Food consumption estimates of Barents Sea harp seals

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ABSTRACT

The consumption of various prey species, required by the Barents Sea harp seal (*Phoca groenlandica*) stock in order to cover their energy demands, has been estimated by combining data on the energy density of prey species and on seasonal variations in the energy expenditure and body condition of the seals. Data on diet composition and body condition were collected in the period 1990-1996 by sampling harp seals during different seasons, in various areas of the Barents Sea. All diet composition data were based on reconstructed prey biomass, and adjustments were made for differences in digestibility of crustaceans and fish. The number of seals representing different age and sex groups were calculated for the entire population, and the monthly food requirements were estimated.

In 1998, the total Barents Sea harp seal stock was estimated to comprise 2.22 million seals based on a mean production of 301,000 pups. After adjustments for a pup mortality of 30% its total annual food consumption was estimated to be in the range of 3.35-5.05 million tonnes (depending on choice of input parameters). Assuming that there are seasonal changes in basal metabolic rate associated with changes in body mass, and that the field metabolic rate of the seals corresponded to two times their predicted basal metabolic rate, the annual food consumption of the Barents Sea harp seal stock was estimated. If capelin (*Mallotus villosus*) was assumed to be abundant, the annual total consumption was estimated to be 3.35 million tonnes, of which 1,223,800 tonnes were crustaceans, 807,800 tonnes were capelin, 605,300 tonnes were polar cod (*Boreogadus saida*), 212,400 tonnes were herring (*Clupea harengus*), 100,500 tonnes were cod (*Gadus morhua*) and 404,200 tonnes were "other fish". A very low capelin stock in the Barents Sea (as it was in the period 1993-1996) led to switches in seal diet composition, with increased consumption of polar cod (from ca. 16%-18 % to ca. 23%-25 % of total consumption), other gadoids (dominated by cod, but also including haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*)), herring, and "other fish". Using the same set of assumptions as in the previous estimate, the total consumption would have been 3.47 million tonnes, divided between various prey species as follows (in tonnes): polar cod 876,000, codfish (cod, saithe and haddock) 359,700, "other fish" 618,800, herring 392,500, and crustaceans 1,204,200. Overall, the largest quantities of food were estimated to be consumed in the period June-September.

In 1999, the total Barents Sea harp seal stock size was estimated to be 2.18 (95% CI, 1.79 to 2.58) million animals, which would give an annual food consumption in the range of 2.69 – 3.96 million tonnes (based on upper and lower 95% confidence limits and adjusted for a pup mortality rate of 0.3) if capelin is assumed to be abundant.

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Introduction

Increased attention is being directed towards the study of multispecies interactions for the management of marine resources. This has encouraged studies of the feeding ecology of important top predators, including marine mammals. The harp seal (*Phoca groenlandica*) is the most abundant seal species in the Barents Sea (Fig. 1). Consequently, studies of its role as a top predator is considered important within a management context (Anonymous 1991). The harp seal is now included in a multispecies model (MULTSPEC) which may provide the basis for future management of marine resources in the area (Bogstad *et al.* 1997). Bioenergetic models have been used in previous attempts to assess the possible impact of Barents Sea harp seals on fish stocks (Markussen and Øritsland 1991; Nordøy *et al.* 1995a). The energy requirements of individual seals have been estimated and subsequently extrapolated to the entire seal stock. However, information on the feeding habits of Barents Sea harp seal was limited when these analyses were performed.

Studies of harp seal feeding habits were carried out in 1986-1988 (Haug *et al.*1991; Lydersen *et al.* 1991; Nilssen *et al.* 1992), and more comprehensive studies have continued in the period 1990-1996 to assess the feeding habits of Barents Sea harp seals throughout the year (Haug and Nilssen 1995; Nilssen 1995; Nilssen *et al.* 1995a,b, 1998a,b; Lindstrøm *et al.* 1998). Seasonal variations in the distribution (Haug *et al.*1994) and body condition of the seals (Nilssen *et al.* 1997) have also been evaluated (Fig. 2).

Fig. 1:
Moulting harp seals occur in great abundance in the loose pack ice of the southern Barents Sea in March, April and May.

Photo:Kjell Arne Fagerheim

Fig. 2:
The condition of harp seals is monitored by measuring blubber thickness.

Photo: Tore Haug

The aim of the present study was to apply the new knowledge concerning seasonal changes in feeding habits, distributions and variations in body condition of Barents Sea harp seals, to estimation of the consumption of different prey species by the seal stock. Different assumptions concerning the energy requirements for activity and basal metabolic rate were used in order to determine the sensitivity of the consumption estimates to variations in metabolic parameters.

MATERIAL AND METHODS

Sampling of seals

The sampling of seals accounted for the seasonal migration pattern of Barents Sea harp seals (Fig. 3) (Chapskii 1961; Benjaminsen 1979; Haug *et al.* 1994; Nordøy *et al.* MS 1995b). Harp seals, taken as by-catch in gill net fisheries were collected in coastal areas of northern Norway in March and April. Harp seals were sampled in the southern Barents Sea (the East Ice) and White Sea from February to early May, and along the pack-ice belt in the northern parts of the Barents Sea between June and October (Table 1). Details on methods of capture, condition measurements, age determination, and the laboratory methods used for analyses of stomach and intestinal contents are given in Haug *et al.* (1991) and Nilssen *et al.* (1995a,b, 1997).

Model inputs and assumptions

Modelling strategy

The energy of the food is converted to heat or mechanical work through oxidative processes, or is deposited in tissues through growth, stored in blubber deposits and, in pregnant females, transferred to the growing foetus and thereafter to the growing pup during lactation. Energy is also transferred to heat during conversion of food to blubber, and when stored blubber is being mobilized. The sum of these energy requirements, the metabolizable energy, is, however, less than the gross energy intake, because energy is also lost in the urine and faeces (Lavigne *et al.* 1982).

The total consumption of the various prey items required by the harp seals to meet their energy demands is estimated by combining information on diet composition (Nilssen *et al.* 1995a,b, 1998a,b; Lindstrøm *et al.* 1998), with information on the energy density of various prey species (Pechenik *et al.* 1973; Mårtensson *et al.* 1996). Diet composition data were calculated as reconstructed prey biomass, and adjustments were made for differences in digestibility between crustaceans and fish (Mårtensson *et al.* 1994). The number of seals belonging to different age and sex groups were calculated, and monthly food requirements modelled based on dietary data, the energy densities of prey, and data on energy requirements.

