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Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model

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Abstract

We simultaneously followed stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in a two-source food web model to determine trophic levels and the relative importance of open water- and ice-associated food sources (phytoplankton vs. ice algae) in the lower marine food web in the European Arctic during four seasons. The model is based upon extensive seasonal data from 1995 to 2001.

Phytoplankton, represented by samples of particulate organic matter from open water (Pelagic-POM) and ice algae, represented by samples from the underside of the ice (Ice-POM), were isotopically different. Ice-POM was generally dominated by the typical ice diatoms *Nitzschia frigida* and *Melosira arctica* and was more enriched than Pelagic-POM in ^{13}C ($\delta^{13}C = -20‰$ vs. $-24‰$), but less enriched in ^{15}N ($\delta^{15}N = 1.8‰$ vs. $4.0‰$). However, when dominated by pelagic algae, Ice-POM was enriched in ^{13}C and ^{15}N similarly to Pelagic-POM.

The derived trophic enrichment factors for $\delta^{15}N$ ($\Delta_N = 3.4‰$) and $\delta^{13}C$ ($\Delta_C = 0.6‰$) were similar in both pelagic and sympagic (ice-associated) systems, although the Δ_C for the sympagic system was variable.

Trophic level (TL) range for zooplankton (TL = 1.8–3.8) was similar to that of ice fauna (TL = 1.9–3.7), but ice amphipods were generally less enriched in $\delta^{15}N$ than zooplankton, reflecting lower $\delta^{15}N$ in Ice-POM compared to Pelagic-POM. For bulk zooplankton, TLs and carbon sources changed little seasonally, but the proportion of herbivores was higher during May–September than in October and March. Overall, we found that the primary carbon source for zooplankton was Pelagic-POM (mean 74%), but depending on species, season and TL, substantial carbon (up to 50%) was supplied from the sympagic system. For bulk ice fauna, no major changes were found in TLs or carbon sources from summer to autumn. The primary carbon source for ice fauna was Ice-POM (mean 67%), although ice fauna with TL > 3 (adult *Onisimus nanseni* and juvenile polar cod) primarily utilized a pelagic food source.

Keywords: Trophic enrichment; Particulate organic matter; Zooplankton; Ice fauna; Marginal ice zone; Barents Sea

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1. Introduction

Two potential carbon sources exist in the offshore Arctic marginal ice zone (MIZ); ice algae growing on the underside and within the sea ice and phytoplankton in open waters (Syvertsen, 1991; Legendre et al., 1992; Hegseth, 1998; Falk-Petersen et al., 2000a; Sakshaug, 2003). Ice and open water environments generally support different algal species (Syvertsen, 1991). Gran (1904) distinguished between obligate ice forms like *Nitzschia frigida* and *Melosira hyperborea* (now *M. arctica*) and planktonic forms such as *Chaetoceros* spp. and *Thalassiosira* spp. Ice algae start to grow in March, as light levels increase, and terminate growth when their sea ice substratum melts (Hegseth, 1998). In contrast, phytoplankton production in the MIZ starts after the onset of sea ice melting (Hegseth, 1998; Engelsen et al., 2002), giving a temporal discontinuity between sea-ice and open-water production.

Pelagic primary production is typified by short intense algal blooms trailing the ice edge as it melts and breaks up, and subsequently spreading throughout the MIZ (Gran, 1931; Sakshaug and Skjoldal, 1989; Engelsen et al., 2002). The ice edge-bloom begins in April/May at the southernmost fringes of the first-year ice, and as late as the beginning of September near the multi-year ice pack in the far north (Zenkevitch, 1963; Sakshaug and Slagstad, 1992; Hegseth, 1997). Ice algal production may equal the pelagic production in duration, although the production and biomass of phytoplankton usually exceeds that of ice algae (Hegseth, 1998). The Arctic ice algal production is patchy and highly variable, averaging 5–10 g C m^{-2} yr^{-1}, compared to the Arctic pelagic production of 12–50 g C m^{-2} yr^{1} depending on the extent of ice-free waters and latitude (Legendre et al., 1992; Gosselin et al., 1997; Hegseth, 1998). However, in the multi-year ice pack of the central Arctic Ocean, ice algae contribute on average 57% of the total primary production (Gosselin et al., 1997).

Ice algae may be a crucial seasonal food source for first-order consumers, particularly in areas with extensive ice cover. Ice algae are known as an important food source for sympagic organisms (Werner, 1997; Poltermann, 2001) and may supply and extend the restricted grazing season for Arctic zooplankton (e.g. Bradstreet and Cross, 1982; Conover et al., 1986; Runge and Ingram, 1991; Michel et al., 1996). During the long and unproductive winter, Arctic zooplankton and ice fauna may switch to alternate prey and/or rely on physiological mechanisms such as reduced metabolism, body shrinkage or use of internal lipid reserves stored the previous summer (Hagen and Auel, 2001; Werner and Auel, 2005; Lee et al., 2006). In the Antarctic, larval krill feed on the underside of the ice in winter, but too little algal food is available to maintain growth (Ross et al., 2004). While multiple mechanisms for surviving the long polar winter are possible, detailed information is limited (Sato et al., 2002; Ross et al., 2004; Werner and Auel, 2005).

The stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide a time-integrated measure of trophic position and have the potential to track energy or mass flows through food webs (Hobson and Welch, 1992; Hobson et al., 1995; Post, 2002). A consumer is typically enriched in ^{15}N by 3–4‰, relative to its diet (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Hobson and Welch, 1992), whereas ^{13}C undergoes relatively little fractionation (<1‰) with trophic level. The $\delta^{13}C$ values can therefore provide information on an organism's major carbon sources, provided that the available carbon sources have distinct $\delta^{13}C$ signatures (Post, 2002). Ice algae and phytoplankton normally have distinctly different $\delta^{13}C$ values, with ice algae being 2–10‰ more enriched in ^{13}C than phytoplankton (Hobson and Welch, 1992; Hobson et al., 1995; Hobson et al., 2002; Tamelander et al., 2006a). Despite the occurrence of both ice algae and phytoplankton in the Arctic MIZ, most Arctic stable isotope studies have used a one-source food web model to estimate trophic levels (Hobson and Welch, 1992; Hobson et al., 1995; Hobson et al., 2002; Iken et al., 2005; Tamelander et al., 2006a). Such a model assumes that organisms utilize exclusively phytoplankton or ice algal source pathways. This is an overly simplistic assumption in the MIZ, with a more realistic scenario being that both sympagic and pelagic production contribute to the overall autotrophic basis for the food web. Exchange of energy among the pelagic, sympagic (i.e. ice-associated) and benthic communities does occur in the Arctic (e.g. Hobson et al., 1995; Werner et al., 2004; Bauerfeind et al., 2005; Werner and Auel, 2005; Tamelander et al., 2006a), but the extent of energy exchange (i.e. coupling) between these components varies spatially and is not well described. Sympagic–pelagic coupling has received particularly little attention.

In the present study, we developed a stable isotope food web model for the European Arctic MIZ, based on the two-source food web model from Post (2002), using phytoplankton and ice algae as food web baselines, to determine trophic levels (TL) and seasonal carbon sources of key Arctic macrozooplankton and ice-fauna.

2. Materials and methods

We collected samples of particulate organic matter suspended in (Pelagic-POM) and settled from the water column (Sedimented-POM), and from the underside of the sea ice (Ice-POM), in addition to zooplankton and ice fauna, during several cruises from 1995 to 2001 to the Barents Sea MIZ and the MIZ north and west of Svalbard, and east of Greenland (Table 1, Fig. 1).

2.1. Particulate organic matter (POM)

In May and October 1999, Pelagic-POM was collected with multiple vertical hauls (0–30 m) with a plankton net (20 μm mesh size). In September 2000 (Stn. 1003), Pelagic-POM was sampled by pumping large volumes of sea water from ca. 6 m depth through a plankton net (20 μm mesh size). Sedimented-POM was sampled by sediment traps moored to the sea ice. The sediment trap consisted of two gimballed Plexiglas cylinders (72 mm θ, 450 mm high) with an aspect ratio of 6.25. The traps were placed at 25–30 m depth just below the pycnocline for 24 h. Ice-POM was collected by SCUBA divers using an electric suction pump equipped with a net of 20 μm mesh size (Lønne, 1988).

In total, 10 Pelagic-POM, 27 Ice-POM, and 6 Sedimented-POM samples were analyzed. A sub-sample of 100 ml from each suspended POM sample was preserved in 4% buffered formaldehyde for species determination. Quantitative POM community samples were analyzed by counting 10-ml sub-samples under an inverted microscope (Utermöhl, 1958). Qualitative POM community samples were analyzed under a microscope, and species identified were assigned relative abundance indices from present (x) to dominant (xxx). The POM community composition was thereafter categorized into major taxonomic groups (see Table 2); with diatoms divided into ice and pelagic diatoms, depending on their primary habitat (Hegseth, 1992; Hegseth, 1998; von Quillfeldt, 2000). Pelagic-, Ice- and Sedimented-POM were filtered onto pre-combusted (450 °C for 4 h) Whatman GF/C filters for stable isotope analysis. Zooplankton visible at 40× magnification were removed from the filter surface prior to freezing (−20 °C).

The stages of the algal bloom in May 1999 and March 2000 were obtained from Engelsen et al. (2002) and Søreide et al. (2003). The stages of the algal bloom at Stns. 882 and 890 were determined from the algal community composition (Booth and Smith, 1997; Booth et al., 2002) and the recent (<3 months) sea ice conditions (obtained from satellite data; Goodman, 1992). At Stns. 978 and 1003, the algal bloom stages were determined from the relative vertical distribution of chlorophyll-*a* recorded with a Sea Tech fluorometer attached to the CTD.

2.2. Zooplankton and ice fauna

Zooplankton was sampled in the upper 300 m by vertical hauls using plankton nets with various mesh sizes (180, 1000 and 1550 μm) and by oblique trawl hauls with a Tucker trawl (1 m^2 mouth opening and 1 mm mesh). Ice amphipods and polar cod (*Boreogadus saida*) were collected by SCUBA divers using electric suction pumps equipped with nets of 500 μm mesh and by hand held nets (5 mm mesh) on rods. Zooplankton and ice fauna were kept in seawater at ambient temperatures and examined under a stereo-microscope within 1–4 h after sampling. Organisms were identified to species, measured to nearest mm and sorted into different size classes or copepodite stages. *Calanus* specimens were identified to species using the prosome lengths in Unstad and Tande (1991). If necessary, several individuals were pooled to obtain sufficient material for analysis. Dead animals and specimens with visible stomach contents were not used for analysis. Whole zooplankton and ice amphipods, and dorsal muscle of polar cod were used for stable isotope analyses, and all samples were stored frozen at −20 °C until analysis.

Table 1
Sampling locations in the Barents Sea (BS), North (N), Northwest (NW) and Northeast (NE) of Svalbard and East (E) Greenland 1995–2001. Bottom (B.) depth, ice concentration (Ice conc.) in tenths, age of ice; First-year ice (FYI) and multi-year ice (MYI), and the algal bloom stage are given (nd, not determined)

Season	Date	Area	Stations	Latitude (N)	Longitude	B. depth (m)	Ice conc.	Ice type	Algal stage
Spring	05–21.05.99	BS	Al–A4, BI–B4, 68,76	75°52′–77°22′	27°00′–34°25′E	100–320	0–9/10	FYI	Pre- to late-bloom
Summer	17–21.06.99	BS	ICE la, 2a	77°60′–78°20′	34°10′–34°30′E	100–320	7–9/10	FYI/MYI	nd
Summer	27.07–08.08.99	BS	ICE lb–3b	78°32′–8l°33′	25°50′–33°48′E	100–320	3–6/10	FYI/MYI	Late-bloom
Summer	11.07.01	BS	D	81°14′	25°11′E	200	9/10	FYI/MYI	nd
Autumn	25–28.09.99	NE Svalbard	882	82°27′	33°l4′E	>2800	7–9/10	FYI/MYI	Bloom to late-bloom
Autumn	25–28.09.00	N-NW Svalbard	978, 1003	81°28′–80°29′	30°11′–07°40′E	342, 779	8/10	FYI/MYI	Late-bloom
Autumn	03–05.10.99	E Greenland	890	76°10′	07°36′W	330	7–9/10	FYI/MYI	Late to post-bloom
Winter	16–20.03.00	BS	Cl–C4	76°30′–78°21′	3l°26′–33°20′E	150–300	0–5/10	FYI	No bloom

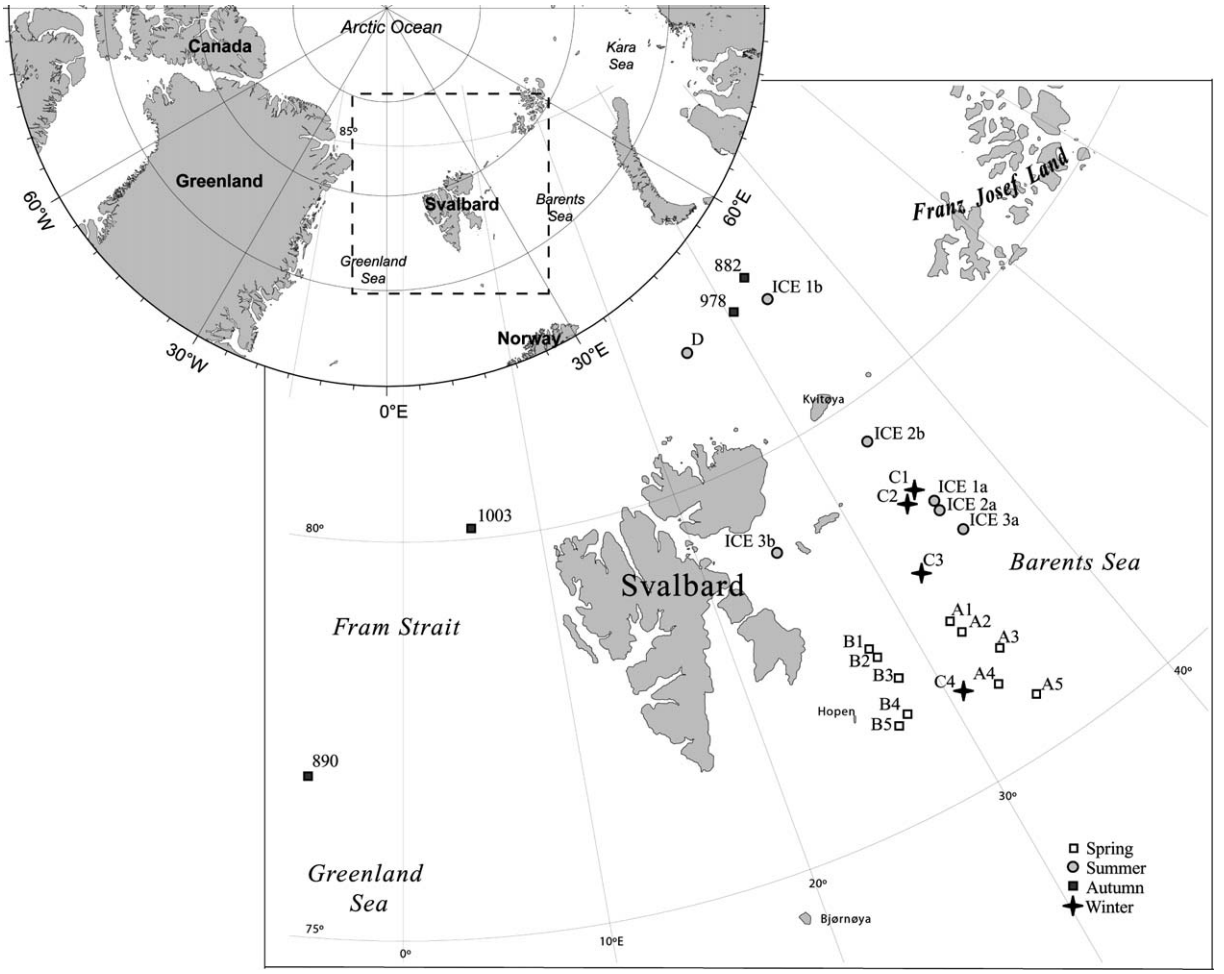

Fig. 1. Map of study area. See Table 1 for details.

