



## Little seasonal variation of mercury concentrations and biomagnification in an Arctic pelagic food web

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### ABSTRACT

Despite numerous studies on mercury in Arctic biota, data from inaccessible, ice-covered regions – especially during the polar night and late winter – remain scarce. This scarcity results in poor understanding of the seasonal dynamics of mercury within the food web. From the Northern Barents Sea, we quantified total mercury and the dietary descriptors  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  as long-term dietary signals (weeks to months) in biota to a) investigate the seasonal pelagic food web structure, b) seasonality in total mercury concentration, c) and its biomagnification in the food web. Mercury and dietary descriptors were analyzed in copepods, macrozooplankton (krill, amphipods, arrow worms, and pteropods) and the fishes, Atlantic cod (*Gadus morhua*), polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) during spring, late summer, early, and late winter. Seasonal changes were observed in  $\delta^{15}\text{N}$  values in some macrozooplankton and capelin, and some seasonal variation was observed across the food web with depleted  $\delta^{13}\text{C}$  values in spring and enriched  $\delta^{13}\text{C}$  values in late summer. Mercury concentrations were lower (range: 2.49 ng/g dw in the krill *Thyssonassa* sp. – 70.55 ng/g dw in the pelagic pteropod *Clione limacina*) than reported from other parts of the Arctic. We found a positive linear relationship between mercury and relative trophic position represented by  $\delta^{15}\text{N}$ , i.e., biomagnification, during all seasons, except in early winter. As *Clione limacina* likely had different turnover rates for mercury and stable isotopes resulting in low  $\delta^{15}\text{N}$ , but high mercury concentrations in early winter, compared to the other species in the food web, the pteropod was omitted from the regression. By omitting *Clione limacina*, biomagnification was similar across all seasons ( $R_{\text{adj}}^2 = 0.45$ ). Thus, we saw clear mercury biomagnification with consistent and little seasonal variation in this high Arctic marine food web despite large seasonal fluctuations in abiotic and biotic conditions.

### 1. Introduction

The Arctic marine ecosystem is shaped by many seasonal processes, such as varying sea ice cover and pronounced variation in irradiance, leading to a range of biological adaptations and dynamics (Johnsen & Kovacs, 2009; Varpe, 2017). Seasonality in the abundance of organisms, such as phytoplankton blooms during the spring and summer, result in lower food abundance during winter, and seasonality of physiological factors and life history traits such as lipid reserves and reproduction (Johnsen & Kovacs, 2009) can impact pollutant dynamics, such as mercury, throughout the year.

During the productive Arctic spring and summer months, generally

from May to August (Reigstad et al., 2008), many Arctic organisms like the herbivore copepod *Calanus hyperboreus* build energy reserves to survive lower food abundance during the winter (Falk-Petersen et al., 1986). Despite the lower food abundance and prey energy density towards spring (Nowicki et al. 2023), organisms like the polar cod (*Boreogadus saida*) and the predatory amphipods *Themisto libellula* and *Themisto abyssorum* continue to feed during the winter (Cusa, Berge & Varpe, 2019; Kraft et al., 2013). Periods of reduced food intake or prolonged starvation could condense remaining tissue and thus elevate mercury concentrations in the organism. These overwintering strategies of Arctic residents may result in different seasonal mercury concentrations and biomagnification in the Arctic food web, compared to

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temperate food webs. For instance, seasonal changes in mercury concentrations in little auks (*Alle alle*) were explained by inter-annual variability of mercury concentrations within the food web, as opposed to a change in food web structure (Fort et al., 2016). Thus, the seasonality of the Arctic marine food web function, structure and its mercury dynamics require further investigation. Stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ), which reflect dietary carbon sources (*i.e.*, energy source) and indicate the relative trophic position over weeks to months in animal tissue, can be used to quantify food web structure and isotopic niche. These integrated dietary tracers are valuable tools for estimating the biomagnification of mercury through food webs via metrics such as trophic magnification factors (TMFs) (Borgå et al., 2012).

Mercury is an element with natural and anthropogenic sources that can potentially harm wildlife and humans, causing neurotoxic effects (Chételat et al., 2022; Dietz et al., 2013). This pollutant biomagnifies in food webs, *i.e.*, increases in concentrations with increasing trophic levels, leaving top predators (including humans) with risks of health effects (*e.g.*, Dietz et al. 2013; Dietz et al., 2022). A major source of Arctic mercury is of anthropogenic origin and legacy mercury emissions, which reach the Arctic via *e.g.*, long-range atmospheric transport, pan-Arctic rivers, erosion, and glacial and sea ice melt (Dastoor et al., 2022). The Arctic's high latitude leads to significant seasonal variations in solar irradiance, resulting in pronounced abiotic and biotic seasonality. Major mercury deposition events in the Arctic, known as atmospheric mercury depletion events (AMDEs), can coincide with seasonality driven events such as the spring bloom (Dastoor et al., 2022). The seasonality of mercury sources may result in seasonal variations of its bioavailability and transformation processes within organisms and thus its biomagnification in the food web. Most studies, including those by Foster et al. (2012), Jæger, Hop, and Gabrielsen (2009), and Ruus et al. (2015), have mainly concentrated on the spring and summer months. The winter season, especially the polar night, has been challenging to study and has only recently started receiving attention from an ecological perspective (Berge et al., 2015).

The highest mercury biomagnification potential through the food web has been observed in high-latitude ecosystems like the Arctic (Clayden et al., 2015; Kidd et al., 2012; Lavoie et al., 2013). The toxic form of mercury is the organic methylmercury, which exhibits a lower proportion to total mercury at lower trophic levels compared to fish (*e.g.*, Ruus et al. 2015).

To our knowledge, only a few studies have reported mercury concentrations in biota from the Arctic winter (but see Gopakumar et al., 2021). Moreover, winter mercury data from zooplankton and fish occupying lower trophic levels, remain scarce (Foster et al., 2012; Pomerleau et al., 2016; Pučko et al., 2014), especially from the European Arctic (Ruus et al., 2015).

The aim of the present study is, therefore, to investigate a) the seasonal food web structure including isotopic niche and other community structure metrics b) seasonality in total mercury concentrations in low- and mid-trophic level species, including various zooplankton and fishes, c) the seasonality in total mercury biomagnification using  $\delta^{15}\text{N}$  as proxy for relative trophic position.

We hypothesize that a) herbivores exhibit greater seasonal variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  compared to carnivores due to herbivores relying on seasonal algae blooms, b) mercury concentrations in biota occupying similar trophic levels increase from winter to spring, shifting from a time of reduced food availability and activity, diapause, extended sea ice, decreasing energy storage, and possible starvation and c) mercury concentrations increase with increasing  $\delta^{15}\text{N}$  values (*i.e.* trophic level), thus biomagnify across all seasons, and finally, if mercury is higher in winter than spring, then we expect a less steep mercury to  $\delta^{15}\text{N}$  biomagnification slope in winter.

## 2. Material and Methods

### 2.1. Study site and sample collection

The Barents Sea is a shallow and productive shelf sea, sustaining large fish stocks of high ecological and commercial value (Hunt et al., 2013; Kvamsdal et al., 2020). Here, the marginal ice zone, where the open water and sea ice meet, is a variable and vital region for Arctic biota and biological productivity (Barber et al., 2015; Gerland et al., 2023). This region is influenced by warmer Atlantic water masses and colder polar water masses (Sundfjord et al., 2020). It experiences seasonal variations in productivity and fluctuations in sea ice coverage and thickness, characterized by open water expanses during summer and autumn, and partial sea ice coverage during winter and spring.

Samples of mainly pelagic zooplankton and fishes were collected in the Northern Barents Sea in late summer (04.08.-27.08.2019), early winter (28.11.-17.12.2019), late winter (02.03.-27.03.2021) and spring (14.04.-07.05.2021) during seasonal research cruises onboard RV *Kronprins Haakon* as part of the Nansen Legacy project. Initially, consecutive seasonal sampling to cover a complete annual cycle was planned, but paused in 2020 due to the coronavirus pandemic. The sampling transect was similar for all seasons and ranged from south of the European polar front (76°N, 31°E) to the Arctic Ocean (82°N, 30°E) (see Supplementary Fig. 1), thus covering Atlantic and Arctic conditions and variable sea ice extent.

