Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed via scat and fatty-acid analyses

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Abstract: This study used hard-part analyses from scats (n = 117) and stomachs (n = 3) to investigate the diet of high Arctic harbour seals (*Phoca vitulina* L., 1758) living on Prins Karls Forland, Svalbard, in early autumn. Additionally, it compared the results of fatty-acid analyses of the seals' blubber versus that of potential prey with the findings of the more traditional diet assessment method. Svalbard harbour seals appear to be opportunistic, polyphagous feeders similar to the situation in other parts of their range. Members of the cod-family, and secondarily the sculpin-family, dominated the diet of harbour seals on Svalbard. Small fish comprised most of the diet of the harbour seals; invertebrates appeared to be insignificant. Atlantic cod (*Gadus morhua* L., 1758) was the most important species in the diet in terms of biomass, whereas polar cod (*Boreogadus saida* (Lepechin, 1774)) was the most frequently consumed prey. Our comparison between hard-part diet analyses and fatty acids is far from definitive, but it indicates a general influence of the diet on the fatty-acid composition of the inner blubber layer. However, it also suggests systematic selective processes in the incorporation of fatty acids into the blubber. Observed differences between the fatty-acid composition of the different blubber layers and possible differences between sex and age classes warrant further investigation.

Résumé : Nous avons analysé les structures dures dans les fèces (n = 117) et les estomacs (n = 3) afin d'étudier le régime alimentaire de phoques veaux marins (*Phoca vitulina* L., 1758) du haut-arctique vivant à Prins Karls Forland, à Svalbard, au début de l'automne. De plus, nous avons comparé les résultats d'analyses d'acides gras du lard des phoques et de leurs proies potentielles avec les résultats des méthodes plus traditionnelles d'évaluation du régime alimentaire. Les phoques veaux marins de Svalbard semblent être des polyphages opportunistes, comme ailleurs dans leur aire de répartition. Le régime alimentaire des phoques veaux marins de Svalbard est dominé par les poissons de la famille de la morue et secondairement de la famille du chabot. Le régime des phoques comprend surtout des poissons de petite taille; l'importance des invertébrés est insignifiante. La morue franche (*Gadus morhua* L., 1758) est l'espèce la plus importante en ce qui a trait à la biomasse, alors que le saïda franc (*Boreogadus saida* (Lepechin, 1774)) est la proie la plus fréquemment consommée. Notre comparaison de l'analyse des structures dures et de l'analyse des acides gras est loin d'être définitive, mais elle montre une influence générale du régime alimentaire sur la composition en acides gras de la couche interne de lard. Elle indique aussi, cependant, l'existence de processus sélectifs systématiques dans l'incorporation des acides gras dans le lard. Les différences observées dans la composition en acides gras des différentes couches de lard et les différences possibles entre les sexes et les différentes classeâge requièrent des études supplémentaires.

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Introduction

Harbour seals (*Phoca vitulina* L., 1758) are a broadly distributed pinniped species that occurs throughout much of the northern hemisphere (Bigg 1981). The northernmost population of this species occurs at Prins Karls Forland, Svalbard. Their occurrence and breeding at this High Arctic archipelago is somewhat surprising given that harbour seals are generally a north-temperate species. Foraging studies have been conducted throughout much of the range of harbour seals, but the diet of harbour seals living on Svalbard is currently totally unknown.

Harbour seals are known to be shallow divers (Bowen et al. 1999; Lesage et al. 1999; Gjertz et al. 2001; Krafft et al. 2002) that feed opportunistically on a wide variety of fish species, as well as some cephalopods and crustaceans. Dominant prey types vary regionally (e.g., Bigg 1981; Bowen and Harrison 1996; Härkönen 1987; Olsen and Bjørge 1995; Tollit et al. 1998) and seasonally (e.g., Pierce et al. 1991; Tollit and Thompson 1996; Brown and Pierce 1998; Hall et al. 1998), as well as interannually (Tollit and Thompson 1996). Harbour seal diet studies considered in combination

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with a specifically designed prey selection study by Tollit et al. (1997) suggest that harbour seals feed on small, schooling, pelagic fishes when these are available, but switch to demersal (benthic) species when the former prey are not abundant in an appropriate form (species, size class, condition, etc.).

Dietary studies on marine mammals have been conducted for several decades using a variety of methodologies (reviewed by Pierce and Boyle 1991). The most frequently used methods have involved the examination of hard-part remains. These prey fragments are usually recovered from scats collected at seal haul-out sites (e.g., Härkönen 1987; Prime and Hammond 1990; Pierce et al. 1991; Hammond et al. 1994; Tollit and Thompson 1996) or retrieved from the contents of stomachs and intestines of dead animals (e.g., Lowry et al. 1980; Finley and Gibb 1982; Gjertz and Lydersen 1986; Bowen et al. 1993; Weslawski et al. 1994; Hjelset et al. 1999). Analyses of hard parts provide important information about diet, but these methods have inherent, well-recognized biases (see da Silva and Neilson 1985; Jobling and Breiby 1986; Dellinger and Trillmich 1988; Harvey 1989; Gales and Cheal 1992; Cottrell et al. 1996). Firstly, hard-part analyses are usually based on scats collected on shore or stomachs collected from seals shot near haul-out areas. Such materials may reflect the last meal ingested from a limited area around the haul-out site (Jobling and Breiby 1986; Murie and Lavigne 1986; Markussen 1993), and hence, only provide information on food habits within a restricted temporal and spatial scale. Secondly, though all otoliths are subject to erosion during digestion, otoliths from different species are degraded at different rates (da Silva and Neilson 1985; Jobling and Breiby 1986; Jobling 1987; Harvey 1989), which can result in a variable and nonrepresentative recovery of ingested otoliths. Additionally, some prey species may not have hard parts or their hard parts may not be ingested. Finally, collected scats can only be definitively assigned to species, sex, or individual by the application of advanced DNA techniques (Reed et al. 1997) or careful observation of the individual animal associated with a particular scat sample. However, despite these shortcomings, the analyses of hard parts retrieved from scats still constitutes a convenient method of diet assessment. Analyses of scat material are at present the most plausible, least invasive means to study diet within small, protected marine mammal populations.

Recently, a new tool has been proposed to investigate marine mammal diet — the analysis of blubber fatty acids (FAs). Marine food webs are generally characterized by great diversity and abundance of long-chained and polyunsaturated FAs, which originate from various forms of unicellular plankton and seaweed (Ackman 1980). The analyses of FAs to explore marine mammal diets is based on the assumption that the relative amounts of the dietary FAs, which are deposited in the tissue of the predator, remain essentially intact through the intermediary metabolic processes of carnivorous mammals (Iverson 1993; Smith et al. 1997). FAs with carbon lengths >14 are thought to be transferred in an especially conservative manner between trophic levels (Iverson 1993; Iverson et al. 1997*a*; Smith et al. 1997; Kirsch et al. 2000). The conservative transfer of a group of FAs called tracer FAs, whose ecological origins can be traced, has suggested the potential for broader applications of FAs to explore feeding habits more generally by using relative ratios of FAs (Iverson 1993; St. John and Lund 1996; Iverson et al. 1997*a*, 2004). Although the presence of some FAs is directly traceable to a specific source, the universality of the use of FAs as dietary tracers is a point of some contention in the recent scientific literature (e.g., Viga and Grahl-Nielsen 1990; Grahl-Nielsen and Mjaavatten 1991; Hove and Grahl-Nielsen 1991; Smith et al. 1997, 1999; Grahl-Nielsen 1999; Grahl-Nielsen et al. 2000).

The present study was part of a broader programme exploring the ecology and population biology of the small harbour seal population on Svalbard. The Svalbard population was estimated to contain some 500–600 animals in the early 1980s (Prestrud and Gjertz 1990). The primary objective of this study was to document the diet of this high Arctic harbour seal population. Because of the small size of this population and its protected status, nondestructive methods of diet assessment were required. To achieve the most complete analyses possible, both hard-part remains and FA composition analyses were performed. The analysis of FAs is a rather new technique in the field of marine mammal diet investigation and few studies have attempted to assess the accuracy of this methodology (Grahl-Nielsen and Mjaavatten 1991; Iverson et al. 1997*a*; Kirsch et al. 1998). The dual assessment approach in this study allowed for a comparison of the results produced by the two methods.

