Individuals matter: investigating individual-level foraging variability in Eastern Canada-West Greenland bowhead whales (*Balaena mysticetus*)

by

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Abstract

The Arctic is one of the fastest changing environments on Earth. For lower trophic level consumers such as zooplankton, local environmental changes in temperature, salinity, and dissolved oxygen push species out of their physiological tolerance range which can alter developmental rates, species distribution, phenology, and community composition. For zooplankton predators like bowhead whales (*Balaena mysticetus*), local replacement of lipid-rich Arctic species by less energetically dense temperate species could result in difficulties to meet their energetic requirements.

The main objective of my thesis was to assess the individual-level foraging variability of Eastern Canada-West Greenland (EC-WG) bowhead whales. Specifically, I tested two mechanisms potentially responsible for explaining inter-individual diet variation: foraging behaviour (i.e., habitat use and foraging dive depth), and individual specialization.

In chapter 2, I used a novel approach combining stable isotopes, fatty acids, satellite telemetry and time-depth recorder data from the same whales to investigate inter-individual variation in dietary biomarkers, habitat use, and foraging dive depth. I found that bowhead whale individuals using distinct summer and fall foraging habitats displayed differences in horizontal movements, foraging dive depth and dietary biomarkers. Individuals using the Canadian Arctic Archipelago habitat (Foxe Basin, Gulf of Boothia, Prince Regent Inlet, Lancaster Sound and Admiralty Inlet, Nunavut) 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 than individuals using the West Baffin Bay habitat (Cumberland Sound, Baffin Bay, Davis Strait), which were more localized in their

horizontal movements and consistent over time in their foraging dive depth, which was generally deeper.

In chapter 3, I investigated individual specialization in EC-WG bowhead whales by quantifying intra- and inter-individual isotopic variation using stable isotopes along baleen plates of harvested bowhead whales. Although sex and body length were not significant predictors of $\delta^{13}C$ and $\delta^{15}N$, individual specialization did not seem to be an important mechanism increasing population-level isotopic niche variation, as most of the remaining $\delta^{13}C$ and $\delta^{15}N$ variation unaccounted for by the fixed effects was attributed to intra-individual variation (79% and 67%, respectively). This isotopic variation within individuals was associated with seasonal migrations between isotopically distinct habitats and variable food intake that cause the yearly isotopic cycles observed in baleen plates. Year was the best predictor of both carbon and nitrogen isotope ratios and drove most of the downward long-term trends in both $\delta^{13}C$ and $\delta^{15}N$ values, likely due to changes in baseline isotopic ratios and/or a possible shift in the feeding ecology of the population. Harvest region was a significant contributor to $\delta^{13}C$ variation, which may indicate long-term site fidelity and foraging in isotopically distinct habitats. The results from this chapter showed a wide isotopic variability within individuals suggesting broad overlapping niche breadths and individual-level plasticity.

Overall, the observed individual-level variation in habitat use, foraging dive depth and dietary biomarker (i.e., stable isotopes and fatty acids) within the EC-WG bowhead whale population suggests high individual-level ecological plasticity which would increase the resilience of the population against changing habitats and prey.

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Thesis format

This thesis follows a grouped manuscript thesis format. Chapter 1 provides a general introduction of the context in which this thesis takes place. Chapters 2 and 3 are distinct manuscripts written with their own abstract, introduction, methods, results, discussion, conclusion, acknowledgements, and references. Chapter 4 presents a general conclusion that summarizes and integrates the conclusions from chapters 2 and 3.

Chapter 1. General introduction

Context

Species around the globe face the threats of climate-induced physical, chemical and biological changes that can alter their ability to efficiently use their habitat to forage, reproduce or even survive (Parmesan 2006). As greenhouse gas concentrations and global temperatures were increasing in the 20th century, an early review released by Hughes (2000) predicted four main consequences on biological systems resulting from those global changes: 1) individual physiological responses to cope with increased temperatures and CO_2 concentrations, 2) population distribution shifts towards higher latitudes and altitudes in response to temperature increases, 3) phenological shifts as life cycle events synchronized with environmental events will be impacted, and 4) microevolutionary adaptions for suitable species with short generation time and fast population growth potential. Those predictions were supported by numerous studies showing that intraspecific responses to human-induced climate changes alter key ecological interactions in ecosystems worldwide (Parmesan 2006).

In this context, the Arctic is one of the fastest changing environments (Previdi et al. 2021). The unproportionally faster warming of Arctic ecosystems compared to the rest of the globe can be referred to as Arctic amplification, which is driven by physical processes such as: 1) sea ice loss, 2) albedo feedback, 3) horizontal heat flux convergence, 4) cloud cover and water vapor, and 5) black carbon aerosols (Serreze & Barry 2011). Most Arctic marine species rely on sea ice, and the earlier melt and later formation of the sea ice cover (e.g., Gagnon & Gough 2005, Laidre et al. 2015) disrupts ecological processes at all trophic levels. For primary producers, the reduction of sea ice cover and the increased water temperatures result in increased primary productivity, which is due to a decrease in the minimum summer sea ice extent and a longer phytoplankton growth period (Arrigo et al. 2008, Arrigo and van Dijken 2015). For lower trophic level 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 and alters species distribution (Reygondeau & Beaugrand 2011) and local zooplankton communities' composition (Daufresne et al. 2009). In 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, Møller & Nielsen 2020).

At higher trophic levels, the loss of sea ice alters predator-prey relationships, which is particularly striking in Arctic marine mammals (Laidre et al. 2008, 2015). For example, pinnipeds rely on sea ice to rest, reproduce, give birth and molt, while polar bears mainly use it as a platform for hunting seals. Therefore, the loss of this habitat not only directly affects these species, but also the inter-specific interactions between them (Laidre et al. 2008). Another example can be found in killer whales and bowhead whales. The sea ice cover that once served as a physical barrier to restrict killer whales from entering subarctic and Arctic waters is no longer preventing their northward expansion. Sightings of killer whales in Arctic waters have increased with the earlier melt and later formation of the sea ice cover (Higdon & Ferguson 2009), and their consumptive and non-consumptive effects on bowhead whales have also been documented (Reinhart et al. 2013, Matthews et al. 2020, Young et al. 2020).

All living organisms have an intrinsic capacity to adapt to biotic and/or abiotic changes in their environment (Williams et al. 2008), but for particularly vulnerable species or populations, rapid ecological alterations can surpass their adaptation ability and lead to extinction. However, extinction risk can be minimized via various processes that can be summarized in two main categories: 1) intra-generational ecological plasticity, and 2) inter-generational evolutionary adaptation (Williams et al. 2008).

Intra-generational ecological plasticity can result from physiological and/or behavioural plastic changes that allow populations to respond to environmental changes by increasing their resilience (Júnior et al. 2022). Ecological plasticity includes processes such as physiological acclimation, phenology shifts, variation in habitat use and biotic interactions, behavioural plasticity, as well as distribution shifts (Williams et al. 2008). Species characteristics and constraints, their behavioural flexibility and physiological limitations all influence the degree of plasticity of ecological traits in a population (Nylin & Gotthard 1998).

Inter-generational evolutionary adaptation can also allow a population to adapt under new selection pressures arising from climate change. The evolutionary potential of a population depends on a number of processes: 1) intraspecific genetic variation for a given trait under selection, 2) trait heritability, 3) the fitness consequences of the trait, 4) intensity and rate of the selection pressure, 5) population size, 6) population growth rate, which depends on the species' life history strategy, and 7) gene flow among populations (Hoffmann & Sgro 2011). Typically, large populations with high genetic variation and short generation times have a higher evolutionary potential to adapt to rapid changes arising with climate change. However, if the rate of change exceeds the rate of evolution potential, then extinction is more likely than evolutionary adaptation (Williams et al. 2008).

Many specialized traits such as stenothermy, diet specialization, complex morphology and behaviour that increase fitness in a limited range of conditions can make a population vulnerable when conditions changes (McKinney 1997) as specialization reduces niche breadth.

However, specialization at the individual level within a population increases resilience against changing habitats and resources as individuals specializing on different resources within a population provide increased population-level niche variation (Araújo et al. 2011, Poisot et al. 2011, Júnior et al. 2022). When inter-individual niche differences are not attributed to sex, age, nor morphology, it is referred to as individual specialization (Bolnick et al. 2003). Studying individual-level variation provides further insight in the ecological dynamics of a population as conspecific individuals may not necessarily be ecologically equivalent (Bolnick et al. 2003). For example, a generalist population may be the result of a homogeneous group of generalist individuals or a heterogeneous collection of specialized individuals (Bolnick et al. 2007), highlighting the need to study variation at the individual-level to better understand population-level dynamics.

General biology of bowhead whales

Bowhead whales (*Balaena mysticetus*, Linneaus 1776) are filter-feeding baleen whales of the Balaenidae family that live year-round in Arctic and subarctic waters (Reeves et al. 1983). They have a circumpolar distribution and are divided into 4 populations by the International Whaling Commission, two of which occur in Canadian waters: the Bering-Chukchi-Beaufort (BCB) and the Eastern Canada-West Greenland (EC-WG) populations. Bowhead whales are easily recognizable with their large head taking up to 1/3 of the body, the absence of dorsal fin, the pronounced arched mouth and unpigmented patches on their chin and tail stock (George et al. 2020). Bowheads are mostly solitary and not gregarious animals, although they socialize in groups at certain times of the year in specific areas (Richardson et al. 1995). They are the longest-lived mammals, with some individuals being estimated living well over a century (George et al. 1999, George & Bockstoce 2008). As Arctic marine mammals, bowhead whales display various adaptations to live in a cold polar environment with highly seasonal productivity. They have the thickest blubber layer of any whale species, which not only acts as an insulative layer for this homeotherm species, but also provides energy reserves in periods of low prey availability (Iverson 2008). They also have the capacity to break through sea ice with their large head which allows them to breathe and move through areas of dense ice cover without risking mortality from ice entrapment (George et al. 1989). Bowhead whales molt their skin annually at the end of the summer, presumably to slough damaged skin to preserve epidermal function, and they facilitate the exfoliation of old skin by rubbing themselves on large boulders in warm shallow coastal areas (Fortune et al. 2017).

Bowhead whales across the Arctic were intensely harvested by commercial whalers from the 16th to the beginning of the 20th century. During this period, thousands of whales were killed for their blubber that provided oil for lighting, and baleen that provided a strong and flexible material widely used in women fashion (Scoresby 1820). The most striking evidence of the impact of commercial whaling on bowhead whales comes from the East Greenland-Svalbard-Barents Sea population, which was heavily hunted by Dutch, German and British whalers from 1611 to 1911 to a point where there was no significant presence of bowhead whales in this area (Allen & Keay 2006). The estimated abundance of the pre-whaling population was 52,500 individuals (Allen & Keay 2006), while recent estimates are only a few hundreds (Boertmann et al. 2015). The EC-WG bowhead whale population was also victim of intense and poorly regulated whaling, and once was designated as endangered, but the slow recovery of the population has led to the recent designation of special concern by the Committee on the Status of Endangered Wildlife in Canada. The current population size is estimated between 9,250 and 12,000 individuals (Ferguson et al. 2021).

EC-WG bowhead whales have a large spatial distribution around Baffin Island (Hudson Strait and Hudson Bay, Foxe Basin, Gulf of Boothia, Prince Regent Inlet, Lancaster Sound, Admiralty Inlet, Cumberland Sound), in north Baffin Bay (Chambault et al. 2018) and on the west coast of Greenland (Reeves et al. 1983, Laidre et al. 2007, Pomerleau et al. 2011, Chambault et al. 2018, Fortune et al. 2020b). Following the annual sea ice ablation and sea surface temperature patterns (Chambault et al. 2018), they undergo large seasonal migrations between those regions. During winter, they select areas with low sea ice concentration within moving ice to minimize the risk of ice entrapment while providing feeding opportunities (Ferguson et al. 2010). In the summer they prefer thick and densely concentrated ice areas to protect themselves from killer whales' predation while foraging (Matthews et al. 2020). Partial sexual segregation and disproportional use of certain areas by different age-reproductive groups of bowheads have also been observed (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010, Fortune et al. 2020c).

