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Blubber fatty acid composition of bowhead whales, *Balaena mysticetus*: Implications for diet assessment and ecosystem monitoring

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ABSTRACT

Fatty acids (FA) have a diversity of structures that are transferred with little modification through food webs, making them valuable in assessing diets of animals that cannot be directly observed feeding. Before using FA to estimate diets, it is necessary to evaluate variation in FA signatures within and among individuals of a given species. To begin assessing diets and foraging of western Arctic bowhead whales (*Balaena mysticetus*), we examined the FA in blubber of 64 bowheads taken in the spring and fall subsistence hunts in 1997–2002 at Barrow and Kaktovik, Alaska. We found no significant differences in FA characteristics of inner blubber layers taken from either duplicate samples on the dorsal surface, or between dorsal and ventral sites. Significant differences were found in the FA composition between inner and outer layers of blubber at the same body site. We also found age, season and year to have significant effects on FA composition; however, gender was not found to be significant. While the importance of the Beaufort Sea as a feeding ground of bowhead whales remains uncertain, our results indicate that adults and sub-adults foraged to some extent on different prey and that both age classes consumed copepods there in summer at sufficient levels to significantly alter their blubber FA profiles. Both of these findings correspond with dietary conclusions reached from the analysis of stomach contents. Furthermore, we found compelling evidence that yearly variation in bowhead FA reflect changes in FA compositions of phytoplankton at the base of the food web, probably in response to climate variation. Variability in phytoplankton-derived FA in blubber was correlated significantly with yearly mean values of the Pacific Decadal Oscillation. FA in bowhead whale blubber, therefore, might be used to monitor effects of climate change on lower trophic levels and production processes in the western Arctic.

1. Introduction

Fatty acids (FA) and FA signature analysis are becoming increasingly important tools in many ecological applications, and have been used as biomarkers to help describe trophic pathways in marine food webs and to assess foraging differences among predators (e.g., Iverson et al., 1997; Dahl et al., 2000; Hooker et al., 2001; Best et al., 2003; Budge et al., 2007). The technique works because most marine FA are synthesized by phytoplankton and other organisms at low trophic levels, FA have a wide variety of structures, and they undergo little biochemical change when passed up the food chain (Dalsgaard et al., 2003; Iverson, in press). Thus, it is possible to recognize FA in a predator's fat stores that were derived from their prey. Most applications of FA analysis are qualitative in nature, investigating spatial or temporal variations in diets among and within individuals or populations. More recently, a new technique, quantitative FA signature analysis (QFASA), has been developed (Iverson et al., 2004, 2007) in which quantitative estimates of diet are derived from FA signatures of predator and prey.

FA analysis and QFASA are particularly useful in evaluating diets of species that cannot be directly observed feeding or which pose other research difficulties. For example, our knowledge of bowhead whale (*Balaena mysticetus*) diets in Alaska is derived from analyses of stomach contents of whales taken in the spring and fall subsistence harvests at villages in the Beaufort Sea (Barrow and Kaktovik), and indirectly from analyses of stable isotopes of baleen and other tissues from those animals (e.g., Hoekstra et al., 2002; Lowry et al., 2004; Lee et al., 2005). However, there are uncertainties associated with these methods. Many whales have nothing in their stomachs and the prey in those that do represent just the most recent feeding. Isotopes provide information on trophic level and general carbon source, but not on the taxonomic identity of the prey. Thus, the interpretations of results from these two methods do not always agree. Also, very little is known about diets outside of the Beaufort Sea (in the northern Bering Sea and Chukchi Sea), where bowheads spend much of the year.

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FA analysis and QFASA should provide valuable insights into bowhead feeding ecology and help resolve conflicting conclusions from the other techniques. Before using these tools, however, one must have an understanding of the variation in FA with the gender and age of individuals, as well as between years, seasons and locations. In addition, it is well known that significant vertical stratification in FA composition exists through the depth of the blubber of many cetaceans (Ackman et al., 1975; Koopman et al., 1996; Hooker et al., 2001; Reynolds et al., 2006), with the innermost layer (i.e., that closest to the muscle) thought to be the most metabolically active and indicative of diet. There is also evidence that FA composition may vary among body sites (Ackman and Lamothe, 1989; Koopman et al., 1996). Thus, both of these issues must also be addressed in bowhead whales prior to undertaking estimates of diet with QFASA.

The principal objectives of this study were to: 1) determine the effect of body site and blubber depth on FA composition; 2) determine the variation in FA composition with gender, age, collection location, season and year and 3) investigate the potential to use blubber FA data to monitor ecosystem change. We also sought to provide preliminary information on bowhead feeding and diet in the Beaufort Sea based on FA analysis, and to begin to reconcile conflicting views based on the analysis of stomach contents and stable isotopes.

2. Methods

2.1. Sample collection

Blubber samples were collected from 64 bowhead whales harvested in 1997–2002 by subsistence hunters in Barrow, AK in spring and fall, and in Kaktovik, AK in fall only (Table 1). A full depth blubber sample (100–600 g, skin and muscle attached) was removed from each whale approximately 1 m posterior to the blowhole. When present, adipose tissue from the hypodermal layer, analogous to the panniculus adiposis, was not included in these analyses. Duplicate blubber samples were taken from three whales in 2002 (02KK1, 02KK2 and 02KK3) by simply dividing the dorsal blubber core into two sections prior to freezing. Ventral samples, collected from the midline between the flippers, were also taken from four other whales in 2001 and 2002 (02B11, 01KK1, 01KK2 and 01KK3). To examine the degree of FA stratification in blubber, each sample was sectioned into five equal portions from the skin to the muscle layer.

2.2. Lipid analysis

Lipids were extracted from all samples using a modified Folch et al. (1957) procedure (Budge et al., 2006). Briefly, blubber samples were extracted with 2:1 chloroform: methanol, washed with salt solution, dried over anhydrous sodium sulphate and evaporated under nitrogen. FA methyl esters (FAME) were prepared from this pure extracted lipid, using H_2SO_4 in methanol (Budge et al., 2006).