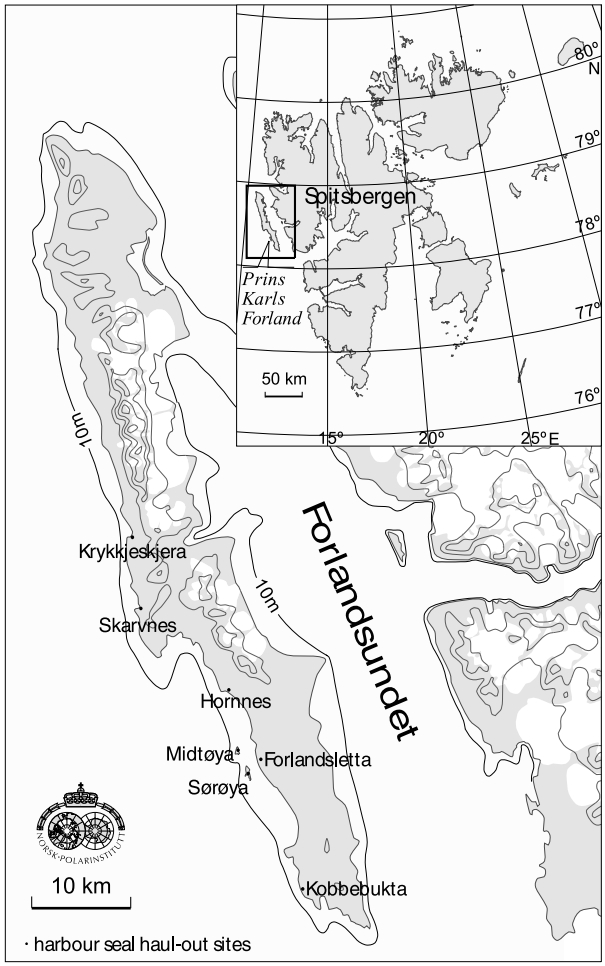
Materials and methods

Prey remains in harbour seal scats and stomachs

During the first 2 weeks in September 1998, a total of 117 scats were collected from harbour seal haul-out sites at Sørøya, on the west coast of Prins Karls Forland, Svalbard (~78°20′N, 11°30′E; Fig. 1). All collections were conducted at or around the time of low tide. Individual scats were placed in polythene bags and frozen at –20 °C until processing. Additionally, three stomachs were opportunistically collected from harbour seals that died during handling (see below); these were also stored at –20 °C prior to analyses.

Scats were thawed in the laboratory, and a few drops of household detergent were added to the samples to emulsify the soft constituents. The scats were then washed through a set of four stacked interlocking sieves (Endecotts) with mesh sizes of 8.00, 2.00, 1.00, and 0.3 mm from top to bottom. Stomach contents were thawed and sorted, initially removing whole, identifiable fish and other prey, and then the unidentifiable components were washed and sieved as described for the scats. Otoliths were identified to the lowest possible taxon, ideally species, using the otolith guide by Härkönen (1986) and the reference collection at the Zoological Museum in Copenhagen, Denmark. The more numerous side (left or right) was used to determine the number of prey consumed by fish species where left- and right-side otoliths could be distinguished. When this was not possible, the number of prey was estimated by dividing the total number of otoliths identified for a given species by 2. Unmatched otoliths were counted as one prey individual. Otolith length was measured (0.01 mm) parallel to the sulcus from the anterior tip of the rostrum to the posterior edge using a dissecting microscope with an ocular micrometer (Carl Zeiss).

Fig. 1. Map showing seven harbour seal (*Phoca vitulina*) haul-out sites on Prins Karls Forland, Svalbard. Sørøya was the primary site where the seals were captured and where the scats were collected for this study. Figure modified from a base map provided by the Norwegian Polar Institute.



Otolith lengths were used to estimate the biomass of the individual prey items consumed by means of otolith length – fish mass correlations obtained from Härkönen (1986) and K.T. Nilssen (personal communication). No correction factors were applied for the degradation of otoliths because of the subjectivity of this sort of adjustment and because appropriate regression equations were not consistently available for the species consumed by the harbour seals in this study. Thus, the size and biomass estimates for species with soft, easily degrading otoliths will be disproportionately underestimated in the calculations presented, and estimates for all species must be considered minimum estimates.

Sampling for FA analyses

During the programme in 1998, a total of 98 harbour seals were caught in tangle nets set from shore near haul-out sites. Captured individuals were brought to land, placed in individual net bags, and processed serially. The harbour seals were weighed and mildly sedated with an intermuscular injection of Zoletil (dose ≤1 mg/kg). Length and girth were measured and sex was determined. One lower incisor was extracted from each harbour seal for age determination. Animals were categorized in the field as being juveniles or adults, based on their body mass, following Bonner (1989). Because blubber biopsies taken through the whole blubber layer are a modestly invasive sampling procedure, sample sizes are kept to a minimum. An a priori sampling protocol was set to select the first five juvenile females, five juvenile males, five adult females, and five adult males captured for blubber biopsy sampling. Samples were to be taken only from animals weighing >40 kg to ensure a sufficient blubber layer thickness. Unfortunately, three animals died during handling. An adult male did not recover from the sedative (this animal is one of the five adult males in the FA analyses) and two small juveniles (one male and one female) were dead upon recovery from the capture net. Although the latter two animals weighed less than our preset sampling mass of 40 kg, the additional blubber samples were collected from these animals and added to the total sample; thus, the total sample size (*n*) for the blubber sampling was 22.

Blubber core samples were taken from the dorsal surface approximately 60% of the way from the nose to the tail using sterile custom-made biopsy punches (diameter of core taken was 8 mm). This specific location on the body was chosen because this region has been shown to be where seasonal changes in blubber thickness are most pronounced (Ryg et al. 1988). Samples were taken through the full depth of the blubber layer (~5 cm). Three equal-sized subsamples (~35 mg), representing the inner (adjacent to the muscle), middle, and outer (adjacent to the skin) blubber layers, were cut from each blubber column. Immediately after sectioning, subsamples were placed in 15 mL thick-walled glass tubes containing a solution of 1 mL anhydrous methanol (MeOH), containing hydrogen chloride (HCl) with a concentration of 2 mol/L, and stored at –20 °C until analysis. All dissecting instruments were cleaned in chloroform prior to handling each subsample. Blanks were prepared on location and were run parallel to the subsequent analysis of blubber samples in the laboratory. Upon completion of fieldwork, air in the glass tubes was replaced by nitrogen gas to prevent oxidation of the FAs. Following this procedure the glass tubes were securely closed with Teflon®-lined screw caps.

Potential harbour seal prey species

The collection of potential harbour seal prey was conducted during two different collecting trips. In October 1998, 106 specimens from a total of 11 species were collected at the mouth of Isfjorden, Svalbard, just south of Prins Karls Forland. These included stout eelblenny, *Anisarchus medius* (Reinhardt, 1837) (*n* = 4); Atlantic poacher, *Leptagonus decagonus* (Bloch and Schneider, 1801) (*n* = 8); sea tadpole, *Careproctus reinhardti* (Krøyer, 1862) (*n* = 4); polar cod, *Boreogadus saida* (Lepechin, 1774) (*n* = 21); long rough dab, *Hippoglossoides platessoides* (Fabricius, 1780) (*n* = 16); capelin, *Mallotus villosus* (Müller, 1776) (*n* = 10); threespot eelpout, *Lycodes rossi* Malmgren, 1865 (*n* = 4); snakeblenny, *Lumpenus lampretaeformis* (Walbaum, 1792) (*n* = 6); starry skate, *Amblyraja radiata* (Donovan, 1808) (*n* = 3); northern pink shrimp, *Pandalus borealis* Krøyer, 1838 (*n* = 21); and sevenline shrimp, *Sabinea septemcarinata* (Sabine, 1824) (*n* = 9). In September 1999, a total of 40 specimens representing 8 additional potential prey species were collected off the west coast of Spitsbergen, just

west of Prins Karls Forland. These included Atlantic cod, *Gadus morhua* L., 1758 (n = 5); Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum, 1792) (n = 5); ribbed sculpin, *Triglops pingelii* Reinhardt, 1837 (n = 5); gelatinous seasnail, *Liparis fabricii* Krøyer, 1847 (n = 5); eelpouts *Lycodes* sp. (n = 5); polka-dot snailfish, *Liparis gibbus* Bean, 1881 (n = 5); daubed shanny, *Leptoclinus maculatus* (Fries, 1837) (n = 5); and deepwater redfish, *Sebastes mentella* Travin, 1951 (n = 5). Prey samples were stored at –20 °C in airtight, lightproof packages until analysis.

In the laboratory, all specimens from each potential harbour seal prey species were homogenized using a mechanical blender. From the resultant mixtures, five replicates were created for each species from the first collecting trip and three replicates were created for each species from the second collecting trip. Each replicate, weighing approximately 50 mg, was transferred to a 15 mL thick-walled glass tube to which a 1.0 mL solution of MeOH:HCl was added.

Methanolysis

Methanolysis of both prey and blubber samples followed the methods outlined in Grahl-Nielsen and Barnung (1985), with the following adjustments: after 5 min at 90 °C, the screw caps were tightened and methanolysis was carried out at 90 °C for an additional 2 h. After methanolysis, approximately half the MeOH:HCl solution was evaporated using nitrogen gas. One and a half millilitres of distilled water was added. The resulting FA methyl esters were extracted twice with 2.0 mL hexane. The phases were mixed on a whirlmixer for 1 min, followed by 5 min of centrifugation (4800 r/m, 2800*g*). The hexane phase was withdrawn using a Pasteur pipette. The two extracts were mixed. Prey samples were methanolysed and extracted using the same methods outlined above for the blubber samples. Blanks were prepared parallel to processing of the prey samples.

