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Harbour seal (*Phoca vitulina*) diet in Vesterålen, north Norway

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Results from analyses of stomach contents and faeces collected from harbour seals (*Phoca vitulina*) in Vesterålen, north Norway, in 1990–1995 revealed a diet comprised mainly of saithe (*Pollachius virens*). Little variation occurred in the diet throughout the year, probably due to a large and stable abundance of saithe in the area. Other prey items that seemed to be important were herring (*Clupea harengus*), cod (*Gadus morhua*), sandeel (*Ammodytes* sp.) and various flatfishes. The harbour seals seemed to prefer small fish, and older seals appeared to have a more varied diet than the younger animals. In a captive study, the recovery of otoliths was only 14.8% when harbour seals were fed whole fish. Recovery rates varied between species: 4.6, 47.7 and 46.6% of herring, haddock (*Melanogrammus aeglefinus*) and cod, respectively. The results from the captive study were used to illustrate potential biases in observed diets based on faeces.

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INTRODUCTION

The harbour seal (*Phoca vitulina*) is one of the most common seal species in the world, and in the northeast Atlantic, harbour seals are coastal residents from northern Portugal to the coast of Kola, Russia, and Svalbard (Bigg 1981; Henriksen & al. 1997). Bjørge (1991) reported an abundance of approximately 4000 harbour seals in Norway. In north Norway, the largest concentration was registered in Vesterålen, where Øynes (1964) suggested a total of 70 animals in the early 1960s and nearly 600 animals were recorded in 1988 (Wiig 1989). Haug & al. (1998) estimated an abundance of approximately 1000 seals in Vesterålen in 1998, thus indicating a possible increase in the stock in recent years.

The resident nature of the harbour seal makes them likely to interact with local fisheries and fish farms (e.g. Henriksen & Moen 1997). Furthermore, harbour seals are final hosts for the sealworm (*Pseudoterranova decipiens*) which may severely affect commercial fishes such as cod (*Gadus morhua*) (Andersen & al. 1995). Sealworm infections have been known to be locally high in Norwegian waters (Jensen & Idås 1991; Andersen & al. 1995; Aspholm & al. 1995). In such areas, the indirect effect of seals as the main host for sealworm infection in fish may be a more significant interaction with commercially valuable populations of fish than their effect as fish predators.

Several studies have suggested that the harbour seal diet composition may reflect differences in the prey species assemblages encountered in different habitats (Brown & Mate 1983; Härkönen 1987; Payne & Selzer 1989; Sievers 1989; Brown & Pierce 1998; Hall & al. 1998). In the southern part of Norway, harbour seals feed on herring (*Clupea harengus*), Norway pout (*Trisopterus esmarkii*), saithe (*Pollachius virens*), cod, whiting (*Merlangius merlangius*) and squid (*Ommatostrephes sagittatus*) (Olsen & Bjørge 1995). No information is, however, available on the diet of harbour seals in north Norway.

Studies of the diets of marine mammals are usually based on analyses of either stomach, intestinal or scat (faeces) contents. Hard remains such as fish otoliths and cephalopod beaks recovered from such samples have been widely used to quantify diets of phocids (e.g. Härkönen 1987; Prime & Hammond 1987; Pierce & al. 1991a; Bowen & Harrison 1996). The method is based on the assumption that relative frequencies of otoliths or beaks in stomachs, intestines or faeces reflect those of fish and cephalopods in the diet. A major problem is, however, that otoliths erode during the passage through the gastrointestinal tract. Otoliths from various fish species erode at different rates, and some may be completely digested (da Silva & Neilson 1985; Prime & Hammond 1987; Harvey 1989). Thus, counts and measurements of otoliths are likely to underestimate the number and size of fish ingested by various amounts

