Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

The summer diet of hooded (*Cystophora cristata*) and harp (*Pagophilus groenlandicus*) seals in the West Ice

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Solveig Enoksen
BIO-3950 Master thesis in Biology
August 2014

UiT
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HAVFORSKNINGSINSTITUTTET
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Front page photos by Solveig Enoksen
Upper: Harp seal mother with pup
Lower: Hooded seal female

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Tromsø, August 2014,

Solveig Enoksen

Summary

The harp seal (*Pagophilus groenlandicus, Erxleben, 1777*) and hooded seal (*Cystophora cristata, Erxleben, 1777*) are both species that inhabit the drift ice areas in the West Ice during certain times of the year. To better understand the role of marine mammal predation in marine systems, and also to better manage them, it is important to know more about their diets. Projects aiming to study the feeding habits of hooded and harp seals in the West Ice were therefore initiated in the mid- to late 1990s, and the present study is part of the Institute of Marine Research's management studies of these seals.

A total of 179 hooded seals were collected in June-July of 2008 and 2010, together with 20 harp seals and 70 harp seal faeces samples in 2010. The contents of the gastrointestinal tracts and faeces samples were identified to the nearest possible taxon, and the prey importance was estimated with both qualitative and quantitative measurements. The diet composition of harp and hooded seals was shown to differ much; polar cod (*Boreogadus saida*) dominated the hooded seal diet, whilst amphipods (mostly *Themisto* sp.) dominated the harp seal diet. Both species had fed upon the squid *Gonatus fabricii*, but the importance of this prey species in the hooded seal diet was lower than in previous years. The occurrence of polar cod, *Themisto* sp. and krill in the diets of the two seal species coincides well with the distribution of these three prey items, as well as the recorded dive depths of the seals. The inclusion of the demersal fishes sculpins and snailfish in the diet of some of the hooded seals was more likely because of temporal availability rather than changes in prey preference, as these seals were collected above shallower waters.

Both seal species showed a rather narrow niche breadth, but when comparing the diets of these species in different areas, it appears as though both species are generalists on a population level. The total prey consumption during June-August 2010 for the hooded seal population was estimated to about 42,000 tonnes (35,000 tonnes polar cod), and almost 300,000 tonnes (283,000 tonnes crustaceans) for the harp seals.

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Introduction

The harp seal (*Pagophilus groenlandicus, Erxleben, 1777*) and hooded seal (*Cystophora cristata, Erxleben, 1777*) are both species closely associated with the drift ice. In March-April, stocks of these species give birth in the West Ice east of Greenland, and around April/May (harp seals) and July (hooded seals) they gather on the ice for their annual moulting season (Rasmussen, 1960, Sergeant, 1991, Folkow and Blix, 1995, Folkow et al., 2004, Haug et al., 2004, 2007, Kovacs, 2009). Hooded and harp seals are so-called pack-ice specialists with short lactation periods, and they display large variations in body mass throughout the year due to the seasonal variation in food availability and significant periods of fasting (Kovacs et al., 2009).

The hooded seal is distributed across the Arctic and sub-Arctic areas of the North Atlantic, with a western stock associated with the areas around Newfoundland and in the Davis Strait, and an easterly stock associated with the areas east of Greenland, the West Ice (Kovacs et al., 2009). Males of this species can grow to a length of 250 cm and reach a body weight of almost 400 kg, averaging 300 kg, whilst the females are much smaller at 2.2 m and an average of 200 kg (Kovacs, 2009). They mainly prey on fish and squid (Kovacs, 2009), and can dive down to around 1,000 m whilst diving (Folkow and Blix, 1999). Hooded seals have been commercially exploited for centuries, at times intensively (Rasmussen, 1960, Kovacs, 2009, Kovacs et al., 2009), but declines in abundance has led to a full stop in commercial hunting of this species (Kovacs, 2009, Kovacs et al., 2009). The hooded seal pup production in the West Ice in 2012 was estimated to 13,655, giving a total population estimate of 84,020 individuals in 2013 (Øigård et al., 2014a).

The harp seal is an abundant species distributed between the North Atlantic in the west, and the Kara and Bering seas in the east. Three geographically separated stocks are recognised; one in the Barents and White Seas (the East Ice), one in the West Ice, and one in the Northwest Atlantic off Newfoundland and in the Gulf of St. Lawrence (Kovacs et al., 2009, Lavigne, 2009). Adult harp seals can grow to a length of 1.9 m and reach a body weight of 200 kg, with both sexes at roughly the same size (Haug and Bjørge, 2010). They mainly prey on fish and crustaceans (Lavigne, 2009), and can reach depths of around 500 m whilst diving (Folkow et al., 2004). The harp seal is currently being exploited commercially (Kovacs et al., 2009, Lavigne, 2009), with current annual catch levels of 5941 individuals in the West Ice (Øigård et al., 2014b). In 2013, the West Ice stock abundance was estimated to 627,410 individuals, from a pup production estimate of 89,590 in 2012 (Øigård et al., 2014b).

Several factors are important to know to better understand the role of marine mammal predation in marine systems; among these are their diets. As marine mammals are large-bodied and homeothermic, they have high energetic requirements, and might thus be significant consumers in marine systems (Haug et al., 2011). Little is known of the ecological significance of the seal stocks in the West Ice, as there have been few diet studies of these seals (Potelov et al., 2000, Haug et al., 2007). Projects aiming to study the feeding habits of hooded and harp seals in these areas were therefore initiated in the mid- to late 1990s (Potelov et al., 2000, Haug et al., 2007). It is also recognized that the inclusion of marine mammals in multispecies models is essential for a realistic modelling of resources (Lindstrøm et al., 1998, 2009). Because of the known importance of the Barents Sea harp seals as fish predators, and also their long exploitation history, the consumption of this stock was included in the multispecies modelling for the Barents Sea in 1997 (Bogstad et al., 1997). Monitoring marine mammal diets could also be important for their conservation and management, as changes in diet due to e.g. changes in sea ice could lead to negative effects on factors such as their survival (Haug, 2010).

Aim of study

The main aim of this study was to gain increased knowledge of harp and hooded seal feeding ecology in the West Ice, and to explore if they compete for food. Also, their prey consumption was estimated to assess possible impact of these apex predators on the West Ice ecosystem during summer. This study is part of the Institute of Marine Research's management studies of hooded and harp seals.

Materials and methods

Seal sampling

The harp and hooded seals included in this study was sampled in drift ice areas off the east coast of Greenland (the West Ice, Figure 1) the 29th June-12th July 2008 and 30th June-18th July 2010, using the research vessel *R/V Jan Mayen* (now *Helmer Hanssen*). The seals were shot on the ice and brought on board for dissection; stomachs and colons were frozen for further analysis. In total, 199 seals were collected these two years: 33 hooded seals in 2008, and 146 hooded seals and 20 harp seals in 2010. Additionaly 70 harp seal faeces samples were collected on the ice in 2010. The catch positions, weight, total length and sex of each animal was recorded (Frie et al., 2008, Haug et al., 2010), and lower jaws with teeth were collected for age determination (see Haug et al., 2004).

As seen in Figure 1, there were two main areas of sampling, one between 76 and 78°N (from now the northern area), and one between 71 and 72°N (from now the southern area). All of the harp seals, including the faeces samples, and eight of the hooded seals in 2010 were collected in the northern area, the rest were collected in the southern area. For comparative reasons, the samples were divided into different sample groups (Table 1).

Table 1: The number of harp and hooded seal gastro-intestinal (stomachs and colons) and faeces samples collected in the southern and northern areas in 2008 and 2010.

Year	Area	Species	Sample	N
2008	South	Hooded seal	Stomachs and colons	33
2010	South	Hooded seal	Stomachs and colons	138
2010	North	Hooded seal	Stomachs and colons	8
2010	North	Harp seal	Stomachs and colons	20
2010	North	Harp seal	Faeces	70

