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ORIGINAL PAPER

Seasonal patterns in fatty acids of *Calanus hyperboreus* (Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut

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Abstract The marine copepod *Calanus hyperboreus* accumulates large quantities of lipids and essential fatty acids during summer months in Northern oceans. However, few data exist regarding their winter fatty acid profiles, which could be informative regarding the use of lipids by *C. hyperboreus* to successfully survive and reproduce during times of ice-cover and limited food. The present study compared fatty acids of *C. hyperboreus* between summer (August 2007 and 2008) and winter (early April 2008 and 2009) in Cumberland Sound, Canada. Summer samples from both years had significantly higher ∑polyunsaturated fatty acids and unsaturation indices (based on μg fatty acid mg dry tissue^{-1}) than winter samples and separated on a principal component analysis due to higher 18:2n-6, 18:4n-3, and 20:5n-3, consistent with phytoplankton consumption. Winter *C. hyperboreus* had significantly higher ∑monounsaturated fatty acids (MUFA) versus summer samples and separated on the principal component analysis due to higher proportions of 16:1n-7, 20:1n-9, and 22:1n-9, suggesting they were not actively feeding. Based on the seasonal fatty acid comparison, *C. hyperboreus* was catabolizing specific fatty acids (e.g. 20:5n-3), conserving others (e.g. 22:6n-3), and maintaining or increasing biosynthesis of certain MUFA (e.g. 18:1n-9) during winter. These findings provide insight into the seasonal strategy of acquisition (summer) and utilization (winter) of specific fatty acids by a key Arctic organism and could become important for monitoring changes in fatty acids associated with decreased ice-cover duration due to climate warming.

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Introduction

Polar oceans are characterized by pronounced seasonal variability in temperature, light, and salinity (Clarke 1983). This inconstancy in physico-chemical conditions drives strong seasonal variability in available food resources, which, in turn, constitutes one of the biggest challenges faced by polar organisms (Clarke 1983). *Calanus hyperboreus* (Krøyer, 1838) is a predominantly herbivorous marine copepod (Falk-Petersen et al. 1987; Stevens et al. 2004b) that inhabits seasonally ice-covered waters in the Arctic and sub-Arctic (Conover 1988). The ephemeral nature of phytoplankton availability in Arctic systems coupled with low water temperatures (low basal metabolic rates) promote most Arctic copepods to accumulate higher amounts of lipids than temperate or tropical copepods (Lee and Hirota 1973).

Lipids are stored by Arctic *Calanus* spp. predominantly as wax esters (Kattner and Hagen 2009), which consist of a fatty acid esterified to a fatty alcohol, and can account for >91% of total lipids in *C. hyperboreus* (Lee 1974). Certain polyunsaturated fatty acids (PUFA) like eicosapentaenoic acid (EPA, 20:5n-3), arachidonic acid (ARA, 20:4n-6) and docosahexaenoic acid (DHA, 22:6n-3) are required for somatic growth and membrane functioning of animals and invertebrates (Parrish 2009). However, it is generally accepted that these 'essential' fatty acids cannot be synthesized from their fatty acid precursors (i.e. alpha-linoleic

acid (ALA, 18:3n-3) and linoleic acid (LIN, 18:2n-6) by animals in amounts sufficient to meet their needs, and must, therefore, be acquired in the diet (Parrish 2009). Aquatic algae are the major source of pre-formed, long-chain (≥20 carbons) n-3 and n-6 PUFA (Arts et al. 2001; Gladyshev et al. 2009). Thus, as a main grazer of primary production in marine Arctic ecosystems, *C. hyperboreus* serves as both a source of energy and essential fatty acids for higher trophic levels (Kattner and Hagen 2009; Søreide et al. 2008). Knowledge concerning food quality obtained by *C. hyperboreus* during summer, with regard to essential fatty acid acquisition, is, therefore, important for identifying potential risks to *C. hyperboreus* populations, and, by extension, to the fish, birds, and mammals that ultimately depend on the fatty acids that *C. hyperboreus* harvests from the oceans.

Calanus hyperboreus feeds only during the productive spring and summer months when phytoplankton are available and synthesizes and stores large amounts of the long-chain MUFAs 20:1n-9 and 22:1n-11 in their wax esters (Graeve et al. 2005; Albers et al. 1996). *C. hyperboreus* enters diapause over the unproductive winter, during which time the copepods do not feed and rely entirely on store lipids to mature and reproduce (Conover and Siferd 1993; Falk-Petersen et al. 2009). Presumably, *C. hyperboreus* relies on both dietary PUFA and biosynthesized MUFA to survive the winter and successfully reproduce (Sargent and Falk-Petersen 1988). However, very few studies to date have explored how *C. hyperboreus* alters specific fatty acids between productive summer and unproductive winter months in ice-covered seas (but see Søreide et al. 2008; Lee 1974). Seasonal fatty acid data are especially needed for the Canadian Arctic because these areas are experiencing decreases in both the extent and duration of ice-cover, and consequently, earlier timing of maximum annual phytoplankton biomass (Kahru et al. 2011), which could affect *Calanus* populations (Søreide et al. 2010). To the best of our knowledge, however, no such data exist.

Quantifying dynamics in fatty acids over multiple seasons across consecutive years could provide important information on the seasonal lipid strategy of *C. hyperboreus*, including identifying which lipids are likely important for their survival. These findings could become important for monitoring how longer open-water periods and earlier phytoplankton growth influence the quality and quantity of lipids accumulated by *C. hyperboreus* annually. Further, it is imperative to identify how *C. hyperboreus* fatty acid profiles change over time (i.e. with seasons and years), because this information contributes important baseline data for future studies focused on the feeding ecology of higher trophic level organisms (Brett et al. 2009). Here we quantify fatty acid profiles of *C. hyperboreus* from Cumberland Sound, Baffin Island, Canada, during summer (i.e. August, open-water) and winter (i.e. April, ice-cover) over two successive years. We suggest that such information can eventually be used to better assess and monitor the cumulative effects of annual variability in physical forcing variables (temperature, light, and nutrients) on copepods and their consumers in the context of climate change.

