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Use and selection of prey by harp seals during summer in the northern Barents Sea

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ABSTRACT

The aim of this study was analyse harp seals prey use and selection during summer in Svalbard waters. A total of 41, 34 and 58 (including 24 faeces samples) from animals were sampled in 1996, 1997 and 2004. Krill was the overall dominant prey species (63%) followed by polar cod (16%) and other fish species (10%) in terms of a combined index (frequency occurrence and weight). Resource mapping was performed in two areas simultaneous with the seal sampling, in 1996 and 1997 by using standard acoustic methods. These surveys suggested that krill was the most abundant prey in both areas and years; krill constituted 84% and 69% of the total prey biomass in 1996 (99.7 tonnes/nm^2) and 1997 (21.4 tonnes/nm^2), respectively followed by parathmisto sp. (13 and 18%) and Gammarus sp. (2 and 12%). The prey preference results suggest that harp seals are not particular prey selective, i.e., harp seals display a random feeding behaviour.

Key words: Harp seals, diets, prey selection, Barents Sea

INTRODUCTION

The resource dynamics in the Barents Sea ecosystem has varied much the past three decades; the dramatic delince in the abundance of capelin and juvenile herring are among the most conspicious. Examination of multi-species predatory interactions in space and time and incorperating this knowledge in to multispecies and eco-trophic models (e.g., Yodzis, 1998; Pauly *et al*., 2000; Begley, 2003) may shed some light into the causes of changes in the Barents Sea ecosystem.

Harp seals are highly mobile predators that undertake extensive seasonal migrations following trhe biological productivity (e.g., Nilssen *et al.*, 1995a,b). Beside northeast Arctic cod, the Barents sea stock of harp seals is the most conspisious high trophic level predator in the Barents Sea ecosystem with an estimated annual prey consumption ranging between 3.5 and 5 million tonnes (Nilssen *et al.,* 2000). To understand harp seals ecosystem function it is important to quantify their use of habitat and prey in time and space as a function of the resource abundance.

Recent studies indicate that harp seals prey use varies in time and space primarily due to seasonal changes in habitat use (Nilssen *et al*., 1995a,b); fish dominate the diet in the southern Barents Sea whereas various crustacean species (mainly krill and amphipods) dominate the diet in the north, along the ice edge (see Nilssen *et al.,* 1995b). From observed seasonal variation in the harp seal body condition, it is evident that the period June-September is the most intensive feeding period for harp seals in the Barents Sea (Nilssen *et al.*, 1997, 2000). However, due to lack of diet data during this period, three research surveys were conducted in Svalbard waters July-August in 1996, August 1997 and June 2004.

To evaluate the interaction strength between harp seals and their prey in the Barents Sea, knowledge of their resource preference in various prey availabilities is needed. The latter follows because the habitat quality in marine ecosystems varies with environmental conditions on a diel, seasonal, and annual basis (e.g., Mehl 1989; Hamre, 1994). To assess the resource preference of harp seals, their diets must be compared with the availability of resources in the environment. Therefore, parallell to the sampling of diet data in two of the areas in 1996 and 1997, the resource availability in the sea was assessed (Figure 2).

The approach described by Lindstrøm *et al.,* (1998) was applied to examine whether harp seals have a prey preference or not; construction of 95% bootstrap based cofidence intervals for a combined index (occurrence and weight). A preference (or antipreference) for a certain prey group is then concluded if the estimated relative abundance for that prey group is outside the range spanned by the diet indices.

MATERIAL AND METHODS

Sampling of harp seals

In the period 26 July to 5 August 1996, 22 harp seals were caught in Storfjord and Olgastredet in the southeastern parts of Svalbard (Fig. 1). In 1997, during the period 8 – 14 August, 11 harp seals were caught in Erik Eriksenstredet between Kong Karls Land and Nordaustlandet, and on the 20 August in a relatively restricted area north of Nordaustlandet 6 harp seals were taken. In early June 2004, 33 harp seals were taken in two areas south if Spitsbergen. The seals were shot on the ice or in the water. The seals were immediately brought on board for dissection where samples of stomachs and intestines were frozen for later examination of contents.

Stomach and intestinal contents analyses

In the laboratory the stomachs and intestines were cut open after thawing. Stomach contents were weighed and, after flushing the intestine with fresh water, the fish and crustaceans were separated. Most of the stomach and intestinal contents were partly or completely digested, and the prey organisms were identified to the lowest possible taxonomic level, preferably species (Enckell, 1980; Pethon, 1985; Breiby, 1985; Härkönen, 1986). A crude estimate of the number of crustaceans present were obtained by counting fresh animals and the carapaces of each species. Mean weights of crustaceans were obtained from fresh prey specimens taken from trawl catches, and these were used to calculate the biomass of crustaceans in the stomach and intestinal contents. The total number of each fish species in each sample were estimated by adding the number of whole specimens, the number of intact skulls and half the number of “free” otoliths. All otoliths were measured, and otolith length to fish wet weight correlations, based on fish material from the trawl hauls or from a published guide (Härkönen, 1986), were used to estimate the initial weight of the fish consumed by the seals.