Mesozooplankton (mainly large copepods) were captured with a midwater ring net (MIK net) with a 3.14 m<sup>2</sup> metal frame rigged with a 1200  $\mu\text{m}$  mesh size and a 500  $\mu\text{m}$  cod end or a WP-3 net (1000  $\mu\text{m}$  mesh size and 1 m<sup>2</sup> opening). The nets were hauled vertically from 20 m above the bottom to the surface at 1–1.5 ms<sup>-1</sup>. On stations that exceeded 1000 m bottom depth, nets were taken from 1000 m or 500 m to the surface.

We collected macrozooplankton with a pelagic macroplankton trawl (3000  $\mu\text{m}$  mesh size) where no sea ice was present. Trawling speed of 3 ms<sup>-1</sup> was kept for 20 min to target mainly krill and amphipods, as they can be quick enough to avoid the MIK net.

Once at the surface, the net or trawl was rinsed with seawater, and zooplankton were quickly transferred into a bucket with seawater and kept at 0 – 4°C until sorting to species within a maximum of six hours. Three groups, including copepods (mainly herbivorous), macrozooplankton (mainly omnivores), and fishes (mainly carnivores), were targeted, and sorted into the following taxa: copepods; *Calanus hyperboreus* (copepodite stage (CIV to adult), *Calanus* sp. (CIV to adult; pooled *Calanus finmarchicus* and *Calanus glacialis*), and paraeuchaeta (*Paraeuchaeta* sp.), macrozooplankton; chaetognaths (*Sagitta elegans* and *Eukhronia hamata*, pooled), amphipods (*Themisto libellula* and *Themisto abyssorum*), krill (*Thyssanoessa* sp. and *Meganctiphanes norvegica*), and pteropods (*Clione limacina*). Only relatively large organisms (clearly recognizable without a microscope) were sampled. After collecting approximately one to two grams of each species, the sample was individually frozen in cryovials at – 20 °C and kept frozen during transport to the Department of Biosciences at the University of Oslo, Norway, where they were analyzed for mercury and bulk stable isotopes.

Target fish species were the abundant species polar cod (*Boreogadus saida*), Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). Mainly, individuals with a total length below 25 cm were sampled, as this size range includes relevant prey for higher trophic level organisms such as seals and seabirds in the Barents Sea (Labansen et al., 2007; Mehlum & Gabrielsen, 1993). Benthopelagic fishes Atlantic cod, and adult polar cod were caught with a demersal (Campelen) trawl at 3 ms<sup>-1</sup> for 20–30 min. Pelagic fishes were targeted with a pelagic (Harstad) trawl at four ms<sup>-1</sup>. Approximately two grams of dorsolateral muscle tissue was dissected and frozen at – 20 °C until further processing. Fish muscle stable isotope and mercury data from early winter 2019 have been obtained from Gopakumar et al., 2021.

## 2.2. Sample preparation

Prior to analysis, all samples were freeze-dried in a Leybold-Heraeus GT2 Freeze dryer with a Leybold Vakuum GmbH vacuum pump (Leybold, Cologne, Germany) for 24 h or until the samples were dry. After that, they were homogenized to a fine powder with a porcelain pestle and mortar. Due to the variable amount and size of available zooplankton species and the minimum required amount of 10–30 mg of dried sample for the mercury analyses, a pool of whole individuals was homogenized together. Here, same species collected in the same season and area were pooled together. Fish muscle tissue was homogenized and analyzed individually. Stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) and total mercury concentrations were analyzed in aliquots from the same homogenate.

## 2.3. Stable isotope analyses

Bulk stable isotope analysis of nitrogen and carbon ratios help in understanding trophic relationships and energy flow within ecosystems. By analyzing the stable isotope ratios in the tissue of organisms, we can infer an organism's position within the food web, as  $\delta^{15}\text{N}$  is enriched > 1.2 ‰ per trophic level and trace dietary carbon sources, as  $\delta^{13}\text{C}$  varies little between trophic levels (<1‰) (Peterson & Fry, 1987). In the Barents Sea, the main carbon sources originate from pelagic algae, whereas ice algae contribute to a lesser extent, particularly in our study species (Kohlbach et al., 2021a; Søreide et al., 2006).

The relative stable isotope abundances of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured in 1 mg ( $\pm 0.1$  mg) of homogenate per sample. After weighing the homogenate in a tin capsule, it was combusted and quantified in a Thermo Fisher Scientific™ EA IsoLink IRMS System™, consisting of a Flash EA (Elemental Analyzer) and a Delta V IRMS (Isotope Ratio Mass Spectrometer).

Stable isotopes were quantified relative to a reference and are reported in the delta notation in parts per thousand (Equation (1)).

$$\delta[X\text{‰}] = \left( \frac{R_{(\text{Sample})}}{R_{(\text{Reference})}} - 1 \right) * 1000 \quad (1)$$

$^{13}\text{C}$  and  $^{15}\text{N}$  are expressed as the delta value in parts per thousand (‰), and R is the molar ratio of  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  in the samples and the international standard, respectively. Each species was measured in triplicates per season, or a triplicate was included in every tenth sample to account for any variability in the sample and equipment. Neither carbonates nor lipids were removed from the samples. Detailed information on quality assurance can be obtained from the [supplementary information](#).

## 2.4. Mercury analysis

Total mercury was analyzed in all freeze-dried sample homogenates (10–30 mg dry weight) by atomic absorption spectrometry with a Milestone Direct Mercury Analyzer DMA-80 (DMA-80, Milestone Srl, Soirsole, Italy) at the University of Oslo, Norway. Each first sample per species was analyzed in triplicates to control for any variability in the homogenate, and the average was used for further analysis. Certified Reference Materials (DORM-4 fish protein; DOLT-5 dogfish liver, National Research Council of Canada, Ottawa, Canada) and an internal reference (TORSK: Cod liver) were included for every batch of samples analyzed for quality assurance. Average recoveries of reference material were within 10 % of their certified value. Each sample run included a set of at least three blanks to account for any background noise and all mercury values were blank corrected. The mean method detection limit was 0.05 ng mercury and the few samples below this limit were excluded from further analyses.

## 2.5. Data treatment and statistical analyses

All data was analyzed using R software version 4.3.1. (R Core Team, 2023). Mercury concentrations are reported in ng/g dry weight (dw) and were  $\log_{10}$ -transformed for statistical analyses to meet the normality and homoscedasticity assumption. Analyses of variance (ANOVA) were conducted to compare mercury concentrations, stable isotope values, and elemental carbon and nitrogen ratios (C:N ratios) among species from the same season and within species across seasons. We grouped the data by species and tested the effect of season and one of the aforementioned response variables and grouped the data by season to test for inter-species differences per response variable. These were followed by *post-hoc* Tukey's honestly significant difference tests. For species sampled in only two seasons, we used Welch's *t*-test. We inspected the residual plots for normality and homoscedasticity and  $\log_{10}$ -transformed  $\delta^{15}\text{N}$  and C:N ratio when the assumptions were violated. To gain better overview of the data, and establish a food web perspective, we pooled all individual measurements of the taxa belonging to copepods, macrozooplankton and fishes in these three groups for the data treatment and ran the same statistical tests, within groups across seasons. The copepod group therefore consists of *Calanus* sp., *Calanus hyperboreus*, *Calanus glacialis*, and the predatory copepod *Paraeuchaeta* sp., of which the two latter species were only sampled in late winter and spring, respectively. The number of different taxa is highest in the macrozooplankton group across the seasons and includes krill, amphipods, chaetognaths, and pteropods. The fish group consists of the three fish species Atlantic cod, polar cod, and capelin, of which Atlantic cod was only sampled in late summer and early winter.

$\delta^{13}\text{C}$  varies little between trophic levels but can be affected by variable lipid content in the samples, which can introduce bias into the  $\delta^{13}\text{C}$  interpretation. The ratio of C:N can be used as a proxy for lipid content, and we found a negative relationship between  $\delta^{13}\text{C}$  and C:N ratio (linear regression, adjusted  $R^2 = 0.56$ ,  $F_{1,172} = 220.3$ ,  $p < 0.001$ ). A correction threshold was set at a C:N ratio exceeding 3.5 to account for lipid interference (Post et al., 2007). Given that the majority of our samples exhibited C:N ratios surpassing this threshold (see Table 2), we applied a correction to all  $\delta^{13}\text{C}$  values using an empirical relationship from Post et al., 2007 (Equation (2));

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C} : \text{N} \quad (2)$$

### 2.5.1. Food web composition

We used Layman's community metrics to assess the sampled food web structure per season (Layman et al., 2007). These metrics included the  $\delta^{15}\text{N}$  range (NR), which indicates the food chain length;  $\delta^{13}\text{C}$  range (CR), indicative of the basal carbon range; mean distance to centroid (CD), which indicates the average degree of trophic diversity, mean nearest neighbor distance (NND), which gives a measure of proximity and clustering of species within the community, the standard deviation of the nearest neighbor distance (SDNND), and total area (TA), which is the area of the convex hull area encompassing the population means of the entire community, thus an indicator for trophic diversity. To determine the isotopic niche space for each species per season, we used the SIBER package in R. We calculated the standard ellipse area corrected for small sample size (SEAc) as well as a Bayesian standard ellipse area (SEAB). SEAB values were derived through 200,000 iterations with a 1000 burn-in and two chains (Jackson et al., 2011).