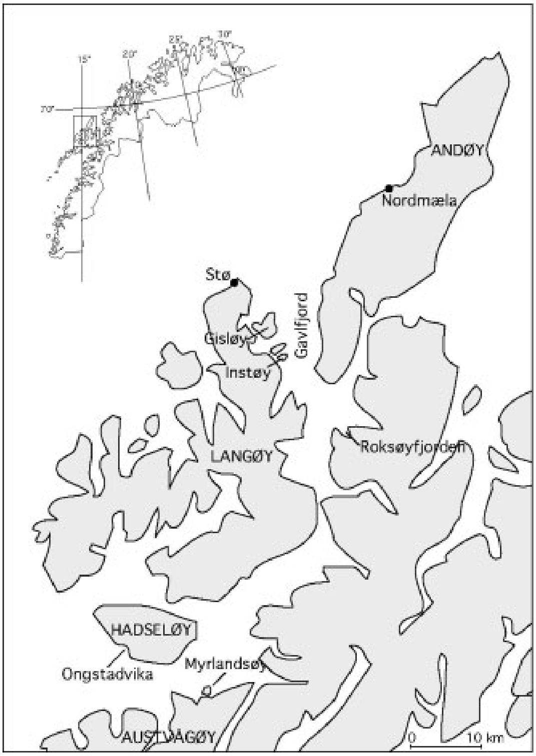

Fig. 1. Map of haul-out sites (Nordmela, Stø, Gisløy, Instøy, Roksøyfjorden, Myrlandsøyene, and Ongstadvika) in Vesterålen, north Norway where harbour seals and scats were sampled in 1990–1995.

(Jobling & Breiby 1986; Jobling 1987). Numerous studies have attempted to quantify the reduction in both number and size of otoliths and beaks recovered from seal faeces (e.g. da Silva & Neilson 1985; Murie & Lavigne 1986; Prime & Hammond 1987; Tollit & al. 1997).

The general lack of knowledge of harbour seal ecology in north Norwegian waters, and the methodological problems involved in the analyses of seal faeces, are the background for the present investigation. The purpose of the study was to evaluate the feeding habits of harbour seals in Vesterålen, north Norway. Also, a feeding experiment was conducted with two captive harbour seals in order to address some of the methodological biases, in particular errors arising from the use of faeces in dietary studies of seals.

MATERIAL AND METHODS

FIELD SAMPLING

Material was collected using inflatable Zodiac boats fitted with outboard motors to survey harbour seal haul-out sites in Vesterålen (Fig. 1). Ship-borne surveys, using a mother ship for transportation and accommodation, were conducted in June 1990, October 1990 and 1994, and in February/March 1995. The field activities were allocated to low tide when harbour seals are most likely to haul-out (Roen & Bjørge 1995). Forty-three seals were shot by rifle from the shore, either when they were in the water or during haul-out. Some of the animals sank but were subsequently collected by a diver.

In all cases, the seals were dissected immediately on board the ship. The stomachs were removed and frozen for later examination. The ages of the seals were determined by examination of the incremental growth layers in the dentine of the lower canine teeth (Bowen & al. 1983). Ages were recorded in years, corresponding to the age at the breeding season in the year of collection (Table 1).

Faeces were collected on haul-out sites where harbour seals had been observed in June, July, August and October 1994 and in February/March 1995. Collected faeces were frozen for later examination.

STOMACH AND FAECES ANALYSES

In the laboratory, the stomach contents were removed and weighed. Fish and crustaceans were then identified using standard identification keys (Enckell 1980; Pethon 1985). Crustaceans were separated from fish

Table 1. Sex and age composition of harbour seals collected in Vesterålen in June 1990, October 1990 and 1994, and February/March 1995.

Month and year	Number	Sex		Age		
		Male	Female	Young-of-the-year	1–5 years	5+ years
June 1990	7	2	5			
October 1990	10	6	4	2	5	2
October 1994	12	9	3	2	7	3
February/March 1995	14	5	9	5	8	2
Total	43	22	21	9	20	7

and identified to the lowest possible taxon. The same methods were used for the faeces samples.

Otoliths and cephalopod beaks were separated from the remainder of the stomach contents or faeces (Treacy & Crawford 1981; Murie & Lavigne 1985), and were identified to the lowest possible taxon, using reference material (Breiby 1985; Clark 1986; Härkönen 1986). All otoliths were length-measured. Otolith length to fish length/wet weight correlations, based either on fish material obtained from trawl hauls performed by the Norwegian Institute of Fisheries and Aquaculture in coastal waters of north Norway during autumn 1995, or from a published guide (Härkönen 1986), were used to estimate the initial lengths and weights of the fish consumed by the seals. The total number of each fish species was reconstructed by adding the number of fresh specimens, the number of intact skulls and half the number of "free" otoliths.