2.3. Stable isotope analysis

Stable isotope analyses were performed at the Institute for Energy Technology (IFE) at Kjeller in Norway, as described in Dahl et al. (2003), including removal of lipids and non-dietary carbon (i.e. carbonates) from all samples prior to analysis. Lipids have a high turnover and are depleted in ^{13}C relative to other body compounds (DeNiro and Epstein, 1977; Griffiths, 1991; Sotiropoulos et al., 2004). To reduce differences in stable isotope composition due to variations in body lipid content (Attwood and Peterson, 1989; Hobson and Welch, 1992), and to make the C:N ratios more comparable among species, lipids were removed prior to analysis.

Stable isotope ratios were expressed in the conventional δ notation as the deviation from standards in ppt (‰) according to the following equation:

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

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. International standards, Pee Dee Belemnite for $\delta^{13}C$ (PDB: USGS 24), and atmospheric air for $\delta^{15}N$ (IAEA-N-1 and 2,) were used to determine R_{standard}. Replicate measurements of internal laboratory standards (muscle tissue of fish) generally run every 10 samples, indicated measurement errors of ±0.2‰ and ±0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Table 2
$\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of particulate organic matter (POM) from open waters (Pelagic), underside of the sea ice (Ice) and sedimenting particles below the pycnocline (Sedim.), sampled from different seasons, stations (Stn.), water depths (w. d.) and ice thicknesses (ice) in 1995–2001. Major POM taxonomic groups; ice and pelagic diatoms, *Phaeocystis pouchetii* (Phaeoc.), dinoflagellates (D. flg.), Flagellates/ciliates (Flag./ciliat.) and detritus (Detr.) are given in percentages of total cell abundance and of carbon cell biomass (in brackets), or as present (x) to abundant (xxx), in addition to the dominating algal species (nd = not determined)

POM	Season	Date	Stn.	w. d./ice (m)	*n*	Diatoms		Phaeoc.	D. flg.	Flag./ciliat.	Detr.	Algae situation	Dominating species	$\delta^{13}C$	$\delta^{15}N$
						Ice	Pelagic								
Pelagic	Spring	21.05.99	B4	0–30	3	1.5 (3.6)	43.4 (68.7)	52.5 (11.9)	1.1 (15.2)	1.4 (0.5)	nd	bloom/late-bloom	*Phaeocystis pouchetii* (*Thallassiosira* spp.)	−23.6 ± 0.0	4.3 ± 0.2
Pelagic	Spring	23.05.99	68, 76	0–50	2		xx	xxx			nd	bloom/late-bloom	*Phacocystis pouchetii*	−24.5 ± 0.0	3.4 ± 0.5
Pelagic	Autumn	27.09.99	882	0–40	1	48.5	51.5				nd	bloom/late-bloom	*Attheya septentrionalis*	nd	nd
Pelagic	Autumn	03.10.99	890	0–40	2	0.8	98.9	0.0	0.2	0.0	nd	late-/post-bloom	*Chaetoceros* spp.	−23.8 ± 0.0	5.7 ± 0.3
Pelagic	Autumn	28.09.00	1003	5	3		xx			xx	xx	late-bloom	Diatom-mix	−24.6 ± 0.2	3.9 ± 0.1
Ice (F)	Spring	11.05.99	A2	~0.5	3	36.7	55.0	8.2	0.0	0.1	nd	nd	*Fragilariopsis oceanica*	−24.3 ± 0.0	3.7 ± 0.2
Ice (O)	Spring	18.05.99	B2	1.5	3	96.7	3.0	0.0	0.2	0.0	nd	nd	*Nitzschia frigida*	−19.9 ± 0.1	2.4 ± 0.1
Ice (O)	Summer	18.06.95	ICE Ia	nd	2	xxx					nd	nd	*Melosira arctica*	−19.0 ± 0.1	0.9 ± 0.5
Ice (O)	Summer	11.07.01	D	1	2	xxx					nd	healthy condition	*Melosira arctica*	−20.0 ± 0.8	1.6 ± 0.3
Ice (–)	Summer	11.07.01	D	1	2	xxx					nd	moderate condition	*Melosira arctica*	−17.1 ± 0.9	4.3 ± 0.1
Ice (–)	Summer	11.07.01	D	1	2	xxx					nd	poor condition	*Melosira arctica*	−12.2 ± 0.3	7.4 ± 0.4
Ice (O)	Autumn	27.09.99	882	~1.5	3	86.8	9.7	0.0	0.7	2.8	nd	nd	*Nitzschia* spp.	−21.0 ± 0.2	4.2 ± 0.1
Ice (F)	Autumn	03.10.99	890	nd	6	9.2	89.3	0.0	0.8	0.7	nd	nd	*Chaetoceros* spp.	−23.5 ± 0.3	5.7 ± 0.3
Sedim.	Autumn	26.09.00	978	20	3	nd	nd	nd	nd	nd	nd	late summer-bloom	nd	−25.5 ± 0.3	3.5 ± 0.7
Sedim.	Autumn	28.09.00	1003	35	3	nd	nd	nd	nd	nd	nd	late summer-bloom	nd	−25.8 ± 0.6	3.2 ± 1.0

(O) = obligate Ice-POM, (F) = facultative Ice-POM and (–) = Ice-POM excluded from the food web baseline estimates in summer.

2.4. Two-source food web model

We assume that energy flows from primary producers through grazers and a chain of predators, generally from small to large organisms (i.e. the basic idea of the classical bottom-up food web), and that zooplankton and ice fauna potentially utilize energy originating from both phytoplankton (Pelagic-POM) and ice algae (Ice-POM). To calculate trophic levels (TL) and proportions (α) contributed by these two available carbon sources, we used food web models from Post (2002). Trophic level (TL) of a consumer was calculated from:

$$\mathrm{TL}_{\mathrm{consumer}} = \lambda + (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - [\delta^{15}\mathrm{N}_{\mathrm{pelagic}} \times \alpha + \delta^{15}\mathrm{N}_{\mathrm{ice}} \times (1-\alpha)])/\Delta_{\mathrm{N}} \quad (2)$$

where λ is the TL of primary producers, i.e. TL = 1, $\delta^{15}\mathrm{N}_{\mathrm{pelagic}}$ and $\delta^{15}\mathrm{N}_{\mathrm{ice}}$ relate to Pelagic-POM and Ice-POM, respectively, Δ_{N} is the estimated δ^{15}N enrichment value per TL, and α is the proportion of nitrogen in the consumer ultimately derived from Pelagic-POM. We assumed that carbon and nitrogen moved through the food web with a similar stoichiometry (Post, 2002), and used the two-member-mixing-model from Post (2002), with fractionation of ^{13}C per TL (Δ_{C}) included, which after reiterations gave:

$$\alpha = \frac{(\Delta_{\mathrm{N}}\delta^{13}\mathrm{C}_{\mathrm{consumer}} - \Delta_{\mathrm{C}}\delta^{15}\mathrm{N}_{\mathrm{consumer}} + \Delta_{\mathrm{C}}\delta^{15}\mathrm{N}_{\mathrm{ice}} - \Delta_{\mathrm{N}}\delta^{13}\mathrm{C}_{\mathrm{pelagic}})}{(\Delta_{\mathrm{N}}\delta^{13}\mathrm{C}_{\mathrm{pelagic}} - \Delta_{\mathrm{N}}\delta^{13}\mathrm{C}_{\mathrm{ice}} - \Delta_{\mathrm{C}}\delta^{15}\mathrm{N}_{\mathrm{pelagic}} + \Delta_{\mathrm{C}}\delta^{15}\mathrm{N}_{\mathrm{ice}})} \quad (3)$$

The food web isotopic baselines and Δ_{C} and Δ_{N} were estimated from samples collected during spring and summer, the peak productive season in the Arctic MIZ (Clarke and Peck, 1991; Dayton et al., 1994; Hegseth, 1998; Sakshaug, 2003). Mean δ^{13}C and δ^{15}N values of POM, consisting primarily of healthy pelagic algae (Pelagic-POM) and ice algae (Ice-POM) were used as food web baselines, and Δ_{C} and Δ_{N} were estimated from the mean isotopic differences between consumers and diets for species with well-known feeding behaviour. Only consumers with δ^{13}C values indicating dietary uptake from one carbon source, assessed from the general assumption of $\Delta_{\mathrm{C}} = 0$–1‰ and $\Delta_{\mathrm{N}} = 3$–4‰ (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Hobson and Welch, 1992), were used in the calculations. Any single trophic transfer is likely to exceed these generally assumed variability ranges for Δ_{C} and Δ_{N}, but $\Delta_{\mathrm{C}} = 0$–1‰ and $\Delta_{\mathrm{N}} = 3$–4‰ are robust and widely applicable assumptions when applied to food webs with multiple trophic pathways and many species (Post, 2002).

The robustness of the two-source food web model to changes in food web baseline values were tested by varying baseline δ^{13}C and δ^{15}N values within the variability ranges found for Pelagic-POM and Ice-POM in this study. The robustness of the two-source food web model to changes in trophic enrichment factors were tested within the variability ranges generally found for Δ_{C} and Δ_{N} (i.e. 0–1‰ and 3–4‰, respectively).

2.5. Data analysis

Species obtained from the same season (i.e. spring, summer, autumn or winter), but from different areas/stations and/or size groups were pooled if no significant differences in the δ^{13}C and δ^{15}N values were found. The predominant, seasonal feeding strategy for species/taxa was determined from their mean TLs (Eqs. (2) and (3)) using the feeding categories: herbivores (TL $\leqslant$ 2.3), omnivores (TL = 2.4–2.8), carnivores (TL = 2.9–3.3) and "top"-carnivores (TL = 3.4–3.8).

Statistical tests were performed using STATISTICA ver. 6.1. *T*-tests were used when comparing two independent groups, and one-way ANOVA with the post-hoc Tukey HSD and Unequal N HSD tests when comparing multiple groups with equal and unequal number of samples, respectively (Winer et al., 1991). If the variance between independent groups was not homogenous (Levene's test, $p < 0.05$), non-parametric statistics were applied. The Mann–Whitney *U* test was used when comparing two independent groups, and a Kruskal–Wallis ANOVA, with a post-hoc multiple comparison test, was applied for comparing multiple independent groups (Siegel and Castellan, 1988). The significance level for all tests was $p \leqslant 0.05$; only the *p*-values are given in the text.

2.6. Food web model comparisons

We compared TLs from the two-source food web model (Eqs. (2) and (3), $\Delta_N = 3.4‰$) with TLs from the commonly used one-source food web model of Hobson and Welch (1992):

$$TL = 1 + (\delta^{15}N_{consumer} - \delta^{15}N_{PP})/\Delta_N \quad (4)$$

where PP denotes primary producers (phytoplankton or ice algae, depending on the anticipated primary food source). We used the two-source food web model with and without fractionation of ^{13}C (i.e. $\Delta_C = 0.6$ and 0‰, respectively) and the one-source food-web model with this study's estimated Δ_N (i.e. 3.4‰) and the Δ_N (3.8‰) commonly used in Arctic marine food web studies (Hobson and Welch, 1992; Hobson et al., 1995; Iken et al., 2005). In addition, the α values estimated from the two-source food web model with and without fractionation of ^{13}C were compared.

Chi-square (χ^2) tests (Snedecor and Cochran, 1989) were used to test for homogeneity of sample frequencies in the selected feeding and carbon source categories for the different food web models.

3. Results

3.1. Particulate organic matter (POM)

Prymensiophytes (*Phaeocystis pouchetti*) and large pelagic diatoms (*Thalassiosira* spp.) dominated the spring bloom in May (Table 2). In September, near the multi-year ice pack, bloom to late-bloom situations prevailed, dominated by oceanic summer diatoms (*Nitzschia granii* and *Chaetoceros decipiens*) and farthest north (Stn. 882) by small ice-associated diatoms (*Attheya septentrionalis*). In October, on the east Greenland shelf (Stn. 890), a late- to post-bloom situation prevailed, dominated by small pelagic diatoms of the genus *Chaetoceros*.

Ice-POM was generally dominated by the typical ice diatoms *Nitzschia frigida* or *Melosira arctica* (obligate Ice-POM), but occasionally Ice-POM was dominated by pelagic-related algae such as *Fragilariopsis oceanica* and *Chaetoceros* spp. (facultative Ice-POM) (Table 2). The algal cell condition of Ice-POM in July 2001, dominated by *M. arctica*, was determined and categorized into healthy, moderate and poor. Healthy *M. arctica* were embedded in little "slime", i.e. polysaccharide mucus known as exopolymeric substances (EPS) (Krembs et al., 2002); *M. arctica* in moderate cell condition contained relatively more EPS; whereas the *M. arctica* in poor cell condition contained abundant EPS and had a lumpy consistency and brownish appearance.

3.1.1. Stable isotope composition of POM

Overall, Pelagic-POM ($n = 10$) and facultative Ice-POM ($n = 9$) had similar $\delta^{13}C$ and $\delta^{15}N$ values ($p \geqslant 0.517$), but were less enriched in ^{13}C and more enriched in ^{15}N than obligate Ice-POM ($n = 10$; Ice-POM dominated by *M. arctica* in moderate and poor condition excluded) ($p \leqslant 0.004$) (Table 2, Fig. 2). Sedimented-POM ($n = 6$) was less enriched in ^{13}C ($p \leqslant 0.007$), but had similar $\delta^{15}N$ values as Pelagic-POM, facultative and obligate Ice-POM ($p \geqslant 0.067$).

Pelagic-POM from productive waters in spring ($n = 5$) and autumn ($n = 9$) had similar $\delta^{13}C$ values ($p = 0.074$), but Pelagic-POM from October was 1.4–2.3‰ more enriched in ^{15}N than Pelagic-POM from May and September ($p \leqslant 0.049$).

Obligate Ice-POM was ~4–12‰ more enriched in ^{13}C than Pelagic-POM (Table 2, Fig. 2). Ice-POM dominated by *M. arctica* in poor condition was particularly enriched in ^{13}C, but the $\delta^{15}N$ values also gradually increased as the *M. arctica*-dominated Ice-POM samples degraded and became more embedded in EPS (Fig. 3).

Sedimented-POM from Stns. 978 and 1003 in autumn had similar $\delta^{13}C$ and $\delta^{15}N$ values ($p \geqslant 0.625$).

