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Ice algae as supplementary food rather than major energy source for the Barents sea zooplankton community

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ABSTRACT

The Barents Sea is a hotspot for environmental change due to global warming. These changes impact the structure and functioning of the marine ecosystem year-round, and it is therefore important to gain knowledge on trophic relationships and the energy flow from primary producers, *i.e.*, ice algae (sympagic algae) and phytoplankton (pelagic algae) to consumers over the entire seasonal cycle. By using different lipid components as trophic markers, we provide seasonal coverage of the carbon and food-source composition of five of the most abundant and ecologically important zooplankton taxa inhabiting the Barents Sea: copepods, krill, amphipods, pteropods and chaetognaths. Based on the composition of algal-produced fatty acid (FA) markers, carbon-source composition of the zooplankton species reflected changes in the production and availability of food resources during different periods of the year. For example, relative proportions of the dinoflagellate/*Phaeocystis* FA marker 18:4(*n*-3) peaked during summer in *Calanus* copepods, the amphipod *Themisto abyssorum* and the chaetognath *Pseudosagitta maxima*, when the production of this FA reached maximum concentrations in phytoplankton. The composition of carnivory FAs (relative contribution of copepod-associated FAs, ratio 18:1(*n*-9)/18:1(*n*-7)) and the ratio of zoo- to phytosterols indicated that most grazers relied more on heterotrophic prey during polar night and spring while switching to a more algae-based diet during the summer. Based on source-specific highly branched isoprenoids (HBIs), sympagic carbon had generally a minor contribution to the nutrition of the zooplankton community, particularly during winter and spring when sympagic HBIs were virtually undetected in the animals. In contrast, sympagic HBI metabolites were detected in krill, amphipods and the pteropod *Clione limacina* during summer and autumn. The krill *Meganyctiphanes norvegica* was unique in terms of its HBI composition as the only species containing both sympagic and pelagic HBIs during spring. Our results indicate that the Barents Sea zooplankton community is largely based on pelagic carbon, while sympagic carbon is only supplementing species-specific diets, mostly during the second half of the year. This relatively low trophic dependency on sea-ice algae might be an indication of the resilience of this food web towards ongoing sea-ice decline that causes changes to the timing and availability of sympagic and pelagic carbon and food sources.

1. Introduction

In the Barents Sea, seasonality drives major variability in environmental conditions. Separated by the Polar Front at about 75°N (Vinje and Kvambekk, 1991), the southern part of the Barents Sea is usually ice-free year-round, while the area north of the Polar Front is ice-covered during winter and spring with the most extensive ice cover in March or April (Ingvaldsen et al., 2021; Mohamed et al., 2022). During the summer months, the sea-ice cover typically retreats as far north as 80°N, with strongest melting in June and July, leading to a largely ice-free Barents Sea in August (Smedsrud et al., 2013). Sea-ice conditions in the Barents Sea show large spatial and temporal variation, not only

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between seasons, but also inter-annually (Koenigk et al., 2009), with direct impacts on the composition of phytoplankton (Kohlbach et al., 2023a) and zooplankton communities (Dalpadado et al., 2020; Skjoldal et al., 2021; van Engeland et al., 2023; Wold et al., 2023). Superimposed on these periodic changes in the environmental conditions, global warming facilitates longer open water seasons due to earlier melting and later sea-ice formation in the study region (Smedsrud et al., 2022). Particularly during winter, the sea ice in the Barents Sea has experienced a strong decline and thinning (Barton et al., 2018). A year-round ice-free Barents Sea is predicted for the end of the century (Onarheim and Årthun, 2017).

In ice-covered regions of the central Arctic, sea-ice algae (sympagic) primary production has been suggested to contribute to over 50 % of the annual primary production (Gosselin et al., 1997; Fernández-Méndez et al., 2015), which exceeds the estimates for regions with seasonal ice such as the Barents Sea (up to 22 %; Hegseth, 1998). Sympagic primary production usually starts in March, peaks in May (McMinn and Hegseth, 2007), and is terminated by ice melt (Sakshaug and Slagstad, 1992; Hegseth, 1998), followed by the phytoplankton bloom in the water column that can also co-occur with the sympagic production underneath ponded or fragmented sea ice (Assmy et al., 2017; Pavlov et al., 2017; Ardyna et al., 2020). In winter, low light conditions limit production both in the water column and sea ice (Castellani et al., 2022). However, recent studies suggest that phytoplankton can quickly respond to increasing light levels after the polar night (Berge et al., 2015; Hoppe et al., 2024). Sympagic protist communities are generally dominated by pennate diatoms, with *Nitzschia frigida* and *Fragilariopsis cylindrus* being particularly prominent in spring (Syvertsen, 1991; Hegseth, 1992; Henderson et al., 1998; McMinn and Hegseth, 2007; Hop et al., 2020). Likewise, seasonal variability also occurs in pelagic protist communities (Ratkova and Wassmann, 2002): During spring, phytoplankton assemblages are often dominated by centric diatoms, while prymnesiophytes, particularly *Phaeocystis pouchetii*, as well as heterotrophic protists become more prominent as the season progresses (von Quillfeldt, 2000; Giraudeau et al., 2016; Vodopyanova et al., 2020; Assmy et al., 2023; Kohlbach et al., 2023a).

Zooplankton are the link between primary production and higher trophic levels. They undergo seasonal changes in activity and ontogenetic development, which closely follows the availability of food sources: Some species, such as *Calanus* copepods, perform deep vertical migration and hibernation (diapause) to overcome food scarcity during the polar night, while others, such as *Themisto* amphipods, stay active and change to a stronger reliance on heterotrophic prey (Kohlbach et al., 2021b), or a generally more opportunistic feeding behaviour (Tarling, 2015; Berge et al., 2020; Hobbs et al., 2020; Kunisch et al., 2023). Due to logistical challenges of sampling during winter, dietary information during the polar night is generally scarce and for many species full seasonal coverage of their feeding strategy is not available to date.

The trophic reliance of zooplankton on sea-ice algae as a food source is stronger in regions with perennial sea-ice cover, such as the central Arctic Ocean (Kohlbach et al., 2016) compared to seasonally ice-covered systems, such as the Barents Sea (Kohlbach et al., 2021a, 2022a, 2023b). Nevertheless, for some species, a seasonal dependence on sympagic food sources in regions with a seasonal ice cover is well documented for both the pelagic (Søreide et al., 2008; Wang et al., 2015) and the benthic realm (Kohlbach et al., 2019; Yunda-Guarin et al., 2020; Cautain et al., 2022; Niemi et al., 2024). With the rapid changes occurring in Arctic ecosystems, there is an urgent need for an improved understanding of trophic dynamics over the full seasonal cycle. The seasonal sampling program in the Norwegian Nansen Legacy project (https://arvenetternansen.com/) provided a unique opportunity to study seasonal changes in trophic relationships of the northwestern Barents Sea and to gain a holistic understanding of the impact of anthropogenic climate change on complex Arctic marine food webs.

Using a multi-trophic marker approach (Kohlbach et al., 2021a and references therein), we inferred the following trophic information: i) the preference for diatom- *vs.* dinoflagellate-produced carbon based on the relative composition of dietary fatty acids (FAs); ii) the importance of heterotrophic food items (*i.e.*, the degree of carnivory) based on the relative contribution of carnivory FAs as well as the composition of phyto- *vs.* zoosterols; and iii) the origin of these food sources based on the presence of sea ice- *vs.* pelagic diatom-derived highly branched isoprenoid (HBI) lipids in the zooplankton.

We followed the composition of lipid-based dietary indicators from the producers (ice algae and phytoplankton) to the consumers (zooplankton) throughout the seasons and hypothesize that there is pronounced seasonality difference in the

1) food-source composition of the zooplankton reflecting changes in the production and availability of food during different periods of the year
2) utilization of sympagic carbon, with strongest reliance on sympagic food during spring when sympagic production is the highest

2. Materials and methods

2.1. Sample collection

As a contribution to the Nansen Legacy project, samples were collected during four seasonal cruises with RV *Kronprins Haakon* north of 76°N in the Barents Sea: Q1 (2 to 24 March 2021, representing late winter), Q2 (27 April to 20 May 2021, representing spring), Q3 (5 to 27 August 2019, representing summer) and Q4 (28 November to 17 December 2019, representing late autumn; Table 1).

2.2. Chlorophyll *a* measurements

For sea-ice chlorophyll (chl) *a* measurements, the bottom 10 cm, cut into 0–3 cm and 3–10 cm sections, of five pooled ice cores were melted for 24–48 h at 4 °C in the dark with 100 mL locally acquired filtered seawater (0.7 μm GF/F) added per 1 cm of sea ice. Seawater chl *a* samples were collected at discrete depths with Niskin bottles attached to a CTD rosette. Samples were collected into plastic bottles and stored in a dark and cold location until further processing (within 1 h).

Between 0.15 and 1 L of melted sea-ice and seawater was filtered through 0.7 μm 25 mm Whatman GF/F filters under low vacuum pressure (~ 30 kPa). Filters were stored in polypropylene tubes with 5 mL of methanol added for chl *a* extraction (overnight at 0–4 °C). Chlorophyll *a* concentrations were determined in the dark according to Holm-Hansen and Riemann (1978) with a Turner Trilogy fluorometer. Depth-integrated chl *a* data is presented in Figure A1. All chl *a* datasets can be found in Vader et al. (2022a,b,c,d).

2.3. Protist community compositions

For the microscopic analysis of sea-ice protists, 90 mL of melted sea-ice was transferred into 100 mL brown glass bottles and fixed with 0.4 mL of 25 % glutaraldehyde and 10 mL of 20 % hexamethylenetetramine-buffered formalin solutions to yield final concentrations of 0.1 and 2 %, respectively. For the analysis of pelagic protists, 190 mL of seawater from each depth was filled into 200 mL brown glass bottles directly from the Niskin bottles. Samples were fixed with 0.8 mL of 25 % glutaraldehyde and 10 mL of 20 % hexamethylenetetramine-buffered formalin solutions to yield final concentrations of 0.1 and 1 %, respectively. All samples were stored cool (ca. 15 °C) and dark until further processing at the Institute of Oceanology, Polish Academy of Sciences (IOPAN) within one year after collection.

Identification and quantification of protists were carried out with a Nikon inverted light microscope equipped with phase and differential interference contrasts and objectives 10–60× (resulting in 100–600 × magnification) following the Utermöhl method (Utermöhl, 1958; Edler and Elbrächter, 2010). Details on the method can be found in Kohlbach

Table 1
Sampling information for the four seasonal cruises Q1 to Q4 in the northwestern Barents Sea.

Station #	Latitude °N	Longitude °E	Q1: Late winter sampling (2021)	Q2: Spring sampling (2021)	Q3: Summer sampling (2019)	Q4: Late autumn sampling (2019)
Zooplankton*						
P1	76.0	31.2	04/03	30/04	08/08	13/12
P2	77.0–77.5	33.6–34.0	07/03	02/05	11/08	10/12
P4	79.5–79.8	33.6–34.6	10/03	05/05	13/08, 14/08	08/12
P5	80.5	33.9–34.4	–	07/05	15/08	06/12
P6	81.5–81.6	30.7–31.5	14/03	11/05	18/08	05/12
P7	81.9–82.2	28.5–30.0	17/03	14/05	20/08, 21/08	01/12
Pelagic particulate organic matter**						
P1	76.0–76.1	31.0–31.2	05/03	30/04	08/08	13/12
P2	77.5	34.0	07/03	02/05	11/08	–
P3+	78.7–78.8	33.9–34.0	08/03	03/05	13/08	09/12
P4	79.8–79.8	33.4–34.3	11/03	06/05	14/08	08/12
P5	80.5–80.6	33.6–34.1	12/03	08/05	16/08	07/12
P6	81.5–81.6	30.8–31.2	14/03	09/05	18/08	05/12
P7	81.9–82.2	29.1–32.0	18/03	15/05	21/08	01/12
Ice-associated particulate organic matter***						
P4_ice	79.7–79.8	33.5–33.7	10/03	05/05	–	–
P5_ice	80.5	34.4	–	08/05+	–	06/12
P6_ice	81.5–81.6	30.7–31.1	14/03	09/05	17/08	–
P7_ice	82.0–82.2	28.7–30.0	17/03	13/05	20/08	02/12

* Sampling with: Bongo net- 64 and 180 μm, Multinet- 180 μm, WP2 net- 90 μm, WP3 net- 1000 μm, MIK net- 1500 μm, Macroplankton trawl- multiple mesh sizes along the net, tapering to 8 mm at its end.
** Sampling with Niskin bottles attached to a CTD rosette.
*** Sampling with 9-cm diameter ice corer, Kovacs Enterprises, Inc. USA.
\+ Only chlorophyll *a* and protist community data.

et al. (2023a). Sea-ice protist taxonomic data can be found in Assmy et al. (2022a–c) for Q1, Q3 and Q4 and Wold et al. (2022) for Q2. Pelagic protist taxonomic data can be found in Assmy et al. (2022d–g) for all seasonal cruises.

2.4. Multi-trophic marker approach

To provide a holistic understanding of seasonal feeding habits and carbon and food-source use, we combined trophic information from varying dietary approaches.

Ice cores were sampled for ice-associated particulate organic matter (IPOM) (Table 1; note: not all stations sampled during all cruises). The bottom 10 cm of the ice was melted in the dark and between 200 mL and 1.2 L melted ice samples were filtered by a vacuum pump through pre-combusted 47 mm GF/F filters (0.7 μm; 3 h, 550 °C). The melting process was conducted without the addition of filtered seawater, which was assumed to have a negligible effect on the bulk biochemical properties of IPOM (Roukaerts et al., 2019). During Q1, two cores were pooled in order to obtain sufficient algal material. Water samples were collected at all P stations at different depths, generally at the chl *a* maximum (Q1: 20 m, Q2: 15 to 95 m, Q3: 14 to 73 m, Q4: 20 m; note: station P2 was not sampled during Q4). Between 1.2 and 3 L of seawater was filtered *via* a vacuum pump through pre-combusted 47 mm Whatman GF/F filters (0.7 μm; 3 h, 550 °C), representing pelagic particulate organic matter (PPOM). All filters were stored at − 80 °C until further processing.

Zooplankton covering five taxonomic groups (copepods, krill, amphipods, pteropods and chaetognaths) were collected at six sampling stations (P1 to P7; note: station P5 was not sampled during Q1 and not all species were present or sampled at all P stations, no sampling at station P3). Different nets of 64 μm, 180 μm and 1500 μm were used to cover all taxa and size groups from small copepods to large amphipods and krill, sorted to the lowest possible taxonomic level and/or stage/size group onboard the ship and immediately frozen at −80 °C in 2 mL cryovials. To obtain sufficient sample material for analyses, small species/individuals were pooled by species and by stage/size group, if applicable (Table 2).

2.4.1. Lipid classes and fatty acids

Lipid classes and fatty acids (FAs) were analysed at the Alfred Wegener Institute, Bremerhaven, Germany. Methods and analytical equipment have been described in detail in Kohlbach et al. (2021a). Data on lipid classes of individual species can be found in Kohlbach et al. (2022e), FA zooplankton data from Q3 can be found in Kohlbach et al. (2022b) and from Q4 in Kohlbach et al. (2022c).

