Prey assemblage isotopic variability as a tool for assessing diet and the spatial distribution of bowhead whale *Balaena mysticetus* foraging in the Canadian eastern Arctic

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ABSTRACT: The eastern Canada-West Greenland (EC-WG) bowhead whale *Balaena mysticetus* population is slowly recovering from the intensive commercial whaling of the 18th and 20th centuries. However, climate change, through effects on ice conditions and prey availability, is one of several threats that might affect bowhead whale recovery. In this study, we exploited the variability observed in isotopic signatures of prey assemblages across the eastern Arctic to examine variability in diet among bowhead whales ($n = 202$) and identify their potential foraging areas. We compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios of biopsied skin samples with those of potential zooplankton prey species collected across the Canadian eastern Arctic, and calculated the proportional contributions of various sources (zooplankton) to the diet of bowhead whales using a Bayesian stable isotope mixing model. A cluster analysis indicated some variability in isotopic composition among groups of individuals, but not between males and females or age classes. The isotopic model discounted Davis Strait and Disko Bay as potential foraging areas for bowhead whales, at least in spring and summer. Lancaster Sound, Baffin Bay and the Gulf of Boothia were the 3 main areas likely used for summer feeding, where bowhead whales fed primarily on large Arctic calanoid copepods (*Calanus hyperboreus*, *C. glacialis*, *Metridia longa*, and *Paraeuchaeta* spp.), mysids and euphausiids. While some inter-individual variability in diet was observed, the strong dependence of this endemic Arctic species on Arctic zooplankton may make them vulnerable to the predicted latitudinal shift in prey species composition caused by ongoing warming.

KEY WORDS: Canadian Arctic · Bowhead whale · Diet · Foraging behaviour · Marine mammal · Zooplankton · Stable isotopes · Bayesian mixing model · SIAR · Trophic ecology

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INTRODUCTION

Environmental conditions and prey abundance are the primary factors influencing the geographic distributions of most species (MacLeod 2009). However,

other ecological, demographic or evolutionary attributes may also shape habitat use and resource partitioning within species (Peterson 2006). For instance, it is expected that for species with wide distribution ranges or with strong social structures, some parti-

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tioning of resources may exist among sex or age classes, or among social groups. Intraspecific differences in feeding location or diet composition are known in a wide array of species and are more frequent in species living in environments where little interspecific competition and strong intraspecific competition exist (Estes et al. 2003).

The bowhead whale *Balaena mysticetus* is endemic to the Arctic, and occurs in Canadian waters as 2 genetically distinct populations: the Bering-Chukchi-Beaufort (BCB) and the eastern Canada-West Greenland (EC-WG) populations (Rugh et al. 2003). Satellite telemetry data indicate that EC-WG bowhead whales are widely distributed throughout the Canadian eastern Arctic and West Greenland where they perform extensive seasonal migrations (NWMB 2000, Heide-Jørgensen et al. 2003). Their winter distribution includes Hudson Strait, northern Hudson Bay, east Baffin Island and the ice edge along West Greenland (Reeves & Heide-Jørgensen 1996, Koski et al. 2006), while in spring they are usually found along the west coast of Greenland (e.g. Disko Bay), in Cumberland Sound, Foxe Basin and Lancaster Sound (see Fig. 1). Their summer range includes the fjords and bays of the Canadian High Arctic, Hudson Bay and Foxe Basin (Cosens et al. 1997, Cosens & Innes 2000, Higdon & Ferguson 2010).

Genetic and satellite telemetry studies indicate significant sex and age class segregation within the EC-WG population, at least at times other than winter (Ferguson et al. 2010a, Heide-Jørgensen et al. 2003, 2006, Postma et al. 2006) (see Fig. 1). For instance, Disko Bay is an important feeding area for adult bowhead whales, and the vast majority of whales aggregating there in the spring are large adult females (>14 m) (Laidre et al. 2008). In summer, Foxe Basin is used mainly by juvenile whales and females with their calves (Cosens & Blouw 2003), whereas the Gulf of Boothia appears to be used by all age and sex classes (Dueck & Ferguson 2009). Hudson Strait is the main wintering ground for this population (Koski et al. 2006) and mating is thought to occur there during late winter within that area (Heide-Jørgensen et al. 2006) as well as in Disko Bay (Heide-Jørgensen et al. 2010).

The seasonal distribution of bowhead whales is largely driven by sea ice (Moore & Reeves 1993, Dyke et al. 1996, Ferguson et al. 2010a). Whales select areas of lower ice concentration and thickness during winter, likely to reduce risks of ice entrapment (Ferguson et al. 2010a). The reverse is observed during summer, possibly to reduce exposure to predators such as killer whales, and to increase feeding

opportunities near the productive marginal sea ice zone (Gosselin et al. 1997, Ferguson et al. 2010b, Pomerleau et al. 2011a).

Over the last several decades, the rapid decline of sea ice extent and thickness at higher latitudes as a result of the continuous warming of both the atmosphere and ocean surface (ACIA 2004) has affected plankton abundance and distribution (Greene & Pershing 2007). Although bowhead whales are adapted to extreme seasonal variability in sea ice cover and associated productivity, they may be impaired by ongoing climate warming (Neibauer & Schell 1993). Bowhead whales feed exclusively on zooplankton, but their degree of specialization on this resource at the population and individual levels, and thus vulnerability to changes in species composition, remains uncertain. Their diet varies among regions, and may include pelagic, sympagic and epibenthic species (Finley 2001, Lowry et al. 2004, Laidre et al. 2007, Pomerleau et al. 2011b). For the EC-WG population, diet has been inferred from short-term, indirect or qualitative approaches such as observation of surface feeding, stomach content analysis, plankton net sampling, dive data or a combination of these approaches (Finley 2001, Lowry et al. 2004, Lee et al. 2005, Laidre et al. 2007, Pomerleau et al. 2011a). Time-integrated studies of diet are lacking for this bowhead whale population.

Stable isotope analysis is used in a wide range of studies to investigate trophic ecology and habitat use of wild species (Hobson 1999), including marine mammals (Newsome et al. 2010). This approach provides time-integrated information on assimilated, not just ingested prey (Peterson & Fry 1987, Dalerum & Angerbjørn 2005) and over periods that vary from a few hours to a lifetime, depending on the tissue used (Tieszen et al. 1983, Hobson 1993). For instance, skin represents the period of epidermal growth, and in beluga whales and dolphins, reflects the diet over a period of 2 to 3 mo prior to skin collection (Hicks et al. 1985, St. Aubin et al. 1990, Hobson et al. 1996, Ruiz-Cooley et al. 2004). The turnover rate is possibly longer than this in balaenids such as bowhead whales, as their epidermis is thicker (15–24 mm) than in beluga (5–12 mm) (Bonin & Vladyskov 1940, Haldiman et al. 1985, Jones & Pfeiffer 1994). The stable isotope approach applied to bowhead whale skin could provide insights into their foraging ecology and the relative importance of various feeding areas, especially considering the variability observed in prey assemblage isotopic signatures across the bowhead whale distribution range in the eastern Arctic (Pomerleau et al. 2011c).

