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Contemporary Diet of Bowhead Whales (*Balaena mysticetus*) from the Eastern Canadian Arctic Inferred from Fatty Acid Biomarkers

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ABSTRACT. The diet and feeding ecology of Eastern Canada–West Greenland bowhead whales were examined using fatty acid (FA) composition of the outer blubber layer of 50 individuals sampled during the summers of 2008 and 2009. Bowhead blubber was rich in the following FAs: 14:0, 16:0, 16:1n–7, 18:0, 18:1n–11, 18:1n–9, 18:1n–7, 20:1n–11, 20:1n–9, 20:1n–7, 20:5n–3, 22:1n–11, 22:1n–9, 22:5n–3, and 22:6n–3, which together accounted for 91% of total FAs identified. Four groups of bowhead whales were identified from their FA signatures using multivariate analysis. Long-chain monounsaturated fatty acids (MUFAs) (20:1n–9, 20:1n–11, 22:1n–9, and 22:1n–11) and polyunsaturated fatty acids (PUFAs) (20:5n–3, 22:5n–3, 22:6n–3) accounted for most of the variance among groups. Whales from a single sampling site segregated into different groups, some of which included whales from other sampling sites, suggesting summer mixing of whales from different wintering areas and prey assemblages, or alternatively, selective feeding. FA composition was similar in males and females and among whales of different age classes, which suggests that these different groups shared foraging areas and had similar diets. The blubber of bowhead whales from the eastern Canadian Arctic was composed of high proportions of calanoid copepod markers (20:1n–9 and 22:1n–11), especially compared to the adipose tissue of western Arctic bowhead whales. This finding suggests that *Calanus* spp. were likely a major prey item. Given the expected change in Arctic zooplankton assemblages with climate warming, bowhead whales, through their FA biomarkers, may serve as sentinels of change in Arctic ecosystems.

Key words: Arctic, bowhead whale, *Balaena mysticetus*, blubber, calanoid copepods, diet, fatty acids, feeding ecology, zooplankton

RÉSUMÉ. Afin d'approfondir les connaissances sur la diète et l'écologie alimentaire de la baleine boréale de la population EC-WG, nous avons examiné la composition en acides gras de la couche de graisse sous-cutanée de 50 animaux échantillonnés durant les étés 2008 et 2009. Les baleines boréales étaient riches en certains acides gras (AG) notamment 14:0, 16:0, 16:1n-7, 18:0, 18:1n-11, 18:1n-9, 18:1n-7, 20:1n-11, 20:1n-9, 20:1n-7, 20:5n-3, 22:1n-11, 22:1n-9, 22:5n-3 et 22:6n-3. Ces 15 acides gras constituaient 91 % de tous les acides gras identifiés. Nous avons identifié quatre groupes de baleines à l'aide d'une analyse composée principale dans une analyse de fonction discriminante. Les acides gras monoinsaturés à longue chaîne (MUFAs) (20:1n-9, 20:1n-11, 22:1n-9 et 22:1n-11) et les acides gras Oméga-3 polyinsaturés (PUFAs) (20:5n-3, 22:5n-3 et 22:6n3) étaient responsables de la majorité de la variance entre les groupes de baleines. Chacun des quatre groupes de baleines était constitué d'animaux provenant d'une même région ainsi que de régions différentes. Ces résultats suggèrent que des baleines boréales avec des sites d'hivernage différents partagent un même site d'alimentation estival et/ou que les baleines boréales ont une alimentation sélective. La composition en acide gras du tissu adipeux était semblable chez les mâles et les femelles ainsi qu'entre les individus de différentes classes de tailles, ce qui suggère une diète similaire ou des aires d'alimentation communes. Le tissu adipeux des baleines boréales de l'Arctique de l'Est canadien était constitué d'une plus grande proportion de marqueurs spécifiques de copépodes calanoides (20:1n–9 et 22:1n–11) comparativement aux baleines boréales de l'Arctique de l'Ouest. Les résultats de notre étude suggèrent que *Calanus* spp. est une proie importante de la diète des baleines boréales de la population de l'est du Canada et de l'ouest du Groenland. Compte tenu de l'évolution attendue dans les assemblages de zooplancton de l'Arctique en raison du réchauffement climatique, les baleines boréales, par leurs biomarqueurs AG, peuvent servir de sentinelles des changements dans les écosystèmes.

Mots clés : Arctique, acides gras, baleine boréale, *Balaena mysticetus*, couche de graisse, copépodes calanoides, diète, écologie alimentaire, lipides, zooplancton

