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Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P. groenlandica* in the Barents Sea

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ABSTRACT: Ringed seals *Phoca hispida* and harp seals *P. groenlandica* were collected for diet analysis along the ice edge in the Barents Sea to investigate possible niche overlap between these 2 seal species. The diet analysis is based on contents from stomachs and intestines. A resource availability survey was conducted concurrently based on an echo survey combined with demersal and pelagic trawling. This survey showed that the potential prey biomass was dominated by pelagic crustaceans (99% of total biomass)—principally *Themisto libellula* and *Thyssanoessa* spp. Despite the prevalence of these crustaceans both seal species showed a strong preference for fish of various species, which constituted only 1% of the biomass in the area. The most common fish in their diet was polar cod *Boreogadus saida*, which had a Manly's prey preference index of 0.87 for ringed seals and 0.42 for harp seals. Pianka's niche overlap index for the 2 seal species in this area was 0.985, indicating an almost complete niche overlap. However, harp seals prey on significantly larger polar cod than ringed seals, and the larger cod were distributed in deeper water than smaller cod. Thus it appears that the 2 seal species exploit different fractions of the same resource.

KEY WORDS: Ringed seal · Harp seal · Diet · Prey preference · Niche overlap · Barents Sea

INTRODUCTION

The ringed seal *Phoca hispida* is found throughout the circumpolar Arctic, and is usually closely associated with sea ice. The global population of this species may be as large as 4 million animals (Reeves 1998). In the Barents Sea (Fig. 1), ringed seals occupy ice-covered areas that vary seasonally, being most extensive during the winter and receding northward during the spring (Belikov & Boltunov 1998). During the summer and autumn, ringed seals are most numerous along the ice edge in the northern and eastern parts of the Barents Sea, as well as deeper into the pack-ice. Harp seals *P. groenlandica* are also an abundant northern pinniped that probably number more than 6 million animals globally. This species migrates on an annual cycle, spending the summer months at the highest northern parts of their range. Many of the harp seals that breed in the White Sea use the ice edge in the Barents Sea as a feeding ground during summer and autumn (Haug et al. 1994).

Several studies have been conducted on the diet of ringed and harp seals in the Barents Sea and adjacent waters (Gjertz & Lydersen 1986, Lydersen et al. 1989, 1991, Weslawski et al. 1994, Nilssen 1995, Wathne 1997, Lindstrøm et al. 1998). The general finding when specimens of these 2 seal species are collected along the ice edge is that polar cod *Boreogadus saida* is the most important prey species, followed by different invertebrates, mainly the amphipod *Themisto libellula* and krill of the *Thysanoessa* spp.

Since there is an overlap in distribution for parts of the year for ringed and harp seals and also an apparent overlap in their diet, the potential for resource competition between these 2 seal species is great. The pur-

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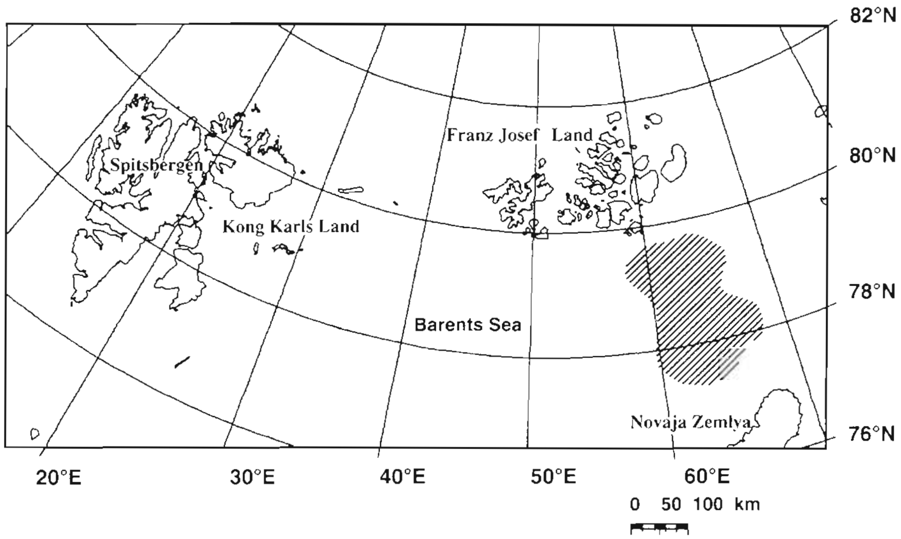