A combined index, C_i, was applied to estimate the diet composition of harp seals:

$$C_i = \frac{B_i \cdot F_i}{\sum_{i=1}^{k} B_i \cdot F_i}$$

where B_i and F_i is percentage weight and occurrence of prey species *i*, respectively, and k is number of prey groups.

To construct 95% confidence intervals (CI) for the relative importance, as the combined index, of each prey group the diet data was bootstrapped 1000 times. All CI's were corrected for possible acceleration and bias (see Efron & Tibishirani 1993).

Estimation of prey abundance

Parallel with the sampling of seals in 1996 and 1997, a standard acoustical survey was conducted with R/V 'Jan Mayen' along predetermined transects in the sub areas where whales were being or had been caught. Continuous acoustic recordings of fish and euphausiids were made by a calibrated echo integration unit consiting of a 38 KHz Simrad EK-500 splitbeam echosounding system (Bodholt *et al.*, 1989), connected to a BEI post processing system (Foote *et al*., 1991). A minimum acoustic threshold of –88dB Sv was applied to detect euphausiids.

The allocation of acoustic values (S_A, area backscattering coefficient) was carried out on the basis of the acoustic character of species and trawl samples. Both pelagic and demersal trawling was performed in response to potential changes in the echo sounder registrations. For pelagic trawling, a 14 fathom trawl (Harstad, Norway) fitted with a Scanmar depth recorder was used, while a "Super Campelin" 1800 mesh shrimp trawl was used for demersal trawling. Both trawls were fitted with an 8 mm net inside the codend thereby making it possible to sample fish juveniles and euphausiids. Pelagic and demersal trawling was standardized to respectively 30 and 20 minutes duration, and the trawling speed was approximately 3 knots.
As a result of different fishing efficiencies of the trawls with respect to fish and euphausiids, and due to the low frequency of the echosounder for detection of euphausiids, the trawl catches was used only to confirm their presence or absence. Therefore, the partitioning of acoustic

values between fish and euphausiids was made subjectively by reducing the volume backscattering coefficient (Sv) to a fix level until euphausiids was assumed to be removed (e.g., Lindstrøm *et al*. 1998). The remaining S_A-values were then partitioned among the different fish species according to standard procedures (see MacLennan and Simmonds, 1992). The recorded S_A-values, averaged over one square nautical mile (nm^2), was converted to numbers (ρ) according to the relation:

$$\rho = \frac{S_A}{4\pi \cdot 10^{0.1 \cdot \overline{TS}}}$$

where $\overline{TS}$ is the mean target strength of scattering organisms, which varies between species and body length.

Statistical analysis of prey selectivity

To simplify statistical analyses of the feeding index, the harp seal prey organisms were combined into different prey categories. The prey organisms were grouped into the following taxa: krill (*Thysanoessa* sp.), *Parathemisto* (*Parathemisto sp.*), various crustaceans (*Pandalus* sp., *Sabinea septemcarinata*, *Gammarus* sp., unidentified crustacean remains), Polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and various fish (*Gadus morhua*, *Lycodes* sp., *Liparis* sp., *Sebastes* sp., *Hippoglossoides platessoides*, *Lumpenus lampraetaeformis*, *Leptoclinus maculatus*, *Leptagonus decanonus* unidentified gadid, cottid, stichaeid, cyclopterid, pleuronectid remains and unidentified fish remains).

Potential dietary preferences of the seals were studied by constructing approximate 95% confidence intervals for the relative diet composition of each prey in terms of prey biomass, and these were compared with the corresponding contribution of prey groups in terms of relative biomass in the sea. The confidence intervals were constructed based on 5000 bootstrap replications of the original diet data (see Lindstrøm *et al.*, 1998).

The applied statistical methods were based on the following assumptions:

i) The examined seals was foraging in the areas where the resource surveys were conducted and represent a random sample of the seals in the area.

ii) The composition and abundance of prey in the sea and seal diets are representative.

RESULTS

Harp seal diets

In a sub-area in Storfjord in 1996, 27.3% of the examined digestive tracts were empty. Four different prey species were identified. All non-empty seals had eaten krill *Thysanoessa inermis* occurred whereas only 25% of the seals had exploited amphipods and polar cod. As expected, krill was by far the most important prey species in the seal diets, and contributed to approximately 98% (CI_{95}=95-100%) of the diet composition in terms of the combined index (Fig. 2).

