ARCTIC SCIENCE NEWS

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The engine of life in the central Arctic Ocean: Ice algae

Algae that live in and under the sea ice also serve as a nutritional basis for animals living at great depths

Algae that live in and under the sea ice play a much greater role for the Arctic food web than previously assumed. In a new study, biologists of the Alfred Wegener Institute (AWI) showed that not only animals that live directly under the ice thrive on carbon produced by so-called ice algae. Even species that mostly live at greater depth depend to a large extent on carbon from these algae. This also means that the decline of the Arctic sea ice may have far-reaching consequences for the entire food web of the Arctic Ocean.

Their results have been published online now in the journal *Limnology & Oceanography*.

The summer sea ice in the Arctic is diminishing at a rapid pace and with it the habitat of ice algae. The consequences of this decline for the Arctic ecosystem are difficult to predict. Scientists of the AWI, Helmholtz Centre for Polar and Marine Research showed the significance of ice algae for the Arctic food web in this context. A number of studies have already speculated that ice algae are an important energy source for the polar ecosystems. These researchers have now been able to show that not only animals associated with ice meet the majority of their carbon needs from ice algae, but that, surprisingly, so do species that mostly live at greater depths.

In a new study, Doreen Kohlbach and her colleagues examined copepods, amphipods, crustaceans and sea angels from the central Arctic Ocean and their dependence on ice algae. A number of these species use the underside of the sea ice as their habitat. Many other species of zooplankton, however, spend their entire lives floating in water depths up to 1000 m and more.

Ice algae play a much more important role for the pelagic food web than previously assumed. This finding also means, however, that the decline of the ice could have a more profound impact on Arctic marine animals, including fish, seals and ultimately also polar bears, than hitherto suspected, says Doreen Kohlbach.

The Arctic pteropod Clione limacina. Image credit: AWI

The AWI researcher was able to establish the close relationship between zooplankton and ice algae using fatty acids as biomarkers, which are passed on unchanged in the food chain. The typical fatty acids in ice algae are thus indicators of whether an animal has ingested carbon from ice algae via food. In order to precisely determine the proportion of ice algae carbon in the diet, Doreen Kohlbach also performed an isotope analysis of these biomarkers. She took advantage of the fact that ice algae inherently have a higher proportion of heavy carbon isotopes incorporated in their cells than algae that float freely in the water. On the basis of the ratio of heavy to light carbon isotopes in the biomarkers it is possible to determine the exact proportion of carbon derived from ice algae in the organisms along the food web.

The result showed that ice-associated animals derive between 60 and 90% of their carbon from the ice. For animals living at greater depths, the percentages were between 20 and 50% - significantly higher than expected. She is most surprised by the percentage in the predatory amphipod *Themisto libellula*, which lives in the open waters and is not known to hunt under the surface of the ice. We now know that it obtains up to 45% of its carbon from ice algae, which had been eaten by its prey. They found that pelagic copepods also obtain up to 50% from these algae, even though we had assumed that they mainly feed on algae from the water column.

These figures were also surprising in view of the fact that ice algae mainly grow in spring when little light penetrates the ice, which is still thick at that time of the year. The samples, however, were taken in the summer -- and the percentage of ice algae carbon in the food chain was still relatively high. The AWI scientists now wonder what the figures look like at other times of the year. They are also interested in whether a greater distinction can be made between the various ice algae and whether perhaps there is a key alga.

Based on the new study, it is now possible to back up the flow of ice algae carbon through the summer food web in the central Arctic using specific figures. AWI biologists can use these figures in model calculations to assess the consequences of the sea ice decline for the Arctic ecosystem.

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The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses

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Abstract

To better predict ecological consequences of changing Arctic sea ice environments, we aimed to quantify the contribution of ice algae-produced carbon (α_{Ice}) to pelagic food webs in the central Arctic Ocean. Eight abundant under-ice fauna species were submitted to fatty acid (FA) analysis, bulk stable isotope analysis (BSIA) of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios, and compound-specific stable isotope analysis (CSIA) of $\delta^{13}C$ in trophic marker FAs. A high mean contribution α_{Ice} was found in *Apherusa glacialis* and other sympagic (ice-associated) amphipods (BSIA: 87% to 91%, CSIA: 58% to 92%). The pelagic copepods *Calanus glacialis* and *C. hyperboreus*, and the pelagic amphipod *Themisto libellula* showed substantial, but varying α_{Ice} values (BSIA: 39% to 55%, CSIA: 23% to 48%). Lowest α_{Ice} mean values were found in the pteropod *Clione limacina* (BSIA: 30%, CSIA: 14% to 18%). Intra-specific differences in FA compositions related to two different environmental regimes were more pronounced in pelagic than in sympagic species. A comparison of mixing models using different isotopic approaches indicated that a model using $\delta^{13}C$ signatures from both diatom-specific and dinoflagellate-specific marker FAs provided the most conservative estimate of α_{Ice}. Our results imply that ecological key species of the central Arctic Ocean thrive significantly on carbon synthesized by ice algae. Due to the close connectivity between sea ice and the pelagic food web, changes in sea ice coverage and ice algal production will likely have important consequences for food web functioning and carbon dynamics of the pelagic system.

Arctic sea ice coverage and thickness have significantly decreased in the past decades (Johannessen et al. 2004; Kwok et al. 2009; Maslanik et al. 2011). This has been accompanied by a dramatic loss of old, thick multi-year sea ice and a transition to a seasonal ice-dominated Arctic Ocean with more open water during summer (Kwok 2007; Lindsay et al. 2009; Maslanik et al. 2011). The loss of summer sea ice has consequences for ice algae that depend on sea ice as habitat and represent an important carbon source in high Arctic regions. Estimates of ice algal primary production range from 3% to 25% of the total primary production within Arctic marine systems (Subba Rao and Platt 1984; Legendre et al. 1992) to as high as 50% to 57% in high Arctic regions (Gosselin et al. 1997; Fernández-Méndez et al. 2015). Climate change is expected to have dramatic consequences in terms of timing, magnitude, and spatial distribution of both ice-associated and pelagic primary production, with a subsequent direct and indirect impact on higher trophic organisms such as zooplankton (Wassmann et al. 2006; Søreide et al. 2013).

The declining sea ice extent could lead to changes in the reproduction and growth cycles of some Arctic zooplankton, such as copepods, that adapt their life cycles to food availability between ice-associated and pelagic blooms (Søreide et al. 2010). Consequently, these changes at the lower trophic level may affect pelagic and benthic food webs. To

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Additional Supporting Information may be found in the online version of this article.

understand how the loss of sea ice and potential changes in primary production may affect zooplankton, we need to gain insight on the importance of sea ice algae carbon to Arctic zooplankton. So far, the contribution of ice algal biomass to higher trophic levels compared to pelagic phytoplankton is scarcely investigated, particularly in the central Arctic basins. The few available studies focused on shelf-bound ecosystems (Hobson et al. 1995; Søreide et al. 2006; Budge et al. 2008).

Fatty acids (FAs) can be used as trophic markers to track predator-prey relationships within marine food webs (e.g., Falk-Petersen et al. 1998; Mayzaud et al. 2013). Certain FAs that are biosynthesized by primary producers are considered to be markers of those primary producers, and are assumed to be transferred conservatively through the marine food web (Graeve et al. 1994a; Bergé and Barnathan 2005; Budge et al. 2012). For example, Bacillariophyceae (simplified to diatoms), which often dominate algal communities in sea ice, express high amounts of the FAs 16:1n-7 and 20:5n-3, accompanied with high levels of C16 polyunsaturated FAs. Dinophyceae (simplified to dinoflagellates) are often more abundant in the water column and contain high amounts of the FA 22:6n-3 and C18 PUFAs (e.g., Dalsgaard et al. 2003). The fatty acid approach alone, however, cannot provide information on the proportional contribution of ice algae—vs. pelagic phytoplankton-produced FAs, because the same FAs can originate from sea ice-diatoms or diatoms in the water column (Søreide et al. 2008). By combining FA biomarker analysis with stable isotope analysis of the bulk organic carbon content (e.g., Dehn et al. 2007; Feder et al. 2011; Weems et al. 2012) or specific compounds, such as FAs (e.g., Budge et al. 2008; Graham et al. 2014; Wang et al. 2015), it is possible to quantify the relative transfer of sea ice- and pelagic phytoplankton-derived organic matter to the consumers.

The isotopic signature of sea ice-produced carbon is assumed to be caused by a carbon-limiting environment of the sea ice system (e.g., Fry and Sherr 1984; Peterson and Fry 1987; Hecky and Hesslein 1995). The semi-closed system in sea ice results in a significantly higher ^{13}C enrichment in ice algae relative to pelagic phytoplankton. This difference in isotope values allows for the tracking of carbon from ice algae and pelagic phytoplankton to higher trophic levels (Hobson et al. 2002; Søreide et al. 2013). The quantification of ice algae-produced carbon based on bulk stable isotope parameters (BSIA), however, can be complicated by the effect of metabolic processes, e.g., isotopic routing (Gannes et al. 1997). Metabolic effects can be largely excluded when the variability of the stable isotope composition is considered only in FAs, which are not biotransformed in consumers. By using gas chromatography-combustion-isotope ratio mass spectrometry (GC-c-IRMS), it is possible to analyze the stable isotope composition of individual FAs (compound-specific stable isotope analysis- CSIA, see description of method in Meier-Augenstein 2002) with high sensitivity regarding both concentration of FAs and isotopic composition (Boschker and Middelburg 2002).

