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Temporal variation in western Hudson Bay ringed seal *Phoca hispida* diet in relation to environment

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ABSTRACT: We present the first study of ringed seal *Phoca hispida* feeding habits in western Hudson Bay (WHB) using stomach content analysis and stable isotope analysis (SIA). Ringed seals were sampled during 9 Inuit subsistence harvests in Arviat, Nunavut, Canada, over the period 1991 to 2006. During the open-water season in summer and fall, ringed seals fed mostly on sand lance *Ammodytes* spp. In the spring, when annual sea ice was still present, Arctic cod *Boreogadus saida* and capelin *Mallotus villosus* were also important in the diet, and consumption of invertebrates was higher than in the open-water period. From SIA, adult ringed seals exploited slightly more benthic habitats than immature individuals. Sand lances were the main prey consumed throughout the study period, but strong interannual variation occurred. When break-up of the sea ice in spring was relatively late, as in the early 1990s, ringed seal consumption of sand lance and total energy input was lower than in subsequent years of the study, despite a higher importance of sculpins (Cottidae) in the diet. The consumption of other fish species changed in the 2000s: Arctic cod declined whereas capelin increased in importance. Our results suggest that ringed seals in WHB are sand lance specialists, and their population dynamics are, at times, strongly regulated by bottom-up processes.

KEY WORDS: Bottom-up regulation · Feeding habit · Stable isotope · Stomach content · Index of global importance · *Ammodytes* spp.

INTRODUCTION

Over the last 40 yr, Hudson Bay (HB), a large Canadian inland sea, ice-covered from November to June (Saucier et al. 2004), has experienced major climatic changes that reflect the warming that is occurring globally (IPCC 2007). Break-up of the sea ice in spring in western Hudson Bay (WHB) is now occurring earlier than it did in the 1970s, at a rate of about 7 to 10 d decade^{-1} (Gagnon & Gough 2005, Stirling & Parkinson 2006). Together with a delayed freeze-up in the fall, the earlier ice break-up resulted in an increase in the length of the open-water season (Gagnon & Gough 2005). A reduction of sea ice extent and snow depth, likely a result of increasing air and water temperatures, has also been reported in HB (Ferguson et al. 2005, Gagnon & Gough 2005, Stirling & Parkinson 2006, Parkinson & Cavalieri 2008, Galbraith & Larouche 2011).

These changes to the atmosphere–ice–ocean coupling are predicted to influence oceanic primary productivity with subsequent cascading effects through the marine food web. As well as possible shifts in prey distribution and availability, loss of sea ice habitat will likely result in changes in distribution, reproduction, and ultimately survival and abundance of

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Arctic species dependent on sea ice (Tynan & DeMaster 1997, Laidre et al. 2008). Evidence of such changes has been reported in HB for ice-associated species, such as thick-billed murres *Uria lomvia* (Gaston et al. 2005) and polar bears *Ursus maritimus* (Stirling et al. 1999, Regehr et al. 2007, Stirling & Derocher 2012).

The ringed seal *Phoca hispida*, one of the smallest phocids (McLaren 1993), is distributed throughout the ice-covered waters of the circumpolar Arctic and is the most abundant pinniped species of the northern polar regions (Frost & Lowry 1981). Sexually mature ringed seals depend on stable ice with sufficient snow cover for females to build subnivean birth lairs that are critical to protect newborn pups from the cold and predators such as polar bears, Arctic foxes *Vulpes lagopus*, and humans (McLaren 1958, Smith & Stirling 1975, Smith et al. 1991, Furgal et al. 1996). Following reproduction and moulting in spring, when minimal feeding occurs, ringed seals feed intensively during the open-water season in late summer and fall to replenish their fat reserves, as reflected by a clear pattern of seasonal variation in the thickness of subcutaneous fat depositions (McLaren 1958, Breton-Provencher 1979, Ryg et al. 1990). Ringed seals consume a large variety of prey species across their range, but only a few prey taxa (2 to 4) generally dominate the diet in a specific location (McLaren 1958, Weslawski et al. 1994, Siegstad et al. 1998). Arctic cod *Boreogadus saida* and invertebrates such as mysids (Mysidae), hyperiid amphipods (Amphipoda), and euphausiids (Euphausiacea) are consistent prey of ringed seals, but diet composition varies with geographical location, season, life stage, and/or sex (Bradstreet & Finley 1983, Smith 1987, Siegstad et al. 1998, Holst et al. 2001, Labansen et al. 2007).

Considering their position near the top of the Arctic food web and their high degree of adaptation to exploit sea ice habitat for reproduction and survival, ringed seals should be good indicators of ecosystem changes (e.g. Harwood et al. 2012). In HB, where ringed seals occur near the southern limit of their distribution (Frost & Lowry 1981), changes in population dynamics because of climate warming will likely occur prior to changes at higher latitudes. Because marked changes in the patterns of sea ice duration and, conversely, of open water have already been documented in HB, this is an appropriate ecosystem in which to test hypotheses related to shifts in ringed seal diet, energy budget, body condition, reproduction, and survival. Low reproductive rates and pup survival have been reported in the 1990s in WHB, and nutritional stress, through decreased marine productivity, was proposed as a possible explanation (Chambellant et al. 2012a). However, ringed seal diet preferences and variation have not been adequately studied anywhere in HB (McLaren 1958, Breton-Provencher 1979, Stirling 2005, Chambellant 2010), preventing the assessment of the proposed nutritional stress hypothesis.

Traditionally, diet studies of pinnipeds have primarily depended on recovery of soft and hard parts in gastrointestinal tracts or faeces, providing both qualitative and quantitative information on prey consumed. However, there are also several limitations associated with this technique which may bias diet determination. Differential digestion rates of large and small, hard and soft prey and rapid transit rate are examples of such limitations (Murie & Lavigne 1986, Tollit et al. 1997, Bowen 2000, Hammill et al. 2005). Furthermore, stomach contents can only provide information on prey ingested shortly before collection and thus may not reflect the diet over time and space. Consequently, indirect methods have recently been developed to provide insight on marine predator diets, including analyses of stable isotope (SI) ratios (Hobson et al. 1996, Lawson & Hobson 2000) and fatty acids in their tissues (Iverson et al. 2004, Thiemann et al. 2008).

Stable isotope analysis (SIA) is based on the natural occurrence of different isotopes of the same element and their differential fractionation during biological processes. In marine food web studies, nitrogen (N) SI ratio ($^{15}N/^{14}N$, labelled $\delta^{15}N$) indicates the relative trophic level of an organism and trophic relationships between organisms in an ecosystem, while carbon (C) SI ratio ($^{13}C/^{12}C$, labelled $\delta^{13}C$) reflects feeding habitat (e.g. benthic vs. pelagic, freshwater vs. marine, inshore vs. offshore) and general geographic locations (water masses of different isotopic signatures; see reviews by Kelly 2000 and Newsome et al. 2010). Due to the specific protein turnover rate of each tissue, the isotopic signature of a specific tissue provides information on prey assimilated over a specific timescale (Kurle & Worthy 2002). Tissues with a high turnover rate (liver, kidney, serum) represent food ingested days or weeks before collection, tissues with a lower turnover rate (muscle, red blood cells) represent food ingested months before, and inert tissues (whisker, fur, tooth) represent the SI signature of prey consumed as they were forming over months or an entire lifetime. Although models have been developed to estimate the contribution of different *a priori* potential prey species to predator diet using C and

N SI ratios (Phillips & Gregg 2003, Moore & Semmens 2008), several limitations (e.g. prey need to have distinct isotopic signatures) hinder the assessment of species composition in the diet using SIA, especially for diversified diets. Using SIA is thus a complementary method to more traditional hard-part reconstruction techniques, and this combination has been successively used to explore pinniped feeding habits (e.g. Dehn et al. 2007).

In this study, we examined the diet of ringed seals in WHB over 9 sampling years between 1991 and 2006, using both stomach contents and C and N SI ratios in muscle tissue. Our objectives were to (1) quantify a baseline for ringed seal diet against which comparisons could be made in future studies, (2) evaluate age-related variability, and (3) assess and interpret the interannual variability of ringed seal diet over time in relation to changes in the sea ice regime.

MATERIALS AND METHODS

Sample collection

Ringed seals were sampled in 1991, 1992, and 1998 to 2000 by the Canadian Wildlife Service and in 2003 to 2006 by Fisheries and Oceans Canada (DFO), Winnipeg, in the HB community of Arviat, Nunavut (NU), Canada (Fig. 1), from the Inuit subsistence fall harvest (September through November), when ringed seals feed in open water. In 1991, 1992, 2004, and 2005, samples were also collected from the spring harvest, when ringed seals haul out on the ice to moult. After collection, stomachs, muscle tissue, and mandibles were labelled, put in individual bags, and kept frozen at −20°C. Muscle tissues were not collected from 1998 to 2000 in the fall and only in 2004 and 2005 in the spring.