Materials and methods

Study site

Copepod sampling was conducted as part of a larger study in Cumberland Sound and occurred within 30 km southwest (65°55′02′′N, 66°27′30′′W) and 30 km northwest (66°12′41″N, 66°35′35′′W) of the mouth of Pangnirtung Fjord (66°4′43′′, 65°57′45′′W, Fig. 1). The southeast coast of Baffin Island is influenced by both Arctic (Baffin Island Current) and Atlantic water masses (Greenland Current; Dunbar 1951), and consequently, the fauna of Cumberland Sound is of both Arctic and Atlantic origin (Aitken and Gilbert 1989). Cumberland Sound is typically ice-covered from November until approximately June. Temperatures in Cumberland Sound typically exceed 3°C in surface waters during summer (Mathias and Keast 1996), but decline to −1.8°C in winter, when the entire water column can reach temperatures near 0°C (Simonsen and Treble 2003). Details on the progression of summer phytoplankton growth do not exist for Cumberland Sound, but in Frobisher Bay, a fjord also on the southeast coast of Baffin Island and ~3° south of Cumberland Sound, primary productivity is typically highest in July and August, with sharp declines in September (Grainger 1971).

Ice coverage and chlorophyll *a*

Satellite data were accessed through the National Oceanographic Atmospheric Administration' Environmental Research Division' Data Access Program to determine the approximate dates of ice breakup (dataset title: Ice Coverage, Aqua AMSR-E, Global (1 Day Composite), Cavalieri et al. 2004, updated daily) and maximum surface chlorophyll *a* (dataset title: Chlorophyll a, Aqua MODIS, NPP, Global, Science Quality (8 Day Composite), O'eilly et al. 2000) in Cumberland Sound during the summers of 2007 and 2008 (Fig. 2). Satellite ice coverage data are daily averages, and chlorophyll *a* data are 8 days averages.

Copepod sampling

Calanus hyperboreus were collected during four sampling trips: during open-water in August 21–27, 2007 and August 10–15, 2008 and during ice-cover in April 10–11, 2008 and April 4–8, 2009. Previous researchers working

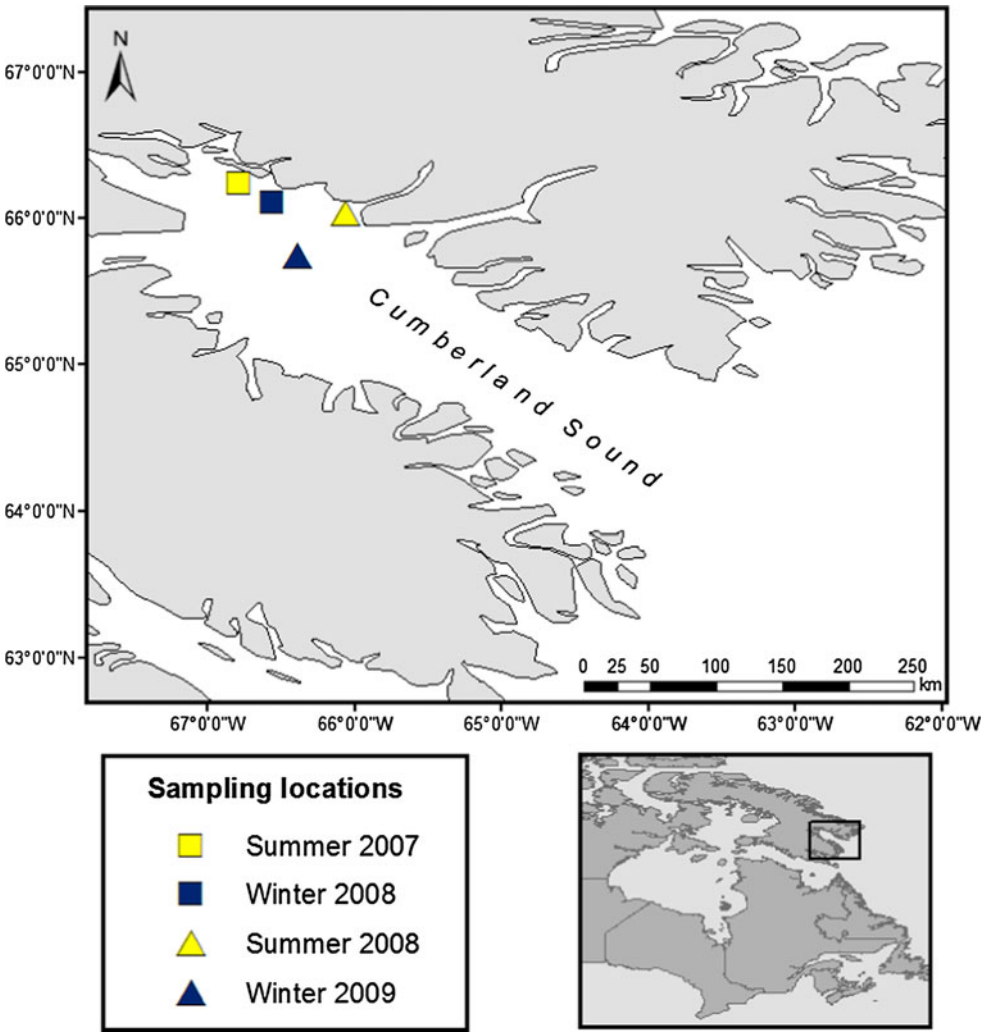

Fig. 1 *Calanus hyperboreus* sampling locations during summer (open-water, August) 2007 and 2008 and winter (ice-cover, April) 2008 and 2009 in Cumberland Sound, Baffin Island, Nunavut, Canada

in southeastern Baffin Island waters (i.e. Frobisher Bay) have referred to winter as occurring in December–March, spring from April–June and summer from July to August (Hsiao 1988, 1992). These designations are somewhat arbitrary, but are useful for referring to the general onset of ice algae (late spring) and phytoplankton production (summer) in this part of the world, with winter referring to a time of low water column primary production (Hsiao 1988) and phytoplankton cell biomass (Hsiao 1992). Considering a turnover time of 11 days for fatty acids in *C. hyperboreus* (Graeve et al. 2005), our April samples reflect activity occurring in late March, and these samples will, hereafter, be referred to as 'winter'. August samples reflect activity in mid-early August and will, hereafter, be referred to as 'summer'. The rationale for our sampling times was to capture the signature of *C. hyperboreus* after they incorporated the signature of summer phytoplankton growth and after the winter low primary production period.

