Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway

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Complete gastro-intestinal tracts (GITs) from 267 ringed seals from five different locations in Spitsbergen were collected during spring of the years 2002–2004. Diet was assessed based on hard part remains from prey. Invertebrates constituted <2% of all prey (relative frequency, N_i). Fish otoliths were found in all seals; 1.7, 34.3, and 64.0% of the recovered otoliths were found in the stomach, small and large intestines, respectively, emphasizing the importance of analysing the whole GIT, not only the stomach. Otoliths from stomachs and small intestines with minimal signs of erosion were measured to back-calculate pre-ingested prey size and biomass. Based on measured polar cod (*Boreogadus saida*) otoliths ($n = 7007$), the ringed seals fed on fish in the length range 44.4–229.2 mm, primarily consuming the youngest year classes. Adult females ate smaller polar cod more often than adult males or juveniles. Polar cod dominated the diet, with a frequency of occurrence (FO) of 100%, N_i of 71.9%, and a biomass contribution of 77.2%. The taxon Stichaeidae was the second most frequent prey type (FO = 55.6%) followed by Cottidae (FO = 35.6%). The diet of ringed seals from one locality markedly differed from the others, with a greater species diversity, low N_i of polar cod (15%), and a dominance of Stichaeidae (N_i = 67%). Location of sampling, as well as sex and age of the seals, had significant influences on ringed seal diet in spring.

Keywords: Arctic, *Boreogadus saida*, diet, foraging, marine ecosystem, *Pusa*, Spitsbergen.

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Introduction

The ringed seal (*Phoca hispida*) has a circumpolar distribution and is the most abundant and widely distributed marine mammal in the Arctic (Reeves, 1998). It is a predator in a strictly marine food chain, and with its broad distribution and year-round availability the ringed seal is itself an important resource for several arctic predators, including polar bears (*Ursus maritimus*), Arctic foxes (*Alopex lagopus*), and man (Smith, 1976, 1980; Lydersen and Gjertz, 1986; Teilmann and Kapel, 1998; Derocher *et al.*, 2002).

Many studies of ringed seal diet have been conducted throughout its range. It feeds on a variety of fish, amphipods, euphausiids, mysids, shrimps, and cephalopods (McLaren, 1958; Lowry *et al.*, 1980; Gjertz and Lydersen, 1986; Smith, 1987; Belikov and Boltunov, 1998; Siegstad *et al.*, 1998; Holst *et al.*, 2001). Spatial and temporal variations are apparent in the diet of ringed seals throughout their range, and some studies have shown an effect of sex and age on diet selection within a given region (Lowry *et al.*, 1980; Holst *et al.*, 2001). Typically, a variety of 10–15 prey species are found, with no more than 2–4 dominant prey taxa for a specific area (Weslawski *et al.*, 1994). Important prey species are generally those that are found in aggregations, e.g. *Parathemisto libellula*, polar cod (*Boreogadus saida*), or saffron cod (*Eleginus gracialis*). Younger age classes of ringed seals feed on a greater proportion of crustaceans in relation to fish than adults (Bradstreet and Cross, 1982; Siegstad *et al.*, 1998; Holst *et al.*, 2001). Further, Holst *et al.* (2001) showed a possible sex-related difference in prey composition for ringed seals in northern Baffin Bay. Previous studies conducted on Spitsbergen, Svalbard, have shown that polar cod dominates the prey, with Cottidae, krill (*Thysanoessa inermis*), and the amphipod *P. libellula* also being important (Gjertz and Lydersen, 1986; Lydersen *et al.*, 1989; Weslawski *et al.* 1994).

It is expected that climate change will impact ringed seals in the near future through changes in the distribution and nature of sea ice, as well as via changes in their prey base (Kelly, 2001; Loeng *et al.*, 2005). Therefore, accurate, current assessments of diet are timely. This study investigated the spring diet of ringed seals collected on land-fast ice at five locations in Spitsbergen, Svalbard. The geographic range of sampling, the relatively large sample size, and the detailed biological information collected on each seal, also allowed us to explore spatial, sex- and age-related variation in the diet of ringed seals from this region of the Arctic.

Material and methods

Complete gastro-intestinal tracts (GITs) were collected from 267 ringed seals from Spitsbergen, Svalbard, Norway (Figure 1) during spring (12 April–24 May of the years 2002–2004). The seals were shot on the land-fast ice in five areas: Wijdefjorden (Wijd); Kongsfjorden (Kong); Forlandsundet and St Jonsfjorden (FSJ); Billefjorden (Bill); and Recherchefjorden and Van

