Oecologia (2016) 180:631–644
DOI 10.1007/s00442-015-3384-5

HIGHLIGHTED STUDENT RESEARCH

Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem

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Received: 22 July 2014 / Accepted: 23 June 2015 / Published online: 26 July 2015

Abstract Spatial and temporal variation can confound interpretations of relationships within and between species in terms of diet composition, niche size, and trophic position (TP). The cause of dietary variation within species is commonly an ontogenetic niche shift, which is a key dynamic influencing community structure. We quantified spatial and temporal variations in ringed seal (*Pusa hispida*) diet, niche size, and TP during ontogeny across the Arctic—a rapidly changing ecosystem. Stable carbon and nitrogen isotope analysis was performed on 558 liver and 630 muscle samples from ringed seals and on likely prey species from five locations ranging from the High to the Low Arctic. A modest ontogenetic diet shift occurred, with adult ringed seals consuming more forage fish (approximately 80 versus 60 %) and having a higher TP than subadults, which generally decreased with latitude. However, the degree of shift varied spatially, with adults in the High Arctic presenting a more restricted niche size and consuming more Arctic cod (*Boreogadus saida*) than subadults (87 versus 44 %) and adults at the lowest latitude (29 %). The TPs of adult and subadult ringed seals generally decreased with latitude (4.7–3.3), which was mainly driven by greater complexity in trophic structure within the zooplankton communities. Adult isotopic niche size increased over time, likely due to the recent circumpolar increases in subarctic forage fish distribution and abundance. Given the spatial and temporal variability in ringed seal foraging ecology, ringed seals exhibit dietary plasticity as a species, suggesting adaptability in terms of their diet to climate change.

Keywords Arctic · Ontogenetic niche shift · Ringed seal · Stable isotopes · Trophic position

Communicated by Helene Marsh.

We quantified large-scale spatial, temporal and within-species variation of trophic relationships for a near-top marine predator within a rapidly changing ecosystem. We highlight latitudinal and temporal (over a 22-year period) trends in the feeding relationships of a marine predator and the complexity of Arctic marine food webs as a result of increased prevalence of sub-Arctic forage fish species at lower latitudes. These results shed new light on the spatial and temporal variability of Arctic ecosystem trophodynamics and the dietary plasticity of Arctic species to changing environmental conditions and resource availability.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3384-5) contains supplementary material, which is available to authorized users.

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Introduction

Quantifying feeding relationships between species in food webs is an important method of increasing our knowledge of the biotic mechanisms that affect ecosystem structure (MacArthur 1955; Paine 1966). Feeding relationships can be quantified by a number of approaches, from consumer–resource connections (Elton 1927) to trophic levels where species are arranged into separate energy groups (Lindemann 1942), which are then evolved into trophic positions (TPs) to account for omnivory (Hobson and Welch 1992). These trophic relationships can be obscured by spatial and temporal variation, where different populations of a species and individuals within a population can vary in terms of their diet, ecological niche size, and trophic position (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 2000; Sweeting et al. 2005).

Trophic omnivory—feeding on multiple trophic levels (Novak 2013)—is prevalent in nature (Gellner and McCann 2012), where one of the significant causes of dietary variation within an omnivorous species is an ecological niche shift in terms of diet and habitat use during ontogeny (Werner and Gilliam 1984). A species' ecological niche is generally defined as an *n*-dimensional hypervolume of environmental and ecological variables (i.e., resources) in which a species can maintain a viable population (Hutchinson 1957). Ontogenetic niche shifts are common in animals where larger, older individuals consume different prey types (Werner and Gilliam 1984; Polis and Strong 1996), thus affecting the overall food web structure (Rudolf and Rasmussen 2013). However, little attention has been focused on whether a species' ontogenetic niche shift remains constant across space and/or over time. Such temporal and spatial variability is important when determining the ecological roles of species in a community, and it is essential to acquire this baseline data to quantify any future changes, especially in rapidly warming climates.

The Arctic undergoes seasonal extremes, with primary production only occurring during a short time period of open water, and full sunlight affecting resource abundance in terms of prey availability (Weslawski et al. 1991). Marine mammals are well adapted to these seasonal extremes, as they intensely forage in the summer and fall, resulting in significant storage of lipids (Ryg and Øritsland 1991). However, a warming climate is causing considerable changes within the Arctic, where (1) air temperatures are increasing by 1.35 °C per decade, (2) sea surface temperatures are increasing (Hinzman et al. 2013), (3) September sea ice extent is declining at a rate of 13.7 % per decade (NSIDC 2013), and (4) snow cover is significantly declining (Iacozza and Ferguson 2014). The physical factors affecting the Arctic climate are in extreme states, with no indication that a reversible shift will occur in the foreseeable future (Hinzman et al. 2013; Polyakov et al. 2013). These marine environmental changes are dramatically altering habitat (Laidre et al. 2008) and causing a higher prevalence of subarctic species (Higdon and Ferguson 2009; Provencher et al. 2012) and parasites/disease (Davidson et al. 2011), which have together negatively impacted the abundances and distributions, decreased the growth and condition, and changed the behavior of numerous Arctic organisms, ranging from phytoplankton to polar bears (Wassmann et al. 2011).

Ringed seals (*Pusa hispida*) are circumpolar and are an indicator species of ecological change (Laidre et al. 2008), as they are a pagophilic ("ice-loving") key species that provide a fundamental link between lower and upper trophic levels (McLaren 1958; Smith 1987). The life history of ringed seals has been strongly shaped by sea ice dynamics (Smith and Hammill 1981), as stable land-fast ice is their preferred breeding habitat over pack ice (Smith and Stirling 1975). Ringed seals are trophic omnivorous consumers (Weslawski et al. 1994; Dehn et al. 2007; Labansen et al. 2007; Thiemann et al. 2007) that have been reported to undergo an ontogenetic shift in diet from invertebrates to fish (Bradstreet and Cross 1982; Holst et al. 2001; Young et al. 2010). Ringed seals consume a wide variety of prey species, from herbivorous and carnivorous invertebrates such as mysid, euphausiid, amphipod, and decapod species to fish such as Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), sand lance (*Ammodytes* sp.), and sculpin (Cottidae; McLaren 1958; Gjertz and Lydersen 1986; Smith 1987; Labansen et al. 2007). The impacts of climate change on sea ice dynamics and marine organisms are of great concern to conservationists (Post et al. 2009). Therefore, it is important to quantify any spatial and temporal variation in the ecological niche and foraging habits of ringed seals in order to better understand the impacts of climate change on the Arctic ecosystem.

