

Ringed Seal Diet and Body Condition in the Amundsen Gulf region, Eastern Beaufort Sea

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ABSTRACT. Diet from stomach contents and body condition from morphometric measurements were obtained for 169 (108 stomachs analysed) ringed seals (*Pusa hispida*) for the Amundsen Gulf region in the western Canadian Arctic from 2015 to 2018. Sampling was from subsistence-harvested seals from the three communities of Paulatuk (spring, summer, and autumn), Sachs Harbour (summer), and Ulukhaktok (winter), Northwest Territories. Stomach contents were separated through sieves and by hand, and taxa identified to the lowest taxonomic level possible and weighed. Stomachs were fullest (by weight and prey count) in the autumn, which suggests that foraging was most intense and successful at that time. A total of 93 prey taxa, including 17 fish and 76 invertebrate species were identified. Several fish and invertebrate species were regularly found together, the most common being Arctic cod (*Boreogadus saida*), sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and hyperiid amphipods (*Themisto* spp.). Condition measurements inferred from blubber thickness, although showing considerable variation among sites and years, had a seasonal relationship with maximal depth during the autumn and winter. Overall, the diet of ringed seals in Amundsen Gulf was broadly similar to those reported from other areas while also indicating some degree of regional specificity. When compared to the diet of ringed seals in the same area in the 1980s, the results presented here were more diverse, with new or increased numbers of subarctic species (e.g., saffron cod, *Eleginus gracilis*) found in the samples. This finding is a likely consequence of climate warming, as increasing numbers of subarctic species move north with warming ocean temperatures in the Arctic.

Key words: ringed seal; *Pusa hispida*; diet; Amundsen Gulf; Beaufort Sea; Arctic; climate change

RÉSUMÉ. La composition du régime alimentaire prélevé à partir du contenu stomacal et la condition corporelle déterminée à partir de mesures morphométriques ont été obtenues pour 169 (108 estomacs analysés) phoques annelés (*Pusa hispida*) de la région du golfe Amundsen, dans l'ouest de l'Arctique canadien, de 2015 à 2018. Cet échantillonnage concernait des phoques récoltés à des fins de subsistance dans trois localités, soit Paulatuk (printemps, été et automne), Sachs Harbour (été) et Ulukhaktok (hiver), dans les Territoires du Nord-Ouest. Les contenus stomacaux ont été séparés à l'aide de tamis et à la main, et les taxons ont été identifiés jusqu'au niveau taxonomique le plus bas possible, puis pesés. Les estomacs étaient plus pleins (en fonction du poids et du nombre de proies) à l'automne, ce qui suggère que la recherche de nourriture était plus intense et plus fructueuse à ce moment-là. En tout, 93 taxons de proies ont été identifiés, dont 17 espèces de poissons et 76 espèces d'invertébrés. Plusieurs espèces de poissons et d'invertébrés ont été régulièrement trouvées ensemble, les plus courantes étant la morue polaire (*Boreogadus saida*), le lançon (*Ammodytes hexapterus*), le capelan (*Mallotus villosus*) et les amphipodes hypéridés (*Themisto* spp.). Même si elles affichaient des variations considérables d'un site et d'une année à l'autre, les mesures de la condition déduites à partir de l'épaisseur du lard avaient une relation saisonnière avec l'épaisseur maximale enregistrée en automne et en hiver. Dans l'ensemble, le régime alimentaire du phoque annelé du golfe Amundsen était grandement comparable à celui signalé dans d'autres secteurs, tout en ayant une certaine spécificité régionale. Comparativement au régime alimentaire du phoque annelé du même secteur dans les années 1980, les résultats présentés ici étaient plus variés, de nouvelles espèces subarctiques ou un plus grand nombre d'entre elles (comme le navaga jaune, *Eleginus gracilis*) se trouvant dans les échantillons. Cette constatation est vraisemblablement une conséquence du réchauffement climatique, car de plus en plus d'espèces subarctiques montent vers le nord en raison du réchauffement des températures océaniques dans l'Arctique.

Mots clés : phoque annelé; *Pusa hispida*; régime alimentaire; golfe Amundsen; mer de Beaufort; Arctique; changement climatique

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INTRODUCTION

Ice conditions in the Arctic are changing with earlier sea ice breakup times, later freeze-up times, and more frequent above-freezing temperatures during winter causing subsequent rain-on-ice events (IPCC, 2019). These changes have the potential to have significant negative impacts on many if not all ice obligate flora and fauna, including all Arctic marine mammals (Tynan and DeMaster, 1997; Laidre et al., 2008, 2015; Kovacs et al., 2011, 2012). The ringed seal (*Pusa hispida*, Schreber, 1775), the smallest phocid pinniped, is a widely distributed circumpolar ice-obligate Arctic marine mammal. Loss of sea ice from warming ocean and air temperatures is a known threat to ringed seals during the neonate stage. Stable sea ice and a sufficient depth of snow for subnivean birth lairs are critical to key life history stages, such as birthing, and for protection from weather and predators throughout the period of pup dependence (Smith and Stirling, 1975; Stirling and Smith, 2004). Less understood is how the changing marine ecosystem will affect ringed seal foraging ecology (Bengtsson et al., 2020). Our goal here is to document ringed seal diet and body condition in order to assess the response of ringed seal foraging behaviour to a changing Arctic ecosystem.

