Dependency of Arctic zooplankton on pelagic food sources: New insights from fatty acid and stable isotope analyses

Doreen Kohlbach [ORCID],[1*] Benoit Lebreton,[2] Gaël Guillou,[2] Anette Wold,[1] Haakon Hop,[1] Martin Graeve [ORCID],[3] Philipp Assmy[1]

[1]Norwegian Polar Institute, Fram Centre, Tromsø, Norway
[2]UMR Littoral, Environnement et Sociétés (CNRS-Université de La Rochelle), Institut du Littoral et de l'Environnement, La Rochelle, France
[3]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar-und Meeresforschung, Bremerhaven, Germany

Abstract

Global warming causes dramatic environmental change to Arctic ecosystems. While pelagic primary production is initiated earlier and its intensity can be increased due to earlier ice melt and extended open-water periods, sea-ice primary production is progressively confined on a spatio-temporal scale, leading to unknown consequences for the ice-associated (sympagic) food web. Understanding ecological responses to changes in the availability and composition of pelagic and sympagic food sources is crucial to determine potential changes of food-web structure and functioning in Arctic marine communities under increasingly ice-free conditions. Focus was placed on the importance of suspended particulate organic matter vs. sympagic organic matter for 12 zooplankton species with different feeding modes covering five taxonomic groups (copepods, krill, amphipods, chaetognaths, and appendicularians) at two ice-covered, but environmentally different, stations in the north-western Barents Sea in August 2019. Contributions of diatom- and flagellate-associated fatty acids (FAs) to total lipid content and carbon stable isotopic compositions of these FAs were used to discriminate food sources and trace flows of organic matter in marine food webs. Combination of proportional contributions of FA markers with FA isotopic composition indicated that consumers mostly relied, directly (herbivorous species), or indirectly (omnivorous and carnivorous species), on pelagic diatoms and flagellates, independently of environmental conditions at the sampling locations, trophic position, and feeding mode. Differences were nevertheless observed between species. Contrary to other studies demonstrating a high importance of sympagic organic matter for food-web processes, our results highlight the complexity and variability of trophic structures and dependencies in different Arctic food webs.

Sea ice is an important feature of Arctic ecosystems as it provides a habitat for foraging and reproduction, as well as shelter from predators for animals across all trophic levels (Laidre et al. 2015; Bluhm et al. 2017). Moreover, microalgae associated with sea ice (sympagic algae) can serve as a food resource for small animals inhabiting the sea ice-water interface and herbivorous zooplankton in the underlying water column, in both perennial sea-ice systems, such as the Central Arctic Ocean (Kohlbach et al. 2016), and seasonal sea-ice systems, such as the Chukchi and Bering Seas (Budge et al. 2008; Wang et al. 2015). Grazers can rely strongly on ice algae during spring, while the role of phytoplankton increases as the season progresses. Phytoplankton can represent the major food source in regions with predominantly ice-free conditions (Michel et al. 1996; Søreide et al. 2006, 2010; Tamelander et al. 2008).

Such a functioning is likely affected by climate change: declining Arctic sea-ice extent and thickness (Onarheim et al. 2018; Stroeve and Notz 2018) lead to longer open-water seasons, which has an impact on the Arctic primary production in the water column (pelagic production) and the sea ice (sympagic production). Such changes affect the spatio-temporal availability, the biomass and the taxonomic composition of these food sources (Leu et al. 2011; Lewis et al. 2020)

---

*Correspondence: doreen.kohlbach@npolar.no; d.kohlbach@googlemail.com

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

leading to implications for seasonal marine food-web structures and dynamics (Stige et al. 2019; Dalpadado et al. 2020). As a result, in an increasingly ice-free Arctic Ocean (Onarheim and Årthun 2017), food sources of sympagic origin may become more confined to some specific regions and periods, while the role of pelagic primary production might increase (Arrigo and van Dijken 2015). Changes currently affecting the primary producers will likely directly impact zooplanktonic communities and their food sources, particularly species that potentially thrive on sympagic organic matter (e.g., Søreide et al. 2010; Kohlbach et al. 2016), with implications for associated pelagic and benthic food webs. As a result, there is a need to establish updated knowledge about zooplankton food resources to predict how changes in primary producers will induce ecological cascades at the scale of entire food webs.

In this study, we compare food-web functioning at two different locations in the north-western Barents Sea during August 2019. These stations were characterized by different environmental conditions, especially ice, allowing us to determine if and how these varying environmental conditions could impact flows of organic matter. Two trophic marker approaches (i.e., fatty acid [FA] analysis and compound-specific stable isotope analysis [CSIA] of FAs) were used to determine the flows of pelagic and sympagic organic matter in these two food webs. Combination of trophic markers has proved to be much more efficient to understand the functioning of food webs, as the information provided by these different methods is rather complementary. Relative proportions of algal FA trophic markers (Dalsgaard et al. 2003; Jónasdóttir 2019) can provide insights on the food resources of consumers (Budge et al. 2007; Kohlbach et al. 2021*a*). Carbon stable isotope compositions (δ^{13}C) of specific FAs can be used to determine energy transfers (Murphy and Abrajano 1994; Burian et al. 2020; Twining et al. 2020) and are very useful to define the origin of food sources (i.e., pelagic vs. sympagic algae) in marine food webs (Wang et al. 2015; Kohlbach et al. 2016).

In this study, the importance of the different food sources (i.e., pelagic particulate organic matter [PPOM] and ice-associated particulate organic matter [IPOM]) for ecologically relevant species of zooplankton collected at the two locations were elucidated based on the relative proportions of algal-specific FA markers and their isotopic compositions in producers and consumers. We focused on species which are important for the energy transfer in the Barents Sea food-web due to their high abundances in this ecosystem, i.e., *Calanus* copepods (Aarflot et al. 2018), krill and *Themisto* amphipods (Wassmann et al. 2006). We also included species that have been less studied so far, i.e., the carnivorous copepods *Paraeuchaeta glacialis* and *P. norvegica*, and the appendicularian *Oikopleura vanhoeffeni*, to gain more information about their role in food-web processes under current environmental conditions and to obtain a broader understanding of the food-web functioning in the Barents Sea.

Materials and methods

Sampling

Two ice-covered stations (i.e., P6 and P7) were sampled with RV *Kronprins Haakon* in the north-western Barents Sea as part of the Norwegian Nansen Legacy project (arvenetternansen.com; Fig. 1). These stations varied in their location (P6: shelf slope vs. P7: deep Arctic Basin); Atlantic water masses dominated at the shelf-regime Station P6, while the surface layer (upper 100 m of the water column) of the Arctic Basin Station P7 was influenced by colder Arctic water masses. The ice edge was located at ca. 79.75°N and 34°E, and first-year ice of < 70 cm dominated the sampling area at both stations, but the sea ice at Sta. P6 was in a more advanced stage of melting compared to P7. Chlorophyll *a* (Chl *a*) concentrations in the water column at the depth of the Chl *a* maximum were similar at P6 (1.3 μg L^{-1}, 10 m) and P7 (1.7 μg L^{-1}, 10 m). Chl *a* concentrations in the bottom 3 cm of the ice were higher at Sta. P7 compared to P6 (2.9 vs. 0.6 μg L^{-1}; Vader et al. 2022).

Five taxonomic groups of zooplankton including copepods (six species), krill (two species), amphipods (one species), chaetognaths (two species), and appendicularians (one species; Table 1) were sampled during the second half of August 17–21, 2019. Animals were collected with Bongo net (180 μm mesh size), MultiNet (180 μm mesh size), and MIK net (1500 μm mesh size). Sampled depth layers were 400–0 m and 50–0 m at Sta. P6 and 1250–0 m, 1000–100 m, and 100–0 m at Sta. P7. Life stages of copepods were determined, and length was measured for the other taxa (Table 1) before being frozen at −80°C until further processing. Dry weights of animals were determined gravimetrically. At the same stations, PPOM was collected by taking water samples at the depth of the Chl *a* maximum (14 m at Sta. P6 and 15 m at Sta. P7) using Niskin bottles attached to a CTD rosette. Ice cores were taken close to these sampling stations with a 9-cm diameter ice corer (Kovacs Enterprises, USA). IPOM was collected by melting the bottom 10 cm of the ice cores in the dark at 4°C without the addition of filtered seawater. Both seawater and ice water samples were filtered through precombusted (3 h, 550°C) 47 mm Whatman® GF/F filters and stored at −80°C until further processing.