Gas chromatographic analysis

One microlitre of each of the mixed hexane extracts was run through a gas–liquid chromatograph (i.e., a Hewlett-Packard 5890A gas chromatograph equipped with a Hewlett-Packard 7673A autosampler and a flame-ionization detector) to separate the individual FA methyl esters in the samples. The column was a 25 m × 0.25 mm (inner diamter) fused silica column coated with polyethylene glycol (CP-WAX 52CB Chrompack) of 0.2 μm thickness, and helium was used as the mobile phase (20 psi; 1 psi = 6.894 757 kPa). The injector temperature was set at 260 °C. After injection, the temperature of the column was kept at 90 °C for 4 min and then increased from 90 to 165 °C at a rate of 30 °C/min followed by a second phase of increase at 3 °C/min to 225 °C. This temperature was maintained for 10.5 min. The flame-ionization detector was set at 330 °C. Samples were analysed in random order with a standard solution (GLC-68D from Nu-Chek-Prep, Elysian, Minnesota, USA, containing 20 FA methyl esters) and pure hexane between every tenth sample. The detector output was coupled to a VG multichrome laboratory data system for storage and treatment of the chromatograms.

The 26 most prominent and well-defined peaks in the chromatograms were selected. They were identified by comparison with chromatograms of known standard mixtures, and named according to the shorthand notation (carbon chain length):(number of double bonds)nX, where nX designates the position of the double bond nearest to the terminal methyl group. Unknown FAs were identified by mass spectroscopy. The detector output was coupled to a VG multichrome laboratory data system for storage and treatment of the chromatograms.

Data analysis

The area units of the 26 peaks were normalized to express the relative (percentage) amounts of the individual FAs within each sample. To compare the various groups of samples on the basis of their FA composition, the data were subjected to multivariate principal component analysis (PCA) (Wold et al. 1987), using Sirius version 6.5 (Kvalheim and Karstang 1987; Pattern Recognition Systems AS 1997–1998). Prior to PCA, the percentage values of the FAs were transformed logarithmically to level out the large numerical differences between FAs.

For statistical analysis of the differences between the inner blubber layer and the prey samples, the data were subjected to soft independent modelling of class analogy (SIMCA) (Wold 1978), within Sirius version 6.5 (Pattern Recognition Systems AS 1997–1998). The percentage values of the FAs of the inner blubber samples were standardized (i.e., for each FA, the percentage value was divided by the standard deviation for that FA). A spatial model of the inner blubber samples was then computed. This model was based on four principle components. This number of components was determined by cross-validation. The outer limit of the model, based on a 95% confidence limit, was determined by the residual standard deviation (RSD_{max}). RSD values for each blubber and prey sample express the distance between the sample and the model. Samples with a RSD value lower than the RSD_{max} value (the rejection criteria) of the model are accepted as belonging within the group.

No attempts were made to assign the scat samples to the sex or age group of the harbour seals producing them; therefore, all sex and age classes were lumped together for the FA analyses, as well as for the comparison of the dietary analysis methods.

All animal handling procedures were conducted in accordance with the principles and guidelines of the Norwegian Council on Animal Care, which parallel those of the Canadian Council on Animal Care.

Results

Prey remains in harbour seal scats and stomachs

Teleost sagittal otoliths were recovered in 92.3% of all scats and in all three stomachs (Table 1). The otoliths of at least 16 species were present in the scat samples and 7 of these species were also found in the stomachs. Additionally, there were cod and sculpin specimens that were placed in two general groupings that we were unable to identify to species which might have included additional species. Because of erosion and breakage, 5.8% and 0.7% of the recovered otoliths were classified as unknown fish in scats and stomachs, respectively. The cumulative number of new prey taxa encountered versus the number of scats analysed

Table 1. Prey information obtained from fish otoliths found in harbour seal, *Phoca vitulina* (Pv), scats (n = 117) and stomachs (n = 3)

	Number of otoliths		Relative frequency (%)		% Frequency of occurrence	
Prey item	Scats	Stomachs	Scats	Stomachs	Scats	Stomachs
Cod-related species						
Unknown cod, species of the family Gadidae	736	226	25.6	53.7	62.4	100
Atlantic cod, *Gadus morhua*	221	105	7.7	24.9	47.0	100
Polar cod, *Boreogadus saida*	908	32	31.6	7.6	54.7	100
Saithe, *Pollachius virens*	66	28	2.3	6.7	10.3	100
Trisopterus sp. (probably Norway pout, *T. esmarkii*)	1	—	0.03	—	0.9	—
Sculpin-related species						
Unknown sculpins, species of the family Cottidae	300	5	10.4	1.2	37.6	66.7
Myoxocephalus sp. (probably bullrout, *M. scorpius*)	70	4	2.4	1.0	18.8	33.3
Gymnacanthus sp. (probably Arctic staghorn sculpin, *G. tricuspis*)	165	10	5.7	2.4	29.9	66.7
Triglops sp. (moustache sculpin, *T. murrayi*,¶ or ribbed sculpin, *T. pingelii*)	21	4	0.7	1.0	12.0	66.7
Unknown flatfish, species of the family Pleuronectidae	2	—	0.1	—	0.9	—
Hippoglossoides sp. (probably long rough dab, *H. platessoides*)	31	—	1.1	—	15.4	—
Lumpenus sp. (probably snake blenny, *L. lampretaeformis*)	105	—	3.7	—	23.9	—
Lycodes sp. (probably Vahl's eelpout, *L. vahli*)	16	—	0.6	—	6.8	—
Capelin, *Mallotus villosus*	3	—	0.1	—	2.6	—
Sebastes sp. (golden redfish, *S. marinus*,¶ or deepwater redfish, *S. mentella*)	13	—	0.5	—	7.7	—
Ammodytes sp. (probably sand lance, *A. marinus*)	2	—	0.1	—	1.7	—
Anarhichas sp. (spotted wolf-fish, *A. minor*,¶ or Atlantic wolf-fish, *A. lupus*)	36	4	1.3	1.0	17.9	100
Sea snails, *Careproctus* sp. (probably *C. reinhardti*)	11	—	0.4	—	5.1	—
Unknown fish species	166	3	5.8	0.7	41.0	66.7
Total	2873	421				

*FM is fish mass, GM is *Gadus morhua*, Bs is *Boreogadus saida*, OL is otolith length, FL is fish length, Ms is *Myoxocephalus scorpius*, Gt is *Gymnacanthus tricuspis*, and Tm is *Triglops murrayi*.

†Biomass of unknown cod or sculpins was calculated proportional to the otolith occurrence of the cod- or sculpin-related species identified in scats or stomachs.

‡Calculated by mean fish length: FL = 16.849 + 20.86OL.

§The equation for *M. scorpius* was used.

‖Calculated for the species marked with a ¶.

reached an asymptote at 58 scats, suggesting that the number of samples analysed in the study was sufficient to identify the majority of prey types in the diet during the early autumn. The seven species identified in the small sample of stomachs (n = 3) were among the nine most commonly identified species within the otoliths recovered in scats.

Cod-related fishes dominated both the scat and the stomach contents, accounting for 67% of the recovered otoliths in scats and 93% of the otoliths in stomachs. The two most important species within the cod grouping were Atlantic cod and polar cod; in combination they accounted for a minimum of 39% of otoliths recovered from scats and 33% from stomachs (plus some proportion of the unknown cod species). In terms of estimated biomass in the diet, these two species represented 39% in the scat samples and 61% in the stomach contents. Polar cod otoliths were proportionally more numerous in the scats than Atlantic cod otoliths, which was the reverse of the situation found in stomachs. Based on the total recovery of otoliths, polar cod was the most commonly taken prey, whereas Atlantic cod was the most important in terms of biomass consumed. Sculpin-related fishes (*Gymnacanthus* sp., species in the family Cottidae, *Myoxocephalus* sp., and *Triglops* sp.) were the second most numerous prey group, representing 19% and 5% of the otoliths recovered and 26% and 4% of the biomass estimated for prey species in scats and stomachs, respectively. The only other fish that accounted for more than 5% of estimated biomass (for scat samples) was the wolf-fish (*Anarhichas* sp.), although this fish species represented only 1.4% of the number of prey consumed.

The estimated size of the fish consumed by the harbour seals, based on the length of the recovered otoliths, ranged from <1 up to 585 g (Table 2). The estimated mean mass of individual prey items from all species was <100 g from both scat and stomach contents. The small size of the fish consumed, suggested by the estimates of length and mass of fishes calculated from otoliths, was consistent with the fresh contents within the few stomach samples that were available. The stomachs all contained only small fishes, including the sample that was from a large adult male.

Polychaete jaws were found in 54 samples. Most of the polychaetes were *Nereis pelagica* L., 1758. The largest individual nereids would have been about 170 mm long and weighed 15 g, based on the jaw sizes. Spines from sea urchins, shrimps parts, carapaces from crabs, and opercula from gastropods were also found in small numbers, but all

collected at Svalbard.