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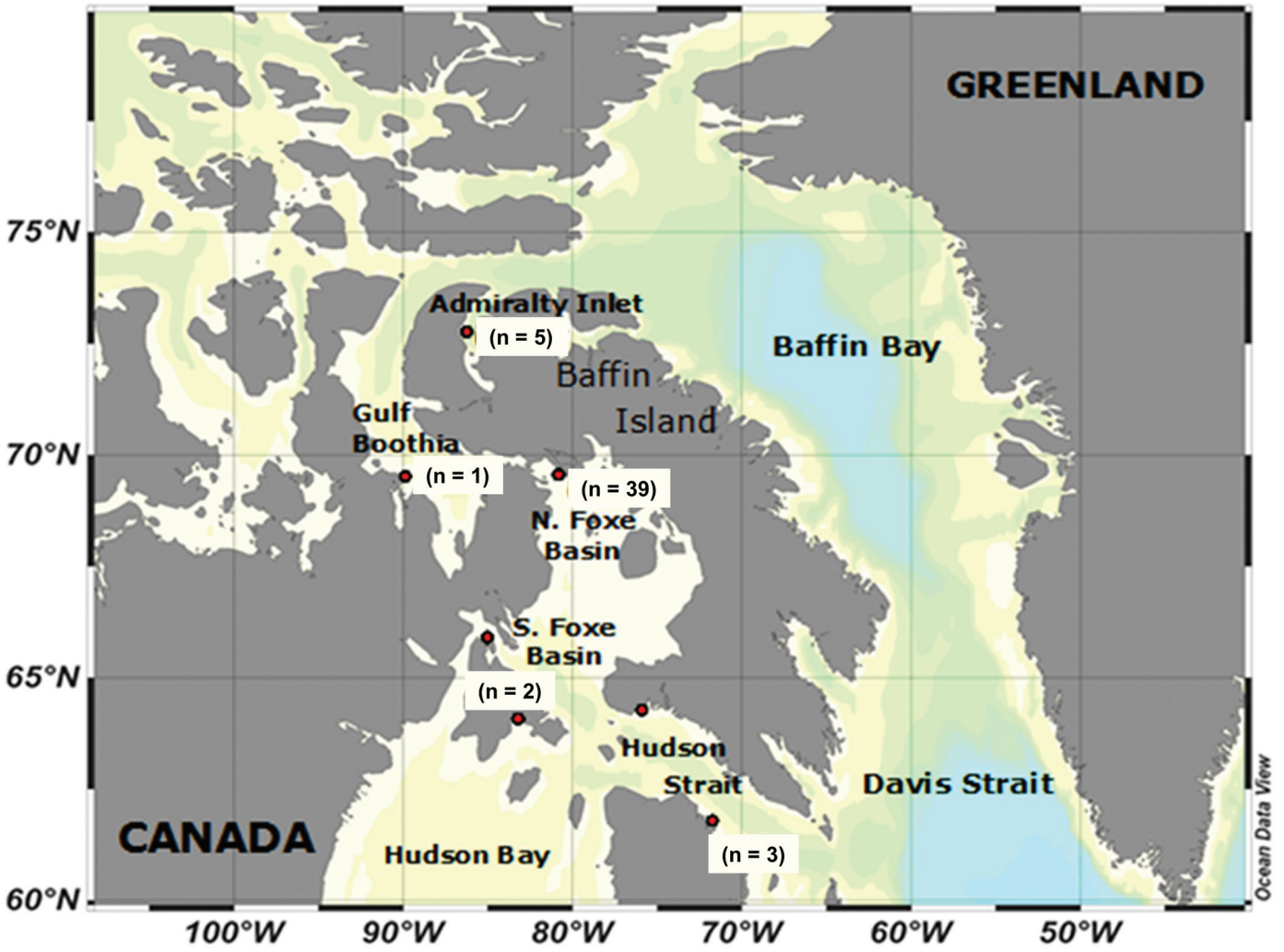

FIG. 1. Sampling locations for bowhead whales (n = 50) in the eastern Canadian Arctic. The five sampling regions are Admiralty Inlet, Gulf of Boothia, Northern Foxe Basin, Southern Foxe Basin, and Hudson Strait.

INTRODUCTION

Feeding ecology of bowhead whales (*Balaena mysticetus*) has been assessed in two different Arctic populations. The diet of the Eastern Canada-West Greenland (EC−WG) population consists primarily of calanoid copepods, mysids, and euphausids, and was inferred using short-term, indirect, and qualitative approaches, such as surface feeding observations, stomach content analysis, plankton net sampling, dive data, and stable isotope ratios (Finley, 2001; Lowry et al., 2004; Lee et al., 2005; Laidre et al., 2007; Pomerleau et al., 2011a, 2012). In the western Arctic, the diet of the Bering−Chukchi−Beaufort (BCB) bowhead whale population has been characterized previously using stable isotopes and stomach contents (Lowry et al., 2004; Lee et al., 2005). Recently, fatty acid composition was also examined and proved to be a useful complement to the other approaches to improving our understanding of BCB bowhead whale diet (Budge et al., 2008a); however, fatty acid composition has not yet been investigated for the EC−WG population.

Fatty acids (FAs) can be used both qualitatively and quantitatively to infer feeding ecology of free-ranging predators (Iverson, 2009). While some FAs can be used as markers for ingestion of specific prey, it is often the relative abundance of some specific long-chain FAs that is used to infer predator-prey relationships and food web structure (Iverson et al., 1997, 2004; Dahl et al., 2000; Hooker et al., 2001; Best et al., 2003; Dalsgaard et al., 2003; Thiemann et al., 2008). However, some specific long-chain polyunsaturated FAs (PUFA), biosynthesized by primary producers (Sargent et al., 1987) are transferred in a relatively conservative way to consumers (Dalsgaard et al., 2003). For instance, the FAs 20:5n−3 (EPA) and 22:6n−3 (DHA) are a diatom and a dinoflagellate marker, respectively (Kates and Volcani, 1966; Graeve et al., 1994), and the ratio of these FAs may provide information on the relative importance of the food webs derived from these phytoplankton resources. Similarly, long chain monounsaturated FAs (MUFAs) of 20:1 and 22:1 are formed de novo in calanoid copepods (Kattner and Hagen, 1995). Thus, direct consumption

of copepods or consumption of copepod predators can be inferred from the relative importance of specific FAs in consumers at higher trophic levels. Also, cetaceans are generally gregarious (Whitehead and Lusseau, 2012), and FAs can be used to gain insights into dietary patterns among whales of different age or sex classes in feeding areas.

