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Differences in individual bowhead whale *Balaena mysticetus* habitat use, foraging dive depth and diet during the peak feeding season

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ABSTRACT: Shifts in zooplankton quantity and quality caused by climate change could challenge the ability of bowhead whales to meet their energetic requirements. When facing such selection pressure, intra-population variation dampens the negative effects and provides population-level resilience. Previous studies observed inter-individual diet variation in bowhead whales, but the mechanism responsible for the variation was undetermined. We investigated foraging variability in Eastern Canada-West Greenland bowhead whales using dietary biomarkers (stable isotopes, fatty acids) and movement data (satellite telemetry with time-depth recorders) from the same individuals. We found that bowhead whale individuals using distinct summer and fall foraging habitats displayed differences in horizontal movements, foraging dive depth, and diet. For individuals using the Canadian Arctic Archipelago habitat (Foxe Basin, Gulf of Boothia, Prince Regent Inlet, Lancaster Sound and Admiralty Inlet, Nunavut), they performed long distance movements across regions, and their foraging dive depth was generally shallow, but increased from July to November. These whales displayed higher $\delta^{13}C$ and $\delta^{15}N$ values and ratios of C16:1n7/C16:0. Individuals using the West Baffin Bay habitat (Cumberland Sound, Baffin Bay, Davis Strait) were more localized in their horizontal movements and consistent over time in their foraging dive depth, which was generally deeper. These whales displayed lower $\delta^{13}C$ and $\delta^{15}N$ values and ratios of C16:1n7/C16:0. Overall, this inter-individual variation in diet and foraging behaviour could indicate some niche variation which would be beneficial for the population under changing habitats and prey availability.

KEY WORDS: Stable isotopes · Fatty acids · Biopsy sampling · HSSSM · Time-depth recorders · Satellite telemetry

1. INTRODUCTION

The Arctic is one of the fastest changing environments on Earth (Previdi et al. 2021). Most Arctic marine species are ecologically dependent on sea ice cover and, thus, the earlier melt and later formation of sea ice (e.g. Gagnon & Gough 2005) alters the timing of ecological processes and the functioning of marine ecosystems. For primary producers, the reduction of sea ice cover and the increased water temperatures commonly result in increased productivity, which is due to a decrease in the minimum summer sea ice extent and a longer phytoplankton growth period (Arrigo et al. 2008). For lower trophic level

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consumers such as zooplankton, local environmental changes in temperature, salinity, and dissolved oxygen, which is a function of water temperature, push species out of their physiological tolerance range which can alter developmental rates (Weydmann et al. 2015), species distribution (Reygondeau & Beaugrand 2011), and community composition (Daufresne et al. 2009). In certain northern marine environments, local water temperature increases resulted in biogeographical changes in zooplankton communities, with temperate species increasing and polar species decreasing locally, suggesting northward distribution shifts (Beaugrand et al. 2002, 2009). For zooplankton predators like bowhead whales (*Balaena mysticetus*) which depend on high consumption rates of lipid-rich copepod species like *Calanus hyperboreus* and *Calanus glacialis*, local replacement of lipid-rich Arctic species by less energetically dense temperate species (i.e. *Calanus finmarchicus*, *Calanus helgolandicus*) (Møller & Nielsen 2020) could result in difficulties in meeting their energetic requirements.

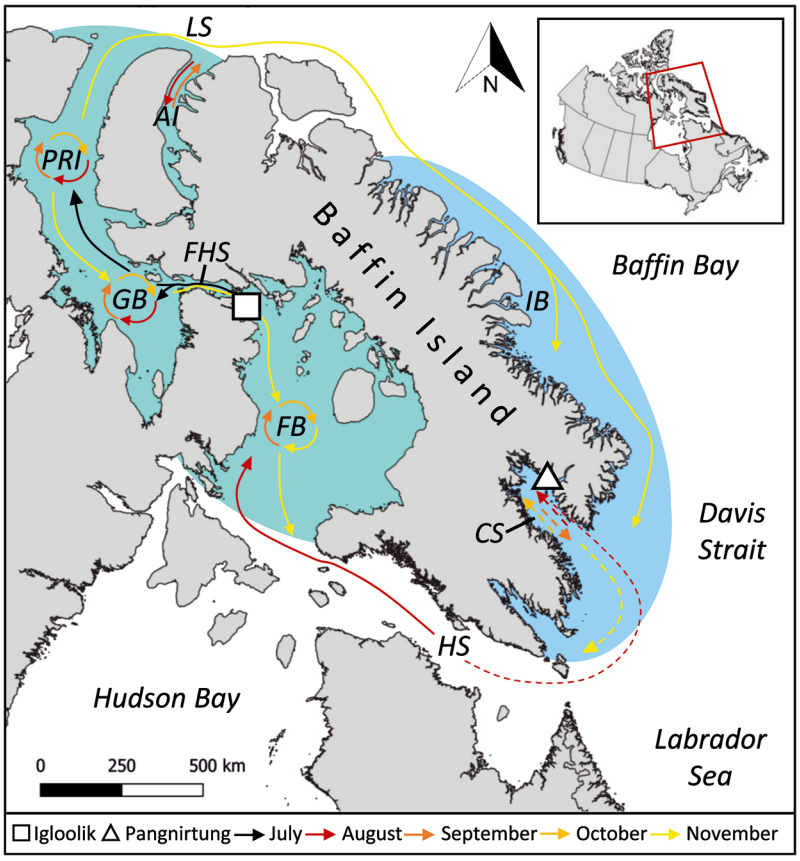

Fig. 1. Sampling locations in the eastern Canadian Arctic. In 2012, 2013 and 2016, a total of 8 bowhead whales were tagged in Igloolik, and 8 bowhead whales were tagged in Pangnirtung. The shaded ocean areas represent the 2 main habitats used: Canadian Arctic Archipelago (CAA) in teal, and West Baffin Bay (WBB) in light blue. Arrows represent general monthly movement patterns for CAA (full arrows) and WBB (dashed arrows) individuals after being tagged. AI: Admiralty Inlet, CS: Cumberland Sound, FB: Foxe Basin, FHS: Fury and Hecla Strait, GB: Gulf of Boothia, HS: Hudson Strait, LS: Lancaster Sound, PRI: Prince Regent Inlet

The Eastern Canada-West Greenland (EC-WG) bowhead whale population is one of 2 populations in the Canadian Arctic along with the Bering-Chukchi-Beaufort population. EC-WG bowhead whales are located around Baffin Island and on the west coast of Greenland. In the winter, they aggregate in Hudson Strait, west Davis Strait, and Disko Bay (Greenland), while in the summer they spread around Baffin Island in different foraging grounds (Fig. 1, Reeves et al. 1983, Pomerleau et al. 2011b, Fortune et al. 2020c).