Trophic marker approaches
Fatty acids

Prior to CSIA, FAs were extracted and analyzed at the Alfred Wegener Institute in Bremerhaven, Germany. Briefly, lipids were extracted from freeze-dried filters and zooplankton with dichloromethane/methanol (2 : 1, v/v); FAs were derivatized to fatty acid methyl esters (FAMEs) and separated via gas chromatography (see Kohlbach et al. 2021*a* for details). PPOM samples were analyzed on triplicates and IPOM samples in duplicates for both stations each. Zooplankton was analyzed on individual samples, except for *Calanus glacialis* at Sta. P7
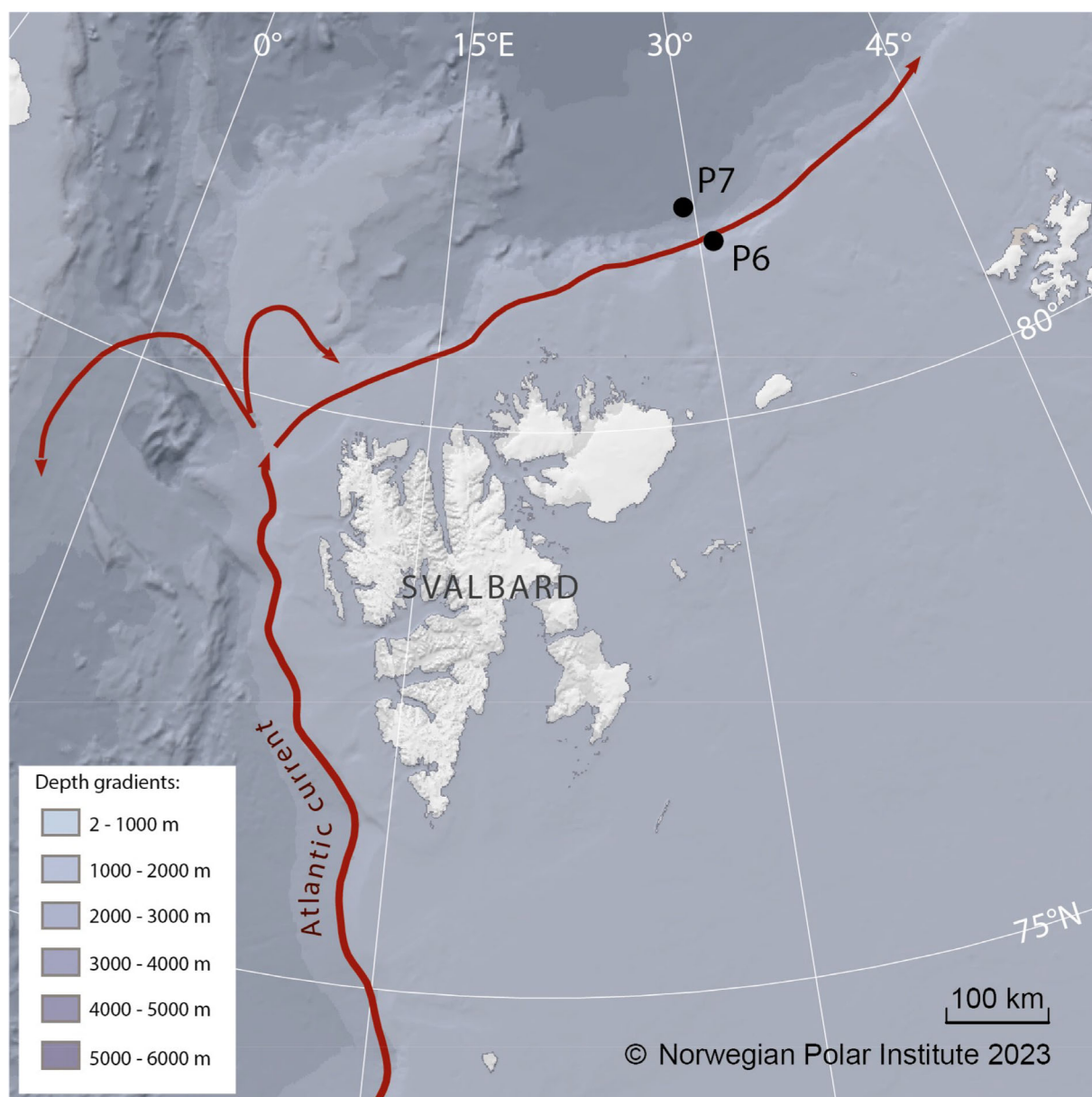
Fig. 1. Location of the two sampling Sta. P6 and P7 in the north-western Barents Sea.

($n = 2$). All FA data can be found in Kohlbach et al. (2021*a*, 2022*b*).

Here we focused on the relative proportions of three FA markers: $16:1(n\text{-}7)$ and $20:5(n\text{-}3)$, mainly produced by diatoms, and $22:6(n\text{-}3)$, predominant in dinoflagellates and other flagellates (e.g., *Phaeocystis* spp.; Reuss and Poulsen 2002; Dalsgaard et al. 2003; thereafter flagellate-associated FA marker). These three FA markers were selected because sympagic communities are often dominated by diatoms (Syvertsen 1991; Tamelander et al. 2009*b*), although diatoms can also contribute significantly to pelagic

communities (Dąbrowska et al. 2020). Dinoflagellates and other flagellates can be abundant in pelagic protist assemblages and can also be found in sea-ice communities (Ratkova and Wassmann 2005; van Leeuwe et al. 2018; Kohlbach et al. 2023*a*).

The following ratios were also computed: $[16:1(n\text{-}7) + 20:5(n\text{-}3)]/22:6(n\text{-}3)$, $16:1(n\text{-}7)/16:0$, $20:5(n\text{-}3)/22:6(n\text{-}3)$ and $\Sigma C16/\Sigma C18$ (including FAs $16:0$, $16:1(n\text{-}9)$, $16:1(n\text{-}7)$, $16:1(n\text{-}5)$, $16:2(n\text{-}4)$, $16:3(n\text{-}4)$, $16:4(n\text{-}1)$, $18:0$, $18:1(n\text{-}9)$, $18:1(n\text{-}7)$, $18:1(n\text{-}5)$, $18:2(n\text{-}6)$, $18:3(n\text{-}6)$, $18:3(n\text{-}3)$, $18:4(n\text{-}3)$). For all these ratios, a value > 1 can indicate

Table 1. Overview of zooplankton collected for trophic marker analyses during the second half of August 2019 in the Barents Sea.

Taxonomic group	Zooplankton taxa	Collected at station	Stage/length or length group (mm)*	Dry weight/ ind. (mg)	Ind./ sample	Trophic type**
Copepods	*Calanus finmarchicus* Gunnerus, 1770	P6, P7	CV-AF	–	25 and 28	H-O
	Calanus glacialis Jaschnov, 1955	P7	CV-AF	–	5 and 10	H-O
	Calanus hyperboreus Krøyer, 1838	P6, P7	CIV-CV	2.7 and 2.9	10 and 18	H-O
	Microcalanus spp.	P7	–	–	100	O
	Paraeuchaeta glacialis Hansen, 1886	P6	AF	16.7	2	C
	Paraeuchaeta norvegica Boeck, 1972	P6	CV-AF	4.9 and 5.0	4	C
Krill	*Meganyctiphanes norvegica* M. Sars, 1857	P7	26	31.7	1	O
	Thysanoessa longicaudata Krøyer, 1846	P6, P7	10–20	5.2 and 5.3	2 and 10	H-O
Amphipods	*Themisto abyssorum* Boeck, 1870	P6, P7	15–20 to 25–30	14.0 and 13.1	3 and 4	C
Chaetognaths	*Eukrohnia hamata* Möbius, 1875	P6, P7	20–30 to 30–40	3.7 and 5.7	10 and 15	O-C
	Pseudosagitta maxima Conant, 1896	P7	80	48.8	1	O
Appendicularians	*Oikopleura vanhoeffeni* Lohmann, 1896	P6	10–20	–	>20	H-O

AF, adult female; CIV-CV, copepodid stages IV–V.
*Copepods measured from the rostrum to the tip of the last prosome segment (not including rostrum); krill and amphipods measured from the base of the rostrum to the end of the urosome; total length or widest diameter were measured on the other species.
**H: herbivore, O: omnivore, C: carnivore; based on the FA carnivory index $18:1(n\text{-}9)/18:1(n\text{-}7)$, the presence/contribution of copepod-associated FAs and the ratio zoosterols/phytosterols (see Kohlbach et al. 2021*a*). Most species could be classified as opportunistic feeders, with both algal and heterotrophic components in their diet. Among the zooplankton, *O. vanhoeffeni* occupied the lowest trophic level. *Calanus* copepods and *T. longicaudata* were likely feeding as omnivores. The copepods *Paraeuchaeta* spp. and the amphipod *Themisto abyssorum* had the highest degree of carnivory based on these indices.

a higher reliance on food sources based on diatoms vs. flagellates. Ratio $[16:1(n\text{-}7) + 20:5(n\text{-}3)]/22:6(n\text{-}3)$ was compared to FA isotopic compositions.