While consumer diets can be determined using mass-balance models, these are often limited by the number of isotopes as they are deterministic, and thus restricted to a small number of possible food sources (Phillips & Gregg 2003). More recently, a robust stable isotope mixing model was developed in a Bayesian framework (Moore & Semmens 2008, Parnell et al. 2010). These models are less limited by the number of dietary sources. They incorporate uncertainty for each parameter and prior information on diet when available, and offer solutions in the form of probability estimates of source contributions to a consumer diet (Parnell et al. 2010).

In the present study, we examined the degree of variability in diet among bowhead whales to identify possible patterns among age and sex classes, and regions most likely exploited as feeding grounds. While individual specialization cannot be specifically addressed in our study given the lack of repeated sampling of individuals over time, some insights into the degree of generalism or specialization at the population level can be gained from the inter-individual variability in diet composition (Bearhop et al. 2004). This was accomplished by first examining patterns in stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures of skin among bowhead whales, and then comparing them to those of potential zooplankton prey from various regions of the eastern Arctic using a Bayesian dietary mixing model.

MATERIALS AND METHODS

Study area and sample collection

Bowhead whale skin samples ($n = 202$) were collected between June and September from 1988 to 2009 at several locations of the Canadian eastern Arctic including Foxe Basin, Admiralty Inlet, Cumberland Sound and Hudson Strait (Fig. 1, Table 1). However, the vast majority of the whales included in this study were sampled in July and August (>94 %) in Foxe Basin (84 %) (Table 1). Samples were obtained using a crossbow darting system (Brown et al. 1991), and were preserved frozen at -20°C until isotopic analyses. Information on age class was collected directly in the field, and was available only for northern Foxe Basin whales and for 43 individuals, including 10 adults (>13 m long) and 33 sub-adults (6–13 m long) (Higdon & Ferguson 2010). Sex was determined genetically (Shaw et al. 2003, Petersen et al. 2011), and could be established for 153 of the 202 whales (Table 1).

Zooplankton samples were collected in July 2007 and September 2009 on board Canadian Coast Guard icebreakers at 24 locations in the Canadian eastern Arctic, including the Labrador Sea, Davis Strait, Baffin Bay and the Canadian Arctic Archipelago (Fig. 1). A complete description of the sampling protocol is presented in Pomerleau et al. (2011c). Briefly, samples were collected with a Bongo net, a

set of 2 adjacent 1 m^2 framed nets (mesh size $2 \times 236\text{ }\mu\text{m}$), towed vertically from 100 m (or near the bottom if sampling was done in a shallower area) to the surface at a speed of 1 m s^{-1} . Each zooplankton item was identified to genus or species, and was placed into 4 ml glass vials and kept frozen at -20°C until analysis.

Pomerleau et al. (2011c) defined 4 biogeographic domains within the EC-WG bowhead whale distribution range, which were characterized by specific prey assemblages and water mass characteristics. These regions included Davis Strait, Baffin Bay, Lancaster Sound and the Gulf of Boothia (Fig. 1). Marine zooplankton stable isotope data from this study were used as sources in a mixing model along with additional data from the literature (Hobson 1993, Hobson et al. 2002). Since bowhead whales may

Fig. 1. Sampling locations for bowhead whale *Balaena mysticetus* skin samples (outliers excluded) in the eastern Canadian Arctic

Table 1. Sample size (n), number of known bowhead whale *Balaena mysticetus* females and males, range of sampling years and months of collection for each of the 6 sampling regions in the Canadian Arctic

Region	Year range	Sample size (n)	Sampling month					Sex		
			June	July	August	September	Unknown	Male	Female	Unknown
North Foxe Basin	1994–1999	19	0	5	1	1	12	3	7	9
	2001–2003	13	0	11	0	0	2	3	3	7
	2007	43	6	37	0	0	0	17	15	11
	2008	7	0	7	0	0	0	2	4	1
	2009	88	0	88	0	0	0	41	37	10
	Total	170	6	154	1	1	8	66	66	38
South Foxe Basin	1999–2001	5	0	0	0	0	5	1	2	2
	2008–2009	7	0	0	3	2	2	2	1	4
	Total	12	0	0	3	2	7	3	3	6
Gulf of Boothia	2008	1	0	0	0	1	0	1	0	0
Lancaster Sound	2008–2009	9	0	0	9	0	0	2	6	1
Hudson Strait	2001–2009	4	0	0	2	1	1	2	1	1
Cumberland Sound	1988–1997	3	0	0	0	0	3	1	0	2
	2003–2006	3	0	3	0	0	0	2	0	1
	Total	6	0	3	0	0	3	3	0	3
Summary		202	6	157	15	5	19	77	76	49

also be found in Disko Bay, West Greenland, during late winter and spring (Laidre et al. 2007), we also incorporated stable isotope data from zooplankton species collected from this area in the spring (Møller 2006).

Sample preparation

Bowhead whale skin samples were freeze-dried to remove moisture, and ground to a fine powder. Nitrogen isotope ratios were determined from dried homogenized sub-samples of bowhead skin, and composite samples of several whole individuals in the case of zooplankton. Carbon isotope ratios were determined from lipid-extracted samples of skin and zooplankton. Lipid extraction was performed following the Folch method (Folch et al. 1957) using approximately 0.2 g of dried material and a solvent consisting of 2:1 chloroform:methanol (volume/volume). The tissue was placed in a glass tube with 10 ml of the solvent mixture, sonicated for 15 min and gently shaken for 4 h at room temperature. The sample was then centrifuged (2500 rpm, $2348 \times g$) for 10 min prior to removing the supernatant. This extraction procedure was repeated 3 times. Once lipids were extracted, zooplankton samples were acidified with the 'drop by drop' technique, using a weak acid solution (1 M HCl) (Mintenbeck et al. 2008), placed in an oven at 60°C to remove moisture, and then analyzed for their carbon isotope ratios.

