



RESEARCH/REVIEW ARTICLE

Foraging ecology of ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian High Arctic determined by stomach content and stable isotope analysis

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Keywords

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Abstract

Stomach content and stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from liver and muscle) were used to identify habitat and seasonal prey selection by ringed seals (*Pusa hispida*; $n=21$), beluga whales (*Delphinapterus leucas*; $n=13$) and narwhals (*Monodon monoceros*; $n=3$) in the eastern Canadian Arctic. Arctic cod (*Boreogadus saida*) was the main prey item of all three species. Diet reconstruction from otoliths and stable isotope analysis revealed that while ringed seal size influenced prey selection patterns, it was variable. Prey-size selection and on-site observations found that ringed seals foraged on smaller, non-schooling cod whereas belugas and narwhals consumed larger individuals in schools. Further interspecific differences were demonstrated by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and indicated that ringed seals consumed inshore Arctic cod compared to belugas and narwhals, which foraged to a greater extent offshore. This study investigated habitat variability and interseasonal variation in the diet of Arctic marine mammals at a local scale and adds to the sparse data sets available in the Arctic. Overall, these findings further demonstrate the critical importance of Arctic cod to Arctic food webs.

The value of multiple and complementary sampling techniques to study foraging behaviours and dietary preferences of Arctic marine mammals has been demonstrated in recent years (e.g., Aubail et al. 2010; Marcoux et al. 2012; Watt & Ferguson 2015). For example, stomach content analysis (SCA) provides direct identification and quantification of prey, which is essential to determine important food items (e.g., Bluhm & Gradinger 2008; Labansen et al. 2011), but can be limited by empty stomachs and unidentified food particles due to rapid digestion (Finley & Gibb 1982; Sheffield et al. 2001). Stable isotope analysis (SIA), which is based on the fact that the chemical composition of a predator reflects the chemical signature of its assimilated prey (Dalerum & Angerbjörn 2005; Newsome et al. 2010),

complements SCA. Nitrogen stable isotopes ($\delta^{15}\text{N}$) can identify trophic position since there is a relatively predictable increase from prey to predator (3–5‰; Newsome et al. 2010), although variation in this enrichment can be significant (Vander Zanden & Rasmussen 2001). Nitrogen stable isotopes can also provide a spatial indication of feeding, such as inshore vs. offshore, because physical/biological processes such as upwelling or phytoplankton blooms can alter nitrogen isotope composition inshore (Chouvelon et al. 2012). Similarly, carbon stable isotopes ($\delta^{13}\text{C}$) serve as a proxy of feeding habitat because values are conserved between predator and prey (0.5–2.0‰; Newsome et al. 2010), reflecting potential sources of carbon at the base of the food web. Further, carbonates (^{13}C) of primary producers

fractionate at different rates during carbon fixation and deposition of organic materials enriches benthic carbon signals (France 1995; Vander Zanden & Rasmussen 1999). For example, benthic food webs, which are derived from algae and detritus, are generally higher in $\delta^{13}\text{C}$ values compared to pelagic food webs, which are derived from phytoplankton (Hobson & Welch 1992; France 1995). However, a limitation of SIA is that it does not necessarily provide detailed information on the prey types consumed by predators (Hussey et al. 2013). Recently, Bayesian framework mixing models such as those in SIAR (Parnell et al. 2010) and MixSIR (Moore & Semmens 2008) have been developed to address this issue by estimating probability distributions of prey contributions based on stable isotope composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) from the predator and a range of potential prey sources (Layman et al. 2012). These models directly incorporate uncertainty in multiple input parameters and different diet–tissue discrimination factors can be specified (Parnell et al. 2010). A further advantage of SIA is that, because of the time it takes for prey to be assimilated into predator tissues, the time-scale represented by SIA is greater than SCA. For example, SCA represents recent diet (hours–days) (Finley & Gibb 1982; Christiansen et al. 2005), SIA of liver provides short-term (weeks) diet assimilation information and

SIA of muscle reflects medium-term diet (months) (Tieszen et al. 1983; Hobson & Clark 1992). Since all dietary techniques have inherent limitations, the combination of several in a multi-approach study improves the assessment of the animal's feeding ecology (see Hyslop 1980; Post 2002).

Beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) migrate to the Canadian Arctic Archipelago during summer mainly from Baffin Bay, Jones Sound, the North Water polynya and off the western coast of Greenland (Innes et al. 1996) (Fig. 1). They typically migrate along coasts or lead in pack ice to summering areas such as Peel Sound (Mansfield et al. 1975; Richard et al. 2001), returning east as the sea ice consolidates. The summer diet of these whale species in the Canadian Arctic is dominated by Arctic cod (*Boreogadus saida*) (Finley & Gibb 1982; Welch et al. 1992; Loseto et al. 2009). Information about diet in wintering areas is limited but suggests that boreoatlantic armhook squid (*Gonatus fabricii*), capelin (*Mallotus villosus*) and Greenland halibut (*Reinhardtius hippoglossoides*) supplement Arctic cod (Heide-Jørgensen & Teilmann 1994; Laidre & Heide-Jørgensen 2005; Gardiner & Dick 2010; Watt & Ferguson 2015). Ringed seals (*Pusa hispida*) are Arctic and sub-Arctic phocids that typically remain in ice-covered waters year-round. Many ringed seals show area fidelity,