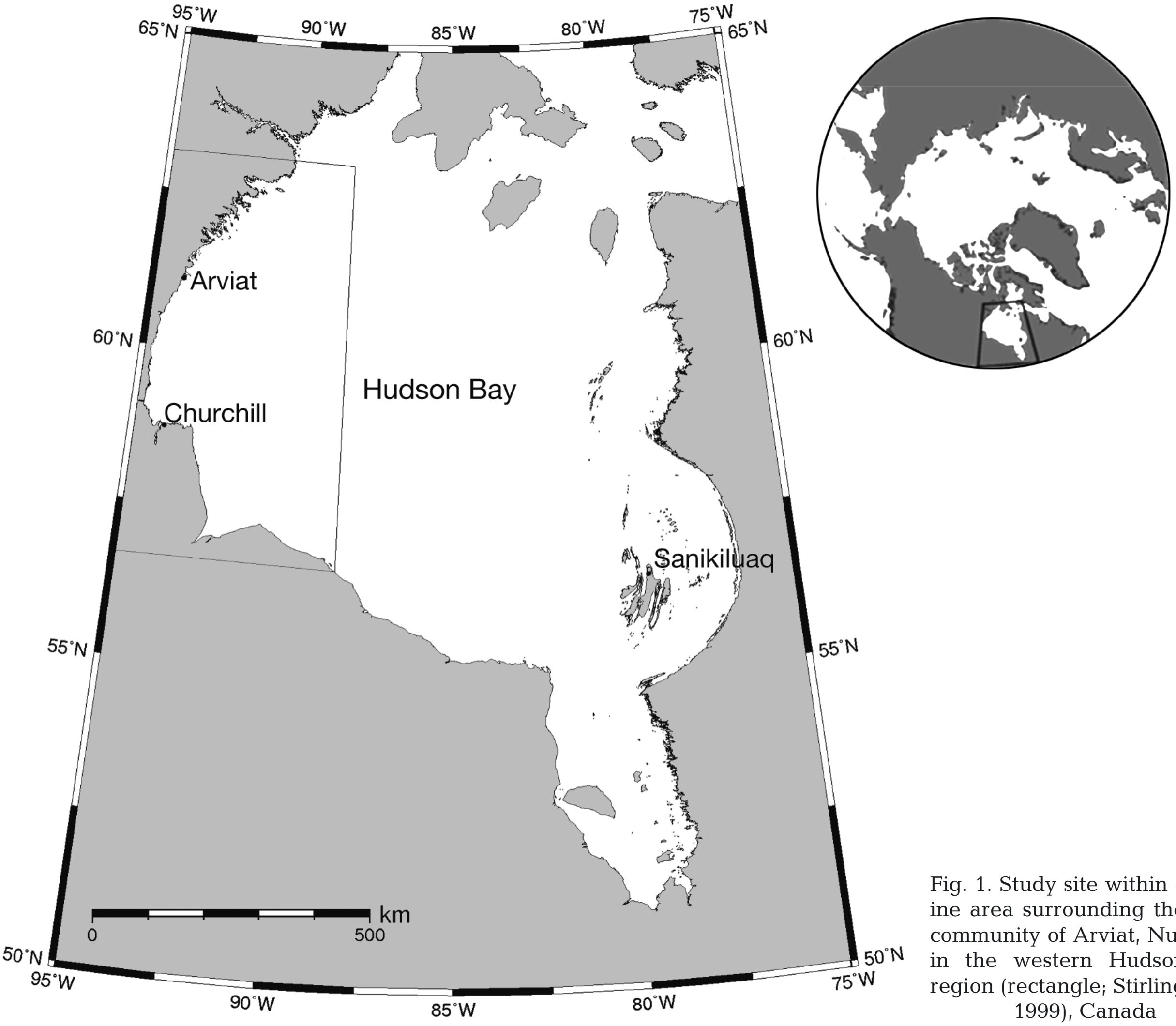

Fig. 1. Study site within a marine area surrounding the Inuit community of Arviat, Nunavut, in the western Hudson Bay region (rectangle; Stirling et al. 1999), Canada

Fish and invertebrate species potentially consumed by ringed seals were collected from 2004 to 2007 at different locations in HB, including Coats Island (see Elliott & Gaston 2008), sample sites from the ArcticNet Leg 2 cruise transect (see Pazerniuk 2007), and opportunistic collections from Arviat, NU; Churchill, Manitoba; and Sanikiluaq, NU. Some fresh items were also recovered from seal stomachs.

Laboratory analysis

Age determination

Ringed seal ages were determined following methods described in Chambellant et al. (2012a).

Ringed seals were grouped according to 3 age classes. Seals born in spring and harvested the same year were referred to as pups, seals 1 to 5 yr of age were considered juveniles, and seals 6 yr of age and older were categorized as adults (Holst et al. 1999).

Analysis of stomach contents

Thawed stomachs were weighed to the nearest 0.1 g using an A&D electronic balance. Each stomach was emptied into a glass tray, and wet weight content was recorded. Large or whole food items were removed; identified to species; weighed to the nearest 0.1 g; and measured, when possible, to the nearest 1 mm (total/fork length for fish and carapace length for crustaceans). Remaining content was washed through graduated, nested sieves of 4.75, 2, and 1 mm. Sagittal otoliths and invertebrate remains, including carapaces, claws, and eyes of crustaceans, were sorted, counted, and identified to the lowest taxonomic level possible using DFO reference collections and published guides (e.g. Campana 2004). Otoliths too eroded for a positive identification were classified as unidentified fish and not measured. Paired otoliths retrieved from fish skulls were kept separately. If possible, otoliths were paired, and the largest one was measured to the nearest 0.01 mm using a Mitutoyo digimatic calliper (>5 mm) or image analysis software (<5 mm; ImagePro© Plus v. 6.0, Media Cybernetics, www.mediacy.com/). When the number of otoliths was >30, a random sample of 30 otoliths was measured, and mean otolith length was assumed for remaining unmeasured otoliths. For otoliths too eroded to be measured but identifiable, we used mean otolith length of the particular prey in the same stomach, or in the same year if no other specimen of the same prey was present in that stomach. If otoliths retrieved from skulls were present, only these measurements were used to determine mean otolith length.

The minimum number of individuals present in a given stomach was determined by adding the number of whole individuals; the number of unique structures (e.g. shrimp telson); the number of otolith pairs; and, when paired structures could not be identified as a pair (e.g. eyes, loose otoliths), the number of such structures divided by 2. When only bones were present, a single individual was recorded.

Body length (fork or total length depending on species) (cm) and wet mass (g) of fish were estimated from regressions, with otolith measurements (mm) taken from published and unpublished data (see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m481p269_supp.pdf). Invertebrates were weighed either individually for large invertebrates (e.g. shrimps) or in bulk for smaller animals (e.g. amphipods). For invertebrates with no measured weight, we took the mean weight of all specimens of that species found in the stomach or in the stomachs for the year or over all years, depending on available sample sizes. We used wet mass of prey to estimate total biomass of prey ingested for each stomach. Total energy consumed by individual seals was estimated by summing the products of total biomass of each prey species by its energy density (kJ g^{-1} wet mass) taken from literature and unpublished data (see Table S2 in the Supplement).

Data analyses

In the spring, adults comprised 83% (15/18) of the sample of ringed seals with identifiable prey items in their stomachs, so only adult diet was considered for this period and no age-class comparison was performed.

Prey grouping was implemented so that each group was present in at least 10 stomachs when all years were pooled.

Diet composition and importance of prey taxa were assessed using (1) percentage abundance of prey ($\%P$ = [minimum number of prey i / total number of prey]*100), (2) percentage of occurrence ($\%O$ = [number of stomachs with prey i / total number of stomachs]*100), (3) percentage biomass contribution ($\%B$ = [wet mass of prey i / total wet mass]*100), (4) percentage energy contribution ($\%E$ = [energy from prey i / total energy from prey]*100), and (5) index of global importance (*IG*; Moreno & Castro 1995) defined as:

$$IG = \frac{(IN + IW)}{2} \quad (1)$$

with *IN* and *IW*, indices of importance by number and by wet mass, respectively, computed as:

$$IN = (\%P * \%O)^{1/2} \quad (2)$$

$$IW = (\%B * \%O)^{1/2} \quad (3)$$

Use of multiple measures to describe ringed seal diet provides information on different aspects of its feeding habits (Cortes 1997), but each has limitations (e.g. %*P* over-emphasizes the contribution of small prey eaten in large numbers, and %*B* over-emphasizes the contribution of single heavy prey to the diet; Hyslop 1980, Joy et al. 2006, Tollit et al. 2007). *IG* was computed to integrate the different information into one single measure and, by averaging *IN* and *IW*, to mitigate their limitations (Moreno & Castro 1995).

Variation in diet composition between age classes and years was assessed using the Bray-Curtis similarity index (*S*) on *IG*. *S* varies from 0 to 1, with $S = 1$ indicating a total similarity in prey consumed. A nonmetric multidimensional scaling was produced based on *S* to visualize the multivariate data, and $S \geq 0.8$ was set to indicate similarity between 2 groups (i.e. age class or year).

