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# DO HARP SEALS *PHOCA GROENLANDICA* EXHIBIT PARTICULAR PREY PREFERENCES ?

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## ABSTRACT

Feeding ecology studies of Barents Sea harp seals *Phoca groenlandica* were carried out in the southeastern Barents Sea in February 1993, and in the northeastern Barents Sea in October 1995. In both years, acoustic surveys aimed to estimate the abundance of potential prey items were conducted concurrently with sealing activities. The abundance of prey differed substantially between the areas. To the west of the southernmost area (CKK), herring *Clupea harengus* was by far the most abundant prey item, while polar cod *Boreogadus saida* predominated to the east (Pechora). In the northern area crustaceans, *Thysanoessa* sp. and *Parathemisto libellula*, were by far the most abundant prey items. Stomach/intestine contents were obtained from 76 and 18 harp seals in 1993 and 1995, respectively. The composition of seal diets varied between areas. In the southeastern Barents Sea, herring and polar cod dominated the diet in the western and eastern sub-area, respectively, with significant contributions also for cod *Gadus morhua*, various other bottom fish and shrimp. In the northeastern Barents Sea, polar cod appeared to be the most important prey accompanied by *P. libellula*. Statistical analyses of potential prey preferences revealed that the harp seals in the northeastern Barents Sea in October 1995 appeared to have a negative preference for krill. Considering two prey species at a time and comparing the difference between diet and abundance composition, the most reliable prey preference conclusion on a 5% test level was that polar cod was preferred before *P. libellula* in the 1995 northern study area if these two species only occurred in the pelagial. In the CKK area, herring was found in a significantly smaller proportion in the seal diet than in the sea. A preference for herring before polar cod was indicated in the Pechora area, but this conclusion is more uncertain due to spatial variation in prey composition in the area. The statistical method used was based on a standardized test statistic where the normal distribution approximation appeared to be appropriate from comparisons of p-values based on the normal distribution with p-values based on bootstrap replications of the real data.

## INTRODUCTION

Understanding the relationship between predator and prey populations is of considerable importance in the management of exploited fish stocks. With the increased attention paid to multispecies interactions, predator-prey relationships are essential both in predictions of yield and in assessment of the ecological effects of exploiting particular species. The modelling effort for resources in the Barents Sea has resulted in an area-structured multispecies model, MULTSPEC, which focuses particularly on the key fish stocks herring *Clupea harengus*, capelin *Mallotus villosus* and cod *Gadus morhua* (Ulltang 1995).

It is, however, recognised that the inclusion of marine mammals is essential for a realistic modelling of the resources in the Barents Sea. The current purpose for including the two most numerous mammal species in the area, harp seals *Phoca groenlandica* and minke whales *Balaenoptera acutorostrata*, in the model is to try to determine what data is necessary to predict the effects of these two species' predation on the stocks of herring, capelin and cod. To a more limited extent, attempts are also made to investigate likely long-term effects of varying exploitation strategies on the fish and mammal stocks on the system through simulation studies.

The development of MULTSPEC has given analysis of feeding ecology of important top predators particular actuality. Previous diet studies have revealed that the harp seals forage mainly on pelagic shoaling prey such as the pelagic crustacean *Parathemisto libellula*, herring, capelin and polar cod *Boreogadus saida* (Nilssen 1995). However, our knowledge regarding harp seal feeding ecology has been mainly descriptive, and multispecies assessments of harp seals predation on different prey populations require more quantitative information about harp seal prey preferences (Bogstad *et al.* 1996).

In recent ecological studies of the northeast Atlantic minke whale, including both whale stomach contents analyses and simultaneous estimations of prey availability, the diet composition and foraging behaviour of the species were successfully assessed (Haug *et al.* 1995a,b, 1996a, b). Questions concerning prey preferences proved, however, much more difficult to address. This is partly due to the difficulties involved in obtaining synoptic results with the chosen survey design, but also to the precision of today's methods of resource mapping (Skaug *et al.* 1996; Haug *et al.* 1996a). Comprehensive Norwegian ecological studies of Barents Sea harp seals were carried out in 1990-1994 (see Nilssen 1995) based on stomach and intestine analyses, and some of the conducted surveys included simultaneous estimates of prey availability. In some cases, the resource maps were only based on trawl hauls (Nilssen *et al.* 1995a), but in February 1993, a more comprehensive resource survey, including the use of acoustic equipment, was carried out during a harp seal survey in the southeastern Barents Sea. A similar harp seal survey with comprehensive and simultaneous acoustical resource mapping was carried out in the northeastern Barents Sea in October 1995.

The 1993 and 1995 resource mapping occurred considerably more synoptic with the sealing activity than any resource mapping connected with previous scientific whaling activities. With reference to the statistical methods developed in the minke whale prey preference studies (see Skaug *et al.* 1996) it is therefore assumed that questions concerning prey preferences can be more effectively addressed, using the harp seal as the top predator model species. A main purpose of this paper is to document developed statistical methods for prey preference analyses, which in our opinion appeared to be appropriate for the available data sets. Additionally, it describes the diets and food availabilities for the harp seal in the areas and years of investigation.

Prey preference is not a self-explanatory term. In this paper two prey species are considered at a time, and prey preference is related to the quotient equal to the amount of one of the two species divided by the amount of both. A prey preference for one of the two prey species considered is defined as an expected difference between the quotient based on diet and abundance data, respectively. Because we aim to assess how prey is exploited in all water masses availabe by the seals, and because we do not know where and when the seals have been feeding, integrated abundance estimates are used and we must assume that all prey have been caught in the area for which representative abundance samples are available.

The following objectives are addressed:

1) Describe the stomach and intestine contents of harp seals.
2) Estimate and evaluate the prey abundance in three areas close to the catch sites.
3) Evaluate possible harp seal prey preferences.

## MATERIAL AND METHODS

### Sampling of harp seals

In 1993, 97 harp seals were caught between Cape Kanin and Kolguyev Island (the CKK area) during the periods 5-7 and 13-17 February, while 13 seals were taken in the Pechora Sea on 10-12 February (Fig. 1). In 1995, 22 harp seals were caught in a relatively restricted area southeast of Franz Josef Land on 21-25 October.

The harp seals were shot on ice floes from the research vessel R/V *Jan Mayen* and immediately brought on board for dissection where samples of stomachs and intestines were frozen for later examination of contents.

### Stomach and intestine contents analyses

In the laboratory the stomachs and intestines were cut open after thawing. The stomach contents were weighed and, after flushing the intestine with fresh water, the fish and crustaceans were separated. Most of the stomach and intestine 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 intestinal crustaceans were obtained by counting the carapaces of each species. The total, or a sub-sample, of the crustaceans in each seal stomach was weighed and the numbers of each species were recorded. In order to estimate the ingested mass of crustaceans found in the seal stomachs and intestines, mean wet masses of fresh crustaceans sampled from trawl catches taken during the survey were used. Similarly, the mean masses of fresh specimens sampled from the trawl catches were used when estimating the initial mass of fish ingested. The total number of each fish species in stomachs and/or intestines were estimated by adding the number of whole specimens, the number of intact skulls and half the number of "free" otoliths. The results from the stomachs and intestines were pooled after identification of the contents.

### Feeding indices

In order to simplify statistical exercises based on the feeding indices, the harp seal prey organisms were combined into different prey categories. Due to differences in species abundance in the two habitats investigated, the 1993 and 1995 groups became different. In 1993 the total number of prey organisms were grouped into the following seven taxa:

SHRIMP (*Sabinea septemcarinata*, *Sclerocrangon boreas*, *Eualus gaimardii*, *Crangon* sp., unidentified crustacean remains), HERRING, CAPELIN, COD, POLAR COD, BOTTOM FISH (*Lycodes* sp., unidentified cottid, stichaeid and pleuronectid remains) and VARIOUS FISH. In 1995, the prey items were grouped into the following five prey taxa: AMPHIPOD (*Parathemisto libellula*), KRILL (*Thysanoessa* sp.), POLAR COD, SNAIL FISH (*Liparis* sp.), VARIOUS FISH and SHRIMP.

Since no feeding indices give a complete or fully realistic picture of the diet compostion, the following five feeding indices were used when analysing the dietary data from 1993 and 1995 (see also Hyslop 1980; Pierce & Boyle 1991):

1) The frequency of occurrence of each prey item, $FO_i$:

$$FO_i = (s_i / s_t) \cdot 100 \qquad \text{(eq 1)}$$

where $s_i$ is the number of examined seals with stomachs and/or intestines containing species i and $s_t$ is the total number of seals examined.

2) The relative frequency of occurrence by number, $N_i$:

$$N_i = (n_i / n_t) \cdot 100 \qquad \text{(eq 2)}$$

where $n_i$ is the total number of individuals of prey category *i* in all seals and $n_t$ is the total number of individuals of all prey categories.

3) The relative frequency of occurrence by mass, $B_i$:

$$B_i = (b_i / b_t) \cdot 100 \qquad \text{(eq 3)}$$

where $b_i$ is the total estimated fresh mass (which includes both undigested and reconstructed mass) of prey category *i* in all seals and $b_t$ is the total estimated mass of all prey categories.

4) The individual number index, $NI_i$:

$$NI_i = \frac{1}{n}\sum_{j=1}^{n}\left(n_{ij} / n_j\right) \cdot 100 \qquad \text{(eq 4)}$$

where $n_{ij}$ is the number of individuals of prey category i in seal no. j, $n_j$ is the total number of individuals of all prey categories in seal no. j, and n is the total number of examined seals with prey content.