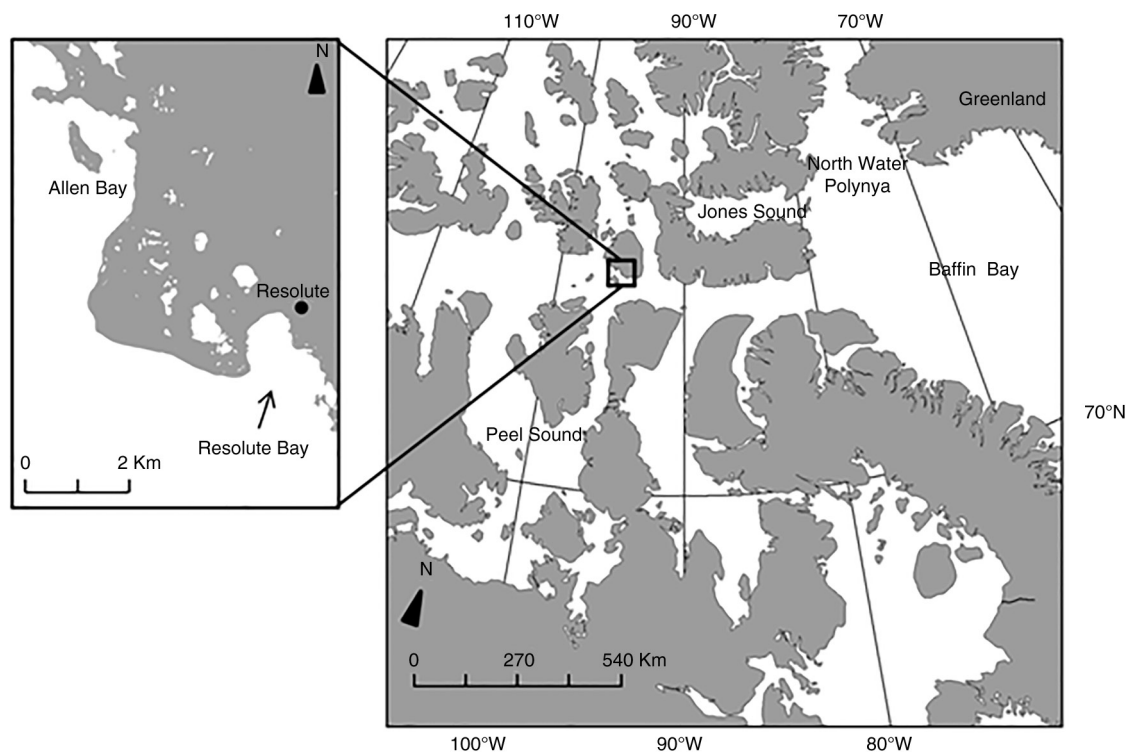


Fig. 1 Map of the eastern Canadian Arctic. Inset indicates the sampling location in Allen Bay and Resolute Bay, off Cornwallis Island.

but long-range movement and changes in seasonal distribution occur (e.g., Heide-Jørgensen et al. 1992). The diet of ringed seals in the High Arctic is dominated by only a few species, including Arctic cod, pelagic amphipods and mysids (Bradstreet & Cross 1982; Marcin 1994; Holst et al. 2001; Labansen et al. 2011).

The purpose of this study was to improve our understanding of the foraging ecology of ringed seals, belugas and narwhals using SCA and SIA in a multi-approach study. Although sampling was mainly limited to the open water period in 2010 and the size of samples was relatively small, the goal was to contribute to the sparse data sets available in the Arctic and explore potential patterns and insights into the foraging ecology of these marine mammals with which future studies could be compared. The main objectives were to: 1) determine intraspecific (ringed seal age and size comparisons) and interspecific (ringed seals vs. whales) prey selection patterns; and 2) determine the importance of prey seasonally (e.g., open water vs. ice-covered water) and spatially (e.g., inshore/benthic vs. offshore/pelagic habitat) within the Resolute and Allen Bay region using SCA and SIA of carbon and nitrogen from liver and muscle tissues.

Materials and methods

Study area

Resolute Bay and Allen Bay are located by Cornwallis Island, Nunavut, near the community of Resolute (74°41'51"N 094°49'56"W; Fig. 1) in the Canadian High Arctic. Belugas and narwhals routinely navigate the shores around Resolute to and from summering grounds, while ringed seals are present year-round. Resolute Bay and Allen Bay are culturally important to Inuit as the main subsistence hunting locations near Resolute. These bays are also frequented by schools of Arctic cod during the open water period and consistently attract marine mammals to the area to feed (Welch et al. 1993; Hop et al. 1997; Simeone pers. comm.).

