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ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis

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Abstract Global warming and the loss of sea ice threaten to alter patterns of productivity in arctic marine ecosystems because of a likely decline in primary productivity by sea ice algae. Estimates of the contribution of ice algae to total primary production range widely, from just 3 to >50%, and the importance of ice algae to higher trophic levels remains unknown. To help answer this question, we investigated a novel approach to food web studies by combining the two established methods of stable isotope analysis and fatty acid (FA) analysis—we determined the C isotopic composition of individual diatom FA and traced these biomarkers in consumers. Samples were collected near Barrow, Alaska and included ice algae, pelagic phytoplankton, zooplankton, fish, seabirds, pinnipeds and cetaceans. Ice algae and pelagic phytoplankton had distinctive overall FA signatures and clear differences in δ^{13}C for two specific diatom FA biomarkers: 16:4n-1 (-24.0 ± 2.4 and -30.7 ± 0.8‰, respectively) and 20:5n-3 (-18.3 ± 2.0 and -26.9 ± 0.7‰, respectively). Nearly all δ^{13}C values of these two FA in consumers fell between the two stable isotopic end members. A mass balance equation indicated that FA material derived from ice algae, compared to pelagic diatoms, averaged 71% (44–107%) in consumers based on δ^{13}C values of 16:4n-1, but only 24% (0–61%) based on 20:5n-3. Our estimates derived from 16:4n-1, which is produced only by diatoms, probably best represented the contribution of ice algae relative to pelagic diatoms. However, many types of algae produce 20:5n-3, so the lower value derived from it likely represented a more realistic estimate of the proportion of ice algae material relative to all other types of phytoplankton. These preliminary results demonstrate the potential value of compound-specific isotope analysis of marine lipids to trace C flow through marine food webs and provide a foundation for future work.

Keywords Pelagic phytoplankton · Diatoms · Trophic linkages · Compound specific · Lipid

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Introduction

Arctic sea ice provides a physical habitat for a community of microalgae that are grazed upon by a variety of herbivorous zooplankton and thus serve as the base of an under-ice food web (Werner 1997; Gradinger 1999). The zooplankton in turn are fed upon by fishes, seabirds, seals and whales (Bradstreet 1980; Bradstreet and Cross 1982; Lowry et al. 1980a, b, 2004; Craig et al. 1982). However,

the contribution of sea ice algae, relative to that from pelagic phytoplankton, to the total primary productivity of arctic marine ecosystems is poorly known geographically and on a seasonal and annual basis. An understanding of that contribution is needed to assess the biological consequences of the rapid decrease in sea ice extent (Johannessen et al. 2004) and the anticipated reduction in ice algae production.

Estimates of the contribution of sea ice algae to total primary productivity in the Arctic vary widely due to a range of factors, including regional and seasonal differences in the amount of ice-free water, nutrient supply and light fields, and methodologies used by different investigators for calculating productivity. For instance, Gosselin et al. (1997) estimated that ice algae contributed on average 57% to the total primary production in the central Arctic Ocean, but $< 5\%$ in the central Chukchi Sea, whereas Parrish (1987) estimated annual production of ice algae in the offshore Chukchi Sea to be as much as 25% of total primary production. McRoy and Goering (1976) estimated that production by ice algae in the Bering Sea was between ~ 3 and 5% of the total for the inner and middle shelf. Even if all of these estimates are correct, we still do not know the proportional contribution of ice algae C to diets of higher trophic level organisms. Thus, we cannot yet achieve the goal of predicting the broader consequences to arctic food webs of a potential decline in ice algal production. To begin to address this issue, new tools and approaches for food web studies are required. Here, we used fatty acid (FA) biomarkers in combination with stable C isotope analyses to investigate the possibility of tracing C flow in an arctic marine food web and to provide a preliminary estimate of the importance of ice algae to higher trophic levels.

Marine FA have a variety of structures and, because of biochemical restrictions on the synthesis of FA in many marine predators, it is possible to recognize FA derived from their prey. Thus, FA are valuable as biomarkers of their source. Numerous studies have demonstrated the transfer of specific FA from prey to predator throughout marine food webs (e.g., St. John and Lund 1996; Auel et al. 2002). Recently, the entire array of FA present (i.e., FA signature) has been used to quantitatively estimate predator diets (Iverson et al. 2004, 2006; Cooper et al. 2005).

δ^{13}C values of the lipid-extracted total organic C (TOC) composing animal tissues are also frequently used in food web studies (e.g., Gannes et al. 1997; Post 2002). Much like FA, isotope signatures are transferred in largely predictable ways from diet to consumer. Where isotopically distinct dietary sources exist, it is possible to determine the relative contribution of different dietary items to a consumer. This can be achieved using mixing models of varying complexity (e.g., Post 2002; Phillips and Gregg 2003; Phillips et al. 2005). Hobson et al. (2002) used bulk stable isotope analysis to examine the proportions of ice algae and pelagic phytoplankton composing total primary production in both the eastern and western Arctic. Søreide et al. (2006) employed a similar approach with bulk stable isotopes to investigate the importance of ice algae versus phytoplankton to low trophic levels in the European Arctic. However, there are limitations to the bulk isotope approaches, including isotopic routing, where isotopes are incorporated differentially into various tissues and compounds (Gannes et al. 1997).

To avoid such limitations of isotopes and to capitalize on both approaches to study food webs, we coupled a qualitative analysis of FA biomarkers of microalgae with stable C isotopes of these individual FA (see Meier-Augenstein 2002 for a review of the technique) to indicate the likely sources of these compounds (i.e., ice algae vs. pelagic phytoplankton) in a number of species known to be associated with arctic pack ice for the entire year and which we expected to be most dependent on ice algae and most affected by its predicted decrease. The application of stable isotope analysis of individual FA to study C input from diatoms, which are responsible for the majority of the production by ice algae and pelagic phytoplankton, is particularly appropriate because they synthesize FA that are produced in limited amounts, or not at all, by other organisms. Most notably, diatoms are the major source of the FA 16:4n-1 and 20:5n-3 (see "Materials and methods" for explanation of FA naming system) in the Chukchi-Bering Sea. Although 20:5n-3 is also produced by other taxa of algae in the area, such as *Phaeocystis* sp., *Amphidinium* sp. and small prasinophytes (Viso and Marty 1993; Booth and Horner 1997; Tang et al. 2001; Sherr et al. 2003), 16:4n-1 has the advantage of being produced almost exclusively by diatoms (Viso and Marty 1993; Dunstan et al. 1994). When this FA is found in the blubber of a marine mammal, for example, we know that it was originally synthesized by diatoms and will preserve the δ^{13}C imparted by algae. Previous δ^{13}C analyses of TOC in ice algae and phytoplankton (Hobson et al. 2002) demonstrated a difference between these end members. We therefore hypothesized that this difference should be maintained at the compound-specific level (i.e., FA). By analyzing the δ^{13}C of these two FA and using a mixing model, we aimed to estimate the contribution of FA from ice algae relative to pelagic diatoms and other phytoplankton to higher trophic levels.