Ringed seals are pelagic foragers that are known to consume a broad variety of prey types across their circumpolar range, while locally a few specific prey species tend to dominate their diet (McLaren, 1958; Weslawski et al., 1994; Siegstad et al., 1998; Thiemann et al., 2007). These include Arctic cod (*Boreogadus saida*), mysids, and amphipods (McLaren, 1958; Smith, 1987; Quakenbush et al., 2011). Prey abundance is also expected to be directly influenced by warming water temperatures, with many species expected to move north with cooler water, and new subarctic species moving into the Arctic (Rose, 2005; Laidre et al., 2008, 2015; Kovacs et al., 2012). Some of this change is already evident, including increasing observations of capelin (Rose, 2005) and salmon (Dunmall et al., 2013, 2018). As a result, monitoring ringed seal diet is useful for understanding their health as well as changes in local prey availability. In addition to diet data, accompanying measures of ringed seal body condition, such as blubber thickness and general morphometrics, are important to relate diet to animal health and reproductive fitness (Ferguson et al., 2020; Harwood et al., 2020).

Ringed seals in the eastern Beaufort Sea region (also known as the Inuvialuit Settlement Region or ISR) are widespread, an important high-trophic-level pelagic predator, and important to local Inuvialuit culture and food security. Although detailed diet studies of ringed seals exist for populations in Alaska, in the Bering, Chukchi, and western Beaufort Seas (e.g., Lowry et al., 1980; Quakenbush et al., 2011; Crawford et al., 2015), as well as for several locations in the eastern Canadian Arctic (Chambellant et al., 2013), the only published substantive diet study in the eastern Beaufort is now over 30 years old (Smith, 1987). As

a result of widespread changing conditions in the marine environment due to climate change, there is a need for comparative and more recent information.

Several methods to infer diet in pinnipeds are used, including identification of hard parts from scat, and stomach contents, stable isotope, and fatty acid analyses. Each technique has its strengths and weaknesses (Cortés, 1997; Bowen, 2000; Bowen and Iverson, 2013). Here, we measure diet directly through stomach contents. One of the advantages of this method is the ability to recover smaller and soft tissue prey items before they are broken down past the point of identification. Conversely, stomach contents represent only a recent snapshot of the animal's diet. Clearance rates of the stomach and intestines of ringed seals are quite rapid, in the order of 4–5 hrs, and dependent on the water content of the food ingested (Helm, 1984). Murie and Lavigne (1986) found that most fish otoliths break down and are digested or are passed within 12 hrs.

For subsistence-hunted species, stomach contents and other relevant measures can be readily available through partnerships with communities (Harwood et al., 2012). We partnered with hunters of three ISR communities—Paulatuk, Sachs Harbour, and Ulukhaktok—to collect stomachs, along with a suite of other morphometric and contextual data, in order to ascertain ringed seal diet and body condition in this region. Our goal is to provide diet and condition measures that can be compared to past and future records and, at the same time, help assess how ringed seals are adapting to a changing marine environment.

METHODS

Field Collection

From 2015 to 2018 we worked with the local communities of Paulatuk, Sachs Harbour, and Ulukhaktok, Northwest Territories, Canada (Fig. 1) and commissioned community members to collect and record data on diet and condition of subsistence-harvested ringed seals. Because sampling was opportunistically based on harvested seals, most sampling occurred during the open-water season (June–October) and to a lesser extent throughout the year (Table 1).

Diet and morphometric/condition sampling involved (1) recording contextual data, (2) condition measurements, and (3) sample collection for post-processing. The context data recorded comprised seal species; date, time, and location the seal was taken; the time the seal was brought in and processed; and any additional circumstantial information noted by the hunter. Condition measurements, conducted immediately by the monitor, included whole animal weight, standard nose-to-tail length, maxillary and hip girth (according to Committee on Marine Mammals, 1967), blubber thickness (depth measured at the sternum), sex (as indicated by the presence or absence of a penile aperture), and an external full body check for abnormalities (e.g., hair loss), which would be photographed. Samples



FIG. 1. Map of Amundsen Gulf area in the eastern Beaufort Sea, showing the Inuvialuit Settlement Region (ISR) and the Anguniaqvia niqiqyuam Marine Protected Area (the ANMPA). Seals sampled are from an approximate 50 km radius of the three communities of Paulatuk, Sachs Harbour, and Ulukhaktok. Service Layer Credits: Esri, GEBCO, DeLorme, NaturalVue, Northwest Territories, HERE, Garmin, FAO, NOAA, USGS, EPA, NRCan, Parks Canada.

taken for post-processing included the entire stomach, muscle and skin tissue, fat, canine teeth or the lower jaw, and blood (collected with blotting sample paper). Each sample was immediately sealed in a labeled airtight bag labeled with seal #, species, date, time, and location), with all sample bags from the same seal stored together in a single bag. Labeled samples were stored frozen at -20°C until analysis. Seals were aged by counting annular growth layers in the dentine of a lower canine tooth (McLaren, 1958; Smith, 1973; Matson's Lab, Manhattan, Montana), and then grouped into three age class categories: pup (< 1 year), juvenile (1–5 years-old), and adult (> 5 years-old (McLaren, 1958; Smith, 1973, 1987).

Diet Analysis

In the lab (North South Consulting, Inc., Winnipeg, Manitoba), the stomach was opened, scraped and the lining rinsed gently over a $500\ \mu\text{m}$ sieve. Stomach contents were drained to minimize water, and total stomach content weight was recorded. All non-prey items, including endoparasites, rocks, sand, plant material, and plastics, were documented,

weighed, and excluded from diet calculations. Prey items were then sorted and identified to the lowest taxonomic level possible, using available reference material and relevant guides (e.g., Campana, 2004). Each large prey item was counted and weighed individually to the nearest 0.1 g; a few small invertebrates such as copepods and mysids were grouped after enumeration and weighed collectively. In cases where prey items could not be consistently identified to species level, several species were together considered a single prey group (e.g., *Mysis* spp.).

Sagittal otoliths, including those found loose in the stomach, were considered in the fish counts, using the following calculation for each species: Total # = # of intact fish of each species + $\frac{1}{2}$ # of otoliths belonging to that species (+1 when an odd number of otoliths were recovered).

When fish remains were too digested for a positive identification, or otoliths too eroded, they were classified as unidentified fish. For each stomach sample, the numbers of each different prey species were recorded. We considered a stomach empty if there was less than 1 g of prey items present.