Kruskal–Wallis statistical tests were applied to test potential variation in back-calculated lengths of the most commonly occurring fish prey, saithe, between seasons (Zar 1996). Statistical tests were conducted using SYSTAT (Wilkinson 1990).

Estimates of absolute abundance of prey composition from gut samples and faeces are not directly comparable. However, techniques developed to assess the relative composition of ecological communities (Legendre & Legendre 1998) can be used to compare the relative abundance of prey composition from both gut samples and faeces. In order to assess the temporal variation in the relative abundance of prey in the diets of seals, hierarchical agglomerative clustering was applied (Legendre & Legendre 1998).

Diet indices

Several feeding indices are commonly used in stomach analyses of top predators (Hyslop 1980; Pierce & Boyle 1991). No index gives a complete or fully realistic picture of dietary composition. Therefore, three different indices were used to estimate the dietary contribution of the different prey items.

The frequency of occurrence (Fo_i) of a given prey was defined as the percentage of stomachs that contained one or more individual of the prey species: $Fo_i = (s_i/s_t) \times 100$, where s_i is the number of stomachs/faeces in which species i occurs and s_t is the total number of samples examined.

The relative numerical frequency of occurrence of each prey item was defined as: $N_i = (n_i/n_t) \times 100$, where n_i is the number of individuals of prey category i and n_t is the total number of individuals of all prey categories.

The biomass index was recorded as the relative contribution of each prey species to the total seal diet expressed in terms of calculated fresh wet weight: $B_i = (b_i/b_t) \times 100$, where b_i is the total weight of prey category i and b_t is the total weight of all prey categories.

Feeding experiment

Two male harbour seals from the Aquarium in Bergen, Norway, were used in a feeding experiment during summer 1996. The seals were kept in identical enclosures (7 × 3 m, 2 m water depth) containing seawater. The experiment comprised two feeding bouts with subsequent faecal collections over a period of 4 days. The seals were fed a maintenance ration of decapitated herring for 2 days before the experimental period. Each feeding trial comprised a test meal where either a multispecies fish diet of known relative composition (seal I), or a unispecies diet with otoliths from other species implanted in the flesh of the given fish (seal II), was given to the seal. The seals were always fed until satiation. Collections of otoliths were made 48 h after each trial, by draining the tank through a 0.25 mm basket sieve. At the end of the experiment the tank was cleaned thoroughly, at least three times, before a new feeding trial started, to ensure no otoliths remained.

To check the otolith sampling procedure, a pilot experiment was conducted before the feeding experiments started. This was carried out by throwing a known number of otoliths (20 otoliths of saithe and herring) into the tank and then collecting them 2 days later using the described method. All otoliths were retrieved.

Seal I (*Ca* 80 kg) was fed with a mixed diet of dead, intact fish comprising herring, cod and haddock. The size of the meals varied between 990 and 3181 g (median 2573 g). Prior to the feeding experiment, all fish were weighed to the nearest gram, and lengths measured to the nearest mm. The total length of herring ranged between 25.4 and 34.4 cm and individual fish mass had a mean weight of 190 g (n = 108). The total length of cod ranged between 29 and 44 cm and the mean mass of individuals was 600 g (n = 15). The total length of haddock ranged between 31.5 and 40.6 cm and individual fish weight averaged 460 g (n = 19).

In the first trial, seal II (*Ca* 50 kg) was fed dead, intact herring. Two otoliths of haddock were implanted into the flesh of each herring before the fish were given to the seal. In the second trial, seal II was fed with whole herring in which the otoliths were transferred from the head to the fish flesh. As in the first trial, two otoliths

Table 2. Percentages of identified prey species in stomachs or faeces of harbour seals in Vesterålen in different periods. The most important prey species within the six periods are in bold.