Fig. 1. Sampling area (hatched) for ringed and harp seals in the northeastern Barents Sea October 1995

pose of this study was therefore to describe the food available for ringed and harp seals in the area, and to compare this food with the gut contents in collected specimens. This would enable us to study whether the 2 species showed any particular preference for different prey organisms, and to evaluate the degree to which the feeding niches of ringed and harp seals overlapped.

MATERIAL AND METHODS

Twenty-seven ringed seals and 18 harp seals were collected along the ice edge in the northeastern Barents Sea during 18 to 28 October 1995 (Fig. 1). The seals were shot using high-powered rifles (Cal. 30-06 and 308) while they were hauled out on ice floes. Seals which had been shot were immediately brought aboard the research vessel, where the stomachs and intestines were extracted, and the lower jaw was collected in order to use teeth for age determination.

Whole stomachs and intestines were frozen at −27°C until analysis. In the laboratory, stomachs and intestines were thawed and their contents were washed through 2 sorting sieves with mesh size 2.0 and 0.5 mm, respectively. The sieved contents were then stored in vials with 96 % ethanol. During a second stage of analysis the contents were divided into fish and invertebrates. Fish material was identified to the lowest possible taxon by studying otoliths under a magnifying glass (Breiby 1985, Härkönen 1986). Total lengths of all otoliths were measured with a digital calliper (Mitutoyo 500). Regressions of otolith length and fish mass were used to calculate the original fish mass based on data from Härkönen (1986). Since each teleost fish contains 2 sagittal otoliths, the number of fish ingested was estimated to be half of the total number of otoliths found in the stomachs and intestines.

The invertebrate fraction of the sieved material was identified to the lowest possible taxon using Enckell (1980) The number of each identified species was recorded.

The age of the seals was determined by examining incremental growth layers in the dentine of transverse sections of the lower canine teeth (Bowen et al. 1983).

To describe and quantify food organisms found in the samples, 2 feeding indices commonly used for stomach analysis of top predators were applied to the material (Hyslop 1980, Pierce & Boyle 1991): (1) frequency of occurrence of each prey item (FO_i)

$$FO_i = \left(\frac{S_i}{S_t}\right) \times 100 \quad (1)$$

where S_i is the number of examined seals with stomach and/or intestines containing species i and S_t is the total number of seals examined; and (2) the relative frequency of occurrence by number (N_i)

$$N_i = \left(\frac{n_i}{n_t}\right) \times 100 \quad (2)$$

where n_i is the total number of individuals of prey category i and n_t is the total number of individuals of all prey categories in the gastrointestinal tract.

A resource survey was carried out on 23 to 24 October 1995 in the area at the same time as the seals were collected in order to identify and quantify available fish and invertebrates occupying this area. It was conducted from onboard the RV 'Jan Mayen' using acoustic techniques for estimating the quantity of fish and invertebrates (Foote 1991) combined with pelagic and demersal trawling for verification/identification of prey organisms detected during echo surveys. The survey area was 1715 km^2. Acoustic measurements were obtained using a Simrad EK-500 split-beam echo sounding system. A minimum acoustic threshold of −88 dB SV was applied, thus allowing for the detection of zoo-plankton. The echo integration surveys were conducted by cruising along predetermined transects in the actual areas. The allocation of acoustic values to species groups was carried out on the basis of the acoustic character of each species group in combination with trawl catches. Trawls were conducted in response to changes in the echo sounder observations. Both pelagic and demersal trawls were used to sample the observed scatters. For pelagic trawling an 18.3 m trawl (Harstadtrål, Norway) fitted with a Scanmar depth monitor was used. For demersal trawling a 'Super Camplin' 1800 mesh shrimp trawl with rubber bobbins was used. Both trawls were fitted with an 8 mm net inside the cod end in order to sample fish fry and zooplankton. The prey biomass was estimated in 4 depth strata: 0–100 m, 100–200 m, 200–300 m, and 300 m–bottom. The partitioning of the depth strata was based mainly on the echogram scatters.

