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First analysis of an Arctic sea ice meiofauna food web based on abundance, biomass and stable isotope ratios

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ABSTRACT: Particulate organic carbon (POC) produced in sea ice is often included in stable isotopic food web studies of polar seas as a single value of particulate organic matter (POM), i.e. 'ice POM'. During 10 field trips to landfast ice off Alaska's north coast, we examined the seasonal contribution of sea ice-associated meiofauna to total POM and the trophic structure within the sea ice using bulk carbon and nitrogen stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$). Algal biomass, POC/particulate organic nitrogen and meiofaunal abundances increased after the polar night, and a suite of different metazoan meiofauna contributed seasonally substantially to total ice POC amount. $\delta^{13}C$ values of meiofauna generally tracked the seasonal enrichment of $\delta^{13}C$ in POC suggesting a trophic relationship, also supported by increasing body mass of meiofauna over the seasons. $\delta^{15}N$ of individual meiofaunal taxa varied by at least 1.5 trophic levels. $\delta^{13}C$ values of some meiofauna were very close to or below POC values suggesting the use of other carbon sources, perhaps including dissolved organic carbon (DOC) and bacteria. Estimated potential grazing rates, based on generated carbon and nitrogen content of individuals in this study, confirmed earlier generally low estimates of grazing impact of the meiofauna on the ice algal spring bloom, leaving large portions of the produced matter as food for pelagic and benthic organisms. These findings suggest a more complex sea ice-based food web structure that should be more commonly incorporated into food web, conceptual and other models.

KEY WORDS: Fast ice · Meiofauna · Stable isotopes · Food web · Arctic

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1. INTRODUCTION

Sea ice-related biological processes have received increasing attention due to the substantial changes in the Arctic sea ice regime and associated biological consequences over the last decades (Bluhm & Gradinger 2008). Observed and projected changes include loss of biodiversity, increased primary production and Atlantification–Pacification of the Arctic Ocean (Slagstad et al. 2015, Polyakov et al. 2017). Most of the observed and suggested biological changes relate to properties observed at the bottom of the ice itself (e.g. under-ice flora and fauna) or in the water column (zooplankton, phytoplankton) and at the sea floor. However, methodological challenges related to working with sea ice make it intrinsically difficult to simultaneously study its wide range of physical, chemical and biological properties. Although recent progress has been made with regards to e.g. remotely sensing ice algal biomass (Cimoli et al. 2017, Meiners et al. 2017) or the non-destructive determination of ice algal primary productivity using eddy correlation approaches (Attard et al. 2018), destruction of the habitat is still applied and required for estimation of e.g. community diversity or activity and biomass measurements in different ice layers (Gradinger & Bluhm 2009, McMinn et al. 2009).

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So far, only a limited number of approaches have been successfully applied to determine biological rates within sea ice under *in situ* conditions (Clasby et al. 1973, Mock & Gradinger 1999, Junge et al. 2004, Meiners et al. 2008, Cummings et al. 2019), and such approaches mainly include the level of bacterial and algal production, which can be assessed by tracers. Likely the best studied aspect of the sea ice-related biological carbon cycle is primary production. Studies have focused on both the physical and chemical control of primary productivity in experimental and field settings (Kudoh et al. 1997, Mock et al. 2003), while field expeditions have aimed at providing regional (Gradinger 2009) or basin-wide (Gosselin et al. 1997) estimates of sea ice primary production. Typical yearly ice algal primary production estimates (Gradinger 2009) range from 1.5 to 10 g C m^{-2}, with differences largely attributed to the snow and ice characteristics and nutrient supply from the water column (e.g. Lavoie et al. 2005). Field and modeling studies revealed that light and inorganic nutrient supply are the main physical forcing parameters in addition to ice temperatures and brine salinities, and that algal growth is largely determined by bottom-up control (Gradinger 2002, Jin et al. 2006). While detailed regional comparisons are partially flawed by inconstant application of adequate methodologies (Campbell et al. 2019), it has been extensively documented that sea ice-produced organic matter is used by, and relevant to, various parts of the Arctic food web (Wang et al. 2015, Schollmeier et al. 2018). Most of the ice-based primary production is released to the water column during ice melt (Michel et al. 2002) and contributes to the nutrition of pelagic and/or benthic consumers. Only a limited amount of organic carbon is utilized by herbivorous sea ice meiofauna, zooplankton and ice-endemic amphipods, with all consumers combined typically consuming less than 10% of the algal production (Gradinger 1999, Werner 1997, Michel et al. 2002). These estimates are based on experimental grazing data for under-ice fauna and allometric equations for meiofauna.

Sea ice meiofauna in general is likely the least studied component of the sea ice-based food web, along with fungi (Hassett et al. 2017). Sea ice meiofauna inhabits the brine channel network within the sea ice and is typically defined as small metzoans including Nematoda, Rotifera, Acoela and Cnidaria, with typical size ranges of 50–500 µm (Bluhm et al. 2018), although some studies also include larger ciliates. So far, allometric equations have been used to calculate potential maximum ingestion rates of meiofaunal taxa based on the biomass of individuals (Gradinger 1999). While these studies have revealed a generally low impact of sea ice metazoans on the accumulation of algal biomass within the ice (Gradinger 1999, Nozais et al. 2001, Michel et al. 2002), they did not provide any insights into the trophic connections between taxa and the number of trophic levels (TLs) present within the ice. Historical information based on gut content (Grainger & Hsiao 1990) or fecal pellet (Carey & Boudrias 1987, Gradinger & Bluhm 2010) analyses indicated that herbivory is the most common feeding mode for many of these ice-inhabiting species. Grainger & Hsiao (1990) found that 13 out of 16 sea ice meiofauna taxa were entirely herbivorous, grazing on a total of 26 genera of algae. However, the recent discovery of a predatory cnidarian, *Sympagohydra tuuli* (Piraino et al. 2008, Siebert et al. 2009, Marquardt et al. 2018), in Arctic sea ice shows that the sea ice food web includes at least one additional TL.

Aiming at providing more detailed information on this threatened, unique and understudied polar food web within sea ice, we applied a stable isotope approach that has been successfully used in other Arctic marine habitats (e.g. Hobson & Welch 1992, Iken et al. 2005, Stasko et al. 2018). The underlying principle using carbon and nitrogen stable isotope tracers is the stepwise enrichment between TLs of about 2–4‰ for $\delta^{15}N$ and 0–1‰ for $\delta^{13}C$ (Peterson & Fry 1987, Hobson & Welch 1992, Post 2002, Tamelander et al. 2008), although fractionation falling outside these ranges has also been measured (Yokoyama et al. 2005). Typically, $\delta^{13}C$ ratios have been used to identify food sources (for example ice algae versus phytoplankton) based on previously observed enriched $\delta^{13}C$ signatures in ice algae during algal blooms, where carbon isotope ratios increase from values below −23‰ to levels above −13‰ (Søreide et al. 2006, Gradinger et al. 2009). $\delta^{15}N$ enrichment does not necessarily show the same seasonal enrichment as $\delta^{13}C$ sea ice ratios; rather, it lends itself to estimating TLs within a community (e.g. Iken et al. 2005). In this study, seasonal observations at a coastal fast ice site near Utqiaġvik, Alaska (formerly Barrow) aimed, first, at applying a stable isotope approach to sea ice meiofauna with the goal of, for the first time, differentiating between different taxa that are commonly blended in a single value of 'ice particulate organic matter' (POM). Second, we aimed to estimate the contribution of sea ice meiofauna to total sea ice particulate organic carbon (POC) and nitrogen (PON) using direct measurements of individual meiofauna carbon and nitrogen content. Third, we used the measured sea ice POC values in a trophic model to determine their potential ingestion rates during different times of seasonal sea ice community development.

2. MATERIALS AND METHODS

2.1. Study site

Sampling took place in fast ice along the Alaskan coastline, which forms in November–December and reaches a thickness of 1.5–1.8 m by April (Macdonald et al. 1999, Mahoney et al. 2007). Break-up usually occurs between late June and mid-July (Mahoney et al. 2007). Attached to the shore and anchored to the sea floor by up to 20–25 m deep keels (Macdonald 2000), the ice extends several km out onto the Chukchi and Beaufort shelves. Samples for this study were collected during 10 field trips to Utqiaġvik, Alaska: 24–28 Apr and 27 May–1 Jun 2002; 12–17 Feb, 1–5 Apr and 27–30 May 2003; 7–12 Dec 2005; 30 Jan–4 Feb, 13–18 Mar, 21–26 Apr and 27 May–1 Jun 2006 at 4 different locations (Fig. 1). In 2002, we sampled Site BASC (Chukchi Sea; 71° 19′ N, 156° 41′ W). In 2003, Site BASC and Site Beaufort (Beaufort Sea; 71° 22′ N, 156° 24′ W) were sampled. During the Dec 2005–Jun 2006 field periods we sampled Site BASC, Site Hanger (Chukchi Sea; 71° 20′ N, 156° 39′ W) and Site Elson (Elson Lagoon; 71° 21′ N, 156° 28′ W). Water depth at these sites ranged from 2.0–6.3 m. All sites were <1 km offshore. Part of the 2002 and 2003 data were used to assess the effect of high concentrations of sea ice sediments for the seasonal development of sea ice communities (Gradinger et al. 2009). Substantial, clearly visible greyish sediment accumulations were observed in 2003 at Site Beaufort and in 2005–2006 at Site Elson. These high accumulations of sediment are often established during sea ice formation (Eicken et al. 2005) and in our study area can form clearly visible dark grey layers within collected ice cores (see example given in Gradinger et al. 2009). Such greyish layering was used as a criterion for classifying cores as 'sediment-impacted' in the context of this study as well; absolute amounts of incorporated sediment were only measured for cores overlapping with those used in Gradinger et al. (2009).