Blubber in marine mammals is a dynamic tissue that serves several functions, including insulation and fat storage (Iverson et al., 1995). Marine mammal blubber reflects the diet composition and dietary intake of prey over a period of weeks to months (Iverson et al., 1995, 2004). Vertical stratification of FAs in the blubber layer of marine mammals has been documented in pinnipeds (Best et al., 2003; Thiemann et al., 2004) and cetaceans (Thiemann et al., 2008; Strandberg et al., 2008), although the degree of stratification appears to be less in larger cetaceans (Hooker et al., 2001; Koopman, 2007). In general, the outer blubber layer is composed of a larger proportion of biosynthesized components and MUFAs less than 18 carbons in length than the inner blubber layer, which is more metabolically active and contains greater amounts of MUFAs with 18 carbons or more, non-branched saturated FAs (SFAs), and PUFAs (Koopman et al., 1996; Smith and Worthy, 2006). In bowhead whales, the FA compositions of the inner and outer layers differ, but the extent of the stratification is relatively small, and one can make reliable general inferences about diet based on the outer layer alone (Budge et al., 2008a). Here we assess the feeding ecology and diet of EC–WG bowhead whales by examining how the FA composition of the outer blubber layer varies among individuals.

METHODS

Study Area and Sample Collection

Bowhead whale blubber samples (n = 50) were collected in July–September of 2008 (n = 7) and 2009 (n = 43) in five regions within the summer range of the EC–WG bowhead whale population in the eastern Canadian Arctic (Fig. 1; Table 1). The vast majority (n = 39) of the samples came from northern Foxe Basin. Blubber samples consisted of the outer layer and were obtained from live individuals using a crossbow darting system (n = 45) (Brown et al., 1991), or from dead carcasses through subsistence harvests (n = 5). Samples from the outer blubber layer of dead whales were measured from beneath the attached epidermis (not included). Average length of all blubber was approximately 1 cm. Samples were preserved frozen in liquid nitrogen or at –80˚C until lipid analysis. Age class was assessed visually (by length) in the field. The sample of 50 whales included 15 adults (> 13 m long), 22 subadults (8 – 13 m long), 12 immature whales (< 8 m long), and one individual of unknown age. Sex was determined genetically (Shaw et al., 2003; Petersen et al., 2011) for 46 of the 50 whales (19 females and 27 males) (Table 1).

TABLE 1. Data collected for bowhead whale specimens: Whale identity number, year, month, and geographical region of sample collection, sex, maturity status, and group identity. Region codes: AI – Admiralty Inlet, GB – Gulf of Boothia, HS – Hudson Strait, NFB – northern Foxe Basin, and SFB – southern Foxe Basin (See Fig. 1). "U" under Sex means undetermined. Group identity was determined through a discriminant analysis of principal components (See Fig. 2).

Specimen ID	Year	Month	Region	Sex	Status	Group
1	2009	August	AI	F	Subadult	3
2	2009	August	AI	M	Adult	4
3	2009	August	AI	F	Subadult	4
4	2009	August	AI	M	Adult	4
5	2009	August	AI	F	Immature	3
6	2008	September	GB	M	Subadult	4
7	2009	August	HS	F	Adult	4
8	2009	September	HS	M	Adult	3
9	2008	August	HS	M	Adult	4
10	2009	July	NFB	M	Subadult	3
11	2009	July	NFB	M	Subadult	4
12	2009	July	NFB	F	Subadult	4
13	2009	July	NFB	F	Subadult	1
14	2009	July	NFB	M	Immature	3
15	2009	July	NFB	F	Immature	3
16	2009	July	NFB	F	Immature	3
17	2009	July	NFB	M	Subadult	3
18	2009	July	NFB	M	Immature	3
19	2009	July	NFB	F	Immature	4
20	2009	July	NFB	M	Immature	4
21	2009	July	NFB	F	Immature	1
22	2009	July	NFB	M	Adult	3
23	2009	July	NFB	M	Subadult	3
24	2009	July	NFB	M	Subadult	3
25	2009	July	NFB	M	Subadult	2
26	2009	July	NFB	M	Subadult	3
27	2009	July	NFB	F	Adult	2
28	2009	July	NFB	U	Subadult	3
29	2009	July	NFB	F	Immature	4
30	2009	July	NFB	U	Immature	4
31	2009	July	NFB	F	Adult (cow)	3
32	2009	July	NFB	M	Immature	4
33	2009	July	NFB	M	Adult	2
34	2009	July	NFB	M	Subadult	3
35	2009	July	NFB	F	Adult (cow)	1
36	2009	July	NFB	F	Subadult	4
37	2009	July	NFB	F	Adult	3
38	2009	July	NFB	U	Adult	1
39	2009	July	NFB	M	Subadult	1
40	2009	July	NFB	M	Subadult	1
41	2009	July	NFB	F	Adult	3
42	2009	July	NFB	M	Immature	2
43	2009	July	NFB	M	Subadult	4
44	2009	July	NFB	M	Subadult	4
45	2008	July	NFB	F	Subadult	3
46	2008	July	NFB	M	Unknown	4
47	2008	July	NFB	F	Subadult	2
48	2008	July	NFB	M	Adult	1
49	2009	August	SFB	F	Adult	2
50	2008	September	SFB	U	Subadult	4

