Multiple Trophic Markers Trace Dietary Carbon Sources in Barents Sea Zooplankton During Late Summer

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We investigated diets of 24 Barents Sea zooplankton taxa to understand pelagic food-web processes during late summer, including the importance of sea ice algae-produced carbon. This was achieved by combining insights derived from multiple and complementary trophic marker approaches to construct individual aspects of feeding. Specifically, we determined proportions of algal-produced fatty acids (FAs) to reflect the reliance on diatom- versus dinoflagellate-derived carbon, highly branched isoprenoid (HBI) lipids that distinguish between ice-associated and pelagic carbon sources, and sterols to indicate the degree of carnivory. Copepods had the strongest diatom signal based on FAs, while a lack of sea ice algae-associated HBIs (IP_{25}, $IPSO_{25}$) suggested that they fed on pelagic rather than ice-associated diatoms. The amphipod *Themisto libellula* and the ctenophores *Beroë cucumis* and *Mertensia ovum* had a higher contribution of dinoflagellate-produced FAs. There was a high degree of carnivory in this food web, as indicated by the FA carnivory index $18:1(n-9)/18:1(n-7)$ (mean value < 1 only in the pteropod *Clione limacina*), the presence of copepod-associated FAs in most of the taxa, and the absence of algal-produced HBIs in small copepod taxa, such as *Oithona similis* and *Pseudocalanus* spp. The coherence between concentrations of HBIs and phytosterols within individuals suggested that phytosterols provide a good additional indication for algal ingestion. Sea ice algae-associated HBIs were detected in six zooplankton species (occurring in krill, amphipods, pteropods, and appendicularians), indicating an overall low to moderate contribution of ice-associated carbon from late-summer sea ice to pelagic consumption. The unexpected occurrence of ice-derived HBIs in pteropods and appendicularians, however, suggests an importance of sedimenting ice-derived material at least for filter feeders within the water column at this time of year.

Keywords: food web, Barents Sea, sea ice, carbon sources, trophic markers, fatty acids, highly branched isoprenoid (HBI) lipids, sterols

INTRODUCTION

The Barents Sea epitomizes a valuable, high latitude system undergoing rapid climatic warming. This sea comprises a highly productive Arctic shelf sea and nursery ground for commercially important fish species (Hunt et al., 2013; Fuglestad et al., 2020; Kvamsdal et al., 2020). While its southern part is influenced by Atlantic waters supporting rich fish stocks, the northern part is governed by a colder Arctic climate. During winter, most of the Barents Sea north of 75°N is covered with sea ice, while the southern part remains ice-free (Vinje and Kvambekk, 1991). Seasonal and interannual variability in ice coverage is large, however, and depends directly on the inflow of Atlantic water as well as atmospheric and oceanic circulation patterns (Schlichtholz, 2011; Årthun et al., 2012; Lind et al., 2018). Increasing atmospheric temperatures and warming Atlantic waters in recent decades have resulted in a decline in sea-ice coverage and a decrease in sea-ice import, which is particularly pronounced in the northern Barents Sea (Long and Perrie, 2017; Onarheim and Årthun, 2017; Lind et al., 2018).

Such environmental changes have major impacts on primary producers (algae) and their interactions with consumers in the Barents Sea ecosystem (Wassmann et al., 2006; Stige et al., 2019; Dalpadado et al., 2020; Dong et al., 2020). Zooplankton are key components of marine ecosystems, transferring energy from algae to fish and ultimately to top predators (Wassmann et al., 2006; Hop and Gjøsæter, 2013; Planque et al., 2014). As such, they are well adapted to the prevailing environmental conditions and the seasonality of food supply, and therefore zooplankton can be sensitive to changes in their habitat, with cascading effects along the food chain (Blanchard, 2015).

As the Barents Sea has warmed, sea-ice retreat and the longer open water season have caused a sharp increase in estimated net pelagic primary production (e.g., Ellingsen et al., 2008; Arrigo and van Dijken, 2015), which can improve feeding conditions for zooplankton and fish in phytoplankton-based food chains. However, organisms with a strong reliance on sea ice can be negatively impacted (Stige et al., 2019; Dalpadado et al., 2020). Many Arctic species, across all trophic levels, are known to have a strong association with sea ice, for feeding, reproduction and refuge (Hop et al., 2000; Poltermann, 2001; Lone et al., 2019). Shrinkage and confinement of the sea-ice habitat to more northern regions will likely have negative consequences for these species. While algae associated with the sea ice may comprise less than 25% of the annual Barents Sea primary production (Hegseth, 1998; Wassmann et al., 2006), they can nevertheless be an important carbon source for the food web both early in the season (Conover et al., 1986; Søreide et al., 2010) and later during summer (Tamelander et al., 2006; Assmy et al., 2013; Kohlbach et al., 2016, 2017b).

In the Barents Sea, pronounced interannual variability in physical conditions is reflected in large fluctuations of zooplankton composition between seasons and years (Dalpadado et al., 2003; Gluchowska et al., 2017; Stige et al., 2019). *Calanus* copepods generally dominate the zooplankton biomass in the northern regions (Aarflot et al., 2018). While *Calanus glacialis* is more abundant in Arctic shelf waters, *C. finmarchicus* dominates in the Atlantic sector of the Barents Sea, and *C. hyperboreus*

is overall less abundant than the former two species as it is predominantly found in waters deeper than the Barents Sea (Hirche, 1997). Moreover, small copepod taxa, such as *Oithona* spp., *Pseudocalanus* spp., *Microcalanus* spp. as well as krill (*Thysanoessa* spp.), amphipods (*Themisto* spp.) and pteropods (*Clione limacina* and *Limacina helicina*) can occur in high abundances (Falk-Petersen et al., 1999; Wassmann et al., 2006).

Gelatinous zooplankton have been less studied, though scientific interest in such species and their function in food-web processes has increased worldwide in recent years (Condon et al., 2012; Jaspers et al., 2015; Aubert et al., 2018). Gelatinous zooplankton, such as ctenophores, are not assumed to be a major prey item for fish, although recent studies suggest that increasing water temperatures might favor ctenophores, as they were found more frequently preyed on by cod (*Gadus morhua*) (Eriksen et al., 2018a). For these reasons, our study compared a wide suite of Arctic zooplankton species, assessing diets of the gelatinous component in a comparative context with the other species.

To study predator-prey relationships of marine organisms, different biochemical methods can be applied. Marine algae produce a number of biomolecules that are transferred along the food chain without significant changes, and can be employed as so-called trophic markers (Ruess and Müller-Navarra, 2019). Marker fatty acids (FAs) can be traced in the consumers across multiple trophic levels (Scott et al., 1999; Haug et al., 2017) and provide information on their carbon and food source preferences (Wang et al., 2015; Kohlbach et al., 2016). Furthermore, distinguishing between pelagic or ice-associated carbon can potentially be achieved by investigating the presence and distribution of certain highly branched isoprenoid (HBI) lipids biosynthesized by specific pelagic and ice-associated diatoms (Brown et al., 2017b, 2018; Schmidt et al., 2018). In contrast, sterols yield less specific dietary information, but can be used to distinguish, to some extent, phytoplankton-produced versus animal-produced carbon (Drazen et al., 2008; Ruess and Müller-Navarra, 2019). Each of these biochemical methods has strengths and weaknesses, but when applied in combination they yield different facets to feeding and are a powerful approach to study food webs (Leu et al., 2020).

Since the Barents Sea has rich fishery resources and is considered a 'climate change hotspot,' it has been the focus of a series of large-scale and long-term ecological surveys as a basis for risk assessment and the prediction of future scenarios (Johannesen et al., 2012; Eriksen et al., 2017; Prozorkevich and Sunnanå, 2017; Eriksen et al., 2018b; Arneberg et al., 2020). Elucidating the present-day variability in diets of the key zooplankton species is crucial to gain a better understanding of the impacts of climate change on the Barents Sea food-web. In this context, the Nansen Legacy Project (arvenetternansen.com) represents a Norwegian research effort to address the impact of climate change on biological, chemical and physical processes in the northern Barents Sea on a seasonal scale. As a contribution to this project, we explored the dietary carbon sources, including sea-ice algae, for Barents Sea zooplankton collected during late summer 2019 to infer food-web interactions at the base of the marine ecosystem during the late summer period. This research question was approached comprehensively by sampling at multiple stations along a south-north transect using a

multi-trophic marker approach. The results are discussed in the context of a reducing Arctic sea-ice cover.