Data visualization was done in Software R, version 4.1.0 (R Core Team 2021), using the package ggplot2 (Wickham 2016).

FA-specific carbon isotope compositions

We determined the carbon stable isotope compositions (δ^{13}C) of the two diatom-associated FA markers $16:1(n\text{-}7)$ and $20:5(n\text{-}3)$ and the flagellate-associated FA marker $22:6(n\text{-}3)$. Isotopic compositions of other diatom- and flagellate-associated FA markers, such as $16:4(n\text{-}1)$ and $18:4$ $(n\text{-}3)$, respectively, were not included in this study due to their low relative proportions in some of the species, hampering reliable evaluation of their respective isotopic signals with concentrations close to the detection limit.

Isotopic compositions were determined directly from the FA extracts at the stable isotope facility of the joint research unit LIENSs (CNRS–University of La Rochelle), France, using a gas chromatograph (Trace GC Ultra, Thermo Scientific, Italy) coupled with an interface (GC Isolink, Thermo Scientific, Germany) to an isotope ratio mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo Scientific, Germany). An Agilent J&W VF-23 ms (60 m × 0.25 mm internal diameter × 0.25 μm film) was used with helium as a carrier gas at a flow of 1 mL min^{-1} (constant flow) for separation of FAMEs. Samples were injected (1 μL) in splitless mode using a SSL injector at 240°C. Oven initial temperature was 100°C and then increased at a rate of 1°C min^{-1} until 210°C, and at a rate of 20°C min^{-1} until 240°C, with a hold time of 1.7 min at 240°C at the end of the ramp. FAME identification was performed by comparing relative retention times of FAME samples with those of two known standard mixtures (37 component FAME mix and PUFA No.3, Sigma Aldrich). Peaks were not overlapping with adjacent peaks, which could lead to ambiguous results. Isotopic compositions are expressed as parts per thousand (‰) in the δ notation (Coplen 2011) as deviations from a standard (Vienna Pee Dee Belemnite) following the formula: $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where R is $^{13}\text{C}/^{12}\text{C}$. Delta values were corrected and normalized using the values of an internal standard ($23:0$, Sigma Aldrich) calibrated in EA-IRMS (mean: -32.39‰, standard deviation: 0.02‰, $n = 5$). Calibration was conducted using reference materials (USGS-24, -61, -62, IAEA-CH6, -600). Analytical precision was < 0.10‰ based on analyses of laboratory internal standards (USGS-61 and USGS-62). This internal standard was added in each sample during lipid extraction. δ^{13}C values (mean ± standard deviation) of

this internal standard in samples—corrected to consider effect of peak amplitude—were $-32.63 \pm 0.51‰$ ($n = 37$). Samples were analyzed once, or in duplicate or triplicates when needed (i.e., adjustment of sample concentrations when compounds of interest had a very different peak amplitude). Statistical significance of differences in $\delta^{13}C$ values between Sta. P6 and P7 was tested with the nonparametric Wilcoxon signed rank test (assuming results with $p \le 0.05$ as significant). CSIA was performed on individual PPOM, IPOM, and zooplankton samples per station, except for *P. norvegica* at Sta. P6 ($n = 2$) and *C. glacialis* at Sta. P7 ($n = 2$). All data can be found in Kohlbach et al. (2023*b*).

Roles of PPOM and IPOM

To contrast the importance of pelagic-derived and sympagic-derived organic matter as food sources to the zooplankton at Sta. P6 and P7, we visualized the trophic marker data using non-metric multidimensional scaling (NMDS) ordination (Bray–Curtis dissimilarity). Three different ordinations were done based on (1) the relative proportions of three FA markers: $16:1(n\text{-}7)$, $20:5(n\text{-}3)$, and $22:6(n\text{-}3)$, (2) the $\delta^{13}C$ values of these three FA markers, and (3) the relative proportions and $\delta^{13}C$ values of these three FA markers. Data visualization was done using the vegan package in R (Oksanen et al. 2020).

Results

Relative proportions of FA markers

Detailed information on PPOM, IPOM, and zooplankton species-specific FA compositions (including output of statistical analyses) are reported in Kohlbach et al. (2021*a*). In brief, proportions of FA diatom markers were much higher (i.e., three times more abundant) in IPOM than in PPOM at both stations, particularly driven by the diatom-associated FA $16:1(n\text{-}7)$. Conversely, at both stations, proportions of the diatom-associated FA $20:5(n\text{-}3)$ were higher in PPOM compared to IPOM. Relative contributions of $22:6(n\text{-}3)$ were higher in PPOM than in IPOM (i.e., $< 2\%$ in IPOM) and twice as high in PPOM at Sta. P6 compared to P7 (Fig. 2).

Among the zooplankton, relative proportions of FA markers suggested that all species relied on a mixture of diatoms and flagellates at both sampling stations. Briefly, *Calanus* copepods had the strongest diatom signal with mean FA ratios of $16:1$ $(n\text{-}7)/16:0$, $\Sigma C16/C18$, and $20:5(n\text{-}3)/22:6(n\text{-}3) \ge 1$ at Sta. P6 and P7 (except for *Calanus hyperboreus* $\Sigma C16/C18 = 0.8$ at P7). All copepod species had high proportions of $16:1(n\text{-}7)$, ranging between 7% and 24% of the total FA content, while contributions of this FA marker in other species ranged from 7% to 17%. Highest proportions of $20:5(n\text{-}3)$ were observed in the appendicularian *O. vanhoeffeni* (27%) and *C. hyperboreus* (26%), both at Sta. P6 (other species: 7% to 22%). The chaetognath *Pseudosagitta maxima* (Sta. P7) and *O. vanhoeffeni* (Sta. P6) had higher proportions of the flagellate-associated FA $22:6(n\text{-}3)$ (i.e., 16% and 18%, respectively) compared to the
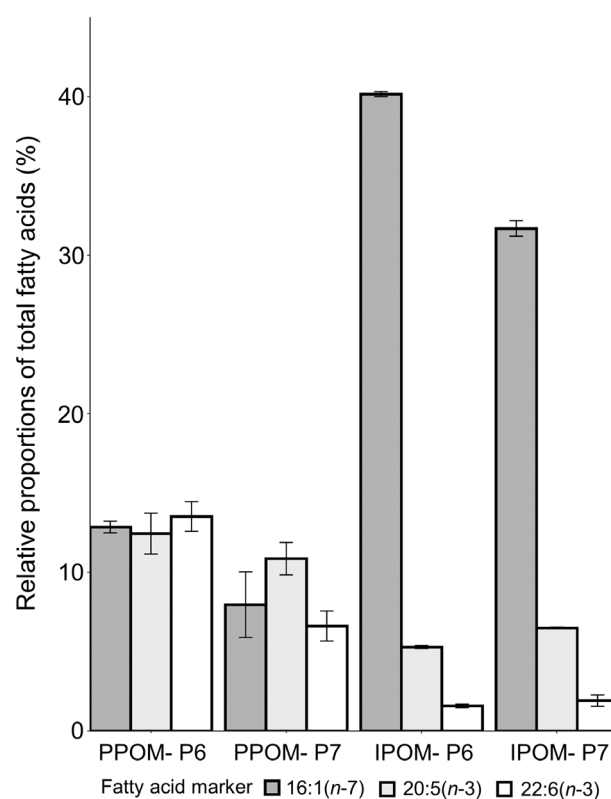

Fig. 2. Relative proportions (mean $\pm$ standard deviation) of the three FA markers in PPOM and IPOM at Sta. P6 and P7 (data reported in (Kohlbach et al., 2021*a*). FA markers $16:1(n\text{-}7)$ and $20:5(n\text{-}3)$ are diatom-derived, $22:6(n\text{-}3)$ is flagellate-derived.

other species (4–13%). In *Calanus finmarchicus*, *C. hyperboreus* and the krill *Thysanoessa longicaudata*, the diatom signal was stronger at Sta. P6 than at P7.

