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PREY CONSUMPTION BY BARENTS SEA HARP SEALS IN THE PERIOD 1990-2005

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Abstract

The Barents Sea ecosystem has experienced major fluctuations in species abundance in the past 20-30 years. The mechanisms behind these fluctuations are complex and arise from numerous interactions between species and the environment. Previous and present attempts to assess multi-species interactions in the Barents sea ecosystem has resulted in increased focus on the foraging ecology of the most conspicuous high trophic-level predators in the ecosystem. The Barents Sea stock of harp seals Pagophilus groenlandicus is, along with Arctic cod Gadus morhua, considered as the most conspicuous high trophic-level predator in the Barents Sea ecosystem. The abundance and feeding ecology of the Barents Sea stock of harp seals has been monitored the past 15 years. Previous prey consumption estimates suggests that harp seals consume range between 3.3 and 5 million tonnes of prey annually, depending on the choice of input parameters in the bioenergetic model. There were a considerable amounnt of uncertainty attached to the input data in the consumption model, in particular the important harp seal diets during summer (May-August). Also, uncertainty estimates of the prey consumption were not given in the previous study. An important objective of this study was to estimate the uncertainty of the prey consumption estimates by using a standard Monte-Carlo framework; random draws from probability distributions of diet and abundance were performed. Additionally, new diet data from May-July has become available and is included in the analysis. The summer consumption was to a large extent dominated by krill, whereas polar cod also contributed importantly. All sampling were performed in a period with low capelin abundance – this may have influenced the results.

Keywords: Barents Sea, harp seals, summer diet, consumption

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Introduction

The Barents Sea is a shallow continental shelf sea of high productivity and low biological diversity (Hamre 1994, Sakshaug et al. 1994). It serves as a nursery area for several commercially important fish that spawn off western and northwestern Norway. These include herring (*Clupea harengus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) (Bergstad et al. 1987, Gjøsæter 1995, Dragesund et al. 1997). Adult cod and haddock reside in the Barents Sea during the feeding and wintering periods, but migrate to spawn along the Norwegian coast in spring. Capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) complete their life cycles in the Barents Sea (Hamre 1994, Gjøsæter 1995). These two species, along with immature herring, are the main planktivorous fish, whereas cod, haddock and saithe tend to prey on these planktivores (Bergstad et al. 1987). There have been substantial changes in species abundances in the Barents Sea during the last three decades; the most dramatic being the disappearance and subsequent reappearance of herring and capelin (e.g., Røttingen 1990, Hamre 1994, Gjøsæter 1995, 1998, Dragesund et al. 1997, Gjøsæter et al. 1998).

In an attempt to better understand and predict food web dynamics in the Barents Sea ecosystem, a multispecies model (GADGET) is presently being parameterised for the ecosystem (Begley & Howel 2004); minke whales (*Balaenoptera acutorostrata*), cod, capelin and herring are included in the model. Beside cod, the Barents Sea / White Sea stock of harp seals (*Pagophilus groenlandicus*), with a recent abundance estimate of 2.06 million individuals (ICES 2006), is the most conspicuous predator in the Barents Sea ecosystem (Nilssen et al. 2000). Thus, quantification of harp seal feeding dynamics in space and time will be important for the performance of the model.

Harp seals are highly mobile predators that undertake extensive annual feeding migrations within the Barents Sea (Haug et al. 1994; ICES 2006). Changes in the abundance and composition of planktivorous fish in the Barents Sea is likely to have had an impact on the harp seals because these fish species represent potential prey (see Nilssen et al. 2000). Possible influences include effects on prey composition, growth, age at maturity, body condition and migratory patterns of the seals. To understand how harp seals use prey in time and space, and to assess the possible effects from the seals on prey populations in the Barents Sea, knowledge of their resource use under different conditions is needed. The habitat quality in marine ecosystems varies with environmental conditions on a diel, seasonal, and annual basis (e.g., Croxall et al. 1988, Mehl 1989), and harp seals have been shown to exhibit both temporal and geographical variations in food selection (Nilssen et al. 2000).

Bioenergetic models have been used in attempts to assess the possible impact of harp seals on fish stocks in the Barents Sea. Data from studies conducted in 1990-1997 on seasonal changes in diet, distribution and variation in body condition of harp seals were applied to estimate the total consumption of various prey species by the entire Barents Sea / White Sea stock (Nilssen et al. 2000). The model was run with various harp seal activity levels (field metabolic rate) to determine the sensitivity of the consumption estimates to variations in metabolic parameters. Due to large variations in the Barents Sea ecosystem during the research period, i.e. the rise and fall of the capelin stock, the model was run with high and low capelin abundanance. The total annual food consumption by the seals was estimated to be in the range of approximately 3.3-5 million tonnes. The highest food intake occurred in the period June-September. The model predicted that more data on the harp seal diet would be required during this intensive feeding period to improve estimates of the consumption of various prey species.