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 and basking sharks (Goldbogen et al. 2017). When feeding with their mouth open, they swim at slow speeds to reduce the drag forces that increase drastically with the modification of their hydrodynamic shape associated with an open mouth (Simon et al. 2009). The filtering apparatus consists of two baleen racks each containing around 300 baleen plates with the lingual edge being eroded into small fringe hair. Plates are attached on the upper jaw and fall on each side of the tongue which sits in the middle (Werth & Sforno 2020). Experimental studies of hydrodynamic flow revealed that bowhead whales use a cross-flow filtration in which the prey-laden water enters the mouth in the middle and is flowing parallel to the baleen racks, which prevents clogging of the baleen (Werth & Potvin 2016). The prey-free water is then expulsed out of the posterior openings on each side of the mouth. When feeding at depth, their foraging behaviour consists of three main dive shapes: V, U and Square, which refer to the profile shape of the dives and are characterized by the percentage of time spent at maximum depth, respectively ≤20%, >20 and ≤50%, and >50% as defined by Wildlife Computers (e.g., Fortune et al. 2020b). V-shaped dives are search dives allowing the whale to locate particularly dense patches of zooplankton in the water column (Laidre et al. 2007). Once that depth is identified, bowheads target it and perform U- or Square-shaped foraging dives in which they open their mouth only at maximum depth, and not during the ascent and descent phases (Simon et al. 2009). To maximize filtering efficiency and prey acquisition while at depth, they periodically close their mouth to clean the baleen plates and swallow the prey, before reopening it to continue filtering (Simon et al. 2009).

Current telemetry technologies combined with mathematical models (e.g., Jonsen et al. 2005) allow us to identify two main behavioural states for bowhead whales based on their traveling speed and turning angle between locations: “transit” or “resident” (also referred to as area restricted movement (ARM)). Transit is characterized by high swim speeds and small turning angles, while ARM is characterized by low swim speeds and high turning angles (Jonsen et al. 2005). Typically, a “transit” behavioural state is associated with uninterrupted linear movements across long distances, mostly when migrating between regions (e.g., Fortune et al. 2020b, Pomerleau et al. 2011). ARM behavioural state is mostly associated with foraging, although it can also include non-feeding behaviours like mating (Richardson et al. 1995) and skin molting related activities like rock-rubbing (Fortune et al. 2017). EC-WG bowhead whales spend most of their time in ARM, mostly conducting shallow dives (≤50 m), suggesting that whales forage on near-surface zooplankton patches when resident (Pomerleau et al. 2011).

Bowhead whales also modulate their diving behaviour seasonally, following the seasonal vertical migration of *Calanus* spp. copepods in the water column: square dives are longer and deeper during fall and winter, and they are shallower during spring and summer (Fortune et al. 2020b). Diel diving behaviour is also observed for certain individuals that conduct deeper and longer dives during daylight in periods of high contrast of daylight and darkness in August, likely following the diel vertical migration (DVM) of zooplankton in the water column (Fortune et al. 2020b). Finally, EC-WG bowhead whales sometimes display a multi-depth feeding strategy. Fortune et al. (2020a) found that when two 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% more) 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 deeper patch with higher biomass was proportionally more exploited, suggesting that zooplankton biomass is the main determinant of bowhead whale selection of prey in the water column (Fortune et al. 2020a). However, the shallower foraging dives could represent an interesting trade-off for some individuals (e.g., juveniles), as even if energetic intake is lower, energetic costs are also reduced compared to long and deep dives.

Most feeding occurs in late summer, and Baffin Bay, Cumberland Sound, Gulf of Boothia are thought to be the key summer foraging areas (Fortune et al. 2020b, Pomerleau et al. 2011). Bowhead whales were originally thought to fast during the winter and use their large blubber reserves as an energy source, but recent studies supported the hypothesis that bowhead whales do in fact forage year-round (Matthews & Ferguson 2015, Pomerleau et al. 2018). Several studies have characterized the diet of EC-WG bowhead whales using various methods such as stomach content analysis (Pomerleau & Ferguson 2011, Fortune et al. 2020a), stable isotope analysis (Pomerleau et al. 2012), and fatty acid analysis (Pomerleau et al. 2014). Overall, they revealed that EC-WG bowhead whales mainly feed on large calanoid copepods such as *Calanus glacialis*, *Calanus hyperboreus*, *Calanus finmarchicus*, *Metridia longa* and *Paraeuchaeta* spp., and that mysids (e.g., *Mysis oculata*) and euphausiids (e.g., *Thysanoessa* spp.) 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 stable isotope ratios or fatty acid profiles. However, none of the groups were dominated by individuals from a specific site, year, sex, or age class, and the mechanism driving inter-individual diet variation could not be identified.

Stable isotope ratios along baleen plates have also provided further insight into the foraging ecology of bowhead whales. Baleen plates are keratinous structures formed from amino acids circulating in the bloodstream, and their isotopic composition reflects the stable isotope ratios from the integrated diet (Schell et al. 1989). They are continuously growing at a rate of > 25 cm/year in juveniles and ~17.5 cm/year in adults and can represent a period up to 20 to 25 years of growth (Lubetkin et al. 2008). Because keratinous tissues are metabolically inert after synthesis, stable isotopes along baleen plates provide a timeline of the integrated diet throughout an individual’s life. Baleen stable isotope ratios have mainly been used to investigate seasonal isotopic cycles and revealed that EC-WG bowhead whales feed year-round across isotopically distinct food webs (Matthews & Ferguson 2015, Pomerleau et al. 2018).

Stable isotope analysis

Stable isotope analysis is a method used in ecology to study the integrated diet variation and composition of consumers over a period determined by the turnover rate of the analyzed tissue. The two main elements used in such studies are carbon (C) and nitrogen (N). In the natural world, those elements are present in multiple forms called isotopes; the same elements with an equal number of protons but unequal number of neutrons, which gives them a slightly different atomic mass (Peterson & Fry 1987). Distinct isotopes therefore have different physical properties that influence parameters of chemical reactions such as reaction rate and bond strength. As opposed to radioactive isotopes which have a nucleus that decays at a steady rate, the nucleus of stable isotopes (SI) does not decay and remains stable over time.

SI are measured as ratios of the heavier isotope over the lighter, more naturally abundant form: $^{13}C/^{12}C$ for carbon, and $^{15}N/^{14}N$ for nitrogen. SI ratios are determined during tissue synthesis and the SI composition of a consumer's tissue is expressed in delta values (δ) as parts per thousand (‰) deviations from a standardized ratio following the equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

Where X is the isotope of interest, and R the ratio of the isotope of interest and its natural form in the sample and in the standard.

When going from a prey to a consumer, the ratio of stable isotopes is altered through a mass-dependent process known as isotopic fractionation, i.e., the preferential use of the heavy or light isotope in certain enzymatic reactions. The magnitude of the fractionation is dependent on various factors such as the amino acid and lipid composition of the sampled tissue, the metabolic routing of the dietary inputs to the sampled tissue, the nutritional quality of the diet, the individual's growth rate, and temporal physiological and ecological variation (Newsome et al. 2010). The SI ratios in a consumer's tissue are the product of the SI ratios of the inputs (from prey items) and the physiological processes involved in assimilating the inputs during tissue synthesis and discarding the wastes (Peterson & Fry 1987). The diet of a consumer can be reconstructed with SI ratios from potential prey species and tissue-specific discrimination factors that account for the change in isotope ratios resulting from isotopic fractionation during tissue synthesis (Phillips 2012).

Carbon is sourced from dietary proteins, carbohydrates and lipids. Lipids have a particular affinity for ^{12}C and are therefore ^{13}C-depleted, which is why it is common to extract lipids from the sampled tissue before measuring δ^{13}C to account for variation in lipid content and not attribute it to dietary variation (DeNiro & Epstein 1978). δ^{13}C is typically an indicator of different carbon sources at the base of the food web, from different primary producers displaying distinct δ^{13}C values based on temperature, concentration of dissolved CO_2, phytoplankton growth rate and cell size, and taxonomic differences in isotopic fractionation (Newsome et al. 2010). δ^{13}C values provide distinctions between benthic- and pelagic-based food webs, as well as neritic and oceanic contributions (Hobson & Welch, 1992), with higher δ^{13}C values found inshore and in benthic environments compared to offshore and pelagic ones (Newsome et al. 2010). A trophic enrichment of the heavier isotope (^{13}C) occurs during respiration and the difference in δ^{13}C between trophic levels is usually low (≈+1‰) (DeNiro & Epstein 1978, McCutchan et al. 2003) but can increase to ≈+4‰ in certain taxa (e.g., Vighi et al. 2016).

Nitrogen is mainly sourced from amino acids in dietary proteins. δ^{15}N is a good indicator of trophic level, although δ^{15}N values are also influenced by location of foraging, physiological state (e.g., starving vs satiated), reproductive status, and age (Newsome et al. 2010). During protein catabolism, the lighter ^{14}N isotope is preferentially excreted in nitrogenous waste (urea), while the heavier ^{15}N is assimilated by the organism, which results in an enrichment of ^{15}N in consumer tissue. $\delta^{15}N$ values increase of about 3‰ to 4‰ per trophic level (Minagawa & Wada 1984, McCutchan et al. 2003). Spatial differences in baseline $\delta^{15}N$ are also observed in marine environments based on nutrient availability (Pruell et al. 2020), between intertidal and pelagic systems (Newsome et al. 2010), and areas with important freshwater inputs (Montoya 2007).

Stable isotopes can be measured in metabolically active or inert tissues. Metabolically active tissues, such as blood, skin, blubber, or muscles, have different turnover rates representing the growth period of the given tissue, and therefore represent the integrated diet of the consumer during that period (Tieszen et al. 1983). The isotope ratios are renewed at the same rate as the tissue's growth. In metabolically inert tissues, such as keratin-based tissues like hair, whiskers, feathers, or baleen plates, the isotopic ratios incorporated during synthesis remain unchanged after their formation. If the growth rate of such tissue is known, it is possible to link the SI ratios of the consumer to a specific period in its lifetime, and to investigate seasonal diet variation and migration between isotopically distinct regions (e.g., Best & Schell 1996).

Stable isotopes are not specific, meaning that inter-individual differences in SI ratios can be attributed to different SI inputs but are not necessarily representative of different diet compositions, as the same prey species in distinct locations can display different SI ratios. Similarly, individuals with identical SI ratios measured in a given tissue do not necessarily have an identical diet composition, as SI ratios provide information on the integrated diet over a period defined by the tissue turnover. Therefore, an assemblage of various prey species with distinct SI ratios can be averaged to similar SI ratios between individuals of distinct diets.

Fatty acid analysis

Similar to stable isotopes, fatty acids (FA) are useful biomarkers for the study of food web dynamics and diet. Their structure is well described in Budge et al. (2006) and Iverson (2008). In brief, FA are the simplest lipid form and the basic components of triacylglycerols (TAGs). Their structure consists of two terminal ends: a methyl (CH_3) and a carboxyl group (COOH), linked by a carbon chain. Their structure can differ in two main ways: 1) the length of the carbon chain, typically ranging from 12 to 24 carbon atoms, and 2) the presence, number, position and configuration (cis or trans) of double carbon bonds along the chain. Saturated FA contain no double carbon bonds, while unsaturated FA contain one (monounsaturated) or multiple (polyunsaturated) carbon bonds. FA are generally part of more complex compounds like triacylglycerols which are the most common FA storage form. TAGs are formed with a glycerol and three fatty acids, in such a way that the carboxyl groups of the fatty acids form ester bonds with the hydroxyl groups of the glycerol.