Estimated number of individuals		Biomass(%)			
Scats	Stomachs	Scats	Stomachs	Otolith length to fish mass relationships*	Source
437	117	23.7	31.4	FM = 0.19Gm + 0.76Bs + 0.05Pv (FM = 0.63Gm + 0.19Bs + 0.17Pv)†	
158	55	29.2	59.7	$FM = 0.006855OL^{4.435}$	Härkönen 1986
526	18	9.7	1.3	$FM = 3.6 \times 10^{-6}FL^{3.12}$‡	Härkönen 1986
39	17	0.4	0.6	$FM = 0.007288OL^{4.501}$	Härkönen 1986
1	—	0.04	—	$FM = 0.002805OL^{4.729}$	Härkönen 1986
187	4	9.7	0.6	FM = 0.27Ms + 0.65Gt + 0.08Tm (FM = 0.22Ms + 0.56Gt + 0.22Tm)†	
49	2	5.3	1.3	$FM = 0.2261OL^{3.496}$	Härkönen 1986
111	5	10.3	1.3	$FM = 0.2261OL^{3.496}$§	
19	3	0.7	0.6	$FM = 0.3307OL^{3.274}$	K.T. Nilssen, personal communication
1	—	—	—	—	
24	—	2.9	—	$FM = 0.166OL^{3.788}$	Härkönen 1986
70	—	1.3	—	$FM = 0.374OL^{3.668}$	K.T. Nilssen, personal communication
12	—	0.4	—	$FM = 1.002OL^{1.933}$	Härkönen 1986
3	—	0.04	—	$FM = 1.163OL^{2.742}$	Härkönen 1986
11	—	0.7	—	$FM = 0.0741OL^{3.295}$‖	Härkönen 1986
2	—	0.02	—	$FM = 0.61215OL^{2.71}$	Härkönen 1986
25	4	5.7	3.1	$FM = 5.290OL^{4.08}$‖	Härkönen 1986
8	—	—	—	—	
83	2	—	—	—	

of these invertebrate remains were too eroded for accurate identification, and hence, were not analysed in further detail. Three samples contained identifiable beaks from the cephalopod *Gonatus fabricii* (Lichtenstein, 1818), and several samples contained eye lenses from cephalopods. The size class of squid represented by the beaks would have weighed about 10 g.

FA composition of harbour seal blubber

A total of 26 different FAs were identified and quantified in all harbour seal blubber subsamples (n = 66 in total consisting of 22 individuals from the inner, middle, and outer blubber areas, respectively; Table 3). The predominant FAs were palmitic (16:0), palmitoleic (16:1n7), oleic (18:1n9), and docosahexaenoic acid (22:6n3). These FAs accounted for approximately 60% of the total FAs.

Significant differences were found in FA composition between the three blubber layers (Tables 3, 4). Generally, the amounts of saturated fatty acids (SFAs) and polyunsaturated fatty acids (PUFAs) increased, whereas the amount of monounsaturated fatty acids (MUFAs) decreased towards the core. PCA employed on all FAs simultaneously confirmed the differences in FA composition between blubber layers (Table 3, Fig. 2). The FA composition changed gradually from the inner to the outer blubber layers in all sex and age classes (Figs. 2*a*–2*d*), with the middle layer being crudely intermediate between the inner and outer blubber layers for each age or sex group. PCA revealed distinctions between the FA composition of the four sex and age classes (Figs. 3*a*, 3*b*). The inner and outer blubber layers of adult females were significantly different than those of adult males. Juvenile males and females overlapped with one another and to some extent with adults of their respective sex.

FA composition of potential harbour seal prey species

The predominant FAs (16:0, 16:1n7, 18:1n9, and 22:6n3) in all of the prey species were similar to those that were dominant in the harbour seal blubber (Table 5). These four FAs represented approximately 50% of the total FAs in the various fish species. Additionally, 20:1n9 and 22:1n11 occurred in high amounts (~9% of total FAs) in capelin, polar cod, spotted snakeblenny, and Greenland halibut. 20:1n9 dominated in deepwater redfish, gelatinous seasnail, and long rough dab. Clear distinctions between the FA compositions of the various prey species existed (Fig. 4).

Table 2. Estimated mean and range of body mass (g) for each species of fish consumed by harbour seals on Prins Karls Forlandet, Svalbard, for which otolith length/fish length and fish length/fish mass regressions are available (see Table 1 for sample sizes and regression sources).

	Scats		Stomachs	
Prey items	Mass (mean ± SD)	Mass range	Mass (mean ± SD)	Mass range
Unknown cod, species of the family Gadidae	15±18	1–105	22±27	1–90
Atlantic cod	61±49	3–234	90±107	10–585
Polar cod	5±6	1–54	7±7	1–28
Saithe	4±1	2–9	5±3	3–13
Trisopterus sp. (probably Norway pout)	18	—	—	–
Unknown sculpins, species of the family Cottidae	15±15	1–193	11±8	2–21
Myoxocephalus sp. (probably bullrout)	35±28	5–194	38±2	36–39
Gymnacanthus sp. (probably Arctic staghorn sculpin)	28±19	6–106	24±11	17–53
Triglops sp. (moustache* sculpin or ribbed sculpin)	15±11	7–59	15±10	5–25
Hippoglossoides sp. (probably long rough dab)	46±22	5–97	—	–
Lumpenus sp. (probably snake blenny)	6±4	1–23	—	–
Lycodes sp. (probably Vahl's eelpout)	15±3	5–16	—	–
Capelin	7±1	6–8	—	–
Sebastes sp. (golden* redfish or deepwater redfish)	19±8	7–27	—	–
Ammodytes sp. (probably sand lance)	7	—	—	–
Anarhichas sp. (spotted* wolf-fish or Atlantic wolf-fish)	72±56	20–274	113±63	50–180

*Values are from this species.

Comparison of FA composition in blubber and potential prey species

The FA composition of the inner blubber layer resembled those of the prey most closely (Fig. 4). However, all prey species had FA compositions that were different from this layer (Figs. 4, 5). Detailed analysis of the innermost blubber layer and the prey species revealed that polar cod, ribbed sculpin, and Atlantic cod were the three species that were the most similar to the innermost blubber layer (Fig. 5).

Discussion

The hard-part analyses, using materials from scats and stomachs, demonstrated that the diet of harbour seals from Prins Karls Forland, Svalbard, includes a wide variety of prey items, and hence, confirms the generally acknowledged polyphagous and opportunistic nature of this species with respect to its foraging activity (Behrends 1985; Payne and Selzer 1989; Sievers 1989; Olsen and Bjørge 1995; Tollit et al. 1997). Harbour seals are thought to consume prey species largely, but not solely, according to their abundance. Fish remains dominated all samples in this study, with few indications that invertebrates were taken. Some polychate worms, shrimp, crab, squid, and other invertebrate parts were present in small numbers and could have been primary prey of harbour seals. But, if these animals were not secondary prey that were consumed initially by the fish, then they were either underrepresented in the analyses or made up only a small fraction of the harbour seal diet at Svalbard.

The contents of both the harbour seal scat samples and the few stomachs that were available were dominated by members of the cod family (Gadidae). This finding is consistent with studies of the diet of harbour seals from other locales; Gadidae are found to dominate the diet in many harbour seal feeding analyses (e.g., Härkönen 1988; Härkönen and Heide-Jørgensen 1991; Olesiuk 1993; Olsen and Bjørge 1995; Tollit et al. 1997; Brown and Pierce 1998). In Svalbard, polar cod were the most frequently consumed fish species, whereas Atlantic cod was the most important in terms of biomass. Three species that were found in all three stomach samples were Atlantic cod, polar cod, and saithe. The first two species were also found in almost half of the scats analysed, although the third species (saithe) were much less common in the scats. The cod family was followed in prevalence by sculpins in both the scats and the stomachs. The other prey species that occurred with lower frequency were mainly benthic dwelling fish. All of the prey types identified in the stomachs were also found in scats. The fish consumed by the harbour seals were small in size. If larger prey was eaten and the heads simply not consumed so that large otoliths were underrepresented, there was no evidence of this in our small stomach collection.

Two non-cod pelagic species were found in the scat samples (i.e., capelin and redfish), but these made up <1% of the biomass consumed by Svalbard harbour seals. Herring (*Clupea harengus* L., 1758; Clupeidae) have been found to be important prey of harbour seals at more southerly locations (Olesiuk 1993; Olsen and Bjørge 1995; Tollit et al. 1997), but these fish do not generally occur at the latitude of Svalbard. However, sand lance (*Ammodytes marinus* Raitt, 1934) are present at Svalbard and are a common prey species for harbour seals elsewhere in the northeast Atlantic, United Kingdom (Tollit et al. 1997; Brown and Pierce 1998), as well as on the eastern coast of the United States (Payne and Selzer 1989). However, they were found in only two of the scat samples and were not present in the stomach samples in this study.

Harbour seals in Svalbard tend to remain in the vicinity of Prins Karls Forland all year round, and most of their dives are to shallow or moderate depths (Gjertz et al. 2001; Jørgensen et al. 2001; Krafft et al. 2002), similar to harbour seal diving at other geographic locations (e.g., Bowen et al. 1999; Lesage et al. 1999). During the early fall, which was the period in which this diet study was conducted, harbour

Table 3. Relative amounts (percentage of sum ± SD) of fatty acids in three blubber layers of four sex and age classes of harbour seals from Prins Karls Forland, Svalbard.