5) The individual mass index, $WI_i$ (see Haug *et al.* 1996):

$$WI_i = \frac{1}{n}\sum_{j=1}^{n}\left(b_{ij} / b_j\right)\cdot 100 \qquad \text{(eq 5)}$$

where $b_{ij}$ is the estimated fresh mass of prey category i in seal no. j, $b_j$ is the total mass of all prey categories in seal no. j, and n is the total number of examined seals with prey content.

The number indices ($N_i$ and $NI_i$) are applied in the diet preference analysis when demersal trawl haul data are used in the abundance estimates, while the mass indices ($B_i$ and $WI_i$) are applied when acoustical abundance data are used. One advantage of the individual indices ($NI_i$ and $WI_i$) is that they give each seal the same importance irrespective of the variation of total prey content (number of individuals or weight) from seal to seal. Using analysis based on both 'total' and individual indices are assumed to give more reliable conclusions from the diet preference analysis in that similar conclusions appear more indicative than opposite ones.

**Estimation of prey abundance**

The estimation of prey abundance in the two main sampling areas were carried out onboard R/V *Jan Mayen*. Standard acoustic survey methods were used (Foote 1991), including a Simrad EK-500 split beam echo sounding system (Bodholt *et al.* 1989) and a BEI post-processing system (Foote *et al.* 1991). In the 1993 study in the southeastern Barents Sea, the acoustic surveys were conducted on 6-7 February in the western CKK area and on 10-11 February in the eastern Pechora Sea. In 1995, in the northeastern Barents Sea, the survey was made on 23-24 October.

A minimum acoustic threshhold of -88 dB SV was applied which also allowed zooplankton to be detected. The echo integration surveys were conducted by cruising along predetermined transects in the actual areas. The allocation of acoustic values to species groups were carried out on the basis of the acoustic character of each species group and the results from trawl hauls. The integration was interrupted each time trawling was carried out, and trawl hauls were taken in response to changes in the echo sounder observations.

Both pelagic and demersal trawls were used to sample the observed acoustic scatterers. For pelagic trawling a 10 fathom trawl (Harstadtrål, Norway) fitted with a Scanmar depth monitor was used. Demersal trawling was carried out in 1993 using a "Super Campelin" 1800 mesh shrimp trawl with rubber bobbins. Both trawls were fitted with an 8 mm net inside the cod end in order to sample fish fry and zooplankton. All trawl hauls lasted for about 30 minutes and the towing speed was approximately 3 knots.

Approximate volumes of fish and crustaceans were recorded from all trawl hauls. The samples were identified to the lowest possible taxon using standard identification keys (Enkell 1980; Pethon 1985). Fish were counted, and for crustaceans, the fraction by number in the trawl haul was estimated by counting a random subsample.

As a measure of the sampling intensity we have calculated the degree of coverage defined by $d = D/\sqrt{A}$ where D is the total length (in nautical miles) of the cruise track and A is the size (in square nautical miles) of the surveyed area (Aglen 1989). The degree of coverage was calculated for all three areas. Aglen (1989) recommended that the degree of coverage should preferably be six or larger.

The standard echo integration method, described in detail by Maclennan & Simmonds (1992), was used to estimate the relative abundance of the most common prey species in the areas. The acoustic parameter measured by the echo integrator is the area backscattering coefficient $S_A$ (see Maclennan & Simmonds 1992).

The relationship between $S_A$ and density of fish, $\rho_A$, is:

$$S_A = \sigma \cdot \rho_A \qquad \text{(eq 6)}$$

where $\sigma$ is the scattering cross section.The target strength (TS), and therefore $\sigma$, varies between species and will also vary with fish body length, according to the relation

$$TS = A + B \cdot \log L = 10 \cdot \log\left(\frac{\sigma}{4\pi}\right) \qquad \text{(eq 7)}$$

where L is fish length and A and B are species-specific constants. All but two of these constants (cod and crustaceans), which were taken from MacLennan & Simmonds (1992), were kindly provided by the Institute of Marine Research, Bergen. Consequently, the length composition of each of the fish scatters is needed in order to convert from $S_A$ to fish density. The total number, N, of fish and zooplankton in the surveyed area is

$$N = \rho_A \cdot A \qquad \text{(eq 8)}$$

where A is the area (square nautical mile). To calculate total biomass, mean mass of fish/zooplankton were used.

The average $S_A$ per square nautical mile and 50 m depth channel was recorded over 5 nautical miles intervals, and in 1993 the $S_A$ was distributed on the following six targets: herring, capelin, cod, polar cod, sandeel and various fish. In 1995 the $S_A$ was distributed on amphipods, krill, polar cod, snail fish and various fish.

In 1993 the biomass was estimated in two depth strata (0-50m, 50-bottom), while in 1995 the water column was stratified in following four depth strata: 0-100 m, 100-200 m, 200-300 m and 300-bottom. The partioning of the depth strata was based mainly on the echogram scatters.

**Statistical analysis of prey selectivity.**

Potential dietary preferences of the seals were tested by comparing two different prey species or prey groups at a time. The applied statistical method considers the quotient equal to the amount (number or biomass) of one of the two prey species divided by the total amount of the two prey species. In each analysis, one diet quotient and one abundance quotient were calculated in order to see if there were significant differences between diet and abundance. This method is similar to a method used in prey preference studies of minke whales documented by Skaug *et al.* (1996).

The test statistic used was the difference between diet and abundance prey species quotients divided by the estimated standard deviation of this difference. It appeared that the abundance quotient variance was negligible compared to the diet quotient variance, and the former was, therefore, neglected in the analysis. The test statistic was assumed to approximately follow the standard N(0,1) normal distribution under the hypothesis that there was no expected difference between diet and abundance composition. The normality assumption was assessed by use of bootstrap techniques (see Efron & Tibshirani 1993, Jiang & Jørgensen 1996), where p-values from the tests estimated on the basis of bootstrap resamples of the real data were compared with p-values based on the N(0,1) distribution.

Biomass as well as number diet indices (eq. 2-5) were used in the analyses. In all cases, indices where each seal is weighted equally irrespective of total prey content (WI and NI) and indices based on total content of all seals (Bi and Ni) were used. The estimated variances needed in the test statistic were based on the real data as well as on bootstrap resamples of the data.

One justification for studying only two prey species at a time was that a very limited number of species dominated both the diet and the abundance data. Another justification was that the method is simpler than multivariate alternatives. A general multivariate method, where any number of prey species can be analyzed simultaneously, is currently under development (Alf Harbitz, unpublished material).

*Assumptions.*

The statistical methods were based on the following assumptions:

i) The examined seals perform a random sample from all seals in the considered area.
ii) The prey abundance estimates used were relevant.

Because we did not know exactly where and when the seals have eaten, integrated prey abundance data were used and prey preference was defined as a significant difference between the expected relative composition of that particular prey in the seal diet and the corresponding abundance composition in the ocean. Because the abundance estimates based on demersal trawl hauls are not comparable with the pelagic abundance estimates based on acoustics, we were not able to estimate the total abundance in the ocean. In addition, acoustics is not an appropriate method to estimate abundance in the uppermost surface layer. We had to assume, therefore, that all seals had been feeding in the same part of the water column, i.e., either along the bottom, or in the pelagic area.

*Notations.*

The following standard mathematical notations are used: Underline as a vector symbol, overbar as a mean value symbol, E for statistical expectation value, Var for variance, sd for standard deviation, the symbol ^ for estimator (e.g. $\hat{sd}$ denotes an estimator for sd) and N(0,1) for a normal distribution with expectation 0 and variance 1.

In addition attempts were made to use logical symbols: a for abundance, b for biomass, n for number of individuals, t for total, Q for quotient and Z for the test statistic because it is assumed to be approximately standard N(0,1) distributed under the hypothesis that there was no prey preference.

| | |
|---|---|
| $a_i$ | abundance estimate of prey species i:<br>- number of prey species i at the bottom based on demersal trawl hauls or<br>- biomass of prey species i in the pelagic area based on acoustics |
| $b_{ij}$ | biomass of prey species i in seal j |
| $b_i$ | total biomass of prey species i in all seals |
| i | prey species no., i = 1, 2 |
| j | seal no., j = 1, 2, ..., n |
| n | number of examined seals with prey content |
| $n_{ij}$ | number of prey species i in seal j |
| $n_i$ | total number of prey species i in all examined seals |
| $\overline{Q}_a$ | $= a_1/(a_1 + a_2)$ = relative abundance variable |
| $Q_{bj}$ | $b_{1j}/(b_{1j} + b_{2j})$ = relative biomass of prey species 1 in seal j |
| $\overline{Q}_b$ | mean value of $Q_{bj}$ averaged over all n seals |
| $Q_{nj}$ | $n_{1j}/(n_{1j} + n_{2j})$ = relative number of prey species 1 in seal j |
| $\overline{Q}_n$ | mean value of $Q_{nj}$ averaged over all n seals |
| $\overline{Q}_s$ | relative diet variable:<br>1) $b_1/(b_1+b_2)$ when diet index $B_i$ is considered<br>2) $n_1/(n_1+n_2)$ when diet index $N_i$ is considered<br>3) $\overline{Q}_b$ when diet index $WI_i$ is considered<br>4) $\overline{Q}_n$ when diet index $NI_i$ is considered |
| Z | $\dfrac{\overline{Q}_s - \overline{Q}_a}{sd(\overline{Q}_s - \overline{Q}_a)}$ test statistic |

*The hypothesis testing model.*

The null and alternative hypothesis. The following null hypothesis $H_0$ and alternative hypothesis H were tested:

$H_0$: E [Z ] = 0 ; i.e. there were no expected preference between any two prey species

H: E [Z ] $\neq$ 0 , i.e. there was an expected preference for at least one prey species

The test statistic Z. The following test statistic, Z, was applied:

$$Z = \frac{\overline{Q}_s - \overline{Q}_a}{sd(\overline{Q}_s - \overline{Q}_a)}$$

For sufficiently large n (number of examined seals) Z is approximately N(0,1) distributed under $H_0$. A verification of the normal approximation was performed by comparing p-values based on the normal assumption with p-values estimated by use of bootstrap replications of the real data.