Simpson's diversity index (*D'*), the probability that 2 randomly selected prey items are from different species, was computed as:

$$D' = 1 - D \quad (4)$$

with *D*, the index of dominance, being:

$$D = \sum_i \left(\frac{n_i}{n}\right)^2 \quad (5)$$

on the number of prey (*P*), using all prey taxa (Hammer et al. 2001, Magurran 2003).

Stable isotope analysis

Muscle tissue from ringed seals collected in the fall and muscle tissue from fish and whole invertebrates (head and telson were removed from shrimps; shell was removed from bivalves) were freeze dried and homogenized. Lipids were removed with chloroform:methanol (2:1 v/v) using a modified liquid-liquid Folch method (Folch et al. 1957).

C and N isotopic analyses on muscle samples were accomplished by continuous flow ion ratio mass spectrometry using a GV Instruments IsoPrime attached to a peripheral temperature-controlled EuroVector elemental analyzer (EA) (University of Winnipeg Isotope Laboratory). Samples (1 mg) were loaded into tin capsules and placed in the EA autosampler along with internally calibrated C/N standards (pharmaceutical and casein proteins: $\delta^{13}C = -22.95$ and -26.98‰ Vienna Pee Dee Belemnite [VPDB] and $\delta^{15}N = 5.00$ and 5.94‰ atmospheric nitrogen, respectively). C and N isotope results were expressed using standard delta (δ) notation in units of per mil (‰). Delta values of C ($\delta^{13}C$) and N ($\delta^{15}N$) represent deviations from a standard, such that:

$$\delta_{\text{sample}}\ (‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000 \quad (6)$$

where *R* is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in the sample and the standard. Standards used for C and N isotopic analyses were VPDB and International Atomic Energy Agency Standard N1, respectively. Accuracy was obtained through analysis of laboratory standards used for calibration of results. Analytical precision, determined from duplicate measurements of laboratory standards run at the same time as samples, was ±0.18‰ for $\delta^{13}C$ and ±0.19‰ for $\delta^{15}N$.

C SI ratios were corrected for (1) the oceanic Suess effect by adding 0.019‰ yr^{-1} (Quay et al. 2003) using year 1991 as our starting point, and (2) the presence of carbonates in invertebrates by adding −0.3‰ (Bunn et al. 1995).

C and N SI ratios in ringed seal muscle tissue integrated prey ingested months before the fall harvest, most likely over the summer months (Tieszen et al. 1983, Kurle & Worthy 2002).

Time of spring break-up

Annual break-up dates in WHB were calculated for the period 1991 to 2006 following the method described in Gagnon & Gough (2005). The WHB region (as defined in Stirling et al. 1999; Fig. 1) was divided into a grid of 0.5° latitude × 1.5° longitude. Weekly ice-concentration maps of HB were retrieved from the Canadian Ice Service (http://ice-glaces.ec.gc.ca/), and ice concentration at 42 points defined by the grid was determined. Break-up date (±1 wk) at each center point was defined as the earliest date with an ice concentration of 50% or less that was maintained for at least 2 wk. Annual break-up dates for the entire WHB region were calculated by taking the median of the 42 values from the grid. Average date of break-up over the period 1990 to 2007 was also calculated.

Statistical analyses

Normality was assessed using the Anderson-Darling test (Stephens 1974).

Frequency of empty stomachs was compared between age class and years using a *G*-test of independence with Williams' correction (Sokal & Rohlf 1995).

Means or medians were compared using a *t*-test with Welch's correction to account for different standard deviations (Zar 1996) when necessary or a Mann-Whitney/Kruskal-Wallis test corrected for ties and large samples with Dunn's multiple comparisons test when normality of residuals was not reached.

Relationships between sand lance *Ammodytes* spp. *IG* and total *P* per stomach (P_{stom}), total biomass, and total energy were explored using sigmoid functions, whereas the Pearson product moment correlation (r_p) was used to describe relationships with the diversity index, the percentage of empty stomachs, and the timing of spring sea ice break-up.

An analysis of similarity (ANOSIM) was performed on the Bray-Curtis similarity matrix on *IG* to test for difference between age classes and years. Difference of *D'* between years and age classes was assessed pairwise by bootstrapping 1000 times with replacement to determine the probability that the difference observed could have occurred by random sampling (Hammer et al. 2001).

Graphs and statistical analyses were performed using Systat 12 (Systat Software) and SigmaPlot 11 (Systat Software). The free statistics package PAST 1.97 (Hammer et al. 2001) was used to perform similarity and diversity analyses. Unless otherwise stated, results are presented as mean ± SD or median (first to third percentiles). Differences were considered significant at $p < 0.05$.

RESULTS

A total of 889 ringed seal stomachs were processed over the 9 yr of the study; most were collected during the fall open-water period (Table 1). Similar to previous findings on ringed seals throughout the Arctic

Table 1. *Phoca hispida*. Characteristics of the spring (May to June) and fall (September to November) ringed seal collection over 1991 to 2006 in Arviat, Nunavut, Canada, and percentage of occurrence (O) of stomachs without prey. n is the total number of stomachs collected. Age classes defined as follows (Holst et al. 1999): adult, ≥6 yr; juvenile, 1 to 5 yr; pup, <1 yr. **Bold** values are for all age classes pooled

Year	Fall				Spring			
Age class	n	Age class (%)	Sex ratio (M:F)	O stomachs without prey (%)	n	Age class (%)	Sex ratio (M:F)	O stomachs without prey (%)
1991	**41**		**0.86**	**75.6**	**81**		**1.19**	**88.9**
Adult	20	48.8		75	74	91.4		90.5
Juvenile	19	46.3		79	6	7.4		83.3
Pup	2	4.9		50	1	1.2		0
1992	**70**		**0.79**	**84.3**	**73**		**1.35**	**90.4**
Adult	39	55.7		87.2	56	76.7		89.3
Juvenile	28	40		78.6	10	13.7		100
Pup	3	4.3		100	7	9.6		85.7
1998	**91**		**1.28**	**48.4**				
Adult	58	73.4		44.8				
Juvenile	15	19		53.3				
Pup	6	7.6		66.7				
1999	**97**		**1.69**	**61.9**				
Adult	77	79.4		61				
Juvenile	15	15.5		60				
Pup	5	5.1		80				
2000	**97**		**1.77**	**52.6**				
Adult	54	56.8		50				
Juvenile	20	21.1		45				
Pup	21	22.1		61.9				
2003	**84**		**0.95**	**60.7**				
Adult	41	51.9		73.2				
Juvenile	25	31.6		48				
Pup	13	16.5		53.8				
2004	**31**		**1.55**	**51.6**	**15**		**0.36**	**86.7**
Adult	5	16.1		40	13	86.6		84.6
Juvenile	19	61.3		57.9	1	6.7		100
Pup	7	22.6		42.9	1	6.7		100
2005	**91**		**1.07**	**49.5**	**70**		**1.5**	**90**
Adult	22	24.7		72.7	62	92.5		90.3
Juvenile	53	59.6		47.2	5	7.5		80
Pup	14	15.7		21.4	0	0		0
2006	**48**		**0.96**	**45.8**				
Adult	17	35.4		52.9				
Juvenile	21	43.8		38.1				
Pup	10	20.8		50				
All years	**650**		**1.2**	**58.3**	**239**		**1.23**	**89.5**
Adult	333	52.9		61.9	205	86.9		89.8
Juvenile	215	34.2		55.3	22	9.3		90.9
Pup	81	12.9		53.1	9	3.8		77.8

(e.g. McLaren 1958, Smith 1987, Ryg et al. 1990), the small sample size of seal stomachs containing prey items in the spring in our study prevented comparison with results from the fall.

Stomachs with no prey

Annual percentages of stomachs without prey (i.e. empty or only containing non-prey items) did not vary in the spring (G_{corr} = 0.28, df = 3, $p > 0.9$) but were significantly different in the fall (G_{corr} = 38.5, df = 8, $p < 0.001$), with the highest percentages in 1992 and 1991 and the lowest in 2006 (Table 1). Overall, fewer than half of the stomachs contained prey items in the fall, whereas in the spring, prey items were found in only about 10% of stomachs (Table 1). Percentage of stomachs without prey was not statistically different among age classes (spring: G_{corr} = 1.1, df = 2, $p > 0.5$; fall: G_{corr} = 3.0, df = 2, $p > 0.1$) despite interannual variation.

Diet composition

A total of 35 prey taxa and 9 groups in the fall (Table 2) and 13 prey taxa and 8 groups in the spring (Table 3) were found in ringed seal stomachs. Mean P taxa per stomach was 1.6 ± 1.0 (n = 232; max = 6) in the fall, with 61.2% of seals having only 1 prey taxon in their stomach, and 1.2 ± 0.4 (n = 15; max = 2) in the spring, with 80% (12/15) of seals having ingested only 1 prey taxon.

Ringed seals fed predominantly on fish, and sand lance were the most important prey species in both fall and spring, when they represented approximately 80 and 45%, respectively, of energy acquired (Tables 2 & 3).

