How adaptable are narwhal?
A comparison of foraging patterns among the world’s three narwhal populations

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Abstract. How organisms will fare in the face of climate change depends on their behavioral adaptability to changing conditions. Adaptability in foraging behavior will be particularly critical as food web changes are already occurring in Arctic regions. Stomach contents from narwhals (Monodon monoceros) in the Baffin Bay (BB) population have suggested that narwhals are dietary specialists with little behavioral flexibility, but there are two other narwhal populations in the world, the Northern Hudson Bay (NHB) and East Greenland (EG) populations, of which very little is known about diet. We investigated whether plasticity in foraging behaviors existed among the world’s narwhal populations and between sexes by comparing their stable isotope values and niches, and running stable isotope mixing models to determine primary prey. Stable isotope analysis was conducted on skin collected by Inuit hunters during their subsistent narwhal hunt in Canada and Greenland. Stable isotope analysis on carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) revealed the three populations have distinct stable isotope values that are not expected based on geographic differences and that males in all populations had significantly higher $\delta^{13}$C. Stable isotope mixing models revealed narwhals in EG forage more on pelagic prey, particularly capelin, while those in NHB typically forage in the benthos. Males, probably because of their size and enhanced diving ability, likely feed more intensively on benthic organisms, resulting in their higher $\delta^{13}$C. Stable isotopic niches were similar between males and females in each population, and between NHB and BB, but EG narwhals had a significantly larger niche, suggesting they either forage across a larger geographical expanse, or whales within the population employ individual dietary specialization. This is the first study to use stable isotopes to evaluate and compare diet in all three narwhal populations, which is vital for understanding how they will fare in the face of changing climate. We discuss how narwhal are adaptable in their preferred prey and how there is potential for narwhal to adjust foraging behavior in the face of the dramatic ecosystem shifts occurring with climate warming.

Key words: adaptability; Arctic; climate change; diet; isotopic niche; mixing models; Monodon monoceros; stable isotopes.

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INTRODUCTION

Historically, rapid climate change has been implicated as a cause of adaptation, range shift, and evolution for mammals (Bruyn et al. 2009). Phenotypic plasticity, which is the capacity for one genotype to produce alternate morphological, physiological or behavioral forms in response...
to variable conditions (West-Eberhard 1989), increases a species chance of survival in a changing environment. Plasticity, in terms of foraging behavior, within a species can result from spatial segregation resulting in individuals experiencing different environmental conditions (MacArthur and Wilson 1967). In these allopatric populations, evolutionary change in foraging behavior with no changes in physiology or morphology can account for differences in preferred prey (Futuyma and Moreno 1988). In some cases, behavioral modifications across groups of organisms precede genetic differentiation into populations (Price et al. 2003).

Narwhals (Monodon monoceros L.) are medium sized, toothed whales that live exclusively in Arctic waters. The species underwent a significant range contraction during the little ice age that accompanied changes in ice conditions (Hay and Mansfield 1989, Laidre et al. 2008). As a species, narwhals have extremely low genetic diversity (Palsbøll et al. 1997, Petersen et al. 2011), which may reduce their ability to evolve in response to environmental changes. In addition, narwhals are believed to be extremely sensitive to environmental changes as a result of their limited distribution, selective diet, and reduced capability for behavioral modification (Laidre et al. 2008). However, the sensitivity of the species as a whole is based exclusively on information from only one of the three narwhal populations and different populations within a species can demonstrate different adaptations, particularly if these populations are spatially segregated and encounter different environmental conditions (Price et al. 2003). We investigated whether plasticity in foraging behaviors exists among the world’s narwhal populations to understand if they may be able to modify their foraging behaviour in a changing Arctic environment.