When facing biotic environmental changes arising from climate change, there are ultimately 2 ways EC-WG bowhead whales can respond. First, they may adapt to these environmental changes. However, with their slow growth rate, late sexual maturity at around 25 years of age, low fecundity, long generation time (George et al. 1999) and small population size (between 9250 and 12 000 individuals, Ferguson et al. 2021), the rate of evolution will likely be slower than the rate of environmental changes currently observed in the Arctic. Second, bowhead whales may benefit from an ability to modulate their behaviour through ecological plasticity within a generation. With high habitat connectivity across their range and high mobility during long distance seasonal migrations (e.g. Reeves et al. 1983), their dispersal potential and ability to shift their distribution to match that of their prey is considerable. For the EC-WG population, the variation in habitat use by different demographic groups in the population based on energetic requirements and predator avoidance (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010, Fortune et al. 2020c), and the inter-individual diet variation observed (Pomerleau et al. 2012, 2014) suggest spatial and dietary flexibility.

Bowhead whales forage on dense patches of zooplankton in the water column using a continuous ram filtration method similar to the unidirectional filter-feeding observed for whale sharks and basking

sharks (Goldbogen et al. 2017). Bowhead whales dives have been classified into 3 categories based on profile shape that reflect different behaviours: V-, U- and square-shaped dives are characterized by the percentage of time spent at maximum depth, ≤20%, >20 and ≤50%, and >50% respectively (e.g. Fortune et al. 2020b). V-shaped dives are considered search dives allowing the whale to locate dense patches of zooplankton in the water column (Laidre et al. 2007). Once prey patches are identified, bowhead whales target them and perform U- or square-shaped foraging dives depending on the vertical distribution of prey (Fortune et al. 2020a). Higher proportions of shorter and shallower U-shaped dives are performed when feeding on near-surface prey aggregations compared to higher proportions of longer and deeper square-shaped dives when feeding near the sea bottom (Fortune et al. 2020b). During foraging dives, bowhead whales only open their mouth at maximum depth to reduce drag in the descent and ascent phases (Simon et al. 2009). To maximize filtering efficiency and prey acquisition while at depth, they periodically close their mouth, presumably to clean the baleen plates and swallow the prey (Simon et al. 2009) or to reduce drag when prey density is low (van der Hoop et al. 2019), before reopening it to continue filtering.

Several studies have characterized the diet of EC-WG bowhead whales using stomach content analysis (Pomerleau & Ferguson 2011a, Fortune et al. 2020a), *in situ* prey sampling near foraging whales (Fortune et al. 2020a), stable isotope (SI) analysis (Pomerleau et al. 2012), and fatty acid analysis (Pomerleau et al. 2014). Results indicate that EC-WG bowhead whales mainly feed on large calanoid copepods such as *C. glacialis*, *C. hyperboreus*, *Metridia longa* and *Paraeuchateta* spp., and that mysids (e.g. *Mysis oculata*) and euphausiids are secondary prey items. Pomerleau et al. (2012, 2014) reported important inter-individual variability in diet, and cluster analyses in both studies revealed distinct groups within the population based on their SI ratios or fatty acid profiles. However, none of the groups were dominated by individuals from a specific region, year, sex, or age class, and, thus, the mechanism driving inter-individual diet variation remained unknown.

The objective of this study was to investigate the drivers of inter-individual diet variability of bowhead whales from the EC-WG population to help assess the potential for the population to cope with future changes in prey composition and availability. A unique dataset combining satellite telemetry, dive data and biopsy samples (SIs, fatty acids [FAs]) from the same individual bowhead whales (n = 16) allowed us to test the hypothesis that foraging behaviour drives dietary variation. More specifically, we hypothesized that differences in horizontal movements (habitat use) and vertical movements (foraging dives) during the peak feeding season drive the inter-individual diet variation. Based on findings from previous studies, we predicted that inter-individual variation in SI ratios and FA profiles were not influenced by sex, age class, sampling year nor sampling region. Instead, we predicted that inter-individual differences in habitat use and foraging dive depth would explain dietary variation and, thus, that foraging behaviour would be a significant predictor of diet.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in the eastern Canadian Arctic centered around Baffin Island. We focused on 2 distinct regions of importance for the EC-WG bowhead whales: (1) Canadian Arctic Archipelago (CAA) which includes Foxe Basin, Gulf of Boothia, Prince Regent Inlet, Lancaster Sound and Admiralty Inlet, and (2) West Baffin Bay (WBB) including Isabella Bay, Cumberland Sound, west Baffin Bay and Davis Strait (Fig. 1). The 2 regions differ considerably in their biotic and abiotic features. Foxe Basin is located more inland in the Canadian Arctic Archipelago and mostly consists of Arctic water masses, with higher terrestrial influences, numerous islands, peninsulas and channels, shallower bathymetry (generally less than 100 m) and denser sea ice cover that persists longer through the summer. Through Fury and Hecla Strait, bowhead whales can reach the adjacent Gulf of Boothia, Prince Regent Inlet and Admiralty Inlet, which offer greater depths up to 700 m. Cumberland Sound is located at the edge of the archipelago in an area more typical of open ocean with its proximity to Davis Strait where Baffin Bay and Labrador Sea meet, providing a mix of Artic and Atlantic water masses (Talley et al. 2011). It is deeper (reaching depths ≥ 1000 m) with lower sea ice cover.

2.2. Sample collection

Whales <8 m long, and mother and calf pairs were not approached and, thus, all tagged individuals were solitary juveniles (≥8 m and <10 m), subadults

(≥10 m and <13 m for females, <12.5 m for males) or adults (≥13 m for females, ≥12.5 m for males) (Fortune et al. 2020c). Whale body length was visually estimated through proportional comparison with the known length of the boat used as a reference. Given the error associated with real-time visual estimation of whale body size, individuals were classified into the broader age-classes mentioned above.

Satellite transmitters were deployed on bowhead whales in Foxe Basin (n = 8) near the community of Igloolik in early July 2012 and 2013, and in Cumberland Sound (n = 8) near the community of Pangnirtung in late August 2012 and 2016 (Table 1, Fig. 1). Platform Transmitter Terminal (PTT) satellite telemetry tags (Wildlife Computers SPLASH MK10) contained time-depth recorders and Argos transmitters to record vertical and horizontal movements. Each tag was deployed using a long fiberglass tagging pole and a ~20 cm stainless steel anchor was embedded into the thick blubber layer on the dorsal surface of the whale (Heide-Jørgensen et al. 2003). Skin and outer blubber layer samples were simultaneously collected from a 4 cm biopsy tip attached to the tag deployment pole.

The tags were programmed to transmit up to 400 times per day, every second hour during the period of absence of sea ice between June 27 and December 27, and reduced to 100 times every second day during the period of near complete sea ice cover between December 28 and March 15 to increase the longevity of the tags (Ferguson et al. 2010, Fortune et al. 2020c). For horizontal movements, the tags provided information on date, time and location (latitude and longitude), allowing us to infer behavioural state using a hierarchical switching-state-space model (HSSSM) (see Fortune et al. 2020c for a detailed description of the procedure). First, the raw locations were filtered to remove biologically improbable locations based on a 2 m s^{-1} swim speed threshold (Heide-Jørgensen et al. 2003, Simon et al. 2009). Then an HSSSM was fit to the filtered telemetry data using a 12 h timestep to distinguish between 2 behavioural states (b) using mean estimates from the Markov Chain Monte Carlo (MCMC): (1) Area Restricted Movement (ARM) based on slow travel speeds and high turning angles (b > 1.75); and (2) Transit based on fast travel speeds and low turning angles (b < 1.25) (Jonsen et al.