FAME were analyzed in duplicate using temperature-programmed gas liquid chromatography according to Budge and Iverson (2003). Analyses were carried out on a Perkin Elmer Autosystem II Capillary gas chromatograph (GC) with a flame ionization detector (FID) using a flexible fused silica column (30 m×0.25 mm ID) coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness; Agilent Technologies, DB-23; Palo Alto, CA, USA). Helium was used as the carrier gas and the gas line was equipped with an oxygen scrubber. Up to 66 FAME were identified according to Iverson et al. (1997) and are reported as weight percent of total FA. Each FA is described using the shorthand nomenclature of A:Bn-X, where A represents the number of carbon atoms, B the number of double bonds and X the position of the double bond closest to the terminal methyl group.

2.3. Statistics

Principal components analysis (PCA) was performed on proportional FA data that were transformed using the following logarithmic function (Aitchison, 1983): $x_t = \log(x_i/g(x))$, where x_i is a given FA expressed as percent of total, $g(x)$ is the geometric mean of the FA data for the sample and x_t represents the transformed FA data. To investigate stratification of FA by depth, PCA was performed on the 12 transformed FA with the greatest variation among layers (14:0, 14:1n-5, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 20:1n-9, 20:5n-3, 22:1n-11, 22:5n-3, 22:6n-3; Table 2). To try to ensure that reliable factors were extracted, we restricted our sample:variable ratio to 5:1

Table 1
Specimen data

	Specimen code	Season	Sex	Location	Body length (m)
1997	97B06	Spring	F	Barrow	16.5
	97B11	Fall	M	Barrow	13.6
	97B12	Fall	M	Barrow	15.3
	97B14	Fall	F	Barrow	8.6
	97B17	Fall	M	Barrow	10.5
	97B18	Fall	M	Barrow	10.8
	97B19	Fall	F	Barrow	9.3
	97B30	Fall	F	Barrow	8.0
	97B31	Fall	F	Barrow	8.8
1999	99B13	Spring	M	Barrow	14.1
	99B14	Spring	M	Barrow	14.2
	99B15	Spring	M	Barrow	14.6
	99B16	Spring	F	Barrow	14.8
	99KK1	Fall	F	Kaktovik	7.7
	99KK1	Fall	M	Kaktovik	12.9
	99KK3	Fall	M	Kaktovik	8.3
2000	00B01	Spring	M	Barrow	9.4
	00B03	Spring	F	Barrow	16.4
	00B05	Spring	F	Barrow	17.5
	00B06	Fall	M	Barrow	14.7
	00B07	Fall	M	Barrow	8.7
	00B08	Fall	U	Barrow	8.6
	00B09	Fall	F	Barrow	7.9
	00B10	Fall	F	Barrow	9.4
	00B11	Fall	M	Barrow	13.8
	00B12	Fall	M	Barrow	10.9
	00B13	Fall	M	Barrow	9.4
	00B14	Fall	F	Barrow	9.9
	00B15	Fall	F	Barrow	8.9
	00B16	Fall	F	Barrow	10.0
	00KK01	Fall	F	Kaktovik	9.2
	00KK02	Fall	M	Kaktovik	12.1
	00KK03	Fall	F	Kaktovik	8.8
2001	01B01	Spring	F	Barrow	9.4
	01B02	Spring	M	Barrow	14.5
	01B03	Spring	F	Barrow	14.6
	01B04	Spring	M	Barrow	17.5
	01B06	Spring	M	Barrow	12.5
	01B07	Spring	M	Barrow	11.3
	01B08	Spring	M	Barrow	10.4
	01B09	Spring	M	Barrow	8.8
	01B11	Spring	M	Barrow	8.4
	01B12	Spring	M	Barrow	9.1
	01B13	Spring	F	Barrow	8.2
	01B15	Spring	M	Barrow	10.6
	01B16	Spring	M	Barrow	8.6
	01B17	Spring	F	Barrow	13.9
	01B19	Spring	M	Barrow	11.9
	01KK01	Fall	F	Kaktovik	13.2
	01KK02	Fall	F	Kaktovik	9.6
	01KK03	Fall	M	Kaktovik	10.0
2002	02B01	Spring	F	Barrow	11.7
	02B02	Spring	F	Barrow	16.7
	02B04	Fall	F	Barrow	8.6
	02B05	Fall	F	Barrow	8.5
	02B06	Fall	M	Barrow	9.0
	02B07	Fall	M	Barrow	8.0
	02B08	Fall	F	Barrow	6.8
	02B11	Fall	F	Barrow	8.1
	02B12	Fall	M	Barrow	7.9
	02B18	Fall	F	Barrow	7.3
	02KK01	Fall	F	Kaktovik	12.0
	02KK02	Fall	M	Kaktovik	9.0
	02KK03	Fall	F	Kaktovik	14.0

Table 2
Variation in FA proportions (mean ± SE, $n = 18$) in each of five blubber layers in bowhead whales collected in the spring of 2001