	June 1990 Stomach	August 1994 Faeces	October 1990 Stomach	October 1994 Stomach	October 1994 Faeces	February/March 1995 Stomach
Total number of stomachs or faeces	2	47	9	12	6	14
% empty stomach or faeces	50.0	14.9	44.4	8.3	66.6	35.7
Mollusca						
Cephalopoda						
Eledone cirrhose		2.5				
Crustacea						
Isopoda						
Idotea baltica sp.						22.2
Euphausiacea						
Thysanoessa sp.						11.1
Pisces						
Clupeidea						
Clupea harengus	**100**	47.5	25	27.3	**100**	22.2
Gadidae						
Trisopterus esmarkii				18.2		11.1
Merlangius merlangius						22.2
Melanogrammus aeglefinus			25	9.1		
Pollacius virens	**100**	**75**	**75**	**90.9**		**88.9**
Gadus morhua			25	27.3		55.5
Unidentified gadoids		20	25	36.4		
Scorpaenidea						
Sebastes viviparus		2.5				
Cottidae						
Myoxocephalus scorpius			25			
Taurulus bubalis				9.1		
Anarhichadidae						
Anarhichas minor		5.0				
Ammodytidae						
Ammodytes sp.	**100**	12.5	50	18.2		22.2
Pleuronectidae						
Limanda limanda			25	9.1		
Platichthys flesus		2.5				
Pleuronectes platessa		5				
Glyptocephalus cynoglossus						11.1
Hippoglossides platessoides						11.1
Unidentified fish (0-group)		55	25	36.4		66.7
Unidentified otholiths			25	9.1		33.4

from haddock were also implanted in the fish flesh of each herring in the second trial. The meal size varied between 1002 and 1680 g (median 1341 g).

The recovery rates of otoliths based on the feeding experiment with seal I were applied to adjust the results from the analyses of faeces collected in Vesterålen (because feeding with whole fish was assumed to be most similar to natural conditions).

RESULTS

PREY OCCURRENCE

Thirteen of 37 seal stomachs were empty, while 11 of 53 faeces were without any hard (otoliths, beaks) remains (Table 2). None of the stomachs contained fresh/whole fish and very few contained only otoliths. Crustaceans were found in one of the sampling periods, but in amounts so small that they may well have been secondary prey. A total of 19 prey species were recorded in the material.

Saithe occurred most frequently in the stomachs (75–100%) in all sampling periods (Table 2). Seals collected in June 1990 also contained herring (100%) and sandeel (*Ammodytes* sp.) (100%). Sandeel occurred frequently in seal stomachs in all periods, while a more sporadic occurrence of herring, haddock, cod, bullrot (*Myoxocephalus scorpius*), and dab (*Limanda limanda*) was observed.

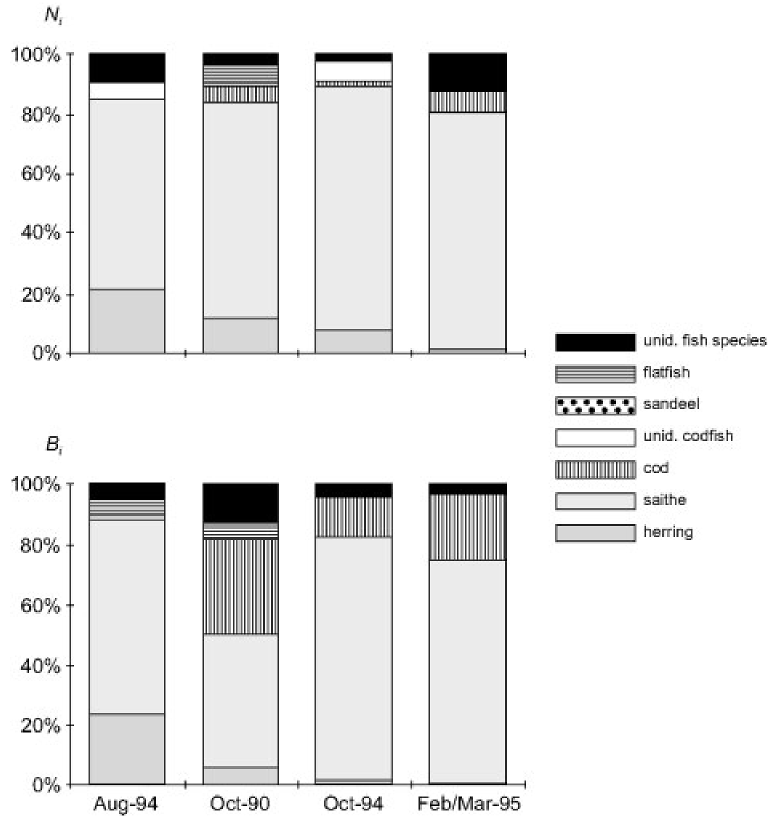

Fig. 2. Relative importance of prey items in harbour seal stomachs (October 1990/1994, February/March 1995) and faeces (August 1994) sampled in Vesterålen, north Norway. N – Relative frequency of occurrence by numbers; B – Relative frequency of occurrence by weight.