We analyzed FAs, bulk and FA-specific stable isotope compositions to describe the trophic relationships between phytoplankton, ice algae, and abundant under-ice fauna species throughout the Eurasian Basin of the Arctic Ocean during summer 2012. We also used this two-dimensional biomarker approach to estimate the relative contribution of carbon produced by sea ice algae vs. pelagic phytoplankton in different macrofauna species at different levels of heterotrophy and ice association, and its sensitivity to the methodological approach chosen. According to David et al. (2015), two environmental regimes could be distinguished in our sampling area. During the sampling period, the Nansen Basin (NB) was characterized by higher salinities and nitrate concentrations compared to the Amundsen Basin (AB), among other properties. The community structure of under-ice faunal organisms was also separated according to these two environmental regimes (David et al. 2015). Besides the basin-wide perspective, we analyzed differences in the FA parameters between the two environmental regimes.

Materials and methods

Study area and sampling

The sample collection was conducted during the RV "Polarstern" expedition IceArc (PS80; 2 August to 7 October 2012) in the Eurasian Basin of the Arctic Ocean north of 80°N (Fig. 1, Table 1). More detailed information on the sampling area, including ice types and properties, is given in David et al. (2015) and Fernández-Méndez et al. (2015).

Ice-associated particulate organic matter (I-POM), representative of the ice algae community, was sampled by taking ice cores at eight sites using a 9 cm interior diameter ice corer (Kovacs Enterprises). Ice thickness of the cores varied between 0.9 m and 2.0 m. Chlorophyll *a* (Chl *a*) concentrations of the entire ice cores varied between 0.4 mg m^{-3} and 6.5 mg m^{-3} (0.3 mg m^{-2} to 8 mg m^{-2}; Fernández-Méndez et al. 2015). Whole ice cores were melted in the dark at 4°C on board the ship and filtered via a vacuum pump through pre-combusted 0.7 μm GF/F filters (3.5 L to 10.5 L, Whatmann, 3 h, 550°C).

Pelagic particulate organic matter (P-POM), representative of the phytoplankton community, was collected at eight sites by a CTD probe (Seabird SBE9+) with a carousel water sampler. Further information about the CTD probe equipment can be found in David et al. (2015). Details of the sampling procedure are accessible in Boetius et al. (2013). The water collection was performed at the surface layer, or at the depth of the Chl *a* maximum (between 30 m and 50 m). The water at the Chl *a* maximum showed Chl *a* concentrations between 0.2 mg m^{-3} and 1.2 mg m^{-3} throughout the sampling area. Depending on the P-POM biomass concentration, between 6.4 L and 11.0 L of water was filtered using

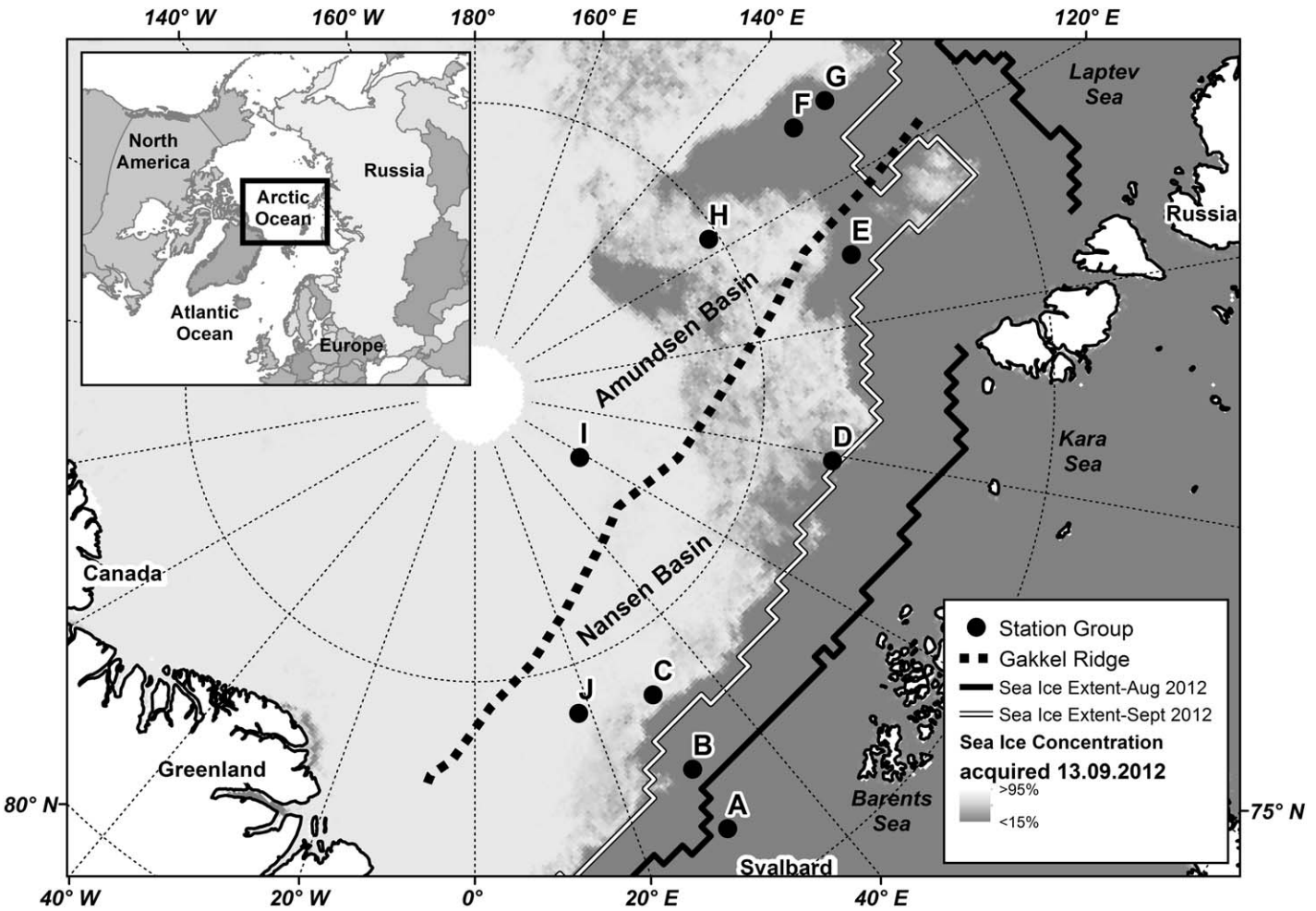

Fig. 1. Map of the sampling area during RV "Polarstern" cruise IceArc (PS80) across the Eurasian part of the Arctic Ocean. The Gakkel Ridge geographically separates the Nansen and Amundsen Basins. Sea ice concentration for 13 September 2012 (concentration data acquired from Bremen University (http://www.iup.uni-bremen.de:8084/amsr/)) and mean sea ice extent for August and September 2012 are represented on the map (data acquired from NSIDC, Fetterer et al. 2002). Letter codes correspond to sampling locations. Station information for the individual sampling sites is given in Table 1.

pre-combusted GF/F filters. All I-POM and P-POM filters were stored at −80°C until further processing.

Samples of dominant species of the under-ice community, such as copepods, ice-associated (sympagic) amphipods, pelagic amphipods, and pteropods were collected at 14 stations, with varying ice conditions, using a surface and under-ice trawl (the SUIT, Van Franeker et al. 2009). Detailed information on the SUIT operation and sampling conditions during the expedition can be found in David et al. (2015).

The copepods *Calanus glacialis* and *C. hyperboreus* were sorted by developmental stages (CV and female). Due to the small organism size, *Calanus* spp. and *Apherusa glacialis* were pooled species-specifically (up to 27 individuals per sample) in order to obtain sufficient sample material for subsequent processing and analyses (Table 2). All samples were immediately frozen on board at −80°C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500°C).

Lipid class and fatty acid analyses

The analytical work was conducted at the Alfred Wegener Institute in Bremerhaven, Germany.

Prior to lipid extraction, all samples were freeze-dried for 24 h. Dry weights were determined gravimetrically (Table 2). The under-ice fauna samples were homogenized mechanically using a Potter-Elvehjem homogenizer. Total lipids were extracted using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2 : 1, v/v). The extracted lipids were cleaned with 0.88% potassium chloride solution. The total lipid content was determined gravimetrically (Table 2).

Lipid classes of the under-ice fauna species were determined directly from the lipid extracts by high performance liquid chromatography using a LaChrom Elite® chromatograph (VWR Hitachi, Germany), equipped with a monolithic silica column Chromolith® Performance-Si (VWR, Germany) and an evaporative light scattering detector Sedex 75

Table 1. Sample information for ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna (UIF) collected in the Eurasian Basin of the Arctic Ocean during PS80 in 2012.

Location	Sample type	Date (dd mon yyyy)	Station no.	Latitude (°N)	Longitude (°E)
A	P-POM	06 Aug 2012	209	81.296	30.103
B	UIF	07 Aug 2012	216	82.483	30.027
C	P-POM	08 Aug 2012	220	83.599	28.500
	UIF	09 Aug 2012	223	84.070	30.434
	I-POM	09 Aug 2012	224	84.051	31.112
	P-POM	11 Aug 2012	230	84.022	31.221
	UIF	11 Aug 2012	233	83.934	31.298
D	I-POM	14 Aug 2012	237	83.987	78.103
	P-POM	16 Aug 2012	244	83.551	75.583
	UIF	16 Aug 2012	248	83.934	75.500
	P-POM	18 Aug 2012	250	83.353	87.271
E	I-POM	20 Aug 2012	255	82.671	109.590
	UIF	20 Aug 2012	258	83.076	109.627
	P-POM	22 Aug 2012	263	83.476	110.899
F	UIF	25 Aug 2012	276	83.076	129.125
	I-POM	25 Aug 2012	277	82.883	130.130
	P-POM	26 Aug 2012	284	82.537	129.462
	UIF	26 Aug 2012	285	82.896	129.782
G	UIF	4 Sep 2012	321	81.717	130.033
	I-POM	4 Sep 2012	323	81.926	131.129
	UIF	5 Sep 2012	331	81.905	130.863
	UIF	6 Sep 2012	333	82.989	127.103
H	I-POM	7 Sep 2012	335	85.102	122.245
	P-POM	7 Sep 2012	341	85.160	123.359
	UIF	9 Sep 2012	345	85.254	123.842
I	I-POM	18 Sep 2012	349	87.934	61.217
	UIF	19 Sep 2012	358	87.341	59.653
	I-POM	22 Sep 2012	360	88.828	58.864
	UIF	25 Sep 2012	376	87.341	52.620
J	UIF	29 Sep 2012	397	84.172	17.922

Table 2. Dry weight, total lipid content (TLC) by dry weight, and fatty acid content (FAC) by dry weight of under-ice fauna species (mean ± 1 SD).