We assumed that the abundance samples could be considered as stochastically independent of each other, and that the diet was stochastically independent of the abundance. The standard deviation in the denominator of Z might then be estimated as follows:

$$\hat{sd}(\overline{Q}_s - \overline{Q}_a) = \sqrt{\hat{Var}(\overline{Q}_s) + \hat{Var}(\overline{Q}_a)}$$

where $\hat{Var}(\overline{Q}_s)$ and $\hat{Var}(\overline{Q}_a)$ are unbiased estimators for the variance of $\overline{Q}_s$ and $\overline{Q}_a$, respectively. Because the abundance variance estimate $\hat{Var}(\overline{Q}_a)$ in most cases appeared to be negligible, compared with the diet variance estimate $\hat{Var}(\overline{Q}_s)$, the former was set to zero in all analyses for which results are listed. The diet variance was estimated based on the real diet data when the individual seal diet indices (eq. 4 and 5) were used, and based on bootstrap replications of the real data when the total (or bulk) indices (eq. 2 and 3) were used.

Rejection area, R. Note that the test was two-sided, i.e. the test was rejected when Z was positive and sufficiently above zero (preference for the first of the two prey categories) as well as when Z was negative and sufficiently below 0 (preference for the latter of the two prey categories). We used a genereal test level of 5 % in all tests. The rejection area R based on the N(0,1) distribution was then defined as:

R: $|Z| > 2$

where $|Z|$ denotes the absolute value of Z. (A more precise test criterion based on the N(0,1) distribution would be $|Z| > 1.96$, but the difference between 2 and 1.96 was negligible compared to other uncertainties).

p-values. The p-value is defined as the probability of obtaining a value of the test statistic (Z) which is at least as extreme as the actual observed value, when $H_0$ is true. The theoretical p-value, $p_{th}$, was calculated based on the N(0,1) distribution as follows:

$p_{th} = 2 \cdot \Phi(|z|)$

where $\Phi$ denotes the cdf (cumulative distribution function) of the N(0,1) distribution. As an example, $p_{th} \approx 0.05$ when $|z| = 2$.

For low $p_{th}$-values, however, corresponding to the tail part of the normal distribution, the validity of the assumed normality assumption is questionable. We have, therefore, estimated the p-values based on bootstrap simulations of the Z-distribution under $H_0$ using the following algorithm:

1. Label the n examined seals with successive integer numbers from 1 to n.
2. Simulate n independent labels from a uniform distribution of integers from 1 to n and use these to pick out the n seals which are used to calculate a bootstrap sample $\overline{Q}_{sboot}$ of $\overline{Q}_s$ .
3. Repeat step 1) and 2) $n_{boot}$ times
4. Translate the simulated distribution of $\overline{Q}_{sboot}$ to have mean value equal to $\overline{Q}_a$
5. Calculate the number of $\overline{Q}_{sboot}$ samples, $n_{Rboot}$, with values equal to or more extreme than the $\overline{Q}_s$ value based on real data.
6. The Bootstrap p-value estimate is then $p_{boot} = 2 \cdot n_{Rboot} / n_{boot}$
7. If $p_{boot}$ appears to be larger than one, then replace it by $2\text{-}p_{boot}$.

Note that in step 2) one specific seal can be used several times in the bootstrap sample, a key feature of the bootstrap technique (Efron & Tibshirani, 1993). The procedure above is quite efficient, because there is no need for estimating variances. If $p_{th}$ did not deviate too much from $p_{boot}$, we have taken this as a reasonable indication that the normal assumption was appropriate.

## RESULTS

### Harp seal diets

*The February 1993 data*

In the CKK area (between Cape Kanin and Kolguyev Island) all stomachs were empty whereas food was found in 67% of the intestines. 15 different prey species were identified (Table 1), and herring occurred in 72.3% of the intestines, while 32.4% of the intestines contained identified crustaceans, mainly decapods. 32.3% of the 97 harp seals in the CKK area had fed on one prey species only (Fig. 2). Of the single-prey intestines, 48% and 38% contained herring and shrimp, respectively.

Applying the mass $B_i$ index to the intestine remains, herring constituted 59% of the calculated fresh mass, while bottom fish and cod contributed 22% and 12%, respectively (Fig. 3). Application of the $WI_i$ index reduced the relative importance of herring (from 59% to 49%) and bottom fish (from 22% to 10%), while the dietary importance of shrimp increased from 10% to 19%.

In the Pechora Sea all but one of the 13 stomachs (containing polar cod otoliths) were empty, while 84.6% of the intestines contained prey remains (Table 1). A total of 13 different prey species were identified in the harp seal intestines where polar cod (100%) and herring (72.7%) occurred most frequently. In this area, most of the harp seal intestines contained 5 or more prey species (Fig. 2).

In terms of reconstructed prey biomass (index $B_i$), polar cod and herring occurred in comparable amounts and constituted approximately 70% of the harp seal intestine contents in the Pechora Sea (Fig. 3). Bottom fish contributed to ca. 18% of the biomass. Substituting the $B_i$ index with the $WI_i$ index revealed that the latter increased the relative importance of polar cod from 35% to 57% and reduced it from 32% to 22% for herring.

The numerical frequency index ($N_i$), used when modelling the interactions between harp seal diet and demersal trawl catches, increased the dietary importance of herring in both areas compared with the two biomass indices (Fig. 4). In the CKK area, herring contributed with 74% to the counts of prey items in the harp seal intestines while the corresponding percentage for shrimp was 9%. In the Pechora Sea, herring contributed with 47%, with 26% polar cod and 16% bottom fish and various fish (Fig. 4).

*The October 1995 data*

Of the 22 harp seals sampled southeast of Franz Josef Land food was found in 18.2% and 72.7% of the stomachs and intestines, respectively (Table 1). In 4 of the 22 seals no food was found. A minimum of 5 prey categories were identified in the stomachs and intestines with polar cod and the amphipod *Parathemisto libellula* being the most frequent. *P. libellula* occurred most frequently in the stomachs (75%) whereas polar cod occurred in 81.3% of the intestines (Table 1). A total of 55% of the harp seals were observed to contain one or two prey species in their digestive tract (Fig. 2).

In terms of calculated fresh prey biomass ($B_i$), polar cod contributed with 62% to the intestinal contents, *P. libellula* 20% and snail fish 11% (Fig. 5). When the $WI_i$ index was applied the contribution from polar cod was reduced to 43% while contribution from *P. libellula* increased to 38%. The relative importance of snail fish and various fish remained more or less unchanged.

**Prey abundance**

*February 1993*

The sizes of the two southern sub-areas, the CKK area and the Pechora Sea, were calculated to be 637 and 600 n. square nautical miles, respectively. The degree to which the transects covered the surveyed areas were close below the value recommended by Aglen (1989) in both areas. The coverage was slightly higher in the Pechora Sea (5.3) than in the CKK area (5.2).

Results from the acoustic surveys in the CKK area, revealed that herring totally dominated the prey biomass (95%), followed by capelin, cod and polar cod which, when pooled, comprised less than 4% of the estimated total prey biomass (Table 2). Other fish, e.g. sandeel, contributed only 1% to the prey biomass. Approximately 71% of the estimated prey biomass was distributed in the lowest depth stratum (Table 2). Furthermore, more than 85% of the estimated prey biomass in the upper 50m was distributed in a relatively restricted area (approximately 80 square nautical miles) near the coast of Cape Kanin, and the prey abundance was generally observed to decrease with distance from the coast. Although the prey biomass was patchily distributed, the relative species composition seemed to be relatively constant during the entire acoustical survey. Although not included in Table 2, one observation of krill in one pelagic trawl haul taken in the northeastern part of the survey area indicated patches of this species.

Twenty-four different prey species were identified in four demersal trawl hauls taken in the CKK area. Herring dominated the contribution by numbers in the catches (92%), followed by shrimp (4%) and bottom fish (2%) (Fig. 4). Most of the herring were 0-group fish (the 1992 year class) with lengths between 8-10cm.

The prey abundance situation in the Pechora Sea differed substantially from that in the western sub-area. The main bulk of the prey biomass (58%) was allocated in the upper 50m. The total estimated prey abundance in the Pechora Sea (18.6 tonnes) was less than 1 o/oo of that in the western area (Table 2), and was nearly totally dominated by polar cod (90%). Herring contributed little to the Pechora Sea prey biomass (10%), and was completely absent in the upper 50m. The Pechora Sea prey biomass was more or less concentrated in three small patches: a western, central and eastern patch. Herring was only present in the western patch whereas polar cod was found in all three patches in both depth strata.

Six demersal trawl catches taken in the Pechora Sea, in which 27 prey species were identified, revealed a more varied bottom fauna than in the CCK area (Fig. 4). By numbers, polar cod and shrimp were the two most important prey items near the bottom and constituted approximately 46% and 30% of the demersal trawl catches, respectively (Fig. 4). Bottom fish contributed 16%, while 0-group herring was only present in low numbers (6%). Most of the polar cod in the Pechora Sea were between 8-14 cm in length.

