

1 First Arctic sea ice meiofauna food web analysis based on abundance, biomass and stable
2 isotope ratios of sea ice metazoan fauna from near-shore Arctic fast ice

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4 Rolf Gradinger¹ *

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6 Bodil A. Bluhm^{1,2}

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8 ¹UiT, the Arctic University of Norway, N-9037 Tromsø, Norway

9 ²College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks AK

10 99775-7220, USA

11 *Rolf.gradinger@uit.no

12

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20 **Abstract**

21 Particulate organic carbon produced in sea ice is often included in stable isotopic food web

22 studies of polar seas as a single ‘ice POM’ value. During ten field trips to landfast ice off

23 Alaska’s north coast, we examined the seasonal contribution of sea ice-associated meiofauna

24 to total POM, and the trophic structure within the sea ice using bulk carbon and nitrogen

25 stable isotope ratios. Algal biomass, POC/PON and meiofaunal abundances increased after

1 the polar night, and a suite of different metazoan meiofauna contributed seasonally
2 substantially to total ice POC amount. $\delta^{13}\text{C}$ values of meiofauna generally tracked the
3 seasonal enrichment of $\delta^{13}\text{C}$ in POC suggesting a trophic relationship, also supported by
4 increasing body mass of meiofauna over the seasons. $\Delta^{15}\text{N}$ of individual meiofaunal taxa
5 varied by at least 1.5 trophic levels. $\delta^{13}\text{C}$ values of some meiofauna were very close to or
6 below POC values suggesting the use of other carbon sources, perhaps including DOC and
7 bacteria among others. Estimated potential grazing rates, based on generated C and N content
8 of individuals in this study, confirmed the earlier estimated generally low grazing impact of
9 the meiofauna on the ice algal spring bloom, leaving large portions of the produced matter as
10 food for pelagic and benthic organisms. The findings suggest a more complex sea ice based
11 food web structure that should be incorporated in food web, conceptual and other models
12 than is currently common.

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1 **1. Introduction**

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4 Sea ice related biological processes have received increasing attention due to the substantial
5 changes in the Arctic sea ice regime and associated biological consequences over the last
6 decades (Bluhm & Gradinger 2008). Observed and projected changes include loss of
7 biodiversity, increased primary production and Atlantification-Pacification of the Arctic
8 Ocean (Slagstad et al. 2015, Polyakov et al. 2017). Most of the observed and suggested
9 biological changes relate to properties observed at the bottom of the ice itself (e.g. under-ice
10 flora and fauna) or in the water column (zooplankton, phytoplankton) and at the sea floor.
11 However, methodological challenges related to working with sea ice make it intrinsically
12 difficult to study simultaneously its wide range of physical, chemical and biological
13 properties. Although recent progress has been made in regards to e.g. remotely sensing ice
14 algal biomass (Cimoli et al. 2017, Meiners et al. 2017) or the non-destructive determination
15 of ice algal primary productivity using eddy correlation approaches (Attard et al. 2018),
16 destruction of the habitat is still applied and required for estimation of, e.g., community
17 diversity or activity and biomass measurements in different ice layers (Gradinger & Bluhm
18 2009, McMinn et al. 2009).

19
20 So far only a limited number of approaches were successfully applied to determine biological
21 rates within sea ice under *in-situ* conditions (Clasby et al. 1973, Mock & Gradinger 1999,
22 Junge et al. 2004, Meiners et al. 2008, Cummings et al. 2019) and such approaches include
23 mainly the level of bacterial and algal production, which can be assessed by tracers. The
24 likely best studied aspect of the sea ice related biological carbon cycle is the primary
25 production. Studies focused on both the physical/chemical control of primary productivity in

1 experimental or field settings (Kudoh et al. 1997, Mock et al. 2003), while field expeditions
2 aimed at providing regional (Gradinger 2009) or basin wide (Gosselin et al. 1997) estimates
3 of sea ice primary production. Typical yearly ice algal primary production estimates
4 (Gradinger 2009) range from 1.5 to 10 g C m⁻², with differences largely being attributed to
5 the snow and ice characteristics and nutrient supply from the water column (e.g., Lavoie et al.
6 2005). Field and modeling studies revealed that light and inorganic nutrient supply are the
7 main physical forcing parameters in addition to ice temperatures and brine salinities and that
8 algal growth is largely determined by bottom-up control (Gradinger 2002, Jin et al. 2006).
9 While detailed regional comparisons are partially flawed by inconstant application of
10 adequate methodologies (Campbell et al. 2019) it has been documented extensively that sea
11 ice produced organic matter is used by, and relevant to, various parts of the Arctic food web
12 (Wang et al. 2015, Schollmeier et al. 2018). Most of the ice-based primary production is
13 released to the water column during ice melt (Michel et al. 2002) and contributes to the
14 nutrition of pelagic and/or benthic consumers. Only a limited amount of organic carbon is
15 utilized by herbivorous sea ice meiofauna, zooplankton and ice endemic amphipods, with all
16 consumers combined typically consuming less than 10% of the algal production (Gradinger
17 1999, Werner 1997, Michel et al. 2002). These estimates are for under-ice fauna based on
18 experimental grazing data, while they are for meiofauna based on allometric equations.
19
20 Sea ice meiofauna in general is likely the least studied component of the sea ice based food
21 web, next to fungi (Hassett et al. 2017). Sea ice meiofauna inhabits the brine channel network
22 within the sea ice and is typically defined as small metzoans inhabiting the sea ice brine
23 channel network including e.g. Nematoda, Rotifera, Acoela and Cnidaria with typical size
24 ranges of 50 to 500 μ m (Bluhm et al. 2018) with some studies also including larger ciliates.
25 So far allometric equations were used to calculate potential maximum ingestion rates of

1 meiofauna taxa based on the biomass of individuals (Gradinger 1999). While these studies
2 revealed a generally low impact of sea ice metazoans on the accumulation of algal biomass
3 within the ice (Gradinger 1999, Nozais et al. 2001, Michel et al. 2002), they did not provide
4 any insights into the trophic connections between taxa and the number of trophic levels
5 present within the ice. Historical information based on gut content (Grainger & Hsiao 1990)
6 or fecal pellet (Carey & Boudrias 1987, Gradinger & Bluhm 2010) analysis indicated that
7 herbivory is the most common feeding mode for many of these ice inhabiting species. Hsiao
8 and Grainger (1990) found that 13 out of 16 sea ice meiofauna taxa were entirely
9 herbivorous, grazing on a total of 26 genera of algae. However the recent discovery of a
10 predatory cnidarian *Sympagohydra tuuli* (Piraino et al. 2009, Siebert et al. 2009, Marquardt et
11 al. 2018) in Arctic sea ice shows that the sea ice food web includes at least one additional
12 trophic level.

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14 Aiming at providing more detailed information on this threatened, unique and understudied
15 polar food web within sea ice, we applied a stable isotope approach that has been
16 successfully used in other Arctic marine habitats (e.g. Hobson & Welch 1992, Iken et al.
17 2005, Stasko et al. 2018). The underlying principle using carbon and nitrogen stable isotope
18 tracers is the stepwise enrichment between trophic levels of about 2-4‰ for $\delta^{15}\text{N}$ and 0-1‰
19 for $\delta^{13}\text{C}$ (Peterson & Fry 1987, Hobson & Welch 1992, Post 2002, Tamelander et al. 2008),
20 although fractionation falling outside these ranges has also been measured (Hisachi et al.
21 2005). Typically, $\delta^{13}\text{C}$ ratios have been used to identify food sources, for example ice algae
22 versus phytoplankton, based on previously observed enriched $\delta^{13}\text{C}$ signatures in ice algae
23 during algal blooms, where carbon isotope ratios increases from values below -23‰ to levels
24 above -13‰ (Soreide et al. 2006, Gradinger et al. 2009). $\delta^{15}\text{N}$ enrichment does not
25 necessarily show the same seasonal enrichment as $\delta^{13}\text{C}$ sea ice ratios, rather it lends itself to

1 estimate trophic levels within a community (e.g. Iken et al. 2005). In this study, seasonal
2 observations at a coastal fast ice site close to Utqiagvik, Alaska (formerly Barrow) aimed,
3 first, at applying a stable isotope approach to sea ice meiofauna with the goal to, for the first
4 time, differentiate between different taxa that are commonly blended in a single value of 'ice
5 particulate organic matter' (POM). Second, we aimed to estimate the contribution of sea ice
6 meiofauna to total sea ice particulate organic carbon (POC) and nitrogen (PON) using direct
7 measurements of individual meiofauna C and N content. Third, we used the measured sea ice
8 POC values in a trophic model to determine their potential ingestion rates during different
9 times of the seasonal sea ice community development.