MATERIALS AND METHODS

Sample Collection

Sampling was carried out as part of the Norwegian Nansen Legacy project during the seasonal cruise Q3 (05–27 August 2019) with RV *Kronprins Haakon* north of 76°N in the Barents Sea (**Figure 1**). During the sampling, areas represented by sampling stations P1 and P2 were ice-free, P4 was located close to the ice edge, and stations P5, P6, and P7 were ice-covered (**Figure 1**). Additional information about individual sampling stations can be found in **Supplementary Table 1**.

Samples of 24 zooplankton taxa including copepods, krill, amphipods, pteropods and gelatinous species (**Table 1**) were collected at six stations. We used MIK nets (1,200 μm with 500 μm cod end) and WP3 net (1,000 μm) for large taxa; Macroplankton trawl for mostly *Thysanoessa* spp. (multiple mesh sizes along the net, tapering to 8 mm at its end); Bongo net

(180 μm) and Multinet (180 μm) for copepods (all species); and WP2 net (90 μm) for small copepods (**Supplementary Table 1**). Samples were sorted into the lowest possible taxonomic level, and/or stage/size groups (where possible) onboard the ship and immediately frozen at −80°C in 2 mL cryovials. The three *Calanus* species were differentiated based on morphology and prosome lengths according to Kwasniewski et al. (2003). Small species/individuals were pooled by species (and by stage/size group, if applicable) in order to obtain sufficient sample material for analyses (**Table 1**).

Pelagic particulate organic matter (PPOM) was collected at the chlorophyll *a* (Chl *a*) maximum with Niskin bottles attached to a CTD rosette, which varied in depth from 14 to 73 m at the six investigated stations. Volumes from 1.2 to 2.5 L of seawater were filtered via a vacuum pump (−20 kPA) through pre-combusted (3 h, 550°C) 47 mm Whatman® GF/F filters. Ice-associated POM (IPOM) was collected at two stations by sampling ice cores using an ice corer of 9 cm interior diameter (Kovacs Enterprises, Inc., United States). The lowest 10 cm of the ice cores were melted in the dark at 4 °C without the addition of seawater, which was assumed to have a negligible effect on the
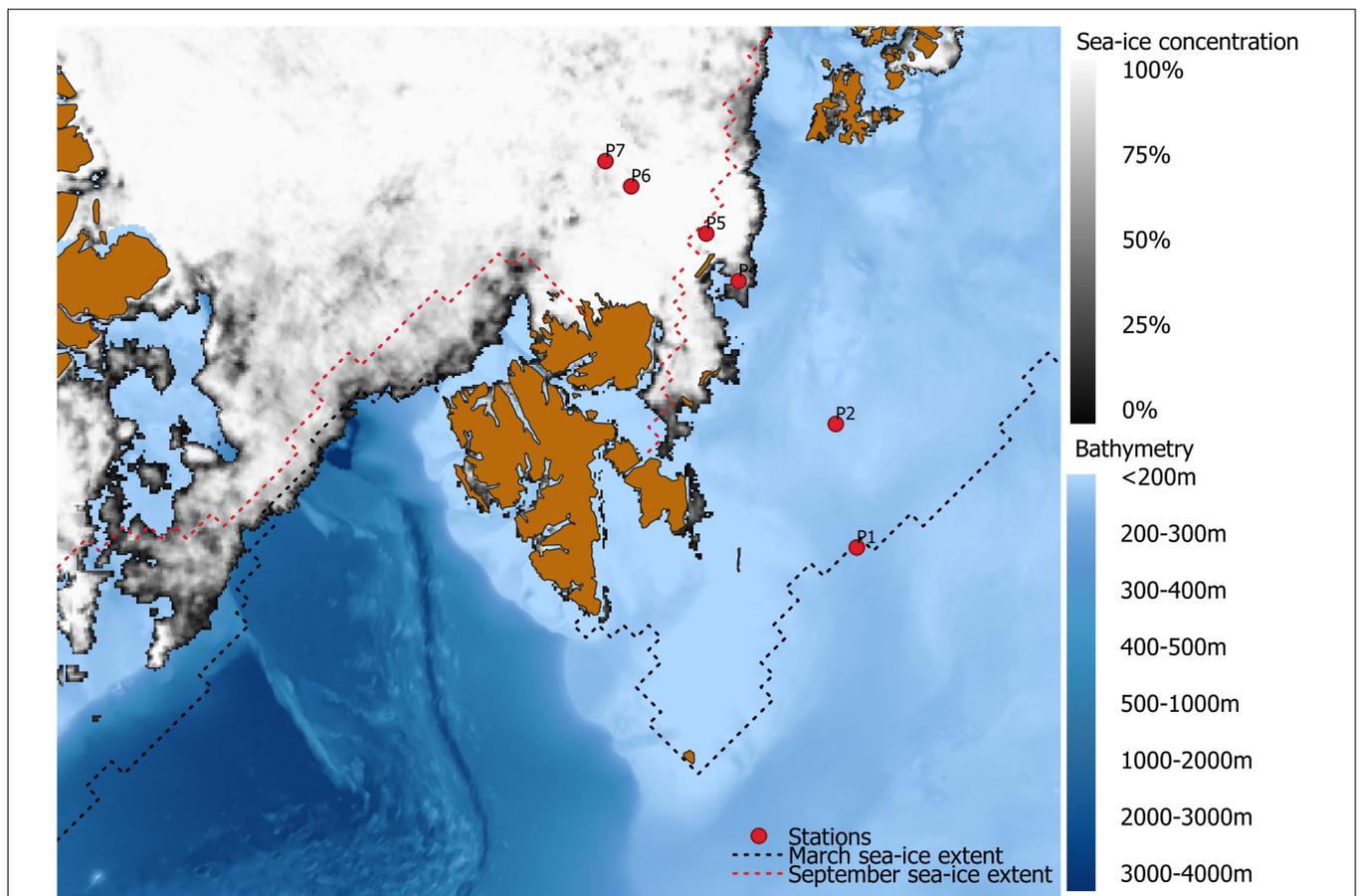
FIGURE 1 | Map showing the Nansen Legacy transect across the Barents Sea in August 2019. Sea-ice concentration (*SIC*%) along the sampling transect is shown for 15 August 2019. *SIC* data was acquired from Bremen University (https://seaice.uni-bremen.de/sea-ice-concentration/amsre-amsr2/) (Spreen et al., 2008). Maximum sea-extent occurred in March (black stippled line), minimum sea-ice extent in September 2019 (red stippled line) [acquired from National Snow and Ice Data Center; Fetterer et al. (2017)].

TABLE 1 | Overview of zooplankton taxa collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea.

Taxonomic group	Zooplankton taxa	Stage/Length group (mm)*	Ind. per sample	Dry weight/ind. (mg)**
Copepods	*Calanus finmarchicus* Gunnerus, 1770	CIV-AF	8–30	–
	Calanus glacialis Jaschnov, 1955	CIV-AF	5–31	–
	Calanus hyperboreus Krøyer, 1838	CIV-AF	4–22	3.7 (2.3–6.2)
	Metridia longa Lubbock, 1854	CV-AF	8–35	–
	Microcalanus spp.	CIV-AF	50–100	–
	Oithona similis Claus, 1866	CIII-AF	50–160	–
	Paraeuchaeta glacialis Hansen, 1886	AF	2	16.7
	Paraeuchaeta norvegica Boeck, 1972	CV-AF	4	4.9 (4.9 and 5.0)
	Pseudocalanus spp.	CIV-AF	18–50	–
Krill	*Meganyctiphanes norvegica* M. Sars, 1857	30–40	1	72.5 (31.7–123.8)
	Thysanoessa inermis Krøyer, 1846	15–20 to 25–30	3–5	36.0 (7.9–58.1)
	Thysanoessa longicaudata Krøyer, 1846	10–15	2–10	5.3 (4.5–6.1)
Amphipods	*Themisto abyssorum* Boeck, 1870	5–10 to 25–30	3–25	11.2 (0.7–17.1)
	Themisto libellula Liechtenstein, 1822	5–10 to 10–20	2–8	3.5 (1.2–6.1)
Pteropods	*Clione limacina* Phipps, 1774	5–10 to 50–60	1–5	62.6 (4.0–104.2)
	Limacina helicina Phipps, 1774	10–15	4–10	5.9 (3.6–8.3)
Cnidarians	*Bougainvillia superciliaris* L. Agassiz, 1849	5–10	8	0.7
	Catablema vesicarium A. Agassiz, 1862	20–25 to 30–40	2	10.2 (6.2 and 14.2)
Ctenophores	*Beroë cucumis* Fabricius, 1780	10–20	1–2	41.8 (8.9–101.8)
	Mertensia ovum Fabricius, 1780	10–20	1 or bulk	12.4 (9.6 and 15.1)
Chaetognaths	*Eukrohnia hamata* Möbius, 1875	20–30 to 30–40	10–15	5.0 (3.7–6.7)
	Parasagitta elegans Verrill, 1873	30–40	5–20	5.3 (2.4–8.3)
	Sagitta maxima Conant, 1896	70–80	1	59.8 (48.8 and 70.8)
Appendicularians	*Oikopleura vanhoeffeni* Lohmann, 1896	10–20	10->20	2.6 (2.5 and 2.8)

AF, adult female; CIII-CV, copepodid stages III–V.
*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 fatty acid analyses. For some samples, a bulk of individuals has been pooled, and no information on dry weight/ind. is available for these samples. For n see **Supplementary Table 3.

bulk biochemical properties of IPOM (Roukaerts et al., 2019). Samples for taxonomic analysis were melted with the addition of filtered seawater to conserve the more delicate algae, such as flagellates, during the melting process (Garrison and Buck, 1986). For each sample, 600 mL of melted ice sample was filtered through pre-combusted GF/F filters. All filters were stored at −80°C until further processing.