The estimated total biomass of potential prey was calculated in tonnes of prey in each 100 m depth stratum. To calculate the number of prey organisms in each depth stratum, the total biomass was divided by the average mass of a particular prey type obtained from specimens taken from the trawls in the same area (n = 100 for each prey type in each stratum; randomly selected). Where numbers from more than 1 depth stratum are shown, they were calculated from summed total biomass from the strata, divided by the average mass of the prey item in question.

Manly's α preference index (Krebs 1989) was used to examine whether the seals were selecting particular prey types. Because the number of prey eaten by a predator is small in relation to prey availability present in the sampling area, Manly's α for constant prey populations was chosen. The formula for this index is:

$$\alpha_i = \frac{r_i}{n_i} \times \frac{1}{\sum (r_j / n_j)} \qquad (3)$$

where α_i is the preference index for prey type i; r_i and r_j are the proportion of prey type i or j, respectively, in the diet (i and j = 1, 2, 3, ... , m); n_i and n_j are the proportion of prey type i or j in the environment; and m is the number of prey types available. The α-values quantify the probability that an individual prey item is selected from a particular prey group when all prey species are equally available. Probability ranges from 0, which means that there is no probability of selecting a given prey group, to 1, which means that the prey group will always be selected. The prey preference estimates are based upon numbers.

To calculate niche overlap between ringed and harp seals Pianka's (1973) index was used:

$$O_{jk} = \frac{\sum_{i=1}^{n} (p_{ij} \times p_{ik})}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}} \qquad (4)$$

where O_{jk} is Pianka's measure of niche overlap index between predator species j and species k; p_{ij} is the proportion of prey species i in relation to the total amount of prey ingested by species j; p_{ik} is the proportion of prey species i in relation to the total amount of prey ingested by species k and n is the total number of prey species.

Pianka's index is symmetrical, i.e. overlap between species j and species k is identical to overlap between species k and j. The index ranges from 0, i.e. no overlap, to 1, i.e. complete overlap. It is generally considered that values of Pianka's index (O_{jk}) higher than 0.6 means that there is a biologically significant niche overlap for the resource(s) examined (Wallace 1981).

Calculation of niche overlap was based on 5 prey groups; *Themisto libellula*, polar cod, *Liparidae* spp., *Thysanoessa* spp. and 'other fish'. The basis for calculation of Pianka's niche overlap index was the number of prey items by group. In this analysis, conversion factors were applied to reduce over-representation of small-sized prey groups. Each prey item was given as an average 'polar cod biomass unit' (6.0 g), i.e. a *T. libellula* with an average mass of 0.291 g got a conversion factor of 20.6, and so on for the other prey species (see Table 5).

Levins' measure (B) was used in order to estimate the niche breadth of the seals (Krebs 1989).

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

where p_i is the fraction of prey item i in the diet ($\Sigma\, p_i = 1.0$), and n is the number of prey groups. This measure varies between 1 and the total number of prey groups found in the diet. If only 1 prey group is eaten, the niche breadth is 1. The more evenly the different prey groups are consumed, the higher the niche breadth.