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11 **2.1 Materials and Methods**

12

13 2.1. Study site

14 Sampling took place in fast ice along the Alaskan coastline which forms in
15 November/December and reaches a thickness of 1.5 to 1.8 m by April (Macdonald et al.
16 1999, Mahoney et al. 2007). Break-up usually occurs between late June and mid-July
17 (Mahoney et al. 2007). Attached to the shore and anchored to the sea floor by up to 20 to 25
18 m deep keels (Macdonald 2000), the ice extends several km out onto the Chukchi and
19 Beaufort shelves. Samples for this study were collected during ten field trips to Utqiagvik,
20 Alaska: 24-28 Apr and 27 May-1 Jun 2002; 12-17 Feb, 1-5 Apr and 27-30 May 2003; 7-12
21 Dec 2005; 30 Jan-4 Feb, 13-18 Mar, 21-26 Apr and 27 May-1 Jun 2006 at four different
22 locations (Fig. 1). In 2002, we sampled the location 'BASC' in the Chukchi Sea (71° 19' N,
23 156° 41' W). In 2003 site 'BASC' and site 'Beaufort' in the Beaufort Sea (71° 22' N,
24 156° 24' W) were sampled. During Dec 2005-Jun 2006 field periods we sampled site
25 'BASC', site 'Hanger' (Chukchi Sea 71° 20' N, 156° 39' W) and site 'Elson' (71° 21' N, 156°

1 28' W) in Elson Lagoon. Water depth at these sites ranged from 2.0-6.3 m. All sites were less
2 than 1 km offshore. Part of the 2002 and 2003 data were used to assess the effect of high
3 concentrations of sea ice sediments for the seasonal development of sea ice communities
4 (Gradinger et al. 2009.). Substantial clearly visible greyish sediment accumulations were
5 observed in 2003 at the site “Beaufort” and in 2005/2006 at “Elson”. These high
6 accumulations of sediment are often established during sea ice formation (Eicken et al. 2005)
7 and can in our study area form clearly visible dark grey layers within collected ice cores (see
8 example given in Gradinger et al. 2009). Such greyish layering was used as criterion for
9 classifying cores as ‘sediment impacted’ in the context of this study as well; absolute
10 amounts of incorporated sediment were only measured for cores overlapping with those used
11 in Gradinger et al. (2009).

12

13 2.2. Sample collection and processing

14 At least three replicate ice cores per variable were collected with an ice corer (10 cm
15 diameter in 2002/3 and 9 cm in 2005/6) at each site and time period. For bulk algal pigment,
16 POC, PON and stable isotope ratio samples, the bottom 10 cm of the cores were melted in the
17 dark and sub-samples of 2-50 ml were filtered onto pre-combusted GF/F filters, which were
18 frozen at -20°C for later determination. The bottom 10 cm sections of a second set of at least
19 3 replicate ice cores were melted in the dark after addition of 1 l of $0.2\ \mu\text{m}$ -filtered seawater
20 to each core section to avoid osmotic stress for the biota (Garrison and Buck 1984). After
21 complete melt, total volume was determined, the samples were concentrated over $20\ \mu\text{m}$
22 mesh and metazoan ice meiofauna was sorted by taxon and enumerated (Gradinger et al.
23 2009) using Wild M3 and Leica MZ12 dissecting microscopes. Individuals of the meiofauna
24 present were picked from the melted samples with Pasteur pipettes and pooled to get
25 sufficient organic mass for later stable isotope analysis. Pooled animals were filtered onto

1 pre-combusted GF/F filters by taxon and frozen until further processing, and the number of
2 individuals per filter noted. At least three replicate filter samples were collected per sampling
3 period whenever animal abundances were sufficient.

4 In 2002/3, under-ice amphipods were collected in screened baited minnow traps that were
5 deployed immediately under the ice for 24-48 hours at a time (Kaufman et al. 2008). In
6 2005/6, amphipods were picked from melted bottom ice core sections or slush of the cored
7 ice holes immediately after core removal. Amphipods were kept in filtered sea water in the
8 dark for several hours to clear their guts before being subsequently frozen (-20°C).

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

12

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

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18 2.3. Stable isotope analysis

19 In the Fairbanks lab, samples were dried at 60°C for 24 hours and subsequently fumed for 24
20 hours with 2N HCl to remove carbonates. All samples were re-dried at 60°C for 24 hours
21 prior to analysis. The stable isotope composition of either filter samples or, in the case of
22 amphipods, of approximately 0.3 mg homogenized, acidified whole organism sample were
23 measured on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with carbon V-PDB
24 and atmospheric N₂ as standards at the Alaska Stable Isotope Facility (ASIF) at the

1 University of Alaska Fairbanks. Analytical error was typically 0.05 ‰ for ¹³C and 0.06 ‰ for
2 ¹⁵N. Sample isotopic ratios are expressed in the conventional δ notation as parts per thousand
3 (‰) according to the following equation:

$$4 \quad \delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \cdot 1000$$

5 where X is ¹³C or ¹⁵N of the sample and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N.

6 For comparisons of δ¹⁵N and δ¹³C values across different sites and seasons with different
7 POM reference samples, we subtracted the mean values of δ¹⁵N and δ¹³C of POC / PON of a
8 particular site and season from the organism values. We assigned trophic levels to each taxon
9 assuming a 3.4‰ enrichment per trophic level (TL) (Post 2002) and using the consumer with
10 the most depleted δ¹⁵N value, Harpacticoida, as TL=2. First-order consumers are regularly
11 used as isotopic baselines in a given habitat (Bell et al. 2015, Stasko et al. 2018). We decided
12 against using the δ¹⁵N of PON as the baseline because our data showed strong seasonal
13 dynamics in its isotopic ratios, with at the same time unknown isotopic turnover times for the
14 meiofauna taxa in question. Earlier studies with ice-associated amphipods demonstrated slow
15 isotopic half-life times of weeks to several months (Kaufman et al. 2008) making POM as the
16 isotopic baseline even more challenging in the dynamic sea ice system than elsewhere. This
17 approach also helped us avoid bias due to the fact that the bulk POC/PON isotopic values do
18 not only reflect algal signature but will include the meiofauna itself.

19

20 2.4. PON, POC and biomass

21 The above-mentioned stable isotope measurements also provided the absolute concentrations
22 of carbon and nitrogen in each sample. C and N content of individual sea ice organisms were
23 calculated by dividing the carbon or nitrogen concentration of the pooled organism samples
24 by the number of organisms on the respective filter. Taxon-specific, average individual

1 carbon and nitrogen amounts were calculated based on all measurements per taxon (between
2 3 and 22 per taxon) and season. Biomass per taxon in a given sample was consequently
3 obtained by multiplying individual C or N content by the abundance for a given site and time
4 period.