Fatty Acid Extraction

Lipids were extracted from 0.5 g of the outer blubber layer using a 2:1 chloroform-methanol solution containing 0.01% butylated hydroxytoluene (BHT) (v/v/w) (Folch et al., 1957). Gas chromatographic analyses were performed following the method developed by Thurnhofer and Vetter (2005). We identified 69 fatty acids with verification via

TABLE 2. Blubber fatty acid (FA) composition of 45 bowhead whales. Mean (± SE) values of the 42 FAs that contributed more than 0.1% of total FA weight are given for each of three age classes of males and females. SFAs = saturated fatty acids, MUFAs = monounsaturated fatty acids, and PUFAs = polyunsaturated fatty acid.

FA	Male			Female		
	Adult (n = 7)	Subadult (n = 13)	Immature (n = 5)	Adult (n = 7)	Subadult (n = 7)	Immature (n = 6)
SFAs:						
14:0	3.08 ± 0.14	3.28 ± 0.07	3.20 ± 0.04	3.53 ± 0.26	3.13 ± 0.07	2.82 ± 0.2
14:0 iso	0.11 ± 0.02	0.09 ± 0.00	0.10 ± 0.00	0.10 ± 0.01	0.09 ± 0.00	0.12 ± 0.1
15:0	0.17 ± 0.01	0.17 ± 0.00	0.17 ± 0.00	0.18 ± 0.01	0.17 ± 0.00	0.16 ± 0.0
16:0	4.64 ± 0.24	5.34 ± 0.12	5.16 ± 0.20	5.23 ± 0.39	4.79 ± 0.22	4.68 ± 0.3
18:0	0.89 ± 0.07	1.17 ± 0.06	1.12 ± 0.12	0.96 ± 0.11	1.08 ± 0.10	1.17 ± 0.3
20:0	0.11 ± 0.01	0.11 ± 0.00	0.10 ± 0.00	0.13 ± 0.01	0.10 ± 0.01	0.11 ± 0.0
23:0	0.22 ± 0.03	0.24 ± 0.02	0.23 ± 0.03	0.24 ± 0.04	0.27 ± 0.02	0.25 ± 0.1
Subtotal	**9.22 ± 0.38**	**10.40 ± 0.21**	**10.08 ± 0.37**	**10.37 ± 0.70**	**9.63 ± 0.37**	**9.31 ± 0.26**
MUFAs:						
14:1n−5	0.62 ± 0.03	0.61 ± 0.03	0.58 ± 0.05	0.72 ± 0.07	0.62 ± 0.06	0.59 ± 0.03
16:1n−11	0.42 ± 0.05	0.39 ± 0.02	0.38 ± 0.01	0.36 ± 0.04	0.39 ± 0.02	0.49 ± 0.05
16:1n−9	0.27 ± 0.01	0.29 ± 0.01	0.27 ± 0.01	0.26 ± 0.01	0.30 ± 0.02	0.34 ± 0.02
16:1n−7	18.90 ± 0.68	19.90 ± 0.44	19.55 ± 0.37	20.64 ± 1.66	19.21 ± 0.81	19.49 ± 0.44
16:1n5	0.26 ± 0.00	0.28 ± 0.01	0.29 ± 0.01	0.29 ± 0.02	0.28 ± 0.01	0.25 ± 0.01
18:1n−11	4.68 ± 0.37	4.26 ± 0.13	4.22 ± 0.18	3.85 ± 0.27	4.72 ± 0.20	5.10 ± 0.21
18:1n−9	9.82 ± 0.59	10.48 ± 0.34	9.84 ± 0.54	9.83 ± 0.59	10.45 ± 0.59	11.76 ± 0.56
18:1n−7	2.85 ± 0.11	3.25 ± 0.10	3.16 ± 0.16	3.07 ± 0.28	3.30 ± 0.21	3.20 ± 0.26
18:1n−5	0.56 ± 0.01	0.61 ± 0.01	0.63 ± 0.04	0.58 ± 0.02	0.63 ± 0.03	0.62 ± 0.03
20:1n−11	3.65 ± 0.32	3.51 ± 0.09	3.55 ± 0.06	3.32 ± 0.30	3.90 ± 0.28	4.05 ± 0.26
20:1n−9	17.08 ± 0.71	15.84 ± 0.47	16.30 ± 0.62	16.80 ± 1.20	15.59 ± 0.97	16.16 ± 1.04