*October 1995*
The degree to which the cruise track covered the survey area (approximately 500 square nautical miles) was 5.8.

The acoustic survey conducted in October 1995 revealed a prey abundance situation dominated by the crustaceans *Thysanoessa* sp. and *P. libellula* (99% of the biomass) whereas the fish component (polar cod, snail fish and various other fishes) consituted only 1% (Table 3). The fish component was dominated by polar cod (73%). Approximately 80% of the estimated prey biomass was distributed in the upper 200m, while less than 1% was below 300m. Although prey organisms were considerably more patchily distributed in the upper 100m and below 300m compared to the two intermediate depth strata, the species composition seemed to be relatively constant in the whole survey area. It should be kept in mind that the resource survey was conducted at night when hunting was impossible, and that prey organisms may have performed diel vertical migrations. This seemed to be particularly evident for a dense scattering layer distributed at 150m at night, which was found at 50m depth during daylight.

Three pelagic and two demersal trawl hauls, in which ten and nine prey species were identified respectively, were taken southeast of Franz Josef Land in 1995. The majority of the fish in the area were between 5-15 cm in length. Krill and *P. libellula* were generally between 2.5-4 cm and 2.3-3.8 cm in length, respectively.

## Predator-prey interactions

*Applicability of the material*

In the predator-prey analyses, only prey items contributing more than 5% to the total diet were included.

The bottom abundance estimates based on demersal trawl hauls are not comparable with the pelagic estimates based on acoustic data. Since we did not know exactly where each seal had been feeding, each prey preference analysis had to be based on the assumption that the content in any seal of the two prey species considered came from the area (bottom or pelagic) used in that particular analysis. If the pelagic and bottom tests were all rejected, however, we could conclude that a test based on a total abundance estimate, integrating bottom and pelagic abundance data, would also have caused test rejection. Due to possible vertical movements of some prey species, and since we did not know where and when the seals had been feeding, the pelagic abundance data are integrated over all depth intervals as well as over all 5 nautical miles samples. Similarly, the abundance estimates based on demersal trawl hauls are integrated values.

*The CKK area in February 1993.*

Of the identified prey groups in the CKK area (Table 4), the prey preference tests were limited to bottom fish, cod, herring and shrimp. A total of 27 acoustical abundance samples, 4 demersal trawl hauls and 65 seals with prey content were included in the analysis. Diet indices and integrated relative prey abundance estimates are given in Table 4. Herring was the dominant species in all diet indices as well as in the abundance estimates. While herring was the only dominant species in the abundance estimates (constituting ca. 95 % of all species), bottom fish, cod and various other fish contributed substantially to the seal diet in the area.

The preference test results comparing two species at a time are listed in Table 5. Tests comparing seal diets and integrated demersal trawl hauls and including the relationships cod vs. shrimp and bottom fish vs. cod were rejected. Thus, if all the seal caught had fed along the bottom only, and the diet and bottom abundance estimates were relevant, it is reasonable to conclude that the seals may have had a preference for cod rather than bottom fish and shrimp.

Tests of cod vs. herring based on the $WI_i$ and $NI_i$ indices, i.e., seal diets vs. pelagic and bottom abundance, respectively, were clearly rejected, thus suggesting a possible preference of cod before herring in both strata. The cod-herring test based on the $N_i$ index (seal diet vs. bottom abundance) was, however, not rejected, and the cod-herring test based on the $B_i$ index (seal diet vs. pelagic abundance) resulted in a 'weak' rejection (bootstrap p-value of 0.049). We have therefore chosen to conclude that there is not sufficient evidence in the data to claim that cod is preferred before herring.

Tests (not given in the tables) were also performed to see if the relative abundance in the sea of the dominante herring (92-95%, see table 4) was significantly larger than the seal diet indices for herring, which corresponds to a comparison of herring with all other prey species integrated. As a conservative estimate for the total relative abundance of herring (pelagic + bottom) the value 0.92 was used. The tests based on all 4 diet indices were rejected, though the bootstrap p-value based on 2000 bootstrap replications was close to 0.05 when the diet index $N_i$ was used. The test results thus indicated that there is a significantly smaller relative abundance of herring in the seal diet than in the sea.

*The Pechora area in February 1993.*

Of the identified prey groups in the Pechora area (Table 6), the prey preference tests were limited to bottom fish, herring, polar cod and shrimp. Integrated acoustical abundance samples, six demersal trawl hauls and 11 seals were involved in the analysis. Diet indices and integrated relative prey abundance estimates are given in Table 6. Polar cod is the dominant species in the sea, but shrimp (at the bottom) and herring (50m-bottom) also contribute considerably to the overall abundance. Herring and polar cod dominate the diet indices, but bottom fish and various fish are also significant prey species.

The preference test results comparing two species at a time are listed in Table 7. All tests comparing herring and polar cod were rejected. This indicates a general preference for herring before polar cod, also when the total abundance (bottom and pelagic) is considered. Using the integrated demersal trawl abundance estimates, all tests except the bottom fish vs. shrimp test were clearly rejected. Assuming that the prey species involved in the analyses only occurred at the bottom, this may indicate that the seals preferred herring more than shrimp and bottom fish, and polar cod more than bottom fish and shrimp. The test gave no evidence to conclude preference of bottom fish before shrimp.

*The Franz Josef Land area in October 1995.*

Of the identified prey groups in the Pechora area (Table 8), the prey preference tests were limited to *P. libellula*, polar cod, snailfish and the various fish group. 18 seals with prey content and 26 acoustical abundance samples for each of the depth intervals 0-100m, 100-200m, 200-300m and 300m-bottom are included in the analysis. Diet indices and integrated relative prey abundance estimates are given in Table 8. Krill and *P. libellula* dominated the abundance data in a proportion of 3:1, while krill was only found in one of the 18 seals, constituting ca. 1% of the total prey biomass in this seal. It appeared, therefore, that the seals examined rejected krill as food. Polar cod and *P. libellula* were the dominant prey species, and snailfish and various fish also contributed significantly to the seal diet.

The preference test results comparing two species at a time are listed in Table 9. The tests comparing *P. libellula* and polar cod, snailfish and various fish, respectively, were all clearly rejected, thus indicating that *P. libellula* was the least preferred. No other tests were rejected. Assuming pelagic predation, the strongest indication is a preference of polar cod before *P. libellula*.

## DISCUSSION

### Seal diet and prey abundance in February 1993

Results from the intestinal contents analyses revealed that herring was the most important harp seal prey species in the southeastern parts of the Barents Sea in February 1993. It is even possible that the contribution of herring to the harp seal diet may have been underestimated due to the rapid digestion of herring otoliths (Murie & Lavigne 1985; Jobling & Breiby 1986; Jobling 1987). Harp seal predation upon herring was also confirmed during commercial sealing in the East Ice in April 1993 where many harp seal stomachs were well filled with herring (K.A Fagerheim, Institute of Marine Research, Bergen, Norway, pers. comm.). The occurrence of polar cod in the Pechora Sea appears to be consistent with previous observations, suggesting that this species may also be an important winter food for the Barents Sea harp seals (Chapskii 1961).

The 1993 results from the southeastern Barents Sea differs from previous observations in this area. During the breeding period (early March) in 1989 and 1993 in the White Sea, limited feeding on crustaceans was observed (Nilssen *et al.* 1995b). In the southeastern Barents Sea between the Varangerfjord in North Norway and the Pechora Sea, capelin has been observed to be an important constituent on the harp seal menus, although amounts eaten vary in accordance with the huge changes in the abundance of the Barents Sea stock of capelin in recent years (Nilssen 1995; Nilssen *et al.* 1995b). Harp seal predation on herring in winter is also known from the beginning of this century (Wollebæk 1907; Chapskii 1961). The stock of the Norwegian spring spawning herring has gradually increased in size since the collapse in the late 1960s and since 1988 the southeastern Barents Sea has served as the main nursery area for the species (Anon. 1994). The present findings may indicate that immature herring is a current key species for harp seals in this area.

The present dominance of young herring, in particular individuals belonging to the 1992 year class, in the survey areas was also documented in the resource mapping. The 1992 year class of Norwegian spring spawning herring was particularly strong (Anon. 1994). Although present, there was much less capelin than herring in the surveyed areas, probably a result of the collapse in the Barents Sea capelin stock during the 1992/1993 winter. All recorded cod during the present survey were young specimens belonging to the very strong 1992 year class (see Anon. 1994). Compared to other species, polar cod was not particularly abundant in the CKK area, while in the much less prey abundant Pechora Sea this species dominated. However, recent Russian surveys suggest that the Barents Sea polar cod stock is relatively large at present (Borkin 1995). Notwithstanding several sources of error inherent in the prey abundance estimates (see MacLennan & Simmonds 1992), it is assumed that the resource surveys in the two southeastern Barents Sea sub-areas gave a reasonably representative picture of the resource situation, possibly with krill as an exception. Krill are known to occur in substantial amounts in these areas (Loeng 1989), and were registered in significant amounts in one pelagic trawl haul taken northeast in the CKK area. However, due to methodological problems inherent in abundance estimates of zooplankton which result in rather crude estimates, it was decided to neglect krill when partitioning the $S_A$ values into species.