Stock size, age composition and length groups
The total stock size of Barents Sea harp seals has been estimated to comprise 2.22 million seals, based on a mean production of 301,000 pups (ICES 1999). This estimate was used in the present study. We furthermore assumed that the number of pups (0-year old animals) would be 210,700 (adjusted for a pup mortality rate of 0.3), and that all pups belonged to the 101-110 cm length group.

The age-composition of 1,189 male and 508 female harp seals (aged 1+ years) taken by Norwegian sealers in the East Ice moulting lairs in April-May 1995 showed a very low representation of one and two years old animals (Nilssen *et al.* 1998a). The year classes born during the late 1980s were also very scarce, in particular the 1987 and 1988 year classes (Kjellqwist *et al.* 1995). We assumed that seals 6 years old (approximately 150 cm standard body length) and younger were immature. Based on the observed 1995 age-composition (Nilssen *et al.* 1998a) and available length at age data, the immatures (excluding the pups) were calculated to comprise 20% (384,400 animals) of the stock. These were assumed to be distributed with 96,100 animals in each of the four body length groups 111-120,...,141-150 cm.

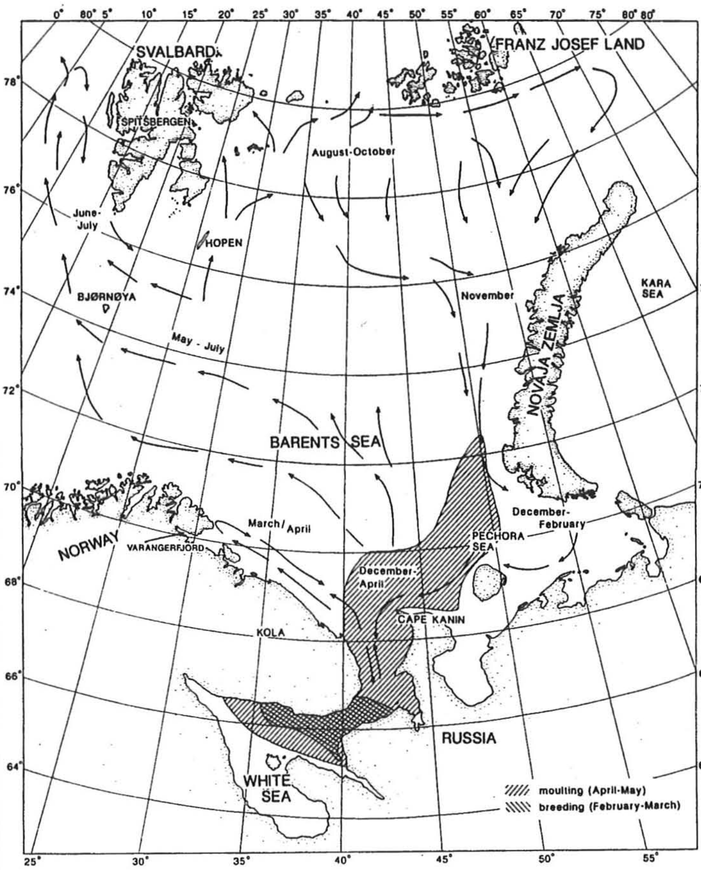


Fig. 3: *Annual migration pattern of the Barents Sea harp seals (from Haug et. al. 1994)*

We assumed that the number of pregnant females were equal to the 301,000 born pups and that they were equally distributed with 75,250 animals in the four body length groups 151-160,...,181-190. Non-pregnant females were treated as males, and together they were calculated to comprise 1,236,600 animals, which yields 309,150 animals in each of the four body length groups longer than 150 cm.

Seasonal variations in body and blubber masses
Previous observations suggest that both blubber thickness and condition of adult harp seals vary on a seasonal basis (Sivertsen 1941; Sergeant 1973, 1991). Recent analyses of harp seal body condition in the Barents and White Seas confirm this seasonality (Nilssen *et al.* 1997). These new body condition studies revealed that harp seals generally are in a poor condition in spring and early summer (May-June). Condition improves during the course of the summer, and the seals are in good condition in August (Nilssen *et al.* MS 1998b) and during the autumn. The energy

Table 1: Information about harp seals from collections along the Norwegian coast and in the Barents and White Seas during 1990-1996. The data on diets include relative composition of the diet based on stomach and intestine contents. The condition data include total body mass, standard length, girth, dorsal bubber thickness and blubber mass.

Year	*Month*	*Area*	*Data collected*	*Number of seals*
1990	*Sep*	*East of Svalbard*	*Diet, condition*	*22*
1991	*Jun*	*East of Hopen*	*Diet, condition*	*239*
1991	*Sep*	*East of Svalbad*	*Diet, condition*	*40*
1992	*Mar*	*Norwegian coast*	*Diet, condtion*	*25*
1992	*Apr*	*Norw. coast/East Ice*	*Diet, condition*	*329*
1992	*Oct*	*East of Svalbard*	*Diet, condition*	*50*
1993	*Feb*	*SE Barents Sea*	*Diet, condition*	*110*
1994	*May*	*White Sea*	*Condition*	*52*
1995	*Mar*	*East Ice*	*Condition**	*40*
1995	*Apr*	*Norw. coast/East Ice*	*Diet, condition**	*82*
1995	*Oct*	*East of Svalbard*	*Diet, condition**	*22*
1996	*Mar*	*Norwegian coast*	*Diet, condition**	*38*
1996	*Apr*	*East Ice*	*Condition**	*75*
1996	*Jul/Aug*	*East of Svalbard*	*Diet, condition*	*22*
Total				***1146***

**data include determination of total blubber mass*

stores built up during the summer and autumn seem to decrease slowly between October and February, after which the seals rapidly become leaner as the stores of blubber decrease during the breeding period (late February - early March). Condition seems to remain relatively constant in the short period between lactation and moult (late March - early April), but the stores of blubber decrease again during moulting, which takes place between late April and mid-May (Nilssen *et al.* 1997).

The condition data used in the present study relate to total sculp mass (blubber with skin) for samples collected in March, April and October 1995, and March/April 1996. In order to provide estimates for other periods, blubber mass ($M_{blubber}$) was estimated from calculated correlations between standard body length (SL) and core mass (M_{core}), where total body mass (M) is the sum of M_{core} and $M_{blubber}$. The relationship between standard body length and core mass could be described by the equation:

$$M_{core} = 2.7747 \cdot \exp^{0.0181\ SL},\ r^2 = 0.76$$

If total body mass of the animals is known, and assuming that the equation is valid for all seasons, the blubber mass can be estimated for all length groups. Mean blubber masses were calculated for all length groups 101-110, ...,181-190 cm, and for all months for which data were available. Linear interpolations between months were carried out in periods where data were lacking (Table 2). The energy density of blubber (wet weight) was taken as 35 kJ/g (Nordøy and Blix 1985).