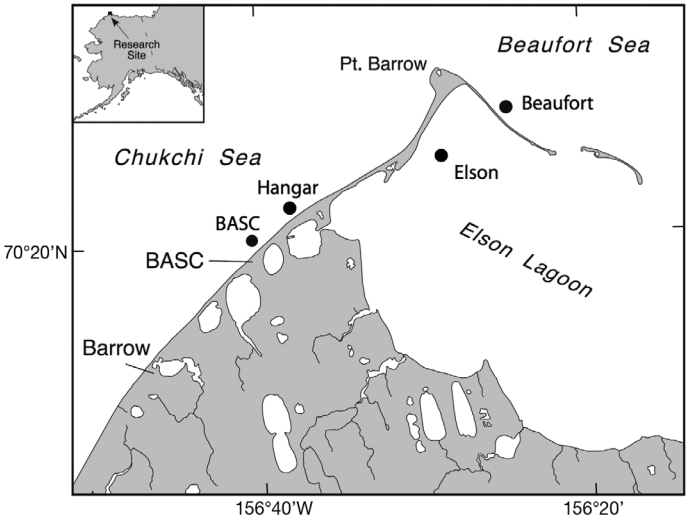

Fig. 1. Study area close to Utqiaġvik, Alaska. Sites BASC (Barrow Arctic Science Consortium) and Hangar are in the Chukchi Sea, while Elson and Beaufort are on the Beaufort Sea side

2.2. Sample collection and processing

At least 3 replicate ice cores per variable were collected with an ice corer (10 cm diameter in 2002–2003; 9 cm in 2005–2006) at each site and time period. For bulk algal pigment, POC, PON and stable isotope ratio samples, the bottom 10 cm of the cores were melted in the dark and sub-samples of 2–50 ml were filtered onto pre-combusted GF/F filters, which were frozen at –20°C for later determination. The bottom 10 cm sections of a second set of at least 3 replicate ice cores were melted in the dark after addition of 1 l of 0.2 µm filtered seawater to each core section to avoid osmotic stress for the biota (Garrison & Buck 1986). After complete melt, total volume was determined, the samples were concentrated over 20 µm mesh and metazoan ice meiofauna were sorted by taxon and enumerated (Gradinger et al. 2009) using Wild M3 and Leica MZ12 dissecting microscopes. Individuals of the meiofauna present were picked from the melted samples with Pasteur pipettes and pooled to get sufficient organic mass for later stable isotope analysis. Pooled animals were filtered onto pre-combusted GF/F filters by taxon and frozen until further processing, and the number of individuals per filter was noted. At least 3 replicate filter samples were collected per sampling period whenever animal abundances were sufficient.

In 2002–2003, under-ice amphipods were collected in screened baited minnow traps that were deployed immediately under the ice for 24–48 h at a time (Kaufman et al. 2008). In 2005–2006, amphipods were picked from melted bottom ice core sections or slush of the cored ice holes immediately after core removal. Amphipods were kept in filtered sea water in the dark for several hours to clear their guts before being subsequently frozen (–20°C).

For chlorophyll *a* (chl *a*) determination, filters were extracted with 7 ml of 90% (v:v) acetone for 24 h in the dark at –18°C (Karl et al. 1990). Chl *a* concentration was subsequently determined with a Turner TD-700 fluorometer (Arar & Collins 1997).

As most variables were determined on material collected with ice corers, they likely underestimate actual values due to the potential loss of communities in unconsolidated sea ice at the bottom of the ice cores (Welch et al. 1988). Thus, our data are only reflective of those communities attached to or within the solid sea ice cores.

2.3. Stable isotope analysis

In the Fairbanks lab, samples were dried at 60°C for 24 h and subsequently fumed for 24 h with 2 N HCl to remove carbonates. All samples were re-dried at 60°C for 24 h prior to analysis. The stable isotope composition of either filter samples or, in the case of amphipods, approximately 0.3 mg homogenized, acidified whole organism sample were measured on a Thermo Finnigan delta isotope ratio mass-spectrometer with carbon V-PDB and atmospheric N_2 as standards at the Alaska Stable Isotope Facility (ASIF) at the University of Alaska Fairbanks. Analytical error was typically 0.05‰ for ^{13}C and 0.06‰ for ^{15}N. Sample isotopic ratios are expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

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

where X is ^{13}C or ^{15}N of the sample and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

For comparisons of $\delta^{15}N$ and $\delta^{13}C$ values across different sites and seasons with different POM reference samples, we subtracted the mean values of $\delta^{15}N$ and $\delta^{13}C$ of POC/PON of a particular site and season from the organism values. We assigned TLs to each taxon assuming a 3.4‰ enrichment per TL (Post 2002) and using the consumer with the most depleted $\delta^{15}N$ value, Harpacticoida, as TL 2. First-order consumers are regularly used as isotopic baselines in a given habitat (Bell et al. 2016, Stasko et al. 2018). We decided against using the $\delta^{15}N$ of PON as the baseline because our data showed strong seasonal dynamics in isotopic ratios with, at the same time, unknown isotopic turnover times for the meiofauna taxa in question. Earlier studies with ice-associated amphipods demonstrated slow isotopic half-life times of weeks to several months (Kaufman et al. 2008), making POM as the isotopic baseline even more challenging in the dynamic sea ice system than elsewhere. This approach also helped us avoid bias due to the fact that the bulk POC/PON isotopic values not only reflect algal signatures but will include the meiofauna itself.

2.4. PON, POC and biomass

The above-mentioned stable isotope measurements also provided the absolute concentrations of carbon and nitrogen in each sample. Carbon and nitrogen content of individual sea ice organisms were calculated by dividing the carbon or nitrogen content of the pooled organism samples by the number of organisms on the respective filter. Taxon-specific, average individual carbon and nitrogen amounts were calculated based on all measurements per taxon (between 3 and 22 per taxon) and season. Biomass per taxon in a given sample was consequently obtained by multiplying individual carbon or nitrogen content by the abundance for a given site and time period.

2.5. Ingestion rates

Potential ingestion rates were estimated using the allometric mass-specific equation by Moloney & Field (1989) following the approach suggested by Gradinger (1999), assuming an ice temperature of −2°C and a Q_{10} value of 2:

$$I_{max} = 63 \times M^{-0.25} \times 0.2177 \times B \quad (2)$$

where I_{max} is the potential maximum ingestion rate (µg C l^{-1} d^{-1}); 63 is biomass-specific ingestion (pg C d^{-1}), M is the body mass of one individual (pg C) and B is the carbon biomass of a taxon in a sea ice sample (µg C l^{-1}), and 0.2177 is the temperature compensation.

2.6. Data analysis

As most of our variables were not normally distributed (based on Kolmogorov-Smirnov tests), we used medians for comparison between seasons and sites. For statistical analyses, data from the individual sampling events were pooled into 3 season groups: winter (Dec–Feb; i.e. polar night), spring (Mar–Apr) and late spring (May–Jun). For each season, data were split into 2 groups based on sediment load (i.e. with and without visible sediment load). We used sediment load as a factor since earlier studies demonstrated the large impact of visible sediment load on the biological development in Alaskan fast ice in the study area (Gradinger et al. 2009). We used the Kruskal-Wallis 1-way ANOVA (H-test) to test for equality of medians between sites with and without sediment and between seasons. Analyses including linear regressions were conducted using SYSTAT v.11.0 and STATA v.15.1.

3. RESULTS

3.1. POM, algal pigments, stable isotope ratios and meiofaunal abundance

All bulk variables (POC, PON, chl *a*) increased at the sediment-free sites from the winter sampling to spring and then late spring, with significant differences for PON and chl *a.* In contrast, no significant changes with season were observed for any bulk variable at the sediment-impacted sites (Fig. 2). In sediment-free ice, median POC concentrations increased from 0.6 mg l^{-1} in winter to 6.5 mg l^{-1} in late spring. Highest PON values occurred in spring with a median of 0.5 mg l^{-1}. Ice algal pigment concentrations increased from a median of 1.0 µg chl *a* l^{-1} in winter to 45.1 µg l^{-1} in spring and dropped to 27.1 µg l^{-1} in later spring. The median $\delta^{13}C$ values increased, though not significantly, over time at the sediment-free sites from −24.9‰ in winter to −14.5‰ in late spring, whereas these values remained virtually constant at the sediment-laden sites. The medians for $\delta^{15}N$ varied little (range: 7.9–8.4‰) at the sediment-free locations, and from 5.5 ‰ (late spring) to 8.6 ‰ (spring) at the sediment sites.