**Seal diet and prey abundance in October 1995**

The October 1995 harp seal diet in the northeastern Barents Sea revealed a diet characterized particularly by the pelagic amphipod *P. libellula* and by polar cod. The importance of *P. libellula* as harp seal food in the northern parts of the Barents Sea, has also previously been suggested by Nilssen *et al.* (1995a). The results also indicate the importance of polar cod on the harp seal diets. Previous studies have suggested that while harp seal diets in the northern areas of the Barents Sea were characterized by amphipods during early autumn (September), a shift to fish, mainly capelin and to a lesser extent polar cod, occurred during October (Nilssen *et al.* 1995a). An October shift from crustaceans to fish appears to be supported by the present material, where polar cod is the prominent fish species, and capelin is absent. The lack of capelin could be due to the recent collapse in the capelin stock (Anon. 1996) and/or the very easterly localisation of the October 1995 survey area which may have been out of the usual distributional range for the Barents Sea capelin (see Dragesund *et al.* 1973; Røttingen 1990; Hamre 1994). Polar cod is, on the other hand, known to be abundant in these areas (Gjøsæter 1995). Furthermore, since 1992, there has been a marked increase in the abundance of polar cod (Borkin 1995; Gjøsæter 1995). These events may also have contributed to the shift in importance from capelin to polar cod on the harp seal October diets between 1992 and 1995.

Compared to the February 1993 resource survey, the October 1995 survey in the northeastern Barents Sea was considerably more susceptible to methodological biases due to the mixture of zooplankton and fish in this habitat. However, some effort was made to estimate the abundance of zooplankton. Due to different fishing efficiencies of the trawl with regard to fish and zooplankton, partitioning of $S_A$ values between fish and zooplankton had to be made subjectively. This was done by reducing the TS values on the computer screen until zooplankton could be assummed to be removed. The remaining $S_A$ values were then partitioned among the different fish species according to normal procedures (see MacLennan & Simmonds 1992). There was a complete dominance of zooplankton, *P. libellula* and *Thysanoessa* sp. in the acoustic survey. This is consistent with investigations made in the northern Barents Sea in September 1990 and 1991 (Nilssen *et al.* 1995a). Based on other, independent surveys in October 1995, the average biomass of zooplankton larger than 2000μ m in the northeastern Barents Sea was estimated to be approximately 7g dry weight $m^{-2}$ (Anon. 1996), which is considerably lower than estimates made in this study (35g dry weight $m^{-2}$). However, not only may zooplankton production vary dramatically between different localities, and 7g dry weight $m^{-2}$ may also be a considerable underestimate due to gear avoidance by large zooplankton such as *P. libellula* and *Thysanoessa* sp. (A. Hassel, Institute of Marine Research, Bergen, Norway, pers. comm.). Nevertheless, it is thought that the abundance of zooplankton compared to that of fish may have been overestimated in the area. The amphipod *P. libellula* is a dominant species in cold water plankton communities in the upper 50m of the water column of the northwest Atlantic (Percy 1993), may reach a peak in late August, and start to decline in early September (Dunbar 1946,1957; Percy & Fife 1985). *P. libellula* has also been suggested to be an important link in the food web between herbivorous zooplankton and fish, sea birds and mammals (Dunbar 1942,1946,1957; Sergeant 1973; Davis *et al.* 1980; Bradstreet & Cross 1982; Lønne & Gulliksen 1989; Ajiad & Gjøsæter 1990; Mehlum & Gabrielsen 1993). The observed consumption of large quantities of *P. libellula* by Barents Sea harp seals supports this. The most abundant krill species in the northern Barents Sea, i.e. *Thysanoessa* sp., is also known to be important link between the herbivorous zooplankton and fish, sea bird and mammals (Sakshaug *et al.* 1992). Krill is normally most abundant in the upper 200m, except in November and December when it seems to be distributed in deeper waters. Adult euphausiids are normally distributed close to the bottom at day, and migrate up to the surface during dusk (Sakshaug *et al.* 1992). However, during this survey we observed the opposite, i.e. the patch which was distributed at 150m at night was to be found at 50m during daylight.

**Predator-prey interactions**

Even though the very abundant herring was undoubtedly an important harp seal prey item in the CKK area in February 1993, it appears that the role of this species was more pronunced in terms of abundance than in terms of seal food. Cod and other fish species also contributed significantly to the seal diet, and the results from prey selectivity tests may indicate that harp seals exhibit a certain preference for cod rather than other fish species, including herring. Particular analyses where the variance estimate of the abundance was included (not shown in Table 5) revealed that none of the conclusions would have been changed. The conclusions should, however, still be interpreted cautiously, since the test results were shown to vary with choice of diet index.

The importance of herring on the seal diet is also emphasized in the Pechora area where polar cod was the most abundant species. The prey selectivity tests seem to indicate a general preference of herring before polar cod, while bottom fishes and shrimps were less preferred. Individual acoustic 5nm samples were not available to the analysis, which may weaken the herring - polar cod conclusion, especially since the prey composition of herring and polar cod was much less homogenous in the Pechora area compared to the CKK area. Particular analyses, where the variance estimate of the bottom abundance was included (not shown in Table 7), revealed that the test of bottom fish vs. polar cod was not longer rejected based on the $NI_i$ index. For the other bottom tests, no conclusions were changed.

Despite the vast occurrence of krill in the investigated Franz Josef Land area, this species was almost completely absent from the harp seal diets. Thus, krill, known to be important food for juvenile harp seals (Nilssen *et al.* 1995a, Haug *et al.* 1996d), may be rejected by the older seals. *P. libellula* is undoubtedly an important food constituent for the harp seals in autumn, although the test results indicate that this species is less preferred than fish species such as polar cod. Particular analyses of the variance of the acoustic abundance estimates revealed that these were negligible.

All tests which were rejected (28 of totally 40) based on the normal assumption of the test statistic were also rejected based on the p-values estimated by bootstrap. In addition, the theoretical p-values based on the normal distribution and the estimated p-values based on bootstrap were reasonably close to each other in most cases. We have interpreted this as a verification of the appropriateness of the method used.

The simple bootstrap technique used could probably be improved. One problem is that the technique applied is not range conserving, i.e., the estimated $H_0$ distribution of the test statistic easily extends the allowable range from 0 to 1. One way to proceed could be to follow the ideas behind sophisticated confidence intervals documented in Efron & Tibshirani (1993). Another approach which will be considered is to use confidence intervals before, or in addition to, hypothesis testing as an inference tool. A confidence interval approach based on bootstrap replications has been used in diet analysis of haddock *Melanogrammus aeglefinus* by Jiang & Jørgensen (1996).

The test results generally depended on the diet index used. Choice of the most appropriate diet index was not obvious, neither speaking of 'total' indices ($B_i$ and $N_i$) versus individual indices ($WI_i$ and $NI_i$) nor of biomass indices ($B_i$ and $WI_i$) versus number indices ($N_i$ and $NI_i$).

An apparent advantage of the individual indices is that all seals are weighted equally, irrespective of the amount of food found in the stomach and intestines at the time of capture. It was reasonable to assume that the examined seals had similar food biomass requirements. Differences in prey content between individual seals were assumed to be caused by different feeding times and variation in prey biomass from meal to meal. If seals with large prey content had a diet composition which deviated significantly from the other seals, this was assumed to be incidental. The use of individual indices prevent such 'incidental' cases from dominating the results.

A possible disadvantage of individual feeding indices, as applied in the present analyses, is, however, that the $H_0$- distribution of the test statistic Z may be biased when based, i.e., the expectation value E[Z] may be different from zero even if no prey preference is present. This would, e.g., be the case if the prey biomass content of the two prey species considered at a time in a random seal are stochastically independent and exponentially distributed, with expectation values proportional to the abundance of these species in the ocean (Alf Harbitz, unpublished material). In addition, if there are systematic differences in the diet composition dependent on, e.g., the size of a meal, seals with a large amount of prey content should count most in the prey preference analyses.

No feeding index will give a completely or fully realistic picture of dietary composition (see Hyslop 1980). In this work we have chosen to apply several indices, where test results which appeared to be similar for all diet indices are particularly emphasized. An interesting task for future investigations will be to compare analyses based on different indices more thoroughly and hopefully find one appropriate diet index for more simplified analyses.

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**Table 1.** Frequency of occurrence of empty stomachs and intestines, and identified species of prey in non-empty stomachs/intestines of 132 harp seals caught in three areas in the northeast Atlantic in 1993 and 1995. N = number of animals examined.