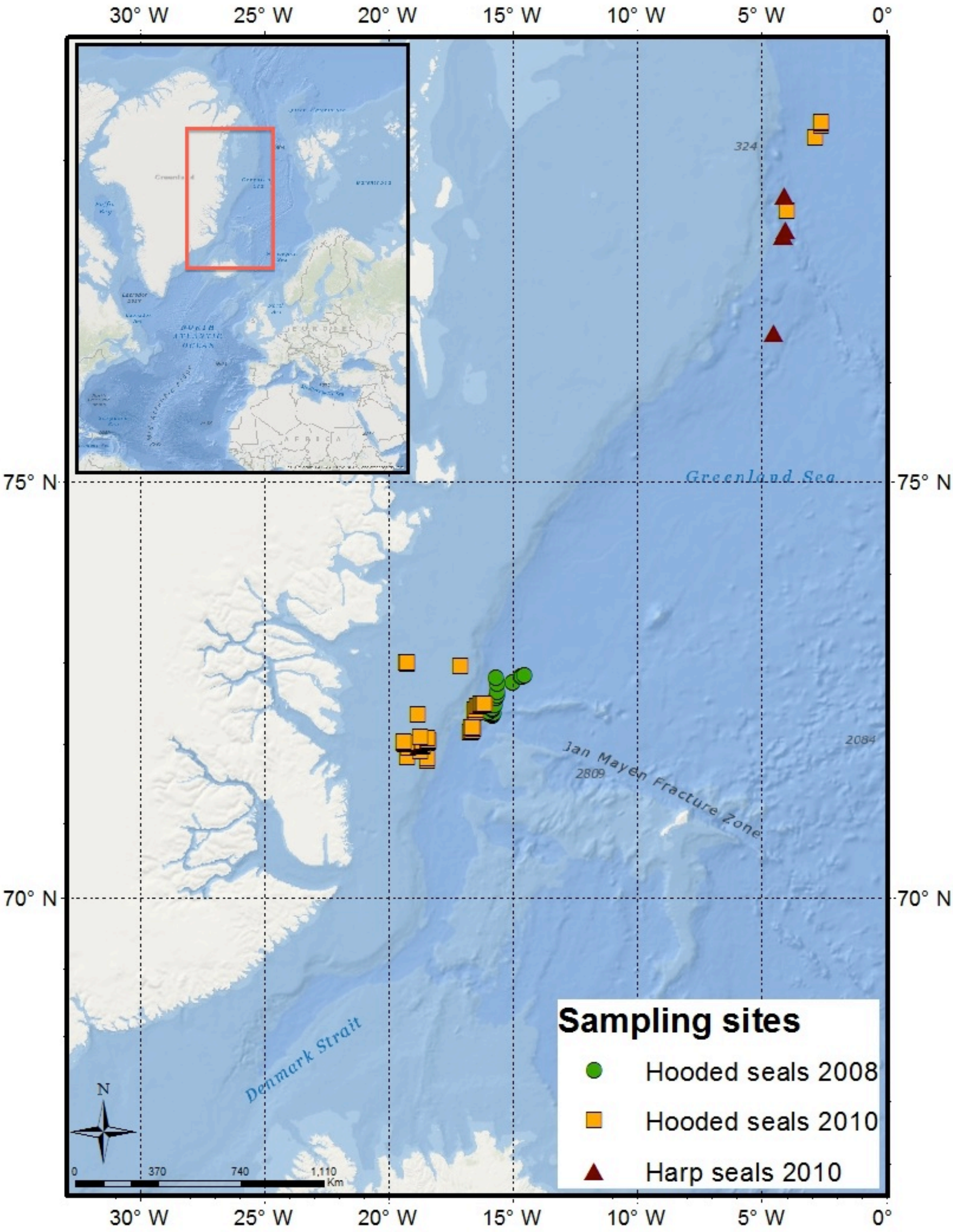

Figure 1: The sampling sites of harp and hooded seals in 2008 and 2010. Green circles mark the catch positions of the hooded seals in 2008, orange squares mark the catch positions of the hooded seals in 2010, and red triangles mark the catch positions of the harp seals in 2010.

All samples in the northern area as well as the southern area in 2008 were collected above water deeper than 1,000 m. Some of the samples collected in the southern area in 2010 were from shallower areas (<300 m depth), whilst the rest were from deeper areas (>500 m depth).

Initial laboratory procedures

The samples were thawed over night, and the stomach and colon contents as well as the faeces samples were filtered through a sieve system of three sieves (0.5 mm, 1 mm and 2 mm). Both stomachs and colons were weighed before and after the removal of contents. Fish sagittal otoliths, fish bones, squid beaks and remains of crustaceans were collected for further analysis.

Laboratory analyses

Samples were identified to nearest possible taxon using Enckell (1980), Clarke (1986) and Härkönen (1986), and the measurements were done using a stereo microscope with a measuring reticle. Otoliths were divided into left and right and then paired. Up to 50 pairs of otoliths from each species or family were measured, and the rest were counted. Wet weight of each fish was calculated using otolith length conversion factors from the Institute of Marine Research's (IMR) earlier material (Table 2). To find the fish wet weight from the counted otoliths, an average of the fish weight calculated from the measured otolith pairs was multiplied by half the amount of counted otoliths. No corrections for otolith degradation were done when calculating the wet weights. Any remains of fish backbones found together with otoliths were assumed to be from the same fish as the otoliths. When there were no otoliths present, any bones found were noted as "unidentified fish".

Hood and rostrum length of upper and lower squid beaks were measured (Figure 2). When there were several beaks, they were divided into groups by size. One from each of these groups was measured, and the rest were counted. Upper and lower beaks were then paired, and the lower beak rostrum length (LRL) for each pair was used to calculate the wet weight using Clarke (1986). When there were only upper beaks in a sample, or the upper beak clearly belonged to a larger squid than the lower beak, a lower beak from another sample paired with the same size upper beak was used to find the wet weight. It must be noted that lower beaks are difficult to measure accurately, especially the smaller ones, as the two points you measure between has to lie horizontally to each other.

Table 2: The regression equations for calculations of individual weights (g) and mean weights (g) of different prey consumed by harp and hooded seals in 2008 and 2010. LRL = lower rostrum length (see Figure 2), OL = otolith length. The regression equations and mean prey weights were taken from earlier work (see Haug et al., 2004, 2007, Windsland et al., 2007), (*) is from Clarke (1986).

Prey item	Equation
Gonatus sp.	Weight = $0.515 \cdot LRL^{3.33}$ (*)
Unknown amphipod	Weight = 0.27
Themisto spp.	Weight = 0.27
Gammarus spp.	Weight = 0.38
Krill	Weight = 0.115
Decapoda	Weight = 2.0
Unknown/other crustacean	Weight = 0.27
Unknown fish	Weight = 5.0
Polar cod	Weight = $0.178 \cdot OL^{2.595}$
Sculpin	Weight = $0.3307 \cdot OL^{3.274}$
Snailfish	Weight = $0.4411 \cdot OL^{6.0788}$
Capelin	Weight = $0.1358 \cdot OL^{2.747}$

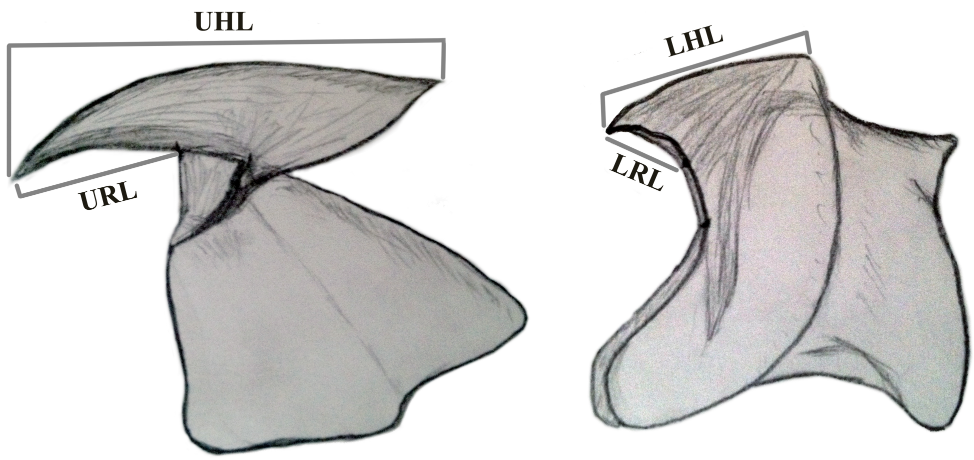

Figure 2: Squid beak measures. UHL = upper hood length, URL = upper rostrum length, LHL = lower hood length, LRL = lower rostrum length. Left: upper beak. Right: lower beak. Only the LRL measurements were used in the regressions to find squid wet weights, but the UHL and URL measurements were used to find the correct LRL measurements for upper beaks when there were no matching lower beaks in the same sample.

To estimate the ingested biomass of crustaceans, the tails were counted, and multiplied with the mean wet weights taken from the IMR's earlier material (Table 2).

The identified prey items were grouped into 6 prey categories: **polar cod** (*Boreogadus saida*), **other fish** (including sculpins (Cottidae), snail fish (Liparidae), capelin (*Mallotus villosus*) and unidentified fish), ***Gonatus fabricii***, **krill** (Euphausiacea), **Amphipoda** (including *Themisto* spp., *Gammarus* spp. and unidentified amphipods) and **Crustacea** (including Isopoda, Decapoda and unidentified crustacean remains).

Data analyses

Sex and age composition

A chi-square (X^2) test that compare observed and expected frequencies in each category was used to test for differences in sex and age composition:

$$\chi^2 = \sum_{i=1}^{n} \frac{(O - E)^2}{E} \qquad \text{(Equation 1)}$$

where *o* denote the observed frequencies, and *e* denote the expected frequencies, in each category or combination of categories, and the summation is over all the categories. The chi-square test assumes that the observed categories are classified independently, and that no more than 20% of the categories have expected frequencies of less than 5 (Quinn and Keough, 2002).

Prey importance

There are several different approaches to measuring prey importance in diet studies, and none of them give a complete overview by themselves (Hyslop, 1980, Pierce and Boyle, 1991). The dietary importance in this study was assessed using the frequency of occurrence and relative prey biomass, as these two are frequently used in diet analyses for marine mammals (Hyslop, 1980, Pierce and Boyle, 1991, Wathne et al., 2000, Berg et al., 2002, Haug et al., 2004, 2007, Windsland et al., 2007).

The frequency of occurrence index (*FO_i*) is a qualitative index calculated as follows:

$$FO_i = \frac{S_i}{S_t} \times 100 \qquad \text{(Equation 2)}$$

where S_i is the number of seals (gastrointestinal tracts/faeces) containing prey species i, and S_t is the total number of seals.

To avoid pseudoreplication, the stomach and colon contents were pooled, and identified prey items were pooled into the six previously mentioned prey categories. To see if there were any differences in prey occurrence between the sample groups (Table 1), a chi-square test was performed on the prey frequency of occurrence data. The same test was performed on the data of the prey occurrence of adult (≥2 years) and juvenile (<2 years) hooded seals to see if there were any differences between adults and juveniles.

The relative biomass index, RB_i, was used to quantify the dietary importance of the seals, and was calculated as follows:

$$RB_i = \frac{B_i}{B_t} \times 100 \qquad \text{(Equation 3)}$$

where B_i is the total mass of prey category i in all gastrointestinal tracts/faeces of one sample group, and B_t is the total mass of all prey items in that sample group.

Bootstrapping and construction of confidence intervals was used to test for differences in the B_i index between the different sample groups. A total of 1,000 replicates were generated from each sample group and used to create 95% confidence intervals for the relative importance (mean) of each prey item (Efron and Tibshirani, 1993, Quinn and Keough, 2002, Haug et al., 2007, Windsland et al., 2007). This resampling technique was introduced in 1979 as a completely automatic, computer-based method for estimating the standard error of a parameter of interest (Efron and Tibshirani, 1993). By randomly drawing many independent bootstrap samples from the original sample, with replacement, it can estimate the standard error by the empirical standard deviation of the corresponding replications (Efron and Tibshirani, 1993, Quinn and Keough, 2002). The confidence intervals were calculated by the percentile method, which means arranging the 1,000 bootstrap samples in ascending order and picking out the 25th (lower percentile) and 975th (upper percentile) values, with $\alpha = 0.05$ (Efron and Tibshirani, 1993, Quinn and Keough, 2002).