Median total metazoan abundances increased slightly in the sediment-free locations from 126 ind. l^{-1} in winter to 371 ind. l^{-1} in late spring (Fig. 2). At the sediment-impacted locations, highest median values occurred in later spring with 427 ind. l^{-1}. No significant changes (Kruskal-Wallis test, $p > 0.05$) were observed for either total abundances or abundances of the individual taxa with regards to seasonality or sediment load (Fig. 3a). In sediment-free ice, Acoela median abundances were highest in late spring (90 ind. l^{-1}), while for all other taxa the highest

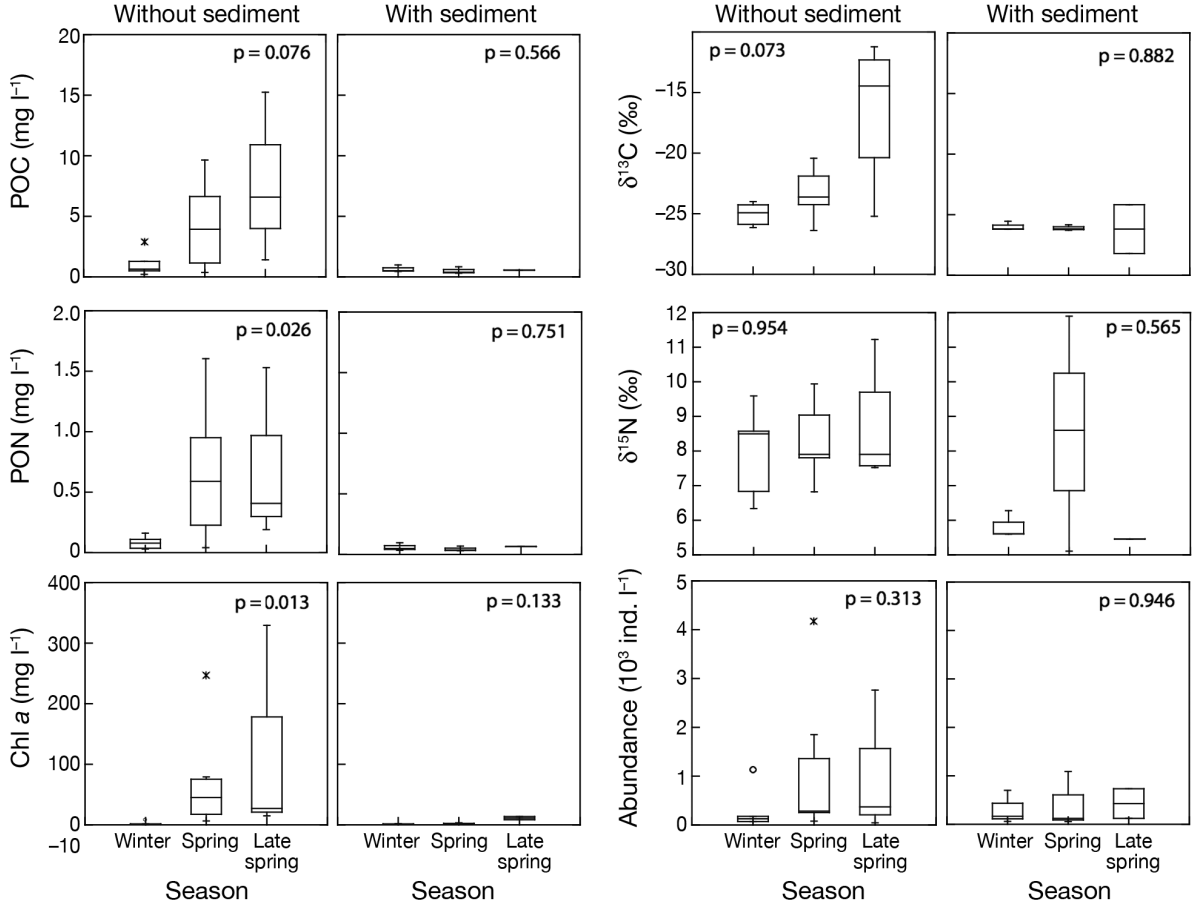

Fig. 2. Seasonal changes in particulate organic carbon and nitrogen (POC and PON) and algal pigment (chl *a*) concentrations, stable carbon and nitrogen isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of POC and PON, respectively, and total meiofauna abundances for sea ice (bottom 10 cm) with and without visible sediment loads. The p-values are based on non-parametric Kruskal-Wallis test with 3 groups (winter, spring, late spring; for definition of seasons see Section 2.6), run separately for ice with and without visible sediment load. Boxes: contain 50 % of the data within the 25 and 75 % quartile as edges (called hinges); center line: median; whiskers: all data that fall in the range of the difference (IQR) between the upper (75 %) and lower (25 %) hinge multiplied by 1.5. Mild outliers (outside 1.5 × IQR from median) are marked as circles, extreme outliers (3 × IQR from median) as crosses

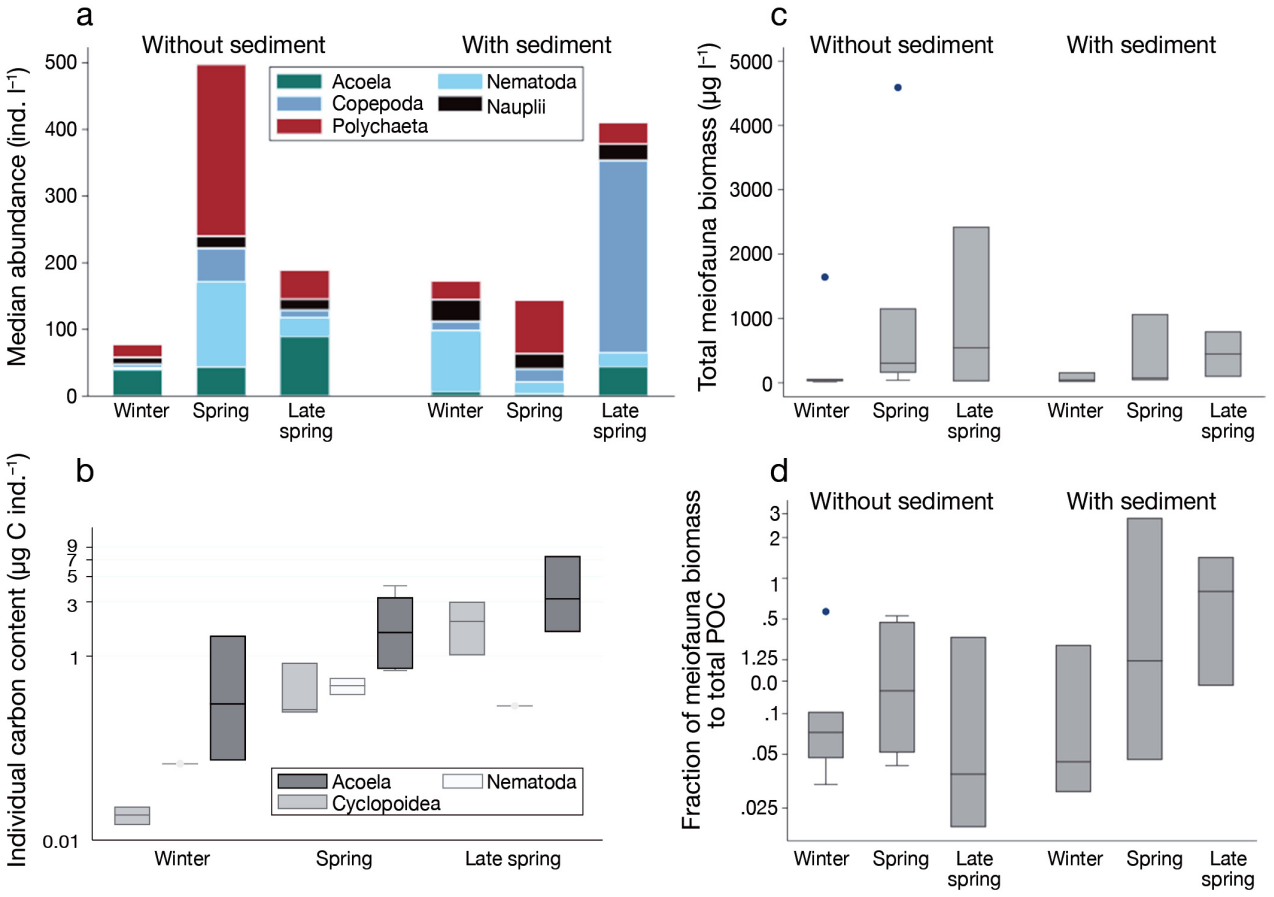

Fig. 3. Seasonal development of ice meiofauna (a) abundance and composition, (b) individual carbon content, (c) individual biomass, and (d) relative contribution to total ice particulate organic carbon (POC) content. Box and whisker plots explained in Fig. 2. Note the log scale for the *x*-axes in panels b and d

median values were observed during the spring period, when Nematoda (127 ind. l^{-1}) and juvenile Polychaeta were most abundant (143 ind. l^{-1}). At the sites with sediment, abundances decreased from winter to later spring for Nematoda and nauplii while copepods (290 ind. l^{-1}) and Acoela (45 ind. l^{-1}) showed highest median abundances in late spring. The polychaete fauna in Elson Lagoon was dominated by juveniles of a hesionid polychaete, while spionid *Scolelepis squamata* juveniles dominated at all other locations.