There are currently three spatially and genetically segregated narwhal populations recognized in the world (Petersen et al. 2011) (Fig. 1). The East Greenland (EG) population inhabits the eastern shores of Greenland and the Greenland Sea with current estimates of about 6,000 individuals (Heide-Jørgensen et al. 2010). The Baffin Bay (BB) population overwinters in the Davis Strait and spends summer in the fiords and inlets of northern Canada and western Greenland and is estimated to be larger than 60,000 individuals (Richard et al. 2010), and the Northern Hudson Bay (NHB) population spends winter in the Hudson Strait and summers in northern Hudson Bay (Richard 1991) and is estimated at 12,500 individuals (Asselin et al. 2012). Narwhals are a culturally and economically important species to the Inuit (Hoover et al. 2013) and the reported annual subsistent harvest of narwhals is approximately 110 for the EG population, 800 for the BB population, and 100 for the NHB population (Heide-Jørgensen et al. 2010, DFO 2012). Narwhals are considered to be one of the most sensitive Arctic marine mammals to climate change and the narwhal’s limited distribution (only occurring in the Atlantic region of the Arctic), small population size (ca. 100,000), and dietary specialization are all contributing factors for their high sensitivity (Laidre et al. 2008).

Current knowledge about narwhal diet comes primarily from stomach content analysis on hunted narwhals from the BB population, with no studies being conducted on the NHB or EG narwhals. Stomach contents from BB narwhals have identified the primary prey as Greenland halibut (Reinhardtius hippoglossoides), Arctic cod (Boreogadus saida), polar cod (Arctogadus glacialis), and squid (Gonatus fabricii) (Finley and Gibb 1982, Laidre and Heide-Jørgensen 2005a). Finley and Gibb (1982) identified a few other species, such as snailfishes (Liparis spp.), redfish (Sebastes marinus), sculpins (Cottidae), eelpout (Lycodes spp.), and skate egg sacs (Raja spp.), and Hay and Mansfield (1989) identified some shrimps (Pasiphaea tarda and Hymenodora glacialis) in narwhal stomachs, albeit in small amounts. Laidre and Heide-Jørgensen (2005a) also identified the shrimp Pandalus borealis as being abundant in narwhal stomachs, and capelin (Mallotus villosus), skate egg sacs, and wolfish (Anahichas lupus and A. minor) as minor prey items.

A sexual size dimorphism exists between male and female narwhals (Garde 2011) and males have an erupted left tooth that results in a spiraled tusk. Few studies have been able to compare diet between male and female narwhals because of low sample size of females (Laidre and Heide-Jørgensen 2005a), and the only study that was able to compare did not find evidence of dietary segregation between narwhal sexes based
on stomach contents, although they also had a relatively small female sample (n = 29) (Finley and Gibb 1982). Although no dietary differences have been noted, a sexual size dimorphism does exist in all populations, and typically hunter collected samples are biased towards males, limiting the ability to detect differences in diet between males and females. Diving capacity is greater for larger animals (Schreer and Kovacs 1997) and male narwhals are likely capable of making deeper dives and potentially foraging more in the benthos in deep waters. In addition, males, because of their larger size, may be able to manipulate larger prey than females.

Stomach content analysis of the BB population, although insightful to give a first understanding of narwhal diet, can result in biased estimates as a result of varying digestion rates, only provides information on what was consumed and not what was assimilated into tissues, and only provides information on the organism’s last meal. This is particularly a problem in Arctic marine mammals that experience seasonal changes in food availability and diet (Laidre and Heide-Jørgensen 2005a, Bluhm and Gradinger 2008) and have high-energy requirements (Laidre et al. 2004a) because stomach contents may not be representative of typical feeding events. More recent studies investigating diet in marine mammals have used stable isotope analysis to...
Stable isotope analysis is a powerful tool for studying animal feeding ecology because predator tissues are directly related to the ratios found in their prey with a progressive enrichment factor. The stable nitrogen isotope ratio ($^{15}$N:$^{14}$N, expressed as $\delta^{15}$N) provides information on an organism’s trophic level and the stable carbon ratio ($^{13}$C:$^{12}$C, expressed as $\delta^{13}$C) reflects its spatial foraging distribution (pelagic versus benthic, or offshore versus coastal) (Peterson and Fry 1987, Newsome et al. 2010). Previous studies investigating stable isotope ratios in narwhals have determined their trophic position (Hobson and Welch 1992, Hobson et al. 2002) and found differences in $\delta^{15}$N and $\delta^{13}$C between narwhals from two different locations in West Greenland (Dietz et al. 2004), but no study has conducted a large-scale comparison of narwhal stable isotope values across the three populations. Stable isotope ratios vary with geography as a result of variable $\delta^{15}$N and $\delta^{13}$C at the base of the food web, and there is known to be a large gradient in $\delta^{13}$C across the narwhal’s geographic span (Graham et al. 2010). An organism’s isotopic niche, or the extent of stable isotope values for all the resources used by an organism, can provide insight into an animal’s dietary niche (Bearhop et al. 2004, Jackson et al. 2011). In general, animals with very small isotopic niches are often dietary specialists that consume only one or a few types of resources and therefore have relatively low variability in their isotopic values, whereas dietary generalists that forage on a variety of organisms have a much larger isotopic niche. This general rule, however, has caveats and depends on the isotopic variability of the environment in which the organisms live and the prey sources they consume and usually stable isotope niche width is not directly comparable to an animal’s trophic niche (Cummings et al. 2012).