All *C. hyperboreus* were collected using a 243-µm plankton net (Wildlife Supply Company®, Buffalo, New York) by performing both surface horizontal tows and vertical hauls in the summer, and vertical hauls through holes cut in the sea ice during winter. The maximum depth of sampling sites was ~400 m, and vertical hauls were conducted down to near-bottom depth. For all samples, the contents of each plankton tow were first rinsed into buckets filled with seawater. The samples were then poured through a 2-mm sieve fitted on top of a 0.5-mm sieve (both Fieldmaster®). Individuals were gently removed from the sieves using tweezers. Approximately 10 *C. hyperboreus* were pooled for each fatty acid sample, placed in cryogenic vials immediately frozen at −80°C in liquid nitrogen, and kept at −80°C until analysis. *Calanus hyperboreus* samples consisted of adult females (AF), and stage IV and V copepodites based on prosome length (Hirche et al. 1994) measured on type specimens. One exception is the two samples from April 2009 that consisted entirely of AF.

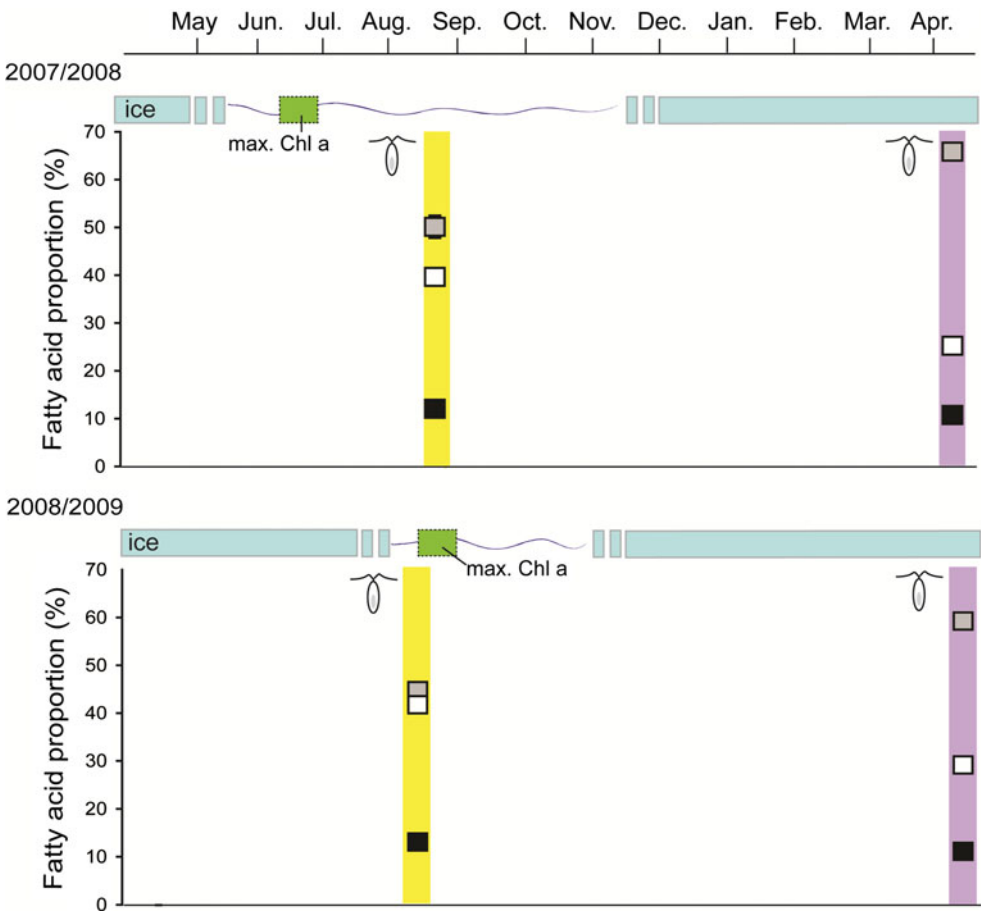

Fig. 2 Mean and standard deviation of relative proportions (fatty acid ∑fatty acids^{-1}, expressed as %) of *Calanus hyperboreus* monounsaturated fatty acids (∑MUFA: *gray symbols*), polyunsaturated fatty acids (∑PUFA: *white symbols*), and saturated fatty acids (∑SAFA: *black symbols*) over four sampling events (highlighted) in Cumberland Sound, Baffin Island, Nunavut. Timing of ice-cover and maximum surface chlorophyll *a* in Cumberland Sound obtained from satellite data is shown from May 2007 to April 2009

Fatty acid analysis

*Calanus hyperboreus s*amples were freeze-dried (48 h) and weighed to the nearest microgram (Sartorious ME5 microbalance). Lipids were extracted from each sample (dry weight of samples: range = 12.11–44.33 mg, mean ± SD = 34.79 ± 9.02 mg) by homogenizing in 2 mL of 2:1 (v/v) chloroform/methanol (C:M) (Folch et al. 1957). The lipid extract was adjusted to 8 mL with 2:1 C:M, 1.6 mL of a 0.9% NaCl in water solution was added, the phases were mixed and centrifuged (2,000 rpm at 4°C) and the upper aqueous layer was removed. The solvent layer was evaporated under nitrogen gas redissolved in 2 mL of 2:1 C:M, and percent total lipid (on a dry weight tissue basis) was determined gravimetrically. Fatty acid methyl esters were generated by adding sulfuric acid in methanol (1:100 mixture) to the vials, flushing the headspace with nitrogen and incubating (16 h) at 50°C in a water bath. After the samples cooled, potassium hydrogen carbonate, isohexane:diethyl ether (1:1), and butylated hydroxy toluene (0.01%) were added, and the vials were vortexed and centrifuged. The upper organic layer was transferred to another centrifuge tube; isohexane/diethyl ether (1:1) was added to the original tube, which was then shaken, vortexed, and centrifuged. FAME were evaporated under nitrogen, dissolved in hexane, transferred to amber glass GC vials, and separated using a Hewlett Packard 6890 GC (splitless injection, column = Supelco (SP-2560 column) 100 m × 0.25 mm ID × 0.20 µm thick film). Fatty acids were identified using a 37-component fatty acid standard (Supelco 47885-U) added with methyl stearidonate (Fluka, 43959), 13-eicosenoic acid methyl ester (Sigma E3512), 9-eicosenoic acid methyl ester (Indofine Chemical, 20-2001-1), 16-docosatetraenoic acid methyl ester (Sigma D3534), and 19-docosapentaenoic acid methyl ester (Supelco, 47563-U). Identification of 11-docosenoic acid methyl was accomplished via a Triple Quadrupole GC/MS (Agilent 7890A with Agilent 7000 mass detector) and confirmed by comparing the mass spectrum to the American Oil Chemists' Society Lipid Library (http://lipidlibrary.aocs.org/index.html). In the present study, 'SAFA' is used to indicate the sum of all fatty acids with zero double bonds, 'MUFA' indicates the sum of all fatty acids with one double bond, and 'PUFA' indicates the sum of all fatty acids with ≥2 double bonds.