A similar procedure was used for calculation of total body masses for seals in all length groups (Table 3).

Basal Metabolic Rate (BMR)

The basal metabolic rate (BMR) of harp seals appears to correspond to that predicted by Kleiber (1975), i.e. about $3.4 \cdot M^{0.75}$ (w) (e.g., Gallivan 1981; Gallivan and Ronald 1981; Renouf and Gales 1994). Thus, BMR is proportional to $M^{0.75}$, and since seasonal variations in body mass were large for all length groups, the model was run under two assumptions for BMR: a) the energy required for BMR was based on the

Table 2: Average blubber masses[1] (kg) of harp seals, for each length group (cm) and month, based on data collected in 1990-1996 in the Barents Sea.

	Months											
Length Groups	*Jan*	*Feb*	*Mar*	*Apr*	*May*	*Jun*	*Jul*	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
101-110	*18*	16	20	13	11	9	*7.8*	6.6	*15.3*	24	*22*	*20*
111-120	*20.8*	20	19	16.9	15.6	14.4	*15.7*	16.9	17.5	23.1	*22.4*	*21.6*
121-130	*22.4*	22	26.8	20.5	15.7	15.6	*17.3*	*19*	20.8	23.6	*23.2*	*22.8*
131-140	*27.2*	24.6	27.2	25.8	12.5	18.8	*23.8*	28.7	31.8	35	*32.4*	*29.8*
141-150	*42.6*	42	33.3	30.4	*25.9*	21.4	*26.3*	*31.1*	36	44.5	*43.8*	*43.2*
151-160	*65.8*	64.3	37.8	35.3	31.4	22.7	*29.2*	35.6	69.2	70.3	*68.8*	*67.3*
161-170	*75.8*	73.8	43.6	34.9	37.2	24.1	*47.3*	70.6	75.9	81.6	*79.8*	*77.8*
171-180	*90.5*	87.1	46.2	38.1	39.5	22.8	*42.1*	61.4	78.9	100.6	*97.5*	*93.5*
181-190	*70.4*	61.5	52.7	47.5	41.1	22.7	*40*	*57.3*	74.6	96.9	*79.2*	*79.2*

[1]Linear interpolations between months (in italics).

Table 3: Average total body masses[1] (kg) of harp seals, for each length group (cm) and month, based on data collected in 1990-1996 in the Barents Sea. Annual mean masses for each length group (cm) are also given.

	Months												
Length Groups	*Jan*	*Feb*	*Mar*	*Apr*	*May*	*Jun*	*Jul*	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*	*Mean Masses*
101-110	*39*	35.6	40	30	*29*	27.9	26.5	24	31	49	*45.6*	*42.3*	*35*
111-120	*43.7*	42.7	40	39	*38.3*	37.7	*38.7*	39.7	41.6	46.9	*45.7*	*44.7*	*41.6*
121-130	*49.1*	48.6	55	48.5	43.7	42.7	*44.5*	*46.2*	48	50.7	*50.1*	*49.6*	*48.1*
131-140	*60*	57	62	56.3	45.3	52.6	*56.9*	61.2	65	*68.8*	*66*	*63*	*59.5*
141-150	*86.8*	81	84.1	67	*63.9*	60.7	*65.1*	*69.6*	74	104.3	*98.4*	*92.6*	*78.9*
151-160	*112.1*	113	94.7	83.6	78.4	69.5	*76.3*	83	116	110	*110.7*	*114.4*	*96.6*
161-170	*131.7*	129	105.1	90.8	92.9	80	121	128	132.3	139.9	*137.2*	*134.5*	*118.5*
171-180	*158.9*	155	112.1	103.4	107.2	88.6	128	126	147.1	170.4	*166.5*	*162.7*	*135.5*
181-190	*145.3*	135.8	126.2	121.5	121.6	103	*119.6*	*136.3*	153	174	*164.4*	*154.9*	*138*

[1]Linear interpolations between months (in italics).

mean M for each length group in each month, and b) the energy required for BMR was based on the annual mean M for each length group (Table 3).

Field metabolic rate (FMR)

The field metabolic rate (FMR) of free-living harp seals in the Barents Sea has not been examined, but energy requirements of various species of adult/subadult captive and wild, unrestrained phocid seals, including captive harp seals, appears to correspond to between 1.7 and 3 times the BMR (e.g., Gallivan 1981; Markussen *et al.* 1990; Castellini *et al.* 1992; Lager *et al.* 1994; Reed *et al.* 1994). Based on this, the model was run under the assumptions that FMR corresponds to either 2 or 3 times BMR throughout the year, in order to assess the effect of variations in energy expenditure. In addition, we used variable multiplicative factors, to account for monthly variations in energy expenditure. These factors were based on subjective evaluations of energy requirements where we assumed that metabolic rates were higher (3 · BMR) during reproduction (e.g., Reilly 1989; Reilly and Fedak 1991; Kovacs *et al.* 1996) in March and lower (1.5 · BMR) during the moult in May (e.g., Ashwell-Erickson *et al.* 1986; Worthy *et al.* 1992). The following factors were chosen for the twelve months January through December: 2.5; 2.5; 3; 2.5; 1.5; 2; 2.5; 2.5; 2.5; 2.5; 2.5 and 2.5.

Growth
The resting metabolic rate of juvenile harp seals appears to be two times the BMR predicted according to Kleiber (1975) (e.g., Irving and Hart 1957; Folkow and Blix 1989). We assumed that the excess energy metabolism reflects the energy required for growth, and we have consequently added a growth factor corresponding to $3.4 \cdot M^{0.75}$ (W) to the predicted BMR for all length groups less than 151 cm (immature animals) to account for such growth. This seems to be valid, as judged from the results obtained in studies of free living ringed seals (*Phoca hispida*) (Lydersen and Hammill 1993), and in captive harbour seal (*Phoca vitulina*) pups (Markussen *et al.* 1990). We assumed that no extra energy was required for growth in adult seals (animals longer than 150 cm).

Foetal growth
We assumed that foetal growth resulted in a foetal body mass of 10 kg in early March. Growth was assumed to be exponential, and occurring mainly in January and February. The energy density of the foetus was assumed to be similar to minke whale foetuses, and constant at 3.8 kJ/g (Nordøy *et al.* 1995c). Pregnant females were assumed to use 130 MJ to meet the requirements of foetal growth in each of the months of January and February. This value includes both the heat of gestation and the energy content of the foetus.