Table 1. Summary information for 16 bowhead whales biopsied and tagged with Wildlife Computers SPLASH Tags (MK10) in 2012, 2013 and 2016. The Habitat column refers to the habitat used from July to November: Canadian Arctic Archipelago (CAA) and West Baffin Bay (WBB). Sex (male (M) and female (F)) was determined genetically from biopsy samples and age class (juvenile (JU), sub-adult (SA), adult (A)) was determined from visual estimation of body length. Median depth and *n* columns refer to Area Restricted Movement (ARM) square-shaped dives performed from July to November

PTT	Tagging date (d/mo/yr)	Tagging location	Habitat	Sex	Age class	$\delta^{13}C$	$\delta^{15}N$	C16:1n7/ C16:0	C18:1n9/ C18:1n7	C20:5n3/ C22:6n3	C22:1n11/ C20:1n9	Median depth (m)	*n* (percentage of total dives)
114497	06/07/2012	Igloolik	CAA	M	SA	−20.18	13.25	4.46	3.40	1.54	2.70	48.5	282 (83)
114498	06/07/2012	Igloolik	CAA	M	SA	−19.56	12.89	3.87	3.28	1.66	3.81	31.0	2953 (86)
114499	06/07/2012	Igloolik	CAA	F	A	−19.94	13.29	4.35	2.98	2.13	3.45	27.0	3601 (70)
128145	03/07/2013	Igloolik	CAA	F	SA	−19.51	13.68	3.83	3.50	1.27	1.77	34.0	1447 (81)
128146	03/07/2013	Igloolik	CAA	F	A	−19.85	13.24	4.17	2.88	1.94	2.22	29.0	1514 (69)
128153	03/07/2013	Igloolik	CAA	M	SA	−19.68	13.08	3.51	3.75	1.45	0.42	39.0	133 (63)
128154	03/07/2013	Igloolik	CAA	M	SA	−19.72	13.24	3.64	3.54	1.36	3.74	17.5	663 (74)
128152	09/07/2013	Igloolik	CAA	M	JU	−20.57	12.24	3.97	3.14	1.75	2.84	62.5	3608 (62)
114502	06/08/2012	Pangnirtung	WBB	M	SA	−20.74	12.88	3.21	3.25	1.66	4.97	251.5	1009 (80)
114503	06/08/2012	Pangnirtung	CAA	F	SA	−19.93	13.44	3.43	3.50	1.73	2.93	40.0	102 (67)
114504	07/08/2012	Pangnirtung	WBB	F	SA	−20.23	12.57	3.76	3.41	1.34	3.34	267.5	691 (76)
114505	08/08/2012	Pangnirtung	WBB	M	SA	−20.54	11.79	3.52	3.26	1.70	3.28	245.5	1620 (69)
114508	12/08/2012	Pangnirtung	WBB	M	JU	−20.58	12.48	3.46	3.22	1.89	2.60	259.5	1963 (73)
148504	23/08/2016	Pangnirtung	WBB	F	JU	−19.96	12.25	3.57	2.96	1.85	3.50	259.5	589 (70)
148505	26/08/2016	Pangnirtung	WBB	M	SA	−20.6	12.17	3.71	3.66	1.59	3.58	251.5	214 (82)
126500	28/08/2016	Pangnirtung	WBB	F	SA	−20.49	12.5	3.88	3.07	1.41	3.65	173.5	728 (76)

2005). Locations with b values between 1.25 and 1.75 were assigned an unclassified behavioural state. For vertical movements in the water column, a summary of dive behaviour for dives ≥8 m deep, including maximum dive depth (m), dive duration (s), and dive shape (Square, U, V) was produced for each dive performed. A minimum dive depth of 8 m was required for the Wildlife Computers tags to classify the dives; therefore, any vertical movement <8 m deep was not recorded, preventing us from quantifying surface skim feeding (e.g. Würsig et al. 1985). The 8 m depth threshold is biologically relevant as it represents the minimum length of individuals tagged in this study, and is the depth threshold for visual detection by observers during aerial surveys (Watt et al. 2015). It also avoids the recording of inter-breath intervals which are not considered dives.

2.3. Dietary biomarkers

Skin biopsy samples were used to genetically determine sex (Shaw et al. 2003) and to measure carbon and nitrogen SI ratios. Samples from the entire skin layer were prepared for SI analysis by cutting into small pieces, freeze drying to remove moisture, and extracting lipids using the Folch method (Folch et al. 1957) by combining the dried sample with a 2:1 chloroform:methanol (volume/volume) solvent. Nitrogen and carbon isotope ratios from lipid-extracted samples were simultaneously measured by continuous flow ion ratio mass spectrometry (Thermo Scientific Delta V Plus) at the Freshwater Institute, Winnipeg, Manitoba, Canada. SI ratios were expressed in delta notation ($\delta^{15}N$, $\delta^{13}C$) as parts per thousand (‰) deviations from international standards: atmospheric N_2 for $\delta^{15}N$ and Vienna Pee Dee Belemnite for $\delta^{13}C$. A consumer's SI ratios are a function of the source's SI ratio (from prey items) and physicochemical reactions that fractionate the isotopic ratios (Peterson & Fry 1987). $\delta^{15}N$ is an indicator of trophic level, with increases of about 3 to 4‰ per trophic level (Minagawa & Wada 1984), while $\delta^{13}C$ is typically an indicator of different carbon sources at the base of the food web, providing distinction between benthic- and pelagic-based food webs (Hobson & Welch 1992). The isotopic turnover rate of bowhead whale skin is unknown, but it is estimated to be between 3.5 and 6 mo for bottlenose dolphin skin (Giménez et al. 2016) and between 3 and 9 mo for blue whale skin (Busquets-Vass et al. 2017). As bowhead whales are bigger than bottlenose dolphins, and isotopic turnover rates increase with body mass (Vander Zanden et al. 2015), skin turnover rates for bowheads are predicted to be longer. Bowhead whales are also thought to have a hypometabolic rate for their size (George & Thewissen 2020) and, thus, the turnover rate of their skin could be longer than the estimated 3 to 9 mo from Busquets-Vass et al. (2017) even though they are shorter than blue whales. As bowhead whales also undergo a molt during summer (Fortune et al. 2017), we assume skin samples represent the isotopic niche integrated over a maximum period of one year, but likely reflects the isotopic niche of the previous summer/fall when skin is re-grown and the most intense foraging occurs (Fortune et al. 2020b).