Isotopic composition of FA markers

$\delta^{13}C$ values of the three FAs were distinctly, but not significantly, higher in IPOM vs. PPOM at Sta. P7, with differences depending on FAs: $\sim8‰$ in $16:1(n\text{-}7)$, $\sim6‰$ in $20:5(n\text{-}3)$ and $\sim5‰$ in $22:6(n\text{-}3)$ (Supplementary Table S1). At Sta. P6, the $\delta^{13}C$ values of $16:1(n\text{-}7)$ and $20:5(n\text{-}3)$ were relatively similar between PPOM and IPOM, while $22:6(n\text{-}3)$ had lower $\delta^{13}C$ values in PPOM (Fig. 3, Supplementary Table S1).

Among all zooplankton species and across both stations (Supplementary Tables S2 and S3), $\delta^{13}C$ values of $16:1(n\text{-}7)$ varied from $-31.2‰$ in *T. longicaudata* (Sta. P7) to $-27.9‰$ in *O. vanhoeffeni* (Sta. P6), $\delta^{13}C$ values of $20:5(n\text{-}3)$ ranged from $-33.3‰$ in *P. maxima* (Sta. P7) to $-29.0‰$ in *T. longicaudata* (Sta. P6), and $\delta^{13}C$ values of $22:6(n\text{-}3)$ varied from $-33.6‰$ in *Themisto abyssorum* (Sta. P7) to $-28.2‰$ in *P. glacialis* (Sta. P6).

Overall, $\delta^{13}C$ values of $16:1(n\text{-}7)$ and $20:5(n\text{-}3)$ in the zooplankton were significantly higher at Sta. P6 ($-29.0 \pm 0.6‰$ and $-30.2 \pm 1.0‰$, respectively) compared to
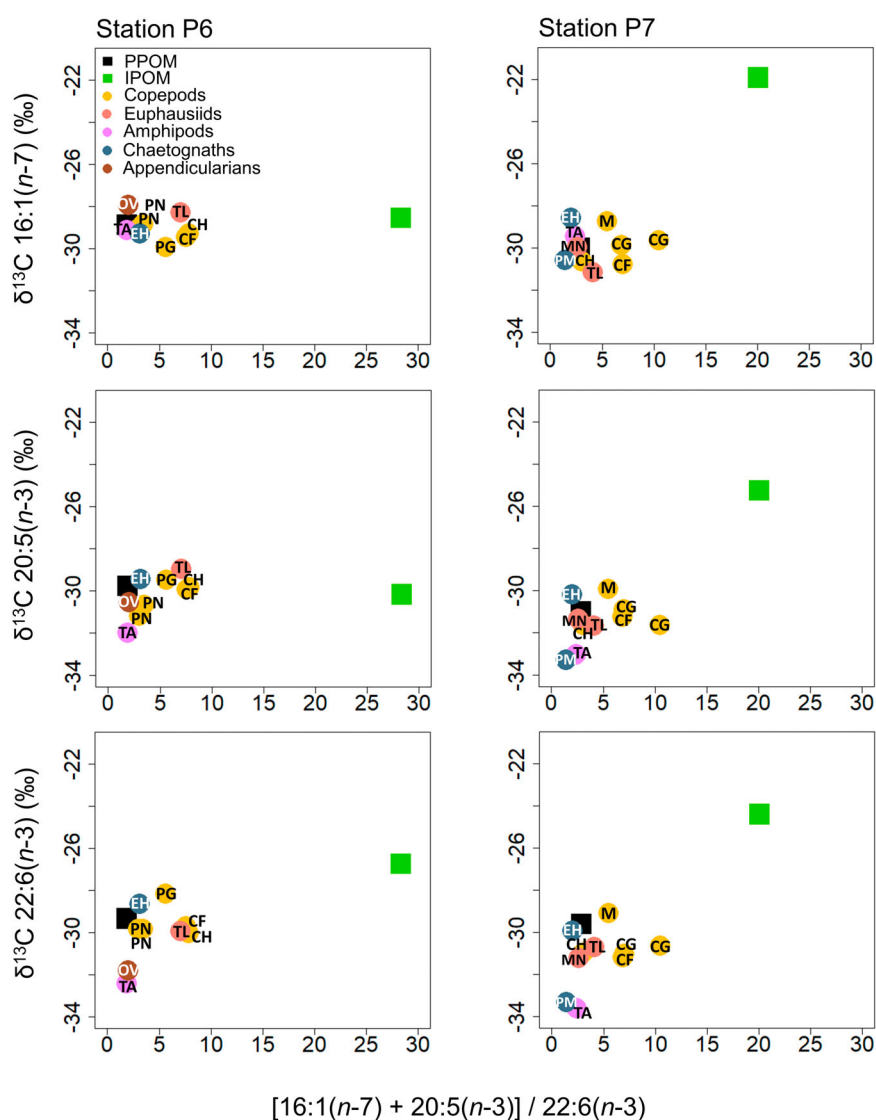
Fig. 3. Ratios of the diatom-associated FAs ($16:1(n\text{-}7) + 20:5(n\text{-}3)$) and the flagellate-associated FA $22:6(n\text{-}3)$ vs. carbon isotopic compositions ($\delta^{13}C$) of these three FAs in PPOM, IPOM, and the zooplankton species at Sta. P6 (left panels) and P7 (right panels).

CF: *Calanus finmarchicus*   CG: *Calanus glacialis*   CH: *Calanus hyperboreus*
EH: *Eukrohnia hamata*   MN: *Meganyctiphanes norvegica*   M: *Microcalanus* spp.
PG: *Paraeuchaeta glacialis*   PM: *Pseudosagitta maxima*   PN: *Paraeuchaeta norvegica*
TA: *Themisto abyssorum*   TL: *Thysanoessa longicaudata*   OV: *Oikopleura vanhoeffeni*

P7 ($-29.9 \pm 0.9‰$ and $-31.5 \pm 1.1‰$, respectively; Wilcoxon, $W = 72$, $p = 0.03$ and Wilcoxon, $W = 74$, $p = 0.02$, respectively). Average zooplankton $\delta^{13}C$ values were also somewhat higher in $22:6(n\text{-}3)$ at Sta. P6 ($-30.0 \pm 1.3‰$) compared to P7 ($-31.2 \pm 1.4‰$), although with no significant differences (Wilcoxon, $W = 67$, $p = 0.08$, respectively).

Comparing $\delta^{13}C$ values of the five species that were sampled at both stations (i.e., *C. finmarchicus*, *C. hyperboreus*, *T. longicaudata*, *T. abyssorum*, and *E. hamata*), between the two stations, only *E. hamata* did not follow the trend of higher

$\delta^{13}C$ values at Sta. P6 vs. P7 in $16:1(n\text{-}7)$ (Supplementary Table S3).

