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Ringed seal (*Pusa hispida*) diet on the west coast of Spitsbergen, Svalbard, Norway

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Olof Bengtsson

Bio-3950 Master's thesis in Biology, Marine Ecology and Resource Biology May 2019

Foreword

This thesis is written following the “instructions for authors” for the journal “Polar Biology”. For improved readability, figures and tables have been incorporated in the text and 12pt font size has been used for the main text.

I am immensely grateful to my supervisors at the Norwegian Polar Institute, Christian Lydersen and Kit M. Kovacs for including me in their important research on marine mammals in the Arctic. It has been an invaluable experience to work with the best! Not only have my knowledge and academic skills benefited greatly from this, I have also been provided with unique opportunities to accompany Kit and Christian in their fieldwork on Svalbard. It has all been unforgettable – especially the stay in Pungvika.

I would also like to thank my supervisor from the University of Tromsø, Ulf Lindström, for taking time to guide me through the jungle of statistical analyses, and for encouraging me in my work. Lotta Lindblom from the Institute of Marine Research guided me through the intestines and their contents.

A big thank you goes out to the Biodiversity group at the Norwegian Polar Institute for being supportive and inclusive during my studies. It has been a privilege to be a part of the team! I especially thank my fellow master students for sharing the office, pain, frustration and laughs with me, and Charmain Hamilton for sharing R-codes and other valuable inputs.

Finally, thank my loved ones for “holding my back” and believing in me.

The sages who have compassed sea and land,
Their secret to search out, and understand -
My mind misgives me if they ever solve
The scheme on which this universe is planned

- Omar Kayyam, translated by Edward Henry Whinfield

Front-page photo taken by: Kit M. Kovacs and Christian Lydersen, Norwegian Polar Institute

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Abstract The diet of 99 coastal-feeding ringed seals (*Pusa hispida*), collected in western Spitsbergen, Svalbard (Norway), was analysed via identification of hard-parts in the contents of their gastrointestinal tracts (GITs). The study animals where shot either in spring (n = 30; April-July) or autumn (n = 69; August-October) during four consecutive years (2014-2017). Thirty different prey types were identified in total, but most individual seals (55.6%) had consumed between 2-4 different prey types. Polar cod (*Boreogadus saida*) dominated in terms of relative biomass (B_i = 60.0%) and frequency of occurrence (FO_i = 86.9%) in the diet, followed by pricklebacks (Stichaeidae; B_i = 23.4%; FO_i = 79.8%). GITs collected in spring contained a lot of krill (*Thysanoessa* spp.) in adults of both sexes and in juvenile seals, but crustaceans were not important prey in terms of biomass. Redundancy analysis (RDA) revealed that year was the only significant predictor explaining variance in diet composition (F-ratio = 4.96, P = ≤ 0.005); i.e. blubber content and sex/age group were not significant. Atlantic herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) occurred in the diet in small quantities; these temperate fish species have not previously been documented in the ringed seals' diet on Svalbard. Atlantic cod (*Gadus morhua*) had the highest B_i (9.2%) among Atlantic prey types. However, despite major changes in the last decade in the fish and zooplankton community in western Svalbard, and consumption of some few temperate prey types by ringed seals, the Arctic seal's diet continues to be dominated by Arctic prey types, especially polar cod.

Keywords Arctic, Climate change, Global warming, Marine foodwebs, Prey preferences, Polar cod

Introduction

The ringed seal (*Pusa hispida hispida*) is an important species in Arctic food-webs, both as a predator of many fish and invertebrate species (McLaren 1958; Labansen et al. 2007; Crawford et al. 2015) and as a primary prey species for polar bears (*Ursus maritimus*; Stirling and Øritsland 1995; Iversen et al. 2013) and coastal people in the Arctic (Teilmann and Kapel 1998). In addition, it is part of the diet for a wide variety of other species, such as Greenland sharks (*Somniosus microcephalus)*, walruses (*Odobenus rosmarus*), Arctic foxes (*Vulpes lagopus*), glaucous gulls (*Larus hyperboreus*), and killer whales (*Orcinus orca*) (Smith 1976; Lowry and Fay 1984; Lydersen and Smith 1989; Melnikov and Zagrebin 2005; Leclerc et al. 2012). The ringed seal is a circumpolar species and one of the most abundant seal species in the Arctic (Reeves 1998). Although few actual abundance estimates exist, and no time series of population trends have been documented, there is concern for the status of ringed seals with regard to global warming and sea ice declines (e.g. Laidre et al. 2015). Local declines have been reported in some areas (e.g. Ferguson et al. 2017) and are suspected in other regions (Hamilton et al. 2019).

Ringed seals give birth in snow lairs on the surface of sea ice in coastal areas with land-fast ice and in some areas, on drifting pack ice (McLaren 1958; Finley et al. 1983; Wiig et al. 1999). In the Svalbard Archipelago, ringed seals are generally born in early April. Lactation lasts for about 39 days (Hammill et al. 1991), after which females mate. During the reproductive season, adult males actively defend territories that encompass the lair complexes used by several females (Ryg and Øritsland 1991; Lydersen 1998). Moulting takes place post breeding, usually starting in late May for the period of approximately one month, though moulting can extend through the end of July (Ryg et al. 1990a; Gjertz et al. 2000; Freitas et al. 2008). Both the breeding season (including lactation and territorial defence) and the moulting period are energetically costly. Sexually mature ringed seals are generally in negative energy balance from April to July, losing a substantial amount of their stored blubber during this period (Ryg et al. 1990a; Hammill et al. 1991; Ryg and Øritsland 1991; Smith et al. 1991), despite some feeding on sympagic prey during this time (Lydersen and Kovacs 1999). After moulting, Svalbard ringed seals remain tied to ice, travelling offshore, to areas along the ice edge (Freitas et al. 2008; Hamilton et al. 2015; Lone et al. 2019), or remaining in the fjords, where they have glacier ice resting platforms and concentrations of prey taking advantage of up-welling from the glaciers (Hartley and Fisher 1936; Freitas et al. 2008; Lydersen et al. 2014; Hamilton et al. 2016).

Arctic sea ice has decreased dramatically in recent decades and predictions for the future suggest that this will continue to be the trend (Wang and Overland 2009; Overland and Wang 2010; IPCC 2014; Bilt et al. 2019). This raises concern for ringed seal populations throughout the Arctic (Tynan and DeMaster 1997; ACIA 2005; Simmonds and Isaac 2007; Laidre et al. 2008; Kovacs et al. 2011; Hamilton et al. 2015; Laidre et al. 2015). Nowhere is this sea ice decline more profound than in the Barents Sea region, including the areas around the Svalbard Archipelago (Laidre et al. 2015; Lind et al. 2018), especially along the west coast of Spitsbergen. The North Atlantic Current (NAC) brings warm, saline Atlantic Water (AW) from the Gulf Stream in to the Arctic Ocean via the Barents Sea. One of the main currents carrying this water northward is the West Spitsbergen Current (WSC), which runs along the coastal shelf slope, west of Spitsbergen (Tverberg et al. 2014). AW from the NAC has recently warmed markedly; AW was warmer at the beginning of this century than it has been during the last 2000 years (Spielhagen et al. 2011). Both the warmer temperatures of the WSC and increased inflow of this water into the fjords on the west coast of Spitsbergen, because of changing and more intense winds, has resulted in reduced sea ice formation (Cottier et al. 2005; Tverberg et al. 2014). In addition, the glaciers in Svalbard are experiencing a net-loss of mass due to the warmer climate (Nuth et al. 2010). This loss of mass is greatest for tidewater glaciers (Błaszczyk et al. 2009; Nuth et al. 2013) and many of these glaciers, whose fronts meet the ocean, are retreating onto land (Lindbäck et al. 2018; Bilt et al. 2019). Thus, ringed seals are likely to lose this important feeding and resting habitat in Svalbard (Hamilton et al. 2016).

Changes linked to the altered water mass regime around Svalbard are being seen in the marine ecosystem, with an increased presence of Atlantic species in the food web (Søreide et al. 2013; Berge et al. 2015; Fossheim et al. 2015; Kortsch et al. 2015; Brand and Fischer 2016; Misund et al. 2016). Potential consequences of this change for ringed seals are unknown. However, there is concern that replacing the generally lipid-rich Arctic prey species with less lipid-rich Atlantic prey species will be negative for the seals and other Arctic top predators (but also see Renaud et al. 2018).

Changes have been documented in ringed seal behaviour concomitant with the ice changes over recent decades. Coastal ringed seals have retracted into glacier front habitats, and exhibit much smaller home ranges than previously following the collapse of the sea ice in 2006 (Hamilton et al. 2016). Ringed seals that travel to the ice edge north of Svalbard must travel longer distances to reach the ice and when they get into ice covered areas they dive more, rest less and exhibit less area-restricted search in these areas, suggesting that they must search more broadly and that they encounter less concentrated prey schools (Hamilton et al. 2015). Additionally, they dive less frequently to just beneath the ice, suggesting that less sympagic prey are available now compared to a decade ago (Hamilton et al. 2015). Changes in spatial distribution patterns have also been documented for white whales (*Delphinapterus leucas*) in Svalbard, another fish feeding marine mammal (Vacquié-Garcia et al. 2018). White whales still use glacier fronts as a feeding ground, but they spend more time out in the fjords than before, presumably targeting recent influxes of Atlantic prey (Vacquié-Garcia et al. 2018, Hamilton et al. 2019).

The diet of ringed seals varies between regions (McLaren 1958; Lowry et al. 1980; Thiemann et al. 2007), as well as seasonally and inter-annually within regions (Węsławski et al. 1994; Siegstad et al. 1998). On the west coast of Spitsbergen, Svalbard, previous studies have shown that the ringed seal diet is dominated by polar cod (*Boreogadus saida*), with varying amounts of other fish species, such as pricklebacks (Stichaeidae), sculpins (Cottidae) and sebastids, in addition to a variety of invertebrate species e.g. *Themisto libellula, Pandalus borealis, Gammarus wilkitzkii* and krill (*Thysanoessa* spp.; Gjertz and Lydersen 1986; Lydersen et al. 1989; Węsławski et al. 1994; Labansen et al. 2007). A recent study of ringed seal diet in this same region, using stable isotope analysis of ringed seal whiskers collected before and after the change in the oceanographic regime occurred suggested that a dietary shift has taken place following the sea ice collapse (Lowther et al. 2017). However, whether this change is due to an altered diet of ringed seals or alternatively an altered diet of their prey, cannot be distinguished through this method. A direct study of ringed seal diet in this region is therefore essential. The purpose of the present study was therefore to study the diet of ringed seals, directly, via analyses of gastrointestinal tracts, to explore whether the diet of this important Arctic species has been impacted by the physical environmental- or food web changes that have taken place in Svalbard over the past decade.

Materials and methods

Gastrointestinal tracts (GITs) from 99 ringed seals were collected from animals shot by local sport hunters, from April to October during the years 2014-2017, at six locations in Isfjorden (Adolfbukta, Borebukta, Ekmanfjorden, Tempelfjorden, Yoldiabukta and Ymerbukta) and in Van Mijenfjorden on the west coast of Spitsbergen (Fig. 1). In the field, animals were weighed to the nearest 0.5 kg using a Salter 100-kg spring scale and standard body length was measured in a straight line from nose to tail to the nearest cm (Scheffer 1967). Blubber thickness to the nearest mm was measured dorsally at a position about 60% of the body length from behind the snout towards the tail, where blubber thickness is most variable (Ryg. et al. 1988). GITs were removed from the seal carcasses and tied shut around the oesophagus and the rectum before being frozen at -20°C until analysis. Reproductive organs and canine teeth (as well as various other tissues – for other studies) were collected and stored frozen at -20°C. In the laboratory, maturity of males was determined by the size of the testes (Ryg et al. 1991). Females were considered mature if *corpus luteum* or *c. albicans* were present in the ovaries (McLaren and Smith 1985), or if they were pregnant. Age was determined by counting cementum layers of decalcified and stained longitudinal sections of canines from the lower jaw (Lydersen and Gjertz 1987).