In Olgastredet in 1996, all collected seals had contents in their digestive tract. Seven different prey species were identified. Krill (90.9%) and *Parathemisto libellula* (72.7%) occurred most frequently but also polar cod (36.4%) and *Liparis* sp. (27.3%) were found. In terms of biomass, polar cod was the predominant species (not shown), whereas in terms of the combined index krill was by far the most important prey species (60%, CI_{95}=13-87%) followed by polar cod (32%, CI_{95}=5-80%) and other crustaceans (3.6%, CI_{95}=2-7%) (Fig. 2).

In a sub-area in Erik Eriksenstredet in 1997, all examined digestive tracts had contents. Sixteen different prey species were identified. Krill (100%), *Parathemisto libellula* (81.8%) and polar cod (81.8%) occurred most frequently but Atlantic cod (18.2%), Stichaeidae sp. (27.3%) and Cyclopteridae sp. (18.2%) were also observed frequently (Table 1). Polar cod was the predominant species and contributed to approximately 45% (CI_{95}=32-66%) of the combined index, while the contribution from krill, codfish and various other fishes were approximately 13% (CI_{95}=6-29%), 3% (CI_{95}=0.3-9%) and 34% (CI_{95}=18-52%), respectively (Fig. 2).

In the 1997 investigations north of Nordaustlandet, all examined digestive tracts had contents. Ten different prey species were found. Krill (100%), *Parathemisto libellula* (50%) and polar cod (66.7%) occurred most frequently followed by *Pandalus* sp. (33.3%) and Stichaeidae sp. (33.3%) (Table 1). Krill and various other fishes were dominating and contributed approximately 51% (CI_{95}=20-83%) and 27% (CI_{95}=7-55%) to the diet composition, respectively, whereas polar cod consituted 13% (CI_{95}=4-21%) of the diet (Fig. 2).

In the hopen area in 2004 (Fig. 1), krill dominated the diet composition 53% (CI_{95}=8-89%) (Fig. 2), in terms of the combined index, followed by capelin 25% (CI_{95}=0.5-71%) and other various fish 15% (CI_{95}=5-37%). In the area south of Spitsbergen (S.Spitsb.) the dietary diversity was much lower; krill completely dominated the diet composition of the seals 97% (CI_{95}=87-100%) followed by various other 3% (CI_{95}=0.1-13%).

Prey abundance

In Storfjord in July/August 1996, all seal hunting and resource surveys were carried out in open waters far away from pack-ice. The size of the sub-area surveyed in Storfjord was calculated to be 224 n. square miles. The degree of which the acoustical transects covered the surveyed area was calculated to be approximately 3.9. This is below the d-value of 6 which was recommended by Aglen (1989).

The total abundance of potential seal prey in the water column (except the lowest 10 meters bottom layer) was estimated to be 99.7 tonnes per n. square miles (Table 2). Krill (c. 84%) totally dominated in the pelagic layers, in waters from approximately 20 to 120 meters depth, with the highest concentrations around 120 meters. Bottom trawl hauls revealed that various fish species, mainly polar cod (Fig. 3) but also other crustaceans such as shrimps, particularly *Pandalus borealis*, were abundant along the bottom (approximately 210 meters depth).

In Erik Eriksenstredet in August 1997, all seals were taken in or close to areas covered by pack-ice. The drifting pack-ice hampered the resource survey, and it was only possible to cover a part of the sealing area by acoustical transects (the size of this area and the d-value were not calculated).

The total abundance of potential seal prey in the water column (except the lowest 10 meters bottom layer) was estimated to be 21.5 tonnes per n. square miles (Table 2). According to the echosounder observations and the pelagic trawl catches, the highest concentrations of potential seal prey were close to the bottom. Krill (c. 68%) totally dominated the estimated biomass in the water column but amphipods such as *Parathemisto libellula* and *Gammarus* sp. (c. 30%) also contributed significantly (Table 2). Results from bottom trawl catches revealed that various fishes, particularly polar cod, were abundant (Fig. 4). Several bentic fish species belonging mainly to the Cottidae, Liparidae and Pleuronectidae families occurred frequently in the trawl catches. *Pandalus borealis* and krill were also abundant along the bottom (200-250 meters depth).

Potential prey preferences

In the analyses of predator-prey interactions, data from distinct pelagic and demersal trawl hauls were applied. A total of 3 pelagic and 2 demersal trawl hauls, and 8 harp seals with stomach contents were included in the predator-prey analyses in Storfjord in 1996. The analyses revealed that the relative abundance of krill in both demersal trawl hauls and two of the pelagic trawl hauls were outside (below) the diet confidence interval for this species. However, the relative abundance in one pelagic trawl haul taken at 120 meters depth (which contained approximately 9 liters of krill compared to less than 0.5 liter in the two other pelagic trawl hauls) fell within the diet confidence interval, and might suggest no strong indication of positive preference for krill (Fig. 3). For the remaining prey groups, there were no strong indications of positive or negative preferences. The result of this analyses may indicate that the harp seals are opportunistic predators foraging on most abundant species (krill) occurring mainly in the pelagic water masses (above 120 meters depth).