Two-dimensional analysis using FA profiles and carbon isotopic composition of FA markers

Combining the relative proportions of the diatom- vs. flagellate-associated FAs (i.e., ratio [$16:1(n\text{-}7) + 20:5(n\text{-}3)$]/$22:6(n\text{-}3)$) and the isotopic composition of the three FA markers (i.e., $16:1(n\text{-}7)$, $20:5(n\text{-}3)$ and $22:6(n\text{-}3)$) allowed to differentiate PPOM and IPOM (Fig. 3). At both stations, the
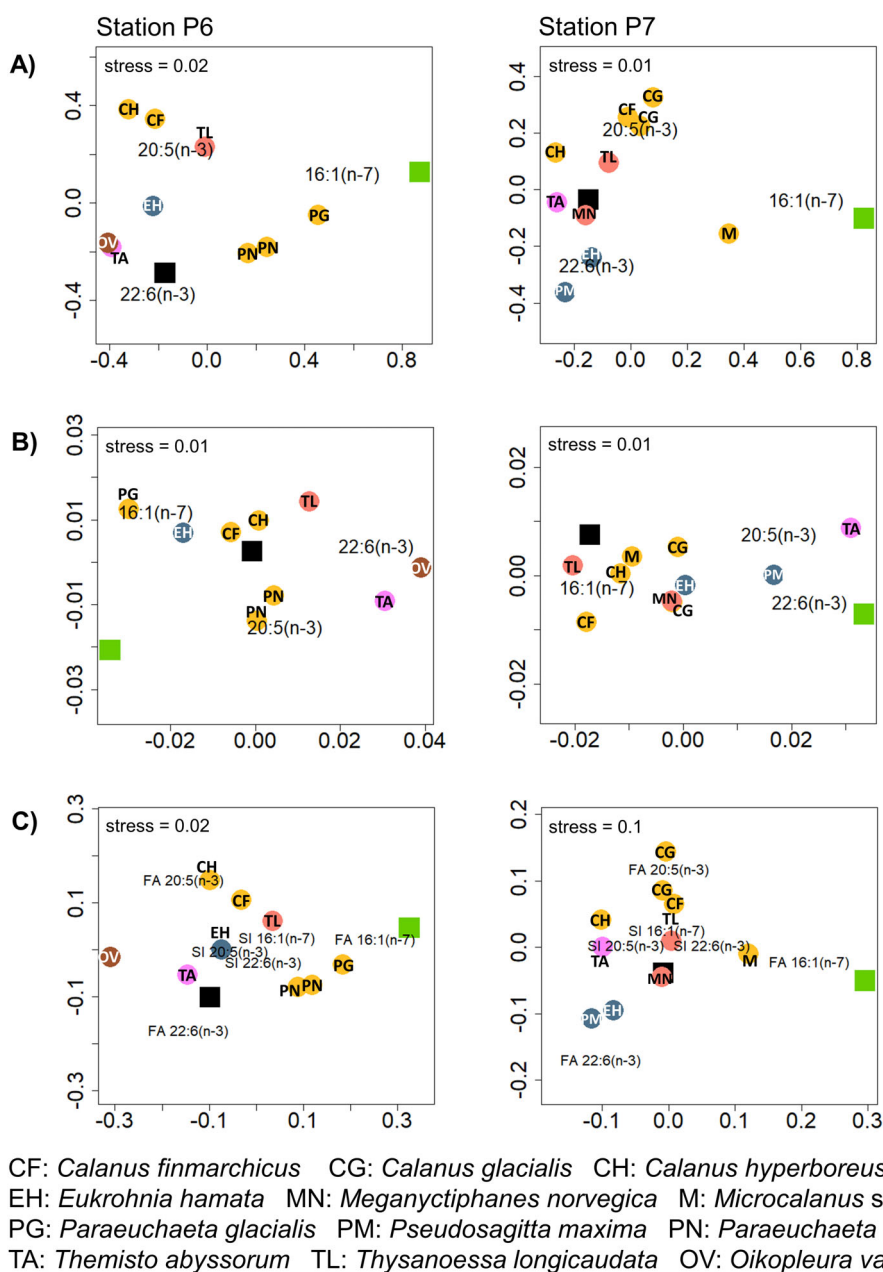
Fig. 4. Nonmetric multidimensional scaling of (A) relative proportions of the FA trophic markers 16 : 1(*n*-7), 20 : 5(*n*-3), and 22 : 6(*n*-3), (B) carbon isotopic compositions of the three above cited FA markers, and (C) relative proportions and carbon isotopic compositions of the three FA markers.

CF: *Calanus finmarchicus*   CG: *Calanus glacialis*   CH: *Calanus hyperboreus*
EH: *Eukrohnia hamata*   MN: *Meganyctiphanes norvegica*   M: *Microcalanus* spp.
PG: *Paraeuchaeta glacialis*   PM: *Pseudosagitta maxima*   PN: *Paraeuchaeta norvegica*
TA: *Themisto abyssorum*   TL: *Thysanoessa longicaudata*   OV: *Oikopleura vanhoeffeni*

ratios [16 : 1(*n*-7) + 20 : 5(*n*-3)]/22 : 6(*n*-3) were much higher in IPOM (P6: 28; P7: 20) than in PPOM (P6: 2; P7: 3).

In the zooplankton, ratios [16 : 1(*n*-7) + 20 : 5 (*n*-3)]/22 : 6 (*n*-3) were similar between Sta. P6 (mean ± standard deviation: 4.6 ± 2.4) and P7 (4.5 ± 2.9; Wilcoxon, *W* = 51, *p* = 0.65), being much closer to the values measured in PPOM than in IPOM (Fig. 3). At the species scale, the ratios [16 : 1(*n*-7) + 20 : 5(*n*-3)]/22 : 6(*n*-3) were higher at P6 than at P7 in *C. hyperboreus* (7.9 vs. 3.1) and *T. longicaudata* (7.1 vs. 4.1), but relatively similar between stations for the other species

(difference < 1.2). All zooplankton species had a more similar biochemical composition to PPOM than IPOM at both sampling stations (Fig. 3).

Importance of pelagic vs. sympagic food sources

NMDS ordination based on relative FA proportions alone (Fig. 4A) and in combination with their isotopic compositions (Fig. 4C) indicated a close biochemical composition between most of the zooplankton species and PPOM at the two stations. The NMDS plot solely based on FA isotopic

compositions indicated weak discrimination power, not allowing to determine food-source uses, especially at Sta. P6 (Fig. 4B).

Among all species, *P. glacialis* (Sta. P6), *P. norvegica* (Sta. P6) and *Microcalanus* spp. (Sta. P7) were the species with the biochemical compositions the most influenced by IPOM (Fig. 4A,C).

Discussion

Trophic marker and community compositions of primary producers

In agreement with the literature (Wang et al. 2014; Kohlbach et al. 2016, 2021a), PPOM and IPOM could clearly be distinguished based on their FA compositions: the diatom-associated FA 16 : 1(*n*-7) dominated in IPOM, while the flagellate marker 22 : 6(*n*-3) had higher concentrations in PPOM. This pattern was robust across the two stations, while differences in FA marker isotopic compositions were not consistent between P6 and P7.

At Sta. P7, $\delta^{13}C$ values of the selected FAs were distinctly higher in IPOM than in PPOM, whereas at Sta. P6, $\delta^{13}C$ values of 16 : 1(*n*-7) and 20 : 5(*n*-3) were very similar between PPOM and IPOM, and slightly lower in PPOM for 22 : 6(*n*-3). Ice algae or ice-associated POM are often found to be more enriched in ^{13}C than pelagic algae due to differences in CO_2 availability in their growth habitat (i.e., lower CO_2 concentrations in ice compared to seawater; Thomas et al. 2003) and variability in algal-specific growth rates and enzymatic apparatus (Thompson and Calvert 1994; Fry 1996). While this was true at P7, the overlapping isotopic compositions of FA markers at P6 may be related to combined effects of several environmental factors. Isotopic fractionation during photosynthesis in algae differs not only among the taxa, but also depends on the isotopic composition of the incorporated CO_2 as well as environmental conditions, such as irradiance levels, ambient nutrient concentrations, and salinity (Burkhardt et al. 1999a,b; Tamelander et al. 2009a; Pineault et al. 2013; Wang et al. 2014), which are subject to large spatial and temporal variability (de la Vega et al. 2019). Despite their geographical proximity, the two sampling stations differed in their water-mass regimes: Atlantic water masses dominated at the shelf-regime Sta. P6 (bottom depth ≤ 1000 m), while the surface layer at the Arctic Basin Sta. P7 (bottom depth > 3000 m) was strongly influenced by colder and fresher Arctic water masses. Moreover, taxonomic composition of pelagic protist communities differed between the stations: Protist biomass was overall higher at P6, with higher abundances and biomass of diatoms, dinoflagellates and other flagellates (Kohlbach et al. 2023a). Differences in algal biomass and composition between the two sampling stations also occurred in sea ice: Protist numbers in the bottom 3 cm of the sea ice were generally higher at P7, with larger contributions of diatoms, but also flagellates and dinoflagellates (P. Assmy, pers. comm.). The higher importance of sympagic

algae at P7 was further reflected in the distinctly higher Chl *a* concentrations at P7 (2.9 $\mu g\ L^{-1}$) compared to P6 (0.6 $\mu g\ L^{-1}$, bottom 3 cm of ice; Vader et al. 2022).