When lipids are ingested, digestive enzymes in the gut breakdown TAGs into their basic components, freeing the FAs which are then transported in the bloodstream to lipid reserves dispersed in the consumer's body where they will be re-integrated in TAGs and absorbed (Budge et al. 2006, Iverson 2008). This is true for most long-chain FA of more than 14 carbon atoms, while short-chain FA of less than 14 carbon atoms are oxidized in the liver and do not make it to fat storage sites (Vance & Vance 2008). The biochemical properties of FA with $\geq$ 14 carbons allow them to be integrated in adipose tissues as they were present in the prey item, with little or no modification (Iverson 2008), which make them particularly useful biomarkers to study diet of consumers. Modifications of FA can occur during the digestion and integration process, with alterations such as adding carbon atoms and double carbon bonds to the chain. However, birds and mammals are limited in their ability to elongate or desaturate exogenous fatty acids (Iverson 2008), which makes the use of FA in consumers tissues even more representative of dietary intake from diverse prey sources. Specifically, carnivorous marine mammals are thought to be highly adapted in the digestion and incorporation of marine-specific FA without any modification (Iverson 2008).

Assuming that individuals of a species all have similar metabolism and capacities to digest and incorporate dietary FA in their tissues, inter-individual differences in FA composition can be attributed to differences in diet, which is supported by experimental studies (e.g., Kirsch et al. 1998). Without trying to specifically reconstruct the diet of an individual, its FA profile, which refers to the relative contribution of specific fatty acids to the overall identified FA in the sampled tissue, can serve as a qualitative and quantitative tool to investigate inter-individual diet differences in the population (Budge et al. 2006, Iverson 2008). Specific FA ratios can also be calculated to distinguish between diatom- or flagellate-based diets (Auel et al. 2002), between carnivory and herbivory (Graeve et al. 1997), and among specific prey species (Falk-Petersen et al. 2009). Finally, as for SI in a given tissue, FA in a specific fat storage site represent an integrated diet over the turnover time of the given lipid tissue.

Objectives

The main objective of my thesis was to assess individual-level variation in the foraging ecology of EC-WG bowhead whales. For zooplankton, local environmental changes in temperature, salinity, and dissolved oxygen push species out of their physiological tolerance range which can alter developmental rates (Weydmann et al. 2015), phenology (Edwards & Richardson 2004), 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 to meet their energetic requirements.

When facing biotic environmental changes arising from climate change, there are two ways EC-WG bowhead whales can respond. First, they may evolve to 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 relatively small population size (between 9,250 and 12,000 individuals, Ferguson et al. 2021), the rate of potential 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 ecology through intra-generational ecological plasticity. 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, reproductive status 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. However, quantification of intra- and inter-individual variability in diet and understanding the drivers of such variation are required to properly assess the ability of EC-WG bowhead whales to cope with current and future changes in prey quality and availability. Therefore, chapters 2 and 3 focused on testing different mechanisms potentially responsible for explaining the observed individual-level diet variation: foraging behaviour (i.e., habitat use and foraging dive depth), and individual specialization.

In chapter 2 I used a novel approach combining stable isotopes, fatty acids, satellite telemetry and time-depth recorder data from the same individuals to investigate inter-individual variation in diet, habitat use, and foraging dive depth and test the hypothesis that foraging behaviour drives dietary variation. More specifically, I 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, I predicted that inter-individual variation in SI ratios and FA profiles were not influenced by sex, age class, sampling year nor sampling region. Instead, I 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.

For chapter 3 I built on the findings from chapter 2 by investigating individual specialization in EC-WG bowhead whales through quantification of intra- and inter-individual variation in stable isotopes along baleen plates of harvested bowhead whales. As I found significant inter-individual differences in dietary biomarkers, habitat use and foraging dive depth with no effect of sex nor age class in chapter 2, I hypothesized that individual specialization was driving inter-individual diet differences within the population, and therefore I predicted greater inter- than intra-individual variation in isotopic ratios unaccounted for by sex and body size (i.e., age) differences.

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Chapter 2. 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. Individuals using the Canadian Arctic Archipelago habitat (Foxe Basin, Gulf of Boothia, Prince Regent Inlet, Lancaster Sound and Admiralty Inlet, Nunavut) performed long distance movements across regions, and their foraging dive depth was generally shallow, but increased from July to November. These whales displayed higher δ^{13}C and δ^{15}N values and ratios of C16:1n7/C16:0 than individuals using the West Baffin Bay habitat (Cumberland Sound, Baffin

Bay, Davis Strait) which were more localized in their horizontal movements and consistent over time in their foraging dive depth, which was generally deeper. 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.

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 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 to meet their energetic requirements.

The Eastern Canada-West Greenland (EC-WG) bowhead whale population is one of two 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 (Fortune et al. 2020c, Pomerleau et al. 2011b, Reeves et al. 1983).

When facing biotic environmental changes arising from climate change, there are ultimately two 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 9,250 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 (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 three 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 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 stable isotope 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 (stable isotopes (SI), fatty acids (FA)) 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.

Material and methods

Study area

This study was conducted in the eastern Canadian Arctic centered around Baffin Island. We focused on two 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 two 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 100m) 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 that 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 $\geq$ 1000 m) with lower sea ice cover.

Sample collection

Whales <8 m long and mother and calf pairs were not approached and, thus, all tagged individuals were solitary juveniles ($\geq$8 m and <10 m), subadults ($\geq$10 m and <13m for females, <12.5m for males) or adults ($\geq$13 m for females, $\geq$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 2m/s swim speed threshold. Then a HSSSM was fit to the filtered telemetry data using a 12hr timestep to distinguish between two 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. 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 to quantify 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 prevents from recording inter-breath intervals which are not considered dives.

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 stable isotope 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 stable isotope ratio (from prey items) and physicochemical reactions that fractionate the isotopic ratios (Peterson & Fry 1987). $\delta^{15}N$ is an indicator of trophic level and 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 1991). The isotopic turnover rate of bowhead whale skin is unknown, but it is estimated to be between 3.5 and 6 months for bottlenose dolphin skin (Giménez et al. 2016) and between 3 and 9 months 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 months 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 (BHT) (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:Bn-X 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 n-X 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 months. 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 stable isotopes 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.

Data analysis

To temporally match the biomarker results from the same seasons in two consecutive years (before and after tagging), 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 (Matthews & Ferguson 2015, 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 three individuals for which we had a record of horizontal and vertical movements over almost two 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 stable isotopes and fatty acids 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 (i.e., female, male), age class (i.e., juvenile, sub-adult, adult), tagging year (i.e., 2012, 2013, 2016) 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 biomarkers (i.e., δ^{15}N, δ^{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 δ^{15}N and δ^{13}C values as dependent variables, and four other MANOVAs on the combined four 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 in RStudio (Fachada et al. 2016, Version 2022.02.3 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 δ^{15}N, δ^{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 and homogeneity of variance of residuals).

Results

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

Horizontal movements

Bowhead whales tagged in two 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, four 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 four 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 (Fortune et al. 2020c, Pomerleau et al. 2011b, Reeves et al. 1983). On the other hand, all individuals tagged in Pangnirtung (except PTT:114503) stayed in the Cumberland Sound 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 Pangnirtung 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).

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=6,088), V (7%, n=2,069) 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 (153-5,862). Most ARM dives were $\leq$ 50 m (54.7%; median: 38 m; 113.66 ± 125.93 m) but ranged from 8-719.5 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, but with higher variability within each month (Fig. 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 less than 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.

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. 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. 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.

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. The significant variation in SI and FA with habitat and foraging dive depth is consistent with diet variation that differs by foraging behavior.

Foraging behaviour

The strong association between foraging dive depth and dietary biomarkers, with shallow dives associated with higher SI and FA ratios, support the hypothesis that foraging behaviour could be a driver of diet variation.

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. Regional 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 bottom depths where bowhead whales occurred based on satellite-telemetry data were 246 m ±263.26 SD (max 1000 m) in Cumberland Sound and only 93 m ± 82.23 SD (max 417 m) in Foxe Basin (Fortune et al. 2022).

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 (Fig. 1 and 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 within month variability in their ARM square-shaped dive depths, and consistency in average dive depth between months. The greater variation within each month could represent the multi-depth foraging strategy presented by Fortune et al. (2020a). When two distinct patches of zooplankton were found in the water column (a shallow (30-40 m) aggregation with high abundance of small calanoid copepods, and a deeper (190-225 m) aggregation with lower abundance but higher biomass (46% more) of larger calanoid copepods, the whales alternated between deep and shallow foraging dives, with 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.

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 biomarker differences. In this study, potential prey items were not sampled, which prevented us from using dietary stable isotope mixing models or quantitative fatty acid signature analysis (QFASA) 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 five 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 two 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 δ^{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 months (Busquets-Vass et al. 2017, Giménez et al. 2016, Nordstrom et al. 2008), the two month 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 δ^{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 epi-benthic euphausiids, mysids and chaetognaths all had higher isotopic ratios than pelagic 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 δ^{13}C and δ^{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 δ^{13}C and δ^{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 EC-WG 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., Geoffroy et al. 2019, Mohan et al. 2016, Søreide et al. 2013) 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 (Auel et al. 2002, Graeve et al. 1997) 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.

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 three 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 used 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 in temporally challenging. 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%, 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.

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 to cope 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 subarctic 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. For instance, WBB individuals displayed limited 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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Tables

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 and *n* columns refer to Area-Restricted Movement (ARM) square-shaped dives performed from July to November.

PTT	Tagging date	Tagging location	Habitat	Sex	Age class	δ^{13}C	δ^{15}N	C16 :1n7/ C16 :0	C18 :1n9/ C18 :1n7	C20 :5n3/ C22 :6n3	C22 :1n11/ C20 :1n9	Median (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%)

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, Nunavut, 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-value	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