	Calanus glacialis	*Calanus hyperboreus*	*Apherusa glacialis*	*Onisimus glacialis*	*Gammarus wilkitzkii*	*Eusirus holmii*	*Themisto libellula*	*Clione limacina*
Ind./sample	15 ± 6	8 ± 5	12 ± 4	1	1	1	1	1
Dry weight/Ind. (mg)	0.6 ± 0.2	1.1 ± 0.7	4.2 ± 1.2	46.0 ± 33.4	103.2 ± 43.5	86.3 ± 21.1	64.6 ± 36.9	26.0 ± 20.6
TLC/dry weight (%)	40.5 ± 16.3	36.4 ± 15.3	42.3 ± 7.0	37.4 ± 7.9	26.5 ± 6.2	26.3 ± 9.7	35.7 ± 4.8	16.1 ± 8.7
FAC/dry weight (%)	16.9 ± 6.5	18.7 ± 9.2	29.1 ± 5.6	22.8 ± 5.6	16.1 ± 3.1	16.4 ± 6.0	24.7 ± 3.5	7.1 ± 4.0

(Sedere, France). Further information about the chromatographic method was given by Graeve and Janssen (2009). Results of the lipid class analysis were provided as supplementary content (Supporting Information Table S1).

The extracted lipids were converted into fatty acid methyl esters (FAMEs) and free alcohols derived from wax esters by transesterification in methanol, containing 3% concentrated sulfuric acid, at 50°C for 12 h.

After a subsequent hexane extraction, the FAMEs and alcohols were separated on an Agilent 6890N Network gas chromatograph (Agilent Technologies, USA) with a DB-FFAP capillary column (30 m, 0.25 mm I.D., 0.25 μm film thickness), equipped with a split injection and a flame ionization detector using a temperature program (160°C to 240°C). The samples were injected at 160°C. Helium was used as a carrier gas. FAMEs were identified via standard mixtures and quantified with an internal standard (23 : 0) that was added prior to lipid extraction.

Fatty acids were expressed by the nomenclature A:Bn-X, where A represents the number of carbon atoms, B the amount of double bonds, and X is giving the position of the first double bond starting from the methyl end of the carbon chain. The proportions of individual FAs were expressed as mass percentage of the total FA content.

Bulk stable isotope analysis

Frozen samples were freeze-dried for 24 h, and under-ice fauna samples were mechanically homogenized prior to the BSIA. In order to get an adequate amount of sample material, individuals of *Calanus* spp. and *A. glacialis* were pooled species-specifically for each sampling site. The powdered material and filters were filled into tin capsules and analyzed with a continuous flow isotope ratio mass spectrometer Delta V Plus, interfaced with an elemental analyzer (Flash EA 2000 Series) and connected via a Conflo IV interface (Thermo Scientific Corporation, Germany).

According to the following equation, the isotopic ratios were conventionally expressed as parts per thousand (‰) in the δ notation (Coplen 2011):

$$\delta_x = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where x represents the heavy carbon isotope ^{13}C or the heavy nitrogen isotope ^{15}N. R_{sample} represents the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotope ratio relative to the corresponding standard ($R_{Standard}$). The international Vienna Pee Dee Belemnite standard was used for carbon measurements and atmospheric nitrogen for nitrogen measurements.

Since lipids have a high turnover and are depleted in ^{13}C relative to proteins and carbohydrates (Deniro and Epstein 1977), they are often removed prior to the analysis in order to reduce the variability of $\delta^{13}C$ due to seasonal fluctuations (Tamelander et al. 2006b), and to make the C:N ratios more comparable among species (Søreide et al. 2006). Previous studies, however, have shown that the extraction can cause fractionations in $\delta^{15}N$ (Pinnegar and Polunin 1999; Sweeting et al. 2006). In our study, the lipids were not removed, since the removal process might create uncertain changes in the isotopic compositions, particularly in small organisms (Madurell et al. 2008; Mintenbeck et al. 2008; Kürten et al. 2012).

The calibration of the stable isotope measurements (Brand et al. 2014) was done by analyzing the secondary reference material USGS40 (certified: $\delta^{15}N = -4.52‰$, $\delta^{13}C = -26.39‰$, measured: $\delta^{15}N = -4.46‰$, $\delta^{13}C = -26.24‰$) and USGS41 (certified: $\delta^{15}N = 47.57‰$, $\delta^{13}C = 37.63‰$, measured: $\delta^{15}N = 47.12‰$, $\delta^{13}C = 37.49‰$), provided by the International Atomic Energy Agency (IAEA, Austria). The analytical errors were indicated as $\pm 0.2‰$ for nitrogen and $\pm 0.3‰$ for carbon measurements for both USGS40 and USGS41 (representing the 1 SD of 7 analyses each). For the verification of accuracy and precision, the laboratory standards Isoleucine and Acetanilide were analyzed every five samples, with analytical errors of $\pm 0.1‰$ for both Isoleucine nitrogen and carbon isotope ratios, and $\pm 0.1‰$ and $\pm 0.2‰$ for Acetanilide nitrogen and carbon isotope ratios, respectively (representing the 1 SD of 7 analyses each). The samples were analyzed in duplicates, and true δ values were obtained after two-point linear normalization (Paul et al. 2007).

Compound-specific stable isotope analysis

Prior to the CSIA, FAMEs were separated from the wax ester-derived fatty alcohols in order to avoid overlapping peaks. An insufficient baseline separation between FAMEs and alcohols can potentially cause carry-over effects and, thus, potentially lead to imprecise calculations of the FAME $\delta^{13}C$ values. For this purpose, FAMEs were isolated from the fatty alcohols via column chromatography with silica gel (6%, deactivated). The FAME fraction was eluted with hexane/dichloromethane (9 : 1, v/v), fatty alcohols with hexane/acetone (1 : 1, v/v).

Carbon stable isotope ratios were determined for selected marker FAs using a Thermo GC-c-IRMS system, equipped with a Trace GC Ultra gas chromatograph, a GC Isolink and Delta V Plus isotope ratio mass spectrometer, connected via a Conflo IV interface (Thermo Scientific Corporation, Germany). The FAMEs, dissolved in hexane, were injected in splitless mode and separated on a DB-FFAP column (60 m, 0.25 mm I.D., 0.25 μm film thickness). The $\delta^{13}C$ values of a free FA and the corresponding FAME can differ slightly due to the added methyl group during the transesterification (e.g., Budge et al. 2011; Wang et al. 2014). However, in a previous study, we did not find significant differences between the $\delta^{13}C$ values of the free FA and the FAME (e.g., 16 : 0 FA: $-28.56 \pm 0.12‰$, 16: 0 FAME: $-28.57 \pm 0.16‰$; C. Albers unpubl.). Therefore, we did not correct for these potential differences.

The $\delta^{13}C$ values of the individual FAMEs were calibrated by analyzing the certified standard FAMEs 14:0 (certified: $\delta^{13}C = -29.98‰$, measured: $\delta^{13}C = -29.54‰$) and 18:0 (certified: $\delta^{13}C = -23.24‰$, measured: $\delta^{13}C = -23.29‰$), supplied by Indiana University, every five samples. The analytical error was $\pm 0.3‰$ for both 14 : 0 and 18 : 0 (representing the 1 SD of 10 analyses each). Furthermore, for quality assurance and analytical precision of the determined carbon stable isotope ratios, the laboratory standard 23 : 0 was measured intermittently during the sample runs with an analytical error of $\pm 0.4‰$ (representing the 1 SD of 10 analyses). The samples were analyzed in duplicates.

Table 3. Statistical parameters of ANOVA tests and Tukey HSD post-hoc tests with significant results.

	ANOVA				
Parameter	***n***	***F***	**df**	***p***	**Tukey HSD**
level FA 16:1*n*−7	98	28.3	7, 90	< 0.001	*A. glacialis* > all amphipod species: $p < 0.001$
					C. limacina < all species: $p < 0.05$
level FA 22:6*n*−3	98	39.3	7, 90	< 0.001	*Calanus* spp.> all amphipod species: $p < 0.01$
					C. limacina > all species (except C. *hyperboreus*): $p < 0.001$

FA: fatty acid, *n*: sample size.

Data analysis

The species-specific FA proportions were used as an indicator of a consumer's carbon sources in the days and weeks before the sampling. Consumers at lower trophic levels, such as *Calanus* copepods, show a quick lipid turnover rate ranging between hours and days (Graeve et al. 2005).

The investigation of the FA composition variations was based on six marker FAs. The FAs 16:1*n*−7 and 20:5*n*−3 are mainly produced by diatoms and can therefore be treated as valid diatom-specific marker FAs (e.g., Graeve et al. 1997; Falk-Petersen et al. 1998; Scott et al. 1999). The FAs 18:4*n*−3 and 22:6*n*−3 are produced in high amounts by dinoflagellates and are therefore used as a dinoflagellate marker FAs (Viso and Marty 1993; Graeve et al. 1994b). Long-chained FAs 20 : 1 and 22 : 1 (all isomers) were used to indicate the presence of *Calanus* spp. within the diets of the investigated under-ice fauna species (e.g., Falk-Petersen et al. 1987; Søreide et al. 2013). A principal component analysis (PCA) was applied on the FA dataset to visualize inter-specific differences. Spatial variability in the FA patterns between the two environmental regimes characterized by David et al. (2015) were visualized with bar plots.