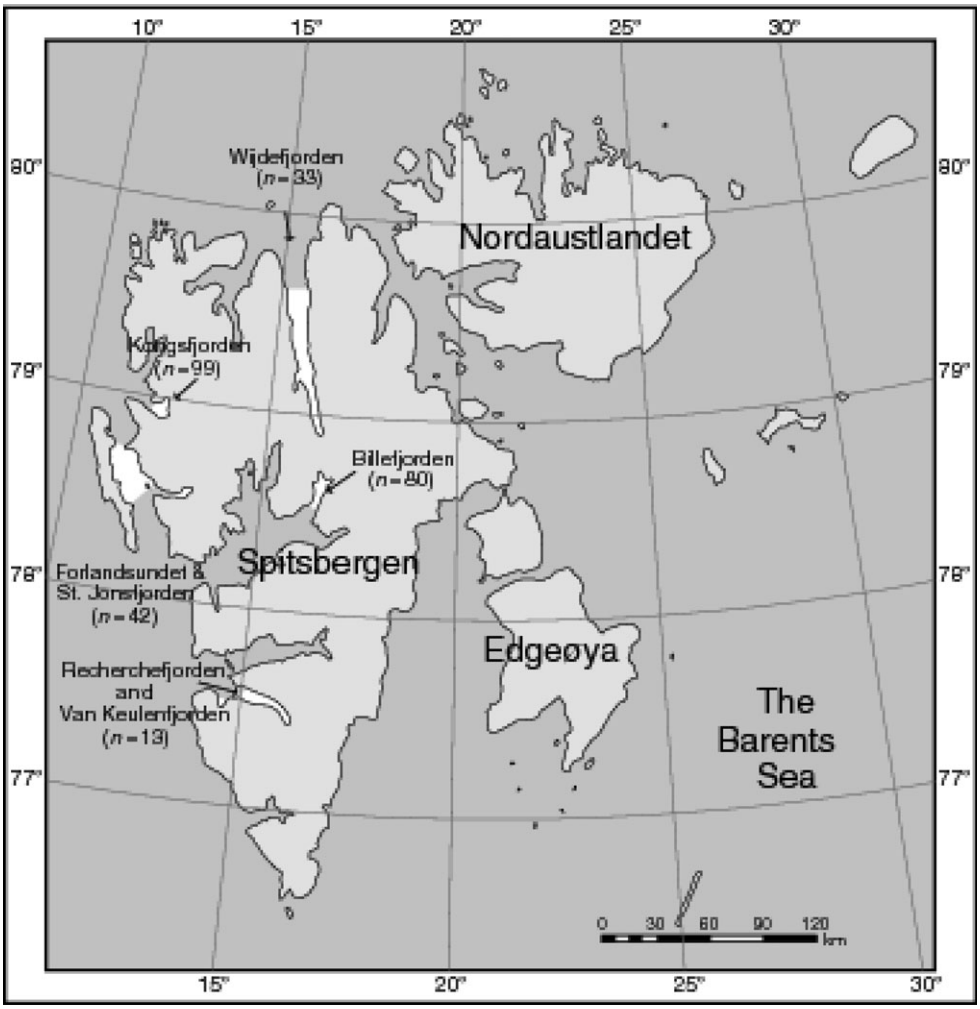

Figure 1. Map of the Svalbard Archipelago with sampling locations on Spitsbergen indicated (sample sizes in parenthesis). The white areas on the map indicate the approximate distribution of land-fast ice at the time of sampling.

Keulenfjorden (RVK). Wijd and Bill were sampled in 2002 and 2003, FSJ in 2003, and Kong and RVK in 2004. Each GIT was tied off at the oesophagus and at the rectum, placed in a plastic bag and kept frozen. Age, sex, maturity status, mass, and length were determined for all seals (see Krafft *et al.*, 2006).

In the laboratory, each GIT was divided so that the stomach with oesophagus, the small intestine, and the large intestine were weighed separately before being opened. The contents of each part were treated separately in subsequent laboratory work. The GIT contents were washed in a dark plastic bowl and poured through an interconnecting sieve system with mesh sizes of 2.0, 1.0, and 0.5 mm from top to bottom, respectively. Most of the fish otoliths were collected directly from the bottom of the plastic bowl. The remaining hard parts were gently washed on the sieves before being preserved. The collected items were sorted into fish (mainly otoliths) and invertebrate remains, and preserved in 96% ethanol for later identification. Invertebrate prey items included hard parts from crustacean exoskeletons, beaks of cephalopods, shells of gastropods and bivalves, and jaws or setae of polychates.

Fish prey were identified using the otolith identification guide of Härkönen (1986) and reference material from the west coast of Greenland collected during fisheries surveys of the Greenland Institute of Natural Resources, with supplementary collections performed by the Institute of Marine Research, Tromsø, Norway. Otoliths were classified to the lowest possible taxonomic level for all sections of the GIT and counted. Those that were too eroded, or damaged, were categorized as "unidentified". Otoliths that had minimal or no signs of erosion were measured (± 0.01 mm) along their longest axis parallel to the sulcus using a dissection microscope (Leica MZ6) with an ocular micrometer, to estimate the pre-ingested size (length and mass) of the fish consumed. Because of the large number of otoliths, only those from the stomach and the small intestine were measured as a representative subsample. Additionally, for most of the GIT samples containing >100 measurable otoliths, a subsample of ~ 50 was measured per seal so that the results of individual seals did not bias the overall results.

The number of fish ingested per seal was estimated for most species by dividing the number of otoliths found by two, assuming that two otoliths per fish were present. Unmatched otoliths were considered to be one individual prey item. For cod (*Gadus morhua*), the number of ingested fish was determined using the most numerous side (left or right).

Otolith length was used to estimate fish length and mass (Härkönen, 1986; K. T. Nielsen, pers. comm.). For fish prey types that were not determined to the level of species, regressions for what was considered the most likely species of prey was used. In samples where the measured otoliths were sorted into left and right, the otoliths were paired in the best possible manner before the average otolith length for each pair was used for estimating fish mass. In cases where the measured otoliths were not identified as left and right, fish mass was calculated for each otolith and the total mass sum was divided by two. The total biomass for each fish prey type ingested was estimated, assuming that eroded otoliths of each species were originally similar in size range and distribution to the non-eroded, measured otoliths of the same species. For otoliths from small Stichaeidae, which were in large numbers in some samples, the size range was determined for the whole group, and the average value was used to estimate the contribution by mass of the taxon. No attempts were made to estimate prey size of rare prey types or prey items that were only identified from eroded material (e.g. most invertebrate material).

Diet indices commonly used in stomach contents analyses (Hyslop, 1980; Pierce and Boyle, 1991) were applied including: (i) frequency of occurrence $(\mathrm{FO}) = \mathrm{FO}_i\ (\%) = (S_i/S_t) \times 100$, where S_i is the number of seals with prey type i, and S_t the total number of seals; (ii) the relative frequency (N_i), the numerical proportion of each prey type in the diet $= N_i\ (\%) = (n_i/n_t) \times 100$, where n_i is the total number of prey type i, and n_t the total number of prey; and (iii) the relative proportion of each prey type in terms of biomass (B_i) in the diet, expressed as total reconstructed biomass for each prey type relative to the estimated total biomass for all prey types $= B_i\,(\%) = (b_i/b_t) \times 100$, where b_i is the total biomass of prey type i, and b_t is the total biomass of all prey types with mass estimations.