Figures

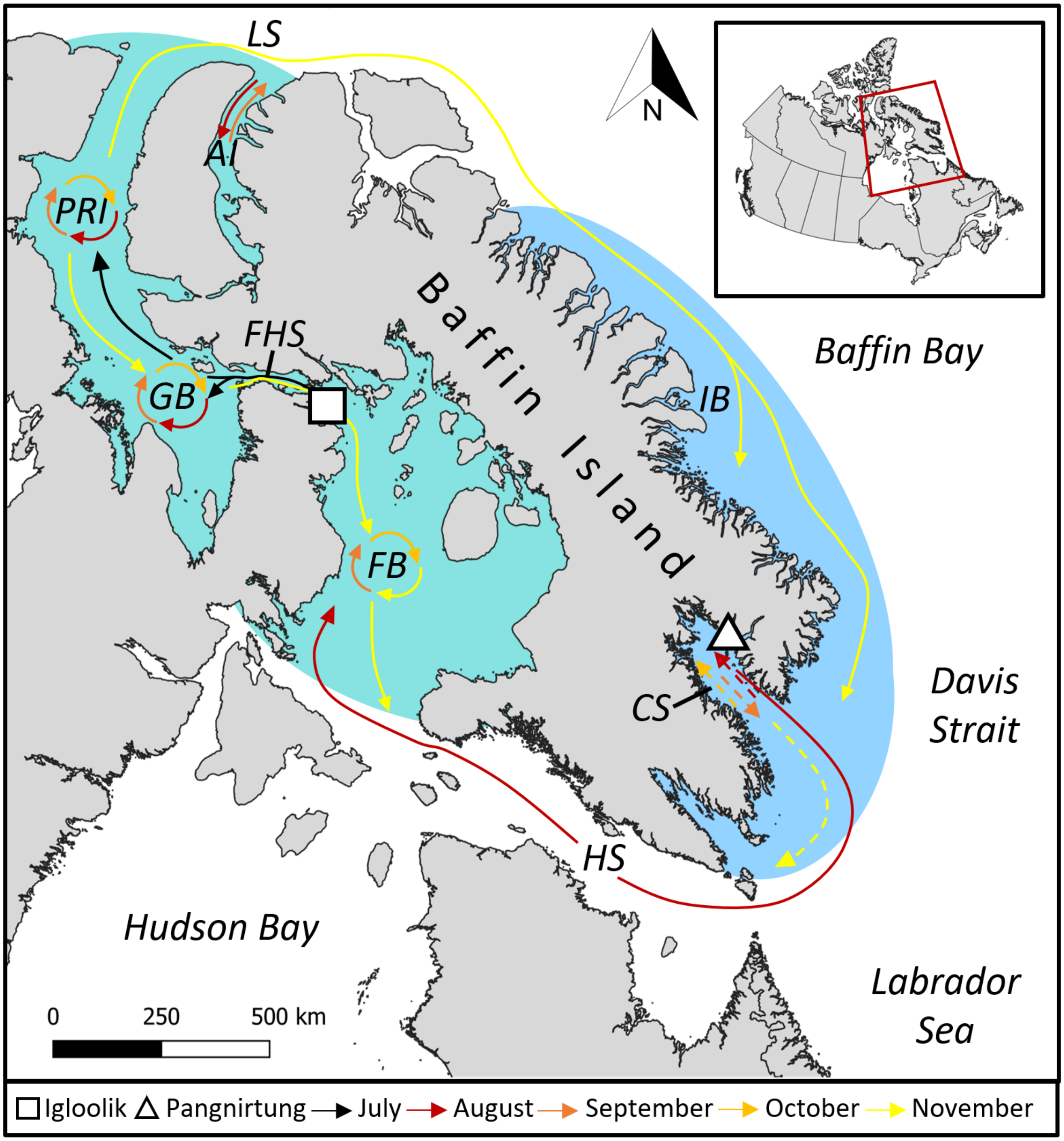

Figure 1: Sampling locations in the eastern Canadian Arctic. In 2012, 2013 and 2016, a total of 8 bowhead whales were tagged in Igloolik, and 8 bowhead whales were tagged in Pangnirtung. The shaded ocean areas represent the two main habitats used: Canadian Arctic Archipelago (CAA) in teal, and West Baffin 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.

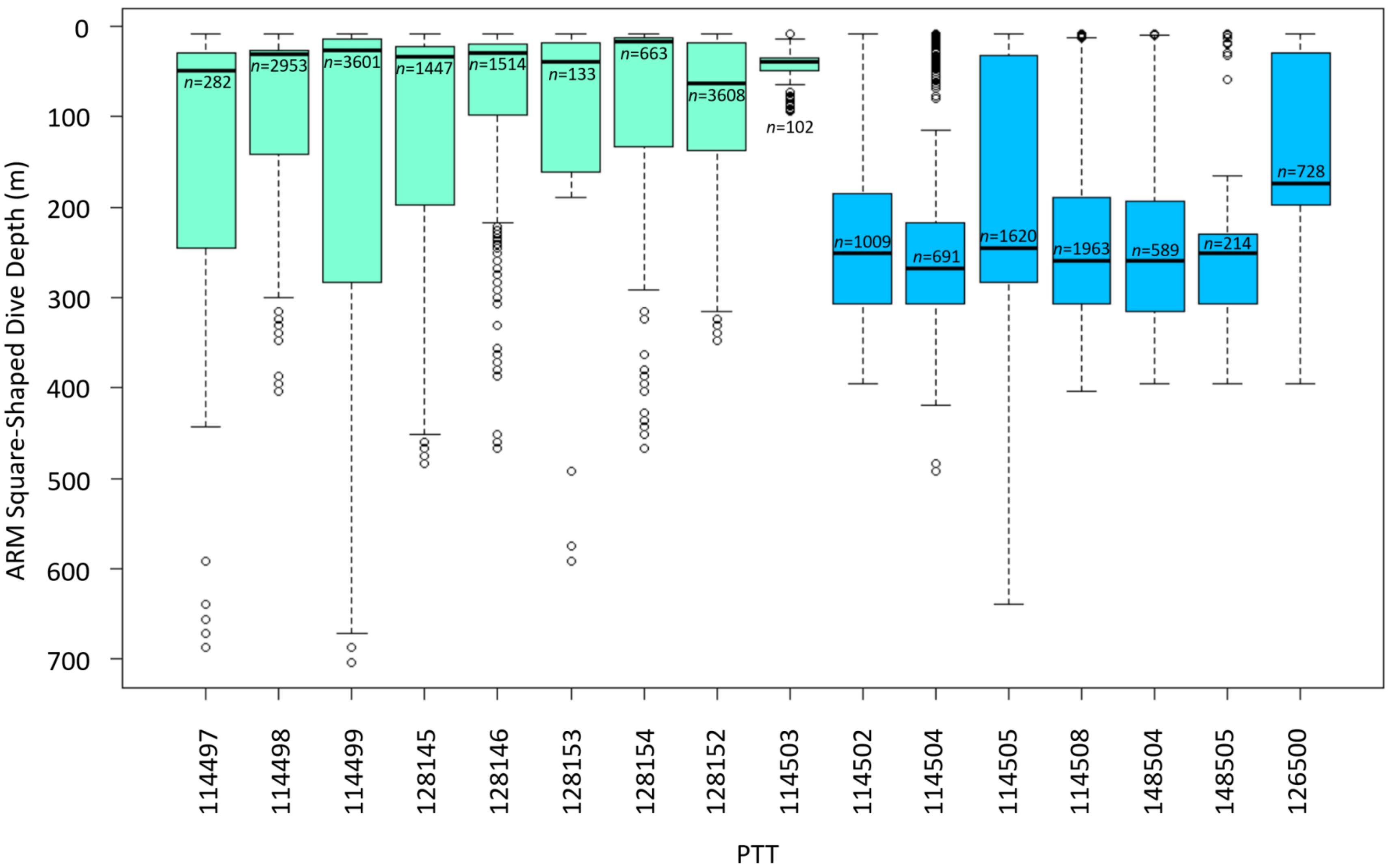

Figure 2: Vertical distribution of Area Restricted Movement (ARM) square-shaped dives performed from July to November following the tagging of 16 bowhead whales using the Canadian Arctic Archipelago (teal boxes) and West Baffin Bay (light blue boxes) in 2012, 2013 and 2016. PTT numbers are the same individual identifiers as in Table 1.

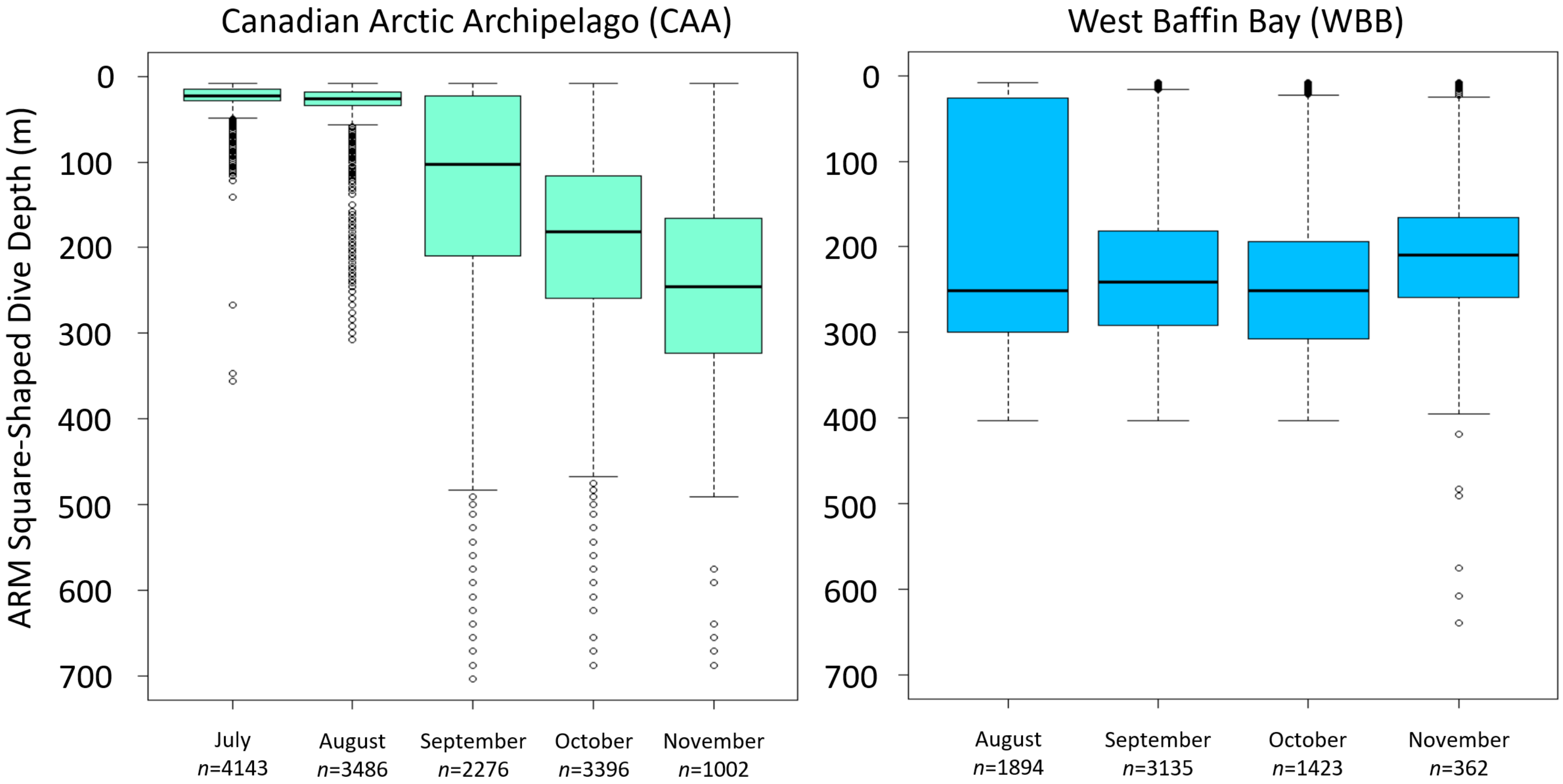

Figure 3: Monthly variation in Area Restricted Movement (ARM) square-shaped dive depth for bowhead whales using the Canadian Arctic Archipelago (CAA, teal boxes) and West Baffin Bay (WBB, light blue boxes) in 2012, 2013 and 2016. All the dives from the 9 individuals using the CAA are pooled together,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