Stomach, small intestine and large intestine were treated separately when their contents were handled in the lab. After thawing, GIT sections were cut open and their contents were washed with cold water and poured over a series of three connected sieves with mesh sizes of 2 mm, 1 mm and 0.5 mm (top to bottom). Otoliths and other prey materials that stuck to the containment bowl were collected directly. The contents on the sieve system were washed carefully with cold water and otoliths and invertebrate remains were collected. All collected material was preserved in 96% ethanol and subsequently examined under a Leica MZ6 stereomicroscope with an ocular micrometer. Sagittal fish otoliths (hereafter otoliths) and crustaceans were identified to the lowest possible taxon with the help of the identification guides by Enckell (1980) and Härkönen (1986) and a reference collection of otoliths from fish caught on surveys around Svalbard and in the Barents Sea, provided by the Institute of Marine Research (IMR), Tromsø, Norway. The number of otoliths found for each species in each GIT was divided by two (and then rounded up to a whole number - assuming both otoliths were ingested for each fish). Otoliths with minimal signs of erosion, found in the stomach and small intestine were measured along the longest axis parallel to the sulcus (Härkönen 1986). Due to digestive erosion, otoliths from the large intestine were not measured. Fish length and mass, on a species specific basis, were back-calculated using otolith length (Härkönen 1986; Windsland et al. 2007). When possible, otoliths from one species in a given part of the GIT were sorted into left and right and paired based on length before being measured.

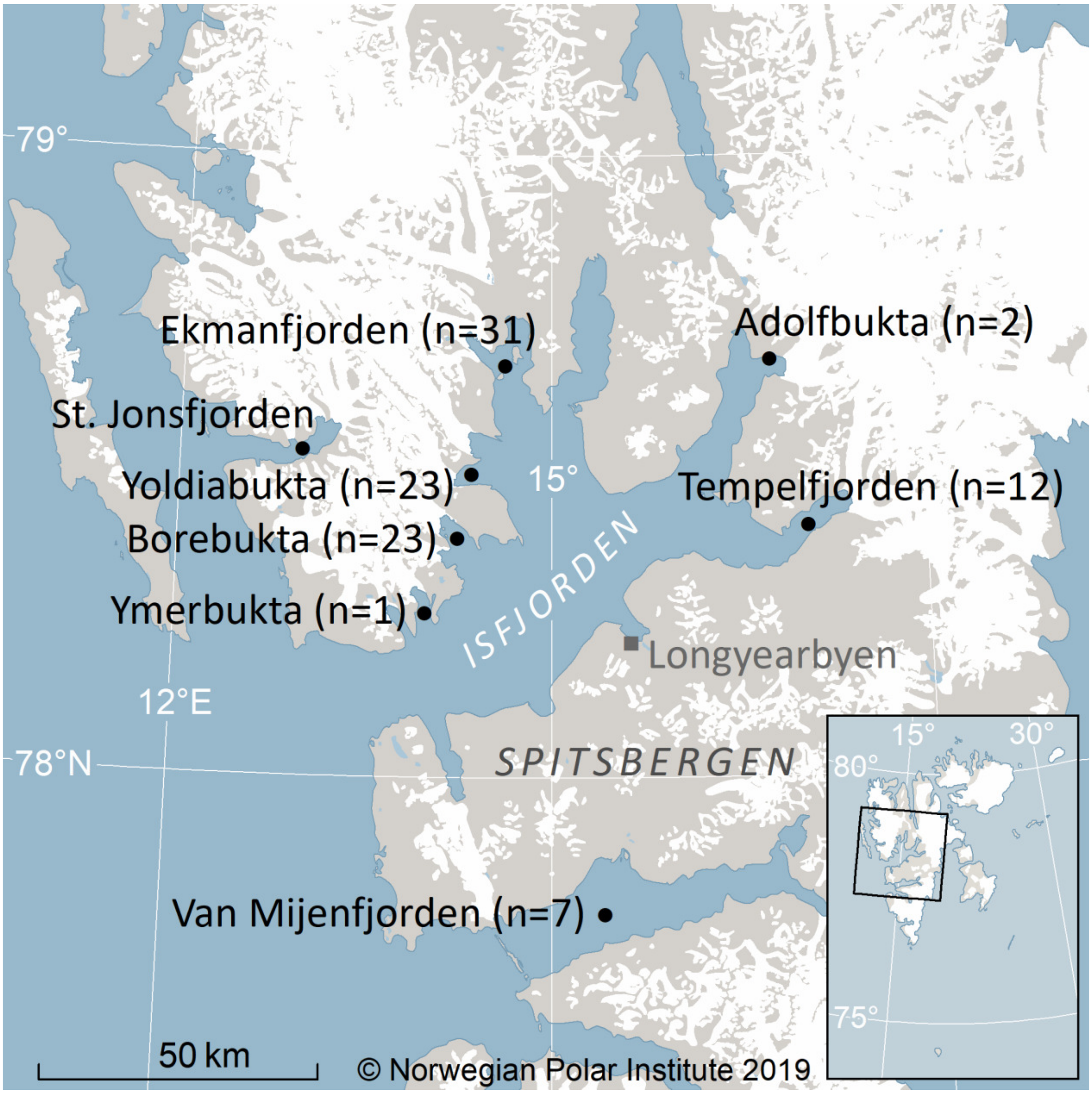

Fig. 1 Map of locations where ringed seals where sampled (2014-2017 - and other locations mentioned in the text) in Spitsbergen, Svalbard, Norway. Sample sizes are in parentheses

A subsample of ~100 otoliths were measured when the number of otoliths from one species was >100 in a given part of the GIT, assuming that the size distribution was representative for all otoliths in the sample. Otoliths in subsamples were not sorted into left and right. When estimating total biomass for each prey type, eroded and damaged otoliths were assumed to have the same overall size distribution as the measured otoliths from the same species in the same GIT. Biomass of various crustaceans were estimated by multiplying the number of individual of a given species found in the GITs with average masses of that species caught in trawls around Svalbard (IMR, unpublished data).

Frequency of occurrence (FO), relative frequency (N_i) and the relative proportion of biomass (B_i) of each prey item were used as diet indices (Hyslop 1980; Pierce and Boyle 1991) and calculated using following formulas: (1) $FO_i(\%) = \left(\frac{S_i}{S_t}\right) * 100$, S_i being the number of seals that had consumed prey type i and S_t the total number of seals; (2) $N_i(\%) = \left(\frac{n_i}{n_t}\right) * 100$, where n_i is the number prey type i consumed by all seals and n_t the total number of prey consumed by all seals; (3) $B_i(\%) = \left(\frac{b_i}{b_t}\right) * 100$, b_i being the total biomass off prey type i and b_t the total biomass of all estimated prey.

Percent blubber content of the seals ($C(\%)$) was used as an indicator of body condition. This variable was calculated using (4) $C(\%) = 5102 * \sqrt{\frac{L}{M}} * d + 8.53$, where L is body length in meters, M body mass in kilograms and d dorsal blubber thickness in meters (Ryg *et al.* 1990b).

Year class (YC) of polar cod was estimated based on estimated fish length (back-calculated from otolith length) based on Falk-Petersen et al. (1986). Length intervals (mm) were: YC 1 ≤ 110.5; 110.5 < YC 2 ≤ 139.5; 139.5 < YC 3 ≤ 156.6; 156.6 < YC 4 ≤ 169.0; 169.0 < YC 5 ≤ 185.5; and YC 6 > 185.5.

Samples (stomachs, small intestines and large intestines) belonging the same GITs were pooled to represent the diet of individual seals. When analysing potential seasonal differences in ringed seal diet, samples collected in the period April to July, were grouped into a “spring-sample” and samples collected in the period from August to October were grouped into an “autumn-sample”. This simplistic two-season division was performed because the total sample size of GITs in this study was small. To investigate whether prey consumed by the ringed seals were of Arctic or Atlantic origin, prey species known to be (or belonged to families that are known to have year-round residency in Svalbard) Arctic - namely: polar cod, pricklebacks, eelpouts (Zoarcidae), sculpins, snailfish (Liparidae), *Themisto libellula* and *Gammarus wilkitzkii* - were classified as Arctic. The rest of the prey species found in the GITs were classified as Atlantic species.

Potential sex/age class (adult males, adult females and juveniles of both sexes) differences in diet of the ringed seals were explored using Chi-squared tests. To better understand what factors (biotic and abiotic) drive the variation in diet composition, a constrained ordination analysis (Legendre and Legendre 1998) was conducted on prey biomass data. Because there was a linear relationship (gradient length <3) between the response matrix (diet matrix) variables and the predictor matrix, a redundancy analysis (RDA) was used for further analyses (Legendre and Anderson 1999; Corfield 2000; Lepš and Šmilauer 2003). The biomass of the five most important prey types (polar cod, pricklebacks, Atlantic cod (*Gadus morhua*), sculpins and krill were used as response variables, and year, percent blubber content and age/sex group of the seals were used as predictor variables. Year and age/sex group were defined as nominal variables. To normalize the data and dampen the effect of outliers, the response variables (diet data) were transformed prior to the analysis and, after exploring various types of data transformations (log, Hellinger and Chi-square) the Hellinger transformation was selected (Legendre and Gallagher 2001). An RDA with untransformed data is presented in Fig. S1 (Supplementary material). Model selection was done by testing predictor variables through forward selection using 1000 Monte Carlo permutations and ranking models by Akaike information criterion (AIC). Prior to statistical testing, the assumption of equal variance was made and normality was tested using Shapiro-Wilk tests. A two-sample t-test was run to investigate whether percent blubber content differed between spring and autumn. To investigate whether there was a difference in blubber content between age/sex groups, and between years for the autumn sample, a Kruskal-Wallis ranked sum test was run, followed by pairwise Kruskal-Wallis ranked tests with Bonferroni correction to detect whether groups were significantly different from each other. All statistical analyses was performed in R (version 3.5.2) and the level of significance (α) was set at 0.05.

Results

The seals in this study ranged in age from 0 (young of the year) to 33 years. The sex ratio was 52 (53%) females and 47 (47%) males. Among the females, 45 (86.5%) were sexually mature whereas for males 29 (61.7%) were mature (Table 1). Details regarding sampling and biological parameters of the seals are presented in Table S1 (Supplementary material). Two of the 99 GITs were empty and were excluded from analyses concerning diet composition. All of the other GITs (97) contained some prey remains: 70.7% of the stomachs; 81.8% of the small intestines and 86.9% of the large intestines had identifiable prey items. Otoliths were found in 92.9% of the GITs and 49.5% contained crustaceans (Table 2). The stomachs, small intestines and large intestines contained 31.78%, 45.20% and 23.02% of the otoliths respectively.

In total, 12 fish groups were recognized; seven of these were identified to the species level and five were recognizable only to the level of the family (Table 2). For crustaceans, 18 prey types were found; ten of these were identified to the species level, six to genus and two to order (Table 2). Most of the otoliths and crustacean parts were identifiable, while only 0.15% of the other fish material and 0.02% of the other invertebrate items were not identifiable. In addition to fish and crustaceans, algal fragments and small (<2 mm), empty bivalve and gastropod shells were found in 10.1%, 58.6% and 14.1% of the seals' GITs, respectively. Gastroliths were found in 61.6% of the seals. It is likely that bivalves and gastropods were secondary prey, as they are regular in the diet of pricklebacks (Pethon 2005), which were found in large numbers in the GITs of the seals. They were therefore not included in further analyses.