Measured polar cod otoliths were sorted into year classes (YCs, I–VI), based on estimated fish lengths. The YC/fish length intervals followed Falk-Petersen *et al.* (1986), except that the separation of YCI and YCII was adjusted based on the observed fish length distribution from the present study. The length intervals (mm) of YCs I–VI were: I $<105.0<$ II $<139.5<$ III $<156.5<$ IV $<169.0<$ V <185.5 and larger = VI.

Microsoft® Excel, SPSS 12.0 for Windows®, CANOCO 4.5 for Windows® and R 2.0.1 were used to analyse the data. Statistical significance level was set at $\alpha \leq 0.05$. Chi-squared tests were applied when testing for differences in seal sex ratios between areas. Analysis of deviance was used to test for differences between the numbers of different prey types consumed per seal by area. Diet as a function of location and seal age/sex was explored via a Constrained Correspondence Analysis (CCA) carried out on log-transformed prey counts. Because CCA is sensitive to species in low abundance, haddock (*Melanogrammus aeglefinus*) were excluded from the analysis along with uncommon invertebrate species. Fish larvae were also excluded because of potentially high detection errors. The remaining fish prey types, decapods (grouped), *P. libellula*, and *Gammarus wilkitzkii* were included. The five locations, the seal sex/age groups and seal length, age, and mass were independent variables in the CCA model. To test the significance of the multivariate model, a Monte Carlo permutation test was applied.

Four generalized linear models (GLM) were run with YC of polar cod as the dependent variable, to explore spatial effects and the effects of age and sex of seals on the type of polar cod consumed: Model I, II (subsample of I, see below), $\mathrm{YC} = \beta_1$ location $+ \beta_2$ seal category; Model III, $\mathrm{YC} = \beta_1$ location $+ \beta_2$ sex of adult seal; Model VI, $\mathrm{YC} = \beta_1$ seal category. Location and seal category (juvenile, adult male, and adult female) were independent variables in Models I and II. The complete dataset of measured polar cod otoliths was included in Model I. In order to avoid some seals with very large numbers of polar cod otolith measurements, potentially biasing the model coefficient estimates, only seals for which fewer than 100 otoliths were measured were included in Model II. Only adult seals from locations with approximately balanced sex ratios, and with fewer than 100 otolith measurements were included in Model III, with location and sex as independent variables. Only seals from Kongsfjord, which had approximately balanced sample sizes for the three seal categories, and samples with fewer than 100 measurements were included in Model IV (with seal category as the independent variable). The frequency distribution of the polar cod YCs approximated a Poisson distribution, so a Poisson distribution of the error term was assumed when running the GLMs. Low values of the independent model coefficients reflect a greater proportion of younger ingested polar cod. A 95% confidence interval (CI) was calculated for all derived coefficient estimates from the models, based on the given standard errors (s.e.). Analysis of deviance was applied on all four models to test for significant effects of the independent variables on the dependent variable.

Results

The ages of the seals in this study ranged from 1 to 30 years, and the sample sex ratio of 166 males to 101 females was significantly different from unity [χ^2 (d.f. 1) = 15.82, $p < 0.01$]. In all, 45 seals were classified as juveniles, 141 as adult males, and 81 as adult females (Table 1). Considering the five sampling locations (see Table 1), the sex ratio of the adult seals differed significantly between areas [χ^2 (d.f. 4) = 11.98, $p < 0.05$], and was significantly different from unity in FSJ and Bill [χ^2 (d.f. 1) = 7.62, $p < 0.01$, and χ^2 (d.f. 1) = 4.97, $p < 0.05$, respectively].

All seals had prey remains in their GITs; 11.2% of the stomachs, 66.3% of the small intestines, and 99.6% of the large intestines had identifiable remains. Fish otoliths were in every seal; 1.7, 34.3, and 64.0% of the recovered otoliths were found in the three respective parts of the GITs. The percentages of unidentified otoliths were 1.5, 0.3, and 0.7% for stomachs, small, and large intestines, respectively. Hard parts of various invertebrate species were found in 39% of the seals ($n = 105$).

Some 12 fish prey types were identified (Table 2); five to species, three to genus and three to family, and one prey type was categorized as unidentified fish larvae. Fewer than 1% of otoliths were classified as unidentifiable (Table 2). In all 20 crustacean

Table 1. Geographical distribution of ringed seals from Spitsbergen, from which GITs were analysed, categorized into three sex/age groups.

Seal category	Area					Total
	Wijd	Kong	FSJ	Bill	RVK	
Adult males	18	35	33	47	8	141
Adult females	13	35	8	21	4	81
Juveniles	2	29	1	12	1	45
Total	33	99	42	80	13	267

Wijd, Wijdefjorden; Kong, Kongsfjorden; FSJ, Forlandsundet and St Jonsfjorden; Bill, Billefjorden; RVK,Recherchefjorden and Van Keulenfjorden.

Table 2. Taxonomic grouping of gastro-intestinal tract contents from 267 ringed seals from Spitsbergen.