	Inner	Middle inner	Middle	Middle outer	Outer
Saturated					
10:0	0.36 ± 0.06	0.22 ± 0.05	0.12 ± 0.02	0.08 ± 0.01	0.08 ± 0.01
14:0[a]	4.34 ± 0.11	4.53 ± 0.10	4.53 ± 0.10	4.31 ± 0.09	4.13 ± 0.07
i−15:0	0.12 ± 0.00	0.13 ± 0.00	0.12 ± 0.00	0.12 ± 0.00	0.12 ± 0.00
15:0	0.24 ± 0.00	0.25 ± 0.00	0.25 ± 0.01	0.24 ± 0.00	0.23 ± 0.00
16:0 [a]	11.30 ± 0.41	11.70 ± 0.37	11.05 ± 0.34	9.62 ± 0.28	8.89 ± 0.22
i−17:0	0.12 ± 0.00	0.11 ± 0.00	0.11 ± 0.00	0.11 ± 0.00	0.10 ± 0.00
17:0	0.15 ± 0.01	0.16 ± 0.01	0.15 ± 0.01	0.13 ± 0.01	0.11 ± 0.01
18:0 [a]	2.91 ± 0.12	2.84 ± 0.11	2.44 ± 0.09	1.90 ± 0.08	1.69 ± 0.08
Subtotal	19.55 ± 0.50	19.93 ± 0.50	18.77 ± 0.48	16.51 ± 0.39	15.35 ± 0.31
Monounsaturated					
14:1n-9	0.27 ± 0.04	0.19 ± 0.03	0.14 ± 0.01	0.13 ± 0.01	0.14 ± 0.01
14:1n-5 [a]	0.19 ± 0.01	0.23 ± 0.02	0.33 ± 0.02	0.51 ± 0.02	0.63 ± 0.02
16:1n-11	0.37 ± 0.01	0.38 ± 0.01	0.41 ± 0.01	0.41 ± 0.01	0.40 ± 0.01
16:1n-9	0.22 ± 0.01	0.21 ± 0.01	0.23 ± 0.01	0.22 ± 0.01	0.23 ± 0.01
16:1n-7 [a]	13.75 ± 0.32	14.73 ± 0.40	16.48 ± 0.35	18.38 ± 0.25	19.31 ± 0.20
17:1n-8	0.13 ± 0.01	0.15 ± 0.01	0.18 ± 0.01	0.20 ± 0.01	0.20 ± 0.01
18:1n-11	2.38 ± 0.14	2.34 ± 0.11	2.26 ± 0.10	2.09 ± 0.10	2.05 ± 0.10
18:1n-9 [a]	11.63 ± 0.91	12.42 ± 0.63	13.26 ± 0.41	13.31 ± 0.47	13.24 ± 0.53
18:1n-7 [a]	4.10 ± 0.15	4.86 ± 0.13	5.43 ± 0.09	5.48 ± 0.10	5.32 ± 0.13
18:1n-5	0.60 ± 0.01	0.59 ± 0.01	0.59 ± 0.01	0.58 ± 0.01	0.58 ± 0.01
20:1n-11	2.69 ± 0.17	2.39 ± 0.13	2.15 ± 0.11	2.09 ± 0.11	2.14 ± 0.11
20:1n-9 [a]	11.19 ± 0.69	9.80 ± 0.48	8.43 ± 0.33	8.11 ± 0.32	8.42 ± 0.37
20:1n-7	1.72 ± 0.09	1.53 ± 0.07	1.32 ± 0.04	1.30 ± 0.05	1.34 ± 0.06
22:1n-11 [a]	5.00 ± 0.74	5.05 ± 0.48	4.83 ± 0.24	5.23 ± 0.28	5.67 ± 0.34
22:1n-9	1.50 ± 0.16	1.28 ± 0.12	1.03 ± 0.05	1.01 ± 0.05	1.07 ± 0.06
22:1n-7	0.31 ± 0.04	0.28 ± 0.03	0.24 ± 0.01	0.25 ± 0.01	0.27 ± 0.02
24:1n-9	0.19 ± 0.03	0.13 ± 0.02	0.10 ± 0.01	0.09 ± 0.00	0.10 ± 0.00
Subtotal	56.24 ± 0.86	56.55 ± 0.65	57.41 ± 0.61	59.39 ± 0.50	61.13 ± 0.41
Polyunsaturated					
16:3n-6	0.61 ± 0.01	0.66 ± 0.01	0.70 ± 0.01	0.72 ± 0.01	0.73 ± 0.01
16:3n-4	0.24 ± 0.02	0.23 ± 0.02	0.20 ± 0.02	0.20 ± 0.01	0.20 ± 0.01
16:4n-1	0.35 ± 0.04	0.32 ± 0.03	0.29 ± 0.03	0.29 ± 0.03	0.29 ± 0.03
18:2n-6	0.69 ± 0.01	0.69 ± 0.01	0.68 ± 0.01	0.67 ± 0.01	0.66 ± 0.01
18:2n-4	0.13 ± 0.01	0.15 ± 0.00	0.17 ± 0.00	0.17 ± 0.00	0.17 ± 0.00
18:3n-6	0.15 ± 0.01	0.14 ± 0.01	0.13 ± 0.00	0.12 ± 0.00	0.12 ± 0.00
18:3n-4	0.25 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.28 ± 0.01	0.27 ± 0.01
18:3n-3	0.31 ± 0.01	0.32 ± 0.01	0.33 ± 0.01	0.34 ± 0.01	0.34 ± 0.01
18:4n-3	0.82 ± 0.07	0.76 ± 0.06	0.67 ± 0.04	0.66 ± 0.04	0.65 ± 0.04
18:4n-1	0.35 ± 0.02	0.38 ± 0.02	0.42 ± 0.02	0.44 ± 0.02	0.43 ± 0.01
20:2n-6	0.15 ± 0.00	0.16 ± 0.00	0.16 ± 0.00	0.16 ± 0.00	0.17 ± 0.00
20:4n-6	0.30 ± 0.02	0.30 ± 0.01	0.31 ± 0.01	0.32 ± 0.01	0.32 ± 0.01
20:4n-3	0.44 ± 0.01	0.47 ± 0.01	0.47 ± 0.01	0.47 ± 0.01	0.43 ± 0.01
20:5n-3 [a]	7.40 ± 0.45	8.15 ± 0.33	9.29 ± 0.27	9.94 ± 0.24	9.40 ± 0.23
21:5n-3	0.44 ± 0.02	0.41 ± 0.02	0.38 ± 0.01	0.36 ± 0.01	0.34 ± 0.00
22:5n-3 [a]	3.68 ± 0.09	3.40 ± 0.08	3.24 ± 0.07	3.08 ± 0.08	3.03 ± 0.09
22:6n-3 [a]	6.19 ± 0.28	5.09 ± 0.13	4.46 ± 0.06	4.26 ± 0.05	4.30 ± 0.05
Subtotal	22.49 ± 0.62	21.87 ± 0.41	22.18 ± 0.34	22.48 ± 0.30	21.86 ± 0.27
Total	98.28 ± 0.03	98.35 ± 0.04	98.36 ± 0.04	98.37 ± 0.03	98.34 ± 0.03

[a] Indicates FA used to assess extent of stratification.

(Stevens, 1996); thus, with a sample size of 64, we were limited to only 12 FA. Repeated measures multivariate analysis of variance (MANOVA) was then carried out on the PC scores with layer, year, season and gender as factors and body length (as a proxy for age) as a covariate. Similarly, to assess variation in FA composition with body site within individuals, these PC scores for inner and outer layers at different body sites were compared using repeated measures MANOVA.