Lipid Classes and Fatty Acids (FAs)

Lipid classes and FAs were analyzed at the Alfred Wegener Institute, Bremerhaven, Germany. Detailed information on analytical procedure and lab equipment can be found in Kohlbach et al. (2016). Samples were freeze-dried and zooplankton dry weights were determined gravimetrically (**Table 1**; no dry weights were available for *C. finmarchicus*, *C. glacialis* and small copepods). Briefly, an internal standard (C23:0) was added and total lipids were extracted using a modified procedure from Folch et al. (1957) with dichloromethane/methanol (2:1, v/v). 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) lipids and polar (i.e., membrane) lipids (**Supplementary Table 2**). Lipid class analysis was not performed on *Metridia longa*, *Microcalanus* spp., *Oithona similis*, and *Pseudocalanus* spp. due to lack of sufficient

sample material. In these taxa, the relative proportions of wax esters were estimated from the relation of FAs to fatty alcohols.

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. After a subsequent hexane extraction, the FAMEs and alcohols were separated by gas chromatography. PPOM samples were analyzed in triplicates per station (total $n = 18$) and IPOM samples in duplicates per station (total $n = 4$).

Fatty acids were expressed by the nomenclature $A{:}B(n{-}X)$; 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.

In this study, we focus on trophic marker FAs that can be used to trace food-source preferences through the food web. The FAs $16{:}1(n{-}7)$, $16{:}4(n{-}1)$, and $20{:}5(n{-}3)$ are mostly produced by diatoms (i.e., diatom-associated FAs), and the FAs $18{:}4(n{-}3)$ and $22{:}6(n{-}3)$ (i.e., dinoflagellate-associated FAs) are predominantly produced by dinoflagellates and the prymnesiophyte *Phaeocystis* (Falk-Petersen et al., 1998; Reuss and Poulsen, 2002; Dalsgaard et al., 2003). Trophic marker ratios of the FAs $16{:}1(n{-}7)/16{:}0$, the sum of C16 FAs (produced in high amounts by diatoms) versus the sum of C18 FAs (produced in high amounts by dinoflagellates;

hereafter referred to as $\Sigma C16/\Sigma C18$), and the FA ratio $20:5(n-3)/22:6(n-3) > 1$ can indicate a dominance of diatom-produced versus dinoflagellate-produced carbon in an algal community or carbon pool of a consumer. The monounsaturated long-chained FAs 20:1 and 22:1, which are isomers synthesized *de novo* by copepods, typically indicate the importance of copepods, such as *Calanus* spp., as a food source for a consumer (Sargent and Falk-Petersen, 1988; Falk-Petersen et al., 1990). The relative proportion of polyunsaturated FAs (PUFAs) can be used as an indicator of food quality of an algal community or as a herbivore index for a consumer based on the assumption that algae are the main producers of PUFAs (Stevens et al., 2004). Additionally, high ratios of $18:1(n-9)/18:1(n-7)$ indicate an omnivorous/carnivorous/detritivorous rather than herbivorous feeding mode (Graeve et al., 1997; Falk-Petersen et al., 2000; Auel et al., 2002).

Highly Branched Isoprenoids (HBIs) and Sterols

Highly branched isoprenoids and sterols were analyzed at the University of Plymouth, United Kingdom. Detailed information about analytical procedure and lab equipment can be found in Brown and Belt (2012) and Schmidt et al. (2018).

Briefly, samples were freeze-dried and homogenized. Two standards, 9-octyl-8-heptadecene and 7-hexylnonadecane, were added for subsequent trophic marker quantification. Total lipids were extracted with chloroform/methanol (2:1, v/v). Thereafter, samples were saponified with 20% potassium hydroxide in water/methanol. Non-saponifiable lipids were extracted with hexane and purified by open column chromatography filled with SiO_2 and HBIs were analyzed by gas chromatography-mass spectrometry (GC-MS). Quantification of HBIs was achieved by integrating individual ion responses in single-ion monitoring mode, and normalizing these to the corresponding peak area of the internal standard and an instrumental response factor obtained from purified standards (Belt et al., 2012). The GC-MS-derived masses of the HBIs were converted to concentrations in body fractions of the zooplankton using the lipid mass of the extracted sample. The two tri-unsaturated HBIs, hereafter referred to as HBIs III and IV (m/z 346.3), can indicate the consumption of pelagic algal material, including that from the marginal ice zone (MIZ) (Brown et al., 2014; Belt, 2018), while the mono- and di-unsaturated HBIs IP_{25} (m/z 350.3) and $IPSO_{25}$ (m/z 348.3) are assumed to be produced exclusively by certain sea-ice diatoms, providing information on the origin of carbon sources in a consumer (Brown et al., 2018; Schmidt et al., 2018).

Sterols were eluted from the same silica column using hexane:methylacetate (4:1,v/v). Sterol fractions were derivatised using *N,O*-bis(trimethylsilyl)trifluoroacetamide (BSTFA) and analyzed by GC-MS. 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 phytoplankton-produced sterols (hereafter referred to as phytosterols) brassicasterol (24-methylcholesta-5,22E-dien-3β–ol; m/z 470), sitosterol (24-ethylcholest-5-en-3β–ol; m/z 396), chalinasterol (24-methylcholesta-5,24(28)-dien-3β–ol; m/z 470) and campesterol (24-methylcholest-5-en-3β–ol; m/z 382) and the phyto- and-zooplankton-produced sterols (hereafter referred to as zoosterols) cholesterol (Cholest-5-en-3β–ol; m/z 458), desmosterol (Cholesta-5,24-dien-3β–ol; m/z 343) and dehydrocholesterol (Cholesta-5,22E-dien-3β–ol; m/z 327).

Statistical Analyses

Spatial variability in PPOM and *Calanus* spp. FAs was 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 $\pm$ 1 SD. FA data were transformed by applying an arcsine square root function to meet normality requirements for parametric statistics (Legendre and Legendre, 2012). Variability in FA datasets of PPOM and IPOM, as well as spatial variability in *Calanus* copepods, was visualized with correspondence analysis (CA), which is suitable for analyzing compositional data (Greenacre and Primicerio, 2014; Greenacre, 2017). Differences in FA composition between zooplankton taxa were visualized with a principal component analysis (PCA) and tested for statistical relevance with ANOSIM (dissimilarity measure: Bray–Curtis). Correlation between total zoosterols/total phytosterols and the FA ratio $18:1(n-9)/18:1(n-7)$ as well as HBI concentrations versus the total abundance of phytosterols and zoosterols was tested using Pearson's correlation; data have been LOG-transformed to appropriately present species-specific distributions. To visually summarize the main results of this study, a PCA was applied to show zooplankton-specific differences in marker FA ratios, HBI concentrations and degree of carnivory. All statistical analyses were run in R v.3.4.3 (R Core Team, 2017) using the vegan (Oksanen et al., 2019) and ggplot2 packages (Wickham, 2016), the map was produced with QGIS version 3.16.1.

RESULTS

FA Composition of Pelagic and Ice-Associated Particulate Organic Matter (PPOM and IPOM)

Our CA explained ∼84% of the variability in the FA dataset, showing that the FA composition in PPOM (P1-P7) differed from that in IPOM (P6_ice, P7_ice; **Figure 2**). While PPOM was associated with higher mean proportional contributions of the dinoflagellate-associated FAs $18:4(n-3)$ and $22:6(n-3)$, the mean relative proportion of the diatom-associated FA $16:1(n-7)$ was more than four times higher in IPOM than in PPOM. In IPOM, all three trophic marker FA ratios indicated a dominance of diatoms over dinoflagellates (**Table 2**). In PPOM, both diatom- and dinoflagellate-associated FA contributed largely to the FA composition, and contributions were more equally distributed compared to IPOM.