Sample collection

Ringed seals ($n = 21$, 2010; $n = 6$, 2011), belugas ($n = 13$, 2010) and narwhals ($n = 3$, 2010) were collected as part of subsistence hunting by Inuit hunters in Resolute Bay and Allen Bay during the summer and early fall in 2010 and 2011 (Table 1). The following tissues were collected from each animal less than four hours after harvesting and frozen (-20°C): whole stomach (ringed seals: $n = 19$, 2010; belugas: $n = 12$; narwhals: $n = 3$), liver

Table 1 Sample collection information of ringed seals, belugas and narwhals in Allen Bay and Resolute bay in 2010 and 2011.

Collection date	Ringed seals		Belugas Sep 1–Sep 16 2010	Narwhals Sep 16–Sep 17 2010
	Aug 9– Sep 14 2010	Jun 15– Sep 31 2011		
	Sample size (n)	21	6	13
Males	17	2	8	3
Adult	9	1	6	3
Juvenile	4	1	2	–
Pup	4	–	–	–
Females	4	2	5	–
Adult	4	2	3	–
Juvenile	–	–	2	–
Pup	–	–	–	–
Unknown	–	2	–	–
Total stomachs with contents	17 (2) ^a	–	5 (7) ^a	3 (0) ^a

^aThe numbers in parentheses represent empty stomachs.

and muscle (ringed seals: $n = 21$, 2010, and $n = 6$, 2011; belugas: $n = 12$; narwhals: $n = 3$), a tooth from the 2nd and 5th position on the right mandible (belugas; following Stewart et al. 2006), and lower and upper canines (ringed seals; following Stewart et al. 1996). The frozen tissue samples were later shipped to the University of Manitoba and stored at -20°C until analyses.

Age, maturity and sex determination

Ringed seals were aged by counting growth layer groups in the lower and upper canines (cementum age analysis; Stewart et al. 1996). If age (x , $n = 4$) or length (L , $n = 2$) was not obtained, the following growth model was used to estimate the missing value: $L_x = 144.5 (1 - e^{-0.099(x+0.61)})^{0.225}$ (see figure 22 in McLaren 1993). This model was selected because of the large sample size (ca. 100 ringed seals) and also because seals were sampled from the Canadian Arctic (McLaren 1993), reducing the effect of regional variability. The maturity of ringed seals was estimated after counting annual growth layers in canine teeth (Stewart et al. 1996) as follows: adult ≥ 6 years, juvenile 1–5 years and pup < 1 year (Holst et al. 2001). Beluga age was estimated by counting annual growth layers deposited in the dentine of mounted tooth sections (Stewart 2012). Belugas were classified as adult if they were ≥ 12 years old (Stewart 1994; Stewart et al. 2006). When teeth were unavailable, age (x , $n = 2$) and length (L , $n = 1$) were estimated as follows: $L_x = 381.5e^{-7.56e^{-0.29x}}$ (female) and $L_x = 432.2e^{-1.16e^{-0.15x}}$ (male) (Luque & Ferguson 2010). The age of narwhals could not be estimated, but the lengths of their tusks (> 1 m) indicated that all three were adult males (Finley & Gibb 1982).

The sex of ringed seals and toothed whales was determined from a skin sample using polymerase chain reaction-based genetic analysis (Shaw et al. 2003).

Stomach content analysis

Whole stomachs were thawed then cut open, and stomach contents and epithelium were washed with water and filtered through three sieves (4 mm, 1.4 mm and 425 μm). Diet items were identified to the lowest possible taxonomic level. Sagittal otoliths showing little or no degradation were measured using an Axio Zoom V16 microscope and AxioCam HR camera (Zeiss, Jena, Germany) to model the fork length (FL, mm) of consumed Arctic cod. When a stomach had >25 otoliths, a subsample of 25 otoliths were measured. Otolith length (OL, mm) was defined as the longest dimension between the posterior and anterior edges of the otolith (Hunt 1992). The FL of Arctic cod was then estimated from OL using $\text{FL} = 24.20 \times \text{OL} - 4.29$ ($r^2 = 0.91$, $n = 251$) (Matley et al. 2013). Amphipods were enumerated by counting whole bodies and disarticulated parts—eyes and telsons (Finley & Gibb 1982).

Frequency of occurrence (FO_i) and percent composition (N_i) were used to determine the importance of prey (e.g., Hyslop 1980; Pierce & Boyle 1991) as follows:

$$\text{FO}_i(\%) = (S_i/S_t) \times 100, \quad (1)$$

where S_i represents the number of ringed seals (or belugas or narwhals) that consumed prey type i , and S_t represents the total number of ringed seals (or belugas or narwhals) sampled; and

$$\text{N}_i(\%) = (n_i/n_t) \times 100, \quad (2)$$

where n_i represents the total number of prey type i , and n_t represents the total number of prey sampled in all stomachs.