Effects of season and year on FA composition were examined with two separate PCA on FA expected to vary with those factors (Table 3). Bowheads spend much of the summer in the Canadian Beaufort Sea where copepods are plentiful and thought to dominate diets (Saupe et al., 1989; Lowry et al., 2004). In fall, on their westward migration back to the Chukchi and Bering seas, euphausiids are apparently consumed in much greater proportions than copepods. Thus, any differences in blubber FA with season should be driven by differences in FA composition of copepods and euphausiids. Iverson et al. (2002) determined the FA composition of copepods and euphausiids from the Chukchi and Bering Seas and, based on this work, 12 FA (16:0, 16:1n-7, 16:3n-4, 16:4n-1, 18:0, 18:1n-9, 18:1n-7, 18:4n-3, 20:1n-9, 20:1n-7, 22:1n-11 and 22:1n-9; Table 3) showing the greatest differences between the two organisms were selected for the analysis. For yearly effects, we expected the FA composition of blubber to vary with yearly changes in phytoplankton FA. In the Bering and Chukchi Seas, ice algal diatoms and spring bloom phytoplankton are the principal sources of primary productivity (Booth and Horner, 1997), with some contribution from autotrophic flagellates and dinoflagellates. The relative abundance of each class is dependant on the extent of yearly ice coverage and each type of phytoplankton has a distinct FA signature (Budge et al., in review) that is expected to vary with changes in water temperature, nutrient content and incident light levels (Mortensen et al., 1988; Harrison et al., 1990; Reitan et al., 1994). Thus, changes in

Table 3
Proportions of FA in the inner blubber layer of bowhead whales collected from 1997–2002 (mean ± SE, $n = 64$)

	1997	1999	2000	2001	2002
	$n = 9$	$n = 7$	$n = 17$	$n = 18$	$n = 13$
Saturates					
10:0	0.22 ± 0.08	0.38 ± 0.10	0.25 ± 0.04	0.35 ± 0.05	0.24 ± 0.11
14:0	4.40 ± 0.19	4.37 ± 0.27	4.46 ± 0.14	4.38 ± 0.10	4.39 ± 0.16
i−15:0	0.12 ± 0.01	0.12 ± 0.01	0.12 ± 0.00	0.12 ± 0.00	0.13 ± 0.01
15:0	0.25 ± 0.01	0.23 ± 0.01	0.25 ± 0.01	0.24 ± 0.00	0.25 ± 0.01
16:0 [a,b]	10.95 ± 0.67	11.02 ± 0.97	11.77 ± 0.51	11.40 ± 0.38	11.82 ± 0.54
i−17:0	0.12 ± 0.00	0.12 ± 0.01	0.12 ± 0.00	0.12 ± 0.00	0.12 ± 0.00
17:0	0.15 ± 0.01	0.14 ± 0.01	0.14 ± 0.01	0.15 ± 0.01	0.16 ± 0.01
18:0[a]	2.53 ± 0.20	2.49 ± 0.16	2.71 ± 0.14	2.92 ± 0.10	2.89 ± 0.14
Subtotal	18.83 ± 1.00	19.03 ± 1.32	19.96 ± 0.65	19.86 ± 0.47	20.12 ± 0.80
Monounsaturates					
14:1n-9	0.18 ± 0.03	0.25 ± 0.04	0.19 ± 0.02	0.26 ± 0.03	0.22 ± 0.05
14:1n-5	0.29 ± 0.04	0.20 ± 0.03	0.24 ± 0.04	0.19 ± 0.01	0.26 ± 0.02
16:1n-11	0.39 ± 0.02	0.38 ± 0.02	0.37 ± 0.01	0.37 ± 0.01	0.38 ± 0.01
16:1n-9	0.20 ± 0.02	0.19 ± 0.02	0.21 ± 0.01	0.22 ± 0.01	0.24 ± 0.01
16:1n-7 [a,b]	15.91 ± 0.76	13.52 ± 0.71	15.07 ± 0.51	13.67 ± 0.27	15.57 ± 0.68
17:1n-8	0.17 ± 0.02	0.13 ± 0.02	0.15 ± 0.01	0.13 ± 0.01	0.17 ± 0.01
18:1n-11	2.23 ± 0.27	2.24 ± 0.22	2.06 ± 0.19	2.38 ± 0.12	2.36 ± 0.21
18:1n-9[a]	11.37 ± 0.80	10.42 ± 1.26	12.13 ± 0.81	11.65 ± 0.78	13.85 ± 0.54
18:1n-7 [a,b]	4.93 ± 0.33	4.01 ± 0.34	4.52 ± 0.15	4.18 ± 0.16	4.77 ± 0.17
18:1n-5	0.59 ± 0.02	0.56 ± 0.02	0.58 ± 0.02	0.60 ± 0.01	0.62 ± 0.02
20:1n-11	2.00 ± 0.22	2.35 ± 0.19	2.12 ± 0.11	2.66 ± 0.14	2.33 ± 0.14
20:1n-9[a]	9.89 ± 1.15	10.91 ± 1.41	9.59 ± 0.72	10.97 ± 0.62	9.03 ± 0.45
20:1n-7 [a,b]	1.81 ± 0.23	2.07 ± 0.24	1.56 ± 0.09	1.69 ± 0.08	1.59 ± 0.08
22:1n-11[a]	4.84 ± 0.49	5.71 ± 1.38	5.19 ± 0.66	5.13 ± 0.63	3.29 ± 0.44
22:1n-9[a]	1.33 ± 0.20	1.79 ± 0.32	1.33 ± 0.14	1.48 ± 0.14	0.99 ± 0.08
22:1n-7	0.32 ± 0.04	0.38 ± 0.06	0.29 ± 0.03	0.31 ± 0.04	0.21 ± 0.02
24:1n-9	0.08 ± 0.01	0.16 ± 0.03	0.14 ± 0.02	0.18 ± 0.02	0.12 ± 0.01
Subtotal	56.44 ± 1.46	55.11 ± 2.11	55.60 ± 0.99	55.90 ± 0.73	55.87 ± 1.18
PUFA					
16:3n-6[b]	0.68 ± 0.02	0.66 ± 0.02	0.66 ± 0.01	0.61 ± 0.01	0.64 ± 0.02
16:3n-4 [a,b]	0.25 ± 0.04	0.30 ± 0.04	0.25 ± 0.02	0.25 ± 0.02	0.21 ± 0.02
16:4n-1 [a,b]	0.35 ± 0.05	0.46 ± 0.07	0.34 ± 0.03	0.37 ± 0.03	0.27 ± 0.03
18:2n-6	0.64 ± 0.02	0.63 ± 0.03	0.67 ± 0.01	0.68 ± 0.01	0.69 ± 0.02
18:2n-4	0.16 ± 0.01	0.13 ± 0.01	0.14 ± 0.01	0.13 ± 0.01	0.14 ± 0.01
18:3n-6[b]	0.14 ± 0.01	0.15 ± 0.01	0.15 ± 0.01	0.15 ± 0.01	0.14 ± 0.00
18:3n-4[b]	0.28 ± 0.01	0.23 ± 0.02	0.23 ± 0.01	0.25 ± 0.01	0.26 ± 0.01
18:3n-3	0.33 ± 0.02	0.29 ± 0.03	0.36 ± 0.01	0.31 ± 0.01	0.30 ± 0.02
18:4n-3[a]	0.69 ± 0.06	0.84 ± 0.15	0.90 ± 0.08	0.82 ± 0.06	0.60 ± 0.05
18:4n-1[b]	0.45 ± 0.03	0.40 ± 0.04	0.36 ± 0.02	0.36 ± 0.02	0.35 ± 0.02
20:2n-6	0.16 ± 0.01	0.15 ± 0.01	0.16 ± 0.00	0.16 ± 0.00	0.16 ± 0.00
20:4n-6	0.29 ± 0.02	0.29 ± 0.02	0.30 ± 0.01	0.29 ± 0.01	0.32 ± 0.01
20:4n-3	0.45 ± 0.02	0.42 ± 0.03	0.46 ± 0.01	0.44 ± 0.01	0.42 ± 0.01
20:5n-3[b]	9.26 ± 0.51	9.42 ± 1.00	8.55 ± 0.42	7.50 ± 0.38	7.78 ± 0.56
21:5n-3	0.42 ± 0.03	0.45 ± 0.03	0.40 ± 0.01	0.44 ± 0.01	0.40 ± 0.02
22:5n-3	3.38 ± 0.15	3.65 ± 0.25	3.23 ± 0.09	3.67 ± 0.08	3.54 ± 0.19
22:6n-3[b]	5.14 ± 0.28	5.74 ± 0.42	5.61 ± 0.19	6.09 ± 0.25	6.10 ± 0.46
Subtotal	23.07 ± 0.66	24.21 ± 1.19	22.74 ± 0.42	22.52 ± 0.53	22.31 ± 0.64
Total	98.34 ± 0.06	98.35 ± 0.04	98.30 ± 0.03	98.28 ± 0.03	98.31 ± 0.05