3.2. Two-source food web model

Mean stable isotope values of Pelagic-POM ($n = 5$), collected in the Barents Sea in spring, and obligate Ice-POM ($n = 9$), collected in the Barents Sea during spring and summer, were selected as isotopic baselines for phytoplankton and ice algae, respectively (Table 2 and Figs. 2, 4). Pelagic-POM and Ice-POM baselines were

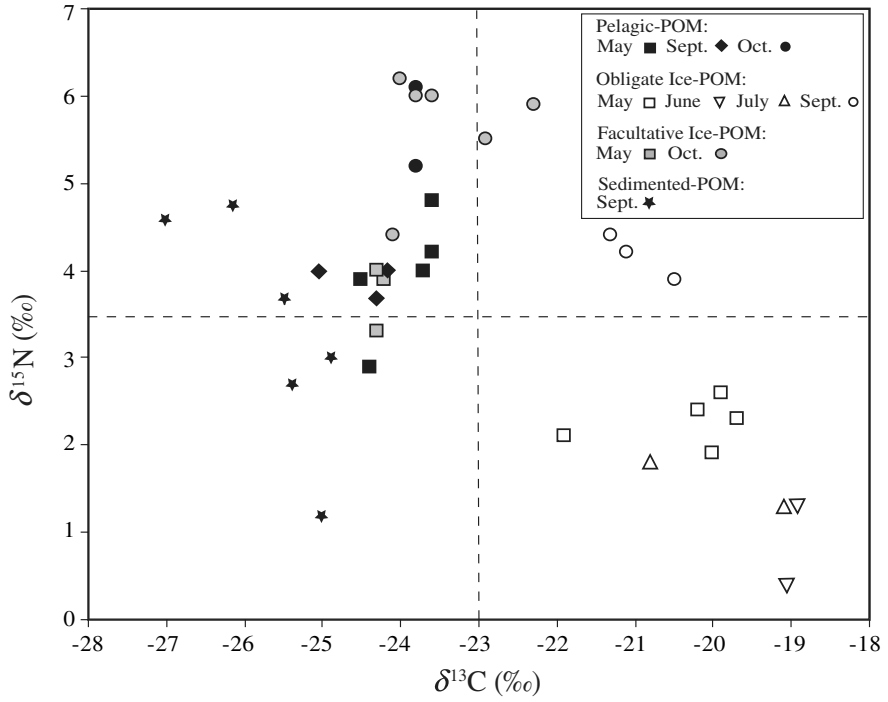

Fig. 2. Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) values of individual particulate organic matter (POM) samples collected in open water dominated by pelagic algae (Pelagic-POM) and from the underside of the sea ice, dominated by either ice diatoms (obligate Ice-POM) or pelagic algae (facultative Ice-POM). See Table 2 for details.

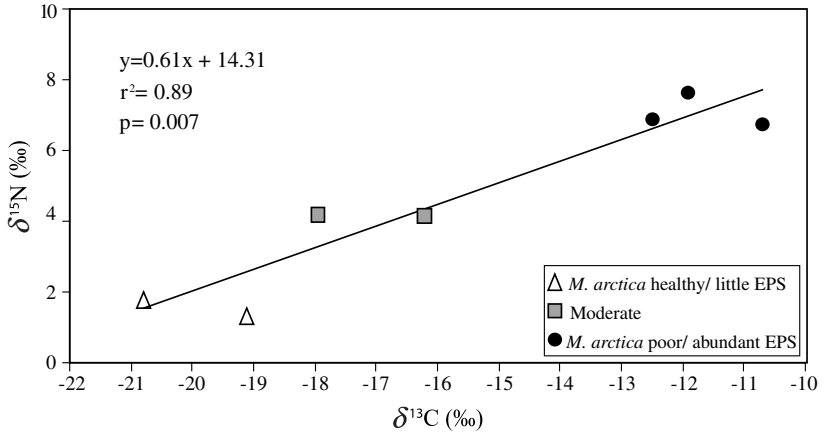

Fig. 3. Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) composition of Ice-POM from summer (Stn. D), consisting primarily of *Melosira arctica*, differentiated into three major categories depending on the algal cell condition (healthy to poor), and the relative amount of polysaccharide mucus known as exopolymeric substances (EPS).

distinctly different in their δ^{13}C and δ^{15}N values ($p \leqslant 0.001$), with Pelagic-POM baseline being 4‰ less enriched in ^{13}C and 2.2‰ more enriched in ^{15}N than Ice-POM baseline (mean $\delta^{13}C = -24.0 \pm 0.2$ vs. -20.0 ± 0.3‰ and mean $\delta^{15}N = 4.0 \pm 0.3$ vs. 1.8 ± 0.2‰, respectively).

The predominant herbivores and carnivores in the pelagic system during spring, those exclusively utilizing Pelagic-POM source pathways, were the copepods *Calanus glacialis* ($n = 4$) and *C. hyperboreus* ($n = 4$) (mean $\delta^{13}C = -23.3 \pm 0.2$‰, and mean $\delta^{15}N = 7.3$‰ ± 0.2‰), and the amphipod *Themisto libellula* ($n = 5$) (mean

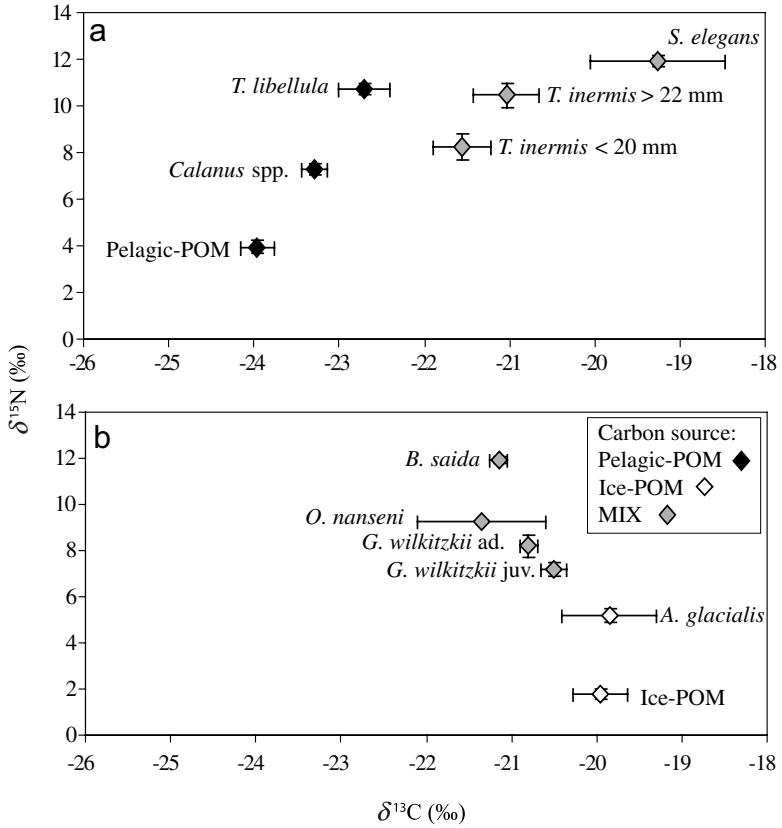

Fig. 4. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values (mean ± SE) of key components of the lower pelagic (a) and sympagic (b) food webs in the European Arctic during spring/summer. Organisms were categorized according to their major carbon source: phytoplankton (Pelagic-POM), ice algae (Ice-POM) or a mixture of the two (MIX). The organisms that primarily utilized Pelagic-POM or Ice-POM source pathways were used to calculate the trophic enrichment factors of $\delta^{13}C$ and $\delta^{15}N$ for the pelagic and sympagic systems, respectively.

$\delta^{13}C = -22.7 \pm 0.3‰$, and $\delta^{15}N = 10.7 \pm 0.2‰$) (Fig. 4), respectively. For the sympagic system, only the predominantly herbivorous ice amphipod *Apherusa glacialis* ($n = 4$) ($\delta^{13}C = -19.9 \pm 0.6‰$, and $\delta^{15}N = 5.2 \pm 0.3‰$) was found to mainly utilize Ice-POM source pathways (Fig. 4). The mean trophic enrichment factor per TL for $\delta^{15}N$ (Δ_N) was estimated to be 3.4‰ for both the pelagic ($3.36 \pm 17‰$) and sympagic ($3.39 \pm 0.34‰$) systems. The mean enrichment factor per TL for $\delta^{13}C$ (Δ_C) was estimated to be 0.6‰ for the pelagic system and 0.1‰ for the sympagic system. However, we determined Δ_C to be similar for both pelagic and sympagic systems, since the $\delta^{13}C$ values in *A. glacialis* used to calculate Δ_C for the sympagic system were variable, and since the difference in $\delta^{13}C$ between individual samples of consumers and the estimated food web baselines in the pelagic (mean $\Delta_C = 0.66 \pm 0.14‰$, $n = 13$) and the sympagic (mean $\Delta_C = 0.15 \pm 0.56‰$, $n = 4$) systems were not significantly different ($p = 0.184$).

3.2.1. Robustness of the two-source food web model

The TL estimates for zooplankton and ice amphipods did not differ significantly when we changed the $\delta^{13}C$ baselines by ±1‰ (Table 3). However, the proportion of Pelagic-POM vs. Ice-POM utilized by zooplankton increased (i.e. higher α) when the Pelagic-POM baseline increased from $\delta^{13}C = -24.0‰$ to $-23.0‰$, and decreased (i.e. lower α) when this baseline decreased from $\delta^{13}C = -24.0‰$ to $-25.0‰$. For ice amphipods, the proportion of Pelagic-POM food sources decreased when the Ice-POM baseline decreased from $\delta^{13}C = -20‰$ to $-21‰$.

The α estimates for zooplankton and ice amphipods did not differ significantly when we changed the $\delta^{15}N$ baselines by ±2‰, except for an increase in the estimated proportion of Ice-POM utilized by ice amphipods

Table 3
Comparison of trophic levels (TL) and proportions (α) of Pelagic- vs. Ice-POM source pathways (means ± SE) for zooplankton (zoopl.) and ice amphipods (Ice amph.), calculated from this study's two-source food web model (in bold) and from the two-source food web model when using other Pelagic- and/or Ice-POM food web baseline values (*p*-values given). Phytoplankton and ice algae, represented by samples of particulate organic matter from open water (Pelagic-POM) and the underside of the sea ice (Ice-POM), were used as food web baselines

Pelagie-POM		Ice-POM		Mean TL		*p*-value		Mean α		*p*-value	
$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	Zoopl.	Ice amph.	Zoopl.	Ice amph.	Zoopl.	Ice amph.	Zoopl.	Ice amph.
−24.0	**4.0**	**−20.0**	**1.8**	**2.7 ± 0.5**	**2.3 ± 0.0**			**0.74 ± 0.02**	**0.33 ± 0.03**		
−24.0	4.0	−19.0	1.8	2.7 ± 0.5	2.2 ± 0.0	1.000	0.959	0.79 ± 0.02	0.45 ± 0.02	1.000	0.070
−24.0	4.0	−21.0	1.8	2.8 ± 0.5	2.4 ± 0.0	1.000	0.625	0.66 ± 0.03	0.13 ± 0.04	0.601	<0.001
−23.0	4.0	−20.0	1.8	2.6 ± 0.5	2.2 ± 0.0	0.171	0.992	0.96 ± 0.03	0.42 ± 0.04	<0.001	0.721
−25.0	4.0	−20.0	1.8	2.8 ± 0.5	2.3 ± 0.0	1.000	1.000	0.60 ± 0.02	0.27 ± 0.02	<0.001	0.977
−24.0	4.0	−20.0	1.0	3.1 ± 0.5	2.6 ± 0.1	<0.001	<0.001	0.41 ± 0.02	0.10 ± 0.03	1.000	<0.001
−24.0	4.0	−20.0	2.4	2.7 ± 0.5	2.1 ± 0.0	1.000	0.790	0.73 ± 0.02	0.31 ± 0.03	1.000	1.000
−24.0	4.0	−20.0	4.0	2.6 ± 0.4	1.8 ± 0.1	0.021	<0.001	0.71 ± 0.02	0.26 ± 0.03	1.000	1.000
−24.0	6.0	−20.0	4.0	2.2 ± 0.5	1.7 ± 0.0	<0.001	<0.001	0.66 ± 0.02	0.24 ± 0.03	0.313	1.000

when the Ice-POM baseline decreased from $\delta^{15}N = 1.8‰$ to 1.0‰ (Table 3). In contrast to the α values, the TL estimates were sensitive to changes in the $\delta^{15}N$ baseline. When the Ice-POM baseline was reduced from $\delta^{15}N = 1.8‰$ to 1.0‰, the mean TL for both zooplankton and ice amphipods increased. When Pelagic-POM and Ice-POM had the same $\delta^{15}N$ (i.e. 4‰), no significant differences in TL for zooplankton were found, although significantly lower TLs were estimated for ice amphipods. By increasing the $\delta^{15}N$ baseline value by approximately 2‰ for both Pelagic-POM and Ice-POM (i.e. an autumn situation with $\delta^{15}N = 6‰$ and 4‰, respectively), the estimated TL for both zooplankton and ice amphipods became significantly lower.

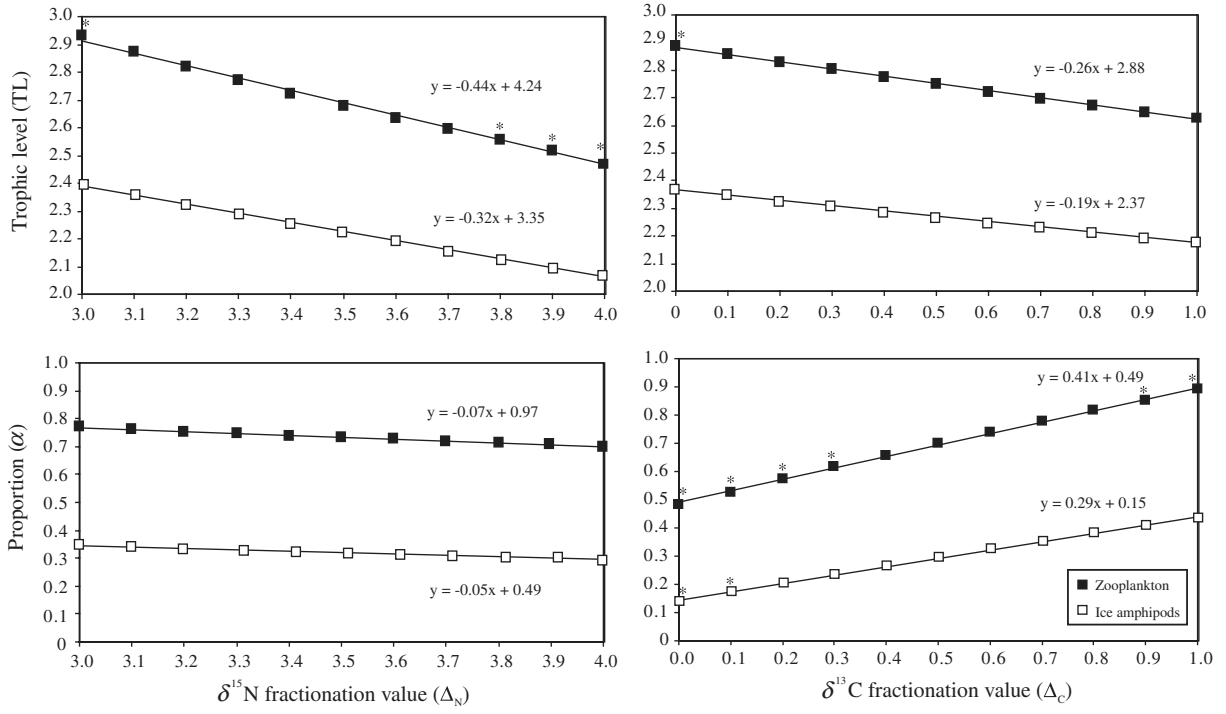

Fig. 5. Mean trophic levels (top panels), and mean proportion of Pelagic-POM vs. Ice-POM source pathways (bottom panels) for bulk zooplankton and ice amphipods, calculated from the two-source food web model when changing the trophic fractionation estimates of ^{13}C (Δ_C) and ^{15}N (Δ_N) respectively from 0 to 1‰ and 3 to 4‰. The TL and α labelled (*) were significantly different from the TL and α calculated from the two-source food web model when using this study's estimated Δ_C (0.6‰) and Δ_N (3.4‰).