Stable isotope analysis

Liver and muscle tissue from each seal and toothed whale were analysed at the Great Lakes Institute for Environmental Research at the University of Windsor, Canada, for quantification of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Tissues were oven-dried at 70°C for 48 h then crushed and ground. Since lipids are depleted in ^{13}C and influence $\delta^{13}\text{C}$ values (Caut et al. 2011), they were extracted from predator and prey tissues using a 2:1 chloroform:methanol solvent as described by McMeans et al. (2009). A continuous flow isotope ratio mass spectrometer (Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with a Costech Elemental Analyzer (Costech Analytical

Technologies, Valencia, CA, USA) determined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2 as standard reference materials. Stable isotope ratio values are expressed in parts per thousand (‰) using δ notation as calculated using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000, \quad (3)$$

where X is ^{15}N or ^{13}C , R_{sample} is the ratio ($^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$) in the sample and R_{standard} is the ratio in the standard. The standard deviation of samples run in triplicate was generally $<0.1\text{‰}$ ($\delta^{13}\text{C}$) and $<0.2\text{‰}$ ($\delta^{15}\text{N}$).

Data analysis

Statistical analyses were not conducted for ringed seals in 2011 because of the small sample size ($n = 6$), but stable isotope values are presented. Tissues from only four female ringed seals were collected in 2010 and consequently no sex comparisons were made. Similarly, the effect of life history traits on stable isotopes and stomach contents were not examined for belugas or narwhals because of small sample sizes. After preliminary data exploration showed that similar food items were consumed by belugas and narwhals, and that stable isotope values did not significantly differ between species, the toothed whales were grouped for statistical analyses. Assumptions of data normality and homogeneity of variances were verified using Q–Q plots and visual analysis of residuals, respectively. General additive modelling (GAM; Gaussian error distribution with an identity link) was used to describe how ringed seal age and length influenced the size of Arctic cod consumed. Candidate models were compared using Akaike information criterion with correction for small sample size (AICc) from the mgcv package (Wood 2000). The models with the lowest AIC values were considered to contain the most important factors influencing the size of Arctic cod consumed; however, uncertainty associated with hypothesis testing in GAMs means that this is only a general guide (e.g., Venables & Ripley 2004). Data from one ringed seal pup which consumed Arctic cod <90 mm was omitted because it had a disproportionate influence on the output (Cook's distance >1). The mean size of Arctic cod consumed (via SCA) by ringed seals and whales was compared with a Mann–Whitney U test.

An analysis of covariance (ANCOVA) determined the effect of maturity (juvenile/pup <6 years old, adult ≥ 6 years old; Holst et al. 2001) on ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for liver and muscle with ringed seal length as the covariate. Finally, the mean liver and muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were compared among ringed seals

and toothed whales by analysis of variance (ANOVA), followed by a Tukey’s test. Statistical analyses were conducted with the R program (R Core Team 2013), and differences $p \leq 0.05$ were considered statistically significant.

To quantify the importance of potential prey of ringed seals in 2010 near Resolute, the Bayesian mixing model SIAR (SIA in R) from the SIAR package (Parnell et al. 2010) was used with diet–tissue discrimination factors estimated from harp seals (*Pagophilus groenlandicus*) by Hobson et al. (1996) (muscle: $\Delta^{15}n = 2.4, \Delta^{13}C = 1.3$; liver: $\Delta^{15}n = 3.1, \Delta^{13}C = 0.6$). An arbitrary standard deviation of 0.2 was selected for each discrimination factor similar to bowhead whale (*Balaena mysticetus*) skin–prey isotopic discrimination estimates (Pomerleau et al. 2012). Stable isotope values (mean \pm SD) of common prey also collected in Allen Bay between July and August 2010 (see Matley et al. 2013) were used to estimate prey proportion as follows: Arctic cod (muscle: $\delta^{15}N = 15.27 \pm 0.61, \delta^{13}C = -20.28 \pm 0.34$); *Themisto libellula* ($\delta^{15}N = 9.6 \pm 1.00, \delta^{13}C = -21.42 \pm 1.00$); *Onisimus* sp. ($\delta^{15}N = 8.58 \pm 1.02, \delta^{13}C = -16.92 \pm 0.93$); and *Gammarus* sp. ($\delta^{15}N = 9.80 \pm 1.83, \delta^{13}C = -19.13 \pm 1.37$). These prey only represent a subset of potential food items of ringed seals in the High Arctic; however, only prey found in SCA were included to reduce contribution of non-prey items to the output. Also, Arctic cod were the focus as they are a dominant biomass in the Arctic Ocean and are well known to be very important in the diet of the marine mammals examined.

Mixing models were also completed for toothed whales using discrimination factors estimated by Caut et al. 2011 (muscle: $\Delta^{15}N = 1.23, \Delta^{13}C = 1.26$; liver: $\Delta^{15}N = 2.78, \Delta^{13}C = 1.27$). Additional prey items were explored to account for dietary changes during seasonal migrations, including *Gonatus fabricii* ($\delta^{15}N = 11.2 \pm 1.3, \delta^{13}C = -19.8 \pm 0.6$; Watt & Ferguson 2015), *Reinhardtius hippoglossoides* ($\delta^{15}N = 15.3 \pm 0.6, \delta^{13}C = -19.6 \pm 0.1$; Watt & Ferguson 2015) and *Mallotus villosus* ($\delta^{15}N = 12.9 \pm 0.1, \delta^{13}C = -19.3 \pm 0.1$; Dennard et al. 2009). Isotope values of Arctic cod and *R. hippoglossoides* were nearly identical, exceeding 90% in the correlation matrix, which made it difficult to differentiate the contribution of the two prey sources. Consequently, only values from Arctic cod were used but the final output is representative of possible contribution from both prey. Isotope values from prey and predators were also plotted after correcting for discrimination factors (described above) to visualize potential prey sources.