Table 1 Geographical distribution of ringed seals sampled on the west coast of Spitsbergen, Svalbard (2014-2017) divided into three groups based on age and sex

Seal category	**Area**							**Total**
	Ado	**Bor**	**Ekm**	**Tem**	**Van**	**Yme**	**Yol**	
Adult Females	1	12	15	3	2	0	13	46
Adult Males	0	5	9	5	3	1	6	29
Juveniles	1	6	7	4	2	0	4	24
Total	2	23	31	12	7	1	23	99

Ado, Adolfbukta; Bor, Borebukta; Ekm, Ekman; Tem, Tempelfjorden; Van, Van Mijenfjorden; Yme, Ymerbukta; Yol, Yoldiabukta

Table 2 Taxonomic grouping and ecological indices of prey found in gastrointestinal tracts from 99 ringed seals from Spitsbergen, Svalbard (2014-2017) FO_i = frequency of occurrence. N_i = relative frequency, B_i = Relative proportion of total prey biomass

Prey item				**Number of prey**	**FO (%)**	**N_i (%)**	**B_i (%)**
Pisces							
		Gadidae	*Boreogadus saida*	14 781	86.9	39.1	60.0
			Gadus morhua	231	23.2	0.61	9.2
			Pollachius virens	2	2.02	0.01	0.07
			Micromesistius poutassou	35	14.1	0.09	0.06
			Gadidae spp.[a]	13	11.1	0.03	-
		Cottidae	Cottidae spp.[b]	206	22.2	0.5	2.8
		Stichaeidae	Stichaeidae spp.[c]	4 203	79.8	11.1	23.4
		Clupeidae	*Clupea harengus*	184	15.2	0.5	0.72
		Osmeridae	*Mallotus villosus*	29	17.2	0.08	0.4
		Liparidae	Liparidae spp.[d]	47	16.2	0.1	0.09
		Zoarcidae	Zoarcidae spp.[e]	18	13.1	0.05	0.2
		Pleuronectidae	*Hippoglossoides platessoides*	3	2.02	0.01	0.05
		Unidentified		36	17.2	0.10	-
Crustacea							
	Euphausiacea	Euphausiidae	*Thysanoessa inermis*	5 309	14.05	14.03	-
			T. longicaudata	19	4.04	0.05	-
			T. raschii	6	2.02	0.02	-
			T. spp.	10 083	21.2	26.7	2.0[f]
	Amphipoda	Hyperiidae	*Themisto libellula*	1 861	17.2	4.9	0.6[g]
		Gammaridae	*Gammarus wilkitzkii*	390	15.2	1.03	0.2[h]
		Amphipoda spp.		182	3.03	0.5	0.05[i]
	Decapoda	Crangonidae	*Sabinea sarsi*	2	2.02	0.01	0.4[j]
			S. septemcarinatus	20	1.01	0.05	-
			S. spp.	74	8.08	0.20	-
			Crangon sp.	17	2.02	0.04	-
		Pandalidae	*Pandalus borealis*	15	2.02	0.04	-
			P. sp.	1	1.01	0.003	-
		Hippolytidae	*Eualus gaimardi*	40	5.05	0.1	-
			Caridion sp.	16	1.01	0.04	-
		Dexaminidae	*Atylus carinatus*	2	2.02	0.01	-
		Decapod larva		1	1.01	0.003	-
	Calanoida	Calanidae	*Calanus sp.*	1	1.01	0.003	-
	Unidentified			3	3.03	0.01	-
Sum	Pisces			19 788	91.9	52.3	96.9
	Crustacea			18 042	49.5	47.7	3.2
	All prey			37 830			

[a]Gadidae spp. otoliths were either broken or too eroded to determine species, in addition to the gadoids found in this study, this grouping might contain *Melanogrammus aeglefinus*, which is also present in the study area. [b]Two most probable species: *Myoxocephalus scorpius* and *M. quadricornis*; other possible species: *Icelus bicornis, Triglops murrayi, T. pingelii* and *Gymnocanthus tricuspis.* [c]Possible species: *Lumpenus lampretaformis, L. fabricii, Leptoclinus maculatus* and *Anisarchus medius.* [d]Probable species: *Liparis liparis, L. fabricii* and *Careproctus reinhardti*. [e]Numerous possible species e.g: *Lycodes vahli, L. frigidus, Zoarces viviparus, Gymnelus retrodorsalis* and *Lycenchelys kolthoffi.* [f]Relative proportion of biomass (B_i (%)) for all euphausids, assumed to have an average weight of 0.115 g. [g]Assumed average weight of 0.27 g. [h]Assumed average weight of 0.38 g. [i]Assumed average weight of 0.27 g. [j]B_i (%) for all adult decapods, assumed average weight of 2 g

Most (55.6%) of the seals had ingested 2-4 different prey types (range 0-11; Fig. 2). There was no significant difference in the number of prey types consumed by different age/sex groups ($\chi^2 = 3.11$, df = 6, p = 0.794).

Polar cod was the dominant prey type regardless of which diet index was used (Tables 2, 3). Pricklebacks were the second most numerous fish prey type (Tables 2, 3) and the prey type with the second highest FO_i (Table 2). In addition several Atlantic fish species were found, the most important in terms of B_i (9.2%) and FO_i (23.2%) was Atlantic cod. Other Atlantic species such as Atlantic herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*) and Capelin (*Mallotus villosus*) had FO_i between 14.1 and 17.2%. Different species of krill (*Thysanoessa* spp.) had the second highest N_i (Table 2).
Estimated lengths of 4159 polar cod, from the stomachs and small intestines of 75 seals, ranged from 36.9 to 231.2 mm (Table 3; Fig. 3a). Most of these fish belonged to YC 1 (58.7%) or YC 2 (28.4%), while approximately 4% belonged to YC 4 or higher (Fig. 3b). The different age and sex classes of seals displayed no difference in the size of polar cod that they ingested (Fig. S2, Supplementary material).

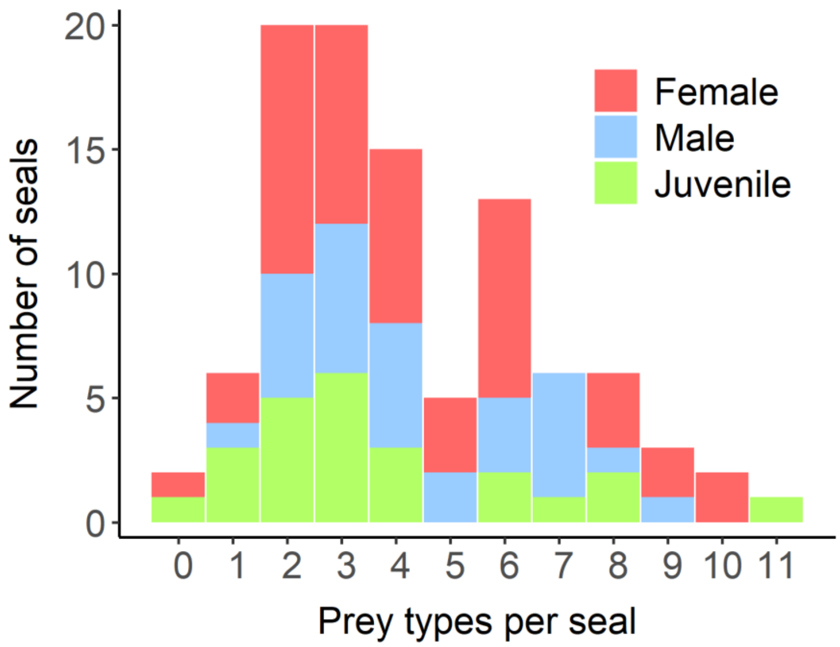

Fig. 2 Number of prey types found in gastrointestinal tracts of 99 ringed seals sampled on the west coast of Spitsbergen, Svalbard (2014-2017)

Table 3 Number of otoliths measured from each fish type and estimated lengths and biomasses and total biomass for each fish species found in gastrointestinal tracts of 99 ringed seals sampled on the west coast of Spitsbergen, Svalbard (2014-2017). N_{fish} = relative frequency of fish prey items, B_{fish} = Relative proportion of total biomass (of fish prey items)

Prey item	Measured otoliths (proportion of total prey group count (%))	Estimated fish length (mm)	Estimated biomass (g)		N_{fish} (%)	B_{fish} (%)
		Mean ± SD (Min-Max)	Mean ± SD	Total		
Boreodadus saida[a]	8 015 (27.2)	94.7 ± 37.4 (36.9 – 231.2)	3.7 ± 8.0	54 105	74.7	61.9
Gadus morhua[a,b]	362 (81.4)	117.5 ± 77.0 (32.1 - 320.3)	36.0 ± 59.3	8 326	1.2	9.5
Pollachius virens[a]	4 (100)	136.7 ± 79.3 (80.6 - 192.8)	32.6 ± 39.5	65.1	0.01	0.07
Micromesitius poutassou[a,c]	45 (75)	58.8 ± 8.7 (42.1 - 73.3)	1.4 ± 0.5	50.4	0.2	0.06
Cottidae spp.[a,d]	142 (35.6)	82.3 ± 34.8 (27.7 - 220.0)	12.2 ± 24.1	2 507	1.04	2.9
Stichaeidae spp.[e]	2 237 (26.9)	106.0 ± 30.3 (43.7 - 285.6)	5.03 ± 2.7	21 073	21.2	24.1
Clupea harengus[f]	17 (4.8)	88.1 ± 10.6 (73.4 - 104.9)	3.6 ± 1.8	653.3	0.9	0.8
Mallotus villosus[g]	25 (56.8)	130.6 ± 13.0 (109.8 - 151.0)	11.1 ± 4.3	320.8	0.2	0.4
Liparidae spp.[h]	37 (43.02)	-	1.9 ± 5.1	85.6	0.2	0.1
Zoarcidae spp.[a,i]	21 (67.7)	100.0 ± 36.7 (66.5 - 193.9)	5.5 ± 4.9	171.7	0.09	0.20
Hippoglossoides platessoids[a]	2 (40)	135	15.3	45.9	0.02	0.05
Sum	10 746 (27.4)	-	-	87 404	-	-

Sources for regressions used to back-calculate fish length (FL) and fish weight (FW) from otolith length (OL): [a]Härkönen (1986). [b]Institute of Marine Research (IMR; unpublished data), regression for OL (mm) to FL (mm), $FL = 25.76 * OL - 18.941$ $(r^2 = 0.9072)$, used when OL < 3 mm; OL to fish weight (mm) (FW), $FW = 0.0294 * OL^{3.5377}$ $(r^2 = 0.8603)$, when OL < 6 mm. [c]OL shorter for all otoliths than for otoliths used to calculate regressions for OL to FL and OL to FW based on Härkönen (1986). [d]Regressions for *Myoxocephalus Scorpius* used. 65 of the otoliths were shorter than the otoliths used to calculate regressions in Härkönen (1986). [e]IMR (unpublished data), regression for *Leptoclinus maculatus* used. $FL = 41.894 * OL + 43.661$ $(r^2 = 0.6724)$; $FW = 3.7735 * OL - 1.3259$ $(r^2 = 0.3705)$. [f]Windsland et al. (2007), $FL = 1.449 * OL^{3.238} (r^2 = 0.96)$; $FW = 49.961 * OL + 23.951$ $(r^2 = 0.95)$. [g]Windsland et al. (2007), $FL = 44.333 * OL + 41.951$ $(r^2 = 0.65)$; $FW = 1.538 * OL^{2.778}$ $(r^2 = 0.78)$. [h]IMR (unpublished data), $FW = 0.4411 * OL^{6.0788}$. [i]16 of the otoliths were shorter than the range of otolith size used to calculate the regressions

For samples collected in spring 2014 and 2015, polar cod was found only in small numbers. Krill made up more than half of the prey items numerically (Fig. 4a), but due to their small size, krill contributed little to the total biomass of prey consumed (Fig. 4b). Pricklebacks had the highest occurrence by biomass for all years during spring (Fig. 4b). Because the sample size for spring was small, and some of the spring material was collected in Van Mijenfjorden (south of Isfjorden), more detailed exploration of diet composition was only conducted on the autumn samples (spring results are presented in Fig. S3, Supplementary material).