There was large variability in PPOM FA proportions along the sampling transect. PPOM from samples collected at stations
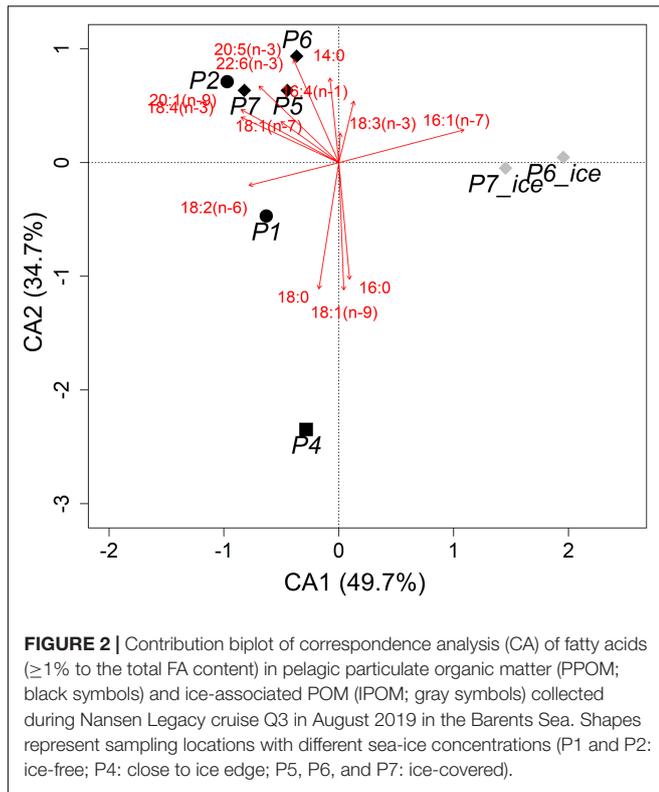
FIGURE 2 | Contribution biplot of correspondence analysis (CA) of fatty acids ($\geq$1% to the total FA content) in pelagic particulate organic matter (PPOM; black symbols) and ice-associated POM (IPOM; gray symbols) collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea. Shapes represent sampling locations with different sea-ice concentrations (P1 and P2: ice-free; P4: close to ice edge; P5, P6, and P7: ice-covered).

TABLE 2 | Relative proportions of trophic marker fatty acids (FAs; mean $\pm$ SD%) and FA ratios (mean $\pm$ SD) in pelagic particulate organic matter (PPOM) and ice-associated POM (IPOM) collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea.

Descriptor	Trophic marker FA proportions (%)	PPOM (n = 6)	IPOM (n = 2)
Diatom-associated FA	16:1(n−7)	8.0 $\pm$ 3.2	35.9 $\pm$ 6.0
	16:4(n−1)	1.0 $\pm$ 1.2	1.0 $\pm$ 0.1
	20:5(n−3)	8.9 $\pm$ 3.7	5.9 $\pm$ 0.9
Dinoflagellate-associated FA	18:4(n−3)	9.9 $\pm$ 5.5	1.7 $\pm$ 0.7
	22:6(n−3)	7.4 $\pm$ 3.9	1.8 $\pm$ 0.2
Food quality	ΣPUFA	32.1 $\pm$ 10.2	16.0 $\pm$ 5.1
	16:1(n−7)/16:0	0.5 $\pm$ 0.2	1.9 $\pm$ 0.2
Diatoms/ dinoflagellates	ΣC16/ ΣC18	1.1 $\pm$ 0.6	2.5 $\pm$ 0.7
	20:5(n−3)/22:6(n−3)	1.4 $\pm$ 0.5	3.4 $\pm$ 0.1

n, number of samples analyzed across the sampling area: PPOM was analyzed in triplicates, IPOM in duplicates.

P1 and P4 were clearly separated from the other stations in the CA plot with significantly higher mean relative contributions of FA 18:1(n−9) (10 and 24%, respectively) compared to most of the other stations (3–5%, respectively, **Figure 2**; ANOVA, $F_{5,12}$ = 55.1, p < 0.001, Tukey HSD p < 0.05). Additionally, PPOM from samples collected at station P4 had significantly higher relative proportions of 18:0 (mean 22%) compared to most other stations (mean 4–14%; $F_{5,12}$ = 7.9, p = 0.002, Tukey HSD p < 0.05). In contrast, the relative proportions of the diatom-associated FAs 16:1(n−7) ($F_{5,12}$ = 12.3, p < 0.001, Tukey HSD p < 0.05) and 20:5(n−3) ($F_{5,12}$ = 21.4, p < 0.001, Tukey

HSD p < 0.001), and the dinoflagellate-associated FAs 18:4(n−3) ($F_{5,12}$ = 14.7, p < 0.001, Tukey HSD p < 0.05) and 22:6(n−3) ($F_{5,12}$ = 9.9, p < 0.001, Tukey HSD p < 0.05) were lower at P4 compared to most of the other stations. At station P1, relative proportions of 16:1(n−7) in PPOM were also lower compared to stations P5 and P6, and relative proportions of 20:5(n−3) were lower compared to stations P5, P6, and P7.

Lipid Class and FA Composition of Barents Sea Zooplankton

In all copepod taxa as well as krill, amphipods and the pteropod *Clione limacina*, the cnidarians, the chaetognath *Eukrohnia hamata*, and the ctenophore *Mertensia ovum*, mean relative proportions of neutral (storage) lipids were higher than those of polar (membrane) lipids. In contrast, the pteropod *Limacina helicina*, the ctenophore *Beroë cucumis*, the chaetognaths *Parasagitta elegans* and *Sagitta maxima* and the appendicularian *Oikopleura vanhoeffeni* had the reverse. Levels of wax esters (neutral lipids) were generally high in all copepod species (mean > 90% in *Paraeuchaeta* spp.) and *E. hamata* (mean 64%). Triacylglycerols (TAGs) dominated the neutral lipid fraction in the amphipods, the krill *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, and *C. limacina* (up to 76%). Among the polar lipids, phosphatidylethanolamine (PE) and phosphatidylcholine (PC) were the most abundant lipid classes, with up to 23% of the total lipids in *O. vanhoeffeni* and up to 48% in *Parasagitta/Sagitta* spp., respectively. Lipid class compositions of individual taxa are reported in **Supplementary Table 2**.

In the PCA (explained ∼65% of the variance in the FA dataset), all taxonomic groups (ANOSIM, R = 0.328, p = 0.001) and most species (ANOSIM, R = 0.878, p < 0.001) could be clearly distinguished from each other based on their FA profiles (**Figure 3**). Except for the copepods *Oithona similis* and *Pseudocalanus* spp. and the cnidarian *Catablema vesicarium*, FA proportions were similar within a species/taxa.

Among all taxa, the copepod *Metridia longa* had the highest mean relative proportion of the diatom-associated FA 16:1(n−7) (26%), and *B. cucumis* had the lowest mean relative level of this FA (2%). The diatom-associated FA 16:4(n−1) showed the maximum mean proportion in the copepod *Calanus hyperboreus* (3%), and the minimum in *B. cucumis* and *C. limacina* (both 0.1%). The proportions of the diatom-associated FA 20:5(n−3) were lower in the copepods *Microcalanus* spp. (7%) and *Paraeuchaeta* spp. (7%) compared to all other taxa (10–24%). *Calanus hyperboreus* had a substantially higher mean relative proportion of the dinoflagellate-associated FA 18:4(n−3) (11%) than all other taxa. Amphipods (11 and 19%), pteropods (15 and 25%) and gelatinous zooplankton (8–24%) had distinctly higher relative proportions of the dinoflagellate-associated FA 22:6(n−3) than most copepods (4–8%) and krill (4–7%). Only in the amphipod *T. libellula* and the ctenophores were all three diatom/dinoflagellate ratios $\leq$ 1. *Clione limacina* was the only species with a mean ratio of 18:1(n−9)/18:1(n−7) < 1 (**Table 3**). Fatty acid compositions of individual taxa are reported in **Supplementary Table 3**.

FIGURE 3 | Principal component analysis (PCA) of fatty acids (FAs; ≥1% to the total FA content) in the zooplankton collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea. Relative proportions of individual FAs are shown in **Supplementary Table 3**.

