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 (\(a_{Ice}\)) 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 (\(d^{15}N\)) and carbon (\(d^{13}C\)) isotopic ratios, and compound-specific stable isotope analysis (CSIA) of \(d^{13}C\) in trophic marker FAs. A high mean contribution \(a_{Ice}\) 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 \(a_{Ice}\) values (BSIA: 39% to 55%, CSIA: 23% to 48%). Lowest \(a_{Ice}\) 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 \(d^{13}C\) signatures from both diatom-specific and dinoflagellate-specific marker FAs provided the most conservative estimate of \(a_{Ice}\). 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-Mén dez 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
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 origi-
nate 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 con-
tent (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 13C 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 com-
positions to describe the trophic relationships between phy-
toplankton, 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 pro-
duced 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 envi-
ronmental regimes could be distinguished in our sampling
area. During the sampling period, the Nansen Basin (NB)
was characterized by higher salinities and nitrate concentra-
tions compared to the Amundsen Basin (AB), among other
properties. The community structure of under-ice faunal
organisms was also separated according to these two envi-
nronmental regimes (David et al. 2015). Besides the basin-
wide perspective, we analyzed differences in the FA parame-
ters 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

Ice-associated particulate organic matter (I-POM), represen-
tative of the ice algal 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 equip-
ment can be found in David et al. (2015). Details of the sam-
pling 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 concentra-
tions between 0.2 mg m⁻³ and 1.2 mg m⁻³ throughout the
sampling area. Depending on the P-POM biomass concen-
tration, between 6.4 L and 11.0 L of water was filtered using
pre-combusted GF/F filters. All I-POM and P-POM filters were stored at $-80^\circ$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 $-80^\circ$C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500 $^\circ$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$^\text{TM}$ chromatograph (VWR Hitachi, Germany), equipped with a monolithic silica column Chromolith$^\text{Hyp}$ Performance-Si (VWR, Germany) and an evaporative light scattering detector Sedex 75.
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.

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.

<table>
<thead>
<tr>
<th>Location</th>
<th>Sample type</th>
<th>Date (dd mon yyyy)</th>
<th>Station no.</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>P-POM</td>
<td>06 Aug 2012</td>
<td>209</td>
<td>81.296</td>
<td>30.103</td>
</tr>
<tr>
<td>B</td>
<td>UIF</td>
<td>07 Aug 2012</td>
<td>216</td>
<td>82.483</td>
<td>30.027</td>
</tr>
<tr>
<td>C</td>
<td>P-POM</td>
<td>08 Aug 2012</td>
<td>220</td>
<td>83.599</td>
<td>28.500</td>
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<tr>
<td></td>
<td>UIF</td>
<td>09 Aug 2012</td>
<td>223</td>
<td>84.070</td>
<td>30.434</td>
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<td>31.221</td>
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<tr>
<td></td>
<td>UIF</td>
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<td>233</td>
<td>83.934</td>
<td>31.298</td>
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<tr>
<td>D</td>
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<td>237</td>
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<tr>
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<td>E</td>
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<td>109.590</td>
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<tr>
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<td>258</td>
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<tr>
<td></td>
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<td>263</td>
<td>83.476</td>
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<td>F</td>
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<td>G</td>
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<td>81.717</td>
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<td></td>
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<td>82.989</td>
<td>127.103</td>
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<tr>
<td>H</td>
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<td>85.102</td>
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<td>85.254</td>
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<td>I</td>
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<td>87.341</td>
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<td>52.620</td>
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<tr>
<td>J</td>
<td>UIF</td>
<td>29 Sep 2012</td>
<td>397</td>
<td>84.172</td>
<td>17.922</td>
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</tbody>
</table>

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).