Results

Stomach contents

Forty-two percent of belugas, 89% of ringed seals and all narwhals had food in stomachs (Table 1). Arctic cod measuring between 160 and 200 mm and amphipods (*Themisto libellula*, *Onisimus* sp. and *Gammarus* sp.) were the main prey species (Fig. 2, Table 2). Results from the GAM demonstrated that age had greater importance

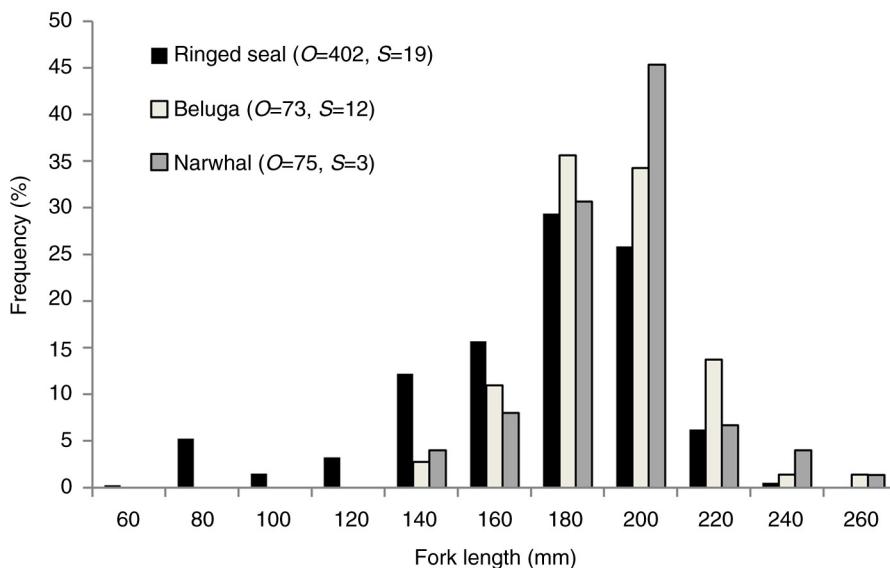


Fig. 2 Frequency distribution of Arctic cod size (fork length [FL], mm) found in the stomachs of ringed seals, belugas and narwhals. The symbol *O* represents the number of otoliths sampled, and *S* represents the number of stomachs collected. Arctic cod fork length was extrapolated from otolith length (OL) using $FL = 24.20 * OL - 4.29$ (Matley et al. 2013).

Table 2 Number of prey, frequency of occurrence (FO_i) and percent composition (N_i) of ringed seal, beluga and narwhal food items.

	Number of prey ^a	FO _i	N _i
Ringed seals			
Juveniles and pups (n = 8)			
Arctic cod	160	87.5	23.6
Amphipods	519 ^b	50	76.4
Adult (n = 11)			
Arctic cod	578	100	91.9
Amphipods	51	36.4	8.1
Belugas (n = 12)			
Arctic cod	556	41.7	93.6
Amphipods	34	16.7	5.7
Squid	4	25	<1
Narwhals (n = 3)			
Arctic cod	257	100	81.6
Amphipods	55	66.7	17.5
Squid	3	66.7	1

^aNumber of Arctic cod calculated by dividing the total number of otoliths by 2 (e.g., 1476/2 = 738 individuals). ^bTwo individuals (a juvenile and a pup) contributed ca. 98% of amphipods collected.

describing the size of Arctic cod consumed by ringed seals (Fig. 3, Table 3); however, the small sample size led to considerable variability in the output and large confidence intervals. The mean length (\pm SE) of Arctic cod consumed by ringed seals (168.0 ± 4.3 mm) was significantly smaller than the toothed whales (182.5 ± 2.0 mm) (Mann–Whitney U test, $W = 21$, $P = 0.01$; Fig. 2).

Stable isotopes

Tissue values of $\delta^{13}C$ were similar among predators except in the livers of ringed seals, which were significantly higher than all other samples (ANOVA, $F_{3,68} = 12.44$, $P < 0.01$; Table 4). Muscle $\delta^{15}N$ values from the toothed whales were significantly lower than $\delta^{15}N$ from ringed seal liver and muscle (ANOVA, $F_{3,68} = 7.97$, $p < 0.01$; Table 4). Ringed seal $\delta^{15}N$ and $\delta^{13}C$ values for liver and muscle did not differ between adults and juveniles when length was included as a covariate (Table 5). Liver $\delta^{15}N$ was positively related to length (ANCOVA, $F_{1,18} = 5.80$, $p = 0.03$; Table 5).