Prey item				**Number of prey**	**FO (%)**	**N_i (%)**
Fish						
		Gadidae	*Boreogadus saida*	55 491	100	71.87
			Gadus morhua	374	22.5	0.48
			Gadidae sp.[a]	1 340	28.5	1.74
			Melanogrammus aeglefinus	2	0.4	0.003
		Stichaeidae	Stichaeidae spp.[b]	15 231	55.6	19.73
		Cottidae	Cottidae spp.[c]	1 571	35.6	2.03
			Fish larvae not determined (n.det.)	595	5.2	0.77
		Pleuronectidae	*Hippoglossoides platessoides*	257	9.0	0.33
		Zoarcidae	*Lycodes* spp.[d]	205	16.9	0.27
		Liparidae	*Liparis* sp.[e]	130	14.2	0.17
		Scorpaedidae	*Sebastes* sp.[f]	36	1.5	0.05
		Osmeridae	*Mallotus villosus*	10	2.2	0.01
			Unidentified	471	31.1	0.61
Crustacea						
	Amphipoda	Hyperiidae	*Parathemisto libellula*	354	6.4	0.46
		Gammaridae	*Gammarus wilkitzkii*	348	1.9	0.45
			Gammarus spp. fragments	16	1.1	0.02
		Lysianassidae	*Onisimus glacialis*	14	0.4	0.02
			Anonyx spp.	17	1.9	0.02
			Lysianassidae n.det.	3	0.7	0.004
		Stegacephalidae	*Stegocephalus inflatus*	1	0.4	0.001
			Amphipod fragments n.det.	11	2.6	0.01
	Decapoda	Crangonidae	*Sabinea septemcarinata*	291	19.8	0.38
			Sclerocrangon spp.	190	7.5	0.25
		Pandalidae	*Pandalus borealis*	113	6.7	0.15
		Hippolytidae	*Eualus gaimardi*	35	3.7	0.05
			Lebbeus polaris	15	2.2	0.02
			Hippolitidae n.det	5	1.9	0.01
		Paguridae	*Eupagurus pubescens*	1	0.4	0.001
			Decapoda fragments	21	4.9	0.03
			All Decapods together	671	28.5	0.87
	Euphausiacea	Euphausiidae	*Thysanoessa inermis*	6	0.7	0.01
			T. longicaudata	2	0.4	0.003
	Isopoda	Idoteidae	*Synidotea nodulosa*	4	0.4	0.01
	Mysidacea	Mysidae	*Mysis oculata*	1	0.4	0.001
Cephalopoda		Gonatidae	*Gonatus fabricii*	7	1.5	0.009
Polychaeta			Polychate jaws	15	4.9	0.02
			Polychate setae	26	8.2	0.03
Sum	Fish			75 713	100.0	98.06
	Crustaceans			1 448	38.2	1.88
	Other invertebrates			48	10.5	0.06
	All prey			77 209		
Others[g]						
		Bivalva	*Astarte* sp.	3	1.1	0.004
			Yoldia sp.	1	0.4	0.001
			Bivalve fragments	248	20.1	0.3
		Gastropoda	*Margarites* sp.	1	0.4	0.001
		Algae	Algal fragments	22	6.0	0.03
			Dictyosiphon sp.	12	4.1	0.02

Continued

Table 2. Continued

Prey item			Number of prey	FO (%)	N_i (%)
	Tunicata	Tunicata fragment	1	0.4	0.001
	Foraminifera	*Rhabdaminia* sp.	1	0.4	0.001

[a]Gadidae sp. was distinguishable from polar cod, but these specimens were too eroded to distinguish between *Gadus morhua* and *Pollachius virens*; [b]three possible species: *Lumpenus lampraeteformis*, *Leptoclinus maculatus*, and *Anisarchus medius*. The last two are more plausible than the first in the sampling areas; [c]primarily *Gymnacanthus* sp. and *Myoxocephalus* sp. (most probably *G. tricuspis* and *Myoxocephalus scorpius*) and a few *Triglops* sp; [d]several species found in Spitsbergen waters (e.g. *L. pallidus*, *L. seminudus*, *L. rossi*); [e]possibly *Liparis liparis* or *Liparis koefoedi*. [f]Two species possible: *Sebastes marinus* and *Sebastes mentella*; [g]likely to be secondary prey. FO_i (%), frequency of occurence; N_i (%), numerical frequency.

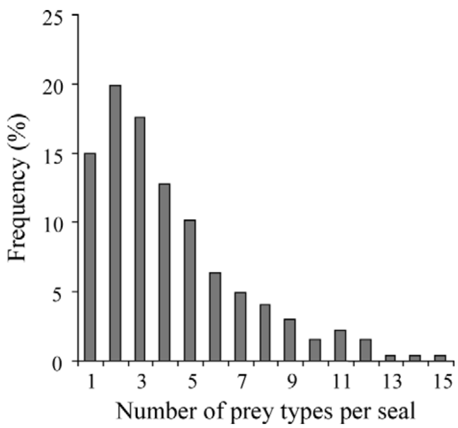

Figure 2. Frequency distribution of the total number of different prey types identified in each of the 267 ringed seals collected in Spitsbergen for gastro-intestinal analysis.

prey types were identified, including representatives from 5 orders and 11 families (Table 2). In addition, remains of cephalopods and polychaetes were found in a few GITs (Table 2). Various fragments of small bivalves (<5.0 mm), a single gastropod, algae, tunicates, and a foraminiferan (see Table 2) were considered to be secondary prey and were not included in subsequent analyses. Gastroliths were found in the GITs of several seals, but were not systematically noted.

More than half the ringed seals (52%) had ingested ≤3 prey types, and the maximum number of different prey types found in one seal was 15 (Figure 2). Only 18.4% of the seals had ≥6 prey types in their GITs. Some 77% of the various prey types had a FO_i of <10, and 86% (30 prey types) had a N_i of <1 (Table 2). Polar cod was the dominant prey type, both in terms of number of individuals ingested and biomass, and it was the only prey species with an FO_i of 100 (Tables 2 and 3). Stichaeidae, Cottidae, and Gadidae (excluding polar cod), in that order, were the three next most important prey types in terms of all three diet indices (Tables 2 and 3). Invertebrate prey constituted just 1.94% of all prey types (N_i, Table 2).

Of fish, the smallest estimated prey length was that of *Hippoglossoides platessoides*, and the largest was a polar cod (Table 3). The biomass index of the prey types for which size estimations were obtained (B_{fish}) and the frequency index (N_{fish}) suggested similar patterns of relative importance of various prey types (Table 3). All prey types for which no size estimations were obtained had a N_i of <1.

Table 3. Number of otoliths from each fish prey type and estimated length range and total biomass of ingested fish based on measured otoliths found in the GITs of 267 ringed seals from Spitsbergen.