In the prey-preference analysis carried out in a sub-area in Erik Eriksenstredet in 1997, which included 2 pelagic and 2 demersal trawl hauls, and 11 harp seals with stomach content, no strong indications of positive or negative preferences for any particular species were found (Fig. 4). However, the more frequent occurrence of polar cod and various bentic fishes in the diet may indicate that the harp seals also feed in deeper waters and close to the bottom if the abundance of alternative prey species are low in the upper layers.

DISCUSSION

To summerise the results of this study: 1. krill is the most important harp seal prey in the northern Barents Sea, or more specifically in Svalbard waters, in July/August, 2. Krill was by far the most abundant prey in the two surveyed areas and 3. Harp seals display a random foraging behaviour; feeding on the most abundant prey in the sea.

Thysanoessa sp., the most abundant krill genus in the northern Barents Sea, is known to be important link in the food chain between herbivorus zooplankton and fish, sea birds and marine mammals. Krill is normally most abundant in the upper 200 meters, except in November and December when it seems to be distributed in deeper waters (Sakshaug *et al.*, 1992). Krill is also known to be important prey for juvenile harp seals in other areas (e.g., Nilssen *et al.*,1995a).

Confirming a previous study in autumn 1995, krill and amphipods completely dominated the prey abundance in the acoustic surveys in 1996 and 1997. The contribution of polar cod, which was the only fish species taken in the pelagic trawl hauls, was less than 1% in the abundance estimates both years. The present results indicate that harp seals may feed in deeper waters and close to the bottom, particularly on polar cod but also on other bentic fishes, when the abundance of alternative prey is low in the upper layers. It was also been suggested by Lindstrøm *et al.*, (1998) that harp seals, despite the occurrence of both amphipods and krill in the upper layers, may prefer to dive down to deeper waters to feed on polar cod.

The pelagic amphipod *Parathemisto libellula* has been suggested to be the most important harp seal food from September to mid-October, when a shift to fish, mainly capelin and to a lesser extent polar cod, occur (Nilssen *et al.*, 1995a). Russian studies carried out during the 1930s in the eastern parts of the Barents Sea suggest that polar cod is the most important harp seal food during late autumn (Chapskii, 1962). Seasonal prey switching in predators as a result of spatial changes in prey abundance, as observed in harp seals (Nilssen, 1995), may have important implications for coexistence of species and predator-prey dynamics (e.g., Vincent *et al.*, 1996, Kotler and Brown 1988, 1999).

The dietary discrepancy between this and another study, conducted further northeast in the Barents Sea in 1995 (see Lindstrøm *et al.*, 1998), indicate that harp seals exhibit foraging threshold towards their prey; krill was equally important, relative to the other prey, in the sea in oct. 1995 and July/august 1996 and 1997, but c. 20 and 3.5 times less abundant in 1995 compared with 1996 and 1997, respectively. Predation thresholds, or frequency dependent selection, may have important ecological consequences via their stabilizing effect on predator-prey systems (e.g., Rosenzweig and MacArthur 1963, Hassel and May 1974, Fryxell and Lundberg 1994, Abrams and Ginzburg 2000).

This study confirms previous studies conducted in the northern Barents Sea; harp seals are opportunistic predators foraging on the most abundant prey when their abundance is above a certain level (Nilssen, 1995; Lindstrøm *et al.*, 1998).

The almost complete absence of capelin, which is known to be important harp seal food when available (e.g., Nilssen *et al.*,1995a,b), in the present harp seal diets and resource surveys, could be due to a low capelin stock these years (Anon, 2005) and low predator-prey overlap in space.

Also, more recent aerial surveys in 2001 and 2002 indicate a low spatial overlap between harp seal and capelin in Sept./Oct. (Anon, 2002a,b).

Given the results of this study and the importance in predator-prey dynamics, future ecological studies of harp seals should aim to quantify harp seals foraging tresholds in space and time.

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Table 1. Frequency of occurrence of empty stomachs and intestines, and identified species in stomachs and intestines of 37 harp seals caught in four sub-areas in Svalbard waters in July-August 1996 and 1997. N = number of seals examined. n = number of stomachs/intestines with content.