Materials and methods

Sample collection

Phytoplankton samples were collected over a 3-day period from 29 to 31 May 2002 off Barrow, Alaska. Ice algae,

composed mainly of the pennate diatom *Navicula* sp., were obtained from cores of sea ice. Sea water (3–5 L) from a depth of approximately 5 m under the ice was filtered to obtain pelagic phytoplankton, composed chiefly of the large centric diatom *Coscinodiscus* sp. These samples were then filtered through pre-combusted GF/C filters and treated with boiling salt water to deactivate lipolytic enzymes (Budge and Parrish 1999). Large zooplankton were removed with tweezers and the filters were stored in chloroform at −20°C until extraction. Copepods were collected on the same dates with nets (mesh < 200 μm) towed from the sea floor to the undersurface of the ice. Samples were concentrated by filtering through a 20-μm mesh and then separated manually using a microscope into general classes (i.e., harpacticoid and cyclopoid copepods). These were then collected on a GF/C filter and stored in chloroform. Sampling information including species, tissue and collection date is summarized in Table 1.

Five types of invertebrates, the euphausiid *Thysanoessa raschii* and the amphipods *Apherusa* sp., *Gammarus* sp., *Onisimus* sp. and *Acanthostepheia behringiensis*, were recovered from the stomachs of 16 arctic cod (*Boreogadus saida*) collected in early August 2002 near Barrow. Euphausiids and amphipods were separated to genus or species and frozen whole. Entire arctic cod, including stomach contents, from Barrow and nearby Cooper Island, 35 km southeast of Barrow, were collected in August 2002, frozen and homogenized prior to lipid extraction (see below). Cod from Barrow (13–16 cm; $n = 10$) were collected with hand lines, while those from Cooper Island (9–17 cm; $n = 15$) were taken from nests of adult black guillemots (*Cepphus grylle*) that had brought the fish to feed their chicks.

During the same period, synsacral fat samples (~100 mg) were collected from adult guillemots that had been killed by peregrine falcons (*Falco peregrinus*) and by horned puffins (*Fratercula corniculata*) that compete for nest sites. Blubber samples were collected from bearded and ringed seals (*Erignathus barbatus* and *Phoca hispida*, respectively) and bowhead whales (*Balaena mysticetus*) taken in the subsistence hunts in Barrow. Seals were sampled in July 2002, while whales were taken in both spring and fall 2002 (Table 1). Blubber samples included the full blubber depth for seals, and only the innermost layer for the whales.

Table 1 Sample information

Species	Tissue type	Collection date
Ice algae	Entire cells	29–31 May 2002
Phytoplankton	Entire cells	29–31 May 2002
Harpacticoid copepods	Whole body	29–31 May 2002
Cyclopoid copepods	Whole body	29–31 May 2002
Thysanoessa raschii	Whole body	August 2002
Apherusa sp.	Whole body	August 2002
Gammarus sp.	Whole body	August 2002
Onisimus sp.	Whole body	August 2002
Acanthostepheia behringiensis	Whole body	August 2002
Arctic cod (Barrow)	Whole body	August 2002
Arctic cod (Cooper I.)	Whole body	August 2002
Black guillemots	Adipose tissue	August 2002
Bowhead whales	Blubber	May and October 2002
Bearded seals	Blubber	July 2002
Ringed seals	Blubber	July 2002

Cooper I. Cooper Island

FA analyses

Lipids were extracted from all plankton types with a modified (Folch et al. 1957; Parrish 1999) method using chloroform and methanol, then transesterified to FA methyl esters (FAME) with anhydrous BF_3. Fish and blubber were also extracted with a modified Folch et al. (1957) method following Budge et al. (2006). FAME proportions were determined using gas chromatography (GC) according to Iverson et al. (2002) and Budge et al. (2006). Up to 65 FAME were routinely identified in all samples; however, we report here the proportions (weight percent of total FAME identified) of 14 selected FAME. The entire dataset is available upon request. Each FAME is described using the shorthand nomenclature of *A*:*B*n-*X*, where *A* represents the number of C atoms, *B* the number of double bonds and *X* the position of the double bond closest to the terminal methyl group. Individual FA proportions of replicate analyses were within 0.1%.

Compound-specific stable C isotope analyses of FA

FAME sub-samples were analyzed for C isotopes by routing the effluent from a GC through a combustion interface (Finnigan GC combustion III) to an isotope ratio mass spectrometer (IRMS) (Thermo Finnigan Delta^{plus} XL). FAME were separated using the same GC column and method as described above. FAME analyzed here differed from the FA present in the source material because of the addition of a methyl group derived from methanol used in transesterification. To correct for the contribution from this extra C and determine any kinetic isotope effects, we transesterified free FA (FFA) standards 20:0 and 22:0 with the same reagents described above. Prior to transesterification, the purity of the FFA was confirmed with thin layer chromatography and $\delta^{13}C$ values for FFA were determined using an elemental analyzer (EA) (Costech ECS4010) attached to the IRMS. The $\delta^{13}C$ of these FFA that had been

transesterified into their respective FAME were then measured using the GC-IRMS system described above. We could not perform this analysis on the FA actually studied here because 16:4n-1 is not commercially available and 20:5n-3 FFA is a liquid at room temperature and thus cannot be analyzed using the EA. As expected for a reaction that goes to completion (Rieley 1994), there was no evidence of a kinetic isotope effect associated with transesterification. We then calculated an average correction to apply to our FAME data (+0.59‰), based on the difference between the δ^{13}C values of the corresponding FFA and FAME. Pure C10 and C20 FAME (supplied by Indiana University Stable Isotope Reference Materials) were analyzed after every ten samples to establish the analytical precision of the GC-IRMS system. Analytical error (consisting of 1 SD of 31 analyses of the C10 and C20 standards interspersed during the samples run) was 0.3‰ for C10 and 0.2‰ for C20. We therefore conservatively estimated our analytical precision to be ≤0.3‰. A hexane blank was also run after every 12th sample. All δ^{13}C values are reported relative to Vienna Pee Dee Belemnite (VPDB) using standard δ notation.