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

\[
\delta x = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000
\]

where x represents the heavy carbon isotope ¹³C or the heavy nitrogen isotope ¹⁵N. \(R_{\text{sample}}\) represents the ¹³C/¹²C or ¹⁵N/¹⁴N isotope ratio relative to the corresponding standard (\(R_{\text{standard}}\)). 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 ¹³C relative to proteins and carbohydrates (Deniro and Epstein 1977), they are often removed prior to the analysis in order to reduce the variability of δ¹³C due to seasonal fluctuations (Tammlander 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 δ¹³C (Pinnegar and Polumin 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: \(\delta^{15}N = -4.52^{\text{oom}}\), \(\delta^{13}C = -28.57^{\text{oom}}\)) and USGS41 (certified: \(\delta^{15}N = 47.57^{\text{oom}}\), \(\delta^{13}C = 37.49^{\text{oom}}\)) provided by the International Atomic Energy Agency (IAEA, Austria). The analytical errors were indicated as \(\pm 0.2^{\text{oom}}\) for nitrogen and \(\pm 0.3^{\text{oom}}\) 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 \(\pm 0.1^{\text{oom}}\) for both Isoleucine nitrogen and carbon isotope ratios, and \(\pm 0.1^{\text{oom}}\) and \(\pm 0.2^{\text{oom}}\) 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 δ¹³C 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 δ¹³C 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 δ¹³C values of the free FA and the FAME (e.g., 16 : 0 FA: \(-28.56^{\pm 0.12^{\text{oom}}}\); 16 : 0 FAME: \(-28.57^{\pm 0.16^{\text{oom}}}\), C. Albers unpubl.). Therefore, we did not correct for these potential differences.

The δ¹³C values of the individual FAMES were calibrated by analyzing the certified standard FAMES 14:0 (certified: \(\delta^{13}C = -29.98^{\text{oom}}\)) and USGS40 (certified: \(\delta^{15}N = 47.57^{\text{oom}}\), \(\delta^{13}C = 37.49^{\text{oom}}\)) supplied by Indian University, every five samples. The analytical error was \(\pm 0.3^{\text{oom}}\) 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 \(\pm 0.4^{\text{oom}}\) (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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>ANOVA</th>
<th>Tukey HSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>level FA 16:1n−7</td>
<td>n: 98, F: 28.3, df: 7, 90, p &lt; 0.001</td>
<td>A. glacialis &gt; all amphipod species: p &lt; 0.001</td>
</tr>
<tr>
<td>level FA 22:6n−3</td>
<td>n: 98, F: 39.3, df: 7, 90, p &lt; 0.001</td>
<td>C. limacina &lt; all species: p &lt; 0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Calanus spp. &gt; all amphipod species: p &lt; 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. limacina &gt; all species (except C. hyperboreus): p &lt; 0.001</td>
</tr>
</tbody>
</table>

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 16:1n−7 and 20:5n−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 18:4n−3 and 22:6n−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 : 2 (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 δ13C and FA-specific δ13C values were determined to estimate the proportional contribution of ice algae-produced carbon (zice) to the diet of the under-ice fauna species. Bayesian multi-source stable isotope mixing models (SIAR; Parnell et al. 2010) were used to determine the zice estimates from both analyses, BSIA and CSIA. For the CSIA modeling, two different FA combinations were used: (a) 20:5n−3 and (b) 20:5n−3 + 22:6n−3, to account for the potentially overlapping compositions of the ice algae and phytoplankton communities. The diatom-specific FA 20:5n−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 22:6n−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 (Tameleon 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 20:5n−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 zice 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 zice 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. Students 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 (ANOVA) 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 16:1n−7, showing significantly higher levels than
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