PREY ITEMS	PERCENTAGE OCCURRENCE							
	STORFJORD N=11		OLGASTR. N=11		E. ERIKS.STR. N=11		N. SPITSB. N=6	
	Stomachs n=8	Intestines n=10	Stomachs n=11	Intestines n=11	Stomachs n=11	Intestines n=9	Stomachs n=6	Intestines n=5
Empty	27.3	9.1				11.2		16.7
Crustacea								
Amphipoda								
Parathemisto libellula	12.5	9.1	72.7	27.3	81.8	22.2	50	
Parathemisto sp.	25		63.6	63.6	72.7	66.7	33.3	20
Gammarus wilkitzkii					9.1			
Gammarus sp.			18.2		9.1			
Unid. amphipod. remains	9.1	11.1						
Euphausiacea								
Thysanoessa inermis	100		81.8	9.1	100	11.1	100	100
Thysanoessa sp.	100	72.7	90.9	81.8	100	88.9	100	100
Decapoda								
Pandalus sp.					9.1		33.3	
Sabinea septemcarinata					9.1			
Unid. crustacea remains	12.5				9.1	11.1		
Mollusca								
Unid. cephalopoda remains					18.2		16.7	
Pisces								
Gadidae								
Gadus morhua					18.2			
Boreogadus saida	25	18.2	36.4	27.3	81.8	66.7	66.7	40
Unid. gadidae remains					9.1	11.1	16.7	
Cottidae								
Unid. cottidae remains			27.3	18.2		11.1		20
Stichaeidae								
Lumpenus lampraetaeformis							33.3	20
Leptoclinus maculatus	12.5			9.1	27.3	11.1		40
Unid. stichaeid. remains							33.3	60
Agonidae								
Leptagonus decanonus					9.1			
Zoarcidae								
Lycodes sp.				9.1	9.1	11.1	16.7	
Liparidae								
Liparis sp.			27.3	9.1	9.1	11.1		
Cyclopteridae								
Unid. Cyclopt. remains					18.2	44.4		
Scorpaenidae								
Sebastes sp.						22.2	16.7	
Pleuronectidae								
Hippoglossoides platessoides			9.1	9.1		9.1		
Unid. pleuronect. remains			9.1			11.1		
Myctophidae								
Benthosema glaciale					9.1			
Unidentified fish remains			18.2	18.2	72.7	44.4	16.7	

Table 2. Standard acoustic survey methods were carried out in two sub-areas in Svalbard wates, in Storfjord 3 August 1996 and in Erik Eriksenstredet 14-15 August 1997. The abundance estimates are given in tonnes per nautical square miles.

	POLAR COD	KRILL	PARATHEMISTO SP.	GAMMARUS SP.	TOTAL
Storfjord 1996	0.3	83.8	13	2.6	99.7
E. Erik.str. 1997	0.15	14.7	4	2.6	21.4