During the fall, sculpins (Cottidea) were the second most important prey for ringed seals (*IG* = 10.7), although their contribution to the total energy content of the diet was slightly less than that of other Gadidae (6.7 and 10.4%, respectively; Table 2). In the spring, ringed seals fed secondarily on capelin *Mallotus villosus* (*IG* = 26.9), followed by other invertebrates (i.e. Decapoda and Mysidae; Table 3). Arctic cod was not a main part of the ringed seal diet, contributing less than 1 and 4% of the overall energy ingested in fall and spring, respectively (Tables 2 & 3). Hyperiid amphipods were a significant invertebrate prey for ringed seals in both seasons, but shrimps (Decapoda) were more important in the spring, when the consumption of invertebrates by ringed seals was more than twice as large as in the fall (*IG* = 12.9 and 5.4, respectively; Tables 2 & 3). Overall, only 15% of ringed seal stomachs contained invertebrates in the fall, whereas they were found in 40% of stomachs collected in the spring. The energy contribution of invertebrates was negligible in both seasons (Tables 2 & 3).

The Simpson's diversity index was $D' = 0.55$ in the spring and $D' = 0.20$ in the fall (Table 4).

Age-class variation in the fall diet

There was no difference in the diet of ringed seals of different age classes (ANOSIM: R = −0.0029 and p = 0.46). However, the P taxa in adult ringed seal stomachs was significantly lower than the number found in juveniles and pups ($n_{adult} = 1.4 \pm 0.9$, $n_{juvenile} = 1.8 \pm 1.1$, $n_{pup} = 2.0 \pm 1.3$; H_c = 14.0, df = 2, p = 0.0009). D' was significantly different between age classes when all years were pooled, with juveniles showing the most diverse diet (Table 4, p = 0.000 for all combinations).

Adult ringed seals had a significantly higher N SI signature (‰) than pups ($\delta^{15}N_{adult}$ = 15.6 [14.8 to 16.3], n = 64; $\delta^{15}N_{juvenile}$ = 15.4 [14.3 to 16.3], n = 86; and $\delta^{15}N_{pup}$ = 14.9 [14.1 to 15.6], n = 32; H_c = 6.7, df = 2, p = 0.04) and a higher C SI signature (‰) than juveniles and pups in their muscle tissue collected in the fall ($\delta^{13}C_{adult}$ = −19.3 [−19.8 to −19.0], n = 64; $\delta^{13}C_{juvenile}$ = −19.8 [−20.4 to −19.3], n = 86; and $\delta^{13}C_{pup}$ = −20.2 [−20.4 to −19.6], n = 32; H_c = 18.7, df = 2, p = 0.0001).

Interannual variation in the diet

Fall

The P taxa per stomach varied over the years (H_c = 27.8, df = 8, p = 0.0005), with a maximum of 2.7 ± 1.7 prey taxa per stomach in 2004 and a minimum of 1.2 ± 0.7 in 1992. The *S* matrix indicated that 1991 and 1992 were different from the other study years ($S < 0.80$), which was confirmed by an ANOSIM between groups 1991 to 1992 and 1998 to 2006 (R = 0.9, p = 0.03). Three other groups emerged from the similarity matrix: 1999, 2000/2006, and 1998/2003/2004/2005. Interannual variations in the different prey group *IG*s are presented in Fig. 2. Diets in 1991 and 1992 were characterized by their relatively low representation of sand lance (*IG* < 70) and relatively high representation of Arctic cod, other fish

Table 2. *Phoca hispida*. Overall number of identified prey (n prey), occurrence (n stomachs), percentage of occurrence (%*O*), percentage prey (%*P*), percentage biomass (%*B*; see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m481p269_supp.pdf), percentage energy (%*E*; see Table S2), and index of global importance (*IG*) of identified prey found in ringed seal stomachs (n = 232) collected in Arviat, Nunavut, Canada, during fall (September to November) 1991 to 2006. Taxa in **bold** indicate the 9 key groups used in the analyses

Prey taxon	n prey	n stomachs	%*O*	%*P*	%*B*	%*E*	*IG*
FISH							
Sand lance (Ammodytidae)							
***Ammodytes* spp.**[a]	**10307**	**203**	**87.5**	**88.0**	**79.6**	**81.2**	**85.6**
Cod (Gadidae)							
Arctic cod *Boreogadus saida*	**16**	**14**	**6.0**	**0.1**	**0.3**	**0.3**	**1.1**
Other Gadidae	**31**	**13**	**5.6**	**0.3**	**10.4**	**9.8**	**4.4**
Unidentified gadids	5	4	1.7	0.04	0.03	0.03	0.3
Atlantic cod *Gadus morhua*	1	1	0.4	0.01	1.2	1.0	0.4
Greenland cod *Gadus Ogac*	25	9	3.9	0.2	9.2	8.7	3.4
Smelts (Osmeridae)							
Capelin *Mallotus villosus*	**35**	**16**	**6.9**	**0.3**	**0.3**	**0.3**	**1.5**
Rainbow smelt *Osmerus mordax*	**188**	**12**	**5.2**	**1.6**	**2.2**	**1.8**	**3.1**
Sculpins (Cottidae)	**378**	**55**	**23.7**	**3.2**	**6.7**	**6.1**	**10.7**
Artediellus sp.	3	2	0.9	0.03	<0.01	<0.01	0.1
Arctic staghorn sculpin *Gymnocanthus tricuspis*	42	10	4.3	0.4	2.1	1.9	2.1
Moustache sculpin *Triglops murrayi*	27	6	2.6	0.2	0.7	0.6	1.04
Arctic sculpin *Myoxocephalus scorpioides*	5	4	1.7	0.04	0.1	0.1	0.3
Shorthorn sculpin *Myoxocephalus scorpius*	104	20	8.6	0.9	1.3	1.2	3.1
Myoxocephalus sp.	8	1	0.4	0.1	0.2	0.2	0.2
Unidentified sculpins	189	35	15.1	1.6	2.4	2.2	5.5
Other Fish	**94**	**24**	**10.3**	**0.8**	**0.4**	**0.4**	**2.5**
Herrings (Clupeidae)							
Atlantic herring *Clupea harengus*	3	1	0.4	0.03	0.1	0.1	0.1
Snailfish (Liparidae)							
Liparis sp.	10	6	2.6	0.1	0.02	0.01	0.4
Sticklebacks (Gasterosteidae)							
Ninespine stickleback *Pungitius pungitius*	60	9	3.9	0.5	0.04	0.1	0.9
Shannies (Stichaeidae)	21	9	3.9	0.2	0.3	0.3	1.0
Fourline snakeblenny *Eumesogrammus praecisus*	4	3	1.3	0.03	0.1	0.04	0.2
Daubed shanny *Leptoclinus maculatus*	4	4	1.7	0.03	0.02	0.02	0.2
Slender eelblenny *Lumpenus fabricii*	8	1	0.4	0.1	0.1	0.1	0.2
Snakeblenny *Lumpenus lampretaeformis*	5	1	0.4	0.04	0.1	0.1	0.2
INVERTEBRATES							
Amphipoda	**471**	**24**	**10.3**	**4.0**	**0.1**	**0.1**	**3.7**
Dexaminidae							
Atylus carinatus	3	1	0.4	0.03	<0.01	<0.01	0.1
Uristidae							
Onisimus litoralis	30	3	1.3	0.26	<0.01	<0.01	0.3
Gammaridae							
Unidentified gammarids	14	6	2.6	0.1	<0.01	<0.01	0.3
Hyperiidae	424	15	6.5	3.6	0.1	0.1	2.8
Unidentified hyperiids	197	14	6.0	1.7	0.02	0.02	1.8
Themisto libellula	227	1	0.4	1.9	0.1	0.1	0.5
Other Invertebrates	**194**	**17**	**7.3**	**1.7**	**0.02**	**0.01**	**1.9**
Decapoda	12	5	2.2	0.1	0.01	<0.01	0.3
Unidentified shrimps	2	2	0.9	0.02	<0.01	<0.01	0.1
Dendrobranchiata	10	3	13	0.1	<0.01	<0.01	0.2
Mysidae	175	8	3.5	1.5	<0.01	<0.01	1.2
Unidentified mysids	167	7	3.0	1.4	<0.01	<0.01	1.1
Mysis litoralis	8	1	0.4	0.1	<0.01	<0.01	0.1
Copepoda	1	1	0.4	<0.01			
Echinoidea	1	1	0.4	<0.01			
Mollusca							
Unidentified Mollusca	1	1	0.4	<0.01			
Bivalvia	3	2	0.9	0.03	<0.01	<0.01	0.1
Polychaeta	1	1	0.4	<0.01			

Table 2 (continued)

Prey taxon	n prey	n stomachs	%*O*	%*P*	%*B*	%*E*	*IG*
Fish total	11049	221	95.3	94.3	99.9	99.9	96.2
Invertebrates total	665	36	15.5	5.7	0.1	0.1	5.4
Other[b]		6	4	1.5	0.1		
Unidentified fish	290	56	21.1	2.4			
Unidentified invertebrates	37	9	3.4	0.3			
Grand total	12047	265					