After correcting for diet–tissue discrimination factors, the biplot of predator and prey isotopes showed that ringed seal and whale tissues were closely associated with Arctic cod (Fig. 4). Similarly, the stable isotope mixing model estimated that Arctic cod was the main contributor to the diet of ringed seals in liver and muscle tissues (95% credibility interval: liver = 65–85%; muscle = 84–96%; Fig. 5a, b). The sympagic (ice-associated) amphipod *Onisimus* sp. was also important in liver tissue of ringed seals (95% credibility interval: 11–31%; Fig. 5a). For the

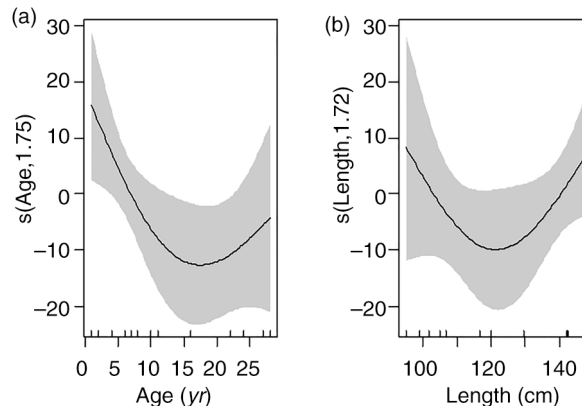


Fig. 3 Smoothing functions ($k = 3$) of general additive modelling on the size of Arctic cod consumed by ringed seals in relation to age (a) and length (b). The y axes represent the smoothing function centred at zero and the estimated degrees of freedom for each explanatory variable. The adjusted R^2 for this model is 0.47. The dark line represents the overall mean, shaded areas are 95% confidence intervals, and small lines on the x axes are observations at each predictor level.

toothed whales, Arctic cod and/or *Reinhardtius hippoglossoides* were the main prey (95% credibility interval: liver = 67–83%; muscle = 83–97%; Fig. 5c, d).

Discussion

Arctic cod was the dominant prey item of ringed seals, narwhals and belugas collected from the Resolute Bay region during the open water period. This is not surprising considering that Arctic cod aggregated in abundant schools in Allen Bay during the sampling period (see Matley et al. 2012) and are known to be heavily exploited by predators in this area (Hobson & Welch 1992; Hop et al. 1997). This research also showed differences in ringed seal feeding patterns among individuals and compared to the toothed whales based on multiple sampling techniques.

Ringed seal life history traits (age and length) did not have a clear influence on the size of Arctic cod consumed or muscle stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values, although

Table 3 Model selection from generalized additive modelling (GAM) examining the effect of ringed seal age and length on the size of consumed Arctic cod (FL). Akaike information criterion accounting for small sample size (AICc) was used to select the best models (i.e., lower AICc), and the relative importance of each model—its weight—is indicated.

	Model	AICc	Δ AICc	Weight
M1	FL ~ s(Age)	140.3	0	0.52
M2	FL ~ s(Length)	141.8	1.52	0.25
M3	FL ~ s(Age) + s(Length)	142.9	2.64	0.14
M4	FL ~ 1 (null model)	143.8	3.57	0.09

Table 4 Sample number (n), mean \pm 1 standard error (SE) of liver and muscle $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) of ringed seals, belugas and narwhals collected near Resolute in 2010 and 2011.

Species	n	Liver		Muscle	
		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Ringed seals (2010)	21	17.45 \pm 0.18	-18.56 \pm 0.10	17.21 \pm 0.18	-19.35 \pm 0.14
Ringed seals (2011)	6	16.50 \pm 0.17	-19.37 \pm 0.14	16.96 \pm 0.43	-19.76 \pm 0.23
Belugas	12	17.00 \pm 0.12	-19.14 \pm 0.10	16.33 \pm 0.20	-19.28 \pm 0.09
Narwhals	3	16.97 \pm 0.12	-19.57 \pm 0.14	16.34 \pm 0.07	-19.59 \pm 0.11

a larger sample size is needed to investigate this further. Similarly, Holst et al. (2001) found no difference in the size of Arctic cod consumed between age classes and between sexes at two High Arctic locations. Also, Dehn et al. (2007) did not find a difference between muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with age of ringed seals in the Canadian Arctic, and suggested that a mixture of krill and gadid fish comprised ringed seal diet independent of life history. Liver $\delta^{15}\text{N}$ values of ringed seals were influenced by length likely because the smaller individuals were eating smaller prey such as amphipods in addition to Arctic cod during the open water period, as supported by SCA. Higher digestion rates of smaller prey may have resulted in overestimation of Arctic cod in the diet, but the isotopic mixing model is consistent with SCA findings.