RESULTS

The mean age of the collected ringed seals was 2.3 ± 3.5 yr (SD), ranging from 0 to 10 yr. The corresponding values for the harp seals were 11.9 ± 7.7 yr (SD), ranging from 1 to 24 yr. All 27 ringed seals had identifiable contents in their gastrointestinal tracts. Polar cod and *Themisto libellula* dominated their diet, with a minor contribution from other fish species (Table 1). All 18 harp seals also had identifiable contents. Polar cod was also the dominant prey item for this species, followed by *T. libellula* and *Liparidae* spp. (Table 1).

The resource survey revealed a great abundance of pelagic crustaceans (*Thysanoessa* spp. and *T. libellula*), which constituted about 99% of the estimated prey biomass available in the area (Table 2). Fish constituted only about 1% of the total biomass. Polar cod were the most abundant fish (73% of all fishes). Approximately 80% of the estimated prey biomass was distributed in the upper 200 m, while less than 1% was below 300 m. Although prey organisms were considerably more patchily distributed in the upper 100 m and below 300 m compared to the 2 intermediate depth layers, the species composition was relatively homogeneous in the whole survey area.

Table 2. Total biomass (tonnes) of prey items estimated from the acoustic resource survey conducted October 1995 in the same area where ringed and harp seals were collected for diet analyses

Depth strata (m)	Prey item *Boreogadus saida*	*Themisto libellula*	*Liparidae* spp.	*Thysanoessa* spp.	Other fish species
0–100	308	16881	71	45580	48
100–200	779	34651	231	103301	111
200–300	479	13675	275	44058	64
300–bottom	1101	36	1	143	165
Total	2667	65243	578	193082	388
Percentage	1.02	24.91	0.22	73.71	0.15

Table 3. Estimated number of specimens within each prey group in the environment (N), and the number of specimens within each prey group ingested by ringed (I_{PH}) and harp seals (I_{PG}) sampled in northeastern Barents Sea in October 1995

	Prey item *Boreogadus saida*	*Themisto libellula*	*Liparidae* spp.	*Thysanoessa* spp.	Other fish species
N	4.44×10^{8}	2.24×10^{11}	1.16×10^{8}	6.41×10^{11}	7.76×10^{7}
I_{PH}	3361	2848	6	0	69
I_{PG}	2340	754	402	2	261

The number of specimens within each prey group taken by seals in relation to the number of specimens within each group found in the resource survey (Table 3) was the basis for calculations of the preference indices. Analyses showed that both ringed and harp seals had a clear preference for fish as prey, with polar cod being the most important (Table 4). *Themisto libellula* and *Thysanoessa* spp. both scored zero on the preference index for both seal species, even though both species were very abundant in the study area.

For the analyses of niche overlap between ringed and harp seals, the numerical results from Table 1 were adjusted into 'polar cod units' based on the size of average specimens within each prey group (Table 5). The dominance of polar cod in the diet of both ringed and harp seals resulted in a nearly complete niche overlap between the 2 seal species (O_{jk} = 0.985). However, the sizes of the polar cod taken by these 2 seal species are quite different. Harp seals fed on significantly larger specimens than ringed seals (Fig. 2; Pearson chi-square, χ^2 = 1075, $p < 0.001$). Polar cod collected by trawling at different levels in the water column were of different size. Those found in deeper water were significantly larger than those found in shallow water (Fig. 2; Pearson chi-square, χ^2 = 133, $p < 0.001$). Levin's niche breadth indices for ringed seals and harp seals were found to be 2.03 and 2.25, respectively.

Table 1. Results from analyses of gastrointestinal tract contents of ringed (n = 27) and harp (n = 18) seals collected along the ice edge in the Barents Sea in October 1995. (FO_i: frequency of occurrence of each prey item; N_i: relative frequency of occurrence by number)

Prey item	Ringed seal FO_i	Ringed seal N_i	Harp seal FO_i	Harp seal N_i
Boreogadus saida	88.9	53.5	77.8	62.3
Themisto libellula	100.0	45.3	66.7	20.1
Liparidae spp.	18.5	0.1	44.4	10.7
Thysanoessa spp.	11.1	0.0	11.1	0.1
Other fish species	14.8	1.1	33.3	6.9