Briefly, total lipids were extracted using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2:1, v/v) and were cleaned with 0.88 % potassium chloride solution. Lipid-class analysis was performed directly on the extracted lipids (Graeve and Janssen, 2009) *via* high performance liquid chromatography. Lipid classes were distinguished into neutral (*i.e.*, storage) and polar (*i.e.*, membrane) lipids. Main storage lipids included wax esters, triacylglycerols (might contain diacylglycerolether), sterols, fatty alcohols, and free FAs. Major membrane lipids included phosphatidylcholine, phosphatidylethanolamine, phosphatidylinositol, and phosphatidylserine (Table A2).

The extracted lipids were converted into fatty acid methyl esters (FAMEs) and free fatty alcohols derived from wax esters by transesterification in methanol, containing 3 % concentrated sulfuric acid. FAMEs and alcohols were separated *via* gas chromatography. FAMEs were identified *via* standard mixtures and total lipid content was quantified with an internal standard (23:0) that was added prior to lipid extraction. Fatty acids were expressed by the nomenclature A:Bn-X; where A represents the number of carbon atoms, B the amount of double bonds, and X is 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 (Table A3).

We focused on trophic marker FAs that can be used to study seasonal change in carbon and food-source use by the pelagic zooplankton. To distinguish preferences for diatom- *vs.* dinoflagellate-produced carbon, we traced the marker FAs 16:1(*n*-7), 16:4(*n*-1) and 20:5(*n*-3), which are produced by diatoms (*i.e.*, diatom-associated FAs), and the marker FAs 18:4(*n*-3) and 22:6(*n*-3) (*i.e.*, dinoflagellate-associated FAs), which are predominantly produced by dinoflagellates and the prymnesiophyte *Phaeocystis* (Dalsgaard et al., 2003 and references therein). Furthermore,

Table 2
Overview of zooplankton taxa collected during the Nansen Legacy cruises Q1 (2 to 24 March 2021; late winter), Q2 (27 April to 20 May 2021; spring), Q3 (5 to 27 August 2019; summer) and Q4 (28 November to 17 December 2019; late autumn) in the Barents Sea.

		Q1 (late winter)		Q2 (spring)		Q3 (summer)		Q4 (late autumn)	
Taxonomic group	**Zooplankton taxa**	**Stage/ Length group (mm)***	**Dry weight/ ind. (mg)****	**Stage/ Length group (mm)***	**Dry weight/ ind. (mg)****	**Stage/ Length group (mm)***	**Dry weight/ ind. (mg)****	**Stage/ Length group (mm)***	**Dry weight/ ind. (mg)****
Copepods	*Calanus glacialis*	AF	0.7 to 1.3	CV-AF	0.7 to 1.2	CIV-AF	–	CV, AF, AM	0.7 to 1.2
	Calanus hyperboreus	AF	1.8 to 3.3	CIV-AF	0.9–3.1	CIV-AF	2.2 to 6.2	CV, AF, AM	2.4 to 6.5
	*Paraeuchaeta glacialis****	AF	7.1	–	–	AF	16.7	CV-AF	1.9 to 5.1
	*Paraeuchaeta norvegica****	AF	4.7 to 6.2	–	–	CV-AF	4.9 to 5.9	CV-AF	1.4 to 5.6
	Paraeuchaeta spp.	AF	3.9 to 5.3	Adult (most with eggs)	3.7 to 5.5	–	–	–	–
Krill	*Meganyctiphanes norvegica*	20 to 30–40	21.3 to 133.2	20–35	7.5 to 87.1	30–40	31.2 to 123.8	20–30 to 30–40	42.5 to 140.3
	*Thysanoessa inermis****	–	–	–	–	15–20 to 25–30	7.9 to 58.1	–	–
	*Thysanoessa longicaudata****	–	–	–	–	10–15	4.5 to 6.1	–	–
	Thysanoessa spp.	0–10 to 20–30	1.8 to 37.4	0–10 to 20–30	1.5 to 23.7	–	–	10–20 to 30–40	4.7 to 59.6
Amphipods	*Themisto abyssorum*	0–10 to 10–20	1.9 to 45	0–10 to 10–20	4.8 to 10.1	5–10 to 25–30	0.7 to 17.1	0–10 to 10–20	2.9 to 12.8
	Themisto libellula	20–30	16.5 to 40.5	0–10 to 30–40	0.2 to 79.9	5–10 to 10–20	1.2 to 6.1	10–20 to 30–40	12.0 to 115.5
Pteropods	*Clione limacina*	16 to 20–30	8.7 to 25.6	0–10 to 35	4.6 to 39.8	5–10 to 50–60	4.0 to 104.2	20–30 to 30–40	11.7 to 91.9
Chaetognaths	*Parasagitta elegans****	–	–	–	–	30–40	2.4 to 8.3	–	–
	Parasagitta spp.	20–30	3.4 to 13.2	0–10 to 20–30	3.2 to 8.9	–	–	10–20 to > 30	2.0 to 17.7
	Pseudosagitta maxima	70	30.7 to 31.4	55 to 70	27 to 68	70–80	48.8 to 70.8	–	–

Note: for some samples, individuals have been pooled, and no information on dry weight/ind. is available for these samples.
AF: adult female, AM: adult male, CIII-CV: copepodid stages III-V.
The two *Calanus* species were differentiated based on morphology and prosome length according to Kwasniewski et al. (2003).
* copepods measured from rostrum to the tip of the last prosome segment (not including rostrum); krill and amphipods measured from base of rostrum to end of urosome; other species measured as total length or widest diameter.
** individuals used for lipid class and FA analyses; for *n* see Table A3.
*** some species were pooled to spp. for presentation of trophic marker results; for results on individual species see Tables A2 (lipid classes), A3 (fatty acids) and A5 (HBIs).

trophic marker ratios of the FAs 16:1(*n*-7)/16:0 and the FA ratio 20:5(*n*-3)/22:6(*n*-3) are computed; ratios > 1 can indicate a dominance of diatom-produced *vs.* dinoflagellate-produced carbon in a consumer. *Calanus* spp. and other calanoid copepods biosynthesize isomers of the monounsaturated long-chain FAs 20:1 and 22:1 *de novo*, which typically indicate the importance of calanoid copepods as a food source for a predatory consumer (Sargent and Falk-Petersen, 1988; Falk-Petersen et al., 1990). High ratios of 18:1(*n*-9)/18:1(*n*-7) were used to estimate an omnivorous/carnivorous/detritivorous rather than herbivorous feeding behavior in the zooplankton (Graeve et al., 1997; Falk-Petersen et al., 2000).

Seasonal variability in the composition of lipid classes and marker FAs as well as carnivory indices in the zooplankton were tested for statistical significance with 1-way ANOVAs followed by Tukey's HSD post hoc tests. Results with $p \leq 0.05$ were considered significant. All measures of statistical variation are reported as means ± 1 SD. Statistical analyses were run in R v.4.1.0 (R Core Team, 2021) and data visualization was done using the ggplot2 package (Wickham, 2016).

2.4.2. Highly branched isoprenoids and sterols

HBIs and sterols were analysed at the University of Plymouth, UK. Methods and analytical equipment have been described in detail in Kohlbach et al. (2021a). HBI and sterol data of individual zooplankton samples can be found in Kohlbach et al. (2022f) for Q3 and Kohlbach et al. (2022d) for Q4.

Briefly, total lipids were extracted with chloroform/methanol (2:1, v/v), cleaned with potassium chloride (0.88 %) and saponified with 20 % potassium hydroxide in water/methanol (1:9, v/v). Extracted lipids were purified by open-column chromatography with SiO_2 and non-polar lipids containing HBIs were analysed *via* gas chromatography-mass spectrometry (GC–MS). Quantification of HBIs was achieved by integrating individual ion responses in single-ion monitoring mode, and normalising these to the corresponding peak area of the internal standard and an instrumental response factor obtained from purified standards (Belt et al., 2012). The two tri-unsaturated HBIs, hereafter referred to as HBIs III and IV (*m/z* 346.3), can indicate the consumption of pelagic diatoms (*i.e.*, phytoplankton), including the marginal ice zone (MIZ), while the mono- and di-unsaturated HBIs IP_{25} (*m/z* 350.3) and $IPSO_{25}$ (*m/z* 348.3) were assumed to be produced exclusively by certain sea-ice diatoms, such as *Haslea* and *Pleurosigma* (*i.e.*, sympagic algae), providing information on the origin of carbon sources in a consumer (Belt, 2018; Brown et al., 2018; Schmidt et al., 2018; Koch et al., 2023).

Sterols were eluted from the same silica column as HBIs and prior to analysis by GC–MS, sterol fractions were derivatised using N,O-bis (trimethylsilyl)trifluoroacetamide (BSTFA, 50 µl; 70 °C, 1 h). Individual sterols were identified by comparison of the mass spectra of their trimethylsilyl-ethers with published data (Belt et al., 2018). The principal identifiable sterols were the algae-produced sterols brassicasterol, sitosterol, chalinasterol and campesterol (combined to phytosterols), and the phyto-and-zooplankton-produced sterols cholesterol, desmosterol and dehydrocholesterol (combined to zoosterols). To some extent, sterols can be used to differentiate between algal- and animal-based

diets (Drazen et al., 2008; Ruess and Müller-Navarra, 2019).

3. Results

3.1. Sea-ice concentrations

During the late winter cruise (Q1), the entire sampling area except for station P1 was sea-ice covered (Fig. 1). Stations P6 and P7 were located close to the sea-ice edge but fully ice-covered during all other seasons. During the spring- (Q2) and autumn cruise (Q4), the sea-ice edge was in close proximity to station P2, while during the summer cruise (Q3), the sea ice had retreated northwards to station P4.

3.2. Chlorophyll *a* concentrations in sea ice and water column

In bottom 10 cm sea ice, chl *a* was the highest during spring (maximum 57.6 μg L^{-1} at station P4) and lowest during late autumn (< 0.3 μg L^{-1}) and winter (< 0.2 μg L^{-1}; Figure A1). Pelagic chl *a* concentrations reflected the typical seasonal cycle of primary production in the Barents Sea with highest values during spring (May; up to 3.2 μg L^{-1} at station P6) and summer (August; up to 2.6 μg L^{-1} at station P5), followed by a gradual decrease in concentration during the rest of the year with the lowest chl *a* biomass during winter (< 0.02 μg L^{-1}; Figs. 2 and A1, Table A1).

3.3. Sympagic and pelagic protist community compositions

Based on microscopic analysis, spring sea-ice protist communities were dominated by diatoms, particularly at stations P4 and P6. Diatoms also played a central role for sea-ice communities at station P7 during late autumn but had a lower overall contribution to the sympagic communities during summer when dinoflagellates, flagellates and ciliates were more prominent. Sympagic protist biomass was very low during late winter (Fig. 3).

Spring pelagic protist communities were dominated by diatoms at most sampling stations (Fig. 3), with the highest diatom biomass at station P6. During summer, diatoms were only important at the ice-covered stations P5 to P7, while ciliates had increased in biomass compared to the spring. Diatoms played a negligible role during late autumn and winter when the overall protist biomass was minimal and dominated by dinoflagellates.

3.4. Composition of storage vs. membrane lipids in zooplankton

In the chaetognath *Pseudosagitta maxima* (sampled during Q1-Q3), the average proportion of storage lipids was lower than the proportion of membrane lipids across all seasons, while this was the case only during summer and autumn in the chaetognaths *Parasagitta* spp. (winter: 50 %) and during spring in the krill *Thysanoessa* spp.

In the copepod *Calanus glacialis* and *Thysanoessa* spp., the relative proportions of storage lipids were significantly lower during spring compared to the rest of the year (Fig. 4). Lower proportions of storage lipids during spring were also apparent in the krill *Meganyctiphanes norvegica*, and the pteropod *Clione limacina* (difference not significant). Storage lipid content was the highest during summer in the amphipod *Themisto abyssorum* and *P. maxima*.

Wax esters dominated the storage lipid fraction in all three copepod species during all seasons and were also abundant in both amphipod species (particularly during winter, spring and autumn) and *Parasagitta* spp. (albeit in variable concentrations; Table A2). Triacylglycerols (TAGs) were generally more important in *M. norvegica* (particularly during summer and autumn) and *C. limacina* year-round but were also abundant in *T. abyssorum* (particularly during summer and autumn; ANOVA, $F_{3,\ 8} = 11.4$, $p < 0.01$). In *Thysanoessa* spp., both wax esters and TAGs contributed largely to the storage lipid fraction. Among the membrane lipids, phosphatidylcholine was the dominant polar lipid class in all species and had high contributions in *Thysanoessa* spp. and both chaetognaths throughout the year, in *T. abyssorum* during winter and spring (ANOVA, $F_{3,\ 8} = 17.4$, $p < 0.001$), and in *M. norvegica* (ANOVA, $F_{3,\ 8} = 4.4$, $p < 0.05$) and *C. limacina* (ANOVA, $F_{3,\ 8} = 4.4$, $p < 0.05$) particularly during spring.

3.5. Carbon and food source composition

3.5.1. Diatom- vs. dinoflagellate-produced fatty acids

The importance of diatom-associated carbon was generally highest in the copepod species indicated by the high relative contributions of the diatom marker FA 16:1(*n*-7) and high ratios of 16:1(*n*-7)/16:0 (ANOVA, $F_{9,\ 250} = 22.1$, $p < 0.001$; Fig. 5, Tables A3 and A4). Average proportions of the diatom-associated FA 16:4(*n*-1) were below 1 % in all species, except in the *Calanus* copepods (maximum values in *Calanus hyperboreus* with 2.4 %; ANOVA, $F_{9,\ 250} = 30.0$, $p < 0.001$). Contributions of 20:5(*n*-3) were relatively evenly distributed among the different species but showed significantly lower proportions in the copepods *Paraeuchaeta* spp. compared to all other species (ANOVA, $F_{9,\ 250} = 16.8$, $p < 0.001$). Average values of the dinoflagellate-associated/*Phaeocystis* FA 18:4(*n*-3) were the highest in *C. hyperboreus* (ANOVA, $F_{9,\ 250} = 10.9$, $p < 0.001$) and maximum values of the second dinoflagellate-associated FA 22:6(*n*-3) were detected in the chaetognath *P. maxima* (ANOVA, $F_{9,\ 250} = 20.7$, $p < 0.001$).

3.5.1.1. Copepods. In *C. glacialis*, contributions of the diatom-associated FAs 16:1(*n*-7) were significantly higher during late winter compared to the other seasons (see Fig. 6 for statistical output). The proportions of 16:4(*n*-1) were significantly higher in summer and late winter than late autumn and spring, and 20:5(*n*-3) was more abundant in spring and summer in comparison to late autumn and winter. Among the dinoflagellate-associated FAs, 18:4(*n*-3) peaked in summer and 22:6(*n*-

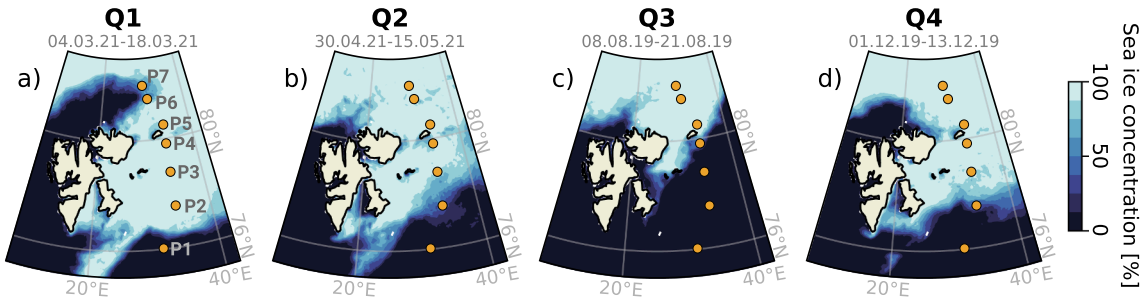

Fig. 1. Maps with sampling stations P1 to P7 (from south to north) and mean sea-ice concentration (SIC) during the sampling in late winter (Q1), spring (Q2), summer (Q3) and late autumn (Q4) using AMSR2 daily 6.25 km SIC based on the ASI algorithm (Spreen et al., 2008), version 5.4 from the University of Bremen (https://seaice.uni-bremen.de/data/amsr2/asi_daygrid_swath/n6250/netcdf/). Time ranges used to compute mean SIC are indicated in the panels above the maps, respectively.