Here, we used stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to (1) quantify dietary prey contributions, (2) determine isotopic niche size, and (3) determine the TP for ringed seals across ontogeny, and assessed the influence of space and then time (22-year sampling period) using sea ice extent data. Stable isotope (SI) analysis provides a robust integrative approach to elucidating spatial and temporal trophic variation in terms of a species' feeding ecology (Layman et al. 2012). We hypothesized that adult ringed seals have a more variable diet, isotopic niche size, and TP than subadults due to their greater physiological capability to utilize more habitats. Alternatively, if these metrics were less variable in adults, we expected this to be attributed to foraging experience, leading to them consuming more energy-rich prey. In addition, we hypothesized that ringed seals from the Low to the High Arctic will have similar diets, isotopic niche sizes, and TPs as a result of them utilizing similar resources. Alternatively, it is possible that ringed seals in the Low Arctic show higher

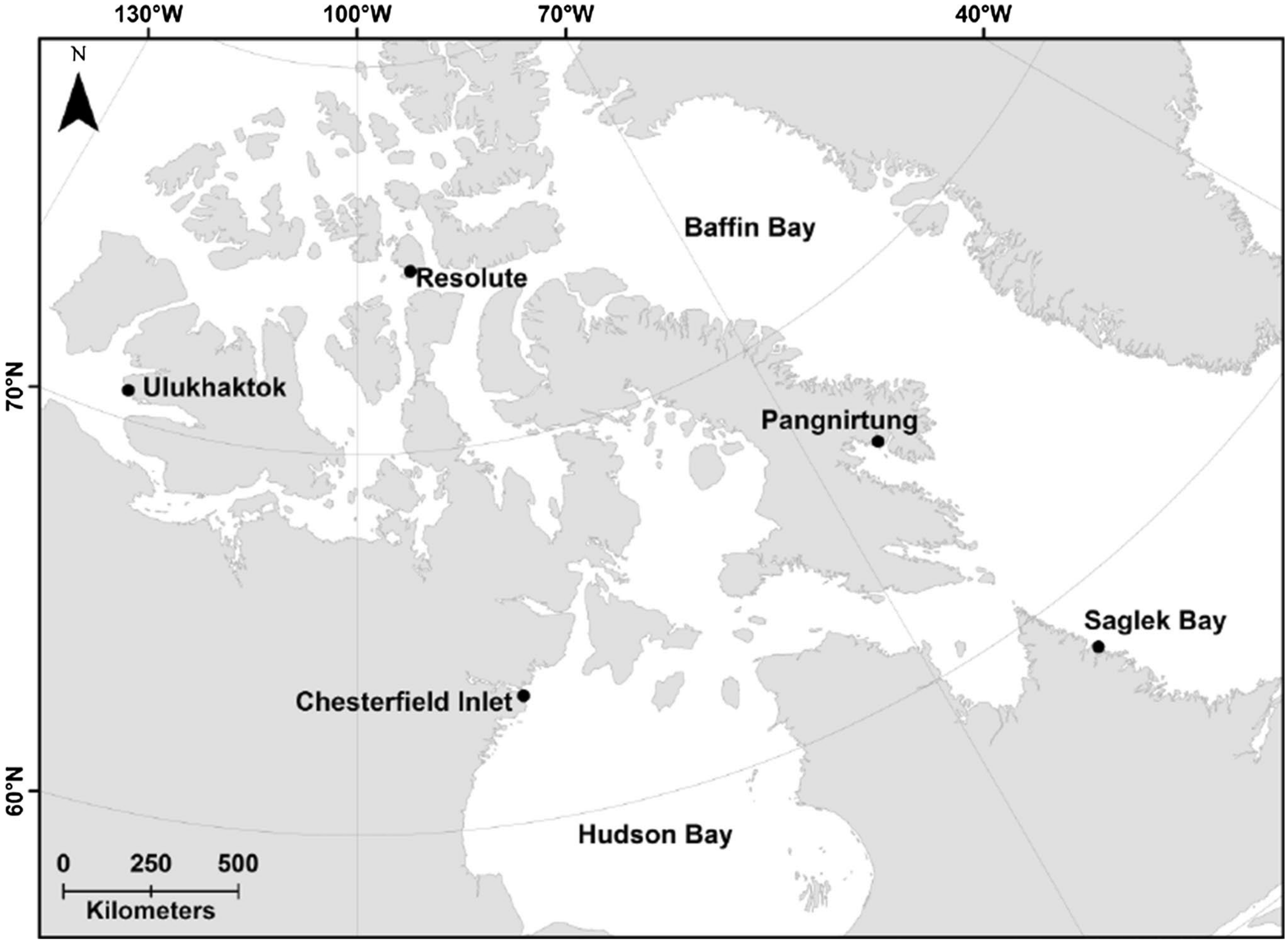


Fig. 1 Map of the Canadian Arctic highlighting the High Arctic (≥70° latitude, Resolute and Ulukhaktok, Mid-Arctic (<70° to ≥60° latitude, Pangnirtung and Chesterfield Inlet), and Low Arctic (<60°, Saglek Bay) communities, where ringed seal samples and prey items were collected for stable isotope analysis

variability in diet and isotopic niche size and they occupy a lower TP due to higher species richness and the incidence of subarctic species expanding northward with climate change. We also hypothesized that ringed seals across the Arctic have increased their isotopic niche size over time, thus exhibiting enough dietary plasticity as a species to change between different prey resources in a rapidly changing ecosystem.

Materials and methods

Sample collection and preparation

Ringed seal liver and muscle samples were collected during the Arctic summer months (June to September; Carmack et al. 2004) by Inuit hunters as part of their subsistence harvests from 1990 to 1996 and 1999 to 2011 from across the Canadian Arctic, ranging from the High Arctic (≥70° Resolute and Ulukhaktok) to the Mid-Arctic (<70° to ≥60° Pangnirtung and Chesterfield Inlet) and the Low Arctic (<60° Saglek Bay; Fig. 1; Table 1). All tissue samples were stored at −20 °C prior to analysis. To group individuals into age classes, seal age was determined by counting the annual growth layer groups in the cementum of decalcified, stained, longitudinal thin sections of the lower right canine by Barbara Stewart (Fisheries and Oceans Canada) and Matson's Laboratory LLC (Missoula, MT, USA). Age estimates from ringed seals collected in Ulukhaktok were provided by counting growth layer groups in the dentine layers of canine teeth. Stewart et al. (1996) indicated that this method underestimates ages of older seals (>10 years of age), but this will have no effect on our results, as all seals have been grouped into separate age classes based on age of sexual maturity: adults (≥6 years of age) and subadults (1–5 years of age; McLaren 1958; Holst and Stirling 2002).

Based on previous stomach content analyses, potential prey items of ringed seals included pelagic and benthic

Table 1 Summary of ringed seal mean δ^{13}C and δ^{15}N values ±SD by tissue, collection location, collection year, and age class used for stable isotope analysis