### 2.5.2. Mercury biomagnification

The lipid content in fish muscle tissue varied between species and affected the mercury content (see Gopakumar et al., 2021 and Supplementary figure 3), as capelin store lipids in muscle tissue, contrary to the gadoids, which mainly store lipids in the liver. We therefore included C:N ratio as a proxy for lipid content in our linear model (Kahilainen et al., 2016). We then used the linear model to investigate the effect of the predictors  $\delta^{15}\text{N}$  and season on mercury concentrations on our entire

dataset and included the C:N ratio as a covariate, to remove mercury variance due to lipid variation (Equation (3)).

$$\log_{10} \text{Hg } \delta^{15}\text{N} + \text{season} + \delta^{15}\text{N} : \text{season} + \text{C} : \text{N ratio} \quad (3)$$

We visually checked the model for normality of residuals and heteroscedasticity, and calculated Cohen's  $f^2$  using the R package 'effectsize' to estimate the predictors effect sizes (Ben-Shachar et al., 2020). Acknowledging the suitability of a linear mixed model for this data set, we chose a simpler model due to the limited sample size.

**2.5.2.1. Calculation of trophic magnification factors.** For ease of comparison to other studies, trophic magnification factors (TMFs) were calculated from the antilog of the slope (b) of the regression of  $\log_{10}$  mercury onto trophic position (TP) of organisms in our food web (Equation (4), e.g., Borgå et al., 2012; Lavoie et al., 2013).

$$\log_{10} \text{Hg} = a + b * \text{TP}, \text{ and } \text{TMF} = 10^b \quad (4)$$

A TMF greater than one indicates biomagnification in the food web.

To generate TMFs, we calculated the trophic position of individuals relative to the assumed primary consumer *Calanus* sp. for each species at each station (therefore *Calanus* sp. was defined to inhabit trophic position 2) (Equation (5)). *Calanus* sp. is a common prey item by other taxa from the food web, e.g. amphipods, krill, and capelin, thus a suitable baseline (Dalpadado et al., 2008; Ogloff et al., 2020). The enrichment factor was set to 3.4 ‰ (Jardine et al., 2006; Post, 2002; Sørreide et al., 2006), assuming constant enrichment of  $^{15}\text{N}$  across trophic levels.

$$\text{TP} = 2 + \frac{\delta^{15}\text{N}_{\text{Consumer}} - \delta^{15}\text{N}_{\text{Calanus sp.}}}{3.4} \quad (5)$$

With  $\delta^{15}\text{N}_{\text{Consumer}}$  representing the analyzed species (zooplankton and fishes) and  $\delta^{15}\text{N}_{\text{Calanus sp.}}$  representing the average  $\delta^{15}\text{N}$  value found in *Calanus* sp. at the same season as the sample.

All results are reported as mean  $\pm$  standard deviation (SD), if not defined else. We used the conventional  $p \leq 0.05$  threshold for statistical significance.




### 3. Results

#### 3.1. General food web structure

Overall, the  $\delta^{15}\text{N}$  values increased from copepods to macrozooplankton to fishes across seasons (Tukey HSD,  $p < 0.001$ ) (Table 1). The macrozooplankton group showed a large variability of  $\delta^{15}\text{N}$  values,

**Table 1**

Summary statistics for organism groups: Mean ( $\pm$  standard deviation) bulk stable isotope values of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) (in ‰), and C:N ratios, as well as total mercury concentrations (ng/g dw) of pooled copepods (including *Calanus glacialis*, *Calanus hyperboreus*, *Calanus* sp., and *Paraeuchaeta* sp.), macrozooplankton (including *Thyssanoessa* sp., *Meganyctiphanes norvegica*, *Themisto libellula*, *Themisto abyssorum*, *Clione limacina*, and chaetognaths) and fishes (including *Mallotus villosus*, *Boregadus saida*, and *Gadus morhua*) collected in the Barents Sea. Results are presented as the mean ( $\pm$  standard deviation).

Organism group	Season	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N ratio	Mercury (ng/g dw)
 Copepods	Late winter 2021	13	$-25.7 \pm 0.7$	$6.9 \pm 0.4$	$7.5 \pm 1.0$	$7.1 \pm 2.6$
	Spring 2021	25	$-22.7 \pm 0.9$	$7.3 \pm 1.4$	$5.9 \pm 1.1$	$12.3 \pm 12.0$
	Late summer 2019	14	$-20.8 \pm 2.4$	$6.6 \pm 0.8$	$2.4 \pm 8.1$	$7.0 \pm 4.1$
	Early winter 2019	10	$-22.0 \pm 1.1$	$7.0 \pm 0.5$	$8.2 \pm 0.7$	$5.5 \pm 3.0$
	Late winter 2021	30	$-22.8 \pm 0.8$	$8.9 \pm 1.2$	$5.0 \pm 0.8$	$21.2 \pm 17.2$
 Macrozooplankton	Spring 2021	19	$-23.4 \pm 0.7$	$7.5 \pm 1.4$	$4.9 \pm 0.8$	$17.4 \pm 17.1$
	Late summer 2019	38	$-21.9 \pm 1.3$	$8.0 \pm 0.9$	$6.2 \pm 1.3$	$12.4 \pm 12.7$
	Early winter 2019	38	$-22.3 \pm 1.3$	$8.6 \pm 1.1$	$6.1 \pm 1.4$	$23.8 \pm 25.6$
	Late winter 2021	19	$-22.4 \pm 0.4$	$11.8 \pm 0.4$	$3.9 \pm 1.1$	$28.4 \pm 11.4$
	Spring 2021	28	$-22.2 \pm 0.4$	$11.8 \pm 0.6$	$3.5 \pm 0.2$	$31.0 \pm 11.8$
 Fishes	Late summer 2019	30	$-21.5 \pm 0.8$	$11.8 \pm 1.2$	$3.5 \pm 0.3$	$42.6 \pm 23.2$
	Early winter 2019	24	$-21.7 \pm 1.1$	$11.9 \pm 0.5$	$4.6 \pm 2.0$	$24.4 \pm 8.1$

ranging from values comparable to copepods, which had the lowest  $\delta^{15}\text{N}$  values, in the herbivore krill *Thyssanoessa* sp. to values comparable to the omnivore krill *Meganyctiphanes norvegica*, and the fish capelin (Table 2, Fig. 1).

A less clear contrast between groups was found for  $\delta^{13}\text{C}$ , with copepods generally having more enriched  $\delta^{13}\text{C}$  values than macrozooplankton within the same season (Tukey HSD, copepods-macrozooplankton,  $p < 0.001$  for late winter, and  $p = 0.029$  for late summer). In spring,  $\delta^{13}\text{C}$  values exhibited significant differences across all groups (Tukey HSD, copepods-macrozooplankton,  $p = 0.002$ ; copepods-fishes,  $p = 0.026$ ; macrozooplankton-fishes,  $p < 0.001$ ). Conversely, during early winter,  $\delta^{13}\text{C}$  values across groups were similar (Tukey HSD,  $p > 0.05$  for all group comparisons).

C:N ratios were highest in copepods, followed by macrozooplankton and fishes (see Table 2).