In all three *Calanus* species, the FA composition varied along the sampling transect (**Figures 4A–C**). In all three species, individuals from stations with low proportions of $16:1(n-7)$, i.e., station P7 for *C. finmarchicus* (**Figure 4A**) and *C. hyperboreus* (**Figure 4C**) and station P1 for *C. glacialis* (**Figure 4C**), were associated with a higher degree of carnivory, i.e., higher ratios of $18:1(n-9)/18:1(n-7)$. Relative proportions of the diatom-associated FA $20:5(n-3)$ were high in all species from station P7. Overall, *C. glacialis* from station P1 had the lowest diatom signal, i.e., low relative proportions of the diatom-associated FAs $16:1(n-7)$, $16:4(n-1)$, and $20:5(n-3)$ [low ratios of $16:1(n-7)/16:0$, $\Sigma C16/\Sigma C18$ and $20:5(n-3)/22:6(n-3)$], but the strongest dinoflagellate signal, i.e., high proportions of the dinoflagellate-associated FAs $18:4(n-3)$ and $22:6(n-3)$, among the four sampled stations (**Figure 4B**). Additionally, in *C. finmarchicus* and *C. hyperboreus*, individuals from station P6 were different in their FA composition from that of the other stations (**Figures 4A,C**). They were associated with higher levels of the diatom-associated FAs $16:4(n-1)$ and also $20:5(n-3)$ compared to the other stations. Furthermore, *C. hyperboreus* from station P6 had a low dinoflagellate signal, i.e., low levels of $18:4(n-3)$ and $22:6(n-3)$. Statistical output is reported in **Supplementary Table 4**.

HBIs and Sterols

None of the pelagic/MIZ and sea ice algae-associated HBIs were detected in PPOM. The pelagic/MIZ HBIs were found in all zooplankton taxa, except for the small copepod species *Microcalanus* spp., *O. similis*, *Pseudocalanus* spp., the pteropod

C. limacina, the chaetognath *S. maxima* and the appendicularian *O. vanhoeffeni*. Maximum concentrations of both HBIs III and IV were found in the cnidarian *C. vesicarium*. The sea ice algae-associated HBI IP$_{25}$ was detected in the amphipod *Themisto abyssorum*, the pteropod *L. helicina* and *O. vanhoeffeni* (**Figure 5A**). The other sea ice algae-associated HBI IPSO$_{25}$ was found in the krill *M. norvegica* and *Thysanoessa inermis*, the amphipods *T. abyssorum* and *T. libellula*, *C. limacina* and *L. helicina* as well as *O. vanhoeffeni*. *Limacina helicina* had the highest concentrations of both sea ice algae-associated HBIs. In all taxa, species-specific variability in HBI concentrations was high. Mean ratios of sea ice algae-associated to pelagic/MIZ HBIs were >1 in *T. abyssorum*, the two pteropod species and *O. vanhoeffeni*. HBI concentrations of individual taxa/species are reported in **Supplementary Table 5**.

In most zooplankton, the most abundant phytosterols were brassicasterol (up to 90% of total phytosterols) and campesterol (up to 69% of total phytosterols). In most taxa, desmosterol had the highest relative contribution to the total zoosterol content (up to 90%), while in krill, cholesterol had the highest relative contributions (up to 93% of total zoosterols). Ratios of the four phytosterols versus cholesterol were generally the highest in *O. vanhoeffeni* and the pteropods and the lowest in *P. norvegica* and krill (**Supplementary Figure 1**).

The relationship of the FA carnivory ratio $18:1(n-9)/18:1(n-7)$ versus total zoosterols/total phytosterols was positively correlated (**Figure 5B**). For both ratios, *P. norvegica* had the highest values. The pteropods and *O. vanhoeffeni* showed lower values than most of the other taxa.

TABLE 3 | Ratios of fatty acids (FAs; mean ± SD) in zooplankton collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea.

Zooplankton taxa	n	16:1(n−7)/16:0	ΣC16/ΣC18	20:5(n−3)/22:6(n−3)
Calanus finmarchicus	12	1.4 ± 0.4	2.4 ± 0.7	3.3 ± 0.7
Calanus glacialis	14	2.4 ± 0.6	1.9 ± 0.5	3.4 ± 1.0
Calanus hyperboreus	16	4.6 ± 1.8	1.3 ± 0.7	2.7 ± 1.2
Metridia longa	4	4.0 ± 1.1	1.1 ± 0.3	1.4 ± 0.3
Microcalanus spp.	4	2.2 ± 0.8	0.8 ± 0.3	1.3 ± 0.2
Oithona similis	5	0.4 ± 0.4	1.3 ± 0.7	1.6 ± 1.2
Paraeuchaeta spp.	3	12.1 ± 1.0	0.7 ± 0.1	0.9 ± 0.2
Pseudocalanus spp.	5	1.4 ± 0.6	1.0 ± 0.8	2.2 ± 0.7
Meganyctiphanes norvegica	4	0.5 ± 0.1	1.2 ± 0.1	1.3 ± 0.3
Thysanoessa inermis	8	0.9 ± 0.3	1.2 ± 0.2	3.6 ± 0.9
Thysanoessa longicaudata	5	0.4 ± 0.1	1.5 ± 0.2	2.5 ± 0.5
Themisto abyssorum	4	0.9 ± 0.3	0.8 ± 0.1	1.7 ± 0.5
Themisto libellula	6	0.5 ± 0.1	0.9 ± 0.1	0.9 ± 0.1
Clione limacina	6	0.7 ± 0.4	2.1 ± 0.9	0.9 ± 0.1
Limacina helicina	4	0.3 ± 0.3	1.9 ± 0.1	1.0 ± 0.2
Bougainvillia superciliaris	2	2.1 ± 0.1	1.4 ± 0.1	1.8 ± 0.2
Catablema vesicarium	2	0.8 ± 0.8	0.8 ± 0.2	1.4 ± 0.1
Beroë cucumis	4	0.2 ± 0.1	0.9 ± 0.2	0.8 ± 0.1
Mertensia ovum	4	0.4 ± 0.3	1.0 ± 0.1	1.0 ± 0.3
Eukrohnia hamata	6	2.0 ± 0.3	1.3 ± 0.1	1.8 ± 0.5
Parasagitta elegans	6	1.1 ± 0.5	1.4 ± 0.1	1.2 ± 0.4
Sagitta maxima	2	0.8 ± 0.1	1.2 ± 0.2	0.8 ± 0.1
Oikopleura vanhoeffeni	3	0.5 ± 0.4	0.9 ± 0.6	1.2 ± 0.4

n, number of samples analyzed across the sampling area. Ratios > 1 indicate the dominance of diatom-associated over dinoflagellate-associated FAs in the zooplankton.

In the zooplankton, the total abundance of phytosterols had a strong positive correlation with the total HBI concentrations (**Figure 5C**), and this significant correlation was found for all four phytosterols. The correlation between phytosterols and total HBIs was stronger than the correlation between zoosterols and total HBIs (**Supplementary Figure 2**).

Carbon Sources of Barents Sea Zooplankton: Summary

Fatty acid ratios indicating the dominance of diatom-associated carbon versus dinoflagellate-associated carbon were the highest in the copepods *Paraeuchaeta* spp. and *Calanus* spp., and the lowest in the ctenophores *B. cucumis* and *M. ovum* as well as the amphipod *T. libellula* (**Figure 6A**).

Pelagic/MIZ HBIs were found in all taxa, except for small copepods, with highest concentrations in the cnidarian *C. vesicarium*. Sea ice algae-associated HBIs were found in the pteropod *L. helicina* in highest concentrations, and further
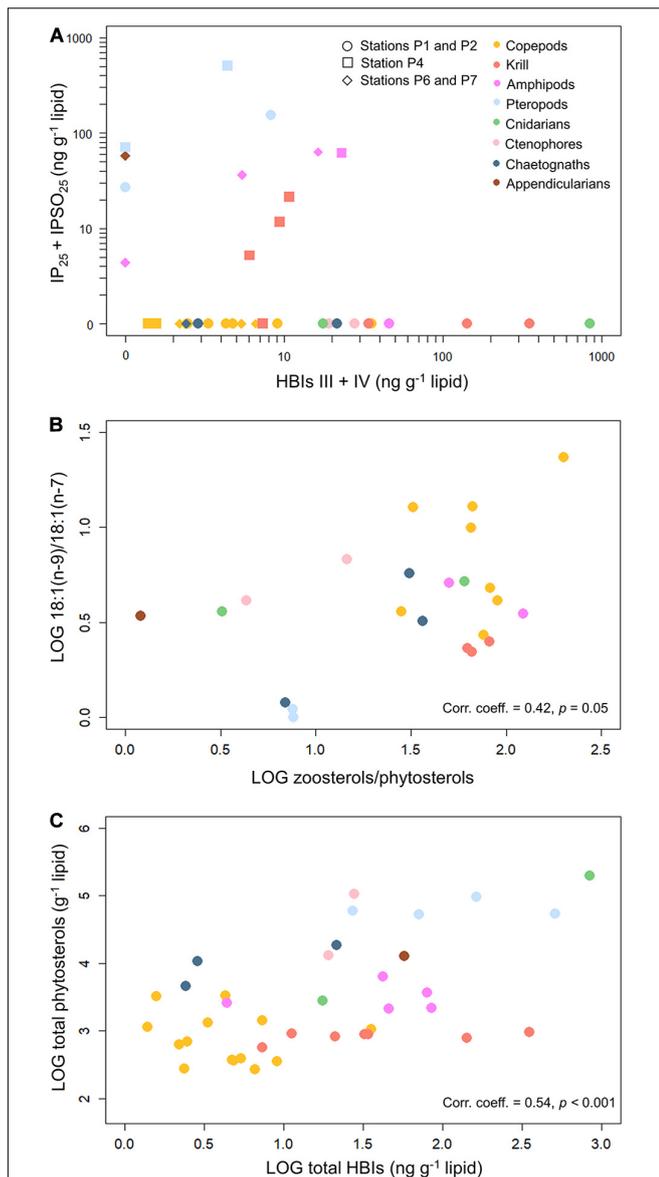