Year	Adult				Subadult			
	n	δ^{13}C (‰)	δ^{15}N (‰)	TP	*n*	δ^{13}C (‰)	δ^{15}N (‰)	TP
Liver								
Resolute								
1990–1996	6	−18.3 ± 1.1	16.3 ± 0.6	–	22	−18.7 ± 1.2	15.7 ± 1.1	–
1999–2011	38	−18.3 ± 0.4	17.9 ± 0.8	–	24	−18.3 ± 0.8	17.3 ± 0.7	–
Ulukhaktok								
1990–1996	18	−20.9 ± 0.2	17.8 ± 0.3	–	1	−20.9	17.3	–
1999–2011	120	−20.8 ± 0.5	17.6 ± 0.7	–	12	−20.7 ± 0.9	16.6 ± 0.9	–
Pangnirtung								
1990–1996	15	−18.9 ± 0.4	16.6 ± 0.8	–	41	−18.6 ± 0.5	15.5 ± 1.1	–
1999–2011	26	−18.8 ± 0.6	15.7 ± 0.9	–	72	−18.6 ± 0.6	15.1 ± 0.7	–
Chesterfield Inlet								
1999–2011	43	−18.9 ± 0.7	16.8 ± 1.3	–	27	−18.9 ± 0.8	17.0 ± 1.1	–
Saglek Bay								
1999–2011	59	−18.0 ± 0.5	14.3 ± 0.9	–	34	−18.3 ± 0.5	13.9 ± 0.3	–
Muscle								
Resolute								
1990–1996	5	−18.7 ± 1.0	16.1 ± 0.8	–	23	−18.4 ± 1.2	16.2 ± 1.3	–
1999–2011	85	−18.4 ± 0.5	17.3 ± 0.7	4.7 ± 0.3	43	−18.6 ± 0.3	16.9 ± 0.7	4.6 ± 0.3
Ulukhaktok								
1990–1996	29	−20.6 ± 0.1	16.5 ± 0.5	–	4	−20.7 ± 0.1	15.7 ± 1.3	–
1999–2011	126	−20.6 ± 0.4	16.7 ± 0.5	4.5 ± 0.2	12	−20.8 ± 0.6	15.7 ± 1.0	4.0 ± 0.4
Pangnirtung								
1990–1996	17	−18.8 ± 0.4	15.8 ± 0.6	–	41	−18.7 ± 0.4	14.8 ± 0.9	–
1999–2011	38	−18.9 ± 0.7	15.7 ± 0.8	3.9 ± 0.4	76	−19.0 ± 0.6	14.9 ± 0.8	3.6 ± 0.3
Chesterfield Inlet								
1999–2011	28	−18.9 ± 0.7	16.5 ± 1.1	4.0 ± 0.5	13	−19.0 ± 0.8	17.3 ± 1.3	4.2 ± 0.5
Saglek Bay								
1999–2011	59	−18.0 ± 0.4	14.5 ± 0.9	3.7 ± 0.4	31	−18.5 ± 0.5	13.6 ± 0.5	3.3 ± 0.2

primary consumers and zooplanktivores, such as *Mysis* sp., shrimp (*Lebbeus* sp.), *Themisto libellula*, Arctic cod, capelin, sand lance, and sculpin (Bradstreet and Cross 1982; Dehn et al. 2007; Chambellant et al. 2013). Prey items were collected in 2009–2010 and 2012 via nets and trawls in the summer (June–September) in Resolute and Saglek Bay. Stable isotope values for the majority of prey items used in analyses have been previously reported in the literature (see Table 2 for references). Arctic cod collected from Saglek Bay were short (7–10 cm long) and likely represented an age class of 1–2 years (Matley et al. 2013).

Stable isotope analysis

For SI analysis, frozen tissue samples were freeze-dried for 48 h and then crushed into a fine powder using a mortar and pestle. With the presence of lipids in Arctic marine mammal liver and muscle (Yurkowski et al. 2015), lipids were extracted with 2:1 chloroform:methanol solvent using a modified version of the Bligh and Dyer (1959) method (see McMeans et al. 2009 for details) and 400–600 µg of tissue were then weighed into tin capsules. The δ^{15}N and δ^{13}C values were measured by a Thermo Finnigan Delta$^{\mathrm{Plus}}$ mass spectrometer (Thermo Finnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA) at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, University of Windsor. Stable isotope ratios are expressed in parts per thousand (‰) in delta (δ) notation using the following equation: $\delta X = [R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R equals ^{13}C/^{12}C or ^{15}N/^{14}N. The standard material for ^{13}C and ^{15}N are Pee Dee Belemnite and atmospheric nitrogen, respectively. A triplicate was run every ten samples and the measurement precision for δ^{13}C and δ^{15}N of liver

Table 2 Mean ± SD of δ^{13}C (‰) and δ^{15}N (‰) values for potential ringed seal prey items at each sampling location after 1996

Species	*n*	δ^{13}C ± SD	δ^{15}N ± SD	Adult contribution (%)	Subadult contribution (%)	TP	References
Resolute							
Onisimus sp.	11	−17.0 ± 0.7	8.7 ± 0.3	0 (0–1)	0 (0–1)	1.9	Matley (2012)
Themisto	3	−21.4 ± 0.1	9.6 ± 0.1	1 (0–2)	3 (0–8)	2.1	Matley (2012)
Gammarus sp.	7	−21.4 ± 0.3	12.0 ± 0.5	5 (0–13)	30 (16–42)	2.8	Matley (2012)
Arctic cod	176	−19.3 ± 0.8	14.6 ± 0.7	87 (74–98)	44 (17–72)	3.6	
Sculpin	21	−18.4 ± 0.8	14.9 ± 0.6	6 (0–15)	22 (5–40)	3.7	
Ulukhaktok							
Themisto	28	−26.1 ± 1.1	10.2 ± 1.1	1 (0–2)	5 (0–12)	2.2	Loseto et al. (2008)
Mysis sp.	15	−23.0 ± 1.5	10.9 ± 1.5	4 (1–7)	22 (4–39)	2.4	Loseto et al. (2008)
Shrimp	3	−21.5 ± 1.2	13.5 ± 0.3	42 (35–47)	34 (12–58)	3.2	Loseto et al. (2008)
Arctic cod	39	−22.0 ± 1.2	14.7 ± 1.2	33 (25–41)	27 (3–49)	3.6	Loseto et al. (2008)
Sculpin	2	−23.0 ± 1.0	16.1 ± 1.3	20 (15–25)	11 (0–25)	4.0	Loseto et al. (2008)
Pangnirtung							
Mysis sp.	5	−20.8 ± 0.1	9.0 ± 0.1	6 (2–11)	21 (11–31)	1.7	McMeans et al. (2013)
Gammarus sp.	7	−18.6 ± 0.3	9.5 ± 0.7	3 (0–8)	5 (0–12)	1.9	McMeans et al. (2013)
Arctic cod	8	−20.5 ± 0.3	13.5 ± 0.5	71 (54–86)	54 (37–70)	3.1	Marcoux et al. (2012)
Capelin	7	−19.4 ± 0.2	13.5 ± 0.3	11 (0–28)	12 (0–28)	3.1	McMeans et al. (2013)
Shrimp	7	−18.2 ± 0.7	13.9 ± 0.4	4 (0–13)	5 (0–13)	3.2	Marcoux et al. (2012)
Sculpin	23	−17.3 ± 0.8	15.4 ± 1.1	4 (0–10)	4 (0–9)	3.6	Marcoux et al. (2012)
Chesterfield Inlet							
Themisto	90	−20.8 ± 0.4	11.4 ± 1.3	3 (0–9)	13 (0–29)	2.2	Chambellant et al. (2013)
Sand lance	35	−20.7 ± 1.3	12.8 ± 1.5	43 (27–58)	21 (1–38)	2.6	Chambellant et al. (2013)
Capelin	34	−19.3 ± 0.7	13.8 ± 0.8	11 (0–29)	17 (0–33)	2.9	Chambellant et al. (2013)
Shrimp	19	−18.4 ± 2.2	13.5 ± 2.1	4 (0–12)	14 (0–31)	2.9	Chambellant et al. (2013)
Sculpin	24	−18.8 ± 1.2	14.3 ± 1.3	9 (0–25)	16 (0–33)	3.1	Chambellant et al. (2013)
Arctic cod	27	−19.2 ± 0.8	14.7 ± 1.3	28 (4–50)	19 (0–36)	3.2	Chambellant et al. (2013)
Saglek Bay							
Mysis sp.	24	−19.0 ± 0.5	8.5 ± 0.5	5 (0–13)	10 (0–14)	1.6	
Themisto	26	−19.7 ± 0.5	9.7 ± 0.9	19 (5–31)	28 (6–47)	2.1	
Arctic cod	5	−19.8 ± 1.2	12.3 ± 0.8	29 (16–42)	33 (12–53)	2.7	
Capelin/snailfish	8	−19.1 ± 0.4	13.1 ± 0.8	39 (21–56)	19 (0–37)	3.0	
Shrimp	8	−17.0 ± 0.9	13.1 ± 1.0	3 (0–7)	5 (0–12)	3.0	
Sculpin	8	−17.5 ± 0.6	14.4 ± 0.6	5 (0–12)	5 (0–14)	3.4	