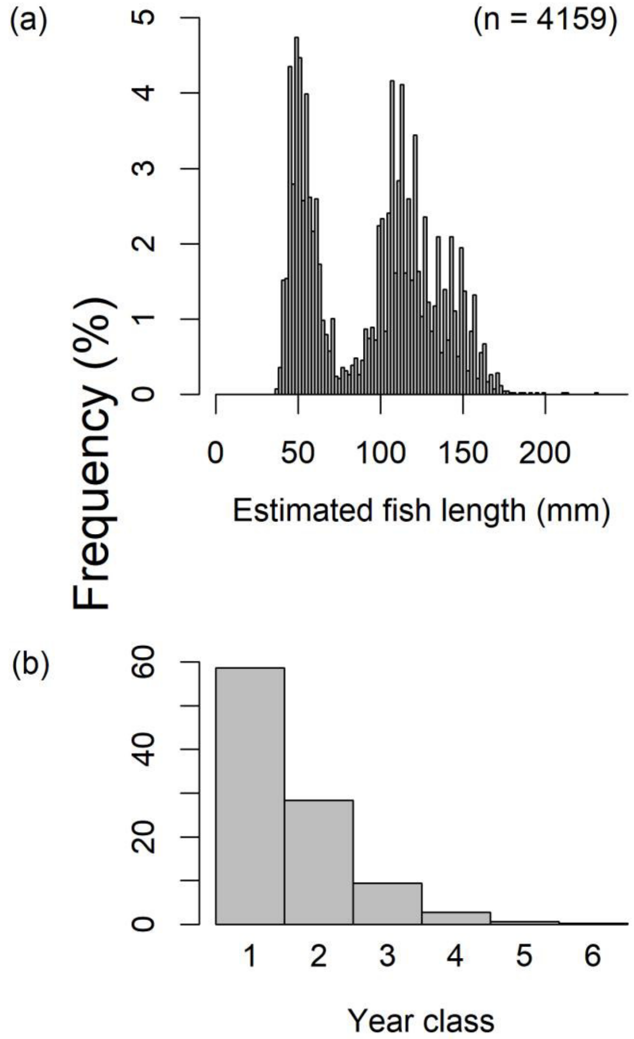

Fig. 3 Frequency distributions of polar cod found in gastrointestinal tracts of ringed seals from the west coast of Spitsbergen, Svalbard (2014-2017) (a) fish length estimated from measured otolith length and (b) year classes calculated based on estimated fish lengths

During autumn, polar cod dominated the diet in all years, except 2014, both in terms of numbers of items and biomass (Fig. 4c, d). High numbers of amphipods and krill were found in the autumn samples from 2014 and 2016, respectively (Fig. 4c), but again, due to their relative small size, these prey types contributed little in terms of biomass (Fig. 4d). Polar cod dominated the diet for all age/sex groups (Fig. 5a, b). Juveniles consumed more krill, while adults of both sexes consumed more amphipods and pricklebacks (Fig; 5a).

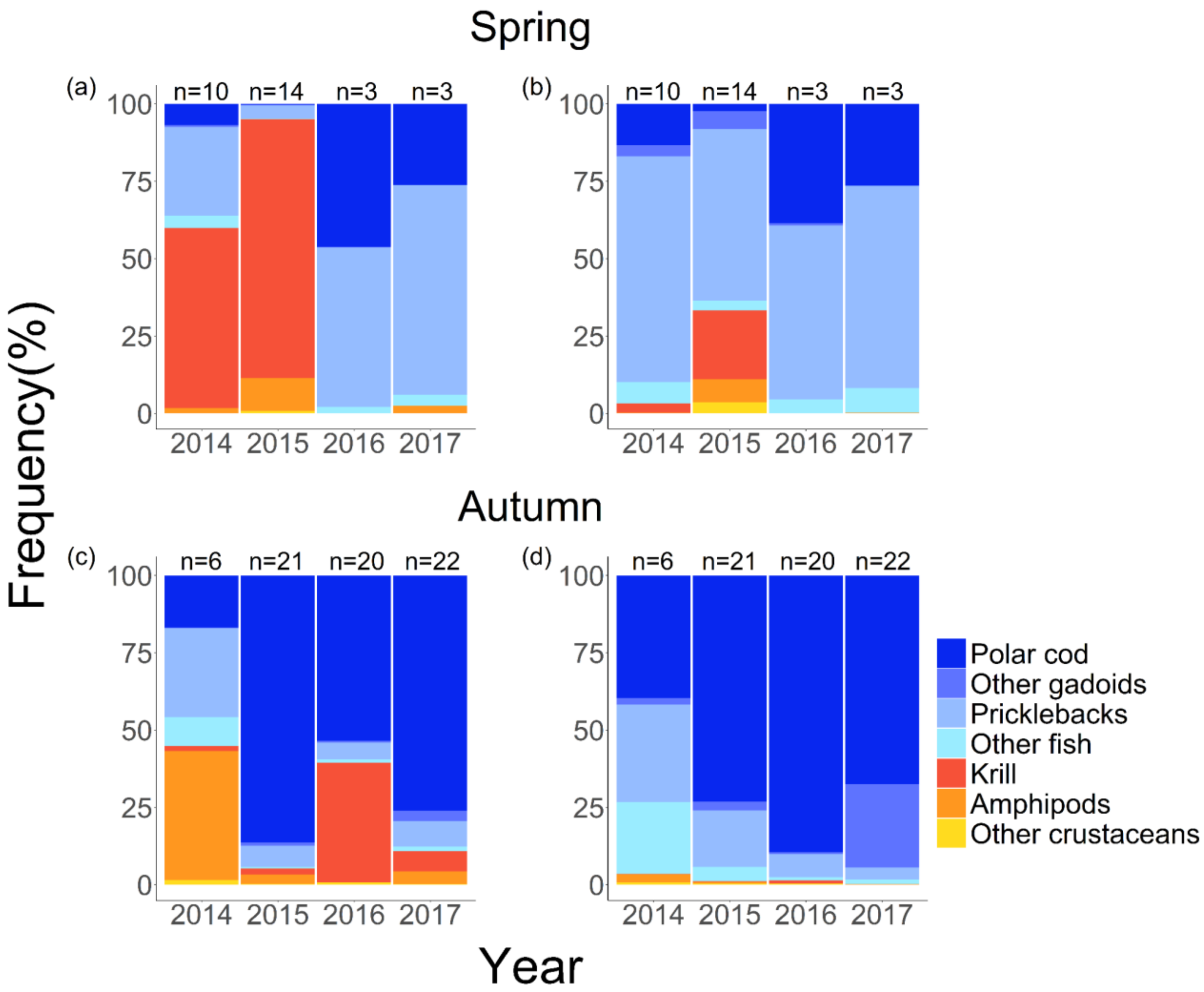

Fig. 4 Relative frequencies of different prey types in the ringed seal diet on the west coast of Spitsbergen, Svalbard (2014-2017) by (a) numerical occurrence during spring; (b) occurrence by biomass during spring; (c) numerical occurrence during autumn and (d) occurrence by biomass during autumn

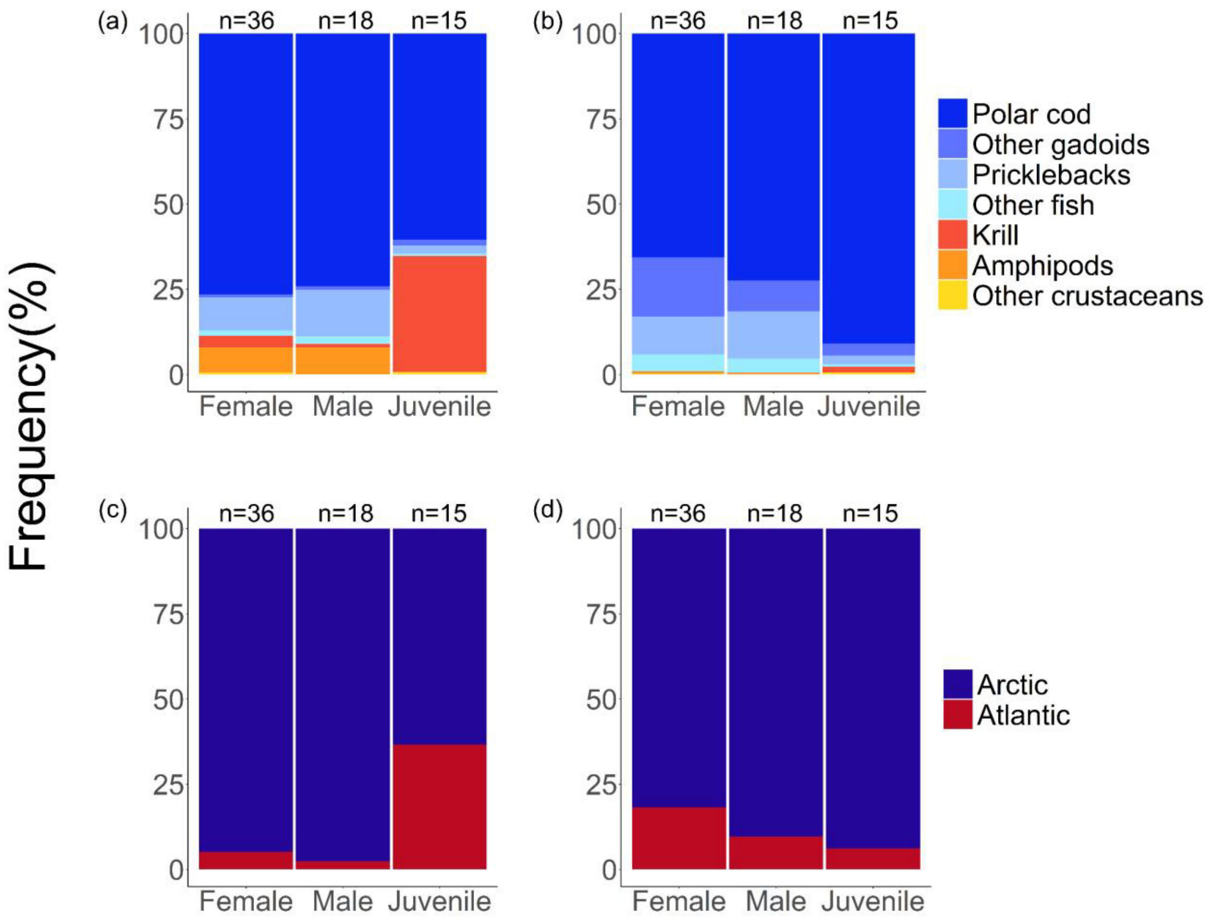

Fig. 5 Relative frequencies of different prey types in the ringed seal diet on the west coast of Spitsbergen, Svalbard, during autumn (2014-2017), divided into sex/age groups (adult females, adult males and juveniles, by (a) numerical occurrence; (b) occurrence by biomass; (c) numerical occurrence for prey types divided into Arctic and Atlantic prey classes and (d) occurrence by biomass for prey types divided into Arctic and Atlantic

Arctic prey types dominated the diet for all seal age/sex groups, both by numbers and biomass (Fig. 5c, d). In terms of numbers, juveniles had consumed more Atlantic species (mainly krill) than adult seals (Fig. 5c). In terms of biomass, females had consumed a slightly greater proportion of Atlantic species than males and juveniles (Fig. 5d).