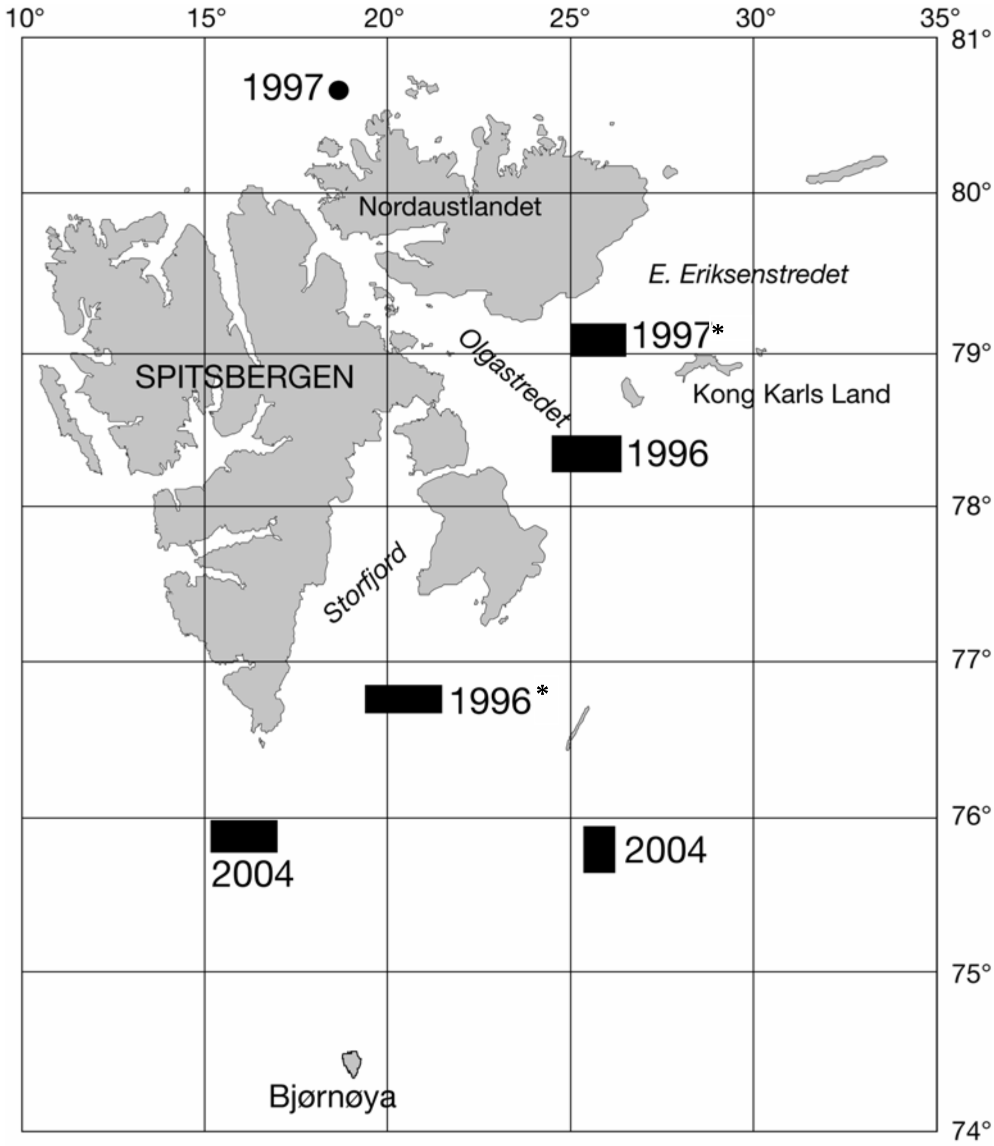

Figure 1. Sampling areas (filled) of harp seals in Svalbard waters in July/August 1996, 1997 and 2004. Acoustic surveys was run parallel to the sampling of seals in Storfjord and E. Eriksenstredet in 1996 and 1997 (*), respectively.