Saithe was also the most abundant prey species observed in the faeces (75%) collected in August 1994 (Table 2), but herring (47.5%) and sandeel (12.5%) were also well represented. The faeces collected in October 1994 contained only herring.

PREY NUMBERS

Saithe dominated in terms of relative numbers in all sampling periods, most in the stomachs collected in October 1994 (81.6%) and least in the faeces collected

Table 3. The relative composition (%) of stomach contents subdivided by age groups of harbour seals sampled in Vesterålen in October 1990 and 1994, and in February/March 1995, based on relative frequencies of occurrence by number (N_i), and by calculated fresh weight (B_i). The most important prey species within the age groups are in bold.

	Young-of-the-year (n = 7)		1–5 years (n = 14)		5+ years (n = 3)	
Prey item	N_i	B_i	N_i	B_i	N_i	B_i
Herring			10.6			
Saithe	**93.9**	**97.4**	**68.3**	**62.4**	**95.6**	**74.6**
Cod				21.1		24.2
Unidentified gadoids			7.2			
Flatfishes				6.8		
Various fishes	6.1	2.6	13.8	9.7	4.4	1.1

n = number of stomachs examined.

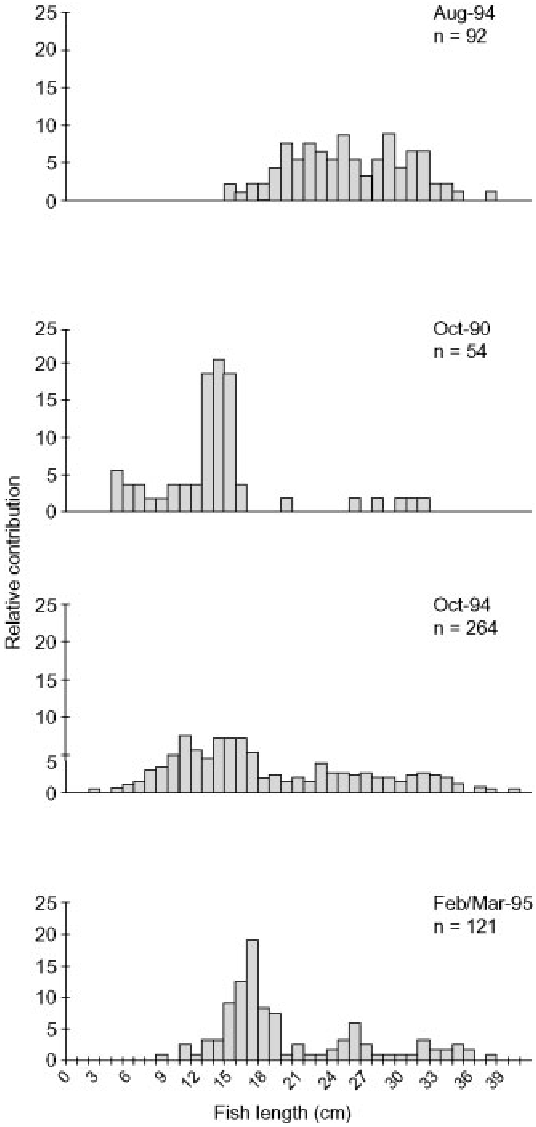

Fig. 3. Estimated length composition for saithe in stomach and faeces samples of harbour seals collected in Vesterålen, north Norway in August 1994 (faeces) and in October 1990 and 1994 and February/March 1995 (stomachs). n – Number of specimens examined.

in August 1994 (63.5%) (Fig. 2). Herring was quite abundant in the faeces collected in August 1994 (21.6%), but less so in the stomachs collected in October 1990 (11.1%), October 1994 (7.6%) and in February/March 1995 (7%).

Prey biomass

Reconstructed fresh weights from individual stomach or faeces samples ranged between 2 and 10,982 g, and between 3 and 1870 g, respectively.