[a,b] FA used to assess seasonal and yearly differences, respectively, in FA signatures.

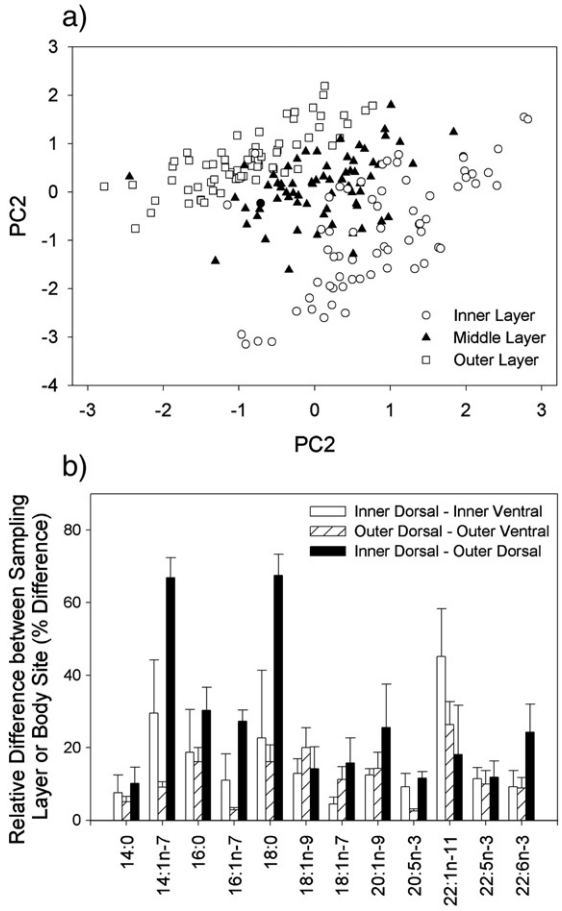

Fig. 1. a) Plot of scores of PC1 and PC2 derived from the analysis of FA for stratification in blubber layers. For clarity, only data for inner, middle and outer layers are shown; b) Comparison of relative differences in FA composition between pairs of samples taken from the same individual at dorsal and ventral sites. Differences between inner layers (inner–inner), outer layers (outer–outer) and inner and outer layers (inner–outer) are shown. Repeated measures MANOVA did not indicate a significant difference in FA composition within inner layers but a significant difference was apparent within the outer layers ($P<0.05$). Comparison of the FA composition of inner with outer layers at the same sampling site also showed a statistically significant difference ($P<0.001$). Comparison of duplicate dorsal samples (data not shown) generated similar results with a significant difference in FA composition apparent between outer samples, while inner samples did not vary significantly.

climate should affect both the species composition and the FA signature of the phytoplankton at the base of the food web, which in turn should be carried through to higher trophic levels, including the bowhead whale. Accordingly, FA that showed the greatest differences between ice algae and spring bloom phytoplankton in a single year (Budge et al., in review), and ice algae over two years (Budge, Springer, Iverson and McRoy, unpublished data) were selected for the PCA (16:0, 16:1n-7, 16:3n-6, 16:3n-4, 16:4n-1 and 20:5n-3; Table 3). Based on the FA composition of the zooplankton consumers, substantial chain elongation of several of these diatom FA seemed likely; thus, those elongated FA, whose levels would also vary with changes in environment and climate, were added to the analysis and included 18:1n-7, 18:3n-6, 18:3n-4, 18:4n-1, 20:1n-7, 22:6n-3. ANOVA and MANOVA were carried out on the resultant PC scores.

Without *a priori* reasons to select particular FA to investigate gender and location effects, the 12 FA with the greatest variance were chosen for PCA. Confounding of data due to season and location effects was avoided by first assessing the effect of collection location on FA composition with season held constant (i.e., only fall samples were analyzed for location effects).