The energetic importance of Arctic cod as prey is well documented in the Arctic food web, and mainly derives from large, dense and readily visible aggregations exploited by seabirds, seals and whales near the surface (Welch et al. 1993; Crawford & Jorgenson 1996). However, smaller and sparsely dispersed non-schooling Arctic cod appear to be a significant source of food, particularly for ringed seals. During several months of observations in Allen Bay (Matley et al. 2012), ringed seals did not forage on schools of Arctic cod near the surface, yet belugas and harp seals often did—an observation also noted by Bradstreet et al. (1986). Interestingly, the mean length of net-captured Arctic cod from schools in Allen Bay was 187.0 mm (Crawford & Jorgenson 1996), while

non-schooling adults in Resolute Bay were 163.5 mm (Hop et al. 1997). Therefore, it appears that ringed seals consumed non-schooling Arctic cod (162.1 mm), and toothed whales exploited Arctic cod schools (183.1 and 181.4 mm, respectively). However, the low number of predator samples available necessitates further studies to validate this preliminary finding. Further differences in feeding patterns between ringed seals and toothed whales were identified from SIA. For example, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from ringed seals were typically higher than values from belugas and narwhals. Considering that Arctic cod were the main prey for all tissues and species, these differences may represent isotopic variation in feeding habitat and not necessarily trophic structure. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are often higher in inshore/benthic habitats compared to offshore/pelagic on account of processes associated with differential fractionation (Vander Zanden & Rasmussen 2001), benthic–pelagic coupling (Hobson et al. 1995) and other physical processes, such as the demand/uptake of dissolved inorganic nitrogen (Montoya 2007; Chouvelon et al. 2012). Therefore, higher values of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the tissues of ringed seals support foraging in coastal areas (e.g., Teilmann et al. 1999), whereas the male-biased toothed whale tissues indicated that foraging occurred mainly offshore in deeper water (e.g., Loseto et al. 2009). Alternatively, variation in baseline $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values associated with distribution patterns—migratory whales and more resident ringed seals—may have contributed to interspecific isotope patterns (e.g., Ruiz-Cooley et al. 2012).

Liver and muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were similar for the toothed whales indicating that prey selection and feeding habitat were consistent over a temporal scale of months. The mixing model for the toothed whale data also supported this finding. However, the relative contribution of Arctic cod/*Reinhardtius hippoglossoides* was difficult to differentiate. Nevertheless, *R. hippoglossoides* has not been documented near Resolute either by SCA (e.g., Welch et al. 1992) or fishing (e.g., Crawford & Jorgenson 1996; Kessel, pers. comm.) and is unlikely to contribute to the tissue isotope values of predators in this area. Seasonal trends were not detected from skin and

Table 5 Summary of ANCOVA results testing the effect of ringed seal maturity (adult \geq 6 years old, juvenile/pup $<$ 6 years old) and length (covariate) on muscle and liver $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Significant relationships ($p \leq 0.05$) are in boldface.

	Parameter	F value	P value
Muscle $\delta^{13}\text{C}$	Length	<0.01	0.93
	Maturity	<0.01	0.99
Muscle $\delta^{15}\text{N}$	Length	3.86	0.07
	Maturity	1.12	0.30
Liver $\delta^{13}\text{C}$	Length	0.22	0.64
	Maturity	<0.01	0.98
Liver $\delta^{15}\text{N}$	Length	5.80	0.03
	Maturity	1.22	0.29