Data analysis and display

A simple two-end member mixing model was used to determine the relative contribution of ice algae and pelagic phytoplankton to the two FA analyzed:

$$\delta^{13}C_{\text{consumer},k} = x_k\delta^{13}C_I + (1 - x_k)\delta^{13}C_{\text{P}}$$

where x_k is the proportion of ice algae C contribution to k, the FA of interest, either 16:4n-1 or 20:5n-3, $\delta^{13}C_{\text{I}}$ is the isotope ratio of C in the ice algae FA and $\delta^{13}C_{\text{P}}$ is the isotope ratio of C in the pelagic phytoplankton FA. To determine the contribution of ice algae to all FA in general in a consumer, the relative amounts of the FA in the ice algae and pelagic phytoplankton must be taken into account:

$$x_{\text{FA}} = \frac{x_k/\text{FA}_{k,I}}{\left[(x_k/\text{FA}_{k,I}) + \left((1 - x_k)/\text{FA}_{k,P}\right)\right]}$$

where x_{FA} is the proportional contribution of ice algae to all FA in a consumer, FA_I is the average proportion of the FA in ice algae and FA_P is the average proportion of the FA in pelagic phytoplankton FA. Ranges in the proportions were calculated using the variation in the δ^{13}C for the two end members.

To investigate the variation in FA composition among samples, Bray–Curtis similarity matrices were calculated on the FA dataset consisting of all FA present at proportions >0.1% and analysis of similarity (ANOSIM; Clarke and Green 1988) was performed using PRIMER 6 (Primer-E). Significant differences in FA profiles were identified using the global R-values and a similarity percentages routine (SIMPER) was used to determine FA contributing to the differences. To improve normality, FA data were transformed using an arcsine square root function (Budge et al. 2007).

Results

Nutrient analysis

From 29 to 30 May, the current was southerly and copepod samples were dominated by harpacticoids. Inorganic nutrient analyses of this water (analyzed in the Nutrient Laboratory of the Institute of Marine Science, University of Alaska Fairbanks) revealed a dissolved silicate content of 25.4 μM. On 31 May, the current switched to a northerly direction with a large influx of small cyclopoid copepods and a silicate content of 4.9 μM. This shift in silicate concentration reflected a change in source water from high-silicate Pacific water with an origin in the Bering Sea to low-silicate Arctic surface water with an Atlantic origin (Jones et al. 2003).

General FA compositions

The FA profiles of ice algal pennate diatoms and pelagic centric diatoms (Table 2) were significantly different (ANOSIM $R = 0.66$, $P < 0.001$), with 16:1n-7, 18:0, 18:1n-9 and 20:5n-3 primarily accounting for the differences (SIMPER with percent dissimilarities for the FA of 13.1, 9.4, 6.4 and 5.7%, respectively). Differences ($P < 0.005$) were also apparent in the levels of 16:4n-1, 18:1n-7 and 22:6n-3 (Table 2). The ratio of FA with 16 versus 18 C atoms (ΣC16/ΣC18) was 3 times greater in ice algae. FA proportions were quite similar between the primary planktonic grazers (harpacticoid and cyclopoid copepods), but differed in both of them from those of the two diatoms. Much lower levels of 16:1n-7 were observed in the copepods, with larger amounts of 18:1n-7, 20:1n-7, 22:1n-7, 20:5n-3 and 22:6n-3. This likely represented biochemical manipulation of the dietary FA in copepods, with contribution from de novo synthesis and selective deposition of polyunsaturated FA.

Few consistencies were obvious in the amphipods, likely reflecting their variable diets. *Acanthostepheia behringiens* shared a characteristic of the copepods—elevated proportions of the n-7 isomers of 18:1, 20:1 and 22:1 relative to the other monounsaturated isomers of the same chain length. The FA of arctic cod from Barrow and Cooper Island were significantly different (ANOSIM $R = 0.32$, $P < 0.005$) with elevated levels of 20:1n-9 and 22:1n-11 in the Cooper I. cod. These particular FA are normally produced in amounts >10% by calanoid copepods and are

Table 2 Proportions of selected fatty acids (FA) in all sample types (mean ± SD). The full data set is available upon request. *Total* Total FA reported for the sample type in this table, *Sats* saturated FA, *Mono* monounsaturated FA, *PUFA* polyunsaturated FA