**Table 4. Statistical parameters of Students t-tests with significant results.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>level FA 16:1(n)-7</td>
<td>19</td>
<td>13.6</td>
<td>&lt; 0.001 I-POM &gt; P-POM</td>
</tr>
<tr>
<td>level FA 18:4(n)-3</td>
<td>19</td>
<td>16.3</td>
<td>&lt; 0.001 I-POM &gt; P-POM</td>
</tr>
<tr>
<td>(\delta^{13})C FA 18:4(n)-3</td>
<td>12</td>
<td>4.7</td>
<td>&lt; 0.001 I-POM &gt; P-POM</td>
</tr>
<tr>
<td>level FA 20:5(n)-3</td>
<td>19</td>
<td>10.9</td>
<td>&lt; 0.05 I-POM &lt; P-POM</td>
</tr>
<tr>
<td>(\delta^{13})C FA 20:5(n)-3</td>
<td>13</td>
<td>9.9</td>
<td>&lt; 0.001 I-POM &lt; P-POM</td>
</tr>
<tr>
<td>level FA 22:6(n)-3</td>
<td>19</td>
<td>12.8</td>
<td>&lt; 0.001 I-POM &lt; P-POM</td>
</tr>
<tr>
<td>(\delta^{13})C FA 22:6(n)-3</td>
<td>11</td>
<td>4.4</td>
<td>&lt; 0.01 I-POM &lt; P-POM</td>
</tr>
</tbody>
</table>

FA: fatty acid, n: sample size.

*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 \(p > 0.05\)).

*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. *Gammaaras 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.
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 18:4n–3, 20:5n–3, and 22:6n–3 were significantly higher in the NB regime in *A. glacialis*, *O. glacialis*, and *G. wilkitzkii*. In *E. holmii*, the proportions of 20:5n–3 and 22:6n–3 were significantly higher in the NB regime samples compared to the AB regime samples. In *T. libellula*, the levels of 18:4n–3, 20:1n–9 and 22:1n–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\(^{\circ/\circ} \) and 6.4\(^{\circ/\circ} \) in I-POM and between 2.1\(^{\circ/\circ} \) and 5.8\(^{\circ/\circ} \) in P-POM, representing the trophic baseline (Table 6). The \( \delta^{13}C \) values in I-POM varied between -22.8\(^{\circ/\circ} \) and -26.8\(^{\circ/\circ} \), the P-POM \( \delta^{13}C \) values varied between -25.4\(^{\circ/\circ} \) and -28.7\(^{\circ/\circ} \).

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

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**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 “–”.