Diet was also inferred from FAs from the outer blubber layer collected from the biopsy using standard protocol (Pomerleau et al. 2014). Samples were kept frozen at −80°C until lipid analysis, then lipids were extracted using a 2:1 chloroform-methanol solution containing 0.01% butylated hydroxytoluene (v/v/w). FAs were identified by gas chromatography with verification via ion mass spectrometry and standards at the Freshwater Institute, Winnipeg, Manitoba, Canada. We used the CA:BnX nomenclature to describe each FA: C to specify carbon is the element of interest, A the length of the carbon chain, B the number of double carbon bonds, and nX the position of the double bond closest to the methyl end. Identified FAs were reported as a percent weight of total FA content, and only the FAs representing >1% of total FA content were retained for further analysis, resulting in 15 FAs that were renormalized over 100%. Four biomarker ratios of interest were also calculated: C16:1n7/C16:0, C18:1n9/C18:1n7, C20:5n3/C22:6n3, and C22:1n11/C20:1n9. C16:1n7 and C20:5n3 are indicators of pelagic or sympagic diatoms (ice algae), while C22:6n3 indicates a flagellate-based diet (Auel et al. 2002). C18:1n7, which is formed by elongation of the precursor C16:1n7, is an indicator of herbivorous feeding on diatoms, while C18:1n9 indicates carnivorous feeding and is a proxy for trophic level (Graeve et al. 1997). Finally, C20:1n9 and C22:1n11 are synthesized *de novo* in calanoid copepods, and can help differentiate diets based on different *Calanus* species (Falk-Petersen et al. 1990). Based on this information, higher C16:1n7/C16:0 values suggest a more diatom-based diet. C18:1n9/C18:1n7 distinguishes between carnivory (>1) and herbivory (<1) and is a proxy for trophic level. C20:5n3/C22:6n3 distinguishes between a diatom-based diet (>1) and flagellate-based diet (<1). C22:1n11/C20:1n9 distinguishes among *Calanus* copepod species in the diet: *C. glacialis* (<0.7), *C. finmarchicus* (≈1.1) and *C. hyperboreus* (>1.8)

(Falk-Petersen et al. 2009). The turnover rate of FAs in the outer blubber layer of bowhead whales is unknown. Blubber in cetaceans can be highly stratified: the inner layer close to the muscles is more metabolically active and has a shorter turnover rate resulting from its dynamic energy storage role, while the outer layer is more static and structural, acting as a thermoregulatory and buoyancy tissue with a longer turnover rate (Budge et al. 2008). The blubber turnover rate of smaller marine mammals has been established in experimental studies on harbour seals (Nordstrom et al. 2008) and is estimated to be 1.5 to 3 mo. However, bowhead whales have a considerably thicker blubber layer and as previously mentioned, an overall lower metabolic rate, so their outer blubber turnover rate is presumably longer. Given the uncertainty in blubber turnover rates, the outer blubber layer likely represents the integrated diet over a similar period as SIs from the skin (i.e. up to a year), but more specifically likely reflects the diet of the previous summer and fall when most of the foraging occurs.

2.4. Data analysis

To temporally match the biomarker results, we restricted dive data to the summer and fall period (June 1–November 30, as defined by Fortune et al. 2020b) following the tagging of the whales. Although bowhead whales forage year-round (Pomerleau et al. 2018), this period is when most of the foraging occurs (Fortune et al. 2020b) and, thus, is more representative of the integrated diet found in skin and blubber samples. Additionally, only dives occurring during an ARM behavioural state based on time stamps were included in the analysis, as foraging behaviour typically occurs in ARM while foraging is limited during the long uninterrupted linear movements typical of a Transit behavioural state (Fortune et al. 2020c). The median depth of ARM square-shaped dives performed during the period of interest was the chosen metric to summarize foraging behaviour, as it provides a reliable measure of a typical value without being skewed by a small number of extreme values (which were present in our positively skewed dataset). Square-shaped dives occurring during ARM likely represent when bowhead acquire most of their prey, as they target a specific depth and maximize the time spent at maximum depth to optimize prey acquisition (Laidre et al. 2007, Simon et al. 2009, Fortune et al. 2020a). In this study, square-shaped dives represented 72% of the 29 408 recorded dives in ARM. As we compared diet of the previous year (before tagging) with foraging behaviour of the following year (after tagging), we assumed that foraging behaviour of an individual is consistent across years. This assumption was confirmed by comparing habitat use between years for 3 individuals for which we had a record of horizontal and vertical movements over almost 2 years. Individuals PTT:128146 and PTT:128152 were both tagged in Igloolik and used the CAA during the summer and fall of both years (2013 and 2014), while individual PTT:114503 was tagged in Pangnirtung and used WBB early in the summer but switched to the CAA from September to November in both consecutive years (2012 and 2013).

We used multiple regression analysis to investigate the drivers of diet variation. As we had a small sample size of tagged and biopsied whales (n = 16), we minimized the number of predictor variables included in our models to prevent overfitting (Babyak 2004). Foraging dive depth (i.e. median depth of ARM square-shaped dives) was included as a fixed effect because its impact on bowhead whale diet has not been investigated yet in similar studies (Pomerleau et al. 2012, 2014). Other potential predictor variables were sex, age class, tagging year and habitat used during the peak feeding season (CAA vs WBB), all as fixed effects. To choose which variables to exclude from the models, we used MANOVAs to investigate differences in dietary metrics (i.e. $\delta^{15}N$, $\delta^{13}C$, and FA ratios of interest) among sexes, age classes, years and regions. Four MANOVAs (one for each potential predictor) were performed on the combined $\delta^{15}N$ and $\delta^{13}C$ values as dependent variables, and 4 other MANOVAs on the combined 4 FA ratios of interest. We tested whether the assumptions of multivariate normality and homogeneity of covariance were met using the 'assumptions_manova' function from the 'micompr package' (v. 2022.02.3) in RStudio (Fachada et al. 2016, R Core Team 2022). Predictors were excluded if no significant diet differences were revealed by the MANOVAs. Once the predictors were chosen, we tested for interactions between them, and built separate general linear models for $\delta^{15}N$, $\delta^{13}C$, and the FA ratios of interest. We tested our hypothesis by model selection based on ΔAICc, the Akaike Information Criterion corrected for small sample sizes. All models with ΔAICc ≤ 2.0 were considered plausible with substantial support (Burnham & Anderson 2004). The null model included the error term (residuals) by itself without any predictor, therefore representing the inter-individual variability in a given biomarker explained by the individuals themselves. We also performed a

residual analysis to graphically verify the assumptions of linear models (normality of residuals and homogeneity of variance).

3. RESULTS

The 16 bowhead whales sampled in 2 distinct regions across years (2012, 2013, 2016) showed variation in habitat use, foraging dive depth, SI ratios and FA profiles (Table 1, Figs. 1–4).

3.1. Horizontal movements

Bowhead whales tagged in 2 distinct locations used different habitats during the summer and fall following their tagging. All individuals tagged in Igloolik used the CAA as their summer and fall foraging habitat (Fig. 1). In July, they all transited through Fury and Hecla Strait to Gulf of Boothia and Prince Regent Inlet where they spent August, September, and October (except PTT: 114499 which went to Admiralty Inlet in August and September). In November, 4 individuals (PTT: 128145, 128146, 128152 and 128154) transited south through Fury and Hecla Strait to reach Foxe Basin and head to Hudson Strait for the winter, while the 4 others (PTT: 114497, 114498, 114499 and 128153) went north through Lancaster Sound to head for the east coast of Baffin Island. This behaviour was consistent with known migratory patterns for this bowhead whale population (Reeves et al. 1983, Pomerleau et al. 2011b, Fortune et al. 2020c). On the other hand, all individuals tagged in Cumberland Sound (except PTT:114503) stayed in the region during the summer and most of the fall (Fig. 1), spending extensive periods of time in Kingnait Fiord (Fortune et al. 2020b) which has a maximum depth around 200 m. They only initiated movement south towards Hudson Strait in late November in preparation for winter. Individual PTT:114503 was tagged in Cumberland Sound but used the CAA as a summer and fall foraging area. This individual went from Cumberland Sound to Foxe Basin through Hudson Strait in late August, and stayed in Foxe Basin through September, October and November (Fig. 1).