Among the explanatory variables in the RDA (year, blubber content and sex/age group) year was the only significant explanatory variable retained after the forward selection procedure (F-ratio = 4.96, P = ≤ 0.005). This variable explained 19.1% of the total variation in diet composition (Fig. 6). The first two axes of the bi-plot (Fig. 6) explained 18.9% of the constrained variation in the model. Seals sampled in 2014 and 2015 consumed more sculpins and pricklebacks compared with the seals in 2016 and 2017. The highest biomasses of Atlantic cod and polar cod were found in GITs from 2016 and 2017, respectively (Fig. 6).

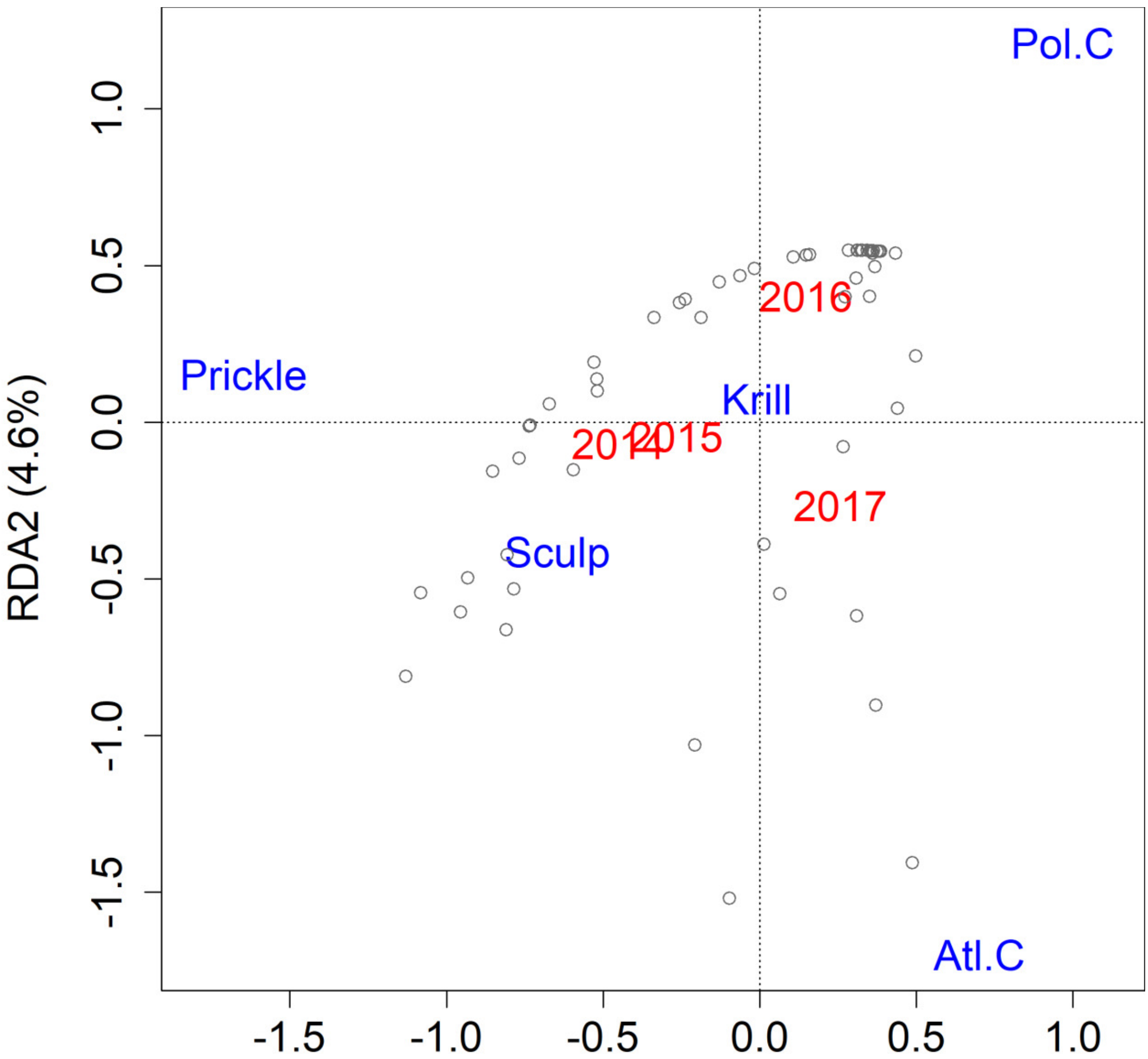

Fig. 6 Redundancy analysis (RDA) bi-plot for biomass of selected prey species (blue) as response variables (for individual seals (grey circles)) by year (red). The independent predictor explained 19.1% of the variance in biomass (Hellinger-transformed) seen in the dependent variables. Prickle, Pricklebacks; Sculp, Sculpins; Atl.C, Atlantic cod; Pol.C, polar cod

Blubber content (%) was calculated for 95 seals (Fig. 7); four samples lacked data on body- mass or length. Blubber content followed a normal distribution during both spring and autumn and within age/sex groups during autumn. The seals caught during autumn had significantly higher blubber contents than seals caught during spring ($t = 10.33$, $df = 93$, $p < 0.001$; Fig. 7a). There was a significant difference in blubber content between the age/sex groups during autumn ($\chi^2 = 10.77$, $df = 2$, $p < 0.001$). Pairwise testing of groups revealed that females and juveniles were significantly different ($\chi^2 = 9.62$, $df = 1$, $p < 0.001$). The sample size was too small to test for potential annual differences (during autumn) in blubber content of age/sex groups. However, analyses of pooled age/sex groups found a significant difference between years ($\chi^2 = 11.19$, $df = 3$, $p = 0.011$); 2015 was significantly lower than 2017 ($\chi^2 = 9.077$, $df = 1$, $p = 0.0026$).

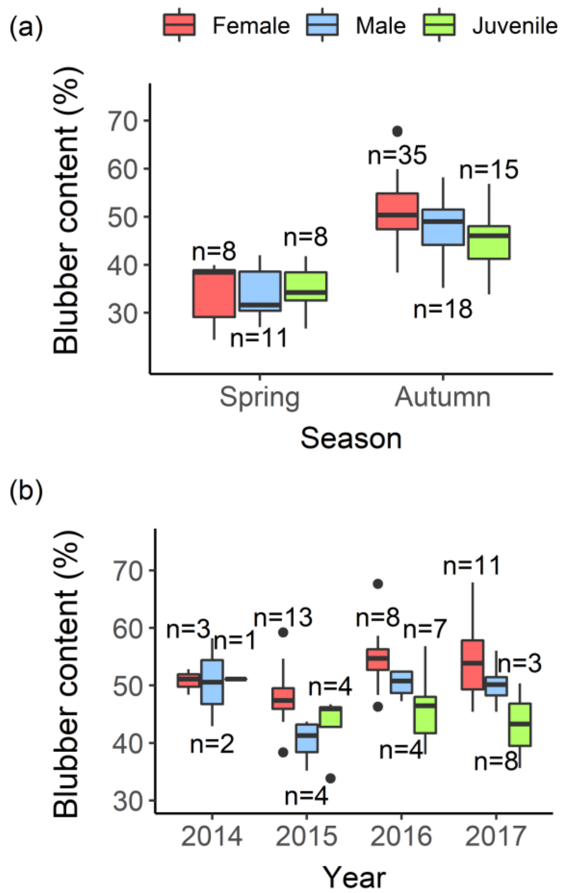

Fig. 7 Blubber content (%) of 95 ringed seals from the west coast of Spitsbergen, Svalbard (2014-2017), divided into sex and age grouping and compared between (a) seasons and (b) year (only autumn samples). Boxes contain values between the upper and the lower quartile and are divided by a line, representing the median value. Vertical lines through the boxes extend to the maximum and the minimum values (excluding outliers). Outliers are represented by dots, and are defined as values more than 1.5 times higher or lower than the upper and lower quartile, respectively

Discussion

Ringed seals diets are known to vary seasonally, interannually and regionally (McLaren 1958; Thiemann et al. 2007)). This suggests that the species is a generalist feeder that exhibits some capacity for dietary plasticity. The very marked environmental changes in the marine environment in Svalbard in recent decades has resulted in a borealization of both the fish and invertebrate communities and an isotopic study of diet in the region by Lowther et al. (2017) detected changes in the ringed seal whisker composition that suggested a change either what ringed seals or their prey were consuming. The current study, which assessed diet directly via hard-part analyses in the GITs, found that spring diet has likely changed quite markedly, and that some Atlantic prey types are making their way into the ringed seals' diet. However, the ringed seal's diet in Svalbard continues to be dominated Arctic prey types, with polar cod being particularly important.

All methods of dietary analyses (DNA, fatty acids, stable isotopes, identification of hard parts) have biases (Trites and Spitz 2018). The analyses of hard-parts from GITs used in this study represents only recent meals and otoliths and other materials are susceptible to partial or complete erosion when moving through the digestive system of a seal (Bowen and Harrison 1994). Gastric acid within the stomach is particularly corrosive (Christiansen et al. 2005). Dissolution rates are affected by the size of the otoliths and the robustness of hard-materials differs between species; gadoid otoliths are generally quite robust while salmonid otoliths are very fragile, for example (Christiansen et al. 2005, Grellier and Hammond 2006). Meal size and feeding mode also have effects on the degree of erosion of prey hard-parts. Experiments on recovery rates of otoliths, collected from seal faeces, showed that a lower percentage of otoliths will be recovered from a small meal, but that a small meal will travel faster through the GIT resulting in otoliths being less affected by erosion (Marcus *et al.* 1998). Additionally, in experiments when seals were fed otoliths inside a carrier (i.e. otoliths are extracted from a number of fish heads and placed inside the body cavity of a "carrier-fish"), otoliths were more digested than when seals were fed whole fish (Grellier and Hammond 2005). This means that otoliths inside intact skull cases are more protected from erosion than otoliths that have come loose, e.g. by rough handling of fish by seals when feeding. It can also be assumed that skulls of fish species with strong bones that take longer to dissolve will be more protected compared to those in more fragile skulls, affording the otoliths differential protection. This can, to some, degree be accounted for by using species-specific recovery rates and digestion coefficients (Grellier and Hammond 2006). Such corrections were not used in this study because the number of otoliths found in each seal varied greatly, indicating a lot of variation in meal size and because such coefficients have not been calculated for ringed seals or their primary prey species. Another issue when using otoliths to identify consumed fish species is that the head of the prey is not always consumed by the seals, especially for larger prey (Pierce and Boyle 1991). This results in a potential underestimate of the contribution of large fish prey. In the context of this study, this issue is a concern regarding Atlantic cod, which have large heads. Ringed seals might eat the soft flesh and leave the heads of Atlantic cod beyond a certain size. The chitinous shells of crustaceans are relatively resistant to digestion within pinniped digestive systems (Sheffield et al. 2001; Staniland 2002), but in this study, samples from the small- and large intestine were broken in many small pieces. Thus, it was challenging to get a good estimate of numbers of telsons, heads or eye pairs. Whichever type of item was the most numerous was assumed to best represent given type of prey consumed. Results on prey abundance and size of fish prey herein should be assessed with these biases in mind.