In this study we investigated three hypotheses. Our first was that narwhals display phenotypic plasticity, in terms of their foraging behavior, and this would result in populations having different $\delta^{13}$C and $\delta^{15}$N values. We expected $\delta^{13}$C and $\delta^{15}$N would differ for the three populations because stable isotope ratios at the base of the food web would likely differ across such a wide geographic expanse; however, if the three populations also have distinct foraging behavior which results in different preferred prey, the magnitude of the differences in $\delta^{13}$C and $\delta^{15}$N should be greater than would be expected by geography alone. Second, we hypothesized that dietary niche sizes for the three populations would differ. We predicted the isotopic niche of the BB population would be larger than the NHB and EG populations because they are part of a much larger population, which may increase competition for resources and result in individuals or groups of individuals specializing on specific prey in order to limit competition with other groups for their preferred prey. Alternatively, narwhals in East Greenland have a larger range compared to the other two populations, which means they may encounter different geographic regions with different baseline $\delta^{13}$C and $\delta^{15}$N values, which would result in this population having a larger isotopic niche. Third, we hypothesized that males, having a larger body size, would be able to exploit a greater range of resources than females, which would result in them having different $\delta^{13}$C and $\delta^{15}$N, as well as a larger isotopic niche. In particular, we expected they might be able dive deeper and spend greater time at depth compared to females, which would result in their skin tissue expressing a higher $\delta^{13}$C value, and that they could forage on larger prey, which may increase the $\delta^{15}$N value of their tissues. Finally, we wanted to estimate the importance of primary prey components for each of the three populations and discuss the potential for narwhal to adjust foraging behavior in the face of the dramatic ecosystem shifts occurring with climate warming.

**Methods**

Inuit hunters and researchers collected narwhal skin samples from narwhals in Pond Inlet, Nunavut, Canada (representative of the BB population), Repulse Bay, Nunavut, Canada,
(representative of the NHB population), and Ittoqqortoormiit, Greenland (representative of narwhals from EG). Since all samples are collected opportunistically, this resulted in a varying number of male and female samples, which spanned various temporal scales; however, we limited our analyses to include only samples collected in the summer months, which we defined as June through September following Finley and Gibb (1982). Unfortunately, samples from other seasons were rare across populations and we were unable to compare seasonal diet.

Narwhal skin tissue was sub-sectioned and a 0.5 g piece of skin was diced, freeze-dried for 48 hours, homogenized with a glass mortar and pestle, and lipid extracted using a 2:1 chloroform:methanol solution. A continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, CA, USA) was used to determine $\delta^{13}C$, $\delta^{15}N$ and% C and N of 400–600 μg of tissue. The standard reference material was Vienna Pee Dee Belemnit carbonate for CO$_2$ and atmospheric nitrogen N$_2$. Every 12th sample was run as a triplicate to assess precision; the mean standard deviation of these samples was 0.1% for $\delta^{13}C$ and 0.4% for $\delta^{15}N$. Internal lab and National Institute of Standards and Technology (NIST) standards were analyzed after every 12 samples for quantification of samples and to assess analytical precision. The analytical precision (standard deviation) for NIST standard 8414 (bovine muscle, $n = 152$) and an internal lab standard (tilapia muscle, $n = 152$) for $\delta^{13}C$ was 0.07‰ and 0.09‰, and for $\delta^{15}N$ was 0.15% and 0.19%. To assess accuracy, certified NIST standards were analyzed during sample analysis. For $\delta^{13}C$, the mean value for NIST 8542 ($-10.48 \pm 0.03$‰; $n = 10$) was within 0.01 of the certified value of $-10.47$ and for NIST 8573 ($-26.26 \pm 0.04$‰; $n = 10$) was within 0.13 of the certified value of $-26.39$‰. For $\delta^{15}N$, the mean value for NIST 8542 (4.58 ± 0.11‰; $n = 10$) was within 0.12 of the certified value of 4.70‰ and for NIST 8548 (20.11 ± 0.38‰; $n = 9$) was within 0.30 of the certified value of 20.41‰. All stable isotope analyses were conducted at the University of Windsor, Great Lakes Institute for Environmental Research. $\delta^{13}C$ values were corrected for the “Suess effect” by applying a correction of 0.02‰ (an average of values reported by Körtzinger and Quay (2003)) and Sonnerup et al. (1999) from the North Atlantic Ocean, per year beyond 1982 (the oldest sample included in the data set).