Carbon-based median individual weights for sea ice meiofaunal taxa derived from pooled samples ranged from 0.23 µg C ind.$^{-1}$ for copepod nauplii to 2.28 µg C ind.$^{-1}$ for Calanoida (Table 1). Nitrogen content ranged from 0.03 µg N ind.$^{-1}$ for copepod nauplii to 0.22 µg N ind.$^{-1}$ for both Acoela and Calanoida. Acoela, Nematoda and Cyclopoida showed an increase in individual body mass with season (Fig. 3b). Using linear regression between individual carbon/nitrogen content and day of the year, Acoela grew by 0.04 µg C d^{-1} ($p = 0.05$) and 0.008 µg N d^{-1} ($p = 0.05$) from winter (median: 0.38 µg C ind.$^{-1}$; 0.13 µg N ind.$^{-1}$) to late spring (median: 3.19 µg C ind.$^{-1}$; 0.65 µg N ind.$^{-1}$). Median Nematoda individual carbon content increased from winter (0.11 µg C ind.$^{-1}$; 0.03 µg N ind.$^{-1}$) to spring (0.55 µg C ind.$^{-1}$; 0.07 µg N ind.$^{-1}$) but decreased in late spring (0.36 µg C ind.$^{-1}$; 0.03 µg N ind.$^{-1}$) due to reproduction and the hatching of juveniles from egg cases. Cyclopoida grew by 0.017 µg C d^{-1} ($p = 0.032$) and 0.003 µg N d^{-1} ($p = 0.031$) to maximum carbon and nitrogen values of 2.01 µg C ind.$^{-1}$ and 0.33 µg N ind.$^{-1}$ in late spring (median values). Low abundances and sporadic occurrence of taxa limited the complete seasonal coverage for carbon and nitrogen bulk and isotope measurements to sediment-free locations.

Across all seasons, median carbon and nitrogen concentrations contributed by the total ice meiofauna biomass in the bottom 10 cm of the sea ice was 152.9 µg C l^{-1} and 22.0 µg N l^{-1} (distribution over season shown in Fig. 3c). This represents a median con-

Table 1. Pooled carbon and nitrogen content of sea ice meiofauna taxa in fast ice close to Utqiaġvik, Alaska. Provided are medians with number of pooled samples in parenthesis regardless of location and season. Trophic levels (TL) were calculated based on the median difference of $\delta^{15}N$ values from particulate organic nitrogen (PON), setting PON as TL 1 and Harpacticoida as TL 2 as the consumer taxon with the lowest difference to PON. Subsequent TLs are estimated assuming a 3.4‰ enrichment per trophic level. nd: no data

Taxon	Median C (µg C ind.$^{-1}$)	Median N (µg N ind.$^{-1}$)	Median $\delta^{13}C$ (‰)	Median $\delta^{15}N$ (‰)	Trophic level
Acoela	1.56 (10)	0.22 (10)	−20.9 (14)	9.5 (14)	2.4
Scolelepis squamata	0.56 (7)	0.09 (7)	−22.6 (12)	8.6 (12)	2.4
Hesionid polychaete	0.55 (5)	0.10 (5)	nd	11.1 (5)	3.1
Nematoda	0.45 (5)	0.05 (5)	−22.2 (7)	12.0 (9)	3.0
Cyclopoida	0.54 (8)	0.05 (5)	−25.3 (9)	10.6 (9)	2.8
Calanoida	2.28 (3)	0.22 (3)	−24.2 (4)	11.3 (4)	2.8
Harpacticoida	0.96 (3)	0.14 (3)	−20.8 (4)	7.8 (4)	2
Nauplii	0.23 (2)	0.03 (2)	−25.2 (3)	10.6 (4)	nd
Onisimus litoralis	nd	nd	−21.7 (5)	12.9 (5)	3.5
Gammaracanthus loricatus	nd	nd	−19.8 (2)	nd	nd

tribution of 11% of total POC and 19% of total PON in sea ice bottom sections (Fig. 3d). The highest median contribution of meiofauna to total POC concentration was estimated for late spring in the sediment-impacted area where it reached 80% (Fig. 3d). With season, meiofauna biomass increased from 46 to 542 µg C l^{-1} at the sediment-free locations and from 42 to 446 µg C l^{-1} at the sediment-laden locations in late spring (Fig. 3c), with no significant differences (Kruskal-Wallis tests, $p > 0.05$) between sediment-free and sediment-laden locations for any season. Acoela contributed the largest fraction to total meiofauna biomass at all sites (median: 17%), followed by *S. squamata* (10%) and Nematoda (9%). At the sediment-free locations, Acoela relative biomass contribution increased with season to a maximum of 53% (median) in late spring; Nematoda had the highest contribution in spring (24%). At the sediment-laden locations in winter and spring, the hesionid polychaete had the highest contribution (11 and 39% respectively), while in late spring Cyclopoidea contributed 20% to total meiofauna biomass.

3.2. Food web structure and carbon flow

The isotopic ratios for both POC and PON differed in their seasonal changes (Fig. 2). The $\delta^{13}C$ ratio of POC was significantly correlated with ice algal pigment concentration (as estimated by linear regression):

$$\delta^{13}C\ (‰) = -24.8\ (‰) + 0.025\ (‰/\mu g\ l^{-1}) \times \text{chl } a\ (\mu g\ l^{-1}) \quad (r^2 = 0.31,\ n = 23,\ p < 0.01) \quad (3)$$

Similarly, this isotopic ratio was even more strongly significantly correlated to POC:

$$\delta^{13}C\ (‰) = -26.0\ (‰) + 0.00078\ (‰/\mu g\ l^{-1}) \times POC\ (\mu g\ l^{-1}) \quad (r^2 = 0.60,\ n = 23,\ p < 0.001) \quad (4)$$

In contrast, no significant relationship was found between $\delta^{15}N$ and chl *a*, or $\delta^{15}N$ and PON concentrations.

The median stable isotope ratios for sea ice meiofauna taxa for the entire data set (Table 1) ranged from −25.3‰ (Cyclopoida) to −19.8‰ (*Gammaracanthus loricatus*) for $\delta^{13}C$, and from 7.8‰ (Harpacticoida) to 12.9‰ (*Onisimus litoralis*) for $\delta^{15}N$. Overall, $\delta^{13}C$ values of sea ice meiofauna increased with heavier $\delta^{13}C$ POC ratios (Fig. 4a). The difference between $\delta^{15}N$ values of taxa and total $\delta^{15}N$ PON did not change significantly with season for any meiofauna taxa (Kruskal Wallis tests, $p > 0.05$) and showed no relationship to the seasonally changing $\delta^{13}C$ POC ratios (Fig. 4b).

The calculated differences between the median $\delta^{15}N$ of sea ice meiofauna taxa and the $\delta^{15}N$ values of PON across the entire data set ranged from −0.14‰ (Harpacticoida) to 5.06‰ (*Onisimus litoralis*), with considerable variation within each taxon (Fig. 4b). The spread of TLs across meiofauna taxa was estimated at 1.5, from TL 2 (as defined by lowest taxa $\delta^{15}N$) to TL 3.5 (Table 1). Acoela, Nematoda and Polychaeta had sufficient data coverage in the sediment-free locations to evaluate seasonal differences in the isotopic ratios between biota and PON (Fig. 5): while little change occurred between winter and spring, this difference decreased for all 3 taxa in late spring (Fig. 5).

The median calculated total sea ice meiofauna ingestion rate across all seasons was 55 µg C l^{-1}d^{-1} (Fig. 6), representing 5.5% of the median POC pool. Ingestion rate varied between <1 and 100% of POC concentrations. For all taxa, ingestion rates were low-

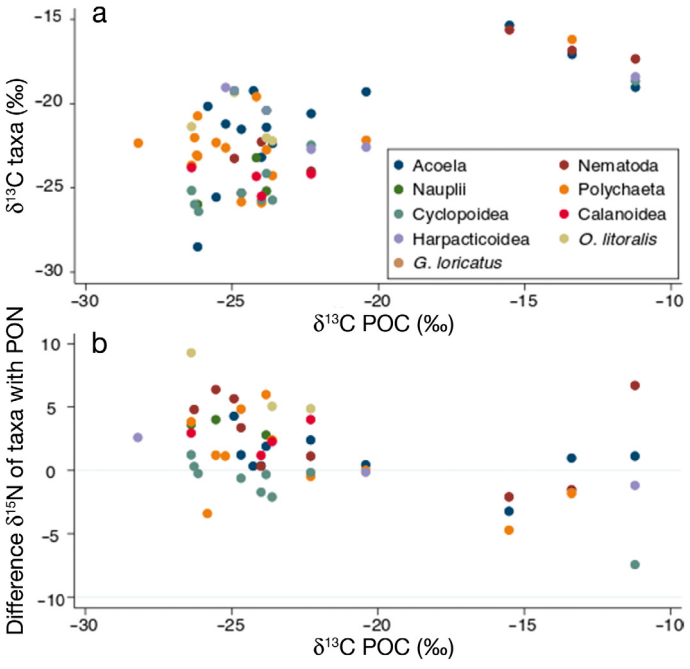

Fig. 4. Changes in the (a) $\delta^{13}C$ and (b) $\delta^{15}N$ ratios in individual sea ice meiofauna taxa in relation to the matching $\delta^{13}C$ particulate organic carbon (POC) ratio from the same locations and time periods. All individually measured isotopic ratios are plotted