20:1n−7	1.96 ± 0.07	1.89 ± 0.05	1.98 ± 0.07	1.99 ± 0.16	1.98 ± 0.13	1.97 ± 0.06
22:1n−11	10.21 ± 0.85	9.12 ± 0.69	9.68 ± 1.01	9.80 ± 1.27	8.83 ± 1.11	7.43 ± 1.13
22:1n−9	2.29 ± 0.14	1.96 ± 0.12	2.02 ± 0.20	2.19 ± 0.33	1.92 ± 0.26	1.87 ± 0.23
22:1n−7	0.42 ± 0.03	0.36 ± 0.02	0.37 ± 0.04	0.38 ± 0.07	0.36 ± 0.05	0.31 ± 0.03
24:1n−9	0.10 ± 0.01	0.11 ± 0.01	0.10 ± 0.01	0.12 ± 0.03	0.12 ± 0.01	0.10 ± 0.01
Subtotal	**74.10 ± 1.69**	**72.84 ± 0.87**	**72.93 ± 1.42**	**74.21 ± 1.03**	**72.58 ± 1.61**	**73.75 ± 1.83**
PUFAs:						
16:2n−4	0.56 ± 0.02	0.59 ± 0.02	0.59 ± 0.03	0.58 ± 0.03	0.59 ± 0.02	0.52 ± 0.02
16:3n−4	0.18 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.20 ± 0.01	0.18 ± 0.01	0.15 ± 0.00
16:4n−3	0.09 ± 0.01	0.11 ± 0.00	0.10 ± 0.01	0.09 ± 0.01	0.12 ± 0.01	0.12 ± 0.01
16:4n−1	0.32 ± 0.03	0.32 ± 0.02	0.31 ± 0.03	0.34 ± 0.03	0.29 ± 0.01	0.23 ± 0.01
18:2n−6	0.80 ± 0.08	0.87 ± 0.04	0.84 ± 0.04	0.94 ± 0.10	0.82 ± 0.04	0.82 ± 0.05
18:2n−4	0.11 ± 0.01	0.12 ± 0.00	0.12 ± 0.01	0.12 ± 0.01	0.12 ± 0.01	0.11 ± 0.01
18:3n−6	0.14 ± 0.01	0.14 ± 0.01	0.14 ± 0.01	0.16 ± 0.01	0.12 ± 0.01	0.12 ± 0.01
18:3n−4	0.14 ± 0.03	0.17 ± 0.01	0.18 ± 0.03	0.13 ± 0.01	0.18 ± 0.02	0.17 ± 0.03
18:3n−3	0.29 ± 0.02	0.31 ± 0.01	0.33 ± 0.02	0.30 ± 0.01	0.35 ± 0.03	0.34 ± 0.03
18:4n−3	0.78 ± 0.09	0.73 ± 0.05	0.80 ± 0.06	0.79 ± 0.08	0.75 ± 0.05	0.65 ± 0.07
18:4n−1	0.38 ± 0.05	0.45 ± 0.03	0.47 ± 0.07	0.36 ± 0.03	0.49 ± 0.06	0.41 ± 0.07
20:2n−9	0.11 ± 0.00	0.12 ± 0.00	0.13 ± 0.00	0.12 ± 0.01	0.13 ± 0.01	0.12 ± 0.00
20:2n−6	0.14 ± 0.01	0.16 ± 0.01	0.17 ± 0.00	0.17 ± 0.01	0.17 ± 0.01	0.16 ± 0.02
20:3n−6	0.12 ± 0.01	0.12 ± 0.00	0.12 ± 0.001	0.12 ± 0.01	0.12 ± 0.01	0.12 ± 0.01
20:4n−6	0.27 ± 0.01	0.28 ± 0.01	0.28 ± 0.00	0.28 ± 0.02	0.29 ± 0.01	0.32 ± 0.02
20:4n−3	0.43 ± 0.06	0.40 ± 0.03	0.43 ± 0.06	0.36 ± 0.03	0.46 ± 0.06	0.45 ± 0.07
20:5n−3	6.02 ± 0.74	5.50 ± 0.31	5.71 ± 0.58	5.06 ± 0.35	5.99 ± 0.64	5.64 ± 0.68
22:5n−3	1.74 ± 0.19	1.93 ± 0.12	1.86 ± 0.13	1.62 ± 0.08	2.24 ± 0.24	2.14 ± 0.29
22:6n−3	3.08 ± 0.29	3.02 ± 0.59	3.14 ± 0.12	2.62 ± 0.24	3.43 ± 0.30	3.40 ± 0.36
Subtotal	**15.72 ± 1.49**	**15.53 ± 0.71**	**15.92 ± 1.02**	**14.36 ± 0.70**	**16.81 ± 1.30**	**15.99 ± 1.59**
Total	**99.04 ± 0.07**	**98.77 ± 0.05**	**98.93 ± 0.08**	**98.94 ± 0.06**	**99.02 ± 0.05**	**99.05 ± 0.03**