Temporal and regional variations in diet

Pairwise bootstrapped-based hypothesis testing was used to test for possible differences in diet composition between the sample groups (Efron and Tibshirani, 1993, Lindstrøm et al., 1998, Haug et al., 2007, Windsland et al., 2007). This was done for each prey item by constructing a confidence interval for the difference between the bootstrapped prey biomass data of the two groups to be compared, and then checking if the null value was in the interval (Efron and Tibshirani, 1993). These confidence intervals were Bonferroni corrected to control Type I error rates, as there were six prey categories in the samples, and thus six pairwise tests, making the lower percentile of these intervals the fourth value, and the upper percentile the 996th value (Quinn and Keough, 2002).

Diet competition and niche breadth

Differences in time, place and trophic level utilised by different animals separate niches (Pianka, 1973). As the harp seals were sampled in the same area as the northern area hooded seals, it would be of interest to see if there is any diet competition between these species. Pianka's niche overlap, O_{jk} (Pianka, 1973, 1974, Krebs, 1999, Wathne et al., 2000), was used:

$$O_{jk} = O_{kj} = \frac{\sum_{i=1}^{n} \left(P_{ij} \times P_{ik} \right)}{\sqrt{\sum_{i=1}^{n} P_{ij}^2 \sum_{i=1}^{n} P_{ik}^2}} \qquad \textbf{(Equation 4)}$$

where O_{jk} is Pianka's measure of niche overlap between predator species j and predator species k and O_{kj} is Pianka's measure of niche overlap between predator species k and predator species j; P_i is the proportion of prey species i in relation to the total amount of prey ingested by either species j (P_{ij}) or k (P_{ik}), and n is the total number of prey species. This measure is symmetrical, meaning that overlap between species j and species k is equal to overlap between species k and species j (Pianka, 1973, Krebs, 1999, Wathne et al., 2000). It is generally considered a biological significant niche overlap of the examined resources when O_{jk} is higher than 0.6 (e.g. Wallace, 1981, Wathne et al., 2000).

Measures of niche breadths attempt to quantitatively measure the degree of specialisation of a species by observing the distribution of individual organisms within a set of resource states (Krebs, 1999). Here, Levin's measure of niche breadth (Krebs, 1999, e.g. Wathne et al., 2000), B, was used to measure the niche breadth of each sample group:

$$B=\frac{1}{\sum_{i=1}^{n} P_i^2} \qquad \text{(Equation 5)}$$

where P_i is the fraction of prey item i in the diet, and n is the number of prey groups. This measure varies between 1 and n; the niche breadth is 1 when only one prey item is consumed. The niche breadth gets closer to n, and thus a high niche breadth, with more, and more evenly consumed, prey groups.

Levin's measure of standardized niche breadth (Krebs, 1999), B_A, was used to get a standardized measure of niche breadth from 0 to 1, with 0 being low niche breadth (few and/or unevenly consumed prey items) and 1 being a high niche breadth with several, evenly consumed, prey items:

$$B_A=\frac{B-1}{n-1} \qquad \text{(Equation 6)}$$

where n is the number of prey items.

Prey consumption

A bioenergetic model (e.g. Lindstrøm et al., 2002) was used to estimate the prey consumption, K_i, by the seals;

$$K_i = N \times \lambda \times GF \times BMR \times D_i \frac{1}{E_{fu} \times E_i} \quad \text{(Equation 7)}$$

where K_i is the prey consumption (in kg per day) of prey item *i; N* is the number of seals in the population, λ is the activity factor, *GF* is the growth factor, *BMR* is the basal metabolic rate, D_i is the fraction of prey item *i* in the diet (based on weight), E_{fu} is the digestion effect for prey item *i*, and E_i is the energy content of prey item *i* (in kilojoule/g, Table 3). The activity factor for the seals in June is 2.0, in July and August it is 2.5 (Nilssen et al., 2000). GF for juvenile seals is 2×BMR. For adult seals, GF = BMR. The BMR (kilojoule/day) was calculated according to Nilssen et al. (2000):

$$BMR = 4.184 \times 70 \times BW^{0.75} \quad \text{(Equation 8)}$$

Table 3: Energy content, E_i, (kilojoule/g) of different prey items (Mårtensson et al., 1996).

Prey	E_i
Crustaceans	4.2833
Other fish/squid	4.2437
Polar cod	5.9638

The digestion coefficient used for fish and *Gonatus fabricii* was 0.85, whereas for crustaceans it was 0.75 (Mårtensson et al., 1994).

Table 4: Total population (*N, Tor Arne Øigård, Institute of Marine Research, pers. comm.*) of juvenile (<2 years) and adult (≥2 years) harp and hooded seals in 2010 and their mean body weight (BW, kg). The mean body weight was calculated from the seal weights from the present dataset and from datasets provided by Tor Arne Øigård, and are based on data sets from summer periods, when the seals are generally slimmer (Kovacs et al., 2009).

	Hooded seals		Harp seals	
	N	BW	*N*	BW
Juvenile	43865	40	378697	30
Adult	38679	170	217975	80
Total	82544		596672	

The seal population numbers used were from 2010 (Table 4), as most of the seals in this study were collected this year. To get a larger dataset, the diet data from the hooded seals collected in 2008 were included in the estimate, as well as the faeces samples from harp seals collected in 2010. Nilssen et al. (2000) also included energy depots in muscles and blubber as well as metabolic costs of pup production in their estimates of the Barents Sea harp seals' food consumption, but this was not done here.

Software used

All calculations were done in Microsoft ® Excel ® for Mac 2011 (Microsoft Corp. Redmond, WA, USA). The bootstrapping was done in R, 3.1.0 (Robert Gentleman and Ross Ihaka, Auckland, USA). All graphs were made using SYSTAT 13 (Cranes Software International Ltd, Chicago, IL, USA). The map was made using ArcGIS for Desktop Advanced, 10.2.2 (Esri, USA).

Results

Sex and age composition

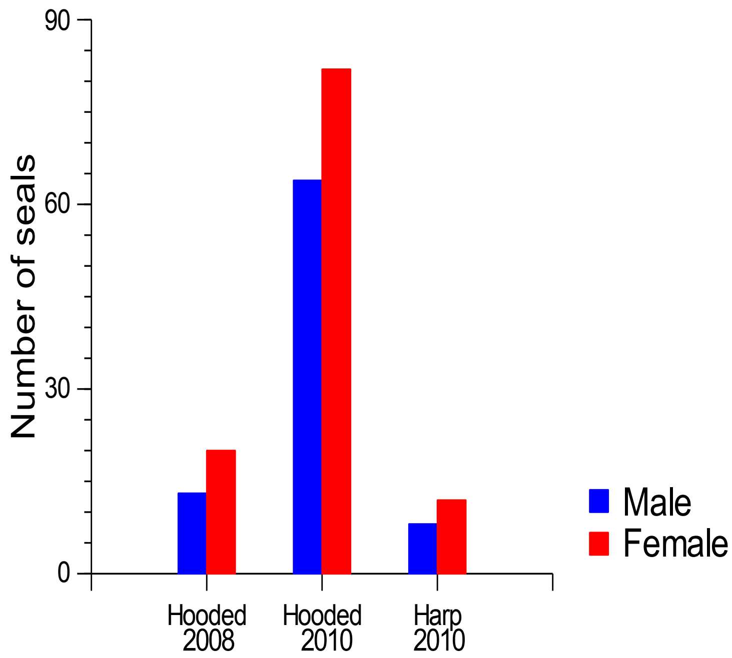

Figure 3: Gender distribution of harp and hooded seals sampled in the West Ice in 2008 and 2010.

There was no significant difference in sex composition among sampling years and species (χ^2=0.28, p=0.87); of the hooded seals, approximately 61% (20 female and 13 male hooded seals) in 2008 and 56% (81 females and 64 males) in 2010 were female (Figure 3). Similarly, 60% of the harp seals caught in 2010 (12 females and eight males) were female. Although the chi-square test shows no significant difference in male:female ratio between the different years and species, there was a difference between the two sampling areas with respect to the hooded seals caught in 2010, as there were more males (five) than females (three) caught in the northern area.

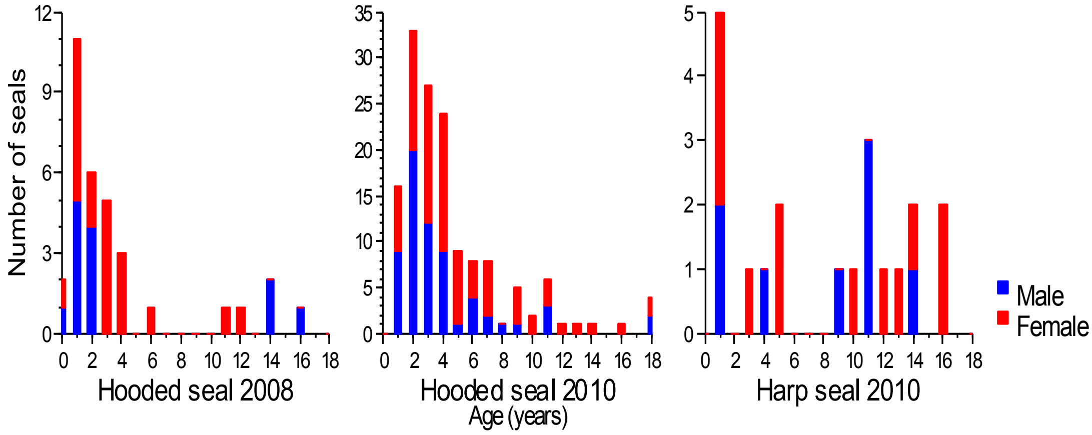

Figure 4: The age and sex distribution of the sampled hooded and harp seals in 2008 and 2010.