Lactation
Energy losses incurred by females during lactation were not included specifically in the model. This is because the energy required for this purpose is mainly drained from blubber deposits (Lydersen and Kovacs 1996), so these energy requirements will largely be reflected in the change in blubber mass of females during lactation.

Urine and faeces
The metabolizable energy represents approximately 92% of the digestible energy, the remaining 8% of which is assumed to be lost in the urine (Lavigne *et al.* 1982). In addition, energy is lost in the faeces. This energy loss corresponds to about 8% of the energy content of fish and about 18% of the energy content of crustaceans (Nordøy *et al.* 1993; Mårtensson *et al.* 1994). Thus, only between 74% and 84% of the energy content of a meal is available for body growth and energy expenditure. This was taken into account in the model.

Feeding habits of harp seals
Our knowledge concerning the feeding habits of harp seals in winter (November-January) and in summer (July-August) is still limited. The decline in condition in spring and early summer (Nilssen *et al.* 1997) suggests that energy intake decreases during this period. The observation that harp seals improve in condition from June to August/September (Nilssen *et al.* 1997; Nilssen *et al.* MS 1998b) indicates that the summer and autumn are periods of intense feeding. The slow decrease in body mass during October-February (Table 3), suggests that feeding is reduced in this period. Such seasonal changes in food intake have been documented in captive harp seals (Lager *et al.* 1994) and grey seals (Nordøy and Blix 1988), maintained under simulated natural light-darkness cycles.

Tables 4 and 5 summarize data on harp seal diets in terms of bulk biomass, based on studies carried out in the Barents Sea and in coastal areas of northern Norway during the period 1990-1996 (Nilssen *et al.* 1995a,b; 1998a; Lindstrøm *et al.* 1998). The Barents Sea stock of capelin (*Mallotus villosus*) collapsed in 1992/1993 (Hamre 1994; Gjøsæter 1995). For this reason, two versions of diet composition were used as inputs in the model. Common dietary compositions were used where adequate data were lacking: July and August were based on observed diets in July and August 1996 (Nilssen *et al.* MS 1998b); the diet in November and December, in periods with capelin available in the ecosystem, was assumed to be similar to the diet observed in late October 1992 (Lindstrøm *et al.* 1998). The diets in November, December and January were assumed to be equivalent to the diet observed in the Pechora Sea in February (Lindstrøm *et al.*

Table 4: Relative harp seal diet composition (percentage wet weight) based on bulk biomass, with capelin abundant in the Barents Sea ecosystem,

					Prey species					
Months	***krill***	***Parath lib.***	***other crust***	***capelin***	***herring***	***cod***	***saithe***	***haddock***	***polar cod***	***other fish***
January			3		61	20			10	6
February			3		61	20			10	6
March				99		1				
April			42	46		10				2
May			42	46		10				2
June			22	18					18	42
July	61	1							37	1
August	61	1							37	1
September	5	47	11	5					10	22
October		20							62	18
November				91					8	1
December				91					8	1

Table 5: Relative harp seal diet composition (percentage wet weight) based on bulk biomass, with a depleted capelin stock in the Barents Sea ecosystem.

					Prey species					
Months	***krill***	***Parath lib.***	***other crust***	***capelin***	***herring***	***cod***	***saithe***	***haddock***	***polar cod***	***other fish***
January			3		61	20			10	6
February			3		61	20			10	6
March			2	6	1	50	2	10		29
April			2	6	1	50	2	10		29
May			42		10	10	10	10		18
June			40						18	42
July	61	1							37	1
August	61	1							37	1
September	5	47	11						15	22
October		20							62	18
November			2		37	6			42	13
December			2		37	6			42	13

1998) when the capelin stock was at a low level.

Energy densities of prey

The energy densities of prey species were taken from Mårtensson *et al.* (1996). In months with several observations of energy densities for a given prey species, mean values were used. For "other crustaceans" the energy density for krill was used. For saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), for which data were lacking, the energy density for cod (*Gadus morhua*) was used, and for "other fish" the energy density was assumed to be 5 kJ/g. Energy density values for polar cod (*Boreogadus saida*) were based on regressions between fat content and energy density (Pechenik *et al.*

1973). The energy densities for polar cod varied between 5.5 and 7.8 kJ/g, with the highest values in the period July-December (J. S. Christiansen, Norwegian Institute of Fisheries and Aquaculture, Tromsø, Norway, pers.comm.).

RESULTS

Estimates of total food consumption

The total food consumption of the Barents Sea harp seal stock (assumed to comprise 2.13 million seals including adjustments for a pup mortality of 30%) was estimated to be in the range of 3.35- 4.84 million tonnes (depending on choice of input parameters) with capelin abundant in the ecosystem in the Barents Sea. With a very low capelin stock in the Barents Sea, the estimated food consumption increased slightly, to values ranging between 3.47-5.05 million tonnes (Tables 6 and 7).

When calculations of BMR were based on annual average body masses for each length group, consumption estimates increased by approximately 1% to 2.5%, compared to a situation where calculations of BMR were based on monthly variations in body masses for each length group throughout the year.

When the value for field metabolic rate was increased from 2 times BMR to 3 times, the consumption estimates increased by between 40.6% and 41.9%. When the consequences of monthly variations in body mass for the BMR estimates were taken into account, the total food consumption was found to be approximately 3.35 million tonnes with FMR = 2 · BMR, compared to an estimated consumption of approximately 4.72 million tonnes with FMR = 3 · BMR. Running the model with both a BMR and FMR that varied throughout the year resulted in consumption estimates 16.7% to 17.4% higher than doing so on the assumption of a variable BMR and a fixed FMR of 2 · BMR (Table 6).

The model predicted that the largest quantities of food were consumed in the period June-September. Use of variable versus constant BMR input values resulted in minor differences but the estimated consumption in June was higher based on annual average M for each length group compared with energy requirements based on mean M for each length group in each month (Fig. 4 and 5).

In 1999, the total Barents Sea harp seal stock size was estimated to be 2.18 (95% CI, 1.79 to 2.58) million animals (ICES 1999). Assuming that the field metabolic rate of the seals corresponds to two times their estimated basal metabolic rate, the annual food consumption of the Barents Sea harp seal stock in 1999 was estimated to be in the range of 2.69 – 3.96 million tonnes (based on upper and lower 95% confidence limits and adjusted for a pup mortality of 30%) if capelin is assumed to be abundant (Table 8).