Adult and subadult ringed seal mean contribution (95 % Bayesian credible intervals) represents the estimated contribution of prey items to the diet according to mixing model analysis

The mean δ^{15} N values for *Calanus* (baseline in TP estimations) were: 9.2 ‰ in Resolute (Hobson and Welch 1992), 9.4 ‰ in Ulukhaktok, 9.9 ‰ in Pangnirtung, 10.6 ‰ in Chesterfield Inlet, and 9.8 ‰ in Saglek Bay

TP trophic position

and muscle was 0.1 and 0.1 ‰, respectively. The analytical precision derived from the standard deviation of replicate analyses of a NIST standard (NIST 8414, $n = 198$) and an internal lab standard (tilapia muscle, $n = 198$) were both 0.1 and <0.1 ‰ for δ^{15}N and δ^{13}C, respectively.

Statistical analysis

To investigate temporal changes in ringed seal diet, and because of the uneven sampling performed by year among sites, we tested whether the ringed seal data could be grouped into separate time frames via minimum sea ice extent data for September from 1979–2013, acquired from the National Snow and Ice Database Centre (Sea Ice Index; NSIDC 2013). Segmented regression analysis was performed to determine any significant sea ice regime shifts over this time period.

Four separate general linear models were used to test the effects of three explanatory variables: (1) sampling location, (2) collection year, and (3) age class, along with interactions (age class × year and age class × location) on $\delta^{13}C$ in liver and muscle, and $\delta^{15}N$ in liver and muscle. Prior to analysis, $\delta^{13}C$ and $\delta^{15}N$ values were normal according to quantile–quantile plots. All four general linear models were assessed for normality and heteroscedasticity of the residuals using normal quantile–quantile plots and residual-fitted value plots, respectively. In addition, we assessed normality in $\delta^{13}C$ and $\delta^{15}N$ using a chi-square quantile–quantile plot prior to multivariate analysis (SIAR and SIBER, see below). To quantify the likely contribution of prey items to the ringed seal diet, we used a Bayesian mixing model approach (iterations = 200,000, a burn-in of 50,000, and thinned by 15) in the package SIAR v4.2 (Parnell and Jackson 2013) in R v.3.0.3 (R Development Core Team 2014). In Saglek Bay, capelin and snailfish (*Liparis* sp.) SI values were not significantly different, so these were combined ($t_6 = 0.2$ and 0.3 for $\delta^{13}C$ and $\delta^{15}N$; $P \geq 0.75$). Diagnostic matrix plots were used to identify any correlations between prey sources in the mixing models where an increase in the contribution to diet of a prey item caused a decrease in contribution of the other prey item due to the requirement of a sum to 1.0 total dietary contribution. For ringed seal diet estimations, only muscle tissue was used, as it provides a more time-integrated approach to diet estimation due to its relatively slow turnover rate in large mammals (178 days; Sponheimer et al. 2006). Diet–tissue discrimination factors, which have been shown to vary by species and protein quality/quantity of the diet (Caut et al. 2009; Florin et al. 2011), have not been reported for ringed seals, so we used previously published values of 1.3 ‰ and 2.4 ‰ for $\delta^{13}C$ and $\delta^{15}N$ in harp seal muscle fed a high-protein diet ($\delta^{13}C = -20.3$ ‰; $\delta^{15}N = 13.0$ ‰; Hobson et al. 1996). Using Bayesian inference to estimate the probability that more of a resource is consumed by adults than by subadults, we calculated the proportion of posterior estimates that were higher than for the other age class relative to the total number of posterior estimates (10,000).

We determined the isotopic niche spaces of adult and subadult ringed seals at each location using Stable Isotope Bayesian Ellipses in R (SIBER) in SIAR, which uses a multivariate ellipse-based approach to compare groups of differing sample sizes (Jackson et al. 2011). The isotopic niche was plotted based on the standard ellipse areas corrected for small sample size (SEA_C), where SEA_C represents 40 % of the data and allows a robust comparison when sample sizes vary between groups. The SEA_C was used to calculate the fractional overlap between the subadult and adult isotopic niches at each location, thus providing a semi-quantitative method of defining ontogenetic differences in feeding ecology. We then estimated the standard ellipse area using a Bayesian approach (1,000,000 iterations) for statistical comparisons between age classes at each location by estimating the mode and 95 % Bayesian credible interval (SEA_B) for each isotopic niche size. We used Bayesian inference to estimate the probability that the isotopic niche size was more restricted by calculating the proportion of posterior estimates that were smaller than the other group relative to the total number of posterior estimates (1,000,000).

Trophic position was calculated for each prey species and ringed seal age class using a one-source TP model (Eq. 1; Post 2002a) to determine the food web structure at each location.

$$TP_{\mathrm{consumer}} = TP_{\mathrm{baseline}} + \frac{\delta^{15}N_{\mathrm{consumer}} - \delta^{15}N_{\mathrm{baseline}}}{\Delta^{15}N}. \quad (1)$$

The $\delta^{15}N$ values of primary consumers such as copepods (*Calanus hyperboreus*) were used as a baseline (TP = 2) for ringed seal prey at each location, as copepods are good integrators of spatial isotopic variability in phytoplankton (McMeans et al. 2013). A diet–tissue discrimination factor ($\Delta^{15}N$) of 3.4 ‰ (Post 2002a) was used for all prey species except in ringed seals, where 2.4 ‰ was applied as a $\Delta^{15}N$ (Hobson et al. 1996), with Arctic cod or capelin employed as a baseline (TP = 2.7–3.6 depending on location; see "Results"). Similarly, under a scaled trophic level framework in the Canadian Arctic, Hussey et al. (2014) estimated a $\Delta^{15}N$ of 3.3 ‰ for species occupying a TP of 3, and a $\Delta^{15}N$ of 2.1 ‰ for species at a TP of 4, which coincides with our TP approach. To determine differences in TP between age classes at each location, a Bonferroni corrected *t* test was used ($\alpha = 0.01$).

Results

Two distinct time periods were identified where September sea ice extent for the circumpolar Arctic had a nonsignificant rate of decline from 1979–1996 (slope = −0.036, $F_{1,17} = 2.59$; $P = 0.13$; $r^2 = 0.14$) but declined significantly thereafter (slope = −0.15, $F_{1,17} = 36.65$, $P < 0.001$, $r^2 = 0.71$). Therefore, we amalgamated ringed seal individuals into two groups in relation to collection year (≤1996 and ≥1999). Muscle $\delta^{15}N$ significantly increased with collection year ($F_{1,618} = 19.5$, $P < 0.001$; Table ESM1 in Online Resource 1 of the Electronic supplementary material, ESM), thus only adult and subadult ringed seals collected from 1999 and thereafter were included in the SI mixing model, isotopic niche, and TP analyses, which also corresponded with prey sample collection years. The change in $\delta^{15}N$ was most pronounced in the High-Arctic location of Resolute, with increases of 1.2 and 0.7 ‰ for adults and subadults, respectively, whereas no change in $\delta^{15}N$ occurred in the other locations (Table 1). Location had the strongest significant effect, followed by age class, on $\delta^{13}C$ and $\delta^{15}N$ for both liver and muscle (Table ESM1 in

Online Resource 1 of the ESM). A significant interaction occurred between sampling location and age class on $\delta^{13}C$ and $\delta^{15}N$ for adult and subadult liver and muscle (Table ESM1 in Online Resource 1 of the ESM).