The age distribution for the sampled hooded seals from both years appears to be skewed towards the lower age groups (less than five years of age), with fewer older individuals (Figure 4). For the hooded seals caught in the northern area in 2010, all eight of them were one-year-old individuals. The one-year-olds constituted 25% of the sampled harp seals, but these seals were more equally distributed with regards to age for the ones that were between three and five years old, and the ones nine years and older.

Diet composition

A total of 13 different prey items were identified from the samples; polar cod, sculpins, snail fish, capelin, unidentified fish, *Gonatus fabricii*, krill (Euphausiidea), unidentified amphipiods, the two amphipods *Themisto* sp. and *Gammarus* sp., Isopoda, Decapoda and unidentified crustaceans.

Most of the unidentified amphipods were probably of the genus *Themisto*, and most likely the species *T. libellula.* However, as the remains were quite degraded and mostly just consisted of tails, no exact identifications were made. Squid in the genus *Gonatus* are hard to distinguish (Clarke, 1986), but squid found in seal samples from this area is most likely *Gonatus fabricii*, as evidenced by Haug et al. (2007) sending a subsample of beaks to a *Gonatus* expert.

Frequency of occurrence

More than half of the harp and hooded seal stomachs were empty, whereas most colons and faeces samples contained food remains (Table 5). A total of six prey items were identified in the gastrointestinal tracts of the hooded seals from 2008. Polar cod (*Boreogadus* saida, 93.9%) was by far the most frequently occurring prey item in the colons, followed by the squid *Gonatus fabricii* (57.6%). Polar cod was also found to be the most frequently occurring prey species in the stomach samples (27.3%), whereas unidentified amphipods and squid occurred in 9.1% of the stomachs. The amphipods *Themisto* sp. and *Gammarus* sp. both occurred less frequently (3%) in the stomach and colon samples. Fish from the family Cottidae (sculpins) only occurred in one of the stomach samples, and in none of the colon samples.

A total of 13 identified prey items were found in the hooded seal gastrointestinal tracts from 2010. Polar cod (36.5%) had the highest frequency of occurrence in the stomach samples, whilst *Gonatus fabricii* (15.8%), sculpins (13.7%) and unidentified amphipods (11%) all had a similar occurrence. The rest of the prey items occurred rarely in the stomach samples. Polar cod also dominated the colon samples (76%), whilst *Gonatus fabricii*, unidentified amphipods and sculpins occurred less frequently (24-37%). The hooded seal gastrointestinal tracts from 2010 were also the only samples containing snailfish and capelin.

A total of seven different prey items were identified in the harp seal stomachs and intestines. Of these, unidentified amphipods (20%), *Themisto* sp. (10%) and krill (15%) were the most frequent in the stomach samples. In the colons, unidentified amphipods were found in 85% of the samples, whilst *Gonatus fabricii* was found in 50%. 35% of the colon samples contained polar cod, whilst krill was found in only 10%. Unidentified amphipods (85.7%) and *Gonatus fabricii* (67.1%) dominated amongst the five prey items identified in the faeces samples. Polar cod was found in 18.6%, unidentified crustaceans were found in 10%, and krill in 2.9% of these.

Table 5: Frequency of occurrence (%) of the different prey items calculated individually for the stomach, colon and faeces samples of harp and hooded seals collected in the West Ice in 2008 and 2010.

	2008		***2010***				
	Hooded seals n=33		Hooded seals n = 146		Harp seals n=20		
	Stomachs	**Colons**	**Stomachs**	**Colons**	**Stomachs**	**Colons**	**Faeces**
Empty	66.7	6.1	53.4	11.6	60.0	10.0	2.9
Mollusca							
Cephalopoda							
Gonatus fabricii	9.1	57.6	15.8	32.9	5.0	50.0	67.1
Crustacea							
Unknown	0	0	0	0.7	5.0	0	10.0
Amphipoda	9.1	27.3	11.0	24.0	20.0	85.0	85.7
Themisto sp.	3.0	3.0	4.8	6.9	10.0	0	0
Gammarus sp.	3.0	3.0	2.1	0.7	0	5.0	0
Euphausiacea	0	0	2.7	0.7	15.0	10.0	2.9
Isopoda	0	0	0	0.7	0	0	0
Decapoda	0	0	0.7	0	0	0	0
Pisces							
Unknown	0	0	1.4	2.1	0	0	0
Gadidae							
B. saida	27.3	93.9	36.3	76.0	5.0	35.0	18.6
Cottidae	3.0	0	13.7	37.0	0	0	0
Liparidae	0	0	4.1	14.4	0	0	0
Osmeridae							
M. villosus	0	0	0	0.7	0	0	0

Of the six pooled prey groups (Table 6), there was a significant difference of occurrence of amphipods ($p<0.05$, Table 7) in the gastrointestinal tract of harp and hooded seals in the northern area in 2010, but no difference was found between the other prey items ($p>0.05$). Thus, harp seals in the northern area had fed significantly more frequently on amphipods (85%) compared with hooded seals (13%), whilst the two seal species had fed upon the other prey items with a similar frequency in this area.

Table 6: Frequency of occurrence (%) of the six pooled prey categories (polar cod, other fish, squid, amphipods, krill and other crustaceans) in the gastrointestinal tract (stomach and colon samples pooled) and faeces samples of harp and hooded seals sampled in the two sub-areas in the West Ice in 2008 and 2010.

	Hooded seals			***Harp seals***	
	2008	2010			
	South n = 33	**South** n=138	**North** n=8	**North** n=20	**Faeces** n=70
Polar cod	97.0	87.7	25.0	35.0	18.6
Other fish	3.0	45.7	12.5	0	0
Gonatus fabricii	60.6	33.3	75.0	50.0	67.1
Amphipoda	36.4	37.0	12.5	85.0	85.7
Krill	0	3.6	0	20.0	2.9
Crustacea	3.0	2.9	0	5.0	10.0

Table 7: Chi-square test results for the frequency of occurrence of the six pooled prey groups (Table 6) for each of the three sample groups; harp and hooded seals in the north, hooded seals in the south and north in 2010 and hooded seals in the south in 2008 and 2010.

	North: hooded VS harp seals		**Hooded seals 2010: north VS south**		**Hooded seals south: 2008 VS 2010**	
Prey	χ^2	**p**	χ^2	**p**	χ^2	**p**
Polar cod	0.262	0.609	22.385	<0.001	2.440	0.118
Other fish	2.593	0.107	3.376	0.066	20.658	<0.001
G. fabricii	1.458	0.227	5.725	0.017	8.358	0.004
Amphipods	13.082	<0.001	1.972	0.160	0.004	0.949
Krill	1.867	0.172	0.300	0.584	1.232	0.267
Other crustaceans	0.415	0.520	0.238	0.625	0.002	0.968

There was no significant spatial difference in occurrence of amphipods, krill and other crustaceans ($p>0.05$) in the hooded seal diets in the southern and northern area in 2010. In contrast, there were significant differences in frequency of prey occurrence ($p<0.05$) for *G. fabricii* (75% in the north, 33% in the south) and polar cod (25% in the north, 88% in the south) for these seals. The occurrence of the prey group "other fish" (snailfish, sculpins, *M. villosus* and unidentified fish, 13% occurrence in the north, 46% in the south) was in the border of significant difference with a p-value just slightly above 0.05.

There was a significant temporal difference in the frequency of occurrence of other fish and squid ($p<0.05$) in the hooded seal diets in the southern area; other fish occurred more frequently in 2010 (46%) compared with 2008 (3%), whereas squid had been preyed upon more frequently in 2008 (61%) than in 2010 (33%). There was no significant difference between these two sample groups with respect to the other prey groups ($p>0.05$). For harp seals, krill ($p<0.05$) occurred significantly more frequently in the gastrointestinal tracts (20%) than in the faeces samples (3%), whilst there was no difference between the other prey items ($p>0.05$).

Table 8: Frequency of occurrence of the six prey groups in the gastrointestinal tracts of adult (≥2 years of age) and juvenile (<2 years of age) hooded and harp seals sampled in the West Ice in 2008 and 2010.

Year	Species	Age	Polar cod	Other fish	*G. fabricii*	Amphipoda	Krill	Crustacea
2008	Hooded seal	<2	100	7.7	46.2	30.8	0	0
		≥2	95	0	70	40	0	0
2010		<2	50	31.3	43.8	25	0	0
		≥2	88.5	44.6	34.6	37.7	3.8	2.3
	Harp seal	<2	20	0	20	60	20	0
		≥2	40	0	60	93.3	20	6.7

To explore whether harp and hooded seals display ontogenetic diet shifts, a chi-square test was performed on the frequency of prey occurrence for the juvenile (<2 years old) and adult (≥2 years old) individuals (Table 8). With the exception of the occurrence of polar cod in juvenile (88.5%) and adult (50%) hooded seals in 2010 ($\chi^2=15.88$, $p<0.001$), there was no significant difference in frequency of prey occurrence between juvenile and adult seals ($p>0.05$).

Relative composition of consumed biomass

Figure 5 shows the relative composition of consumed biomass (%) for the different sample groups. Polar cod dominated the biomass in the hooded seal gastrointestinal samples (>80%) independent of area and year: 98% in the northernmost area in 2010, 82% in the southernmost area in 2010, and 96% in 2008. Other fish (mainly sculpins and snailfish) contributed 14% to the hooded seal diet in the southern area in 2010, and <1% in the other areas and years. The squid *G. fabricii* contributed 2-3%, and amphipods, krill and crustaceans <1% to the diet of hooded seals these two years. Independent of area in 2010, polar cod contributed 84%, other fish 13%, *G. fabricii* 3%, and amphipods, krill and other crustaceans <1% each.