Consumption estimates of various prey species

For each of the two diets used in the various model runs, only minor variations occurred in the relative contribution of different prey species to the total harp seal consumption estimates. When capelin was abundant in the ecosystem, the contribution of crustaceans was ca. 35% to 37% of the total consumption estimates. Capelin contributed ca. 23% to 27%, polar cod ca. 17% to 18%, herring (*Clupea harengus*) ca. 6%, cod ca. 3% and "other fish" ca. 11% to 12%, to the total consumption estimates (Table 6)..

When taking monthly variations in body mass into account in predicting BMR, and assuming a FMR of 2 · BMR, the estimated consumption by harp seals of crustaceans was ca. 1,223,800 tonnes, capelin ca. 807,800 tonnes, polar cod ca. 605,300 tonnes, herring ca. 212,400 tonnes, cod ca. 100,500 tonnes and "other fish" ca. 404,200 tonnes (Fig. 6). It should be noted that "other fish" also includes gadoids such as cod, haddock and saithe, which were impossible to identify to species because of the extent of the digestion of the otoliths recovered in the stomach contents of the seals (Nilssen *et al.* 1995a,b).

When the capelin stock was at a very low level (as it was in the period 1993-1996), consumption of capelin seemed to be replaced with an increased consumption of, particurlarly, polar cod (from ca. 17%-18% to ca. 23%-25% of the total consumption), followed by gadoids (dominated by cod, but also including haddock and saithe), "other fish" and herring (Table 7). Using the same assumptions as above, the harp seal consumption of polar cod increased to 876,000 tonnes, codfishes (cod, saithe and haddock) to 359,700 tonnes, "other fish" to 618,800 tonnes

Table 6: Estimated consumption (in 1,000 tonnes) of various fish species by the Barents Sea harp seal stock under various assumptions concerning basal metabolic rate (BMR) and the field metabolic rate (FMR), when capelin was abundant in the Barent Sea ecosystem Var=BMR was predicted based on the observed monthly variations in the mean body mass for each length group. Mean=BMR was predicted based on the annual mean body mass for each length group. Percentage contributions of each prey group are given in paranthesis.

BMR	FMR	Krill	Parath.	Oth. crust	Capelin	Herring	Cod	Polarcod	Oth. fish	Total
var	2	601.6	311.4	310.8	807.8	212.4	100.5	605.3	404.2	3353.9
		(17.9)	(9.3)	(9.3)	(24.1)	(6.3)	(3)	(18)	(12.1)	
var	3	755.9	414.1	472.7	1284.8	318.1	162.5	790.5	525.5	4724.2
		(16)	(8.8)	(10)	(27.2)	(6.7)	(3.4)	(16.7)	(11.1)	
var	1.5-3	678.7	362.7	334.7	1033.1	265.2	121.7	686.4	436.3	3918.7
		(17.3)	(9.3)	(8.5)	(26.4)	(6.8)	(3.1)	(17.5)	(11.1)	
mean	2	620.5	294.3	359.9	812.7	200.0	105.1	615.5	427.3	3435.3
		(18.1)	(8.6)	(10.5)	(23.7)	(5.8)	(3.1)	(17.9)	(12.4)	
mean	3	783.1	388.7	545.3	1293.3	300.0	169.4	805.2	559.5	4844.5
		(16.2)	(8)	(11.3)	(26.7)	(6.2)	(3.5)	(16.6)	(11.5)	
mean	1.5-3	701.7	341.4	372.7	1018.9	250.0	122.9	695.7	456.4	3959.6
		(17.7)	(8.6)	(9.4)	(25.7)	(6.3)	(3.1)	(17.6)	(11.5)	

Table 7: Estimated consumption (in 1,000 tonnes) of various fish species by the Barents Sea harp seal stock under various assumptions concerning basal metabolic rate (BMR) and the field metabolic rate (FMR), when capelin was depleted in the Barent Sea ecosystem Var=BMR was predicted based on the observed monthly variations in the mean body mass for each length group. Mean=BMR was predicted based on the annual mean body mass for each length group. Percentage contributions of each prey group are given in paranthesis.

BMR	FMR	Krill	Parath.	Oth. crust	Capelin	Herring	Cod	Saithe	Haddock	Polarcod	Oth. fish	Total
var	2	546.9	302.6	354.7	22.9	392.5	296.3	16.4	47.0	876.0	618.8	3474.1
		(15.7)	(8.7)	(10.2)	(0.7)	(11.3)	(8.5)	(0.5)	(1.4)	(25.2)	(17.8)	
var	3	687.3	403.6	508.3	37.2	610.0	480.1	36.7	86.2	1212.0	878.0	4939.2
		(13.9)	(8.2)	(10.3)	(0.8)	(12.3)	(9.7)	(0.7)	(1.7)	(24.5)	(17.8)	
var	1.5-3	617.1	353.1	358.2	33.5	490.6	405.8	16.6	61.3	1031.2	715.6	4082.9
		(15.1)	(8.6)	(8.8)	(0.8)	(12)	(9.9)	(0.4)	(1.5)	(25.3)	(17.5)	
mean	2	564.1	285.5	406.3	26.0	364.0	320.0	22.7	57.4	847.0	657.3	3550.3
		(15.9)	(8)	(11.4)	(0.7)	(10.3)	(9)	(0.6)	(1.6)	(23.9)	(18.5)	
mean	3	712.0	378.0	584.5	41.8	568.1	515.7	45.9	101.8	1169.3	935.2	5052.3
		(14.1)	(7.5)	(11.6)	(0.8)	(11.2)	(10.2)	(0.9)	(2)	(23.1)	(18.5)	
mean	1.5-3	638.1	331.7	393.8	37.6	450.6	432.4	19.6	69.7	991.8	747.7	4113.0
		(15.5)	(8.1)	(9.6)	(0.9)	(11)	(10.5)	(0.5)	(1.7)	(24.1)	(18.2)	

Table 8: Estimated total consumption of prey by the Barents Sea harp seals based on the 1999 stock size estimates (based on upper and lower 95% confidence limits and adjusted for a pup mortality rate of 0.3) and assuming that capelin is abundant in the Barents Sea. Field metabolic rate (FMR) corresponds to two times their estimated basal metabolic rate (BMR).

		TOTAL CONSUMPTION (tonnes)	
Number of pups	Number of seals (1+) one year and older	Annual average BMR	Monthly average BMR
174,650	1,541,000	2,758,825	2,693,478
216,510	1,876,000	3,361,693	3,282,092
258,370	2,211,000	3,964,521	3,870,667

and herring to 392,500 tonnes, after collapse of the capelin stock (Fig. 7).