3. Results

3.1. Variation within individuals — blubber depth and body site

The FA compositions of bowhead whales were characterized by typical marine FA, and were dominated by 14:0, 16:0, 16:1n-7, 18:0, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 22:1n-11, 22:1n-9, 20:5n-3, 22:5n-3 and 22:6n-3 (Tables 2 and 3). To assess variation among blubber layers, PCA of the entire data set (5 blubber layers X 62 whales) was carried out on specific FA (see Methods). This generated 2 PC that explained 86% of the variance (Fig. 1a). The FA with the highest loadings on PC1 were 16:0, 18:0, 22:1n-11 and 22:6n-3 and on PC2 were 14:1n-5, 16:1n-7, 18:1n-9 and 18:1n-7. To address the confounding of data, a preliminary repeated measures MANOVA was carried out on the PC scores of only fall data to assess the effect of collection location on FA blubber composition (see below). A significant effect was not found and thus collection location was not used as a factor in the subsequent analysis. Repeated measures MANOVA on all data showed a significant effect (Wilks' $\lambda=0.431$, $P<0.001$) of layer on FA composition. A significant interaction of layer with body length was also found (Wilks' $\lambda=0.64$, $P<0.005$).

Relative differences in FA proportions were used to illustrate variation in FA composition with body sites within a single whale (Fig. 1b). Repeated measures MANOVA on the PC scores from above did not indicate a significant differences among inner layers taken at two separate body sites, while comparison of outer layers did reveal a statistically significant difference (Wilkes' $\lambda=0.279$, $P<0.05$).

3.2. Variation among individuals — gender, body length, geographic location, season and year

Since clear differences were apparent among the blubber layers, only the innermost layer, thought to best represent more recent diet (Iverson et al., 2004; Cooper, 2004), was analyzed. The 12 FA with the greatest variance in that layer included 14:0, 16:0, 16:1n-7, 18:1n-11, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:5n-3, 22:1n-11, 22:1n-9 and 22:6n-3. PCA of these FA generated two PC that accounted for 82% of the variance in the data. MANOVA on the PC scores of samples collected in the fall using location, gender, year and body length as factors did not show any significant differences due to geographic location. Subsequent MANOVA on the full data set using the same factors, plus season, did not reveal any significant differences. In all of the following analyses with PCA and MANOVA, the data failed to show a significant difference due to location or gender.

PCA on FA expected to vary by season generated one PC, accounting for 76% of the variance. The FA 18:1n-9, 22:1n-11 and 22:1n-9 had the highest loadings on that component. ANOVA on the single PC revealed seasonal ($F=5.33$, $P<0.05$) and body length ($F=11.06$, $P<0.01$) effects. Similarly, PCA on FA that were expected to vary by year produced

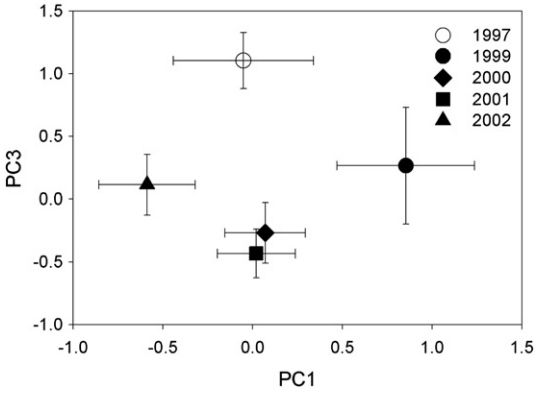

Fig. 2. Plot of scores of PC1 and PC3 (mean ± SE) representing the influence of year on FA composition. Years 2000 and 2001 clearly separate on plots of PC1 vs PC2.

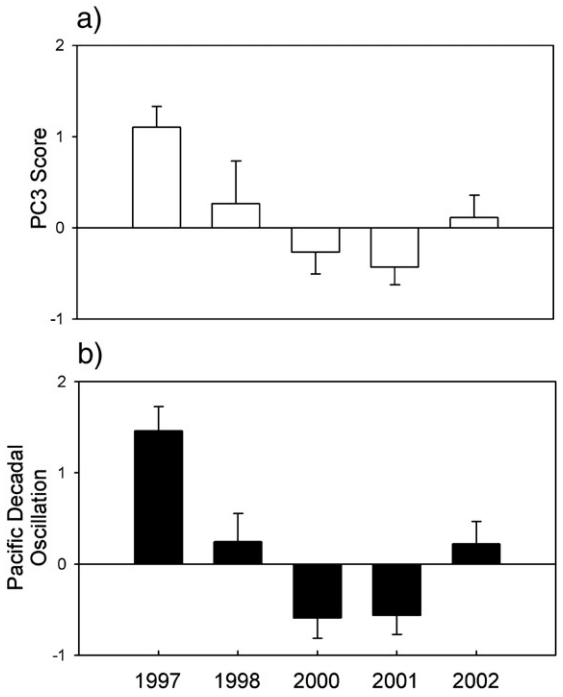

Fig. 3. Correlation of the scores of PC3 (mean±SE, $n=64$) for yearly effects on FA signature with the Pacific Decadal Oscillation (mean±SE; $r=0.99$, $P<0.005$): a) the third component derived from a PCA of plankton FA in bowhead blubber was found to vary significantly with year and is plotted against sampling year; and b) the Pacific Decadal Oscillation, an index of climate variation, is calculated monthly. The averages of the PDO for the first four months of each year are plotted against year.

three PC, representing 83% of the variance (Fig. 2). On PC1, 16:3n-4 and 16:4n-1 were heavily loaded, while PC2 was influenced by 16:0 and 20:5n-3. Only 18:4n-1 loaded high on PC3. MANOVA on the three components yielded a significant length ($\lambda=4.63$, $P<0.005$) and year effect ($\lambda=2.5$, $P<0.001$). Only PC3 had a significant influence on the year effect. A significant year*season effect was also apparent ($\lambda=2.27$, $P<0.05$), also driven by PC3. To investigate a possible link between this significant interannual variability of FA signatures of bowhead whale blubber and climatic change, the scores of PC3 were compared with the mean values of the Pacific Decadal Oscillation (PDO; Fig. 3) for January through April of each year. The PDO is an index of climate, based on variability in sea surface temperature in the North Pacific and is known to mirror ecological changes such as zooplankton biomass and fish recruitment (Hare and Mantua, 2000). We assumed that the PDO in those four winter months preceding sampling would best reflect environmental conditions that would be affecting primary production and, indirectly, the FA composition of blubber (i.e., extent of sea ice, sea surface temperature, etc.). The correlation was highly significant ($r=0.99$, $P0.005$).