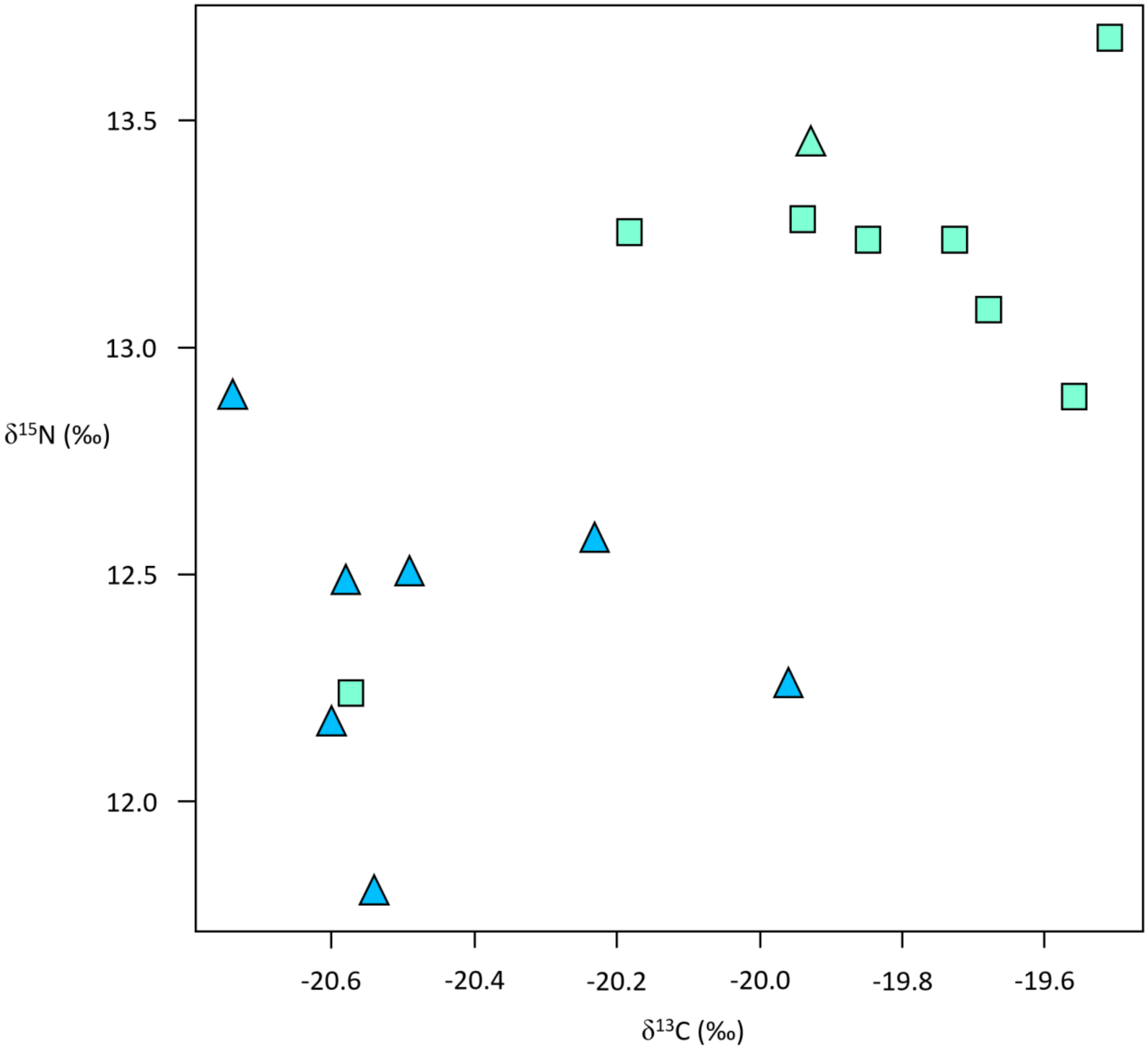

Figure 4: Isotopic biplot for the 16 bowhead whales biopsied in Igloolik (squares) and Pangnirtung (triangles) in 2012, 2013 and 2016. Individuals that used the Canadian Arctic Archipelago (CAA) habitat during the summer and fall are displayed in teal, while the individuals that used the West Baffin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

Chapter 3. Long-term baleen plate stable isotopes records suggest greater isotopic variation within than among individuals in a bowhead whale (*Balaena mysticetus*) population

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Abstract

In the context of climate change, shifting prey species composition and abundance may jeopardize the ability of plankton-feeding bowhead whales to meet their high energetic requirements. However, intra-population variation in resource-use via individual-level specialization or generalization could dampen the effects of climate-induced shifts in prey, thereby providing resilience at the population level. Previous studies showed that Eastern Canada – West Greenland (EC-WG) bowhead whales display inter-individual diet differences that could not be explained by sex, age class or body length, suggesting that diet variation in the population could be attributed to individual specialization. Our objective was to quantify the inter- and intra-individual isotopic variation within the EC-WG bowhead whale population using stable isotope ratios of carbon and nitrogen along baleen plates of harvested individuals. This approach provided the longitudinal data required to compare intra- and inter-individual variation over time to investigate the presence of individual specialization or generalization. Although sex and body length were not significant predictors of $\delta^{13}C$ and $\delta^{15}N$, individual specialization does not seem to be an important mechanism increasing population-level isotopic niche variation, as most of the remaining $\delta^{13}C$ and $\delta^{15}N$ variation unaccounted for by the fixed effects was attributed to intra-individual variation (79% and 67%, respectively). This isotopic variation within individuals was associated with seasonal migrations between isotopically distinct habitats and variable food

intake that cause the yearly isotopic cycles observed in baleen plates. Year was the best predictor of both carbon and nitrogen isotope ratios and drove most of the downward long-term trends in both $\delta^{13}C$ and $\delta^{15}N$ values, likely due to changes in baseline isotopic ratios and/or a possible shift in the feeding ecology of the population. Harvest region was a significant contributor to $\delta^{13}C$ variation, which may indicate long-term site fidelity and foraging in isotopically distinct habitats. Overall, the results showed a wide isotopic variability within individuals suggesting broad overlapping niche breadths and individual-level plasticity, another mechanism through which the population could increase its resilience.

Introduction

Species around the globe face threats of climate-induced physical, chemical or biological changes that can alter their ability to efficiently use their habitat to forage, reproduce or even survive (Parmesan 2006). Many specialized traits such as stenothermy, diet specialization, complex morphology and behaviour that increase fitness in a limited range of conditions can make a species vulnerable when conditions changes (McKinney 1997) as population-level specialization reduces niche breadth. However, specialization at the individual level within a population increases resilience against changing habitats and resources as individuals specializing on different resources within a population provide increased population-level niche variation and presumably less intra-specific competition for resources (Araújo et al. 2011, Poisot et al. 2011, Júnior et al. 2022). Individual specialization is often identified as inter-individual niche differences that are not attributed to sex, age, nor morphology (Bolnick et al. 2003).

With warmer waters and extended periods without ice cover, Arctic zooplankton communities experience altered developmental rates (Weydmann et al. 2015), phenology (Edwards & Richardson 2004), distribution (Reygondeau & Beaugrand 2011) and composition (Daufresne et al. 2009), with temperate species increasing in abundance while polar species decline locally (Beaugrand et al. 2002, 2009, Møller & Nielsen 2020). For a zooplankton predator like the bowhead whale (*Balaena mysticetus*, Linneaus 1776), individual specialization would be a mechanism that could dampen the effects of climate-induced prey shifts. The diet of Eastern Canada-West Greenland (EC-WG) bowhead whales mainly consists of large calanoid copepods such as *Calanus hyperboereus*, *Calanus glacialis*, *Calanus finmarchicus*, *Metridia longa* and *Paraeuchateta* spp., of mysids (e.g., *Mysis oculata*), and of euphausiids (e.g., *Thysanoessa* spp.) (Pomerleau & Ferguson 2011, Pomerleau et al. 2012, Pomerleau et al. 2014, Fortune et al. 2020a).

A recent study investigated the inter-individual variability in foraging behaviour and diet of the EC-WG bowhead whale population (Pontbriand et al. *In review*) and found significant regional differences in habitat use, foraging dive depth and diet among individuals within the population during the peak feeding season (July – November). Sex and age class were not significant predictors of dietary variation, while habitat use and foraging dive depth were significant. However, a large portion of the variation in dietary biomarkers remained unexplained suggesting the presence of individual specialization. Other studies also found non-significant effects of sex and age class on stable isotopes and fatty acids variation (Pomerleau et al. 2012, 2014), suggesting that the remaining inter-individual variation could be attributed to individual-level processes like individual specialization.

Even though bowhead whales are large predators feeding on dense aggregations of very small prey, individual specialization is expected to be present in the EC-WG population, as individuals use distinct foraging grounds (Pontbriand et al. *In review*, Heide-Jørgensen et al. 2010, Cosens & Blouw 2006, Fortune et al. 2020b) and feed at different depths (Fortune et al. 2020a, Pontbriand et al. *In Review*). Arctic zooplankton communities are horizontally and vertically variable (Pomerleau et al. 2011, Darnis et al. 2022, Kosobokova & Hopcroft 2010), providing sufficient ecological opportunity to promote individual specialization (Araújo et al. 2011). Different prey species also display important isotopic variation (Pomerleau et al. 2011, 2012) supporting the use of stable isotopes to investigate the degree of specialization in the population. To do so, it is also crucial to quantify both inter- and intra-individual variation over time from longitudinal data (Bolnick et al. 2003). These longitudinal data can be obtained from continuously growing structures like baleen plates. The filtering apparatus of bowhead whales consists of two symmetrical racks of baleen each containing around 300 plates with the lingual edge being eroded into small fringe hair. Plates are attached on the upper jaw and fall on each side of the tongue which sits in the middle (Werth and Sforno 2020). The baleen plates are keratinous structures formed from amino acids circulating in the bloodstream, and their isotopic composition reflects the stable isotope ratios from the integrated diet (Schell et al. 1989). The stable isotope ratios found in consumer tissue are a function of the source (i.e., prey) stable isotope ratios and physicochemical reactions that fractionate the isotopic ratios (Peterson & Fry 1987), allowing inferences on average assimilated diet from the measured isotopic ratios in the consumer. Each baleen plate is thought to provide an accurate record of temporal isotopic variation as adjacent baleen plates and plates from either side of the mouth display nearly identical isotopic records (Caraveo-Patino & Soto 2005, Schell et al. 1989). Bowhead baleen plates are continuously growing at a rate of > 25 cm/year in juveniles and ~17.5 cm/year in adults and can represent a period of 20 to 25 years of growth (Lubetkin et al. 2008). Because keratinous tissues are metabolically inert after synthesis, stable isotope ratios along baleen plates provide a timeline of the integrated diet throughout an individual’s life. Baleen stable isotope ratios have mainly been used to investigate seasonal isotopic cycles and revealed that EC-WG bowhead whales feed year-round across isotopically distinct food webs (Matthews & Ferguson 2015, Pomerleau et al. 2018).

Previous studies on EC-WG bowhead whales found inter-individual differences in dietary biomarkers that were not related to sex nor age class (Pontbriand et al. *In review*, Pomerleau et al. 2012, 2014), but to region used in autumn during peak feeding (Pontbriand et al. In review). The objective of this study was to quantify the inter- and intra-individual variation in carbon and nitrogen isotope ratios for the EC-WG bowhead whale population. Results will quantify the level of observed diet variation in the population attributed to individuals varying diet over time or to different individuals specializing. To do so, we used stable isotope ratios of carbon and nitrogen along baleen plates of individuals harvested across the range of the population between 1998-2011. We hypothesized that individual specialization is driving variation in stable isotope ratios within the population, and therefore we predicted greater among than within individual variation in isotopic ratios unaccounted for by sex and body size (i.e., age) differences.

Material and methods

Data collection

Baleen plates were collected from 19 bowhead whales harvested between April and September during Inuit subsistence hunts between 1998 and 2011 across the range of the EC-WG bowhead whale population (Table 1, Fig. 1). The sampling protocol is described in Matthews & Ferguson (2015). In brief, within 48 h of death, the longest baleen plate from each individual was selected and extracted either from within the gum or cut at the gum before being frozen at -25°C until sampling. The collected baleen plates varied in length (170 – 326 cm) which affected the duration of recorded stable isotope ratios (from 8 to 21 years based on yearly nitrogen cycles). Total whale length was measured from the tip of the rostrum to the fluke notch with a measuring tape, and their sex was determined genetically (Shaw et al. 2003, Frasier et al. 2020). The 19 whales varied in body length (9.04 – 17.29 m) and females were generally larger than males (15.19 m on average compared to 13.55 m). A close to even sex ratio of bowhead whales was harvested (n=9 males, n=10 females).