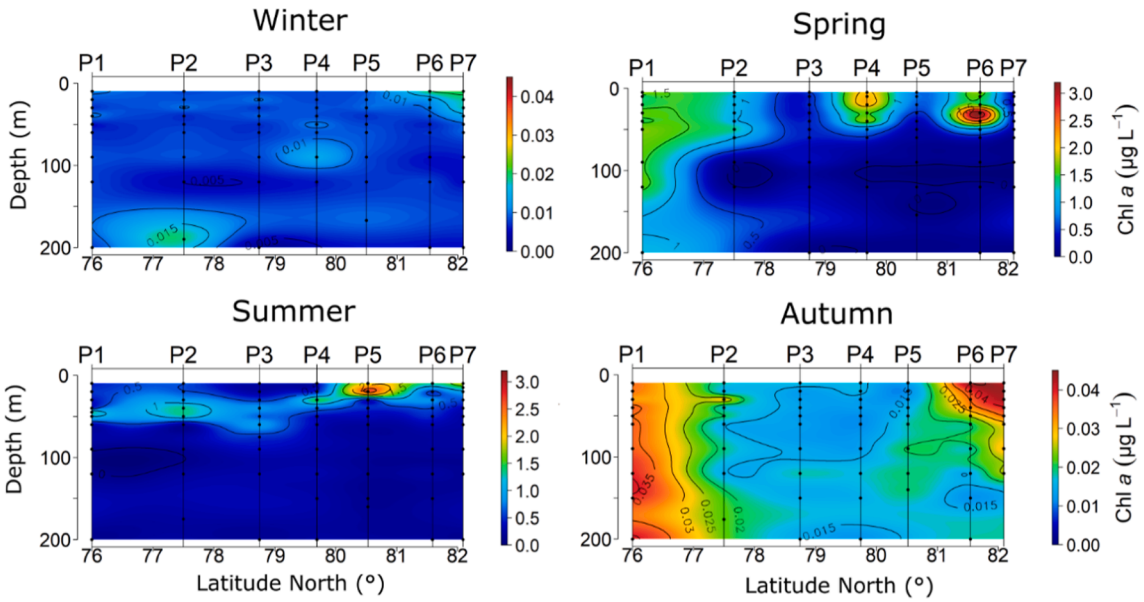

Fig. 2. Seasonal chlorophyll (chl) *a* concentrations (µg L^{-1}) along the sampling transect in the uppermost 200 m of the water column. Note different scales for late winter and autumn *vs.* spring and summer.

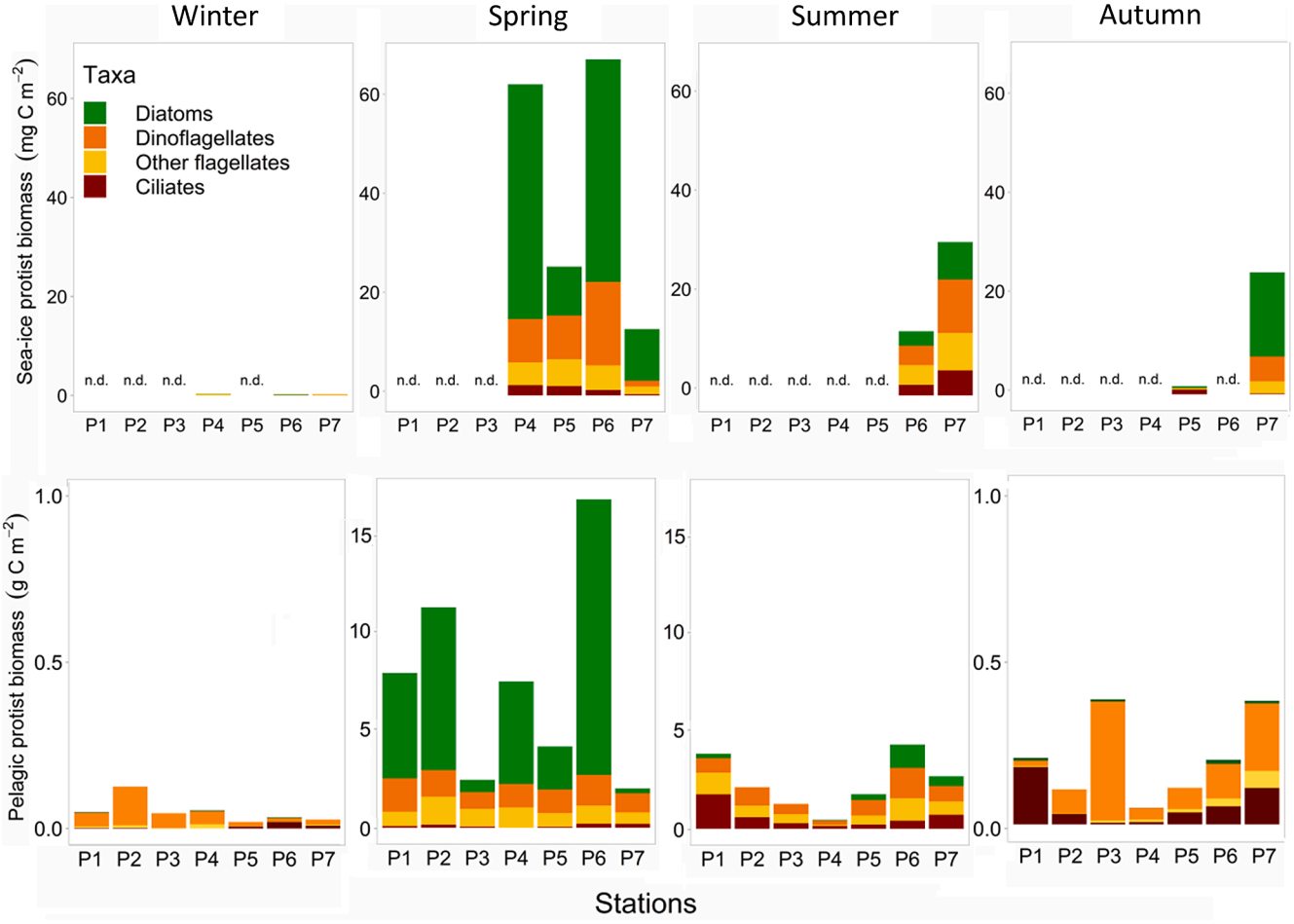

Fig. 3. Seasonal depth-integrated biomass of sympagic protists (mg C m^{-2}; top panel) for the bottom 10 cm of the sea ice, and pelagic protist biomass (g C m^{-2}; bottom panel) for the upper 90 m surface layer. Note: for stations P2 and P4 in summer, protist biomass was integrated over shallower depth (0–60 m and 0–30 m, respectively). Note different scales for sea-ice and pelagic protist figure panels as well as among different seasons for pelagic protist biomass. n.d. = no data.

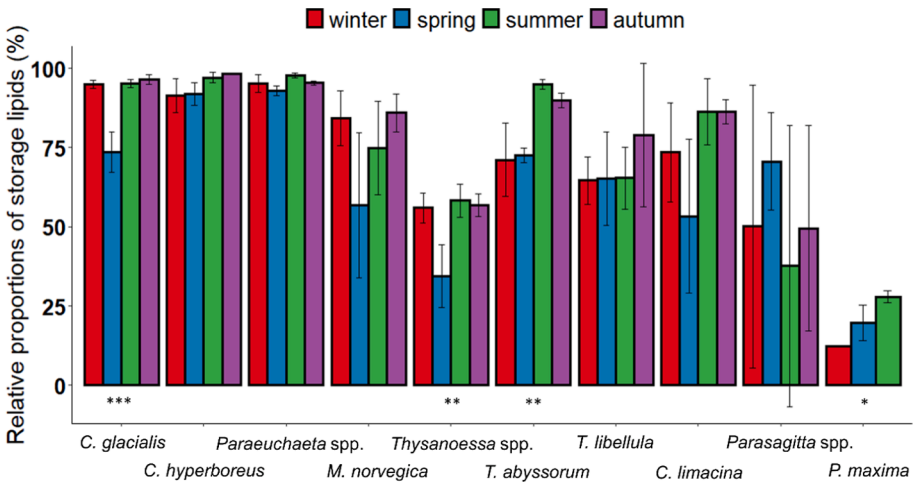

Fig. 4. Seasonal variability in the average relative proportions (%; error bars represent SD) of storage lipids (*i.e.*, wax esters, triacylglycerols, diacylglycerolethers, sterols, fatty alcohols, free fatty acids) in the pelagic zooplankton species. Note: no autumn data available for *Pseudosagitta maxima*. Associated bars marked with asterisk '*' represent significant differences among the seasons (ANOVA, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

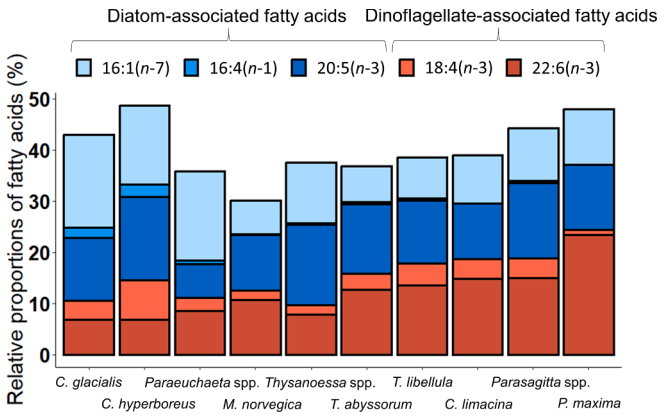

Fig. 5. Average relative proportions (%) of diatom- [16:1(*n*-7), 16:4(*n*-1), 20:5(*n*-3)] and dinoflagellate-associated fatty acids [18:4(*n*-3), 22:6(*n*-3)] in the pelagic zooplankton species. Note: no autumn data available for *Pseudosagitta maxima*. See individual relative proportions (± SD) in Table A3.

3) showed highest proportions during spring. In *C. hyperboreus*, 16:4(*n*-1) proportions were significantly lower in late winter than in summer. Proportions of 18:4(*n*-3) were significantly higher in summer and late autumn *vs.* late winter and spring. In *Paraeuchaeta* spp., levels of 16:1(*n*-7) were significantly higher in summer and late winter compared to autumn, proportions of 16:4(*n*-1) reached highest concentrations in winter compared to the rest of the year, while 20:5(*n*-3) had highest proportions during late autumn. Both dinoflagellate-associated FAs peaked during late autumn.

3.5.1.2. Krill. In *M. norvegica*, the two spring samples differed significantly from samples collected in the other seasons due to their higher proportions of 20:5(*n*-3) and 22:6(*n*-3). In *Thysanoessa* spp., higher relative proportions of 16:1(*n*-7) were recorded in summer compared to spring, while relative contribution from 16:4(*n*-1) was lower in late winter compared to the other seasons. Maximum concentrations of 20:5(*n*-3) and 22:6(*n*-3) were observed during spring.

3.5.1.3. Amphipods. In this amphipod, relative proportions of 16:4(*n*-1), 20:5(*n*-3) and 18:4(*n*-3) were significantly higher during summer than during the other seasons while proportions of 22:6(*n*-3) were the highest during late winter. In *T. libellula*, significant differences between the seasons were restricted to contributions from 20:5(*n*-3), which were higher in summer than in spring and late autumn, and proportions of 22:6(*n*-3), which were higher in late winter and summer compared to late autumn.

3.5.1.4. Other zooplankton. In *C. limacina*, relative proportions of 16:1(*n*-7), 20:5(*n*-3) and 22:6(*n*-3) were significantly lower in late autumn compared to the other seasons. In *Parasagitta* spp., seasonal variability was restricted to proportions of 16:1(*n*-7), which were significantly higher during summer than spring. In *P. maxima*, proportions of 18:4(*n*-3) were significantly higher during summer than spring and late winter, while those of 22:6(*n*-3) were somewhat lower during summer compared to the other two seasons (no significant differences).

3.5.2. Importance of heterotrophic food items/degree of carnivory

To estimate the importance of heterotrophic food items in the zooplanktons' diet, three carnivory indices have been used: i) the relative importance of copepod-associated FAs, ii) the ratio of 18:1(*n*-9) to 18:1(*n*-7) and iii) the ratio of zoosterols to phytosterols; the latter two both increase with increasing degree of carnivory. Considering all three carnivory indices, the copepods *Paraeuchaeta* spp. and the amphipod *T. libellula* were most reliant on heterotrophic prey throughout the year (Table 3). In the krill *Thysanoessa* spp. and the pteropod *C. limacina*, FAs derived from calanoid copepods were generally not found abundantly in any season. The overall lowest degree of carnivory was indicated for *C. limacina* and the chaetognath *P. maxima*.