4. Discussion

4.1. Variation in FA composition within individuals

4.1.1. Stratification and body site

Vertical stratification of FA composition in blubber has been reported in pinnipeds (Käkelä and Hyvärinen, 1996; Best et al., 2003; Thiemann et al., 2004) and especially cetaceans (Ackman et al., 1975; Koopman et al., 1996; Hooker et al., 2001; Olsen and Grahl-Neilsen, 2003; Reynolds et al., 2006), and likely occurs to some degree and in various FA in most marine mammals that deposit blubber. The patterns of stratification differ among species but some consistencies do exist. For example, all marine mammals examined in those studies had higher monounsaturated FA 14:1n-5, 16:1n-7 and occasionally 18:1n-9, and lower saturated FA 16:0 and 18:0 in the outer than in the inner blubber layers. The same patterns were present in the bowheads. In addition, bowheads showed some variation with depth in levels of PUFA such as 16:3n-6, 21:5n-3, 22:5n-3 and 22:6n-3 (Table 2). Reynolds et al. (2006) also noted stratification in levels of 20:5n-3 and 22:6n-3, albeit opposite of that identified here; such discrepancy can likely be attributed to the low sample size ($n=1$) in that report.

A number of explanations have been proposed for this structure. For instance, Pond (1998) has suggested that a particular arrangement of FA might enhance membrane fluidity in the outer blubber layers, while Käkelä and Hyvärinen (1996) have proposed that FA stratification improves the insulation properties of blubber. It is also possible that this distribution might be due, in part, to both mobilization and replenishment of dietary polyunsaturated FA (PUFA) from the inner layer of blubber, perhaps with an accumulation of readily biosynthesized FA (e.g., 14:0, 14:1n-5, 16:0, 16:1n-7 and 18:0) in the outer layer (Koopman et al., 1996). Although FA stratification was apparent in bowheads, the magnitude of this stratification was relatively small, similar to that found in other large whales such as bottlenose whales (*Hyperoodon ampullatus*, Hooker et al., 2001) and sperm and right whales (*Physeter macrocephalus* and *Eubalaena glacialis*, respectively, S.J. Iverson, unpublished data). In contrast, stratification is much more extensive in smaller cetaceans. For example, Koopman et al. (1996) found up to 4-fold differences in the amounts of certain FA between inner and outer blubber layers in the harbour porpoise (*Phocoena phocoena*), perhaps relating to increased insulative properties required by small species.

We did not find significant differences in FA composition among inner blubber layers sampled at different body locations (i.e., duplicate samples on the dorsal surface or opposite dorsal and ventral sites near the abdomen) on the same animal. In contrast, Reynolds et al. (2006) reported a difference between dorsal and ventral FA composition but, with their small sample size, we are unable to evaluate if that difference was significant. In our data set, differences due to stratification were much more obvious, demonstrating that stratification exerts a much stronger effect on FA composition than body site (Table 1 and Fig. 1b). Site-specific FA compositions have been noted in other cetaceans (Ackman and Lamothe, 1989; Olsen and Grahl-Neilsen, 2003), but this variation seems to only be apparent when body sites with very different functions are compared (e.g., the highly structured caudal peduncle vs. the fat storage area of the thorax; Koopman et al., 1996). Our samples were not collected from body sites that would be expected to have any function other than insulation and energy storage. Certainly, if one considers that variation in FA composition due to stratification is small, the comparative difference in FA composition observed with body site is irrelevant. The relatively small FA stratification encountered in these large whales raises the possibility that diet could be qualitatively inferred or perhaps even estimated from more outer blubber layers, as suggested by Hooker et al. (2001). This can be evaluated more clearly in the future with QFASA modeling and a comprehensive prey database for bowheads.

4.2. Variation in FA composition among individuals

4.2.1. Gender, geographic location and body length

To minimize the slight variation in FA composition due to stratification, only the innermost layer, thought to best reflect diet, was analyzed to assess variation among individual bowheads. Within this layer, the gender of the whale did not have a significant effect on the FA profile. Male and female bowhead whales are not size dimorphic and, although they do not necessarily migrate together as a group, they do share the same ranges (Moore and Reeves, 1993). Thus, we expect the whales to consume similar diets, regardless of gender. Lowry et al. (2004) reported that the stomach contents of males and females were virtually identical and our analysis of blubber FA supports this.

Bowheads were collected in Kaktovik in the fall only, so to assess variation in FA composition with location we were restricted to comparisons of those whales to others collected in the fall at Barrow. The subsequent PCA and MANOVA of the inner blubber layers did not show a significant difference due to location. This might suggest that the diets of whales in the two locations are similar. However, Lowry et al. (2004) found the stomachs of whales collected in Kaktovik more frequently contained copepods, while euphausiids and amphipods occurred more often in stomach contents in whales taken near Barrow. Nevertheless, these seemingly contrasting results may be providing complimentary information. The FA data suggest that over time, the average diet of whales migrating through both areas was rather constant, while stomach content analyses suggest a shift from a diet high in copepods in Kaktovik to one high in euphausiids in Barrow. Zooplankton surveys have shown that copepods dominate the zooplankton of the Canadian and eastern Alaskan Beaufort Sea where most bowheads summer (Saupe et al., 1989). If bowheads do feed on copepods for several months while in that area (see below), we would expect the FA composition in the blubber of whales harvested at Barrow to be similar to that of whales harvested at Kaktovik. Barrow and Kaktovik are only 500 km distant and a whale might travel between the two areas in as little as one week (see Mate et al., 2000 for estimated swim speeds). It is doubtful that even extensive feeding on euphausiids in such a short time would have a large impact on blubber FA. It is this integrated record of diet over time preserved in blubber that makes FA analysis particularly useful in examining foraging ecology.