5

6 2.5. Ingestion rates

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

$$10 \quad I_{\max} = 63 \times M^{-0.25} \times 0.2177 \times B$$

11 with:

12 I_{\max} : potential maximum ingestion rate ($\mu\text{g C l}^{-1} \text{ d}^{-1}$), 63: biomass specific ingestion ($\mu\text{g C d}^{-1}$)
13 l^{-1}), M: body mass of one individual (pg C), and B: carbon biomass of taxon in sea ice sample:
14 ($\mu\text{g C l}^{-1}$), 0.2177 = Q_{10} factor.

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16 2.6. Data analysis

17 As most of our variables were not normally distributed (based on Kolmogorov Smirnov
18 tests), we used medians for comparison between seasons and sites. For statistical analyses
19 data from the individual sampling events were pooled into three season groups: winter (Dec-
20 Feb – i.e. polar night), spring (Mar-Apr), and late spring (May-Jun). For each season data
21 were split into two groups based on sediment load (with and without visible sediment load).
22 We used sediment load as factor as earlier studies demonstrated the large impact of visible
23 sediment load on the biological development in Alaskan fast ice in the study area (Gradinger
24 et al. 2009). We used the Kruskal Wallis one-way analysis of variance (H-test) to test for

1 equality of medians between sites with and without sediment and between seasons. Analyses
2 including linear regressions were conducted using SYSTAT 11.0 and STATA15.1.

3

4 **3. Results**

5

6 **3.1. Particulate organic matter, algal pigments, stable isotope ratios and meiofauna** 7 **abundance**

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9 All bulk variables (POC, PON, chl *a*) increased at the sediment free sites from the winter /
10 polar night sampling to spring and then late spring with significant differences for PON and
11 chl *a*. In contrast, no significant changes with season were observed for any bulk variable at
12 the sediment impacted sites (Fig. 2). In sediment free ice, median POC concentrations
13 increased from 0.6 mg l⁻¹ in winter to 6.5 mg l⁻¹ in late spring. Highest PON values occurred
14 in spring with a median of 0.5 mg l⁻¹. Ice algal pigment concentrations increased from a
15 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
16 spring. The median carbon isotopic values increased, though not significantly, over time at
17 the sediment free sites from -24.9 ‰ in winter to -14.5‰ in late spring while it remained
18 virtually constant at the sediment laden site. The medians for δ¹⁵N varied little (range of 7.9
19 to 8.4 ‰) at the sediment free locations, and from 5.5 ‰ (late spring) and 8.6 ‰ (spring) at
20 the sediment sites.

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22 Median total metazoan abundances increased slightly in the sediment free locations from 126
23 Ind l⁻¹ in winter to 371 Ind l⁻¹ in late spring (Fig. 2). At the sediment impacted locations,
24 highest median values occurred in later spring with 427 Ind l⁻¹. No significant changes
25 (Kruskal Wallis test) were observed for either total abundances or abundances of the

1 individual taxa in regard to seasonality or sediment load (Fig. 3a). In sediment free ice,
2 Acoela median abundances were highest in late spring (90 Ind l⁻¹), while for all other taxa
3 highest median values were observed during the spring period, when Nematoda (127 Ind l⁻¹)
4 and juvenile Polychaeta were most abundant (143 Ind l⁻¹). At the sites with sediment,
5 abundances decreased from winter to later spring for Nematoda and nauplii while copepods
6 (290 Ind l⁻¹) and Acoela (45 Ind l⁻¹) showed highest median abundances in late spring. The
7 polychaete fauna in Elson Lagoon was dominated by juveniles of a hesionid polychaete,
8 while spionid *Scoelelepis squamata* juveniles dominated at all other locations.

9

10 Carbon-based median individual weights for sea ice meiofaunal taxa derived from pooled
11 samples ranged from 0.23 µg C ind⁻¹ for copepod nauplii to 2.28 µg C ind⁻¹ for Calanoida
12 (Table 1). Nitrogen content ranged from 0.03 µg N ind⁻¹ for copepod nauplii to 0.22 µg N ind⁻¹
13 for both Acoela and Calanoida. Acoela, Nematoda and Cyclopoida showed an increase in
14 individual body mass with season (Fig. 3b). Using linear regression between individual
15 carbon / nitrogen content and day of the year, Acoela grew by 0.04 µgC d⁻¹ (p=0.05) and
16 0.008 µgN d⁻¹ (p=0.05) from winter (median: 0.38 µgC ind⁻¹; 0.13 µgN ind⁻¹) to late spring
17 (median C: 3.19 µgC ind⁻¹; 0.65 µgN ind⁻¹). Median Nematoda individual carbon content
18 increased from winter (0.11 µgC ind⁻¹; 0.03 µgN ind⁻¹) to spring (0.55 µgC ind⁻¹; 0.07µgN
19 ind⁻¹) but decreased in late spring (0.36 µgC ind⁻¹; 0.03 µgN ind⁻¹) due to reproduction and the
20 hatching of juveniles from egg cases. Cyclopoida grew by 0.017 µgC d⁻¹ (p=0.032) and
21 0.003 µgN d⁻¹ (p=0.031) to maximum C and N values of 2.01 µgC ind⁻¹ and 0.33 µgN ind⁻¹ in
22 late spring (median values). Low abundances and sporadic occurrence of taxa limited the
23 complete seasonal coverage for carbon and nitrogen bulk and isotope measurements to
24 sediment free locations.

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1 Across all seasons median carbon and nitrogen concentrations contributed by the total ice
2 meiofauna biomass in the bottom 10 cm of the sea ice was $152.9 \mu\text{gC l}^{-1}$ and $22.0 \mu\text{gN l}^{-1}$
3 (distribution over season shown in Fig 3c). This represented a median contribution of 11% of
4 total POC and 19% of total PON in sea ice bottom sections (Fig. 3d). The highest median
5 contribution of meiofauna to total POC concentration was estimated for late spring in the
6 sediment impacted area where it reached 80% (Fig 3d). With season, meiofauna biomass
7 increased from $46 \mu\text{gC l}^{-1}$ to $542 \mu\text{gC l}^{-1}$ at the sediment free locations and from $42 \mu\text{gC l}^{-1}$ to
8 $446 \mu\text{gC l}^{-1}$ at the sediment laden locations in late spring (Fig. 3c) with no significant
9 differences (Kruskal Wallis tests) between sediment free and sediment laden locations for
10 any season. Acoela contributed the largest fraction to total meiofauna biomass at all sites
11 (median: 17%) followed by *S. squamata* (10%) and Nematoda (9%). At the sediment free
12 locations, Acoela relative biomass contribution increased with season to a maximum of 53%
13 (median) in late spring and Nematoda had the highest contribution in spring (24%). At the
14 sediment laden location in winter and spring, the hesionid polychaete had the highest
15 contribution (11% and 39%), while in late spring Cyclopoidea contributed 20% to total
16 meiofauna biomass.

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18 **3.2. Food web structure and carbon flow**

19 The isotopic ratios for both POC and PON differed in their seasonal changes (Fig. 2). The
20 $\delta^{13}\text{C}$ ratio of POC was significantly correlated with ice algal pigment concentration (as
21 estimated by linear regression) with

22

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

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

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$$\delta^{13}\text{C} (\text{‰}) = -26.0 (\text{‰}) + 0.00078 (\text{‰}/(\mu\text{g l}^{-1})) * \text{POC} (\mu\text{g l}^{-1}), R^2=0.60, n=23, p<0.001.$$

In contrast, no significant relationship was found between $\delta^{15}\text{N}$ and chl *a*, and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and from 7.8‰ (Harpacticoida) to 12.9‰ (*Onisimus litoralis*) for $\delta^{15}\text{N}$. Overall, $\delta^{13}\text{C}$ values of sea ice meiofauna increased with heavier $\delta^{13}\text{C}$ POC ratios (Fig. 4a). The difference between $\delta^{15}\text{N}$ values of taxa and total $\text{PO}\delta^{15}\text{N}$ did not change significantly with season for any meiofauna taxa (Kruskal Wallis tests, $p>0.05$) and showed no relation to the seasonally changing $\delta^{13}\text{C}$ POC ratios (Fig. 4b).