Normal quantile plots for $\delta^{13}C$ and $\delta^{15}N$ were normally distributed across populations and between sexes. Variances were also homogenous for the three populations across both sexes for $\delta^{13}C$ (Levene’s test: $F_{5,211} = 0.38$, $P = 0.86$) and $\delta^{15}N$ (Levene’s test: $F_{5,211} = 1.31$, $P = 0.26$), thus no data transformations were required. A generalized linear model, which included population, sex and the interaction between the two factors, was used to assess if $\delta^{13}C$ and $\delta^{15}N$ values differed among populations and between sexes. When significant differences were detected in the full model, Tukey’s HSD tests were used to determine which populations differed. Niche widths were calculated and statistically compared using a Bayesian framework, which uses a multivariate ellipse-based metric that is useful for comparing populations of different sizes (Jackson et al. 2011). Ellipse standard areas, which are the bivariate equivalent to standard deviations, were calculated using the SIBER package within SIAR in R (Parnell et al. 2010).

Next, we compared predator and prey stable isotope values to understand what prey may be contributing to the differences in stable isotope ratios among populations. Potential prey was identified based on stomach content analyses of hunted narwhals from the BB population conducted by Finley and Gibb (1982) and Laidre and Heide-Jørgensen (2005a) and included Arctic cod ($B. salrei$), polar cod ($A. glacialis$), Greenland halibut ($R. hippoglossoides$), shrimp ($P. borealis$), squid ($Gonatus spp.$), and capelin ($M. villosus$). Discrimination factors of 2.6‰ for $\delta^{15}N$ and 1.9‰ for $\delta^{13}C$ were added to the potential prey. These values were calculated by taking an average of fractionation factors reported by the only two studies that have investigated trophic enrichment in the skin of odontocetes (studies were conducted in killer whales (Orcinus Orca) and bottlenose dolphins (Tursiops truncatus) (Caut et al. 2011, Fernández et al. 2011)). Since prey stable isotope values may vary with geography, we attempted to obtain prey from the specific regions, unfortunately this was not always possible, and in these cases we relied on values reported in the literature (Table 1). SIAR was used to assess the contribution of each prey to the diet of narwhals.
Table 1. Collection location, date, and stable isotope values (mean ± SD) for potential narwhal prey used in isotope mixing models for each population.