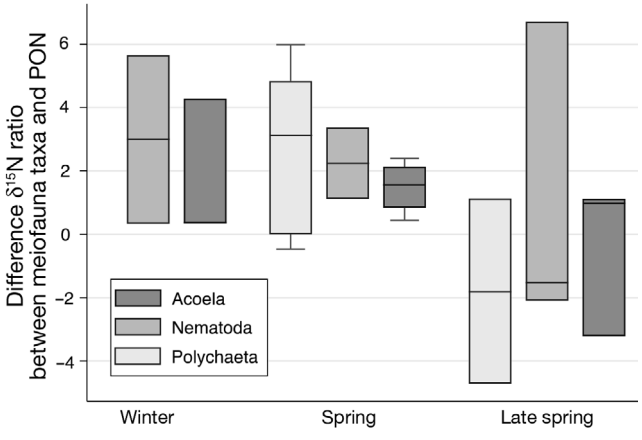

Fig. 5. Seasonal difference in the $\delta^{15}N$ ratio of 3 selected sea ice meiofauna taxa to $\delta^{15}N$ ratio of ice particulate organic nitrogen (PON). Box and whisker plots explained in Fig. 2

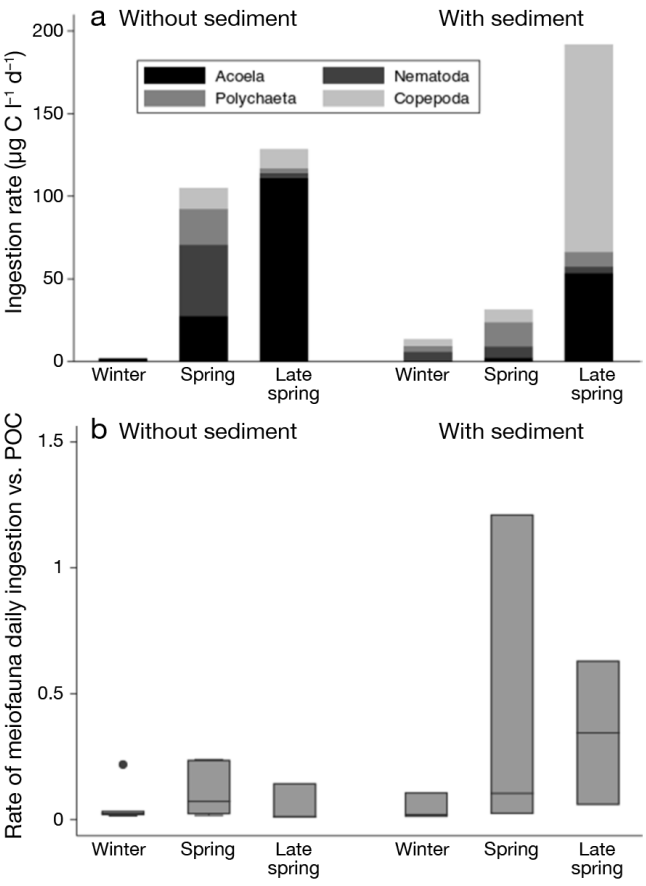

Fig. 6. Seasonal changes of (a) calculated meiofauna ingestion rates and (b) the daily ratio of ingested carbon versus the particulate organic carbon (POC) pool. Box and whisker plots explained in Fig. 2

est in winter with a median total ingestion rate of 15 µg C $l^{-1}d^{-1}$, and increased towards spring with the highest median total ingestion rate of 149 µg C $l^{-1}d^{-1}$ in late spring at the sediment-free ice sites. At these sites, Nematoda (highest median: 43 µg C l^{-1} d^{-1}), Copepoda (13 µg C $l^{-1}d^{-1}$) and Polychaeta (22 µg C $l^{-1}d^{-1}$) ingestion rates peaked in spring, while Acoela showed the overall highest median ingestion rates at 111 µg C l^{-1} d^{-1} in late spring. A similar pattern was found at sites with sediment in the ice; however, overall rates were lower in spring but higher in late spring, with the highest total median ingestion rate of 192 µg C $l^{-1}d^{-1}$ mainly caused by a high contribution of Copepoda (126 µg C l^{-1} d^{-1}) and Acoela (54 µg C l^{-1} d^{-1}).

4. DISCUSSION

The present study provides first insights into trophic dynamics inside the sea ice by looking in detail at the contribution of different meiofauna taxa to ice-derived particulate matter characteristics. In the following, we first discuss the seasonal changes in sea ice meiofaunal properties within the bottom 10 cm of the coastal fast ice in relation to available food resources. We infer close trophic coupling between available food and metazoan grazers via their matching seasonal evolution of $\delta^{13}C$ and $\delta^{15}N$. We then resolve the seasonally changing composition of what is often indiscriminately referred to as 'ice POM'; specif-

ically, we document the shifting contribution of metazoan meiofauna to ice POM. Finally, we quantify the grazing capacity of ice meiofauna based on actual carbon content of ice organisms rather than literature-based assumptions, leading to improved estimates.

4.1. Seasonal role of ice meiofauna related to food resources

4.1.1. Winter

Winter sea ice sampling occurred during the polar night season in the months of December–February. Our winter data agree well with the overall scenario developed for ice algal phenology by Leu et al. (2015), demonstrating a largely heterotrophic phase of the ecosystem during the dark season. Ice algal biomass and POC levels were very low at both the sediment-laden and sediment-free sites. Despite these low values, stable isotope values of POC and PON corresponded largely with typical water column values reported for Arctic marine pelagic particulate matter from nearshore and offshore areas, which mainly come from spring and summer (Gradinger 2009, Iken et al. 2010, Bell et al. 2016). Although substantial sediment load was detected at some sites, the marine signature of Arctic POC and PON stable isotope ratios (e.g. Kumar et al. 2016) indicate a marine origin of these particles, while terrestrial input through rivers or coastal erosion in Arctic areas have lighter $\delta^{13}C$ values (Vonk et al. 2014, Divine et al. 2015, Bell et al. 2016). We suggest fall/winter suspension freezing during ice formation as the likely pathway of incorporation of marine sediments into the fast ice at these shallow sites (for detailed discussion see Gradinger et al. 2009). Further indication of the marine origin of the incorporated sediment in the ice and the POC and PON comes from the ice meiofauna taxa observed at these sites. Here, we observed mainly Nematoda of likely benthic origin (Hajduk 2015) in abundances exceeding the sediment-free sites. Overall, at both sediment-free and sediment-laden locations, meiofauna occurred at low abundances and with the lowest carbon content per individual during winter months. Stable isotopic ratios were roughly the same for Nematoda and Acoela and 1 TL above PON. For both taxa, direct feeding on bacteria, Protozoa, other meiofauna and detritus has been suggested in addition to grazing on algae, both by sea ice studies (e.g. Tchesunov & Riemann 1995) and benthic meiofauna studies (Achatz et al. 2013, Majdi & Traunspurger 2015). Given that algal food sources were scarce in winter, as indicated by the low chl *a* concentrations and the resulting very high POC to chl *a* ratio (medians: sediment-laden site: 510; sediment-free site: 474), we infer that meiofauna food was dominated by heterotrophic/detrital contributors.

4.1.2. Spring

In spring (March–April), sufficient daylight for sea ice algal primary production allowed for the build-up of a strong ice algal bloom, shifting the ice system from a heterotrophic to a phototrophic phase (c.f. Leu et al. 2015) and enhancing food availability for sea ice meiofauna. Algal build-up was delayed in the sediment-laden ice regions due to light limitation (Gradinger et al. 2009). The substantial increase in ice algal biomass in terms of chl *a* and POC corresponded to a reduction in the POC to chl *a* ratio, mainly at the sediment-free site (medians: sediment-free site: 58; sediment-laden site: 270). We also observed enrichment in $\delta^{13}C$ ratios but not $\delta^{15}N$ ratios at the sediment-free sites. Earlier studies already demonstrated this enrichment of the dissolved inorganic carbon pool within the brine channel system (Gradinger 2009, Pineault et al. 2013, Wang et al. 2015) in the semi-confined brine channel space as a consequence of the preferential incorporation of ^{12}C during photosynthesis by sea ice algae. Surprisingly, no such enrichment was evident for $\delta^{15}N$, which remained nearly constant throughout the entire study period in the sediment-free areas, as also observed in other parts of the Arctic (Gradinger 2009, Pineault et al. 2013). Nitrate concentrations as major inorganic nitrogen sources in early spring are reduced by algal uptake within the ice during the ice algal bloom and can cause limitation of ice algal growth (Manes & Gradinger 2009, Gradinger 2009). Consequently, the nitrate pool itself becomes enriched over time and should lead to an enriched signature in the ice algae, which we, however, did not observe. This observation points towards use of an alternative nitrogen source. The direct use of dissolved N_2 by Arctic marine algae has recently been established through observation of a haptophyte–cyanobacterial consortium fixing atmospheric N_2 in the Chukchi and Beaufort Seas (Harding et al. 2018), questioning the past paradigm based on the lack or very low abundances of free-living marine pico-cyanobacteria from Arctic waters (Gradinger & Lenz 1995). Direct fixation of N_2 would strongly lower the isotopic values due to the very modest fractionation of ^{14}N versus ^{15}N during