In addition, the sea ice at sampling Sta. P6 was likely in a more advanced stage of melting compared to the northernmost Sta. P7, indicated by the distinctly lower Chl *a* concentration in the bottom sea-ice. The fact that flagellates dominated numerically, and that the bottom 3 cm of the ice did not stand out in terms of abundance compared to the middle and upper parts of the ice (P. Assmy et al., pers. comm.) indicated that the biomass-rich diatom-dominated bottom layer had already sloughed off. More porous sea ice in an advanced stage of melt probably allowed for a stronger mixing with the underlying water column and increased CO_2 uptake in the ice (Loose et al. 2011), which could have caused IPOM $\delta^{13}C$ values to be more similar to PPOM. Another explanation could be an increased migration of pelagic protists and therefore larger contribution of pelagic algae to the sea-ice community at P6 (Søreide et al. 2006; Hardge et al. 2017).

These results contribute to our knowledge on the strong spatio-temporal variability of $\delta^{13}C$ values of primary producers in polar ecosystems that needs to be considered when using isotopic compositions as a tool to distinguish food sources in polar food webs (de la Vega et al. 2019; Leu et al. 2020) and further highlights the importance to combine several trophic markers in studies focusing on the fate of pelagic and sea ice-derived organic matter. Indeed, the approach based on CSIA needs PPOM and IPOM isotopic compositions to differ and this difference to be consistent in the entire food web, as well as being robust over time and space (Twining et al. 2020). While the combination of FA compositions and isotopic compositions of selected FAs allowed to differentiate between PPOM and IPOM at Sta. P7, only the FA compositions of PPOM and IPOM allowed to separate food sources at Sta. P6.

Pelagic organic matter: Major food resource of zooplankton at the community scale

Dietary information derived from FA compositions and isotopic compositions of FAs highlighted that the zooplankton mostly relied on pelagic food sources at both stations. In addition, the relative proportions of FA markers indicated that the animals utilized both diatom-derived (most important in copepod taxa) and dinoflagellate-derived organic matter during summer 2019 at the two sampling locations in the Barents Sea, directly by feeding on microalgae or indirectly by preying on other zooplankton relying on these microalgae (see Table 1 for trophic types; Kohlbach et al. 2021a).

The predominant role of PPOM (at both stations) was confirmed by the low contents of highly branched isoprenoids (HBIs) of sympagic origin (details on method in Brown et al. 2017; Belt 2018; Schmidt et al. 2018) in almost all zooplankton species (see Kohlbach et al. 2021a). Such a result is likely related to the dominantly pelagic lifestyle of most of the studied animals and the relatively poor quality of the leftover

ice-algal material in late August, reflected by its low content of polyunsaturated FAs in IPOM (16%) in comparison to PPOM (37%; Kohlbach et al. 2021*a*). In addition, gross pelagic primary production in the northern Barents Sea typically largely exceeds the seasonal sympagic production (Hegseth 1998), so that the species we focused on are likely adapted to rely on pelagic food sources rather than exclusively feeding on ice algae, which are only available seasonally (i.e., abundant during the spring sympagic bloom).

A minor contribution of sympagic organic matter to the carbon budget of copepods and amphipods in the same region has also been observed during early winter (Kohlbach et al. 2021*b*) (note: most *Calanus* were likely in diapause, but *C. finmarchicus* might have been more reliant on heterotrophic carbon), and phytoplankton-derived food dominated the zooplankton diets during spring/summer in the marginal ice zone of the Barents Sea (Tamelander et al. 2008). Similarly, ice amphipods and polar cod showed little reliance on sympagic organic matter during spring at the same two locations (Kohlbach et al. 2022*a*). Combined with information gained from this study carried out in late summer, this low intake of sympagic organic matter by zooplankton and fish suggests a lesser role of sympagic food sources in the seasonally ice-covered Barents Sea in comparison to perennial sea-ice systems, such as the Central Arctic Ocean (Kohlbach et al. 2016, 2017).

Disparities at the species level

While HBIs of pelagic origin were found in almost all of the zooplankton species, except for the copepod *Microcalanus* spp., the chaetognath *P. maxima* and the appendicularian *O. vanhoeffeni*, HBIs of sympagic origin were detected in varying concentrations in two consumers among the 12 investigated species, namely the amphipod *T. abyssorum* (both stations; concentrations higher at P6) and *O. vanhoeffeni* (Sta. P6; Kohlbach et al. 2021*a*). Besides this evidence highlighting that sympagic organic matter had a role in the diet of these consumers, their FA δ^{13}C values were in the range of those from all other consumers. This discrepancy between the information provided by FA δ^{13}C values and HBIs may be related to the grazing of organic matter of sympagic origin following its release in the open water, after the melting of ice. Ice algae released in the water column may mix with pelagic assemblages and rely on the dissolved CO_2 from the seawater and synthesize FAs with isotope compositions close to those of strictly pelagic phytoplankton (Pineault et al. 2013). For example, Søreide et al. (2006) reported high δ^{13}C values in sympagic POM (obligate ice-POM: $\sim -20‰$) and much lower δ^{13}C values in sedimented POM ($\sim -26‰$), suggesting that algal habitat and respective environmental conditions have a strong impact on algal isotopic compositions. During late summer, other processes like bacterial degradation and remineralization during sedimentation may also alter isotopic composition of sinking or suspended senescent ice algae (Michener and Kaufman 2007). As a result, animals relying on

sympagic organic matter from sinking sea-ice material, possibly as marine snow (Lampitt et al. 1993; Lee et al. 2004), might exhibit a different isotopic composition than animals relying exclusively on fresh sympagic material, such as ice algae-grazing amphipods (Werner 1997; Kohlbach et al. 2016), with lower δ^{13}C values thus overlapping those of species relying exclusively on pelagic food sources. This could have been the case for the two species listed above (Kohlbach et al. 2021*a*). During our samplings, we found multiple algal taxa, typically associated with sea ice, such as the diatom *Shionodiscus bioculatus* (Kohlbach et al. 2023*a*), throughout the water column, confirming this cryo-pelagic coupling due to ice melt.

Another discrepancy between information provided by FA isotopic compositions and FA proportional compositions and HBIs was observed in *Microcalanus* spp., *P. glacialis*, and *P. norvegica*. FA isotopic compositions and/or FA compositions indicated that these species were relying the most on food sources of sympagic origin, but HBIs of sympagic origin were not found (Kohlbach et al. 2021*a*). *C. finmarchicus* and *C. hyperboreus* had FAs with higher δ^{13}C values and a stronger diatom FA signal at Sta. P6 than at Sta. P7 (Kohlbach et al. 2021*a*), suggesting a somewhat higher trophic dependence on sympagic diatoms at this station. However, as for the other copepod species mentioned above, no HBIs of sympagic origin were measured in *Calanus* spp. at P6. One explanation for the seemingly contrasting results derived from HBI vs. CSIA approach could be dietary flexibility/opportunistic feeding behavior of the zooplankton dependent on ambient food availability including the reliance on sympagic algae that did not produce HBIs, as not the same individuals could be used for both types of analyses.

Interests to combine trophic markers in ecological studies and recommendations

As previously highlighted, the combination of different biochemical methods including analyses of FA compositions, isotopic compositions of FAs and the presence/absence of HBIs of pelagic and sympagic origin is more advantageous for the assessment of food-source uses in marine food webs than the use of a single method, which could potentially lead to misleading results and data interpretation (e.g., Leu et al. 2020). The multitrophic marker approach helps to understand, which food resources are utilized, as well as the complexity of the system, i.e., the variability between species and at the species scale (Kohlbach et al. 2016, 2021*a*; Schoo et al. 2018).