#### 3.1.1. Seasonal food web structure

Between-season comparison of organism groups reveals no seasonal difference of  $\delta^{15}\text{N}$  values in the copepod group (ANOVA,  $F = 1.34$ ,  $p = 0.27$ ). More variability in  $\delta^{15}\text{N}$  was seen in the macrozooplankton group. Here, the  $\delta^{15}\text{N}$  values followed a U-shape pattern across the seasons. High  $\delta^{15}\text{N}$  values of  $8.9 \pm 1.2$  ‰ were measured in late winter, which decreased to  $7.5 \pm 1.4$  ‰ in spring (Tukey HSD,  $p < 0.001$ ), increasing slightly to  $8.0 \pm 0.9$  ‰ in late summer and further to  $8.6 \pm 1.1$  ‰ (Tukey HSD,  $p = 0.001$ ) in early winter, reaching similar values as in late winter (Tukey HSD,  $p = 0.831$ ). This pattern was well reflected by *Thyssanoessa* sp., which had at least 1.3-fold lower  $\delta^{15}\text{N}$  values in spring compared to all other seasons (Tukey HSD,  $p < 0.001$  spring vs. late winter,  $p < 0.001$  spring vs. late summer, and  $p < 0.001$  spring vs. early winter). However, the amphipods *Themisto abyssorum* and *Themisto libellula* had a reverse pattern, with lowest  $\delta^{15}\text{N}$  values in late summer and highest during late winter (Tukey HSD,  $p < 0.001$  and  $p = 0.005$ , respectively) (see Table 2, Fig. 1). While no seasonal changes of  $\delta^{15}\text{N}$  were observed in the fish group, we saw seasonal differences in  $\delta^{15}\text{N}$  values at the species level for capelin, which had lower  $\delta^{15}\text{N}$  values during late summer compared to late winter and early winter (Tukey HSD,  $p < 0.001$ , and  $p < 0.001$ , respectively), but similar  $\delta^{15}\text{N}$  values in early winter and spring (Tukey HSD,  $p = 0.199$ ).

Some seasonal changes in  $\delta^{13}\text{C}$  values were observed across the organism groups, with depleted  $\delta^{13}\text{C}$  values in spring and enriched  $\delta^{13}\text{C}$  values in late summer. We observed seasonal variation in the copepod group, which had the most enriched  $\delta^{13}\text{C}$  values in late summer, as opposed to high depletion in spring ( $-22.7 \pm 0.8$  ‰) (Tukey HSD,  $p = 0.001$ ). This pattern was well reflected in *Calanus* sp., which had more

**Table 2**

Bulk stable isotope values of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ), C:N ratio, and total mercury concentrations (ng/g dw), and ecological parameters of fish and zooplankton collected in the Barents Sea during field campaigns in late summer 2019 (Aug), early winter 2019 (Dec), late winter 2021 (Mar), and spring 2021 (May). Results are presented as the mean of each sample ( $\pm$ standard deviation). The feeding mode was determined from the organisms' feeding ecology and trophic position and modified after (Søreide et al., 2006).

Taxonomic group	Taxa	Feeding mode	Habitat	No. of samples				$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)				C:N ratio				Mercury (ng/g dw)			
				Mar	May	Aug	Dec	Mar	May	Aug	Dec	Mar	May	Aug	Dec	Mar	May	Aug	Dec	Mar	May	Aug	Dec
	<i>Calanus glacialis</i>	Herbivore, pelagic	Arctic, Native	3	5	NA	NA	-22.6 $\pm$ 0.3	-22.7 $\pm$ 0.4	NA	NA	7.4 $\pm$ 0.2	5.9 $\pm$ 0.8	NA	NA	7.5 $\pm$ 0.3	4.1 $\pm$ 0.1	NA	NA	5.1 $\pm$ 0.3	6.0 $\pm$ 0.5	NA	NA
	<i>Calanus hyperboreus</i>	Herbivore, pelagic	Arctic, Native	8	7	9	3	-21.5 $\pm$ 1.2	-22.0 $\pm$ 0.7	-20.8 $\pm$ 2.9	-23.0 $\pm$ 1.6	6.6 $\pm$ 0.2	6.6 $\pm$ 0.4	6.3 $\pm$ 0.6	6.9 $\pm$ 0.3	7.4 $\pm$ 1.3	6.2 $\pm$ 0.9	7.6 $\pm$ 0.9	7.9 $\pm$ 1.0	8.6 $\pm$ 2.2	9.3 $\pm$ 4.0	9.0 $\pm$ 3.5	8.9 $\pm$ 3.2
	<i>Calanus</i> spp.	Herbivore, pelagic	Arctic, Native	2	6	5	7	-20.8 $\pm$ 0.6	-23.6 $\pm$ 0.2	-20.8 $\pm$ 1.5	-21.5 $\pm$ 0.6	7.2 $\pm$ 0.1	7.6 $\pm$ 0.4	7.2 $\pm$ 0.7	7.0 $\pm$ 0.6	7.8 $\pm$ 0.7	6.4 $\pm$ 0.6	9.0 $\pm$ 0.7	8.3 $\pm$ 0.5	4.4 $\pm$ 0.5	5.3 $\pm$ 0.4	3.3 $\pm$ 2.0	4.0 $\pm$ 1.5
	<i>Paraeuchaeta</i> spp.	Carnivore, pelagic	Arctic, Native	NA	7	NA	NA	NA	-22.7 $\pm$ 0.8	NA	NA	NA	8.8 $\pm$ 1.3	NA	NA	NA	6.3 $\pm$ 0.8	NA	NA	NA	25.9 $\pm$ 16.0	NA	NA
	Chaetognatha	Omnivore, pelagic	Arctic, Native	8	7	7	9	-23.3 $\pm$ 0.3	-23.4 $\pm$ 0.2	-22.5 $\pm$ 0.8	-23.1 $\pm$ 0.7	7.5 $\pm$ 1.0	6.6 $\pm$ 1.4	7.4 $\pm$ 1.2	8.4 $\pm$ 1.2	4.5 $\pm$ 0.4	5.0 $\pm$ 0.8	5.1 $\pm$ 0.8	4.8 $\pm$ 0.8	9.4 $\pm$ 1.5	8.0 $\pm$ 0.7	7.3 $\pm$ 3.6	7.5 $\pm$ 2.1
	<i>Clione limacina</i>	Omnivore, pelagic	Arctic, Native	3	6	4	9	-24.3 $\pm$ 0.1	-24.2 $\pm$ 0.2	-23.3 $\pm$ 0.9	-23.6 $\pm$ 0.9	8.3 $\pm$ 0.1	8.4 $\pm$ 0.4	7.8 $\pm$ 0.6	7.0 $\pm$ 0.8	5.5 $\pm$ 0.5	5.4 $\pm$ 0.5	5.3 $\pm$ 1.8	6.3 $\pm$ 1.0	23.5 $\pm$ 1.9	20.9 $\pm$ 2.2	28.5 $\pm$ 8.2	70.6 $\pm$ 28.4
	<i>Thysanoessa</i> spp.	Herbivore, pelagic	Arctic, Native	6	4	15	14	-22.3 $\pm$ 0.8	-22.4 $\pm$ 0.7	-21.5 $\pm$ 1.2	-21.5 $\pm$ 1.7	9.0 $\pm$ 0.2	6.9 $\pm$ 0.4	8.4 $\pm$ 0.7	8.9 $\pm$ 0.5	5.7 $\pm$ 0.5	4.0 $\pm$ 0.1	6.8 $\pm$ 1.0	7.1 $\pm$ 1.6	4.8 $\pm$ 3.6	6.5 $\pm$ 2.9	6.0 $\pm$ 2.5	2.5 $\pm$ 1.9
	<i>Meganycitiphanes norvegica</i>	Omnivore, pelagic	Sub-Arctic	7	NA	3	6	-22.5 $\pm$ 0.4	NA	-20.2 $\pm$ 1.1	-21.7 $\pm$ 0.7	10.1 $\pm$ 0.2	NA	8.2 $\pm$ 1.8	10.0 $\pm$ 0.3	5.3 $\pm$ 1.2	NA	6.4 $\pm$ 1.3	6.6 $\pm$ 0.3	30.8 $\pm$ 13.4	NA	24.9 $\pm$ 12.8	27.0 $\pm$ 10.1
	<i>Themisto abyssorum</i>	Omnivore, pelagic	Sub-Arctic	3	2	3	12	-22.0 $\pm$ 0.7	-22.5 $\pm$ 1.2	-21.8 $\pm$ 0.6	-21.9 $\pm$ 0.8	10.2 $\pm$ 0.3	9.4 $\pm$ 0.2	7.7 $\pm$ 0.9	9.2 $\pm$ 0.6	4.8 $\pm$ 0.2	5.0 $\pm$ 0.9	6.1 $\pm$ 0.3	5.6 $\pm$ 1.6	44.4 $\pm$ 23.6	62.0 $\pm$ 6.0	36.8 $\pm$ 21.3	28.0 $\pm$ 10.4
	<i>Themisto libellula</i>	Omnivore, pelagic	Arctic, Native	3	NA	6	8	-22.2 $\pm$ 0.5	NA	-22.1 $\pm$ 1.1	-22.2 $\pm$ 0.9	8.7 $\pm$ 0.3	NA	7.7 $\pm$ 0.2	8.3 $\pm$ 0.4	4.4 $\pm$ 0.6	NA	6.2 $\pm$ 1.9	5.8 $\pm$ 0.9	37.6 $\pm$ 16.3	NA	5.5 $\pm$ 1.7	17.8 $\pm$ 5.0
	<i>Mallotus villosus</i>	Carnivore, pelagic	Sub-Arctic, migratory	4	11	10	10	-21.8 $\pm$ 0.4	-22.1 $\pm$ 0.4	-21.5 $\pm$ 0.2	-21.1 $\pm$ 1.3	11.6 $\pm$ 0.2	11.2 $\pm$ 0.3	10.5 $\pm$ 0.4	11.7 $\pm$ 0.4	5.7 $\pm$ 1.3	3.5 $\pm$ 0.3	3.7 $\pm$ 0.4	6.4 $\pm$ 2.0	18.4 $\pm$ 1.1	24.8 $\pm$ 4.6	18.3 $\pm$ 5.4	22.6 $\pm$ 6.6
	<i>Boreogadus saida</i>	Carnivore, pelagic	Arctic, Native	15	17	10	10	-22.5 $\pm$ 0.2	-22.3 $\pm$ 0.2	-22.4 $\pm$ 0.4	-22.4 $\pm$ 0.5	11.9 $\pm$ 0.3	12.1 $\pm$ 0.4	11.9 $\pm$ 0.6	11.8 $\pm$ 0.5	3.4 $\pm$ 0.1	3.4 $\pm$ 0.2	3.4 $\pm$ 0.1	3.4 $\pm$ 0.1	31.1 $\pm$ 11.5	35.0 $\pm$ 13.3	50.6 $\pm$ 16.6	23.9 $\pm$ 7.0
	<i>Gadus morhua</i>	Carnivore, benthopelagic	Sub-Arctic, migratory	NA	NA	10	4	NA	NA	-20.7 $\pm$ 0.3	-21.5 $\pm$ 0.2	NA	NA	13.0 $\pm$ 0.5	12.3 $\pm$ 0.8	NA	NA	3.2 $\pm$ 0.1	3.3 $\pm$ 0.1	NA	NA	59.0 $\pm$ 20.4	30.0 $\pm$ 13.0