3.2. Vertical movements

The 16 individual bowhead whales performed a combined total of 53 559 dives during the period of summer and fall following tagging, 29 408 (54.9%) of which occurred during an ARM behavioural state. Within ARM dives, square-shaped dives were the dominant dive shape (71.8%, n = 21 117), followed by U (20.7%, n = 6088), V (7%, n = 2069) and uncategorized dives (0.5%, n = 134), which supported the use of the median depth of ARM square-shaped dives to characterize foraging behaviour. The number of recorded ARM dives between July and November varied considerably among individuals (153 to 5862). Most ARM dives were ≤ 50 m (54.7%; median: 38 m; 113.66 ± 125.93 m) but ranged from 8 to 719.5 m. The median depth of ARM square-shaped dives over the period of summer and fall following tagging ranged from 17.5 to 267.5 m (Table 1, Fig. 2). When pooled, the individuals using the CAA displayed a monthly increase in their dive depth, while the individuals using WBB showed more consistency in foraging dive depth between months (Fig. 3).

3.3. Dietary biomarkers

$\delta^{13}C$ values ranged from −20.74 to −19.51‰ while $\delta^{15}N$ values ranged from 11.79 to 13.68‰ (Table 1, Fig. 4). The isotopic ratios of carbon and nitrogen of the sampled individuals did not differ significantly among years (MANOVA, Pillai = 0.16804, F = 1.3129, p = 0.303), among age classes (MANOVA, Pillai = 0.26444, F = 0.99039, p = 0.430), and between sexes (MANOVA, Pillai = 0.11542, F = 0.8481, p = 0.451), but differed between habitats used during the peak feeding season (MANOVA, Pillai = 0.61016, F = 10.174, p = 0.002) by <1‰ for both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 4). General linear models (multiple regressions) were conducted separately with $\delta^{13}C$ and $\delta^{15}N$ as response variables and with habitat (CAA vs WBB) and median depth of ARM square-shaped dives (foraging dive depth) as predictor variables. There was a significant interaction between the predictors, as whales using the CAA performed shallower foraging dives than the whales using WBB (Wilcoxon Rank Sum Test, W = 24424504, p < 0.001).

For $\delta^{13}C$, the median depth of ARM square-shaped dives was the best predictor of the observed variation (R^2 = 0.47, p = 0.002, AICc = 12.813; Table 2), and $\delta^{13}C$ decreased with an increase in median depth of ARM square-shaped dives. The other plausible models (ΔAICc < 2.0) included (1) the interaction between foraging dive depth and habitat, and (2) habitat, where the CAA bowhead whales had higher $\delta^{13}C$ values than those using WBB.

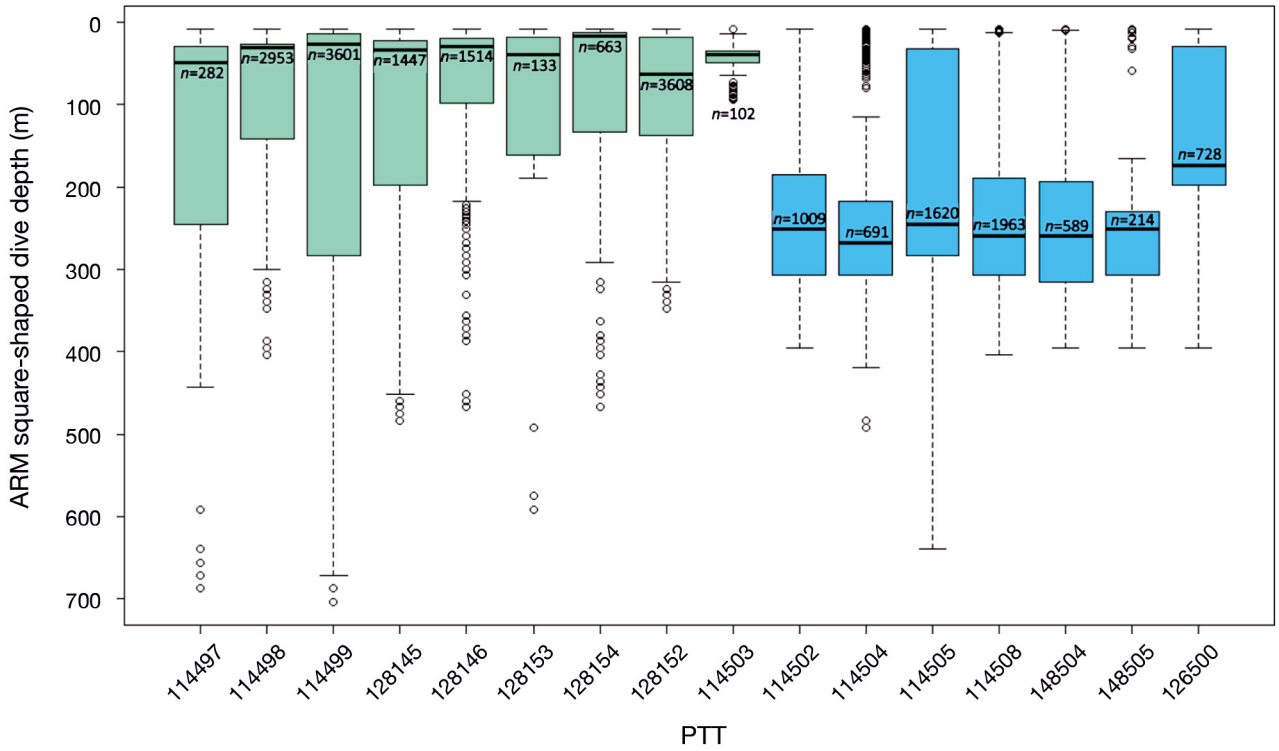

Fig. 2. Vertical distribution of Area Restricted Movement (ARM) square-shaped dives performed from July to November following the tagging of 16 bowhead whales using the Canadian Arctic Archipelago (teal boxes) and West Baffin Bay (light blue boxes) in 2012, 2013 and 2016. Boxes show the interquartile range with the center horizontal line representing the median. Whiskers delimit maximum and minimum values, and circles are outliers. PTT numbers are the same individual identifiers as in Table 1