The TL estimates were most sensitive to changes in Δ_N, and moderately sensitive to changes in Δ_C (Fig. 5). Increasing Δ_N and Δ_C resulted in somewhat lower TL for both zooplankton and ice amphipods. The α estimates were most sensitive to changes in Δ_C and not sensitive to changes in Δ_N.

3.3. Zooplankton and ice fauna

In May 1999, zooplankton did not differ significantly in their stable isotope composition between Transect A ($n = 25$) and Transect B ($n = 27$), between Atlantic ($n = 10$) and Arctic ($n = 39$) water masses ($p \geqslant 0.065$), among different ice-cover regimes ($n = 10$, 30 and 10 from ice categories 1/10, 4–7/10 and 7–9/10, respectively) ($p \geqslant 0.824$), or among different algal bloom situations ($n = 8$, 24 and 17 from pre-bloom, bloom and late-bloom situations, respectively) ($p \geqslant 562$) (for station details see Søreide et al., 2003), and were, thus, categorized into one group, i.e. spring (Table 4).

The zooplankton samples from June 1995 ($n = 6$) and July 1996 ($n = 12$) were similarly enriched in ^{13}C and ^{15}N ($p \geqslant 0.067$) and were categorized into one summer-group (Table 4). Ice amphipods from June 1995 ($n = 7$), July 1996 ($n = 16$) and July 2001 ($n = 6$) did not differ significantly in their $\delta^{13}C$ and $\delta^{15}N$ values ($p \geqslant 0.138$), and were also pooled as one summer group (Table 5).

Zooplankton from Stn. 882 ($n = 42$) were less enriched in ^{13}C and ^{15}N than zooplankton from Stn. 890 ($n = 36$) ($p \leqslant 0.004$), so zooplankton were divided into two separate autumn groups (Table 4). Too few zoo-

Table 4
Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values, and calculated trophic levels (TL) and proportions (α) of Pelagic vs. Ice-POM source pathways (means ± SE; minimum and maximum values in brackets) from this study's two-source food web model for bulk, herbivorous (TL ⩽ 2.3), omnivorous (TL = 2.4–2.8), carnivorous (TL = 2.9–3.3) and top-carnivorous (TL = 3.4–3.8) arctic macrozooplankton (>1 mm). Number of species (taxa) and samples (n) are given. The minimum and maximum values are based on mean species/taxa values. Zooplankton samples from Stns. 978 ($n = 3$) and 1003 ($n = 2$) in autumn were included in total zooplankton

Season	Species (taxa)		n	$\delta^{13}C$	$\delta^{15}N$	TL	α
Spring	Bulk	13 (13)	52	−21.9 ± 0.2 (−23.8/−19.3)	9.6 ± 0.2 (7.1–11.9)	2.9 ± 0.1 (1.9–3.8)	0.75 ± 0.05 (0.20–1.14)
	H	3 (3)	11	−23.4 ± 0.5 (−23.8/−23.0)	7.3 ± 0.2 (7.1–7.5)	2.0 ± 0.1 (1.9–2.1)	1.00 ± 0.10 (0.90–1.14)
	O	3 (3)	15	−22.3 ± 0.4 (−23.0/−22.0)	9.3 ± 0.4 (8.2–10.1)	2.7 ± 0.1 (2.5–2.8)	0.83 ± 0.08 (0.64–1.04)
	C	5 (5)	17	−21.5 ± 0.3 (−22.7/−19.7)	10.3 ± 0.2 (9.2–10.5)	3.1 ± 0.0 (2.9–3.2)	0.67 ± 0.07 (0.48–0.90)
	T	2 (2)	9	−20.3 ± 0.5 (−20.9/−19.3)	11.4 ± 0.0 (11.2–11.9)	3.5 ± 0.1 (3.4–3.8)	0.46 ± 0.10 (0.20–0.60)
Summer	Bulk	5 (5)	15	−21.9 ± 0.2 (−22.7/−20.5)	9.2 ± 0.3 (8.2–12.2)	2.7 ± 0.1 (2.3–3.7)	0.74 ± 0.05 (0.44–0.94)
	H	1 (1)	1	−22.1	8.0	2.3	0.73
	O	3 (3)	12	−22.1 ± 0.3 (−22.7/−20.6)	8.7 ± 0.1 (8.6–8.8)	2.5 ± 0.0 (2.5–2.7)	0.75 ± 0.06 (0.44–0.94)
	T	1 (1)	2	−20.5 ± 0.0	12.0 ± 0.0	3.7 ± 0.0	0.51 ± 0.01
Autumn (882)	Bulk	13 (14)	42	−22.5 ± 0.2 (−24.0/−20.5)	8.5 ± 0.2 (6.6–10.7)	2.4 ± 0.1 (1.8–3.2)	0.84 ± 0.05 (0.41–1.23)
	H	5 (5)	16	−22.7 ± 0.3 (−24.0/−21.2)	7.8 ± 0.3 (6.6–8.9)	2.2 ± 0.1 (1.8–2.3)	0.86 ± 0.08 (0.51–1.20)
	O	7 (7)	21	−22.7 ± 0.2 (−23.7/−21.5)	8.8 ± 0.2 (8.4–10.2)	2.5 ± 0.1 (2.4–2.7)	0.88 ± 0.05 (0.61–1.23)
	C	2 (2)	5	−21.1 ± 0.4 (−21.6/−20.5)	10 ± 0.5 (9.0–10.2)	3.0 ± 0.0 (2.9–3.2)	0.58 ± 0.10 (0.40–0.90)
Autumn (890)	Bulk	10 (11)	36	−21.7 ± 0.2 (−23.0/−20.0)	9.4 ± 0.2 (6.4–12.6)	2.7 ± 0.1 (2.0–3.8)	0.68 ± 0.05 (0.30–1.04)
	H	1 (1)	2	−21.6 ± 0.3	6.2 ± 0.4	2.0 ± 0.0	0.53 ± 0.04
	O	5 (5)	17	−22.1 ± 0.3 (−23.0/−21.4)	9.0 ± 0.2 (8.4–9.6)	2.6 ± 0.1 (2.4–2.8)	0.77 ± 0.06 (0.61–1.04)
	C	4 (4)	16	−21.1 ± 0.2 (−22.2/−20.0)	9.8 ± 0.3 (9.1–11.1)	3.0 ± 0.1 (2.9–3.2)	0.57 ± 0.05 (0.30–0.91)
	T	1 (1)	1	−20.8	12.6	3.8	0.61
Winter	Bulk	15 (15)	50	−21.7± 0.2 (−23.2/−19.7)	9.8 ± 0.1 (8.2–12.2)	2.9 ± 0.1 (2.2–3.71)	0.70 ± 0.05 (0.27–1.04)
	H	1 (1)	3	−23.2 ± 0.8	8.2 ± 0.2	2.2 ± 0.0	1.00 ± 0.19
	O	5 (5)	22	−22.4 ± 0.3 (−22.8/−21.9)	9.4 ± 0.2 (9.0–9.8)	2.7 ± 0.0 (2.7–2.8)	0.85 ± 0.06 (0.70–1.02)
	C	7 (7)	20	−20.9 ± 0.2 (−22.4/−19.7)	10.0 ± 0.1 (9.4–10.5)	3.1 ± 0.0 (2.9–3.2)	0.53 ± 0.06 (0.27–0.90)
	T	2 (2)	5	−20.3 ± 0.3 (−20.8/−19.7)	11.7 ± 0.3 (11.0–12.2)	3.6 ± 0.0 (3.4–3.8)	0.48 ± 0.08 (0.31–0.61)
Total	Bulk	17 (58)	203	−21.9 ± 0.1 (−24.0/−19.3)	9.3 ± 0.1 (6.4–12.6)	2.7 ± 0.0 (1.8–3.8)	0.74 ± 0.02 (0.20–1.23)
	H	6 (11)	36	−22.8 ± 0.2 (−24.0/−21.2)	7.5 ± 0.2 (6.4–8.9)	2.1 ± 0.0 (1.8–2.3)	0.88 ± 0.05 (0.50–1.20)
	O	11 (23)	94	−22.3 ± 0.1 (−23.7/−20.6)	9.1 ± 0.1 (8.2–10.2)	2.6 ± 0.0 (2.4–2.8)	0.82 ± 0.03 (0.44–1.23)
	C	13 (18)	57	−21.1 ± 0.1 (−22.7/−19.7)	10.1 ± 0.1 (9.0–11.0)	3.1 ± 0.0 (2.9–3.2)	0.59 ± 0.03 (0.27–1.02)
	T	3 (6)	16	−20.4 ± 0.3 (−20.9/−19.3)	11.6 ± 0.1 (11.0–12.6)	3.6 ± 0.5 (3.4–3.8)	0.47 ± 0.06 (0.20–0.65)

Table 5
As in Table 4, but for ice amphipods

Season	Species (taxa)		n	$\delta^{13}C$	$\delta^{15}N$	TL	α
Summer	Bulk	3 (5)	29	−20.5 ± 0.1 (−21.4/−18.3)	6.9 ± 0.2 (4.8–9.3)	2.3 ± 0.1 (1.9–2.8)	0.32 ± 0.03 (−0.28–0.64)
	H	2 (3)	15	−20.3 ± 0.2 (−20.5/−18.3)	6.1 ± 0.3 (4.8–6.5)	2.1 ± 0.1 (1.9–2.1)	0.25 ± 0.04 (−0.28–0.31)
	O	2 (2)	14	−20.7 ± 0.2 (−21.4/–20.6)	7.7 ± 0.3 (7.5–9.3)	2.5 ± 0.3 (2.4–2.8)	0.40 ± 0.04 (0.37–0.64)
Autumn	Bulk	4 (10)	33	−20.6 ± 0.2 (−21.9/−19.0)	6.7 ± 0.3 (5.7–12.8)	2.2 ± 0.1 (2.0–3.7)	0.33 ± 0.04 (0.01–0.92)
	H	3 (5)	26	−20.6 ± 0.2 (−21.1/−20.0)	6.0 ± 0.1 (5.7–6.7)	2.1 ± 0.0 (2.0–2.2)	0.30 ± 0.04 (0.01–0.40)
	O	3 (3)	4	−21.1 ± 0.7 (−22.0/−19.0)	8.0 ± 0.4 (7.6–8.2)	2.5 ± 0.1 (2.4–2.8)	0.49 ± 0.17 (0.01–0.73)
	C	1 (1)	2	−19.1 ± 0.9	8.9 ± 0.4	3.0 ± 0.2	0.07 ± 0.07
	T	1 (1)	1	−21.9	12.8	3.7	0.92
Total	Bulk	4 (15)	62	−20.6 ± 0.1 (−22.0/−18.3)	6.8 ± 0.2 (4.8–12.8)	2.3 ± 0.0 (1.9–3.7)	0.33 ± 0.03 (−0.28–0.92)
	H	3 (8)	41	−20.5 ± 0.1 (−21.1/−18.3)	6.1 ± 0.1 (4.8–6.7)	2.1 ± 0.0 (1.9–2.2)	0.29 ± 0.03 (−0.28–0.40)
	O	3 (5)	18	−20.6 ± 0.2 (−22.0/−19.0)	7.8 ± 0.2 (7.5–9.3)	2.5 ± 0.0 (2.4–2.8)	0.42 ± 0.05 (0.01–0.73)
	C	1 (1)	2	−19.1 ± 0.9	8.9 ± 0.4	3.0 ± 0.2	0.07 ± 0.07
	T	1 (1)	1	−21.9	12.8	3.7	0.92

plankton samples existed from Stns. 978 ($n = 3$) and 1003 ($n = 2$) to make meaningful comparisons. Ice amphipods from Stns. 882 ($n = 13$), 890 ($n = 12$) and 1003 ($n = 8$) did not differ significantly in their $\delta^{13}C$ and $\delta^{15}N$ values ($p \geqslant 0.089$) and were thus pooled as one autumn group (Table 5).

In March 2000, different zooplankton species were sampled at Stns. C2 ($n = 28$), C3 ($n = 15$) and C4 ($n = 5$), so only Stns. C2 and C3 with relatively many samples were meaningful to compare. Zooplankton from these two stations were similarly enriched in ^{13}C ($p = 0.734$), but zooplankton from Stn. C2 were less enriched in ^{15}N than zooplankton from Stn. C3 (9.4‰ vs. 10.4‰, $p = 0.003$). Nevertheless, we pooled all March zooplankton samples in one category, i.e. winter, since only significant differences in TL ($p = 0.030$) and not α ($p = 0.789$) were found between Stns. C2 and C3.

3.3.1. Seasonal patterns in zooplankton

Carnivorous and omnivorous taxa dominated in the large zooplankton fraction (Table 4). The proportion of herbivorous taxa was highest in spring and summer, and also at Stn. 882 in autumn (>20%), and lowest at Stn. 890 in autumn and in winter (<10%). No seasonal differences in $\delta^{13}C$, $\delta^{15}N$, TL and α were found for herbivorous, omnivorous, or carnivorous zooplankton ($p \geqslant 0.07$; only seasons with >3 samples per feeding category were compared). Herbivorous, omnivorous, carnivorous and top-carnivorous zooplankton were distinctly different in their $\delta^{15}N$ values ($p \leqslant 0.001$). Herbivorous and omnivorous zooplankton had similarly low $\delta^{13}C$ values and high α ($p \geqslant 0.233$), whereas carnivorous and top-carnivorous zooplankton had similarly high $\delta^{13}C$ values and relatively low α ($p \geqslant 0.218$).

For bulk zooplankton, no seasonal differences in α were found ($p = 0.129$), but zooplankton from Stn. 882 in autumn was more depleted in ^{13}C than zooplankton from Stn. 890 in autumn and winter ($p \leqslant 0.044$) (Table 4). Seasonal differences in $\delta^{15}N$ and TL for bulk zooplankton were not found, except for lower $\delta^{15}N$ and TLs in zooplankton from Stn. 882 in autumn ($p \leqslant 0.02$).

3.3.2. Seasonal patterns in ice amphipods

Herbivores dominated in summer and autumn, followed by omnivores (Table 5). No significant differences in $\delta^{13}C$, $\delta^{15}N$, α or TL from summer to autumn were found for herbivorous ($p \geqslant 0.412$), or omnivorous ice amphipods ($p \geqslant 0.476$). Carnivorous and top-carnivorous ice amphipods were few, and only found in autumn.

Herbivorous ice amphipods had similar $\delta^{13}C$ values as omnivorous ice amphipods ($p = 0.207$), but significantly lower α, $\delta^{15}N$ and TLs ($p \leqslant 0.019$). Too few carnivores and top-carnivores were sampled for meaningful comparisons. No differences in $\delta^{13}C$ and α or $\delta^{15}N$ and TL were found for bulk ice amphipods from summer to autumn ($p \geqslant 0.421$).

Overall, ice amphipods in summer and autumn were more enriched in $\delta^{13}C$ and less enriched in $\delta^{15}N$ than zooplankton in summer and at Stns. 882 and 890 in autumn ($p \leqslant 0.001$) (Tables 4 and 5).