| Prey                     | Species              | Location              | n  | Year       | δ13C ± SD (%) | δ15N ± SD (%) | Source |
|--------------------------|----------------------|-----------------------|----|------------|---------------|---------------|--------|
| BB                       |                      |                       |    |            |               |               |        |
| Polar cod†               | A. glacialis         | Davis Strait          | 8  | 2004       | −20.5 ± 0.3  | 13.5 ± 0.5    |        |
| Arctic cod†              | B. saida             | Davis Strait          | 15 | 2004–2011  | −20.5 ± 0.4  | 14.0 ± 1.0    |        |
| Squid†                   | G. fabricii          | Davis Strait          | 15 | 1999–2011  | −20.3 ± 1.3  | 11.9 ± 1.9    |        |
| Capelin†                 | M. villosus          | Cumberland Sound      | 7  | 2008       | −19.3 ± 0.1  | 12.9 ± 0.1    | 1      |
| Shrimp                   | P. borealis          | Davis Strait          | 10 | 1999       | −18.7 ± 0.2  | 14.5 ± 0.5    |        |
| Greenland halibut        | R. hippoglossoides   | Davis Strait          | 20 | 1996–2011  | −20.0 ± 0.8  | 15.0 ± 1.7    |        |
| NHB                      |                      |                       |    |            |               |               |        |
| Arctic cod               | B. saida             | Hudson Strait         | 5  | 2011       | −19.9 ± 1.3  | 13.5 ± 0.5    |        |
| Squid                    | G. fabricii          | Hudson Strait         | 11 | 2004–2011  | −19.1 ± 1.3  | 12.0 ± 1.8    | 2      |
| Capelin                  | M. villosus          | Hudson Strait         | 5  | 2011       | −19.0 ± 0.5  | 12.1 ± 0.3    |        |
| Shrimp                   | P. borealis          | Northeast Greenland Offshore | 10 | 1995      | −17.9 ± 0.3  | 11.3 ± 0.2    | 3      |
| Greenland halibut        | R. hippoglossoides   | Hudson Strait         | 5  | 2011       | −19.4 ± 0.7  | 14.2 ± 0.5    |        |
| EG                       |                      |                       |    |            |               |               |        |
| Polar cod                | A. glacialis         | Northeast Greenland fiords | 60 | 2003      | −21.1 ± 0.4  | 14.6 ± 0.6    | 4      |
| Arctic cod               | B. saida             | Northeast Greenland fiords | 60 | 2003      | −21.4 ± 0.3  | 13.9 ± 0.6    | 4      |
| Squid                    | G. fabricii          | West Greenland       | 26 | 2003       | −18.8 ± 0.5  | 13.1 ± 1.7    | 5      |
| Capelin                  | M. villosus          | Northern Iceland     | 16 | 1994–1995  | −21.3 ± 0.3  | 10.8 ± 0.1    | 6      |
| Shrimp                   | P. borealis          | Northern Iceland     | 8  | 1994–1995  | −19.4 ± 0.1  | 11.0 ± 0.1    | 6      |
| Greenland halibut        | R. hippoglossoides   | West Greenland       | 13 | 2003       | −18.4 ± 0.9  | 13.9 ± 1.0    | 5      |

Notes: Population abbreviations are: BB, Baffin Bay; NHB, Northern Hudson Bay; EG, East Greenland. Sources are: 1, Dennard et al. (2009); 2, Chambellant, Elliott and Ferguson unpublished data and this study; 3, Lawson and Hobson (2000); 4, Christiansen et al. (2012); 5, Møller (2006); 6, Thompson et al. (1999). All other values came from this study.

† Arctic and polar cod stable isotope values were not distinct and were combined to define an individual cod value.
‡ Squid and capelin values were not distinct and were combined.

for the three populations (Parnell et al. 2010).

RESULTS

The three populations had significantly different δ13C ($F_{2,211} = 319.88$, $P < 0.0001$) and δ15N ($F_{2,211} = 201.10$, $P < 0.0001$) (Fig. 2). NHB had the highest mean δ13C (−17.0%) and BB had the highest mean δ15N (16.6‰); EG had the lowest mean δ13C (−19.1%) and δ15N (14.6‰). Males and females differed in δ13C ($F_{1,211} = 9.72$, $P < 0.01$) with males having significantly higher δ13C (−17.9%) than females (−18.1%) (Fig. 2). Sexes did not differ significantly in their δ15N values ($F_{1,211} = 1.28$, $P = 0.26$) and there was no significant interaction between sex and population for δ13C ($F_{2,211} = 0.69$, $P = 0.50$) or δ15N ($F_{2,211} = 0.37$, $P = 0.69$) (Fig. 2). Standard ellipse area of the EG population ($n = 25$) was larger than the ellipse for the BB population ($n = 127$), although this result was not quite significant ($P = 0.06$), and significantly larger than the NHB ellipse ($n = 65$; $P = 0.04$). There was no significant difference between ellipse area for narwhals from NHB and BB ($P = 0.66$) (Fig. 3). Male and female narwhals did not differ in their isotopic niche size in the BB ($n = 69$ and 58, respectively; $P = 0.15$), EG ($n = 17$ and 8, respectively; $P = 0.78$) or NHB ($n = 41$ and 24, respectively; $P = 0.90$) populations (Fig. 3).