Saithe dominated the biomass in all sampling periods, ranging from 44% in October 1990 to 81% in October 1994 (Fig. 2). Herring contributed considerably in the faeces collected in August 1994 (23.5%) but less in the stomachs sampled in other periods. Cod was absent in the faeces collected in August 1994, but contributed to the biomass in the stomachs collected in October 1990 and 1994 and in February/March 1995 with 31.8, 13.3 and 22.3%, respectively. Flatfishes contributed 6.8% to the estimated weight in the faeces in August 1994 and 5.3% to the stomach contents in October 1990.

Temporal variation in diet

In the hierarchical agglomerative clustering used to assess potential temporal variation in diets, a matrix of prey species abundance (in terms of numbers and biomass) in columns, and individual seals or faeces samples in rows, was analysed. A Bray–Curtis coefficient, standardized by rows as association measure and an unweighted arithmetic average clustering algorithm, was used to produce dendograms showing clustering of gut contents and faecal samples, based on the estimated abundance of prey species in the samples. Only the samples from August 1994 (faeces), October 1994 (gut contents) and February/March 1995 (gut contents) were included in the analyses. No temporal variation in diet could be detected. Most samples clustered together, based on their preponderance of saithe.

Number and size of prey

Individual faeces and stomach samples contained from one to three prey species each. One (40–52.5%) or two (40–45%) prey species per sample were the most common.

The estimated median length of the most common prey items ranged from 11.1 cm for herring to 28 cm for cod. The median length for flatfish was 17.9 cm, for sandeel 16.9 cm and for saithe 15.7 cm. The smallest and largest prey items observed were a 2.8 cm saithe and a 58 cm cod, respectively. Significant variation (Kruskal–Wallis test, $p < 0.05$) in the length of saithe was observed between the different sampling periods (Fig. 3). Thus, faeces collected in August 1994 contained otoliths from longer saithe (median 24.9 cm) than saithe from the stomachs collected in

October 1990 (13 cm), October 1994 (15.2 cm) and February/March 1995 (16.9 cm).

DIET VARIATION WITH SEAL AGE

Saithe dominated in the stomachs of all age classes of seals, both numerically (68.3–95.6%) and in calculated weight (62.4–97.4%) (Table 3). Apparently, seals younger than 1 year old tended to include particularly large amounts of saithe in their diets, while in older seals, other prey species, mainly flatfishes (6.8%) and cod (21.1–24.2%), also occurred.

FEEDING EXPERIMENT

Only 14.8% of the fish fed to seal I were recovered as otoliths in the feeding tank. Recovery rates varied between the species: 4.6, 47.7 and 46.6% of herring, haddock and cod, respectively. The recovery rate for whole herring fed to seal II in the first trial was 10%, but when herring and haddock otoliths were implanted in the fish flesh of herring (the second trial), a recovery rate of 18.4% was observed for herring. The recovery rate for haddock in the two trials combined was 91.4%.

The observed species composition of prey, as determined from faecal samples collected in Vesterålen in August 1994, was adjusted in accordance with the results from the feeding experiment with seal I. Numerical correction factors for herring and saithe (the latter based on the combined haddock and cod results from the experiment) were calculated to be 21.6 and 1.5, respectively. If the diet was assumed to consist of only two prey items (i.e. herring and saithe), the estimated relative contribution by herring, based on data from faecal samples and the recovery experiments, would be a little over 80%. This represents a 57% increase in the estimated fraction of the diet made up of herring, based solely on the data from faecal samples.

DISCUSSION

METHODOLOGICAL ASPECTS

The field work was generally allocated to areas where harbour seals are known to congregate during breeding and moult in Vesterålen (see Wiig 1989; Haug & al. 1998). Few seals were, however, observed at these sites in October 1990 and 1994 and in February/March 1995, when they also hauled out in other areas. None of the collected seals contained intact prey in the stomach. One reason may be that the animals were shot close to the haul-out sites at low tide, i.e. after the active foraging period. Seals have a fast digestion (Helm 1984). Havinga (1933) showed that harbour seal stomachs were empty 3 h after the intake of food, while after 6 h the meals were found in the faeces (initial defecation time; IDT). After 14 h the gastrointestinal tracts were completely empty. Helm (1984) and Markussen (1993) found that harbour seal IDTs were 5 h and 3 h and 50 min, respectively.