ion mass spectroscopy and known standard mixtures and report these as percent weight of total FAs. The shorthand nomenclature of A:Bn−X is used to describe each FA, with A representing 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.

Statistical Analyses

Statistical analyses were performed using R version 2.15.1 (R Development Core Team, 2010). Only the most abundant FAs known to be associated with diet (Iverson et al., 2004) were used in our analyses. We retained 15 FAs (> 1.0% of total FA content) that accounted for ~ 91% of total FAs for statistical analyses: 14:0, 16:0, 16:1n−7, 18:0, 18:1n−11, 18:1n−9, 18:1n−7, 20:1n−11, 20:1n−9, 20:1n−7, 20:5n−3, 22:1n−11, 22:1n−9, 22:5n−3, and 22:6n−3 (Table 2). Values for the selected FAs were renormalized over 100%. Then proportional FA data were transformed using the centered log ratio transformation (Aitchison, 1983, 1986; Budge et al., 2008a): $x_t = \log (x_i/g(x))$, where x_i is a given FA expressed as percent of total FAs, g(x) is the geometric mean of the FA data for the sample, and x_t represents the transformed FA data.

TABLE 3. Summary of the key variables contributing to the first three principal components of the principal component analysis of 15 FAs in 50 bowhead whales.

PC	Loading	Variable	Proportion of variance (%)	Cumulative variance (%)
PC1	+	22:5n−3, 18:0, 20:5n−3	57.4	57.4
	−	22:1n−11, 22:1n−9, 20:1n−9		
PC2	+	18:1n−11, 20:1n−11, 18:0	17.9	75.3
	−	22:1n−11, 14:0, 22:1n−9		
PC3	+	22:6n−3, 20:5n−3, 22:5n−3	13.4	88.7
	−	18:1n−9, 16:1n−7, 18:1n−7		

Differences between genders and between different age classes were tested using a two-way multiple analysis of variance (MANOVA) on FA signatures (all 15 FAs simultaneously). Since no significant differences were found between genders or age classes, a discriminant analysis of principal components (DAPC) was performed to identify individuals with similar FA composition. We used this method to identify relationships among groups of individual whales (Jombart et al., 2010). First, a principal component analysis (PCA) (covariance matrix) was used on the 15 transformed FAs to reduce the dataset to a set of uncorrelated principal components retaining most of the variance in the original data. The scree test (scree plot) as part of the DAPC analysis and Kaiser's criterion (eigenvalues > 1) were used to determine the number of principal components best describing our dataset. Once eigenvectors were extracted from the covariance matrix, they were ordered by eigenvalue (highest to lowest) to assess the best low-dimensional space. The number of clusters best describing our dataset and membership of individual whales in those clusters were determined using a k-means cluster analysis and the Bayesian Information Criterion (BIC). The variables included in a DAPC are the principal component scores for each individual. The linear combinations of the original 15 FAs best separating the bowhead whale groups identified through the k-means cluster analysis were determined using a linear discriminant function analysis.

RESULTS

A total of 69 FAs were identified from the outer blubber layer of bowhead whales. The 42 most abundant FAs (> 0.1%) are presented for males and females of three different maturity classes (Table 2). MUFAs were the most abundant FAs, averaging 73.4 ± 3.9% of the total FA content. The most abundant MUFAs were 16:1n−7, 20:1n−9, 18:1n−9, and 22:1n−11. PUFAs comprised 15.6 ± 3.0% of the total FA content and were dominated by 20:5n−3, 22:6n−3, and 22:5n−3. SFAs were the least abundant class of FAs, averaging 9.9 ± 0.4% of total FA content, and 16:0, 14:0, and 18:0 were the dominant SFAs. A two-way MANOVA with gender and age class as independent variables indicated no significant difference in FA composition between males and females (Pillai = 0.389, F = 1.059, p = 0.436) or the three age classes (Pillai = 0.905, F = 1.434, p = 0.125). The interaction between these two treatments was also not significant (Pillai = 0.485, F = 0.747, p = 0.803).

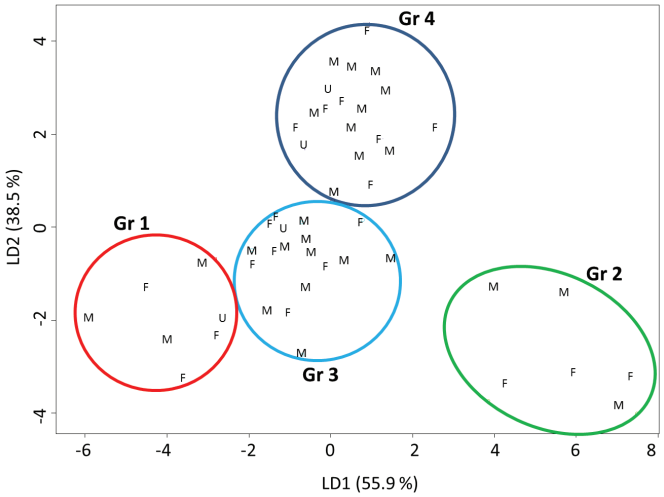

FIG. 2. Discriminant analysis of principal components using the 15 most abundant FAs identifying four groups of bowhead whales (see Table 3). Scatterplot shows the first two discriminant functions, which explain 94.4% of the variance. Each circle represents a group of whales.

Regional patterns in FA composition could not be investigated, given the small sample size for all regions except northern Foxe Basin. A PCA reduced the 15 FAs to three uncorrelated principal components (PCs), retaining 89% of the total variance (Table 3). The first PC separated individuals largely on the basis of their levels of 22:5n−3, 18:0, and 20:5n−3, which had a strong negative correlation with content in 22:1n−11, 22:1n−9, and 20:1n−9. FAs strongly correlated with PC2 included 18:1n−11, 20:1n−11, and 18:0 (positive correlation) and 22:1n−11, 14:0, and 22:1n−9 (negative correlation). For PC3, 22:6n−3, 20:5n−3, and 22:5n−3 were positively correlated, while 18:1n−9, 16:1n−7, and 18:1n−7 were negatively correlated with this factor.

Four distinct groups of bowhead whales, comprising approximately equal numbers of males and females, were identified using PC scores in a k-means cluster analysis (Table 1, Fig. 2). All individuals of Group 1 (n = 7) and Group 2 (n = 6) were sampled in Foxe Basin, whereas groups 3 and 4 had a mixture of individuals sampled in different regions. Group 3 encompassed 18 individuals: 15 from Foxe Basin, two from Admiralty Inlet, and one from Hudson Strait. Group 4 (n = 19) was similar in size to Group 3 and included 13 whales from Foxe Basin, three from Admiralty Inlet, one from the Gulf of Boothia, and

TABLE 4. Values in percent weight (mean ± standard deviation) of the 15 FAs for each of the four groups of bowhead whales.