FIGURE 4 | Contribution biplot of correspondence analysis (CA) of fatty acids (≥1% to the total FA content) representing spatial variability in **(A)** *Calanus finmarchicus*, **(B)** *C. glacialis* and **(C)** *C. hyperboreus* collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea. Shapes represent sampling locations with different sea ice concentrations (P1 and P2: ice-free; P4: close to ice edge; P6 and P7: ice-covered).

FIGURE 5 | (A) Concentrations of the pelagic/MIZ HBIs III and IV versus the sea ice algae-associated HBIs IP$_{25}$ and IPSO$_{25}$ in the zooplankton collected during Nansen Legacy cruise Q3 in August 2019 in the Barents Sea. Considered are only samples that contained either pelagic/MIZ or sea ice algae-associated HBIs or both. Datapoints represent individual samples. All data can be found in **Supplementary Table 5**. (B) Pearson's correlation of the mean ratio of zoosterols/phytosterols versus the mean carnivory index 18:1(*n*–9)/18:1(*n*–7) in the zooplankton. (C) Pearson's correlation of total phytosterols versus total HBIs in the zooplankton. Considered are only samples that either contained pelagic/MIZ or sea ice algae-associated HBIs or both. Datapoints represent individual samples.

FIGURE 6 | Summary of results representing principal component analysis (PCA) of (A) the carbon source composition based on diatom- versus dinoflagellate-associated fatty acids (FAs; trophic marker FA ratios are shown in **Table 3**), (B) the origin of these carbon sources based on concentrations of pelagic/MIZ highly branched isoprenoids (HBIs III and IV) and sea ice algae-associated HBIs (IP$_{25}$, IPSO$_{25}$; HBI concentrations are shown in **Figure 5A** and **Supplementary Table 5**) and (C) the degree of carnivory versus herbivory in the zooplankton taxa based on concentrations of zoosterols/phytosterols, and relative proportions of the carnivory FA 18:1(*n*–9) versus the algal-produced FA 18:1(*n*–7), and calanoid copepod-associated FAs 20:1 and 22:1 (FA proportions are shown in **Supplementary Table 3**).

in the pteropod *C. limacina*, the krill *M. norvegica* and *T. inermis*, the amphipods *Themisto* spp. and the appendicularian *O. vanhoeffeni* (**Figure 6B**).

Fatty acid- and sterol-based carnivory ratios were the highest in the copepod *P. norvegica* and other copepods and the lowest in *O. vanhoeffeni*. The highest proportions of

copepod-associated FAs were found in *M. norvegica*, and the lowest proportions in the krill *Thysanoessa* spp., the pteropods and *O. vanhoeffeni* (**Figure 6C**).

DISCUSSION

Composition of PPOM and IPOM

During our sampling period, pelagic and sea ice-associated algal communities, referred to as PPOM and IPOM, respectively, differed in their FA composition (**Figure 2**). The diatom-associated FA 16:1(n−7) has frequently been found to be strongly associated with Arctic sea-ice diatoms (Henderson et al., 1998; Budge et al., 2008; Kohlbach et al., 2016), suggesting a diatom-dominated sea-ice community in the current study, in agreement with microscopic analysis which revealed high abundances of typical sea ice-associated pennate diatoms, such as *Nitzschia* spp. However, diatom-produced marker FAs accounted for almost 20% of the PPOM FAs, suggesting that diatoms also played an important part in structuring the pelagic algal community (Ratkova and Wassmann, 2002). Furthermore, elevated levels of the FAs 18:4(n−3) and 22:6(n−3) in PPOM indicated the presence of flagellates/prymnesiophytes in the water column, typical for European Arctic protistan plankton during summer (Wassmann et al., 2005, 2006). Taxonomic analysis confirmed the importance of diatoms, including *Thalassiosira* and *Fragilariopsis* genera, and dinoflagellates, e.g., *Gymnodinium* spp. and taxa of the order Peridiniales, for the phytoplankton community composition. The prymnesiophyte *Phaeocystis* was found in high abundances at stations P4, P6, and P7.

Carbon Sources of Barents Sea Zooplankton During Late Summer

In this study, all of the diatom- and dinoflagellate-associated trophic marker FAs were found in all investigated zooplankton. Thus, all taxa are capable of utilizing carbon of different origin, directly obtained and/or, more likely based on the generally high carnivory indices in this study (presence of copepod-associated FAs, high 18:1(n−9)/18:1(n−7) ratios, presence of zoosterols), indirectly by feeding on other organisms. The overall high degree of carnivory among the zooplankton agrees with findings that dominant species prefer microzooplankton (if abundant) over phytoplankton (Campbell et al., 2009; Stoecker and Pierson, 2019). Additionally, it could reflect a high abundance of heterotrophic protists in the sampling region (Wassmann et al., 2005), and it is noteworthy that heterotrophic or mixotrophic dinoflagellates of the genus *Gymnodinium* were a key component of the phytoplankton community in this and other studies in the Arctic (Kubiszyn and Wiktor, 2016; Hardge et al., 2017).

Copepods, Krill and Amphipods

Overall, the diverse taxonomic group of copepods showed the strongest diatom signal in their FA pool among the different zooplankton groups (**Table 3** and **Figure 6A**). Diatoms have been identified as major food items for *Calanus* spp. (Søreide et al., 2008; Cleary et al., 2017), and most of the other copepods have also been reported to utilize diatom-derived carbon (Atkinson, 1996; Cleary et al., 2016). *Calanus hyperboreus* was more likely to graze directly on autotrophic algae according to its lower degree of carnivory [lower 18:1(n−9)/18:1(n−7), higher levels of PUFAs] and its high proportions of the short-term FA 18:4(n−3)

compared to all other copepods (Stevens et al., 2004), suggesting also the ingestion of fresh flagellate material and/or *Phaeocystis* (Hansen et al., 1994; Søreide et al., 2008).

Variability in FA composition in all three *Calanus* species along the transect (**Figures 4A–C**) showed high species-specific consistency, and likely reflects spatial and temporal variations in carbon and food sources, i.e., composition of algal communities and prey species. Variability in FA composition was also pronounced in PPOM (**Figure 2**) and suggested differences in community structure, which was likely the result of varying environmental factors, e.g., Atlantic versus Arctic water masses and water-mass characteristics (temperature and salinity), mixing processes, sea-ice concentrations and nutrient availability (Engelsen et al., 2002; Ardyna et al., 2011). In all three *Calanus* species, stations with higher 18:1(n−9)/18:1(n−7) ratios were also linked to a lower diatom signal: in *C. glacialis* at station P1 and in the other two *Calanus* species at station P7, where a high proportion of unidentified (possibly heterotrophic or mixotrophic) eukaryotic species contributed to the pelagic protist composition. This might mirror an increased availability of preferred heterotrophic prey at these sampling locations other than diatoms, resulting in a higher degree of carnivory in these species (Søreide et al., 2008).