Another biasing factor in diet investigations based on stomach contents or scat samples is that different parts of the food ingested have different transit times in the gastrointestinal tract (Markussen 1993). Bigg & Fawcett (1985) showed that squid beaks can remain in the stomach for at least a day longer than fish otoliths. Some hard remains tend to accumulate in the stomach, while others pass quickly through the gastrointestinal tract, making diet investigations even more complex.

The presented experiments with captive seals, even though restricted with only two animals involved, illustrate some of the methodological problems in diet analyses of seals. When seals were fed with intact herring, only 4.2–10% of the ingested herring otoliths were retrieved in the experimental tank. The recovery rate tended to increase (to 18.4%) when the herring otoliths were transferred from the head into the fish flesh, although the significance of this increase was not tested statistically. Herring otoliths are generally much less resistant to erosion than gadoid otoliths (Murie & Lavigne 1985; Jobling & Breiby 1986; Jobling 1987). It is, therefore, not surprising that more gadoid otoliths were recovered from seal I, 47.4 and 43.3% for haddock and cod, respectively, than for herring in the present study. Still, these are relatively low gadoid recovery rates compared with other experiments with grey seals (65–98.3%; Prime & Hammond 1987) and with harbour seals (70–92%; Tollit & al. 1997). Different results from various feeding experiments with seals may be related to factors such as differences between species, variations in digestion between individuals, and, maybe even more importantly, differences in experimental design (Helm 1984; Tollit & al. 1997). Certainly, because the present experiments were based on only two animals, and lasted for only 8 days, the results should be treated with caution.

To illustrate the possible magnitude of the bias introduced by the use of faeces in the present study, a correction factor, found in the feeding experiment, was applied. This resulted in a 57% increase (from 23.5% to more than 80% of the total biomass) of herring and a corresponding reduction in saithe in the diet observed in August 1994. Assuming that the results from the experiment are representative, herring is severely underrepresented as compared with gadoids when scat samples are used to assess seal diets. This was also suggested by Jobling (1987), who warned against using faeces in quantitative diet investigations. It should be emphasized that saithe was not used as prey in the feeding experiment. In the Vesterålen faeces samples, therefore, saithe had to be corrected numerically based on the results from cod and haddock. Cod, haddock and saithe have similar otoliths, but the fish used in the experiment were larger than the back-calculated size of saithe found in the stomachs and faeces in Vesterålen. This may have affected the results (see also Tollit & al. 1997).

Diet composition

Given the methodological uncertainties involved and the small sample sizes, it is evident that interpretation of the results must be carried out with caution. The majority of the biomass eaten by harbour seals in Vesterålen appeared to be comprised of relatively few species, where saithe was particularly important. Similar observations have been made in coastal waters of Iceland (Hauksson 1984) and Atlantic Canada (Bowen & Harrison 1996). However, the Vesterålen results differ from studies performed elsewhere in Europe (Sievers 1989; Olsen & Bjørge 1995; Tollit & Thompson 1996; Brown & Pierce 1998; Hall & al. 1998) and in Pacific Canada (Olesiuk 1993; Iverson & al. 1997) where harbour seals were shown to consume a wide range of fish species depending on area, season and sometimes year. Thus, the low varation observed in the relative composition of the diet by season is in contrast to previous investigations in other areas.

The observed low seasonal variation is most likely due to the availability of saithe in Vesterålen throughout the year. Immature saithe are known to be relatively stationary with a coastal distribution in northern Norway, Vesterålen included (Bergstad & al. 1987). The total saithe stock in the area produced strong year classes for the entire period 1988–1993 (Anonymous 1996), and acoustic/trawl surveys carried out in Vesterålen in 1993–1995 revealed that saithe contributed significantly to the fish biomass in the area (J. E. Eliassen, Norwegian Institute of Fisheries and Aquaculture, Tromsø, Norway, pers. comm.). Saithe often aggregate, which may be advantageous to the harbour seals. The high number of small saithe recorded in the seal diet suggests that seals are able to ingest many fish in a relatively short time, which has also been observed in other investigations (Pierce & al. 1990).