	Adult males			Adult females			Adult males			Adult females		
Fatty acid*	Inner	Middle	Outer	Inner	Middle	Outer	Inner	Middle	Outer	Inner	Middle	Outer
14:0	2.4±0.7	2.1±0.3	2.0±0.2	2.3±0.4	2.2±0.2	2.1±0.3	2.8±0.3	2.7±0.2	2.4±0.3	2.8±0.5	2.7±0.1	2.5±0.2
14:ln5	0.3±0.1	1.0±0.4	1.4±0.2	0.5±0.3	1.5±0.9	1.7±0.3	0.6±0.3	2.1±0.6	1.8±0.5	0.9±0.5	2.2±0.5	1.9±0.6
15:0	0.26±0.06	0.21±0.04	0.21±0.01	0.25±0.05	0.21±0.03	0.23±0.03	0.25±0.03	0.21±0.02	0.21±0.2	0.24±0.03	0.20±0.02	0.21±0.04
i-15:0	0.19±0.01	0.18±0.01	0.15±0.02	0.17±0.02	0.16±0.01	0.15±0.03	0.18±0.03	0.16±0.02	0.13±0.01	0.17±0.02	0.15±0.02	0.15±0.02
16:0	10±2	5±2	5.2±0.8	10±3	7±2	4.8±0.4	9±1	7.3±0.8	6±1	8±1	7.4±0.4	6.5±0.8
16:ln7	10±3	16±2	20±1	14±1	21±5	26±2	15±3	26±4	26±3	18±3	28±5	28±4
16:3n4	0.44±0.09	0.56±0.5	0.62±0.05	0.51±0.05	0.56±0.06	0.66±0.04	0.41±0.04	0.47±0.04	0.51±0.06	0.43±0.07	0.46±0.02	0.49±0.03
17:0	0.23±0.05	0.12±0.4	0.11±0.02	0.20±0.04	0.13±0.04	0.12±0.02	0.16±0.04	0.11±0.03	0.11±0.01	0.14±0.03	0.10±0.01	0.14±0.03
18:0	2.5±0.8	0.8±0.4	1.2±0.6	1.6±0.6	0.9±0.4	0.7±0.3	1.3±0.3	0.7±0.2	1.0±0.2	1.1±0.3	0.7±0.1	1.0±0.3
18:ln9	29±6	29±2	31±3	25±3	25±1	29±3	24±3	23±1	28±3	24±2	23±1	27±3
18:ln7	8±1	6.9±0.6	6.9±0.5	7.2±0.3	7.4±0.8	7.3±0.5	6±1	6.9±0.3	7.1±0.4	6.5±0.7	6.7±0.3	6.9±0.3
18:2n6	1.4±0.2	1.6±0.2	1.8±0.2	1.7±0.3	1.6±0.2	1.9±0.3	1.4±0.2	1.2±0.2	1.4±0.2	1.4±0.2	1.2±0.1	1.4±0.1
18:3n3	0.5±0.1	0.8±0.1	0.66±0.07	0.9±0.2	0.7±0.2	0.7±0.1	0.7±0.3	0.5±0.1	0.5±0.1	0.7±0.1	0.5±0.1	0.44±0.03
18:4n3	1.3±0.4	1.7±0.1	1.2±0.5	1.9±0.4	1.5±0.2	1.0±0.2	1.9±0.5	1.3±0.2	0.9±0.1	1.9±0.4	1.2±0.4	0.83±0.08
20:0	0.14±0.07	0.05±0.2	0.07±0.04	0.06±0.02	0.04±0.02	0.04±0.01	0.05±0.01	0.03±0.01	0.06±0.02	0.05±0.01	0.03±0.01	0.06±0.02
20:ln9	10±2	7±1	4.4±0.7	5±1	4±1	2.8±0.3	7.9±0.6	3.6±0.8	4±1	7±3	3±1	4±1
20:2n6	0.40±0.09	0.35±0.07	0.25±0.04	0.42±0.04	0.33±0.09	0.24±0.04	0.29±0.04	0.22±0.05	0.19±0.02	0.28±0.07	0.20±0.04	0.17±0.02
20:4n6	0.9±0.4	0.9±0.2	1.7±0.6	1.5±0.7	1.5±0.4	1.9±0.7	0.65±0.08	1.02±0.08	1.5±0.3	0.9±0.4	1.2±0.4	1.6±0.2
20:3n3	0.08±0.01	0.11±0.02	0.08±0.01	0.18±0.06	0.15±0.04	0.11±0.02	0.10±0.03	0.09±0.02	0.07±0.01	0.11±0.03	0.09±0.02	0.08±0.02
20:5n3	4±2	6.8±0.4	6±1	9±1	8.4±0.3	6.5±0.4	7±1	7.0±0.9	5.8±0.5	7.7±0.4	6.7±0.6	5.8±0.3
22:0	0.03±0.01	0.02±0.01	0.02±0.01	0.02±0.01	0.02±0.01	0.02±0.01	0.02±0.01	0.02±0.01	0.03±0.01	0.01±0.01	0.02±0.01	0.03±0.01
22:lnl1	1.9±0.8	0.5±0.3	0.2±0.1	0.5±0.3	0.2±0.1	0.09±0.04	1.8±0.5	0.3±0.1	0.3±0.1	2±1	0.3±0.3	0.3±0.1
22:ln9	0.7±0.3	0.2±0.1	0.2±0.1	0.18±0.08	0.11±0.05	0.05±0.01	0.37±0.8	0.10±0.03	0.13±0.09	0.3±0.2	0.10±0.05	0.09±0.03
22:5n3	6±1	6.9±0.4	5.1±0.9	6±1	5.8±0.9	4.6±0.4	6.0±0.2	4.8±0.9	4.1±0.3	5.6±0.8	4.6±0.6	3.8±0.1
22:6n3	8±2	10.8±0.9	9±2	11±2	10.1±0.7	7.8±0.5	11±2	9±1	7.5±0.5	10.3±0.8	9±1	7.0±0.5
24:ln9	0.4±0.1	0.09±0.03	0.3±0.3	0.15±0.05	0.06±0.06	0.2±0.1	0.2±0.1	0.03±0.01	0.2±0.1	0.11±0.05	0.03±0.02	0.2±0.2
ΣSFA	16±2	9±2	9±1	14±3	10±2	8±1	13±1	11±1	11±11	13±1	11±1	11±1
ΣMUFA	61±7	61±3	65±4	53±3	59±6	66±3	57±4	63±5	67±5	58±5	64±5	68±6
ΣPUFA	23±4	30±1	26±2	33±3	30±1	26±1	30±2	26±2	22±1	29±1	25±2	22±1

*Fatty acids are as follow, with common names in parentheses if available: 14:0, tetradecanoic acid (myristic acid); 14:1n5, 9c-tetradecenoic acid (myristoleic acid); 15:0, pentadecanoic acid; i-15:0, 13-methyltetradecanoic acid; 16:0, hexadecanoic acid (palmitic acid); 16:1n7, 9c-hexadecenoic acid (palmitoleic acid); 16:3n4, 6c,9c,12c-hexadecenoic acid; 17:0, heptadecanoic acid (margaric acid); 18:0, octadecanoic acid (stearic acid); 18:1n9, 9c-octadecenoic (oleic acid); 18:1n7, 11c-octadecenoic acid (*cis*-vaccenic acid); 18:2n6, 9c,12c-octadecadienoic acid (linoleic acid); 18:3n3, 9c,12c,15c-octadecatrienoic acid (α-linolenic acid); 18:4n3, 6c,9c,12c,15c-octadecatetraenoic (stearidonic acid); 20:0, eicosanoic acid (arachidic acid); 20:1n9, 11c-eicosenoic acid (gadoleic acid); 20:2n6, 11c,14c-eicosadienoic acid (dihomolinoleic acid); 20:4n6, 5c,8c,11c,14c-eicosatetraenoic acid (arachidonic acid); 20:3n3, 11c,14c,17c-eicosatrienoic acid; 20:5n3, 5c,8c,11c,14c,17c-eicosapentaenoic acid (timnodonic acid); 22:0, docosanoic acid (behenic acid); 22:1n11, 11c-docosenoic acid (cetoleic acid); 22:1n9, (13c-docosenoic acid (erucic acid); 22:5n3, 7c,10c,13c,16c,19c-docosapentaenoic acid (clupadonic acid); 22:6n3, 4c,7c,10c,13c,16c,19c-docosahexaenoic acid (cervonic acid); 24:1n9, 13c-tetracosenoic acid (nervonic acid); ΣSFA, sum of the saturated fatty acids; ΣMUFA, sum of the monounsaturated fatty acids; and ΣPUFA, sum of the polyunsaturated fatty acids.

Table 4. Statistical overview of the differences in SFA, MUFA, and PUFA contents in three blubber layers of four sex and age classes of harbour seals from Prins Karls Forland, Svalbard.