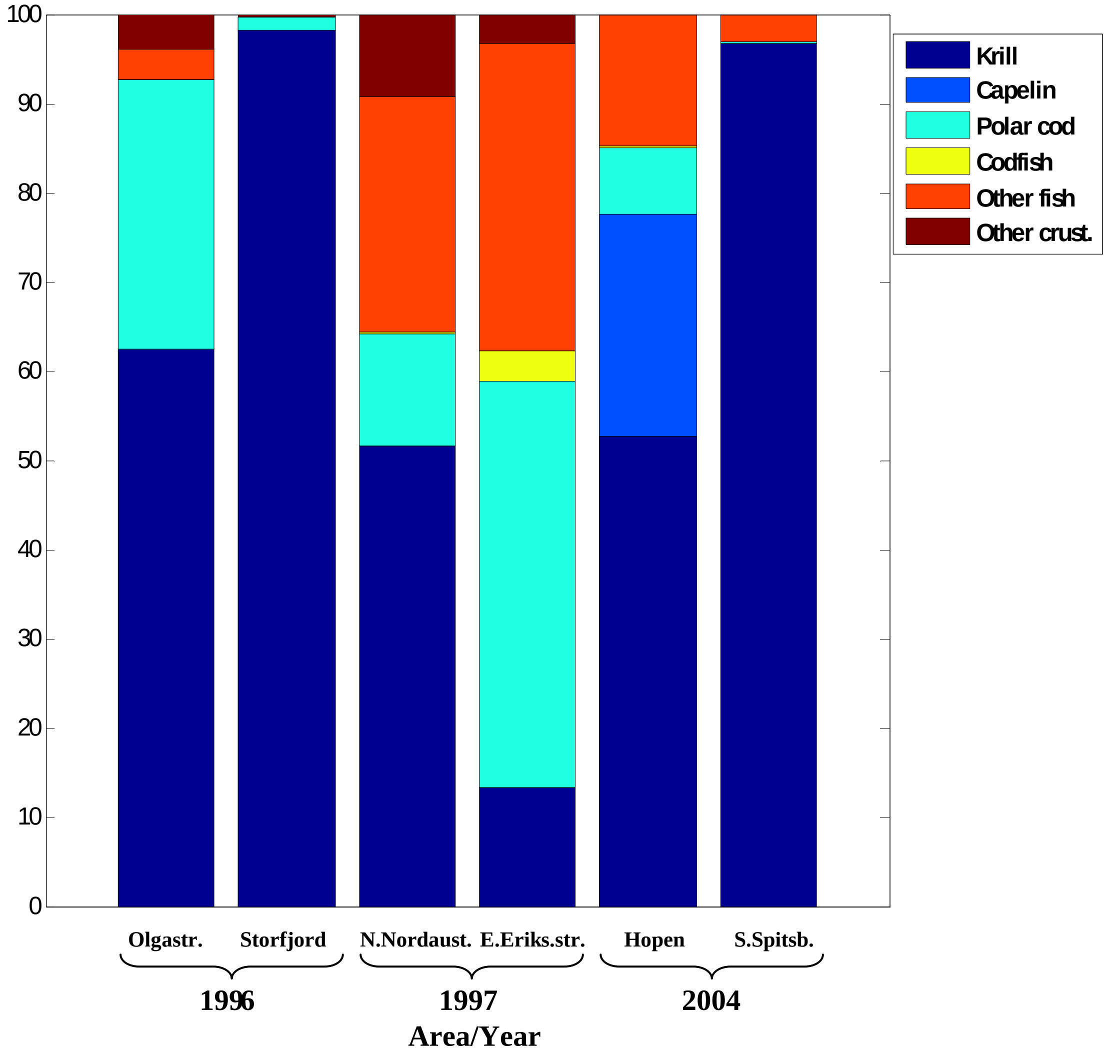

Figure 2. Harp seals diet composition, as percentage combined index (see text for explanation), in the northern Barents Sea during summer in 1996, 1997 and 2004.

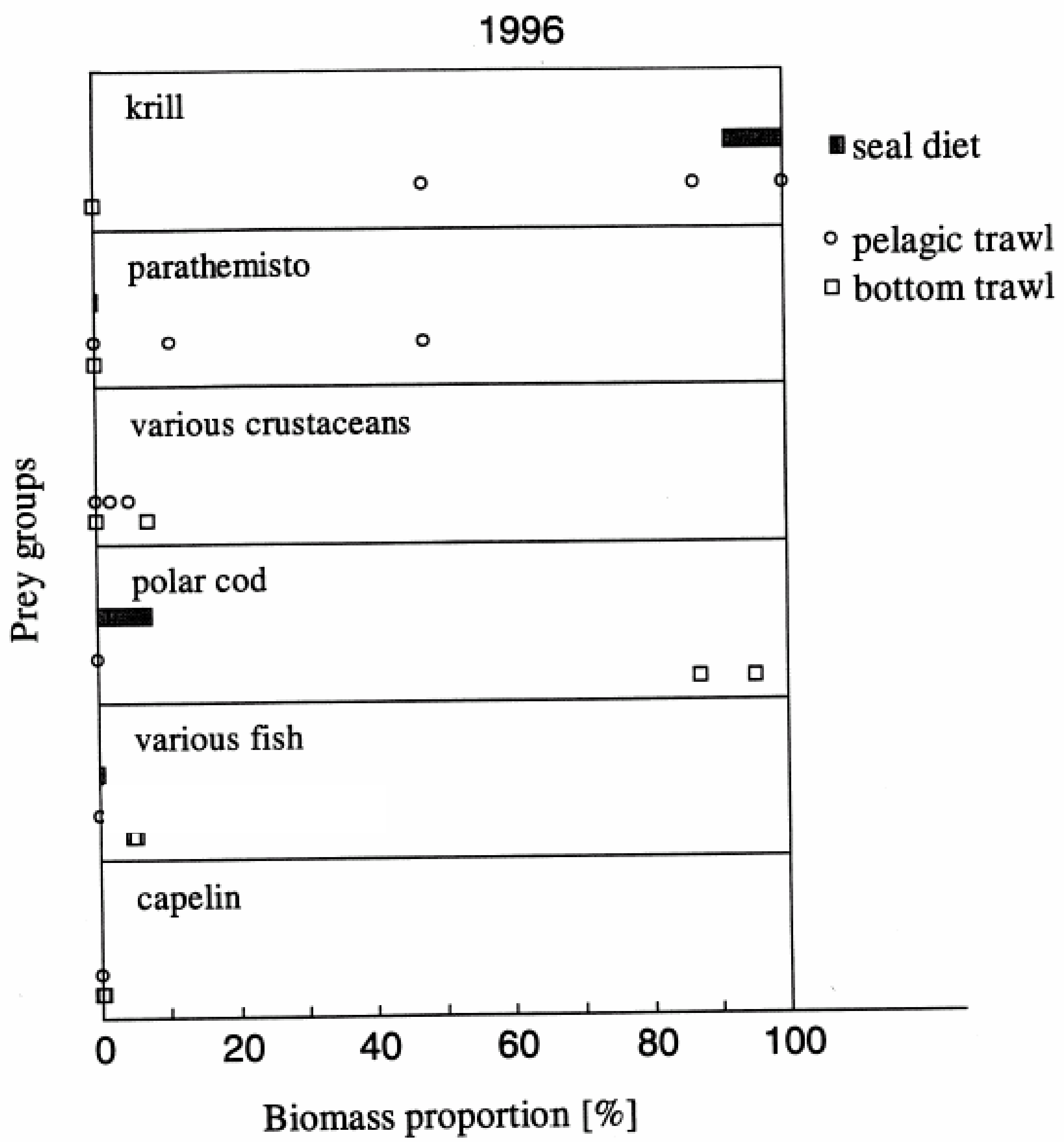

Figure 3. Harp seals prey preference in Storfjord in Svalbard waters in July/August 1996. approximate 95% confidence intervals for the diet, in terms of percentage weight, are compared with relative prey biomasses in 3 pelagic and 2 demersal trawl hauls.