In comparison to our study, samples from the central Arctic Ocean (CAO) in August/September (Kohlbach et al., 2016) had a considerably higher contribution of the diatom-associated FA 16:1(n−7) in both IPOM (mean over 50% versus mean 36% in this study) and *Calanus* copepods (e.g., mean 26% in *C. glacialis* versus mean 16% in this study). Based on FA-specific stable isotope mixing models, ice-associated carbon contributed up to 48% of the copepods' carbon budget in the CAO (Kohlbach et al., 2016), and was similar to what was reported for the Bering Sea during summer ice-free conditions with up to 54% (Wang et al., 2015). However, the lack of sea ice algae-associated HBIs in all of the investigated copepod taxa indicates that carbon was mainly obtained from phytoplankton and pelagic prey during our study representative of the late summer season. In contrast to the Barents Sea, ice algal primary production in the CAO can constitute over half of the total primary production during August/September due to the extensive sea-ice coverage, somewhat counteracting the relatively poor pelagic primary production in the CAO (Fernández Méndez, 2014; Fernández-Méndez et al., 2015). Consequently, the generally high availability of sea-ice algae in a sea ice-dominated ecosystem such as the CAO likely promotes and necessitates an increased dependency on ice-associated carbon sources, which could rapidly change with further reduction in sea ice and longer open-water season. However, it needs to be noted that one of the dominant sea-ice diatoms during the above-mentioned studies from the CAO, *Melosira arctica*, is not known to produce HBIs and is therefore not captured by our biomarker approach.

HBIs produced by algae in open waters or the MIZ (HBIs III and IV) were found in all sampled taxa except for the small copepods *Microcalanus* spp., *O. similis* and *Pseudocalanus* spp. (**Figure 5A**). Along with their high ratios of 18:1(n−9)/18:1(n−7) and elevated levels of zoosterols, this suggests further that these small copepod species were feeding to a greater extent

as omnivores, carnivores or detritivores (Norrbin et al., 1990; Lischka and Hagen, 2007). *Oithona similis* has been described as an ambush feeder (Svensen and Kiørboe, 2000), preferring mobile prey such as ciliates, and is only rarely found to feed on diatoms (Zamora-Terol et al., 2013), in line with the lower diatom FA signal compared to the other copepods in our study. Furthermore, phytoplankton assemblages containing smaller protist taxa might have hampered efficient grazing by copepods with a different prey-size preference, such as *O. similis* (10–40 μm; Zamora-Terol et al., 2013).

Despite the common co-occurrence of the two sea ice algae-associated HBIs IP_{25} and $IPSO_{25}$ in Arctic sea-ice diatoms (Belt and Müller, 2013; Brown et al., 2014; Belt et al., 2016), only $IPSO_{25}$ was detected, for example in the krill species, whereas IP_{25} was absent. This could have many reasons, such as lack or unavailability of source taxa, differing nutrient availability affecting metabolite production (Brown et al., 2020), or selective feeding of these zooplankton taxa. It could also point to different metabolic turnover rates or concentrations of the two HBIs in the consumer, retaining $IPSO_{25}$ in the animal's tissue while concentrations of IP_{25} were already below the detection limit as $IPSO_{25}$ can be several times more abundant than IP_{25} in Arctic animals (Brown et al., 2015). Pelagic HBIs were found in substantially higher concentrations in *M. norvegica* in comparison to *Thysanoessa* spp., and its stronger pelagic signal was supported by the FA compositions.

Based on all three diatom/dinoflagellate ratios being <1, low levels of the diatom-associated FA $16:1(n-7)$, but high levels of the dinoflagellate-associated FA $22:6(n-3)$, the amphipod *T. libellula* and the ctenophores *B. cucumis* and *M. ovum* had the highest dinoflagellate, i.e., pelagic signal, in their FA pool (**Figure 6A** and **Supplementary Table 3**). In previous studies, the link between the predominantly carnivorous *T. libellula* and sea-ice primary production varied during summer in the Bering Sea (mean contribution of ice-associated carbon between 38 and 79%, depending on stable isotope model parameters; Wang et al., 2015) and the CAO (mean contribution of ice-associated carbon between 23 and 55%, depending on stable isotope parameters; Kohlbach et al., 2016). In this study, sea ice algae-associated and pelagic/MIZ HBIs were detected in both *Themisto* species, showing that they utilized carbon of different origin, likely by preying on *Calanus* spp., based on their high proportions of copepod-associated FAs and elevated wax ester levels (Scott et al., 1999; Auel et al., 2002) and/or possibly also on krill and pteropods (Marion et al., 2008) based on the presence of HBIs in these taxa. Differences in lipid class, FA composition and HBI concentrations between *T. abyssorum* and *T. libellula*, however, reflect differences in energy storage mode and their highly diverse feeding behavior (Auel et al., 2002; Havermans et al., 2019). HBI concentrations in *T. abyssorum* were only analyzed for samples from the ice-covered stations P6 and P7, so that a strictly pelagic feeding style of this species in the more southern Barents Sea cannot be excluded.

Pteropods and Gelatinous Zooplankton

Based on high amounts of phytosterols and a ratio of $18:1(n-9)/18:1(n-7) < 1$, the pteropod *C. limacina* was

characterized by a herbivorous rather than carnivorous feeding strategy, challenging the idea that *C. limacina* is exclusively feeding on *L. helicina* (Conover and Lalli, 1972; Böer et al., 2005), at least during the summer period when phytoplankton should be abundant. Correspondingly, the lipid class and FA composition were distinctly different between the two pteropods (e.g., more TAGs in *C. limacina*, more polar lipids in *L. helicina*), suggesting that *L. helicina* was not a major food item for *C. limacina* in our study. The significantly higher proportions of the PUFAs $20:5(n-3)$ and $22:6(n-3)$ in *L. helicina* were at least partly the result of the large proportion of polar lipids in *L. helicina* compared to *C. limacina*, since these long-chain FAs are mainly incorporated into cell membranes (Stübing et al., 2003). Furthermore, *L. helicina* had substantially higher proportions of free FAs (average 19%) than all other taxa (mean 0.2 to 10.7%), except for *C. vesicarium*, which could indicate gonad maturation during summer (Gannefors et al., 2005).

Interestingly, *C. limacina* is assumed to be a true pelagic species, with relatively low (trophic) interaction with the sea-ice system (mean contribution of ice-associated carbon between 14 and 30% during summer in the CAO, depending on stable isotope model parameters; Kohlbach et al., 2016). Yet, in this study, *C. limacina* alongside six other species out of 24, including *L. limacina* and the appendicularian *O. vanhoeffeni*, were the only species containing sea ice algae-associated HBIs. In both pteropod species, sea ice algae-associated HBIs were determined in individuals collected at station P2, where sea ice was absent during the sampling period. This might reflect the great mobility of these species, able to cover large distances with varying sea-ice coverage, or a low turnover rate of HBIs in these species if it is assumed that sea ice-associated material was ingested prior to sampling when sea ice was still present at this station.

In the ctenophores *B. cucumis* and *M. ovum*, the strong pelagic signal in their FA compositions as well as the absence of sea ice algae-associated HBIs likely reflects that they fed on pelagic prey, probably copepods, but also amphipods and krill, as reported previously (Swanberg and Båmstedt, 1991). The two cnidarian species were largely different in their lipid class and FA composition with an overall stronger diatom signal in *Bougainvillia superciliaris* compared to *Catablema vesicarium*. In accordance with previous studies, both species were likely feeding as omnivores/carnivores, and phytoplankton-derived carbon contributed largely to their diets (Hansson et al., 2005; Prudkovsky and Neretina, 2016). Among the chaetognaths, *E. hamata* had a stronger diatom signal compared to *Parasagitta/Sagitta* spp., likely as a result of its higher trophic dependency on *Calanus* spp. (Connelly et al., 2014) or other copepods, corresponding to its higher relative proportions of wax esters and somewhat higher proportions of copepod-associated FAs, while *Parasagitta* and *Sagitta* have been found to rather rely on smaller copepods (*Pseudocalanus* and *Oithona*) (Falkenhaug, 1991; Alvarez-Cadena, 1993). In *Parasagitta elegans*, the presence of the diatom-derived HBI III suggests that this species also utilized food sources other than small copepods.

The failure to detect IP_{25} and $IPSO_{25}$ in PPOM suggests that zooplankton containing HBIs received these lipid components by feeding on sea ice-derived material. This does not necessarily

mean that these species were actively grazing on sea-ice biota (where sea ice was present) but rather that the animals fed on ice algae that had sunk to deeper water or the seabed, possibly as marine snow (Olli et al., 2002; Tamelander et al., 2006; Tamelander et al., 2009; Schmidt et al., 2018). In ice-covered regions, the phytoplankton community is strongly influenced by water stratification due to ice melt, while more porous ice conditions during summer could have triggered the release and vertical export of ice algal material, thus contributing to the PPOM community composition (Hegseth, 1998; Tamelander et al., 2009). *Limacina helicina* is described as a flux-feeder with the ability to consume fast-sinking food particles (Stukel et al., 2019), such as ice algal aggregates dominated by pennate diatoms (Assmy et al., 2013), which have been shown to contain HBI-producing diatoms albeit in low abundances (Brown et al., 2017a), providing an explanation for the highest concentrations of sea ice algae-associated HBIs in *L. helicina* in this study. The absence of sea ice algae-associated HBIs does not exclude the possibility of the other taxa to feed on sea ice-derived carbon. The so far identified ice-associated HBIs are specific for certain sea-ice diatoms (Belt et al., 2007; Brown et al., 2014) and these diatom species have usually a relatively low contribution to the ice algal community (Volkman et al., 1994; Brown et al., 2014). Thus, the lack of these trophic markers could simply indicate that the organisms were feeding on ice-associated algae that did not produce these HBIs.