Stable isotope analysis

Samples were analyzed for carbon and nitrogen isotope ratios at the University of Waterloo Environmental Isotope Laboratory, Ontario, Canada, by continuous flow ion ratio mass spectrometry, using a GV-Instruments IsoPrime coupled to a peripheral temperature-controlled Euro Vector elemental analyzer. Stable isotope ratios are expressed as delta (δ) notations, the normalized ratio of an unknown sample to an internationally accepted standard. Standards were atmospheric N_2 for $\delta^{15}N$, and Vienna Pee Dee Belemnite for $\delta^{13}C$. Analytical error based on replicate analyses of samples and laboratory standards was 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Statistical analysis

Statistical analyses were performed using R version 2.13.1 (R Development Core Team 2010). Normality of isotopic data was assessed using Shapiro-Wilk normality tests. A dissimilarity matrix based on Euclidean distances was constructed from the isotopic signatures of all 202 bowhead whales, and used in a single linkage non-hierarchical cluster analysis (nearest neighbor) to remove outliers, as the latter are known to bias hierarchical cluster analysis results (Hair et al. 1995). A second dissimilarity matrix was then constructed while excluding outliers ($n = 12$), and used in a hierarchical cluster analysis to identify

groupings among bowhead whales. We used 3 statistical indicators to assist with objective determination of the appropriate number of clusters: cubic-clustering criterion (CCC) (Sarle 1983), pseudo F statistic (Calinski & Harabasz 1974), and pseudo t^2 statistic (similar to Hotelling's T^2) (Duda & Hart 1973).

Statistical analyses testing for various effects were conducted exclusively on the 110 bowheads of known sex obtained from northern Foxe Basin during 2007 and 2009, given this site and these years dominated our sample, and because whales were all biopsied during July. Sex and year effects were tested in this sample using a 2-way ANOVA, whereas comparisons among age classes were made using a Student's t -test, or a Wilcoxon rank sum test when data were not normally distributed. As a result of the small sample size for other seasons and sites (Table 1), no attempts were made to statistically assess seasonal or site effects. Nevertheless, results from the cluster analysis were scrutinized to ensure particular clusters of bowhead whales were not biased towards specific seasons, sampling sites, sex or age classes.

Stable isotope mixing model

Diet composition was quantitatively assessed for each bowhead group identified through the cluster analysis, using a Bayesian dietary multi-source SI mixing model (SIAR: Stable Isotope Analysis in R) (Parnell et al. 2010). Each bowhead group was evaluated against prey from each of the 5 biogeographical regions (Davis Strait, Disko Bay, Baffin Bay, Lancaster Sound and the Gulf of Boothia) to identify plausible feeding areas and diet composition associated with each set of prey. Input parameters to Bayesian models may include prior knowledge about diet composition, but none was available for bowhead whales. Therefore, input parameters included isotopic signatures of each of the consumers, each potential prey (entered as mean $\pm$ SD), and the discrimination factors (DF) between the consumer tissue and that of the prey, with a measure of uncertainty (SD).

To our knowledge, the only study on DFs for skin of cetaceans was conducted using a captive female killer whale, and resulted in discrimination factors of $+2.4\text{‰}$ for $\delta^{13}\text{C}$ (after lipid removal) and $+3.05\text{‰}$ for $\delta^{15}\text{N}$ between the whale skin and whole fish prey (Caut et al. 2011). These results need to be interpreted with caution, since the whale was sick for 3 mo prior to death from a bacterial infection. We used a DF ($\pm$ SD) between bowhead whale skin and their zooplankton prey of $+2.5 \pm 0.2\text{‰}$ for $\delta^{15}\text{N}$, and

$+1.0 \pm 0.1\text{‰}$ for $\delta^{13}\text{C}$. The DF value for $\delta^{15}\text{N}$ corresponds to the DF predicted based on prey isotopic value for mammals (Caut et al. 2009), and is close to the value obtained in the study on captive killer whales (i.e. 2.4‰) (Caut et al. 2011), and the estimated $+2.3\text{‰}$ obtained for skin of seals maintained in captivity under controlled conditions (Hobson et al. 1996). We used a DF value of 1.0‰ for $\delta^{13}\text{C}$, the average enrichment predicted for mammals based on isotopic prey value (Caut et al. 2009), as we suspected the value obtained from captive seal skin ($+2.7\text{‰}$) to be overestimated because lipids were extracted from prey but not skin. Error terms for discrimination factors were determined arbitrarily, but were set to a higher value for $\delta^{15}\text{N}$ than $\delta^{13}\text{C}$ given the larger discrimination associated with the former.

SIAR mixing models include diagnostic matrix plots for exploring the covariance structure between each pair of sources (Parnell et al. 2010). For instance, a strong negative correlation between 2 prey sources implies that for a given iteration, the contribution of one source negatively affects the contribution of the other, a phenomenon that inflates the uncertainty around the proportional contribution of each source to the diet. Sources that were strongly negatively correlated were combined *a posteriori* for each iteration to reduce uncertainty. Contributions of dietary sources are reported as mean and 95 % credibility interval (CI).

RESULTS

Stable isotope analysis

Isotopic signatures of bowhead whales sampled in Foxe Basin during the same month (July) were consistent across the 2 years of sampling (2007 and 2009), as well as among age and sex classes. Carbon isotopic signatures were similar among sex classes in both years (sex: $F_{1,106} = 0.0065$, $p = 0.936$; year: $F = 3.0287$, $p = 0.085$), and the same was obtained for $\delta^{15}\text{N}$ values (sex: $F_{1,106} = 0.0078$, $p = 0.929$; year: $F = 0.0471$, $p = 0.829$). Isotope ratios of these 2 elements were also similar among adult and sub-adult whales ($\delta^{13}\text{C}$: $t = -0.47$, $p = 0.644$; $\delta^{15}\text{N}$: $W = 204$, $p = 0.273$). Assuming a similar trend for sites, years or seasons with insufficient sample sizes, all whales were pooled together in the cluster analysis to investigate individual isotopic variability further.

The hierarchical cluster analysis of bowhead whale isotopic signatures segregated bowhead whales into 4 groups, all of which were approximately composed

of an equal number of males and females among the sexed individuals (Fig. 2, Table 2). Examination of the outliers removed prior to this analysis did not reveal any bias towards a particular site, year, sex or age class (not shown). There was also no clear pattern in the distribution of individuals from specific sites, years or age classes among the clusters, indicating that none of the groups were dominated by individuals from a particular site, year or age class. Group 1 was the largest, and encompassed 103 individuals, the majority ($n = 92$) of which were biopsied in the northern Foxe Basin. Group 2 comprised 44 whales, with about half ($n = 26$) being biopsied in areas other than Foxe Basin. This group had $\delta^{13}\text{C}$ values similar to Group 1, but was less enriched in $\delta^{15}\text{N}$. The only calf included in this study was part of Group 2. Group 3 included 28 individuals, all from northern Foxe Basin, and was the most enriched in $\delta^{15}\text{N}$. Group 4 comprised 15 individuals, including 12 from northern Foxe Basin, and had the most depleted average $\delta^{13}\text{C}$.