| PREY ITEMS | PERCENTAGE OCCURRENCE | | | | | |
|---|---|---|---|---|---|---|
| | CAPE KANIN-KOLGUYEV N=97 | | PECHORA SEA N=13 | | FRANZ JOSEF LAND N=22 | |
| | (Stomachs) | (Intestines) | (Stomachs) | (Intestines) | (Stomachs) | (Intestines) |
| Empty | 100.0 | 33.0 | 92.3 | 15.4 | 81.8 | 27.3 |
| Crustacea | | | | | | |
| Amphipoda | | | | | | |
| *Parathemisto libellula* | | | | | 75.0 | 62.5 |
| Unid. amphipod. remains | | 3.1 | | 9.1 | | |
| Euphausiacea | | | | | | |
| *Thysanoessa* sp. | | | | | 5.6 | |
| Decapoda | | | | | | |
| *Sabinea septemcarinata* | | 13.9 | | 9.1 | | |
| *Sclerocrangon boreas* | | | | 9.1 | | |
| *Eualus gaimardii* | | 9.2 | | 9.1 | | |
| *Crangon* sp. | | 6.2 | | | | |
| Unid. decapod. remains | | | | | | 5.6 |
| Unid. crustacea remains | | 35.3 | | 54.5 | | |
| Pisces | | | | | | |
| Clupeidae | | | | | | |
| *Clupea harengus* | | 72.3 | | 72.7 | | |
| Osmeridae | | | | | | |
| *Mallotus villosus* | | 7.7 | | 27.3 | | |
| Gadidae | | | | | | |
| *Gadus morhua* | | 29.2 | | 54.5 | | |
| *Boreogadus saida* | | 1.5 | 100 | 100.0 | 50.0 | 81.3 |
| Cottidae | | | | | | |
| Unid. cottid. remains | | 10.7 | | 36.4 | 25.0 | 25.0 |
| Stichaeidae | | | | | | |
| Unid. stichaeid. remains | | 6.1 | | 27.3 | | |
| Liparidae | | | | | | |
| *Liparis* sp. | | 12.2 | | 36.4 | 25.0 | 43.8 |
| Zoarcidae | | | | | | |
| *Lycodes* sp. | | 6.1 | | 18.2 | | |
| Ammodytidae | | | | | | |
| *Ammodytes* sp. | | 4.6 | | | | |
| Pleuronectidae | | | | | | |
| *Hippoglossoides platessoides* | | 4.6 | | 9.1 | | |
| Unid. pleuronectid. remains | | 3.1 | | | | |
| Unid. fish remains | | 21.5 | | 54.5 | | 25.0 |

**Table 2.** Acoustic resource surveys conducted during feeding ecology studies of harp seals in two sub-areas in the southeastern Barents Sea in February 1993: total average biomass (tonnes) of prey items in two depth strata, above and below 50m.

| AREA | DEPTH (m) | PREY ITEMS | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | HERRING | CAPELIN | COD | POLAR COD | SANDEEL | VARIOUS FISH | TOTAL |
| CAPE KANIN-KOLGUYEV | 0-50 | 6238 | 154 | 34 | 46.5 | 68 | 1.3 | 6541.8 |
| | 50-bottom | 15130 | 375 | 134 | 118 | 145 | 4.5 | 15906.5 |
| PECHORA SEA | 0-50 | | | | 10.8 | | | 10.8 |
| | 50-bottom | 1.8 | | | 6 | | | 7.8 |

**Table 3.** Acoustic resource surveys conducted during feeding ecology studies of harp seals in the northeastern Barent Sea in October 1995: total biomass (tonnes) of prey items in 100m depth strata.

| DEPTH (m) | PREY ITEMS | | | | | |
|---|---|---|---|---|---|---|
| | AMPHIPODS | KRILL | POLAR COD | SNAIL FISH | VARIOUS FISH | TOTAL |
| 0-100 | 16881 | 45580 | 308 | 71 | 48 | 62888 |
| 100-200 | 34651 | 103301 | 779 | 231 | 111 | 139073 |
| 200-300 | 13675 | 44058 | 479 | 275 | 64 | 58551 |
| 300-bottom | 36 | 143 | 1101 | 1 | 165 | 1446 |

**Table 4.** CKK area in February 1993: Diet composition, illustrated by 4 feeding indices (see text for explanation), of harp seals, and relative prey abundance in various depth layers (acoustic estimation) and along the bottom (from demersal trawl hauls).

| %Diet index | bottom fish | capelin | cod | herring | polar cod | shrimp | snailfish | various fish | sand eel |
|---|---|---|---|---|---|---|---|---|---|
| $B_i$ | 22 | 0.6 | 12 | 59 | 0.6 | 3 | | 3 | |
| $N_i$ | 4 | 0.6 | 4 | 74 | 0.4 | 9 | 3 | 4 | |
| $WI_i$ | 10 | 1 | 13 | 49 | 0.5 | 19 | | 7 | |
| $NI_i$ | 5 | 0.9 | 8 | 48 | 0.8 | 27 | 3 | 8 | |
| **%Abundance** | | | | | | | | | |
| 0-50 m | | 2 | 0.5 | 95 | 0.9 | | | 0.02 | 1 |
| 50m-bottom | | 2 | 0.8 | 95 | 0.8 | | | 0.02 | 0.9 |
| 0m-bottom | | 2 | 0.8 | 95 | 0.8 | | | 0.02 | 0.9 |
| bottom | 2 | 0.03 | 0.2 | 92 | 0.03 | 4 | 1 | 0.01 | |

**Table 5.** CKK Area in February 1993: Test results (Z and p values) of pairwise prey preference tests based on 4 different feeding indices for harp seals. The acoustic biomass abundance estimates used are denoted 0m-bottom and include all 5 nm samples integrated. Correspondingly, the number abundance estimates used are denoted bottom and include all demersal trawl hauls integrated. A positive sign of Z indicates preference for the first of the two compared prey species, while a negative sign of Z indicates preference for the latter. $p_{th}$ denotes "theoretical" p-values based on the N(0,1)-distribution, while $p_{boot}$ denotes p-values based on 5000 bootstrap simulations. Tests which are not rejected at a 5% level are in bold italic. See text for further explanations.

| Diet index: | Abundance: | | bott. fish - cod | bott. fish - herring | bott. fish - shrimp | cod - herring | cod - shrimp | herring - shrimp |
|---|---|---|---|---|---|---|---|---|
| $B_i$ | 0m-bottom | Z | | | | 2.4 | | |
| | | $p_{th}$ | | | | 0.019 | | |
| | | $p_{boot}$ | | | | 0.049 | | |
| $WI_i$ | 0m-bottom | Z | | | | 4.6 | | |
| | | $p_{th}$ | | | | <.0002 | | |
| | | $p_{boot}$ | | | | <.0002 | | |
| $N_i$ | bottom | Z | -5.4 | 1.0 | -0.8 | 1.9 | 3.4 | -1.5 |
| | | $p_{th}$ | <.0002 | ***0.33*** | ***0.42*** | ***0.05*** | 0.0007 | ***0.13*** |
| | | $p_{boot}$ | <.0002 | ***0.30*** | ***0.43*** | ***0.10*** | <.0002 | ***0.17*** |
| $NI_i$ | bottom | Z | -6.0 | 2.8 | -3.5 | 4.0 | 3.9 | -6.0 |
| | | $p_{th}$ | <.0002 | 0.0052 | 0.0005 | 0.0001 | 0.0001 | <.0002 |
| | | $p_{boot}$ | <.0002 | 0.0084 | <0.0002 | <.0002 | <.0002 | <.0002 |

**Table 6.** Pechora area in February 1993: Diet composition, illustrated by 4 feeding indices (see text for explanation), of harp seals, and relative prey abundance in various depth layers (acoustic estimation) and along the bottom (from demersal trawl hauls).

| | bottom fish | capelin | cod | herring | polar cod | shrimp | snailfish | various fish |
|---|---|---|---|---|---|---|---|---|
| %Diet index | | | | | | | | |
| $B_i$ [1)] | 9 | 0.5 | 6 | 32 | 47 | 2 | | 4 |
| $N_i$ [1)] | 4 | 1 | 6 | 45 | 33 | 5 | 1 | 4 |
| $WI_i$ | 10 | 0.3 | 3 | 22 | 57 | 4 | | 4 |
| $NI_i$ | 7 | 0.8 | 4 | 29 | 45 | 9 | 0.8 | 5 |
| %Abundance | | | | | | | | |
| 0-50m | | | | | 100 | | | |
| 50m-bottom | | | | 30 | 70 | | | |
| 0m-bottom | | | | 10 | 90 | | | |
| bottom | 16 | 0.6 | 0.3 | 6 | 46 | 30 | 2 | 0.03 |

[1)] One of the 11 seals with prey content is omitted because it constituted about 2/3 of the total prey content.

**Table 7.** Pechora Area in February 1993: Test results (Z and p values) of pairwise prey preference tests based on 4 different feeding indices for harp seals. The acoustic biomass abundance estimates used are denoted 0m-m-bottom and include all 5 nm samples integrated. Correspondingly, the number abundance estimates used are denoted bottom and include all demersal trawl hauls integrated. A positive sign of Z indicates preference for the first of the two compared prey species, while a negative sign of Z indicates preference for the latter. $p_{th}$ denotes "theoretical" p-values based on the N(0,1)-distribution, while $p_{boot}$ denotes p-values based on 10000 bootstrap simulations. Tests which are not rejected at a 5% level are in bold italic. See text for further explanations.

| Diet index: | Abundance: | | bott. fish - herring | bott. fish - polar cod | bott. fish - shrimp | herring - polar cod | herring - shrimp | polar cod - shrimp |
|---|---|---|---|---|---|---|---|---|
| $B_i$ | 0m-bottom | Z | | | | 2.3 | | |
| | | $p_{th}$ | | | | 0.020 | | |
| | | $p_{boot}$ | | | | 0.0006 | | |
| $WI_i$ | 0m-bottom | Z | | | | 2.1 | | |
| | | $p_{th}$ | | | | 0.034 | | |
| | | $p_{boot}$ | | | | 0.030 | | |
| $N_i$ | bottom | Z | -5.8 | -3.8 | 1.0 | 3.1 | 6.0 | 6.0 |
| | | $p_{th}$ | <.0001 | 0.0001 | ***0.33*** | 0.0022 | <.0001 | <.0001 |
| | | $p_{boot}$ | <.0001 | <.0001 | ***0.27*** | <.0001 | <.0001 | <.0001 |
| $NI_i$ | bottom | Z | -3.4 | -2.7 | 1.3 | 2.5 | 3.8 | 5.3 |
| | | $p_{th}$ | 0.0007 | 0.0062 | ***0.19*** | 0.012 | 0.0002 | <0.0001 |
| | | $p_{boot}$ | <.0001 | <.0001 | ***0.17*** | 0.007 | <.0001 | <.0001 |