Similar to FAs, stable isotope compositions can provide dietary information over a longer period (Tieszen et al. 1983). Bulk $\delta^{13}C$ and FA-specific $\delta^{13}C$ values were determined to estimate the proportional contribution of ice algae-produced carbon (α_{Ice}) to the diet of the under-ice fauna species. Bayesian multisource stable isotope mixing models (SIAR; Parnell et al. 2010) were used to determine the α_{Ice} estimates from both analyses, BSIA and CSIA. For the CSIA modeling, two different FA combinations were used: (a) 20:5*n*−3 and (b) 20:5*n*−3 + 22:6*n*−3, to account for the potentially overlapping compositions of the ice algae and phytoplankton communities. The diatom-specific FA 20:5*n*−3 was used in the model, because I-POM is typically dominated by diatoms (Horner 1985; Gosselin et al. 1997; Arrigo et al. 2010). However, diatoms can also be present in P-POM (Gosselin et al. 1997; Wang et al. 2014). The dinoflagellate-specific FA 22:6*n*−3 was used, because the water column can contain high amounts of dinoflagellates and flagellates (Sherr et al. 1997). Besides, sea ice systems may also be dominated by flagellates, particularly during ice melt (Tamelander et al. 2009).

The models allow the incorporation of trophic enrichment factors (TEFs) to account for isotopic turnover rates in the consumers that are tissue-specific. From lower to higher trophic level, an enrichment of the heavy carbon stable isotope between 0.1‰ and 1‰ was often observed (Deniro and Epstein 1978; Rau et al. 1983; Post 2002). Since the true value of the carbon TEFs in the under-ice fauna species is unknown, carbon TEFs for both BSIA and CSIA models were assumed to be zero (Budge et al. 2011; Wang et al. 2015).

The models also allow the incorporation of concentration dependencies to account for different levels of the investigated marker FAs in the primary producers. The discrepancy in the proportions of 20:5*n*−3 between I-POM and P-POM during maximum ice in 2010 reported by Wang et al. (2015) was higher than in our dataset. However, Wang et al. (2015) did not find substantial differences between the results using models with and without concentration data. Thus, we did not incorporate concentration dependencies in our models.

Due to the small sample size, the calculation of α_{Ice} was based on the mean stable isotope values, with no differentiation between the two environmental regimes, for both BSIA and CSIA data.

The ice algae-produced carbon demand of the most abundant herbivores, *C. glacialis*, *C. hyperboreus* and *A. glacialis*, was estimated by multiplying our proportional α_{Ice} derived from CSIA model b with ingestions rates (Olli et al. 2007) and observed species abundances under sea ice and in the water column (David et al. 2015; Ehrlich 2015).

All data analyses were conducted using the open-source software "R", version 3.2.0 (R Core Team 2015). Intra-specific and inter-specific variations in fatty acid and stable isotope compositions were tested using 1-way ANOVAs followed by Tukey HSD post-hoc tests. Student's t-tests were applied for comparisons between two groups. Prior to testing, the FA data were transformed applying an arcsine square root function following Budge et al. (2007) to improve normality. The statistical output reported in the text was summarized in Tables 3 (ANOVAs) and 4 (*t*-tests).

Results

Marker fatty acid compositions

Ice-associated and pelagic particulate organic matter

The I-POM samples were dominated by the diatom-specific FA 16:1*n*−7, showing significantly higher levels than

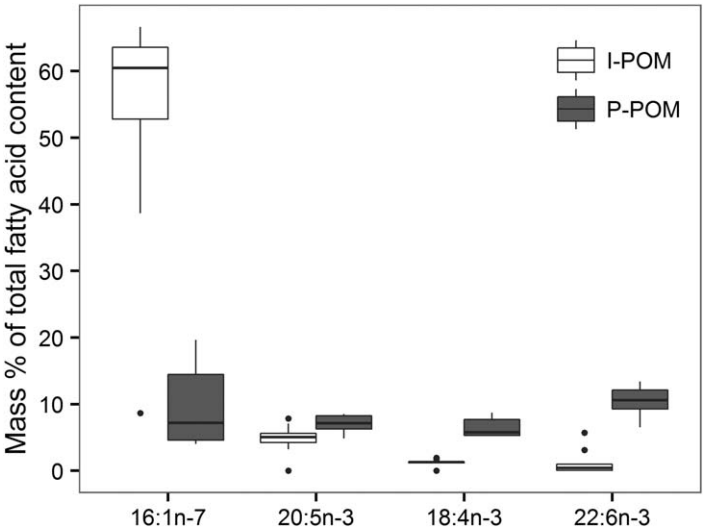

Fig. 2. Relative composition of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM) and pelagic particulate organic matter (P-POM). 16:1$n-7$ and 20:5$n-3$ represent diatom marker FAs, 18:4$n-3$ and 22:6$n-3$ represent dinoflagellate marker FAs. Horizontal bars in the box plots indicate median proportional values. Upper and lower edges of the boxes represent the approximate 1st and 3rd quartiles, respectively. Vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (R Core Team 2015). Outliers are represented by the dots outside the boxes. Sample size is reported in Table 5.

the P-POM samples. The proportional contributions of the second diatom-specific FA 20:5$n-3$ were, however, significantly lower in the I-POM samples compared to the P-POM samples. The proportions of the dinoflagellate-specific FAs 18:4$n-3$ and 22:6$n-3$ showed significantly higher values in P-POM compared to I-POM (Fig. 2, Tables 4 and 5).

Under-ice fauna species

In all species, the bulk of the determined FAs were incorporated into neutral (storage) lipids, whose proportions far exceeded the levels of polar (membrane) lipids (Supporting Information Table S1).

The largest variability among all species was observed in the diatom-specific FA 16:1$n-7$ and the dinoflagellate-specific FA 22:6$n-3$. The levels of the diatom-specific FA 20:5$n-3$ were comparable among all species, and the proportions of the dinoflagellate-specific FA 18:4$n-3$ were generally low in all species (Fig. 3, Table 5).

The mean levels of 16:1$n-7$ in both *Calanus glacialis* and *C. hyperboreus* were lower than in all other species, except for *Clione limacina*. In contrast, their content in 20:5$n-3$ was high compared to the other species, with *C. hyperboreus* reaching the maximum mean value of this study. *C. glacialis* and *C. hyperboreus* contained significantly higher amounts of 22:6$n-3$ compared to all amphipod species (Tables 3 and 5). The mean level of the *Calanus*-specific FA 20:1$n-9$ was only higher in *Themisto libellula* relative to *Calanus* spp., and in *Onisimus glacialis* relative to *C. hyperboreus*. The second *Calanus*-specific FA 22:1$n-11$ was detected in generally higher amounts in both *Calanus* spp. compared to all other species. There was no significant difference found in the FA patterns between CV and female within the same *Calanus* species (*t*-test $p > 0.05$).

Table 4. Statistical parameters of Student's *t*-tests with significant results.

		t-test			
Parameter	***n***	***t***	**df**	***p***	
level FA 16:1$n-7$	19	7.1	13.6	< 0.001	I-POM > P-POM
level FA 18:4$n-3$	19	9.8	16.3	< 0.001	I-POM < P-POM
δ^{13}C FA 18:4$n-3$	12	7.3	4.7	< 0.001	I-POM > P-POM
level FA 20:5$n-3$	19	2.3	10.9	< 0.05	I-POM < P-POM
δ^{13}C FA 20:5$n-3$	13	6.4	9.9	< 0.001	I-POM > P-POM
level FA 22:6$n-3$	19	9.0	12.8	< 0.001	I-POM < P-POM
δ^{13}C FA 22:6$n-3$	11	5.9	4.4	< 0.01	I-POM > P-POM

FA: fatty acid, *n*: sample size.

A. glacialis had a significantly higher proportion of 16:1$n-7$ than all other amphipod species, in addition to relatively high levels of 20:5$n-3$ (Tables 3 and 5). The levels of 20:1$n-9$ and 22:1$n-11$ were close to the detection limit in this species. *Gammarus wilkitzkii* and *Eusirus holmii* were generally similar to each other in their FA composition. *E. holmii* had the second-highest proportional content of 16:1$n-7$ among all amphipod species. *T. libellula* had a higher proportional content of 22:6$n-3$ than all other amphipods, and high levels of 20:1$n-9$ and 22:1$n-11$.

The FA 16:1$n-7$, which was dominant in all investigated copepods and amphipods, showed significantly lower levels in *C. limacina* compared to all other investigated species (Tables 3 and 5). Conversely, the proportional contribution of 22:6$n-3$ was significantly higher in *C. limacina* compared to all other investigated species, except for *C. hyperboreus* (Tables 3 and 5). The FAs 20:1$n-9$ and 22:1$n-11$ were only found in small amounts in this species.

The first two principal components of the PCA explained 69.8% of the variance in the FA data among the samples (Fig. 4). The first axis (PCA 1) separated the sympagic amphipods with high levels of 16:1$n-7$ on one side from the pelagic copepods with high levels of 22:6$n-3$, 20:1$n-9$, and 22:1$n-11$ on the other side. The second axis (PCA 2) emphasized the difference in the marker FA proportions between the pelagic species *T. libellula* with higher levels of 16:1$n-7$ and both *Calanus*-marker FAs, and *C. limacina* with distinctly higher levels of 22:6$n-3$. In general, the FA profile of *C. limacina* was clearly isolated from all other species.