Suitability of Trophic Marker Methods for Tracing Food-Web Relationships

By combining dietary information derived from different biochemical approaches, we gained insights on (a) differences in energy storage modes between the zooplankton taxa based on lipid class composition (wax esters versus TAGs), (b) the taxonomic composition of carbon sources in zooplankton based on FA compositions (diatoms versus dinoflagellates), (c) the origin of these carbon sources based on HBI compositions (sea ice versus water column), and (d) tendencies regarding herbivory versus carnivory based on sterol compositions, FA carnivory indices and the presence of copepod-associated FAs (**Figures 6A–C**). To reveal food-web relationships, FAs have been traced from producer to consumer in numerous food-web studies in both the Arctic (Falk-Petersen et al., 1987; Graeve et al., 1994; Kohlbach et al., 2016) and the Antarctic (Schmidt et al., 2006; Kohlbach et al., 2018). Recent literature, however, suggests that marine invertebrates have the potential to *de novo* synthesize certain PUFAs (Kabeya et al., 2018), which is somewhat contradictory to the general assumption that these FAs are exclusively produced by marine algae and thus essentially obtained as dietary components in the marine environment. Kabeya et al. (2018) reported that numerous zooplankton possess the respective genes for PUFA biosynthesis, however, actual concentrations of zooplankton-produced PUFAs and the relation of zooplankton-produced versus algal-produced PUFAs in the FA composition of a consumer are unknown and are likely to vary greatly from species to species. Since the ability of herein

investigated species to biosynthesize their own PUFAs is unclear at this point, we assume that their trophic marker PUFAs were primarily obtained from dietary sources.

Compared to lipid class and FA compositions, the use of HBI and sterol lipid data in Arctic food-web studies is relatively new (e.g., Brown et al., 2018; Schmidt et al., 2018; Kohlbach et al., 2019), and likely benefits from a multidimensional application as employed here. The recent literature on HBIs and their role in Arctic marine processes (e.g., Brown and Belt, 2012; Brown et al., 2015, 2017a) strongly suggests their potential, and crucially these markers are highly stable; if a polar bear or a paleo-sediment sample contains ice marker, we can be fairly sure that some of the organic carbon was indeed originally sourced from sea-ice algae. All the trophic marker approaches have their strengths and weaknesses, and our study highlights the value of combining them into a multi-biomarker approach, whereby independent approaches provide both alternative insights and complementary information (Schmidt et al., 2018).

One key methodological issue for HBIs concerns their specificity to particular diatom species. The number of HBIs found to be produced by Arctic algae is continuously growing (Belt, 2018; Belt et al., 2019; Brown et al., 2020), but while the presence of the ice markers IP_{25} and $IPSO_{25}$ is believed to provide unequivocal sourcing from ice algae, their absence is not so straightforward to interpret (Belt, 2018). Also, species-specific turnover rates of HBIs in the consumers are still unknown. It might be assumed, however, that turnover times of these lipids lengthen with increasing trophic level (c.f. FAs), reaching up to several weeks in polar zooplankton (Boissonnot et al., 2016, 2019; Graeve et al., 2020). The failure to detect pelagic/MIZ HBIs in PPOM suggests that either HBI-producing algae were not present at the depth of the Chl *a* maximum, where the PPOM samples were collected, or that HBI concentrations were below the detection limit, both of which might be related to the seasonality of some HBI production. The presence of pelagic/MIZ HBIs in most of the zooplankton species could reflect the animals' vertical mobility (e.g., Fortier et al., 2001) to encounter differing algal assemblages consisting of different algal taxa throughout the water column.

Even though phytosterols can potentially be metabolically changed by herbivorous consumers (Ruess and Müller-Navarra, 2019), they can support biomarker studies by informing about plant-derived food intake in comparison to a rather animal-based diet (Nichols et al., 1993). In this study, PPOM and zooplankton clustered according to their sterol composition, with the overall pattern being robust across taxa and sampling locations (**Supplementary Figure 2**). Moreover, we found an internal consistency and strong positive correlation between the animals' HBI content and phytosterols (**Figure 5C**), further suggesting the suitability of phytosterols as an indicator for algal ingestion. The most abundant phytosterols found in Arctic sea ice are brassicasterol, chalinasterol, and sitosterol (Belt et al., 2013), and brassicasterol is also produced by pelagic algae (Müller et al., 2011). However, cholesterol can also be abundant in algal assemblages (Brown et al., 2011; Belt et al., 2018), offering an explanation for the presence of zoosterols in, e.g., *C. limacina* and *O. vanhoeffeni* that indicated the overall lowest

degree of carnivory in this study. Sterols have been found to be predominantly produced by, but not restricted to diatoms (Volkman et al., 1998; Rampen et al., 2010). The importance of diatoms in both sea-ice and pelagic protist communities was apparent from microscopic analysis and their FA compositions, suggesting that algae from both the sea ice and the pelagic habitat could have contributed to the overall sterol content in the zooplankton.

Conclusion

Tracing FAs, stable isotopes and/or HBIs, previous studies have indicated the role of sea ice-derived organic matter for Arctic ice-associated invertebrates (Tamelander et al., 2006; Kohlbach et al., 2016), pelagic animals in Arctic (Budge et al., 2008; Tamelander et al., 2008; Wang et al., 2015) and Antarctic marine environments (Schmidt et al., 2018), and Arctic benthic consumers (Brown and Belt, 2012; Kohlbach et al., 2019) across multiple trophic levels during spring and summer. In the present study, we found sea ice algae-specific metabolites (i.e., HBIs IP_{25} and $IPSO_{25}$) in filter-feeders of the mid-water column (pteropods, appendicularians) and in mobile omnivorous crustaceans (krill, pelagic amphipods), extending present knowledge about the role of ice algae as a food source for pelagic consumers in the Barents Sea during summer. Despite the 'heavy' sea-ice conditions in the Barents Sea during summer 2019 compared to previous years, the investigated pelagic food web showed a taxon-specific but relatively weak trophic relation to sea ice-derived carbon. During the time of the sampling, most of the sea-ice algae had already sloughed off and the remaining ice algae material seemed decayed. This corresponds to the lower PUFA levels in IPOM (average 16%) compared to PPOM (average 32%). Thus, not surprisingly, ice algae were providing a less abundant and attractive carbon source, in terms of lower food quality, than food of pelagic origin for the zooplankton grazers during the late summer melting season.

Until now, little information is available about direct consequences of declining sea ice on food-web interactions in the Arctic (e.g., Wassmann et al., 2011; Stige et al., 2019; Dalpadado et al., 2020). Overall, ice-associated species are expected to be more susceptible to sea-ice decline than pelagic ones (Dalpadado et al., 2020) and might be forced to a stronger association with the pelagic environment (Hop and Gjøsæter, 2013), with consequences for associated pelagic and benthic food webs and trophic interactions (Michalsen et al., 2013; Blanchard, 2015). With the change in primary production, i.e., the composition and availability of carbon sources, species with opportunistic feeding behavior, such as *O. similis* and *Pseudocalanus* spp. (Castellani et al., 2005; Lischka and Hagen, 2007; Cornwell et al., 2020) might further have a higher tolerance to more variable environmental conditions and an advantage over highly specialized (ice-associated) species.

Due to great uncertainties of consequences for individual species, it is crucial to continuously monitor and assess climate vulnerability on a species level during the transition to a warmer Arctic Ocean to reliably inform about changes in food-web structure and functioning (Eamer et al., 2013; Poloczanska, 2020).

Ultimately, the understanding of present food-web processes through the seasons will be the requisite for meaningful projections of winners and losers in the future Barents Sea with less sea ice and changing sea-ice properties.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

PA, HH, and DK were responsible for study design. AW conducted sampling. HH and PA provided sampling logistics. DK is the main author of this manuscript and did the fatty acid laboratory analyses and data evaluation. MW carried out lipid class analysis with support of MG. KS did the HBI and sterol analysis and data evaluation with the help of LS, SB, and AA. Taxonomic analysis of POM samples was carried out by AD and AT. MG and SB provided laboratory materials, methodological expertise, and laboratory space. The map was created by AKA-H. Data analyses and figure assemblage was done by DK with the help of the other authors. All authors contributed significantly to data interpretation and to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

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