Fatty acids	Gr 1 (n = 7)	Gr 2 (n = 6)	Gr 3 (n = 18)	Gr 4 (n = 19)
14:0	3.31 ± 0.52	3.44 ± 0.75	3.23 ± 0.35	3.11 ± 0.35
16:0	5.15 ± 0.54	5.33 ± 0.72	5.08 ± 0.60	4.90 ± 0.66
18:0	1.09 ± 0.24	1.10 ± 0.22	1.09 ± 0.27	1.06 ± 0.28
16:1n−7	19.86 ± 2.36	20.32 ± 1.03	19.95 ± 2.48	19.62 ± 2.31
18:1n−11	4.71 ± 0.73	4.28 ± 1.25	4.20 ± 0.93	4.38 ± 0.69
18:1n−9	10.83 ± 1.77	11.04 ± 0.59	10.54 ± 1.87	10.12 ± 1.26
18:1n−7	3.25 ± 0.39	3.45 ± 0.45	3.17 ± 0.59	3.11 ± 0.51
20:1n−11	3.67 ± 0.61	3.45 ± 0.90	3.63 ± 0.83	3.54 ± 0.55
20:1n−9	15.92 ± 1.43	14.73 ± 2.32	15.98 ± 2.61	16.55 ± 2.33
20:1n−7	1.91 ± 0.22	1.80 ± 0.32	1.95 ± 0.30	1.95 ± 0.23
22:1n−11	8.56 ± 2.73	7.80 ± 1.83	8.87 ± 2.52	10.02 ± 2.85
22:1n−9	1.85 ± 0.48	1.68 ± 0.35	2.03± 0.56	2.16 ± 0.58
20:5n−3	5.37 ± 0.71	6.29 ± 1.43	5.82± 1.26	5.44± 1.70
22:5n−3	2.00 ± 0.40	2.12 ± 0.37	1.93 ± 0.50	1.85 ± 0.59
22:6n−3	2.98 ± 0.88	3.33 ± 0.87	3.22 ± 0.65	2.99 ± 0.66

two from Hudson Strait. None of these four groups was biased towards one particular gender or age class.

The first two discriminant functions of the DAPC accounted for 94.4% of separation among the four groups of whales. The FAs that had the highest discrimination power were the long-chain MUFAs 20:1n−9, 20:1n−11, and 22:1n−11, along with 16:0, for the first discriminant axis (55.9% separation), and FAs 16:0, 18:0, 18:1n−11, and 20:1n−9 for the second axis (38.5%). While all four groups of whales comprised mostly individuals from Foxe Basin, they varied in FA composition (Table 4). Overall, Group 2 had the highest proportion of PUFAs (11.8%) but the lowest proportion of long-chain MUFAs (29.4%) compared to all other groups. Group 4 had the highest proportion (34.5%) of long-chain MUFAs (e.g., 20:1n−9, 22:1n−9, and 22:1n−11).

DISCUSSION

The FA composition of the outer blubber layer of bowhead whales from the eastern Canadian Arctic was composed of typical marine FAs and was similar to the common array of FAs found in other species of marine mammals, including pinnipeds (e.g., Iverson et al., 1997), odontocetes (e.g., Dahl et al., 2000; Hooker et al., 2001; Smith and Worthy, 2006), and mysticetes (Lockyer et al., 1984; Borobia et al., 1995). Bowhead whales from the EC−WG population shared similarities in their blubber FA composition with whales from the BCB population (Budge et al., 2008a), although differences were also noted. Several factors may explain the observed differences between the two populations of bowhead whales in outer blubber FA composition; these factors include sampling season (summer for EC−WG versus spring or autumn, or both, for BCB) and differences in FA metabolism according to nutritional status (Budge et al., 2008a). The 15 most abundant FAs identified in the outer blubber layer of bowhead whales in this study were the same most abundant FAs found in the outer blubber of bowhead whales from the western Arctic (Budge et al., 2008a), although their proportions varied. SFAs and PUFAs accounted for a larger proportion of total FA in bowhead whales from the BCB than in those from the EC−WG population. In contrast, for long-chain MUFAs such as 20:1n−9 and 22:1n−11, which are trophic markers of calanoid copepods, the proportion was higher in bowhead whales from the EC−WG population (~ 25%) than in those from the BCB population (~15%), suggesting that EC−WG whales consumed and incorporated a higher proportion of calanoid copepods than BCB whales.

The outer blubber of bowhead whales from the BCB population (Budge et al., 2008a) showed a larger fraction of PUFAs than that of EC−WG whales. This was the case especially for 20:5n−3 (9.4% ± 0.2% in BCB vs. 5.7% ± 1.4% in EC−WG), and to some extent for 22:6n−3 (4.3% ± 0.1% in BCB vs. 3.1% ± 0.7% in EC−WG), resulting in a mean 20:5n−3/22:6n−3 ratio of 2.2 in BCB whales, compared to 1.8 in the EC−WG whales. Given that 20:5n−3/22:6n−3 ratios were greater than 1 in both populations, bowhead whales in the Canadian Arctic probably rely more generally on diatom-derived as opposed to flagellate-derived food webs, and possibly even more so in the western Canadian Arctic. Marine diatoms, which comprise both ice algae and planktonic species, are rich in the FAs 14:0, 16:0, 16:1n−7, and 20:5n−3 (Kates and Volcani, 1966). In contrast, autotrophic flagellates and dinoflagellates tend to be poor in 16:1n−7, but rich in 22:6n−3, 18:4n−3, and 18:5n−3 (Harrington et al., 1970; Graeve et al., 1994). Future research using techniques such as compound-specific stable isotope analysis (Budge et al. 2008b) may improve our understanding of the relative contributions of ice algae and phytoplankton to the bowhead whale diet.