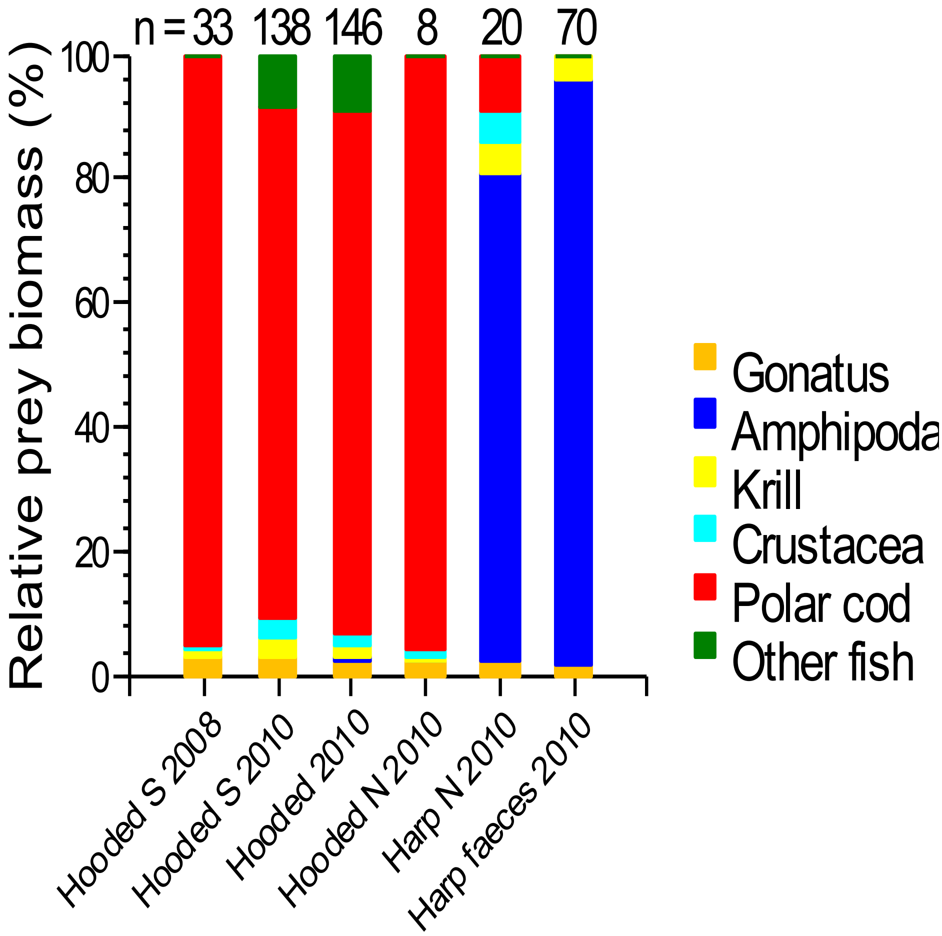

Figure 5: Relative prey biomass (%) of the six prey categories (squid, amphipods, krill, other crustaceans, polar cod and other fish) in the gastrointestinal tracts and faeces samples for the different sample groups of harp and hooded seals collected in the West Ice in 2008 and 2010.

For the harp seals, amphipods dominated in both gastrointestinal (78%) and faeces (94%) samples. Polar cod contributed 16% in the gastrointestinal samples and only 4% in the faeces samples. There were no other fish present in either of the harp seal samples, and the squid contributed about 3% in each of them. Krill contributed about 2% in the gastrointestinal content and less than 1% in the faeces samples. Other crustaceans also contributed much less than 1% in each.

The relative prey importance derived from the bootstrapping of the diet (Figure 6) gave a similar result to the relative consumed biomass seen in Figure 5, with the hooded seals feeding mostly on polar cod and the harp seals feeding mostly on amphipods. As there were only 20 harp seal samples, the confidence intervals are larger than for both the hooded seal samples, but this might also be due to higher individual diet variation. The somewhat larger confidence intervals for the hooded seal samples from 2010 compared to the 2008 samples suggest a higher individual variation in diet composition for the 2010 seals.

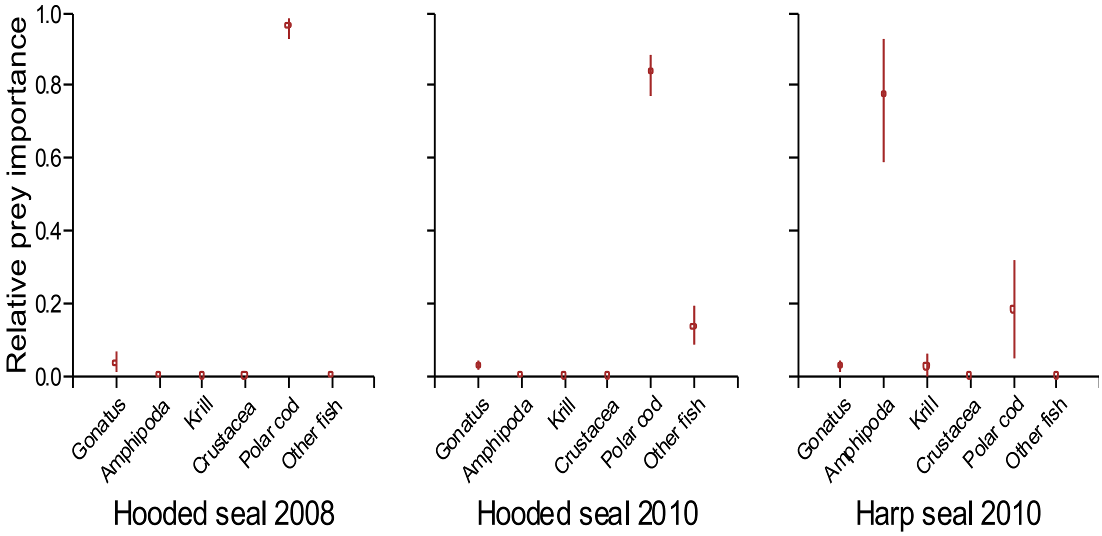

Figure 6: Relative prey importance in terms of biomass of the different prey goups. The error bars (95% confidence intervals) were determined from 1,000 bootstrappings of the diet data.

Temporal and regional variations in diet

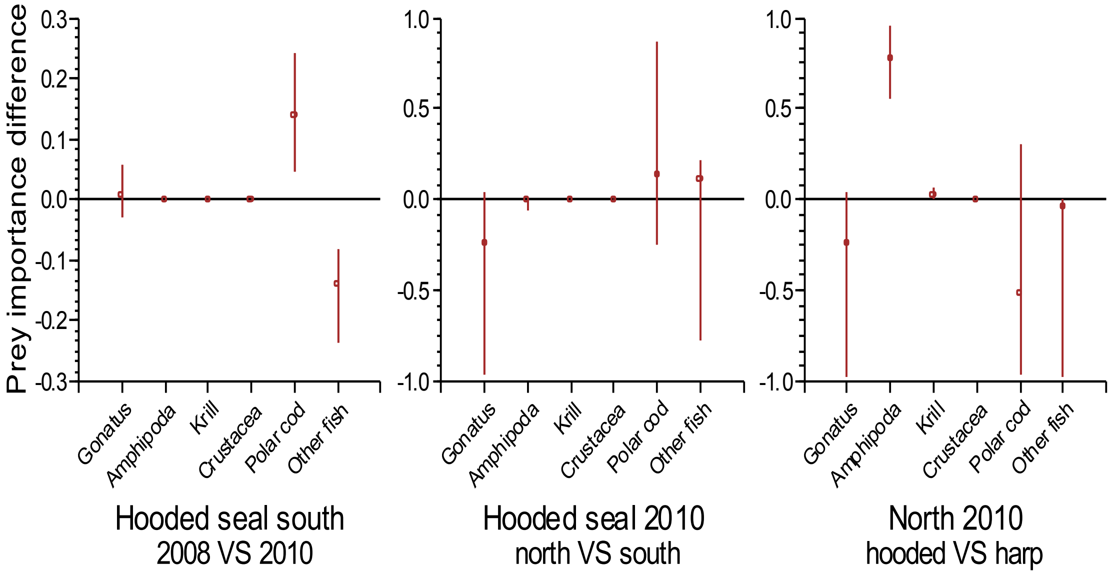

Figure 7: Spatio-temporal differences in prey importance of harp and hooded seal sample groups from two sub-areas (south and north) in the West Ice during the summers of 2008 and 2010. The error bars (95% confidence intervals) are based on 1,000 bootstrap replicates of the diet data seen in Figure 8. Where the error bars overlap the zero horizontal line there is no significant difference for that prey group. Non-overlapping error bars suggest significant temporal or spatial difference in prey importance.

Comparing the hooded seal diets in the southern area in 2008 and 2010 showed that polar cod had been consumed in significantly greater amounts in 2008, and that other fish had been consumed in significantly greater amounts in 2010. This can be seen in Figure 7, where the confidence intervals of polar cod and other fish do not overlap the horizontal line of zero difference. There was no significant temporal difference in importance with respect to the other prey groups for these two sample groups. For the hooded seal samples from 2010, there was no significant difference between any of the prey items in the northern and southern areas, but the confidence intervals are large. For the harp and hooded seals from the northern area, squid, polar cod and other crustaceans have no significant difference. The prey preference test results for amphipods, krill and other fish are significantly different for these samples.

Diet overlap and niche breadth

The dominance of polar cod in the hooded seal diets, and amphipods in the harp seal diets, resulted in no niche overlap in diet between these two seal species (O_{jk}=0.16).

Table 9: Niche breadth of the harp and hooded seal sample groups from two subareas (south and north) in the West Ice during the summers of 2008 and 2010. Both the Levin measure (0-*n*) and the standardized measures (0-1) are given.

Species	Area	Year	Levin	Stand.
Hooded seal	S	2008	1.08	0.02
		2010	1.43	0.08
	N		1.05	0.01
	N&S		1.39	0.08
Harp seal	N		1.56	0.11

The niche breadths of all sample groups were low, ranging from 1.05 to 1.56 (Levin's measure) and 0.01 to 0.11 (standardized), suggesting a low niche breadth and thus high prey specificity (Table 9).