We grouped prey species into 10 broad prey groups (shown in bold in Table 2; Fig. 2) and assessed the dietary contribution of each prey species using a global importance index (IG, Moreno and Castro, 1995; for examples, see Chambellant et al., 2013; Young and Ferguson, 2013). This index was selected because it incorporates information on both prey size (mass) and numeric abundance into a single metric and, in doing so, mitigates some of the problems associated with these individual measures—prey abundance overemphasizes the contribution of small prey eaten in large numbers, while biomass contribution overemphasizes the contribution of heavy prey to the diet. IG is calculated as:

$$IG = [(\%P \times FO)^{1/2} + (\%B \times FO)^{1/2}] / 2,$$

where %P (prey abundance) = [number of prey i / total number of prey] \times 100; %B (biomass contribution) = [wet weight of prey i / total wet weight] \times 100; and FO (% occurrence) = [number of stomachs with prey i / total number of non-empty stomachs] \times 100.

Statistical Analyses of Diet and Condition

All statistical analyses were performed on ringed seals that had at least one identifiable prey item in their stomach and were conducted in R statistical software (version 3.6.1; R Core Team, 2019). We attempted to answer the following three questions: 1) How does ringed seal diet vary between sites, seasons, and age groups? 2) How does ringed seal body condition vary between sites, seasons, and age groups? and 3) How does ringed seal body condition vary by diet? We expand on the analyses used to answer each of these questions below.

In our first analysis examining ringed seal diet, we first examined different groupings of prey to test which groupings explained the most variation but were also most parsimonious. We examined three different groupings: 1) fish or invertebrates; 2) cod species (*Gadidae*), other fish, amphipod species (*Amphipoda*), and other invertebrates; and 3) Arctic cod, other cod species (*Gadidae*), capelin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), sculpin species (*Cottoidea*), other fish, amphipod species (*Amphipoda*), and other invertebrates. We compared linear models with the count of each category in each group as the dependent variable and the grouping as the independent variable. The third group was best according to R^2_{adj} (group 1 = 0.25, group 2 = 0.38, group 3 = 0.42), so we only used this grouping for the subsequent analysis.

We built linear models with the \log_{10} -transformed counts of prey items within each prey group as the dependent variable, and with the prey group and age (categorical; pup: < 1 year, juvenile: 1–5 years, adult: > 5 years), including their two-way interaction, as independent variables. We started with a fully saturated model and then removed nonsignificant variables, which allowed us to not only have a better model fit and more parsimonious model, but

also allowed the models to have more degrees of freedom since age was not measured on all seals. We did not include year, site, or season in this analysis because one of the sites (Ulukhaktok) only had seals collected from a single year, and two sites only had seal stomachs collected and analyzed from a single season (summer for Sachs Harbour, winter for Ulukhaktok). Given the high likelihood that seal diet varies by season (Smith, 1987), we could not statistically test for differences in diet across sites given that the sites were sampled in different months. However, in a follow-up analysis, we examined models with each site individually. Since the Paulatuk site had more than one season of data collection, we included season as an independent variable. For these analyses, the seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

In our second analysis, we used linear models to examine variability in ringed seal body condition by seal age, using blubber thickness as our metric of body condition. We used blubber thickness as our metric of body condition because it is a direct measure of the body fat reserves of ringed seals. We opted not to use other metrics, such as ratios of girth by body length, because they are more indirect measurements of body condition than blubber thickness. As in the first analysis, we also examined patterns individually for both Sachs Harbour and Paulatuk, and also seasonal patterns for seals sampled at the community of Paulatuk. We did not examine patterns within the Ulukhaktok site because only one pup and three juveniles were included in the sample.

In our final model, we examined whether blubber thickness was related to the different diets evident from the stomach contents. In order to do so, we included the count of prey items (\log_{10} -transformed) within each diet group identified in the first analysis as independent variables.

RESULTS

Diet Results

Of the 108 ringed seal stomach samples analyzed (Table 1), the mean weight of stomach contents was 115.4 g (\pm 192.8 g SD; range: 0–1146.2 g). When the 16 empty stomachs (< 1 g of prey present) were excluded, the mean weight of stomach contents was 135.2 g (\pm 202.6 g SD; range: 1.1–1146.2 g). More than half (59.3%) of the 108 stomachs contained only small amounts of food (< 50 g), and 14.8% were completely empty. All empty stomachs, with the exception of two, were from seals in the spring. Many of the seals had consumed non-prey items, such as rocks, sand, and plant material, which made up less than 1% (0.41%) of the total weight of stomach contents. We found nematodes or other endoparasites in 65.7% of the stomachs examined. Two stomachs, both from Sachs Harbour, contained small plastic (macro) or metal fragments.

We identified 93 prey taxa, including 17 fish and 76 invertebrate species (Table 2). Additional but unconfirmed

TABLE 1. Ringed seals (*Pusa hispida*) harvested in Paulatuk, Sachs Harbour, and Ulukhaktok, Northwest Territories, 2015–18 (n = 169). Since, in some cases, physical data and morphometric measurements were made but stomachs were not collected, the number of stomachs collected and assessed for diet analysis is shown in brackets. All seals were considered in the calculation of sex ratio (M/F) and percent of pups.