Data analysis

Calanus hyperboreus fatty acids were expressed as both µg fatty acid mg dry tissue^{-1} (abbreviated here as µg mg^{-1})

and relative proportions (individual fatty acid ∑ fatty acids^{-1}, expressed as a %). Statistical analyses were performed primarily on proportional data, with the exception of analysis of variance (ANOVA) and Tukey's post hoc tests performed on total fatty acids (∑μg fatty acids mg^{-1}) and unsaturation index (∑(μg fatty acid mg^{-1} × number of double bonds)). The 'summary' fatty acid proportions (i.e. ∑n-3 and ∑n-6 PUFAs, ∑SAFA, ∑MUFA, and ∑PUFA), and % lipid were also compared among sampling dates via ANOVA and Tukey's post hoc tests. Principal component analysis (PCA) was used to investigate seasonal patterns in individual *C. hyperboreus* fatty acids. Data were standardized to a mean of zero and unit variance prior to their inclusion in the PCAs, and fatty acids that had unscaled weights (i.e. scaling = 0) ≥0.3 (which corresponded to correlations/loadings >0.5) were considered influential to that principal component (McGarigal and Cushman 2000). The sample scores extracted for principal components 1 (PC1) and 2 (PC2) were compared among sampling dates using ANOVA and post hoc tests. The 'mixed' samples containing multiple stages (AF, CV, and CVI) and the AF samples from April 2009 were coded differently in the ANOVAs. Ten separate ANOVAs were performed, and *P* values were corrected accordingly using a sequential Bonferroni procedure (Holm 1979). Statistical analyses were performed in R (R Development Core Team 2010), and the package 'vegan' was used for PCA (Oksanen et al. 2010).

Results

Ice breakup occurred in late May of 2007 and in early August of 2008, and sampling was, therefore, conducted closer to the time of ice breakup in 2008 (Fig. 2). Maximum surface chlorophyll *a* based on satellite data was reported on June 30 of 2007 and August 24 of 2008 (Fig. 2, O'eilly et al. 2000). Ice began to reform in late November of 2007 and in early November of 2008 (Fig. 2, Cavalieri et al. 2004, updated daily).

Summer samples were dominated by high EPA, 16:1n-7, 22:1n-11, 20:1n-9, DHA and 16:0, whereas winter samples were dominated by high 16:1n-7, 20:1n-9, EPA, 22:1n-11, DHA and 18:1n-9, when expressed as both relative proportions (Table 1) and μg mg^{-1} (Table 2). Summer *C. hyperboreus* had significantly higher ∑n-3 s ($F_{4,14} = 21.64$, $P < 0.01$), ∑n-6 s ($F_{4,14} = 276.25$, $P < 0.005$), and ∑PUFAs ($F_{4,14} = 41.94$, $P < 0.006$), and unsaturation index ($F_{4,14} = 26.30$, $P < 0.007$), and significantly lower ∑MUFAs ($F_{4,14} = 25.54$, $P < 0.008$) than winter samples (Fig. 2). Total fatty acids (∑μg mg^{-1}, Table 2) were higher in summer than winter samples ($F_{4,14} = 18.13$, $P < 0.01$), although the difference between summer and winter 2008 was not significant ($P > 0.01$). Percent (%) lipid was also higher in summer samples (Table 1), but only differed significantly between summer 2008 and winter 2009 ($F_{4,14} = 4.21$, $P < 0.03$). ∑SAFA did not differ among sampling dates ($P > 0.05$). Winter AF samples had a lower unsaturation index and lower total fatty acids than winter mixed samples (Table 2), but these differences were not significant ($P > 0.05$).

The first three principal components extracted by the PCA of *C. hyperboreus* fatty acid proportions explained 70.3% of the variance in the data (Table 3). PC1 separated summer (positive scores) from winter *C. hyperboreus* (negative scores), due to positive loadings of LIN, 18:4n-3 and EPA in summer, and negative loadings of 16:1n-7, 20:1n-9 and 22:1n-9 in winter (Fig. 3). Sample scores extracted for PC1 were significantly higher in summer versus winter copepods ($F_{4,14} = 35.20$, $P < 0.006$) and did not differ between the winter mixed and AF samples ($P > 0.05$). Principal component 2 was characterized by negative loadings of 16:0 and positive loadings of ALA, 18:4n-3 and 22:1n-11 (Table 3), but PC2 scores did not differ among sampling dates ($P > 0.01$). 18:1n-7, ARA, and DHA did not load significantly on the first two PC axes extracted, reflecting their similar proportions among samples (Table 1). Average proportions of 18:1n-9 were higher in winter samples, although these fatty acids did not load significantly on the first two PC axes (Table 3).

Non-metric multidimensional scaling performed on the *C. hyperboreus* fatty acid proportions (Euclidean distances, dimensions = 2, stress = 0.06, results not shown) produced a similar ordination to the PCA, lending confidence to the above results. Furthermore, the μg mg^{-1} data generally supported results of the PCA and ANOVAs performed on proportions, because summer samples tended to have higher PUFA, including LIN, 18:4n-3, and EPA, and because 18:1n-7 was similar among sampling dates (Table 2). Similar to proportional data, winter samples (excluding AF) were also higher in μg mg^{-1} of 18:1n-9 (Table 2), but were not consistently higher in μg mg^{-1} of 16:1n-7, 20:1n-9, and 22:1n-9 versus summer *C. hyperboreus* (Table 2). Finally, there were slightly lower μg mg^{-1} values of ARA and DHA in winter versus summer samples (Table 2), whereas proportions were similar among sampling dates (Table 1).