Both *Calanus* species had significantly higher ratios of zoosterols/phytosterols in late autumn compared to the other seasons (Table 3). The higher zoosterols/phytosterols ratio in *Paraeuchaeta* spp. during late autumn was supported by their higher 18:1(*n*-9)/18:1(*n*-7) ratio compared to the other seasons, indicating more carnivory. Both krill species showed the highest ratios of zoosterols/phytosterols during late winter. The krill *M. norvegica* was also more reliant on copepods during late winter, while their 18:1(*n*-9)/(*n*-7) ratios peaked during late autumn. In the amphipod *T. abyssorum*, only the relative proportions of copepod-associated FAs showed seasonal variability, with significantly higher levels in spring than in summer and late autumn. In the amphipod *T. libellula*, the higher degree of carnivory reflected by higher zoosterols/phytosterols ratios during spring and late autumn was mainly driven by a stronger reliance on *Calanus* copepods during these seasons (Table 3). All three carnivory indices suggested a lower importance of heterotrophic prey during summer in this species. In *C. limacina*, their relative proportions of copepod-associated FAs were generally low, while zoosterols/phytosterols ratios were significantly higher during summer and late autumn compared to late winter and spring. The

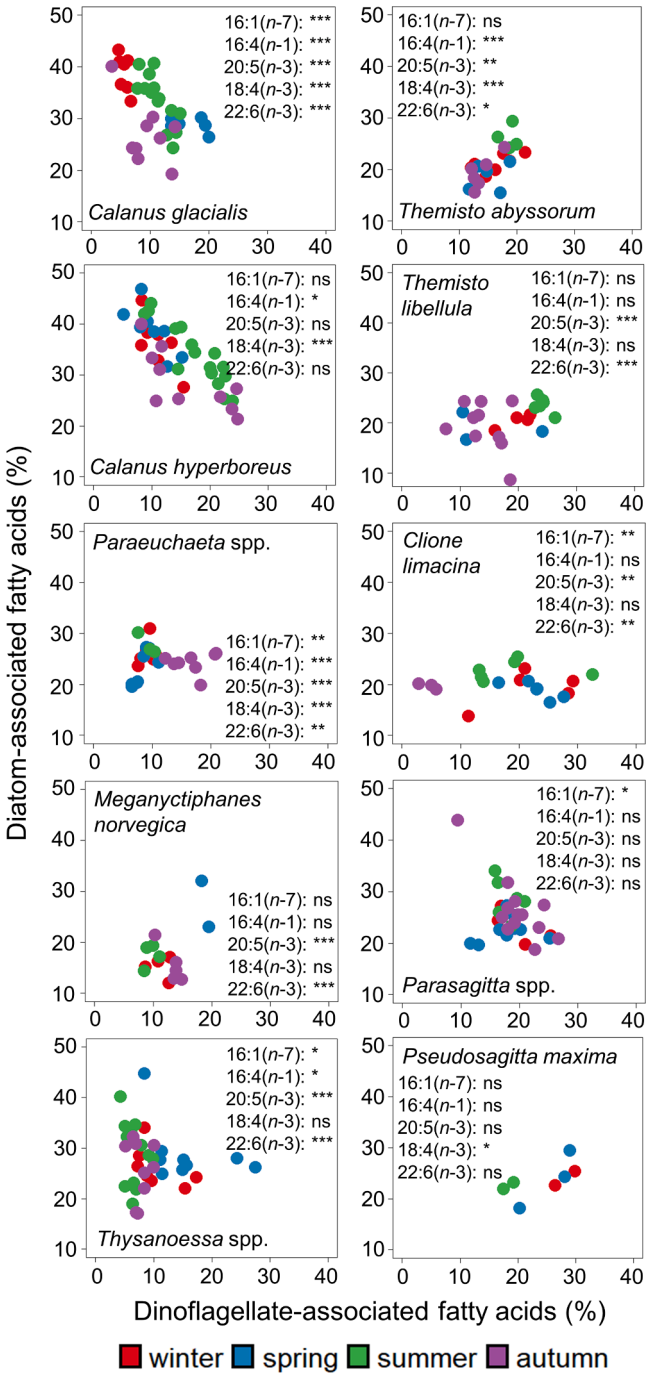

Fig. 6. Seasonal variability in the relative contributions (%) of diatom- *vs.* dinoflagellate-produced fatty acids (FAs) in the pelagic zooplankton species. Diatom-associated FAs: 16:1(*n*-7), 16:4(*n*-1), 20:5(*n*-3); dinoflagellate-associated FAs: 18:4(*n*-3), 22:6(*n*-3). Note: no autumn data available for *Pseudosagitta maxima*. FA-specific significant differences among the seasons are presented for each species (ANOVA, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns-not significant).

chaetognaths *Parasagitta* spp. indicated the lowest reliance on copepods during summer, while ratios of 18:1(*n*-9)/(*n*-7) were highest in spring. Seasonal variability of carnivory indices was insignificant in *P. maxima* (Table 3).

3.5.3. Importance of sympagic vs. pelagic food sources

During late winter, none of the four HBIs (IP_{25}, $IPSO_{25}$, HBIs III and IV) were detected in IPOM ($n = 4$). In spring, IP_{25} (4.6 pg ml^{-1}) was the only HBI detected in one ice core collected from station P7. At P6, however, each of the IPOM samples ($n = 5$) collected in the under-ice environment by divers contained all four HBIs, with IP_{25} ranging from 26 to 36 pg ml^{-1}, $IPSO_{25}$ from 208 to 279 pg ml^{-1}, HBI III from 1546 to 2413 pg ml^{-1} and HBI IV from 571 to 859 pg ml^{-1} (see Kohlbach et al., 2022a). During summer, low concentrations of IP_{25} were also detected in one IPOM sample collected at station P6 (0.02 pg ml^{-1}) while $IPSO_{25}$ was detected in IPOM samples from stations P6 and P7 (0.8 and 1.6 pg ml^{-1}). In contrast, HBIs specific to pelagic producers (HBIs III and IV) were not detected. One of the three late autumn IPOM samples contained 0.6 pg ml^{-1} of $IPSO_{25}$ (station P7) but lacked detectable concentrations of the other HBIs. None of the four HBIs were detected in PPOM across all seasons (late winter $n = 5$, spring $n = 6$, summer $n = 17$, late autumn $n = 15$).

In the zooplankton, sea ice-associated HBIs (IP_{25} and $IPSO_{25}$) were virtually absent during late winter and spring, except for one sample of the krill *M. norvegica* at station P6 containing $IPSO_{25}$ but no IP_{25}. This was accompanied by relatively large concentrations of HBIs III and IV (Fig. 7, Table A5), however, despite elevated concentrations of these HBIs in other *M. norvegica* samples and krill *Thysanoessa* spp. sampled during spring, no sympagic HBIs were detected. During summer and late autumn, the sympagic HBIs IP_{25} and/or $IPSO_{25}$ were found in krill species (*Thysanoessa inermis*, *M. norvegica* not in late autumn), both amphipod species (*T. abyssorum*, *T. libellula*) and the pteropod *C. limacina* (not in late autumn) derived from various sampling locations across the northwestern Barents Sea (both ice-covered and ice-free stations). During late autumn, maximum sympagic HBI concentrations were detected in *T. abyssorum* from stations P6 and P7. In *Thysanoessa* spp. and the amphipod species, mean concentrations of sympagic HBIs were slightly higher in late autumn than in summer. Pelagic HBIs (*i.e.,* HBIs III and IV) were found across all seasons, in one third of all samples collected during late winter, half of the samples measured from spring and about three quarters of the samples from summer and late autumn. Across all seasons, the average concentrations of pelagic HBIs (HBIs III and IV) in zooplankton were generally higher than sympagic HBIs (IP_{25} and $IPSO_{25}$), with highest quantities detected in spring (Fig. 7, Table A5). During late winter, spring and summer, maximum concentrations of pelagic HBIs were detected in *M. norvegica* while during late autumn, the highest amounts of pelagic HBIs were found in *Thysanoessa* spp.

4. Discussion

4.1. Seasonality in sympagic and pelagic protist communities reflected in food-source use by pelagic zooplankton

The observed large interspecific differences in our trophic marker data suggested that the zooplankton species were using (a mix of) different strategies to cope with seasonal fluctuations in food availability, including diapause, continuous feeding, reduced metabolism, starvation, the utilization of energy reserves during winter *vs.* a stronger algal-based diet during summer, which largely reflects known feeding strategies (e.g., Hagen, 1999; Lee et al., 2006; Grigor et al. 2015).

Previous research suggests that (some) zooplankton can stay active and even reproduce during the polar night, likely facilitated through opportunistic feeding and/or utilization of accumulated lipid reserves (Hagen, 1999; Tarling, 2015; Berge et al., 2020; Hobbs et al., 2020). To counteract the scarcity of (sympagic and pelagic) algae during polar night, and in line with hypothesis 1 of a seasonal variation in carbon and food-source use as well as recent research (Kunisch et al., 2023), the winter-active krill species *Meganyctiphanes norvegica* and *Thysanoessa* spp. both had a stronger reliance on heterotrophic prey during late winter, indicated by a higher contribution of copepod-associated FAs (*M. norvegica*) and higher ratios of zoosterols/phytosterols (both species). Lipid stores in the copepod *Calanus glacialis*, *M. norvegica* and *Thysanoessa* spp. were depleted in spring compared to the other seasons,

Table 3
Carnivory indices (mean ± SD) in the pelagic zooplankton species. ns = no significant seasonal variability. Note: no autumn data available for *Pseudosagitta maxima*.

Species	Season	*n*	Copepod-associated FAs (%)	18:1(*n*-9)/18:1(*n*-7)	*n*	Zoosterols/phytosterols
Calanus glacialis	Late winter	8	31.5 ± 4.9	3.3 ± 0.3	4	69.0 ± 7.4
	Spring	6	27.7 ± 3.3	1.8 ± 0.5	2	66.7 ± 13.5
	Summer	14	24.1 ± 2.7	4.8 ± 1.6	4	93.2 ± 15.6
	Late autumn	9	33.7 ± 5.9	3.8 ± 0.8	5	117.8 ± 13.1
	Mean		**28.6 ± 5.7**	**3.7 ± 1.5**		**91.4 ± 24.6**
ANOVA			$F_{3, 33} = 11.1$, $p < 0.01$	$F_{3, 33} = 10.6$, $p < 0.001$		$F_{3, 11} = 14.0$, $p < 0.001$
Calanus hyperboreus	Late winter	7	32.0 ± 4.2	2.2 ± 0.2	3	49.2 ± 6.7
	Spring	8	29.9 ± 2.9	2.4 ± 0.4	3	34.8 ± 11.9
	Summer	16	25.8 ± 3.8	2.7 ± 0.7	6	77.7 ± 15.9
	Late autumn	10	31.7 ± 4.8	2.9 ± 0.6	2	109.1 ± 2.6
	Mean		**29.1 ± 4.7**	**2.6 ± 0.6**		**66.9 ± 27.6**
ANOVA			$F_{3, 37} = 6.4$, $p < 0.01$	ns		$F_{3, 10} = 16.8$, $p < 0.001$
Paraeuchaeta spp.	Late winter	6	28.6 ± 4.9	19.6 ± 7.4	4	158.4 ± 20.4
	Spring	8	31.0 ± 7.9	22.3 ± 4.4	4	260.3 ± 27.8
	Summer	3	20.0 ± 5.6	22.3 ± 2.9	1	200.8
	Late autumn	8	16.7 ± 8.4	35.6 ± 9.5	4	325.2 ± 110.1
	Mean		**25.0 ± 9.5**	**26.0 ± 9.5**		**244.4 ± 90.6**
ANOVA			$F_{3, 21} = 7.5$, $p < 0.01$	$F_{3, 21} = 7.3$, $p < 0.01$		$F_{3, 9} = 4.4$, $p < 0.05$
Meganyctiphanes norvegica	Late winter	4	33.5 ± 11.1	2.3 ± 0.3	3	282.8 ± 68.9
	Spring	2	10.1 ± 12.9	2.1 ± 0.5	2	119.9 ± 37.6
	Summer	4	26.7 ± 6.2	2.5 ± 0.4	2	83.0 ± 31.4
	Late autumn	5	16.3 ± 4.7	3.1 ± 0.5	2	173.9 ± 35.3
	Mean		**22.8 ± 11.3**	**2.6 ± 0.6**		**178.0 ± 94.2**
ANOVA			$F_{3, 11} = 5.2$, $p < 0.05$	$F_{3, 11} = 4.0$, $p < 0.05$		$F_{3, 5} = 7.3$, $p < 0.05$
Thysanoessa spp.	Late winter	7	5.4 ± 2.6	2.3 ± 0.3	8	297.0 ± 114.7
	Spring	9	3.1 ± 1.6	2.2 ± 0.3	7	120.5 ± 63.2
	Summer	13	3.5 ± 1.5	2.2 ± 0.2	5	65.4 ± 16.2
	Late autumn	9	4.8 ± 2.6	2.5 ± 0.3	4	111.7 ± 37.8
	Mean		**4.0 ± 2.1**	**2.3 ± 0.3**		**166.4 ± 120.8**
ANOVA			ns	ns		$F_{3, 20} = 11.8$, $p < 0.001$
Themisto abyssorum	Late winter	7	25.0 ± 4.7	5.6 ± 0.9	3	47.3 ± 17.0
	Spring	5	29.3 ± 2.8	6.8 ± 1.6	5	78.3 ± 28.7
	Summer	4	19.9 ± 3.8	5.1 ± 0.7	3	66.0 ± 66.9
	Late autumn	6	21.0 ± 4.8	6.4 ± 1.1	3	98.4 ± 32.5
	Mean		**23.9 ± 5.3**	**6.0 ± 1.2**		**73.3 ± 38.4**
ANOVA			$F_{3, 18} = 5.0$, $p < 0.05$	ns		ns
Themisto libellula	Late winter	4	19.0 ± 7.3	5.6 ± 1.5	3	183.8 ± 138.2
	Spring	3	31.1 ± 10.9	4.0 ± 0.9	3	250.1 ± 170.5
	Summer	6	10.7 ± 2.2	3.5 ± 0.3	2	122.3 ± 62.5
	Late autumn	10	28.1 ± 8.6	4.9 ± 1.5	5	277.5 ± 145.3
	Mean		**22.3 ± 10.7**	**4.5 ± 1.4**		**225.7 ± 137.4**
ANOVA			$F_{3, 19} = 8.3$, $p < 0.01$	$F_{3, 19} = 3.1$, $p = 0.05$		ns
Clione limacina	Late winter	5	6.3 ± 1.6	1.2 ± 0.2	2	2.2 ± 0.6
	Spring	6	5.6 ± 0.9	1.0 ± 0.2	4	2.4 ± 0.6
	Summer	6	4.9 ± 1.3	0.9 ± 0.3	2	7.6 ± 0.2
	Late autumn	3	7.6 ± 0.2	0.9 ± 0	2	6.8 ± 0.9
	Mean		**5.9 ± 1.4**	**1.0 ± 0.2**		**4.3 ± 2.5**
ANOVA			$F_{3, 16} = 3.7$, $p < 0.05$	ns		$F_{3, 6} = 45.5$, $p < 0.01$
Parasagitta spp.	Late winter	4	25.5 ± 6.9	6.2 ± 1.9	2	28.3 ± 4.9
	Spring	9	30.9 ± 6.3	7.3 ± 2.0	6	27.0 ± 4.0
	Summer	6	12.7 ± 5.4	3.2 ± 1.1	3	42.3 ± 18.6
	Late autumn	13	25.3 ± 7.4	4.4 ± 2.0	6	43.1 ± 11.5
	Mean		**24.6 ± 8.9**	**5.2 ± 2.4**		**36.5 ± 12.3**
ANOVA			$F_{3, 28} = 8.9$, $p < 0.001$	$F_{3, 18} = 7.3$, $p < 0.001$		
Pseudosagitta maxima	Late winter	2	13.2 ± 0.9	1.8 ± 0.6	1	12.0
	Spring	3	16.2 ± 11.7	2.4 ± 0.7	2	8.5 ± 0.5
	Summer	2	19.5 ± 0.2	1.2 ± 0	1	7.0
	Late autumn	–	–	–		–
	Mean		**16.3 ± 1.9**	**1.9 ± 0.7**		**9.0 ± 2.2**
ANOVA			ns	ns		ns

indicating that these predominantly omnivorous species also utilized their accumulated lipids throughout the winter.