In May-August, most harp seals are known to be distributed in open waters in central and northwestern parts of the Barents Sea (Haug et al. 1994, ICES 2006), i.e., where also capelin and cod are abundant (see Bergstad et al 1987, Gjøsæter 1998). This may therefore, be the most important period of interaction between harp seals and cod/capelin.

Because data on harp seal diets are very limited during this period, the input in the model was based on the assumption that the diet was equal to that observed in the previous or following months. Also, the diet data obtained in June-July were mainly sampled in pack ice waters in northern parts of the Barents Sea (Svalbard waters), where the potential prey species differ from the southern areas.

In order to improve the estimates of potential capelin and cod consumption by harp seals, relevant diet data are required in open waters in spring and early summer in the central and western Barents Sea. To obtain such data, a new project was initiated in Norway in 2004. The main purpose of this project is to study the feeding habits and the potential consumption of capelin and cod by harp seals when all three species are abundant in open waters in spring and summer in the Barents Sea. The investigations have proceeded over three years (2004-2006) and have covered the southwestern, central and northwestern Barents Sea in spring and early summer. The data obtained supplement similar data obtained in open waters east of Svalbard in July and August in 1996 and 1997.

The overall goal for the project is to improve the data base necessary for an evaluation of the entire ecological impact of harp seals in the Barents Sea throughout the year. The purpose of this particular paper is, however, to focus on the estimation of the total prey consumption by harp seals in the western and northwestern Barents Sea in their intensive feeding period in May-August. The bioenergetic model introduced by Nilssen et al. (2000) will be used to estimate the total prey consumption in the period. The data on diet composition, length composition and body condition used were those sampled in July-August in 1996 and 1997, supplemented with new samples obtained in boat-based surveys in May-July in 2004, 2005 and 2006 (the 2006 data on diet, collected in May-June southeast of Svalbard are, however, not yet available). In addition, condition and length data from Nilssen et al (1997, 2000) were applied. Monte Carlo simulation with respect to diet composition and body condition was used to generate uncertainty estimates.

Material and methods

Recent sampling and examinations of seals

The material to assess diets originate from four dedicated, boat-based research expeditions performed in 1996, 1997, 2004 and 2005. In late July and August in 1996 and 1997, only the ice-filled areas south and east of Svalbard were surveyed (Fig. 1), and 22 (1996) and 17 (1997) seals were captured. In 2004 (May/June) and 2005 (June/July), when much larger areas were covered, very few seals were observed along the coast of Finnmark, and no seals were seen in the open, ice-free areas. In the areas south east of Svalbard, however, very large numbers of seals were observed along the ice edge and 20-30 nautical miles south of this. In these areas, 33 (2004) and 55 (2005) harp seals were shot and sampled (Fig. 1). Additionally, samples of faeces were taken from the haul out sites on the ice.

The seals were shot in the water or on ice floes and immediately brought on board the research vessel for dissection where samples of digestive tracts were frozen. During the 2004 and 2005 surveys, also blubber cores were sampled for later diet studies based on fatty acid analyses (see Falk-Petersen et al. 2004). The lower jaw (with teeth) were collected from each seal for age determination (see Bowen et al. 1983), and weights and body measurements to be used in analyses of condition were recorded as described in Nilssen et al (1997). In the laboratory the stomachs and intestines were cut open after thawing and the contents analysed according to procedures described in Lindstrøm et al. (1998) and Haug et al. (2004).

Estimation of prey consumption by harp seals

A bioenergetic model, proposed by Nilssen et al. (2000) and the modelling framework by Lindstrøm et al. (2002), was used to estimate the consumption of prey i by the Barents sea stock of harp seals in the northern Barents Sea:

$$C_{i} = \sum_{j=1}^{k} \sum_{t=1}^{n} \frac{\left[\lambda_{t} \cdot (GF_{j} + BMR_{j}) + P_{j,t}\right]}{E_{f+u} \cdot E_{i,t}} \cdot R_{i,t} \cdot N_{j,t}$$
(1)

Where C_i is annual prey consumption, summarised across k length groups of seals (j=1,...,19) and n equally spaced time steps (t=1,...,150), E_{f+u} is faecal and urinary efficiency, λ_i is a multiplicative factor, GF_j is growth factor (the additional energy required by immature animals, <151 cm), BMR_j is the basal metabolic rate, $P_{j,t}$ is energy deposition (blubber and foetus growth), $R_{i,t}$ is relative importance of prey i in the whale seal diets, $E_{i,t}$ is energy density of prey i, and $N_{j,t}$ is the number of seals in length group j at time t in the study areas.