Site and year	# Seals	Dates	Sex ratio	% pups	Age ¹	% empty stomachs ²
Paulatuk:						
2015	19 (17)	autumn: 22 September–22 October	2.8	0	–	0
2016	28 (23)	summer-autumn: 25 June–13 October	0.6	25.0	9.7 ± 9.0 (7)	4.3
2017	21 (15)	summer-autumn: 8 July–5 September	2.0	57.1	1.1 ± 1.9 (0)	0
2018	9 (8)	most spring: 8 April–16 July	3.5	33.3	7.6 ± 7.6 (6.5)	87.5
	77 (63)	–	1.7	25.3	6.1 ± 7.9	12.7
Sachs Harbour:						
2015	17 (6)	summer-early autumn: 25 July–18 August	1.1	0	10.7 ± 7.0 (9)	16.7
2016	22 (6)	summer: 6–22 July	1.4	36.4	7.1 ± 8.0 (6)	50
2017	15 (2)	summer: 27 June–3 July	2.0	40	6.3 ± 7.8 (5)	0
2018	16 (16)	summer: 22 July–5 August	1.3	37.5	6.1 ± 7.2 (4.5)	12.5
	70 (30)	–	1.4	28.6	7.6 ± 7.6	20
Ulukhaktok (2017)	15 (15)	winter: 6 December 2017–2 March 2018	2.0	6.7	6.3 ± 4.0 (6)	13.3
All Sites Total	169 (108)	–	1.7	25.0	6.9 ± 7.4	14.8

¹ For seals aged by canine cementum analysis, this is average age in years ± SD (median).

² We classified a stomach as empty if it contained 1.0 g or less identifiable prey items, even if other non-prey items such as rocks, sand, or parasites were present. Sixteen empty stomachs were excluded from diet calculations and analysis.

species of fish included polar cod (*Arctogadus glacialis*), ribbed sculpin (*Triglops pingelii*), Arctic staghorn sculpin (*Gymnocanthus tricuspis*), kelp snailfish (*Liparis tunicatus*), hookear sculpin (*Artediellus* sp.), and Arctic alligatorfish (*Aspidophoroides olrikii*). Most seals had consumed a diversity of prey items. Six seals had 15 or more different types of prey in their stomachs, and only five had a single prey type. The average number of different prey species observed in all stomach contents was 7.3 ± 4.2.

Fish were found in all but two seal stomachs (97.8% occurrence) and comprised 78.0% of the total prey weight and 30.4% of the total count (Table 2; summarized in Fig. 2). The majority of fish biomass (82.1%), however, was highly digested and unidentifiable; most fish species were identified by otoliths alone. Arctic cod was, by far, the most common fish consumed (75.2% of total fish count and in 70.6% of stomachs), although capelin contributed more by weight (Fig. 2). The number of fish consumed varied between sites ($F_{2,89} = 8.143, p < 0.001$) and years ($F_{3,88} = 17.26, p < 0.001$); this was also true for the total number of prey items ($F_{2,89} = 5.95, p < 0.01$; and $F_{3,88} = 3.44, p < 0.05$, respectively).

Hyperiid amphipods were important during all years of study (Fig. 2). *Themisto libellula*, in particular, was found in 47.8% of the stomachs sampled, and comprised 8.4% of the total stomach content weight and 31.9% of the total count. Mysids and copepods were also commonly encountered (in 56.5% and 66.3% of stomachs, respectively) but are smaller and contributed less overall. Collectively, invertebrates made up of 11.0% of diet by weight and 69.4% by count, and were present in all but 11 of the stomachs (88.0%).

The results based on counts of prey items show that ringed seals (pooled across years, sites, and seasons) had significant preferences for some prey items over others ($F_{7,672} = 38.57, p < 0.01$), with Arctic cod, amphipods, and other invertebrates being the most commonly consumed

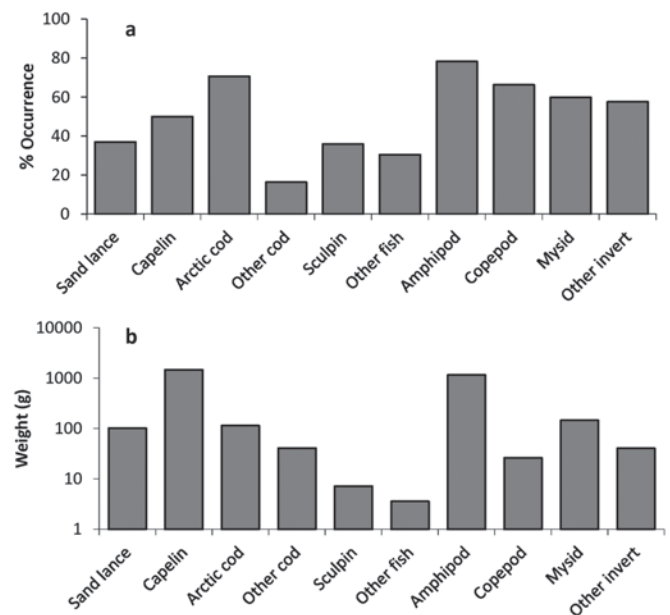


FIG. 2. Summary of ringed seal diet by (a) wet weight and (b) percent occurrence showing the main prey groups found in the stomachs of seals harvested in the eastern Beaufort Sea, Northwest Territories, 2015–18 (n = 92). See Table 2 for breakdown of these broad taxonomic groups.

prey items ($p < 0.05$), and the counts of these three prey items were not significantly different ($p > 0.05$). Seal age had no impact on diet. Seals at Paulatuk ate all prey categories, but ate Arctic cod and other invertebrates the most, followed closely by amphipods. Capelin were also quite common at Paulatuk. Paulatuk was the only site with a decent sample of stomachs across multiple seasons (summer and autumn), so we also examined seasonal effects at this site (Table 3). Arctic cod, amphipods, and other invertebrates remained important prey items in both

TABLE 2. Count, weight, and frequency of occurrence for prey species found in the stomachs of ringed seals (*Pusa hispida*) harvested in the eastern Beaufort Sea, 2015–18 (n = 92). Global Importance (IG) is an index that incorporates all of these measures in its assessment of contribution by species (see equation in text; Moreno and Castro, 1995). Taxa in bold are the broad taxonomic groups used in the descriptive analysis (e.g., Fig. 2). Note that the otolith sizes indicate that the majority of Arctic cod are small in size while saffron cod and “Other fish” and are more variable but generally much larger.