In addition to the differences between the species, there was an intra-specific spatial variability of certain marker FA proportions observed. SUIT station 258 was located close to the Gakkel ridge, on the border between the Nansen Basin

Table 5. Relative composition of the most abundant fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD mass % of total FA content) collected in the Nansen Basin (NB) and Amundsen Basin (AB). Not detected FAs are reported as "–".

	I-POM	P-POM	*Calanus glacialis*	*Calanus hyperboreus*	*Apherusa glacialis*	*Onisimus glacialis*	*Gammarus wilkitzkii*	*Eusirus holmii*	*Themisto libellula*	*Clione limacina*
n_{NB}	1	7	3	2	4	7	5	5	2	3
n_{AB}	9	2	7	4	8	9	3	9	14	13
14:0	5.3 ± 1.5	6.0 ± 2.1	8.1 ± 1.2	4.6 ± 1.9	4.2 ± 0.4	3.4 ± 0.9	3.9 ± 0.5	3.8 ± 0.6	4.9 ± 1.3	2.6 ± 1.8
16:0	16.3 ± 4.1	20.3 ± 1.9	8.8 ± 1.5	7.3 ± 3.2	13.4 ± 0.5	11.5 ± 2.1	12.2 ± 0.8	12.7 ± 1.6	9.2 ± 1.3	12.1 ± 1.6
16:1*n*−7*	53.6 ± 17.9	9.8 ± 6.0	26.2 ± 7.3	20.3 ± 10.2	48.1 ± 8.1	27.0 ± 9.6	31.4 ± 5.6	36.4 ± 8.5	27.9 ± 8.5	10.3 ± 2.9
18:0	4.5 ± 7.5	5.3 ± 1.2	1.2 ± 0.5	1.6 ± 1.1	0.7 ± 0.2	0.5 ± 0.2	0.6 ± 0.1	0.6 ± 0.2	0.5 ± 0.1	2.8 ± 1.9
18:1*n*−9	7.0 ± 4.5	6.5 ± 2.5	3.6 ± 0.4	3.3 ± 0.6	7.9 ± 1.5	18.1 ± 4.4	16.1 ± 2.9	9.8 ± 1.4	8.1 ± 1.5	4.2 ± 1.3
18:1*n*−7	0.4 ± 0.4	1.8 ± 1.1	1.5 ± 0.4	1.8 ± 0.7	2.0 ± 0.5	3.4 ± 0.7	4.0 ± 0.5	3.0 ± 0.6	3.0 ± 0.7	4.6 ± 1.4
18:4*n*−3†	1.2 ± 0.5	6.4 ± 1.4	2.2 ± 1.6	3.0 ± 1.6	1.9 ± 0.7	1.5 ± 0.9	1.9 ± 0.5	1.5 ± 0.7	2.4 ± 1.3	1.8 ± 1.5
20:1*n*−9‡	–	–	9.8 ± 4.3	8.7 ± 5.6	0.7 ± 0.4	8.9 ± 4.5	3.2 ± 2.1	4.9 ± 4.5	11.3 ± 4.1	2.7 ± 0.7
20:1*n*−7	–	–	0.5 ± 0.4	1.0 ± 0.9	0.5 ± 0.2	1.4 ± 0.6	0.7 ± 0.1	1.0 ± 0.5	1.5 ± 0.8	2.5 ± 0.6
20:5*n*−3*	4.8 ± 2.2	7.1 ± 1.3	11.9 ± 1.9	15.3 ± 3.7	11.7 ± 3.6	9.7 ± 3.8	12.8 ± 3.4	11.8 ± 3.3	9.7 ± 1.6	12.1 ± 2.9
22:1*n*−11‡	–	–	4.3 ± 2.3	6.2 ± 4.8	0.2 ± 0.1	2.5 ± 1.6	2.1 ± 1.9	1.8 ± 1.8	3.7 ± 1.6	0.2 ± 0.2
22:6*n*−3†	1.2 ± 1.8	10.4 ± 2.1	11.4 ± 3.5	14.1 ± 7.8	2.0 ± 0.8	3.4 ± 1.3	3.3 ± 0.8	4.3 ± 1.8	7.1 ± 2.7	17.5 ± 7.0
Total	94.3	73.6	89.5	87.2	93.3	91.3	92.2	91.6	89.3	73.4

*diatom marker FA.
†dinoflagellate marker FA.
‡*Calanus* marker FA, *n*: sample size.

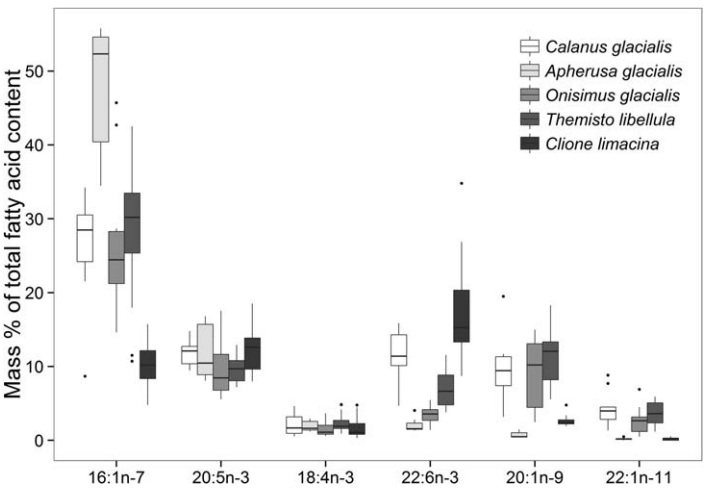

Fig. 3. Relative composition of marker fatty acids (FAs) in selected under-ice fauna species. 16:1*n*−7 and 20:5*n*−3 represent diatom marker FAs, 18:4*n*−3 and 22:6*n*−3 represent dinoflagellate marker FAs, 20:1*n*−9 and 22:1*n*−11 represent *Calanus*-marker FAs. Box plot design as in Figure 2. Sample size is reported in Table 5.

(NB) and the Amundsen Basin (AB). In general, the FA composition of individuals from station 258 demonstrated a higher similarity to the FA profiles of the same species from the AB regime. Thus, station 258 was considered as an AB regime sample for the statistical tests. In *Calanus* spp. and all five amphipod species, the proportional amount of 16:1*n*−7 was higher in the AB regime samples than in the NB regime samples. This pattern was significant (*t*-test $p < 0.05$) in *C. hyperboreus*, *A. glacialis, G. wilkitzkii*, *E. holmii*, and *T. libellula*, and near-significant in *O. glacialis* ($p = 0.06$). Conversely, the levels of 18:4*n*−3, 20:5*n*−3, and 22:6*n*−3 were significantly higher in the NB regime in *A. glacialis, O. glacialis*, and *G. wilkitzkii*. In *E. holmii*, the proportions of 20:5*n*−3 and 22:6*n*−3 were significantly higher in the NB regime samples compared to the AB regime samples. In *T. libellula*, the levels of 18:4*n*−3, 20:1*n*−9 and 22:1*n*−11 were significantly higher in the NB regime than in the AB regime (Fig. 5). As all but one station in the AB regime were sampled later in the season than stations in the NB regime, these patterns could reflect the seasonal progression of the system (e.g., Basedow et al. 2010). In addition, the fundamental differences in the environmental characteristics of the two regimes probably played an important role. The AB regime was characterized by lower nitrate and phosphate concentrations and lower Chl *a* concentrations in the surface layer compared to the NB regime (David et al. 2015).

Bulk stable isotope compositions

Both POM types displayed the lowest $\delta^{15}N$ values between 3.5‰ and 6.4‰ in I-POM and between 2.1‰ and 5.8‰ in P-POM, representing the trophic baseline (Table 6). The $\delta^{13}C$ values in I-POM varied between −22.8‰ and −26.8‰, the P-POM $\delta^{13}C$ values varied between −25.4‰ and −28.7‰.

Among the under-ice fauna species, *A. glacialis* showed the lowest $\delta^{15}N$ values between 5.0‰ and 5.7‰, *E. holmii*

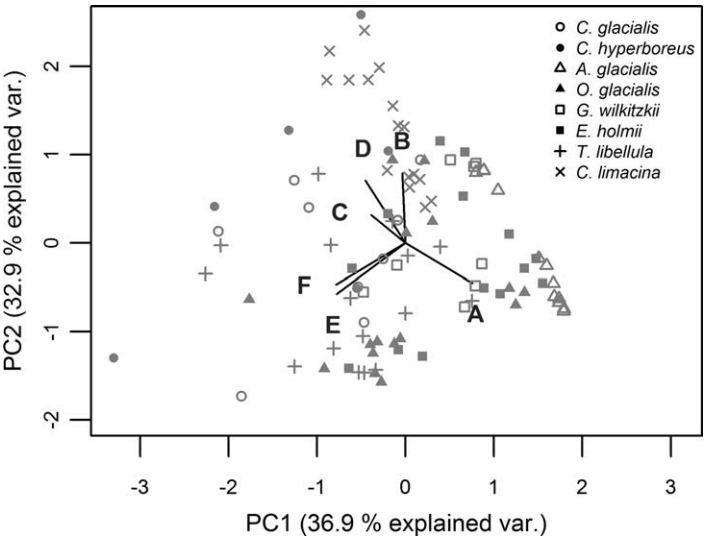

Fig. 4. PCA biplot of marker fatty acid (FA) proportions in under-ice fauna species. Biplot arrows correspond to gradients of FAs in the PCA ordination. Diatom marker FAs: 16:1$n-7$ (A), 20:5$n-3$ (B); dinoflagellate marker FAs: 18:4$n-3$ (C), 22:6$n-3$ (D); *Calanus*-marker FAs: 20:1$n-9$ (E), 22:1$n-11$ (F). Sample size is reported in Table 5.

showed the highest δ^{15}N values between 8.9‰ and 12.2‰ (Table 6).