A total of 30 different prey types were identified in the GITs of the ringed seals in the present study. However, only five prey types constituted more than 1% in terms of numbers and biomasses. Polar cod was the dominant prey type in terms of biomass overall, and during autumn. These findings are similar to previous studies of ringed seal diet in Svalbard and elsewhere across the Arctic (Lowry et al. 1980; Gjertz and Lydersen 1986; Lydersen et al. 1989; Węsławski et al. 1994; Siegstad et al. 1998; Wathne et al. 2000; Holst et al. 2001; Labansen et al. 2007, 2011). Most of the seals in this study had consumed between one to four different prey types. This is similar to what Labansen et al. (2007) reported from Svalbard. This suggests that in this area, ringed seals are generalist feeders, but that they have strong preferences for a few key species and might be considered specialists at an individual level.

Polar cod is the most important food source for ringed seal on the west coast of Spitsbergen during autumn, followed by other Arctic fish species in the prickleback and sculpin families, even though presence of Atlantic species has increased in the area in recent years (Renauld et al. 2012; Fossheim et al. 2015). Polar cod in and around Svalbard are dispersed in the water column according to age class; smaller, younger fish (YC 1 and 2) are found in shallow water, sometimes associated with drifting sea ice, whereas older fish resides at greater depths (Falk-Petersen et al. 1986; Lønne and Gulliksen 1989; Renaud et al. 2012). A similar size- and age-related distribution pattern in the water column has been documented for pricklebacks (Eriksen et al. 2012). Most of the polar cod in this study belonged to YC 1 and 2, as has been observed in previous studies in Svalbard (Gjertz and Lydersen 1986; Węsławski et al. 1994; Labansen et al. 2007). This is consistent with observations of Svalbard ringed seals feeding mostly in the upper part of the water column (Gjertz et al. 2000; Wathne et al. 2000; Hamilton et al. 2015, 2016).

The contribution of polar cod to the ringed seal diet in this study was relatively low during spring, both in terms of biomass and numbers. This is in contrast to what was observed a decade ago by Labansen et al. (2007). Comparing the total estimated biomass of polar cod and the total number of polar cod in this study with Labansen et al. (2007) suggests that ringed seals are eating much less polar cod in spring now compared to a decade ago and that the polar cod they are consuming in recent year is of lower average weight. Assuming that ringed seals are generalist predators around Svalbard, feeding on the most available prey (e.g. Middlemas et al. 2006), i.e. no prey preference, the relatively low numbers of polar cod in spring in this study suggests that krill is much more readily available compared to polar cod in this season. However, it must be noted that ringed seal feeding studies conducted at the ice edge in the Northeast Barents Sea, suggest that in this area ringed seals display a strong preference for polar cod, regardless of its relative availability (Wathne et al. 2000), so the dominance of krill in the spring diet in this study is noteworthy. However, given the lack of knowledge regarding actual availability of the various potential prey types, it is not possible to determine the degree of selectivity that the ringed seals might be displaying. The results herein for spring are likely linked to interannual variation in Atlantic water influxes, and hence krill vs polar cod densities, in the various years of this study in spring.

Pricklebacks were the dominant prey type during spring in terms of biomass. Overall, it was the second most important prey type in terms of biomass and FO_i and the second most numerous fish prey type. The otoliths of these fishes are small and hard to distinguish between species. Species of pricklebacks known to reside in Svalbard include: *Lumpenus lampraeteformis, L. fabricii, Leptoclinus maculatus* and *Anisarhus medius* (Pethon 2005; Eriksen et al. 2012). Labansen et al. (2007) suggested that pricklebacks in the diet of ringed seals in Svalbard waters might be a local phenomenon in Forlandsundet and St Jonsfjorden, because these fishes did not contribute substantially to the ringed seal diet in previous studies or in other fjord systems in their study. The current study show that these prey species are also important for ringed seals in Isfjorden, which is geographically close to Forlandsundet and St Jonsfjorden. Two other phocid seal species, bearded seals (*Erignathus barbatus*) and harbour seals (*Phoca vitulina*) also feed on pricklebacks in western Svalbard (Hjelset et al. 1999, Andersen et al. 2004).

This is the first time Atlantic herring and blue whiting have been recorded as prey for ringed seals in Svalbard. Atlantic herring and blue whiting are both Atlantic species with distributions that stretch across much of the Barents Sea (Dragesund et al. 1980; Pethon 2005; Dolgov et al. 2009). An increase in the presence of these species around Svalbard is likely connected with the documented, increased inflows of AW in this area.

Krill was the dominant crustacean found in the GITs of the ringed seals from Svalbard. In the Barents Sea, krill are associated with AW and their abundance around Svalbard is highly variable from year to year at present, largely correlated with the variations in the inflow of AW (Dalpadado and Skjordal 1996; Ellingsen et al. 2008). Crawford et al. (2015) found that FO_i of crustaceans had decreased over time in ringed seal diet in the Bering and Chukchi seas off Alaska. In contrast, the FO_i occurrence and N_i of crustaceans in the present study were both higher in our study than what Labansen et al. (2007) found in Svalbard about 15 years ago. Furthermore, most of the krill in the study were consumed by seals caught during spring, whereas the study by Labansen et al. (2007), which was conducted during April and May, found only eight individual krill.

In contrast to what was observed during spring by Labansen et al. (2007), no significant sex and age related differences were detected by the multivariate analysis of diet composition during autumn in the current study. The choice to explore diet composition in terms of biomass, as opposed to prey counts (Labansen et al. 2007), was made because biomass was considered to better represent the relative importance of each prey type. This was especially relevant considering the low counts, but high biomass contribution, of Atlantic cod and the high counts but low biomass contribution of krill to the diet composition of the ringed seal in this study.

The sample size(s) in this study are small compared to many studies of pinniped diets. This was due to the fact that a targeted hunt on ringed seals for research purposes was not deemed ethically acceptable at this time because the ringed seal population in Svalbard is thought to be declining due to reduction in their breeding habitat. Thus, samples were only available from a low-level sport hunt conducted by Svalbard residents. This meant that analyses of spring diets were limited to descriptive assessments, and that samples for age/sex classed, even the larger autumn sample had to be pooled for some analyses.

The results of the RDA showed that neither blubber content, nor sex/age contributed significantly to explaining the variation in diet composition. This is in contrast with what has been observed in another Arctic seal present in the Barents Sea, the harp seal (*Pagophilus groenlandicus*; Lindstrøm et al. 2013). It should be pointed out that the RDA results were sensitive to the choice of data transformation (log, Hellinger, square root and Chi-square distance). Independent of transformation, year was significant, and sex/age group was not. Blubber content was on the border of being significant when applying log and square root-transformed data ($p < 0.08$). Prey availability may be considered a latent variable inferred by the predictor variable “year”, i.e. the inter-annual variation in diet composition (during autumn) is most likely a result of changes in prey availability rather than changes in prey preference. It appears that ringed seals prefer polar cod, but will feed opportunistically on other types of prey when necessary (also see Wathne et al 2000).

Blubber content of the seals in this study was lower during spring compared to autumn, especially for sexually mature seals, which is a normal seasonal pattern for all Arctic phocid seals and many other Arctic animals (Ryg et al. 1990a). Due to small sample sizes during autumn in the study by Ryg et al. (1990a), it is impossible to draw firm conclusions regarding longer-term temporal trends, but seals from all groups in the current study generally seem to have higher average blubber contents than the ringed seal studies by Ryg et al. (1990a). This is consistent with Crawford et al. (2015), who found an increase in ringed seal blubber thickness during recent periods (2003-2012) compared to historical periods (1975-1984) in areas around the Bering Strait. These findings are in contrast to the temporal patterns found by Ferguson et al. (2017) from in Hudson Bay from 2004 to 2013, where condition has declined. This highlights the importance of studying individual ringed seal populations across the Arctic, as there is no uniform response of the different populations to the environmental changes observed. On first reflection body condition of ringed seals on Svalbard does not in any case seem to be a cause of concern for the local population. However, paradoxically, females with higher blubber content than normal during autumn might in fact be a cause of concern. This is because the largest energy output in an adult ringed seal female's annual cycle is by far lactation (Lydersen and Kovacs 1999). In recent years the snow and ice condition in Svalbard have been unfavourable for ringed seal reproduction. Ice forms late (if at all) and it generally does not have enough snow on it for construction of ringed seal birth lairs. Thus, the majority of the pups are born on the open ice and are killed by predators. As a result, females do not undergo a full lactation period. Consequently, they are in much better condition at the end of the breeding period and likely also in the following autumn. Another potential factor in seals being fatter in the recent past, is that if ringed seals are unable to successfully raise pups, there will naturally be fewer seals, reducing potential interspecific competition for food resources. There is currently little knowledge of ringed seal population size around Spitsbergen. The last time the area was surveyed was during the peak moulting period in 2002 and 2003, when there was still considerable amounts of sea ice in the fjords. At that time it was estimated that a minimum of between 6 332 and 9 085 ringed seals occupied the fjords around Spitsbergen (Krafft et al. 2006). New surveys are necessary to estimate the current status of this population, though how these would be designed and implemented without the presence of spring sea ice remains an unsolved challenge.

Blubber content results in this study suggest that 2015 stands out as a year when adult seals were in a poorer condition during autumn than the others years. The spring diet for this particular year, with its' large numbers of krill, indicates that this was a year with high influx of AW. Some Atlantic species that were found in this study, such as krill and Atlantic cod, have lower caloric value than many of the Arctic prey species, such as polar cod and pricklebacks (Lowry et al. 1980; Elliot and Gaston 2008). Thus, having a less lipid-rich diet during spring could explain why the ringed seals had poorer fat reserves during autumn. Another factor that may play a role is that the ice-cover in Isfjorden and the neighbouring fjords, Van Mijenfjorden and St Jonsfjorden in March to May was greater during 2015 than the other years (Skoglund pers. comm.). It is likely that favourable ice-conditions resulted in more of the seals going through a normal breeding season with complete lactation and territorial defence periods, resulting in somewhat poorer, but more normal body condition the coming autumn.

Lowther et al. (2017) documented a dietary shift in ringed seals over recent decades. The current study found that the contribution of polar cod to the diet in terms of biomass has declined somewhat, especially during spring, compared to what was found in this area in 2002-2004 (Labansen et al. 2007), while the importance of pricklebacks has increased. Additionally, new Atlantic species have been found in the diet, e.g. Atlantic herring and blue whiting and other Atlantic species have relatively higher importance, e.g. krill and capelin. It is also likely that the increase in AW around Svalbard has affected the diet of the main prey of ringed seals, i.e. polar cod. This fish species has been described as an opportunistic feeder (Ajiad and Gjøsæter 1990) and it might be eating more Atlantic crustacean species, which are increasing in abundance in Svalbard (Dalpadado et al. 2016).

Recent tracking studies of ringed seals in Svalbard have shown that they have altered their space use patterns following the marked sea ice declines that have occurred in the region, likely as a response to the increased influx of AW in this area (Hamilton et al. 2016, 2019). Especially adult animals now spent virtually all of their time at tidewater glacier fronts, where polar cod concentrate (Lydersen et al. 2014; Fey and Węsławski 2017). This is in clear contrast to another endemic marine mammal in Svalbard, the white whale, which now spends more time away from the glacier fronts (Vacquié-Garcia et al. 2018), and have apparently incorporated new AW prey resources into their diet (Hamilton et al. 2019).