Discussion

Between seasons, variability in fatty acid proportions (i.e. winter vs. summer) was greater than within-season variability (e.g. summer vs. summer) because the first PC axis completely separated summer from winter *C. hyperboreus*. The separation of summer samples on PC1 due to high proportions of LIN, 18:4n-3, and EPA, as well as high ∑n-3,

Table 1 Fatty acid proportions (fatty acid ∑fatty acids^{-1}, expressed as a %, mean ± SE) of *Calanus hyperboreus* sampled during summer (i.e. August) and winter (i.e. April) over 2 years in Cumberland Sound

Date	Summer 2007	Winter 2008	Summer 2008	Winter 2009	Winter 2009 ♀
n	5	2	5	5	2
16:0	5.6 ± 0.3	5 ± 0.2	6.1 ± 0.3	5.9 ± 0.5	4.1 ± 0.3
16:1n-7	16.6 ± 0.6	22.9 ± 0.5	17.3 ± 0.3	17.8 ± 0.3	20.5 ± 0.6
18:1n-9	2.4 ± 0.2	5.9 ± 2.1	3.9 ± 0.1	7.6 ± 1.8	4.8 ± 0.4
18:1n-7	2.3 ± 0.1	1.9 ± 0.3	1.4 ± 0	2.4 ± 0	2.3 ± 0.1
18:2n-6	3.9 ± 0.1	1.1 ± 0.5	3.5 ± 0.1	1.2 ± 0.1	1.6 ± 0.1
20:1n-9	10.5 ± 1.1	17.3 ± 1.3	11.3 ± 0.4	16.1 ± 1.4	15.1 ± 0.3
18:3n-3	1.2 ± 0.3	1.3 ± 0.5	0.9 ± 0.3	0.8 ± 0.3	0.3 ± 0
18:4n-3	5.4 ± 0.6	1.2 ± 0.2	1.5 ± 0.1	1.2 ± 0.2	1.7 ± 0.2
22:1n-11	14.5 ± 1.5	12.1 ± 0	8.7 ± 0.5	9.9 ± 0.6	9.8 ± 0.5
22:1n-9	1.8 ± 0.4	3.3 ± 0.7	1.6 ± 0.1	2.2 ± 0.3	5.2 ± 0.1
20:4n-6	0.2 ± 0	0.1 ± 0	0.2 ± 0	0.2 ± 0	0.3 ± 0
20:5n-3	16.9 ± 1	10.7 ± 0.7	20.8 ± 0.3	12.6 ± 0.5	13.8 ± 0.1
22:5n-3	1 ± 0.1	0.4 ± 0.1	0.7 ± 0	0.5 ± 0	1 ± 0.1
22:6n-3	9.3 ± 0.3	8.4 ± 0.3	8.9 ± 0.4	10.5 ± 0.4	9.4 ± 0
∑n-3	34.1 ± 1.2	22.5 ± 0.4	33.2 ± 0.6	26.1 ± 1	26.4 ± 0.2
∑n-6	4.9 ± 0.1	2.3 ± 0.6	8.6 ± 0.1	2.6 ± 0.1	3.4 ± 0.1
∑SAFA	11.8 ± 1.2	10.6 ± 0.7	13.2 ± 0.7	13.4 ± 1.3	9 ± 0.3
∑MUFA	49.2 ± 2.3	64.7 ± 0.9	44.9 ± 0.7	57.8 ± 0.7	61.1 ± 0
∑PUFA	38.9 ± 1.2	24.8 ± 0.2	41.9 ± 0.5	28.8 ± 1.2	29.8 ± 0.3
% lipid	33.7 ± 2.0	29.3 ± 4.5	36.0 ± 1.3	27.2 ± 1.5	27.4 ± 3.0

Percent (%) lipid: mass of lipid dry weight of sample^{-1}

Each individual sample (number of samples = '*n*') was comprised of ca. 10 individuals of copepodite stages CIV, CV, and adult females, except for the samples from winter 2009 marked with '♀' that consisted entirely of adult females

Table 2 Mean ± 1SE µg fatty acid mg $^{-1}$ dry tissue of *Calanus hyperboreus* collected in Cumberland Sound during summer (i.e. August) and winter (i.e. April) of two consecutive years

Date	Summer 2007	Winter 2008	Summer 2008	Winter 2009	Winter 2009 ♀
n	5	2	5	5	2
16:0	9.3 ± 0.8	7.1 ± 1	12.4 ± 0.4	7 ± 0.6	4.4 ± 0.2
16:1n-7	27.7 ± 2	33 ± 4.9	35.2 ± 1.4	21.2 ± 1.4	21.8 ± 3.1
18:1n-9	4 ± 0.4	9 ± 4.5	8 ± 0.3	9.2 ± 2.5	5.2 ± 1
18:1n-7	3.7 ± 0.2	2.8 ± 0.8	2.8 ± 0.1	2.8 ± 0.1	2.5 ± 0.2
18:2n-6	6.6 ± 0.5	1.7 ± 0.9	7.1 ± 0.3	1.4 ± 0.2	1.7 ± 0.2
20:1n-9	17.2 ± 1.4	24.6 ± 2.3	23.1 ± 1.4	19 ± 1.8	16 ± 1.5
18:3n-3	1.8 ± 0.5	2 ± 1.1	2 ± 0.8	0.9 ± 0.4	0.4 ± 0
18:4n-3	9.2 ± 1.4	1.8 ± 0.5	3.2 ± 0.2	1.5 ± 0.2	1.9 ± 0.4
22:1n-11	23.8 ± 2	17.5 ± 2.9	17.9 ± 1.6	11.7 ± 0.9	10.4 ± 0.7
22:1n-9	2.8 ± 0.6	4.6 ± 0.1	3.2 ± 0.3	2.6 ± 0.3	5.5 ± 0.5
20:4n-6	0.4 ± 0.1	0.2 ± 0.1	0.4 ± 0	0.3 ± 0	0.3 ± 0
20:5n-3	28.3 ± 2.7	15.3 ± 1.6	42.4 ± 1.7	15 ± 1.2	14.7 ± 1.8
22:5n-3	1.6 ± 0.1	0.6 ± 0	1.5 ± 0.1	0.6 ± 0.1	1 ± 0.1
22:6n-3	15.4 ± 0.5	12 ± 1.6	18 ± 0.6	12.4 ± 0.5	10 ± 1.1
∑n-3	56.7 ± 4.2	32.3 ± 4.9	67.8 ± 2.9	30.9 ± 2.1	28.1 ± 3.4
∑n-6	8.1 ± 0.5	3.4 ± 1.3	17.5 ± 0.8	3.1 ± 0.3	3.6 ± 0.6
∑SAFA	19.8 ± 2.4	15.4 ± 3.5	26.8 ± 1.2	15.8 ± 1.6	9.6 ± 0.7
∑MUFA	81.2 ± 3.5	93 ± 14.6	91.7 ± 4.3	68.6 ± 3.8	65 ± 7.3
∑PUFA	64.8 ± 4.6	35.8 ± 6.4	85.6 ± 3.6	34.2 ± 2.4	31.7 ± 3.9
UI	385	268	478	239	221
Total FA	165.8 ± 7.9	144.2 ± 24.5	204.1 ± 7.8	118.6 ± 6	106.4 ± 12