		Count ¹	% Weight ²	% Occurrence ³	IG
FISH:		14336	78.0	97.8	71.0
Ammodytidae	Sand lance (<i>Ammodytes hexapterus</i>)	574	0.8	37.0	6.1
Smelt (Osmeridae)	Capelin (<i>Mallotus villosus</i>)	1204	11.8	50.0	17.8
	Sculpin (Cottidae)	759	0.1	35.9	4.5
	Spatulate sculpin (<i>Icelus spatula</i>)	14	–	2.2	–
	<i>Triglops</i> sp.	17	–	4.3	–
	<i>Myoxocephalus</i> sp.	2	–	1.1	–
Cod (Gadidae)		11588	1.2	76.1	26.5
	Arctic cod (<i>Boreogadus saida</i>)	10797	0.9	70.7	24.2
	Other cod	791	0.3	16.3	3.8
	Saffron cod (<i>Eleginus gracilis</i>)	599	0.3	9.8	2.6
Other fish		115	0.0	30.4	1.8
	Poacher (Agonidae)	3	–	3.3	–
	Snailfish (Liparidae)	97	0.0	26.1	1.5
	Variegated snailfish (<i>Liparis gibbus</i>)	13	0.0	5.4	0.3
	<i>Liparis</i> sp.	7	0.0	3.3	0.2
	Fourline snakeblenny (<i>Eumesogrammus praecisus</i>)	1	–	1.1	–
	Prickleback (Stichaeidae)	8	0.0	4.3	0.2
	Eelpout (Zoarcidae)	7	0.0	6.5	0.3
	<i>Lycodes</i> sp.	1	–	1.1	–
INVERTEBRATE:		32698	11.0	88.0	54.7
Amphipoda		16235	9.3	78.3	39.5
Hyperiididae		15005	8.5	63.0	34.0
	<i>Themisto</i> sp.	221	0.0	10.9	1.4
	<i>Themisto libellula</i>	14614	8.4	47.8	29.3
	<i>Hyperia galba</i>	1	0.0	1.1	0.0
Urstidae		42	0.1	2.2	0.4
	<i>Anonyx</i> sp.	31	0.1	4.3	0.6
	<i>Onisimus</i> sp.	1	0.0	1.1	0.0
	<i>Onisimus glacialis</i>	1	0.0	1.1	0.0
	<i>Onisimus litoralis</i>	27	0.0	6.5	0.5
Pontoporeiididae		3	0.0	1.1	0.0
	<i>Monoporeia affinis</i>	5	0.0	3.3	0.1
Gammaridae		2	0.0	2.2	0.1
	<i>Gammarus loricatus</i>	106	0.1	21.7	1.6
	<i>Gammarus wilkitzkii</i>	3	–	3.3	–
Melitidae		3	0.0	2.2	0.1
	<i>Quasimelita quadrispinosa</i>	1	0.0	1.1	0.0
	<i>Melita</i> sp.	2	0.0	2.2	0.1
	<i>Melita dentata</i>	2	0.0	2.2	0.1
Oedicerotidae		329	0.4	4.3	1.6
	<i>Acanthostephea malmgreni</i>	5	0.0	4.3	0.1
Unidentified Oedicerotidae		5	0.0	4.3	0.1
Corophiidae		15	0.0	1.1	0.1
	<i>Crassikorophium</i> sp.	593	0.0	7.6	1.7
Ischyroceridae		12	0.0	3.3	0.2
	<i>Ischyrocerus</i> sp.	12	0.0	3.3	0.2
Priscilliniidae		19	0.0	4.3	0.4
	<i>Priscillina</i> sp.	19	0.0	4.3	0.4
Eusiridae		1	0.0	1.1	0.0
	<i>Rhachotropis aculeata</i>	1	0.0	1.1	0.0
Calliopiidae		1	0.0	1.1	0.0
	<i>Weyprechtia heuglini</i>	1	0.0	1.1	0.0
Mysida		3549	1.2	56.5	14.4
	<i>Mysis</i> spp.	3545	0.7	54.3	13.2
	<i>Neomysis</i> sp.	1	0.0	1.1	0.0
Copepoda		12387	0.2	66.3	22.8
Calanoida		87	0.0	3.3	0.4
	<i>Calanus</i> sp.	1	0.0	1.1	0.0
	<i>Calanus hyperboreus</i>	1076	0.0	7.6	2.3
	<i>Metridia longa</i>	5	–	2.2	–
	<i>Paraeuchaeta glacialis</i>	1	0.0	1.1	0.0
Cyclopoida		1	–	1.1	–
	Chondracanthidae	1	–	1.1	–
	Unidentified Cyclopoida	1	–	1.1	–
Siphonostomatoida		345	0.0	13.0	1.8
	<i>Clavella adunca</i>	1	0.0	1.1	0.0
	Lernaeopodidae	1	0.0	1.1	0.0
Harpacticoida		19	–	5.4	–
Other Invertebrate		206	0.3	50.0	4.4
Isopoda spp.		12	0.0	6.5	0.2
	Unidentified Bopyridae	3	0.0	1.1	0.1
	<i>Dajus mysidis</i>	7	–	3.3	–
	<i>Gnathia</i> sp.	2	0.0	2.2	0.1

TABLE 2 – *continued*: Count, weight, and frequency of occurrence for prey species found in the stomachs of ringed seals (*Pusa hispida*) harvested in the eastern Beaufort Sea, 2015–18 (n = 92). Global Importance (IG) is an index that incorporates all of these measures in its assessment of contribution by species (see equation in text; Moreno and Castro, 1995). Taxa in bold are the broad taxonomic groups used in the descriptive analysis (e.g., Fig. 2). Note that the otolith sizes indicate that the majority of Arctic cod are small in size while saffron cod and “Other fish” and are more variable but generally much larger.