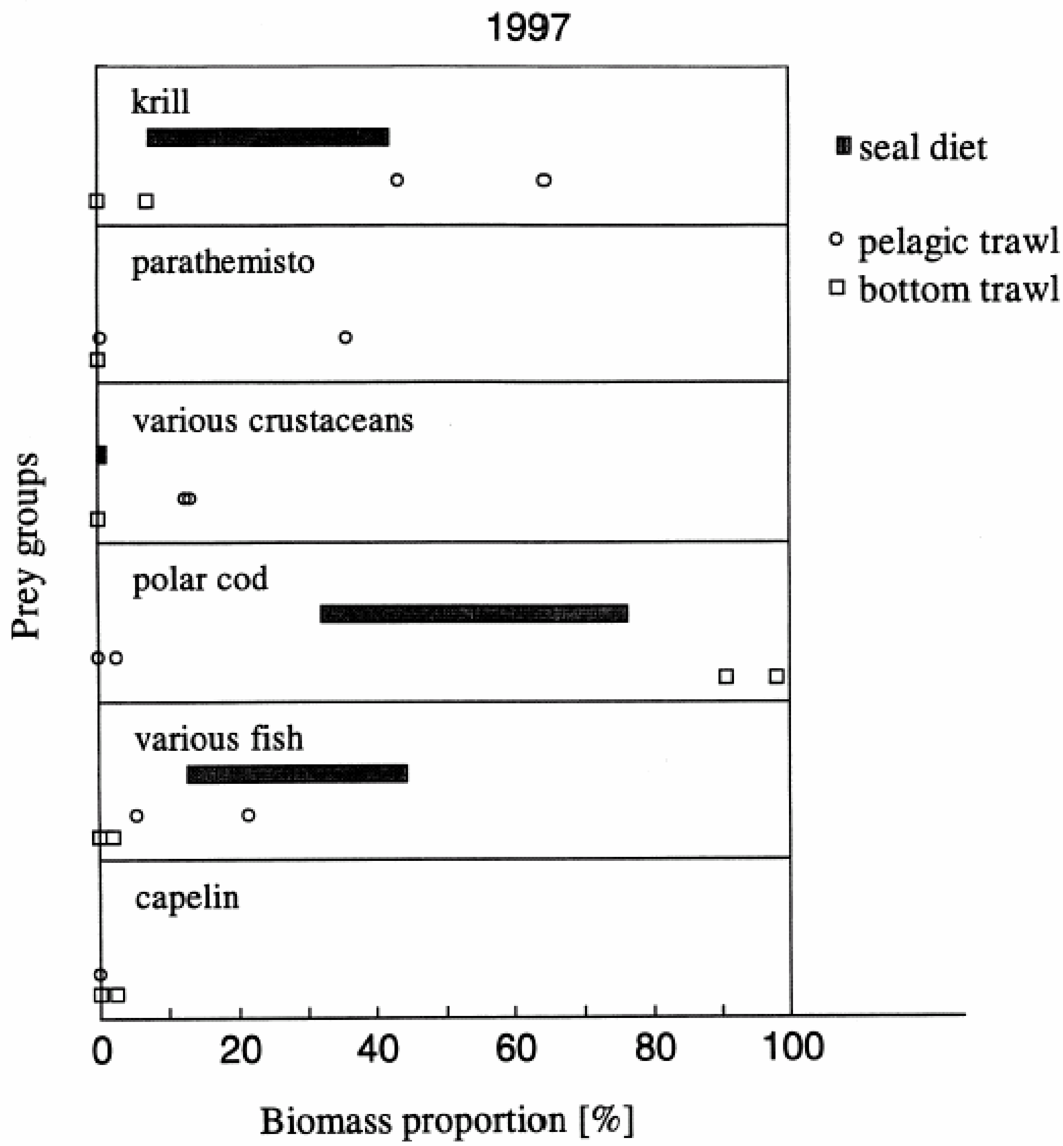

Figure 4. Harp seals prey preference in E. Eriksenstredet in Svalbard waters in July/August 1997. Approximate 95% confidence intervals for the diet, in terms of percentage weight, are compared with relative prey biomasses in 2 pelagic and 2 demersal trawl hauls.