In marine mammals, the PUFAs 20:5n−3, 22:5n−3, and 22:6n−3 and the long-chain MUFAs C20 and C22 are assimilated exclusively from the diet (Iverson et al., 2004). These long-chain MUFAs are formed de novo by calanoid copepods (e.g., *C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) (Kattner and Hagen, 1995). In our study, the long-chain MUFAs 20:1n−9 and 22:1n−11 accounted for more than 25% of the fatty acids in the outer blubber layer of bowhead whale, suggesting herbivorous calanoid copepods as a key food source (Sargent and Whittle, 1981; Lee et al., 2006). There is also some evidence that omnivorous

and carnivorous zooplankton may play a role in the diet of bowhead whales. Several FAs, including SFAs 16:0 and 18:0 and MUFAs such as 16:1n−7 and 18:1n−9, can be produced endogenously and may also originate significantly from dietary sources in marine mammals (Kirsch et al., 2000; Iverson, 2009). SFAs 16:0 and 14:0 are the most common alcohols of wax esters found in omnivorous and carnivorous zooplankton, and they were the most abundant SFAs in bowhead whales. Similarly, the endogenously produced MUFA 18:1n−9 (oleic acid) is also a major FA in omnivorous or carnivorous zooplankton, including euphausids and amphipods (Falk-Petersen et al., 2000), and was observed in bowhead whales (~ 10.5% of total FAs). The FA 18:1n−9 may derive from the sympagic food web (Søreide et al., 2008) because ice-related amphipod species, such as *Apherusa* sp., *Gammarus* sp., and *Onisimus* sp., are usually richer in 16:1n−7 and 18:1n−9 than herbivorous copepods. However, even if the occurrence of 16:0, 18:0, 16:1n−7, and 18:1n−9 in bowhead whales reflects prey intake, an unknown proportion of these FAs most likely also originated from biosynthesis. Since blubber samples were obtained primarily using a remote darting technique, this study was limited to the examination of the outer blubber layer composition of whales. Although the extent of the stratification in the blubber of bowhead whale is relatively small (Budge et al., 2008a), the outer layer is composed of a larger proportion of biosynthesized components compared to the inner blubber layer, the most metabolically active layer.

Bowhead whales from different regions clustered together on the basis of their FA composition. However, further analyses of a larger dataset are needed for a proper assessment of geographical patterns in whale FA composition. Cluster analysis identified four groups of whales even though the vast majority of whales were sampled from northern Foxe Basin. One explanation for this pattern is that the diet is integrated over a time period when whales likely fed in different regions. Thus the different groups of whales might reflect feeding in other parts of their range in the eastern Canadian Arctic before their arrival in Foxe Basin, rather than specific dietary selection. Previous movement studies have shown that bowhead whales found on the same wintering grounds were not necessarily using the same summering grounds, but rather mixed widely in the eastern Canadian Arctic (Heide-Jørgensen et al., 2003). The rate of blubber FA turnover is approximately 1.5 to 3 months in pinnipeds (Nordstrom et al., 2008), but has not been established in large whales. The outer layers of blubber are more structural and less metabolically active than the inner layers and therefore have slower turnover rates. The period of integration of diet in large mammals is expected to be at least the same or longer than in smaller mammals because of their lower mass-specific metabolic rate. Satellite telemetry data indicate that EC−WG bowhead whales undertake extensive seasonal migrations throughout the eastern Canadian Arctic and West Greenland (Heide-Jørgensen et al., 2003). The species composition of zooplankton assemblages varied across the distribution range of EC−WG bowhead whales (Pomerleau et al., 2011b).

Quantitative fatty acid signature analysis (QFASA) has been recently developed through controlled feeding studies in captivity to permit statistical comparison of the FA signatures of a predator and those of various prey species (Iverson et al., 2007; Nordstrom et al., 2008). While this analysis was not possible in our study, the comparison of proportions of FAs among individuals provided a qualitative understanding of bowhead whale feeding ecology, including basic information on likely prey. Our results are in accordance with the recent findings on bowhead whale diet from studies of stomach content and stable isotopes. Previous work on stomach contents revealed that bowhead whales feed on pelagic and epibenthic preys and that stomach contents of males and females were nearly identical (Lowry et al., 2004; Pomerleau et al., 2011a). Similarly, FA and stable isotope results indicated that diet composition of males and females, adult and subadult whales were similar, but individual diets varied. The segregation among groups of whales in this study was based largely on diatom and copepod markers, suggesting different use of regional food webs. These results emphasize the value of using several approaches in combination to assess feeding ecology and diet.

The results of this study provide an important set of contemporary EC−WG bowhead whale biomarkers that will be of value in assessing changes in bowhead diet, behavior, and food web structure that might occur in the future. The FA data suggest that bowhead whales may have a social organization through the use of different feeding grounds that is being reflected in their adipose tissue.

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