this process, leading to N_2-fixed $\delta^{15}N$ values close to 0‰ (Sigman & Casciotti 2001). Given the clear dominance, however, of diatoms within the local fast ice system (Manes & Gradinger 2009), we consider this process not very likely to cause the stability in the PON isotopic ratios. A more likely explanation in our view is the tight recycling of nitrogen within the sea ice-based food web, and the release of relatively light $^{14}NH_4$ from consumed organic matter by sea ice heterotrophs. As determined for marine zooplankton, released NH_4 is typically lighter than consumed PON, as the lighter ^{14}N is preferentially metabolized and excreted by animals (Sigman & Casciotti 2001). Thus, the use of released NH_4 for regenerated algal production could act as a stabilizing factor, explaining the near-constant sea ice PON isotopic ratios. This argument is further supported by direct ammonia and nitrate uptake measurements from this area, which showed low mean *f*-ratios of 0.34 for Utqiaġvik bottom ice algal communities (Lee et al. 2008) and 0.11 for phytoplankton (Baer et al. 2017) in spring, indicating preferred incorporation of ammonia. Our estimated meiofaunal ingestion rates of ca. 7% (sediment-free site) of POC point towards a small potential role of meiofauna excretion in this process.

Coincident with the onset of the ice algal bloom and POM increase in spring months, meiofauna reached their seasonal abundance maximum in sediment-free ice, and individuals had increased carbon and nitrogen content. Isotopic enrichment in both POC and meiofauna carbon suggests the latter increase was a result of grazing on ice algae and not of metabolic turnover. Polychaete juveniles dominated in March–April in the ice, as benthic adults had released their meroplanktonic larvae, and juveniles entered the bottom ice to feed (Gradinger et al. 2009, McConnell et al. 2012). Fast growth of juveniles of the sea ice-inhabiting polychaete *Scolelepis squamata* based on herbivory was demonstrated in experimental studies from the same area (McConnell et al. 2012) and from a Svalbard fjord system (V. Pitusi et al. unpubl. data). Interestingly, juvenile polychaetes of a different family entered the sea ice system at the sediment-laden ice locations, leading to an increase in meiofauna biomass at these sites as well, although food sources, as indicated by POC and chl *a* concentrations, remained low at these sites. Nematoda reached their maximum individual body weights in spring with a median of 0.54 µg C ind.$^{-1}$. This value is similar to those from inter- and subtidal beaches in North America (0.56–0.78 µg C ind.$^{-1}$; Sikora et al. 1977), but exceeds individual biomass values reported for Arctic benthic deep-sea Nematoda (0.03–0.15 dry weight [DW] ind.$^{-1}$, Vanreusel et al. 2000 with ca. 40% carbon content in DW; Kennedy 1994) and calculated biomass–carbon conversion based values of ice nematodes used by Gradinger (1999: 0.13 µg C ind.$^{-1}$). We assume that these heavy animals were reproductive adults, as we later observed egg cases and increased abundances of juveniles (see Section 4.1.3).

Although the stable isotopic values revealed a near-constant difference between $\delta^{15}N$ of major meiofauna taxa and PON for winter and spring, we argue that a major shift in nutrition occurred between winter and spring, as now the increased POC and PON in the bottom layer of the fast ice was largely contributed by microalgae, mainly diatoms (Manes & Gradinger 2009). The close relationship of both $\delta^{15}N$ and $\delta^{13}C$ indicates direct feeding on microalgae, as also supported by gut contents analyses (Grainger & Hsiao 1990) and limited experimental evidence (McConnell et al. 2012, V. Pitusi et al. unpubl. data).

4.1.3. Late spring

Late spring conditions were characterized by high variability in several biological factors, including POC, chl *a*, $\delta^{13}C$ and meiofauna abundance, specifically at the sediment-free sites. This is not surprising, as several processes co-occur at this time causing substantial spatial and temporal variability in sea ice, both within and between years (Fortier et al. 2002). In spring as well as late spring/summer, variability in environmental factors (specifically snow depth, melt pond formation and the consequently variable light availability) lead to changes in the rate of build-up of algal and sea ice meiofauna biomass (Riedel et al. 2008). Heavy snow load and corresponding low light intensities, for example, lead to delayed algal bloom formation, similar to the effect demonstrated for sediment-laden sea ice (Gradinger et al. 2009, this study). Further, factors related to the end of the ice algal growing season contribute to increased variability (Leu et al. 2015): while algal growth continues and biomass further accumulates within the ice, increased nutrient limitation (Cota et al. 1987, Gradinger 2009) and increased release of algae due to ice melt of the bottom layer (Michel et al. 2002, Juhl et al. 2011) or increased brine drainage due to snow melt (Tamelander et al. 2009) will either slow down biomass build-up or reduce algal biomass. Even small melt events at the ice bottom due to the increased temperatures and self-heating due to light absorption (Zeebe et al. 1996) in the bottom layer can

release large fractions of the ice biota (Tremblay et al. 1989, Michel et al. 2002, R. Gradinger et al. unpubl data). Such melt events make sea ice-derived POM available as food to under-ice, pelagic and/or benthic biota (Gradinger & Bluhm 2010, Schollmeier et al. 2018, Rybakova et al. 2019). With progressing time and increased algal biomass, we observed further enrichment of $\delta^{13}C$ values of ice POM. Interestingly, we saw similar increases in the carbon isotopes in the sea ice meiofauna taxa, indicating — as expected — that the algal-dominated sea ice particulate matter is indeed the major food source for the sea ice-based food web.

The sea ice meiofauna community composition changed from spring to late spring. Major shifts included the reduced abundance of polychaete juveniles and large Nematoda (which presumably left the ice for benthic settlement) and increased contributions of Acoela and smaller Nematoda. The observed weight reduction for Nematoda was related to the occurrence of smaller individuals due to reproduction occurring with the ice in April–May (Kern & Carey 1983, Riemann & Sime-Ngando 1997, authors' pers. obs.). Acoela, in contrast, continued to grow and reached a maximum median weight of 3.19 µg C ind.$^{-1}$, substantially (by factor of 8) exceeding the estimated individual biomass used in older meiofauna grazing studies (Gradinger 1999). The $\delta^{15}N$ of sea ice meiofauna showed lower values compared to PON of the matching time, with often negative differences. The unexpectedly low or often lacking enrichment observed in our data could be explained in several different (and not necessarily exclusive) ways. First, relatively low enrichment could be expected as $\delta^{15}N$ enrichment is reduced in ammonia-excreting taxa (Vanderklift & Ponsard 2003) like most sea ice meiofauna (Crustacea: Aarset 1991; Turbellaria, now Acoela: Holley 2016; Nematoda: Rothstein 1963). A second possible explanation might lie in the use of resources other than sea ice algae; namely, the role of the microbial food web, which we did not sample. Different sea ice meiofauna taxa can consume either dissolved organic matter (DOM), or bacteria, flagellates and/or ciliates as part of their food spectrum, all of which can occur in high abundance in sea ice (see Gradinger et al. 1999 for complete spectrum of ice inhabitants). Freshly produced dissolved organic nitrogen (DON) may be an unsampled but important nitrogen source during the late spring season. Unfortunately, the isotopic changes related to DON production and uptake are poorly understood, although they are considered important parts of the marine nitrogen cycling (Sigman et al. 2009). DON from subtropical areas had $\delta^{15}N$ ratios of ca. 4‰ (Sigman et al. 2009) and were similar to values in the North Atlantic (4.1–6.6‰, Aluwihare & Meador 2008). In late spring and during the melting season, sea ice does harbor a very active microbial network, with preferential retention of extracellular particulate substances (EPS), POC and dissolved organic carbon (DOC) (Juhl et al. 2011), which could lead to a more heterotrophic food base of the meiofauna. If DON in sea ice had values as low as observed in the North Atlantic, this could lead to lower ratios in meiofauna as well, through food web interactions. A third explanation for lower meiofaunal than PON $\delta^{15}N$ values could be related to the (unknown) turnover time of $\delta^{15}N$. As mentioned above, the isotopic half-life (50% of the entire change happens in this period) of the partially under-ice, partially benthic Arctic littoral amphipod *Onisimus litoralis* was over 20 d to several months. While we assume that meiofauna likely has a faster metabolic and growth-related turnover, comparatively slow turnover at low temperatures can still lead to a time lag in isotopic composition and the potential for misinterpreting snapshot isotope data in food web analysis. Given that the PON isotopic ratios did not change with season, however, we suggest that the increased activity of the microbial food web may be causing the observed meiofauna $\delta^{15}N$ ratios in late spring.