Meganyctiphanes norvegica had the lowest reliance on wax ester-rich calanoid copepods during spring, which was reflected in their minimal levels of storage lipids and consequently stronger relative contribution of the polyunsaturated FAs (PUFAs) 20:5(*n*-3) and 22:6(*n*-3) to their FA content, which are predominantly associated with membrane lipids rather than storage lipids (Stübing et al., 2003). These results could

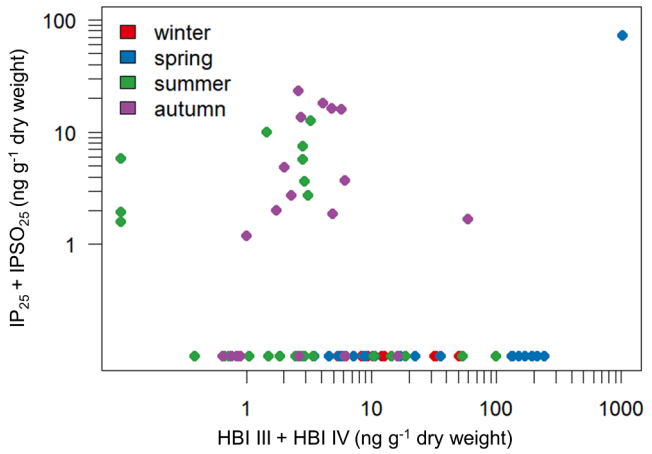

Fig. 7. Concentrations (ng g^{-1} dry weight) of the sympagic highly branched isoprenoids (HBIs) IP_{25} and $IPSO_{25}$ *vs.* the pelagic HBIs III and IV in the zooplankton community during all seasons. Note: only samples that contained sympagic or pelagic HBIs or both are shown in the figure. Late winter: sympagic HBIs: not detected, pelagic HBIs: 5.4–50.9 ng g^{-1} dry weight ($n = 10$); spring: sympagic HBIs: 72.4 ng g^{-1} dry weight ($n = 1$), pelagic HBIs: 3.5–1034.4 ng g^{-1} dry weight ($n = 20$); summer: sympagic HBIs: 1.6–12.7 ng g^{-1} dry weight ($n = 9$), pelagic HBIs: 0.4–100.4 ng g^{-1} dry weight ($n = 22$); late autumn: sympagic HBIs: 1.2–23.1 ng g^{-1} dry weight ($n = 12$), pelagic HBIs: 0.6–59.9 ng g^{-1} dry weight ($n = 19$).

further indicate that this krill species was taking advantage of the spring blooms in sea ice and/or the ice-water interface (Schmidt, 2010). In IPOM, the maximum production of PUFAs during spring coincided with the peak biomass of sympagic protists (Kohlbach et al., 2022a). The elevated proportional contributions of 20:5(*n*-3) and 22:6(*n*-3) in combination with the detection of sympagic HBI metabolites (see 4.2) could thus point to the utilization of ice algae as a food source during spring by this species. However, other species including *C. glacialis* and *Thysanoessa* spp. also displayed high proportions of these two PUFAs during spring with associated lower proportions of storage lipids, but with no detectable amounts of sympagic HBIs, suggesting the reliance on under-ice phytoplankton rather than ice algae for these species (e.g., under-ice bloom at station P6 dominated by pelagic diatoms; Kohlbach et al., 2022a) and/or a remaining late winter signal reflecting depleted energy stores. Although being valuable dietary proxies due to their source specificity, it should be noted that the interpretation of HBI results is challenging due to typically low and variable contributions from their diatom sources potentially leading to consumer concentrations below the detection limit (for more details on method limitations see also Schmidt et al., 2018; Kohlbach et al., 2021a).

Besides differences in dietary compositions between the seasons due to fluctuations in the availability of food, species-specific variability in the trophic marker composition can further be the result of ontogenetic differences reflecting varying dietary requirements of the different developmental stages of zooplankton throughout the year and with life cycle (e.g., shown for Antarctic krill: Kohlbach et al., 2017). For example, based on length and dry weights, individuals of *M. norvegica* sampled during spring were in an earlier life stage than during the other seasons, and their lower reliance on copepods during spring could reflect that younger individuals are not able to ingest relatively large prey such as copepods (Schmidt, 2010). Intraspecific variability can further reflect opportunistic feeding behaviour, *i.e.,* spatial variability in food-source use at ice-free *vs.* ice-covered sampling stations along the Barents Sea sampling transect (Kohlbach et al., 2021a).

Relative contributions of the copepod-associated FAs in the amphipods *Themisto abyssorum* and *T. libellula* remained high in late autumn and winter, suggesting that *Themisto* amphipods fed actively throughout the dark season (business-as-usual), largely relying on wax ester-rich *Calanus* copepods (Kraft et al., 2013; Mayzaud & Boutoute 2015; Dischereit et al., 2022). The high proportions of *Calanus*-associated FAs in *Parasagitta* spp. during late winter also suggested continuous feeding through the polar night, which is in agreement with previous findings (Grigor et al., 2015; Choi et al., 2020). The fairly low seasonal variability in FA marker composition in comparison to most other species investigated in our study further confirms the notion that the carnivorous *Parasagitta* spp. might be relatively unaffected by seasonal change. This can be primarily attributed to the constant availability of prey throughout the year (Hagen, 1999) and their plastic dietary composition, indicated by the highly variable wax-ester content within and between the seasons, as well as their non-visual predatory behaviour (Terazaki, 2004).

The predatory amphipods *T. abyssorum* and *T. libellula* as well as *Parasagitta* spp. had lower degrees of carnivory during summer, based on the majority of the carnivory indices, mirroring the increased availability and utilization of phytoplankton rather than heterotrophic prey in their diet (e.g., Dalpadado et al. 2008). Further confirming our assumption of zooplankton mirroring seasonal variation in the availability of food items (hypothesis 1) and showing a clear link to the pelagic primary production, concentrations of the dinoflagellate/*Phaeocystis* marker 18:4(*n*-3) peaked during summer in the *Calanus* copepods as well as *T. abyssorum* and *Pseudosagitta maxima*, when the production of this FA also reached maximum values in phytoplankton (Kohlbach et al., 2022a). This larger contribution of flagellates/dinoflagellates to the pelagic protist communities during summer was also evident in the microscopy samples (Kohlbach et al., 2023a). Low carnivory indices in *P. maxima* complement recent studies demonstrating that chaetognaths feed more herbivorously than previously assumed (Grigor et al., 2020).

4.2. Ice algae as alternative food rather than major energy resource

Partly in accordance with hypothesis 2 of a sympagic HBI production peak in spring, sea ice-associated production in terms of algal biomass and HBI concentrations was the highest during spring. However, detection of sympagic HBIs was mostly restricted to the under-ice environment in samples collected by divers using slurp guns (see Kohlbach et al., 2022a). These differences are likely a result of different sampling techniques by which the under ice *vs.* ice core samples have been collected. While divers can specifically target the collection of visibly concentrated ice-algae assemblages, algal biomass in individual ice cores is considerably lower, reflected in low amounts or even undetectable HBIs. By specifically targeting areas with visibly higher ice algal biomass, a more diverse sympagic community is more likely to be captured, increasing the probability of collecting HBI-producing taxa. In contrast, the bottom layer of ice algae is often loosely attached and lost when the core is retrieved from the surface, particularly when the ice has interconnected brine channels. We further note that HBI-producing sea-ice diatoms, such as *Haslea* and *Pleurosigma* (Brown et al., 2014; Limoges et al., 2018) likely had a minor contribution to the sea-ice communities sampled during this study (all seasons; Assmy et al., 2022a, b, c; Wold et al., 2022), and were in fact only detected in sea-ice protist community samples from Q2 (Wold et al., 2022).

The presence of $IPSO_{25}$ in *M. norvegica* collected during the spring sampling at station P6 tallied with elevated concentrations of sympagic HBIs (*i.e.*, $IPSO_{25} > IP_{25}$) in the IPOM (under-ice) samples at this station. However, this was the only sample linking the zooplankton to the sympagic environment during spring. It further aligned with accompanying elevated concentrations of HBIs III and IV in the same sample and the general profile of HBIs in under-ice IPOM (Kohlbach et al., 2022a). At station P6, the occurrence of an under-ice phytoplankton bloom, dominated by pelagic diatoms of the genus *Thalassiosira*, possibly presented an alternative food source to ice-associated algae for the majority of grazers, as it has been suggested for the ice-associated amphipod *Apherusa glacialis* and polar cod collected during the same sampling

campaign (Kohlbach et al., 2022a). An under-ice bloom is easier accessible for pelagic grazers and thus likely preferred over ice algae. Another explanation for the absence of sympagic HBIs in the majority of the spring samples could be the preferential uptake and retention of IP_{25} and/or $IPSO_{25}$ in *M. norvegica* as these sympagic metabolites were also detected during summer in this species. Furthermore, *M. norvegica* had the highest concentrations of pelagic HBIs during late winter, spring and summer among all zooplankton species, suggesting a somewhat higher storage efficiency of HBI lipids in comparison to the other species.

Contrary to our hypothesis 2 of a maximum consumption of sympagic food items during spring, the reliance of the zooplankton community on ice algae was, despite the highest production of sympagic HBIs, negligible during spring. Already elevated phytoplankton concentrations in the water column in May 2021, particularly at stations P1 to P4 and P6, likely counteracted the utilization of sea-ice associated algae. The presence of sympagic HBIs IP_{25} and $IPSO_{25}$ in krill, amphipods and *C. limacina* during summer and late autumn (only krill and amphipods) with the simultaneous lack of dominant HBI-producing diatom taxa in the ice, lack of IP_{25} and $IPSO_{25}$ in PPOM and low concentrations in IPOM during both seasons suggests that concentrations of sympagic HBIs must have been higher in algae associated with the under-ice environment, which was not sampled during summer and late autumn. It is rather unlikely that the HBI signal in the summer and late autumn animals reflected the spring HBI production as it is assumed that HBIs are not retained for long periods but represent the recent algal production (Koch et al., 2023).

Absence of HBIs in primary producers and animals does not necessarily imply that these metabolites were not produced or obtained but could also point to concentrations below the detection limits of the current analytical approaches. Based on current knowledge, HBIs are only produced by a handful of sympagic and pelagic diatom species, which are usually not among the dominating algal taxa in sea-ice and pelagic communities (Brown et al. 2014, Limoges et al., 2018). In accordance with that, HBI concentrations in POM samples collected in short-term sediment traps throughout the water column were generally low (during spring and summer; restricted to few stations) or zero (during late autumn and winter; Y. V. Bodur, UiT The Arctic University of Norway, pers. comm.). $IPSO_{25}$ has been found (in low concentrations) in short-term sediment traps deployed directly underneath the ice at station P6 during spring (Y. V. Bodur, pers. comm.). Since no $IPSO_{25}$ was detected in the bottom 0–3 cm of sea-ice samples analysed from P6, the HBI signature from the traps points towards the HBI signature observed from under-ice material (phytoplankton under-ice bloom) at station P6. In agreement with our HBI results, FA specific carbon stable isotopes showed that zooplankton was isotopically closer to PPOM than IPOM during summer (stations P6 and P7; Kohlbach et al., 2023b), further providing evidence of PPOM being the major carbon source for these species in the Barents Sea.

At a first glance, the poor utilization of sympagic food sources during all seasons seems to be in contrast to previous findings suggesting the (high) importance of ice-algal carbon in different Arctic food webs spanning all trophic levels and seasons. For example, Søreide et al. (2006) described a strong utilization of ice algae by ice amphipods and its importance as supplementary dietary source for carnivorous species in the Barents Sea and Svalbard waters based on bulk stable isotopes. A high contribution of IPOM to the carbon budget of ice amphipods and zooplankton sampled off Barrow, Alaska (Budge et al., 2008) and the central Arctic Ocean (Kohlbach et al., 2016) as well as in Svalbard seals (Kunisch et al., 2021) was quantified using FA specific stable isotope analysis and, finally, based on HBIs, Koch et al. (2023) suggested an overall strong ice algal reliance of consumers on a pan-Arctic scale independent of trophic position. Two of these studies (Søreide et al., 2006; Budge et al., 2008) were based on datasets from more than 20 years ago, at a time when sea ice was more extensive in the Barents Sea than in the current situation (Ingvaldsen et al., 2023). In our study, analysis of food-source origin at the species level revealed that sympagic food did play a role for e.g., filter feeders during summer (Kohlbach et al., 2021a) and amphipods and krill during summer and late autumn (Kohlbach et al., 2021b). Zooplankton in the Barents Sea are more adapted to the absence/lower availability of ice algal carbon during the ice-free period than it would be expected in a perennial sea-ice system. In addition, phytoplankton production in the Barents Sea typically exceeds the sympagic production (Hegseth, 1998; Dalpadado et al., 2014; de la Guardia et al., 2023) and is likely sufficient to fully support the energetic requirements of the zooplankton community. In this study, we focused on species with a predominantly pelagic lifestyle, which inherently have a stronger association with pelagic carbon and food sources. However, typical autochthonous sympagic grazers, such as *Apherusa glacialis*, likewise predominantly relied on food sources of pelagic origin during spring when the bottom sea ice in the sampling area had the highest sea-ice algae biomass (Kohlbach et al., 2022a). With prevailing trophic structures being subject to change with ice retreat, these seasonal results suggest a strong adaptation potential of the pelagic lower-trophic food web to a future ice-free Barents Sea associated with a lower availability of sea-ice algae.

5. Conclusions

Our study suggests that the year-round food-source composition of Barents Sea zooplankton was strongly driven by seasonal change in the production and availability of food resources. The trophic marker data indicated a stronger heterotrophic component in the diet of most grazers during polar night and in spring, with a switch to a more algae-based dietary composition during the summer. Further intra- and interspecific differences in consumer trophic marker composition were likely related to ontogenetic differences, varying dietary requirements throughout the year as well as spatial variability in available food items along the sampling transect. The zooplankton community was mainly reliant on phytoplankton and pelagic carbon and food sources year-round while sympagic food was only utilized by some species to supplement their diet during summer and late autumn. Algal production of sympagic HBI lipids was the highest during spring but did not translate into a high importance of sympagic food for the zooplankton community during this season. Utilization of sympagic carbon during summer and late autumn was mostly restricted to krill and amphipods. This overall relatively low trophic reliance on ice-associated food and trophic plasticity throughout the year might reflect the resilience of the Barents Sea pelagic food web toward ongoing changes to the availability of sympagic and pelagic carbon and food sources.