The calculated differences between the median $\delta^{15}\text{N}$ of sea ice meiofauna taxa and the $\delta^{15}\text{N}$ 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 trophic levels across meiofauna taxa was estimated at 1.5 trophic levels from TL 2 (as defined by lowest taxa $\delta^{15}\text{N}$) to TL 3.5 (Table 1). Acoela, Nematoda and Polychaeta had sufficient data coverage in the sediment free locations to evaluate seasonal differences between the isotopic ratios between biota and PON (Fig. 5): While little change occurred between winter and spring, this difference decreased for all three taxa in late spring (Fig. 5).

The median calculated total sea ice meiofauna ingestion rate across all seasons was 55 $\mu\text{gC l}^{-1}\text{d}^{-1}$ (Fig. 6), representing 5.5% of the median POC pool. Ingestion rate varied between <1%

1 to 100% of POC concentrations. For all taxa, ingestion rates were lowest in winter with a
2 median total ingestion rate of $15 \mu\text{gC l}^{-1}\text{d}^{-1}$ which increased towards spring with the highest
3 median total ingestion rate of $149 \mu\text{gC l}^{-1}\text{d}^{-1}$ in late spring at the sediment free ice sites. At
4 these sites, Nematoda (highest median: $43 \mu\text{gC l}^{-1}\text{d}^{-1}$), Copepoda ($13 \mu\text{gC l}^{-1}\text{d}^{-1}$) and
5 Polychaeta ($22 \mu\text{gC l}^{-1}\text{d}^{-1}$) ingestion rates peaked in spring, while Acoela showed the overall
6 highest median ingestion rates with $111 \mu\text{gC l}^{-1}\text{d}^{-1}$ in late spring. A similar pattern was found
7 at sites with sediment in the ice, however overall rates were lower in spring, but higher in late
8 spring with the highest total median ingestion rate of $192 \mu\text{gC l}^{-1}\text{d}^{-1}$, mainly caused by a high
9 contribution of Copepoda ($126 \mu\text{gC l}^{-1}\text{d}^{-1}$) and Acoela ($54 \mu\text{gC l}^{-1}\text{d}^{-1}$).

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11 **4. Discussion**

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13 The present study provides first insights into trophic dynamics *inside* the sea ice by looking
14 in detail at the contribution of different meiofauna taxa to ice derived particulate matter
15 characteristics. In the following we first discuss the seasonal changes in sea ice meiofaunal
16 properties within the bottom 10 cm of the coastal fast ice in relation to available food
17 resources. We infer close trophic coupling between available food and metazoan grazers via
18 their matching seasonal evolution of carbon and nitrogen stable isotopes. We then resolve the
19 seasonally changing composition of what is often indiscriminately referred to as ‘ice POM’,
20 specifically we document the shifting contribution of metazoan meiofauna to ice POM.
21 Finally we quantified grazing capacity of ice meiofauna based on actual carbon content of ice
22 organisms rather than literature based assumptions, leading to improved estimates.

23

24 **4.1. Seasonal role of ice meiofauna related to food resources**

25 **4.1.1. Winter**

1 Winter sea ice sampling occurred during the Polar Night season in the months of December
2 to February. Our winter data agree well with the overall scenario developed for ice algal
3 phenology by Leu et al. (2015), demonstrating a largely heterotrophic phase of the ecosystem
4 during the dark season. Ice algal biomass and POC levels were very low both at the sediment
5 laden and sediment free sites. Despite these low values, stable isotope values of POC/PON
6 corresponded largely with typical water column values reported for Arctic marine pelagic
7 particulate matter from nearshore and offshore areas which mainly come from spring and
8 summer (Gradinger 2009, Iken et al. 2010, Bell et al. 2016). Although substantial sediment
9 load was detected at some sites, the marine signature of Arctic POC/N stable isotope ratios
10 (e.g. Kumar et al. 2016 and citations before) indicate a marine origin of these particles, while
11 terrestrial input through rivers/coastal erosion in Arctic areas have lighter $\delta^{13}\text{C}$ values (Vonk
12 et al. 2014, Divine et al. 2015, Bell et al. 2016). We suggest fall/winter suspension freezing
13 during ice formation as the likely pathway of incorporation of marine sediments into the fast
14 ice at these shallow sites (for detailed discussion see Gradinger et al. 2009). Further
15 indication of the marine origin of the incorporated sediment in the ice and the POC and PON
16 comes from the ice meiofauna taxa observed at these sites. Here we observed mainly
17 Nematoda of likely benthic origin (Hajduk et al. in prep.) in abundances exceeding the
18 sediment free sites. Overall at both sediment free and sediment laden locations, meiofauna
19 occurred at low abundances and with the lowest carbon content per individual during winter
20 months. Stable isotopic ratios were roughly the same for Nematoda and Acoela and one
21 trophic level above PON. For both taxa, direct feeding on bacteria, Protozoa, other
22 meiofauna, and detritus has been suggested in addition to grazing on algae both by sea ice
23 studies (e.g. Tchessunov and Riemann 1995) and benthic meiofauna studies (Achatz et al.
24 2013, Majidi and Traunspurger 2015). Given algal food sources were scarce in winter as
25 indicated by the low chl *a* concentrations and the resulting very high POC to chl *a* ratio

1 (medians: sediment laden site: 510, sediment free site: 474), we infer that meiofauna food
2 was dominated by heterotrophic/detrital contributors.

3

4 **4.1.2. Spring**

5 In spring (March/April) sufficient daylight for sea ice algal primary production allowed for
6 the build-up of a strong ice algal bloom, shifting the ice system from a heterotrophic to a
7 phototrophic phase (c.f. Leu et al. 2015) and enhancing food availability for sea ice
8 meiofauna. Algal build-up was delayed in the sediment laden ice regions due to light
9 limitation (Gradinger et al. 2009). The substantial increase in ice algal biomass in terms of
10 chl *a* and POC corresponded to a reduction in the POC to chl *a* ratio, mainly at the sediment
11 free site (median sediment free site: 58; sediment laden site: 270). We also observed
12 enrichment in $\delta^{13}\text{C}$ ratios but not $\delta^{15}\text{N}$ ratios at the sediment free sites. Earlier studies already
13 demonstrated this enrichment of the inorganic dissolved carbon pool within the brine channel
14 system (Gradinger 2009, Pineault et al. 2013, Wang et al. 2015) in the semi-confined brine
15 channel space as a consequence of the preferential incorporation of ^{12}C during photosynthesis
16 by sea ice algae. Surprisingly no such enrichment was evident for $\delta^{15}\text{N}$ which remained
17 nearly constant throughout the entire study period in the sediment free areas, as also observed
18 in other parts of the Arctic (Gradinger 2009, Pineault et al. 2013). Nitrate concentrations as
19 major inorganic N source in early spring are reduced by algal uptake within the ice during the
20 ice algal bloom and can cause limitation of ice algal growth (Manes & Gradinger 2009,
21 Gradinger 2009). Consequently, the nitrate pool itself becomes enriched over time and should
22 lead to an enriched signature in the ice algae, which we however did not observe. This
23 observation points towards use of an alternative nitrogen source. The direct use of dissolved
24 N_2 by Arctic marine algae has recently been established through observation of a haptophyte-
25 cyanobacterial consortium fixing atmospheric N_2 in the Chukchi and Beaufort Seas (Harding