[a] *Ammodytes dubius* and *Ammodytes hexapterus* are found in Hudson Bay (Coad & Reist 2004)
[b] Includes fish eggs, stomach of a fish, and an unknown prey item

Table 3. *Phoca hispida.* Overall number of identified prey (n prey), occurrence (n stomachs), percentage of occurrence (%*O*), percentage prey (%*P*), percentage biomass (%*B*; see Tables S1 & S2 in the Supplement), percentage energy (%*E*; see Table S2 in the Supplement), and index of global importance (*IG*) of identified prey found in adult ringed seal stomachs (n = 15) collected in Arviat, Nunavut, Canada, during spring (May to June) 1991, 1992, 2004, and 2005. Taxa in **bold** indicate the 8 groups used in the analyses

Prey taxon	n prey	n stomachs	%*O*	%*P*	%*B*	%*E*	*IG*
FISH							
Sand lances (Ammodytidae)							
***Ammodytes* spp.**[a]	**178**	**4**	**26.7**	**61.4**	**43.2**	**44.6**	**37.2**
Cod (Gadidae)							
Arctic cod *Boreogadus saida*	**5**	**1**	**6.7**	**1.7**	**4.1**	**4.0**	**4.3**
Unidentified gadids[b]	**2**	**1**	**6.7**	**0.7**	**20.8**	**20.0**	**7.0**
Smelts (Osmeridae)							
Capelin *Mallotus villosus*	**77**	**4**	**26.7**	**26.6**	**27.7**	**27.7**	**26.9**
Sculpins (Cottidae)							
Arctic staghorn sculpin *Gymnocanthus tricuspis*	**2**	**1**	**6.7**	**0.7**	**2.9**	**2.6**	**3.3**
Sticklebacks (Gasterosteidae)							
Ninespine stickleback *Pungitius pungitius*	**1**	**1**	**6.7**	**0.3**	**0.02**	**0.03**	**0.9**
INVERTEBRATES							
Amphipoda	**15**	**2**	**13.3**	**5.2**	**0.1**	**0.1**	**4.7**
Hyperiidae							
Unidentified hyperiids	2	1	6.7	0.7	<0.01	<0.01	1.2
Themisto libellula	13	1	6.7	4.5	0.1	0.1	3.1
Other Invertebrates	**10**	**4**	**26.7**	**3.5**	**1.2**	**1.1**	**7.6**
Decapoda (Hippolytidae)	8	3	20.0	2.8	1.2	1.1	6.2
Arctic eualid *Eualus fabricii*	1	1	6.7	0.3	0.1	0.03	1.2
Spiny lebbeid *Lebbeus groenlandicus*	5	1	6.7	1.7	0.8	0.8	2.8
Polar lebbeid *Lebbeus polaris*	1	1	6.7	0.3	0.2	0.2	1.3
Punctate blade shrimp *Spirontocaris phippsii*	1	1	6.7	0.3	0.2	0.1	1.3
Mysidae							
Mysis litoralis	2	1	6.7	0.7	<0.01	<0.01	1.1
Fish total	265	10	66.7	91.4	98.7	98.8	79.6
Invertebrates total	25	6	40.0	8.6	1.3	1.2	12.9
Unidentified fish	133	7	36.8	31.2			
Unidentified invertebrates	3	2	10.5	0.7			
Grand total		426	19				

[a] *Ammodytes dubius* and *Ammodytes hexapterus* are found in Hudson Bay (Coad & Reist 2004)
[b] Likely *Gadus ogac* (M. Chambellant pers. obs.; Coad & Reist 2004)

Table 4. *Phoca hispida*. Total number of prey (*P*), number of prey per stomach, total biomass (kg) and energy (MJ) of identified prey, number of taxa found, and Simpson's diversity index (*D'*; *italicized* values indicate similarity between age classes, superscripts ^{a,b} indicate similarity between years) in ringed seal stomachs collected in fall (September to November) 1991 to 2006 in Arviat, Nunavut, Canada, per year and age class. n stomachs and n stomachs with identified prey are the total number of stomachs collected containing prey items and the number of stomachs with identified prey, respectively. **Bold** values are for all age classes pooled

Year Age class	*P*	n stomachs	n stomachs with identified prey	n prey stomach^{-1}	Biomass of identified prey (kg)	Energy of identified prey (MJ)	n taxa present	*D'*
1991	**275**	**10**	**7**	**27.5**	**0.24**	**1.24**	**6**	**0.50**^{a}
Adult	241	5	4	48.2	0.18	0.92	5	0.52
Juvenile	18	4	2	4.5	<0.01	<0.01	1	
Pup	16	1	1	16.0	0.06	0.32	2	0.12
1992	**63**	**11**	**8**	**5.7**	**0.14**	**0.68**	**7**	**0.78**
Adult	43	5	4	8.6	0.03	0.13	2	0.44
Juvenile	20	6	4	3.3	0.12	0.55	6	0.72
Pup	0	0	0	0.0	**0.00**	**0.00**	0	–
1998	**4107**	**46**	**42**	**89.3**	**16.11**	**81.25**	**11**	**0.02**
Adult	3415	31	27	110.2	12.24	61.71	10	*0.02*
Juvenile	383	7	7	54.7	2.21	11.15	3	*0.02*
Pup	141	2	2	70.5	0.70	3.55	2	*0.01*
1999	**492**	**37**	**29**	**13.3**	**1.53**	**7.60**	**8**	**0.60**
Adult	333	30	22	11.1	0.57	2.77	6	0.47
Juvenile	157	6	6	26.2	0.96	4.82	5	0.14
Pup	2	1	1	2.0	<0.01	<0.01	1	
2000	**954**	**46**	**38**	**20.7**	**8.66**	**41.25**	**12**	**0.36**
Adult	462	27	22	17.1	4.15	19.87	7	*0.28*
Juvenile	218	11	9	19.8	2.87	13.48	9	0.63
Pup	274	8	7	34.3	1.63	7.9	8	*0.21*
2003	**1477**	**30**	**26**	**49.2**	**11.28**	**56.93**	**7**	**0.26**^{b}
Adult	686	11	8	62.4	4.69	23.71	5	0.36
Juvenile	436	11	10	39.6	4.00	20.20	6	*0.09*
Pup	231	6	6	38.5	1.58	8.00	3	*0.11*
2004	**1490**	**15**	**15**	**99.3**	**11.29**	**55.54**	**15**	**0.18**
Adult	348	3	3	116.0	2.92	14.08	9	*0.10*
Juvenile	737	8	8	92.1	6.84	33.71	10	0.25
Pup	405	4	4	101.3	1.53	7.74	5	*0.12*
2005	**2905**	**44**	**44**	**66.0**	**16.49**	**81.95**	**14**	**0.24**^{b}
Adult	224	5	5	44.8	1.64	8.26	4	*0.06*
Juvenile	1727	28	28	61.7	10.35	50.92	11	0.34
Pup	905	10	10	90.5	4.49	22.69	9	*0.03*
2006	**284**	**26**	**23**	**10.9**	**1.68**	**8.17**	**12**	**0.54**^{a}
Adult	62	8	6	7.8	0.38	1.93	4	*0.30*
Juvenile	147	13	12	11.3	0.85	4.17	11	*0.31*
Pup	75	5	5	15.0	0.45	2.07	8	0.80
All years	**12047**	**265**	**232**	**45.5**	**67.42**	**334.6**	**35**	**0.22**
Adult	5814	125	101	46.5	26.79	133.37	25	0.20
Juvenile	3843	94	86	40.9	28.21	139.02	25	0.29
Pup	2049	37	36	55.4	10.45	52.27	19	0.14

(exclusively represented by ninespine stickleback *Pungitius pungitius*), and benthic invertebrates (mostly decapods and Mysidae; Table 5, Fig. 2). In 1992, sculpins were second in importance after sand lances but contributed to the total energy consumed twice as much as sand lances (64.7 and 29.6%, respectively). In 1999, 2000, and 2006, sand lance *IG* was also relatively low (~70). Sculpins were the second most important prey item in terms of *IG* and percentage energy consumed for 2000 and 2006, while in 1999, amphipods had the second highest *IG* but the energy contribution of sculpins was greater