Two-dimensional plots of mean isotopic signatures of the 4 bowhead groups relative to potential prey from the 5 biogeographic regions indicate that Baffin Bay, Lancaster Sound and the Gulf of Boothia represent plausible feeding areas for bowhead whales sampled in our study (Fig. 3c–e). In contrast, Davis

Table 2. *Balaena mysticetus*. Sample size (n), number of known females and males, mean $\delta^{13}\text{C} \pm \text{SD}$ and mean $\delta^{15}\text{N} \pm \text{SD}$ of bowhead whale skin samples in the 4 groups resulting from the hierarchical cluster analysis

Group	n	Females	Males	$\delta^{13}\text{C} (\text{‰})$	$\delta^{15}\text{N} (\text{‰})$
1	103	37	44	-19.4 ± 0.3	13.2 ± 0.2
2	44	18	15	-19.4 ± 0.3	12.4 ± 0.3
3	28	11	9	-19.7 ± 0.3	14.1 ± 0.2
4	15	7	5	-20.4 ± 0.2	12.9 ± 0.4

Fig. 2. *Balaena mysticetus*. Stable isotopes ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of bowhead whale skin samples divided into 4 groups by hierarchical cluster analysis

Strait and Disko Bay are unlikely to be important feeding areas (Fig. 3a,b). As a result, diet composition using Bayesian mixing models was evaluated for each of the 4 bowhead whale groups, but against only 3 of the 5 regional prey assemblages: Baffin Bay, Lancaster Sound and the Gulf of Boothia (Fig. 3c–e). Potential prey base varied among regions from 9 to 12 species (Fig. 3c–e).

Using potential prey as sources in mixing models, we found similarities and differences among the diets of the 4 groups of bowhead whales. Groups 1 and 3 consumed primarily a mixture of euphausiids, mysids, *Paraeuchaeta* spp. and chaetognaths, but the contribution of the different species was different between the 2 groups. Bowhead whales from Groups 2 and 4 consumed a large amount of calanoid copepods (*Calanus* spp. [here and hereafter comprised of *C. hyperboreus* and *C. glacialis*] and *Metridia longa*), but individuals from Group 2 also consumed various amounts of amphipods, pteropods and chaetognaths. Bowhead whales in Group 4 consumed the largest amount of euphausiids.

Contributions of a given species also varied depending on the biogeographic region being considered. For Group 1, euphausiids and *Paraeuchaeta* spp. contributed 27% (CI 20–36%) of the diet of whales in Lancaster Sound and 18% (6–31%) in Baffin Bay. *Mysis oculata* contributed the same amount in the Gulf of Boothia and Baffin Bay (16%, CI 2–30%) but was more important in the diet of whales from Lancaster Sound (26%, CI 9–43%). Larvaceans and the pteropod *Limacina helicina* also contributed to bowhead whale diets in the Gulf of Boothia (17%, CI 4–29%) (Fig. 4).

For Group 2, the most important dietary sources were *Apherusa glacialis*, *Calanus* spp., *Limacina helicina* and chaetognaths (Fig. 5). The ice amphipods *A. glacialis* and *Onisimus glacialis* contributed 19% (CI 13–25%) in the Gulf of Boothia, and a similar amount (18%, CI 7–28%) in Baffin Bay. *Calanus* spp. and *L. helicina* were important dietary sources in both Lancaster Sound (24%, CI 12–36%) and Baffin Bay (14%, CI 2–27%).

For Group 3, euphausiids accounted for half of the diet in Lancaster Sound (51%, CI 42–60%) and about one-quarter of food consumed in Baffin Bay (27%, CI 11–41%) (Fig. 6). Chaetognaths and *Paraeuchaeta* spp. contributed nearly half of the diet (47%, CI 37–57%) of this group in the Gulf of Boothia, and possibly also substantially in Lancaster Sound and Baffin Bay, although the similarity of their isotopic signature with other species precluded firm conclusions about their relative contributions. *Metridia*

Fig. 3. *Balaena mysticetus*. Stable isotope input data of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of bowhead whales (within ellipse). Means (squares) and standard deviations (lines) are shown for each source (prey), corrected for diet-tissue discrimination (data from Pomerleau et al. 2011c). Polygons represent the geometric space of mixing models with feasible solutions, i.e. those where predator signatures are included in the polygon formed by the prey. Note the different scales of the isotope ratios. (a) Davis Strait, (b) Disko Bay, (c) Baffin Bay, (d) Gulf of Boothia and (e) Lancaster Sound

longa was also an important prey item (20%, CI 8–33%) in the Gulf of Boothia, followed by *Mysis oculata* (13%, CI 2–25%).

Finally, *Metridia longa*, *Calanus* spp. and euphausiids were the most important prey items for

Group 4 (Fig. 7). Most of the species attributed to the diet of whales feeding within Lancaster Sound and Baffin Bay were euphausiids (>50%) followed by *M. longa* in the Gulf of Boothia (41%, CI 26–57%) and Baffin Bay (27%, CI 15–40%).

Fig. 4. Dominant prey items of bowhead whale Group 1. Mean percentage of total and credibility interval (in square brackets) indicated above boxes. Dark grey, grey and light grey boxes: 50, 75 and 95 % credibility interval, respectively. Curved lines: violin plot of kernel density; values calculated from mixing models

Fig. 5. Dominant prey items of bowhead whale Group 2. Details as in Fig. 4

DISCUSSION

Our study revealed a significant amount of inter-individual diet variability in bowhead whales and indicated that for a given group of animals, targeted prey was mainly the same regardless of the region potentially exploited. The lack of clear differentiation among sampling sites, age or sex classes, even when natural groupings of individuals were revealed through cluster analysis, suggest that there is no ontogenic shift nor sex differences in diet among the bowhead whales sampled in this study.