	Count ¹	% Weight ²	% Occurrence ³	IG	
Decapoda spp.	60	0.3	17.4	1.8	
	<i>Argis</i> sp.	2	0.0	2.2	0.1
	<i>Argis dentata</i>	1	0.0	1.1	0.1
	<i>Sabinea septemcarinata</i>	29	0.1	5.4	0.7
	Unidentified Crangonid	4	0.0	4.3	0.3
	<i>Eualus</i> sp.	11	0.0	2.2	0.2
	<i>Eualus gaimardii</i>	4	0.0	2.2	0.2
	<i>Spirontocaris spinus</i>	2	0.0	2.2	0.2
	<i>Hyas</i> sp.	2	0.0	2.2	0.1
	<i>Hyas coarctatus</i>	3	0.0	1.1	0.0
Cumacea spp.	51	0.0	13.0	0.7	
	<i>Eudorella</i> sp.	1	–	1.1	–
	<i>Lamprops</i> sp.	2	–	2.2	–
	<i>Lamprops fuscatus</i>	35	0.0	8.7	0.4
Euphausiacea	Unidentified Euphausiidae	?	–	–	–
Ostracoda		26	0.0	13.0	0.4
Branchiopoda	Diplostraca	1	0.0	1.1	0.0
Insecta	Diptera	1	0.0	1.1	0.0
Annelida		1	0.0	1.1	0.0
Polychaeta spp.		2	0.0	2.2	0.0
	Pectinariidae	1	0.0	1.1	0.0
Ophiuroidea		1	–	1.1	–
Mollusca spp.		47	0.0	23.9	1.0
	Cephalopoda	1	0.0	1.1	0.1
	Octopoda	2	0.0	2.2	0.1
	Bivalvia	23	0.0	14.1	0.5
	Gastropoda	18	0.0	10.9	0.4

¹ Count = Number # of prey *i*. For each species of fish, count was # identifiable remains + 0.5 × # sagittal otoliths (+1 if there was an odd count).

² Percent (%) weight = wet weight of prey *i* (g)/ total wet weight of stomach contents (prey only in g).

³ Percent (%) occurrence = # of stomachs with prey *i* present/ total # of non-empty stomachs. Sixteen empty stomachs, which contained only non-prey items such as rocks, parasites or mucus, were excluded from analysis.

summer and autumn. An important seasonal effect is that capelin became a larger part of the diet in the autumn, at which time its occurrence was no longer significantly different than Arctic cod or other invertebrates, but still remained lower in abundance than amphipods. Seals at Sachs Harbour ate mostly amphipods, Arctic cod, other invertebrates, sand lance, and some other fish, but rarely ate capelin, other cod, or sculpins; amphipods and other invertebrates were eaten most frequently. Every seal at Ulukhaktok with food in their stomach ate Arctic cod and other invertebrates, and most also ate amphipods. Sand lance, sculpins, and other fish were also common in their diets, but capelin was never found at Ulukhaktok, and other cod were only found once.

Body Condition Results

Blubber thickness tended to increase with seal age ($F_{2,163} = 14.04$, $p < 0.01$); pups had significantly thinner blubber than both juveniles ($p = 0.03$) and adults ($p < 0.01$), but juveniles and adults were not significantly different ($p = 0.58$). The average blubber thickness for pups was 3.1

± 0.1 cm (median = 3.0 cm), for juveniles was 3.9 ± 0.2 cm (median = 3.9 cm), and for adults was 4.2 ± 0.1 cm (median = 4.0 cm; Fig. 3). For seals sampled at Paulatuk, blubber thickness was affected by season ($F_{2,73} = 16.84$, $p < 0.01$), age ($F_{2,73} = 11.45$, $p < 0.01$), and the interaction between season and age ($F_{4,73} = 5.10$, $p < 0.01$). Adult seals sampled in autumn at Paulatuk had thicker blubber than adults sampled in summer and spring ($p < 0.01$), whereas juveniles and pups showed no difference in blubber thickness in the different seasons ($p > 0.90$; Table 4). Adult seals at Paulatuk had thicker blubber than pups ($p < 0.01$), but blubber in juveniles was not significantly different than in either adults ($p = 0.18$) or pups ($p = 0.27$). Similarly, at Sachs Harbour, adults had significantly thicker blubber than pups ($p = 0.02$), but blubber in juveniles (n = 4) was not significantly different from adults ($p = 0.92$) or pups ($p = 0.59$).

Influence of Diet on Condition

Blubber thickness had a significant, positive relationship with both the number of Arctic cod (slope = 0.63 ± 0.14 log₁₀ Arctic cod, $t_{81} = 4.59$, $p < 0.01$) and the number of other

TABLE 3. Mean \pm SE and median (med) counts (3a) and weight in g (3b) of prey items in stomachs of harvested ringed seals (*Pusa hispida*). The number of stomachs (n) is shown in parentheses. na = no stomachs collected for that site or period.

Site	Spring	Summer	Autumn	Winter	Site total
3a) Counts of prey items:					
Paulatuk	2 (1)	648 \pm 110 med = 827 (16)	824 \pm 210 med = 434 (32)	na	750 \pm 142 med = 498 (49)
Sachs Harbour	na	113 \pm 56 med = 34 (24)	na	na	113 \pm 56 med = 34 (24)
Ulukhaktok	na	na	na	322 \pm 100 med = 230 (12)	322 \pm 100 med = 230 (12)
Total	2 (1)	327 \pm 69 med = 60 (40)	824 \pm 210 med = 434 (32)	322 \pm 100 med = 230 (12)	510 \pm 90 med = 220 (85)
3b) Weight (g) of prey items:					
Paulatuk	0.4 \pm 0.2 med = 0.2 (7)	244.4 \pm 63.7 med = 140.2 (23)	165.0 \pm 29.8 med = 116.2 (33)	na	175.7 \pm 29.2 med = 107.1 (63)
Sachs Harbour	na	28.6 \pm 10.2 med = 8.9 (30)	na	na	28.6 \pm 10.2 med = 8.9 (30)
Ulukhaktok	5.4 (1)	na	na	37.7 \pm 9.0 med = 33.8 (14)	35.6 \pm 8.6 med = 31.6 (15)
Total	1.0 \pm 0.7 med = 0.2 (8)	122.2 \pm 31.6 med = 23.7 (53)	165.0 \pm 29.8 med = 116.2 (33)	37.7 \pm 9.0 med = 33.8 (14)	115.4 \pm 18.6 med = 34.7 (108)

cod (slope = $0.69 \pm 0.28 \log_{10}$ other cod, $t_{81} = 2.48$, $p < 0.01$) found in the stomach of those seals ($R^2_{adj} = 0.22$).