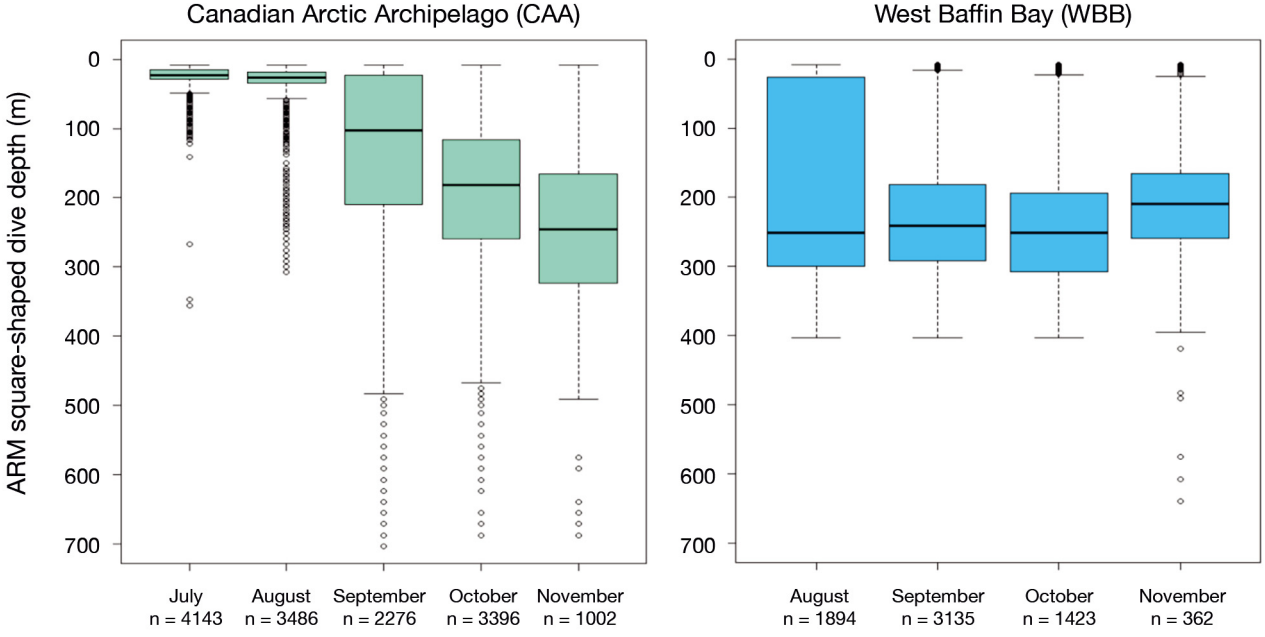

Fig. 3. Monthly variation in Area Restricted Movement (ARM) square-shaped dive depth for bowhead whales using the Canadian Arctic Archipelago (CAA, teal boxes) and West Baffin Bay (WBB, light blue boxes) in 2012, 2013 and 2016. All the dives from the 9 individuals using the CAA are pooled together, and the same was done for the 7 individuals using WBB. Boxplots as in Fig. 2

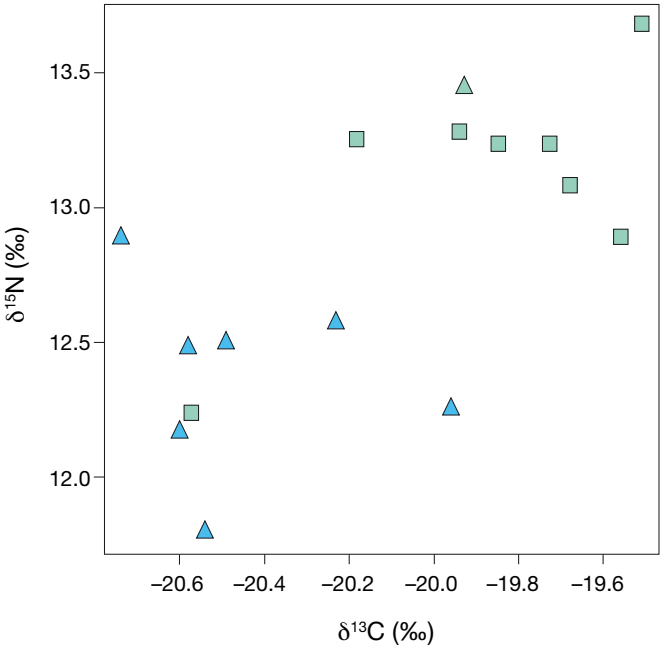

Fig. 4. Isotopic biplot for the 16 bowhead whales biopsied in Igloolik (squares) and Pangnirtung (triangles) in 2012, 2013 and 2016. Individuals that used the Canadian Arctic Archipelago (CAA) habitat during the summer and fall are displayed in teal, while the individuals that used the West Baffin Bay habitat are displayed in light blue

For $\delta^{15}N$, the median depth of ARM square-shaped dives was also the best model (R^2 = 0.53, p = 0.001, AICc = 19.510; Table 2), and $\delta^{15}N$ decreased with an increase in median depth of ARM square-shaped dives. The other plausible model (ΔAICc < 2.0) included habitat, where $\delta^{15}N$ values were higher in the CAA compared to WBB.

The FA ratios of interest did not differ significantly among years (MANOVA, Pillai = 0.085712, F = 0.25781, p = 0.899), between sexes (MANOVA, Pillai = 0.27331, F = 1.0343, p = 0.432) or between habitats (MANOVA, Pillai = 0.44951, F = 2.2455, p = 0.1302). The ratios did differ significantly among age classes (MANOVA, Pillai = 1.0466, F = 3.019, p = 0.019) but the difference was only significant for the C18:1n9/C18:1n7 and C20:5n3/C22:6n3 ratios, and is likely unreliable due to unbalanced small sample sizes among age classes. As there were no reliable general trends in FA ratios across predictors, the same predictors used for the SI ratios were used in the multiple regressions for the FA ratios. For C16:1n7/C16:0, ratios ranged from 3.21 to 4.46 (Table 1) suggesting feeding in a pelagic or sympagic diatom-based food web. The best predictor of the observed variation was the median depth of ARM square-shaped dives (R^2 = 0.21, p = 0.044, AICc = 13.251; Table 2) where ratios decreased with an increase in foraging dive depth. Other plausible models (ΔAICc < 2.0) included (1) habitat, where the ratios were higher for individuals in the CAA compared to WBB, and (2) the null model. For C20:5n3/C22:6n3, ratios ranged from 1.27 to 2.13 (Table 1), showing a predominance of C20:5n3 which suggests feeding in a pelagic or sympagic diatom-based food web. No predictor successfully explained the observed variation and the null model had the lowest AICc value (Table A1 in the Appendix). For C18:1n9/C18:1n7, ratios ranged from 2.88 to 3.75 (Table 1), showing a predominance of the C18:1n9 FA suggesting carnivorous feeding. No predictor successfully explained the observed variation and the null model had the lowest AICc value (Table A1). For C22:1n11/C20:1n9, the ratios varied considerably and ranged from 0.42 to 4.97 and suggested mostly feeding on *C. hyperboreus* (Table 1). Habitat was the best predictor of the observed variation, but the difference was not statistically significant (Table A1).