Ontogenic shifts in trophic niche are common in animals that exhibit large increases in size through-

out their lifetime (Jackson et al. 2004) as predator body size is one of the main factors influencing predator–prey relationships (Peters 1983, Werner & Hall 1988). They are documented in a number of marine mammal species including killer whales (Newsome et al. 2009), sea lions (Hobson & Sease 1998, Drago et al. 2009, Orr et al. 2011), sperm whales (Mendes et al. 2007) and bottlenose dolphins (Knoff et al. 2008). Considering that the diet of bowhead whales is composed primarily of zooplankton (Finley 2001, Lowry et al. 2004, Pomerleau et al. 2011b), a very small prey relative to the size of the predator, bowhead whales might not adhere to this pattern. In bowhead whales from the western Arctic, a greater variability in isotopic signatures over the approximately 15 yr record represented by their baleens suggests the use of a wider range of habitat by sub-adults compared to adults (Lee et al. 2005). However, their muscle tissue suggests that both age classes acquire their food largely from the same area (the Bering-Chukchi Sea) and likely similar trophic levels (Lee et al. 2005). Thus, our findings for the EC-WG population, of exploitation of a similar isotopic niche by sub-adult and adult bowhead whales, are consistent

with what was described previously for the species.

Differences in trophic niche between males and females may occur as a result of significant body size dimorphism between sexes, differences in spatial distribution and habitat use and other factors including energy requirements and intra-specific competition (Ruckstuhl & Neuhaus 2005). Bowhead whales exhibit only a small and reversed size dimorphism, with females being slightly larger than males (Koski et al. 1993). Given the similarity in diet documented in many monomorphic species (Michaud 2005), similar isotopic niches between male and female bowhead whales in this study were not totally unexpected. Similar results were obtained for marine

Fig. 6. Dominant prey items of bowhead whale Group 3. Details as in Fig. 4

Fig. 7. Dominant prey items of bowhead whale Group 4. Details as in Fig. 4

mammal species with mild or no sexual dimorphism, including bowhead whales from the western Arctic (Hicks et al. 1985, Todd et al. 1997, Lawson & Hobson 2000, Lowry et al. 2004, Budge et al. 2008, Witteveen et al. 2009). In bowhead whales of this population, stomach contents of males and females were nearly identical (Lowry et al. 2004) suggesting similar diets between sexes, a result supported by the similarity of the dietary fatty acid composition of their blubber (Budge et al. 2008).

Differences in spatial distribution and habitat use among age and sex classes are documented in bowhead whales, including the EC-WG population (Cubbage & Calambokidis 1987, Heide-Jørgensen et al. 2010). Baffin Bay and Davis Strait are generally used by adult males and resting or pregnant females from

Disko Bay, West Greenland, whereas the Hudson Bay complex, including Prince Regent Inlet and the Gulf of Boothia, is also used by nursing females, calves and sub-adults. During the autumn, bowhead whales either travel southeast from Foxe Basin toward Hudson Strait (Ferguson et al. 2010a) or move along the east coast of Baffin Island and/or travel towards the West Greenland coast (Reeves et al. 1983). Bowhead whales overwinter in Hudson Strait, Cumberland Sound, West Greenland and the North Water Polynya (Koski et al. 2006, Ferguson et al. 2010a, Wiig et al. 2011). Little is known about spring movements, but the lack of difference in isotopic niche among sex and age classes for a period likely representing mostly spring and early summer feeding may indicate a more diffuse spatial structure of age and sex classes at that time, when movements between wintering and spring/summer feeding grounds are likely to occur (Heide-Jørgensen et al. 2003, 2006). Mating is thought to occur during late winter (Heide-Jørgensen et al. 2006), suggesting a co-occurrence of adult males and females. The spring migration may be spatially structured, as sug-

gested by observations of bowhead whales in the western Arctic, where sub-adult whales migrate past Point Barrow, Alaska, first, and mother-calf groups last (Koski et al. 1993, George et al. 2004). While spring movements of adult males remain largely undocumented, there is no reason to believe they cannot overlap with those of females and younger individuals. Whales wintering in Hudson Strait could be moving west and north as the ice retreats to reach Foxe Basin in late spring and early summer (Heide-Jørgensen et al. 2010). It is also possible that these animals move into Foxe Basin from the North via Lancaster Sound, Prince Regent Inlet, the Gulf of Boothia and Fury and Hecla Strait.

Bowhead whales sampled during summer, and mostly in northern Foxe Basin, were unlikely to have

used Davis Strait or Disko Bay as a feeding ground in the preceding months, as indicated by the mixing model results, and acknowledging the predominance of 1 sampling site in our study. The results from the mixing models might have been different if more samples were obtained from other areas, such as Disko Bay. Whether bowhead whales sampled in Foxe Basin in summer foraged in Lancaster Sound, Baffin Bay, the Gulf of Boothia or in other areas in the spring or early summer (the period reflected by the skin isotopic ratios) could not be ascertained. No zooplankton samples were available from Hudson Strait and Foxe Basin, which prevented us from estimating diet composition based on these prey assemblages.

The cluster analysis identified isotopically distinct groups among the bowhead whales which indicate variability in diet among individuals within the population. The similarities observed in diet composition for a given bowhead whale group, regardless of the biogeographic region against which it was evaluated, suggest that differences in diet composition among groups of bowhead whales were unlikely driven by the region exploited, but more by a preference of each of these groups for specific sets of prey species. This inter-individual variability was also unlikely related to the timing of sampling and thus, the period reflected by the sampled tissue, given that the vast majority of the whales were sampled in late summer (July and August). Variability was also not related to sampling site, given that diet was similar for a given group regardless of the area considered as a feeding ground.

Since the years of prey collection (2007–2009) did not always corresponded to those of bowhead whales (1994–2009), the observed group differences in diet should be interpreted with caution. Differences in $\delta^{15}\text{N}$ among the 4 clusters may result from regional differences at the base of the food web (Post 2002). Spatial and temporal variations in primary producers strongly depend on differences in productivity, including nitrogen sources, and may influence the isotopic values in consumers (Montoya 2007, Auriolles-Gamboa et al. 2009). Thus, variability in $\delta^{15}\text{N}$ is derived from diet but is also influenced by foraging locations. Future studies should include concurrent sampling of primary producers and zooplankton.