DISCUSSION

Our results on ringed seal diet and condition are limited in time span, sample size, and geography with respect to a species with a circumpolar distribution, but they do provide a useful snapshot of year-round diet and condition for the Amundsen Gulf region between 2015 and 2018. Comparing these results with earlier records from the same area (e.g., Smith, 1987), as well as other regions, provides insight into potential changes in ringed seal diet and may also help to predict the ability of ringed seals to adapt to a warming Arctic marine ecology. One of the first things that stands out in our data is the lack of pups (young of the year) at both Paulatuk and Sachs Harbour during 2015. If the hunter-based samples are representative of the population, it raises the question of a potentially widespread reproductive failure in this year, similar to those documented by Harwood et al. (2020) in other years among ringed seals from the Ulukhaktok area. Harwood et al. (2020) found that the percentage of pups in the harvest tracked ovulation rate but their data did not indicate anything unusual for 2015 in the relatively nearby Ulukhaktok area. Although nothing diet- or condition-related stood out in our 2015 data, our inference abilities are limited by sample size. The previous year of 2014, however, was an anomalous year for prey and predator species in the region with unusually high numbers of beluga whales harvested in eastern Amundsen Gulf near Ulukhaktok as well as these whales foraging primarily on sand lance rather than Arctic cod (Loseto et al., 2018).

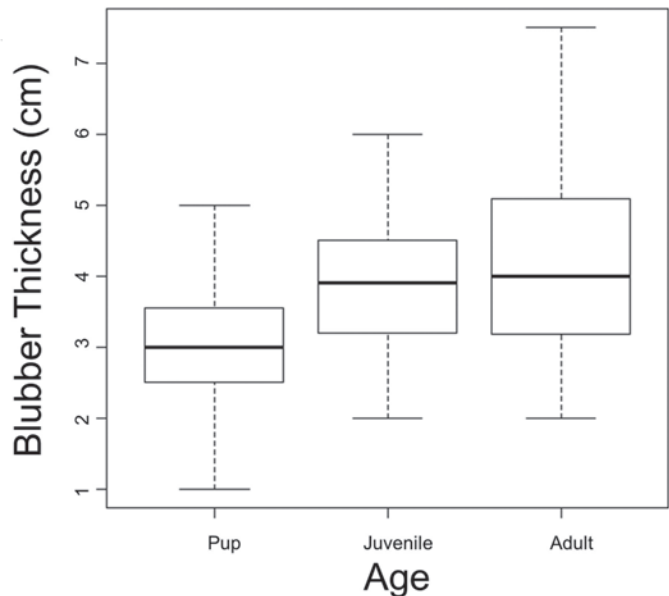


FIG. 3. Blubber thickness by age class. Blubber thickness (in cm) was measured at the sternum. Age class groupings are: pups (< 1 year), juveniles (1–5 years), and adults (> 5 years). Box plots show the median, 1st, and 3rd quartiles (25th and 75th percentiles), and minimum and maximum values.

The time of year and frequency when seals were not foraging, as indicated by empty stomachs, varied. Our data, although representative of but not evenly distributed across all months of the year, found a total proportion of 14.8% of stomachs were completely empty (< 1 g of prey present). Stomachs were most likely to be empty during the spring, the period of breeding and molt (Tables 3a and b), as well as the time of year when seals' blubber layers were minimal (Table 4). Our results agree with Smith's (1987) findings

TABLE 4. Mean \pm SE and median (med) blubber thickness (cm) of harvested ringed seals (*Pusa hispida*). The number of harvested ringed seals (n) is shown in parentheses. na = no harvested ringed seals for that site or period.

Site	Spring	Summer	Autumn	Winter	Site Total
Paulatuk	3.42 \pm 0.13 med = 3.5 (15)	3.42 \pm 0.16 med = 3.5 (32)	4.66 \pm 0.24 med = 5.08 (36)	na	3.96 \pm 0.14 med = 3.81 (83)
Sachs Harbour	na	3.39 \pm 0.10 med = 3.5 (70)	na	na	3.39 \pm 0.10 med = 3.5 (70)
Ulukhaktok	5 (1)	na	na	5.5 \pm 0.35 med = 5.75 (15)	5.47 \pm 0.33 med = 5.5 (16)
Total	3.53 \pm 0.16 med = 3.5 (16)	3.4 \pm 0.13 med = 3.5 (102)	4.66 \pm 0.24 med = 5.08 (36)	5.5 \pm 0.35 med = 5.75 (15)	3.86 \pm 0.10 med = 3.81 (167)

from a larger sample size from the same region. However, due to the known positive relationship between blubber thickness and age (Fig. 3) and the unequal representation of age groups across sites and seasons (primarily a lack of pup samples during winter in Ulukhaktok), blubber thickness during winter may be overestimated (Table 4). The proportion of empty stomachs was similar in the Alaska region (Bering and Chukchi Seas; Quakenbush et al., 2011). A number of other studies from Alaska, the eastern Canadian Arctic, and Greenland (Siegstad et al., 1998; Holst et al., 2001; Dehn et al., 2007; Chambellant et al., 2013) found that empty stomachs were more common (45%–86%), including during the autumn when feeding appeared to be maximal (Tables 3a and b; Smith, 1987; Chambellant et al., 2013).