Table 2. Model selection for $\delta^{13}C$, $\delta^{15}N$ and C16:1n7/C16:0 ratios obtained from skin and outer blubber samples of 16 bowhead whales from Igloolik and Pangnirtung in 2012, 2013 and 2016. Foraging dive depth represents the median depth of Area Restricted Movement square-shaped dives, while Habitat refers to the habitat used (Canadian Arctic Archipelago or West Baffin Bay)

Model	R^2	p	AICc	ΔAICc
$\delta^{13}C$ ~				
Foraging dive depth	0.47	0.002	12.813	0
Habitat × Foraging dive depth	0.62	0.002	12.889	0.076
Habitat	0.46	0.002	13.238	0.425
Habitat + Foraging dive depth	0.43	0.010	16.423	3.610
Null	–	–	21.024	8.211
$\delta^{15}N$ ~				
Foraging dive depth	0.53	0.001	19.510	0
Habitat	0.50	0.001	20.381	0.871
Habitat + Foraging dive depth	0.49	0.005	23.147	3.637
Habitat × Foraging dive depth	0.55	0.005	24.250	4.740
Null	–	–	29.611	10.101
C16:1n7/C16:0 ~				
Foraging dive depth	0.21	0.044	13.251	0
Habitat	0.19	0.054	13.656	0.405
Null	–	–	14.960	1.709
Habitat + Foraging dive depth	0.15	0.142	16.861	3.610
Habitat × Foraging dive depth	0.11	0.232	20.539	7.288

4. DISCUSSION

Inter-individual variability in dietary biomarkers was associated with spatial and behavioural differences that influenced where and how individual bowhead whales acquired their prey during the period of summer and fall. As predicted, habitat use and foraging dive depth were important predictors of dietary biomarker variability, with no significant effect of year, sex or age class.

4.1. Foraging behaviour

The median depth of ARM square-shaped dives was the key predictor of isotopic ratio ($\delta^{13}C$, $\delta^{15}N$) and C16:1n7/C16:0 variation, and interacted significantly with region. Shallower dives were conducted in the CAA, and were associated with higher $\delta^{13}C$ and $\delta^{15}N$ values and C16:1n7/C16:0 ratios, while individuals using the WBB habitat conducted deeper dives and displayed lower biomarker values. Differences in the median depth of ARM square-shaped dives could be a feature of the location where the dives occurred, as maximum dive depth is restricted by the bathymetry. As the CAA is generally shallower than WBB, it is expected that foraging dives might be shallower for individuals using this habitat. A recent study examined the relationship between bowhead whale square-dive depth and bathymetry and found that bottom depths where bowhead whales occurred based on satellite-telemetry data were 246 ± 263.26 m (±SD) (max. 1000 m) in Cumberland Sound and only 93 ± 82.23 m (max. 417 m) in Foxe Basin (Fortune et al. unpubl. data).

Additionally, the large-scale horizontal movements of the individuals using the CAA between regions with distinct bathymetry could partially explain their monthly increase in ARM square-dive depth, while the horizontal movements in a smaller region could explain the monthly consistency in dive depth for the WBB individuals (Figs. 1 & 3). The monthly increase in foraging dive depth of the CAA individuals from July to November is consistent with findings from Fortune et al. (2020b), whereby square dives were longer and deeper during the fall, and shallower during the spring and summer. This behaviour is likely a response to the seasonal vertical migration of calanoid copepods. *Calanus* spp. copepods accumulate important lipid reserves during the summer and fall before entering a form of dormancy at greater depths in cooler water masses for the winter (Baumgartner & Tarrant 2017). Those lipid-rich diapausing copepods represent an important source of energy for bowhead whales (Laidre et al. 2007).

In contrast, individuals using WBB showed more variability in their ARM square-shaped dive depths within each month but consistency between months. The greater variation within each month could represent the multi-depth foraging strategy presented by Fortune et al. (2020a). When 2 distinct patches of zooplankton were found in the water column (a shallow [30–40 m] aggregation with high abundance of small prey species, and a deeper [190–225 m] aggregation with lower abundance but higher biomass [46% greater] of larger prey species), the whales alternated between deep and shallow foraging dives, with mean dive depths coinciding with the depths of both zooplankton patches. The within-month variation in foraging dive depth could also be a behavioural strategy to follow the diel vertical migration (DVM) of calanoid copepods (e.g. Bollens & Frost 1989, Baumgartner & Tarrant 2017) that are known to occur in August in this region (Fortune et al. 2020b). In Cumberland Sound, a seasonal increase in foraging dive depth was also documented, as dive depths in May, June and July were generally shallow (<100 m) and increased in August through November (> 200 m), following the seasonal vertical migration of diapausing copepods (Fortune et al. 2020b). As we did not cover the months of May to July for the individuals using WBB in this study, we cannot assess if a shallower dive pattern occurred, as the one observed for the whales in the CAA.

4.2. Regional diet variation

The regional differences in foraging behaviour were also reflected in diet, as groups of whales exploiting distinct summer and fall foraging habitats (CAA or WBB) displayed significant dietary differences. In this study, potential prey items were not sampled, which prevented us from using dietary SI mixing models or quantitative fatty acid signature analysis to characterize the diet composition of individual bowhead whales and link differences in dietary biomarkers to specific prey species. However, information gathered from previous dietary studies on EC-WG bowhead whales allowed us to interpret our findings.

Individuals in the CAA exhibited higher $\delta^{13}C$ and $\delta^{15}N$ values compared to the WBB individuals. These differences could be due to regional differences in zooplankton species assemblages resulting from oceanographic features unique to both habitats.

Pomerleau et al. (2011c) found a relationship between zooplankton species composition and water mass properties in the eastern Canadian Arctic, identifying 5 regions with significantly distinct species assemblages: Gulf of Boothia, Labrador Sea, Arctic Archipelago, Davis Strait, and Baffin Bay. This spatial variation in species composition could therefore be a driver of diet variation in individuals using distinct foraging habitats. The variation in isotopic ratios between habitats could also originate from differences at the base of the food web that would influence the biomarker values in the same prey species found at 2 different locations. Pomerleau et al. (2011c) observed an enrichment of almost 3‰ in $\delta^{15}N$ for *C. glacialis* and *C. hyperboreus* in the Gulf of Boothia compared to Davis Strait. The cause of such enrichment could have originated from changes in particulate nitrogen at the base of the food web, but was likely due to seasonality, as zooplankton sampled later in the summer usually have higher $\delta^{15}N$ values (Schell et al. 1998). The sampling design in our study did not allow us to distinguish between regional and seasonal effects, as tagging in Igloolik occurred in early July while tagging in Pangnirtung occurred in mid to late August. Assuming the turnover rate of both the skin and outer blubber layer is likely between 6 and 12 mo (Nordstrom et al. 2008, Giménez et al. 2016, Busquets-Vass et al. 2017), the 2 mo time difference between early July and late August is likely not sufficient for diet changes to be reflected in the sampled tissues, suggesting minimal impact of seasonality on the observed results. Pomerleau et al. (2012) also recorded higher $\delta^{15}N$ ratios in a group of whales biopsied in Foxe Basin compared to other sampling sites around the Eastern Canadian Arctic. Potential prey items such as euphausiids, mysids and chaetognaths all had higher isotopic ratios than calanoid copepods (*Calanus* spp., *Metridia longa*) and represented a higher proportion of the diet of bowhead whales biopsied in Foxe Basin, as revealed by dietary mixing models (Pomerleau et al. 2012). Overall, the higher values in $\delta^{13}C$ and $\delta^{15}N$ found in bowhead whales using the CAA could be attributed to both isotopically enriched diet from baseline values differing between habitats and varying dietary compositions with CAA individuals potentially foraging on higher isotopic prey. The higher $\delta^{13}C$ and $\delta^{15}N$ values in CAA individuals also suggest a more diversified diet by incorporating those isotopically enriched prey (e.g. mysids, euphausiids, chaetognaths) in their diet, while the WBB individuals likely fed mainly on calanoid copepods, resulting in their lower SI values.