The highest carbon stable isotope values were found in *A. glacialis* (−20.0‰ to −23.3‰). The lowest δ^{13}C values were found in *Calanus* spp., *T. libellula* and *C. limacina* (−24.1‰ to −31.2‰).

A comparison of the bulk stable isotope ratios in POM and the under-ice fauna species between the two environmental regimes was provided in Supporting Information Table S2.

Compound-specific stable isotope compositions

The δ^{13}C values of 18:4$n-3$, 20:5$n-3$, and 22:6$n-3$ were significantly higher in the I-POM samples compared to the P-POM samples (Tables 4 and 7). The stable isotope values of 16:1$n-7$ demonstrated little variation between the two source communities.

There was no significant difference in the carbon stable isotope values of the individual marker FAs between the two *Calanus* species (*t*-test $p > 0.05$). The mean δ^{13}C values of 18:4$n-3$, 20:5$n-3$, and 22:6$n-3$ were lower in both *Calanus* spp. compared to all other species, except for *T. libellula* and *C. limacina*. Among all species, *A. glacialis* displayed the highest mean δ^{13}C values of 18:4$n-3$, 20:5$n-3$, and 22:6$n-3$. Among the amphipods, *T. libellula* displayed the lowest mean δ^{13}C values of 18:4$n-3$, 20:5$n-3$, and 22:6$n-3$ (Table 7).

A comparison of the fatty acid-specific stable isotope ratios in POM and the under-ice fauna species between the two environmental regimes was provided in Supporting Information Table S3.

Proportional contribution of ice algae-produced carbon

All three approaches indicated that the sympagic amphipods *A. glacialis*, *O. glacialis*, *G. wilkitzkii*, and *E. holmii* showed the highest dependency on ice algal carbon, *Calanus* spp. and *T. libellula* took an intermediate position, and *C. limacina* showed the lowest dependency (Table 8). The results from the SIAR models using the carbon stable isotope values of FA 20:5$n-3$ (model a) were similar to those from the BSIA models, and were generally higher than the α_{Ice} estimates derived from model b, which combined 20:5$n-3$ and 22:6$n-3$ (Table 8).

A. glacialis showed the highest α_{Ice} estimates among all species, accompanied with the lowest variation between the α_{Ice} estimates derived from the BSIA model and the two CSIA models (overall mean >85%). Both *Calanus* spp. indicated high similarity between the estimates derived from the BSIA model and CSIA model a (BSIA: mean 43%, CSIA model a: mean 44%). Furthermore, all approaches provided similar α_{Ice} estimates for *O. glacialis*, *G. wilkitzkii*, and *E. holmii* (BSIA: mean ~90%, CSIA model a: mean ~80%, CSIA model b: mean ~60%).

A high discrepancy between the BSIA model and CSIA model b was found in the pelagic species *T. libellula* (BSIA: mean 55%, CSIA model b: 23%) and *C. limacina* (BSIA: mean 30%, CSIA model b: mean 14%).

Ice algae-produced carbon demand

We calculated a tentative estimate of the overall demand of ice algae-produced carbon by the most abundant grazers *C. glacialis*, *C. hyperboreus* and *A. glacialis* based on the α_{Ice} values derived from CSIA model b (Table 8). Altogether, these species consumed between 2.9 mg and 8.5 mg ice algae-produced carbon m^{-2} d^{-1}. Due to its high abundance, the bulk of the ice algal carbon demand was attributed to *C. glacialis* (Table 9).

Discussion

Variability in marker fatty acid compositions among algal communities and under-ice fauna species

In our study, the FA profiles of the I-POM samples suggested a diatom-dominated ice algal community. The small amounts of the dinoflagellate-specific FAs 18:4$n-3$ and 22:6$n-3$ in the I-POM samples indicated that a small part of the sea ice flora consisted of dinoflagellates, which was in agreement with the results of molecular analyses of the primary community structures (K. Hardge et al. unpubl.). Based on the marker FA proportions, the phytoplankton community consisted of a mixture of both diatoms and flagellates. The dominance of dinoflagellates in the water column and a substantially higher proportion of diatoms in the sea ice community compared to the pelagic community during our sampling were also confirmed by genome sequencing (K. Hardge et al. unpubl.). The lower levels of the diatom-specific FA 20:5$n-3$ accompanied with the distinctly higher levels of the diatom-FA 16:1$n-7$ in the I-POM samples

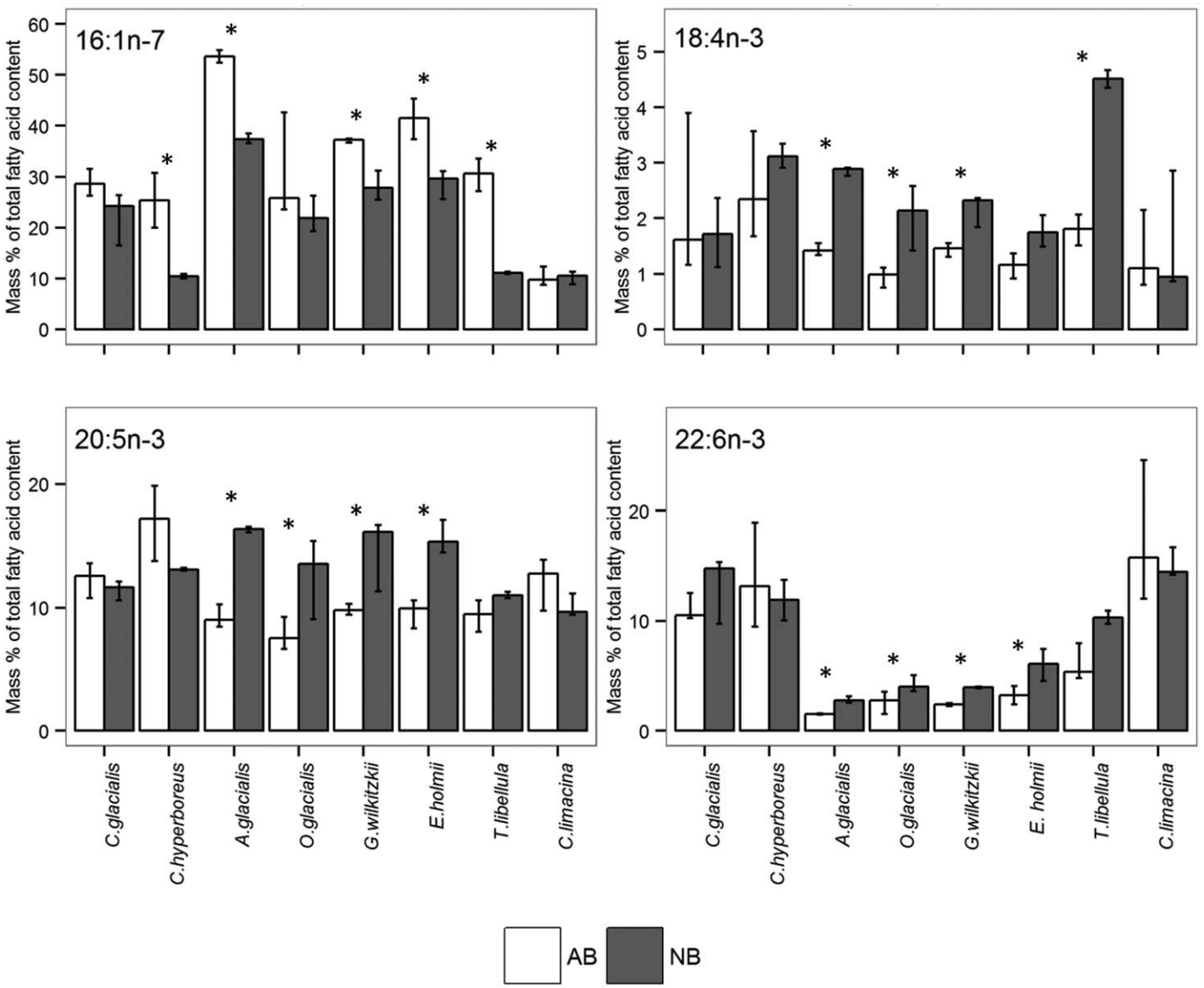

Fig. 5. Intra-specific differences in the proportions of marker fatty acids (FAs) in under-ice fauna species between Nansen Basin (NB) and Amundsen Basin (AB) regimes. Columns and error bars correspond to the median and interquartile ranges, respectively. Note: *y*-axes have different scales. Associated bars marked with asterisk "*"represent significant differences between the regimes (*t*-test $p < 0.05$). Sample size is reported in Table 5.

compared to the P-POM samples could indicate a different diatom-community in sea ice compared to the water column. Supporting our assumption, previous studies found a dominance of pennate diatoms in sea ice vs. a dominance of centric diatoms in the water column (Gosselin et al. 1997; Arrigo et al. 2010).

The FA profiles of the under-ice fauna species revealed variable associations with diatom-and dinoflagellate-related marker FAs. Although it may be possible for herbivorous invertebrates to synthesize 20:5$n-3$ and 22:6$n-3$ from 18:3$n-3$ (Moreno et al. 1979), FA 18:3$n-3$ was only found in trace amounts (< 1%) in the species from this study. This indicates that biosynthesis of 20:5$n-3$ and 22:6$n-3$ likely did not occur, and these FAs were derived through the trophic chain from algal sources.

Both *Calanus* spp. are known to be key Arctic grazers, utilizing both ice algae- and pelagic phytoplankton-derived carbon (Søreide et al. 2010; Durbin and Casas 2013). There was little difference in the FA profiles between *C. glacialis* and *C. hyperboreus*, indicating that the primary carbon sources were similar for both *Calanus* species. As frequently shown, the FA composition of Arctic *Calanus* spp. was characterized by high amounts of the diatom-specific FAs 16:1$n-7$ and 20:5$n-3$ (Graeve et al. 1994b; Wang et al. 2015).