	Juvenile females (n = 6)			Juvenile males (n = 6)			Adult females (n = 5)			Adult males (n = 5)			All harbour seals (n = 22)			Adult males excluded (n = 17)		
	Inner–outer	Inner–middle	Middle–outer	Inner–outer	Inner–middle	Middle–outer	Inner–outer	Inner–middle	Middle–outer	Inner–outer	Inner–middle	Middle–outer	Inner–outer	Inner–middle	Middle–outer	Inner–outer	Inner–middle	Middle–outer
SFA	*	*	ns	*	*	ns	*	*	ns	*	*	ns	*	*	ns	*	*	*
MUFA	*	*	*	*	*	*	*	*	*	ns	ns	ns	*	*	*	*	*	*
PUFA	*	*	*	*	*	*	*	*	*	ns	*	ns	*	ns	*	*	*	*

Note: Significance (*, $p < 0.05$) of the data was tested using a Kruskal–Wallis test followed by a Tukey's a posteriori test; ns indicates no significant difference.

Fig. 2. Principal component (PC) plots of inner (solid symbols), middle (half-filled symbols), and outer (open symbols) harbour seal blubber layers of adult males (*a*), adult females (*b*), juvenile males (*c*), and juvenile females (*d*). The first two PCs represent at least 85% of the variance in the samples for each age or sex class.

seals forage intensively. Most of the diving done (at least by juvenile animals) during this season is to average depths of about 40 m, although some diving is done to depths beyond 150 m (Krafft et al. 2002). Additionally, most of the diving is done in the evening and in the very early morning hours, with a lull in diving activity around midday. The depths of the dives during a bout of diving, which usually lasts about 12 h (Krafft et al. 2002), are remarkably consistent from dive to dive within a bout, which is likely because they are diving to the bottom. This is consistent with the fact that most of the prey found in this diet analysis is benthic prey.

The FAs that dominated the harbour seal blubber composition in this study were the same FAs that have been reported to be the most prevalent in other harbour seal populations (West et al. 1979; Fredheim et al. 1995; Iverson et al. 1997*b*), as well as in a number of other marine mammals (West et al. 1979; Fredheim et al. 1995; Dahl et al. 2000). Relative abundances of different FAs in seals and other marine mammals have been attributed to sex-specific patterns (West et al. 1979), age-specific patterns (Grahl-Nielsen and Mjaavatten 1995), reproductive state (Aguilar and Borrell 1990), species- or population-specific genetic determination (West et al. 1979; Innis and Kuhnlein 1987; Grahl-Nielsen and Mjaavatten 1995; Fredheim et al. 1995; Borobia et al. 1995), habitat type (limnic, marine) (Käkelä et al. 1993, 1995), the seasonal time of sampling (e.g., fasting and fattening up; see Iverson et al. 1997*b*), and to dietary differences (e.g., Ackman et al. 1971, 1975; Innis and Kuhnlein 1987; Käkelä et al. 1993; Iverson et al. 1995; Dahl

Fig. 3. Graphical representations of soft independent modelling of class analogy (SIMCA) models of the fatty-acid composition of the inner (*a*) and outer blubber (*b*) layers of habour seals from Svalbard (squares are adult males; circles are adult females; triangles are juvenile females; diamonds are juvenile males). The dotted lines indicate 95% confidence limits around the models.

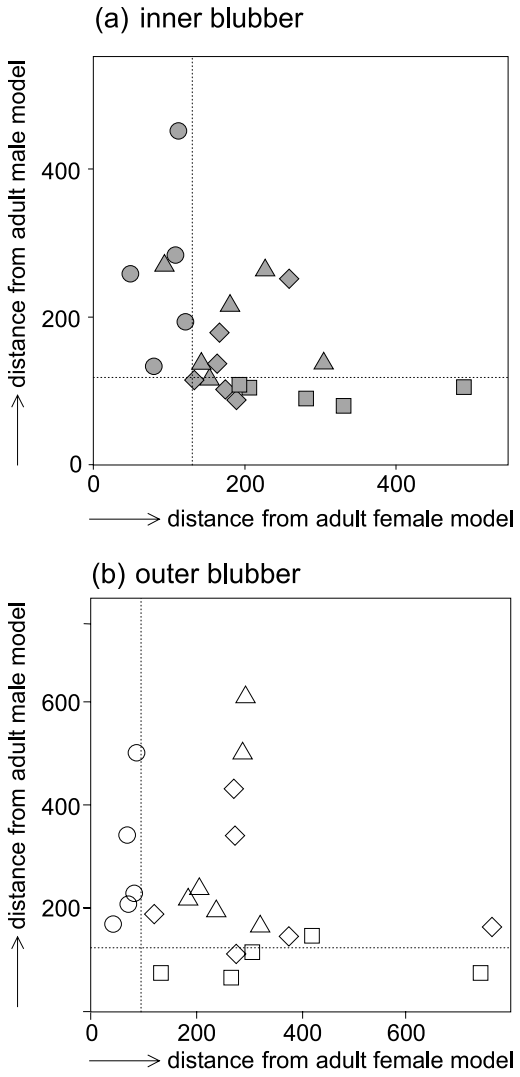
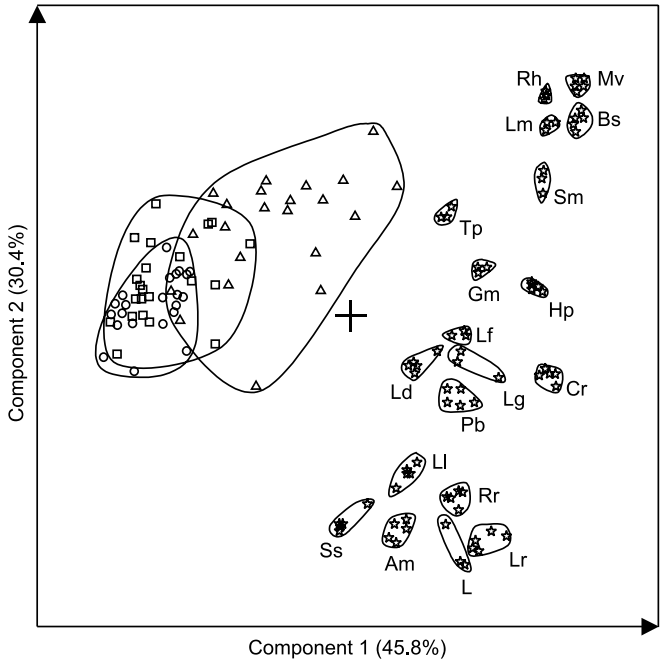


Fig. 4. Principal component plot of inner (△), middle (□), and outer (○) harbour seal blubber layers versus potential prey species (☆). Three principal components were retained in the analyses, which explained 83.5% of the variance, although only the two most important PCs are illustrated here. The prey species are *Mallotus villosus* (Mv), *Gadus morhua* (Gm), *Boreogadus saida* (Bs), *Lycodes rossi* (Lr), *Lycodes* sp. (L), *Sebastes mentella* (Sm), *Triglops pingelii* (Tp), *Leptagonus decagonus* (Ld), *Liparis gibbus* (Lg), *Liparis fabricii* (Lf), *Careproctus reinhardti* (Cr), *Lumpenus lampretaeformis* (Ll), *Lumpenus maculatus* (Lm), *Anisarchus medius* (Am), *Hippoglossoides platessoides* (Hp), *Reinhardtius hippoglossoides* (Rh), *Raja radiata* (Rr), *Pandalus borealis* (Pb), and *Sabinea septemcarinata* (Ss).



et al. 2000). These parameters should not be considered mutually exclusive, of course, in that the diet of an animal is often influenced by its age, sex, the seasonal availability of food, etc., simultaneously (e.g., Thompson et al. 1998).

Similar to other studies, this study documented distinct differences in the FA compositions of the various layers in the blubber (e.g., Borobia et al. 1995; Fredheim et al. 1995; Olsen and Grahl-Nielsen 2003). This finding is not surprising given that blubber serves a variety of functions, including thermoregulation, streamlining the body, and energy storage; hence, its composition varies with the different functions that dominate as one moves from the metabolically active, warm core outwards to the more structural, less metabolically active, and cooler conditions at the skin.

Although age and sex differences observed in our study needed to be treated with caution because sample sizes were small for each age and sex classes, some interesting trends were observed. Adult males and adult females had significantly different compositions in their inner and outer blubber layers. This may be due to the females' blubber stores being dramatically depleted during the nursing period from mid-June to mid-July. During the short, intense lactation period in phocid seals, lipid metabolism is intensified and the FA composition of the blubber changes as a consequence of a selective utilization of particular depot FAs (Iverson et al. 1995; Grahl-Nielsen et al. 2000). Depot fats of adult males would not be as dramatically affected by the reproductive period as those of females. The similarity in the FA compositions of juvenile males and juvenile females in this study suggests a lack of inherent sexual differences, although juveniles of each sex appear to be most similar to adults of their respective sex. The differences among age and sex classes suggested in this study warrant further investigation with larger sample sizes.