Prey item	Number of otoliths		Fish length (mm)		Estimated biomass (g)	N_{fish} (%)	B_{fish} (%)	Source
	Total	Number measured	Min	Max				
B. saida	110 846	7 007	44.5	229.2	546 978	74.5	77.2	Härkönen (1986)
G. morhua	724	65	36.5	161.2	1 719	0.5	0.2	Härkönen (1986)
Gadidae sp.[a]	2 653	–	–	–	6 299	1.8	0.9	Härkönen (1986)
M. aeglefinus	4	4	120.6	130.2	29	0.003	0.004	Härkönen (1986)
Stichaeidae spp.[b]	30 377	543	96.5	157.4	97 985	20.4	13.8	K. T. Nielsen (pers. comm.)
Cottidae spp.[c]	3 107	95	89.6	169.4	53 031	2.1	7.5	Härkönen (1986)
H. platessoides	506	93	14.2	125.4	165	0.3	0.02	Härkönen (1986)
Lycodes spp.[d]	394	17	104.0	226.3	2 134	0.3	0.3	Härkönen (1986)
Sebastes sp.[e]	70	12	75.6	104.0	273	0.2	0.04	Härkönen (1986)
Mallotus villosus	18	1	114.8	–	90	0.05	0.01	Härkönen (1986)
Liparis sp.	243	–	–	–	–	–	–	
Fish larvae, not determined	1 182	–	–	–	–	–	–	
Sum	148 699	7 837			708 703			

[a]Based on the *G. morhua* fish mass estimation relationship; [b]equations for the species *L. maculatus* used here. FL (mm) = 25.564 OL (mm) + 74.561 (r^2 = 0.3023). Fish mass (g) = 3.7735 OL (mm) = 1.3259 (r^2 = 0.3705). [c]Equations for the species *M. scorpius* used; [d]equations for the species *Lycodes vahli* used; [e]equations for the species *Sebastes marinus* used. N_{fish}, relative numerical frequency; B_{fish}, relative proportion in terms of biomass of the various fish prey types.

When the GIT contents were sorted according to sampling location, polar cod completely dominated all areas except for FSJ (Table 4). There, N_i for polar cod was only 15.5 (Table 4). The number of different prey types found per seal in FSJ was significantly higher than in the other areas (Analysis of deviance, $p < 0.01$), and all seals from that area had remains of at least one fish species other than polar cod (Table 4). Stichaeidae was the dominant prey type in terms of N_i in FSJ (Table 4). The FSJ samples also had the largest mean number of decapod crustaceans per seal. The dominant decapods were *Sclerocrangon* spp. and *Sabinea septemcarinata*. Wijd had more crustacean prey types than other locations, but few types of fish other than polar cod. All GITs that contained *G. wilkitzkii* and most of those with *P. libellula* were from this area, and all but one of the amphipod species found were in Wijd samples.

The CCA model explained 20.3% of the total variation in selected prey counts (Monte–Carlo test, $p < 0.01$), 80.8% of which was explained by the first two axes (Figure 3). Location had a significant influence on prey type composition of the GITs, as did sex and age of the seals, but to a lesser degree (Figure 3, see below). The GIT contents of the ringed seals from the FSJ area were characterized by few polar cod and the presence of the two prey types *H. platessoides* and *Sebastes* sp., which were not common elsewhere. GIT contents of Wijd were characterized by the presence of the two amphipod species and relatively low counts of polar cod. Stichaeidae, which were most abundant in seals from FSJ, did not deviate in particular on the bi-plot, being the second most important species found in the GITs in general.

Measurements of polar cod otoliths ($n = 7007$) were obtained from 141 ringed seal GITs, including seals from all areas and categories. The pre-ingested fish length estimates, based on the measured polar cod otoliths, ranged from 44.4 to 229.2 mm (Figure 4a). YC I was the most frequent age group of polar cod taken by the seals (see Figure 4b). The analysis of deviance applied to the GLM Model I showed a significant effect of both location ($p < 0.01$) and seal category ($p < 0.01$) on YC. There was a decreasing trend in the coefficient estimates when moving from north to south (Wijd, Kong, FSJ, Bill, and RKV), more small polar cod being found in the diet as one moved south (Table 5). Values for Wijd and Kong were both significantly higher than that of Bill, and RKV was significantly lower than for all the other locations (Table 5). The seal category coefficient estimates overlapped, with adult males having slightly higher values and juveniles somewhat lower values than the adult females. The male and juvenile coefficients were significantly different from each other (Table 5).

When only ringed seals that had ingested fewer than 100 polar cod were included in the analyses (Model II), the sample size decreased to 121 seals (2952 otoliths), but it still included representatives from all five areas and all seal categories. The effect of both location ($p < 0.01$) and seal category ($p < 0.01$) on polar cod size remained significant in Model II, with the same latitudinal trend exhibited; Wijd, Bill, and RVK were significantly different from each other (Table 4). However, the relationship between the coefficient estimates for the seal categories differed from the previous model; both juvenile and male values were significantly higher than values for females, though they were not significantly different from each other (Table 5).

In model III, where only locations with an approximately even adult sex ratio were included (Wijd, Kong, and Bill), a significant effect of sex remained; adult males ate significantly older/larger polar cod than adult females ($p < 0.01$; Table 5). Model IV, run with Kong data that included juveniles, showed a significant effect of seal category on YC of ingested polar cod ($p < 0.01$); the coefficient estimate for females was significantly lower than for both males and juveniles (Table 5).

Discussion

Our analysis of diet was based on GITs from ringed seals collected during April and May, a period of the year when all ages and sex groups of this seal species (except pups of the year) are in a period of negative energy balance (Ryg *et al.*, 1990). Most adult female ringed seals pup during the first week of April in Svalbard (Lydersen, 1995), then go through an energically demanding lactation period, that is, on average 39 days in duration (Hammill *et al.*, 1991; Lydersen and Hammill, 1993). During this period, the adult males are also in a negative energy balance (Ryg and Øritsland, 1991); they are busy defending their underwater territories (Kelly and Wartzok, 1996) and interacting with adult females as they become available for copulation. Following the breeding season, all animals one year of age and older go through their annual moult (Carlens *et al.*, 2006), and during this time their energy intake is low (Ryg *et al.*, 1990). Being in negative energy balance implies that the seals are relying on energy stored in their blubber (Ryg and Øritsland, 1991), but these stores are not sufficient to cover all the energetic costs of this part of the ringed seals' annual cycle, so they must feed (Ryg and Øritsland, 1991; Lydersen, 1995; Lydersen and Kovacs, 1999). This is confirmed in the present study by the fact that all the ringed seals sampled had prey remains in their GITs.