Cod (A. glacialis and/or B. saida), Greenland halibut (R. hippoglossoides), shrimp (P. borealis), squid (Gonatus spp.), and capelin (M. villosus) were all considered potential prey for narwhals in each population (Table 1, Fig. 4A). Results from the stable isotope mixing models revealed that narwhals from EG consume significantly more capelin than other populations, and less shrimp (Fig. 4A). Narwhals from BB consumed slightly more Arctic and polar cod (the two could not be distinguished for this population) than NHB narwhals, and NHB narwhals consumed more Greenland halibut (Fig. 4A). Male and female narwhals typically had similar diets within a population, however, in BB males appeared to consume more shrimp than females, while females ate more cod, and in NHB males ate more halibut and less capelin and squid compared to females (Fig. 4A). Males and females in EG were difficult to distinguish based on their prey proportions (Fig. 4A). When prey were assigned to their respective habitats (pelag-
ic or benthic), and mean proportion of prey was assessed it was evident that male and female narwhals from EG feed in the pelagic zone to a greater extent, while narwhals in NHB forage more in the benthos (Fig. 4B). Males in BB spend more time foraging in a benthic food web, while females in this population forage similarly in a benthic and pelagic food web (Fig. 4B).

**DISCUSSION**

The world’s three narwhal populations have very different $\delta^{13}$C and $\delta^{15}$N values suggesting they have different preferred prey and thus, may be more flexible in their foraging behaviour than previously thought. Narwhal flexibility in preferred prey may help them face changing food web structure and prey distribution that are accompanying climate change (Tynan and De-Master 1997). $\delta^{13}$C values change as you move from benthic or inshore food webs to pelagic food webs, with organisms in the benthic environment displaying a higher $\delta^{13}$C value (France 1995). Mean $\delta^{13}$C was lowest in the EG population suggesting narwhals in this region feed within a more pelagic food web compared to the NHB and BB populations and this was confirmed by the stable isotope mixing model results that showed EG narwhals preferentially feed on capelin. The NHB population had the highest $\delta^{13}$C values suggesting they feed in a more benthic food web, which is consistent with them inhabiting a much shallower ecosystem compared to BB and EG. NHB narwhals consumed a large proportion of shrimp, while pelagic prey such as capelin and squid played a minor role in their diet. The NHB food web has been changing in the last 30 years as a result of climatic change in the region, which has resulted in an increase in capelin and sand lance (Ammodytes sp.) and a decrease in Arctic cod and some benthic species (Gaston et al. 2003). It is possible that, if necessary, narwhals may be able to switch primary prey and monopolize on the increase in capelin abundance, which may mitigate the negative impacts of reduced cod and benthic species. BB narwhals had intermediate $\delta^{13}$C values and the highest $\delta^{15}$N values indicating they feed at a higher trophic level than the other two populations. These values are consistent with narwhals in this population consuming high proportions of Greenland halibut (Laidre and Heide-Jørgensen 2005a); however, the mixing models did not show that Greenland halibut is the primary prey. This may be indicative of the timing of sample collection (restricted to summer months) and the time frame that this tissue represents in the diet. Stable isotope turnover rates are unknown in this species; however, St. Aubin et al. (1990) found that complete tissue
Fig. 3. A) δ¹³C and δ¹⁵N biplot with all male and female narwhals from the BB (n = 69 and 58), EG (n = 17 and 8), and NHB (n = 41 and 24) populations. Thin dashed lines indicate convex hulls of total niche width (Layman et al. 2007). Solid lines (males) and thick dashed lines (females) indicate standard ellipse area, representative of isotopic niches (Jackson et al. 2011) and B) boxplot indicating the area (per mil²) of the isotopic niche for male and female narwhals in each population. Boxes indicate 50%, 75%, and 95% credibility intervals.
turnover in the skin of beluga whales (*Delphinapterus leucas*), the narwhal’s closest relative, was approximately 2–3 months. In this case, the stable isotope values in narwhal skin in BB would not necessarily reflect a large proportion of Greenland halibut, which is primarily consumed in the winter (Laidre and Heide-Jørgensen 2005a), because it would only reveal foraging in the late spring and summer. Alternatively, much longer turnover rates (~1 year) have been
determined in large mammals (Sponheimer et al. 2006), which may indicate that narwhals in BB have a more variable diet than stomach content studies have revealed and Greenland halibut is not the major prey item. A more variable diet than stomach samples from one area/season is likely given the opportunities narwhal have to vary diet over seasons and the large space afforded by migrations; however, in our assessment we have included all high trophic level potential prey species, such as halibut, that could be resulting in BB narwhals having a high $\delta^{15}\text{N}$ value.