Table 6
Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of dominating Arctic macrozooplankton species (>1 mm), their trophic level (TL) and proportion (α) of Pelagic- vs. Ice-POM source pathways calculated from this study's two-source food web model. Species obtained from the same season (i.e. spring, summer, autumn or winter), but from different areas/stations and/or size groups were pooled as long as no significant differences were found in their $\delta^{13}C$ or $\delta^{15}N$ values

Species	Size/stage	Season	Stn./area	*n*	$\delta^{13}C$	$\delta^{15}N$	TL	α
Calanus finmarchicus (cf)	CVIF	Spring	BS 99	3	-23.8 ± 1.9	7.4 ± 0.4	2.0 ± 0.4	1.14 ± 0.43
	CVIF	Autumn	890, 1003	5	-21.6 ± 0.1	6.4 ± 0.2	2.0 ± 0.1	0.50 ± 0.02
	CVIF	Winter	BS 00	2	-20.1 ± 0.4	9.7 ± 0.3	3.1 ± 0.0	0.35 ± 0.12
Calanus glacialis (cg)	CVIF	Spring	BS 99	4	-23.6 ± 0.2	7.1 ± 0.3	1.9 ± 0.1	1.00 ± 0.04
	CV, CVIF	Autumn	882	6	-21.2 ± 0.3	7.4 ± 0.3	2.3 ± 0.1	0.51 ± 0.07
	CVIF	Autumn	890, 978	6	-21.4 ± 0.3	9.1 ± 0.1	2.8 ± 0.0	0.63 ± 0.08
	CV	Autumn	890	3	-21.1 ± 0.2	10.2 ± 0.3	3.1 ± 0.1	0.61 ± 0.05
	CVIF	Winter	BS 00	3	-21.7 ± 0.7	9.7 ± 0.2	2.9 ± 0.1	0.73 ± 0.18
Calanus hyperboreus (ch)	CVIF	Spring	BS 99	4	-23.0 ± 0.2	7.5 ± 0.4	2.1 ± 0.1	0.90 ± 0.03
	CVIF	Summer	BS 96		-22.1	8.0	2.3	0.76
	CV, CVIF	Autumn	882	6	-24.0 ± 0.1	8.9 ± 0.2	2.3 ± 0.1	1.20 ± 0.02
	CV, CVIF	Autumn	890	6	-21.2 ± 0.2	9.4 ± 0.4	2.9 ± 0.1	0.60 ± 0.05
	CVIF	Winter	BS 00	3	-21.9 ± 0.8	9.3 ± 0.2	2.7 ± 0.1	0.70 ± 0.21
Paraeuchaeta norvegica (pn)	CVIF	Spring	BS 99	1	-20.6	9.8	3.1	0.48
	CVIF	Autumn	882	3	-21.6 ± 0.4	10.7 ± 0.6	3.2 ± 0.2	0.70 ± 0.10
	CVIF	Winter	BS 00	3	-20.7 ± 0.7	10.5 ± 0.3	3.2 ± 0.1	0.54 ± 0.10
Paraeuchaeta glacialis (pg)	CVIF	Autumn	882	3	-23.7 ± 0.1	10.2 ± 0.2	2.7 ± 0.1	1.23 ± 0.02
	CVIF	Autumn	890	3	-22.2 ± 0.4	11.1 ± 0.3	3.2 ± 0.1	0.91 ± 0.08
Thysanoessa inermis (ti)	10–19 mm	Spring	BS 99	6	-21.6 ± 0.3	8.2 ± 0.6	2.5 ± 0.1	0.64 ± 0.09
	>22 mm	Spring	BS 99	3	-21.0 ± 0.4	10.5 ± 0.5	3.2 ± 0.2	0.61 ± 0.08
	n.m.	Summer	BS 95,96	3	-20.6 ± 0.1	8.6 ± 0.1	2.7 ± 0.0	0.44 ± 0.02
	l6–19 mm	Autumn	882	3	-23.1 ± 0.8	6.9 ± 0.8	1.9 ± 0.3	0.97 ± 0.17
	>22 mm	Autumn	890	3	-20.0 ± 0.3	9.1 ± 0.1	3.0 ± 0.0	0.30 ± 0.08
	17–19 mm	Winter	BS 00	3	-21.9 ± 0.2	9.4 ± 0.1	2.8 ± 0.0	0.70 ± 0.06
Thysanoessa longicaudata (tl)	9–13 mm	Spring	BS 99	2	-20.8 ± 0.5	9.2 ± 0.1	2.9 ± 0.1	0.50 ± 0.12
	12–17 mm	Autumn	882, 890	7	-22.5 ± 0.4	8.4 ± 0.4	2.4 ± 0.2	0.80 ± 0.09
	12–13 mm	Winter	BS 00	3	-22.1 ± 0.3	9.2 ± 0.2	2.7 ± 0.1	0.81 ± 0.07
Themisto abyssorum (ta)	6–9 mm	Autumn	882, 978	2	-23.1 ± 0.1	6.6 ± 0.1	1.8 ± 0.0	0.90 ± 0.03
	9–15 mm	Autumn	882, 890	4	-22.9 ± 0.3	8.6 ± 0.2	2.4 ± 0.0	0.93 ± 0.08
	12–15 mm	Winter	BS 00	3	-19.7 ± 0.0	11.0 ± 0.1	3.5 ± 0.0	0.31 ± 0.00
Themisto libellula (tli)	26–27 mm	Spring	BS 99	5	-22.7 ± 0.3	10.7 ± 0.2	3.0 ± 0.1	1.02 ± 0.07
	n.m.	Summer	BS 96	6	-22.7 ± 0.1	8.7 ± 0.2	2.5 ± 0.0	0.94 ± 0.03
	11–17 mm	Autumn	882	3	-21.5 ± 0.1	8.5 ± 0.6	2.6 ± 0.2	0.63 ± 0.01
	13–26 mm	Autumn	890	6	-23.0 ± 0.5	9.6 ± 0.4	2.7 ± 0.1	1.04 ± 0.13
	15–26 mm	Winter	BS 00	3	-22.8 ± 0.7	9.8 ± 0.5	2.7 ± 0.2	1.02 ± 0.10
Hyperia galba (hg)	<10 mm	Spring	BS 99	2	-21.2 ± 0.4	9.9 ± 0.5	3.0 ± 0.1	0.62 ± 0.10
	<10 mm	Winter	BS 00	3	-22.4 ± 0.2	10.5 ± 0.2	3.0 ± 0.1	0.90 ± 0.05
Aglantha digitale (ad)	13–21 mm	Spring	BS 99	6	-21.0 ± 0.4	10.4 ± 0.1	3.2 ± 0.1	0.60 ± 0.11
	l4–16 mm	Winter	BS 00	3	-19.7 ± 0.6	9.6 ± 0.4	3.1 ± 0.1	0.27 ± 0.17
Beroë cucumis (bc)	15–45 mm	Spring	BS 99	6	-20.9 ± 0.5	11.2 ± 0.2	3.4 ± 0.1	0.60 ± 0.11
	70–80 mm	Autumn	882	2	-20.5 ± 0.6	9.0 ± 0.1	2.9 ± 0.1	0.41 ± 0.16
	70–80 mm	Winter	BS 00	3	-20.8 ± 0.3	10.3 ± 0.3	3.2 ± 0.1	0.54 ± 0.07
Mertensia ovum (mo)	n.m.	Spring	BS 99	2	-23.0 ± 0.6	9.7 ± 0.4	2.7 ± 0.2	1.04 ± 0.14
	15–45 mm	Autumn	882	2	-22.5 ± 0.6	8.1 ± 0.4	2.3 ± 0.0	0.80 ± 0.17
	35–40 mm	Winter	BS 00	3	-23.2 ± 0.8	8.2 ± 0.2	2.2 ± 0.2	1.04 ± 0.18
Clione limacina (cl)	10–40 mm	Spring	BS 99	7	-22.8 ± 0.6	10.1 ± 0.3	2.8 ± 0.1	1.02 ± 0.14
	n.m.	Summer	BS 95, 96	3	-22.3 ± 0.3	8.8 ± 0.4	2.5 ± 0.1	0.80 ± 0.08
	35 mm	Autumn	882	2	-22.8 ± 0.1	8.6 ± 0.3	2.4 ± 0.1	0.90 ± 0.04
	20–40 mm	Winter	BS 00	6	-22.5 ± 0.6	9.4 ± 0.2	2.7 ± 0.1	0.91 ± 0.10

Table 6 (*continued*)

Species	Size/stage	Season	Stn./area	*n*	$\delta^{13}C$	$\delta^{15}N$	TL	α
Limacina helicina (lh)	10 mm*	Autumn	882	3	-22.6 ± 0.2	8.7 ± 0.2	2.5 ± 0.1	0.91 ± 0.04
Eukrohnia hamata (eh)	15–30 mm	Autumn	882, 890	5	-21.5 ± 0.2	8.6 ± 0.2	2.6 ± 0.1	0.61 ± 0.06
	15–30 mm	Winter	BS 00	2	-20.3 ± 0.2	9.4 ± 0.0	3.0 ± 0.0	0.36 ± 0.04
Sagitta elegans (se)	30–40 mm	Spring	BS 99	3	-19.3 ± 0.8	11.9 ± 0.2	3.8 ± 0.1	0.20 ± 0.19
	n.m.	Summer	BS 95	2	-20.5 ± 0.0	12.0 ± 0.0	3.7 ± 0.0	0.54 ± 0.01
	26–30 mm	Autumn	890	1	-20.8	12.6	3.8	0.65
	30–40 mm	Winter	BS 00	3	-20.8 ± 0.3	12.2 ± 0.1	3.7 ± 0.0	0.62 ± 0.07

n.m., not measured.
BS, Barents Sea.
* Shell diameter.

3.3.3. Seasonal patterns at species level

The zooplankton species *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* changed one or more TL between seasons, while the krill *Thysanoessa inermis*, and the amphipod *Themisto abyssorum* varied by one or more TL between size groups (Table 6, Fig. 6). Among ice fauna, only *Onisimus nanseni* changed markedly in TL, with a 2× TL difference between small and large specimens in autumn (Table 7, Fig. 6). The other species changed by TL $\leqslant 0.5$ among seasons or size groups.

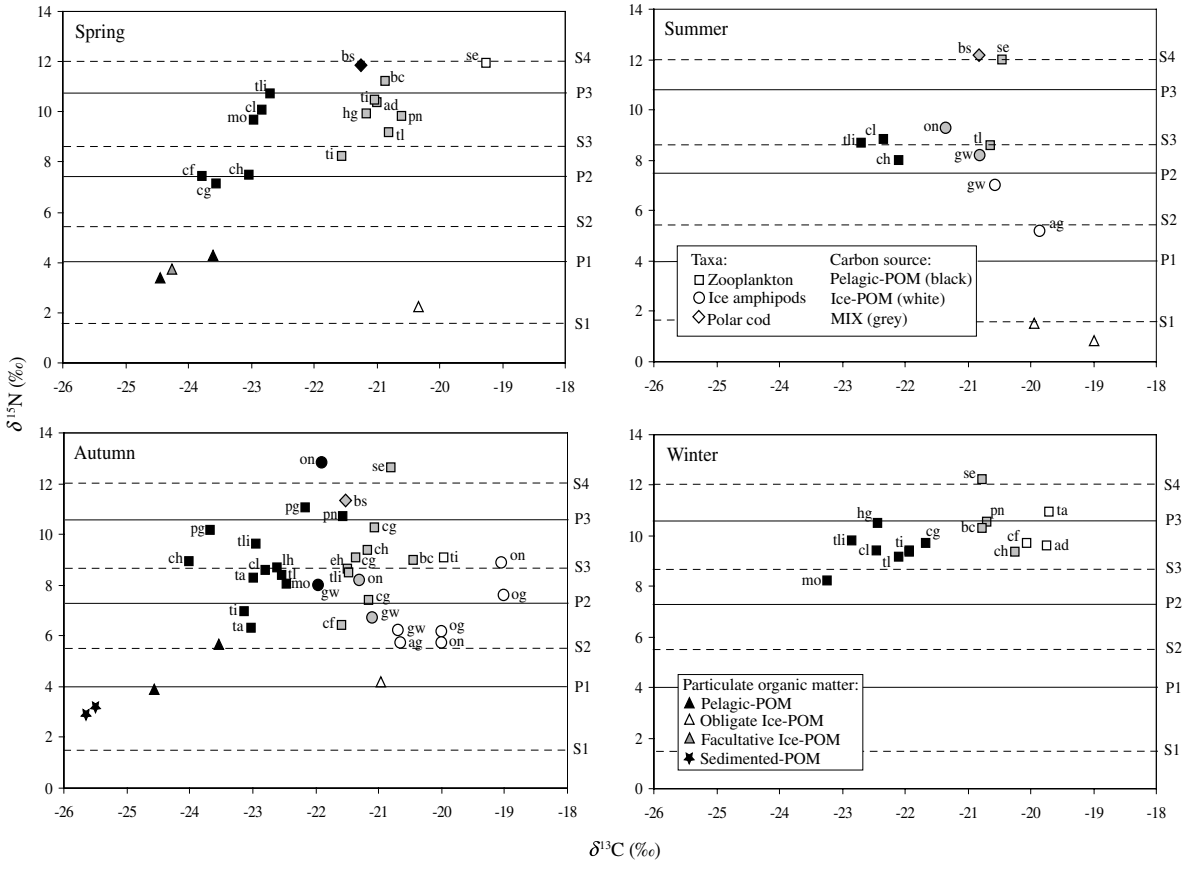

Fig. 6. Seasonal overview of the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values (means) of species/taxa (see Tables 6 and 7 for abbreviations and details). Species with $\alpha \geqslant 0.7$, $\alpha = 0.4$–0.6 and $\alpha \leqslant 0.3$ were assumed to primarily utilize Pelagic-POM, mixed Pelagic- and Ice-POM (MIX) and Ice-POM source pathways, respectively. Trophic levels for the pelagic (P) and sympagic (S) systems are marked on the opposite *y*-axis.

Table 7
As in Table 6, but for dominating Arctic ice fauna (>1 mm)

Species	Size stadium	Season	Stn./area	*n*	$\delta^{13}C$	$\delta^{15}N$	TL	α
Apherusa glacialis (ag)	Juv.–Ad.	Summer	BS 96	3	-19.9 ± 0.6	5.2 ± 0.3	1.9 ± 0.0	0.10 ± 0.05
	5–13 mm	Autumn	882, 890, 1003	7	-20.6 ± 0.3	5.7 ± 0.2	2.0 ± 0.1	0.32 ± 0.07
Gammarus wilkitzkii (gw)	Juv.	Summer	BS 95, 96	11	-20.5 ± 0.2	6.5 ± 0.3	2.1 ± 0.1	0.31 ± 0.04
	Ad. up to 40 mm	Summer	BS 95, 96, 01	12	-20.6 ± 0.1	7.5 ± 0.2	2.4 ± 0.1	0.37 ± 0.03
	10–41 mm	Autumn	882, 1003	15	-20.7 ± 0.2	6.2 ± 0.1	2.1 ± 0.0	0.30 ± 0.06
	35–62 mm	Autumn	890	2	-22.0 ± 0.3	8.0 ± 0.8	2.4 ± 0.2	0.73 ± 0.09
Onisimus glacialis (og)	7–8 mm	Autumn	890	2	-20.0 ± 0.8	6.2 ± 0.4	2.2 ± 0.0	0.04 ± 0.20
	10–11 mm	Autumn	890	1	−21.1	6.7	2.2	0.40
	12 mm	Autumn	890	1	−19.0	7.6	2.7	0.01
Onisimus nanseni (on)	Juv–ad	Summer	BS 95, 96	2	-21.4 ± 0.8	9.3 ± 0.0	2.8 ± 0.1	0.64 ± 0.20
	6–8 mm	Autumn	890	1	−20.0	5.7	2.0	0.16
	16 mm	Autumn	890	1	−21.3	8.2	2.5	0.58
	18 mm	Autumn	890	1	−21.9	12.8	3.7	0.92
	20–21 mm	Autumn	882	2	-19.1 ± 0.9	8.9 ± 0.4	3.0 ± 0.2	0.07 ± 0.19
Boreogadus saida (bs)	n.m.	Spring	B5 99	13	-21.2 ± 0.1	11.8 ± 0.1	3.5 ± 0.0	0.72 ± 0.02
	n.m.	Summer	BS 95	4	-20.8 ± 0.2	12.2 ± 0.4	3.7 ± 0.1	0.64 ± 0.04
	99–112 mm	Autumn	882	3	-21.5 ± 0.3	11.3 ± 0.2	3.3 ± 0.0	0.70 ± 0.07

n.m., not measured; BS, Barents Sea; Juv., juvenile; Ad., adult.