As a result, when combining several biochemical methods is not possible, the choice of the most relevant trophic marker is of high importance. This choice may vary depending on sea ice and other environmental conditions, as observed in our study. The single use of FA isotopic compositions yielded relatively little ecological information to distinguish the roles of PPOM and IPOM at Sta. P6, which was likely the result of overlapping δ^{13}C values of FAs from PPOM and IPOM.

Environmental conditions, such as ambient nutrient concentrations and salinity, change drastically with season and have an impact on the $\delta^{13}C$ values of primary producers (Hinga et al. 1994; Tamelander et al. 2009*a*; Pineault et al. 2013). For example, sea-ice algae $\delta^{13}C$ values varied from $-25‰$ to $-13‰$ over the course of a May/June spring bloom in the North Water Polynya (Tremblay et al. 2006). To get the most relevant data, it is therefore recommended that future studies consider sea-ice conditions to adapt the trophic markers which should be used.

Future studies should also focus on limitations related to the methods themselves, some being already quite well known (i.e., detection limits for metabolites), to improve the quality of the data interpretation. For example, some knowledge should be gained about the turn-over of lipid metabolites in consumer's tissues and its effect on isotopic compositions. Species-specific turnover rates for most of the animals investigated in this study are yet to be determined, but are likely to range from days to few weeks (Boissonnot et al. 2016).

Additional trophic tools, such as stomach content analysis (Kohlbach et al. 2017) or metabarcoding of food items, could also provide a more holistic understanding of complex diet compositions on different time scales, especially when investigating higher trophic animals. Indeed, if herbivores have relatively specific diets with only few potential food sources, predatory animals can rely on a much larger diversity of prey items. This complexity can consequently lead to less clear data interpretation when relying only on trophic markers.

Conclusions

We observed an overall low reliance of zooplankton on sympagic food sources in the north-western Barents Sea during late summer. This is likely a consequence of the (expected) high abundance of pelagic food sources during summer in the seasonally ice-covered Barents Sea. This low dependence on sympagic food resources was not only robust among the two environmentally different sampling locations but also among zooplankton taxa: Species with a previously shown trophic sea-ice association (e.g., *C. glacialis*) had seemingly no stronger reliance on sympagic food sources than species with a pronounced pelagic food preference. These conclusions are in accordance with observations made during other seasons in the sampling area (Kohlbach et al. 2021*b*, 2022*a*). Contrarily to our observations, many other studies have highlighted that ice algae play a central role in Arctic marine food webs, for example during spring or in perennial sea-ice systems of the Central Arctic Ocean. Our somewhat contrasting results highlight the regional and seasonal complexity of trophic pathways in the Arctic Ocean.

To avoid misleading results and obtain the most realistic and accurate outputs from biochemical methods, the combination of varying trophic marker approaches is strongly recommended for reliable data interpretation when assessing food source compositions in the marine environment. If a combination of several biochemical methods is not possible, the selection of the most appropriate trophic marker approach for the given environmental context is of high importance. Moreover, it appears crucial to support the trophic marker data with physical data of the study region, including knowledge on the typology of the ice, such as ice conditions, and the production of pelagic/sympagic food sources.

Data availability statement

The isotopic data are available at the Norwegian Polar Data Center (https://data.npolar.no/ and https://doi.org/10.21334/npolar.2023.d8e07ee1).

References

Aarflot, J. M., H. R. Skjoldal, P. Dalpadado, and M. Skern-Mauritzen. 2018. Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. ICES J. Mar. Sci. **75**: 2342–2354.

Arrigo, K. R., and G. L. van Dijken. 2015. Continued increases in Arctic Ocean primary production. Prog. Oceanogr. **136**: 60–70.

Belt, S. T. 2018. Source-specific biomarkers as proxies for Arctic and Antarctic Sea ice. Org. Geochem. **125**: 277–298.

Bluhm, B. A., K. M. Swadling, and R. R. Gradinger. 2017. Sea ice as a habitat for macrograzers, p. 394–414. *In* D. N. Thomas [ed.], Sea Ice. Wiley-Blackwell.

Boissonnot, L., B. Niehoff, W. Hagen, J. Søreide, and M. Graeve. 2016. Lipid turnover reflects life-cycle strategies of small-sized Arctic copepods. J. Plankton Res. **38**: 1420–1432.

Brown, T. A., P. Assmy, H. Hop, A. Wold, and S. T. Belt. 2017. Transfer of ice algae carbon to ice-associated amphipods in the high-Arctic pack ice environment. J. Plankton Res. **39**: 664–674.

Budge, S., M. Wooller, A. M. Springer, S. J. Iverson, C. McRoy, and G. Divoky. 2008. Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia **157**: 117–129.

Budge, S. M., A. M. Springer, S. J. Iverson, and G. Sheffield. 2007. Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. Mar. Ecol. Prog. Ser. **336**: 305–309.

Burian, A., J. M. Nielsen, T. Hansen, R. Bermudez, and M. Winder. 2020. The potential of fatty acid isotopes to trace trophic transfer in aquatic food-webs. Philos. Trans. R. Soc. B **375**: 20190652.

Burkhardt, S., U. Riebesell, and I. Zondervan. 1999*a*. Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim. Cosmochim. Acta **63**: 3729–3741.

Burkhardt, S., U. Riebesell, and I. Zondervan. 1999*b*. Stable carbon isotope fractionation by marine phytoplankton in

response to daylength, growth rate, and CO_2 availability. Mar. Ecol. Prog. Ser. **184**: 31–41.

Coplen, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Commun. Mass Spectrom. **25**: 2538–2560.

Dąbrowska, A. M., J. M. Wiktor, M. Merchel, and J. M. Wiktor. 2020. Planktonic protists of the eastern Nordic seas and the Fram Strait: Spatial changes related to hydrography during early summer. Front. Mar. Sci. **7**: 557.

Dalpadado, P., K. R. Arrigo, G. L. van Dijken, H. R. Skjoldal, E. Bagøien, A. V. Dolgov, I. P. Prokopchuk, and E. Sperfeld. 2020. Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea. Prog. Oceanogr. **185**: 102320.

Dalsgaard, J., M. St John, G. Kattner, D. Muller-Navarra, and W. Hagen. 2003. Fatty acid trophic markers in the pelagic marine environment. Adv. Mar. Biol. **46**: 227–237.

de la Vega, C., R. M. Jeffreys, R. Tuerena, R. Ganeshram, and C. Mahaffey. 2019. Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies. Glob. Change Biol. **25**: 4116–4130.

Fry, B. 1996. $^{13}C/^{12}C$ fractionation by marine diatoms. Mar. Ecol. Prog. Ser. **134**: 283–294.

Hardge, K., I. Peeken, S. Neuhaus, B. A. Lange, A. Stock, T. Stoeck, L. Weinisch, and K. Metfies. 2017. The importance of sea ice for exchange of habitat-specific protist communities in the Central Arctic Ocean. J. Mar. Syst. **165**: 124–138.

Hegseth, E. N. 1998. Primary production of the northern Barents Sea. Polar Res. **17**: 113–123.

Hinga, K. R., M. A. Arthur, M. E. Pilson, and D. Whitaker. 1994. Carbon isotope fractionation by marine phytoplankton in culture: The effects of CO_2 concentration, pH, temperature, and species. Glob. Biochem. Cycle **8**: 91–102.

Jónasdóttir, S. H. 2019. Fatty acid profiles and production in marine phytoplankton. Mar. Drugs **17**: 151.

Kohlbach, D., M. Graeve, B. A. Lange, C. David, I. Peeken, and H. Flores. 2016. The importance of ice algae-produced carbon in the Central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses. Limnol. Oceanogr. **61**: 2027–2044.

Kohlbach, D., F. Schaafsma, M. Graeve, B. Lebreton, B. A. Lange, C. David, and others. 2017. Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: Evidence from stomach content, fatty acid and stable isotope analyses. Prog. Oceanogr. **152**: 62–74.

Kohlbach, D., and others. 2021*a*. Multiple trophic markers trace dietary carbon sources in Barents Sea zooplankton during late summer. Front. Mar. Sci. **7**: 1216.