The degree to which blubber FAs can be used as a diagnostic tool for determining the diet of marine mammals is a subject that is currently under debate (Grahl-Nielsen and Mjaavatten 1991; Smith et al. 1997, 1999; Grahl-Nielsen 1999; Iverson et al. 2004). Some studies suggest that even fine-scale shifts in diet can be detected using ratios of spe-

Table 5. Relative amounts (percentage of sum ± SD) of fatty acids in potential prey species of harbour seals from Prins Karls Forland,

Fatty acid	Mv	Gm	Bs	Lr	Ls	Sm	Tp	Ld	Lg	Lf
14:0	7.4±0.04	2.54±0.05	3.09±0.03	1.64±0.02	2.0±0.3	2.8±0.2	3.27±0.06	2.72±0.05	2.3±0.1	1.92±0.05
14:ln5	0.15±0.01	0.39±0.05	0.07±0.01	0.05±0.01	0.33±0.04	0.15±0.02	0.25±0.01	0.19±0.01	0.2±0.1	0.4±0.2
15:0	0.45±0.01	0.06±0.02	0.35±0.01	0.53±0.01	0.08±0.01	0.07±0.01	0.05±0.01	0.40±0.01	0.04±0.01	0.04±0.02
i-15:0	0.27±0.01	0.08±0.01	0.23±0.01	0.16±0.01	0.12±0.02	0.04±0.01	0.07±0.01	0.26±0.01	0.06±0.01	0.08±0.01
16:0	16.35±0.08	14.0±0.2	11.8±0.2	14.5±0.4	14.6±0.7	11.44±0.06	15.00±0.09	13.1±0.1	14.1±0.3	12.13±0.09
16:ln7	8.27±0.04	8.40±0.05	10.7±0.2	8.5±0.5	10±2	14.0±0.5	11.9±0.1	14.3±0.2	3.95±0.08	8.67±0.03
16:3n4	0.30±0.01	0.35±0.01	0.22±0.01	0.87±0.75	0.67±0.08	0.33±0.01	0.31±0.01	0.58±0.01	0.44±0.02	0.5±0.2
17:0	0.15±0.01	0.32±0.01	0.17±0.01	0.75±0.04	0.81±0.05	0.20±0.01	0.18±0.01	0.25±0.01	0.47±0.01	0.35±0.08
18:0	1.50±0.01	3.06±0.06	2.37±0.04	4.5±0.2	4.9±0.4	3.1±0.1	2.06±0.01	2.08±0.07	3.3±0.2	2.47±0.04
18:ln9	14.5±0.1	11.9±0.2	10.53±0.09	9.2±0.1	7.5±0.2	14.1±0.2	20.28±0.09	16.9±0.3	17.6±0.6	14.8±0.2
18:ln7	4.12±0.02	5.22±0.01	3.69±0.05	8.4±0.2	8.5±0.2	5.86±0.08	6.88±0.06	10.70±0.06	5.68±0.09	8.9±0.1
18:2n6	1.54±0.02	1.13±0.01	0.99±0.01	1.18±0.02	0.63±0.07	0.75±0.01	1.12±0.02	1.01±0.02	1.10±0.02	0.9±0.4
18:3n3	1.09±0.01	0.86±0.01	0.49±0.02	0.20±0.01	0.19±0.04	0.31±0.01	0.67±0.01	0.31±0.01	0.70±0.01	0.18±0.01
18:4n3	4.74±0.02	2.49±0.02	1.71±0.01	0.81±0.07	0.7±0.1	1.81±0.09	2.31±0.02	0.86±0.03	1.98±0.06	0.54±0.03
20:0	0.11±0.01	0.05±0.001	0.05±0.01	0.08±0.01	0.13±0.01	0.11±0.02	0.03±0.01	0.10±0.01	0.03±0.02	0.08±0.03
20:ln9	9.03±0.09	6.65±0.07	16.4±0.4	2.5±0.2	1.9±0.1	12.2±0.4	6.4±0.3	4.58±0.06	4.4±0.01	8.9±0.1
20:2n6	0.23±0.01	0.37±0.01	0.24±0.01	0.40±0.02	0.62±0.07	0.30±0.08	0.23±0.03	0.40±0.01	0.47±0.01	0.38±0.02
20:4n6	0.36±0.01	0.81±0.04	0.55±0.03	7.3±0.2	5.4±0.6	1.33±0.08	0.41±0.01	2.63±0.03	1.5±0.2	3.00±0.07
20:3n3	0.12±0.01	0.13±0.01	0.08±0.01	0.10±0.01	0.15±0.02	0.05±0.01	0.09±0.01	0.08±0.01	0.20±0.01	0.07±0.01
20:5n3	9.63±0.06	14.5±0.2	10.6±0.2	14.3±0.3	18.4±0.7	11.4±0.5	13.1±0.2	14.0±0.2	15.6±0.3	14.5±0.3
22:0	0.07±0.01	0.05±0.01	0.04±0.01	0.43±0.01	0.40±0.03	0.16±0.06	0.03±0.01	0.19±0.01	0.07±0.01	0.19±0.01
22:ln11	9.5±0.1	2.08±0.02	8.9±0.4	0.60±0.07	0.37±0.06	7.7±0.4	3.0±0.2	1.67±0.04	0.52±0.02	2.30±0.05
22:ln9	0.83±0.03	0.43±0.01	1.45±0.05	0.54±0.06	0.50±0.04	1.41±0.05	0.73±0.06	0.65±0.05	0.66±0.01	0.57±0.01
22:5n3	0.3±0.2	1.03±0.02	1.00±0.01	1.72±0.01	2.0±0.2	1.00±0.07	1.02±0.04	1.58±0.03	1.00±0.03	2.05±0.03
22:6n3	8.3±0.1	22.3±0.1	13.4±0.3	18.2±0.6	17±1	8.7±0.6	10.2±0.2	9.7±0.3	22.4±0.5	15.0±0.3
24:ln9	0.75±0.04	0.72±0.07	0.97±0.06	2.5±0.2	1.9±0.3	0.62±0.08	0.42±0.02	0.77±0.06	1.2±0.6	1.09±0.06
Σ SFA	26.3±0.1	20.2±0.2	18.1±0.2	22.6±0.5	23.1±0.9	18.0±0.2	20.7±0.1	19.1±0.1	20.4±0.4	17.2±0.1
Σ MUFA	47.2±0.2	35.8±0.2	52.6±0.6	32.3±0.6	31±2	56.1±0.8	49.8±0.4	49.8±0.4	34.2±0.8	45.6±0.4
Σ PUFA	26.5±0.3	44.0±0.2	29.3±0.4	45.1±0.7	46±2	26.9±0.8	29.6±0.3	31.1±0.4	45.4±0.6	37.2±0.6

Note: Refer to Table 3 for the list of fatty acids. The species are as follows: Mv, *Mallotus villosus*; Gm, *Gadus morhua*; Bs, *Boreogadus saida*; Lr, *Careproctus reinhardti*; Ll, *Lumpenus lampretaeformis*; Lm, *Lumpenus maculatus*; Am, *Anisarchus medius*; Hp, *Hippoglossoides platessoides*; Rh,

cific FAs in the blubber because the blubber mirrors the FA composition of the diet (Iverson et al. 1995, 1997*b*; Smith et al. 1997). Other studies, however, suggest that dietary effects are masked by differential absorption, breakdown, and storage of different FAs, which occur at least in part on a species-specific basis and result in FA ratios that at best would be crude dietary indicators, beyond the tracer FAs. Diet-induced changes have been demonstrated in blubber FA compositions through feeding experiments in fish (Kirsch et al. 1998), and low-fat diets fed to harp seals (*Pagophilus groenlandicus* (Erxleben, 1777); Kirsch et al. 2000) and various fish and invertebrate species have been shown to have distinctive FA signatures (Budge et al. 2002; Iverson et al. 2002). However, a diet composed of known ratios of FAs does not necessarily translate into similar blubber compositions in marine mammals (Grahl-Nielsen et al. 2000; Olsen and Grahl-Nielsen 2003). Several authors have stressed that blubber FA compositions do not precisely match those of the prey items (Viga and Grahl-Nielsen 1990; Kirsch et al. 2000). Kirsch et al. (2000) suggested that this might be due to differential utilization of FAs or the synthesis of specific FAs. The FA composition analysis performed in this study revealed that the innermost blubber layer of the harbour seals resembled the prey most closely, suggesting that dietary lipids likely influence this layer most directly. This is consistent with the innermost layer being the most metabolically active blubber layer (Fredheim et al. 1995; Koopman et al. 1996; Käkelä and Hyvärinen 1996).

The analyses of potential prey versus blubber FA compositions did have some limitations in this study. Some of the fish species found in the hard-part analyses were not available to run in the FA analyses. Three fish species that, in combination, made up 20% of the biomass estimates for the diet of the harbour seals from the scat analyses were not collected during potential prey sampling. In hindsight, it would have been useful to run known outliers, such as an Antarctic or tropical fish species, in our analyses to see where they would fall in the comparative PCA plots. However, fish species that made up 80% of the diet according to the hard-part analyses from the same time of year and the same area where the harbour seals were foraging were run in the FA analyses, in addition to some invertebrate species that were

Svalbard.