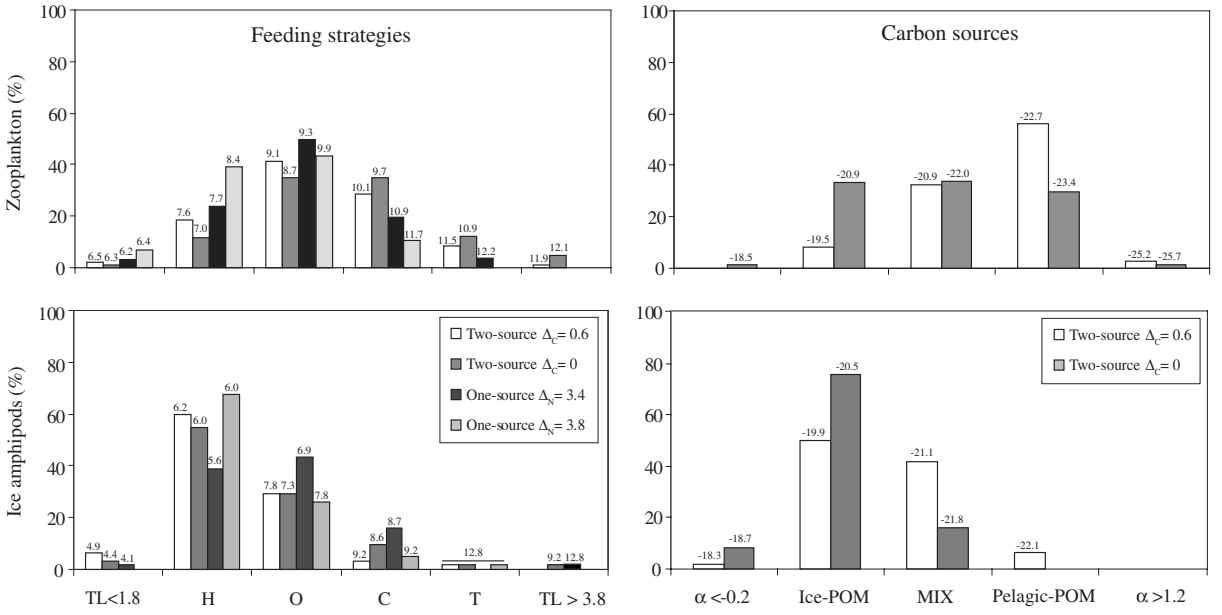

Fig. 7. Distributions of zooplankton ($n = 203$) and ice amphipod samples ($n = 62$) with regard to feeding strategies (left panels): herbivores (TL = 1.8–2.3), omnivores (TL = 2.4–2.8), carnivores (TL = 2.9–3.3) and top-carnivores (TL = 3.4–3.8), and primary carbon sources (right panels): Pelagic-POM ($\alpha = 0.7$–1.2), Ice-POM ($\alpha = -0.2$–0.3), and a mixture (MIX) of them ($\alpha = 0.4$–0.6). Values were calculated from this study's two-source food web model with ($\Delta_C = 0.6‰$) and without trophic fractionation of $\delta^{13}C$ ($\Delta_C = 0‰$), and from the one-source food web model (Hobson and Welch, 1992) with this study's $\delta^{15}N$ trophic fractionation value ($\Delta_N = 3.4‰$) and the Δ_N (3.8‰) used in Hobson and Welch (1992). Mean $\delta^{15}N$ values for each feeding strategy, and mean $\delta^{13}C$ for each carbon source, are shown above the bars.

Zooplankton that switched between mainly utilizing Pelagic-POM ($\alpha \geqslant 0.7$) and Ice-POM ($\alpha \leqslant 0.3$) source pathways were *C. finmarchicus*, *T. inermis* and *T. abyssorum*. No zooplankton species were found to exclusively utilize Ice-POM, but *Paraeuchaeta norvegica*, *Aglantha digitale*, *Beroë cucumis*, *Eukrohnia hamata*

and *Sagitta elegans* mainly utilized mixed Pelagic-POM and Ice-POM (MIX) source pathways ($\alpha = 0.4$–0.6). The other zooplankton primarily utilized a Pelagic-POM based carbon source, or occasionally a mixture (e.g. *C. glacialis*). Ice amphipod species that switched between mainly utilizing Ice- and Pelagic-POM source pathways were *Gammarus wilkitzkii* and *O. nanseni*. The other two, *Apherusa glacialis* and *Onisimus glacialis*, utilized primarily Ice-POM as carbon source.

The stable isotope composition of juvenile polar cod changed little with seasons. It occupied TL = 3.3–3.7, utilizing primarily Pelagic-POM source pathways ($\alpha = 0.7$, mean for spring, summer and autumn).

3.4. Food web model comparisons

3.4.1. Zooplankton

Lowest TLs were calculated from the one-source food web model with $\Delta_N = 3.8‰$, and highest TLs from the two-source food web model assuming no fractionation of ^{13}C (i.e. $\Delta_C = 0‰$) (mean TL = 2.4 and 2.9, respectively; $n = 203$). The one-source food web model with $\Delta_N = 3.4‰$ and the two-source food web model with $\Delta_C = 0.6‰$ calculated only slightly different TLs (mean TL = 2.6 and 2.7, respectively; $n = 203$).

The frequency distribution of samples in the different feeding categories (Fig. 7) were significantly different among the four models ($\chi^2 = 134.68$, df = 15, $p \leqslant 0.001$). The one-source food web models gave higher percentages of herbivores and omnivores, and lower percentages of carnivores than the two-source food-web models. In particular, the one-source food web model with $\Delta_N = 3.8‰$ calculated high proportions of herbivores compared to the two-source food web model both with and without fractionation of ^{13}C (39% vs. 19% and 11%, respectively). The one-source food web model with $\Delta_N = 3.8‰$ determined ca. 7% of the zooplankton samples to have unrealistically low TLs (<1.8), whereas <3% of the zooplankton samples were estimated to have such low TLs in the other models.

3.4.2. Ice amphipods

The two-source food web model with and without fractionation of ^{13}C, and the one-source food web model with $\Delta_N = 3.8‰$ produced similar TLs (mean TL = 2.3, 2.4 and 2.3, respectively; $n = 63$) and similar relative proportions of herbivores (58–66%), omnivores (25–29%) and carnivores (3–9%) ($\chi^2 = 9.4$, df = 10, $p \leqslant 1$; Fig. 7). The one-source food web model with $\Delta_N = 3.4‰$, however, calculated slightly higher TLs (mean TL = 2.5, $n = 63$) with lower proportion of herbivores (38%) and higher proportions of omnivores (29%) and carnivores (16%) compared to the other models ($\chi^2 = 25.4$, df = 15, $p \leqslant 0.05$). However, the $\delta^{15}N$ values for herbivores, omnivores and carnivores did not differ significantly among the four models ($p \geqslant 0.189$).

3.4.3. Carbon sources

The proportions of zooplankton primarily utilizing Pelagic-POM, Ice-POM or MIX (Fig. 7) were significantly different between the two-source food web model applied with and without fractionation of ^{13}C ($\chi^2 = 51.4$, df = 4, $p \leqslant 0.001$). The two-source food web model with $\Delta_C = 0.6‰$ determined Pelagic-POM to be the most important carbon source for zooplankton, whereas the two-source food web model excluding Δ_C (i.e. $\Delta_C = 0‰$) determined that Pelagic-POM, Ice-POM and MIX were equally important source pathways for zooplankton.

The proportions of ice amphipods primarily utilizing Pelagic-POM, Ice-POM or MIX (Fig. 7) were also significantly different between the two models ($\chi^2 = 17.1$, df = 3, $p \leqslant 0.001$). According to the two-source food web model with $\Delta_C = 0.6‰$, Ice-POM and MIX were similarly important carbon source pathways for ice amphipods, whereas the two-source food web model excluding Δ_C determined Ice-POM to be the major carbon source for ice amphipods during summer and autumn.

4. Discussion

Because ^{13}C has not shown a predictable stepwise enrichment pattern similarly to ^{15}N in Arctic marine organisms, it is generally disregarded as a quantitative tracer for trophic position (i.e. Hobson and Welch, 1992; Hobson et al., 1995; Hobson et al., 2002; Iken et al., 2005; Tamelander et al., 2006a). However, this study's two-source food web model showed that the combined $\delta^{13}C$ and $\delta^{15}N$ values gave realistic estimates

of trophic levels for zooplankton (TL = 1.8–3.8), comparable to those reported for zooplankton in the above studies, in addition to realistic estimates of major carbon sources for zooplankton and ice fauna without *a priori* assumptions. For ice amphipods, our two-source food web model calculated generally higher and more realistic TLs (1.9–3.7) than those previously reported from the Barents Sea (TL = 0.9–2.1) (Hop et al., 2002; Tamelander et al., 2006a).

The importance of ice algae as a carbon source for zooplankton is not well described. The proportion of Pelagic-POM and Ice-POM utilized by zooplankton and ice amphipods in our study did, however, support the general understanding that Pelagic-POM is the primary carbon source for zooplankton and Ice-POM for ice amphipods. However, a significant proportion of Ice-POM source pathways was found in several zooplankton species, particularly in carnivorous zooplankton. Conversely, Pelagic-POM was shown to be an important additional carbon source for ice amphipods, particularly for those with TL > 2.4. Juvenile polar cod (ages 1 and 2) use the sea ice as a feeding site and as a refuge to avoid predators. Their diet, however, consists primarily of pelagic copepods and hyperiid amphipods (Lønne and Gulliksen, 1989; Scott et al., 1999), which was supported in our study by a relatively high α (0.6–0.7) and high TL (3.3–3.7). Their diet may also include ice amphipods, particularly in multi-year ice (Lønne and Gulliksen, 1989).

One important assumption for the two-source food web model is that carbon and nitrogen move through the food web with similar stoichiometry, an assumption which is only acceptable when working with organisms with similar C:N (Post, 2002). However, high latitude organisms may experience relatively large differences in C:N among species, developmental stages and seasons due to differences in body lipid content (Lee, 1974; Hagen, 1999; Walve and Larsson, 1999; Matthews and Mazumder, 2005). Lipids have a high turnover (Attwood and Peterson, 1989; Graeve et al., 1994; Graeve et al., 2004) and are strongly depleted in ^{13}C relative to other body components (Sato et al., 2002; van Dongen et al., 2002; Sotiropoulos et al., 2004). In particular, herbivorous zooplankton accumulate large lipid stores during spring and summer, whereas carnivores generally store less lipids because they experience less seasonal resource limitation (Falk-Petersen et al., 1990; Clarke and Peck, 1991; Lee et al., 2006). The nitrogen content, however, is more or less independent of the lipid content and is relatively stable, constituting 5–10% of dry weight (Omori and Ikeda, 1984; Walve and Larsson, 1999; Postel et al., 2000). The significantly lower $\delta^{13}C$ values in herbivorous and omnivorous zooplankton compared to carnivorous zooplankton in our study may suggest that removal of lipids was not sufficient in order to obtain comparable C:N between herbivores and carnivores. However, a similar variability and range in the $\delta^{13}C$ values was found in lipid-rich (e.g. *Calanus* spp. and *Thysanoessa* spp.) and relatively lipid-poor zooplankton (e.g. *Clione limacina*, *Eukrohnia hamata*, *Mertensia ovum*). Dietary quality may also influence the stable isotope fractionation (Adams and Sterner, 2000; Scott et al., 2003; Robbins et al., 2005). Vander Zanden and Rasmussen (2001) found lower Δ_C, and Δ_N, in herbivores than in carnivores, although Post (2002) did not. However, Post (2002) did find larger variability in Δ_C for herbivore-detritivores than for carnivores.

The ranges in $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton and ice amphipods in our study were within the ranges found for zooplankton and ice amphipods in the Canadian Arctic (Hobson and Welch, 1992), northern Baffin Bay (Hobson et al., 2002), the Northeast Water Polynya of Greenland (Hobson et al., 1995) and in the Barents Sea (Tamelander et al., 2006a). Zooplankton and ice amphipods from Canada Basin had similar $\delta^{15}N$ values, but much lower $\delta^{13}C$ values (Iken et al., 2005), which most likely can be explained by lack of lipid removal prior to stable isotope analyses in their study in contrast to the others. The few stable isotope data existing for zooplankton in winter, from Fram Strait and West-Spitsbergen waters in January (Sasaki et al., 2001; Sato et al., 2002), were comparable to our copepod stable isotope data from the Barents Sea in March.

We removed lipids not only from the animal tissue samples, but also from the POM samples, which makes it difficult to compare our POM $\delta^{13}C$ values with those of other studies, except for the study by Tamelander et al. (2006a) from the Barents Sea in July, who also analyzed lipid-extracted POM samples. Algae may contain 5–20% lipids, depending on the algal growth stage (Siegenthaler and Murata, 1998). POM may also contain a significant proportion of animal remains and/or micro-heterotrophs, which additionally influence the total POM lipid content. For instance Hobson et al. (1995) found a relatively large gap between the $\delta^{13}C$ values of non-lipid-extracted POM samples ($< -27.7‰$) and lipid-extracted zooplankton samples ($> -24.2‰$) from the Northeast Water Polynya of Greenland, which may indicate presence of ^{13}C-depleted terrestrial organic matter in the POM samples (Gõni et al., 2000) or $\delta^{13}C$-depleted POM due to presence of lipids.

However, the $\delta^{15}N$ values in our lipid-extracted POM samples should be comparable to the $\delta^{15}N$ values in non-lipid-extracted POM samples, since the N-content is largely independent of the lipid content.

In our study, POM taxonomic data were important for interpreting POM $\delta^{15}N$ and $\delta^{13}C$ values. Although qualitative POM community analysis may have led to under- or overestimates of some of the POM taxonomic groups in Table 2, the major community pattern in these POM samples were most likely identified. A different sampling technique for Pelagic-POM was used at Stn. 1003 in autumn (pump) than at the other stations (net). Sampling from one depth (~6 m) at Stn. 1003, compared to the integrated upper 30 m at the other stations, may have given less representative $\delta^{13}C$ and $\delta^{15}N$ values for Pelagic-POM available for zooplankton at Stn. 882 compared to the rest. However, this had little impact on the overall interpretation of the results, since the Pelagic-POM values from Stn. 1003 were not used for estimating food web baselines or Δ_C and Δ_N.