Unsaturation index (UI): ∑(µg fatty acid mg $^{-1}$ × number of double bonds)

Individual samples (total number of samples = '*n*') were comprised of ca. 10 individuals of copepodite stages CIV, CV, and adult females, except for the samples from winter 2009 marked with '♀', which consisted entirely of adult females

Table 3 Eigenvalues, proportion explained and unscaled weights of each fatty acid variable on the first three principal components (PC) of a PCA performed on *Calanus hyperboreus* fatty acid proportions

Principal components	PC1	PC2	PC3
Eigenvalue	4.57	2.52	2.06
Cumulative proportion	0.35	0.55	0.70
Fatty acid			
16:0	0.2	−0.3	0.0
16:1n-7	−0.3	−0.1	0.2
18:1n-7	−0.2	0.2	−0.6
18:1n-9	−0.2	−0.2	−0.2
18:2n-6	0.4	0.2	0.1
20:1n-9	−0.4	0.0	0.1
18:3n-3	0.0	0.4	0.1
18:4n-3	0.3	0.3	−0.3
22:1n-11	0.0	0.6	−0.1
22:1n-9	−0.4	0.2	0.1
20:4n-6	0.2	−0.2	−0.5
20:5n-3	0.4	−0.2	0.2
22:6n-3	−0.1	−0.2	−0.46

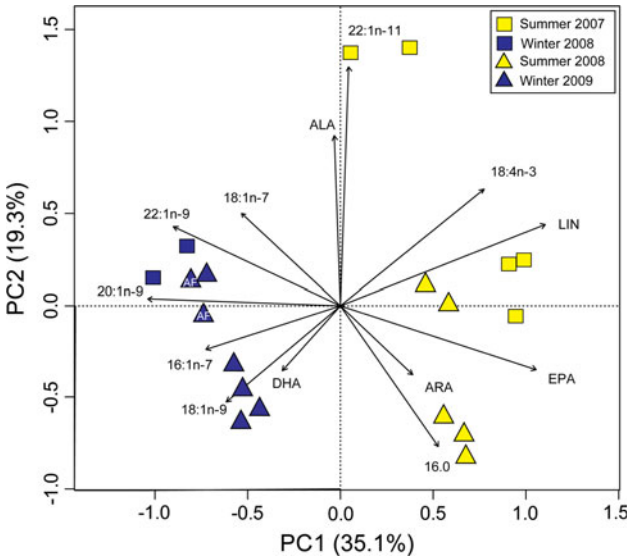

Fig. 3 Biplot of the component scores (*symbols*) and fatty acid variable loadings (*vectors*) on the first two principal components from a PCA performed on fatty acid proportions (%) in *Calanus hyperboreus*. Both scores and variables are scaled by the square root of the eigenvalues (i.e. scaling = 3). All samples consisted of pooled copepodite stage VI, V, and adult females except for two winter 2009 samples that consisted entirely of adult females (marked with 'AF')

∑n-6, ∑PUFA, and unsaturation index, is consistent with phytoplankton consumption and agrees with previous reports (Lee 1974; Søreide et al. 2008) that summer *C. hyperboreus* have higher EPA and 18 PUFAs relative to winter samples. Fatty acid data for phytoplankton and other potential food sources (e.g. bacteria) are needed to differentiate the contribution of specific taxa to the diet of summer *C. hyperboreus*. However, phytoplankton were available in Cumberland Sound during our field operations based on chlorophyll *a* (integrated over 0–40 m) measured at the *C. hyperboreus* sampling locations (67.6 mg m^{-2} on August 14, 2007, B. McMeans, unpublished data; 53.4 mg m^{-2} on July 31, 2008, J. Brush, unpublished data), supporting the contention that summer fatty acid profiles reflected consumption of phytoplankton.

The *C. hyperboreus* fatty acid data presented here are, to the best of our knowledge, the first for eastern Canadian waters outside of the NOW (Stevens et al. 2004a, b). Both *C. hyperboreus* from Cumberland Sound and from the NOW during autumn (Stevens et al. 2004b) had 16:1n7, 20:1n-9, 22:1n-11, and EPA in the highest proportions. Summer 2007 Cumberland Sound samples had the most similar proportions of the above fatty acids (although 22:1n-11 was higher) relative to conspecifics from NOW station 54a (Stevens et al. 2004b), where *C. hyperboreus* were concluded to be feeding on ciliates, flagellates, and/or dinoflagelles. On the other hand, summer 2008 Cumberland Sound samples were more similar to those from NOW station 68 (Stevens et al. 2004b), where *C. hyperboreus* were feeding on diatoms (Stevens et al. 2004b). It is prudent to note here that comparisons among studies that analyzed different lipid fractions are acceptable because the total fatty acid fraction (as reported here) and wax ester fraction (e.g. Stevens et al. 2004b) have similar proportions of most fatty acids (Graeve et al. 1994). One exception is 16:1n-7, which is lower in total fatty acids versus wax esters (Graeve et al. 1994), indicating that our 16:1n-7 values are lower than would be expected if the wax ester fraction was analyzed. Zooplankton fatty acids respond rapidly to changes in the composition and/or availability of phytoplankton (Lee et al. 1972; Stevens et al. 2004b), which likely explains the observed differences between summer 2007 and 2008 samples reported here. This explanation is especially likely because we sampled closer to the time of ice breakup in summer 2008 (Fig. 2). There is a need for future efforts to better categorize the progression of the phytoplankton bloom in Cumberland Sound, and the associated changes in the fatty acid profile of herbivorous zooplankton.