DISCUSSION

The type of resource survey conducted during this study is sensitive to methodical bias caused by the mixture of zooplankton and fish in the sampling environment. Due to different fishing efficiencies of the pelagic and demersal trawls with regard to fish and zooplankton, partitioning of backscattering coefficient values between fish and zooplankton had to be made subjectively (Lindstrøm et al. 1998). In addition, sympagic prey organisms were not included in the resource survey, since methods for assessing biomass or collecting specimens from the underside of the ice were not available. Nevertheless, pelagic crustaceans

Table 4. Prey preference by ringed and harp seals sampled in the northeastern Barents Sea in October 1995, measured by Manly's preference index (α)

Prey item	Manly's α for ringed seals	Manly's α for harp seals
Boreogadus saida	0.87	0.42
Themisto libellula	0.00	0.00
Liparidae spp.	0.01	0.31
Thysanoessa spp.	0.00	0.00
Other fish species	0.13	0.26

Table 5. Diet composition, expressed as relative frequency of occurrence as numbers of prey items of each species identified in ringed and harp seal gastrointestinal tracts, sampled in the northeastern Barents Sea in October 1995. Conversion factors compensate for size differences between specimens of different prey groups

Prey item	Ringed seal	Harp seal	Conversion factor
Boreogadus saida	94.37	79.00	1.00
Themisto libellula	3.88	1.23	20.61
Liparidae sp.	0.14	12.42	1.09
Thysanoessa spp.	0.00	0.00	19.93
Other fish species	1.61	7.34	1.20

heavily dominated the pelagic ecosystem during the period of investigation and the dominant species overall were *Themisto libellula* and *Thyssanoessa* spp. Both these invertebrates are key species in the Barents Sea ecosystem, and represent an important link between herbivorous zooplankton and fish, birds and marine mammals including harp and ringed seals (Bradstreet & Cross 1982, Lønne & Gulliksen 1989, Lydersen et al. 1991, Sakshaug et al. 1992, Mehlum & Gabrielsen 1993, Percy 1993, Nilssen 1995).