<table>
<thead>
<tr>
<th>I-POM</th>
<th>P-POM</th>
<th>Calanus glacialis</th>
<th>Calanus hyperboreus</th>
<th>Apherusa glacialis</th>
<th>Onisimus wilkitzkii</th>
<th>Gammarus holmii</th>
<th>Eusirus holmii</th>
<th>Themisto libellula</th>
<th>Clione limacina</th>
</tr>
</thead>
<tbody>
<tr>
<td>( n_{NB} )</td>
<td>9</td>
<td>17</td>
<td>3</td>
<td>11</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>( n_{AB} )</td>
<td>9</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>14:0</td>
<td>5.3 ± 1.5</td>
<td>6.0 ± 2.1</td>
<td>8.1 ± 1.2</td>
<td>4.6 ± 1.9</td>
<td>4.2 ± 0.4</td>
<td>3.4 ± 0.9</td>
<td>3.9 ± 0.5</td>
<td>3.8 ± 0.6</td>
<td>4.9 ± 1.3</td>
</tr>
<tr>
<td>16:0</td>
<td>16.3 ± 4.1</td>
<td>20.3 ± 1.9</td>
<td>8.8 ± 1.5</td>
<td>7.3 ± 3.2</td>
<td>13.4 ± 0.5</td>
<td>11.5 ± 2.1</td>
<td>12.2 ± 0.8</td>
<td>12.7 ± 1.6</td>
<td>9.2 ± 1.3</td>
</tr>
<tr>
<td>16:1n–7*</td>
<td>53.6 ± 17.9</td>
<td>9.8 ± 6.0</td>
<td>26.2 ± 7.3</td>
<td>20.3 ± 10.2</td>
<td>48.1 ± 8.1</td>
<td>27.0 ± 9.6</td>
<td>31.4 ± 5.6</td>
<td>36.4 ± 8.5</td>
<td>27.9 ± 8.5</td>
</tr>
<tr>
<td>18:0</td>
<td>4.5 ± 7.5</td>
<td>5.3 ± 1.2</td>
<td>1.2 ± 0.5</td>
<td>1.6 ± 1.1</td>
<td>0.7 ± 0.2</td>
<td>0.5 ± 0.2</td>
<td>0.6 ± 0.1</td>
<td>0.6 ± 0.2</td>
<td>0.5 ± 0.1</td>
</tr>
<tr>
<td>18:1n–9</td>
<td>7.0 ± 4.5</td>
<td>6.5 ± 2.5</td>
<td>3.6 ± 0.4</td>
<td>3.3 ± 0.6</td>
<td>7.9 ± 1.5</td>
<td>18.1 ± 4.4</td>
<td>16.1 ± 2.9</td>
<td>9.8 ± 1.4</td>
<td>8.1 ± 1.5</td>
</tr>
<tr>
<td>18:1n–7</td>
<td>0.4 ± 0.4</td>
<td>1.8 ± 1.1</td>
<td>1.5 ± 0.4</td>
<td>1.8 ± 0.7</td>
<td>2.0 ± 0.5</td>
<td>3.4 ± 0.7</td>
<td>4.0 ± 0.5</td>
<td>3.0 ± 0.6</td>
<td>3.0 ± 0.7</td>
</tr>
<tr>
<td>18:4n–3†</td>
<td>1.2 ± 0.5</td>
<td>6.4 ± 1.4</td>
<td>2.2 ± 1.6</td>
<td>3.0 ± 1.6</td>
<td>1.9 ± 0.7</td>
<td>1.5 ± 0.9</td>
<td>1.9 ± 0.5</td>
<td>1.5 ± 0.7</td>
<td>2.4 ± 1.3</td>
</tr>
<tr>
<td>20:1n–9‡</td>
<td>–</td>
<td>–</td>
<td>9.8 ± 4.3</td>
<td>8.7 ± 5.6</td>
<td>0.7 ± 0.4</td>
<td>8.9 ± 4.5</td>
<td>3.2 ± 2.1</td>
<td>4.9 ± 4.5</td>
<td>11.3 ± 4.1</td>
</tr>
<tr>
<td>20:1n–7</td>
<td>–</td>
<td>–</td>
<td>0.5 ± 0.4</td>
<td>1.0 ± 0.9</td>
<td>0.5 ± 0.2</td>
<td>1.4 ± 0.6</td>
<td>0.7 ± 0.1</td>
<td>1.0 ± 0.5</td>
<td>1.5 ± 0.8</td>
</tr>
<tr>
<td>20:5n–3*</td>
<td>4.8 ± 2.2</td>
<td>7.1 ± 1.3</td>
<td>11.9 ± 1.9</td>
<td>15.3 ± 3.7</td>
<td>11.7 ± 3.6</td>
<td>9.7 ± 3.8</td>
<td>12.8 ± 3.4</td>
<td>11.8 ± 3.3</td>
<td>9.7 ± 1.6</td>
</tr>
<tr>
<td>22:1n–11‡</td>
<td>–</td>
<td>–</td>
<td>4.3 ± 2.3</td>
<td>6.2 ± 4.8</td>
<td>0.2 ± 0.1</td>
<td>2.5 ± 1.6</td>
<td>2.1 ± 1.9</td>
<td>1.8 ± 1.8</td>
<td>3.7 ± 1.6</td>
</tr>
<tr>
<td>22:6n–3‡</td>
<td>1.2 ± 1.8</td>
<td>10.4 ± 2.1</td>
<td>11.4 ± 3.5</td>
<td>14.1 ± 7.8</td>
<td>2.0 ± 0.8</td>
<td>3.4 ± 1.3</td>
<td>3.3 ± 0.8</td>
<td>4.3 ± 1.8</td>
<td>7.1 ± 2.7</td>
</tr>
<tr>
<td>Total</td>
<td>94.3</td>
<td>73.6</td>
<td>89.5</td>
<td>87.2</td>
<td>93.3</td>
<td>91.3</td>
<td>92.2</td>
<td>91.6</td>
<td>89.3</td>
</tr>
</tbody>
</table>