depleted values in spring compared to late summer (Tukey HSD,  $p = 0.008$ ).  $\delta^{13}\text{C}$  values were highly variable in *Calanus hyperboreus* in late summer, ranging from  $-25.0$  to  $-17.5$  ‰. Macrozooplankton had more depleted  $\delta^{13}\text{C}$  in spring compared to late summer and early winter (Tukey HSD,  $p < 0.001$ ,  $p = 0.002$ , respectively). In the fish group,  $\delta^{13}\text{C}$  values were similar, lowest in late winter and spring (Tukey HSD,  $p = 0.911$ ), and highest in late summer compared to late winter and spring (Tukey HSD,  $p < 0.001$  and  $p = 0.001$ , respectively), following the copepod and macrozooplankton group pattern. Atlantic cod had depleted  $\delta^{13}\text{C}$  values, from  $-20.7 \pm 0.3$  ‰ in late summer to  $-21.5 \pm 0.3$  ‰ during the early winter (Welch  $t$ -test,  $p = 0.004$ ).

Seasonal variation in C:N ratios was only observed in *Calanus* sp., *Thysanoessa* sp., and capelin (Table 2). *Calanus* sp. had lower C:N ratios in spring than in late summer and early winter (Tukey HSD,  $p = 0.001$  and  $p = 0.005$ , respectively). *Thysanoessa* sp. had lower C:N ratios in spring compared to late summer and early winter (Tukey HSD,  $p < 0.001$ ) and higher C:N ratios in early winter compared to late winter and spring (Tukey HSD,  $p = 0.026$  and  $p < 0.001$ , respectively). Capelin had higher C:N ratios in early winter, compared to late spring and late summer (Tukey HSD,  $p < 0.001$ ).

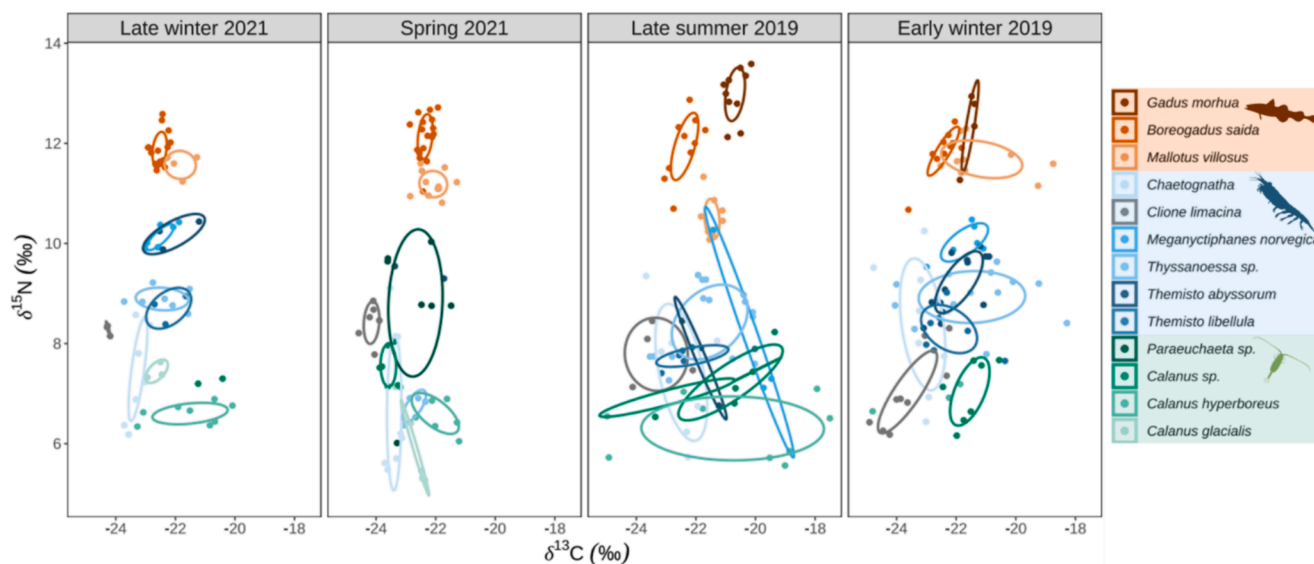
Food web structure based on the Layman's metrics was very similar across the seasons, aside from the late summer food web (Table 3, Supplementary Fig. 2), which had the most trophic links as indicated by the  $\delta^{15}\text{N}$  range (NR) (6.7 ‰, 95 % CI [5.6, 8.0]).  $\delta^{13}\text{C}$  range was lowest in spring, increasing in the late summer, followed by a decrease to 2.8 ‰, 95 % CI [1.8, 4.1] in early winter, and reaching similar values to late summer in late winter. No seasonal variation was observed in the food web in the mean distance to centroid (CD), indicating trophic diversity, and the species redundancy (NND). Total area was smallest in spring (9.4 ‰<sup>2</sup>, 95 % CI [4.2, 17.6]) and 1.5-fold larger in late summer (14.3 ‰<sup>2</sup>, 95 % CI [8.8, 22.1]), followed by a similar total area to spring in early winter and late winter.

### 3.2. Mercury concentrations in the Barents sea pelagic food web

Mercury concentrations varied widely among the different species but only in some species across the seasons. Generally, *Thysanoessa* sp., *Calanus* sp., followed by chaetognaths, had lowest mercury concentrations, and *Themisto abyssorum*, *Meganycitiphanes norvegica* and *Clione limacina* had mercury concentrations comparable to or exceeding those of the fishes (Fig. 2, Table 2).

In the copepod group, mercury concentrations were similar across seasons, except between spring and early winter (Tukey HSD,  $p = 0.04$ ), when mercury concentrations of the predatory copepod *Paraeuchaeta* sp. exceeded fish mercury concentrations.