CRediT authorship contribution statement

Doreen Kohlbach: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Haakon Hop:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization. **Anette Wold:** Writing – review & editing, Validation, Methodology, Data curation. **Katrin Schmidt:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Lukas Smik:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Simon T. Belt:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Matthias Woll:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Martin Graeve:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Lucie Goraguer:** Writing – review & editing, Visualization, Investigation, Formal analysis, Data curation. **Øyvind Foss:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation. **Philipp Assmy:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Author contribution

This study was designed by DK, PA and HH. Sampling was carried out by AW, HH, DK and PA; HH and PA provided sampling logistics. KS and LS run the HBI and sterol analyses and were responsible for data evaluation with the help of STB. MW analysed lipid classes; DK analysed fatty acids and evaluation of lipid datasets were carried out with the support of MG. MG and STB provided laboratory materials, methodological expertise, and laboratory space. Data analyses and figure assemblage was done by DK, LG and ØF with the help of the other authors. DK is the main author of this paper. All authors contributed significantly to data interpretation and to the writing of the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

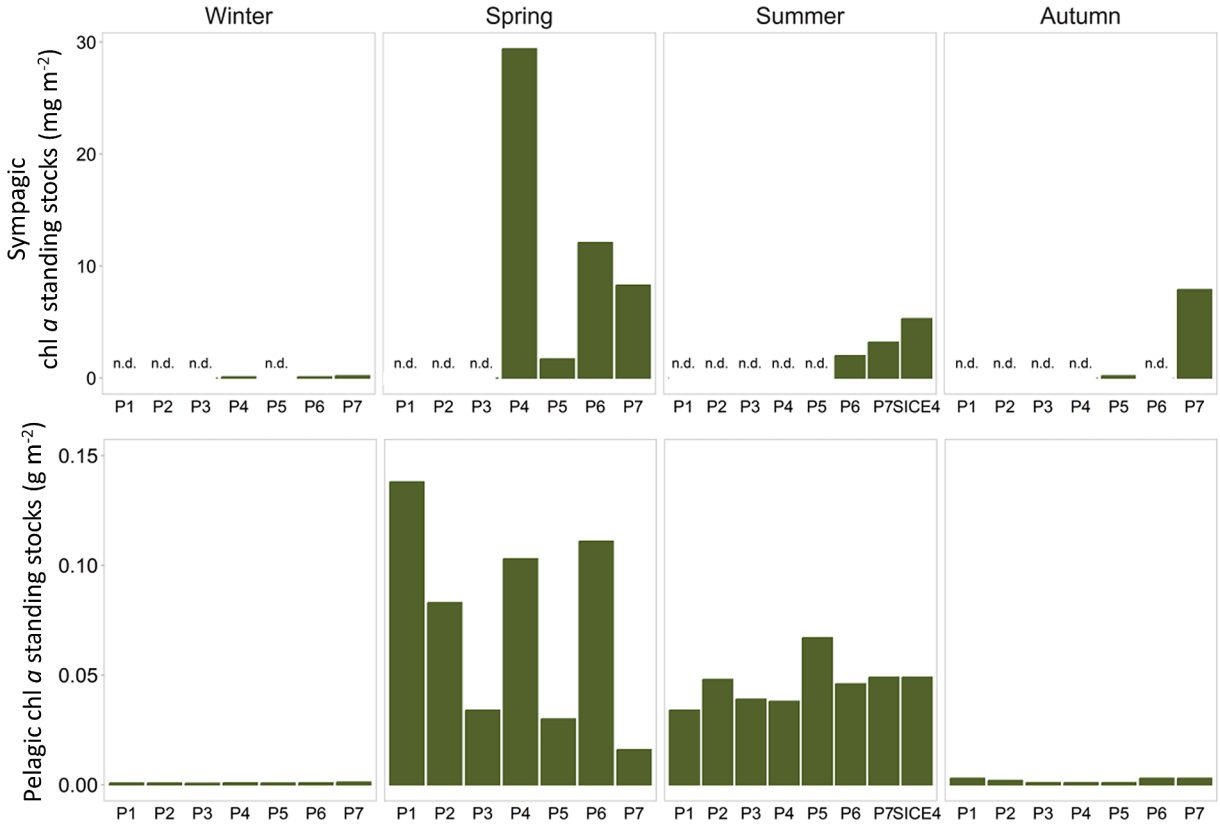

Fig. A1. Seasonal depth-integrated sympagic chlorophyll (chl) *a* concentrations (mg m^{-2}; top panel) for the bottom 30 cm of the sea ice, and pelagic chl *a* concentrations (g m^{-2}; bottom panel) for the upper 90 m surface layer. Note different scales for sea-ice and pelagic chl *a* figure panels. During Q3, samples for chl *a* were collected at an additional station; SICE4: latitude 91.98 °N, longitude 24.64 °E.

Table A1
Maximum chlorophyll *a* values (µg L^{-1}) in the water column (sampling depths) and sea ice during Q1 (Vader et al., 2022c), Q2 (Vader et al., 2022d), Q3 (Vader et al., 2022b) and Q4 (Vader et al., 2022a). * Late winter seawater chl *a* values were < 0.02 µg L^{-1} at all depths.

Chlorophyll *a* (µg L^{-1})	Q1 (late winter)	Q2 (spring)	Q3 (summer)	Q4 (late autumn)
Seawater				
P1	*	1.7 (50 m)	1.2 (45 m)	0.04 (40 m)
P2		1.3 (50 m)	1.2 (50 m)	0.03 (30 m)
P4		2.1 (10 m)	1.4 (30 m)	0.02 (20 m)
P5		0.7 (10 m)	2.6 (20 m)	0.02 (40 m)
P6		3.2 (30 m)	1.3 (10 m)	0.04 (30 m)
P7		0.3 (10 m)	1.7 (10 m)	0.04 (40 m)
Sea ice (bottom 0–3 cm)				
P4_ice	0.03	57.6	–	–
P5_ice	–	3.5	–	0.05
P6_ice	0.1	19.6	0.6	–
P7_ice	0.2	15.4	2.9	0.3

Table A2
Relative proportions (%) of storage and membrane lipid classes in the pelagic zooplankton during all four seasons. '-' no data available; * might contain diacylglycerolethers.

			Q1 (late winter)	Q2 (spring)	Q3 (summer)	Q4 (late autumn)
Taxonomic group	**Zooplankton taxa**	**Lipid class**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**
Copepods	*Calanus glacialis*	**Wax ester**	91.9 ± 2.7 (3)	68.5 ± 8.2 (3)	78.7 ± 6.0 (3)	89.4 ± 0.9 (3)
		Triacylglycerol*	0	3.0 ± 1.4	14.9 ± 6.4	6.2 ± 3.1
		Sterol	0	1.5 ± 0.3	0.1 ± 0.1	0
		Fatty alcohol	1.4 ± 1.2	0.5 ± 0.8	0.2 ± 0.2	0
		Free fatty acid	1.6 ± 0.2	0	0.2 ± 0.3	0.3 ± 0.5
		Phosphatidylcholine	2.8 ± 0.7	16.4 ± 4.2	2.7 ± 0.7	2.1 ± 0.7
		Phosphatidylethanolamine	2.3 ± 0.6	7.0 ± 0.4	1.9 ± 0.3	1.5 ± 0.8
		Phosphatidylinositol	0	3.0 ± 1.8	0.2 ± 0.3	0
		Phosphatidylserine	0	0	0.1 ± 0.1	0
	Calanus hyperboreus	**Wax ester**	87.8 ± 5.4 (3)	86.8 ± 6.0 (3)	90.0 ± 3.3 (3)	96.7 ± 1.1 (3)
		Triacylglycerol*	0.8 ± 0.7	1.6 ± 0.4	4.7 ± 2.7	0.8 ± 0.9
		Sterol	0.6 ± 0.7	0.8 ± 0.4	0	0
		Fatty alcohol	2.2 ± 0.3	1.8 ± 1.1	0.4 ± 0.8	0.5 ± 0.5
		Free fatty acid	0	0.9 ± 0.9	0.3 ± 0.3	0
		Phosphatidylcholine	5.5 ± 3.8	5.5 ± 3.0	1.9 ± 1.2	1.0 ± 0.1
		Phosphatidylethanolamine	3.0 ± 1.7	2.6 ± 0.8	1.0 ± 0.5	0.7 ± 0.1
		Phosphatidylinositol	0.1 ± 0.2	0	0.1 ± 0.1	0
		Phosphatidylserine	0	0	0	0
	Paraeuchaeta norvegica	**Wax ester**	72.9 (1)	–	91.7 (1)	87.2 ± 4.7 (3)
		Triacylglycerol*	19.2		3.7	2.7 ± 3.6
		Sterol	0.4		0.5	0.2 ± 0.4
		Fatty alcohol	0.5		1.3	0.4 ± 0.6
		Free fatty acid	2.9		0.7	5.4 ± 0.7
		Phosphatidylcholine	2.4		1.5	2.4 ± 0.4
		Phosphatidylethanolamine	1.7		0.3	1.8 ± 0.4
		Phosphatidylinositol	0		0	0
		Phosphatidylserine	0		0	0
	Paraeuchaeta spp.	**Wax ester**	89.3 ± 5.1 (3)	85.1 ± 6.9 (3)	–	–
		Triacylglycerol*	3.4 ± 2.3	6.8 ± 8.0		
		Sterol	0.3 ± 0.3	0.5 ± 0.1		
		Fatty alcohol	0.3 ± 0.6	0.5 ± 0.2		
		Free fatty acid	3.2 ± 1.2	0		
		Phosphatidylcholine	2.2 ± 0.5	3.4 ± 0.3		
		Phosphatidylethanolamine	1.3 ± 0.5	2.3 ± 0.3		
		Phosphatidylinositol	0	0.8 ± 0.4		
		Phosphatidylserine	0	0.7 ± 0.6		
		Lyso-Phosphatidylcholine	0	0		
Krill	*Meganyctiphanes norvegica*	**Wax ester**	1.6 ± 1.8 (3)	3.5 ± 6.0 (3)	0.3 ± 0.3 (3)	5.3 ± 9.3 (3)
		Triacylglycerol*	66.2 ± 23.2	28.4 ± 43.5	53.6 ± 42.0	74.2 ± 13.8
		Sterol	1.4 ± 0.5	6.3 ± 3.8	8.0 ± 12.3	0.8 ± 0.7
		Fatty alcohol	1.2 ± 0.7	0	1.5 ± 0.8	1.2 ± 0.1

(*continued on next page*)

Table A2 (*continued*)

Taxonomic group	Zooplankton taxa	Lipid class	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		Free fatty acid	12.1 ± 14.5	18.7 ± 21.2	10.7 ± 14.2	3.9 ± 0.5
		Phosphatidylcholine	11.7 ± 5.6	35.4 ± 17.5	10.6 ± 3.8	12.8 ± 5.7
		Phosphatidylethanolamine	3.2 ± 1.7	7.8 ± 5.4	6.0 ± 4.0	1.3 ± 0.4
		Phosphatidylinositol	0.3 ± 0.5	0	4.6 ± 7.6	0
		Phosphatidylserine	0.6 ± 1.0	0	3.9 ± 6.7	0
	Thysanoessa inermis	**Wax ester**	–	–	32.1 ± 2.1 (3)	–
		Triacylglycerol*			21.2 ± 1.0	
		Sterol			0.2 ± 0.2	
		Fatty alcohol			0.2 ± 0.2	
		Free fatty acid			1.2 ± 0.6	
		Phosphatidylcholine			38.3 ± 1.3	
		Phosphatidylethanolamine			5.3 ± 1.5	
		Phosphatidylinositol			0.2 ± 0.2	
		Phosphatidylserine			0	
	Thysanoessa longicaudata	**Wax ester**	–	–	3.0 ± 0.7 (2)	–
		Triacylglycerol*			55.0 ± 8.2	
		Sterol			0.8 ± 0.3	
		Fatty alcohol			0.4 ± 0.5	
		Free fatty acid			1.9 ± 0.2	
		Phosphatidylcholine			33.2 ± 6.6	
		Phosphatidylethanolamine			3.9 ± 0.9	
		Phosphatidylinositol			0.5 ± 0.1	
		Phosphatidylserine			0.2 ± 0.3	
	Thysanoessa spp.	**Wax ester**	14.5 ± 12.7 (3)	14.0 ± 10.8 (3)	–	28.3 ± 8.2 (3)
		Triacylglycerol*	29.6 ± 8.9	13.4 ± 7.2		27.2 ± 9.5
		Sterol	2.2 ± 1.6	2.5 ± 1.3		0.5 ± 0.7
		Fatty alcohol	0.3 ± 0.5	0		0
		Free fatty acid	8.7 ± 6.8	4.4 ± 5.9		0.1 ± 0.1
		Phosphatidylcholine	38.4 ± 3.4	46.8 ± 4.4		37.3 ± 2.1
		Phosphatidylethanolamine	5.5 ± 1.3	16.0 ± 5.6		5.8 ± 1.4
		Phosphatidylinositol	0	2.9 ± 1.3		0.1 ± 0.1
		Phosphatidylserine	0	0		0
Amphipods	*Themisto abyssorum*	**Wax ester**	32.3 ± 3.2 (3)	37.9 ± 10.7 (3)	17.5 ± 5.9 (3)	33.1 ± 11.3 (3)
		Triacylglycerol*	25.6 ± 17.7	25.1 ± 12.4	76.3 ± 6.5	52.9 ± 11.2
		Sterol	3.8 ± 1.5	3.5 ± 0.9	0.6 ± 0.4	0.7 ± 1.1
		Fatty alcohol	1.6 ± 0.8	1.0 ± 0.9	0.3 ± 0.2	0
		Free fatty acid	7.8 ± 4.6	4.3 ± 3.8	0.4 ± 0.3	0.6 ± 1.0
		Phosphatidylcholine	15.7 ± 4.8	13.3 ± 1.1	3.3 ± 1.1	5.1 ± 0.4
		Phosphatidylethanolamine	9.3 ± 2.7	6.9 ± 0.7	1.6 ± 0.3	5.0 ± 2.6
		Phosphatidylinositol	1.6 ± 1.8	1.9 ± 1.8	0.1 ± 0.1	0.1 ± 0.1
		Phosphatidylserine	2.2 ± 3.0	5.4 ± 0.3	0	0.1 ± 0.1
	Themisto libellula	**Wax ester**	44.5 ± 7.1 (3)	35.9 ± 3.4 (2)	19.0 ± 8.2 (4)	33.9 ± 18.8 (3)
		Triacylglycerol*	6.3 ± 8.3	21.4 ± 14.9	35.1 ± 14.7	39.5 ± 18.5
		Sterol	6.5 ± 4.7	2.1 ± 0.4	1.7 ± 0.5	1.7 ± 2.0
		Fatty alcohol	0	1.5 ± 0.2	2.1 ± 3.0	0.2 ± 0.3
		Free fatty acid	7.2 ± 1.0	4.2 ± 3.2	1.3 ± 0.2	2.8 ± 3.9
		Phosphatidylcholine	22.3 ± 6.5	9.7 ± 3.3	17.7 ± 3.7	12.5 ± 13.1
		Phosphatidylethanolamine	11.8 ± 2.1	15.0 ± 9.5	12.6 ± 3.5	6.5 ± 6.9
		Phosphatidylinositol	1.3 ± 1.2	1.7 ± 0.5	1.1 ± 1.5	1.0 ± 1.7
		Phosphatidylserine	0	8.4 ± 8.0	2.5 ± 1.8	0.9 ± 0.7
Pteropods	*Clione limacina*	**Wax ester**	0.1 ± 0.2 (3)	0 (3)	0.3 ± 0.6 (3)	0 (3)
		Triacylglycerol*	62.5 ± 21.8	41.6 ± 22.5	76.3 ± 11.0	57.6 ± 19.7
		Sterol	5.6 ± 3.0	9.5 ± 3.5	0.8 ± 1.1	4.9 ± 3.0
		Fatty alcohol	0.6 ± 1.1	0.8 ± 1.3	0	7.7 ± 4.6
		Free fatty acid	4.5 ± 5.9	1.5 ± 2.7	1.1 ± 0.7	16.1 ± 11.2
		Phosphatidylcholine	16.2 ± 8.8	28.3 ± 11.0	9.2 ± 5.8	7.7 ± 2.8
		Phosphatidylethanolamine	9.1 ± 6.2	15.7 ± 10.9	3.5 ± 3.6	5.6 ± 1.2
		Phosphatidylinositol	0	0	1.0 ± 1.0	0
		Phosphatidylserine	1.2 ± 1.4	2.7 ± 4.6	0	0.4 ± 0.6
Chaetognaths	*Parasagitta elegans*	**Wax ester**	–	–	27.6 ± 46.7 (3)	25.5 ± 21.6 (3)
		Triacylglycerol*			2.0 ± 2.8	1.0 ± 0.6
		Sterol			2.3 ± 1.9	10.0 ± 13.6
		Fatty alcohol			0.1 ± 0.1	1.5 ± 1.9

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Table A2 (*continued*)

Taxonomic group	Zooplankton taxa	Lipid class	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		Free fatty acid			5.8 ± 3.8	11.5 ± 7.1
		Phosphatidylcholine			48.3 ± 35.7	33.9 ± 24.8
		Phosphatidylethanolamine			8.0 ± 5.3	10.8 ± 3.9
		Phosphatidylinositol			3.7 ± 1.8	1.9 ± 1.6
		Phosphatidylserine			0	0.6 ± 1.0
	Parasagitta spp.	**Wax ester**	28.7 ± 40.6 (2)	57.5 ± 13.0 (3)	–	–
		Triacylglycerol*	1.8 ± 1.3	1.3 ± 0.4		
		Sterol	2.5 ± 1.3	2.0 ± 0.5		
		Fatty alcohol	3.0 ± 4.2	3.3 ± 1.2		
		Free fatty acid	14.2 ± 0.2	6.6 ± 1.4		
		Phosphatidylcholine	36.2 ± 38.2	21.1 ± 12.6		
		Phosphatidylethanolamine	11.5 ± 6.5	6.9 ± 2.4		
		Phosphatidylinositol	1.7 ± 0.9	1.4 ± 1.3		
		Phosphatidylserine	0.6 ± 0.8	0		
		Lyso-Phosphatidylcholine	0	0		
	Pseudosagitta maxima	**Wax ester**	0 (2)	0.2 ± 0.4 (3)	0.8 ± 1.1 (2)	–
		Triacylglycerol*	0	1.4 ± 1.7	12.8 ± 6.0	
		Sterol	6.2 ± 1.8	6.4 ± 3.3	4.1 ± 1.7	
		Fatty alcohol	0	0	0	
		Free fatty acid	6.2 ± 1.9	11.7 ± 3.5	10.2 ± 5.0	
		Phosphatidylcholine	56.3 ± 0.4	50.1 ± 5.0	48.3 ± 0.9	
		Phosphatidylethanolamine	26.1 ± 0.4	20.9 ± 5.2	16.2 ± 2.9	
		Phosphatidylinositol	5.3 ± 0.1	6.4 ± 1.6	5.5 ± 2.4	
		Phosphatidylserine	0	2.9 ± 2.7	0	

Bold: neutral (storage) lipids, *italics: polar (membrane) lipids*.