1 et al. 2018), questioning the past paradigm based on the lack or very low abundances of free
2 living marine pico-cyanobacteria from Arctic waters (Gradinger & Lenz 1995). Direct
3 fixation of N₂ would strongly lower the isotopic values due to the very modest fractionation
4 of ¹⁴N versus ¹⁵N during this process, leading to N₂-fixed δ¹⁵N values close to 0‰ (Sigman
5 and Casciotti 2001). Given the clear dominance, however, of diatoms within the local fast ice
6 system (Manes & Gradinger 2009), we consider this process not very likely to cause the
7 stability in the PON isotopic ratios. A more likely explanation in our view is the tight
8 recycling of N within the sea ice-based food web, and the release of relatively light ¹⁴NH₄
9 from consumed organic matter by sea ice heterotrophs. As determined for marine
10 zooplankton, released NH₄ is typically lighter than consumed PON, as the lighter ¹⁴N is
11 preferentially metabolized and excreted by animals (Sigman & Casciotti 2001). Thus, the use
12 of released NH₄ for regenerated algal production could act as the stabilizing factor explaining
13 the near constant sea ice PON isotopic ratios. This argument is further supported by direct
14 ammonia and nitrate uptake measurements from this area, which showed low mean f-ratios of
15 0.34 for Utqiagvik bottom ice algal communities (Lee et al. 2008) and of 0.11 for
16 phytoplankton (Baer et al. 2017) in spring, indicating preferred incorporation of ammonia.
17 Our estimated meiofauna ingestion rates of ca. 7% (sediment free site) of POC points towards
18 a small potential role of meiofauna excretion in this process.

19
20 Coincident with the onset of the ice algal bloom and POM increase in spring months,
21 meiofauna reached their seasonal abundance maximum in sediment free ice and individuals
22 had increased C and N content. Isotopic enrichment in both POC and meiofauna carbon
23 suggests the latter increase was a result of grazing on ice algae and not of metabolic turnover.
24 Polychaete juveniles dominated in March-April in the ice as benthic adults had released their
25 meroplanktonic larvae, and juveniles entered the bottom ice to feed (Gradinger et al. 2009,

1 McConnell et al. 2012). Fast growth of juveniles of the sea ice-inhabiting polychaete
2 *Scoelepis squamata* based on herbivory was demonstrated in experimental studies from the
3 same area (McConnell et al. 2012) and from a Svalbard fjord system (Pitusi et al. in prep.).
4 Interestingly, juvenile polychaetes of a different family entered the sea ice system at the
5 sediment laden ice locations, leading to an increase in meiofauna biomass also at these sites,
6 although food sources as indicated by POC and chl a concentrations remained low at these
7 sites. Nematoda reached their maximum individual body weight in spring with a median of
8 $0.54 \mu\text{g C ind}^{-1}$. This value is similar to those from inter- and subtidal beaches in North
9 America ($0.56\text{-}0.78 \mu\text{g C ind}^{-1}$, Sikora et al. 1977), but exceeds individual biomass values
10 reported for Arctic benthic deep-sea Nematoda ($0.03\text{-}0.15 \text{ DW ind}^{-1}$, Vanreusel et al. 2000
11 with ca 40% carbon content in DW, Kennedy 1994) and calculated biomass-carbon
12 conversion based values of ice nematodes used by Gradinger (1999: $0.13 \mu\text{g C ind}^{-1}$). We
13 assume that these heavy animals were reproductive adults, as we later observed egg cases and
14 increased abundances of juveniles (see late spring section).

15

16 Although the stable isotopic values revealed near constant difference between $\delta^{15}\text{N}$ of major
17 meiofauna taxa and PON for winter and spring we argue that a major shift in nutrition
18 occurred between winter and spring, as now the increased POC and PON in the bottom layer
19 of the fast ice were largely contributed by microalgae, mainly diatoms (Manes & Gradinger
20 2009). The close relationship of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicates direct feeding on microalgae as
21 also supported by gut contents analyses (Grainger & Hsiao 1990) and limited experimental
22 evidence (McConnell et al. 2012, Pitusi et al. in prep.).

23

24 **4.1.3. Late spring**

1 Late spring conditions were characterized by high variability in several biological factors
2 including POC, chl *a*, $\delta^{13}\text{C}$ and meiofauna abundance, specifically at the sediment free sites.
3 This is not surprising as several processes co-occur at this time causing substantial spatial and
4 temporal variability within sea ice, both within one year but also interannually (Fortier et al.
5 2002). Both in spring and late spring/summer, variability in environmental factors,
6 specifically snow depth, melt pond formation and the consequently variable light availability
7 lead to changes in the rate of build-up of algal and sea ice meiofauna biomass (Riedel et al.
8 2008). Heavy snow load and corresponding low light intensities for example lead to delayed
9 algal bloom formation, similar to the effect demonstrated for sediment laden sea ice
10 (Gradinger et al. 2009, this study). Further, factors related to the end of the ice algal growing
11 season contribute to increased variability (Leu et al. 2015): while algal growth continues and
12 biomass further accumulated within the ice, increased nutrient limitation (Cota et al. 1987,
13 Gradinger 2009) and increased release of algae due to ice melt of the bottom layer (Michel et
14 al. 2002, Juhl et al. 2011) or increased brine drainage due to snow melt (Tamelander et al.
15 2009) will either slow down biomass build-up or reduce algal biomass. Even small melt
16 events at the ice bottom due to the increased temperatures and self-heating due to light
17 absorption (Zeebe et al. 1996) in the bottom layer can release large fractions of the ice biota
18 (Tremblay et al. 1989, Michel et al. 2002, Gradinger et al. unpubl data). Such melt events
19 make sea ice-derived particulate organic matter available as food to under-ice, pelagic and or
20 benthic biota (Gradinger & Bluhm 2010, Schollmeier et al. 2018, Rybakova et al. 2019).
21 With progressing time and increased algal biomass, we observed further enrichment of $\delta^{13}\text{C}$
22 values of ice POM. Interestingly, we saw similar increases in the carbon isotopes in the sea
23 ice meiofauna taxa, indicating – as expected – that the algal dominated sea ice particulate
24 matter is indeed the major food source for the sea ice-based food web.

25

1 The sea ice meiofauna community composition changed from spring to late spring. Major
2 shifts included the reduced abundance of polychaete juveniles and large Nematoda, which
3 presumably left the ice for benthic settlement, and increased contributions of Acoela and
4 smaller Nematoda. The observed weight reduction for Nematoda was related to the
5 occurrence of smaller individuals due to reproduction occurring with the ice in April/May
6 (RG & BB personal observations, Kern & Carey 1982, Riemann & Sime-Ngando 1997).
7 Acoela, in contrast, continued to grow and reached a maximum median weight of 3.19 $\mu\text{g C}$
8 ind^{-1} , substantially (by factor of 8) exceeding the estimated individual biomass used in older
9 meiofauna grazing studies (Gradinger 1999). $\delta^{15}\text{N}$ of sea ice meiofauna showed lower values
10 compared to PON of the matching time, with often negative differences. The unexpectedly
11 low or often lacking enrichment observed in our data could be explained in several different
12 (and not necessarily exclusive) ways. First, relatively low enrichment could be expected as
13 $\delta^{15}\text{N}$ enrichment is reduced in ammonia excreting taxa (Vanderklift & Ponsard 2003) like
14 most sea ice meiofauna taxa (Crustacea: Aarset 1991, Turbellaria, now Acoela: Holley 2016,
15 Nematoda: Rothstein 1963). The second possible explanation might lie in the use of
16 resources other than sea ice algae, namely the role of the microbial foodweb which we did
17 not sample. Different sea ice meiofauna taxa can consume either DOM, or bacteria,
18 flagellates and /or ciliates as part of their food spectrum, all of which can occur in high
19 abundance in sea ice (e.g. Gradinger et al. 1999, for complete spectrum of ice inhabitants).
20 Freshly produced DON may be an unsampled but important nitrogen source during the late
21 spring season. Unfortunately, the isotopic changes related to the DON production and uptake
22 are poorly understood, although they are considered important parts of the marine N cycling
23 (Sigman et al. 2009). DON from subtropical areas had $\delta^{15}\text{N}$ ratios of ca. 4‰ (Sigman et al.
24 2009, Karl et al. 2002) and were similar to values in the North Atlantic (4.1 to 6.6‰,
25 Aluwihare & Meador 2008). In late spring and during melting season, sea ice does harbor a