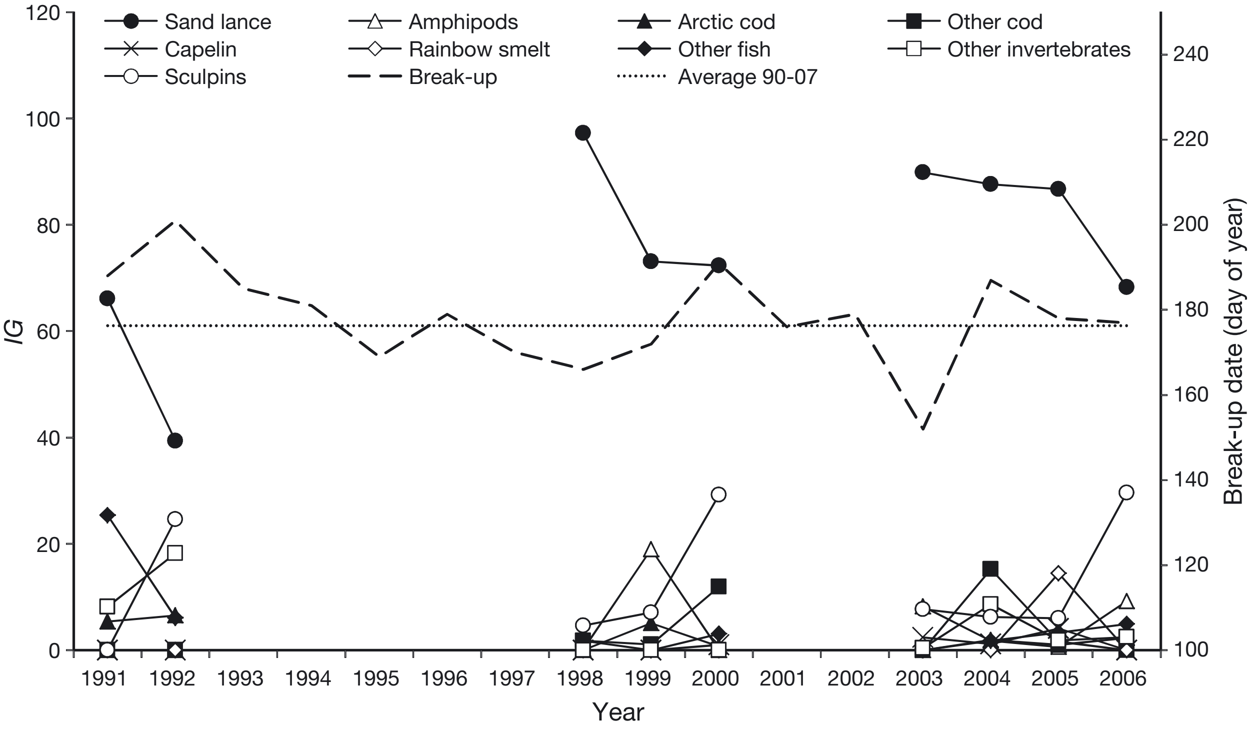

Fig. 2. *Phoca hispida*. Variation in the index of global importance (*IG*) of the 9 prey groups (see Table 2 for species) identified in ringed seal stomachs collected in fall (September to November) 1991 to 2006 in Arviat, Nunavut, Canada, and in dates of spring sea ice break-up in western Hudson Bay. Average 90-07: average date of sea ice spring break-up over 1990 to 2007

(2.9 % and 7.4 %, respectively). Arctic cod *IG* was relatively high in 1999. The last group, years 1998 and 2003 to 2005, showed a diet for which sand lances largely dominated (*IG* > 85), especially in 1998 (*IG* = 97.3). The second most consumed prey item of ringed seals in 2005 was rainbow smelt *Osmerus mordax* (*IG* = 14.5), a fish that was part of the diet for that year only. The importance of capelin in the diet was also the highest in 2005 (*IG* = 4.1; Table 5, Fig. 2). Capelin was not part of the ringed seal diet before 2000 (Table 5).

The total P_{stom} showed strong interannual variation, from fewer than 6 prey per stomach in 1992 to nearly 100 in 2004, and was generally lower in the 1990s (Table 4). Sand lance *IG* was negatively related to percentage of empty stomachs ($r_p = -0.74$, $p = 0.02$), and a sigmoid function best described the relationship between sand lance *IG* and total P_{stom} ($r^2 = 0.80$), total biomass ($r^2 = 0.86$), and total energy consumed ($r^2 = 0.86$; Fig. 3).

D' varied from 0.02 in 1998 to 4.59 in 1992 (Table 4) and was different between years, except for 1991/2006 and 2003/2005, years that were similar ($p = 0.61$ and $p = 0.37$, respectively; Table 4). Apart from 1998, D' was generally higher in the 1990s compared to the 2000s. D' was negatively correlated with P_{stom} ($r_p = -0.89$, $p = 0.001$) and with sand lance *IG* ($r_p = -0.93$, $p = 0.0002$).

Sand lance *IG*s in the ringed seal diet were significantly greater in years when the break-up occurred earlier in WHB ($r_p = -0.72$, $p = 0.03$).

C and N SI ratios (‰) were significantly lower in the 2000s (2003 to 2006) than in the 1990s (1991 to 1992), with $\delta^{13}C_{1990s} = -19.3$ (−19.7 to −19.0), n = 52 and $\delta^{13}C_{2000s} = -19.8$ (−20.4 to −19.3), n = 132 ($U = 2047.5$, $p < 0.0001$); and $\delta^{15}N_{1990s} = 16.3$ (15.8 to 17.1), n = 52 and $\delta^{15}N_{2000s} = 15.0$ (14.2 to 15.8), n = 132 ($U = 1433.5$, $p < 0.0001$; Fig. 4). Mean C and N SI ratios of fish and invertebrate species potentially consumed by ringed seals, and of seal muscle tissue collected in the 1990s and 2000s, are presented in Fig. 4 and in Table S3 in the Supplement.

Spring

In 1992, sand lance and other invertebrates were the only 2 prey groups consumed by ringed seals, with *IG*s of 60 and 45.8 and %*E*s of 74.9 and 25.1 %, respectively. In 1991 and 2005, sand lance

Table 5. *Phoca hispida*. Index of global importance (*IG*) per year and age class for the different prey groups (see Table 2 for species) identified in ringed seal stomachs collected in fall (September to November) 1991 to 2006 in Arviat, Nunavut, Canada. A: adult; J: juvenile; P: pup. Groupings were made to increase sample size

Age class/ year	Sand lance *Ammodytes* spp.	Arctic cod *Boreogadus saida*	Gadidae	Capelin *Mallotus villosus*	Rainbow smelt *Osmerus mordax*	Sculpins (Cottidae)	Other fish	Amphipods (Amphipoda)	Other invertebrates
A91	74.0	8.2	0	0	0	0	21.2	0	0
A92	68.2	0	0	0	0	0	0	0	22.4
A98	96.4	0	1.4	0	0	5.2	2.5	0	0
A99	60.6	6.9	0	0	0	5.1	0	25.2	0
A00	73.9	0	11.0	0	0	21.0	0.9	0	0
A03	87.5	0	0	2.3	0	2.8	0	9.3	0
A04	83.5	4.3	33.6	0	0	10.5	4.9	1.7	0
A05	76.4	0	0	0	8.1	5.7	1.9	0	0
A06	76.5	4.8	0	0	0	15.6	0	8.5	0
J91-92	19.8	9.0	0	0	0	33.2	21.2	0	8.3
J98	98.4	0	5.3	0	0	2.6	0	0	0
J99	88.2	0	3.5	0	0	12.9	0	3.6	0
J00	58.9	0	9.4	4.1	0	44.8	6.1	0	0
J03	87.8	0	0	4.4	0	8.1	0	2.1	1.2
J04	86.2	1.8	12.4	0	0	5.8	0	2.7	11.9
J05	83.2	0	1.7	5.6	19.8	6.2	3.9	1.0	1.7
J06	73.7	2.2	0	0	0	22.4	6.0	5.3	4.8
P91	97.2	0	0	0	0	0	0	0	23.7
P98-99	81.2	4.7	0	0	0	0	0	2.8	0
P00	84.2	3.5	16.4	0	0	26.7	2.8	0	0
P03	98.4	0	0	0	0	2.2	0	5.3	0
P04	98.1	0	0	5.2	0	2.3	2.8	0	9.1
P05	99.2	4.0	0.9	1.9	1.4	2.8	2.0	0	0
P06	41.8	0	0	0	0	36.0	7.4	16.2	0
Adult	86.9	1.1	4.4	0.3	0.4	8.2	2.2	4.5	0.4
Juvenile	80.3	0.6	4.9	3.0	7.2	12.9	3.2	1.6	3.5
Pup	89.3	2.6	3.2	1.2	0.4	11.4	2.3	2.0	2.5

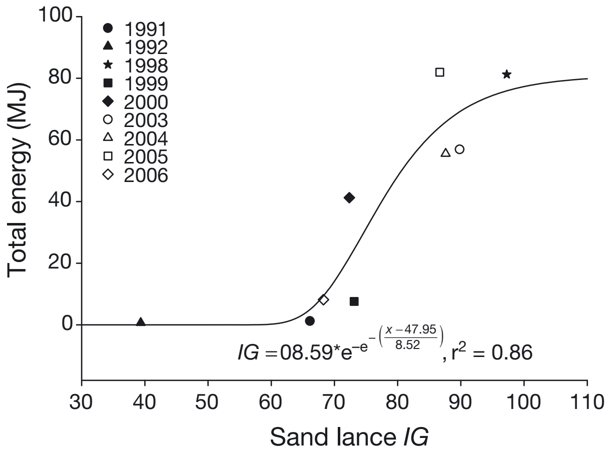

Fig. 3. *Phoca hispida*. Relationship between sand lance *Ammodytes* spp. index of global importance (*IG*) in the diet of ringed seals and the total energy consumed in western Hudson Bay during fall 1991, 1992, 1998 to 2000, and 2003 to 2006, best described by a Gompertz model with 3 parameters

did not dominate the spring diet, and their importance was reduced (*IG* < 35). This was particularly evident in 1991, when sand lance were fourth out of 5 prey groups in the diet (*IG* = 17.7). Arctic cod (*IG* = 29.3), followed by sculpins (*IG* = 22.1) and amphipods (*IG* = 20.8), were the most important prey groups. In 2005, however, the most consumed prey by ringed seals in the spring was capelin (*IG* = 35.5). No Arctic cod were recorded in the 2005 spring diet.