4.1. Food web baseline

It is a challenge to find appropriate food web baselines (Post, 2002). Collecting "pure" samples of primary producers from field habitats is difficult. However, the Arctic MIZ with distinct ice edge spring blooms presents good opportunities to obtain relatively pure primary producer samples, since these ice edge blooms generally have high algal biomass and little detritus (Rysgaard et al., 1999). As the algal bloom progresses, the algal degradation, detritus and microbial activity generally increase (Gradinger et al., 1992; Nielsen and Hansen, 1999; McMinn and Hegseth, 2004). Some studies have used primary consumers instead of primary producers as a baseline, since primary consumers are easier to sample, and may have less variable stable isotope composition than POM (Hobson et al., 2002; Hop et al., 2002; Post, 2002; Jennings and Warr, 2003). For instance, Hobson et al. (2002) use the predominantly herbivorous copepod *Calanus hyperboreus* as baseline in the North Water Polynya food web ($\delta^{15}N = 7.7‰$, which is similar to our spring *Calanus* spp. values), assuming it to occupy TL = 2. This approach works well as long as the $\delta^{15}N$ values in the assumed primary consumers are low. However, low $\delta^{15}N$ values are not always found in *C. hyperboreus* or the two other *Calanus* species *C. finmarchicus* and *C. glacialis* (Hobson et al., 2002; Tamelander et al., 2006a; our study).

4.1.1. $\delta^{13}C$ composition in POM

One important condition for using the two-source food web model is a significant difference in the $\delta^{13}C$ values of the two available food sources (Post, 2002). In our study, obligate Ice-POM, dominated by *Nitzschia frigida* and *Melosira arctica*, was significantly more enriched in ^{13}C (−21.0‰ to −19.0‰) than Pelagic-POM (−24.6‰ to −23.6‰). A similar difference in the ^{13}C enrichment patterns between Pelagic-POM and Ice-POM has been found previously in the Barents Sea (Tamelander et al., 2006a) and in other regions of the Arctic (Hobson et al., 1995; Cooper et al., 2002), as well as the Antarctic (Fischer, 1991; Gibson et al., 1999). However, Ice-POM dominated by pelagic-related diatoms such as *Fragilariopsis oceanica* and *Chaetoceros* spp. (i.e. facultative Ice-POM) were similarly enriched in ^{13}C as Pelagic-POM. Ice-POM collected from young and thin ice in the North Water Polynya (Canada), dominated by *Fragilariopsis* sp., also had similar $\delta^{13}C$ values as Pelagic-POM (Tremblay et al., 2006). Similar $\delta^{13}C$ values for Pelagic-POM and Ice-POM have also been found in the Canada Basin, although the taxonomic composition of POM was not presented (Iken et al., 2005).

It is hypothesized that ice algae are more enriched in ^{13}C than open water algae, because ice algae have a thicker boundary layer and thus grow in a more CO_2-limited environment than pelagic algae (France, 1995; Gibson et al., 1999; Kennedy et al., 2002). However, growth rate, irradiance and type of carboxylating enzymes also influence the $\delta^{13}C$ composition in algae (Thompson and Calvert, 1994; Fry, 1996). Ice algae growing at extremely low light intensities may use bicarbonate as substrate for carbon fixation, bicarbonate being more enriched in ^{13}C than CO_2 (Thompson and Calvert, 1994; Arrigo, 2003). Below thicker sea ice (0.8–1.5 m), the algal populations are typically dominated by the obligate ice diatoms *N. frigida* and *M. arctica*, which are adapted to low irradiance (Horner, 1985; Syvertsen, 1991; Hegseth, 1992; Michel et al., 2002). Pelagic-related algae such as *Thalassiosira* spp. and *Chaetoceros* spp. are, if present, mostly found below thin and young ice (<0.8 m) (Syvertsen, 1991; Hegseth, 1992). Pelagic algae in an exponential growth phase, trapped in a shallow melt water layer, may also temporarily become enriched in ^{13}C because of local depletion of CO_2 and decreasing discrimination against ^{13}C with increasing growth rate (Fischer, 1991; Fry, 1996). However, it is unknown whether pelagic algae

can be as enriched in ^{13}C as ice algae, since few comprehensive stable isotope studies of phytoplankton and ice algae exist from the Arctic (Schubert and Calvert, 2001; Tremblay et al., 2006).

It is difficult to assess whether the $\delta^{13}C$ baseline values determined for Pelagic-POM and Ice-POM in our study are representative food web baselines in a pan-Arctic perspective, since only Tamelander et al. (2006a) and our study have analyzed the $\delta^{13}C$ composition of lipid-extracted POM. However, the $\delta^{13}C$ baseline value determined for Pelagic-POM seems appropriate for the geographical area and time period that both we and Tamelander et al. (2006a) studied, since Pelagic-POM from the Barents Sea, NW Spitsbergen and East Greenland, near the Greenland Sea, were similarly enriched in ^{13}C.

Tamelander et al. (2006a) found similarly large variability in Ice-POM $\delta^{13}C$ values in the Barents Sea in July as we did. They did not analyze the POM community composition, but the heavily enriched $\delta^{13}C$ values in Ice-POM ($-12.6‰$ to $-17.3‰$) correspond to the enrichment we found in Ice-POM dominated by *M. arctica* in moderate to poor condition embedded in high quantities of mucilage-bound EPS, and the relatively depleted Ice-POM $\delta^{13}C$ values ($-20.4‰$ to $-21.7‰$) correspond to the $\delta^{13}C$ values of Ice-POM we found in autumn (Stn. 882), when there was greater representation of facultative species. Tremblay et al. (2006) also found similarly large variability in $\delta^{13}C$ values of Ice-POM from the North Water Polynya, Canada, but they explained the increased enrichment in ^{13}C by increased ice thickness. In our study, enriched ($-20.0‰$), moderately enriched ($-17.1‰$) and highly enriched ($-12.2‰$) $\delta^{13}C$ values of *M. arctica* assemblages were found below ice of similar thickness (~1 m). A qualitative microscopic investigation of the *M. arctica*-dominated Ice-POM samples from July 2001 did not reveal microfauna in notable concentrations, although we cannot rule out high numbers of bacteria and nanoflagellates. The major difference was that the highly ^{13}C-enriched samples had a more "lumpy" consistency and brownish appearance, and consisted of algal cells in generally poorer condition than the moderate and less ^{13}C- enriched samples. Several diatom species can secrete high quantities of mucilaginous EPS, which may play a crucial role in the formation of a thin algal sheet and the attachment of the sheet to the under-ice surface (McConville and Wetherbee, 1983; McConville, 1985). Diatoms have also been shown to release large amounts of polysaccharides when degrading (Ciglenečki et al., 2003), and ice algal assemblages in older and thicker ice generally have higher amounts of EPS (Syvertsen, 1991). The stable carbon isotope compositions of individual monosaccharides are generally enriched in ^{13}C by 0–9‰ compared to the total algal cell material (van Dongen et al., 2002), which may explain the much heavier $\delta^{13}C$ in the EPS-rich *M. arctica* assemblages. In our study, the $\delta^{13}C$ values of zooplankton and ice-fauna indicated that these EPS-rich *M. arctica* communities were of minor importance as food source. The animals may feed on these EPS-rich algal assemblages, but McConville et al. (1986) found that under-ice herbivores were unable to digest the complex polysaccharides/proteglycans (i.e. EPS) that ice diatoms secrete.

Sedimented-POM (20–35 m depth) was significantly depleted in ^{13}C compared to Pelagic-POM and Ice-POM in autumn. In July in the Barents Sea, Tamelander et al. (2006a) found that Sedimented-POM was 0.9–5.6‰ more enriched in ^{13}C than Pelagic-POM, but they also collected ^{13}C-enriched Ice-POM ($-21.7‰$ to $-12.6‰$) at these stations. In our study, no ice algae were visible by direct observation under the ice where the sediment traps were placed. Sedimented-POM tends to consist of faecal pellets, sedimented algal cells, and detritus (e.g. Andreassen et al., 1996; Olli et al., 2002). A high proportion of faecal pellets in the Sedimented-POM samples could have resulted in depleted $\delta^{13}C$ values compared to Pelagic-POM, since copepod faecal pellets are depleted in ^{13}C relative to the algal food ingested (Klein Breteler et al., 2002; Tamelander et al., 2006b). Zooplankton (e.g. *C. hyperboreus* and *C. finmarchicus*), which occasionally had $\alpha > 1.0$, may have fed on faecal pellets since the retention potential may be 50–70% of the produced faecal pellets in the Barents Sea (Wexels Riser et al., 2002). Detritus may be enriched or depleted in ^{13}C, which potentially makes the $\delta^{13}C$ values in detritus-feeding organisms highly variable (Post, 2002). In the Arctic, a significant input of terrestrial POM, depleted in ^{13}C, can be incorporated in sea ice and transported offshore (Schubert and Calvert, 2001; Bauerfeind et al., 2005). Carbon sources other than phytoplankton and ice algae may therefore exist offshore in the Arctic MIZ. However, the phytoplanktonic and ice algae carbon sources explained quite well the variability in organismal $\delta^{13}C$ composition in our study, suggesting that other potential carbon sources were of minor importance.

4.1.2. $\delta^{15}N$ composition in POM

Pelagic-POM $\delta^{15}N$ baseline values used in other Arctic marine food web studies are generally 4–5.4‰ (Hobson and Welch, 1992; Hobson et al., 1995; Iken et al., 2005; Tamelander et al., 2006a), which is similar

to the range found in our study. This suggests a relatively uniform $\delta^{15}N$ value for Pelagic-POM in the Arctic. Hobson et al. (2002) and Tamelander et al. (2006a) found relatively high Pelagic-POM $\delta^{15}N$ values in the North Water Polynya and the Barents Sea (6.8‰ and 8.3‰, respectively), but excluded these values from baseline estimates for their one-source food web models. Hobson et al. (2002) chose to use the slightly more enriched *C. hyperboreus* ($\delta^{15}N = 7.7‰$, TL = 2.0) as food web baseline, whereas Tamelander et al. (2006a) chose to treat the high $\delta^{15}N$ values as outliers. In our study, Pelagic-POM from the East Greenland shelf in October was more enriched in ^{15}N than Pelagic-POM from the Barents Sea in May and from waters north of Svalbard in September. Different water masses in East Greenland vs. Barents Sea/Svalbard area may cause differences in the Pelagic-POM ^{15}N values, but it is more likely that differences in seasons, ice cover and the algal bloom stages led to the enriched Pelagic-POM values on the East Greenland shelf. The station on the East Greenland shelf in October had only been partly covered by sea ice since July, and subsurface chlorophyll-*a* maxima were recorded by Richardson et al. (2005) in June and August the same year relatively close to our Stn. 890. In comparison, the stations in the Barents Sea in May and north of Svalbard in September had been covered by very close drift ice (7–9/10) until 1–3 weeks before sampling, which also explains the findings of ice diatoms at these stations. In the North Water Polynya, Canada, Tremblay et al. (2006) found that Pelagic-POM was most depleted in ^{15}N (4–5‰) at the onset of the bloom, and Bauerfeind et al. (2005) found that $\delta^{15}N$ values of sedimented matter on the East Greenland Shelf gradually increased from summer (3.4‰) to winter (7.2‰). Pelagic-POM from detritus-rich waters west of Spitsbergen in January was enriched in ^{15}N ($6.7 \pm 1.6‰$) similarly to sedimented matter from the East Greenland shelf in winter (Sasaki et al., 2001). Bacterial degradation of algae and increased microbial activity can increase both the $\delta^{13}C$ and $\delta^{15}N$ values in POM (Owens, 1985; Rolff, 2000). *Nitzschia*-dominated Ice-POM was more ^{15}N-enriched in autumn than in spring, which can be explained by less viable cells late in the season, as well as by less dominance of ice diatoms in obligate Ice-POM in autumn than in spring (87% vs. 97%). Ice-POM consisting of *M. arctica* in moderate to poor condition was significantly more enriched in ^{15}N compared to healthy *M. arctica* communities.

During spring and summer, obligate Ice-POM had surprisingly low $\delta^{15}N$ values (0.9–2.4‰). Such low $\delta^{15}N$ values have not previously been recorded to our knowledge in Arctic Ice-POM, except that Iken et al. (2005) reported $\delta^{15}N$ values as low as 2.3‰ in one Ice-POM sample from the Canada Basin. In the Antarctic, however, similarly low $\delta^{15}N$ values in Ice-POM (1.7–2.1‰) have been found during the Austral winter by Frazer (1996), who explained the depleted $\delta^{15}N$ values by low light intensities, referring to Wada and Hattori (1991). They found depleted $\delta^{15}N$ values in diatoms cultured under low-light intensities compared to those grown under high light intensities.

The $\delta^{15}N$ composition of marine algae depends mainly on the source of nitrogen used, i.e. the isotopically heavy nitrate (NO_3^-) or the isotopically lighter ammonium (NH_4^+) (Checkley and Miller, 1989; Waser et al., 1999). POM with low $\delta^{15}N$ values has been found in oligotrophic waters rich in zooplankton-excreted ammonium (Checkley and Miller, 1989). High concentrations of ammonium are frequently measured in sea ice, particularly when covered by dense, actively growing algae (Demers et al., 1989; Mock and Gradinger, 1999; Thomas and Papadimitriou, 2003). Simultaneous uptake of NO_3^- and NH_4^+ in ice algae has been reported (Demers et al., 1989), although high levels of ammonium can inhibit nitrate assimilation by algae (Thompson et al., 1989; Flynn, 1991). Sea ice may be one of the few environments where ammonium-dominated nitrogen metabolism prevails (Thomas and Papadimitriou, 2003). In the Arctic, Ice-POM is generally found to be similarly or more enriched in ^{15}N than Pelagic-POM (Hobson and Welch, 1992; Hobson et al., 1995; Hobson et al., 2002; Tamelander et al., 2006a; Tremblay et al., 2006). The low $\delta^{15}N$ values of Ice-POM in our study, however, were supported by lower $\delta^{15}N$ values in ice amphipods than in zooplankton. Others have also found similarly low $\delta^{15}N$ values in Arctic ice amphipods (Iken et al., 2005; Tamelander et al., 2006a), and as a result they estimated unrealistically low trophic levels for ice amphipods (e.g. TL = 0.9–2.0; Tamelander et al., 2006a) compared to our study (TL = 1.9–3.7).

4.2. Trophic enrichment in ^{13}C and ^{15}N

Our Δ_C (0.6‰) and Δ_N (3.4‰) estimates are comparable to previously published Δ_C and Δ_N estimates (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001; Post, 2002). However, more knowledge about tissue turnover times and the underlying physiological and

biochemical mechanisms that account for trophic increases in stable isotope values of zooplankton and ice amphipods are needed for validation of these fractionation estimates. Nevertheless, the Δ_N showed low variability and was consistent across comparisons in spring (Fig. 4). The trophic enrichment factor of 3.4‰ is considered to be a robust and valid approximation for trophic fractionation of ^{15}N (Post, 2002). However, it is important to keep in mind that occasionally any single trophic transfer may range between $\Delta_N = \sim 2–5‰$ (Post, 2002). We determined Δ_C to be similar for the pelagic and sympagic systems, despite a possibly lower Δ_C in the sympagic system. Fractionations of ^{13}C and ^{15}N are relatively similar in a wide range of animals (Ponsard and Averbuch, 1999; Post, 2002). The small ice amphipod used for estimating Δ_N and Δ_C for the sympagic system, *A. glacialis*, was sampled relatively late in the productive season for ice algae (i.e. summer), which may explain the relatively large variability in $\delta^{13}C$ values of this species. In autumn, *A. glacialis* was more depleted in ^{13}C than in summer, suggesting that Pelagic-POM source pathways increased in importance toward the end of the productive season. Had we used $\Delta_C = 0.1‰$ for the sympagic system, a similar TL would have been estimated as when using $\Delta_C = 0.6‰$, although a slightly higher proportion of Ice-POM source pathway would have been calculated for the ice fauna ($\alpha = 0.2$ vs. 0.3).