	Ice algae ($n = 15$)	Phytoplankton ($n = 8$)	Copepods		Euphausids	Amphipods				Arctic cod					
			Harpacticoid ($n = 3$)	Cyclopoid ($n = 3$)	*T. raschii* ($n = 3$)	*Apherusa* sp. ($n = 4$)	*Gammarus* sp. ($n = 5$)	*Onisimus* sp. ($n = 3$)	*A. behringiensis* ($n = 3$)	Barrow ($n = 10$)	Cooper I. ($n = 15$)[a]	Black guillemot ($n = 10$)	Bowhead whale ($n = 10$)	Bearded seal ($n = 5$)	Ringed seal ($n = 4$)
16:0	18.94 ± 1.24	15.21±1.15	15.10 ± 1.48	15.20 ± 0.74	17.39 ± 0.23	13.33 ± 0.38	13.78 ± 0.58	14.00 ± 0.17	12.85 ± 1.11	14.47 ± 1.17	14.63 ± 1.89	18.64 ± 0.59	11.77 ± 2.18	4.76 ± 1.33	4.32 ± 2.30
18:0	1.32 ± 1.68	4.40 ± 2.37	0.92 ± 0.06	0.84 ± 0.10	0.89 ± 0.07	0.57 ± 0.04	0.71 ± 0.08	0.71 ± 0.07	1.27 ± 0.14	2.84 ± 0.59	2.46 ± 0.55	5.80 ± 0.92	2.98 ± 0.49	0.50 ± 0.06	0.46 ± 0.19
16:1n-7	50.03 ± 6.38	34.17 ± 4.21	23.88 ± 0.31	27.07 ± 2.38	24.43 ± 3.06	42.02 ± 1.44	29.41 ± 2.46	26.92 ± 1.16	16.16 ± 1.64	14.64 ± 8.52	11.44 ± 3.68	12.94 ± 1.17	15.82 ± 2.61	18.69 ± 1.38	17.76 ± 1.08
18:1n-9	1.88 ± 1.59	3.97 ±0.51	1.28 ±0.39	1.26 ± 0.15	8.20 ± 1.19	7.86 ± 0.73	11.91 ± 1.38	15.38 ± 0.28	6.53 ± 0.33	9.84 ± 1.40	10.29 ± 1.61	24.97 ± 1.89	14.15 ± 1.92	14.82 ± 1.17	15.63 ± 2.26
18:1n-7	0.53 ± 0.28	1.24±0.87	6.26±1.25	5.24 ± 0.81	5.63 ± 0.59	2.52 ± 0.12	4.60 ± 0.27	3.28 ± 0.11	7.06 ± 0.12	4.77 ± 0.68	3.92 ± 0.87	4.25 ± 0.25	4.70 ± 0.60	4.79 ± 0.51	4.52 ± 0.68
20:1n-11	0.04 ± 0.05	0.04 ± 0.02	0.24 ± 0.10	0.17 ± 0.06	0.20 ± 0.09	0.21 ± 0.09	0.22 ± 0.11	1.10 ± 0.16	1.36 ± 0.16	0.60 ± 0.27	0.86 ± 0.28	1.29 ± 0.14	2.40 ± 0.56	1.14 ± 0.15	1.36 ± 0.22
20:1n-9	0.12 ± 0.13	0.14 ±0.07	0.58 ± 0.08	0.27 ± 0.03	1.11 ± 0.24	1.04 ± 0.28	1.87 ± 0.61	3.41 ± 0.56	0.97 ± 0.03	4.49 ± 2.21	7.85 ± 2.67	8.99 ± 0.93	8.81 ± 1.89	5.01 ± 1.01	4.38 ± 0.77
20:1n-7	0.10 ± 0.11	0.16 ±0.09	1.05 ± 0.17	1.26 ± 0.34	0.42 ± 0.02	0.60 ± 0.07	0.73 ± 0.06	0.86 ± 0.04	2.42 ± 0.25	0.65 ± 0.15	0.43 ± 0.14	0.44 ± 0.03	1.57 ± 0.33	0.39 ± 0.03	0.33 ± 0.05
22:1n-11	0.14 ± 0.29	0.09 ±0.04	0.09 ± 0.01	0.12 ± 0.05	0.33 ± 0.11	0.26 ± 0.07	0.59 ± 0.25	0.91 ± 0.15	0.19 ± 0.06	1.94 ± 1.22	4.26 ± 1.71	4.03 ± 0.91	2.88 ± 1.42	0.57 ± 0.32	0.49 ± 0.24
22:1n-9	0.07 ± 0.09	0.21 ±0.03	0.13 ± 0.02	0.17 ± 0.01	0.13 ± 0.03	0.13 ± 0.04	0.25 ± 0.07	0.30 ± 0.03	0.13 ± 0.01	0.62 ± 0.31	0.89 ± 0.25	0.82 ± 0.18	0.91 ± 0.28	0.21 ± 0.08	0.18 ± 0.09
22:1n-7	0.10 ± 0.06	0.09±0.05	0.43± 0.12	0.53 ± 0.14	0.09 ± 0.01	0.08 ± 0.01	0.11 ± 0.01	0.08 ± 0.02	0.33 ± 0.05	0.14 ± 0.02	0.13 ± 0.03	0.11 ± 0.02	0.20 ± 0.07	0.02 ± 0.01	0.02 ± 0.01
16:4n-1	2.12 ± 0.56	3.54 ± 0.45	2.31 ± 0.26	2.48 ± 0.48	0.70 ± 0.14	1.28 ± 0.08	0.79 ± 0.17	0.76 ± 0.09	0.44 ± 0.08	0.53 ± 0.30	0.26 ± 0.12	0.15 ± 0.03	0.25 ± 0.10	0.38 ± 0.06	0.32 ± 0.06
20:5n-3	9.62 ± 2.43	14.08 ± 0.68	19.53 ± 2.49	17.84±0.17	16.46 ± 0.96	14.24 ± 0.59	14.62 ± 0.40	13.24 ± 0.94	22.73 ± 1.05	14.25 ± 1.58	12.53 ± 2.38	2.72 ± 1.11	7.46 ± 1.75	10.39 ± 0.97	11.14 ± 0.80
22:6n-3	1.24 ± 0.84	2.62 ± 0.52	11.22 ± 0.39	7.84 ± 1.15	10.36 ± 1.16	3.88 ± 0.22	5.95 ± 0.63	5.48 ± 0.12	12.41 ± 1.06	16.06 ± 4.56	14.46 ± 4.61	3.39 ± 1.29	6.41 ± 1.66	13.74 ± 2.15	14.41 ± 1.68
Total	85.87 ± 2.09	79.97 ± 0.63	83.01 ± 0.16	80.29 ± 0.31	86.35 ± 0.59	88.02 ± 0.32	85.53 ± 1.13	86.45 ± 0.12	84.86 ± 0.40	85.83 ± 1.19	84.41 ± 1.48	88.55 ± 0.59	80.33 ± 1.51	75.41 ± 0.92	75.31 ± 0.85
Sats	27.01 ± 2.60	28.90 ± 2.81	21.59 ± 1.26	22.72 ± 0.20	23.90 ± 0.48	18.61 ± 0.61	18.72 ± 0.61	19.28 ± 0.39	18.06 ± 0.79	21.39 ± 1.10	22.16 ± 2.29	28.40 ± 1.40	20.27 ± 3.09	9.49 ± 2.22	8.75 ± 3.85
Mono	53.70 ± 4.41	41.17 ± 3.53	34.88 ± 0.59	37.43 ± 1.57	42.17 ± 1.39	55.78 ± 0.54	51.26 ± 2.24	55.08 ± 1.05	37.45 ± 1.61	41.06 ± 6.50	44.07 ± 7.04	60.38 ± 2.17	56.08 ± 4.43	51.16 ± 2.82	50.52 ± 3.01
PUFA	18.48 ± 5.20	28.62 ± 1.45	42.08 ± 1.74	38.23 ± 1.34	33.08 ± 1.90	24.78 ± 0.65	28.97 ± 1.76	24.76 ± 1.37	43.25 ± 1.88	36.54 ± 5.69	32.80 ± 6.47	10.40 ± 2.75	22.13 ± 1.79	38.13 ± 3.63	39.51 ± 3.23
Σ C16/C18	12.82 ± 5.17	4.02 ± 0.86	3.40 ± 0.23	3.58 ± 0.40	2.45 ± 0.40	4.15 ± 0.40	2.10 ± 0.26	1.81 ± 0.07	1.65 ± 0.11	1.58 ± 0.85	1.35 ± 0.25	1.97 ± 0.07	1.08 ± 0.10	1.03 ± 0.08	0.95 ± 0.15
16:1/16:0	2.66 ± 0.29	2.30 ± 0.41	1.61 ± 0.17	1.81 ± 0.25	1.44 ± 0.19	3.17 ± 0.04	2.17 ± 0.20	1.97 ± 0.07	1.31 ± 0.16	1.06 ± 0.60	0.85 ± 0.34	0.72 ± 0.07	1.47 ± 0.44	4.51 ± 1.74	5.38 ± 2.88

[a] All arctic cod samples from Cooper I. were taken from the nests of guillemots

considered biomarkers of them (Sargent and Falk-Petersen 1988; Albers et al. 1996).