1 very active microbial network, with preferential retention of EPS (extracellular particulate
2 substances), POC and DOC (Juhl et al. 2011), which could lead to a more heterotrophic food
3 base of the meiofauna. If DON in sea ice had values as low as observed in the North Atlantic,
4 this could lead to lower ratios also in meiofauna through food web interactions. A third
5 explanation for lower meiofaunal than PON $\delta^{15}\text{N}$ values could be related to the (unknown)
6 turnover time of $\delta^{15}\text{N}$. As mentioned above, the isotopic half-life (50% of the entire change
7 happens in this period) of the partially under-ice, partially benthic Arctic litoral amphipod
8 *Onisimus litoralis* was over 20 days to several months. While we assume that meiofauna has
9 likely a faster metabolic and growth related turnover, comparatively slow turnover at low
10 temperatures can still lead to a time lag in isotopic composition and the potential for
11 misinterpreting snap shot isotope data in food web analysis. Given the PON isotopic ratios
12 did not change with season, however, we suggest that the increased activity of the microbial
13 food web may be causing the observed meiofauna $\delta^{15}\text{N}$ ratios in late spring.

14

15 **4.2. Grazing impact**

16 Despite large changes and variability in algal biomass and meiofauna abundance and
17 composition, we did not observe significant changes in the relative amount of ingested
18 carbon by the sea ice meiofauna grazing related to the algal biomass/POC with season.
19 Instead, the ingestion rate followed the seasonal change in algal biomass, although the
20 contribution of individual taxa shifted in their relative importance. The large variability in
21 physical and biological processes contributing to the seasonal occurrence of meiofauna and
22 algae within the ice indirectly also explain the very broad range of observed potential grazing
23 impact. The highest ingestion rate was found in spring at the sediment free locations (median
24 7.1% of POC) and in late spring in sediment laden sea ice (34.3% of POC). These estimates
25 demonstrate again that meiofauna has only a minor grazing impact during algal spring bloom

1 build up, where daily primary productivity rates in the coastal sites exceed the estimated
2 grazing rates by at least one order of magnitude (Lee et al. 2008). Other studies using a
3 similar approach, however, reported considerably lower grazing impact (Nozais et al. 2001:
4 less than 0.9%, Michel et al. 2002: 2.6%) for coastal ice meiofaunal communities. We
5 suggest that this disparity may not necessarily represent a difference between regions but is
6 due to the relatively high individual carbon content estimates we determined directly for our
7 study area compared to those used from other areas in the past.

8

9 **4.3. Composition of sea ice-derived POM**

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

23

24 **5. Conclusion and outlook**

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

16

17

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17

18

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24

1 Table 1: Pooled carbon and nitrogen content of sea ice meiofauna taxa in fast ice close to
 2 Utqiagvik, Alaska. Provided are medians with number of pooled samples in parenthesis
 3 regardless of location and season. Trophic levels (TL) were calculated based on the median
 4 difference of $\delta^{15}\text{N}$ values from PON, setting PON as TL=1 for and Harpacticoida as TL2 as
 5 the consumer taxon with the lowest difference to PON. Subsequent TL are estimated
 6 assuming a 3.4‰ enrichment per trophic level. n.d.= no data

7

Taxon	Median C ($\mu\text{g C/ind}$)	Median N ($\mu\text{g N/ind}$)	Median $\delta^{13}\text{C}$ (‰)	Median $\delta^{15}\text{N}$ (‰)	Trophic level
Acoela	1.56 (10)	0.22 (10)	-20.9 (14)	9.5 (14)	2.4
<i>Scolecopsis squamata</i>	0.56 (7)	0.09 (7)	-22.6 (12)	8.6 (12)	2.4
Hesionid polychaete	0.55 (5)	0.10 (5)	n.d.	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)	n.d.
<i>Onisimus litoralis</i>	n.d.	n.d.	-21.7 (5)	12.9 (5)	3.5
<i>Gammarcanthus loricatus</i>	n.d.	n.d.	-19.8 (2)	n.d.	n.d.

8

9

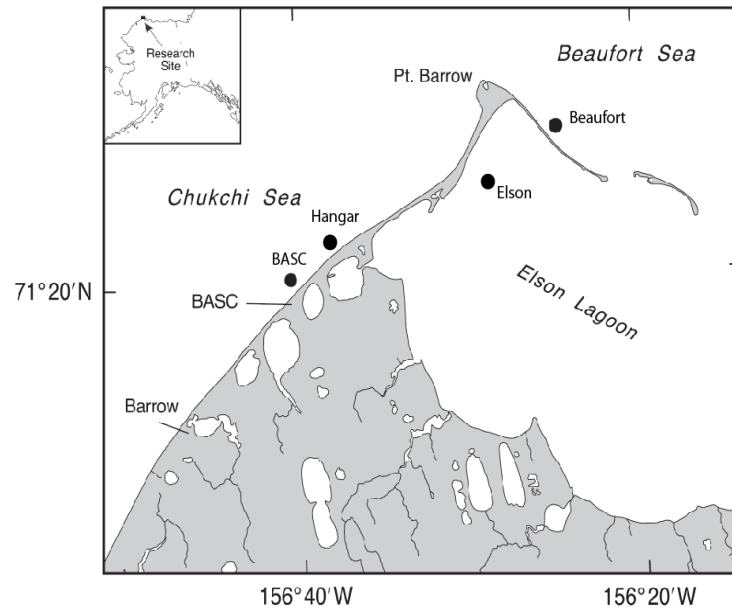


Fig 1 Bluhm/Gradinger

- 1
- 2 Fig. 1: Map of the study area close to Utqiagvik, Alaska. Study sites named BASC and
- 3 Hangar are in the Chukchi Sea, while Elson and Beaufort on the Beaufort Sea side. BASC is
- 4 Barrow Arctic Science Consortium.