Consistent with other ringed seal diet studies where material is collected from animals hauled out on the ice (Vibe, 1950; Nazarenko, 1967; Gjertz and Lydersen, 1986; Siegstad *et al.*, 1998; Holst *et al.*, 2001), most stomachs examined in this study were empty. The clearance rate of the GIT in ringed seals, similar to other pinniped species, is very fast, and the initial defaecation time for food consumed can be as short as 4 h, i.e. 2–5 times faster than most other mammals of similar size (Parsons, 1977; Helm, 1984). The present study, therefore, clearly shows the importance of inspecting the whole GIT for prey remains, not just the stomach. A possible issue of concern when analysing the whole GIT is that a lot of the diet information will be derived from material that had been in the digestive system for a long period. However, the chemical composition of fish otoliths makes time spent in the acidic environment of the stomach a greater source of erosion than the effects of enzymatic breakdown in the intestines (Härkönen, 1986; Christiansen *et al.*, 2005).

Identification of pinniped prey by recovered hard parts from faecal or GIT sampling is a widely used method, and identification of otoliths in particular is an important means of analysing diet (e.g. Härkönen, 1986). However, such analyses have a number of inherent potential biases that must be kept in mind, including partial or complete digestion of otoliths of some species, a greater possibility of identifying species with otoliths with distinctive morphological characteristics or larger size, and the fact that fish heads of larger fish may not always be ingested (see Pierce and Boyle, 1991; Browne *et al.*, 2002). Otolith digestion can also be affected by prey species and size, meal size and composition, and predator behaviour (Marcus *et al.*, 1998; Bowen, 2000; Christiansen *et al.*, 2005). Species with fragile otoliths (e.g. clupeids, salmonids such as *Salvelinus alpinus*, pleuronectids,

Table 4. Results from analyses of GIT contents from 267 ringed seals from Spitsbergen split into the five geographical sampling areas.

Prey item	Number of prey per seal					FO$_i$ (%)					N_i (%)				
	Wijd	Kong	FSJ	Bill	RVK	Wijd	Kong	FSJ	Bill	RVK	Wijd (5 339)	Kong (22 978)	FSJ (18 487)	Bill (27 527)	RVK (2 878)
FISH															
B. saida	121	210	68	316	194	100	100	100	100	100	75	91	15	92	88
G. morhua	4	0	4	0	0	45	5	79	8	8	3	0	1	0	0
Gadidae sp.	4	2	12	7	–	33	6	74	35	–	2	1	3	2	–
M. aeglefinus	–	–	0	–	–	–	–	2	–	–	–	–	0	–	–
Stichaeidae spp.	2	15	293	13	24	33	66	83	40	62	1	6	67	4	11
Cottidae spp.	4	0	26	4	0	27	15	98	35	15	2	0	6	1	0
Fish larvae not determined (n.det)	0	–	14	0	–	3	–	24	4	–	0	–	3	–	–
H. platessoides	0	–	6	–	–	3	–	55	–	–	0	–	1	0	–
Lycodes spp.	1	1	1	0	1	33	20	14	6	23	1	1	0	0	0
Liparis sp.	1	0	1	1	0	39	3	24	14	8	1	0	0	0	0
Sebastes sp.	–	–	1	–	–	–	–	10	–	–	–	–	0	–	–
Mallotus villosus	0	0	0	–	0	6	1	2	–	15	0	0	0	–	0
Unidentified	2	1	5	1	1	52	25	50	21	23	1	1	1	0	0
INVERTEBRATES															
P. libellula	10	0	0	0	–	33	1	5	4	–	6	0	0	0	–
Gammarus wilkitzkii	11	–	–	–	–	15	–	–	–	–	7	–	–	–	–
Gammarus spp. fragments	0	0	–	–	–	6	1	–	–	–	0	0	–	–	–
Onisimus glacialis	0	–	–	–	–	3	–	–	–	–	0	–	–	–	–
Anonyx spp.	0	–	0	0	–	3	–	5	3	–	0	–	0	0	–
Lysianassidae n.det.	0	0	–	–	–	3	1	–	–	–	0	0	–	–	–
Stegocephalus inflatus	–	–	–	0	–	–	–	–	1	–	–	–	–	0	–
Amphipod fragments n.det.	0	–	0	0	–	12	–	5	1	–	0	–	0	0	–
S. septemcarinata	0	1	4	1	0	6	16	45	19	8	0	0	1	0	0
Sclerocrangon spp.	0	0	4	0	–	6	2	29	5	–	0	0	1	0	–
Pandalus borealis	–	1	–	0	–	–	15	–	4	–	–	0	–	0	–
Eualus gaimardi	–	0	1	0	–	–	1	12	5	–	–	0	0	0	–
Lebbeus polaris	–	–	0	0	–	–	–	5	5	–	–	–	0	0	–
Hippolitidae n.det	–	–	0	0	–	–	–	7	3	–	–	–	0	0	–
Eupagurus pubescens	–	–	0	–	–	–	–	2	–	–	–	–	0	–	–
Decapoda fragments	0	0	0	0	–	9	1	14	4	–	0	0	0	0	–
All decapods together	0	2	9	1	0	18	29	67	28	8	0	1	2	0	0
T. inermis	–	–	–	0	–	–	–	–	3	–	–	–	–	0	–
T. longicaudata	0	–	–	–	–	3	–	–	–	–	0	–	0	–	–
Synidotea nodulosa	–	–	0	–	–	–	–	2	–	–	–	–	0	–	–
Mysis oculata	–	–	–	0	–	–	–	–	1	–	–	–	0	0	–
Gonatus fabricii	0	0	–	–	–	9	1	–	–	–	0	0	–	–	–
Polychate jaws	–	0	0	0	–	–	2	24	1	–	–	0	0	0	–
Polychate setae	0	0	0	0	–	9	4	31	3	–	0	0	0	0	–
Non *B. saida* fish prey	18	20	363	26	27	91	73	100	85	69	11	9	82	8	12
Sum fish	139	230	431	343	221	100	100	100	100	100	86	99	98	100	100
Sum crustaceans	22	2	9	1	0	55	30	71	29	8	14	1	2	0	0
Sum other invertebrates	0	0	1	0	0	18	6	33	3	0	0	0	0	0	0
Prey total	162	232	440	344	221	100	100	100	100	100	100	100	100	100	100

$<$0.5 = 0; not detected, "–"; FO$_i$ (%), frequency of occurrence; N$_i$ (%), numerical frequency.