Bowhead whales relied exclusively on zooplankton, and on a limited number of these species, and thus had a relatively restricted or specialized diet compared to some pinnipeds or odontocetes consuming tens of different species (Lawson & Hobson 2000, Loseto et al. 2008). The range of potential diet solutions and estimations of zooplankton species contri-

butions generated by the mixing models generally concur with the results from the small number of studies on bowhead whale diet in the Eastern Arctic (Finley 2001, Pomerleau et al. 2011b). This, combined with the variability in diet composition among groups of whales, suggests that bowhead whales as a population, although relatively specialized, may be considered generalists of Type B, i.e. groups of bowhead whales feed on a subgroup of zooplankton species. This is in opposition to Type A generalists, where all individuals exploit the same set of prey, and to specialist populations, where all individuals eat the same and reduced number of prey species (Bearhop et al. 2004). The different prey assemblages and prey proportions of each group may be influenced by prey availability and abundance. Predators may feed randomly on the most abundant prey in their environment or exert selective feeding on a certain aggregation of preys despite their abundance (MacLeod et al. 2006). Some of the variations found between groups of bowhead whales may be a sign of individual and persistent specialization, a known mechanism of intra-population variation (Roughgarden 1972, Bolnick et al. 2003). However, it was not possible in this study to examine the degree of temporal specialization of individual whales given the absence of longitudinal records for each whale.

Bowhead whales are adapted to extreme seasonal variability in sea ice cover and associated productivity, but they may be impaired by ongoing climate warming (Neibauer & Schell 1993). Results from the present study indicate that bowhead whales specialize on zooplankton, relying generally on large Arctic calanoid copepods (*Calanus hyperboreus*, *Calanus glacialis*, *Metridia longa* and *Paraeuchaeta* spp.), mysids and euphausiids, with some degree of flexibility in the species consumed. One group of bowhead whales depended largely on sea ice plankton species. Zooplankton community composition and abundance are tightly coupled with water mass characteristics, thus are highly influenced by changes in water temperature and salinity and freshwater/sea ice melt water inputs (Hagen & Auel 2001, Beaugrand et al. 2002, Fetzer et al. 2002). The Arctic sea ice has drastically decreased over the last decade and this trend may lead to ice-free summers in the Arctic within 20 yr (Perovich & Richter-Menge 2009). The Arctic food web is characterized by key ice-covered adapted species driving a lipid-rich system (Falk-Petersen et al. 2007), where *Calanus* spp. likely play an important role. Changes in sea ice regimes will impact the timing of bloom events, which are tightly linked with the reproductive cycles

of *Calanus* spp. (Kattner & Hagen 2009), including *C. glacialis* and *C. hyperboreus*, which are important prey of bowhead whales. Along with another prey, the ice amphipods, calanoid copepods have large amounts of lipids and are known to feed under the sea ice (Runge & Ingram 1991). The warming of the Arctic is expected to favour smaller and leaner zooplankton species from more temperate waters, thus changing the lipid flux within the food web. Two groups of bowhead whales consumed the Arctic pteropod *Limacina helicina*. By the end of this century, *L. helicina* may have disappeared as a result of ocean acidification (Comeau et al. 2011). Bowhead whales, as zooplankton specialists, will have to cope with potentially large spatio-temporal changes in productivity and associated prey assemblages.

CONCLUSIONS

Dietary information from the model results provided new insights into diet and potential foraging grounds of bowhead whales from the EC-WG population during summer in the Canadian Arctic. Our study established that diet of bowhead whales varied among groups of individuals, and that for a given group, targeted prey were largely the same regardless of the region exploited. Modelled diets inferred the existence of regional differences in prey selection, as each whale group exhibited preferences in prey species. The model results from this study may not apply to the entire EC-WG bowhead whale population, and reflect spring and early summer feeding behaviour and diet. Thus, further investigation of the seasonal variation of stable isotope ratios in bowhead whale skin samples, especially in autumn, winter and early spring, will improve our understanding of the feeding ecology of this species throughout the year.

Sea-ice habitat loss, together with increased predation exposure and increased competition for food resources (through immigration of non-Arctic baleen whale species as a result of longer ice-free summers), may leave bowhead whales vulnerable to forthcoming environmental changes (ICES 2008). Bowhead whales encounter different water masses and associated prey assemblages in their summer range (Pomerleau et al. 2011c). Results indicate that Lancaster Sound, the Gulf of Boothia and Baffin Bay may be spring and early summer feeding grounds, although their importance relative to other potential feeding sites such as Hudson Strait or Foxe Basin could not be ascertained. Bowhead whales from all 4 groups relied to some extent on

large Arctic calanoid copepod species (e.g. *Calanus hyperboreus*, *Calanus glacialis*, *Metridia longa* and *Paraeuchaeta* spp.). The continuous warming trend in the Arctic may cause the replacement of the larger Arctic copepods *C. glacialis* and *C. hyperboreus* by the smaller and leaner *Calanus finmarchicus* (Beaugrand et al. 2002, Beaugrand 2009). Smaller calanoid copepods from more temperate (*Calanus helgolandicus*) and boreal waters (*C. finmarchicus*) are mostly limited to Davis Strait, with low abundance in the Canadian Arctic (*C. finmarchicus*). How these smaller and less lipid-rich species will expand their range into that of bowhead whales and whether bowhead whales can adapt to the shift in distribution or disappearance of Arctic prey species is uncertain and needs to be monitored.

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LITERATURE CITED

- ACIA (Arctic Climate Impact Assessment) (2004) Impacts of a warming Arctic. Cambridge University Press, New York, NY
- Auriolles-Gamboa D, Newsome SD, Salazar-Pico S, Koch PL (2009) Stable isotope difference between sea lions (*Zalophus*) from the Gulf of California and Galapagos Islands. *J Mammal* 90:1410–1420
- Bearhop S, Adam CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73: 1007–1012
- Beaugrand G (2009) Decadal changes in climate ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res II* 56:656–673
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296:1692–1694
- Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- Bonin W, Vladykov VD (1940) Étude sur les mammifères aquatiques. La peau du marsouin blanc ou beluga. *Nat Can* 67:253–287
- Brown MW, Kraus SD, Gaskin DE (1991) Reaction of North Atlantic right whales (*Eubalaena glacialis*) to skin biopsy