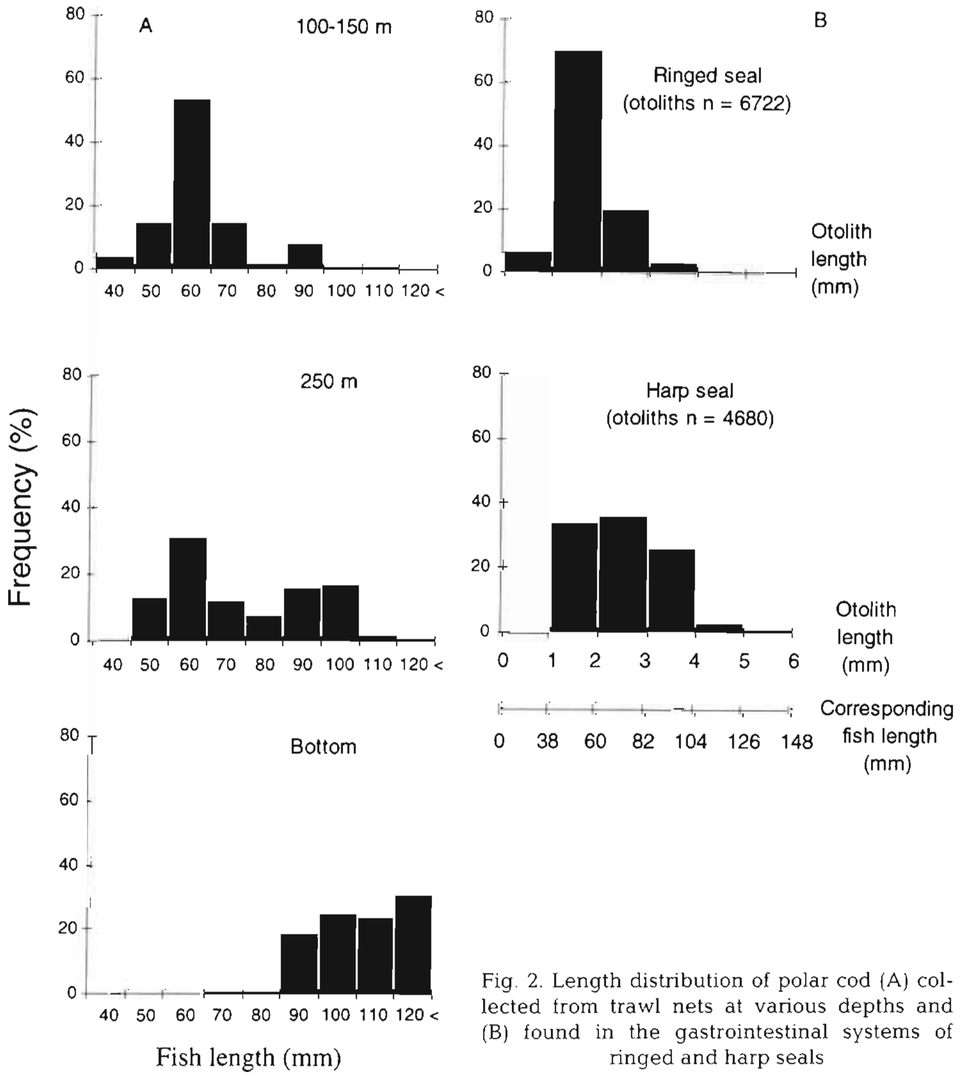

Fig. 2. Length distribution of polar cod (A) collected from trawl nets at various depths and (B) found in the gastrointestinal systems of ringed and harp seals

The resource survey showed that fish species accounted for less than 2% of the biomass available as potential food for seals, and most of the fish were polar cod. Polar cod fry are found throughout much of the northern and eastern Barents Sea in autumn, especially in the upper water column (0 to 50 m). In the spring and summer they undertake feeding migrations from the southeast to the north and west and thereby spread widely across the Barents Sea. Ecological studies conducted in Spitsbergen coastal waters found that 0-group polar cod were found in the upper echo layer (15 to 80 m), while older and larger polar cod were distributed in deeper waters (215 to 370 m) (Falk-Petersen et al. 1986). A similar age and size versus depth distribution of polar cod was also observed in the present study (see Fig. 2).

Based on the diet analysis of the seals in this study, polar cod and *Themisto libellula* were found to be the dominant prey species. This analysis was based on the relative frequency of occurrence by number, which gives relatively small prey organisms, e.g. *T. libellula*, a disproportionate large importance compared to larger prey, e.g. polar cod. When the preference indices were considered, polar cod dominated the diet. *Thyssanoessa* spp. were not eaten at all, and *T. libellula* had a preference index of zero, even though the numerical frequency of occurrence based on stomach and intestine analysis might suggest that this prey species is important. So why, in this large soup of potential prey organisms, do the seals feed on a prey species that constitutes only 1% of the total biomass available as food? Part of the explanation for this selectivity might be found in the differences in the energy content of the prey organisms. Both polar cod and *T libellula* vary seasonally in energy content, and in the autumn polar cod represent nearly twice as much energy per mass unit as *T libellula* (7.0 MJ vs 3.9 MJ kg^{-1}, respectively) (Sakshaug et al. 1992). A second factor related to energetics is that the digestible energy (DE) is probably higher in polar cod than in *T. libellula*. A study measuring DE in harp seals fed capelin *Mallotus villosus* and *T libellula* resulted in higher values for the fat fish than for the amphipod (94 and 81%, respectively) (Mårtensson et al. 1994). It is therefore reasonable to assume that the relatively fatter polar cod has a higher DE than *T libellula* when digested by the seals. From an energetic point of view, this further increases the advantages of preferring polar cod to amphipods. A third factor is the size difference between these prey types. The average mass of a *T. libellula* was found to be 0.291 g, which was on average 20.6 times less than that of an average polar cod (see Table 2). If we consider the difference in energy content and DE for these 2 prey types, the seal would have to capture about 43 specimens of *T. libellula* to obtain an energy intake similar to that from a single polar cod. It is not known how these seals capture such small food objects, but if they pick them one by one, the energetic costs of prey capturing per unit of energy is probably much higher for the amphipods than for the larger fish.