The multiplicative factor, which converts from BMR to field metabolic rate, is assumed to be time dependent and range between 2 and 3 (see Markussen et al. 1990; Lager et al. 1994).

A growth factor of $2 \cdot BMR$ was applied on juvenile seals (<151 cm) in order to compensate for a higher *BMR* in growing animals (see Irving & Hart 1957, Folkow & Blix 1989).

Energy deposition

Seals store energy as blubber (Iverson 2002). Thus, the blubber mass (including the skin) and various morphometric measurements, such as length, blubber and girth, are taken in order to assess the body condition of the seals (see Nilssen et al. 1997). In this study the blubber mass data were taken from Nilssen *et al.* (2000).

The energy cost of carrying a foetus in the study period (May-August) is low and was not taken into consideration in this study.

Estimation of energy density in prey

The energy content of prey vary much in both time and space (Mårtensson et al. 1996). Previous modeling attempts (see Nilssen et al. 2000) have suggested that the consumption estimates is sensitive to changes in energy content in the prey. Data from Mårtensson et al. (1996) was used to parameterise polynomial models for energy density:

$$E_{\text{krill}} = \exp^{(3.329 - 1.246 \cdot t + 0.204 \cdot t^{2} + 0.009 \cdot t^{3})}, \quad (\mathbb{R}^{2} = 0.45, p = 0.03)$$
$$E_{\text{capelin}} = 10.81 - 1.58 \cdot t + 0.10 \cdot t^{2}, \quad (\mathbb{R}^{2} = 0.92, p < 0.001)$$
$$E_{\text{codfish}} = 5 \text{ KJ} / \text{ g}$$

 E_{krill} , $E_{capelin}$ and $E_{codfish}$ are the energy densities (KJ/g) of krill, capelin and cod fish, respectively, and t is month. The energy density of krill was applied to other crustaceans as well, whereas the energy density of cod fish was applied to the other fish groups (flat fish and other fish). Because there was no significant time effect on the energy density of codfish, the mean energy density was used.

Uncertainty estimation

Standard Monte-Carlo methods were used estimate some of the uncertainty in the prey consumption estimates. We ran 1000 Monte-Carlo simulations with respect to three input variables:

1. Harp seal abundance $(N_{i,t})$.

Thousand normally distributed abundance estimates were generated for harp seals of age 0 (pups of the year, N_0) and 1+ (one year old and older animals, N_{1+}). We used the parameterisation applied in the population model used to assess the status of the stock by the Joint ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP, see ICES 2006). We assumed the entire harp seal stock was present in the northern part of the Barents Sea in May-August (see haug et alø. 1994, ICES 2006).

2. Diet composition $(R_{i,t})$.

The diet data sampled in 1996/1997 and 2004/2005 were bootstrapped 1000 times, thus generating a 1000*7 matrix for each month. Due to lack of diet data in May, we assumed that the harp seals feed upon the same prey in May as in June.

3. Multiplicative factor (λ_t)

There is no data on the field metabolic rate of free-living harp seals as far as we know. In this study λ_t was treated as a log-normal variable over simulations, $\log \lambda \sim N(\mu, \sigma^2)$, where μ and σ were set to 0.65 and 0.2, respectively.

Results and Discussion

The current total stock size of Barents Sea harp seals has been estimated to comprise 2.064.600 (95% conf.int. 1.486.520 – 2.633.480) N₁₊ animals with an annual pup production (N₀) of 360.880 (95% conf.int. 298.600 – 423.160) animals (ICES 2006). This estimate was used in the present analyses, and the animals were distributed on length groups based on the length compositions observed in the assumed randomly collected scientific catches obtained in the northern areas of the Barents Sea in the entire period from 1990 to 2005 for the N₀ group and in the samplings performed in 1996, 1997, 2004 and 2005 for the N₁₊ animals (Fig. 2). The N₀ group included samples taken also in September and October (see Nilssen et al. 1997, 2000) - this may explain the large size range of the group.

Previous observations have shown that blubber thickness and condition of harp seals vary on a seasonal basis (see Nilssen et al. 1997): the animals are generally thin in spring and early summer (May–June) - their condition improves over the summer, and the seals are quite fat by September–October. The energy stores built up during the summer and autumn are maintained until February, but then the seals become thinner as the stores of

blubber decrease rapidly during the breeding and moulting periods (March-June). The presented results on seasonal changes in fat deposition (Fig. 3) confirms previous observations: The animals appears still to be using of their deposited energy stores in May – positive deposition of fat reserves starts slowly in June and increases substantially in July/August.