Similar to results from Cumberland Sound and the NOW, *C. hyperboreus* sampled during June and July in the Fram Strait also had EPA, 16:1n-7, 20:1n-9, 22:1n-11, and DHA in the highest proportions (Kattner et al. 1989). One difference is that 18:4n3 was a major fatty acid in *C. hyperboreus* from the latter study, contributing almost 30% to copepods in areas where *Phaeocystis pouchetii* was abundant (Kattner et al. 1989). This fatty acid only contributed a maximum of 5.4% to Cumberland Sound samples (summer 2007, Table 1) and 9.7% to surface NOW *C. hyperboreus*

(Stevens et al. 2004b), which supports the suggestion that large-scale differences in fatty acids can exist between the Canadian and Norwegian Arctic (Sargent and Falk-Petersen 1988). These differences likely reflect different compositions of algal species (Sargent and Falk-Petersen 1988), which warrants further investigation.

Few studies have reported fatty acids for *C. hyperboreus* during winter months, but both Lee (1974) and Søreide et al. (2008) observed that proportions of fatty acids like LIN, 18:4n-3, and EPA decreased and C18 and C22 MUFA increased in *C. hyperboreus*' wax esters during the winter. It is unknown whether Cumberland Sound *C. hyperboreus* were in diapause at depth or had recently ascended to surface waters when sampled in winter 2008 and 2009. However, lower ∑PUFA, unsaturation index, and % lipid of winter versus summer samples provide evidence that these individuals were not actively feeding on ice algae or phytoplankton when sampled (which both have high PUFA, Søreide et al. 2008). A previous report from the Beaufort Sea showed that *C. hyperboreus* were feeding at a very low rate (0.2 μg C $^{-ind\ -h}$, perhaps on microzooplankton) in mid-April prior to spring phytoplankton growth (Seuthe et al. 2007). Further, vertical ascent in *C. hyperboreus* is related to the timing of primary productivity (Hirche and Niehoff 1996), and active accumulation of lipid likely does not start until phytoplankton growth begins. Late March and early April are generally a time of low water column chlorophyll *a* and primary productivity in Frobisher Bay, when sea ice is still ~1–1.5-m thick (Grainger 1971). Sea ice thickness was ~0.8 and 1.3 m at our sampling locations in Cumberland Sound during winter 2008 and 2009, respectively (snow thickness ~15–30 cm), and we, therefore, assume that water column productivity was low, and subsequently that *C. hyperboreus* were not actively feeding. The observed fatty acid profiles of winter samples support this assumption and, therefore, reflect the overwintering strategy of *C. hyperboreus* with regard to lipid metabolism. Additional work is needed in Cumberland Sound to identify the depth of overwintering, the timing of vertical ascent to surface waters, and the commencement of feeding by *C. hyperboreus*.

The comparison between summer and winter fatty acids in the present study supports previous perceptions about lipid dynamics in *C. hyperboreus* during winter months. First, *C. hyperboreus* is known to incorporate and retain dietary PUFA in their phospholipids to maintain membrane function (Scott et al. 2002). For example, proportions of EPA, ARA, and DHA in *C. hyperboreus* phospholipids can remain similar all year (Lee 1974). Therefore, observed values of EPA, ARA, and DHA in winter *C. hyperboreus* from Cumberland Sound could reflect the portions that were retained in the phospholipids. Previous work in freshwater systems has also shown that zooplankton selectively retain certain essential fatty acids (Kainz et al. 2004) and conserve ARA and EPA during starvation (Schlechtriem et al. 2006).

Second, lower observed proportions and μg mg^{-1} of LIN, 18:4n-3, EPA in winter samples agrees with reports that *C. hyperboreus* catabolizes a portion of dietary PUFA from their wax esters to meet energetic demands during the winter (Lee 1974), and during other times of little to no feeding (Kattner et al. 1989). The energetic cost of maintaining bodily functions during diapause is thought to be low, with molting and gonad formation the major causes of wax ester depletion during winter in *Calanus* spp. (Hopkins et al. 1984; Sargent and Falk-Petersen 1988). In high Canadian Arctic (i.e. Resolute Bay) *C. hyperboreus*, stage IV is the dominant overwintering stage, stage V molt all winter to adult males and females (some of which will wait to reproduce until the following winter), and egg production and release in AF occurs from March to mid-May (Conover and Siferd 1993). Eggs were still observed in the oviducts of AF during both winter 2008 and 2009 sampling operations (i.e. egg release was not complete, B. McMeans, personal observation). Therefore, lower LIN, 18:4n-3, and EPA in winter versus summer Cumberland Sound *C. hyperboreus* likely reflects the selective catabolization of these PUFA to fuel maturation in stage V copepodites and egg formation in AF.

Our seasonal comparison of fatty acids also provided two findings regarding the potential role of MUFAs during the winter that have not been thoroughly discussed in the literature. First, proportions of 16:1n-7, 18:1n-7, 20:1n-9, 22:1n-9, and 22:1n-11 were not consistently lower in winter versus summer Cumberland Sound samples, which agrees with previous reports for *C. hyperboreus* from the Norwegian Arctic (Søreide et al. 2008). This result is notable because all of these MUFA are found predominantly in storage molecules (wax esters and TAG, Albers et al. 1996) and should have decreased in winter copepods if they serve as energy stores to fuel reproductive process as presumed (e.g. for C20 and C22 MUFA, Sargent and Falk-Petersen 1988). AF from Cumberland Sound did have lower 20:1n-9 and 22:1n-11 than mixed winter samples on a μg mg^{-1} basis (Table 2), supporting this presumption. Further, although C20 and C22 MUFA are not a major component of *Calanus* eggs (Sargent and Falk-Petersen 1988), lipids in AF are at their lowest once egg release is complete (Lee et al. 1972), and proportions of the above MUFA may be expected to decrease further in winter AF to fuel egg release. Analysis of separate stages of *C. hyperboreus* would have provided more insight into the role of these MUFA in specific overwintering and reproductive processes. However, because AF in the present study had already formed eggs (although we cannot assume that egg formation was complete), it appears that MUFA are not the major fuel for overwintering, maturation, or egg formation in *C. hyperboreus*.