The FA profile of the guillemot adipose tissue was unusual compared to the other higher vertebrates, with large amounts (~25%) of 18:1n-9 and lower levels of 20:5n-3 and 22:6n-3. Levels of the calanoid copepod biomarkers 20:1n-9 (9%) and 22:1n-11 (4%) were also highest in the guillemots compared to the other species at high trophic levels. Like the guillemots, the bowhead whale blubber also contained elevated levels of 20:1n-9 and 22:1n-11. At the highest trophic level, the bearded and ringed seals had similar FA profiles, and as a group were quite different from the bowheads or guillemots.

Compound-specific stable C isotope analyses of FA

The δ^{13}C values for 16:4n-1 in the two end member taxa of primary producers were significantly different (Wilks' $\lambda = 0.13$; $P < 0.001$), ranging from a high of -24.0 ± 2.4‰ in ice algae to a low of -30.7 ± 0.8‰ in pelagic phytoplankton (Table 3). All other sample types, except guillemots (-23.2 ± 1.5‰), fell within this range, with a general trend of more depleted values for organisms at higher trophic levels for 16:4n-1, as well as for 20:5n-3 (Fig. 1). δ^{13}C values of 20:5n-3 in ice algae (-18.3 ± 2.0‰) and phytoplankton (-26.9 ± 0.7‰) bracketed all other taxa except bowhead whales (-27.2 ± 1.2‰), which were somewhat isotopically lighter. The average δ^{13}C value of 16:4n-1 in amphipods and euphausiids collected from the stomachs of Barrow arctic cod was almost identical to that of the cod (-26.1 ± 1.1 vs. -26.2 ± 1.1‰) and was not significantly different for 20:5n-3 (-24.0 ± 1.2 vs. -24.9 ± 0.4‰), suggesting minimal isotopic fractionation during metabolism of these FA.

The estimated contributions of FA material from ice algae and pelagic phytoplankton to higher trophic levels varied depending on which FA was used in the mass balance calculations and on within-species variation in δ^{13}C (Fig. 1). Based on 16:4n-1, ice algae contributed 44–107% of the C to higher trophic levels, whereas based on 20:5n-3 they contributed only 0–61% (Table 3).

Discussion

FA composition among trophic levels

The differences in FA composition of the ice algal diatoms and pelagic diatoms are consistent with previous studies that demonstrated that algal taxa typically have unique FA compositions (e.g., Viso and Marty 1993; Dunstan et al. 1994). Both types displayed FA profiles typical of diatoms, with greater amounts of FA 16:1 than

Table 3 δ^{13}C values of 16:4n-1 and 20:5n-3 (mean ± SD) and the subsequent estimates of the percent relative contribution [mean (range[a])] of ice algal FA to the higher trophic levels from the two-end member mixing model

FA δ^{13}C (‰)			Relative (%) contribution from ice algae compared to pelagic phytoplankton			
Species	16:4n-1	20:5n-3	16:4n-1		20:5n-3	
Ice algae	−24.0 ± 2.4	−18.3 ± 2.0				
Phytoplankton	−30.7 ± 0.8	−26.9 ± 0.7				
Harpacticoid copepods	−26.3 ± 5.1	−26.0 ± 1.1	76	(18–126)	14	(1–33)
Cyclopoid copepods	−28.4 ± 0.1	−25.2 ± 1.4	47	(45–48)	26	(4–45)
T. raschii	−26.5 ± 2.8	−25.6 ± 0.7	74	(45–95)	20	(10–29)
Apherusa sp.	−26.6 ± 0.8	−22.5 ± 0.6	72	(58–82)	61	(51–67)
Gammarus sp.	−26.1 ± 0.8	−23.7 ± 0.6	79	(68–89)	46	(36–54)
Onisimus sp.	−25.9 ± 0.3	−24.5 ± 0.2	80	(76–83)	36	(34–39)
A. behringiensis	−25.3 ± 1.5	−24.5 ± 0.6	88	(68–97)	35	(27–43)
Arctic cod (Barrow)	−26.2 ± 1.1	−24.9 ± 1.7	77	(61–95)	30	(6–62)
Arctic cod (Cooper I.[b])	−27.1 ± 1.8	−26.4 ± 1.1	65	(22–94)	8	(−22–32)
Black guillemots	−23.2 ± 1.5	−24.9 ± 0.4	107	(66–119)	30	(15–33)
Bowhead whales	−28.6 ± 0.8	−27.2 ± 1.2	44	(11–58)	−6	(−49–11)
Bearded seals	−27.8 ± 1.0	−26.9 ± 1.2	57	(30–72)	0	(−25–23)
Ringed seals	−27.4 ± 0.3	−26.4 ± 0.5	62	(56–65)	7	(−5–12)

[a] Ranges associated with the percent calculations are estimated based on the δ^{13}C variation within the sample type (Fig. 1). Ranges >100 or < 0% result from δ^{13}C values that are either less than or greater than the value for ice algae or phytoplankton, respectively

[b] All arctic cod samples from Cooper I. were taken from the nests of guillemots