*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. 16:1n–7 and 20:5n–3 represent diatom marker FAs, 18:4n–3 and 22:6n–3 represent dinoflagellate marker FAs, 20:1n–9 and 22:1n–11 represent *Calanus*-marker FAs. Box plot design as in Figure 2. Sample size is reported in Table 5.
A comparison of the fatty acid-specific stable isotope 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 18:4n–3 and 22:6n–3 in the I-POM samples indicated that a small part of the sea ice flora consisted of diatoms and flagellates, 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 20:5n–3 accompanied with the distinctly higher levels of the diatom-FA 16:1n–7 in the I-POM samples showed the highest δ13C values of 18:4n–3 in the I-POM samples compared to all other species, except for *C. limacina*. Among all species, *A. glacialis* 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 20:5n–3 (model a) were similar to those from the BSIA models, and were generally higher than the zice estimates derived from model b, which combined 20:5n–3 and 22:6n–3 (Table 8).

*A. glacialis* showed the highest zice estimates among all species, accompanied with the lowest variation between the zice 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 zice 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 zice 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 18:4n–3 and 22:6n–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 20:5n–3 accompanied with the distinctly higher levels of the diatom-FA 16:1n–7 in the I-POM samples.
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 20:5n−3 and 22:6n−3 from 18:3n−3 (Moreno et al. 1979), FA 18:3n−3 was only found in trace amounts (<1%) in the species from this study. This indicates that biosynthesis of 20:5n−3 and 22:6n−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 16:1n−7 and 20:5n−3 (Graeve et al. 1994b; Wang et al. 2015).

**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.
Furthermore, our results showed that both copepod species contained high amounts of the dinoflagellate-specific marker FA 22:6n−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 16:1n−7 and 20:5n−3, accompanied by low levels of the dinoflagellate-specific FA 22:6n−3. A diatom-dominated diet is in agreement with several studies showing that A. glacialis primarily feeds on the under-ice flora and phyto- detritus (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 16:1n−7 and 20:5n−3, with considerably lower levels of the dinoflagellate-specific FA 22:6n−3.

Table 6. Bulk stable nitrogen (δ15N) and carbon isotope values (δ13C) in ice-associated particulate organic matter (I-POM), pelagic particulate organic matter (P-POM), and under-ice fauna species (mean ± 1 SD, n).

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

Note: Not detected FAs are reported as “−”.

Table 7. Carbon stable isotope values (δ13C) 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, n). Not detected FAs are reported as “−”.

Table 8. Proportional contribution of ice algae-produced carbon (fice) 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) 20:5n−3 and (b) 20:5n−3 + 22:6n−3 (Table 7). Ranges of fice are shown in parentheses.
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 16:1n−7 and the highest proportion of the dinoflagellate-specific FA 22:6n−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 *L. helicina* community. All amphipod species and *Calanus* spp. from the Amundsen Basin regime had higher proportions of the FA 16:1n−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 16:1n−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 $\%_{ice}$ 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 $\delta^{15}N$ (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 $\%_{ice}$ 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 $\%_{ice}$ estimates yielded a consistent hierarchical order of the investigated species, ranging from a highly sea ice algae-related

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

<table>
<thead>
<tr>
<th></th>
<th>Ingestion rate* (µg C ind.−1 d−1)</th>
<th>Abundance (ind. m−2)</th>
<th>Ice algal carbon demand (mg C m−2 d−1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td><em>Calanus glacialis</em></td>
<td>0.33</td>
<td>6.0</td>
<td>18.0</td>
</tr>
<tr>
<td><em>Calanus hyperboreus</em></td>
<td>0.25</td>
<td>2.8</td>
<td>8.4</td>
</tr>
<tr>
<td><em>Apherusa glacialis</em></td>
<td>0.86</td>
<td>13.0</td>
<td>13.0</td>
</tr>
<tr>
<td>Total</td>
<td>21.8</td>
<td>39.4</td>
<td>8.0</td>
</tr>
</tbody>
</table>

*Olli et al. (2007), †David et al. (2015), ‡Ehrlich (2015).*
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 \( z_{\text{ice}} \) 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 algal 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 Thetis 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.

**References**


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