Prey consumption

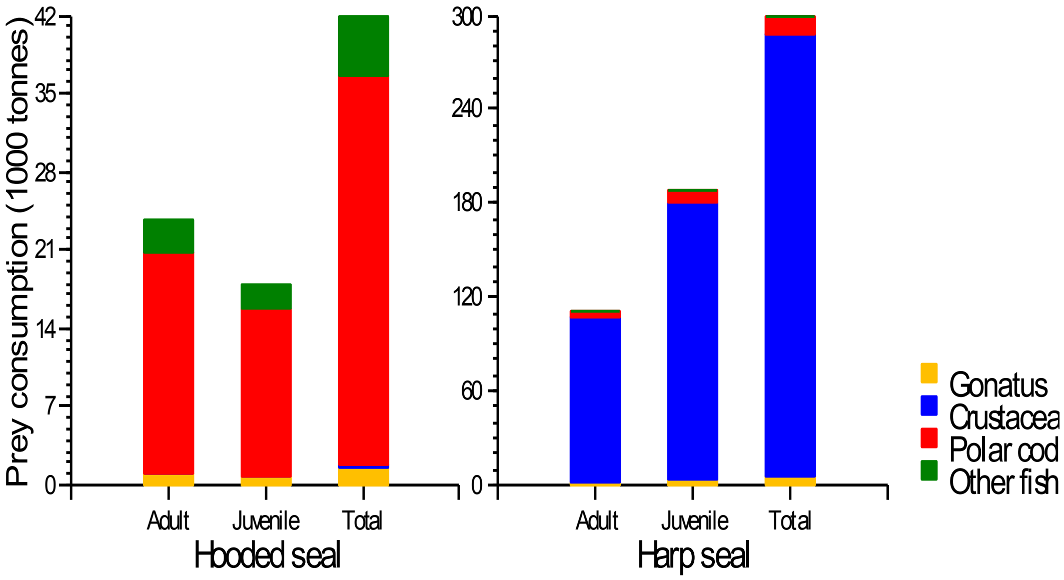

Figure 8: Estimated prey consumption (1,000 tonnes) of juvenile (<2 years old) and adult (≥2 years old) hooded and harp seals in the West Ice during summer (June-August) of 2010.

The total estimated prey consumption for the summer of 2010 was around 42,000 tonnes for the hooded seal population in the West Ice, and around 300,000 tonnes for the harp seal population (Figure 8). Of this, the juvenile hooded seals consumed 18,000 tonnes and the adult hooded seals 24,000 tonnes. Polar cod dominated both age groups, with a total consumption of about 35,000 tonnes. In contrast to the hooded seals, the prey consumption by juvenile harp seals were almost two thirds of the total harp seal consumption, close to 190,000 tonnes, whilst the adults had consumed about 110,000 tonnes. Crustaceans completely dominated the harp seal prey consumption; a total consumption of almost 283,000 tonnes crustaceans was estimated for the three summer months.

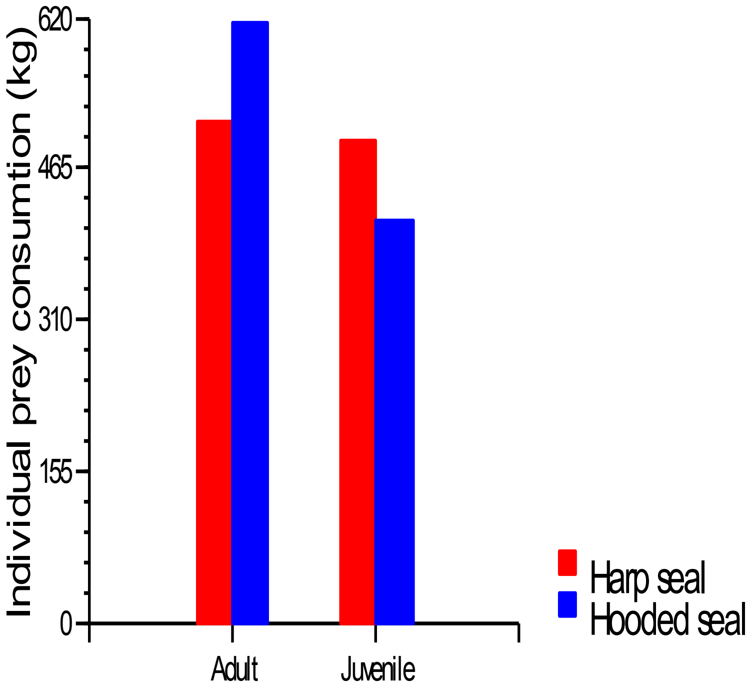

Figure 9: Estimated total prey consumption (kg) by individual juvenile (<2 years old) and adult (≥2 years old) harp and hooded seals in the West Ice in June-August of 2010.

The mean individual prey consumption of adult and juvenile harp and hooded seals during the three summer months of 2010 is shown in Figure 9. One juvenile hooded seal with a body weight of 40 kg was calculated to have consumed about 410 kg of prey. In an average day, this seal would have consumed about 4.5 kg of prey, and of this, about 3.7 kg would have been polar cod. One adult hooded seal with a body weight of 170 kg would have consumed about 615 kg for these three months, with an average of 6.7 kg (5.5 kg polar cod) per day. One juvenile harp seal with a body weight of 30 kg would have consumed about 495 kg prey for the summer months, and 5.4 kg (5.1 kg crustaceans) on average per day. An average adult harp seal with a body weight of 80 kg was calculated to have consumed about 512 kg of prey for this period, with an average of 5.6 kg (5.3 kg crustaceans) per day.

The consumption for adult and juvenile harp seals is fairly close, whilst there is a higher gap between the prey consumption of adult and juvenile hooded seals. An individual juvenile harp seal was calculated to have eaten more per day than a slightly larger juvenile hooded seal, whilst an adult hooded seal was calculated to have eaten more than a much smaller adult harp seal.

Discussion

The major findings in this study suggest that:

1. Hooded seals display little spatio-temporal variation in prey use.
2. There is no significant diet overlap between hooded and harp seals, and both species have narrow niche breadths.
3. Harp seals in the West Ice consume almost 300,000 tonnes of prey during June-August, with the majority being crustaceans, whilst hooded seals consume about 42,000 tonnes of prey during the same time, with the majority being polar cod.

Diet composition

The diet composition of hooded and harp seals in this study differed much; polar cod dominated the hooded seal diets, whereas amphipods dominated the harp seal diets in terms of biomass. The narrow confidence intervals of the hooded seal diet suggest small intraspecific variation in diet composition, whereas the broader confidence intervals of the harp seals may be either due to low sample size and/or greater intraspecific variation in prey use. The apparent temporal difference in diet composition of hooded seals is more likely a result of temporal difference in prey availability than changes in prey preference; some of the hooded seals in 2010 were collected above shelf areas that allowed them to feed on demersal prey items such as sculpins and snailfish, whereas in 2008 the seals were collected above deeper water, constraining their feeding to epi- and/or mesopelagic prey (e.g. squid and polar cod). The occurrence of polar cod, *Themisto* sp. and krill in the diets of the two seal species coincides well with the distribution of these three prey items, as well as the recorded dive depths of the seals. The dominance of smaller squid also coincides with both the recorded dive depths of seals in these areas and the life history of *Gonatus fabricii.*

Hooded seals

This study confirms previous studies of hooded seal summer diets conducted in 1987, 1992 and 2000 (Potelov et al., 2000, Haug et al., 2004, 2007) in that polar cod is a key hooded seal prey item during summer. Polar cod (*Boreogadus saida*) is endemic to the Arctic region where it is widely distributed and the most abundant fish species (Ajiad et al., 2011). This species is closely associated with the sea ice at times during its life (Lønne and Gulliksen, 1989, Christiansen et al., 2012, Renaud et al., 2012) but is found in greater concentrations both pelagically and benthic (Renaud et al., 2012). Very little is known about the polar cod stock in the West Ice (Haug et al., 2007), but, as the seal diet studies performed in this area have shown, it is a major prey constituent of both hooded and harp seal diets, and it is of central importance in the transfer of energy from lower to higher trophic levels (Bradstreet and Cross, 1982).

Gonatus fabricii appears to have been preyed upon frequently by the hooded seals in both 2008 and 2010, but in small quantities. This is in contrast to a previous study (Potelov et al., 2000) conducted during the summers of 1987 and 1992, where squid, in terms of relative biomass, dominated the hooded seal diets; polar cod also occurred quite frequently, whereas the amphipod *Themisto* sp. and krill were found only sporadically. *G. fabricii* has a circumpolar distribution (Gardiner and Dick, 2010), and is the most abundant squid in the Arctic and subarctic areas of the North-Atlantic Ocean (Kristensen, 1983, 1984). It is mainly distributed above the continental slope in 200-3,000 m deep water (Kristensen, 1983), however, Dalpadado et al. (1998) recorded the highest biomasses of this squid in the upper 30 m of the water column in 1994 and 1995. Two more recent studies of hooded seal summer diet (Haug et al., 2004, 2007) found that polar cod dominated the hooded seal diet in the same area during the summer of 2000, however, *G. fabricii* contributed importantly compared with the present study. Small, demersal fish species, like sandeels (*Ammodytes* spp.), sculpins and snailfish were also found in those studies, to some extent. There have been few diet studies of hooded seals in other areas, but Kapel (2000) found that hooded seals west of Greenland during the summers of 1986-1993 had eaten redfish, Greenland halibut, wolffish (*Anarhichas* sp.), *Pandalus* sp., pelagic crustaceans, polar cod and squid.

The frequent predation on sculpins and snailfish in 2010 suggests that small, demersal fish species might be important alternative prey for hooded seals when they are feeding in shallow waters (<300 m depth). To support this statement, Haug et al. (2007) found that hooded seals collected above the continental shelf during the autumns of 2002 and 2003 had consumed larger amounts of demersal fishes, particularly sculpins, and suggested that the hooded seals feed on demersal fish species when they are closer to coastal waters. This is further evidenced in that all but one of the individuals that had eaten sculpins and snailfish in 2010 were collected above the continental shelf, where the depth was 300 m or less. This might also explain the greater individual variation in diet composition with respect to polar cod and other fish in 2010 compared with 2008 (illustrated by the wider error bars in Figure 7), as all seals in 2008 were collected in areas where the water depth was 1,000-1,500 m. With the exception of one individual both years, the hooded seal samples collected above deeper water contained neither sculpins nor snailfish, and the majority of the squid was also found in these samples. The two seals that had consumed sculpins in these deep-water areas might have arrived from a shallower area not long before collection, as the deeper areas were close by the shallower areas (Figure 1).