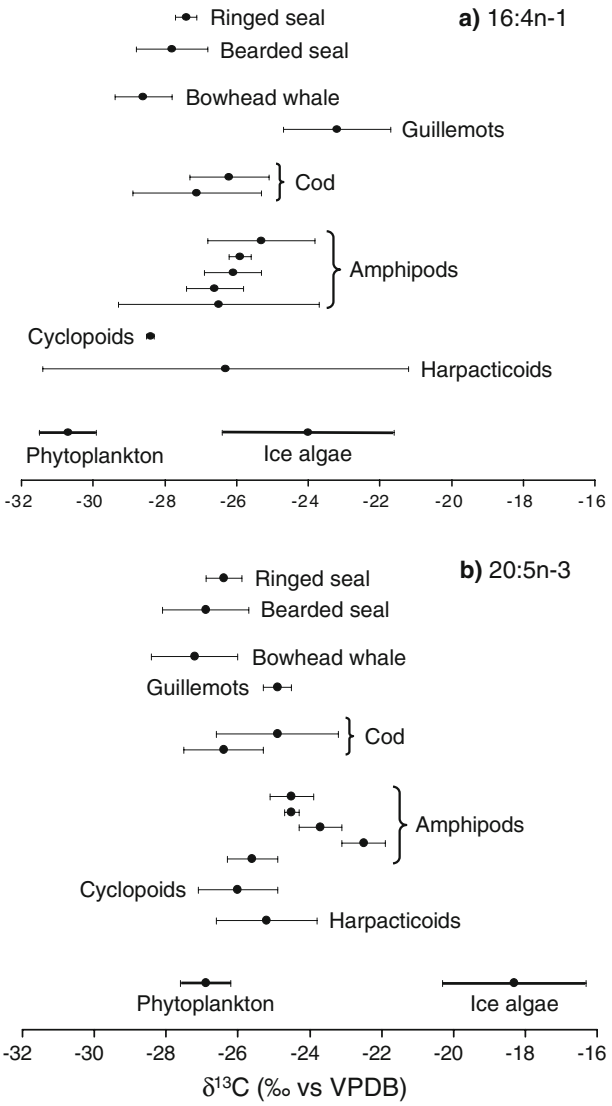

Fig. 1 Distribution and ranges (mean ± SD) of $\delta^{13}C$ values among sample types for **a** 16:4n-1 and **b** 20:5n-3. All $\delta^{13}C$ values are reported relative to Vienna Pee Dee Belemnite (*VPDB*) using standard δ notation. Samples types are plotted vertically in order of known relative trophic level

16:0 and low levels of C18. However, the very high level (~50%) of 16:1n-7 in ice algae was unusual. Only Falk-Petersen et al. (1998) reported a similar level of 46% in *Nitzschia figida* collected in the Antarctic. Combined with the low levels of polyunsaturated FA present, this composition might suggest an extreme in the growth conditions, perhaps because of a collection date late in the season. Because environmental conditions such as temperature, incident light and nutrient availability influence the FA composition of phytoplankton (Harrison et al. 1990; Thompson et al. 1992), the cold, low-light environment in the sea ice may also contribute to the unusual FA composition.

The contrasting FA composition of ice algae and pelagic phytoplankton suggests that it would be possible to recognize signatures of each taxon in species at higher trophic levels. For example, the higher amounts of 22:6n-3 in the phytoplankton, and the even higher levels in harpacticoid copepod consumers, might suggest that phytoplankton was a more significant source of FA to the harpacticoids than was ice algae. However, the much larger amount of 22:6n-3 in the copepods might also arise from differential metabolism (Moreno et al. 1978). The consumers at the lowest trophic levels in this study (zooplankton) have a greater capacity to modify and biosynthesize FA than those at the higher trophic levels, such as fish (Tocher 2003); thus, such simple comparisons are most problematic between these lower levels.

Within species, differences in FA proportions can be useful in assessing spatial and temporal variability in diets (e.g., Walton et al. 2000; Iverson et al. 2002). For example, cod caught near Cooper Island contained higher levels of FA 20:1n-9 and 22:1n-11, that are normally produced in large amounts by calanoid copepods (Sargent and Falk-Petersen 1988; Albers et al. 1996), than cod from Barrow, suggesting that the Cooper Island fish were relying to a greater extent on calanoids than those from Barrow. In like manner, similarities in FA composition between species usually indicate similar diets—the FA compositions of bearded and ringed seals were not significantly different, suggesting that the diets of these sympatric pinnipeds overlapped to some degree. Bearded seals are normally thought to consume benthic molluscs in addition to pelagic fish and shrimp that are the principal dietary items of ringed seals (Lowry et al. 1980a, b). Budge et al. (2007) showed that a particular group of non-methylene interrupted (NMI) FA may be used to indicate feeding on molluscs by bearded seals. However, NMI FA were not detected in the bearded seal blubber in this study. Combined with the similar FA composition in the two seals, these results suggest that both species were relying on similar fish and crustacean prey. Despite the fact that guillemots and bowhead whales in general feed at different trophic levels (high vs. low, respectively), both contained elevated levels of 20:1 and 22:1 isomers. These results suggest that both included calanoid copepods in their diets and/or that guillemots consumed fish which had concentrated these copepods biomarkers through their diets. Unfortunately, without sampling of the entire prey database for each species, it is not possible to assess these contributions with these FA data alone (see below).

A more rigorous use of FA signatures to estimate dietary sources is quantitative FA signature analysis (QFASA), which estimates predator diets by statistically comparing the entire suite of FA of predator and potential prey (Iverson et al. 2004). Among the requirements to use this

technique, one must understand and account for predator metabolism, as well as have a FA database of all potential prey species. In theory, if all such requirements were met for each consumer in our study, we could model diets of each predator at each subsequently higher trophic level, and then iterate backwards to produce an estimate of ice algae contribution to the food web. However, in such a broad sampling as ours, this would require analyzing the FA composition of all prey items of the copepods, euphausiids, amphipods, arctic cod, guillemots, seals and whales. Such a large-scale collection and analysis were beyond the scope of our project. Additionally, while the FA metabolism of fish, birds, and mammals is fairly well understood, relatively little is known about lipid metabolism of zooplankton (see Sargent and Henderson 1986 for a review). For instance, the high levels of n-7 FA (18:1n-7, 20:1n-7, 22:1n-7) in the harpacticoid and cyclopoid copepods are unusual and, while it is possible that these may arise from de novo synthesis (Sargent and Henderson 1986), it seems more likely that elongation of 16:1n-7 that was present at levels near 50% in ice algae was occurring. There is also evidence that copepods are capable of synthesizing long chain polyunsaturated FA, such as 22:6n-3, through elongation and desaturation of FA precursors (Moreno et al. 1978). Because of these complications and the need for further study of FA metabolism, especially at the lower trophic levels, we tested the use of FA-specific stable C isotope analyses to determine trophic linkages and, ultimately, the contribution of ice algal C to higher trophic levels.

Using FA-specific stable C isotopes to understand trophic linkages

The combination of FA and isotope analyses we used was important in clarifying trophic relationships in the local food web that might have been overlooked otherwise. For example, the adult guillemots and the arctic cod collected from the their nests on Cooper Island had similar proportions of 20:1n-9 and 22:1n-11, and one might be tempted to interpret these limited data as indicating that the adult guillemots were consuming those fish also (the cod that were being brought for chicks). Such a conclusion would be reinforced by stomach contents' data from adult guillemots that have been killed by predators at Cooper Island, which indicate that cod are typically their most important prey (G. J. D. unpublished data). However, in this case, the very different δ^{13}C of 16:4n-1 and 20:5n-3 in the two sample types (Table 3) indicated that cod were unlikely to be important diet components for adults. Hobson (1993) also reported that during the breeding season adult guillemots fed their chicks a high proportion of fish, but consumed a large amount of low-trophic-level invertebrates themselves. The high levels of both 20:1n-9 and 22:1n-11 in Cooper Island guillemots and arctic cod could also have resulted from both species consuming similar zooplankton species. However, very different levels of other FA, such as 20:5n-3 and 22:6n-3 in cod and guillemots (Table 2), combined with the isotope data, suggest that arctic cod and guillemots were actually consuming different invertebrate prey. These findings point to the potential pitfalls of using proportions of only one or two FA, in exclusion to others, to infer predator–prey linkages, and underscore the need to consider all prey and FA in a comprehensive model (e.g., such as QFASA) or to use complimentary analyses such as we have here with compound-specific stable isotopes.