DISCUSSION

Barents Sea harp seals are known to display opportunistic feeding patterns in that different species are consumed in different areas and at different times of the year (Haug *et al.*1991; Lydersen *et al.* 1991; Nilssen 1995; Nilssen *et al.* 1992, 1995a,b, 1998a,b; Lindstrøm *et al.* 1998). However, the consumption estimates in this study, based on results from diet studies (Nilssen *et al.* 1995a,b, 1998a; Lindstrøm *et al.* 1998), energy densities in the various prey species (Pechenik *et al.* 1973; Mårtensson *et al.* 1996), and energy requirements (e.g., Lager *et al.* 1994) revealed that the bulk of the harp seal diet comprised relatively few species, in particular capelin, polar cod, herring, cod, krill and *Parathemisto libellula.*

Crustaceans, mainly krill and *Parathemisto libellula*, seem to be important prey of harp seals during summer and autumn (July-October). The estimates of consumption of crustaceans showed little relative variation between the two diets applied in the model (Tables 6 and 7). The consumed biomass of crustaceans was estimated to be between ca. 1,223,800 and ca. 1,717,100 tonnes, or ca. 32% to 37% of the total consumption. This is comparable to the estimate made by Nordøy *et al.* (1995a), who found that crustaceans contributed about 35% of the biomass eaten by the Barents Sea harp seals. However, it should be kept in mind that the knowledge about the harp seal diet in June and July is poor, and that the contribution of krill to the harp seal diet in July was based only on the assumption that their diet in July was equivalent to that observed in August 1996 (Nilssen *et al.* MS 1998b).

Among the commercial harvested fish species in the Barents Sea, capelin, when abundant, seems to be one of the most important prey species of harp seals. Capelin contributed ca. 24% to 27% to the total harp seal consumption. The consumed capelin biomass was estimated to vary between ca. 807,800 – 1,293,300 tonnes, when the species was available in the ecosystem. This is substantial when compared to the total fisheries (1,094,000 tonnes) and estimated total stock biomass (3.9 million tonnes of 2+) of Barents Sea capelin in 1992 (Anonymous 1993). The capelin stock collapsed during the winter of 1992/1993 (Hamre 1994; Gjøsæter 1995; Gjøsæter *et al.* 1998). The total Barents Sea capelin stock size was estimated to be only ca. 195,000 tonnes in 1995, and with very poor production in the period 1993-1995 (ICES 1996). The annual harp seal consumption estimates of capelin, after this, decreased significantly to approximately 22,900 - 41,800 tonnes.

Krill of the genus *Thysanoessa* are known to be an important part of the diet of many commercially and ecologically important fish species in the Barents Sea, including the capelin (Gjøsæter 1998). Coinciding with a strong reduction in the older age-groups of the capelin stock in the late 1980s (Gjøsæter *et al.* 1998), there was a subsequent increase in abundance and biomass of *Thysanoessa,* and a possible predator – prey interrelationship between capelin and krill in the Barents Sea was suggested (Dalpadado and Skjoldal 1996). This may imply that a reduction of the capelin stock is more or less automatically followed by an increase in krill abundance, and may also to some extent explain the apparent large consumption of krill by harp seals in the area in the mid-1990s.

The lack of capelin as potential harp seal prey in the period 1993 - 1996, seems also to have been compensated for by increased consumption of polar cod. The annual consumption of polar cod was estimated to increase from a level of ca. 605,300 – 805,200 tonnes in 1990-1992 to ca. 876,000 – 1,212,000 tonnes in 1993-1996, depending on input parameters. This is very high considering the stock size evaluations (ca. 600,000-1,000,000 tonnes) of polar cod in the eastern Barents Sea in 1992-1993 (Sunnanå and Christiansen 1997). The polar cod is known to be an important prey for many of the top predators in Arctic marine ecosystems (Ponomarenko 1968; Bradstreet and Cross 1982). In the Barents Sea, the polar cod spawn in early winter along the west and south coast of Novaja Zemlja (Ponomarenko 1968). Russian studies, conducted during the 1930s, provided evidence that polar cod was the most important prey of harp seal in these areas during late autumn (Chapskii 1961).

The consumption of other gadoids, mainly cod, was estimated to increase from a range of ca.

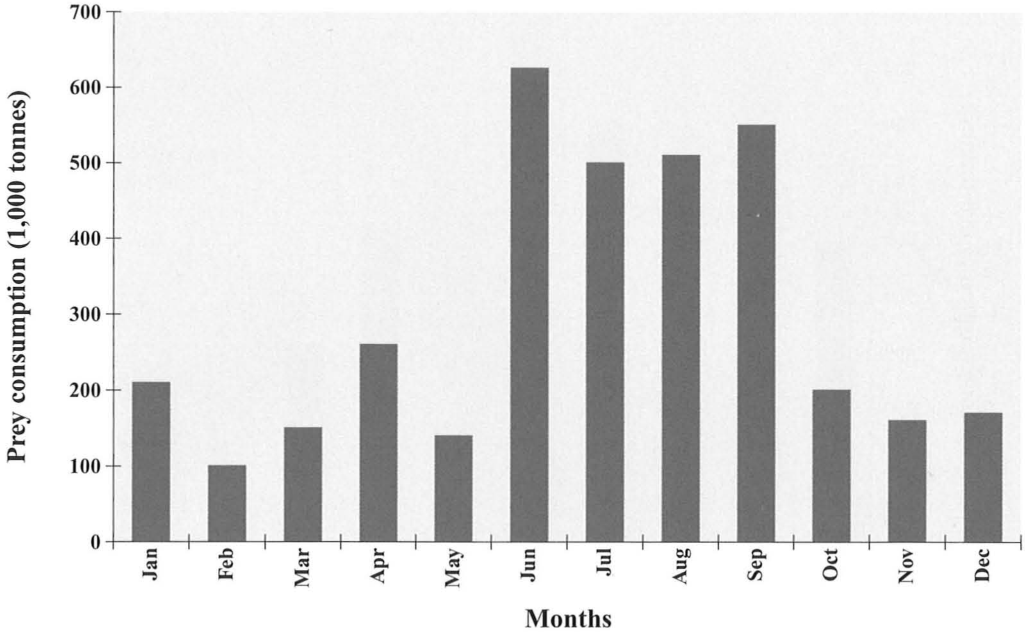


Fig. 4
Monthly consumption of prey biomass (in 1,000 tonnes) by harp seals, when capelin was abundant in the Barents Sea. Energy requirements for basal metabolic rate (BMR) were calculated on the basis of annual mean body mass (M) for each length group of seals, and field metabolic rate (FMR) was assumed to correspond to 2 times BMR. The total consumption of all prey species was 3.43 million tonnes.