Small Δ_C (<0–1‰) generally has little effect on calculations of TL, so long as the differences in $\delta^{15}N$ values are small and the differences in $\delta^{13}C$ values are large between the two available food sources (Post, 2002). However, in our study the difference in $\delta^{15}N$ was relatively large (i.e. 2.2‰) and the difference in $\delta^{13}C$ small (i.e. 4‰) between Pelagic-POM and Ice-POM compared to the isotopic differences found for the two food sources in the study of Post (2002) (<1.5‰ and >6‰, respectively). It was therefore important in our study to include trophic fractionation of ^{13}C in our two-source food web model, particularly for calculating realistic α. The high $\delta^{13}C$ values in carnivorous compared to herbivorous and omnivorous zooplankton lead to a significantly lower proportion of Pelagic-POM source pathway in carnivorous compared to herbivorous and omnivorous zooplankton. This may indicate that our Δ_C was underestimated, which would suggest a lower $\delta^{13}C$ baseline value for Pelagic-POM, or as previously mentioned that differences in dietary quality or C:N, as well as physiological status, may influence Δ_C.

4.3. Seasonal patterns in trophic structures and sympagic–pelagic coupling

4.3.1. Zooplankton

Few of the macrozooplankton (>1 mm) species we studied are considered to be predominantly herbivorous, except for the copepods *Calanus* spp. (Kattner and Hagen, 1995; Scott et al., 2002) and the krill *Thysanoessa inermis* (Falk-Petersen et al., 2000b). The other macrozooplankton species are considered to be omnivorous or predominantly carnivorous. We expected to find the largest shift in feeding strategies between the vegetative and non-vegetative seasons (Hopkins and Torres, 1989; Sasaki et al., 2001; Werner and Auel, 2005), but no pronounced seasonality in TL and carbon sources was found for bulk zooplankton in our study. However, the majority of the zooplankton species were omnivorous-carnivorous, and they generally experience less seasonal food limitation than herbivores (Clarke and Peck, 1991).

In our study, early season sampling was performed in winter (March) with very low phytoplankton and ice algal biomass, although we cannot rule out that ice algae were present further inside the MIZ (e.g. Hegseth, 1998). In May, the phytoplankton biomass was high, but relatively little ice algae was present since the ice melt was advanced (Engelsen et al., 2002; Søreide et al., 2003). Periods with high ice algal biomass and very low phytoplankton biomass were not investigated in our study. No herbivorous zooplankter was found by us to graze extensively on Ice-POM in March or mid-May, but March may have been too early and mid-May too late to detect possible grazing on Ice-POM. At the time of sampling in May the phytoplankton bloom was advanced, suggesting that a relatively high phytoplankton biomass had been available for 2–3 weeks (Engelsen et al., 2002). Intensive feeding and growth in spring may have led to rapid tissue turnover and full incorporation of the phytoplankton stable isotope signature in *Calanus* spp. at the time of sampling (e.g. Klein Breteler et al., 2002). Carnivorous zooplankton, however, will incorporate the POM signatures later than herbivores due to time lags (Falk-Petersen et al., 1990). The chaetognath, *Sagitta elegans*, which is strictly carnivorous (TL = 3.7–3.8), had particularly enriched $\delta^{13}C$ values (−19.3‰) and low α (0.2) in May. It is known to feed extensively on nauplii, and small copepods such as early stages of *Calanus*, *Pseudocalanus* and *Oithona*, in addition to appendicularians in the Barents Sea (Falkenhaug, 1991). In early spring, particularly

Pseudocalanus can graze extensively on ice diatoms (Runge and Ingram, 1988; Runge and Ingram, 1991), which may explain the dominant Ice-POM source pathway in *S. elegans* in spring compared to the other seasons. Few stable isotope studies exist for *Pseudocalanus* in the Arctic, but Iken et al. (2005) categorized *Pseudocalanus* from the Canada Basin as herbivorous sympagic fauna due to its stable isotope signature. Other carnivores, such as *Paraeuchaeta norvegica*, *Thysanoessa longicaudata* and *Hyperia galba*, were also markedly more enriched in ^{13}C and had correspondingly lower α (0.5–0.6) in spring than in autumn and winter.

In spring and summer, the stable isotope signatures in zooplankton generally suggested feeding strategies as expected, except for the carnivorous diet of large specimens (>22 mm) of *T. inermis*. In autumn, latitudinal differences in feeding strategies were found between bloom to late-bloom waters near the multi-year ice pack to the north (82°N) and late- to post-bloom waters farther south (76°N). In the north (Stn. 882), zooplankton were mainly herbivorous-omnivorous (mean TL = 2.4), whereas in the south (Stn. 890) they were mainly omnivorous-carnivorous (mean TL = 2.7). In winter, only carnivorous-omnivorous zooplankton (mean TL = 2.9) were found, except for the surprisingly low TL (2.3) of the ctenophore *Mertensia ovum*. As previously mentioned, ice algae could have been growing farther inside the MIZ in March, out of the reach of the swells, but the α calculated for *M. ovum* suggests an exclusively Pelagic-POM source pathway. However, the phytoplankton biomass in March was very low (Søreide et al., 2003), and *M. ovum* is known to be a carnivore mainly feeding on *Calanus* spp. (Swanberg and Båmstedt, 1991; Falk-Petersen et al., 2002). In spring, *M. ovum* occupied a higher TL (2.7), but in autumn it had the same depleted stable isotope values as in winter. Since *M. ovum* can metabolize its own tissue and actually shrink during times of food shortage (Hoeger, 1983), it is not unlikely that the isotopic signal of the autumn diet was reflected in *M. ovum* in winter. In the North Water Polynya, during spring-summer, similarly low TL (2.3) was estimated for *M. ovum*, although it had slightly higher $\delta^{15}N$ (8.9‰) and much higher $\delta^{13}C$ (−19.0‰) values (Hobson et al., 2002).

Zooplankton may reduce or cease feeding in autumn and go into a hibernating stage utilizing stored body energy to survive the dark and long unproductive winter (Hagen, 1999; Hagen and Auel, 2001; Lee et al., 2006). Polar zooplankton commonly utilize stored lipid reserves for overwintering and spawning the next spring, although some euphausiids and gelatinous zooplankton may also rely on reducing their body mass and volume (Falk-Petersen, 1985; Clarke and Peck, 1991). Fasting animals may show a progressive increase in $\delta^{13}C$ and $\delta^{15}N$ value, since mainly the lighter isotopes are used in catabolism, and during starvation these are not replaced (Hobson et al., 1993; Gannes et al., 1997; Adams and Sterner, 2000). However, insignificant changes in the $\delta^{13}C$ and $\delta^{15}N$ values of starved calanoid copepods (Tamelander et al., 2006b), mysids (Gorokhova and Hansson, 1999) and krill (Frazer et al., 1997), suggest that the isotopic composition of some invertebrates is unaffected by the metabolic processes during prolonged periods of starvation. The TLs and α estimated for organisms collected during the unproductive season, particularly in winter, should therefore be interpreted with caution.

Parts of the *Calanus* population may not descend to depth in autumn to hibernate, but remain in the surface waters during winter (Sato et al., 2002). These surface-dwelling copepods may not have accumulated large enough lipid stores for successful overwintering in diapause, and thus continue to feed (Pasternak et al., 2001). Sasaki et al. (2001) conclude from stable isotope studies of *Calanus* spp. and Pelagic-POM from the upper 300 m, West of Svalbard in January, that *C. glacialis* occasionally feeds on POM (e.g. detritus) in winter, whereas *C. finmarchicus* utilizes lipid reserves. In March (0–300 m), we found elevated $\delta^{15}N$ values in all three *Calanus* species, similarly high as those Sato et al. (2002) measured in *C. glacialis* in January, suggesting TL = 2.7–3.1. Omnivory in *Calanus* spp. is found to be inversely related to the availability of diatoms (Stevens et al., 2004). In response to phytoplankton shortages, copepods may switch to alternate prey including nauplii (Landry, 1981), ciliates (Atkinson, 1996) and heterotrophic dinoflagellates (Levinsen et al., 2000). In autumn, *C. glacialis* and *C. hyperboreus* were predominantly herbivorous in bloom/late-blooming waters and omnivorous in late- to post-blooming waters. *Calanus finmarchicus*, however, was predominantly herbivorous regardless of the algal bloom situation, which may indicate that it had stopped feeding and started to descend at the time of sampling in autumn. Even though similarly high $\delta^{15}N$ values were found in the three *Calanus* species in March, *C. finmarchicus* had significantly lower $\delta^{13}C$ values ($\alpha = 0.35$) than *C. glacialis* and *C. hyperboreus* ($\alpha = 0.73$ and 0.70, respectively), which may suggest species-specific differences in carbon sources and/or metabolic processes. Of the three *Calanus* species, only *C. finmarchicus* has been found in the ice-water interface (0–5 m) in the Barents Sea in March (Werner, 2005). High concentrations of particulate organic matter (POC, PON) were found in this 0–5 m layer below sea ice in March, POM most likely

dominated by detritus given its high C:N ratios and very low concentrations of algal pigments (Werner, 2005). If POM released from the sea ice in late winter is similarly enriched in ^{13}C as is obligate Ice-POM, this could explain the enriched $\delta^{13}C$ values and low α of *C. finmarchicus* and other zooplankton in March.

Runge and Ingram (1988, 1991) concluded from gut analyses that ice algae were a regular and principal food source for *C. glacialis* in Hudson Bay, Canada. In our study, substantial grazing on Ice-POM was only indicated for *C. glacialis* sampled in autumn, far to the north (82°N) in the multi-year ice pack (i.e. TL = 2.3, $\alpha = 0.5$). At this location (Stn. 882), ice diatoms were commonly found on the underside of the ice, and a substantial proportion of the suspended algal cells were ice-associated diatoms, with the small *Attheya septentrionalis* being particularly abundant. However, *C. hyperboreus* sampled at Stn. 882 did not seem to graze on ice diatoms (TL = 2.3, $\alpha = 1.2$). It most likely grazed on pelagic algae or had stopped feeding.

Differences in body size will naturally lead to differences in feeding strategies, even in the same species (Omori and Ikeda, 1984). Since some of the macrozooplankton species can grow to a relatively large size, their feeding strategies can change markedly from juvenile to adult. In our study, medium-sized specimens (10–19 mm) of *T. inermis* were predominantly herbivorous or omnivorous–herbivorous during spring and autumn, whereas larger *T. inermis* (>22 mm) sampled at the same time were carnivorous (TL = 3–3.2). The hyperiid amphipod *Themisto abyssorum* also showed large differences in feeding strategies with size. Small specimens of *Themisto libellula* were not analyzed in our study, but Tamelander et al. (2006a) found significantly lower $\delta^{15}N$ values in small than in large *T. libellula*, indicating a shift from herbivory to omnivory–carnivory with increasing body size.

The ctenophore *Beroë cucumis* may prey on *M. ovum* (Falk-Petersen et al., 2002), but our stable isotope data indicated that *M. ovum* was not an important prey. *Beroë cucumis* was >2‰ more enriched in ^{13}C and only 0.9–2.1‰ more enriched in ^{15}N than *M. ovum*. The pteropod *Clione limacina* is known to feed exclusively on *Limacina helicina* (Conover and Lalli, 1974; Lalli and Gilmer, 1989). However, from the one location (Stn. 882) where we sampled both *C. limacina* and *L. helicina*, similarly enriched $\delta^{13}C$ and $\delta^{15}N$ values were found for these two species. Fatty acid analyses have also not revealed a clear predator–prey relationship between these two species (Falk-Petersen et al., 2001; Böer et al., 2005).

4.3.2. Ice amphipods

Gut content analyses (Poltermann, 2001), feeding experiments (Werner, 1997) and fatty acid analyses (Scott et al., 1999; Scott et al., 2001; Werner and Auel, 2005) support the feeding strategies we determined for *Apherusa glacialis*, *Onisimus nanseni*, *Onisimus glacialis* and *Gammarus wilkitzkii* in this study. In general, herbivorous ice amphipods had lower α than omnivores and particularly carnivores, suggesting increased importance of Pelagic-POM source pathways with increasing TL, although exceptions were found. We detected no significant switch in feeding strategy for *A. glacialis* from summer to autumn, although a slight increase in α from summer to autumn indicated increased grazing on Pelagic-POM later in the season. Lipid and fatty acid analyses confirm that *A. glacialis* is strictly herbivorous, and that it overwinters on internal lipid reserves stored during the productive season (Werner and Auel, 2005). Small specimens of *O. glacialis* (<9 mm) also primarily grazed on Ice-POM, but its TL increased with increasing body size. Of the four ice amphipod species, *O. nanseni* seemed to be the most opportunistic feeder, which has been confirmed by others (Werner and Auel, 2005). It switched from grazing on Ice-POM to carnivory in the sympagic system, and even to "top" predator status in the pelagic system. Besides *O. nanseni*, *G. wilkitzkii* could assimilate substantial energy from the pelagic system ($\alpha = 0.7$). Small specimens of *G. wilkitzkii* generally had lower TLs than the larger ones (2.1 vs. 2.4, respectively), but even relatively large *G. wilkitzkii* could be predominantly herbivorous (TL = 2.1), which resulted in low overall TL for *G. wilkitzkii* and relatively low α (0.3–0.4). Fatty acid analyses confirm that Ice-POM is a major diet component in *G. wilkitzkii* in summer and autumn (Scott et al., 2001; Werner and Auel, 2005), but winter studies show that *G. wilkitzkii* switches to feed mainly on available ice fauna and planktonic copepods when ice algae are scarce (Werner and Auel, 2005).

5. Conclusions

Zooplankton and ice fauna had a similar TL range, but macrozooplankton were mainly omnivorous–carnivorous, whereas ice fauna were herbivorous–omnivorous. During all seasons, zooplankton primarily utilized

open water food sources, whereas ice amphipods mainly utilized ice-source pathways, although ice fauna with TL > 3 primarily fed on pelagic organisms.

The two-source food web model of this study gave realistic TL and α estimates for larger zooplankton and ice fauna species in the European Arctic MIZ, demonstrating the advantage of combining $\delta^{13}C$ and $\delta^{15}N$ values in Arctic marine food web models. However, large stable isotope variability in Pelagic-POM and, particularly, Ice-POM was found, which showed that to determine representative baselines for primary producers it is essential to know the POM community composition as well as the algal cell condition and the stage of the algal bloom. The period of the spring bloom, characterized by high algal biomass and little detritus, was found to be the most appropriate time for determining food web baselines and trophic enrichment factors for the Arctic MIZ. The tissue turnover times and the underlying physiological and biochemical mechanisms that account for trophic increases in $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton and ice amphipods are poorly known. A better understanding of these processes is important in order to fully exploit stable isotope techniques for determining food web structures.

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