Between season comparison of mercury in the macrozooplankton group revealed no clear pattern, as mercury concentrations within and across species varied widely. For instance, mercury concentrations in the krill *Thysanoessa* sp. were 2.4-fold higher in late summer than in early winter (Tukey HSD,  $p < 0.001$ ) but remained generally very low. The opposite was observed for the amphipod *Themisto libellula*, which had 3.2-fold higher mercury concentrations during early winter compared to late summer (Tukey HSD,  $p < 0.001$ ) and 6.8-fold higher mercury concentrations in late winter compared to late summer (Tukey HSD,  $p < 0.001$ ). The pteropod *Clione limacina* had 3.4-fold higher mercury concentrations in early winter compared to spring (Tukey HSD  $p < 0.001$ ) and 2.5-fold higher concentrations than in August (Tukey HSD,  $p = 0.002$ ). Mercury concentrations in early winter exceeded those in Atlantic cod two-fold. However, *Clione limacina* is a gelatinous zooplankton and contains 91–92 % moisture; thus, when presented on a wet weight basis, the mercury concentrations are comparable to the fishes. Highest mercury concentrations were measured in the fish group. In both Atlantic cod and polar cod, mercury concentrations in late summer were 1.7-fold higher than in early winter (Welch  $t$ -test,  $p = 0.05$  for Atlantic cod and Tukey HSD,  $p < 0.001$  for polar cod), leading to overall higher mercury concentrations in the fish group in late summer



**Fig. 1.** Ellipse plot of mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (‰) values per species, fitted with a standard ellipse corrected for small sample sizes (SEAC), derived from the SIBER R package, encompassing approximately 40 % of the data. Each dot represents the mean concentration of one sample. Copepods are depicted in green, macrozooplankton in blue, and fishes in orange colors.

compared to early winter (Tukey HSD,  $p = 0.001$ ). Polar cod mercury concentrations varied most, with the highest concentrations in late summer (Tukey HSD,  $p = 0.002$ , late summer vs. late winter,  $p = 0.02$  late summer vs. spring), lowest in early winter (Tukey HSD,  $p = 0.031$  early winter vs. spring), and similar values in late winter and spring (Tukey HSD,  $p = 0.758$ ). In capelin, mercury concentrations were slightly higher in the spring than in late summer (Tukey HSD,  $p = 0.025$ ).

### 3.3. Mercury biomagnification

Mercury concentrations increased with increasing  $\delta^{15}\text{N}$  in all seasons except in early winter when all species were included (Fig. 2). Changes in mercury concentrations were best explained by  $\delta^{15}\text{N}$  ( $p = 0.001$ ) and the covariate C:N ratio had a significant negative effect ( $p < 0.001$ ) (Table 4). The interaction term between  $\delta^{15}\text{N}$  and early winter was significant ( $p = 0.031$ ). Of the two predictors,  $\delta^{15}\text{N}$  had the largest effect size (Cohen's  $f^2 = 0.35$ ). Season had a small effect (Cohen's  $f^2 = 0.02$ ), and the interaction term between  $\delta^{15}\text{N}$  and season had a medium effect (Cohen's  $f^2 = 0.19$ ) (Cohen, 1988).

We observed a wide spread in the data, specifically among the macrozooplankton group, with high mercury concentrations measured in *Clione limacina* despite very low  $\delta^{15}\text{N}$  values in early winter, so we repeated the same analysis without this species. This resulted in no interaction between season and  $\delta^{15}\text{N}$  (Fig. 2, Table 4) but increased the  $R^2$  adjusted of the model from 0.35 to 0.45.

Mean trophic magnification factors decreased to half between late

summer and early winter when all species were included, and a constant enrichment factor across trophic levels of 3.4‰ was assumed for  $\delta^{15}\text{N}$  (Post, 2002; Sørense et al., 2006). The late summer food web TMF was highest with 2.9, 95 % CI [2.3, 3.8], whereas the early winter TMF was half, at 1.5, 95 % CI [0.9, 2.2]. The TMF increased to 2.5, 95 % CI [1.9, 3.3] in late winter and remained similar in spring. When calculating the TMF while omitting the outlier pteropod *Clione limacina*, season was no longer a significant predictor. Therefore, the TMF for all seasons (without *Clione limacina*) was 2.6, with a 95 % CI of [2.2, 3.0].

## 4. Discussion

This study was designed to contrast food web structure, mercury concentrations and mercury biomagnification across different seasons in a pelagic food web in the European Arctic marginal ice zone. We showed that food web structure was similar across the seasons, and that mercury concentrations in biota varied in direction and magnitude without a clear seasonal pattern. Mercury biomagnification in the food web occurred regardless of season after the pteropod *Clione limacina* was excluded. Previous studies have shown mercury biomagnification in Arctic food webs, but to our knowledge, no study has provided year-round data from the Barents Sea that includes the polar night.

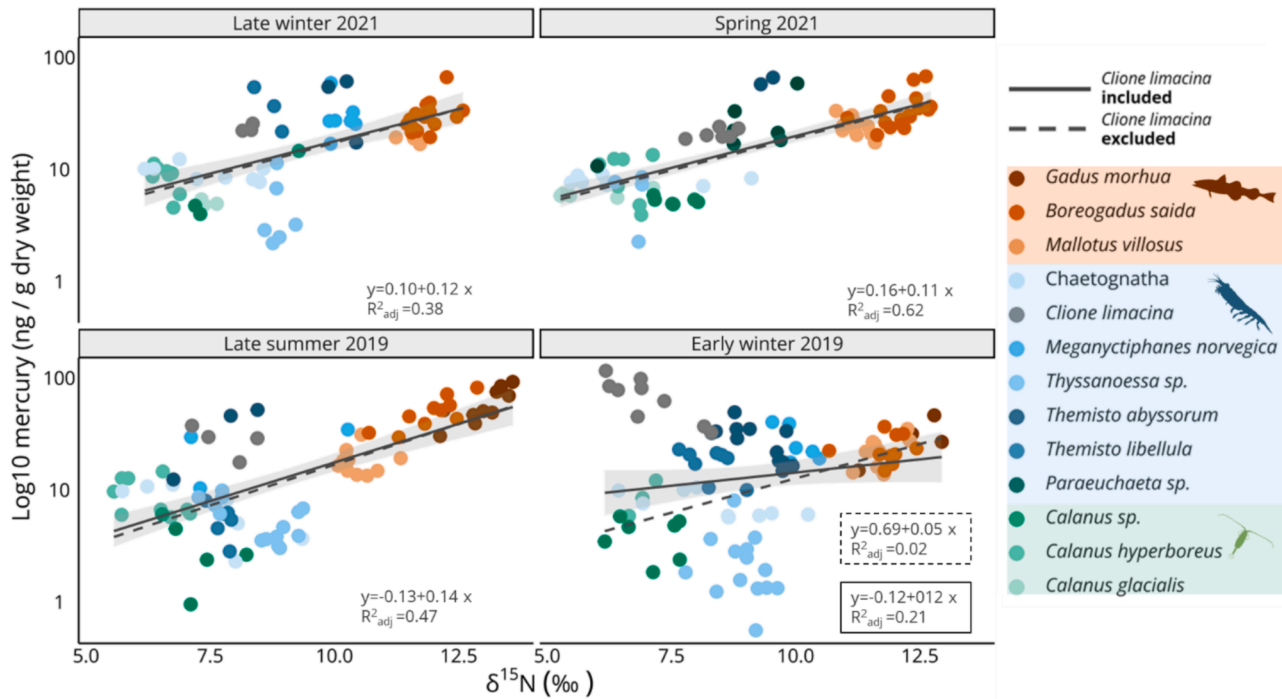
### 4.1. Food web structure

The  $\delta^{15}\text{N}$  values were consistent in the copepods across species, except during spring when they matched those of the macrozooplankton

**Table 3**

Overview table of calculated Layman metrics (Layman et al., 2007) with 95 % credible intervals for each seasonal food web, with number of samples, number of taxa,  $\delta^{15}\text{N}$  range,  $\delta^{13}\text{C}$  range, mean distance to centroid (CD), mean nearest neighbor distance (NND), the standard deviation of the nearest neighbor distance (SDNND) and the total area (TA).