In every comparison, body length of individuals was found to have a significant effect on bowhead blubber FA composition, suggesting that diets vary with the age of the whale. Although there has been little support for diet variation with age from bulk stable isotope analysis (Hoekstra et al., 2002; Lee et al., 2005), analyses of stomach contents have suggested that size-related differences in diet might exist. While not statistically significant, Lowry et al. (2004) reported that benthic taxa, such as fish and isopods, occurred more frequently in bowheads <13 m in length. In addition, young bowheads of lengths up to 8 m may still be nursing (Koski et al., 1993); Lowry and Sheffield (2002) found only milk in the stomach of one whale 7 m in length. Thus, smaller whales in the present study may have been consuming milk and proportionally more benthic invertebrates and fish than the larger whales. Although milk FA signatures arise largely from the mothers' diet, we would expect FA signatures in bowhead milk to be somewhat different from the prey (e.g., Smith et al., 1997), and this might contribute to the significant differences in FA profiles of shorter, younger individuals.

4.2.2. Season and year effects

The annual migration of bowheads through the Bering, Chukchi and Beaufort Seas is well known; however, it is the relative importance of the Beaufort Sea vs. the Bering and Chukchi Sea as feeding habitat that remains an issue of debate. Based on bulk stable isotope analysis of muscle, Lee et al. (2005) contended that the eastern Beaufort is unimportant as a feeding ground, while Hoekstra et al. (2002), using the same technique, suggested that their data indicated significant feeding in the Beaufort Sea. A third study, using stomach content analysis, also suggested that extensive feeding occurs in the Beaufort (Lowry et al., 2004). The seasonal differences we found in blubber FA of whales taken in spring and fall at Barrow support the notion that the eastern Beaufort Sea is an important feeding ground.

We based our PCA analysis on FA that displayed the greatest variation between euphausiids and copepods (see Methods), simply because any change in bowhead blubber FA composition due to diet should be most easily detected with those FA. Thus, the significant effect of season on blubber FA composition was interpreted as indicating distinct diets. If bowheads were not feeding to any significant extent in the eastern Beaufort, they would be forced to mobilize FA from blubber for energy. Although differential mobilization of specific FA from fat stores during fasting has been documented in penguins and, over time, might be expected to result in altered blubber FA profiles (Groscolas, 1990), no data is available to evaluate its influence in cetaceans. Differential mobilization has been known to primarily influence 20:1n-9 and 20:5n-3, where 20:1n-9 is selectively retained and 20:5n-3 selectively mobilized (Groscolas, 1990). In the PCA conducted to assess seasonal effects, 20:5n-3 was not included and 20:1n-9 had minimal influence on the PC extracted. Furthermore, the average levels of 20:1n-9 in bowhead blubber were greater in the spring, displaying the opposite trend to that expected if differential mobilization was occurring. Thus, we are confident that our results represent a real change in diet, rather than simply the effects of fasting.

FA analysis of plankton at the base of the food web has shown dramatic differences in FA profiles among organisms (Budge et al., in review) and between years (Budge, Springer, Iverson and McRoy, unpublished data). These differences were chiefly represented in phytoplankton by FA synthesized by diatoms (16:1n-7, 16:3n-6, 16:3n-4, 16:4n-1) and in zooplankton by the elongation products of the diatom FA (18:1n-7, 18:3n-6, 18:3n-4, 18:4n-1 and 20:1n-7). We expected these changes in plankton FA to be reflected also in the FA profiles of whales that feed near the base of the food web. Indeed, the data did show a significant effect for year, driven mostly by changes in 18:4n-1. The yearly variations in plankton FA profiles that were reflected in the bowhead blubber were likely due to yearly variations in climate. It is well known that subtle differences in incident light, nutrients, water temperature and salinity, that can be expected with a variable climate, influence the FA composition of phytoplankton (Harrison et al., 1990; Thompson et al., 1992; Reitan et al., 1994; Renaud and Parry, 1994). For example, Skerratt et al. (1998) showed that the lipid content of *Chaetoceros simplex*, a common Antarctic diatom, increased with UV-B irradiation, while Mortensen et al. (1988) found that silicate limitation of *C. gracilis* resulted in lower PUFA levels. More recently, Rousch et al. (2003) have demonstrated that an increase in culture temperature for a period as short as 2 h produced significant decreases in levels of 16:1 and 20:5n-3 in another marine diatom, *Phaeodactylum tricornutum*. Yearly climate variation will also affect the relative distribution of phytoplankton species (e.g., Tynan, 1998), most of which have species-specific FA compositions (e.g., Viso and Marty, 1993). Shifts in their proportions will result in an overall shift in FA signature of the general algae pool. Thus, effects of climate shifts should be apparent in the FA profiles of phytoplankton. When the phytoplankton are consumed, these variations are passed to the zooplankton grazers and, in turn, to carnivorous zooplankton and filter-feeding whales, such as the bowhead. This tight link to the base of the food web implies that interannual variability of FA signatures of bowhead whale blubber should reflect climatic change.

To further investigate this possibility, we compared the scores of PC3 that showed a significant yearly effect with the mean values of the PDO for January through April of each year (Fig. 3). The highly significant correlation ($r=0.99$, $P<0.005$) showed clear synchrony in variation of blubber FA with this climate index and indicates that climate is having an effect on plankton FA composition that is subsequently preserved in the bowhead whale blubber. Correlations between fluctuations in fish stocks and plankton biomass (Hare and Mantua, 2000), marine mammals (Francis et al., 1998) and seabirds (Vandenbosch, 2000) with variation in the PDO have been demonstrated. Indeed, Hare and Mantua (2000) have suggested that climate shifts may be best studied by monitoring marine organisms and ecosystems rather than the physical or oceanographic characteristics of climate. However, this is the first demonstration of a correlation of PDO with a biochemical index and suggests that these FA patterns may be used to monitor environmental change at the base of the food web. Analyses of our archived blubber samples collected in 2003–2008 will allow us to further evaluate this application of bowhead blubber FA in monitoring climate change in the Arctic.

In conclusion, FA evidence from bowhead whales suggests that diets vary with both age and season, but not by gender, and that bowheads do feed extensively in the eastern Beaufort Sea in summer. More interesting is the potential to use bowhead blubber FA to monitor ecological change at the base of the food web that is driven by climate variation. Although a longer time series would be necessary to conclusively demonstrate such a result, preliminary data over a 6 year period are extremely promising.

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