Cod contributed considerably to the harbour seal diet, particularly in October 1990 and February/March 1995. Thus, the present investigation in Vesterålen seems to accord with previous observations that gadoids, when available, are important components of harbour seal diets (Härkönen 1987; Pierce & al. 1991b; Bowen & Harrison 1996; Brown & Pierce 1998).

The enhanced contribution from herring in August 1994, as compared with October 1994 and February/March 1995, could be related to the migrational route of adult herring. Mature herring usually occur in Vesterålen in late summer and autumn on their migrational route to Vestfjorden/Ofotfjorden (a little further to the south) where most of the mature stock spend the winter (Dragesund & al. 1997). Hall & al. (1998) suggested that harbour seal diets in the North Sea generally changed seasonally in accordance with the availability of actual prey species. Other investigations have documented that harbour seals may prefer herring (Härkönen & Heide-Jørgensen 1991; Thompson & al. 1991) but they eat small gadoids and sandeels when clupeoids are not available (Härkönen 1988). A faecal sample collected in October 1994 also contained otoliths from herring but this was found above the littoral zone and may, therefore, not necessarily be representative for the period of collection.

Sandeels contributed little to the observed diets, which contrasts with investigations in many other areas where the species has been observed to be seasonally important as prey for harbour seals (Brown & Mate 1983; Payne & Selzer 1989; Pierce & al. 1991a; Tollit & Thompson 1996; Brown & Pierce 1998). Such seasonal importance has also been observed for flatfish (Brown & Mate 1983; Härkönen 1987; Tollit & Thompson 1996), which in the present analyses contributed occasionally.

The observed predation on bullrot (*Myoxocephalus scorpius*) in October resembles observations made in the North Sea where the species was particularly observed to be eaten by harbour seals during late autumn and winter, possibly as a result of increased availability in shallow coastal waters due to spawning (Hall & al. 1998). Bullrot occurring in the vicinity of harbour seal colonies are known to be heavily infected by the sealworm, and it has been suggested that sealworm transmission may involve a large and long-lived reservoir of parasites in small benthic non-exploited fish species such as bullrot (Andersen & al. 1995; Aspholm & al. 1995).

Relatively small variations were observed in the seal diets between October 1990 and October 1994. This is in accordance with the results of Härkönen (1987) who found little inter-annual variation in harbour seal diets in southwestern Sweden. However, considerable changes in the diet were observed in these Swedish areas between 1977–1979 and 1989 (Härkönen & Heide-Jørgensen 1991). Olsen & Bjørge (1995), Tollit & Thompson (1996), Brown & Pierce (1998) and Hall

& al. (1998) have also demonstrated inter-year variations in harbour seal diets that may result from variations in abundance and distribution of potential prey species. The apparently small inter-annual variation in the diet of harbour seals in Vesterålen is most likely due to the stable abundance and distribution of prey in this particular area.

THE SIZE OF PREY SPECIES

Even though the material is restricted, the results tend to suggest that older seals may consume prey species different from those of younger seals. Similar observations were made by Gol'tsev (1971). More clearly, the otoliths found indicate that harbour seals in Vesterålen in general eat relatively small fish (median 15.2 cm). Similar observations have been made in other areas (Brown & Mate 1983; Pierce & al. 1990; Olsen & Bjørge 1995; Tollit & Thompson 1996; Brown & Pierce 1998; Hall & al. 1998). Some observations have indicated that harbour seals do not eat the heads of big fish as often as the heads of smaller fish (Pitcher 1980), which may cause an underrepresentation of larger fish in the observed seal diet.

Apparently, 0-group (3.5–5 cm), 1 year old (14–22 cm) and 2 year old (35 cm) saithe occurred in the harbour seal diet. In Norwegian waters, saithe spawn offshore in February to April, but in contrast to fry from most other fish species, which drift northwards due to the Norwegian coastal current, saithe drift or swim to shallow waters after metamorphosis (Pethon 1985). Young saithe gradually move to deeper waters such that the 0-group specimens live in more shallow water than 1 year olds (Godø & al. 1989). These distributional patterns of young saithe probably contribute to the importance of the species as food for harbour seals in Vesterålen. 0-group saithe did not occur in the seal faeces collected in August 1994, thus suggesting that this year class had not yet arrived into shallow waters at this time of the year.

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