The diet indices displayed different results with respect to hooded seal diet composition in the south and north in 2010; the qualitative index (frequency of occurrence) suggested significant difference in the prey groups polar cod and squid between the two sample groups, whereas the biomass index did not. Only two individuals in the northern area had eaten polar cod, but one of them had eaten large amounts (>2 kg), which probably explains the high biomass and low occurrence. All the seals in the northern area were collected above deeper water, which might explain why a greater share of these animals had eaten squid, compared with the southern area. However, the northern sample group consisted of only eight individuals, which gives the results some degree of uncertainty, as also seen in the very broad confidence intervals in Figure 7 (Zar, 2010), although some of this might be due to higher individual variations. The prey group “other fish” was in the border of significant difference, and in the northern area, this group consisted solely of unidentified fish. As there were no identified sculpins or snailfish present in the samples from this area, as opposed to in the south, there was obviously a difference with regards to these two prey items. The water depth in the northern area might explain the lack of sculpins and snailfish here. The significant difference in occurrence of polar cod between adult and juvenile hooded seals in the southern and northern areas in 2010 is most likely also explained by the differences in sample sizes.

Based on satellite-linked dive recordings, Folkow and Blix (1999) found that, in partially ice-covered areas during moulting season, Greenland Sea hooded seals mostly did short, shallow dives to depths above 52 m. As Bjørke (2001) in 1994 found the smaller (<50 mm) squid individuals in the upper 30 m of the water column, these dive depths coincides with the findings of mostly smaller squid in both this and previous studies (e.g. Haug et al., 2007). Folkow and Blix (1999) also found that the seals performed long forage migrations to the continental shelf between breeding and moulting, where the dive depths frequently exceeded 968 m. Based on these data, they suggested that hooded seals in this area probably preyed upon Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* spp.), polar cod (*B. saida*) and *G. fabricii*. As seen in the samples from 2008 and 2010, and in Haug et al. (2004, 2007), of these prey items only polar cod and squid have been found in hooded seals collected in the West Ice, but as seen above, Kapel (2000) showed that hooded seals west of Greenland had eaten both Greenland halibut and redfish.

Only one of all seal samples contained capelin. The capelin stock in the Icelandic, Jan Mayen and East Greenland areas spawn in the areas off the south and west of Iceland, and are otherwise distributed from the Denmark Strait and up north to Jan Mayen (Vilhjalmsson, 2002), see Figure 1. In later years, the capelin distribution in this area appear to have moved further southwest, and the abundance has been low since 2006 (Carscadden et al., 2013). Capelin in the Barents Sea feed in the northern parts of the sea in summer and autumn, overwinter in the central parts, and spawn in late winter/early spring along the coasts of Northern Norway and Russia (Carscadden et al., 2013). Capelin in the Northwest Atlantic Ocean is abundant in the areas west of Labrador and Newfoundland, where their feeding grounds, overwintering areas and spawning grounds are (Carscadden et al., 2013). These distributions explain the lack of capelin found in the summer diet of harp and hooded seals in the West Ice, as well as the findings of capelin in the winter diets of West Ice hooded seals (Haug et al., 2007) and in the diets of seals in both the Barents Sea (Lindstrøm et al., 2013) and west of Greenland (Kapel, 2000). The one capelin otolith found in the colon of a hooded seal collected in 2010 might have come from a lost capelin, secondary ingestion, or a seal that had just returned from a longer feeding journey to an area closer to the capelin distribution.

Harp seals

This study confirms previous studies of harp seal summer diets conducted between 1987 and 2000 (Potelov et al., 2000, Haug et al., 2004) in that the amphipod *Themisto* sp. dominates the diet of these seals during summer. In terms of occurrence, amphipods (mostly *Themisto* sp.), squid and polar cod were the most important harp seal prey groups. The most important prey group with regards to biomass was amphipods by far, followed by polar cod and krill. Krill was more frequently found in the faeces samples than in the gastrointestinal samples, but had a higher biomass in the latter. This might be because one faeces sample can consist of parts of one meal, and/or several meals, and thus one meal might be spread out over several faeces samples (Grellier and Hammond, 2006). It could also be due to digestion and underreports of number of krill in the faeces samples, as heavily digested specimens made it difficult to count the exact number. This was also a problem with the amphipods in some, but not all, faeces samples, as some of these samples consisted mainly of heavily digested bits and pieces not possible to count as individuals, or even identify the source of in some instances. Potelov et al. (2000) found a domination of the amphipod *Themisto* sp. in harp seals collected in the West Ice in 1987, 1990-1992 and 1997. Krill and polar cod also occurred in most of these samples. Haug et al. (2004) found that *Themisto* sp. and polar cod were very important in the diet of the West Ice harp seals collected in 2000.

Amphipods are a major prey item for polar cod, sea birds, harp seals and ringed seals (Bradstreet and Cross, 1982, Dalpadado et al., 2001). Both amphipods and krill constitute a major fraction of the total zooplankton biomass in the Nordic seas, and *Themisto libellula* together with the two krill species *Thysanoessa inermis* and *T. longicaudata* are the most widespread species in the colder, Arctic waters of these areas (Dalpadado et al., 1998). *T. libellula* has a shallower distribution (<50 m) than the more subarctic *T. abyssorum* (>200 m) and it also has a higher abundance in summer (Dalpadado et al., 2001). Satellite-linked dive recordings of harp seals found that in ice-covered areas of the Greenland Sea, these seals did short, frequent dives to depths above 50 m (Folkow et al., 2004). This coincides well with the previous diet studies that show a domination of *Themisto* sp. in the harp seal diets, and the data from the present study further confirms this. The dive recordings together with the distribution differences between the *Themisto* species also makes it likely to assume that most of the *Themisto* species found in the diet studies from the West Ice are *T. libellula*. The *Gammarus* species found is most likely *G. wilkitzkii*, as this species is found close to the ice edge together with *T. libellula* (Dalpadado et al., 2001).

Finley et al. (1990) found that harp seals collected northwest of Greenland in August, September and early October of 1978 and 1979 had eaten mostly polar cod (*B. saida*) and Arctic cod (*Arctogadus glacialis*). They also found seasnails (Cyclopteridae), eelpouts, Greenland halibut and sculpins, mysids, *Themisto* spp., a few octopus beaks and some gastropod parts in the sampled harp seal stomachs. Kapel (2000) found capelin and krill to be a major part of the harp seal diet in the southwest of Greenland during the summers of 1986-1993. In the western part of Central West Greenland, euphausids and *Themisto* sp. dominated the harp seal diet, whilst in offshore waters, sandeel (*Ammodytes* sp.) was a very important food item. In the northern parts of West Greenland, polar cod and, to some extent, Arctic cod (*Arctogadus glacialis*), dominated. Other prey items eaten by the harp seals west of Greenland were prawns (mainly *Pandalus borealis*), codfishes (*Gadus morhua* and *G. ogac*), redfish (*Sebastes* spp.), Greenland halibut (*Reinhardtius hippoglossoides*), sculpins, snailfish and eelpouts. Lindstrøm et al. (2013) reported krill and polar cod as dominating the harp seal diet east and north of Svalbard in the summers of 1996 and 1997, and south and east of Svalbard in the summers of 2004-2006. Other prey items identified in this study were capelin, other fishes (mainly Stichaeidae, Cyclopteridae and Cottidae), flatfishes, gadoids and amphipods; these were found to have spatio-temporal variations in importance.

Arctic cod as a prey item appear to only have been found northwest of Greenland. In the northern parts of both Svalbard and West Greenland, polar cod, krill and *Themisto* sp. still appear to be dominant prey items for harp seals, whilst other species become more important south of these areas. Whether the seals were collected from offshore or inshore areas also appeared to make a difference in their diet, and this suggests that water depth on foraging grounds, and thus availability of demersal and benthic species, is important in the diet composition of harp seals, as seen with the hooded seal samples from 2008 and 2010.

Diet overlap and niche breadth

The diet overlap estimate, based on the prey biomass in the northern area in 2010, suggests that there was no particular competition between the harp and hooded seals. This was as expected, as the previous summer diet studies mentioned above have shown that harp and hooded seals have different diet compositions, with harp seals preferring crustaceans whilst hooded seals prefer fish and small squid. When comparing the occurrence of the prey groups in the northern hooded and harp seal samples, there was only a significant difference in amphipod occurrence, meaning that the individual harp and hooded seals in this area had eaten mostly the same prey items. The biomass consumed, on the other hand, was significantly different between these two sample groups for amphipods, krill and other fish, meaning that, although they had eaten the same prey, the amounts, and thus the importance, were different for these three prey groups. It must be noted that sample sizes of these sample groups were low, which resulted in broad confidence intervals and thus uncertain results. This was particularly true for polar cod, as there is a clear difference in consumed biomass between these sample groups seen in Figure 5, whilst Figure 7 shows no significant difference. The dietary comparison of ringed and harp seals done by Wathne et al. (2000) found an almost complete dietary overlap between the two species, however, harp seals had been preying upon larger polar cod than ringed seals, thereby reducing the interspecific competition. On the other hand, when comparing hooded and harp seal diets in the present study, the significant differences in biomass of amphipods, krill and other fish, together with Figure 5 showing a clear difference in polar cod as well, suggests that it is rather unlikely that harp and hooded seals compete for food during summer in the northern part of the West Ice ecosystem.