SIAR dietary contributions

Mixing model analyses revealed that among all locations, both age classes generally consumed resources from the pelagic environment, with pelagic forage fish—mainly Arctic cod—being the most common prey item and zooplankton/shrimp being of secondary importance for both adults and subadults (Table 2). Adults had a higher probability of consuming more pelagic forage fish than subadults, with the highest occurring in Resolute (1.0) relative to the other locations (0.65–0.70). Subadults were more likely to consume pelagic zooplankton in higher quantities than adults, with probabilities generally decreasing with latitude (0.87 Resolute, 0.95 Holman, 0.79 Pangnirtung, 0.81 Chesterfield Inlet, 0.73 Saglek Bay). Adults and subadults from Ulukhaktok generally fed epibenthically on shrimp in the highest proportions, followed by Arctic cod and sculpin (Table 2). Isotopic values among Arctic cod, sculpin, and shrimp had coefficients of correlation ranging from −0.55 to −0.79 (for other locations, see Table ESM2 in Online Resource 1 of the ESM). Despite high negative correlations between some isotopically distinct prey sources at each location, Phillips et al. (2014) stated that valid food sources should not be removed, as this can significantly alter dietary contribution estimates for the other prey sources.

SIBER niche metrics

The subadult isotopic niche moderately overlapped the isotopic niche of adults within each location, but the degree of overlap varied spatially, with the overlap being smallest in Ulukhaktok (33 and 19 % for muscle and liver) and largest in Resolute (44 and 55 % for muscle and liver; Fig. 2). Within both age classes at each location, the SEA_B estimates were very similar for the tissues, as the largest deviation occurred in Chesterfield Inlet and Resolute (1 ‰^{2}) for subadults and in Ulukhaktok (0.5 ‰^{2}) for adults (Fig. 3). The probability of isotopic niche size being smaller in adults than in subadults was much higher in the High-Arctic communities of Resolute (98 % for liver) and Ulukahtok (100 % for both liver and muscle) than at the lower latitudes (35 % and 21 % for liver and muscle in Pangnirtung; 21 % and 76 % for liver and muscle in Chesterfield Inlet; 11 % and 57 % for liver and muscle in Saglek Bay; Fig. 3). The probability of adult isotopic niche size being larger after 1999 than during the 1990–1996 time period was high in Ulukhaktok (98 % and 91 % for liver and muscle) and in Pangnirtung (85 % and 98 % for liver and muscle; Fig. 4). The probability of an increase in isotopic niche size over time was mixed for subadults in Pangnirtung based on tissue type (12 % and 90 % for liver and muscle), whereas subadults in Resolute were 100 % more probable to decrease in isotopic niche size over time (Fig. 4).

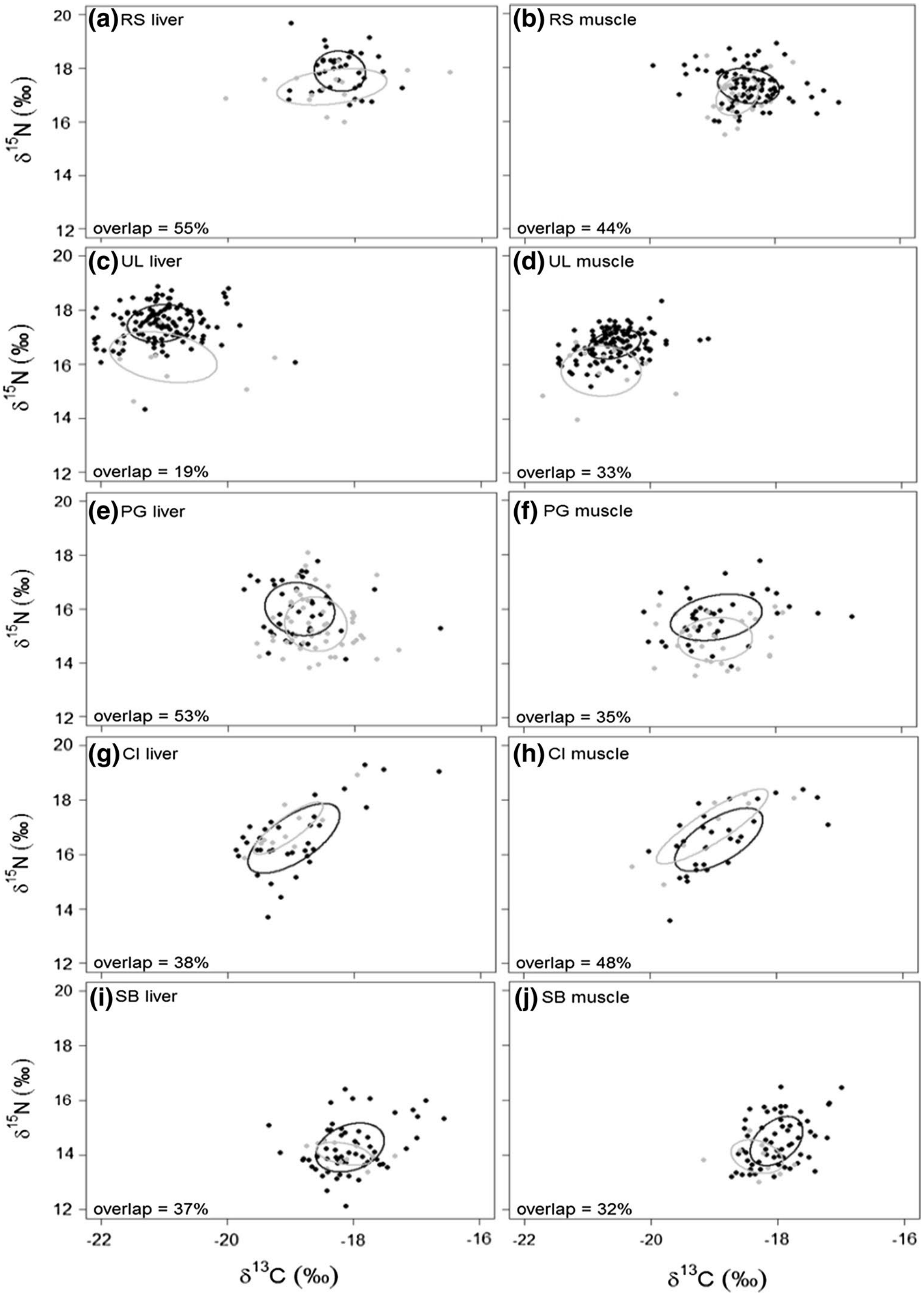
Trophic position

Adult ringed seals had a significantly higher TP than subadults in Ulukhaktok ($t_{13} = 3.72$, $P < 0.01$), Pangnirtung ($t_{64} = 4.04$, $P < 0.01$), and Saglek Bay ($t_{88} = 5.93$, $P < 0.01$), but not in Resolute ($t_{39} = 2.37$, $P = 0.02$) or in Chesterfield Inlet ($t_{10} = 0.98$, $P = 0.35$; see Table 1 for TP estimates). The highest TPs for adults and subadults occurred in the High Arctic (Resolute and Ulukhaktok) and generally decreased with latitude, whereas the lowest TPs occurred in Saglek Bay. The highest $\delta^{15}N$ values and TP for Arctic cod also occurred in the High Arctic (Table 2). The TP range between Arctic cod and both ringed seal age classes varied spatially: the highest occurred in Resolute (1.1 adults, 1.0 subadults) and the lowest in Ulukhaktok (0.8 adults, 0.4 subadults) and Pangnirtung (0.8 adults, 0.5 subadults).