- sampling for genetic and pollutant analysis. Rep Int Whal Comm Spec Issue 13:81–89
- Budge SM, Springer AM, Iverson SJ, Sheffield G, Rosa C (2008) Blubber fatty acid composition of bowhead whales, *Balaena mysticetus*: implications for diet assessment and ecosystem monitoring. J Exp Mar Biol Ecol 359:40–46
- Calinski T, Harabasz J (1974) A dendrite method for cluster analysis. Commun Stat 3:1–27
- Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443–453
- Caut S, Laran S, Garcia-Hartmann E, Das K (2011) Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). J Exp Mar Biol 214:538–545
- Comeau S, Gattuso JP, Nisumaa AM, Orr J (2011) Impact of aragonite saturation state changes on migratory pteropods. Proc R Soc Lond B Biol Sci 279:732–738
- Cosens SE, Blouw A (2003) Size and age class segregation of bowhead whales summering in northern Foxe Basin: a photogrammetric analysis. Mar Mamm Sci 19: 284–296
- Cosens SE, Innes S (2000) Distribution and numbers of bowhead whales (*Balaena mysticetus*) in northwestern Hudson Bay in August 1995. Arctic 53:36–41
- Cosens SE, Qamukaaq T, Parker B, Dueck LP, Anardjuak B (1997) The distribution and numbers of bowhead whales, *Balaena mysticetus*, in northern Foxe Basin in 1994. Can Field Nat 111:381–388
- Cubbage JC, Calambokidis J (1987) Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. Mar Mamm Sci 3:179–185
- Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658
- Drago M, Cardona L, Crespo EA, Aguilar A (2009) Ontogenetic dietary changes in South American sea lions. J Zool (Lond) 279:251–261
- Duda RO, Hart PE (1973) Pattern classification and scene analysis. John Wiley & Sons, New York, NY
- Dueck L, Ferguson SH (2009) Habitat use by bowhead whales (*Balaena mysticetus*) of the eastern Canadian Arctic. Canadian Science Advisory Secretariat Research Document, 2008/082, Fisheries and Oceans Canada, Winnipeg
- Dyke AS, Hooper J, Savelle JM (1996) A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of the bowhead whale (*Balaena mysticetus*). Arctic 49:235–255
- Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BT (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol 72: 144–155
- Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (eds) (2007) Climate variability and the effect on Arctic food chains. The role of *Calanus*. Springer-Verlag, Berlin
- Ferguson SH, Dueck L, Loseto LL, Luque SP (2010a) Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. Mar Ecol Prog Ser 411:285–297
- Ferguson SH, Higdon JW, Chmelnitsky EG (2010b) The rise of killer whales as a major Arctic predator. In: Ferguson SH, Loseto LL, Mallory ML (eds) A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Springer, New York, NY, p 117–136
- Fetzer I, Hirche HJ, Kolosova EG (2002) The influence of freshwater discharge on the distribution of zooplankton in the southern Kara Sea. Polar Biol 25:404–415
- Finley KJ (2001) Natural history and conservation of the Greenland whale, or bowhead, in the northwest Atlantic. Arctic 54:55–76
- Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509
- George JC, Zeh J, Suydam R, Clark C (2004) Abundance and population trend (1978–2001) of western Arctic bowhead whales surveyed near Barrow, Alaska. Mar Mamm Sci 20:755–773
- Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res II 44: 1623–1644
- Greene CH, Pershing AJ (2007) Climate drives sea change. Science 315:1084–1085
- Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313–326
- Hair JF, Tatham RL, Anderson RE, Black W (1995) Multivariate data analysis, 5th edn. Prentice-Hall, Upper Saddle River, NJ
- Haldiman JT, Henk WG, Henry RW, Albert TF, Abdelbaki YZ, Duffield DW (1985) Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). Anat Rec 211:391–402
- Heide-Jørgensen MP, Laidre KL, Wiig Ø, Jensen MV, and others (2003) From Greenland to Canada in ten days: tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. Arctic 56:21–31
- Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD (2006) Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. Mar Mamm Sci 22:34–45
- Heide-Jørgensen MP, Laidre KL, Wiig Ø, Postma L, Dueck L, Bachman L (2010) Large-scale sexual segregation of bowhead whales. Endang Species Res 13:73–78
- Hicks BD, St Aubin DJ, Geraci JR, Brown WR (1985) Epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. J Invest Dermatol 85:60–63
- Higdon JW, Ferguson SH (2010) Past, present, and future for bowhead whales (*Balaena mysticetus*) in northwest Hudson Bay. In: Ferguson SH, Loseto LL, ML Mallory (eds) A little less Arctic: top predators in the world's largest northern inland sea, Hudson Bay. Springer, New York, NY, p 159–177
- Hobson KA (1993) Trophic relationships among high Arctic seabirds: insights from tissue-dependant stable isotope models. Mar Ecol Prog Ser 95:7–18
- Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326
- Hobson KA, Sease JL (1998) Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using stellar sea lions. Mar Mamm Sci 14:116–129
- Hobson KA, Schell DM, Renouf D, Noseworthy E (1996) Stable carbon and nitrogen fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can J Fish Aquat Sci 53:528–533
- Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Res II 49:5131–5150