In the study period (May-August), most harp seals are known to be distributed in open waters in central and northwestern parts of the Barents Sea (Haug et al. 1994, ICES 2006), i.e., where also capelin and cod are abundant (see Bergstad et al 1987, Gjøsæter 1998). This may therefore, be an important period of interaction between harp seals and cod/capelin. Because data on harp seal diets has been very limited during this period, the input in previous model runs has been based on the assumption that the diet was equal to that observed in the previous or following months (Nilssen et al. 2000). Also, the diet data obtained in June-August were mainly sampled in pack ice waters in northern parts of the Barents Sea (Svalbard waters), where the potential prey species differ from the southern areas.

The new diet data (from 2004 and 2005) were collected in order to improve the estimates of prey consumption by harp seals in open waters in spring and early summer in the central and western Barents Sea. An important purpose of these new data collections were to study potential consumption of capelin and cod by the seals when all three species are abundant in open waters in spring and summer in the Barents Sea. The new data, obtained supplement similar data obtained in open waters east of Svalbard in July and August in 1996 and 1997, and used in the first model runs designed to estimate the annual consumption by harp seals in the Barents Sea (see Nilssen et al. 2000).

The results indicate a harp seal summer diet which restrict their consumption almost exclusively to krill and polar cod, while other gadoids and capelin seems to be of very little importance at this time of the year (Fig. 4). This is in good agreement with suggestions made by Nilssen et al. (2000) that krill is a very important source of food for harp seals during the period May-August. This food item occurred in significantly higher amounts in the seal consumption than any other prey species except for July when polar cod dominated (see Fig. 5). It should be kept in mind that all months were not sampled in the same year or area: Late July and August were sampled in 1996-1997 and considerably further to the north (due primarily to different ice conditions) than the 2004/2005 samples which were obtained in June and early July. Certainly, this may have effected the diet compositions. The present model predicts somewhat lower consumption in June/July, but higher in August, than the previous model used by Nilssen et al. (2000).

Nilssen et al. (2000) concluded that the composition of the biomass consumed annually by harp seals in the Barents Sea varied considerably between years with large capelin abundance and years when this planktivorous fish stock was at a low level – for example it was suggested that the seals increased their consumption of polar cod when capelin were scarce. In both recent study periods (1996/1997 and 2004/2005) the capelin stock was at a very low level (Gjøsæter 2006). This may certainly have influenced the observed seal diets – so far no summer samples are available in periods with good capelin abundance in the Barents Sea.

As in previous samplings, also the new data wetre obtained from animals taken near the ice edge. Although the surveys in 2004-2006 revealed very scarce occurrence of harp seals in open waters in May-July, the possibilities that the animals occur and feed in areas without ice cannot be ruled out. If the food they rely on here is different from what we have observed in the present study (primarily krill and polar cod) is difficult to decide with the diet study methods used. However, blubber profiles and samples of all potential prey animals were secured during field work. When these have been analysed for fatty acid compositions (see Falk-Petersen et al. 2004), we may be in a better position to answer these important questions.

Other important work in the future will be to to make the applied consumption model predictive, and to implement the prey consumption by the Barents Sea stock of harp seals into the stock assessment model of important fish species (e.g. spring spawning herring and capelin).

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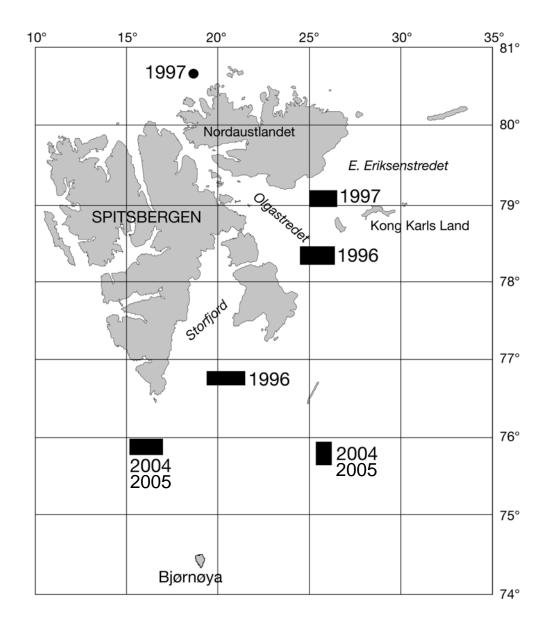


Figure 1. Sampling areas (filled) of harp seals in the northern Barents Sea in May-August 1996, 1997, 2004 and 2005.