The fact that there are more, primarily, Atlantic crustaceans in the ringed seal diet now than over a decade ago (Labansen et al. 2007), despite seals spending more time at glacier fronts could indicate that more krill occur in this habitat than before. It is also possible that seals feed during transit swims between glacier fronts. However, these transitions are short and primarily take place between glacier fronts that are geographically close to each other (Hamilton et al. 2016). It is also important to stress that high numbers of krill in the diet of ringed seals feeding at glacier fronts on Svalbard has been observed before (Węsławski et al. 1994). Tracking results also suggest that younger seals spend more time further away from glacier fronts than adult seals, probably due to competitive exclusion (Hamilton et al. 2016). If juveniles feed further out in the fjords, where the influence of AW is greater than at the glacier fronts, it could explain why juveniles had higher relative numbers of krill in their diet during autumn than adult seals. However, it should also be noted that plumes of glacial discharge water combined with katabatic winds from glaciers drive an outflow of surface water away from the glacier front, which is compensated for by an inflow of AW (Lydersen et al. 2014). Therefore, it is not contradictory to find an increased presence of krill in the ringed seal diet, despite their tighter association with glacier fronts.

Atlantic species, especially gadoids like Atlantic cod, Atlantic herring and krill have increased in frequency and biomass in the diet of ringed seals in Svalbard, suggesting some degree of plasticity in responding to changing availability of these prey types. However, ringed seals still display a strong preference for Arctic species, especially polar cod. This is a concern for the future of the ringed seal population in areas where polar cod is in decline, such as the Barents Sea. The ringed seal's ability to adapt to further borealisation of Svalbard is unknown, but the major changes to their breeding habitat in addition to their preferred prey base is cause for concern.

Acknowledgements

This study was sponsored by the Svalbard Environmental Protection Fund and the Norwegian Polar Institute. We thank hunters that contributed to the collection program (Martin Munck, Tommy Jordbrudal, Eike Stubner and Tommy Sandal). We also thank: Lotta Lindblom for assisting with the labwork and helping with identification of prey species; Magnus Andersen for his contributions to the generation of the biological data on the seals and for handling/transport of samples; Anders Skoglund for providing the map of the sampling region; Charmain Hamilton for sharing her extensive R knowledge; and Heidi Gabrielsen for helping with identification of some of the crustacean species.

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Supplementary material

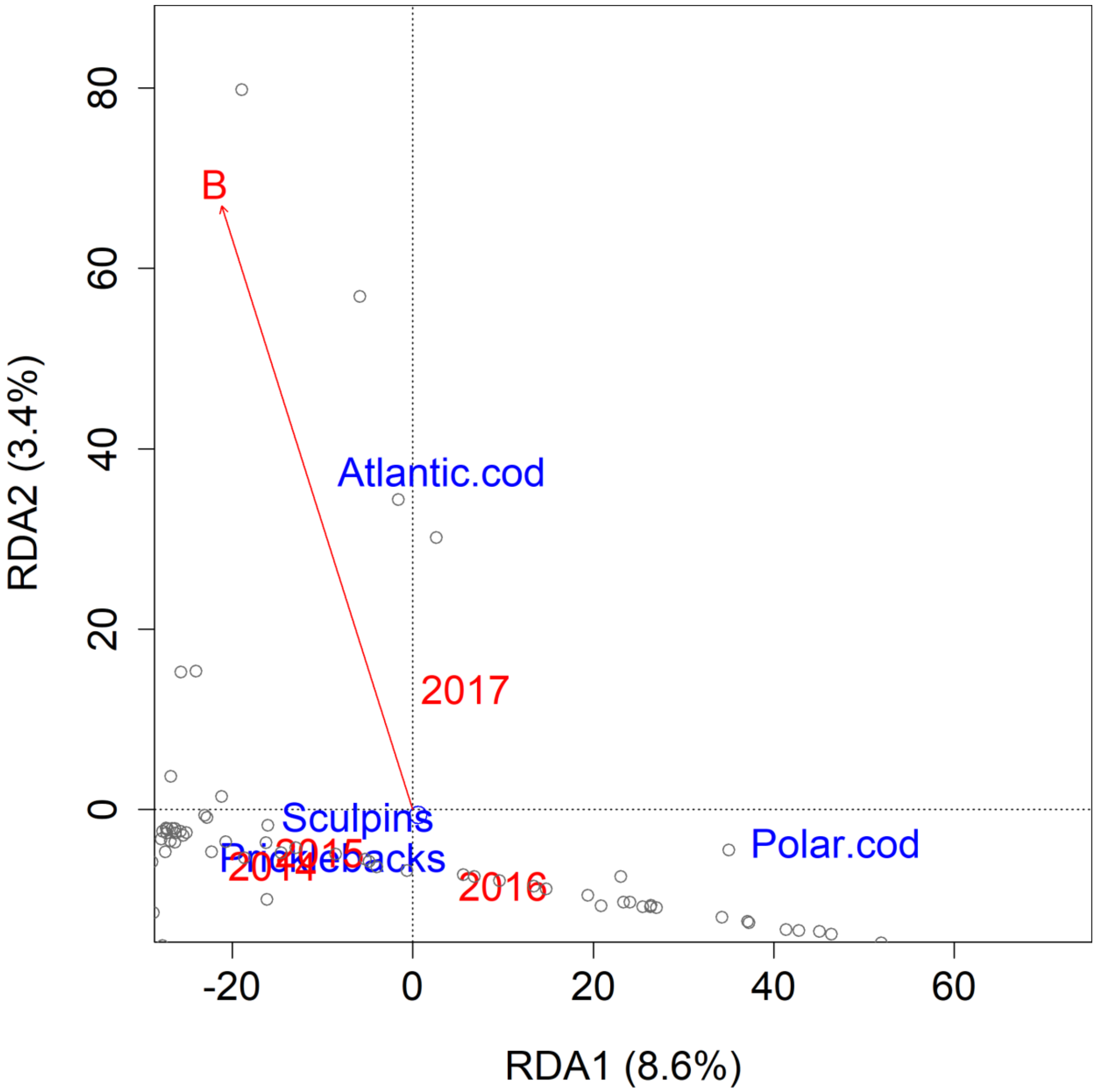

Fig. S1 Redundancy analysis (RDA) bi-plot run on untransformed data for biomass of selected prey species (blue) as response variables (for individual seals (grey circles) by year (red) and blubber content (red B). Blubber content was included as an independent predictor in the model by forward selection, but was not significant. The independent predictors explained 12.5% of the variance in biomass seen in the dependent variables

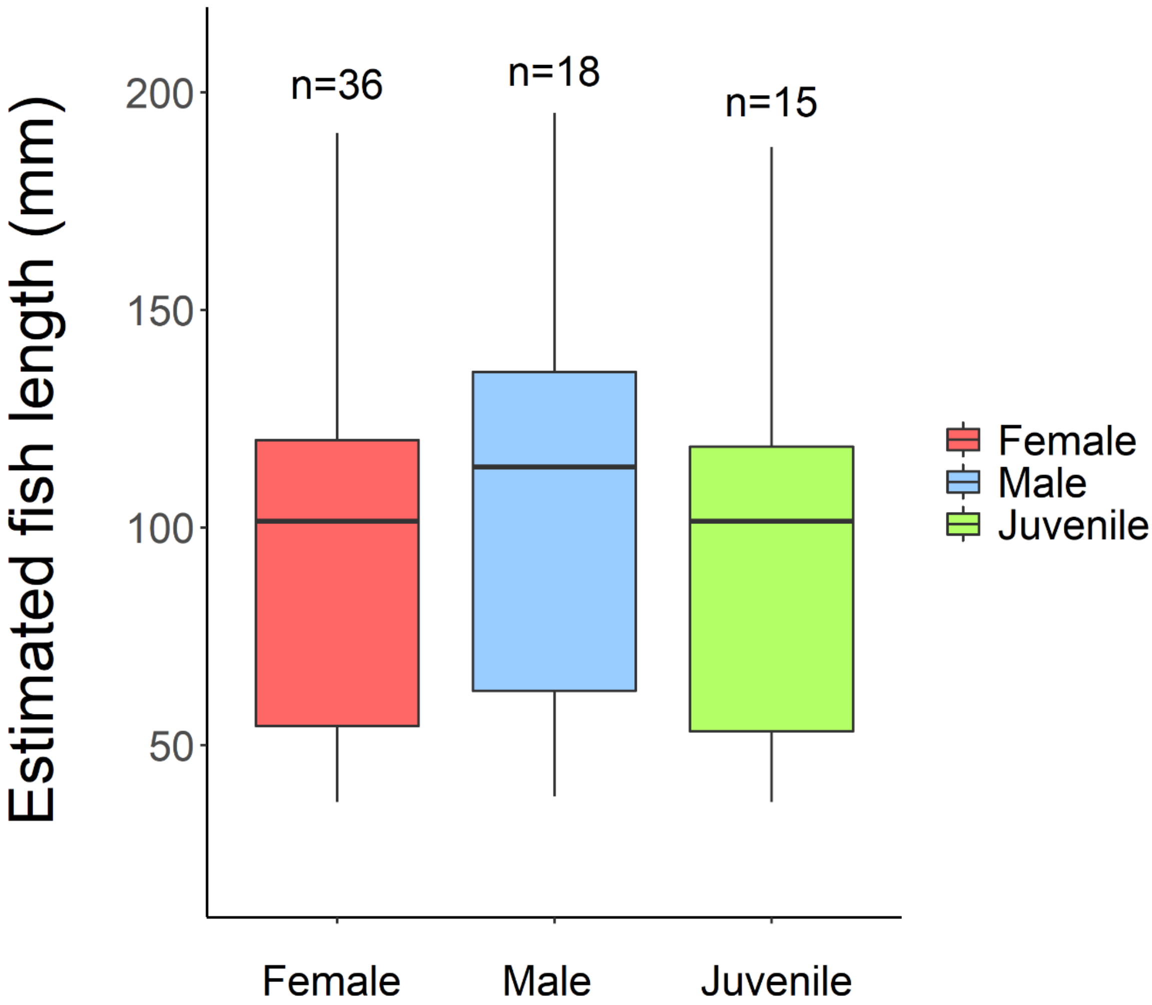

Fig. S2 Estimated fish length of ingested polar cod of 69 ringed from the west coast of Spitsbergen, Svalbard, during autumn (2014-2017), divided into sex/age groups (adult males, adult females and juveniles). Boxes contain values between the upper and the lower quartile and are divided by a line, representing the median value. Vertical lines through the boxes extend to the maximum and the minimum values