Previous studies on ringed seals show a pattern where diet diversity varies widely across their range but is much less variable within specific regions (McLaren, 1958; Weslawski et al., 1994; Siegstad et al., 1998; Holst et al., 2001). A comparison of fatty acid signatures across the Canadian Arctic supports this pattern (Thiemann et al., 2007). In the same region where we sampled Smith's (1987) research during the 1980s found that ringed seal stomachs mostly contained a single prey type (31%) or two prey types (30%), usually a crustacean and Arctic cod. Which prey type depended on the time of year, with Arctic cod being more prevalent after freeze-up and crustaceans during open-water periods. In contrast, our findings for the same region (although sampling over a broader area) indicated a more diverse diet even though the key species of fish (Arctic cod) and invertebrates (*Themisto libellula*) remain important. We also found distinct differences in location (e.g., capelin primarily limited to Paulatuk area diets). In the eastern Canadian Arctic, Chambellant et al. (2013), from a larger sample covering a longer time period, found even less diversity with a minimum in the spring. In Greenland, Siegstad et al. (1998) also found low diversity with a total of 21 different prey species identified. In the Svalbard area, Weslawski et al. (1994) found ringed seals typically prey on no more than 10–15 prey species, with a focus on only two to four species. Bengtsson et al. (2020) more recently found similar results for the same Barents Sea region. In contrast, Quakenbush et al. (2011), whose sampling range extended

into the subarctic Bering Sea region, found a high level of diversity (155 fish prey species, 99 common) suggesting an inverse latitudinal gradient in diet diversity. Yurkowski et al. (2016) also showed a latitudinal gradient in diet diversity by comparing multiple populations of ringed seals and beluga whales using stable isotope analyses, as well as an apparent climate change-driven shift in diet diversity over time (Yurkowski et al., 2018).

Consistent with the overall high diversity of ringed seal diets across their range but in contrast to this species being widely considered a pelagic predator, there are many accounts of benthic foraging being an important component of ringed seal diets (Lowry et al., 1980; Smith, 1987; Weslawski et al., 1994; Young and Ferguson, 2013; this study). Young and Ferguson (2013; 2014) found that patterns of $\delta^{13}\text{C}$ indicate pelagic feeding during the open-water season (August–December), increased benthic foraging during the period of ice cover (January–May), and a period of fasting during the spring molt (June–July). Following the molting and fasting period, the open-water season is considered an important feeding period for ringed seals as they replenish fat and energy stores in preparation for the coming winter (McLaren, 1958; Smith, 1987; Ryg et al., 1990). The change in blubber mass between peak condition in January and the lowest condition in June through August found by Young and Ferguson (2014) agrees with our findings of seasonal variation (Table 4). In terms of the pattern and degree of change in blubber thickness over seasons, Amundsen Gulf ringed seals appear to follow the pattern of peripheral as compared to core seals described in high and low eastern Canadian Arctic populations (Ferguson et al., 2020). Whether this phenological pattern and the associated life history traits, including growth and age of maturity, will change with environmental conditions or whether the pattern is reflective of a specific and stable ecotype is an important question.

How ringed seals will respond to a changing ecosystem with increased temperatures is one of the most pressing current questions (Laidre et al., 2008). Crawford et al. (2015) found a measureable diet shift to fish from invertebrates over a roughly 30-year period, consistent with increasing open water and a transition from a largely benthic to a pelagic ecosystem. In the Barents Sea region,

Bengtsson et al. (2020) found that despite substantial changes in the fish and zooplankton communities and the addition of new species in ringed seal diets, their diets were largely consistent with past records. Our results indicate that invertebrates, with among the highest scores in the global importance index (Table 2), still play an important role in ringed seal diets. Furthermore, when compared to those of Smith (1987), our results show an increasingly diverse diet with respect to both fish and invertebrate species. This finding is consistent with the observed increase in subarctic fish species moving north in response to warming temperatures (Mueter et al., 2009; Grebmeier, 2012; Crawford et al., 2015). Such a trend may be common throughout the Arctic but regional differences in ringed seal diet diversity and fish assemblages limit us to regional temporal comparisons. For example, although sand lance have been known to be a regular part of ringed seal diet in the eastern Canadian Arctic for some time (McLaren, 1958; Chambellant et al., 2013), they appear to be a recent addition in the eastern Beaufort Sea region. Other recent additions in the eastern Beaufort region include capelin and saffron cod, which along with sand lance, are also recent additions to the diets of other species in the area (e.g., beluga; Loseto et al., 2018). Furthermore, Harwood et al. (2015) provide evidence for the Amundsen Gulf that Arctic cod abundance has been decreasing, causing several knock-on effects including Arctic char (*Salvelinus alpinus*) shifting their diet to capelin and sand lance, beluga whales shifting their diet to other forage fish, and black guillemots (*Cepphus grylle*) consuming more sculpin.

Many of the new prey species have high nutritional values, with energy content comparable to those of Arctic cod and the principal invertebrates consumed by ringed seals (e.g., Chambellant et al., 2013: Supplement), although it is important to keep in mind that the values may vary for the same species in the western Arctic. Yet, long-term sampling by Harwood et al. (2020) indicates a slow but consistent decrease in blubber thickness for Amundsen Gulf ringed seals, which suggests that either the current diet is less nutritionally sufficient or that other life history stressors are significant. Other stressors could include changing weather, with increased storms in summer and rain in winter, new or increased numbers of competitors and predators (e.g., killer whales, sharks), and increased pathogens (Laidre et al., 2008, 2015; Kovacs et al., 2012; VanWormer et al., 2019).

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