Determining stable isotope ratios of individual FA in our study further enabled us to estimate the relative contributions of ice algal FA to higher trophic levels. However, to do so it was necessary to make several assumptions.

Assumption 1: The ice algae and pelagic phytoplankton represented end members of the possible ranges of isotope values. Thus, all δ^{13}C of samples in higher trophic levels must fall between these two components. This was in fact the case. Although the values for 20:5n-3 in bowhead whales and 16:4n-1 in guillemots were slightly outside of these limits, when analytical precision and variability between samples were taken into account, the result was negligible. This assumption also implies that there is no variation in the isotope values of these end members with changes in the physiological state of the algae. Søreide et al. (2006) reported little change in the bulk stable C isotope value of pelagic particulate organic matter (POM) from spring to fall in the European Arctic, but did find considerable variation in ice POM. However, when results from only the obligate ice-POM were considered, analogous to our data, the isotope values were quite consistent (-20.0 ± 0.8‰). Thus, while we acknowledge that sample collection at other times of the year would have provided a more complete view of the isotope variation exhibited by primary producers in our system and a more reliable estimate of contribution to higher trophic levels, our values are likely representative of at least a "spring isotope signal" and possibly a reasonable approximation of values found throughout the year. A future study could be dedicated to compound-specific isotope analyses of primary producers and primary consumers in the Arctic.

Assumption 2: Ice algae and pelagic diatoms are the predominant sources of the FA in question, and contributions from other types of algae are not important. For 16:4n-1, this assumption is met—only diatoms produce it in this area (Viso and Marty 1993; Dunstan et al. 1994; Graeve et al. 2002). However, 20:5n-3 is produced by a number of different classes of phytoplankton that are present in the Chukchi Sea, including flagellates,

haptophytes, prasinophytes and prymnesiopytes (Hill et al. 2005; Booth and Horner 1997). Booth and Horner (1997) pointed out that although autotrophic flagellates and dinoflagellates can be found in the Chukchi Sea, centric diatoms dominate the biomass on the shelf. If the conditions were static, the contribution of these other types of phytoplankton to the isotope ratio of 20:5n-3 in our study would likely be insignificant. However, advection might bring algae from off the shelf into the area and introduce classes other than diatoms. We observed such a shift in current during our study; thus, the possible contribution to 20:5n-3 from other algal sources cannot simply be ignored.

This raises two potential problems—we do not know the δ^{13}C of 20:5n-3 or the relative proportions of that FA in these other algal classes. We expect other classes of algae to have a δ^{13}C value similar to pelagic phytoplankton since they are not ice associated. However, Kukert and Riebesell (1998) have shown a $\sim$2‰ depletion in small flagellates compared to centric diatoms, indicating that other algal classes can have an effect on the δ^{13}C of 20:5n-3. We expect this effect to be minimal when considered relative to the $\sim$9‰ difference between ice algae and pelagic phytoplankton. If other algal classes, for example flagellates, were making a substantial contribution to total FA, the slight depletion in 20:5n-3 in them would have resulted in an underestimation of ice algal contribution to higher trophic levels and might help explain some of the discrepancies between the estimates of ice algae FA contribution calculated with 16:4n-1 and 20:5n-3. The second issue regarding unknown proportions of 20:5n-3 in other types of phytoplankton may be more problematic. That is, a species that makes a small contribution to biomass, but synthesizes a much larger proportion of 20:5n-3 than pelagic diatoms, would appear to make a much larger proportional contribution to biomass. In our study, we know that the proportion of 20:5n-3 in pelagic diatoms is $\sim$14% and we have incorporated that into our calculations. In a survey of the literature, we found that proportions of 20:5n-3 for the other potential algal contributors were rarely >15% (Dunstan et al. 1992; Conte et al. 1994; Viso and Marty 1993; Tang et al. 2001). Therefore, we can assume that the impact of other types of open water phytoplankton on the δ^{13}C of 20:5n-3 would be similar, or less than that of the pelagic phytoplankton we sampled here. If we accept that the δ^{13}C value and the proportion of 20:5n-3 are similar in pelagic diatoms and other open water contributors, then we can think of the δ^{13}C of 20:5n-3 as representing the contribution of all other non-ice algal species to total FA, with some error included because of the more depleted C in small-celled species. Alternatively, 16:4n-1 would represent the contribution of FA by ice algal diatoms and pelagic diatoms only. These rationales assume that lipid content may serve as a proxy for C content, even though the ratio of lipid relative to total C fluctuates among algal classes (e.g., Viso and Marty 1993). This is of course a greater issue in the application of 20:5n-3 as an indicator of non-ice associated algal contribution that may encompass many algae classes.

Assumption 3: Isotope fractionation associated with the metabolism of 16:4n-1 and 20:5n-3 is negligible. In animals there is generally an increase in ^{13}C relative to ^{12}C in TOC at successively higher trophic levels. With FA metabolism the opposite effect is encountered, because enzymes preferentially utilize the lighter precursor when FA are modified through chain elongation or desaturation (Monson and Hayes 1982). The obvious way to avoid the problem of fractionation in food web studies such as ours is to use a FA whose structure is not modified in any way (i.e., one that arises only from plants and cannot be produced by animals). The FA 16:4n-1 is produced only by algae (Viso and Marty 1993; Dunstan et al. 1994), so it meets this requirement. There is some evidence that 20:5n-3 can be produced by chain elongation and desaturation of precursors such as 18:3n-3 in higher vertebrates (Sprecher 2000). However, in marine vertebrates, where 20:5n-3 is plentiful, this synthesis does not seem to occur to any significant extent (Tocher 2003). There is other evidence to suggest that several species of zooplankton are capable of synthesizing 20:5n-3 from precursors (Moreno et al. 1978; Norsker and Støttrup 1994) but, as in higher vertebrates, this elongation appears to be quite limited when 20:5n-3 is abundant (Nanton and Castell 1999). Thus, we can expect no change in the δ^{13}C of 16:4n-1 and very little change in 20:5n-3 due to direct modification of their structures.