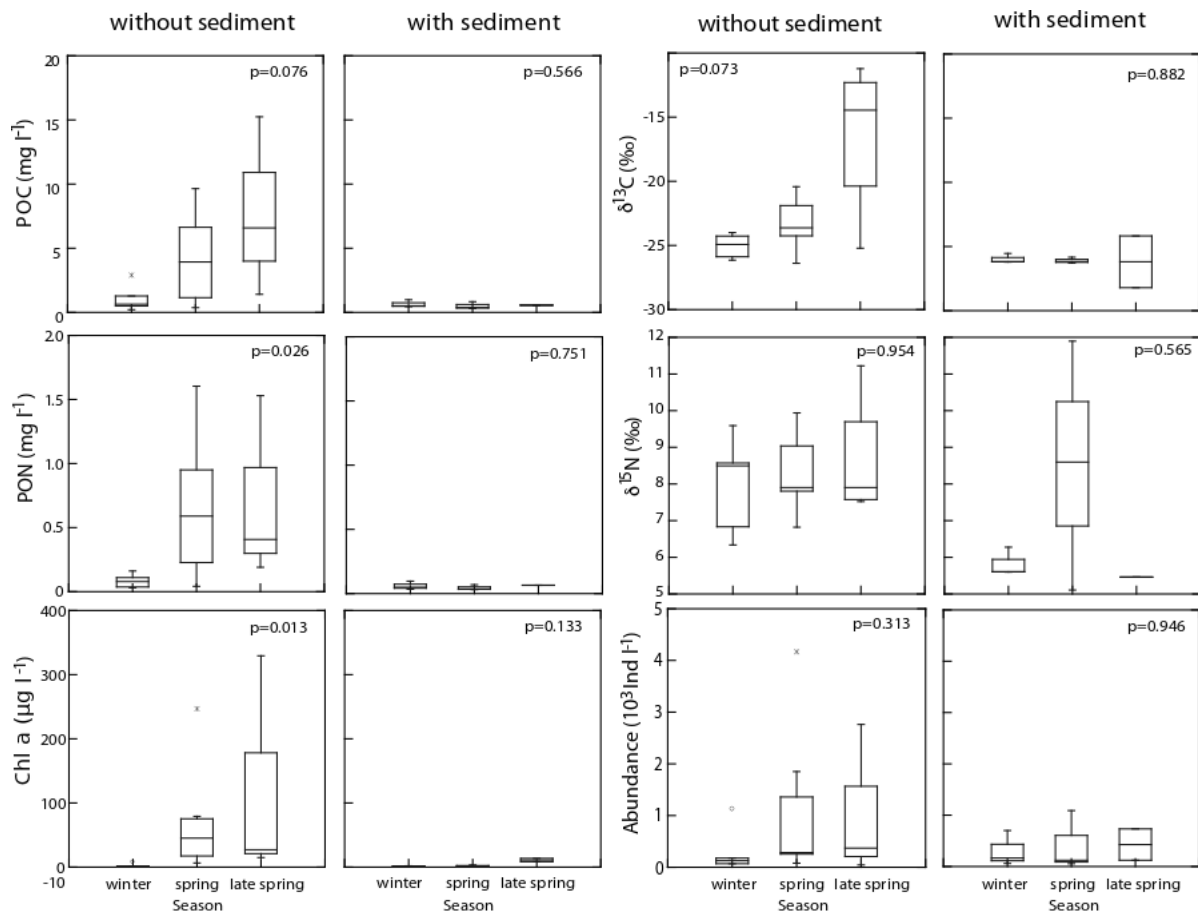


Fig. 2

1

2 Fig. 2: Seasonal changes in POC, PON and algal pigment (Chl a) concentrations, stable
3 carbon and nitrogen isotope ratios of POC and PON, respectively, and total meiofauna
4 abundances for sea ice (bottom 10 cm) with and without visible sediment loads. P-values are
5 based on non-parametric Kruskal Wallis test with three groups (winter, spring, late spring; for
6 definition of seasons see Material and methods section), run separately for ice with and
7 without visible sediment load. In the box and whisker plots, the box contains 50% of the data
8 within the 25% and 75% quartile as edges (called hinges) and the center line representing the
9 median. Whiskers include all data that fall in the range of the difference between the upper
10 (75%) and lower (25%) hinge multiplied with 1.5. Data points outside the whiskers are
11 plotted as circles.

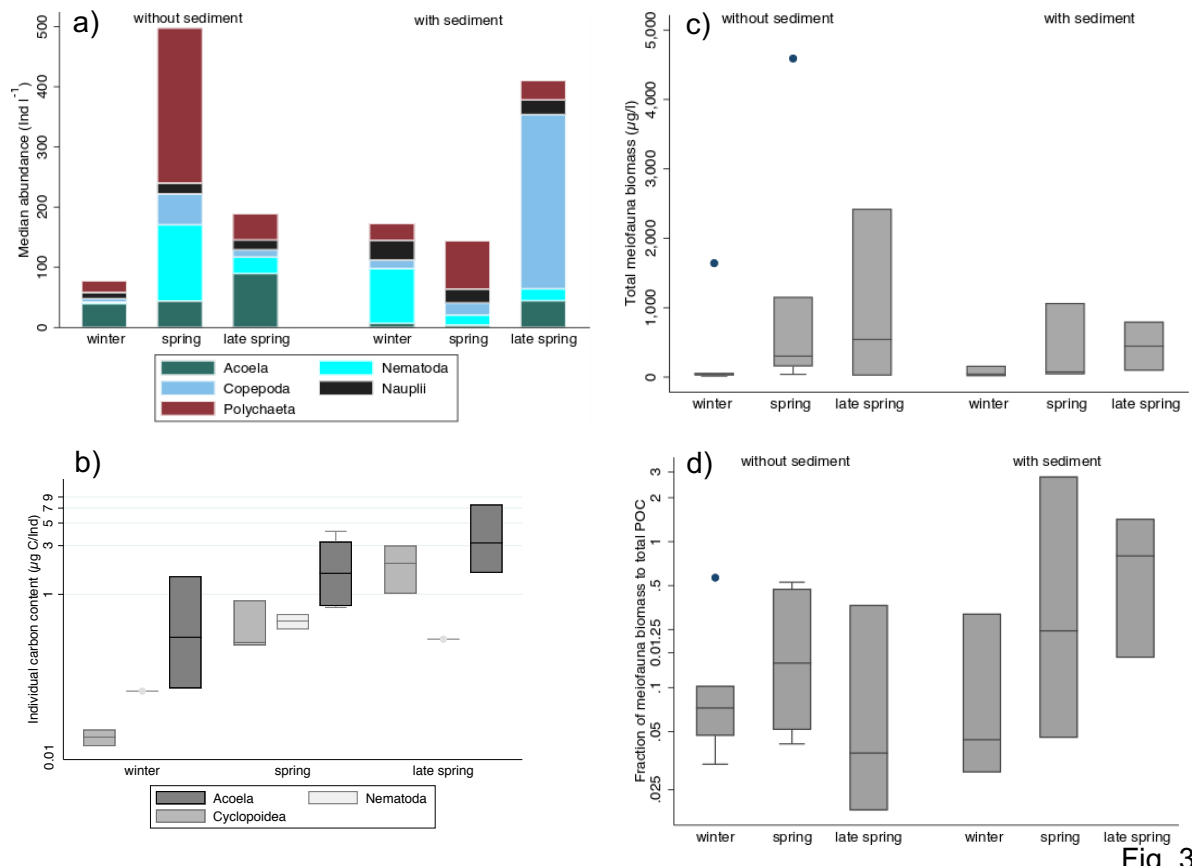


Fig. 3

- 1
- 2 Fig. 3: Seasonal development of ice meiofauna (a) abundance and composition, (b) individual
- 3 carbon content, (c) individual biomass, and (d) relative contribution to total ice POC content.
- 4 Box and whisker plots explained in Fig. 2.