The niche breadth of a species is low if its prey items are few and/or unevenly distributed. There was a dominance of a few prey items in the diets of both the hooded and harp seals from 2008 and 2010, thus resulting in a very low niche breadth of both species. This would suggest that both species have very specialized diets that focus on one or two main prey items. However, as there is no knowledge of prey availability at the times and areas of sampling, such assumptions should be made with caution. For instance, there was an increase in the niche breadth calculated for the hooded seals from the southern area in 2010 compared with the calculations from

2008. This increase is most likely explained by some of the hooded seals from 2010 being collected above shallower areas, and thus having access to demersal fishes. This shows that availability could have an impact on the importance of different prey items and thus the niche breadth. Nevertheless, the niche breadth calculated for these seals was low. The harp seals also had a slightly higher niche breadth than the hooded seals, as polar cod appeared to be an important prey item together with the very important amphipods. In previous studies where more prey items have been identified for both hooded and harp seals, there still appear to be a dominance of one or two prey items, with other prey merely supplementing the diets. Further, Wathne et al. (2000) found that both ringed and harp seals in the North-Eastern Barents Sea in October 1995 had a strong preference for polar cod, even though this fish species only constituted about 1% of the available prey biomass. However, according to Wathne et al. (2000), other studies have suggested that the ringed seal is a generalist, and they suggest caution in their findings as there were only five prey species found during their resource survey. The present study suggests that both harp and hooded seals are specialists, but as previous studies both in the West Ice and other areas have found that both seal species feed on a variety of prey items with a varying degree of intensity, this would suggest that they are generalists on a population level but specialists on an individual level.

Prey consumption

Nilssen et al. (2000) estimated that the Barents Sea population of harp seals (about 2.13 million seals in 1999) during June-August consumed a total of 1.67 million tonnes of food in the Barents Sea ecosystem, and 1.56 million tonnes during years with low capelin abundance. When taking the differences in population size into account, this amounts to 468,000 tonnes, and 438,000 tonnes in years with low capelin abundance. In contrast to the study by Nilssen et al. (2000), the present study did not account for factors such as energy depots and metabolic costs of pup production, which might explain why the estimates are lower (about 300,000 tonnes). Differences in sample size composition between the studies might also have had an effect on the estimated consumption, as e.g. a population consisting mainly of large juvenile seals would result in higher consumption estimates because of the higher metabolic costs compared with adult seals. Stenson et al. (1997) estimated the annual harp seal prey consumption in the Northwest Atlantic to be about 6.9 million tonnes in 1994, given a population size of about 4.8 million individuals. The annual prey consumption in the Barents Sea was estimated to 4 million tonnes, and a little more in years with low capelin abundance (Nilssen et al., 2000). When taking into account the differences in population size, the Northwest Atlantic consumption is a little less than the Barents Sea consumption, which is probably due to the importance of the more energy rich fish in the former study and crustaceans in the latter.

As previously mentioned, the polar cod is the most abundant fish species in the Arctic region (Ajiad et al., 2011), but as the abundance is not known for the Greenland Sea (Haug et al., 2007), the impact of predation by the harp and hooded seals is difficult to predict. However, comparing the consumption with that from other areas could give a general idea. The harp seal consumption of polar cod in the Barents Sea in June-August 1990-2005 was estimated to be around 450,000 tonnes (Lindstrøm et al., 2006). When taking differences in population size into account, this only amounts to about half of the estimated polar cod consumption by hooded seals in the West Ice. However, the Barents Sea harp seal polar cod consumption amounts to about ten times as much as the West Ice harp seal consumption. Thus, when looking at the West Ice hooded and harp seal populations as a whole, the estimated consumption is clearly much lower than the Barents Sea consumption.

Both amphipods and krill constitute a major fraction of the total zooplankton biomass in the Nordic seas, and in 1994 *Themisto libellula* was recorded with the highest mean biomass of 110 g m^{-2} at 30-200 m depth in Arctic waters (Dalpadado et al., 1998). The West Ice harp seals were estimated to have consumed about 283,000 tonnes of crustaceans (mostly *Themisto* sp.) during June-August 2010, whilst Lindstrøm et al. (2006) estimated the Barents Sea harp seal consumption to be about 950,000 tonnes of crustaceans (mostly krill) during the same months in 1990-2005. Considering differences in population size, the Barents Sea harp seals consumption was a little less than the West Ice harp seal consumption, which probably can be explained by the higher polar cod consumption in the Barents Sea. It is also noteworthy that krill was the dominant crustacean prey in the Barents Sea, whilst *Themisto* sp. dominated in the West Ice.

Dalpadado et al. (1998) also recorded the highest mean biomass of *Gonatus fabricii* at 5.5 g m^{-2} in the surface layers of Arctic waters in 1994. Based on trawling in deep waters, Bjørke (2001) suggested that the hooded seals in ice-covered areas off east Greenland annually consume at least 100,000 tonnes of *G. fabricii*. With an estimated consumption of 6,500 tonnes during the three summer months in 2010, 100,000 tonnes annually seems implausible. However, as previous studies have shown the squid to have constituted a higher biomass of the hooded seal prey in earlier years, it might well be that the annual consumption was at the suggested level before.

The much larger difference in estimated prey consumption during summer between adult and juvenile hooded seals than harp seals is most likely explained by the much greater difference in body weight between the former species. An immature, 30 kg harp seal was calculated to consume more prey weight than an immature, 40 kg hooded seal, and an adult hooded seal was calculated to only consume about 1 kg more prey/day than an adult harp seal less than half its weight. This is most likely due to the differences in the energy content of prey items consumed by the hooded and harp seals; the dominant prey of hooded seals (polar cod) was almost 1.4 times more energy rich than the dominant prey of harp seals (amphipods).

Uncertainties in diet estimates

Folkow et al. (2004) found that harp seals appear to be feeding in open water during extended periods of time, particularly during summer and autumn, and implied that diet data from animals from the pack ice thus would not be fully representative. As pinnipeds have been shown to have a short transit time (around five hours) from food item ingestion to defecation (Helm, 1984, Markussen, 1993), this might very well be the case. Many pinnipeds, especially phocids, also fast for extended periods during breeding or moulting (Crocker and Costa, 2009), and harp and hooded seals are among those that eat little to nothing when hauled out during the moult (Rasmussen, 1960, Sergeant, 1991). The large amount of empty or near empty stomachs found was thus expected, and also coincides with earlier findings (Lindstrøm et al., 1998, 2013, Haug et al., 2000, 2004, 2007, Kapel, 2000, Potelov et al., 2000), although it reduces the amount of data it is possible to get out of each sample. Both Helm (1984) and

Markussen (1993) also reported several different factors affecting the digestion efficiency, among these size and composition of the meal, caloric content, prey species and activity of the seal, thus making the estimation of ingestion time difficult.

Studies of captive pinnipeds have found that the recovery rates and size reduction of otoliths during digestion is related to initial otolith size and robustness, as well as the fish species (Tollit et al., 1997, 2007, Berg et al., 2002, Grellier and Hammond, 2005, 2006). Recovery rates and variation in size reduction were greater for species with large otoliths, whilst smaller sized otoliths exhibited little size reduction, but low recovery rates (Tollit et al., 1997, 2007, Grellier and Hammond, 2005, 2006). It was also found that the digestion of otoliths might not always be uniform with respect to width and length, as for instance whiting otoliths were recovered with broken/digested tips (Tollit et al., 1997, Grellier and Hammond, 2006). A study of digestion rates of polar cod (*B. saida*), capelin (*M. villosus*) and herring (*Clupea harengus*) otoliths in a simulated Arctic seal stomach also showed a difference between prey species in size reduction rate as well as a higher likelihood of complete digestion by prey species with smaller otoliths, including polar cod (Christiansen et al., 2005). These findings clearly show the need to use degradation coefficients and number correction factors to account for the size reduction and complete digestion of otoliths. However, they also show the need for these to be species-specific, and as these are not available for all prey fishes found in the present study, no corrections for size reduction or complete digestion were made. It can thus be expected that the importance of some or all prey fishes be underestimated.

Tollit et al. (1997) reported that cephalopod beak recovery rates were greater than the mean recovery rate for fish in a captive harbour seal (*Phoca vitulina*) study, and that rostral lengths of the beaks were not reduced in size. However, Pitcher (1980) reported that cephalopod beaks occurred more frequently in harbour seal stomach contents than in faeces, and suggested that most beaks were regurgitated rather than passed through the intestinal tract. Yonezaki et al. (2003) discovered that there were large cephalopod beaks present in stomachs, but not in intestines of the northern fur seal (*Callorhinus ursinus*), and there have also been reports of cephalopod beaks found in regurgitated material from pinnipeds (Clarke and Trillmich, 1980, cited by Yonezaki et al. (2003), Pitcher, 1980). Most of the cephalopod beaks recovered from the gastrointestinal tracts of the seals in this study, and all of the beaks recovered from the faeces samples, were small in size. This suggests that the seals ate mostly smaller squid individuals, but, as noted above, there is also a chance of beaks from larger individuals being regurgitated. As Folkow and Blix (1999) found that shallow dives were most frequent for both seal species in ice-covered areas, and Bjørke and Gjøsæter (1998) concluded that adult squid do not shoal, it is very likely that the small sized squid that dominated the findings in this study is representative of the mean size of squid consumed by these seals during their stay in the ice.

The effect on crustaceans passing through a pinniped gastrointestinal tract compared with e.g. fish is unknown (Haug et al., 2004), and it might thus be difficult to compare the importance of each of these prey items. However, as crustaceans are generally smaller than fish, it would be likely to assume that the former are digested more rapidly due to the smaller volume and thus larger area that comes into contact with digestive fluids. On the other hand, there was also a clear difference in degree of crustacean digestion between the individual samples in the present study, thus making it clear that a precise biomass estimate of crustaceans can be difficult to obtain when relying on ingested specimens, especially when using faeces samples.

Conclusions

This study has shown that harp and hooded seals do not appear to compete for food. It also confirms previous studies that have shown polar cod to be a key prey item for the hooded seals, and *Themisto* sp. to be a key prey item for harp seals. Other findings include that hooded seals in shallower areas tend to feed on demersal fishes like sculpins, and that squid appears to have a lower importance for this seal species compared with previous years. The niche breadth found in this study was low for both seals, but as other studies have shown several other prey items to be important in other areas, it appears that both the hooded and harp seals are generalists on a population level, and specialists on an individual level. The total prey consumption during June-August 2010 for the hooded seal population was about 42,000 tonnes, and almost 300,000 tonnes for the harp seals. The total harp seal consumption was fairly similar to that of harp seals in other areas.

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