	Number of samples	Number of taxa	$\delta^{15}\text{N}$ range	$\delta^{13}\text{C}$ range	CD	NND	SDNND	TA
Late winter 2021	63	11	5.7 [4.4–7.2]	3.2 [1.6–5.7]	1.8 [1.4–2.2]	0.9 [0.5–1.3]	0.4 [0.1–0.9]	10.5 [5.1–19.3]
Spring 2021	72	10	6.3 [5.2–7.7]	2.5 [1.3–4.8]	2 [1.6–2.4]	0.9 [0.6–1.3]	0.4 [0.1–0.9]	9.4 [4.2–17.6]
Late summer 2019	82	11	6.7 [5.6–8.0]	3.3 [1.9–5.5]	2 [1.7–2.4]	1.1 [0.7–1.4]	0.6 [0.3–0.9]	14.3 [8.8–22.1]
Early winter 2019	92	11	5.7 [4.6–7.4]	2.8 [1.8–4.1]	1.9 [1.6–2.2]	0.9 [0.6–1.2]	0.4 [0.1–0.7]	9.7 [6.2–14.3]



**Fig. 2.** Linear regressions of  $\delta^{15}\text{N}$  (‰) and mercury (ng/g dw) presented on a  $\log_{10}$ -scale. Each dot represents the concentration per sample. Copepods are depicted in green, macrozooplankton in blue, fishes in orange, and *Clione limacina* in grey. Respective 95% confidence intervals are shown in light grey for each regression line. The dashed regression line depicts the regression without the pteropod *Clione limacina*.

group. Here, the predatory copepod *Paraeuchaeta* sp. elevated the copepod groups' values, while macrozooplankton were almost absent during sampling. This pattern is well reflected in the reduced macrozooplankton biomass estimated from the same survey (Van Engeland et al., 2023). In macrozooplankton,  $\delta^{15}\text{N}$  values varied widely, likely caused by the diversity and species-specific adaptations to seasonal windows in productivity of that group. For instance, the herbivorous krill *Thyssanoessa* sp., relies on long-term lipid stores in the form of wax esters to survive winter's low food abundance. It can shrink, and switch to alternative food sources (Falk-Petersen et al., 2000; Huenerlage et al., 2015; Kunisch et al., 2023), potentially reducing  $\delta^{15}\text{N}$  values to those of copepods at the spring bloom onset. Omnivorous *Meganyctiphanes norvegica* feeds year-round, using triacylglycerols for short-term energy storage, and feeds on a mixed diet of copepods and phytoplankton, likely elevating their  $\delta^{15}\text{N}$  values to capelin values in late summer and early winter. Overall, zooplankton  $\delta^{15}\text{N}$  values were slightly lower or within the lower ranges of what Søreide et al., 2006 reported from the same region and similar seasons.

Atlantic cod and polar cod  $\delta^{15}\text{N}$  values showed no seasonal change. For Atlantic cod, a complete seasonal sampling was not possible, but we

did not expect to find a sizeable  $\delta^{15}\text{N}$  variation despite seasonally changing prey preferences (Holt et al., 2019), due to consumption of prey occupying similar trophic positions. Seasonal metabolic changes can also influence the  $\delta^{15}\text{N}$  signature, but dietary influences have a more significant impact (Vanderklift & Ponsard, 2003). Longer tissue turnover rates in polar cod may obscure seasonal  $\delta^{15}\text{N}$  changes, particularly in muscle tissue, which has slower turnover rates compared to other tissues, such as the liver (Hobson & Clark, 1992; Perga & Gerdeaux, 2005). However, shifts are likely as their diet changes from a *Themisto libellula*-dominated diet in the fall to copepods in the summer driven by prey abundance and winter visual limitations (Cusa, Berge & Varpe, 2019; Geoffroy et al., 2019; Matley et al., 2013). The  $\delta^{15}\text{N}$  turnover rate for adult polar cod is 49 days, (Ziegler et al., 2023), making the late winter and spring sampling periods too close together to accurately measure  $\delta^{15}\text{N}$  shifts for polar cod. We assume that changes in isotopic ratios illustrate a change in the predators' diet or in the preys' diet, thereby a change in the food web structure. For instance, for capelin we observed a change in  $\delta^{15}\text{N}$  values, with lower values during late summer, likely due to dominant foraging on abundant copepods (Van Engeland et al., 2023) after the spring bloom and a more generalist diet during winter, where

**Table 4**  
Linear model summary, with and without the pteropod *Clione limacina* included.

Predictors	Linear model (all data included)			Linear model ( <i>Clione limacina</i> included)		
	Estimates	Conf. Int(95 %)	P-value	Estimates	Conf. Int(95 %)	P-value
Intercept	0.83	0.32–1.35	0.001	0.61	0.14–1.09	0.011
C:N ratio	−0.07	−0.10–0.04	<0.001	−0.06	−0.09–0.03	<0.001
$\delta^{15}\text{N}$	0.08	0.03–0.12	0.001	0.09	0.05–0.13	<0.001
Spring 2021	−0.1	−0.63–0.42	0.695	−0.06	−0.54–0.43	0.820
Late summer 2019	−0.1	−0.63–0.42	0.693	−0.16	−0.64–0.32	0.504
Early winter 2019	0.61	0.06–1.16	0.031	−0.10	−0.63–0.44	0.726
$\delta^{15}\text{N}$ :Spring 2021	0.01	−0.04–0.07	0.670	0.01	−0.04–0.06	0.779
$\delta^{15}\text{N}$ :Late summer 2019	0.01	−0.04–0.07	0.698	0.02	−0.03–0.07	0.530
$\delta^{15}\text{N}$ :Early winter 2019	−0.06	−0.12–0.01	0.029	0.00	−0.05–0.06	0.979
Observations	309			287		
R <sup>2</sup> /R <sup>2</sup> adjusted	0.364/0.347			0.469/0.454		

food and visibility are limited. They further undergo ontogenetic migrations to spawn at the Norwegian coast (Gjøsæter, 1998), which can reflect stronger changes in  $\delta^{15}\text{N}$  values compared to polar cod, which mostly reside in Arctic waters year-round. Fish  $\delta^{15}\text{N}$  were generally lower than previously observed (Jæger et al., 2009; Matley et al., 2013; Tاملander et al., 2006).

Across organisms,  $\delta^{13}\text{C}$  values were most depleted during spring. This can indicate a shift in carbon sources, potentially due to vertical migration patterns that make various carbon sources available – from benthic POM and settled ice algae or pelagic algae, or the onset of the spring bloom. In the Northern Barents Sea, the beginning of spring, marked by the sun's return and subsequent algae blooms trailing the receding ice edge, typically occurs from May to July (Reigstad et al., 2008). This period likely coincided with our field campaign in spring 2021 (Bodur et al., 2023). Further, macrozooplankton were relatively absent during that time, which could have led to a skewed  $\delta^{13}\text{C}$  distribution, as macrozooplankton tended to have more enriched  $\delta^{13}\text{C}$  values than copepods and fishes.  $\delta^{13}\text{C}$  values in Atlantic cod were depleted in early winter compared to late summer. Here, a more mixed diet between benthic and pelagic prey could explain our observed shift (Link & Garrison, 2002).

Overall, we observed lower  $\delta^{13}\text{C}$  values in the zooplankton taxa compared to Søreide et al., 2006. This could, however, be due to different methodologies in sample treatment, as Søreide et al. chemically removed lipids, and we used lipid corrected  $\delta^{13}\text{C}$  values using the equation provided by Post et al., 2007. We further did not separate individual species into size classes.  $\delta^{13}\text{C}$  values can also be affected by metabolic processes, seasonal changes, temporal decline (De La Vega et al., 2019) and methodological differences.

Layman's metrics are useful tools in understanding food web structure, enhancing our comprehension of mercury biomagnification which relies on the efficiency of energy and pollutant transfer among organisms. While food web structure remained similar across seasons, as most ranges of the individual metrics overlapped, some seasonal trends emerged. For instance, as seen in the carbon ranges, all food webs had considerable overlap, but particularly *Calanus hyperboreus* had larger carbon ranges in summer. The Arctic summer provides abundant food, with varied carbon sources from post-bloom pelagic and ice algae, as well as other detritus and particulate organic matter (POM) (e.g., Bodur et al. 2023). The late summer food web had the highest trophic diversity, with a large  $\delta^{15}\text{N}$  range and total area, compared to early winter and spring. Biomass and abundance data from the same survey support this, with peak zooplankton biomass in late summer and early winter (Van Engeland et al., 2023). Thus, although our food web exhibited seasonal changes in species composition and position in the isoscape, the food webs remain comparable across seasons.