Furthermore, our results showed that both copepod species contained high amounts of the dinoflagellate-specific marker FA 22:6$n-3$, which together suggests sources of carbon from both diatoms and dinoflagellates.

The FA composition of the amphipod *A. glacialis* indicated a diet dominated by diatom-derived carbon, evident by high proportions of the diatom-specific FAs 16:1$n-7$ and 20:5$n-3$, accompanied by low levels of the dinoflagellate-specific FA 22:6$n-3$. A diatom-dominated diet is in agreement with several studies showing that *A. glacialis* primarily feeds on the under-ice flora and phytodetritus (Bradstreet and Cross 1982; Scott et al. 1999; Tamelander et al. 2006a). Together with *O. glacialis* and *G. wilkitzkii*, *A. glacialis* is known to live permanently associated with the Arctic sea ice (Poltermann 2001; Gradinger and Bluhm 2004). Thus, it is not surprising that *O. glacialis* and *G. wilkitzkii* contained high levels of the diatom markers 16:1$n-7$ and 20:5$n-3$, with considerably lower levels of the dinoflagellate-specific FA 22:6$n-3$.

Calanus copepods are able to synthesize the long-chain FAs 20:1$n-9$ and 22:1$n-11$ in large amounts de novo. These FAs can also be used as trophic indicators for a copepod-related diet in higher consumers (Sargent et al. 1977; Wold et al. 2011). Accordingly, high values of the FA 20:1$n-9$ indicated a partly *Calanus*-based diet in the omnivorous amphipod *O. glacialis*. *G. wilkitzkii* has been reported to also feed extensively on copepods, primarily during adult stages (Scott et al. 2001). However, we found only small amounts of the *Calanus*-specific FAs 20:1$n-9$ and 22:1$n-11$ in this amphipod, indicating that *Calanus* may not have been important in their diets before the sampling.

Carnivorous amphipods, such as *E. holmii* and *T. libellula*, constitute important links between lipid-rich herbivores and top predators (Noyon et al. 2011). These two amphipod species also showed high levels of the diatom-specific FAs 16:1$n-7$ and 20:5$n-3$. In *T. libellula*, a higher proportion of the dinoflagellate-specific FA 22:6$n-3$ indicated a greater importance of dinoflagellate-derived carbon than in *E. holmii*.

Table 6. Bulk stable nitrogen (δ^{15}N) and carbon isotope values (δ^{13}C) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰).

	n	δ^{15}N	δ^{13}C
I-POM	6	4.8 ± 1.3	−24.9 ± 1.6
P-POM	17	4.0 ± 1.2	−27.3 ± 0.9
Calanus glacialis	4	7.5 ± 0.9	−26.8 ± 3.1
Calanus hyperboreus	4	7.8 ± 1.4	−26.6 ± 1.1
Apherusa glacialis	4	5.4 ± 0.3	−22.3 ± 1.5
Onisimus glacialis	4	7.1 ± 1.8	−22.4 ± 1.7
Gammarus wilkitzkii	4	7.1 ± 0.6	−24.4 ± 0.4
Eusirus holmii	4	10.0 ± 1.5	−23.3 ± 0.7
Themisto libellula	4	8.8 ± 1.5	−25.7 ± 1.8
Clione limacina	4	8.6 ± 0.8	−26.9 ± 0.5

n: sample size.

Table 8. Proportional contribution of ice algae-produced carbon (α_{Ice}) in under-ice fauna species (mean %) from SIAR mixing models based on bulk stable isotope analyses (BSIA; Table 6) and stable isotope compositions of marker fatty acids (a) 20:5$n-3$ and (b) 20:5$n-3$ + 22:6$n-3$ (Table 7). Ranges of α_{Ice} are shown in parentheses.

Model	BSIA	(a) 20:5$n-3$	(b) 20:5$n-3$ + 22:6$n-3$
Calanus glacialis	47 (10–76)	48 (20–53)	33 (26–43)
Calanus hyperboreus	39 (6–86)	40 (35–48)	25 (20–27)
Apherusa glacialis	90 (85–95)	92 (91–94)	86 (80–90)
Onisimus glacialis	87 (79–95)	77 (73–81)	61 (53–68)
Gammarus wilkitzkii	91 (88–93)	76 (63–81)	58 (48–66)
Eusirus holmii	90 (87–92)	79 (74–84)	60 (56–64)
Themisto libellula	55 (6–87)	45 (40–50)	23 (20–28)
Clione limacina	30 (16–53)	18 (13–28)	14 (10–21)

Table 7. Carbon stable isotope values (δ^{13}C) of marker fatty acids (FAs) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD ‰). Not detected FAs are reported as "–".

	n	16:1$n-7$	20:5$n-3$	18:4$n-3$	22:6$n-3$
I-POM	7	−24.9 ± 4.1	−26.6 ± 2.7	−28.4 ± 3.2	−23.4 ± 3.7
P-POM	7	−26.4 ± 3.4	−35.6 ± 2.3	−39.3 ± 1.1	−35.5 ± 2.3
Calanus glacialis	10	−25.0 ± 3.8	−32.2 ± 1.7	−35.6 ± 1.8	−32.0 ± 2.1
Calanus hyperboreus	6	−27.3 ± 3.6	−32.1 ± 1.2	−36.2 ± 1.1	−33.8 ± 2.3
Apherusa glacialis	10	−24.2 ± 2.6	−26.6 ± 1.3	−29.2 ± 1.9	−28.5 ± 1.6
Onisimus glacialis	8	−22.9 ± 3.0	−28.4 ± 1.6	−32.4 ± 3.6	−30.4 ± 1.0
Gammarus wilkitzkii	4	−24.8 ± 2.1	−29.0 ± 1.0	−31.2 ± 0.9	−31.3 ± 1.5
Eusirus holmii	8	−23.4 ± 2.1	−28.9 ± 1.0	−30.1 ± 1.2	−30.4 ± 1.3
Themisto libellula	7	−23.9 ± 2.3	−31.4 ± 1.4	−35.6 ± 2.2	−33.7 ±± 1.8
Clione limacina	9	−28.7 ± 1.9	−34.1 ± 1.6	–	−33.8 ± 1.1

n: sample size.

Table 9. Ice algae-produced carbon demand in abundant herbivores. In *Calanus* spp., only adults and CV stages were included in abundance estimates. α_{Ice} = proportional contribution of ice algae-produced carbon derived from SIAR model b (Table 8).

		Ingestion rate* (μg C ind.$^{-1}$ d^{-1})		Abundance (ind. m^{-2})		Ice algal carbon demand (mg C m^{-2} d^{-1})					
						Under-ice		Pelagic		Total	
	α_{Ice} Mean	Min	Max	Under-ice† Mean	Pelagic‡ Mean	Min	Max	Min	Max	Min	Max
Calanus glacialis	0.33	6.0	18.0	6.4	1180	0.01	0.04	2.34	7.01	2.35	7.05
Calanus hyperboreus	0.25	2.8	8.4	1.0	700	0.00	0.00	0.49	1.47	0.49	1.47
Apherusa glacialis	0.86	13.0	13.0	0.6	0	0.01	0.01	0.00	0.00	0.01	0.01
Total		21.8	39.4	8.0	1880	0.02	0.05	2.83	8.48	2.85	8.53

*Olli et al. (2007).
†David et al. (2015).
‡Ehrlich (2015).

Both species, but particularly *T. libellula*, displayed elevated levels of the *Calanus*-specific marker FAs. Our findings are consistent with other feeding studies, which identified *T. libellula* as a part of the *Calanus*-based food web (Scott et al. 1999; Dalpadado et al. 2008; Kraft et al. 2013).

The carnivorous pteropod *C. limacina* is assumed to feed exclusively on *Limacina helicina* (Conover and Lalli 1974; Phleger et al. 2001). In our study, the FA composition of *C. limacina* was characterized by the lowest proportion of the diatom-specific FA 16:1$n-7$ and the highest proportion of the dinoflagellate-specific FA 22:6$n-3$, possibly reflecting a pelagic-based diet of diatoms and dinoflagellates in *L. helicina*. The pteropod *L. helicina* was first described as a pure herbivore, but more recent studies reported an omnivorous diet consisting of small copepods and juvenile *L. helicina* (Gilmer 1974; Gilmer and Harbison 1991; Falk-Petersen et al. 2001). The low levels of the *Calanus*-specific FAs found in our study in *C. limacina*, however, indicated that *Calanus* copepods were not important in the *L. helicina*-based pathway of the food web during the weeks before our sampling.

Besides the expected inter-specific variations largely confirming known feeding patterns, we also found considerable intra-specific variability in the FA profiles of the investigated under-ice fauna species. All amphipod species and *Calanus* spp. from the Amundsen Basin regime had higher proportions of the FA 16:1$n-7$ compared to the samples from the Nansen Basin regime. Additionally, all amphipods from the AB regime showed lower proportions of all other algal FAs than those sampled in the NB regime. The FA 16:1$n-7$ was largely limited to I-POM samples in our dataset. Hence, the observed variability between the two environmental regimes was probably driven by variability in ice algal communities rather than phytoplankton, assuming lipid turnover rates in these herbivores were fast compared to changes in algal composition (Graeve et al. 2005). An impact of the variability of sea ice communities on the FA composition is corroborated by pronounced differences in the community composition of protists in sea ice between the two environmental regimes (K. Hardge et al. unpubl.), as well as by differing drift pathways of sea ice between the NB and the AB in 2012 (David et al. 2015).