Discussion

Ringed seals underwent an ontogenetic diet shift, with adults consuming more forage fish, generally having a more restricted isotopic niche size, and occupying a different isotopic niche space than subadults. However, the degree of ontogenetic diet and niche shift varied spatially. Our mixing model results revealed that pelagic forage fish, mainly Arctic cod, are the principal prey for both age classes, but that subadults consume more zooplankton than adults, in agreement with previous research (Lowry et al. 1980; Bradstreet and Cross 1982; Weslawski et al. 1994; Holst et al. 2001; Dehn et al. 2007; Chambellant et al. 2013). In the Arctic, among ringed seal prey items, Arctic cod possesses a higher energy content than zooplankton and crustaceans (24.2 and 12.3–21.1 kJ/g dw^{-1}, respectively; Weslawski et al. 1994) and other pelagic fish such as capelin (21.2 kJ/g dw^{-1}; Hedeholm et al. 2011) and sand lance (20.1 kJ/g dw^{-1}; Anthony et al. 2000). The higher dietary contribution of Arctic cod suggests that optimal foraging by adults is likely due to foraging experience, where individuals maximize the acquisition of resources, so that the energy gained exceeds that of the energy expended (MacArthur and Pianka 1966). The physiological dive capabilities of younger ringed seals (Teilmann et al. 1999) are more limited than those of adults, likely contributing to their higher dietary proportion of zooplankton and larger isotopic niche size than adults.

Fig. 2 Isotopic niche sizes of adult (*closed circles* and *solid line*) and subadult (*open circles* and *dashed line*) ringed seal liver (**a**, **c**, **e**, **g**, **i**) and muscle (**b**, **d**, **f**, **h**, **j**) samples from each location with decreasing latitude. The percentage overlap of the subadult niche with the adult niche is provided. Refer to Table 1 for sample sizes. *CI* Chesterfield Inlet, *PG* Pangnirtung, *RS* Resolute, *SB* Saglek Bay, *UL* Ulukhaktok



Consequently, subadults exhibit a more generalistic feeding strategy than adults. Although the TPs of ringed seals estimated from δ^{15}N values vary spatially, the TP estimates of adults across the Arctic were generally higher than those of subadults.

Spatial variation

The difference in fish and pelagic zooplankton consumption between adults and subadults decreased with latitude: at the highest latitude (Resolute), adults consumed more forage fish (almost exclusively Arctic cod), whereas subadults consumed more pelagic zooplankton. In addition, adult isotopic niche size was more restricted than it was for subadults in the High Arctic (Resolute and Ulukhaktok), but similar niche sizes were seen for the Mid-Arctic (Pangnirtung and Chesterfield Inlet) and Low Arctic (Saglek Bay), despite similar ranges and variations of pelagic and benthic baseline SI values across the Arctic. The restricted isotopic niche size of adults suggests that adult ringed seals

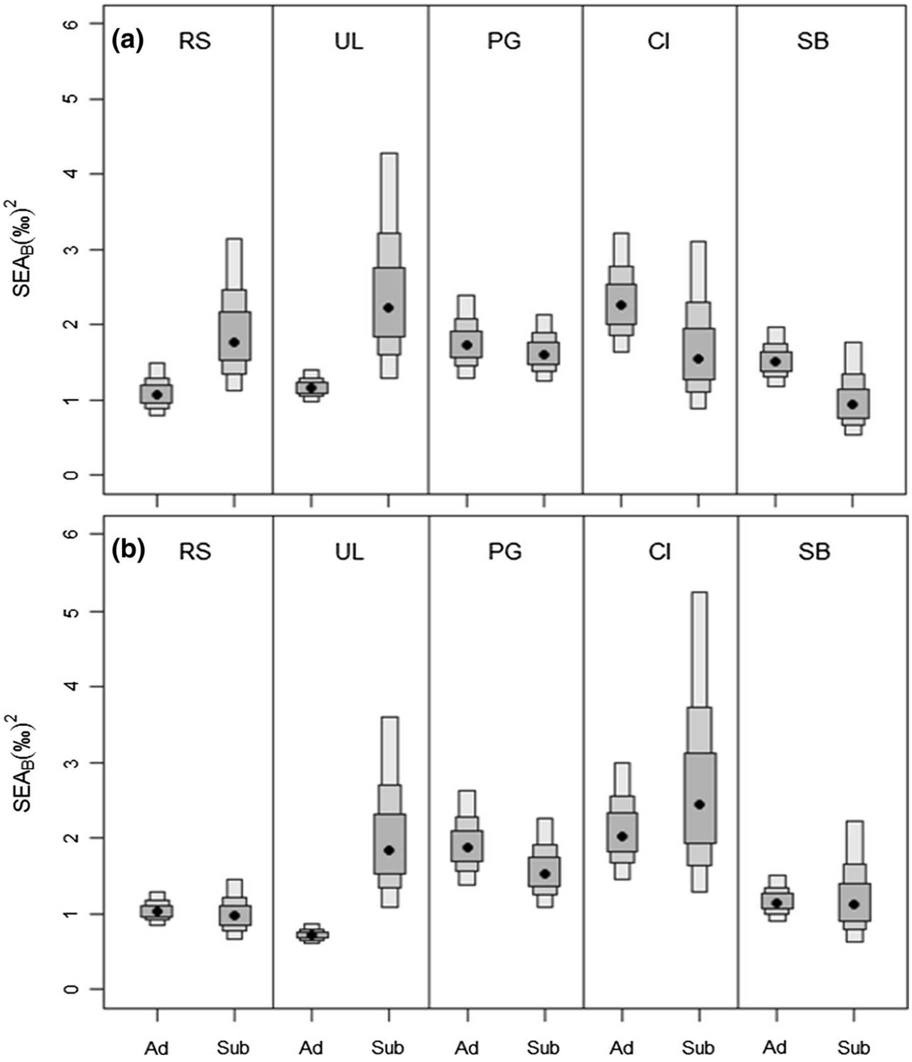


Fig. 3 Boxplots representing Bayesian mode estimates for isotopic niche sizes of adult and subadult liver (**a**) and muscle (**b**) in successive order from the High to the Low Arctic. *Boxes* indicate Bayesian credible intervals at 50 % (*dark gray*), 75 % (*medium gray*), and 95 % (*light gray*). Refer to Table 1 for sample sizes. Scale is the same for all plots. *CI* Chesterfield Inlet, *PG* Pangnirtung, *RS* Resolute, *SB* Saglek Bay, *UL* Ulukhaktok

in the High Arctic target particular resources such as Arctic cod (up to 70,000 tonnes of Arctic cod are consumed annually by ringed seals—more than any other animal—in the High Arctic; Welch et al. 1992), in contrast to subadults and adults at lower latitudes, where subarctic fish species have become prevalent.