Kohlbach, D., and others. 2021*b*. Winter carnivory and diapause counteract the reliance of Barents Sea zooplankton on ice algae. Front. Mar. Sci. **8**: 266.

Kohlbach, D., and others. 2023*a*. Earlier sea-ice melt extends the oligotrophic summer period in the Barents Sea with low algal biomass and associated low vertical flux. Prog. Oceanogr. **213**: 103018.

Kohlbach, D., B. Lebreton, G. Guillou, A. Wold, H. Hop, M. Graeve, and P. Assmy. 2023*b*. Fatty acid-specific stable isotopes in particulate organic matter and pelagic Barents Sea zooplankton, summer 2019 [data set]. Norwegian Polar Institute. doi:10.21334/npolar.2023.d8e07ee1

Kohlbach, D., L. Smik, S. T. Belt, H. A. Hop, A. Wold, M. Graeve, and P. Assmy. 2022*a*. A multi-trophic marker approach reveals high feeding plasticity in Barents Sea under-ice fauna. Prog. Oceanogr. **208**: 102895.

Kohlbach, D., A. Wold, M. Graeve, H. Hop, and P. Assmy. 2022*b*. Fatty acids in pelagic Barents Sea zooplankton, summer 2019 [data set]. Norwegian Polar Institute. doi:10.21334/npolar.2022.53bfa233

Laidre, K. L., and others. 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv. Biol. **29**: 724–737.

Lampitt, R. S., W. R. Hillier, and P. G. Challenor. 1993. Seasonal and diel variation in the open ocean concentration of marine snow aggregates. Nature **362**: 737–739.

Lee, C., S. Wakeham, and C. Arnosti. 2004. Particulate organic matter in the sea: The composition conundrum. AMBIO J. Human. Environ. **33**: 565–575.

Leu, E., J. E. Søreide, D. O. Hessen, S. Falk-Petersen, and J. Berge. 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Prog. Oceanogr. **90**: 18–32.

Leu, E., and others. 2020. Spatial and temporal variability of ice algal trophic markers—With recommendations about their application. J. Mar. Sci. Engin. **8**: 676.

Lewis, K. M., G. L. van Dijken, and K. R. Arrigo. 2020. Changes in phytoplankton concentration now drive increased Arctic Ocean primary production. Science **369**: 198–202.

Loose, B., and others. 2011. Gas diffusion through columnar laboratory sea ice: Implications for mixed-layer ventilation of CO_2 in the seasonal ice zone. Tellus B Chem. Phys. Meteorol. **63**: 23–39.

Michel, C., L. Legendre, R. G. Ingram, M. Gosselin, and M. Levasseur. 1996. Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers. J. Geophys. Res. Oceans **101**: 18345–18360.

Michener, R. H., and L. Kaufman. 2007. Stable isotope ratios as tracers in marine food webs: An update, p. 238–282. *In* R. Michener and K. Lajtha [eds.], Stable isotopes in ecology and environmental science. Blackwell.

Murphy, D. E., and T. A. Abrajano Jr. 1994. Carbon isotope compositions of fatty acids in mussels from Newfoundland estuaries. Est.Coast. Shelf Sci. **39**: 261–272.

Oksanen, J., and others. 2020. Vegan: Community ecology package. R Package Version **2**: 5–7.

Onarheim, I. H., and M. Årthun. 2017. Toward an ice-free Barents Sea. Geophys. Res. Lett. **44**: 8387–8395.

Onarheim, I. H., T. Eldevik, L. H. Smedsrud, and J. C. Stroeve. 2018. Seasonal and regional manifestation of Arctic Sea ice loss. J. Climate **31**: 4917–4932.

Pineault, S., J.-É. Tremblay, M. Gosselin, H. Thomas, and E. Shadwick. 2013. The isotopic signature of particulate organic C and N in bottom ice: Key influencing factors and applications for tracing the fate of ice-algae in the Arctic Ocean. J. Geophys. Res. **118**: 287–300.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ratkova, T. N., and P. Wassmann. 2005. Sea ice algae in the white and Barents seas: Composition and origin. Polar Res. **24**: 95–110.

Reuss, N., and L. Poulsen. 2002. Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar. Biol. **141**: 423–434.

Schmidt, K., T. A. Brown, S. T. Belt, L. C. Ireland, K. W. R. Taylor, S. E. Thorpe, P. Ward, and A. Atkinson. 2018. Do pelagic grazers benefit from sea ice? Insights from the Antarctic Sea ice proxy IPSO$_{25}$. Biogeosciences. **15**: 1987–2007.

Schoo, K. L., M. Boersma, A. M. Malzahn, M. G. J. Löder, K. H. Wiltshire, and N. Aberle. 2018. Dietary and seasonal variability in trophic relations at the base of the North Sea pelagic food web revealed by stable isotope and fatty acid analysis. J. Sea Res. **141**: 61–70.

Søreide, J. E., H. Hop, M. L. Carroll, S. Falk-Petersen, and E. N. Hegseth. 2006. Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog. Oceanogr. **71**: 59–87.

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

Stige, L. C., E. Eriksen, P. Dalpadado, and K. Ono. 2019. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. ICES J. Mar. Sci. **76**: i24–i36.

Stroeve, J., and D. Notz. 2018. Changing state of Arctic Sea ice across all seasons. Environ. Res. Lett. **13**: 103001.

Syvertsen, E. E. 1991. Ice algae in the Barents Sea: Types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. Polar Res. **10**: 277–288.

Tamelander, T., M. Reigstad, H. Hop, M. L. Carroll, and P. Wassmann. 2008. Pelagic and sympagic contribution of organic matter to zooplankton and vertical export in the Barents Sea marginal ice zone. Deep Sea Res. II **55**: 2330–2339.

Tamelander, T., C. Kivimäe, R. G. J. Bellerby, P. E. Renaud, and S. Kristiansen. 2009*a*. Base-line variations in stable isotope values in an Arctic marine ecosystem: Effects of carbon and nitrogen uptake by phytoplankton. Hydrobiol. **630**: 63–73.

Tamelander, T., M. Reigstad, H. Hop, and T. Ratkova. 2009*b*. Ice algal assemblages and vertical export of organic matter from sea ice in the Barents Sea and Nansen Basin (Arctic Ocean). Polar Biol. **32**: 1261–1273.

Thomas, D. N., S. Papadimitriou, and C. Michel. 2003. Biogeochemistry of sea ice, p. 267–302. *In* D. N. Thomas and G. S. Dieckmann [eds.], Sea ice: An introduction to its physics, chemistry, biology, and geology. Wiley-Blackwell.

Thompson, P. A., and S. E. Calvert. 1994. Carbon-isotope fractionation by a marine diatom: The influence of irradiance, daylength, pH, and nitrogen source. Limnol. Oceanogr. **39**: 1835–1844.

Tremblay, J.-E., C. Michel, K. A. Hobson, M. Gosselin, and N. M. Price. 2006. Bloom dynamics in early opening waters of the Arctic Ocean. Limnol. Oceanogr. **51**: 900–912.

Twining, C. W., S. J. Taipale, L. Ruess, A. Bec, D. Martin-Creuzburg, and M. Kainz. 2020. Stable isotopes of fatty acids: Current and future perspectives for advancing trophic ecology. Philos. Trans. R. Soc. B **375**: 20190641.

Vader, A., M. Marquardt, and Y. Bodur. 2022. Chlorophyll *a* and phaeopigments, Nansen legacy cruise 2019706. Norwegian Marine Datacentre. doi:10.21335/NMDC-1109067467

van Leeuwe, M. A., and others. 2018. Microalgal community structure and primary production in Arctic and Antarctic Sea ice: A synthesis. Elem. Sci. Anthr. **6**: 4.

Wang, S. W., S. M. Budge, R. R. Gradinger, K. Iken, and M. J. Wooller. 2014. Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: Tools for estimating sea ice algal contribution to Arctic food web production. Oecologica **174**: 699–712.

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

Wassmann, P., and others. 2006. Food webs and carbon flux in the Barents Sea. Prog. Oceanogr. **71**: 232–287.

Werner, I. 1997. Grazing of Arctic under-ice amphipods on sea-ice algae. Mar. Ecol. Prog. Ser. **160**: 93–99.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.