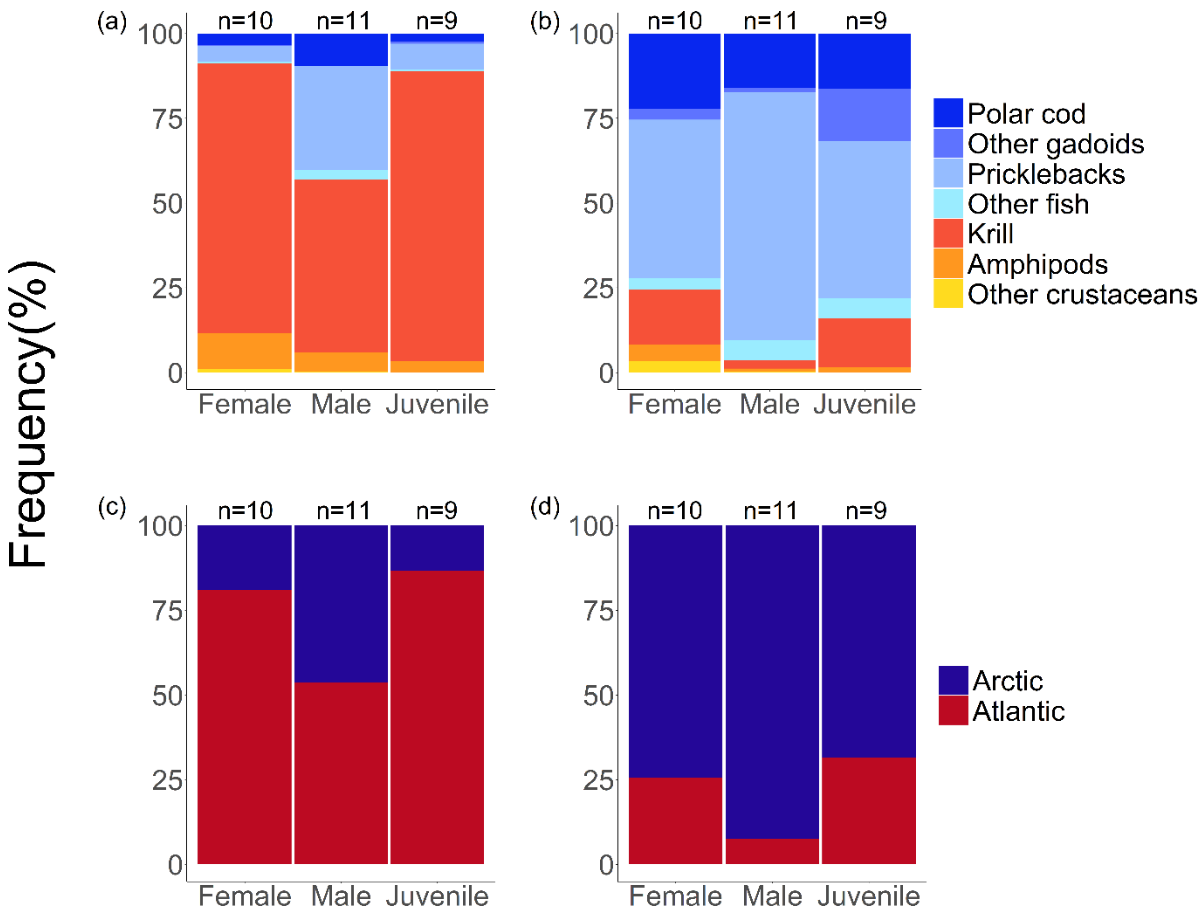

Fig. S3 Relative frequencies of different prey types in the ringed seal diet on the west coast of Spitsbergen, Svalbard, during spring (2014-2017), divided into age/sex groups (adult males, adult females and juveniles): (a) numerical occurrence; (b) occurrence by biomass; (c) numerical occurrence for prey types divided into Arctic and Atlantic prey classes and (d) occurrence by biomass for prey types divided into Arctic and Atlantic

Table S1 Sampling and biological parameters of 99 ringed seals sampled on the west coast of Spitsbergen, Svalbard (2014-2017)

ID	Year	Month	Area	Maturity[a]	Sex[b]	Weight (Kg)	Length (cm)	Blubber thickness (mm)	Blubber content (%)	Age
Sel1	2015	9	Borebukta	J	M	45	123	30	33.8	3
Sel2	2015	9	Borebukta	M	F	75	140	60	50.4	-
Sel3	2015	6	Tempelfjorden	J	F	35	115	25	31.7	8
Sel4	2015	5	Tempelfjorden	M	F	56	124	29	30.5	20
Sel5	2015	5	Tempelfjorden	M	F	53	123	21	24.9	18
Sel6	2015	9	Adolfbukta	M	F	68	122	60	49.5	22
Sel7	2014	9	Borebukta	M	F	57	118	58	51.1	17
Sel8	2015	6	Tempelfjorden	M	M	45	122	22	27.0	22
Sel9	2014	9	Borebukta	M	F	71.5	110	63	48.4	7
Sel10	2015	9	Yoldiabukta	M	M	65	137	36	35.2	6
Sel11	2014	9	Borebukta	M	F	79	125	69	52.8	17
Sel12	2017	8	Yoldiabukta	M	F	52	118	48	45.4	6
Sel13	2017	9	Ekmanfjorden	M	F	87	139	70	53.7	20
Sel14	2015	5	Tempelfjorden	M	M	49	128	28	31.6	18
Sel15	2014	7	Borebukta	J	F	27	104	30	38.6	1
Sel16	2017	10	Ekmanfjorden	M	F	82	132	70	53.8	24
Sel17	2015	6	Yoldiabukta	M	F	35	108	34	39.0	4
Sel18	2017	10	Ekmanfjorden	M	F	57	125	55	50.1	5
Sel19	2017	9	Ekmanfjorden	J	M	23	92	41	50.4	1
Sel20	2017	10	Ekmanfjorden	M	F	82	140	77	59.9	11
Sel21	2017	9	Ekmanfjorden	M	F	92	138	95	67.9	11
Sel22	2017	6	Yoldiabukta	M	M	57	130	27	29.3	12
Sel23	2015	9	Borebukta	M	F	53	124	45	43.6	28
Sel24	2017	9	Ekmanfjorden	M	F	65	123	70	57.7	9
Sel25	2017	10	Ekmanfjorden	M	M	98	142	70	51.5	26
Sel26	2017	6	Yoldiabukta	J	M	28	102	25	32.9	0
Sel27	2017	6	Yoldiabukta	M	F	54	128	40	40.0	19
Sel28	2017	9	Ekmanfjorden	M	M	86	142	58	46.6	23
Sel29	2017	10	Ekmanfjorden	M	M	78	138	70	56.0	6
Sel30	2017	9	Yoldiabukta	M	M	75	133	60	49.3	12
Sel31	2017	8	Yoldiabukta	M	F	58	125	52	47.5	5
Sel32	2014	6	Borebukta	M	M	45	123	29	33.0	7
Sel33	2015	9	Borebukta	M	F	73	140	50	43.9	8
Sel34	2017	8	Yoldiabukta	M	F	72	128	68	54.8	24
Sel35	2015	5	Tempelfjorden	M	M	47	118	40	40.9	12
Sel36	2016	9	Ekmanfjorden	M	F	102	145	75	54.2	8

Continued

Table S1 Continued

ID	Year	Month	Area	Maturity[a]	Sex[b]	Weight (Kg)	Length (cm)	Blubber thickness (mm)	Blubber content (%)	Age
Sel37	2016	9	Ekmanfjorden	J	M	44	110	47	46.4	3
Sel38	2016	9	Ekmanfjorden	M	F	82	135	-	-	15
Sel39	2016	9	Ekmanfjorden	J	M	27	80	55	56.8	0
Sel40	2016	8	Ymerbukta	M	M	90	135	65	49.1	8
Sel41	2016	9	Ekmanfjorden	M	F	59	115	53	46.3	5
Sel42	2016	8	Borebukta	J	F	48	119	50	48.7	3
Sel43	2015	9	Borebukta	M	F	45	102	49	46.2	3
Sel44	2015	6	Tempelfjorden	M	M	44	132	26	31.5	14
Sel45	2014	9	Borebukta	M	M	79	120	79	58.2	26
Sel46	2016	9	Ekmanfjorden	J	M	49	122	38	39.1	4
Sel47	2016	9	Ekmanfjorden	M	M	78	145	63	52.4	9
Sel48	2016	5	Borebukta	M	M	65	148	30	31.6	10
Sel49	2016	9	Ekmanfjorden	M	F	78	135	70	55.5	17
Sel50	2016	9	Ekmanfjorden	J	M	42	120	45	47.3	5
Sel51	2016	9	Ekmanfjorden	M	M	75	120	60	47.3	14
Sel52	2016	9	Ekmanfjorden	M	F	61	120	70	58.6	23
Sel53	2016	9	Ekmanfjorden	M	M	59	122	60	52.5	10
Sel54	2016	9	Ekmanfjorden	M	F	82	136	70	54.5	24
Sel55	2017	8	Yoldiabukta	M	F	58	125	66	58.0	25
Sel56	2015	9	Yoldiabukta	M	F	77	136	68	54.6	9
Sel57	2015	6	Tempelfjorden	M	M	49	126	25	29.0	17
Sel58	2015	9	Yoldiabukta	M	M	77	140	45	39.5	9
Sel59	2015	9	Borebukta	M	F	67	130	42	38.4	22
Sel60	2015	9	Adolfbukta	J	M	30	100	40	45.8	0
Sel61	2017	9	Ekmanfjorden	M	M	77	133	55	45.4	11
Sel62	2016	5	Borebukta	M	F	60	141	38	38.3	22
Sel63	2015	6	Tempelfjorden	J	M	11	76	20	35.4	0
Sel64	2016	9	Ekmanfjorden	M	F	82	122	95	67.7	16
Sel65	2017	9	Ekmanfjorden	M	M	95	145	68	51.4	10
Sel66	2014	4	Van Mijenfjorden	J	F	45	-	58	-	1
Sel67	2014	4	Van Mijenfjorden	M	F	-	143	59	-	23
Sel68	2015	9	Borebukta	M	M	70	133	50	43.7	9
Sel69	2015	9	Borebukta	M	F	55	119	50	46.1	6
Sel70	2017	9	Ekmanfjorden	M	M	111	157	70	51.0	19
Sel71	2015	6	Yoldiabukta	J	M	35	110	33	38.4	2

Continued

Table S1 Continued

ID	Year	Month	Area	Maturity[a]	Sex[b]	Weight (Kg)	Length (cm)	Blubber thickness (mm)	Blubber content (%)	Age
Sel72	2015	6	Tempelfjorden	J	M	38	121	20	26.7	5
Sel73	2014	9	Borebukta	M	M	66	120	50	42.9	11
Sel74	2015	6	Yoldiabukta	M	F	50	122	38	38.8	14
Sel75	2014	5	Van Mijenfjorden	J	M	32	105	36	41.8	1
Sel76	2015	9	Borebukta	M	F	65	116	57	47.4	11
Sel77	2015	9	Borebukta	J	M	29	98	40	46.0	0
Sel78	2017	9	Yoldiabukta	M	M	80	130	62	48.9	19
Sel79	2015	9	Borebukta	J	M	62.5	120	54	46.7	3
Sel80	2016	6	Yoldiabukta	M	F	-	107	42	-	11
Sel81	2017	8	Yoldiabukta	J	F	42	116	41	43.3	3
Sel82	2017	8	Yoldiabukta	M	F	76	130	60	48.6	19
Sel83	2016	9	Ekmanfjorden	J	F	30	98	32	38.0	0
Sel84	2016	9	Ekmanfjorden	M	F	52	119	60	54.8	4
Sel85	2016	9	Ekmanfjorden	M	F	81	137	60	48.3	33
Sel86	2017	8	Yoldiabukta	J	M	52	120	35	35.7	4
Sel87	2015	9	Yoldiabukta	M	F	72	138	55	47.4	12
Sel88	2015	9	Yoldiabukta	M	M	73	145	48	43.0	16
Sel89	2015	9	Yoldiabukta	M	F	66	133	70	59.2	8
Sel90	2014	5	Van Mijenfjorden	M	F	39	117	34	38.6	5
Sel91	2015	9	Yoldiabukta	M	F	68	135	52	45.9	22
Sel92	2015	10	Borebukta	M	F	71	125	60	49.1	24
Sel93	2016	9	Ekmanfjorden	J	M	49	119	45	44.3	4
Sel94	2015	6	Tempelfjorden	M	F	42	125	18	24.4	15
Sel95	2014	9	Tempelfjorden	J	M	55	110	59	51.1	3
Sel96	2014	5	Van Mijenfjorden	M	M	50	120	40	40.1	7
Sel97	2014	5	Van Mijenfjorden	M	M	41	122	38	42.0	4
Sel98	2014	5	Van Mijenfjorden	M	M	82	160	40	37.0	17
Sel99	2014	7	Borebukta	J	M	27	100	25	33.1	2

[a]M, Mature; J, Juvenile. [b]F, Female; M, Male; J, Juvenile.