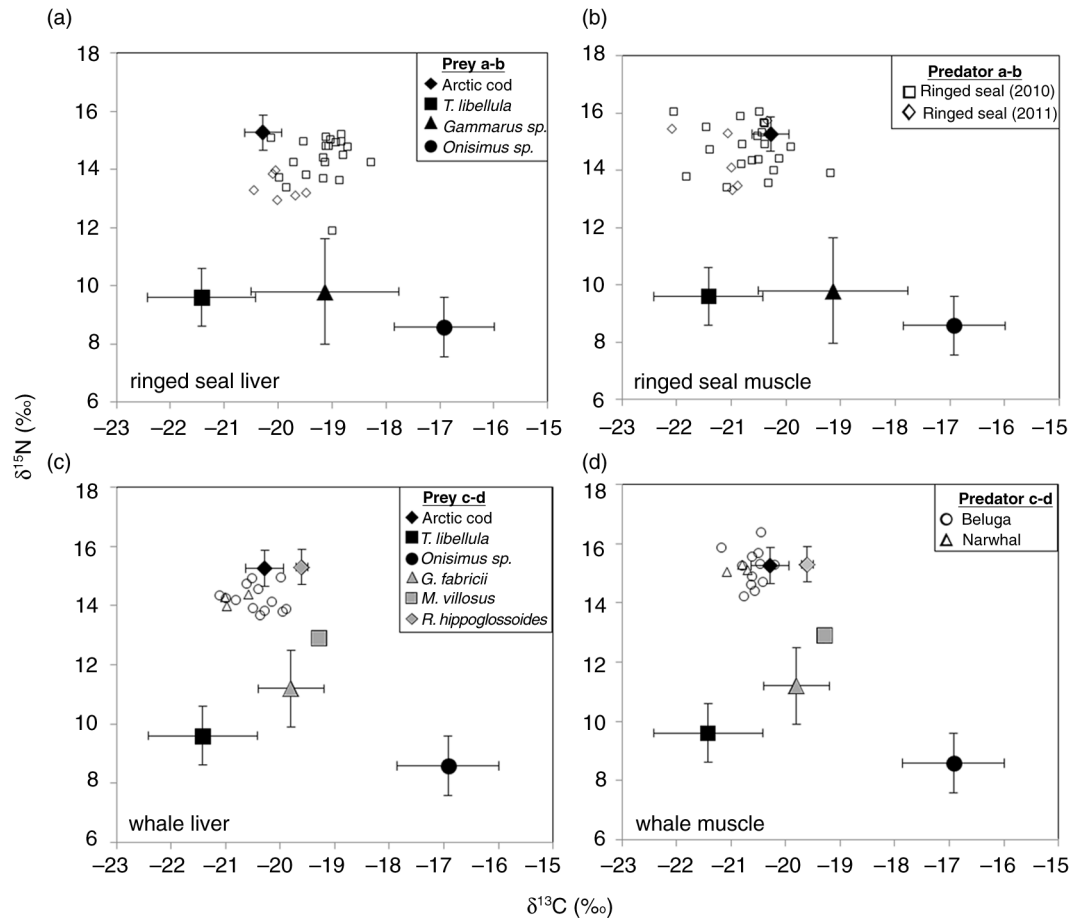


Fig. 4 Isotope biplot of potential prey sources (mean \pm SD) of ringed seals, belugas and narwhals, corrected for trophic discrimination by subtracting 3.1 and 0.6‰ from ringed seal values for liver $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, as well as 2.4 and 1.3‰ for muscle (Hobson et al. 1996). The discrimination factors used for the toothed whales were 2.78 and 1.27‰ for liver $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, and 1.23 and 1.26‰ for muscle (Caut et al. 2011). Prey were collected from Allen Bay in 2010, except for the following species: *Gonatus fabricii* and *Reinhardtius hippoglossoides* collected in Davis Strait in 2011 (Watt & Ferguson 2015) and *Mallotus villosus* collected in Cumberland Sound 2008 (Dennard et al. 2009).

muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of belugas sampled in Cumberland Sound (Marcoux et al. 2012). However, seasonal differences (as indicated by skin and muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) were identified in Baffin Bay narwhals, where the contribution of capelin to the diet appeared to differ between winter and spring (Watt & Ferguson 2015).

Understanding the trophic ecology of migratory animals such as belugas and narwhals is difficult as large-scaled sampling is required to account for prey availability and baseline isotopic differences (e.g., Ruiz-Cooley et al. 2012) throughout geographic distributions. Additional caveats associated with dietary sampling make matters more difficult. For example, diet–tissue discrimination factors and turnover rates are largely unknown for marine mammals (Newsome et al. 2010). Nevertheless, our results are interesting in that diet and habitat of both

belugas and narwhals were similar along migratory routes. Further, dietary similarities between belugas and narwhals indicated by SCA and SIA suggest that both species share a trophic niche, at least in the Resolute and Allen Bay area, which could have important conservation implications.

This study used SIA for liver and muscle tissues from three Arctic marine mammals in conjunction with SCA, to investigate how diet, prey composition and habitat vary seasonally around Resolute Bay and Allen Bay. While sample sizes were small these preliminary data have provided new insights into feeding patterns from traditionally harvested animals that are impossible to acquire through large-scale scientific collections in the High Arctic today. Further, this research provides baseline prey selection patterns, at a local scale, from a highly

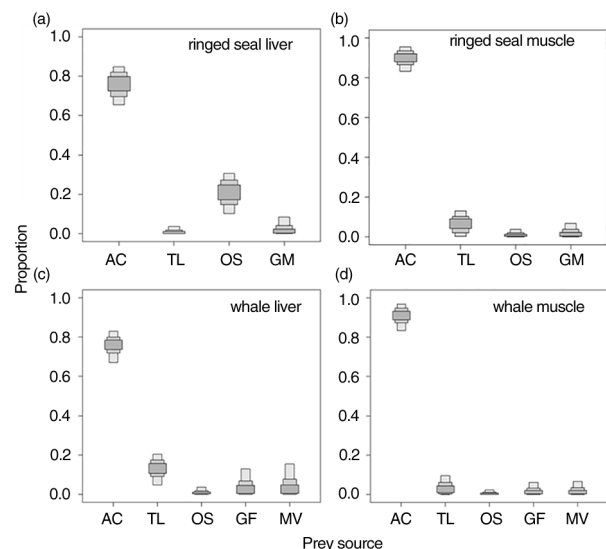


Fig. 5 Contribution of common prey sources based on isotopic mixing model output for ringed seal and toothed whale (belugas and narwhals combined) liver and muscle from 2010. Prey sources used in the models were Arctic cod and/or *Reinhardtius hippoglossoides* (AC), *Themisto libellula* (TL), *Onisimus* sp. (OS), *Gammarus* sp. (GM), *Gonatus fabricii* (GF) and *Mallotus villosus* (MV). The boxplots represent probability densities for credibility intervals of 95% (lighter boxes), 75%, and 50% (darker boxes).

valued traditional resource use area in the Canadian Arctic. It also highlights the ecological significance of Arctic cod.

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