In the spring, *D′* was significantly higher in the period 1991 to 1992 (*D′* = 0.7) than in 2004 to 2005 (*D′* = 0.6; p = 0.02).

Sand lance body length

The estimated body length of sand lances found in ringed seal stomachs varied from 4.8 cm to 21.4 cm. We found no seasonal difference in

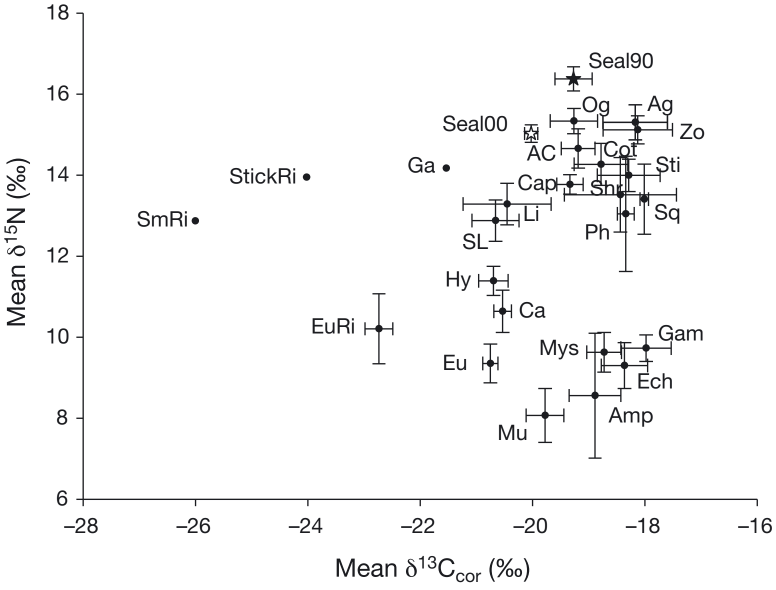

Fig. 4. *Phoca hispida*. Mean (± 1.96 SE) nitrogen (δ^{15}N) and carbon (δ^{13}C) stable isotope ratios in ringed seal muscle tissue collected in the fall (September to November) in Arviat, Nunavut, Canada, in the 1990s (closed star; Seal90, n = 52) and in the 2000s (open star; Seal00, n = 132) and in potential prey taxa collected in Hudson Bay over the period 2004 to 2007 (see Table S3 in the Supplement). Carbon isotope ratios were corrected for the oceanic Suess effect and the presence of carbonates for invertebrates (C_{cor}). AC: Arctic cod *Boreogadus saida*; Ag: Agonidae; Amp: amphipods (Amphipoda); Ca: *Calanus* sp.; Cap: capelin *Mallotus villosus*; Cot: Cottidae; Ech: starfish (Asteroidea); Eu: Euphausiidae; EuRi: Euphausiidae from river; Ga: gastropod; Gam: Gammaridae; Hy: Hyperiidae; Li: *Liparis* sp.; Mu: mussel (Bivalvia); Mys: Mysidae; Og: Greenland cod *Gadus ogac*; Ph: Pholidae; Shr: shrimps (Decapoda); SL: sand lance *Ammodytes* spp.; SmRi: smelt *Osmerux mordax* from river; Sq: squid (Teuthida); Sti: Stichidae; StickRi: ninespine stickleback *Pungitius pungitius* from river; Zo: Zoarcidae

sand lance body lengths over the study period ($\text{median}_{\text{spring}}$ = 12.5 [11.3 to 14.4], n = 127 and $\text{median}_{\text{fall}}$ = 13.1 [11.0 to 15.5], n = 3050; U = 207807.5, p = 0.16). Overall, juvenile ringed seals consumed larger sand lances than adults and pups (H_c = 162.0, df = 2, p = 0.0000), but the difference was not apparent for all years studied. Sand body lengths showed strong interannual variation (H_c = 433.2, df = 8, p = 0.0000), with adult, juvenile, and pup ringed seals consuming the largest sand lances in 2003 ($\text{median}_{\text{adult}}$ = 15.5 [13.8 to 16.9], n = 126; $\text{median}_{\text{juvenile}}$ = 16.1 [13.4 to 17.2], n = 134; and $\text{median}_{\text{pup}}$ = 15.8 [14.0 to 17.1], n = 61).The body lengths of sand lances consumed by ringed seals of all ages in the 2000s were significantly larger than those of fish consumed in the 1990s ($\text{median}_{\text{1990s}}$ = 11.9 [10.3 to 14.4], n = 1620; $\text{median}_{\text{2000s}}$ = 13.9 [11.6 to 15.8], n = 1557; U = 891735.5, p = 0.0000).

DISCUSSION

Diet composition

In WHB, the diet of ringed seals reconstructed from stomach contents and SIA was dominated by sand lance, especially during the open-water season (summer and fall). Arctic cod is typically reported as the primary prey of ringed seals (northern Foxe Basin and southwestern Baffin Island: McLaren 1958; western Canadian Arctic: Smith 1987; high Canadian Arctic: Bradstreet & Finley 1983; Barents Sea: Wathne et al. 2000; northern Greenland: Siegstad et al. 1998; northern Baffin Island: Holst et al. 2001; Svalbard: Labansen et al. 2007). However, studies on ringed seals sampled at lower latitudes (Ungava Bay and northern Labrador: McLaren 1958; southeastern Hudson Bay: Breton-Provencher 1979) revealed that sand lance were the main fish prey, whereas records of Arctic cod were anecdotal or absent. Our results, from similar low latitudes, support the suggestion of a latitudinal gradient in ringed seal feeding habits based on preference and/or availability of fish (McLaren 1958, Siegstad et al. 1998). In years when the importance of sand lance in the diet was comparatively low, ringed seals diversified their diet but were not able to fully compensate for the energy loss by consuming alternative prey taxa. This result, together with the overall low D', suggested that ringed seals in WHB are sand lance specialists, which could have important implications for their body condition and reproductive performances in years when the availability of sand lance is low. In general, specialists are more vulnerable to rapid environmental changes, such as that currently occurring with the warming and loss of sea ice in the Arctic (Kovacs & Lydersen 2008, Laidre et al. 2008).

Sculpins were the second most important food resource for ringed seals in WHB during the open-water season. Sculpins are reported to be an important fish prey for ringed seals (McLaren 1958, Gjertz & Lydersen 1986, Siegstad et al. 1998). The importance of sculpins was particularly high in years when the energy contribution of sand lance was low, suggesting that ringed seals may have attempted to compensate for a shortage of sand lance by foraging more benthically on sculpins.

Invertebrates did not represent an important food resource for ringed seals in WHB. This result is similar to Labansen et al. (2007) but contrasted with most previous studies that found invertebrates, and particularly hyperiid amphipods and mysids, to be major contributors to the ringed seal diet (Lowry et al. 1980, Bradstreet & Finley 1983, Smith 1987, Weslawski et al. 1994, Siegstad et al. 1998, Holst & Stirling 2002). Invertebrates can be underestimated in diet reconstructed from stomach contents because of their usually small size and because they leave few identifiable and quantifiable remains (Lawson et al. 1995). Therefore, invertebrates might be more important in the diet of ringed seals in WHB than indicated in our analysis. However, we think it is not likely to be a major source of bias in our study because (1) using stomach contents to reconstruct the diet of ringed seals in southeastern HB, Chambellant (2010) found that invertebrates constituted the major part; and (2) when using fractionation values of 2.4‰ for δ^{15}N and 1.3‰ for δ^{13}C on ringed seal muscle (Hobson et al. 1996), the value obtained is consistent with a diet in which invertebrates did not constitute an important food resource, at least during the open-water season (see Fig. 4).

Age variation

Previous studies have reported either no age-related differences in the ringed seal diet (McLaren 1958, Gjertz & Lydersen 1986, Siegstad et al. 1998, Holst et al. 2001) or that pups fed more on invertebrates and less on fish than adults (Lowry et al. 1980, Bradstreet & Finley 1983, Smith 1987, Siegstad et al. 1998, Holst et al. 2001).

In our study, reconstruction of stomach contents did not show any age-related difference in ringed seal fall diet in WHB. In summer, however, the timescale muscle SI signature likely provides that when seals are collected in fall, C and N SI ratios showed that adult ringed seals tended to feed at a slightly higher trophic level than pups and foraged more benthically compared to the 2 younger age classes. Despite being statistically significant, the differences (Δ) in N and C SI ratios between adult and pup ringed seals might not be biologically significant (ΔN = 0.7‰ and ΔC = 0.9‰), since the diet-tissue fractionation values for ringed seal muscle have been found to be 2.4‰ for δ^{15}N and 1.3‰ for δ^{13}C (Hobson et al. 1996).