Table A3
Relative proportions (%) of the most abundant fatty acids in the pelagic zooplankton during all four seasons. '-' no data available; * includes 20:1(*n*-11), 20:1(*n*-9), 20:1(*n*-7);** includes 22:1(*n*-11), 22:1(*n*-9), 22:1(*n*-7).

Taxonomic group	Zooplankton taxa	Fatty acid	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
Copepods	*Calanus glacialis*	14:0	7.7 ± 3.0 (8)	7.9 ± 0.9 (6)	8.6 ± 2.8 (14)	9.8 ± 1.6 (9)
		16:0	5.5 ± 0.3	8.3 ± 1.1	6.9 ± 1.0	6.1 ± 0.7
		16:1(*n*-7)	26.5 ± 3.8	14.5 ± 2.7	15.9 ± 3.5	16.9 ± 7.1
		16:4(*n*-1)	3.7 ± 0.4	0	2.7 ± 0.8	0.7 ± 0.6
		18:0	0.1 ± 0.1	0.6 ± 0.5	0.4 ± 0.1	0.5 ± 0.3
		18:1(*n*-9)	4.0 ± 0.3	3.0 ± 0.7	4.3 ± 1.3	3.5 ± 0.8
		18:1(*n*-7)	1.2 ± 0.1	1.7 ± 0.3	0.9 ± 0.1	0.9 ± 0.1
		18:4(n-3)	0.3 ± 0.4	0.4 ± 0.5	6.8 ± 1.8	3.6 ± 3.3
		Sum 20:1*	19.9 ± 2.9	17.2 ± 2.3	15.9 ± 1.8	23.3 ± 5.8
		20:5(*n*-3)	8.9 ± 1.3	14.4 ± 2.6	15.1 ± 2.6	9.5 ± 2.3
		Sum 22:1**	11.6 ± 2.3	10.5 ± 1.0	8.2 ± 1.3	10.4 ± 1.3
		22:6(n-3)	5.2 ± 1.0	16.3 ± 2.7	4.5 ± 0.7	5.9 ± 3.7
	Calanus hyperboreus	14:0	3.9 ± 0.5 (7)	3.8 ± 0.3 (8)	3.3 ± 0.8 (16)	3.9 ± 0.4 (10)
		16:0	3.6 ± 0.8	4.0 ± 1.0	3.2 ± 0.4	3.2 ± 0.3
		16:1(*n*-7)	18.6 ± 5.9	17.2 ± 8.1	14.7 ± 6.0	12.7 ± 4.4
		16:4(*n*-1)	1.2 ± 0.4	2.8 ± 2.5	2.9 ± 0.7	2.1 ± 0.8
		18:0	0.1 ± 0.2	0.3 ± 0.3	0.3 ± 0	0.2 ± 0.1
		18:1(*n*-9)	3.1 ± 0.3	2.6 ± 0.3	2.9 ± 0.6	2.9 ± 0.5
		18:1(*n*-7)	1.4 ± 0.2	1.1 ± 0.2	1.1 ± 0.3	1.0 ± 0.2
		18:4(n-3)	3.5 ± 1.6	2.0 ± 1.2	11.1 ± 3.9	10.2 ± 5.6
		Sum 20:1*	16.7 ± 1.8	15.9 ± 1.3	13.3 ± 1.3	16.5 ± 3.1
		20:5(*n*-3)	16.4 ± 1.8	18.8 ± 4.0	16.4 ± 4.8	14.0 ± 2.8
		Sum 22:1**	15.3 ± 2.7	14.0 ± 2.7	12.5 ± 2.6	15.2 ± 2.1
		22:6(n-3)	7.5 ± 2.6	8.1 ± 2.1	6.4 ± 1.4	6.0 ± 1.3
	Paraeuchaeta glacialis	14:0	5.4 (1)	–	1.4 (1)	0.5 ± 0.5 (3)
		16:0	5.5		1.9	1.3 ± 0.2
		16:1(*n*-7)	16.9		23.7	14.7 ± 2.2
		16:4(*n*-1)	0.9		0.8	0.4 ± 0.3
		18:0	0		0.3	0.2 ± 0.2
		18:1(*n*-9)	12.9		30.4	31.5 ± 10.9
		18:1(*n*-7)	1.7		1.5	0.9 ± 0.1
		18:4(n-3)	1.9		2.4	3.7 ± 0.1
		Sum 20:1*	17.3		8.4	7.6 ± 5.5

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Table A3 (*continued*)

Taxonomic group	Zooplankton taxa	Fatty acid	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		20:5(*n*-3)	7.1		5.7	7.7 ± 2.0
		Sum 22:1**	15.8		5.2	8.4 ± 7.4
		22:6(n-3)	8.3		5.2	12.3 ± 3.2
	Paraeuchaeta norvegica	14:0	3.0 ± 0.1 (2)	–	1.0 ± 0.1 (2)	0.7 ± 0.3 (5)
		16:0	3.9 ± 0.6		1.6 ± 0.2	1.3 ± 0.1
		16:1(*n*-7)	18.1 ± 1.0		19.2 ± 0.7	15.0 ± 1.1
		16:4(*n*-1)	1.2 ± 0.1		0.8 ± 0.1	0.6 ± 0.1
		18:0	0		0.3 ± 0	0.3 ± 0.3
		18:1(*n*-9)	21.3 ± 5.2		25.5 ± 1.4	27.1 ± 3.1
		18:1(*n*-7)	1.3 ± 0.2		1.1 ± 0.1	0.8 ± 0.1
		18:4(n-3)	1.5 ± 0.1		1.9 ± 0.2	5.4 ± 0.7
		Sum 20:1*	13.8 ± 4.5		9.8 ± 0.2	8.0 ± 2.6
		20:5(*n*-3)	5.0 ± 0.1		6.7 ± 0.4	9.6 ± 2.0
		Sum 22:1**	16.8 ± 2.3		13.4 ± 0.8	9.2 ± 3.8
		22:6(n-3)	6.3 ± 0.3		8.1 ± 0.8	11.8 ± 3.3
	Paraeuchaeta spp.	14:0	1.3 ± 0.3 (3)	1.6 ± 0.8 (9)	–	–
		16:0	1.6 ± 0.5	2.1 ± 0.5		
		16:1(*n*-7)	19.6 ± 1.9	17.7 ± 2.8		
		16:4(*n*-1)	1.7 ± 0.3	0.3 ± 0.2		
		18:0	0	0.5 ± 0.2		
		18:1(*n*-9)	24.6 ± 3.1	23.5 ± 4.1		
		18:1(*n*-7)	1.0 ± 0.1	1.1 ± 0.2		
		18:4(n-3)	2.2 ± 0.7	1.3 ± 0.5		
		Sum 20:1*	12.2 ± 1.0	14.1 ± 1.9		
		20:5(*n*-3)	6.5 ± 0.7	4.8 ± 0.7		
		Sum 22:1**	13.9 ± 3.1	18.2 ± 5.7		
		22:6(n-3)	7.6 ± 0.2	6.8 ± 1.2		
Krill	*Meganyctiphanes norvegica*	14:0	4.7 ± 0.6 (4)	2.2 ± 1.2 (2)	5.9 ± 1.0 (4)	5.9 ± 0.9 (5)
		16:0	12.1 ± 3.4	15.9 ± 4.1	15.6 ± 2.6	17.0 ± 1.6
		16:1(*n*-7)	6.6 ± 2.2	5.6 ± 0.8	7.4 ± 0.9	6.0 ± 2.2
		16:4(*n*-1)	0 ± 0.1	0.2 ± 0.3	0.4 ± 0.1	0.1 ± 0.1
		18:0	1.3 ± 0.9	1.3 ± 0.7	1.4 ± 0.4	1.8 ± 0.2
		18:1(*n*-9)	10.0 ± 3.5	11.5 ± 2.5	10.3 ± 1.1	14.7 ± 1.9
		18:1(*n*-7)	4.2 ± 1.0	5.8 ± 2.5	4.3 ± 1.0	4.8 ± 1.3
		18:4(n-3)	1.2 ± 0.7	1.1 ± 0.4	2.2 ± 0.6	2.2 ± 0.4
		Sum 20:1*	20.1 ± 5.6	5.3 ± 6.0	13.2 ± 4.4	9.7 ± 2.8
		20:5(*n*-3)	8.6 ± 1.8	21.7 ± 5.8	9.8 ± 2.1	9.4 ± 1.3
		Sum 22:1**	13.5 ± 5.6	4.9 ± 6.9	13.5 ± 2.9	6.5 ± 1.9
		22:6(n-3)	10.1 ± 1.8	17.8 ± 1.3	7.4 ± 0.7	11.1 ± 1.7
	Thysanoessa inermis	14:0	–	–	2.2 ± 0.3 (8)	–
		16:0			20.0 ± 1.2	
		16:1(*n*-7)			18.2 ± 4.3	
		16:4(*n*-1)			0.4 ± 0.1	
		18:0			1.6 ± 0.4	
		18:1(*n*-9)			18.9 ± 1.5	
		18:1(*n*-7)			8.6 ± 0.4	
		18:4(n-3)			2.7 ± 0.7	
		Sum 20:1*			1.9 ± 0.9	
		20:5(*n*-3)			14.0 ± 0.7	
		Sum 22:1**			0.8 ± 0.6	
		22:6(n-3)			4.2 ± 1.3	
	Thysanoessa longicaudata	14:0	–	–	3.6 ± 0.3 (5)	–
		16:0			30.7 ± 1.8	
		16:1(*n*-7)			11.0 ± 3.6	
		16:4(*n*-1)			0.2 ± 0.1	
		18:0			2.0 ± 0.2	
		18:1(*n*-9)			16.0 ± 2.1	
		18:1(*n*-7)			7.1 ± 0.5	
		18:4(n-3)			0.9 ± 0.2	
		Sum 20:1*			2.5 ± 1.1	
		20:5(*n*-3)			12.6 ± 1.8	
		Sum 22:1**			2.1 ± 0.3	
		22:6(n-3)			5.2 ± 0.7	
	Thysanoessa spp.	14:0	3.1 ± 0.7 (7)	1.9 ± 0.6 (9)	–	2.7 ± 0.7 (9)
		16:0	24.0 ± 3.8	21.6 ± 3.4		22.8 ± 5.6

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Table A3 (*continued*)