4.2. Grazing impact

Despite large changes and variability in algal biomass and meiofaunal abundance and composition, we did not observe significant changes in the relative amount of ingested carbon by the sea ice meiofauna grazing related to the algal biomass/POC with season. Instead, the ingestion rate followed the seasonal change in algal biomass, although the contribution of individual taxa shifted in their relative importance. The large variability in physical and biological processes contributing to the seasonal occurrence of meiofauna and algae within the ice also indirectly explains the very broad range of observed potential grazing impacts. The highest ingestion rate was found in spring at the sediment-free locations (median: 7.1% of POC) and in late spring in sediment-laden sea ice (34.3‰ of POC). These estimates demonstrate again that meiofauna has only a minor grazing impact during algal spring bloom build-up, where daily primary productivity rates in the coastal sites exceed the estimated grazing rates by at least one order of magnitude (Lee et al. 2008). Other stud-

ies using a similar approach, however, reported considerably lower grazing impacts (Nozais et al. 2001: less than 0.9%; Michel et al. 2002: 2.6%) for coastal ice meiofaunal communities. We suggest that this disparity may not necessarily represent a difference between regions, but rather is due to the relatively high individual carbon content estimates we determined directly for our study area compared to those used from other areas in the past.

4.3. Composition of sea ice-derived POM

Although the overall $\delta^{15}N$ ratio did not change seasonally for PON, its composition underwent substantial changes with season. This is not surprising given the above outlined shift of the sea ice ecosystem from a heterotrophic stage through a stage of new production to a stage of mainly regenerated production, thus providing different food source compositions for the meiofauna. Characterizing PON is challenging because PON data in this and most other studies (e.g. Pineault et al. 2013) do not represent a single food source (i.e. sea ice algae) but rather the entire spectrum of sea ice POM, ranging from gel-like particles (Meiners et al. 2008), bacteria, algae, protozoans and fungi to metazoans (e.g. Gradinger et al. 1999). A further complication arises from the fact that meiofauna represent a considerable fraction of the sea ice POC (this study) and thus itself influences the POC/PON values, while not necessarily directly feeding on itself. Consequently, the POC/PON values can only be considered a proxy for the true isotopic ratio of ice algae but do not represent a single endmember.

5. CONCLUSIONS AND OUTLOOK

This study documents that the POM often summarized as 'ice POM' in trophic studies is comprised of a suite of different metazoan meiofauna in addition to the algal/protist community. The composition of these 2 components is generally dominated by algae/protists, but with seasonally substantial proportions of meiofauna. Our stable isotope approach showed the individual meiofaunal taxa to span at least 1.5 TLs, in addition to the primary producer level. We also suggest that food sources not specifically sampled in this study, namely bacteria, DOM, detritus and EPS, may be relevant for sea ice meiofauna, specifically in winter and post-bloom periods as shown in other habitats (e.g. Tenore et al. 1977). To close this gap, we suggest feeding experiments with adequate methodologies to provide more direct evidence of the feeding spectrum of the different ice meiofauna taxa, including the likely top predatory meiofauna taxon *Sympagohydra tuuli*, which was not included in this study due the lack of biomass for isotope analysis. Combining experimental with trophic marker studies would be necessary to complete the here-started sea ice food web model and to finally move beyond the currently strongly simplified algal-focused production models.

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LITERATURE CITED

Aarset AV (1991) The ecophysiology of under-ice fauna. Polar Res 10:309–324

Achatz JG, Chiodin M, Salvenmoser W, Tyler S, Martinez P (2013) The Acoela: on their kind and kinships, especially with nemertodermatids and xenoturbellids (Bilateria incertae sedis). Org Divers Evol 13:267–286

Aluwihare L, Meador T (2008) Chemical composition of marine dissolved organic nitrogen. In: Capone DG, Bronk DA, Mulholland MR, Carpenter EJ (eds) Nitrogen in the marine environment, 2nd edn. Academic Press, Burlington, MA, p 95–140

Arar EJ, Collins GB (1997) Method 445.0: *in vitro* determination of chlorophyll *a* and phaeophytin *a* in marine and freshwater by fluorescence. National Exposure Research Laboratory Office of Research and Development, US Environmental Protection Agency, Cincinnati, OH

Attard KM, Søgaard DH, Piontek J, Lange BA and others (2018) Oxygen fluxes beneath Arctic land-fast ice and pack ice: towards estimates of ice productivity. Polar Biol 41:2119–2134

Baer SE, Sipler RE, Roberts QN, Yager PL, Frischer ME, Bronk DA (2017) Seasonal nitrogen uptake and regeneration in the western coastal Arctic. Limnol Oceanogr 62: 2463–2479

Bell LE, Bluhm BA, Iken K (2016) Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. Mar Ecol Prog Ser 550:1–24

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18: S77–S96

Bluhm BA, Hop H, Vihtakari M, Gradinger R, Iken K, Melnikov IA, Søreide JE (2018) Sea ice meiofauna distribution on local to pan-Arctic scales. Ecol Evol 8:2350–2364

Campbell K, Mundy CJ, Juhl AR, Dalman LA and others (2019) Melt procedure affects the photosynthetic response of sea ice algae. Front Earth Sci 7:21

Carey AGJ, Boudrias MA (1987) Feeding ecology of *Pseudalibrotus* (=*Onisimus*) *litoralis* Kroyer (Crustacea: Amphipoda) on the Beaufort Sea inner continental shelf. Polar Biol 8:29–33

Cimoli E, Lucieer A, Meiners KM, Lund-Hansen LC and others (2017) Towards improved estimates of sea-ice algal biomass: experimental assessment of hyperspectral imaging cameras for under-ice studies. Ann Glaciol 58: 68–77

Clasby RC, Horner R, Alexander V (1973) An *in situ* method for measuring primary production of Arctic sea ice algae. J Fish Res Board Can 30:835–838

Cota GF, Prinsenberg SJ, Bennett EB, Loder JW, Lewis MR, Anning JL, Watson NHF (1987) Nutrient fluxes during extended blooms of Arctic ice algae. J Geophys Res 92: 1951–1962

Cummings VJ, Barr NG, Budd RG, Marriott PM, Safi KA, Lohrer AM (2019) *In situ* response of Antarctic under-ice primary producers to experimentally altered pH. Sci Rep 9:6069

Divine LM, Iken K, Bluhm BA (2015) Regional benthic food web structure on the Alaska Beaufort Sea shelf. Mar Ecol Prog Ser 531:15–32

Eicken H, Gradinger R, Gaylord A, Mahoney A, Rigor I, Melling H (2005) Sediment transport by sea ice in the Chukchi and Beaufort Seas: Increasing importance due to changing ice conditions? Deep Sea Res II 52:3281–3302

Fortier M, Fortier L, Michel C, Legendre L (2002) Climatic and biological forcing of the vertical flux of biogenic particles under seasonal Arctic sea ice. Mar Ecol Prog Ser 225:1–16

Garrison DL, Buck KR (1986) Organism losses during ice melting: a serious bias in sea ice community studies. Polar Biol 6:237–239

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res 44: 1623–1644

Gradinger R (1999) Integrated abundances and biomass of sympagic meiofauna from Arctic and Antarctic pack ice. Polar Biol 22:169–177

Gradinger R (2002) Sea ice microorganisms. In: Bitten G (ed) Encyclopedia of environmental microbiology. Wiley & Sons, New York, NY, p 2833–2844

Gradinger R (2009) Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep Sea Res II 56:1201–1212

Gradinger R, Bluhm B (2009) Assessment of the abundance and diversity of sea ice biota. In: Eicken H, Gradinger R, Salganek M, Shirasawa K, Perovich D, Leppäranta M (eds) Field techniques for sea ice research. University of Alaska Press, Fairbanks, AK, p 283–300

Gradinger R, Bluhm B (2010) Timing of ice algal grazing by the Arctic nearshore benthic amphipod *Onisimus litoralis.* Arctic 63:355–358

Gradinger R, Lenz J (1995) Seasonal occurrence of picocyanobacteria in the Greenland Sea and central Arctic Ocean. Polar Biol 15:447–452

Gradinger R, Friedrich C, Spindler M (1999) Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep Sea Res II 46:1457–1472

Gradinger RR, Kaufman MR, Bluhm BA (2009) Pivotal role of sea ice sediments in the seasonal development of nearshore Arctic fast ice biota. Mar Ecol Prog Ser 394:49–63

Grainger EH, Hsiao SIC (1990) Trophic relationships of the sea ice meiofauna in Frobisher Bay, Arctic Canada. Polar Biol 10:283–292

Hajduk M (2015) Density and distribution of meiofauna in the northeastern Chukchi Sea. MSc thesis, University of Alaska Fairbanks

Harding K, Turk-Kubo KA, Sipler RE, Mills MM, Bronk DA, Zehr JP (2018) Symbiotic unicellular cyanobacteria fix nitrogen in the Arctic Ocean. Proc Natl Acad Sci USA 115:13371–13375

Hassett BT, Ducluzeau AL, Collins RE, Gradinger R (2017) Spatial distribution of aquatic marine fungi across the western Arctic and sub-arctic. Environ Microbiol 19: 475–484

Hobson KA, Welch H (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9–18

Holley D (2016) General zoology. Investigating the animal world. Dog Ear Publishing, Indianapolis, IN

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol 28:238–249

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res II 57:71–85

Jin M, Deal CJ, Wang J, Shin KH and others (2006) Controls of the landfast ice-ocean ecosystem offshore Barrow, Alaska. Ann Glaciol 44:63–72

Juhl AR, Krembs C, Meiners KM (2011) Seasonal development and differential retention of ice algae and other organic fractions in first-year Arctic sea ice. Mar Ecol Prog Ser 436:1–16