For the measured FA ratios, differences between habitats were also found in C16:1n7/C16:0 and C22:1n11/C20:1n9 but the relationship was not significant in the C22:1n11/C20:1n9 ratio. All individuals but one had C22:1n11/C20:1n9 ratios > 1.8 which suggests that *C. hyperboreus* is the most important calanoid copepod species in the diet of the sampled individuals (Falk-petersen et al. 2009), regardless of the region occupied during summer and fall. High values of C16:1n7/C16:0 found in this study are consistent with findings from Pomerleau et al. (2014) and confirm that diatoms are the main type of phytoplankton at the base of these food webs in which ECWG bowhead whales forage (Auel et al. 2002). Carnivorous marine mammals are thought to be highly adapted in the digestion and incorporation of marine-specific FAs without any modification (Iverson 2008), meaning that inter-individual differences in FA composition can be attributed to differences in diet. The significant regional difference in the importance of diatom-based diet, with individuals using the CAA displaying higher C16:1n7/C16:0 ratios than individuals using WBB, therefore supports regional differences in dietary composition. Different herbivorous/omnivorous prey species (i.e. mysids, euphausiids, copepods) metabolize FAs differently, and studies of FAs in Arctic zooplankton species show that different species sampled at the same location during the same time of the year display differences in their C16:1n7 and C16:0 FA content (e.g. Søreide et al. 2013, Mohan et al. 2016, Geoffroy et al. 2019) that would be reflected in the FA content of their predators. While prey sampling would have been necessary to identify specific prey items from FAs in the outer blubber of bowhead whales, the significant differences in FA ratios between individuals using different habitats support the results from the SI ratios of distinct diet compositions between habitats used. Variability in C20:5n3/C22:6n3 and C18:1n9/C18:1n7 could not be explained by any predictors or combination of predictors, but the values of C20:5n3/C22:6n3 and C18:1n9/C18:1n7 >1 indicate carnivorous feeding in a diatom-based food web (Graeve et al. 1997, Auel et al. 2002) which is consistent with the current knowledge on the diet of bowhead whales from this population.

If individuals exploiting different summer and fall foraging habitats do in fact have different diet composition, the way that they acquire different types of prey would likely be reflected in their vertical movements in the water column and horizontal movements between regions. The strong relationship between habitat use, foraging dive depth and dietary

biomarkers ($\delta^{13}C$, $\delta^{15}N$, C16:1n7/C16:0) therefore supports the hypothesis that individuals using the CAA and WBB fed on different prey.

4.3. Limitations and uncertainties

Without temporal overlap between the dietary biomarkers and the foraging behaviour data, the influence of foraging behaviour on diet variation could only be assumed. SI and FA integrated dietary information from the months prior to the biopsy collection, whereas foraging behaviour was obtained for the period after tagging. However, the validity of our approach was supported by showing consistency in habitat use between consecutive years for 3 individuals (PTT: 128146, 128152 and 114503), and by traditional Inuit knowledge which also suggests site fidelity between years in Hudson Bay and Baffin Bay (Nunavut Wildlife Management Board 2000).

Without prey sampling at relevant spatial and temporal scales, biotic habitat differences between the areas frequented by the CAA and WBB individuals can only be inferred but not directly assessed. This prevents us from concluding on the influence of different prey assemblages on diet and foraging behaviour variation. However, since diet and foraging behaviour differences were associated with divergent patterns in summer and fall habitat use, habitat is likely driving the observed variation, specifically varying in biotic (predator, prey) and abiotic (bathymetry, connectivity, oceanographic conditions) features. The observed patterns in diet and foraging behaviour suggest a subpopulation structure and a group specialization associated with different summer and fall foraging habitats. The reason behind this structure and how long it persists remains unknown. Some social structure or cultural component in the population could explain the grouping, although since bowhead whales are the longest living mammal, understanding this pattern is temporally challenging and would require extensive monitoring over multiple generations. One possible explanation is that more closely related individuals associate with each other, and this assumption could be confirmed by assessing genetic distance and relatedness among individuals using distinct summer and fall habitats.

Even in the best models for $\delta^{13}C$, $\delta^{15}N$ and C16:1n7/C16:0, a large portion of the observed inter-individual variation in biomarkers remained unexplained (respectively 53, 47 and 79%, Table 2). Inter-individual niche differences can indicate individual specialists which have narrower niches than their population's niche that is not related to their sex, age, or morphology (Bolnick et al. 2003). Individual specialization could therefore be another mechanism driving inter-individual diet variation in the EC-WG bowhead whale population. With predator and prey sampling at relevant spatial and temporal scales, it would be possible to quantify the degree of individual specialization to provide further insight into EC-WG bowhead whale's ability to cope with changes in prey.

5. CONCLUSION

Bowhead whales using distinct summer and fall foraging habitats displayed differences in foraging dive depth and dietary biomarkers, which suggested feeding on different prey. From a conservation perspective, this intra-population variation in habitat use, foraging dive depth and diet would be beneficial for coping with changes in the quality and quantity of prey in the context of climate change. The high mobility of the EC-WG bowhead whales that perform long seasonal migrations throughout the year would also allow them to track the distribution shifts of their prey (Beaugrand et al. 2002, 2009) as the conditions in sub-arctic waters become more temperate. However, the results also suggest that some individuals in the population may experience unequal impacts from climate induced shifts in prey. WBB individuals were limited in their horizontal movements and had a potentially narrow diet, which would make them more vulnerable compared to CAA individuals that travelled long distances between regions and likely fed on more diversified prey species. Future work should focus on prey sampling at relevant spatial and temporal scales, coupled with the whale sampling to test whether distinct prey assemblages occurring across the population's range are ultimately driving diet and foraging behaviour variation in EC-WG bowhead whales.

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Appendix.

Table A1. Model selection for 3 fatty acid ratios obtained from outer blubber samples of 16 bowhead whales from Igloolik and Pangnirtung in 2012, 2013 and 2016. Foraging dive depth represents the median depth of Area Restricted Movement square-shaped dives, while Habitat refers to the habitat used (Canadian Arctic Archipelago or West Baffin Bay)

Model	R^2	p	AICc	ΔAICc
C18:1n9/C18:1n7 ~				
Null	–	–	5.572	0
Habitat	–0.05	0.611	8.343	2.771
Foraging dive depth	–0.06	0.714	8.490	2.918
Habitat + Foraging dive depth	–0.10	0.724	11.492	5.920
Habitat × Foraging dive depth	–0.18	0.873	15.751	10.179
C20:5n3/C22:6n3 ~				
Null	–	–	3.703	0
Habitat	–0.07	0.916	6.767	3.064
Foraging dive depth	–0.07	0.956	6.777	3.074
Habitat + Foraging dive depth	–0.10	0.743	9.686	5.983
Habitat × Foraging dive depth	–0.19	0.886	13.952	10.249
C22:1n11/C20:1n9 ~				
Habitat	0.15	0.075	49.161	0
Foraging dive depth	0.12	0.106	49.806	0.645
Null	–	–	49.830	0.669
Habitat + Foraging dive depth	0.11	0.189	52.436	3.275
Habitat × Foraging dive depth	0.06	0.311	56.321	7.160

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