Ringed seals in Ulukhaktok mainly fed on benthic fauna, such as shrimp, sculpin, and deeper-water Arctic cod, which undergo size-related segregation in habitat use (Benoit et al. 2010). The most pronounced ontogenetic niche shift (i.e., lowest amount of SEA_C overlap) occurred in Ulukhaktok ringed seals, potentially signifying different ecological roles for adults and subadults in this area. Adults consumed 95 % deeper-water prey and may be more specialized or reliant on resources in the benthic zone, whereas subadults acted more as habitat couplers (Rooney et al. 2006) between the pelagic and benthic energy pathways. Ringed seals have been reported to feed benthically in Alaska (Lowry et al. 1980), the Amundsen Gulf near Ulukhaktok (Brown et al. 2014a), and Svalbard (Weslawski et al. 1991), likely due to higher resource productivity in the benthic zone. Whitehouse et al. (2014) used mass-balance food web modeling in the Bering and Chukchi seas, and determined that the productivity and biomass of the benthic zone in the eastern Chukchi Sea, and likely Beaufort Sea near the Amundsen Gulf, were much higher than those of the pelagic zone.

In the Mid- and Low Arctic, adults consumed slightly more pelagic forage fish than subadults, underwent a moderate ontogenetic niche shift, and had a similar isotopic niche size to subadults. In Pangnirtung, both age classes mainly consumed Arctic cod and principally foraged in pelagic habitats, similar to the observations reported by Brown et al. (2014b), obtained using highly branched isoprenoid fatty acid analysis, and those of McMeans et al. (2013), obtained using SI analysis. In Chesterfield Inlet, sand lance was the most important prey item for both age classes, followed by Arctic cod and capelin, similar to reported stomach content

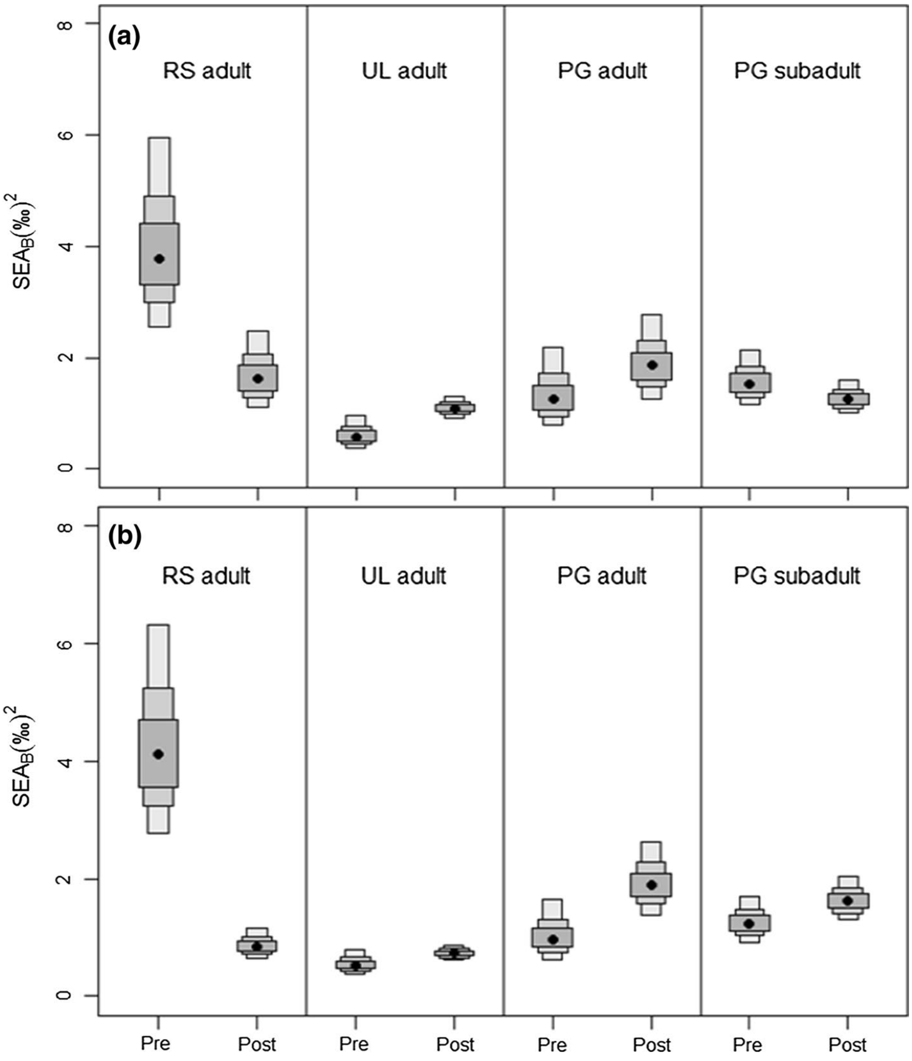


Fig. 4 Boxplots representing Bayesian mode estimates for adult and subadult isotopic niche size during two time periods (1990–1996 and 1999–2011) for liver (**a**) and muscle (**b**) in successive order from the High to the Low Arctic. *Pre* indicates the time period 1990–1996, whereas *Post* represents the time period 1999–2012. *Boxes* indicate Bayesian credible intervals at 50 % (*dark gray*), 75 % (*medium gray*), and 95 % (*light gray*). Refer to Table 1 for sample sizes. *PG* Pangnirtung, *RS* Resolute, *UL* Ulukhaktok

analyses (Chambellant et al. 2013). However, prey species contributions were similar in proportions for subadults, suggesting a more generalistic feeding strategy relative to adults. In southeastern Hudson Bay, adult and subadult ringed seals had different isotopic niche sizes (1.6 and 1.0 ‰^{2}, respectively), a high niche overlap (58 %), and primarily consumed pelagic forage fish, with amphipods being of secondary importance (Young and Ferguson 2014), comparable to our results from Chesterfield Inlet. In the Low Arctic, the δ^{15}N values for adult and subadult ringed seals and Arctic cod (Saglek Bay) were the lowest of all sampling locations despite similar δ^{15}N values for zooplankton, suggesting less complexity in the lower trophic levels. Saglek Bay adult and subadult ringed seals consumed higher proportions of zooplankton compared to all other locations, thus both age classes may forage more opportunistically and exhibit a higher degree of trophic omnivory, causing a lower TP (3.7 and 3.3). However, the low δ^{15}N values for Arctic cod in Saglek Bay may be a result of an ontogenetic niche shift in this species, where smaller age classes have been reported to consume lower-trophic-level prey, causing a lower TP (Matley et al. 2013).

Trophic position (TP) estimates from δ^{15}N values for the ringed seal varied widely (3.3–4.7) across the Canadian Arctic, with a general trend of higher TPs at the northernmost locations. The TPs of forage fish (e.g., Arctic cod and capelin) from Pangnirtung, Chesterfield Inlet, and Saglek Bay were near 3.0, but those TPs were highest in the High Arctic (3.6 in Ulukhaktok and Resolute). Thus, the change in the TP of ringed seals was likely driven by the trophic complexity of its common prey items in the lower part of the food web rather than its feeding ecology. Both adults and subadults at the highest latitude (Resolute) occupied the highest TPs and TPs of 1.1 and 1.0 higher than Arctic Cod, suggesting a reliance on this trophic guild (Vander Zanden and Rasmussen 1996) and a lower degree of trophic omnivory. A similar result occurred in Hobson et al. (2002), where ringed seals inhabiting the nearby North

Water Polynya were estimated at TP 4.6 and predominately consumed Arctic cod. In contrast, both adults and subadults in the Low Arctic (Saglek Bay) had the highest degree of trophic omnivory and occupied the lowest TPs of any location, which may be an artefact of the lower complexity in the zooplankton community (Post 2002b). The degree of complexity in the zooplankton community structure of the High Arctic may be higher due to increased cannibalism and reciprocal predation causing increased omnivory (Sprules and Bowerman 1988). These factors in the zooplankton community have been shown to increase the trophic position of top predators and food chain length in freshwater communities (Hairston and Hairston 1993; Vander Zanden et al. 1999; Post et al. 2000).