Based on Pianka's index for niche overlap, the ringed seals in this study were found to almost completely overlap with that of harp seals collected in the same area (O_{jk} = 0.985). Because comparable studies on niche overlap in marine mammals are lacking, a niche overlap value of greater than or equal to 60% was regarded as a significant overlap, based on Wallace's (1981) study of 2 fish species in Mississippi. Accordingly we can assume that a significant niche overlap exists between ringed and harp seal diet based on analyses of their gastrointestinal tracts. Both seal species in this study show a clear preference for polar cod, and their feeding niches overlap almost 100%. However, when considering the size of the polar cod preyed upon by these 2 seal species, a picture emerges that brings some nuances into this apparent 100% exploitation of the same resource. Harp seals feed on significantly larger polar cod than ringed seals. If we consider the depth distribution of different size/age classes of polar cod, we find that the smaller cod are found in the upper water masses (Falk-Petersen et al. 1986), while the larger cod are found deeper and closer to the bottom (see also Fig 2). Recently acquired data on the diving behaviour of these seal species support the separation suggested. For harp seals tracked along the ice edge in the Barents Sea 50% of all dives are between 100 and 300 m (Nordøy unpubl. data), while more than 90% of ringed seal dives along the autumn ice edge north of Svalbard were shallower than 100 m (Lydersen unpubl. data). These 2 studies were performed on adult specimens of the 2 species. The ages of the seals in the present study showed that most of the ringed seals were juveniles, while the majority of the harp seals were adults. Since juvenile seals are likely to be poorer divers than adults (Lydersen et al. 1992), the proportion of dives shallower than 100 m for the ringed seals in this study is probably even higher than 90%. Thus it seems that the ringed seals are exploiting the upper and harp seals the lower part of the water column. By introducing space and a differentiated age/size approach on the polar cod resource into the niche overlap discussion, the overlap between these two seal species diminishes.

The difference in age distribution between these 2 species in our sample probably reflects the real age distribution of these 2 species along the ice edge in the Barents Sea at this time of the year (See Wathne 1997, Lindstrøm et al. 1998).

The niche breadth measurement expresses to what degree a predator is a generalist or a specialist. A generalist exploits various prey items regardless of species identity, while specialists are very species selective.

Generalists are characterised by high values of niche breadth measurements, whereas specialists have low values of niche breadth. The relatively low niche breadth value found for both ringed (2.03) and harp (2.25) seals could indicate that they are specialists, but due to the low number of species in this pelagic food web (N = 5), we should be cautious in making a generalisation concerning this finding. Studies of ringed seal diets in coastal regions in Svalbard (Gjertz & Lydersen 1986, Lydersen et al. 1989, Weslawski et al. 1994) and from other Arctic regions (see Reeves 1998) have identified a much larger prey species diversity than that found in this study. Those studies suggested that ringed seals are generalists.

In this study we have shown that even though the ice edge areas occupied by ringed and harp seals were totally dominated by pelagic crustaceans, the seals preferred to feed on fish. Polar cod constituted only 1% of the available prey biomass, but was the preferred prey. Niche overlap calculations based on prey found in the gastrointestinal systems of ringed and harp seals showed an almost 100% overlap between these 2 predator species. However, harp seals prey on significantly larger polar cod than ringed seals, and the larger cods are distributed in deeper waters than the smaller ones. These 2 seal species therefore appear to exploit different fractions of the same resource.

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