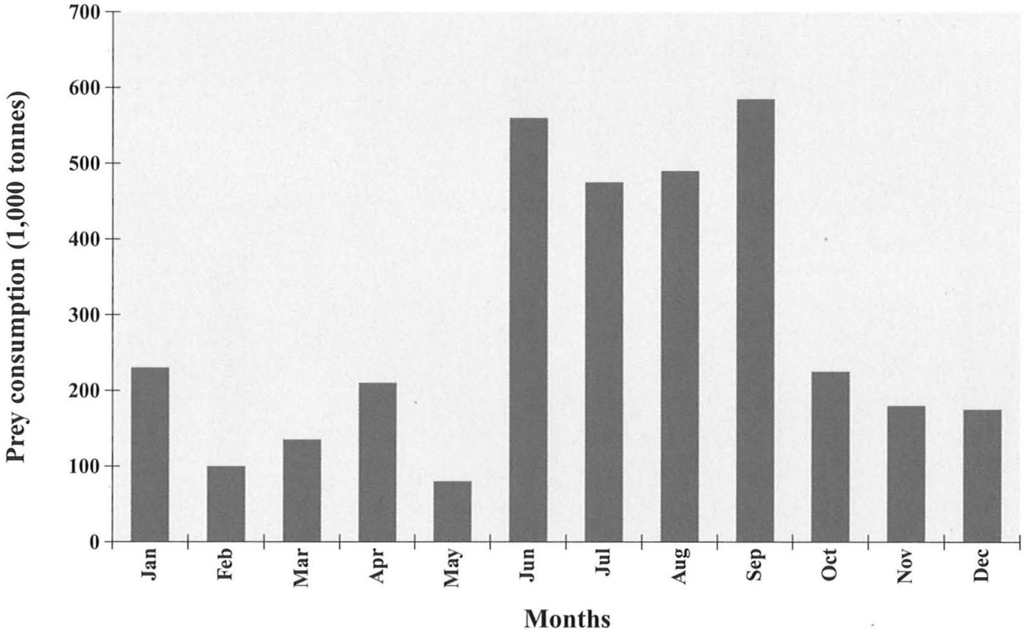


Fig. 5.
Monthly consumption of prey biomass (in 1,000 tonnes) by harp seals, when capelin was abundant in the Barents Sea. Energy requirements for basal metabolic rate (BMR) were calculated on the basis of observed monthly variations in the mean body mass (M) for each length group of seals, and field metabolic rate (FMR) was assumed to correspond to 2 times BMR. The total consumption of all prey species was 3.35 million tonnes.

100,500 - 169,400 tonnes to ca. 296,300 - 515,700 tonnes, when the capelin stock had diminished. The estimated annual consumption of cod by harp seals was comparable to that taken annually by the minke whale (*Balaenoptera acutorostrata*) (ca. 256,000 tonnes) in the period 1992-1995 (Folkow *et al.* this volume), and substantial when compared with the total cod fisheries (735,100 tonnes in 1995). The estimated cod stock biomass was approximately 2 million tonnes in 1995 (Anonymous 1996). The total consumption of gadoids is most likely larger, since the group denoted "other fish" also includes gadoids. In June-July harp seals are distributed in open waters in the central and the southern part of the Barents Sea, in pack-ice waters from Novaja Zemlja in the east, along the pack-ice belt to the north, and in Svalbard waters (Haug *et al.* 1994). The more westerly distribution of the seals dur-

Fig. 6.
Annual consumption of various prey items (in 1,000 tonnes) by harp seals, when capelin was abundant in the Barents Sea. The energy requirements for the basal metabolic rate (BMR) were calculated on the basis of observed monthly variations in the mean body mass (M) for each length group of seals, and field metabolic rate (FMR) was assumed to correspond to 2 times BMR. The total consumption of all prey species was 3.35 million tonnes.

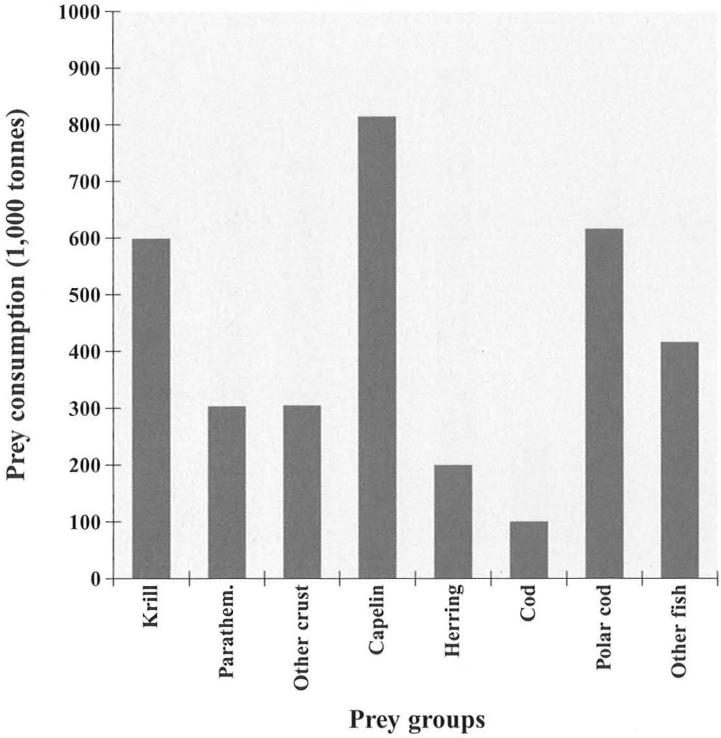
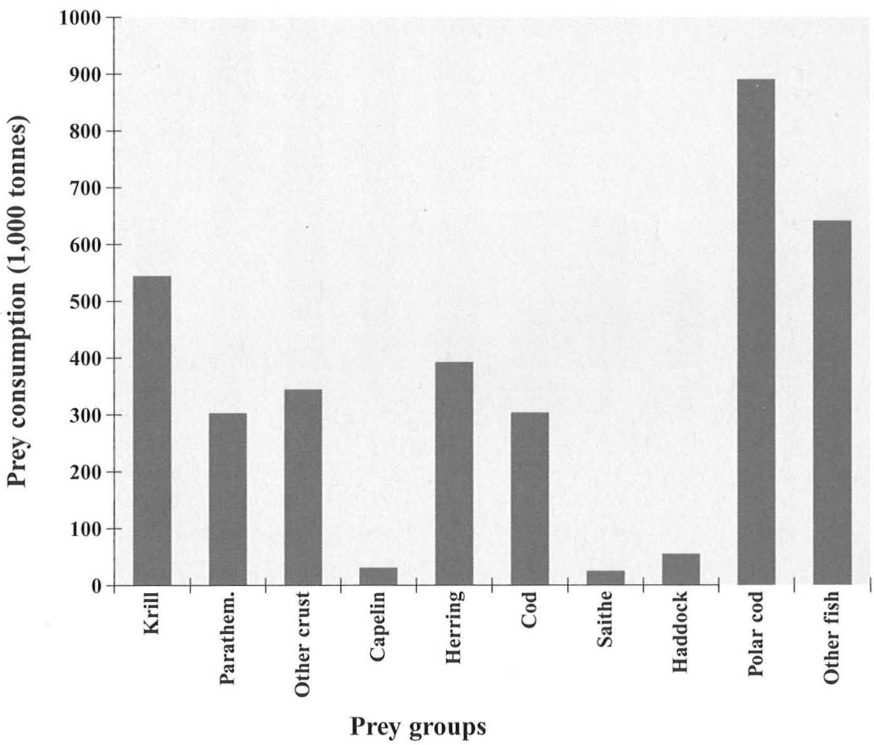