The largest differences in TP between age classes occurred in Ulukhaktok, Pangnirtung, and Saglek Bay, with subadults at the same trophic position as sculpin and adults nearly half a trophic level higher, suggesting an ontogenetic effect on ringed seal diet and use of habitat in these areas. For example, adults primarily utilized the benthic environment in Ulukhaktok and mainly consumed pelagic forage fish in Pangnirtung and Saglek Bay. As a result, functional differences between ringed seal age classes may exist in these areas, and changes in their respective population structures can then lead to congruent changes in community interactions and structure, which requires further investigation.

Our results from the High Arctic, similar to those of Hobson et al. (2002), indicate a longer food chain with ringed seals near trophic level 5. Assuming that top predators are more vulnerable to ecosystem change than lower-trophic-level species, our results suggest that High-Arctic ringed seals may be at greater risk than lower-Arctic populations from current and impending ecosystem perturbations, particularly in terms of the effects of climate change, invasive species, and overexploitation of resources (i.e., overfishing). With the High Arctic having a longer food chain, the predator–prey mass ratios and energy transfer efficiencies to the apex of the trophic pyramid (Trebilco et al. 2013) likely differ between the High and Low Arctic. The size-based energy flow at higher trophic levels in a trophic pyramid will be more constrained and more sensitive to biomass changes at lower trophic levels caused by ecosystem perturbations in the High Arctic. This phenomenon likely has implications for overall Arctic ecosystem conservation and management.

Temporal variation

There was no significant change in δ^{13}C values for ringed seals between 1990 and 2011 for much of the Arctic, despite a rapid rate of sea ice decline. A significant increase in δ^{15}N values occurred between both collection periods ($\leq$1996 and $\geq$1999) and was most pronounced in Resolute, suggesting that both age classes may currently be feeding at a slightly higher trophic position, or this may be an artefact of a baseline increase in δ^{15}N. However, Hobson and Welch (1992) reported similar δ^{15}N (17.3 ‰) but different δ^{13}C (−17.3 ‰) values for ringed seals collected in Lancaster Sound from 1988 to 1990. Moreover, the δ^{15}N values for Arctic cod were higher in 1988–1990 (15.2 ‰; Hobson and Welch 1992) than those for the Arctic cod samples we collected in 2012 (14.6 ‰). As a result, the significant changes in High-Arctic ringed seal and Arctic cod stable isotope values over time is most likely a result of interannual variation in sea ice dynamics influencing resource availability for near-top predators (Roth 2002), but it may also be related to shifts in diet or analytical variability in stable isotope values between studies. Chambellant et al. (2013) reported that the proportion of sand lance in the Hudson Bay ringed seal diet was lowest in 1992, when the September sea ice extent (7.5 Mkm^2) was the highest among all years (3.6–7.5 Mkm^2). Using stomach content analysis, Quakenbush et al. (2010) reported a significant increase in fish consumption from 1960 to 2009 for ringed seals in the Bering and Chukchi seas. In our study, the isotopic niche size of subadult ringed seals from Resolute decreased over time. With Arctic cod now being prevalent in the diet of ringed seals in the High Arctic, this suggests that ringed seals principally feed on more forage fish in years with relatively small sea ice extents.

The isotopic niche size of adults from Ulukhaktok and Pangnirtung has increased over time, which is most likely attributable to a recent increase in subarctic forage fish abundance across the Arctic, with increased prevalence of capelin and sand lance in (1) Ulukhaktok within the Amundsen Gulf, (2) Pangnirtung within Cumberland Sound, and (3) Hudson Bay over the last two decades (Gaston et al. 2003; Marcoux et al. 2012; Harwood et al. 2015). However, the change in adult isotopic niche size over time could also be attributed to potential changes in baseline δ^{13}C and δ^{15}N values. Capelin is a subarctic species that can spawn in a wide range of sea temperatures and has been labeled a “canary” for marine ecosystem changes at higher latitudes (Rose 2005). In the Amundsen Gulf, Arctic cod abundance has been decreasing over time, causing Arctic charr (*Salvelinus alpinus*) to shift theirdiet to capelin and sand lance, beluga whales to shift their diet to other forage fish, and black guillemots (*Cepphus grylle*) to consume more sculpin (Harwood et al. 2015). The recent high abundance of capelin near Pangnirtung has caused a dietary shift from Greenland halibut (*Reinhardtius hippoglossoides*) and Arctic cod to capelin in beluga (Marcoux et al. 2012) and from zooplankton to capelin in Arctic charr (Ulrich 2013) over the last decade. In addition, Chambellant et al. (2013) found that the importance of Arctic cod to ringed seal diet declined after 2000 in western Hudson Bay, while capelin and sand lance became more prevalent thereafter. Similarly, several sea bird populations in Hudson Bay have switched from an Arctic-cod-dominated diet to capelin since the late 1990s (Gaston et al. 2003; Provencher et al. 2012). Overall, ringed seals, as a species, employ dietary plasticity to changing resource availability and environmental conditions.

Summary

Ringed seals underwent an ontogenetic niche shift, with adults generally having a smaller isotopic niche size than subadults due to higher adult consumption of forage fish, likely due to foraging experience. Our findings varied spatially, with the likelihood of fish consumption in adults and probability of zooplankton consumption in subadults both decreasing with latitude. Also, isotopic niche size for adults was smaller than that for subadults in the High Arctic, but was similar for both age classes in the Mid- and Low Arctic. A general trend of lower ringed seal TPs occurring at lower latitudes, likely due to reduced trophic complexity in the zooplankton community. Given the interannual variation in ringed seal diet and an increased adult isotopic niche size over time, ringed seals exhibit dietary plasticity, suggesting adaptability in terms of their diet to climate change. However, long-term monitoring of ringed biological parameters (such as body condition indices) which have declined over time in some areas of the Arctic (Harwood et al. 2015) is required in order to gain more insight into Arctic ecosystem dynamics in our rapidly changing climate.

Acknowledgments We thank the Hunters and Trappers Associations and Organizations around the Canadian Arctic and their hunters for collecting seal samples. In addition, we thank B. Dunn, L. Harwood, H. Cleator, S. Atchison, and A. Gaden for sample collection and preparation. We thank B. Charron, J. Laramie, S. Isaac, A. Tanner, and especially A. Hussey for stable isotope analysis in the Chemical Tracers Lab at the Great Lakes Institute for Environmental Research at the University of Windsor. We thank Helene Marsh, Sam Rossman and an anonymous reviewer for comments that considerably improved this manuscript. This study was supported by funding from NSERC-Ocean Tracking Network, NSERC-Discovery, Fisheries and Oceans Canada, Government of Nunavut, and ArcticNet to ATF and SHF, as well as The Northern Contaminants Program of Aboriginal Affairs and Northern Development Canada to DCGM and TMB, and University of Windsor, Ontario Graduate Scholarships, and The W. Garfield Weston Foundation to DJY.

Author contribution statement DY, SF, and AF conceived and designed the study. DY and CS performed the statistical analysis. DY, SF, AF, TB, and DM were involved in sample collection. DY wrote the manuscript, with SF, CS, TB, DM, and AF contributing editorial advice.

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