FA rarely exist in free form in live organisms and are normally esterified to a glycerol backbone to form structures such as triacylglygerols or phospholipids. Various enzymes catalyze the esterification and hydrolysis of FA to the glycerol molecule. Therefore, some small kinetic isotope effect must be anticipated because of these processes during metabolism, and it might partially explain the slight trend to lighter values at higher trophic levels. However, we expect this effect to be minimal compared to that seen with biosynthesis, catabolism or structure modification. Certainly, the similarity in δ^{13}C of the FA in the Barrow cod and in the amphipods and euphausiids recovered from their stomachs supports this (Fig. 1).

Assumption 4: Effects of isotopic routing are negligible. As in Assumption 3, by using FA that can only arise from primary producers, we know that the FA we analyzed could not consist of C from another non-lipid source. Certainly, with 16:4n-1 arising only from diet, isotopic routing is of little concern. Any elongation of FA precursors to create 20:5n-3 would incorporate either two or four Cs from another source, but as described above, this process is unlikely to occur to a significant extent. In fact, instead of

avoiding dietary routing we are making use of it by determining isotope ratios in FA that are "routed" to fat storage. Because we know that the FA were acquired from diet and remained intact, their stable C isotopic signature must be very similar to the original, with no influence from C arising from carbohydrates or proteins.

Assumption 5: Lipid turnover in a consumer is instantaneous. By sampling algae and herbivorous copepods at the same time, we are assuming that the consumer assimilates the algal lipids immediately so that we will observe a stable C isotope ratio that is representative of diet. Of course, the process is not instantaneous, but at low trophic levels, it does seem to occur in a matter of hours to days. For instance, Graeve et al. (2005) reported the incorporation of isotopically-labeled lipids from diet into copepods in as little as 24 h. At higher trophic levels, we expect the whole-body FA signature of fish to turn over in $\sim$3 weeks (Kirsch et al. 1998). For seals, whales and birds, it was logistically impossible to retrieve and analyze whole-body samples so we instead sampled fat depots, such as adipose tissue or blubber, that we expected to be replaced more rapidly than structural lipids. Estimates for FA turnover rates in these types of predators are more difficult to find but it is generally accepted that blubber FA can reflect a dietary shift in as little as a month (Iverson 2002). For the higher predators, which we sampled months after the algae was collected, there is likely to have been ample time for their lipids to acquire the C isotope signal generated by primary producers. Fortunately, turnover seems faster at lower trophic levels, so we can expect zooplankton to acquire quite quickly an isotope signal representative of the algae they consume. Thus, while lipid turnover in our consumers is not instantaneous, it likely occurs fast enough to incorporate the algae FA C isotopic signature.

Importance of ice algae to food web production

Our estimates based on 16:4n-1 suggest that ice algae contributed an average of 71% (44–107%) of the FA to the species analyzed here (Table 3). This value likely represents the contribution of ice algae relative to pelagic diatoms, rather than total (including non-diatom) primary producers. Our estimates based on 20:5n-3 suggest that an average of just 24% (0–61%) of FA in higher trophic levels was derived from ice algae. This estimate for the Chukchi Sea might be more reasonable considering that classes of algae other than diatoms are known to make significant contributions to primary production (Booth and Horner 1997). When one considers that ice algal diatoms are only present to contribute organic material for such a short period of time (April–May), a contribution of even 24% of FA to higher trophic levels is quite remarkable. One would also expect turnover of ice algal lipids and their replacement with lipids from non-ice associated phytoplankton to cause more depleted δ^{13}C of both 16:4n-1 and 20:5n-3 as the season progressed and less ice algae were present. For instance, in samples consisting of small organisms that feed near the base of the food web, such as the amphipods and euphausiids collected in August, we would have expected a more depleted δ^{13}C of both FA, since little fresh ice algae would be available at that time for consumption. However, we actually found a fairly consistent δ^{13}C for both FA in the amphipods, in some cases with higher δ^{13}C in the amphipods than their potential diets of copepods or algae-derived detritus (Fig. 1).

The relatively enriched levels of 16:4n-1 at all trophic levels, regardless of collection time, suggests that this ice algae FA is effectively recycled within the system. In this respect, it would be informative to determine δ^{13}C of FA in sediments at Barrow to examine the contributions of ice algal C to organic material removed by deposition or taken up by benthic organisms. There are variable reports on the importance of ice algae to the benthos (e.g., Michel et al. 1996; McMahon et al. 2006) and analysis of stable isotopes of individual FA may offer a means to determine the proportion of ice algae FA assimilated there.

Bowhead whales, with the most depleted δ^{13}C of both FA in higher trophic level consumers, did not appear to rely on FA with an ice algae source, but instead assimilated FA derived mostly from pelagic diatoms. This was expected for two reasons. First, bowheads migrate annually from over-wintering areas in the northern Bering Sea, far south of our study area, to summer areas in the eastern Beaufort Sea, following the retreating sea ice (Moore and Reeves 1993). Although they are in close proximity to the ice edge during much of winter and spring, their prey, large calanoid copepods and euphausiids, are mainly supplied to the region by advection in the Anadyr Current from the shelf edge (Springer et al. 1989), which is commonly beyond the reach of winter ice. Furthermore, this current carries abundant nutrients that fuel prolific pelagic diatom productivity that dwarfs that of ice algae and provides abundant food for grazers (Springer and McRoy 1993). Second, the whale samples were not temporally well coupled with the presence of ice algae in the Beaufort Sea where they summer, with most whales collected in October rather than late spring or summer. While there is some debate over the extent that bowheads feed in the summer in the Beaufort Sea, they do feed there (Hoekstra et al. 2002; Lowry et al. 2004; Lee et al. 2005), and presumably these whales were feeding on copepods and euphausiids that had been consuming pelagic phytoplankton blooms. Several months of reliance on such food would likely be enough to alter the δ^{13}C of blubber FA, since FA are known to turn over in blubber in a matter of weeks (Cooper 2004).

Conclusion

This study demonstrated the value of compound-specific isotope analysis of marine lipids and their potential application to food web studies. Relationships derived from FA composition were generally supported by stable C isotope values, and the compound-specific isotope values allowed us to use mass balance calculations to estimate the contributions of ice algae to higher trophic levels, an accomplishment that was not possible with FA proportions alone. With this technique, we made a preliminary estimate that FA derived from ice algal pennate diatoms comprised ~71% of that found in higher trophic levels, relative to FA from pelagic centric diatoms, based on δ^{13}C of 16:4n-1. Using δ^{13}C values of 20:5n-3, we likewise calculated an ice algae contribution of ~24%, which likely reflects contributions from other non-diatom classes of algae. This value might represent a more realistic approximation of the contribution of ice algal FA to higher trophic levels. With oceanic warming and the observed loss of sea ice and ice algae, the more conservative estimate still results in a potential decrement to arctic food web production of at least 24%. The consequences for benthic and pelagic food webs that rely on ice algae are unknown.

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