#### 4.2. Seasonal mercury concentrations

While some taxa, like the pteropods, amphipods, and fishes showed seasonal shifts in mercury concentrations, low-trophic level taxa such as copepods and chaetognaths did not, likely due to their phytoplanktivorous diet, and mercury's biomagnification. *Themisto libellula* exhibited increased mercury concentrations from summer to early and late winter, coinciding with higher  $\delta^{15}\text{N}$  values, indicating a shift to carnivory (Kohlbach et al., 2021b). Zooplankton species such as *Meganyctiphanes norvegica* and the pteropod *Clione limacina* had mercury concentrations equal to or higher than fish, particularly during the winter. *Clione limacina* presented a special case and will be discussed further below. *Meganyctiphanes norvegica* might have comparable mercury concentrations to fish because of its more carnivorous diet, as they prey on copepods, and potentially lower ability to metabolize mercury. *Clione limacina* can starve for almost one year and use its lipid stores as energy buffer (Böer et al., 2007). As food availability is reduced during the Arctic winter, *Clione limacina* might be in a phase of starvation, which can remobilize and elevate mercury concentrations in some organisms

(Peterson et al., 2018). Thus, the pteropod might have different turnover rates both for mercury and stable isotopes than other organisms of the food web. Variability in exposure, such as water column position or water mass (Arctic vs. Atlantic water masses) can affect mercury concentrations, as it has been shown that total and methyl mercury concentrations in the water column vary seasonally and with depth (Kohler et al., 2022; Kohler et al., 2024). Overall, high variability in macrozooplankton mercury concentrations was expected, as we sampled a range of organisms with very different adaptations to survive low food abundance (e.g., lipid storage in wax esters for long-term energy storage vs. triacylglycerols for short-term storage), varying detoxification mechanisms and capacities, as well as various forms and times of the year of reproduction. However, the implications of similar mercury concentrations in some macrozooplankton and fishes must be treated cautiously, as we only quantified total mercury, not the toxic and biomagnifying methylmercury (MeHg). The proportion of methylmercury to mercury in the food web is lowest in low trophic level taxa like *Calanus* sp., while it exceeds 90 % in fish muscle tissue (Bowles et al., 2001; Pomerleau et al., 2016; Ruus et al., 2015; Žizek et al., 2007). Therefore, total mercury serves as proxy for the biomagnifying methylmercury in fish muscle but is less informative for zooplankton.

Polar cod and Atlantic cod had the highest mercury concentrations during late summer, compared to early winter, which could be connected to a change in feeding behavior. However,  $\delta^{15}\text{N}$  values remained similar across seasons for both fish species. As  $\delta^{15}\text{N}$  turnover rates take weeks to months to propagate through the food web, we might observe a lag in the system here, which we might not have captured with our study design. Polar cod had generally higher mercury concentrations than capelin, a result that Pedro et al., 2017 reported previously, explaining it with the migration of capelin and the higher mercury concentrations in Arctic waters compared to lower latitudes (Lavoie et al., 2013). Higher mercury concentrations in capelin during spring compared to summer could stem from different sizes of fish that were sampled. Mercury is known to increase with increasing body size and thus age in fish (e.g., Trudel and Rasmussen, 2006), and although we aimed to sample similar-sized fish across the seasons, capelin from spring was relatively small. They could thus either prey on different organisms, have reduced detoxification capacities, or simply be too young to have accumulated as much mercury as the adults.

Mercury concentrations in our study were generally lower than reported from other parts of the Arctic. For instance, *Calanus* sp. and chaetognaths had less than half the total mercury concentrations measured in the Canadian Arctic (Foster et al., 2012; Pomerleau et al., 2016) and only polar cod total mercury concentrations from winter were comparable to previous results from total mercury muscle concentrations in polar cod from the Alaskan Arctic (Fox et al., 2017).

#### 4.3. Mercury biomagnification in the Barents sea

Mercury concentrations increased with increasing  $\delta^{15}\text{N}$ , indicating biomagnification across all seasons except in the early winter when all species were included. After exclusion of the pteropod *Clione limacina* biomagnification was constant across the seasons. Constant biomagnification across the seasons can result from the multitude of processes that impact mercury uptake and elimination in biota, as well as drastically changing abiotic factors. For instance, during the polar night, when parts of the Barents Sea are ice-covered, air-mercury exchange will be reduced, but methylmercury concentrations in sea water were similar to those in late summer (Kohler et al., 2022). In spring and summer, when the sea ice retreats, the Arctic Ocean has reportedly been a source of mercury to the atmosphere, potentially reducing mercury availability for uptake. On the contrary, the bioavailability of mercury might increase due to increased particulate organic matter during the productive spring and summer (Bodur et al., 2023), melting sea ice that releases potentially trapped mercury, and the occurrence of AMDEs (Schroeder et al., 1988). These mechanisms could result in a constant



biomagnification of mercury during the winter, spring, and summer months.

Although abundant across the Arctic, *Clione limacina* is little studied. It is assumed to be prey for other Arctic predators, but due to its high water content, it is difficult to capture in stomach content analyses. The proportion of the toxic methylmercury to total mercury in *Clione limacina* can be 44 % (Foster et al., 2012). The majority of total mercury might thus be inorganic, not biomagnifying into fish if *Clione limacina* is not a large part of their diet, or *Clione limacina* simply has different turnover rates, as suggested above. In our study, the highest trophic magnification factor was calculated for the late summer food web, when all species were included, which had the widest niche width indicated by the total area and most trophic linkages, as indicated by the larger nitrogen range. Biomass during the summer months can be 12-fold higher compared to the winter (Geoffroy et al., 2019), which could contribute to more efficient mercury transfer due to sheer prey abundance and increased dietary uptake. The TMF for all seasons, when omitting *Clione limacina*, was almost half of the TMF reported by Jæger et al. 2009, which is one of the few mercury biomagnification studies from the European Arctic. However, their study included seabirds, which likely elevated the TMF due to their warm-blooded physiology with elevated energy demands and thus increased bioaccumulation (Braune & Norstrom, 1989; Hop et al., 2002). TMFs of total mercury in pelagic food webs including only cold-blooded species from the eastern Canadian Arctic and sub-Arctic were comparable to (Van Der Velden et al. 2013, TMF = 2.8), or lower than (Clayden et al. 2015, TMF = 1.4) TMFs from this study. However, we only quantified total mercury concentrations, which generally result in lower TMFs than methylmercury TMFs (e.g., Clayden et al. 2015; Fox et al. 2017). Our food web mainly consists of species at or below trophic level three, which can introduce bias of the total mercury TMF estimation, as the proportion of methylmercury in total mercury increases with trophic level (Fox et al., 2017; Ruus et al., 2015). Despite our limited dataset and the significant biological variability in our food web, which can affect TMF estimation (Borgå et al., 2012), the simplicity of the TMF provides robustness when assessing mercury dynamics within the food web, particularly in light of trophic structure.

C:N ratio remained a significant covariate, regardless of inclusion or exclusion of the pteropod, and increased model fit, reducing interference of lipids in the mercury biomagnification assessment. This is particularly important when seasonal variations in lipid tissue, such as in *Calanus* or capelin muscle, can significantly impact measured mercury content, which is primarily associated with proteins (Amlund et al., 2007).

Our findings indicate that food web structure remains similar across the seasons, although abiotic and biotic processes change significantly. We assumed those changes to influence the biomagnification of mercury, thereby modifying the dynamics of mercury within the food web. However, we found little change in mercury biomagnification across the seasons, thus the structural changes within the food web could be masked by dietary changes, or potential phases of starvation as exemplified in some study species.

With climate change altering mercury pathways and thus uptake and elimination in biota (McKinney et al., 2022), an increased understanding on resulting mercury concentrations in biota is necessary. Although no strong seasonal differences in mercury food web biomagnification were observed in this study, we find that species-specific mercury concentrations vary across the seasons. In the future, we might observe stronger seasonal changes in biomagnification as a result of climate change, thus continuous monitoring of not only the productive spring and summer months, but also the polar night is needed to inform mercury pollution mitigation strategies.

## 5. Conclusion

We here provide the first Arctic marine food web mercury concentrations from the polar night and new data on abundant low-trophic

level species from the European Arctic, including zooplankton and fishes. This study provides an essential piece of the puzzle for understanding seasonal mercury dynamics in the Arctic marine food web. Here, we showed that mercury biomagnifies in the pelagic food web across all seasons, with no clear seasonality across taxa. Mercury concentrations were highly variable among taxa and seasons, which highlights the importance of broad sampling, including a diverse species representation through the year. Species composition, sea ice dynamics, sampling locations, and seasons thus need to be registered for future mercury monitoring studies. The multi-tracer approach highlighted how seasonal changes impact trophic interactions and mercury biomagnification in the northern Barents Sea.

## CRedit authorship contribution statement

**Julia Giebichenstein:** Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Tom Andersen:** Writing – review & editing, Supervision, Software, Resources, Conceptualization. **Øystein Varpe:** Writing – review & editing, Supervision. **Geir W. Gabrielsen:** Writing – review & editing, Supervision. **Katrine Borgå:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.poccean.2024.103381>.

## Data availability

Data will be made available on request.

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