Fig. 7.
Annual consumption of various prey items (in 1,000 tonnes) by harp seals with a low capelin stock in the Barents Sea. The energy requirements for the basal metabolic rate (BMR) were calculated on the basis of observed monthly variations in the mean body mass (M) for each length group of seals, and field metabolic rate (FMR) was assumed to correspond to 2 times BMR. The total consumption of all prey species was 3.47 million tonnes.



ing early summer, and the fact that diet data from June and July are poor, may imply that the assumed consumption of mainly crustaceans in this very important feeding period could be debatable. The possibility of a diet comprised of, for example, a larger portion of gadoids and immature herring in the summer period should be examined.

The stock of Norwegian spring spawning herring collapsed in the late 1960s (Hamre 1994; Gjøsæter 1995; Dragesund *et al.* 1997). However, since 1988 the stock size has gradually increased to a level comparable to that in the early 1960s, and the stock size was estimated to be about 2.8 million tonnes in 1994 (Anonymous 1994). Thus, increasing quantities of immature herring (0-group and recruits up to 4 years old) have been present in the southern Barents Sea (Anonymous 1993), and it is possible that immature herring may have been one of the most important winter prey species for harp seals since 1989 (Nilssen 1995). The estimated annual consumption of herring in this study increased from a level of ca. 212,400 – 318,100 tonnes, depending on model input parameters when capelin was abundant, to a level of ca. 392,500 – 610,000 tonnes when the capelin stock was at a low level. These annual consumption estimates were lower than the estimated consumption by minke whales (ca. 633,000 tonnes) (Folkow *et al.* this volume). The total herring fishery was approximately 900,000 tonnes in 1995 and the spawning stock size was estimated to be ca. 3.9 million tonnes (ICES 1996).

The total annual food consumption of Barents Sea harp seals, as estimated to be within the range of ca. 3.35 – 5.05 million tonnes for 2.22 million seals in the present study, seems reasonable compared with the estimate by Nordøy *et al.* (1995a) who calculated the total food consumption to be approximately 1 million tonnes for 600,000 seals (1+). Markussen and Øritsland (1991) estimated the total food consumption, based on restricted knowledge about the feeding habits at that time, to vary from 1.4 to 4.4 million tonnes per year for 1 million harp seals in the Barents Sea. These estimates seem to be too high. In eastern Canada, the total prey consumption by 4.8 million harp seals was estimated to be 6.9 million tonnes in 1994 (Stenson *et al.* 1997), which seems reasonable with the lower range of the estimates in the present study.

The food consumption estimates are sensitive to the model assumptions. The most critical parameter for the total consumption estimates examined in the model, was the choice of multiplier for prediction of field metabolic rate from basal metabolic rate (FMR = a · BMR). If "a" was increased from 2 to 3, the food consumption estimate increased by approximately 41%. Stenson *et al.* (1997) estimated an increased food consumption of 25% when they increased "a" from 2 to 2.5. The consumption estimates based on the lowest FMR ("a" = 2) in our study, seem to be most similar to estimates based on monitored energy expenditures of immature harp seals in captivity throughout the year (Nordøy *et al.* 1995a). The consumption estimates showed little sensivity to variations in the procedure for calculating basal metabolic rate (BMR) in the model (annual average BMR or monthly average BMR).

A contributing factor to the decline in harp seal body mass during spring may be seasonal variations in the energy content of prey species. Some of the prey species consumed by the seals display very low energy densities at this time of the year (Henderson *et al.* 1984; Mårtensson *et al.* 1996). Variations in energy densities, influenced by season, as well as size, geography and year, have also been observed for important prey species of marine vertebrate predators such as harp seals in the northwest Atlantic (Lawson *et al.* 1998). Seasonal changes in feeding intensity have also been observed in captive harp seals. Lager *et al.* (1994) reported that food intake in subadults fed *ad libitum* was generally low during moult (May-June). This was followed by a pronounced increase in feeding in the period July-October. During the period October-April, the food intake of captive seals was observed to be relatively stable. Thus, the decline in mass observed during the moult is probably due to reduced food intake, in addition to consumption of prey that are not particularly energy-rich.

Apparently, there are several fish species (included in the group "other fish") that may serve as prey for harp seals throughout the year. Given the variability in abundances of species such as capelin and herring (Røttingen 1990;

Dragesund *et al.* 1997; Gjøsæter *et al.* 1998), and the current low stock size of Barents Sea capelin stock (Anonymous 1994), the catholic tastes of the harp seals are probably important in ensuring adequate energy intake for these seals in the Barents Sea.

Results from the present study suggest that Barents Sea harp seals consume substantial amounts of commercially exploited fish species, such as capelin, herring and cod. Data on the energy requirements of harp seals throughout the year, and increased knowledge of their feeding habits during summer and early winter, are essential in order to improve our estimates of the food consumption of this seal stock. Satellite tracking and remote sensing - a method which has been successful applied in studies of hooded seals (*Cystophora cristata*) (Folkow *et al.* 1996) - has also been applied to study Barents Sea harp seals (e.g. Nordøy *et al.* MS1995b). The results are now being analysed and will improve our knowledge of harp seal activity and distribution patterns. Regular collection surveys are also required in order to monitor changes in feeding habits and consumption of harp seals in the Barents Sea, in particular when the capelin stock has recovered.

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