Stable isotope mixing models provide best estimates of diet for the three narwhal populations; however, there is uncertainty surrounding the discrimination factor used and these models are known to be sensitive to the specified discrimination factor (Bond and Diamond 2011). Discrimination factors are known to be species and tissue specific (Hobson and Clark 1992) and there is currently no study evaluating tissue specific discrimination factors for narwhal, or for beluga. We used an average of published discrimination factors for odontocete skin for whales that consume higher trophic level prey (Caut et al. 2011, Fernández et al. 2011), which is currently the best estimate available. Stable isotope mixing models are also sensitive to the number of prey included, and it is possible that some potential prey were excluded from the models, especially for the EG and NHB populations where no studies investigating stomach contents have been conducted. We did investigate many other prey stable isotope values for the two populations (including sand lance (Fergusson, unpublished data), Atlantic cod (Gadus morhua) (Thompson et al. 1999, Sarà et al. 2009), the shrimps H. glacialis and P. multidentata (Rau et al. 1989), and Atlantic halibut (Hippoglossus hippoglossus) (Sarà et al. 2009)); however, none of these prey had stable isotope values within the range seen for narwhals in the two populations and thus they were excluded from the stable isotope mixing models. Overall the model results are insightful but should be interpreted with caution.

The size of a species isotopic niche can provide insight into the extent of their dietary diversity (Newsome et al. 2012). However, the isotopic niche, although related to the ecological niche, is not directly comparable and to interpret the variance seen within narwhal populations, we have to consider the variability of the stable isotope values within the prey. We corrected $\delta^{13}\text{C}$ values using the mean and range of $\delta^{13}\text{C}$ for the prey from each region (Olsson et al. 2009) and $\delta^{15}\text{N}$ to trophic level using baseline $\delta^{15}\text{N}$ from Graham et al. (2010). We present uncorrected data for comparative purposes and because the baselines presented by Graham et al. (2010) are only roughly estimated; however, relative niche area differences among the regions did not qualitatively change for corrected data (results on file). The EG narwhal population had the largest niche width, which is consistent with these whales having the greatest geographical range; however, our EG samples came from a restricted area where narwhals are hunted, near the community of Ittoqqortoormiit, Greenland. This particular subpopulation of narwhals has been equipped with satellite transmitters and data suggests these whales move very little throughout the year (M.P. Heide-Jørgensen, unpublished data). Although it is generally assumed that a larger isotopic niche can be interpreted as larger trophic niche where organisms are typically generalists that feed on array of prey, it has been shown that populations confined to one site may display greater isotopic variances within their population due to individual specialization, whereby individuals exploit different aspects of the niche to reduce intraspecific competition (Cummings et al. 2012). This may be the case in EG, however, further evidence, such as that from fatty acids or stomach contents, is needed to confirm this hypothesis.

The BB population had a relatively small isotopic niche despite its population being vastly larger than the other two, which suggests that there is little intraspecific competition to result in individual specialists; however, there may be strong interspecific competition resulting in specialization at the population level. From stomach content analysis, the BB population is assumed to gain much of their energy reserves over the winter when they feed heavily on Greenland halibut (Laidre and Heide-Jørgensen 2005a) and, as a population, appears to specialize on this species. The supply of Greenland halibut in the winter must be substantial enough to
sustain the current population in this region; however, an expanding halibut fishery in the Arctic has the potential to compete with narwhal feeding (Dennard et al. 2010).