Importance of ice algae-produced carbon to the Arctic under-ice community

In most investigated species, the α_{Ice} estimates based on BSIA were higher than those based on the single FAs. Unlike CSIA of FAs, which is limited to molecules assumed to be unchanged by metabolic processes, the interpretation of BSIA results can be more complicated. Besides the lipid components, proteins and carbohydrates are also subject to various mass-dependent metabolic processes, influencing the carbon stable isotope signal of a species. Compared to proteins and carbohydrates, lipids are more depleted in the heavy carbon stable isotope (Deniro and Epstein 1977; Søreide et al. 2006). To correct for a potential bias in the BSIA results introduced by variability in lipid content, both a priori lipid removal and post-analytical corrections, e.g., with the normalization algorithm proposed by McConnaughey and McRoy (1979), have been used in previous studies. Several studies showed, however, that the extraction can cause fractionations in δ^{15}N (Pinnegar and Polunin 1999; Sweeting et al. 2006; Post et al. 2007). On the other hand, there are studies indicating that normalization models do not account for different lipid levels in different species in an appropriate way (Sweeting et al. 2006; Post et al. 2007). Therefore, we based our calculations on the non-corrected data. It remains difficult to conclude to which degree and in which species BSIA-based estimates of α_{Ice} were influenced by lipid content, taxon-specific, habitat-related, and/or trophic level-related effects on metabolically active compounds. Yet, both BSIA and CSIA-derived α_{Ice} estimates yielded a consistent hierarchical order of the investigated species, ranging from a highly sea ice algae-related

trophic dependency in *A. glacialis* to a considerably lower trophic dependency on sea ice algae in *C. limacina* within the food web.

Based on the CSIA results, the isotopic values of carbon in the FAs 20:5*n*−3 and 22:6*n*−3 were used to investigate the proportional contributions of sea ice algae-produced carbon α_{Ice} vs. phytoplankton-produced carbon to the body tissue of abundant under-ice fauna species. Budge et al. (2008) traced the carbon flux in an Alaskan coastal ecosystem using the stable isotope values of carbon in the FA 20:5*n*−3, which they assumed to represent a realistic estimate of the ice algae contribution relative to all other types of phytoplankton. Wang et al. (2015) also suggested that the use of only FA 20:5*n*−3 could be most accurate if diatoms dominated the POM composition. Due to the mixed taxonomic composition of the primary communities in our dataset, we additionally calculated α_{Ice} using the FA 22:6*n*−3 in combination with 20:5*n*−3 to account for the contribution of the dinoflagellate-dominated pelagic communities in our samples.

To estimate the relative contribution of carbon sources to higher trophic levels, Budge et al. (2008) made several assumptions and simplifications that we also included in our study. We assumed that the major sources of FA 20:5*n*−3 were either ice-related diatoms or pelagic diatoms, and isotopic fractionation and routing processes were negligible. Furthermore, we assumed that our measured carbon stable isotope ratios actually reflected the ratio at the base of the food web. This means that the algae-derived lipid composition during the time of sampling was representative of the time when they were ingested. Consumers at lower trophic levels show a quick lipid turnover rate ranging between hours and days (Graeve et al. 2005), indicating that this was indeed the case for the more herbivorous species.

The highest α_{Ice} estimates were found when only the diatom-specific FA 20:5*n*−3 was used (model a). The dinoflagellate-specific FA 22:6*n*−3 showed generally lower $\delta^{13}C$ values compared to I-POM in all under-ice fauna species. Thus, α_{Ice} estimates were considerably lower in some species when 20:5*n*-3 was used in combination with 22:6*n*−3 (model b). This indicates that the sole use of the diatom-specific FA 20:5*n*−3 underestimates the contribution of dinoflagellate-produced carbon when the proportion of diatoms vs. dinoflagellates varies between sea ice and water column, causing a potential bias towards ice algae-produced carbon.

As expected, the sympagic amphipods showed a high trophic dependency on the ice algal production. Surprisingly, many species classified as rather pelagic also showed a considerable input of ice algae-produced carbon, further emphasizing the importance of ice algae for the entire food web. In *Calanus* spp., the estimated relative contribution of ice algae-derived carbon based on the BSIA and the CSIA profiles indicated a mix of pelagic and ice-associated carbon sources. Our results were comparable to a recent study in the Bering Sea, suggesting that the mean proportion of 20:5*n*−3, which originated from ice algae, was between 39% and 57% in *Calanus* spp., depending on the ice conditions (Wang et al. 2015). The reported mean α_{Ice} values for the combination of 20:5*n*−3 and 22:6*n*−3 were somewhat higher than our values, ranging between 31% and 63% (Wang et al. 2015). The ice algae-dependency of *Calanus* spp., however, seems to have a high variability, depending on region, season, and environmental properties. For example, Søreide et al. (2006) found a higher ice algae contribution for both *Calanus* copepods in autumn compared to spring, based on bulk stable isotope values.

Among the amphipods, *A. glacialis* showed the highest dependency on ice algal-produced carbon. *O. glacialis*, *G. wilkitzkii*, and *E. holmii* showed also high α_{Ice} values for both BSIA and CSIA, indicating a generally high trophic dependency on the ice algae production for all investigated sympagic amphipods, which is consistent with previous studies (Søreide et al. 2006; Tamelander et al. 2006a). In contrast, Budge et al. (2008) estimated the mean ice algae carbon contribution in *Apherusa* sp. near Barrow, Alaska, based on FA 20:5*n*−3, to be distinctly lower (61%) than our results. The mean proportional contributions of ice algae-produced carbon in *Onisimus* sp. and *Gammarus* sp., estimated by Budge et al. (2008), were also clearly lower than our findings (*Onisimus* sp.: 36%, *Gammarus* sp.: 46%). These differences could be explained by a combination of regional, seasonal, or inter-annual variability. In a shelf system, pelagic production may be higher due to higher nutrient and light availability, and amphipods have better access to recycled pelagic POM. In the ice-covered high Arctic deep-sea, however, ice algae represent a highly important carbon source for species, such as *A. glacialis* or *Onisimus* spp., and pelagic production is low (Fernández-Méndez 2014).

Based on FA 20:5*n*−3, Wang et al. (2015) reported that *T. libellula* consumed substantial amounts of ice algae-produced FAs with a proportional contribution between 47% and 63% in the Bering Sea, with variations according to ice conditions. These values correspond well to the results of our BSIA analysis and our model a, which is based on the same FA. Our results from model b, however, indicate that the true dependency of this species on sea ice-produced carbon was probably lower when the proportional consumption of dinoflagellate-produced FAs is considered. In fact, a previous study, based on bulk stable isotope compositions, also indicated that *T. libellula* primarily depends on pelagic carbon sources (Søreide et al. 2006).

In the pteropod *C. limacina*, we found the lowest trophic dependency on ice algae-produced carbon compared to all other species, irrespective of the method and the mixing model used. A low trophic dependency (<20%) on ice algae-produced carbon based on BSIA values was also found by e.g., Søreide et al. (2006). However, the subsequent loss of

shelter from predators might be more pronounced in certain species than the dependency on sea ice in terms of food supply.

Altogether, a CSIA-based approach including the effect of multiple potential carbon producing taxa at the base of the food web (such as our model b) appears to be the most conservative approach to estimate the contribution of sea ice algae in food web studies.

We estimated the overall demand of ice algae-produced carbon by the most abundant herbivores *C. glacialis*, *C. hyperboreus* and *A. glacialis* (David et al. 2015). Due to its high abundance in the water column, the bulk of the ice algal carbon demand was attributed to *C. glacialis*. The outcome of this estimation should be considered as a minimum range, because the carbon demand of other abundant potential ice algal grazers, such as *Onisimus* spp. and *Oithona* spp., was not included in our tentative calculation (David et al. 2015). Because *C. glacialis* is known to constantly change its vertical position in the water column, it is unlikely that the estimate of α_{Ice} was biased by our sampling in the under-ice water layer. At an integrated (median) primary production rate by ice algae of about 0.7 mg C m^{-2} d^{-1} (Fernández-Méndez 2014), the minimum ice algal carbon demand of the three species in our study exceeded the ice algal primary production by a factor of 4 to 12 during the sampling period. To some extent, the apparent discrepancy between low sea ice primary production rates and high carbon demand of herbivores may reflect high ice algae production rates prior to our sampling, inferred by Boetius et al. (2013), who observed a high export of ice algae to the sea floor during August and September 2012. In the light of less than one day turnover times in herbivores (Graeve et al. 2005), however, minimum ice algal carbon demand rates ranging potentially an order of magnitude above measured in situ primary production rates of ice algae, indicating that the interaction between ice algal production and food web dynamics is far from understood. To improve the quantitative understanding of this interaction, efforts to quantify the spatio-temporal dynamics of both ice algal production and grazer populations must be considerably increased.

Conclusions

The results of this study showed an Arctic under-ice community with gradual differences in the dependency on sea ice algae-produced carbon, ranging from nearly 100% in sympagic amphipods to less than 30% in the pelagic pteropod *Clione limacina*. Particularly in ecologically important pelagic carbon transmitters, such as *Calanus* spp. and *Themisto libellula*, the dependency on sea ice algae-produced carbon was overall significant, leading to a cumulative carbon demand that considerably exceeded sea ice algae primary production estimated in the field. With a significant dependency on sea ice algae-produced carbon in almost all investigated species, our results show that the Arctic sea ice-water interface is a functional node transmitting carbon from the sea ice into the pelagic food web. Hence, the role of zooplankton and under-ice fauna in the central Arctic Ocean may change significantly in the future, as the spatio-temporal extent of sea ice declines and its structural composition changes. Our results indicate that these changes will likely first have the most pronounced impact on sympagic amphipods, but will consequently affect food web functioning and carbon dynamics of the pelagic system.

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