- ICES (International Council for the Exploration of the Sea) (2008) An assessment of the changes in the distribution and abundance of marine species in the OSPAR maritime area in relation to changes in hydrodynamics and sea temperature. ICES Advice 2008, Book 1, section 1.5.5.1. ICES, Copenhagen
- Jackson AC, Rundle SD, Attrill MJ, Cotton PA (2004) Ontogenetic changes in metabolism may determine diet shifts for a sit-and-wait predator. *J Anim Ecol* 73:536–545
- Jones FM, Pfeiffer CJ (1994) Morphometric comparison of the epidermis in several cetacean species. *Aquat Mamm* 20:29–34
- Kattner G, Hagen W (2009) Lipids in marine copepods: latitudinal characteristics and perspective to global warming. In: Arts MT, Brett MT, Kainz MJ (eds) *Lipids in aquatic ecosystems*. Springer, Dordrecht, p 257–280
- Knoff A, Hohn A, Macko SA (2008) Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. *Mar Mamm Sci* 24:128–137
- Koski WR, Davis RA, Miller GW, Withrow DE (1993) Reproduction. In: JJ Burns, JJ Montague, CJ Cowles (eds) *The bowhead whale*. Society for Marine Mammalogy, Spec Publ No. 2, Allen Press, Lawrence, KS, p 239–274
- Koski WR, Heide-Jørgensen MP, Laidre KL (2006) Winter abundance of bowhead whales, *Balaena mysticetus*, in the Hudson Strait, March 1981. *J Cetacean Res Manag* 8: 139–144
- Laidre K, Heide-Jørgensen MP, Nielsen TG (2007) Role of the bowhead whale as a predator in West Greenland. *Mar Ecol Prog Ser* 346:285–297
- Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol Appl* 18:S97–S125
- Lawson JW, Hobson KA (2000) Diet of harp seals (*Pagophilus groenlandicus*) in nearshore northeast Newfoundland: inferences from stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analyses. *Mar Mamm Sci* 16:578–591
- Lee SH, Schell DM, McDonald TL, Richardson WJ (2005) Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. *Mar Ecol Prog Ser* 285:271–287
- Lowry LF, Sheffield G, George JC (2004) Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J Cetacean Res Manag* 6:215–223
- MacLeod CD (2009) Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endang Species Res* 7:125–136
- MacLeod CD, Santos MB, López A, Pierce GJ (2006) Relative prey size consumption in toothed whales: implications for prey selection and level of specialization. *Mar Ecol Prog Ser* 326:295–307
- Mendes S, Newton J, Reid RJ, Zuur AF, Pierce GJ (2007) Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. *Oecologia* 151:605–615
- Michaud R (2005) Sociality and ecology of the odontocetes. In: Ruckstuhl KE, Neuhaus P (eds) *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge University Press, Cambridge, p 303–326
- Mintenbeck K, Brey T, Jacob U, Knust R, Struck U (2008) How to account for the lipid effect on carbon stable-isotope ratio ($\delta^{13}\text{C}$): sample treatment effects and model bias. *J Fish Biol* 72:815–830
- Møller P (2006) Lipids and stable isotopes in marine food webs in West Greenland. Trophic relations and health implications. PhD thesis, Technical University of Denmark, Kongens Lyngby
- Montoya JP (2007) Natural abundance of ^{15}N in marine planktonic ecosystems. In: Michener R, Lajtha K (eds) *Stable isotope in ecology and environmental science*. Blackwell Publishing, Oxford, p 176–201
- Moore SE, Reeves RR (1993) Distribution and movement. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Society for Marine Mammalogy Spec Publ No. 2, Allen Press, Lawrence, KS, p 313–386
- Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol Lett* 11:470–480
- Neibauer HJ, Schell DM (1993) Physical environment of the Bering Sea population. In: Burns JJ, Montague JJ, Cowles CJ (eds) *The bowhead whale*. Society for Marine Mammalogy Spec Publ No. 2, Allen Press, Lawrence, KS, p 23–44
- Newsome SD, Etnier MA, Monson DH, Fogel ML (2009) Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Mar Ecol Prog Ser* 374:229–242
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- NWMB (Nunavut Wildlife Management Board) (2000) Final report of the Inuit bowhead knowledge study, Nunavut, Canada. NWMB, Iqaluit
- Orr AJ, Newsome SD, Laake JL, VanBlaricom GR, DeLong RL (2011) Ontogenetic dietary information of the California sea lion (*Zalophus californianus*) assessed using stable isotope analysis. *Mar Mamm Sci* 28:714–732
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with variation. *PLoS ONE* 5:e9672
- Perovich DK, Richter-Menge JA (2009) Loss of ice in the Arctic. *Ann Rev Mar Sci* 1:417–441
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Petersen SD, Tenkula D, Ferguson SH (2011) Population genetic structure of narwhal (*Monodon monoceros*). DFO Can Sci Advis Sec Res Doc 2011/021. Fisheries and Oceans Canada, Ottawa
- Peterson AT (2006) Uses and requirements of ecological niche models and related distributional models. *Biodiversity Informatics* 3:59–72
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Ann Rev Ecol Syst* 18:293–320
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261–269
- Pomerleau C, Patterson TA, Luque S, Lesage V, Heide-Jørgensen MP, Dueck LL, Ferguson SH (2011a) Bowhead whale *Balaena mysticetus* diving and movement patterns in the eastern Canadian Arctic: implications for foraging ecology. *Endang Species Res* 15:167–177
- Pomerleau C, Ferguson SH, Walkutz W (2011b) Stomach contents of bowhead whales (*Balaena mysticetus*) from four locations in the Canadian Arctic. *Polar Biol* 34: 615–620
- Pomerleau C, Winkler G, Sastri A, Nelson RJ, Vagle S, Lesage V, Ferguson SH (2011c) Spatial patterns in zooplankton communities across the eastern Canadian sub-

- arctic and Arctic waters: insights from stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios. *J Plankton Res* 33:1779–1792
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718
- Postma LD, Dueck LL, Heide-Jørgensen MP, Cosens SE (2006) Molecular genetic support of a single population of bowhead whales (*Balaena mysticetus*) in western Canadian Arctic and western Greenland waters. DFO Can Sci Advis Sec Res Doc 2006/051. Fisheries and Oceans Canada, Ottawa
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at www.R-project.org
- Reeves RR, Heide-Jørgensen MP (1996) Recent status of bowhead whales, *Balaena mysticetus*, in the wintering grounds off West Greenland. *Polar Res* 15:115–125
- Reeves RR, Mansfield A, McLaughlin M (1983) Distribution and migration of the bowhead whale (*Balaena mysticetus*) in the eastern North American Arctic. *Arctic* 36:5–64
- Roughgarden J (1972) Evolution of niche width. *Am Nat* 106:683–718
- Ruckstuhl KE, Neuhaus P (2005) Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge
- Rugh D, DeMaster D, Rooney A, Breiwick J, Sheldon K, Moore S (2003) A review of bowhead whale (*Balaena mysticetus*) stock identity. *J Cetacean Res Manag* 5: 267–279
- Ruiz-Cooley RI, Gendron D, Aguiñiga S, Mesnick S, Carriquiry JD (2004) Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Mar Ecol Prog Ser* 277:275–283
- Runge JA, Ingram RG (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar Biol* 108:217–225
- Sarle W (1983) Cubic clustering criterion. SAS Technical report A-108. SAS Institute, Cary, NC
- Shaw CN, Wilson PJ, White BN (2003) A reliable molecular method of gender determination for mammals. *J Mammal* 84:123–128
- St. Aubin DJ, Smith TG, Geraci JR (1990) Seasonal epidermal moult in beluga whales, *Delphinapterus leucas*. *Can J Zool* 68:359–367
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implication for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32–37
- Todd S, Ostrom P, Lien J, Abrajano J (1997) Use of biopsy samples of humpback whale (*Megaptera novaeangliae*) skin for stable isotope ($\delta^{13}\text{C}$) determination. *J Northwest Atl Fish Sci* 22:71–76
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging-rate predation risk trade-off. *Ecology* 69:1352–1366
- Wiig Ø, Heide-Jørgensen MP, Lindqvist C, Laidre KL and others (2011) Recaptures of genotyped bowhead whales *Balaena mysticetus* in eastern Canada and West Greenland. *Endang Species Res* 14:235–242
- Witteveen BH, Worthy GAJ, Wynne KM, Roth JD (2009) Population structure of North Pacific humpback whales on their feeding grounds revealed by stable carbon and nitrogen isotope ratios. *Mar Ecol Prog Ser* 379:299–310

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