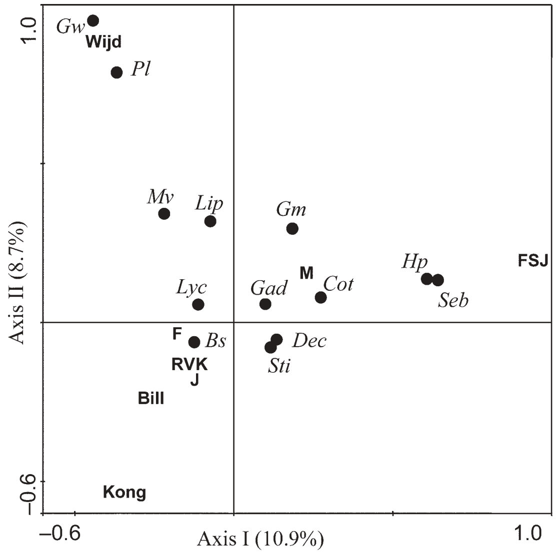

Figure 3. Bi-plot of the CCA on log-transformed prey counts from GITs contents of 267 ringed seals from Spitsbergen as a function of location and seal sex/age categories. The selected prey types (*Gw*, *Gammarus wilkitzkii*; *Pl*, *Parathemisto libellula*; *Mv*, *Mallotus villosus*; *Lip*, *Liparis* sp.; *Gm*, *Gadus morhua*; *Hp*, *Hippoglossoides platessoides*; *Seb*, *Sebastes* sp.; *Lyc*, *Lycodes* spp.; *Gad*, Gadidae; *Cot*, Cottidae; *Dec*, Decapoda; *Sti*, Stichaeidae; *Bs*, *Boreogadus saida*) are marked as filled circles. Emboldened are the independent variables, which include the five locations (Wijd, Wijdefjorden; Kong, Kongsfjorden; FSJ, Forlandsundet and St Jonsfjorden; Bill, Billefjorden; RVK, Recherchefjorden and Van Keulenfjorden) and the seal sex/age categories (M, males; F, females, J, juveniles). The independent variables explain 20.3% of the total variation in the dependent variables. The percentage of the total variation explained by the two first axes are indicated on Axes I and II, respectively.

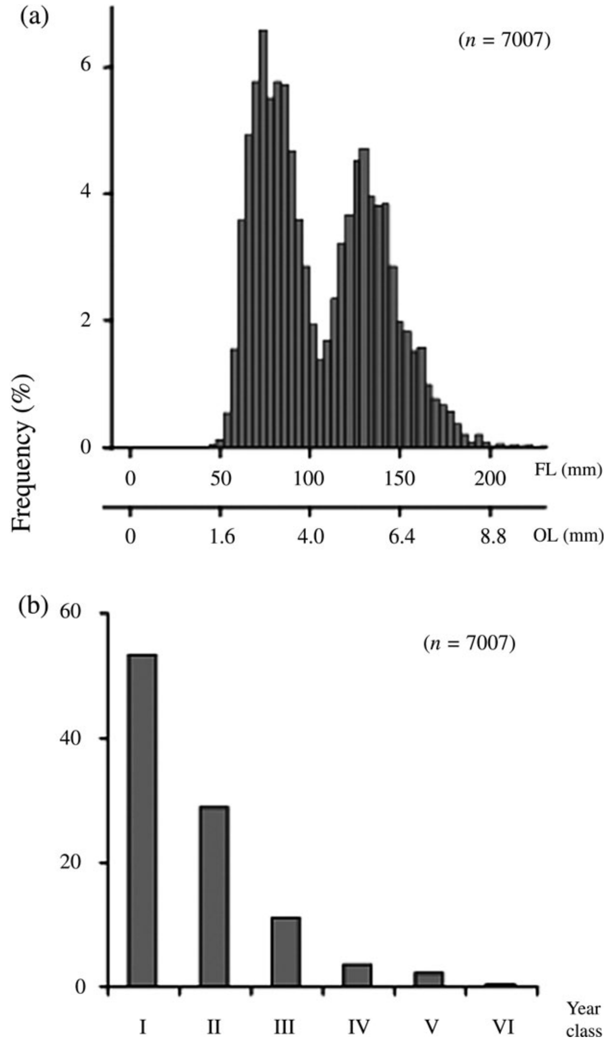

Figure 4. Frequency distributions of polar cod found in the GITs of 141 ringed seals from Spitsbergen, Svalbard by (a) fish length (FL) with corresponding otolith length (OL) and (b) year class.

i.e. dabs and flounders) could be underestimated in the present study, but with the large amount of material from a large collection of seals analysed here, it is unlikely that any frequent prey types were totally missed in the analyses.

Many species were found in the GITs of the sampled ringed seals, but similar to most other studies of ringed seal feeding, only a few species dominated the diet. Polar cod was the most important prey species, consistent with previous studies of ringed seal diet in northwest Spitsbergen (Gjertz and Lydersen, 1986; Lydersen *et al.*, 1989; Weslawski *et al.*, 1994) and many other studies of ringed seal diet in the Arctic (McLaren, 1958; Lowry *et al.*, 1980; Smith, 1987; Belikov and Boltunov, 1998; Siegstad *et al.*, 1998; Holst *et al.*, 2001). This small fish occurs in both ice-free and ice-covered waters, and especially at ice edges (Ponomarenko, 1968). It is an important prey species not only for ringed seals, but also for a wide range of other marine mammals, seabirds, and fish (Bradstreet and Cross, 1982; Haug and Gulliksen, 1982; Gabrielsen and Lønne, 1992; Hjelset *et al.*, 1999; Andersen *et al.*, 2004).