There is sexual segregation in diet for all populations, which may be related to the diving ability of males and females. Studies investigating dive behavior in narwhal sexes have been limited by sample size and perhaps, as a result, have documented conflicting results. It has been shown that female narwhals have significantly lower dive rates than males (Heide-Jørgensen and Dietz 1995) and they typically make dives <400 m (Laidre et al. 2004b), but another study reported no difference in diving performance between female narwhals and their male counterparts (Laidre et al. 2003). Further evidence is required to support differences in dive behavior between males and females, but given the sexual size dimorphism (Garde et al. 2007), males are likely capable of making deeper dives and therefore capable of foraging in the benthos even in deep waters. It has also been suggested the supinate swimming behavior of narwhals may be related to foraging. By swimming upside-down, males can orientate their tusk toward the bottom to guide benthic prey towards their mouth (Dietz et al. 2007). Increased benthic foraging for males would explain their increased Δ13C value (France 1995). We predicted males would have higher Δ15N values and a larger isotopic niche than females, however results indicated no differences. Males may be as specialized as females in their preferred prey and suction feeding may limit the size of prey that both male and female narwhals can manipulate, resulting in them displaying a similar trophic level.

Beluga whales are considered to eat a much more diverse range of prey than narwhals (Laidre et al. 2008). Polar and Arctic cod were found to contribute more than any other item to the diet of beluga in Greenland, the Canadian high Arctic, Russia, Svalbard and the Beaufort Sea (Heide-Jørgensen and Teilmann 1994, Dahl et al. 2000, Boltunov and Belikov 2002, Loseto et al. 2009, Marcoux et al. 2012). These beluga populations are geographically isolated and inhabit very different environments, yet in all cases the dominant prey across populations is cod. Overall belugas consume a greater range of prey than narwhal, but based on our results, narwhal may also be flexible in their preferred prey. Although there is some range overlap between narwhals and belugas, typically the species have different preferred habitats (Reeves et al. 1994), which has reduced competition for food. However, our study and a study conducted by Thiemann et al. (2008) suggest there is substantial overlap in preferred prey, and competition may become more intense when both prey and the predators shift their distribution with changing climate.

Stable isotope ratios fluctuate with geography as a result of variable Δ15N and Δ13C at the base of the food web (Graham et al. 2010) and therefore we have to consider that differences among populations may be a result of the isotopic differences across the large geographical span. Although there are only crude estimates for baseline Δ15N and Δ13C in the ocean, generally Δ15N is greater in NHB compared to BB and EG, and Δ13C is higher in EG compared to BB and NHB (Graham et al. 2010). In this case, correcting for baseline differences in Δ15N and Δ13C would result in NHB narwhals to have slightly lower mean Δ15N and EG narwhals to have lower mean Δ13C. If these differences are taken into account there is even greater separation in stable isotope ratios among the populations. In addition, dietary differences determined by stable isotope mixing models incorporated prey from each of the three respective regions, suggesting that narwhals in each of the populations do have different preferred prey and this is not a result of underlying spatial patterns in stable isotopes.

We restricted our comparisons to narwhal samples collected in summer months, which eliminated any confounding that may be caused by seasonal changes in diet, but annual changes in diet could also have impacted differences among the populations. To assess this possibility we compared samples for the EG population from 1994 and 1995 with samples from 1994 and 1995 for the BB population (unfortunately there were no samples for the NHB population from these exact years) and still found significant differences between the populations for Δ13C and Δ15N, indicating these results are not a result of annual changes in diet within a population (data on file).

Fuller et al. (2010) identified four possible outcomes for a species that is experiencing
climate change: the species can shift distribution, genetically adapt, go extinct, or employ phenotypic plasticity. For narwhals, their distribution is already relatively restricted (Laidre et al. 2008) and although some populations may be able to move further north, range shift will only be a temporary solution for dealing with climate change. Genetic adaptation takes many generations, and given the long lifespan and generation time for narwhals (Garde et al. 2007, Garde 2011) and the speed of current climate changes (IPCC 2007), it is unlikely they will be able to genetically adapt to an ice-free life style. Narwhals are thought to be quite rigid in terms of their behavior, particularly given their high site fidelity (Laidre and Heide-Jørgensen 2005b); however, they may be more adaptable in terms of their foraging behavior than previously thought. We showed that stable isotope values differ among the populations and this difference is related to differences in preferred prey and foraging behavior among the populations. Future studies should monitor changes in preferred prey of narwhals in NHB, the most southerly narwhal population, that is currently experiencing documented food web modifications as a result of changes in climate (Gaston et al. 2003). In addition, investigations of stomach contents and fatty acids from narwhals in the EG and NHB populations would provide a clearer picture of how flexible narwhal are in their foraging behavior.

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