Cr	Ll	Lm	Am	Hp	Rh	Rr	Pb	Ss
1.90±0.01	2.35±0.04	3.3.±0.1	2.7±0.1	2.77±0.06	3.12±0.01	1.32±0.01	2.64±0.04	1.79±0.02
0.06±0.01	0.17±0.01	0.20±0.01	0.13±0.01	0.09±0.01	0.17±0.01	0.03±0.01	0.22±0.01	0.11±0.01
0.36±0.01	0.77±0.02	0.08±0.01	1.07±0.04	0.46±0.01	0.07±0.01	0.34±0.01	0.58±0.01	0.66±0.01
0.19±0.01	0.63±0.01	0.05±0.01	0.28±0.01	0.24±0.01	0.04±0.01	0.19±0.01	0.31±0.01	0.46±0.01
14.6±0.2	15.5±0.2	11.1±0.2	13.9±0.4	14.5±0.2	12.7±0.1	16.51±0.09	16.4±0.2	15.17±0.07
7.95±0.05	14.7±0.4	15.5±0.4	15.1±0.6	10.7±0.1	12.20±0.06	7.8±0.1	17.4±0.2	21.3±0.2
0.36±0.01	0.78±0.01	0.26±0.01	1.13±0.02	0.37±0.01	0.18±0.01	0.41±0.01	0.97±0.01	0.90±0.01
0.35±0.01	0.67±0.02	0.20±0.01	0.74±0.03	0.32±0.01	0.12±0.01	0.51±0.02	0.46±0.01	0.56±0.01
3.86±0.05	3.64±0.05	2.10±0.04	3.9±0.1	3.11±0.02	2.79±0.05	4.0±0.2	2.90±0.04	3.02±0.02
12.5±0.1	13.0±0.3	7.4±0.3	10.9±0.3	12.1±0.1	15.8±0.2	12.32±0.09	12.6±0.2	11.97±0.09
6.35±0.07	9.08±0.09	4.4±0.2	9.8±0.3	6.60±0.05	3.85±0.03	10.5±0.1	8.5±0.1	11.02±0.04
0.96±0.02	0.54±0.02	0.69±0.2	0.66±0.2	0.87±0.01	0.55±0.01	1.19±0.02	0.74±0.01	0.59±0.01
0.25±0.01	0.17±0.01	0.35±0.01	0.21±0.01	0.29±0.01	0.27±0.01	0.28±0.01	0.32±0.01	0.21±0.01
0.91±0.01	0.77±0.06	3.1±0.2	1.02±0.02	1.00±0.02	1.70±0.02	1.07±0.04	0.92±0.02	0.57±0.01
0.09±0.01	0.22±0.01	0.09±0.01	0.20±0.01	0.09±0.01	0.11±0.01	0.09±0.01	0.19±0.01	0.28±0.01
6.75±0.02	1.66±0.04	13.4±0.2	1.49±0.06	9.3±0.2	15.0±0.4	2.09±0.06	2.79±0.03	0.92±0.01
0.31±0.01	0.53±0.01	0.28±0.01	0.75±0.01	0.36±0.01	0.23±0.01	0.41±0.03	0.42±0.01	0.69±0.02
5.35±0.04	3.3±0.1	1.05±0.04	4.9±0.2	2.95±0.01	0.36±0.06	5.0±0.2	2.15±0.02	3.47±0.01
0.08±0.01	0.11±0.1	0.08±0.01	0.40±0.01	0.12±0.01	0.08±0.01	0.08±0.01	0.13±0.01	0.21±0.01
12.9±0.4	14.2±0.4	12.1±0.2	19±1	11.0±0.1	8.1±0.1	10.9±0.3	15.60±0.08	15.5±0.2
0.32±0.03	0.29±0.02	0.07±0.01	0.48±0.01	0.35±0.01	0.06±0.01	0.32±0.02	0.59±0.08	0.40±0.01
3.4±0.1	1.2±0.2	11.0±0.3	0.50±0.06	5.37±0.09	9.7±0.1	0.67±0.02	1.9±0.2	0.38±0.01
1.1±0.2	1.1±0.2	2.13±0.06	0.5±0.1	1.2±0.1	1.94±0.06	1.14±0.07	1.0±0.2	0.33±0.04
1.90±0.02	4.0±0.2	2.57±0.09	2.6±0.1	2.48±0.06	1.40±0.02	1.83±0.08	1.15±0.01	2.10±0.01
15.4±0.3	9.8±0.5	8.1±0.3	6.4±0.6	11.9±0.1	8.7±0.3	20.0±0.3	8.6±0.2	7.2±0.2
1.9±0.2	1.0±0.2	0.45±0.06	1.0±0.2	1.5±0.2	0.64±0.03	1.0±0.2	0.48±0.06	0.20±0.05
21.6±0.2	23.8±0.2	16.9±0.3	23.2±0.5	21.8±0.2	19.0±0.1	23.3±0.2	24.1±0.2	22.3±0.1
40.0±0.3	41.9±0.6	54.4±0.6	39.5±0.8	46.9±0.3	59.4±0.5	35.5±0.3	44.9±0.4	46.2±0.2
38.4±0.5	34.2±0.7	28.6±0.4	37±1	31.2±0.2	21.6±0.3	41.2±0.4	31.0±0.2	31.5±0.2

Lycodes rossi; Ls, *Lycodes* sp.; Sm, *Sebastes mentella*; Tp, *Triglops pingelii*; Ld, *Leptagonus decagonus*; Lg, *Liparis gibbus*; Lf, *Liparis fabricii*; Cr, *Reinhardtius hippoglossoides*; Rr, *Raja radiata*; Pb, *Pandalus borealis*; and Ss, *Sabinea septemcarinata*.

consumed directly or indirectly by the harbour seals in small amounts.

Several things are clear from our FA analyses. One is that all of the potential prey species had FA compositions that were significantly different from the blubber of the harbour seals, even when only the innermost layer was considered. Additionally, the PCA plot comparing the innermost blubber with potential prey showed that all prey samples were systematically found on one side of the blubber samples, implying that the harbour seals had metabolically altered the FA composition of the prey during incorporation into the blubber. This could be via selective uptake, chain elongation/desaturation, or through differential breakdown of some FAs during uptake. The FA results suggested that gadoids and sculpins were the two fish groups that were most similar to the harbour seals in terms of their FA compositions. This is consistent with the findings of diet assessment via hard-part analyses and indicates an influence of the prey on the blubber composition. However, the FA results also suggested that Greenland halibut, the spotted snakeblenny, and the Atlantic poacher had FA compositions that were quite similar to the harbour seal blubber even though these species were not identified in the harbour seal scat or stomach samples. These fishes might be underrepresented in our hard-part analyses, but the reasons why this might be the case is unclear. The fish species that dominated biomass consumption estimates in the scats and the small sample of stomachs (i.e, Atlantic cod) was third in line in terms of the similarity to the harbour seals innermost blubber layer. This qualitative rating might have been higher if total lipid biomass was incorporated into the analyses because Atlantic cod is a lean fish with low lipid content. Methodological improvements in FA analyses might also be required in future studies of marine mammal tissue FA constituents (see Wetzel and Reynolds 2004).

In summary, harbour seals in the high Arctic, at Svalbard, appear to be opportunistic, polyphagous feeders similar to the situation in other parts of their range. It is interesting that the species that dominate their diet in terms of biomass is the Atlantic cod, which is also found throughout temperate areas where harbour seals are found in the Atlantic region. However, ringed seals, *Pusa hispida* (Schreber, 1775),

Fig. 5. Distance plot of all samples to the SIMCA model of the samples from the inner blubber layer of harbour seals. Three principal components were used for the model. The rejection criterion (95% confidence limit) was 65 and is indicated by the horizontal line. The prey species are *Boreogadus saida* (Bs), *Triglops pingelii* (Tp), *Gadus morhua* (Gm), *Reinhardtius hippoglossoides* (Rh), *Lumpenus maculatus* (Lm), *Leptagonus decagonus* (Ld), *Liparis gibbus* (Lg), *Mallotus villosus* (Mv), *Sebastes mentella* (Sm), *Liparis fabricii* (Lf), *Raja radiata* (Rr), *Careproctus reinhardti* (Cr), *Hippoglossoides platessoides* (Hp), *Lumpenus lampretaeformis* (Ll), *Sabinea septemcarinata* (Ss), *Lycodes* sp. (Ls), *Lycodes rossi* (Lr), *Anisarchus medius* (Am), and *Pandalus borealis* (Pb).

and other Arctic fish predators seem to specifically target polar cod and other fat-rich, typically Arctic fish species more exclusively in this same geographic area (Hop et al. 2002). Our comparison between hard-part diet analyses and FAs is far from definitive, but it indicates a general influence of diet on the FA composition of the inner blubber layer. The degree to which FA analyses will reveal fine-scale structure in the diets of marine mammals will not be resolved with data from a catholic feeder such as the harbour seal in the wild. It is likely to require carefully designed feeding experiments performed in captivity. The differences between the FA composition of the different blubber layers and the possible differences between sex and age classes suggested in this study warrant further investigation.

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