Junge K, Eicken H, Deming JW (2004) Bacterial activity at –2 to –20°C in Arctic wintertime sea ice. Appl Environ Microbiol 70:550–557

Karl DM, Winn CD, Hebel DVW, Letelier R (1990) JGOFS Hawaii ocean time-series program field and laboratory protocols. http://hahana.soest.hawaii.edu/hot/protocols/protocols.html

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis.* Oecologia 158:11–22

Kennedy AD (1994) Carbon partitioning within meiobenthic nematode communities in the Exe Estuary, UK. Mar Ecol Prog Ser 105:71–78

Kern JC, Carey AGJ (1983) The faunal assemblage inhabiting seasonal sea ice in the nearshore Arctic Ocean with emphasis on copepods. Mar Ecol Prog Ser 10:159–167

Kudoh S, Robineau B, Suzuki Y, Fujiyoshi Y, Takahashi M (1997) Photosynthetic acclimation and the estimation of temperate ice algal primary production in Saroma-ko Lagoon, Japan. J Mar Syst 11:93–109

Kumar V, Tiwari M, Nagoji S, Tripathi S (2016) Evidence of anomalously low $\delta^{13}C$ of marine organic matter in an Arctic fjord. Sci Rep 6:36192

Lavoie D, Denman K, Michel C (2005) Modeling ice algal growth and decline in a seasonally ice-covered region of the Arctic (Resolute Passage, Canadian Archipelago). J Geophys Res 110:C11009

Lee SH, Whitledge TE, Kang SH (2008) Spring time production of bottom ice algae in the landfast sea ice zone at Barrow, Alaska. J Exp Mar Biol Ecol 367:204–212

Leu E, Mundy CJ, Assmy P, Campbell K and others (2015) Arctic spring awakening — steering principles behind the phenology of vernal ice algal blooms. Prog Oceanogr 139:151–170

Macdonald RW (2000) Arctic estuaries and ice: a positive-negative estuarine couple. In: Lewis EL (ed) The freshwater budget of the Arctic Ocean. Kluwer, Amsterdam, p 383–407

Macdonald RW, Carmack EC, McLaughlin FA, Falkner FK, Swift JH (1999) Connections among ice, runoff and atmospheric forcing in the Beaufort Gyre. Geophys Res Lett 26:2223–2226

Mahoney A, Eicken H, Shapiro L (2007) How fast is landfast sea ice? A study of the attachment and detachment of nearshore ice at Barrow, Alaska. Cold Reg Sci Technol 47:233–255

Majdi N, Traunspurger W (2015) Free-living nematodes in the freshwater food web: a review. J Nematol 47:28–44

Manes SS, Gradinger R (2009) Small scale vertical gradients of Arctic ice algal photophysiological properties. Photosynth Res 102:53–66

Marquardt M, Majaneva S, Pitusi V, Søreide JE (2018) Pan-Arctic distribution of the hydrozoan *Sympagohydra tuuli*? First record in sea ice from Svalbard (European Arctic). Polar Biol 41:583–588

McConnell B, Gradinger R, Iken K, Bluhm B (2012) Growth rates of Arctic juvenile *Scolelepis squamata* (Polychaeta: Spionidae) isolated from Chukchi Sea fast ice. Polar Biol 35:1487–1494

McMinn A, Gradinger R, Nomura D (2009) Biogeochemical properties of sea ice. In: Eicken H, Gradinger R, Salganek M, Shirasawa K, Perovich D, Leppäranta M (eds) Field techniques for sea ice research. University of Alaska Press, Fairbanks, AK, p 259–282

Meiners K, Krembs C, Gradinger R (2008) Exopolymer particles: microbial hotspots of enhanced bacterial activity in Arctic fast ice (Chukchi Sea). Aquat Microb Ecol 52: 195–207

Meiners KM, Arndt S, Bestley S, Krumpen T and others (2017) Antarctic pack ice algal distribution: floe-scale spatial variability and predictability from physical parameters. Geophys Res Lett 44:7382–7390

Michel C, Nielsen TG, Nozais C, Gosselin M (2002) Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). Aquat Microb Ecol 30:57–68

Mock T, Gradinger R (1999) Determination of Arctic ice algal production with a new and easy *in situ* incubation technique. Mar Ecol Prog Ser 177:15–26

Mock T, Kruse M, Dieckmann GS (2003) A new microcosm to investigate oxygen dynamics at the sea ice water interface. Aquat Microb Ecol 30:197–205

Moloney CL, Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. Limnol Oceanogr 34:1290–1299

Nozais C, Gosselin M, Michel C, Tita G (2001) Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay. Mar Ecol Prog Ser 217:235–250

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

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

Piraino S, Bluhm BA, Gradinger R, Boero F (2008) *Sympagohydra tuuli* gen. nov. and sp. nov. (Cnidaria: Hydrozoa) a cool hydroid from the Arctic sea ice. J Mar Biol Assoc UK 88:1637–1641

Polyakov IV, Pnyushkov AV, Alkire MB, Ashik IM and others (2017) Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the Arctic Ocean. Science 356: 285–291

Post DM (2002) Using stable isotopes to estimate trophic position models, methods, and assumptions. Ecology 83: 703–718

Riedel A, Michel C, Gosselin M, LeBlanc B (2008) Winter-spring dynamics in sea-ice carbon cycling in the coastal Arctic Ocean. J Mar Syst 74:918–932

Riemann F, Sime-Ngando T (1997) Note on sea-ice nematodes (Monhysteroidea) from Resolute Passage, Canadian high Arctic. Polar Biol 18:70–75

Rothstein M (1963) Nematode biochemistry. III. Excretion products. Comp Biochem Physiol 9:51–59

Rybakova E, Kremenetskaia A, Vedenin A, Boetius A, Gebruk A (2019) Deep-sea megabenthos communities of the Eurasian Central Arctic are influenced by ice-cover and sea-ice algal falls. PLOS ONE 14:e0211009

Schollmeier T, Oliveira ACM, Wooller MJ, Iken K (2018) Tracing sea ice algae into various benthic feeding types on the Chukchi Sea shelf. Polar Biol 41:207–224

Siebert S, Anton-Erxleben F, Kiko R, Kramer M (2009) *Sympagohydra tuuli* (Cnidaria, Hydrozoa): first report from sea ice of the central Arctic Ocean and insights into histology, reproduction and locomotion. Mar Biol 156:541–554

Sigman DM, Casciotti KL (2001) Nitrogen isotopes in the ocean. In: Steele JH, Thorpe SA, Turekian KK (eds) Encyclopedia of ocean sciences. Academic Press, San Diego, CA, p 1884–1894

Sigman D, Karsh K, Casciotti K (2009) Ocean process tracers: nitrogen isotopes in the ocean. In: Steele J, Thorpe S, Turekian K (eds) Encyclopedia of ocean sciences. Academic Press, San Diego, CA, p 4138–4153

Sikora JP, Sikora WB, Erkenbrecher CW, Coull BC (1977) Significance of ATP, carbon, and caloric content of meiobenthic nematodes in partitioning benthic biomass. Mar Biol 44:7–14

Slagstad D, Wassmann PFJ, Ellingsen I (2015) Physical constrains and productivity in the future Arctic Ocean. Front Mar Sci 2:85

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59–87

Stasko AD, Bluhm BA, Michel C, Archambault P and others (2018) Benthic–pelagic trophic coupling in an Arctic marine food web along vertical water mass and organic matter gradients. Mar Ecol Prog Ser 594:1–19

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

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

Tchesunov AV, Riemann F (1995) Arctic sea ice nematodes (Monhysteroidea) with descriptions of *Cryonema crassum* gen. n. sp. n. and *C. tenue* sp. n. Nematologica 41:35–50

Tenore KR, Tietjen JH, Lee U (1977) Effect of meiofauna on incorporation of aged eelgrass, *Zostera marina*, detritus by the polychaete *Nephthys incisa*. J Fish Res Board Can 34:563–567

Tremblay C, Runge JA, Legendre L (1989) Grazing and sedimentation of ice algae during and immediately after a bloom at the ice-water interface. Mar Ecol Prog Ser 56: 291–300

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia 136:169–182

Vanreusel A, Clough L, Jacobsen K, Ambrose W and others (2000) Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep Sea Res I 47:1855–1879

Vonk JE, Semiletov IP, Dudarev OV, Eglinton TI and others (2014) Preferential burial of permafrost-derived organic carbon in Siberian-Arctic shelf waters. J Geophys Res Oceans 119:8410–8421

Wang SW, Budge SM, Iken K, Gradinger RR, Springer AM, Wooller MJ (2015) Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. Mar Ecol Prog Ser 518: 31–50

Welch H, Bergmann M, Jorgenson J, Burton W (1988) A subice suction corer for sampling epontic ice algae. Can J Fish Aquat Sci 45:562–568

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

Yokoyama H, Tamaki A, Harada K, Shimoda K, Koyama K, Ishihi Y (2005) Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Mar Ecol Prog Ser 296: 115–128

Zeebe RE, Eicken H, Robinson DH, Wolf-Gladrow D, Dieckmann GS (1996) Modelling the heating and melting of sea ice through light absorption by microalgae. J Geophys Res 101:1163–1181

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