In the lab, baleen plates were cleaned with water and scrubbing pads. After removing surface baleen with a scalpel blade, each plate was sampled every 2 cm along the outside edge by drilling small holes with a hand-held rotary tool with a 1/16-inch drill bit. For each sample, 1 mg of extracted baleen plate material was weighed and analyzed using a Vario EL III elemental analyzer (Elementar, Germany) interfaced with a DELTA plus XP isotope ratio mass spectrometer (Thermo Fisher Scientific) at the G.G. Hatch Stable Isotope Laboratory, University of Ottawa, Ontario, Canada. Stable isotope 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 $\delta^{13}C$. For more information on the standards used and measurement precision, see Matthews & Ferguson (2015).

Data analysis

To account for temporal variation in isotopic ratios, $\delta^{15}N$ cycles along baleen plates were used to specify a calendar year to each datapoint, based on the premise that peaks in $\delta^{15}N$ represent summer values and that low $\delta^{15}N$ represent winter values (Matthews & Ferguson 2015). Given that whales were harvested in spring or summer (Table 1) and therefore that peak was incomplete, we used the first low $\delta^{15}N$ value on the baleen plate as a reference point for the previous winter during the harvest year. Then we used the previous peak $\delta^{15}N$ value to indicate the previous year's summer and repeated this process along the length of each baleen plate. $\delta^{15}N$ cycles in all baleen plates had more consistent periods with clear distinct peaks compared to $\delta^{13}C$ cycles, so the accompanying $\delta^{13}C$ values were assigned the same calendar year.

We included the harvest region as a fixed effect in the models to control for spatial variability in harvest location and account for known isotopic differences among individuals using distinct summer-fall habitats (Pontbriand et al. *In review*). Harvest sites were grouped into broader regions using the following method: two groups were identified using a cluster analysis (kmeans) on the combined $\delta^{13}C$ and $\delta^{15}N$ values, and the two groups were further divided resulting in four regions that matched knowledge of the spatial segregation of individual bowhead whales in the EC-WG population. In the summer, individuals are spread across the range of the population, mainly in the Canadian Arctic Archipelago, or on the southeast side of Baffin Island, while they are more concentrated in Hudson Strait during winter (Pontbriand et al. *In review*, Heide-Jørgensen et al. 2010, Cosens & Blouw 2006, Fortune et al. 2020b). Based on this information and the results from the cluster analysis, the harvest regions were divided as follows: 1- Canadian Arctic Archipelago (CAA), 2- Hudson Strait (HS), 3- East Baffin Island (EBI), 4- Greenland and North Baffin (GL) (Table 1, Fig. 1).

Linear mixed effect models were used to quantify inter- and intra- individual variability in stable isotope ratios while controlling for covariates. Models were fit to $\delta^{13}C$ and $\delta^{15}N$ values separately with year, harvest region, body length (as a proxy for age) and sex as fixed effects and individual as a random effect using maximum likelihood (ML) estimation. We compared model fit using the Akaike Information Criterion (AIC), and we selected the full models to perform the variance component analysis as they provided similar fit to the best models ($\Delta AIC < 3.0$, Burnham & Anderson 2004). The full models were re-fit using restricted maximum likelihood estimation (REML). Autocorrelation between data points was controlled by specifying an autocorrelation structure to the full models. Based on autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the models' residuals, we fitted high order autoregressive processes AR(*p*) to the models. For $\delta^{13}C$, an autoregressive process of order 7 (AR(7)) successfully removed the autocorrelation in the residuals, while for $\delta^{15}N$ we could only fit an autoregressive process of order 6 (AR(6)) to the residuals which removed most of the autocorrelation in the residuals. As argued by Zuur et al. (2009) and Schabenberger & Pierce (2002), perfectly modelling the correlation structure of the residuals is not required; as long as the correlation structure is modelled in a reasonable and meaningful way, differences in the output metrics would only differ marginally. Furthermore, the orders of the autoregressive processes are within the range of orders used in Matthews & Ferguson (2015) who successfully fit AR models of order 2-13 to individual baleen isotopic records.

A variance component analysis was performed to quantify inter- and intra-individual variation. Variance associated with the random effect "individual" quantified inter-individual variation unaccounted for by the fixed effects, while the residual error variance represented a measure of intra-individual variation. Model assumptions of homoscedasticity and normality were visually assessed with residual plots.

Results

Variation in both $\delta^{13}C$ and $\delta^{15}N$ values unaccounted for by fixed effects was mainly attributed to intra-individual variation (respectively 78.96% and 67.25%), while inter-individual variation only accounted for 21.04% and 32.75% of the residual isotopic variation (Table 2). Important isotopic niche overlap was also observed (Fig. 2), supporting the results from the variance component analysis.

Sex and body length were not significant predictors in both $\delta^{13}C$ and $\delta^{15}N$ models (Table 2). For $\delta^{13}C$, year and region were significant predictors of isotopic variation (Table 2). Overall, the stable isotope ratios from baleen plates of all individuals ranged from 1985 to 2011 and $\delta^{13}C$ values decreased at a rate of -0.035‰ per year (Pearson's correlation r= -0.362, p-value<0.001). $\delta^{13}C$ differences between harvest regions were observed (mean ± SD: CAA = -18.40 ± 0.59‰, HS = -18.80 ± 0.39‰, EBI = -18.59 ± 0.60‰, GL = -19.00 ± 0.46‰). For $\delta^{15}N$, year was the only significant predictor (Table 2) and $\delta^{15}N$ values decreased at a rate of -0.017‰ per year (Pearson's correlation r=-0.199, p-value<0.001).

Discussion

Our hypothesis was not supported as most of the variation (> 67%) unaccounted for by fixed effects was attributed to intra-individual variation for both $\delta^{13}C$ and $\delta^{15}N$, suggesting a low contribution of individual specialization to isotopic niche breadth at the population level (Bolnick et al. 2002, 2003). These results are similar to what Yurkowski et al. (2016) observed in ringed seals (*Pusa hispida*) and beluga whales (*Delphinapterus leucas*) where intra-individual variation in $\delta^{13}C$ and $\delta^{15}N$ was greater than inter-individual variation, suggesting dietary generalization. However, our results differ from the important individual specialization observed in two ringed seal populations in the low Arctic (Yurkowski et al. 2016). Matthews (2014) also found a similar pattern in dentine growth layers in beluga whale teeth, where $\delta^{13}C$ and $\delta^{15}N$ variation was mostly due to inter-individual differences, suggesting dietary specialization. Similarly, Newsome et al. (2009) found strong evidence of individual specialization in California sea otters (*Enhydra lutris nereis*) using $\delta^{13}C$ and $\delta^{15}N$ along vibrissae, where most of the isotopic variation was attributed to differences between individuals. In comparison, EC-WG bowhead whales do not seem to display important individual specialization, as we observed isotopic niche overlap and minimal isotopic variation among individuals. However, inter-individual isotopic variation was possibly underestimated as predators feeding on different prey can display similar stable isotope ratios falsely interpreted as similar integrated diet (Matich et al. 2021).

The important intra-individual isotopic variation recorded in baleen plates manifested as annual cycles. For $\delta^{13}C$, the cyclic variation is likely due to seasonal migrations between isotopically distinct habitats (Matthews & Ferguson 2015, Pomerleau et al. 2018), where the individuals spend the spring, summer and fall in isotopically distinct foraging habitats spread across the range of the population, but the entire population is restricted to specific areas during winter (Hudson Strait, east Baffin Island, west coast of Greenland, Reeves & Heide-Jørgensen 1996, Koski et al. 2006). Spatial differences in zooplankton assemblages and baseline isotopic ratios have been reported in the regions frequented by EC-WG bowhead whales (Pomerleau et al. 2011), which would be reflected in the isotopic ratios of a consumer. Similarly, cycles in $\delta^{15}N$ values could be attributed to baseline isotopic differences between summer and winter grounds, but the intra-individual variation in $\delta^{15}N$ was more likely associated with annual cycles related to variable food intake, with peak $\delta^{15}N$ values in the summer associated with intense foraging, and low $\delta^{15}N$ values in the winter when foraging is limited (Matthews & Ferguson 2015, Aguilar et al. 2014). Individuals likely maintain a positive nitrogen balance in the winter through limited foraging, allowing them to meet their energetic requirements while avoiding endogenous protein catabolism through protein sparing (Aguilar et al. 2014). If bowhead whales were fasting in the winter (i.e., usage of endogenous protein reserves), we would observe a ^{15}N enrichment in the winter, which is not the case (Matthews & Ferguson 2015). When intense seasonal foraging resumes in the summer, urea excretion and protein catabolism increase and lead to higher ^{15}N enrichment (Aguilar et al. 2014). Baleen plates from all 19 harvested individuals showed strong and clear annual cycles in $\delta^{15}N$.

The fixed effects included in our models provided further insight into long-term isotopic variation in EC-WG bowhead whales. The strongest predictor of isotopic variation in our models was year, with $\delta^{13}C$ and $\delta^{15}N$ values both showing a significant yearly decrease at a rate of -0.035‰ yr^{-1} and -0.017‰ yr^{-1} respectively between 1985 and 2011. Similar long-term declines in consumers' isotopic ratios have been recorded in other marine mammals. Nelson et al. (2018) recorded a decrease of -0.06‰ yr^{-1} for $\delta^{13}C$ and -0.028‰ yr^{-1} for $\delta^{15}N$ between 1962 and 2007 for Cook Inlet beluga whales, which was mainly attributed to a change in their feeding ecology and prey sources. Newsome et al. (2007) recorded a decrease of -0.0215‰ yr^{-1} in $\delta^{13}C$ values between 1948 and 2007 for northern fur seals, but no long-term trend in $\delta^{15}N$ values. The decrease in $\delta^{13}C$ was attributed to anthropogenically-driven changes food web baseline values associated with the Suess effect. Similarly, Matthews & Ferguson (2014) found long term $\delta^{13}C$ declines in Eastern Canadian Arctic/Northwest Atlantic killer whales (*Orcinus orca*) (-0.0184‰ yr^{-1}, 1944-1999), and beluga whales from two populations: Western Hudson Bay (-0.0186‰ yr^{-1}, 1963-2008) and Eastern High Arctic – Baffin Bay (-0.0285‰ yr^{-1}, 1976-2001).

For EC-WG bowhead whales, the observed decline in $\delta^{13}C$ values between 1985 and 2011 is also likely due in part to the oceanic ^{13}C Suess effect, which is caused by the large anthropogenic input of ^{13}C depleted fossil fuels in the atmosphere (Gruber et al 1999). Temporal changes in ocean water $\delta^{13}C$ values have been reported in the Arctic Ocean (-0.011‰ yr^{-1} between 1977-2014, de la Vega et al. 2019), in the Nordic seas (-0.018‰ yr^{-1} in the Norwegian Basin and -0.024‰ yr^{-1} in the Lofoten Basin between 1981 and 2033, Olsen et al. 2006), and in the North Atlantic (-0.022‰ yr^{-1} on average between the 1960s and 1990s, Sonnerup et al. 1999; Gruber et al. 1999; Quay et al. 2003; Körtzinger et al. 2003). Those baseline changes in $\delta^{13}C$ are similar to the -0.035‰ yr^{-1} $\delta^{13}C$ decrease observed in bowhead whale baleen plates. The decline in $\delta^{13}C$ could also partially be attributed to a long-term decrease in primary productivity as argued by Schell (2000, 2001), and by a reduction in sea ice cover limiting the primary production of sympagic phytoplankton and increasing the importance of pelagic primary productivity with lower $\delta^{13}C$ values (Newsome et al. 2007).