A second finding from the present study that merits discussion is the higher average proportions of 18:1n-9 in winter *C. hyperboreus* versus summer, although the variability in winter samples was high (Table 1). Average μg mg^{-1} values of 18:1n-9 were also higher in winter mixed samples (but not in AF) versus summer (Table 2), and previous researchers have also reported higher 18:1n-9 in winter *C. hyperboreus* (Søreide et al. 2008; Lee 1974) and *C. finmarchicus* (Stage V and AF, Falk-Petersen et al. 1987). Increasing 18:1n-9 in winter could be accomplished if *C. hyperboreus* were desaturating 18:0 to 18:1n-9 (Kattner and Hagen 1995; Sargent and Falk-Petersen 1988), although the reason *C. hyperboreus* would increase, or at least maintain, proportions of this MUFA from summer to late winter is unknown. Perhaps there is a biochemical role of 18:1n-9 in winter *C. hyperboreus* in addition to serving as an energy source. For example, the retention of ARA and DHA in winter-sampled *C. hyperboreus* from the present study, coupled with the increase in 18:1n-9, provide field evidence to support recent laboratory observations that fishes and mammals alter the combinations of specific MUFA-PUFA pairings in the *sn-1* and *sn-2* positions of phospholipids in response to cold exposure (Arts and Kohler 2009). Additionally, the combination of PUFA with cis Δ9 MUFA in the sn-1 position of carp liver phospholipids was found to have the greatest effect on membrane physical properties (Fodor et al. 1995). However, further experimental work is required to validate this observation for *C. hyperboreus*.

Implications for monitoring *Calanus hyperboreus* populations

Ice-cover duration has decreased in the Canadian Arctic (Kahru et al. 2011), and a discussion of the potential effects of changing ice conditions on *C. hyperboreus* populations is warranted. Earlier ice breakup is anticipated to cause a mismatch between the emergence of first-feeding *C. glacialis* naupulii and the timing of algae blooms (Søreide et al. 2010). Changing ice-cover duration would likely affect *C. hyperboreus* differently, however, because female *C. hyperboreus* do not need access to food for successful reproduction during the winter (Conover 1967). However, nauplii might rely on ice algae in late winter/early spring for their first feeding (at stage NIII–NVI) (Conover and Siferd 1993). No study has addressed the effect of ice algae duration on *C. hyperboreus* nauplii survival, but it seems reasonable that earlier ice breakup could result in a shorter duration for nauplii to exploit ice algae. Of course, earlier ice breakup could also result in earlier phytoplankton productivity, which could provide a food source for first-feeding *C. hyperboreus* nauplii.

The effects of earlier ice breakup on *C. hyperboreus* populations are unclear, but *C. hyperboreus* is considered highly adapted to interannual variability in resource availability (Falk-Petersen et al. 2009) due to plasticity in the timing of their reproductive cycle (Conover and Siferd 1993). However, the large amounts of lipid accumulated by *Calanus* species are related to the short and variable duration of their food supply in polar seas (Albers et al. 1996). Less ice-cover and longer periods of open-water could, therefore, influence the quantity of lipids accumulated by *C. hyperboreus* annually. Further, food quality (i.e. PUFA content) can affect the survival of *C. glacialis* naupulii (Daase et al. 2011). Thus, any change in the quantity or quality of lipids associated with changing ice conditions could affect *C. hyperboreus* populations and the amount of lipids made available to upper trophic levels. It is, therefore, important to monitor how the fatty acid profile of *C. hyperboreus* changes over time.

Data presented here will be useful for monitoring the acquisition of fatty acids by *C. hyperboreus* in the summer, and utilization in the winter. We recommend summer *C. hyperboreus* monitoring to focus on changes in PUFA like ARA, EPA, and DHA because *C. hyperboreus* fatty acids vary with phytoplankton availability and composition (Stevens et al. 2004b; Kattner et al. 1989) and should, therefore, reflect changes in phytoplankton quality. Monitoring of winter *C. hyperboreus* fatty acids would provide insight into changes in lipid strategy (i.e. which fatty acids are catabolized, conserved, and/or biosynthesized) and could reflect underlying changes in ability to acquire lipids in the summer. Winter monitoring should focus on PUFA, because they are the major fuel for overwintering and reproduction, based on our results. Additionally, the unsaturation index (Treen et al. 1992) could be useful for monitoring overall changes in the degree of fatty acid unsaturation over time and should be a highly sensitive indicator of change because it is based on μg mg^{-1} fatty acid values. Changes in 18:1n9 and long-chain MUFA should also be noted because, based on the observation that they are not consistently depleted in winter *C. hyperboreus*, they could be important for winter survival.

In conclusion, *C. hyperboreus* from Cumberland Sound exhibited similar seasonal patterns in fatty acids over 2 years, which provides evidence that specific fatty acids are consistently catabolized (e.g. EPA), conserved (e.g. DHA), and maintained (or increased) (e.g. 18:1n-9) between summer and winter. Our sampling was coarse, at only two times annually, but still revealed that PUFA are selectively catabolized to a greater degree than biosynthesized C20 and C22 MUFA to fuel maturation and egg formation during winter. The observation that *C. hyperboreus* maintains or increases proportions of certain MUFA during the winter (this study; Lee 1974; Søreide et al. 2008)

suggests that these fatty acids have some purpose for successful overwintering or reproduction and indicates that the role of MUFA in winter *C. hyperboreus* should be further explored. The data presented here are novel for this part of the world and are important for monitoring short- and long-term changes in *C. hyperboreus*, as well as other zooplankton taxa and their higher trophic level consumers in Arctic ecosystems. Additional work combining fatty acids with other dietary metrics (e.g. stable isotopes, sterols) collected over a more frequent (e.g. monthly) and prolonged (i.e. years) time scale, combined with data for the composition, abundance, and fatty acids for phytoplankton, would greatly improve our understanding of the mechanisms governing *C. hyperboreus* fatty acids, and how this might relate to changes in environmental conditions.

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Conflict of interest The authors declare that they have no conflict of interest.

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