Three species of the second most important prey type, Stichaeidae, are present in Svalbard waters, namely *Leptoclinus maculatus*, *Anisarchus medius*, and *Lumpenus lampraeteformis*, the latter being least common (Hognestad, 1961; Pethon, 1985; Klekowski and Weslawski, 1990). The Stichaeidae have not been recorded as an important food item for ringed seals in Svalbard in previous investigations, and their occurrence in FSJ might be a local phenomenon. Diet studies of both bearded seals (*Erignathus barbatus*) and harbour seals (*Phoca vitulina*) collected from areas close to FSJ have documented a significant contribution to diets by this prey group (Hjelset *et al.*, 1999; Andersen *et al.*, 2004).

Other fish species, in addition to all the invertebrates, occurred in small numbers, and their overall contribution to the diet of the ringed seals was negligible. Crustaceans are an important part of the diet of very young ringed seals in other areas (Siegstad *et al.*, 1998; Holst *et al.*, 2001), and the underrepresentation of this age group in the present study may explain this discrepancy. However, fish generally seem to be the preferred prey if ringed seals are in a situation where they can choose between fish and crustaceans (Wathne *et al.*, 2000).

The geographic variation observed in this study of the diet of ringed seals along the west coast of Spitsbergen might be expected because of the varying influences of Atlantic and Arctic waters characteristic of the various fjords along the coast (Svendsen *et al.*, 2002). The influence of the two water masses varies seasonally and annually, and the extent of water exchange between the

Table 5. Summary table of the estimated model coefficients (Coeff.) derived from the generalized linear models (Poisson distribution of error assumed) used to analyse the effect of location (models I and II), sex (model III), and seal category (models I, II, and IV) on YC of ingested polar cod. CIs (95%) for the model coefficients were derived from s.e (Coeff. ± 1.96 s.e.).

Variable	Model I		Model II		Model III		Model IV	
	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI
Wijd	**0.58**	**0.519–0.647**	**0.49**	**0.413–0.57**	**0.49**	**0.409–0.568**	–	–
Kong	0.57	0.525–0.607	0.37	0.317–0.43	0.38	0.318–0.436	–	–
FSJ	0.53	0.459–0.601	0.28	0.201–0.35	–	–	–	–
Bill	**0.47**	**0.424–0.514**	**0.33**	**0.266–0.39**	**0.32**	**0.255–0.387**	–	–
RVK	**0.24**	**0.140–0.339**	**0.02**	**−0.085 to0.12**	–	–	–	–
Juveniles	**0.39**	**0.336–0.453**	0.64	0.558–0.72	–	–	0.67	0.57–0.76
Females	0.47	0.424–0.514	**0.33**	**0.266–0.39**	**0.32**	**0.255–0.387**	**0.32**	**0.24–0.39**
Males	**0.55**	**0.508–0.597**	**0.67**	**0.610–0.73**	**0.67**	**0.605–0.730**	**0.75**	**0.66–0.85**

Coefficient estimates with non-overlapping CIs are emboldened.

water masses of the various fjords with these coastal water masses additionally varies according to the geomorphology and size of a fjord (Svendsen *et al.*, 2002). Wijdefjorden on the north coast of Spitsbergen (see Figure 1) is the least influenced by Atlantic water; it is a site notable for the number of crustaceans consumed by the ringed seals. The other locations are probably all influenced by Atlantic water to some degree, with FSJ probably being most influenced by Atlantic water with its open coastal connection (see Figure 1). This might explain the greater species diversity in the diet of ringed seals from this area. Additionally, glacial impacts have a substantial effect on biological processes in fjords in Svalbard (Hop *et al.*, 2002), and FSJ is the least influenced of the five collection sites in terms of glacial activity.

The relative abundance of the various size/age classes of polar cod in Spitsbergen coastal waters varies from year to year (Falk-Petersen *et al.*, 1986). However, generally speaking, large polar cod are distributed deeper than smaller fish, and small polar cod (YC I and II) dominate the pelagic zone and shallow areas, and are more tightly associated with sea ice (Falk-Petersen *et al.*, 1986; Lønne and Gulliksen, 1989). The large fraction of young polar cod in the GIT of the ringed seals in this study is consistent with earlier ringed seal diet studies, and suggests that ringed seals in Svalbard primarily forage in the upper parts of the water column or in association with ice (Gjertz and Lydersen, 1986; Gjertz *et al.*, 2000; Wathne *et al.*, 2000). The geographical variation in year-class distribution of polar cod ingested by ringed seals in this study is most likely an expression of the YCs present in the various locations. However, there is still a significant effect of seal sex on ingested YCs of polar cod, even when location is accounted for in the statistical models (Table 5). At the time of sampling, most adult females remain in areas of the fjords where they rear their young. This tight association with ice over a long period of time likely explains, at least in part, the significantly larger fraction of the youngest YC of polar cod found in the GITs of adult females. Adult males and juveniles are in all likelihood less restricted in their movements during the spring season generally, so have the opportunity to exploit the older YCs of polar cod that reside in deeper waters.

Location of sampling and sex and age of seals significantly influenced the spring diet of ringed seals in Svalbard. However, those factors explained just 20% of the variance in prey compositions reflected in the GITs. Additional influences on diet might include individual prey preferences and feeding strategies, variation in prey availability by depth not accounted for by location alone, short-term variations in inflow of different quatities of Atlantic and Arctic water into the fjords that could radically alter prey type availability over short periods of time, and small-scale temporal influences such as the time of feeding in relation to tide, time of day, and weather. More information is certainly needed on the distribution of polar cod, as well as other prey groups identified in this study, before it would be possible to provide reliable information on potential selectivity in the choice of prey by this keystone Arctic predator.

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