For $\delta^{15}N$, the observed trend of -0.017‰ yr^{-1} is similar to the -0.0288‰ yr^{-1} observed by Schell (2001). This downward but less pronounced trend in $\delta^{15}N$ is likely associated with shifts in baseline nitrogen values through various processes reducing $\delta^{15}N$ in phytoplankton and up the food web to bowhead whales. Such processes include an increase in ^{15}N depleted atmospheric nitrogen from anthropogenic sources (Paerl & Fogel 1994, Russell et al. 1998), a gradual reduction in phytoplankton $\delta^{15}N$ values associated with increased nutrient availability (Pruell et al. 2020), and an increase in terrestrial and freshwater inputs with lower $\delta^{15}N$ values (Montoya 2007). However, the simultaneous decrease in both $\delta^{13}C$ and $\delta^{15}N$ could possibly suggest a shift in the feeding ecology of the population (Nelson et al. 2018, Newsome et al. 2007), switching to a less isotopically enriched diet like calanoid copepods as opposed to isotopically enriched mysids and euphausiids (Pomerleau et al. 2011). With climate change, subarctic marine ecosystems become more temperate, and some regions experience shifts in zooplankton assemblages, with temperate smaller bodied and less energetically dense prey replacing Arctic large bodied and more energetic prey locally, suggesting northward distribution shifts (Beaugrand et al. 2002, 2009, Møller & Nielsen 2020). If the larger Arctic zooplankton species are locally replaced by smaller temperate species due to oceanographic changes, bowhead whales could have slowly shifted their diet to feed on those smaller, less isotopically enriched prey (Pomerleau et al. 2011).

Harvest region was added to the models to account for spatial variation in individual summer habitat use as a recent study identified significant stable isotopes and fatty acids differences between individual bowhead whales using distinct habitats during the summer and fall foraging seasons (Pontbriand et al. *In review*). Our results showed that region was a significant predictor of inter-individual variation in $\delta^{13}C$ values, but not $\delta^{15}N$. This result suggests that individuals in this study foraged in isotopically distinct food webs, likely spatially segregated across the range of the population. Zooplankton assemblages across the eastern Canadian Arctic spatially differ in terms of species compositions and stable isotope ratios

(Pomerleau et al. 2011) which would be reflected in the isotopic ratios of a zooplankton consumer like the bowhead whale using distinct habitats. Since the isotopic values measured in baleen plates record changes over long periods of time (from 8 to 21 years in this study), the fact that harvest region is a significant predictor could also indicate the consistent use of distinct habitats (i.e., site fidelity) over the recorded years in the baleen plates.

Ecological sexual dimorphism and ontogenetical niche segregation, which are observed in other cetaceans (e.g., Lesage et al. 2001, Pirotta et al. 2020) do not seem to be processes observed in EC-WG bowhead whales as we found no significant effect of sex and body length. Similar diet studies on EC-WG bowhead whales have also recorded no effect of sex and age class on diet variation (Pontbriand et al. *In review*, Pomerleau et al. 2012, 2014), even if spatial segregation of different demographic groups has been observed (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010, Fortune et al. 2020b). The absence of sexual and ontogenetic differences in stable isotope ratios despite strong spatial segregation of sex-age groups highlights the need to investigate potential social and genetic structures within the population.

Although we found a low level of among-individual isotopic variation, one might expect changes in the occurrence of individual specialization in EC-WG bowhead whales in the future. The main causes of individual specialization are competition, predation, and ecological opportunity (Araújo et al. 2011) and these ecological processes will affect the magnitude of individual specialization in EC-WG bowhead whales in different ways. The population has been increasing in abundance since the end of the commercial whaling era (Ferguson et al. 2021) and is expected to continue doing so, increasing intra-specific competition for resources which would promote individual specialization. The increasing presence of killer whales (*Orcinus orca*) in Arctic waters (Higdon & Ferguson 2009) will however increase predation on bowhead whales

(Matthews et al. 2020, Young et al. 2020), likely decreasing individual specialization by restricting individuals in safer habitats to reduce predation risk (Araújo et al. 2011). Finally, the changes in zooplankton communities associated with northward distribution shifts of temperate species towards Arctic ecosystems (Beaugrand et al. 2002, 2009, Møller & Nielsen 2020) would increase prey diversity and ecological opportunity in subarctic waters, promoting individual specialization.

Conclusion

Individual specialization does not seem to be as significant a process compared to variation within an individual in contributing to the population-level isotopic niche of EC-WG bowhead whales. The higher importance of intra-individual variation suggests dietary generalization with important isotopic niche overlap among individuals. Most of the isotopic variation unaccounted for by sex, body length, region and year was attributed to intra-individual variation (79% for $\delta^{13}C$ and 67% for $\delta^{15}N$) associated with yearly isotopic cycles mainly originating from seasonal movements between isotopically distinct habitats ($\delta^{13}C$) and variable food intake ($\delta^{15}N$). Long-term declining in $\delta^{13}C$ and $\delta^{15}N$ values likely resulted from a shift in baseline isotopic ratios, but could also suggest a shift in the feeding ecology of EC-WG bowhead whales, consuming more smaller-bodied and isotopically-depleted prey. Differences among harvest regions appear to have been responsible for a portion of the $\delta^{13}C$ variation, which may indicate long-term site fidelity. Despite a potentially low contribution of individual specialization to the population's isotopic niche breadth, important intra-individual variation suggests behavioural and potentially dietary plasticity at the individual-level, which would increase the population's resilience under changing habitats and prey due to climate change. In this context, the magnitude of individual specialization is also expected to change due to an increase in intra-specific competition, predation and ecological opportunity.

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Tables

Table 1: Summary information for 19 bowhead whales harvested during Inuit subsistence hunts across the Eastern Canada-West Greenland bowhead whale range. Site numbers and regions match with the ones presented in Fig. 1. CAA: Canadian Arctic Archipelago, HS: Hudson Strait, EBI: East Baffin Island, and GL: Greenland and North Baffin.

Site #	Sample ID	Community	Region	Harvest date	Sex	Total length (m)	Baleen plate length (cm)	Record (years)
1	NSA-BM-98-01	Pangnirtung, *Cumberland Sound, NU*	EBI	07/1998	M	12.75	258	1985-1998 (13)
2	BM-CH-2000-001	Coral Harbor, *Hudson Bay, NU*	CAA	08/2000	M	11.65	256	1985-2000 (15)
3	BM-IG-HB-2002-001	Igloolik, *Foxe Basin, NU*	CAA	08/2002	F	14.19	240	1988-2002 (14)
4	BM-RB-2005-001	Repulse Bay, *Foxe Basin, NU*	CAA	08/2005	F	16.40	266	1989-2005 (16)
5	BM-01-2008	Kangiqsujuak, *Hudson Strait, QC*	HS	08/2008	M	14.88	302	1987-2008 (21)
6	BM-NSA-2008-001	Kugaaruk, *Gulf of Boothia, NU*	CAA	09/2008	M	10.51	180	1995-2008 (13)
7	BM-NSA-2008-002	Hall Beach, *Foxe Basin, NU*	CAA	08/2008	M	13.43	228	1996-2008 (12)
8	BM-01-2009	Kangiqsujuak, *Hudson Strait, QC*	HS	08/2009	F	17.29	326	1992-2009 (17)
9	BM-NSA-2009-02	Rankin Inlet, *Hudson Bay, NU*	CAA	08/2009	F	16.15	222	1994-2009 (15)
10	BM-NSA-2009-03	Cape Dorset, *Hudson Strait, NU*	HS	09/2009	M	15.77	314	1988-2009 (21)
11	BM-NSA-2010-01	Pond Inlet, *Eclipse Sound, NU*	GL	08/2010	M	12.80	210	1997-2010 (13)
12	BM-NSA-2010-02	Repulse Bay, *Foxe Basin, NU*	CAA	08/2010	F	14.32	280	1996-2010 (14)
13	BM-NSA-2011-01	Iqaluit, *Frobisher Bay, NU*	EBI	08/2011	M	14.33	286	1993-2011 (18)
14	BM-NSA-2011-03	Kugaaruk, *Gulf of Boothia, NU*	CAA	08/2011	F	9.04	170	2003-2011 (8)
15	BH1_whale 501	Aasiaat, *Disko Bay, GL*	GL	04/2010	F	15.85	262	1996-2010 (14)
16	BH2_whale 500	Aasiaat, *Disko Bay, GL*	GL	04/2010	F	14.35	236	1995-2010 (15)
17	BH3_whale 322	Qeqertarsuat, *Disko Bay, GL*	GL	04/2009	M	14.10	204	1997-2009 (12)
18	BH4_whale 325	Ilulissat, *Disko Bay, GL*	GL	05/2009	F	15.50	192	1995-2009 (14)
19	BH5_whale 502	Ilulissat, *Disko Bay, GL*	GL	05/2010	F	16.10	284	1995-2010 (15)

Table 2: Fixed effects estimates and variance component analysis from the full linear mixed effect models fit to δ^{13}C and δ^{15}N values from baleen plates of 19 EC-WG bowhead whales.

	F-value	df	p	Variance	% of variance
δ^{13}C ~ Year + Region + Body Length + Sex, random = ~1 | Individual					
Intercept	75648.88	2355	<0.001		
Year	36.55	2355	<0.001		
Region	4.28	13	0.026		
Body Length	3.58	13	0.081		
Sex	0.34	13	0.630		
Intercept, Individual (*Inter-Individual*)				0.05783	21.04
Residuals (*Intra-Individual*)				0.21707	78.96
δ^{15}N ~ Year + Region + Body Length + Sex, random = ~1 | Individual					
Intercept	34320.04	2355	<0.001		
Year	79.80	2355	<0.001		
Region	2.57	13	0.099		
Body Length	0.91	13	0.357		
Sex	0.10	13	0.755		
Intercept, Individual (*Inter-Individual*)				0.08615	32.75
Residuals (*Intra-Individual*)				0.17689	67.25