**Table 8.** Franz Joef Land area in February 1993: Diet composition, illustrated by 4 feeding indices (see text for explanation), of harp seals, and relative prey abundance in various depth layers (acoustic estimation) and along the bottom (from demersal trawl hauls).

| | krill | *Parathemisto* | polar cod | snailfish | various fish |
|---|---|---|---|---|---|
| %Diet index | | | | | |
| $B_i$ | 0.02 | 20 | 62 | 11 | 7 |
| $N_i$ | 0.02 | 19 | 61 | 11 | 8 |
| $WI_i$ | 0.005 | 38 | 43 | 11 | 8 |
| $NI_i$ | 0.005 | 32 | 47 | 12 | 9 |
| %Abundance | | | | | |
| 0-300 m | 74 | 25 | 0.6 | 0.2 | 0.1 |
| 300m-bottom | 10 | 2.5 | 76 | 0.1 | 11.4 |
| 0m-bottom | 74 | 25 | 1 | 0.2 | 0.1 |

**Table 9.** Franz Josef Land Area in October 1995: Test results (Z and p values) of pairwise prey preference tests based on 4 different feeding indices for harp seals. The acoustic biomass abundance estimates used are denoted 0m-bottom and include all 5 nm integrated. Correspondingly, the number abundance estimates used are denoted bottom and include all demersal trawl hauls integrated. A positive sign of Z indicates preference for the first of the two compared prey species, while a positive sign of Z indicates preference for the latter. $p_{th}$ denotes "theoretical" p-values based on the N(0,1)-distribution, while $p_{boot}$ denotes p-values based on 10000 bootstrap simulations. Tests which are not rejected at a 5% level are in bold italic. See text for further explanations.

| Diet index | Abundance: | | *Parath.* - polar cod | *Parath.* - snailfish | *Parath.* - var. fish | polar cod - snailfish | polar cod - var. fish | snailfish - var. fish |
|---|---|---|---|---|---|---|---|---|
| $B_i$ | 0m-bottom | Z | -7.8 | -4.0 | -2.3 | 0.6 | 0.5 | 0.05 |
| | | $p_{th}$ | <.0001 | 0.0001 | 0.019 | ***0.54*** | ***0.59*** | ***0.96*** |
| | | $p_{boot}$ | <.0001 | 0.001 | 0.030 | ***0.55*** | ***0.63*** | ***0.98*** |
| $WI_i$ | 0m-bottom | Z | -5.4 | -3.0 | -2.9 | -0.3 | 0.2 | -0.4 |
| | | $p_{th}$ | <.0001 | 0.0024 | 0.0033 | ***0.76*** | ***0.88*** | ***0.68*** |
| | | $p_{boot}$ | <.0001 | 0.0038 | 0.0050 | ***0.73*** | ***0.91*** | ***0.70*** |

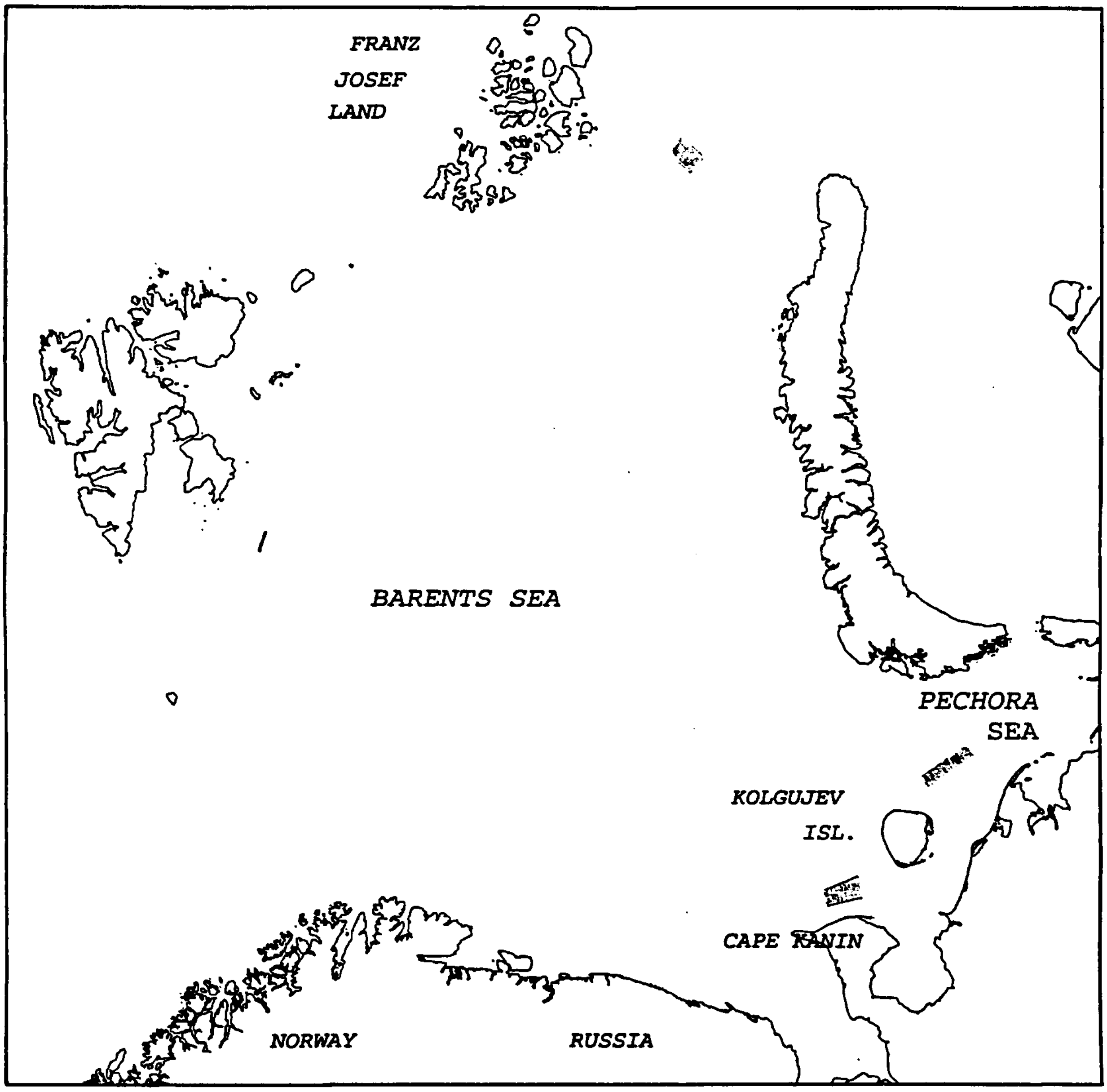


**Fig. 1.** Sampling areas (hatched) in the southeastern (Cape Kanin and Kolgujev Island, denoted CKK in the text, and Pechora Sea) Barents Sea in February 1993, and in the northeastern (Franz Josef Land) Barents Sea in October 1995.

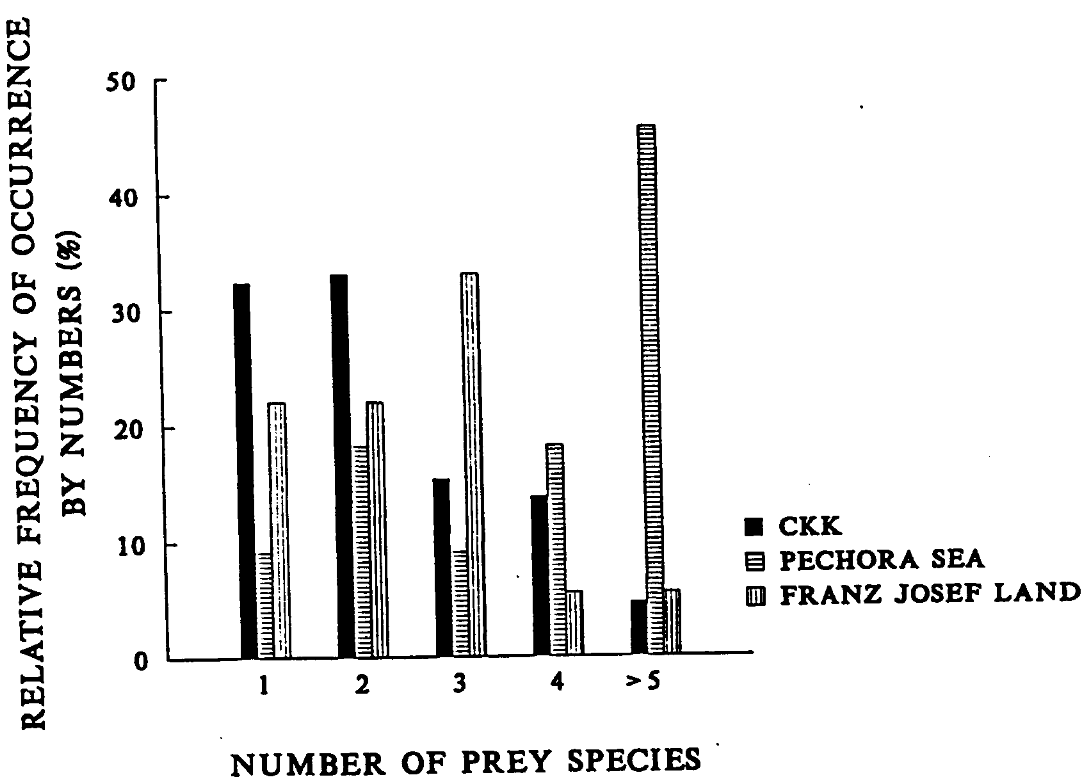


**Fig. 2.** Distribution of the number of prey species found in harp seal intestines sampled in the Barents Sea in two subareas in the southeast (CKK and Pechora Sea) in February 1993 and in one northeastern area in October 1995.