Taxonomic group	Zooplankton taxa	Fatty acid	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		16:1(*n*-7)	10.6 ± 5.4	7.5 ± 6.6		11.6 ± 3.8
		16:4(*n*-1)	0.1 ± 0.2	0.3 ± 0.2		0.3 ± 0.2
		18:0	1.6 ± 0.3	1.7 ± 0.4		1.7 ± 0.3
		18:1(*n*-9)	16.7 ± 3.5	15.8 ± 3.6		20.1 ± 1.7
		18:1(*n*-7)	7.2 ± 1.5	7.1 ± 1.6		8.1 ± 1.3
		18:4(n-3)	1.2 ± 0.9	1.7 ± 1.1		2.4 ± 1.0
		Sum 20:1*	3.1 ± 1.6	2.1 ± 0.9		3.1 ± 1.7
		20:5(*n*-3)	15.5 ± 3.2	21.1 ± 2.5		13.9 ± 2.1
		Sum 22:1**	2.3 ± 1.0	1.0 ± 0.9		1.7 ± 0.9
		22:6(n-3)	9.4 ± 4.4	13.8 ± 6.7		5.4 ± 1.4
Amphipods	*Themisto abyssorum*	14:0	4.0 ± 0.9 (7)	4.9 ± 1.0 (5)	4.4 ± 0.2 (4)	5.1 ± 0.7 (6)
		16:0	10.2 ± 0.8	9.3 ± 1.1	9.2 ± 2.1	11.3 ± 0.8
		16:1(*n*-7)	7.8 ± 1.5	7.2 ± 2.8	7.4 ± 0.9	5.9 ± 2.5
		16:4(*n*-1)	0.1 ± 0.2	0	1.3 ± 0.7	0.3 ± 0.2
		18:0	1.5 ± 0.2	1.3 ± 0.3	0.8 ± 0.2	1.7 ± 0.7
		18:1(*n*-9)	13.5 ± 1.5	13.7 ± 3.2	8.1 ± 2.2	14.4 ± 3.7
		18:1(*n*-7)	2.4 ± 0.2	2.0 ± 0.2	1.6 ± 0.3	2.2 ± 0.3
		18:4(n-3)	1.6 ± 0.8	1.5 ± 1.0	7.9 ± 2.2	3.0 ± 1.5
		Sum 20:1*	16.9 ± 4.3	19.4 ± 3.6	12.4 ± 2.2	13.9 ± 3.1
		20:5(*n*-3)	13.2 ± 2.4	11.5 ± 2.3	17.5 ± 1.2	13.3 ± 2.0
		Sum 22:1**	8.1 ± 1.5	9.9 ± 1.2	7.5 ± 1.6	7.0 ± 1.8
		22:6(n-3)	14.6 ± 3.0	13.6 ± 2.6	10.8 ± 2.0	10.9 ± 2.0
	Themisto libellula	14:0	3.8 ± 1.2 (4)	5.0 ± 2.4 (3)	3.9 ± 0.8 (6)	4.2 ± 1.9 (10)
		16:0	13.1 ± 4.6	10.4 ± 2.5	14.5 ± 0.9	9.7 ± 2.1
		16:1(*n*-7)	6.6 ± 0.9	7.5 ± 3.7	6.5 ± 0.7	9.5 ± 3.2
		16:4(*n*-1)	0.3 ± 0.4	1.0 ± 0.6	0.3 ± 0.3	0.5 ± 0.2
		18:0	1.4 ± 0.3	0.9 ± 0.5	0.9 ± 0.1	0.5 ± 0.3
		18:1(*n*-9)	14.3 ± 4.1	10.0 ± 2.9	9.9 ± 1.4	11.7 ± 3.9
		18:1(*n*-7)	2.6 ± 0.9	2.5 ± 0.7	2.9 ± 0.5	2.5 ± 0.9
		18:4(n-3)	1.6 ± 1.4	0.7 ± 0.5	4.9 ± 1.8	6.1 ± 4.2
		Sum 20:1*	12.3 ± 5.0	21.1 ± 7.1	8.1 ± 1.6	19.5 ± 4.5
		20:5(*n*-3)	13.5 ± 2.2	10.6 ± 1.9	16.9 ± 1.2	9.4 ± 3.0
		Sum 22:1**	6.7 ± 3.5	10.0 ± 3.8	2.5 ± 0.6	8.6 ± 4.5
		22:6(n-3)	18.3 ± 3.0	14.6 ± 8.0	19.3 ± 1.4	8.1 ± 3.7
Pteropods	*Clione limacina*	14:0	3.5 ± 1.3 (5)	3.4 ± 1.1 (6)	3.7 ± 3.0 (6)	3.9 ± 2.3 (5)
		16:0	15.1 ± 3.6	12.4 ± 1.3	13.1 ± 2.2	16.3 ± 5.7
		16:1(*n*-7)	7.3 ± 2.3	8.0 ± 2.1	9.1 ± 3.9	14.8 ± 2.1
		16:4(*n*-1)	0	0	0.1 ± 0.1	0
		18:0	2.8 ± 0.8	1.9 ± 0.3	2.1 ± 0.9	1.6 ± 0.4
		18:1(*n*-9)	3.7 ± 1.4	3.2 ± 0.9	3.5 ± 0.9	4.6 ± 0.5
		18:1(*n*-7)	3.2 ± 1.3	3.1 ± 1.1	4.2 ± 1.6	5.3 ± 0.5
		18:4(n-3)	4.6 ± 2.6	4.7 ± 2.5	3.4 ± 2.6	1.3 ± 0.5
		Sum 20:1*	6.2 ± 1.7	5.6 ± 0.9	4.8 ± 1.2	6.3 ± 1.8
		20:5(*n*-3)	12.0 ± 3.6	10.9 ± 1.9	13.6 ± 4.4	6.0 ± 3.3
		Sum 22:1**	0.1 ± 0.2	0	0.2 ± 0.2	0
		22:6(n-3)	17.5 ± 6.5	18.2 ± 3.3	15.3 ± 5.2	7.7 ± 6.3
Chaetognaths	*Parasagitta elegans*	14:0	–	–	3.4 ± 1.3 (6)	2.8 ± 1.3 (13)
		16:0			12.1 ± 2.3	8.3 ± 3.5
		16:1(*n*-7)			12.3 ± 2.2	10.0 ± 2.0
		16:4(*n*-1)			0.6 ± 0.8	0.5 ± 0.8
		18:0			0.9 ± 0.2	1.0 ± 0.3
		18:1(*n*-9)			6.5 ± 1.3	5.8 ± 1.7
		18:1(*n*-7)			2.2 ± 0.6	1.5 ± 0.6
		18:4(n-3)			4.2 ± 2.2	3.9 ± 2.9
		Sum 20:1*			8.7 ± 5.4	15.9 ± 4.9
		20:5(*n*-3)			15.8 ± 1.3	16.0 ± 4.9
		Sum 22:1**			4.1 ± 1.9	9.4 ± 5.1
		22:6(n-3)			13.7 ± 3.0	15.8 ± 5.2
	Parasagitta spp.	14:0	3.8 ± 1.0 (4)	5.4 ± 2.6 (9)	–	–
		16:0	8.0 ± 2.8	6.5 ± 1.9		
		16:1(*n*-7)	10.1 ± 1.9	9.2 ± 1.3		
		16:4(*n*-1)	0.3 ± 0.4	0.4 ± 0.3		
		18:0	1.2 ± 0.3	1.1 ± 0.3		
		18:1(*n*-9)	7.1 ± 0.6	6.1 ± 0.9		
		18:1(*n*-7)	1.3 ± 0.5	0.9 ± 0.2		
		18:4(n-3)	3.1 ± 2.3	3.9 ± 2.5		

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Table A3 (*continued*)

Taxonomic group	Zooplankton taxa	Fatty acid	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		Sum 20:1*	13.1 ± 2.5	15.0 ± 2.2		
		20:5(*n*-3)	12.8 ± 1.1	13.0 ± 2.6		
		Sum 22:1**	12.4 ± 4.5	15.9 ± 4.4		
		22:6(n-3)	16.8 ± 6.3	13.9 ± 5.3		
	Pseudosagitta maxima	14:0	0.7 ± 0 (2)	1.1 ± 0.4 (3)	1.7 ± 0.1 (2)	–
		16:0	11.5 ± 1.4	9.7 ± 1.7	12.9 ± 0.2	
		16:1(*n*-7)	10.0 ± 0.3	11.8 ± 4.3	10.2 ± 0.7	
		16:4(*n*-1)	0	0	0.2 ± 0.1	
		18:0	2.9 ± 0.1	2.6 ± 0.2	2.3 ± 0.1	
		18:1(*n*-9)	7.7 ± 3.7	8.4 ± 1.1	5.5 ± 1.7	
		18:1(*n*-7)	4.1 ± 0.6	3.8 ± 1.4	4.6 ± 1.3	
		18:4(n-3)	0	0.5 ± 0.8	2.5 ± 0.8	
		Sum 20:1*	8.9 ± 1.0	11.3 ± 4.9	11.2 ± 0.7	
		20:5(*n*-3)	14.1 ± 1.6	12.2 ± 2.0	12.2 ± 0.2	
		Sum 22:1**	4.4 ± 0.1	4.9 ± 6.9	8.3 ± 0.9	
		22:6(n-3)	28.2 ± 2.4	25.3 ± 5.5	15.9 ± 0.5	

Bold: diatom-associated FAs, *italics: dinoflagellate-associated FAs*

Table A4
Ratios of fatty acids (FAs; mean ± SD) in the pelagic zooplankton during all four seasons. '-' no data available. FA ratios > 1 indicate the dominance of diatom-over dinoflagellate-associated fatty acids in the zooplankton.

Species	Season	*n*	16:1(*n*-7)/16:0	20:5(*n*-3)/22:6(*n*-3)
Calanus glacialis	Late winter	8	4.8 ± 0.7	1.8 ± 0.5
	Spring	6	1.8 ± 0.6	0.9 ± 0.9
	Summer	14	2.4 ± 0.6	3.4 ± 1.0
	Late autumn	9	2.9 ± 1.3	2.0 ± 0.9
	Mean		**2.9 ± 1.4**	**2.3 ± 1.2**
Calanus hyperboreus	Late winter	7	5.5 ± 2.1	2.3 ± 0.6
	Spring	8	4.7 ± 2.6	2.4 ± 0.7
	Summer	16	4.6 ± 1.8	2.7 ± 1.2
	Late autumn	10	4.0 ± 1.3	2.5 ± 0.9
	Mean		**4.6 ± 1.9**	**2.5 ± 0.9**
Paraeuchaeta spp.	Late winter	6	8.6 ± 5.4	0.8 ± 0.1
	Spring	8	9.2 ± 3.6	0.7 ± 0.1
	Summer	3	12.1 ± 1.0	0.9 ± 0.2
	Late autumn	8	11.8 ± 1.6	0.8 ± 0.2
	Mean		**10.2 ± 3.6**	**0.8 ± 0.1**
Meganyctiphanes norvegica	Late winter	4	0.6 ± 0.3	0.8 ± 0.1
	Spring	2	0.4 ± 0.1	1.2 ± 0.4
	Summer	4	0.5 ± 0.1	1.3 ± 0.3
	Late autumn	5	0.3 ± 0.1	0.9 ± 0.3
	Mean		**0.5 ± 0.2**	**1.0 ± 0.3**
Thysanoessa spp.	Late winter	7	0.5 ± 0.3	1.9 ± 0.7
	Spring	9	0.4 ± 0.4	1.8 ± 0.7
	Summer	13	0.7 ± 0.9	3.2 ± 1.0
	Late autumn	9	0.6 ± 0.2	2.8 ± 1.1
	Mean		**0.5 ± 0.3**	**2.5 ± 1.1**
Themisto abyssorum	Late winter	7	0.8 ± 0.2	0.9 ± 0.1
	Spring	5	0.8 ± 0.4	0.8 ± 0.1
	Summer	4	0.9 ± 0.3	1.7 ± 0.5
	Late autumn	6	0.5 ± 0.2	1.2 ± 0.1
	Mean		**0.7 ± 0.3**	**1.1 ± 0.4**
Themisto libellula	Late winter	4	0.6 ± 0.2	0.7 ± 0.1
	Spring	3	0.8 ± 0.5	0.8 ± 0.2
	Summer	6	0.5 ± 0.1	0.9 ± 0.1
	Late autumn	10	1.0 ± 0.3	1.2 ± 0.3
	Mean		**0.7 ± 0.4**	**1.0 ± 0.3**
Clione limacina	Late winter	5	0.5 ± 0.2	0.7 ± 0.1

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Table A4 (*continued*)

Species	Season	*n*	16:1(*n*-7)/16:0	20:5(*n*-3)/22:6(*n*-3)
	Spring	6	0.7 ± 0.2	0.6 ± 0.2
	Summer	6	0.7 ± 0.4	0.9 ± 0.1
	Late autumn	3	1.0 ± 0.3	1.0 ± 0.3
	Mean		**0.7 ± 0.3**	**0.8 ± 0.2**
Parasagitta spp.	Late winter	4	1.5 ± 0.8	0.9 ± 0.4
	Spring	9	1.5 ± 0.5	1.0 ± 0.3
	Summer	6	1.1 ± 0.5	1.2 ± 0.4
	Late autumn	13	1.6 ± 1.2	1.2 ± 0.9
	Mean		**1.5 ± 0.9**	**1.1 ± 0.7**
Pseudosagitta maxima	Late winter	2	0.9 ± 0.1	0.5 ± 0.1
	Spring	3	1.2 ± 0.4	0.5 ± 0.1
	Summer	2	0.8 ± 0.1	0.8 ± 0.1
	Late autumn	–	–	–
	Mean		**1.0 ± 0.3**	**0.6 ± 0.1**

Table A5
Concentrations (ng g^{-1} dry weight) of sympagic (IP_{25}, $IPSO_{25}$) and pelagic (HBI III, HBI IV) highly branched isoprenoids (HBIs) in the pelagic zooplankton during all four seasons. Numbers in brackets represent sample size. nd = not detected, '-' no data available.

			Q1 (late winter)	Q2 (spring)	Q3 (summer)	Q4 (late autumn)
Taxonomic group	**Zooplankton taxa**	**HBI (ng g^{-1} dry weight)**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**	**Mean ± SD (*n*)**
Copepods	*Calanus glacialis*	**IP_{25}**	nd (4)	nd (2)	nd (4)	nd (5)
		$IPSO_{25}$	nd	nd	nd	nd
		HBI III	3.3 ± 3.9	nd	1.3 ± 0.9	0.1 ± 0.3
		HBI IV	1.5 ± 2.9	nd	0.7 ± 0.8	nd
	Calanus hyperboreus	**IP_{25}**	nd (3)	nd (3)	nd (6)	nd (2)
		$IPSO_{25}$	nd	nd	nd	nd
		HBI III	nd	36.3 ± 63.0	2.3 ± 4.1	0.4 ± 0.6
		HBI IV	nd	8.5 ± 14.7	0.7 ± 1.7	nd
	Paraeuchaeta glacialis	**IP_{25}**	nd (1)	–	–	nd (4)
		$IPSO_{25}$	nd			nd
		HBI III	nd			0.7 ± 0.7
		HBI IV	nd			0.4 ± 0.4
	Paraeuchaeta norvegica	**IP_{25}**	nd (1)	–	nd (1)	–
		$IPSO_{25}$	nd		nd	
		HBI III	nd		1.3	
		HBI IV	nd		1.5	
	Paraeuchaeta spp.	**IP_{25}**	nd (2)	nd (4)	–	–
		$IPSO_{25}$	nd	nd		
		HBI III	nd	5.3 ± 4.5		
		HBI IV	nd	nd		
Krill	*Meganyctiphanes norvegica*	**IP_{25}**	nd (3)	nd (2)	nd (2)	nd (2)
		$IPSO_{25}$	nd	36.2 ± 51.2	2.8 ± 4.0	nd
		HBI III	21.5 ± 19.7	473.5 ± 449.9	37.8 ± 50.1	7.3 ± 3.9
		HBI IV	6.3 ± 6.1	150.1 ± 131. 1	13.9 ± 18.9	4.0 ± 3.2
	Thysanoessa inermis	**IP_{25}**	–	–	0 (3)	–
		$IPSO_{25}$			2.1 ± 1.9	
		HBI III			1.6 ± 0.2	
		HBI IV			1.6 ± 0.2	
	Thysanoessa spp.	**IP_{25}**	0 (8)	0 (7)	0 (2)	0 (4)
		$IPSO_{25}$	0	0	0	1.9 ± 0.6
		HBI III	6.3 ± 8.4	92.5 ± 65.3	20.5 ± 16.6	8.5 ± 13.8
		HBI IV	3.0 ± 3.0	37.3 ± 26.7	15.8 ± 8.3	8.6 ± 14.8
Amphipods	*Themisto abyssorum*	**IP_{25}**	0 (3)	0 (5)	0.6 ± 1.0 (3)	0.6 ± 1.0 (3)
		$IPSO_{25}$	0	0	7.5 ± 5.1	14.1 ± 8.4
		HBI III	0	8.7 ± 6.7	1.0 ± 1.0	2.2 ± 1.4

(*continued on next page*)

Table A5 (*continued*)

Taxonomic group	Zooplankton taxa	HBI (ng g^{-1} dry weight)	Q1 (late winter) Mean ± SD (*n*)	Q2 (spring) Mean ± SD (*n*)	Q3 (summer) Mean ± SD (*n*)	Q4 (late autumn) Mean ± SD (*n*)
		HBI IV	0	0.9 ± 2.1	0.6 ± 0.6	1.3 ± 0.9
	Themisto libellula	**IP_{25}**	0 (3)	0 (3)	0 (2)	0.7 ± 0.6 (5)
		$IPSO_{25}$	0	0	3.8 ± 5.3	9.9 ± 6.9
		HBI III	0	16.9 ± 10.8	4.4 ± 3.3	1.9 ± 1.0
		HBI IV	0	2.8 ± 4.9	2.3 ± 2.2	2.0 ± 1.3
Pteropods	*Clione limacina*	**IP_{25}**	0 (2)	0 (4)	0 (2)	0 (2)
		$IPSO_{25}$	0	0	3.9 ± 2.7	0
		HBI III	0	0	0	0
		HBI IV	0	0	0	0
Chaetognaths	*Parasagitta elegans*	**IP_{25}**	–	–	0 (3)	0 (6)
		$IPSO_{25}$			0	0
		HBI III			1.1 ± 1.6	0
		HBI IV			0	0
	Parasagitta spp.	**IP_{25}**	0 (2)	0 (6)	–	–
		$IPSO_{25}$	0	0		
		HBI III	0	0.7 ± 1.7		
		HBI IV	0	0		
	Pseudosagitta maxima	**IP_{25}**	0 (1)	0 (2)	0 (1)	–
		$IPSO_{25}$	0	0	0	
		HBI III	0	0	0	
		HBI IV	0	0	0	

Bold: sea ice-associated (sympagic) HBIs, *italics: pelagic/MIZ HBIs*.

Data availability

Data will be made available on request.

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