Figures

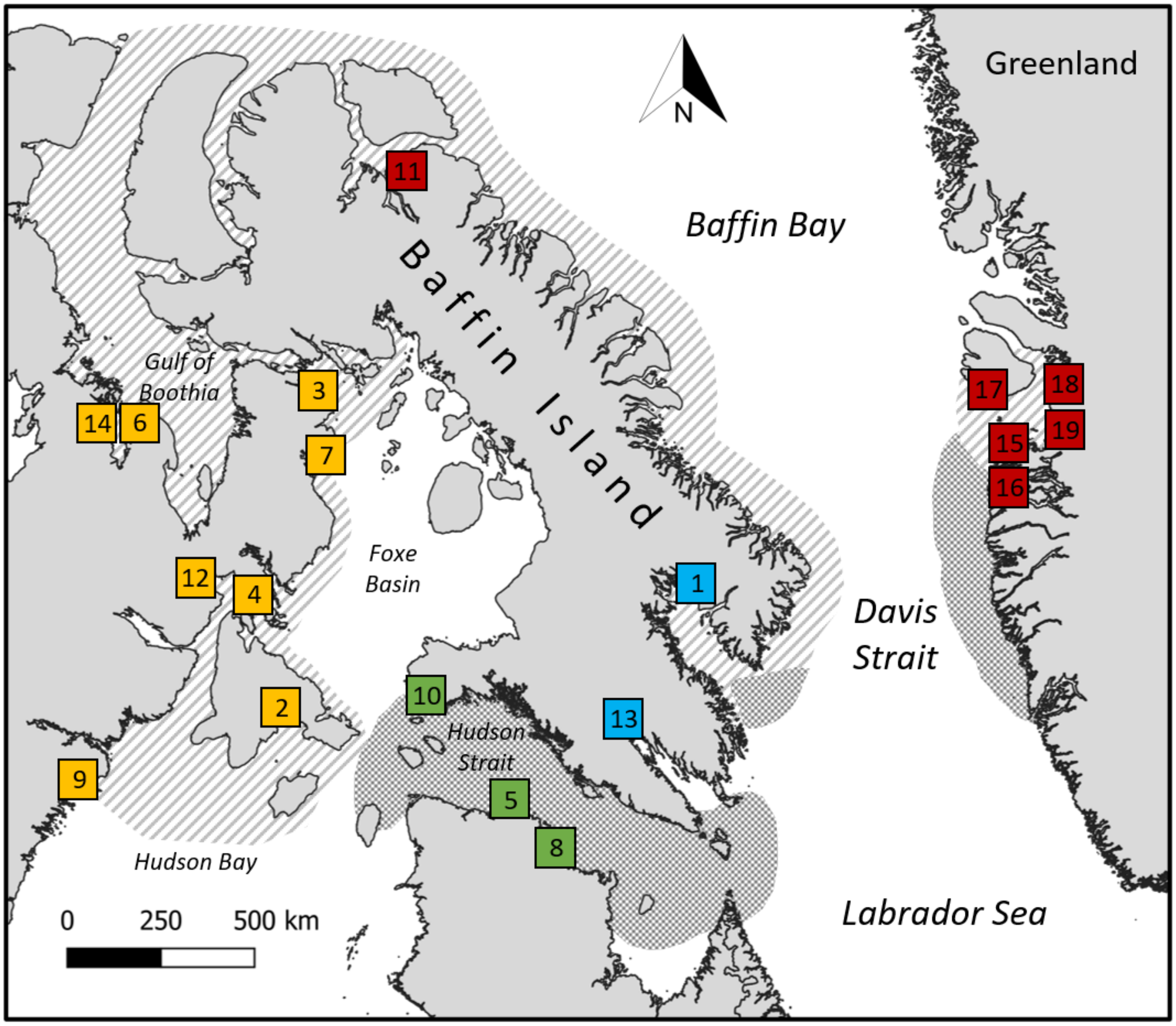

Figure 1: Harvest sites of the 19 Eastern Canada-West Greenland bowhead whales from which baleen plates were collected for stable isotope analysis. Summer and winter distributions are shown in light grey hatching and black hatching, respectively. The numbers in the colored squares represent the site numbers presented in Table 1. The colors represent the regions: Canadian Arctic Archipelago (CAA, yellow), Hudson Strait (HS, green), East Baffin Island (EBI, blue), and Greenland and North Baffin (GL, red).

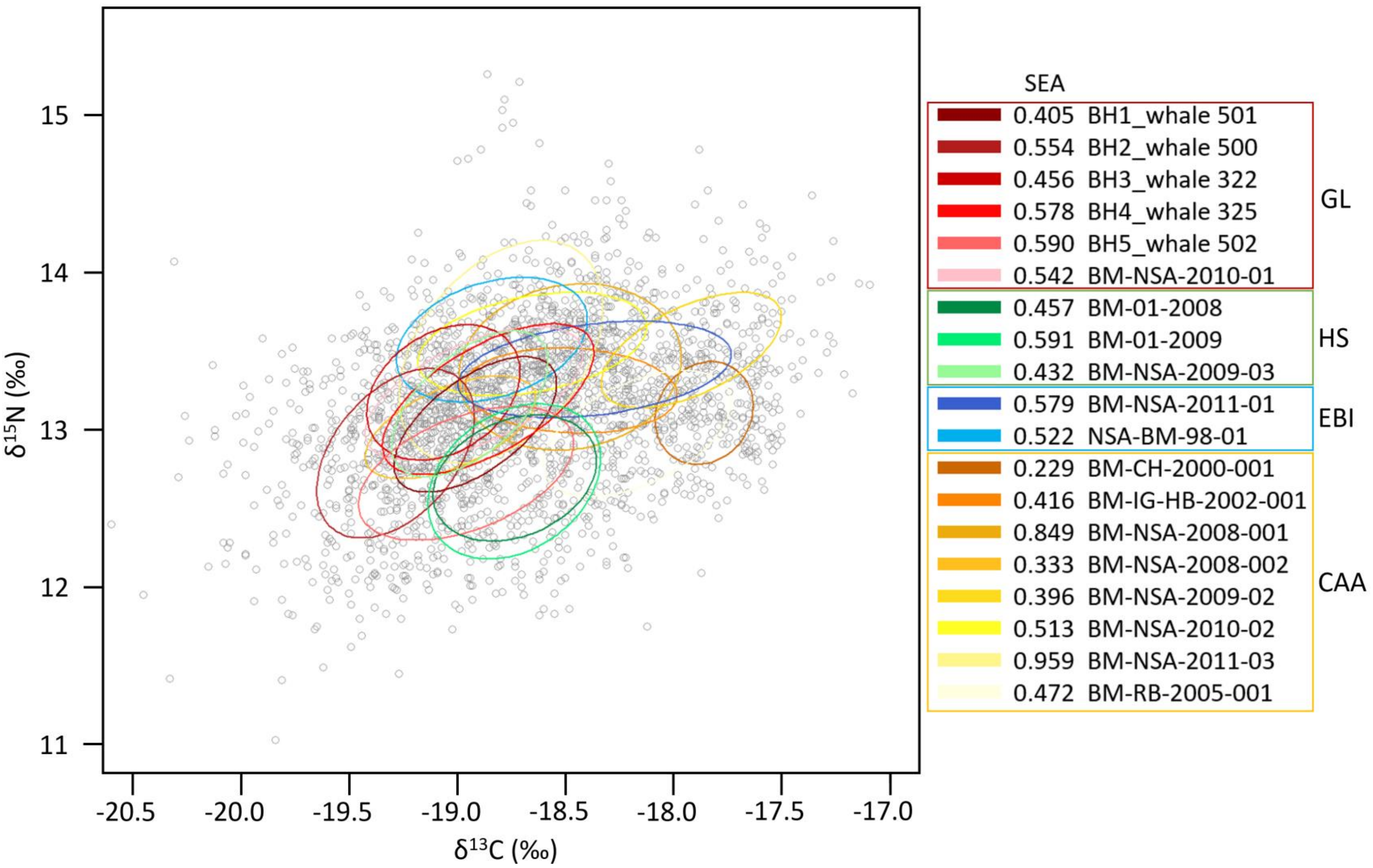

Figure 2: Isotopic niche breadth (Standard Ellipse Area (SEA)) from δ^{13}C and δ^{15}N values measured longitudinally along baleen plates of 19 harvested Eastern Canada-West Greenland bowhead whales. Individuals are color coded by harvest region: Greenland and North Baffin (GL, shades of red), Hudson Strait (HS, shades of green), East Baffin Island (EBI, shades of blue), Canadian Arctic Archipelago (CAA, shades of yellow). Individuals show considerable overlap (i.e., low variation among individuals) with large ellipses indicating greater within individual variability.

Chapter 4. General conclusion

When facing a selection pressure such as changes in prey driven by climate change, individual-level variation within a population increases resilience, and an understanding of individual-level processes is essential to assess the ability of a population to cope with such changes. For EC-WG bowhead whales, evolutionary adaption is unlikely to contribute to coping with climate-induced changes in prey because of their slow growth rate, late sexual maturity, low fecundity, long generation time (George et al. 1999) and relatively small population size (between 9,250 and 12,000 individuals, Ferguson et al. 2021). However, individuals displaying ecological plasticity through variation in their diet, habitat use, foraging behaviour, and specializing on different resources would increase the resilience of the population (Araújo et al. 2011, Poisot et al. 2011, Júnior et al. 2022). Previous studies have already observed inter-individual diet differences (Pomerleau et al. 2011, 2012, 2014) and variation in habitat use by different demographic groups (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010, Fortune et al. 2020), suggesting dietary and spatial flexibility within the EC-WG bowhead whale population. However, quantification of intra- and inter-individual variability in diet and foraging behaviour and understanding the drivers of such variation are required to properly assess the ability of this population to cope with current and future changes in prey quality and availability.

The primary objective of this thesis was to study the resilience of EC-WG bowhead whales under climate-driven changes in prey by assessing the individual-level variation in their foraging ecology. In chapters 2 and 3, I tested two mechanisms potentially responsible for driving inter-individual diet differences within the population: foraging behaviour (i.e., habitat use and foraging dive depth), and individual specialization.

In chapter 2, I found that bowhead whale individuals using distinct summer and fall foraging habitats displayed differences in horizontal movements, foraging dive depth and biomarkers, which suggested feeding on different prey. 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. Despite observing a strong association between habitat use, foraging dive depth, and diet, without prey sampling at relevant spatial and temporal scales, biotic habitat differences between the areas frequented by the CAA and WBB individuals could 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.

In chapter 3, I found that individual specialization did not seem to be an important process contributing to the population-level isotopic niche of EC-WG bowhead whales. The higher importance of intra-individual variation suggested dietary generalization with important isotopic niche overlap among individuals. Most of the isotopic variation unaccounted for by sex, body length, region and year was attributed to intra-individual variation associated with yearly isotopic cycles mainly originating from seasonal movements between isotopically distinct habitats (δ^{13}C) and variable food intake (δ^{15}N). Long-term declining in δ^{13}C and δ^{15}N values likely resulted from a shift in baseline isotopic ratios but could also suggest a shift in the feeding ecology of EC-WG bowhead whales, consuming more smaller-bodied and isotopically-depleted prey. Differences among harvest regions appear to have been responsible for a portion of the δ^{13}C variation, which may indicate long-term site fidelity. Despite a potentially low contribution of individual specialization to the population's isotopic niche breadth, important intra-individual variation suggests behavioural and potentially dietary plasticity at the individual-level.

Overall, results from both chapters 2 and 3 tend towards the same conclusion that significant individual-level ecological plasticity is present in the EC-WG bowhead whale population through individual differences in habitat use, foraging dive depth, and potentially diet as revealed by variation in dietary biomarkers (i.e., stable isotopes and fatty acids). This individual-level variation will contribute to increasing the population's resilience and ability to cope with the observed changes in prey composition and availability due to climate change.

Future research

This thesis highlighted the importance of sampling potential prey when using dietary biomarkers to study the foraging ecology of predators. Without proper spatial and temporal characterization of isotopic and fatty acid composition of prey, interpretation of inter-individual differences in predator biomarkers values is challenging and cannot directly be attributed to differences in diet compositions, limiting the strength of the conclusions. Regional differences in prey assemblages and abundance in areas used by EC-WG bowhead whales could be driving differences in foraging behaviour (i.e., habitat use and foraging dive depth), but this cannot be confirmed without an updated spatial characterization of zooplankton communities' species composition. To add a level of precision to the study of bowhead whale diet using dietary biomarkers, other approaches such as compound specific stable isotopes (Close 2019) and quantitative fatty acid signature analysis (QFASA; Zhang et al. 2020) should be considered.

In both chapters 2 and 3, habitat use seemed to play and important role in explaining the inter-individual variability in dietary biomarkers. In chapter 2, differences in stable isotope ratios and fatty acid signatures were linked with differences in habitat use during the peak feeding season, and in chapter 3 isotopic data along baleen plates suggested long-term site fidelity. Even if the sampled individuals are all part of one single population, there is important spatial variation in habitat use during the summer and fall, suggesting a subpopulation structure. Previous studies have described the spatial segregation of certain demographic groups based on energetics, reproductive status, and predator avoidance (Cosens & Blouw 2003, Heide-Jørgensen et al. 2010, Fortune et al. 2020), but the lack of significance of sex and age on biomarker variation in chapters 2 and 3 suggest that another mechanism could be responsible for the spatial grouping observed in this thesis. Some social structure or cultural component in the population could explain the grouping and use of distinct habitats. One possible explanation is that more closely related individuals associate with each other and this hypothesis could be tested by assessing genetic distance and relatedness among individuals using distinct habitats.

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