When age differences were found in the ringed seal diet, the limited foraging experience and diving capabilities of pups and/or the spatial segregation of the different age classes at different times of the year were proposed as possible, but non-exclusive, explanations. During the open-water season, particularly in autumn, ringed seals of all ages have been observed feeding offshore together, sometimes in large aggregations (McLaren 1958, Smith 1973, 1987, Harwood & Stirling 1992), whereas when ice starts to form in late fall, adults move toward the prime breeding habitat to possibly establish territories from which they would exclude younger age classes (McLaren 1958, Smith 1973, 1987, Holst et al. 1999, Krafft et al. 2007). The high percentage of adults (86%) in our spring samples suggested that segregation of young seals during the spring breeding time occurs in WHB. However, in the fall, the percentage of adult ringed seals in our sample was overall approximately 50% (Table 1), which suggests an absence of spatial segregation of age classes. Physiological and behavioural constraints due to their smaller body size and inexperience, respectively, limit the diving capacities and abilities of ringed seal pups (Kelly & Wartzok 1996, Burns 1999, Jorgensen et al. 2001). Although ringed seal pups were found to dive as deep as 90 m to the sea floor and remain under water for up to 12 min, mean dive duration was close to 1 min (Lydersen & Hammill 1993, Kelly & Wartzok 1996). Adult and subadult ringed seals were found to dive deeper than 250 m for durations of more than 39 min (Teilmann et al. 1999), which would enable them to exploit the benthic community more efficiently than younger age classes.

Interannual variation

Stomach content analysis and SIA indicated that the diet of ringed seals in WHB was different in the early 1990s relative to the 2000s. Although a baseline change in N and C ratios over time could not be excluded, the changes in δ^{15}N and δ^{13}C between the 1990s and the 2000s are supported by results from stomach content analysis and are more likely to reflect a change in the ringed seal diet.

Benthic feeding habits dominated in the early 1990s, with ninespine stickleback, Mysidae, shrimps, and sculpins having their highest or one of their highest *IG*s and sand lance having low importance relative to the other years of the study period, particularly in 1992. Using fractionation values of +2.4 and +1.3‰ from prey to seal muscle tissue for δ^{15}N and

$\delta^{13}C$, respectively (Hobson et al. 1996), the isotope signature of seal muscle collected in the 1990s is consistent with a pattern of a mixed diet of sand lance and Gadidae and/or benthic species, whereas in the 2000s, seal muscle isotopic signature indicated a diet strongly focused on sand lance, supporting the stomach content analysis.

The importance of Arctic cod in the diet of ringed seals in WHB seemed to be reduced in the 2000s relative to the 1990s. This trend was more apparent in the spring, when Arctic cod was the most important prey in 1991 but was not present in the diet in 2005, having been replaced by capelin. Capelin did not appear in the diet of ringed seals prior to 2000 and were then consumed every year with the exception of 2006. Rainbow smelt was present in the ringed seal diet in 2005 only and was mostly consumed by juveniles, although adults and pups did prey on this species as well. The sample sizes were large enough to allow us to be confident that changes in prey composition of ringed seal diet over the years were real and reflected real changes in availability, distribution, and/or abundance of these prey items in the WHB ecosystem. These results also suggest that the ice-adapted Arctic cod, typical of Arctic waters, could have been replaced by more sub-Arctic species in the 2000s. Similar observations and interpretation have been reported by previous studies, which found that thick-billed murres preyed more on capelin and sand lances than on Arctic cod in northern HB (Gaston et al. 2003, Provencher et al. 2012), a switch that occurred at the end of the 1990s (Gaston et al. 2003). Those studies concluded that a change in fish community occurred at the end of the 1990s due to changes in oceanographic and ice conditions driven by the continued warming trend in water temperatures. Inuit also reported a decline of Arctic cod in southeastern and northwestern HB (McDonald et al. 1997). The occurrence of capelin in ringed seal stomachs was described in southeastern HB in the late 1970s (Breton-Provencher 1979). Dunbar (1983) also reported large numbers of capelin in the same region and suggested they might belong to a relict population from a warmer period. Capelin are known to be sensitive to water temperature, and important changes in their abundance, distribution, growth, and spawning time have been observed and linked to changes in water temperatures (Carscadden et al. 2001). Rainbow smelt were illegally introduced into the HB water drainage in the early 1990s and, starting in 2002, expanded their distribution from the Nelson and Churchill river systems to the WHB coast (see Stewart & Lockhart 2005). Both species may profit from the current warming trend in water temperature to expand their range northward in the HB ecosystem, while Arctic cod distribution may have shifted to higher latitudes, supporting the Gaston et al. (2003) and Provencher et al. (2012) hypothesis of a shift in the fish community in HB.

In this study, we found that the importance of sand lance in the ringed seal diet was lower in years with a late spring sea ice break-up. This was particularly the case in 1992, when the ice broke up 25 d later than average (Fig. 2) due to the combined effect of a strong positive phase of the North Atlantic Oscillation and El Niño event in 1991/1992 and the eruption of Mount Pinatubo in June 1991, which created colder than normal and heavy ice conditions over the eastern Arctic in the early 1990s (Mysak et al. 1996, Gough et al. 2004). Sand lance are zooplanktivores that feed in pelagic waters in large schools (see Nelson & Ross 1991, McKenzie & Wynne 2008). In HB, sand lance spawn under the ice surface in the spring before break-up occurs (Drolet et al. 1991). Development of eggs and larvae depend on water temperature, which under the ice is relatively constant. Therefore, sand lance larvae start feeding around the same date every year, usually shortly after the sea ice break-up and the phytoplankton bloom, matching the emergence of earlier stages of copepods, their main prey. Thus, variability in sand lance recruitment is affected by variability in the timing of ice break-up (Drolet et al. 1991). In years with a late break-up, the phytoplankton bloom is delayed, creating a mismatch between the time sand lance larvae start to feed and the emergence of their prey and leading to starvation of the entire cohort of larvae. From the body lengths of sand lance consumed, ringed seals appeared to target principally the subadult and young adult age classes (i.e. 1 to 2 yr old; Winters 1989, Nelson & Ross 1991). This result suggests that by affecting the timing of the phytoplankton bloom and subsequently the growth and abundance of zooplankton (Drolet et al. 1991), the timing of ice break-up could also affect the abundance, distribution, and/or availability of sand lance to ringed seals in the fall. Effects of a late ice break-up on sand lance populations are likely to last for several years, since growth, recruitment, and possibly adult survival are affected. Sculpins and other benthic species will be less affected by the timing of ice break-up, since their larvae emerge after the break-up during the phytoplankton bloom (Drolet et al. 1991). Moreover, during cold and heavy ice years, the herbivorous zooplankton community is less abundant, and reduced ice-algae grazing allows transfer of primary productivity to the benthos, leading to a benthic-dominated food web (see Tynan & DeMaster 1997, Bluhm & Gradinger 2008). The differences in ecology between benthic and pelagic prey and the cryo–pelagic–benthic coupling could be important in understanding why ringed seals increased their consumption of benthic species, particularly sculpins, in cold years when the importance of sand lance was reduced. A similar pattern was described in the western Arctic, where ringed seals switched from Arctic cod to benthic species in 1974, a year of heavy ice and late break-up (Smith 1987).

In years of late ice break-up and therefore lower availability of sand lance, such as in the early 1990s in WHB, ringed seal food consumption was reduced, as shown by a higher percentage of empty stomachs, a lower P_{stom}, and a lower biomass ingested. Reduced energy consumption by ringed seals is expected to be reflected in their body condition, reproduction, survival, and abundance. Poor reproductive performances, low recruitment, and a decline in ringed seal density occurred in WHB in the 1990s (Ferguson et al. 2005, Stirling 2005, Chambellant et al. 2012a,b). Chambellant et al. (2012a) proposed that a decrease in productivity triggered by the cold and heavy ice conditions that prevailed in WHB in the early 1990s (nutritional stress hypothesis) and an increase in predation pressure by polar bears and Arctic foxes could be involved in the poor reproduction and survival of ringed seals observed in the 1990s. Our results support the nutritional stress hypothesis and provide evidence that ringed seals in WHB are, at times, strongly regulated by bottom-up processes driven by variation in the sea ice regime.

In conclusion, ringed seals appeared to be sand lance specialists in WHB, and their feeding habits differed in response to changes in environmental conditions, particularly the sea ice regime. Ringed seals could therefore be good indicators of environmental changes in the ecosystem. Our results also enable inferences to be made on the dynamics of marine fish communities, as well as on regulatory mechanisms for ringed seals in the WHB ecosystem. C and N SI ratios provided a more integrative perspective of ringed seal diet and a good temporal complement to the traditional stomach content diet reconstructions. Future studies exploring marine mammal feeding habits would gain from combining traditional and biomarker techniques, including SI of different elements, fatty acid, and/or mercury in multiple tissues.

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