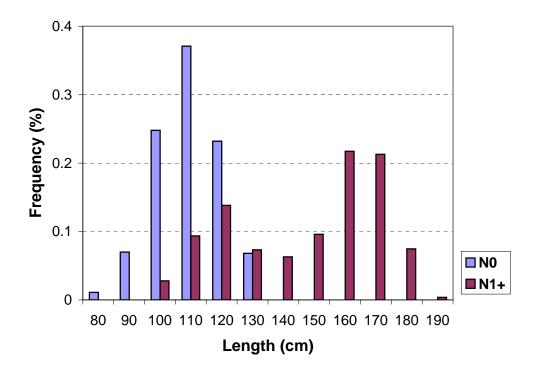


Figure 2. Length distribution of the Barents stock of harp seals, determined from animals obtained in assumed random, scientific catches. N_0 and N_{1+} are pups and one year and older animals, respectively.

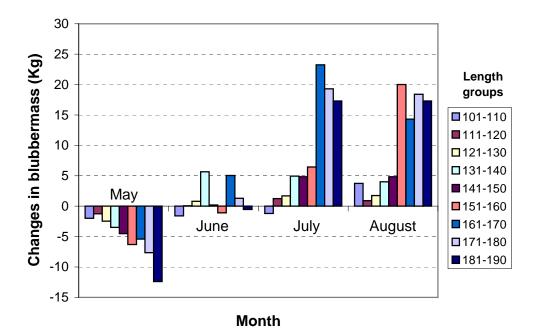


Figure 3. Monthly changes in blubber mass (kg) of the Barents Sea stock of harp seals in the period May-August. The blubber mass data were taken from Nilssen et al. (1997, 2000).

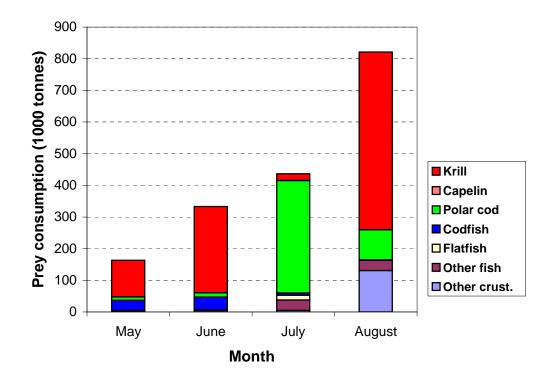


Figure 4. Total prey consumption (1000 tonnes) by the Barents Sea stock of harp seals in the period May-August.

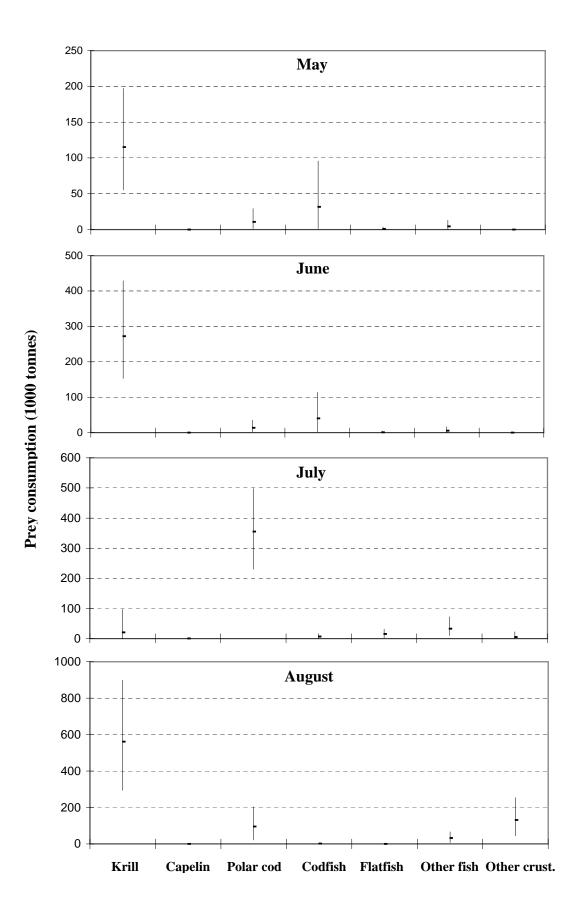


Figure 5. Prey consumption (1000 tonnes) by the Barents Sea stock of harp seals in the northern Barents sea in May-August. The mean consumption estimates are plotted with 95% confidence intervals, determined from 1000 bootstrap replicates.