1

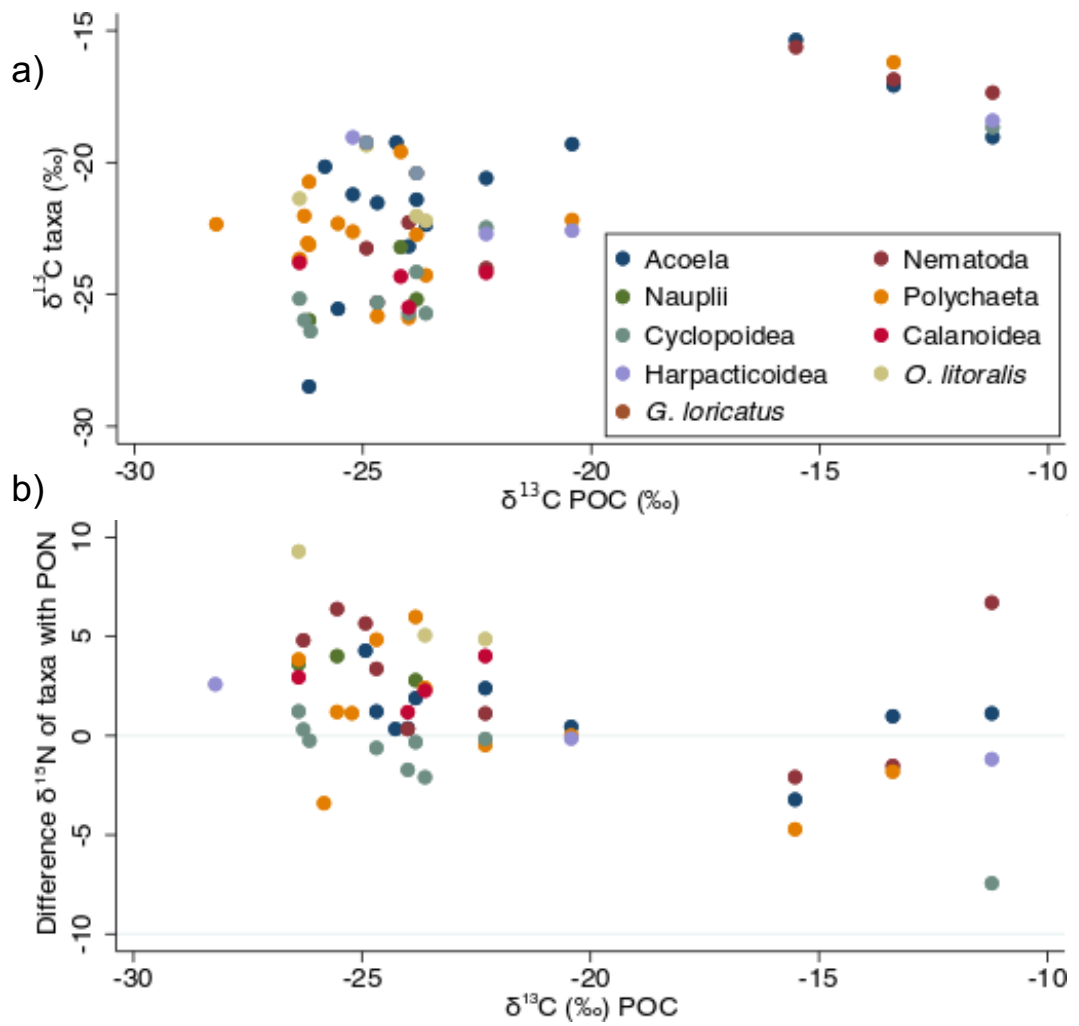


Fig. 4

2

3 Fig. 4: Changes in the (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ ratios in individual sea ice meiofauna taxa in

4 relation to the matching $\delta^{13}\text{C}$ POC ratio from the same locations and time periods. All

5 individually measured isotopic ratios are plotted.

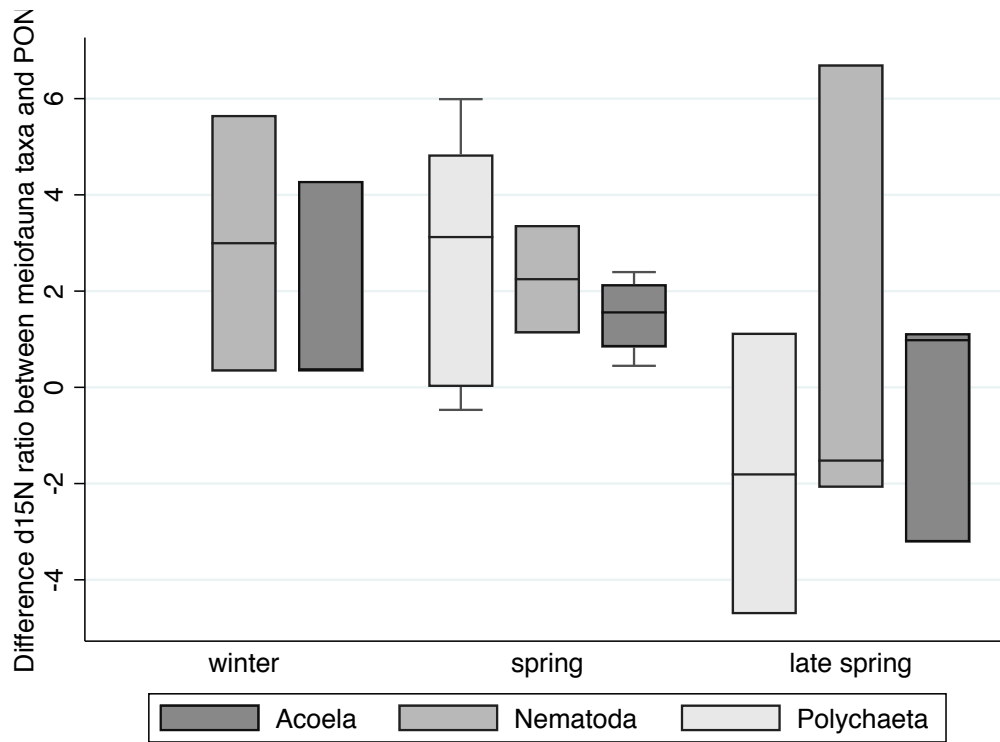
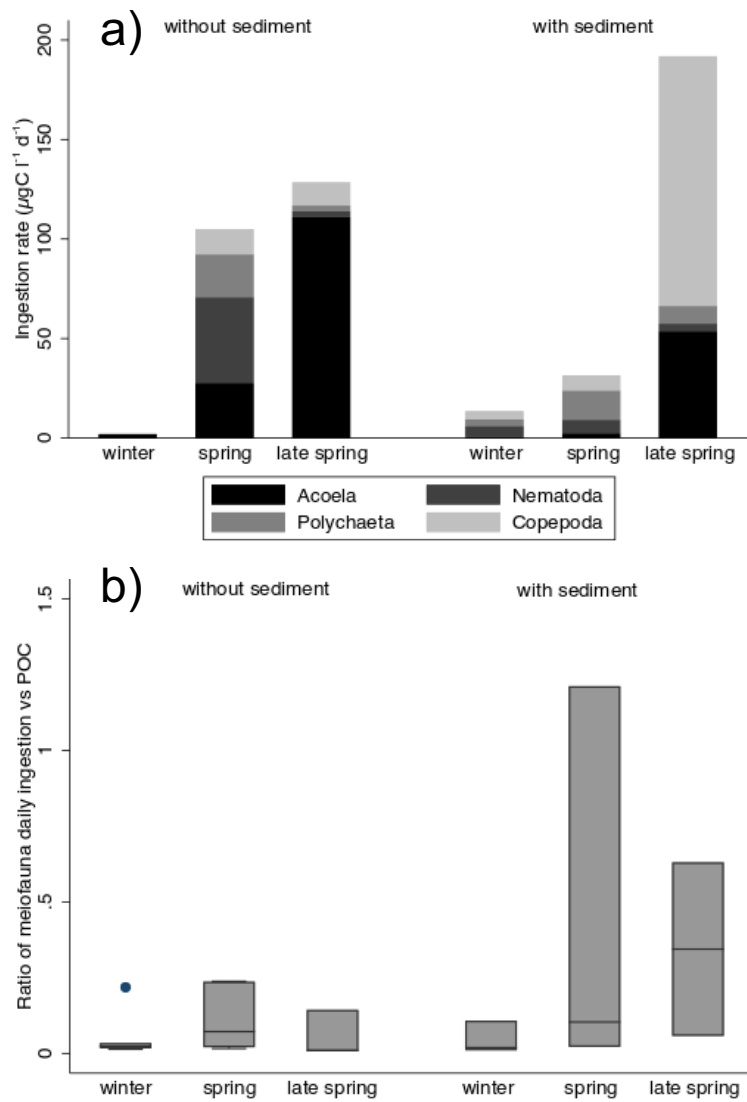


Fig. 5

1

2 Fig. 5: Seasonal difference in the $\delta^{15}\text{N}$ ratio of three selected sea ice meiofauna taxa to $\delta^{15}\text{N}$

3 ratio of ice PON. Box and whisker plots explained in Fig. 2



1

2

3 Fig. 6: Seasonal changes of (a) calculated meiofauna ingestion rates and (b) the daily ratio of

4 ingested C versus the POC pool. Box and whisker plots explained in Fig. 2.