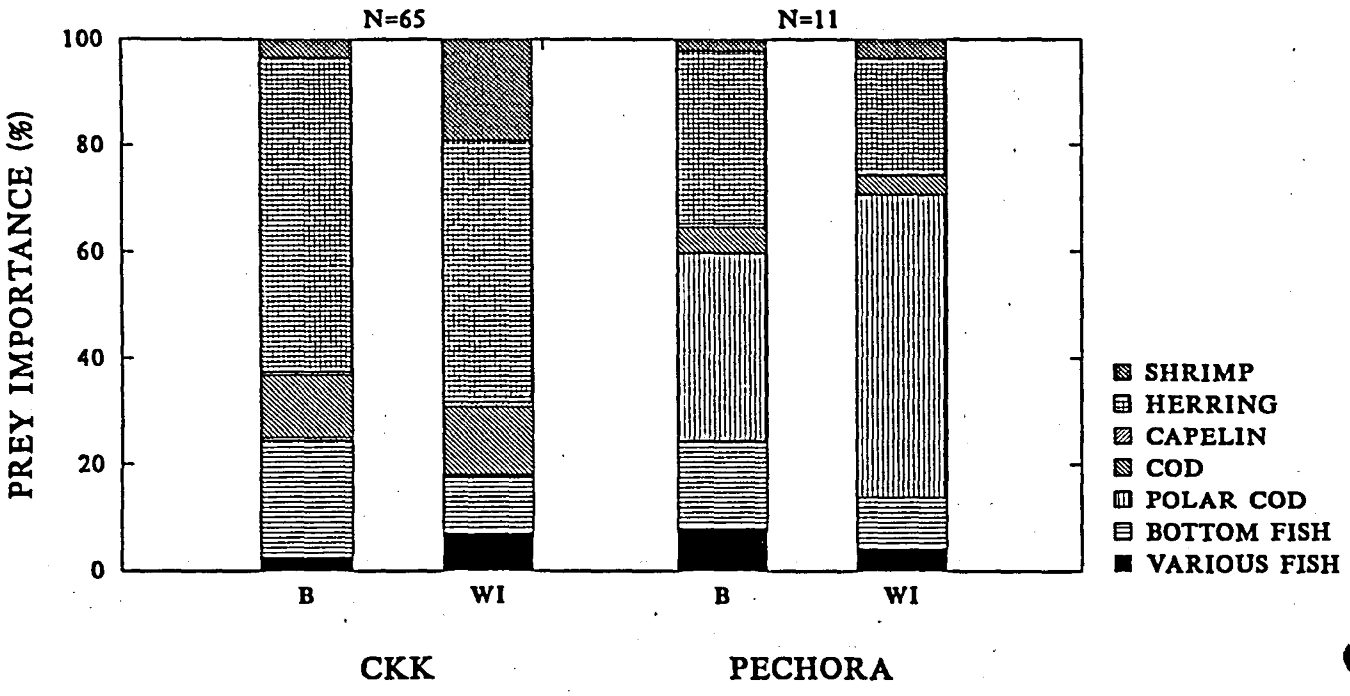


**Fig. 3.** Prey composition, illustrated by two biomass feeding indices (see text for explanation), from intestine contents analyses of harp seals caught in two subareas (CKK and Pechora Sea) in the southeastern Barents Sea in February 1993. N = number of seals examined.

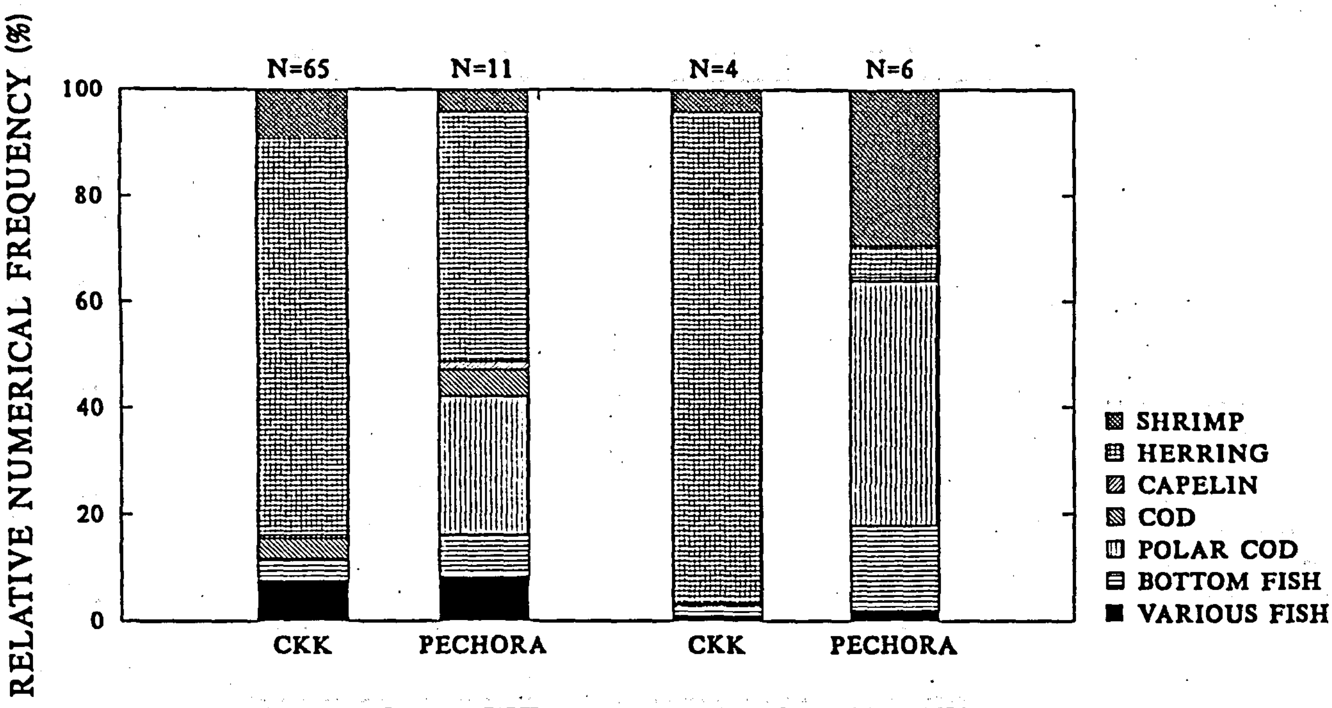


**Fig. 4.** Prey composition, expressed as the relative frequency of occurrence by numbers, in harp seal intestines and in demersal trawl catches in two subareas (CKK and Pechora Sea) in the southeaster Barents Sea in February 1993. N = number of seals or trawl hauls examinied or taken, respectively.

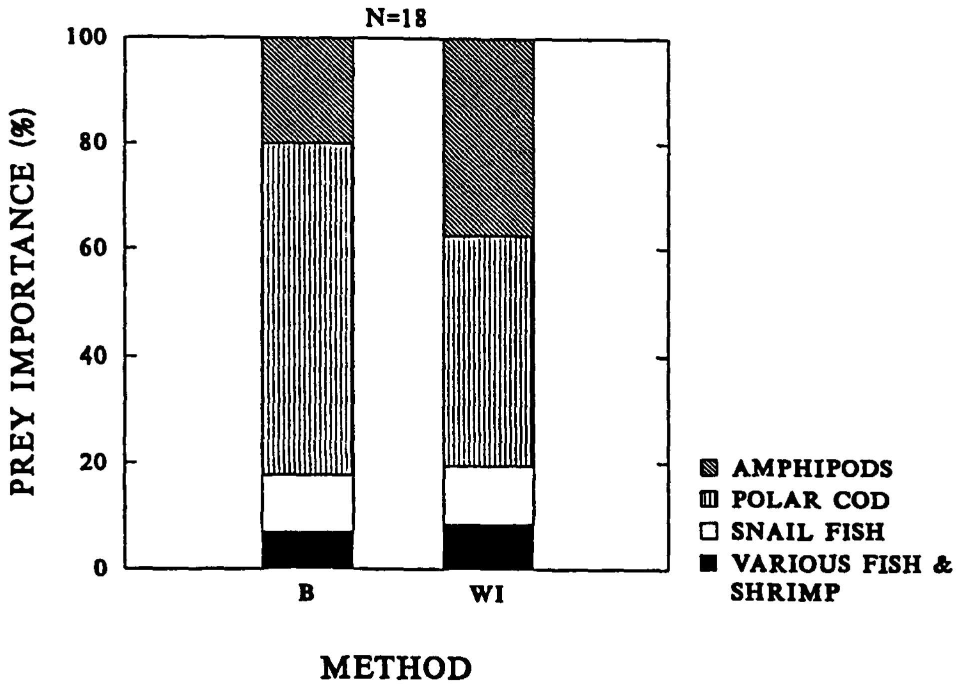


**Fig. 5.** Diet composition, illustrated by two feeding indices (see text for explanation), from stomach/intestine content analyses of harp seals caught in the northeastern Barents Sea (Franz Josef Land area) in October 1995. N = number of seals examined.