Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland

Article *in* Canadian Journal of Zoology · June 1996

DOI: 10.1139/z96-123

2 authors:

Dominic J. Tollit
62 PUBLICATIONS 3,175 CITATIONS
SEE PROFILE

Paul M. Thompson
University of Aberdeen
219 PUBLICATIONS 14,462 CITATIONS
SEE PROFILE

Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland

D.J. Tollit and P.M. Thompson

Abstract: Predictions concerning the effect of seals upon prey stocks require an understanding of temporal variations in diet composition. This study examined the extent of between-year and seasonal variations in the diet of harbour seals (*Phoca vitulina*) from the Moray Firth, Scotland, between 1989 and 1992. Analyses of fish otoliths and cephalopod beaks collected from 1129 faecal samples were used to derive estimates of the contribution made by each of 35 prey species, based on the number and mass consumed. The key prey, by mass, were sand eels (Ammodytidae) (47%), lesser octopus (*Eledone cirrhosa*) (27%), whiting (*Merlangius merlangus*) (6%), flounder (*Platichthys flesus*) (5%), and cod (*Gadus morhua*) (4%). Between-year and seasonal fluctuations in the contributions of these species were observed. Sand eels contributed 86–20% in summer and 91–49% in winter. Lesser octopus contributed 0–62% in summer and <5% in winter, whilst whiting and cod contributed 2–34% in winter and 1–4% in summer. In contrast to 1988, clupeids were unimportant in winter. Differences in diet composition appeared to reflect local changes in the availability of food, especially overwintering clupeids. Results indicate that dietary information obtained from short-term studies can be a poor indicator of subsequent diet composition and should be treated with caution when used to predict the effect of seals on prey populations.

Résumé : L'étude des effets des phoques sur les stocks de proies nécessite une meilleure compréhension des variations temporelles du régime alimentaire. On trouvera ici les résultats d'une étude des variations interannuelles et saisonnières du régime alimentaire des Phoques communs (*Phoca vitulina*) dans le golfe de Moray, Écosse, entre 1989 et 1992. L'analyse des otolithes de poissons et des becs de céphalopodes recueillis dans 1129 échantillons fécaux a servi à estimer la contribution apportée par chacune des 35 espèces de proies, d'après le nombre et la masse consommés. Les principales proies, d'après la masse consommée, étaient les lançons (Ammodytidae) (47%), la pieuvre *Eledone cirrhosa* (27%), le Merlan *Merlangius merlangus* (6%), le Flétan (*Platichthys flesus*) (5%) et la Morue franche (*Gadus morhua*) (4%). Des variations annuelles et saisonnières de la contribution de ces espèces dans le régime ont été enregistrées. Les lançons constituaient 86–20% du régime en été et 91–49% du régime en hiver. Les pieuvres composaient 0–62% du régime en été et moins de 5% en hiver, alors que les merlans et les morues constituaient de 2 à 34% du régime en hiver et de 1 à 4% en été. Contrairement aux résultats obtenus en 1988, cependant, les clupéidés ont été peu nombreux en hiver. Ces différences semblent refléter les variations locales dans la disponibilité de la nourriture, particulièrement celle des clupéidés en hiver. Les résultats indiquent que les études à court terme de l'alimentation des phoques peuvent fournir des résultats qui sont de mauvais indicateurs de la composition future du régime alimentaire et la prudence s'impose avant d'utiliser ces résultats pour prédire l'impact des phoques sur les populations de proies.
[Traduit par la Rédaction]

Introduction

Pinnipeds consume prey that are the target of commercial and recreational fisheries and, consequently, are often viewed as competitors with man (Harwood and Greenwood 1985; Harwood and Croxall 1988). To estimate the effect of seals on fish stocks, bioenergetic models have been developed to determine the annual consumption of key prey species by certain seal populations (e.g., Lavigne et al. 1985; Harvey 1988; Härkönen and Heide-Jørgensen 1991; Markussen and Øritsland 1991; Olesiuk 1993). However, if such models are to be used as a predictive management tool, it is crucial that we understand the extent of temporal and spatial variations in key parameters such as diet composition (Harwood 1987). Such variations in a population's diet may have a direct effect on a seal's predatory impact upon each prey population. In addition, differences in diet may reflect variations in foraging behaviour (Stephens and Krebs 1986), which could affect the seals' energy requirements and thus total food consumption. However, to make specific statements about prey selection, more detailed information is needed on changes in diet in relation to variations in prey abundance and on the net energetic benefits of feeding on different prey (Pyke 1984).

Studies of several pinniped species have recorded seasonal (e.g., Brown and Mate 1983; Härkönen 1987; Prime and Hammond 1987, 1990; Benoit and Bowen 1990; Pierce et al. 1991*c*; Beck et al. 1993; Bowen et al. 1993) and widescale regional (e.g., Härkönen 1987; Pierce et al. 1990; Prime and Hammond 1990) variations in diet composition. However, few investigations have been conducted for long enough to assess the extent to which these patterns remain consistent between years. Where between-year changes in pinniped

Received July 31, 1995. Accepted January 2, 1996.

D.J. Tollit and P.M. Thompson. University of Aberdeen, Department of Zoology, Lighthouse Field Station, Cromarty, Ross-shire IV11 8YJ, U.K. (e-mail: lighthouse@adbn.ac.uk).

foraging have been documented, these have generally been for species that specialize on one or two key prey species (North et al. 1983; Costa et al. 1989; Trillmich and Dellinger 1991). In such cases, changes in food availability have resulted in variations in energy expenditure and the length of foraging trips rather than in diet composition (Costa et al. 1989). In contrast, many perceived fisheries interactions involve seal species with more catholic diets, and the extent to which between-year variations in diet composition and foraging behaviour occur in these species remains unclear.

In European waters, populations of both harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are implicated in fisheries interactions (e.g., Rae 1968; Harwood and Croxall 1988; Hammond et al. 1994) and both are known to take a wide variety of prey species (e.g., Härkönen 1987; Prime and Hammond 1987, 1990; Pierce et al. 1991*c*; Hammond et al. 1994). In northeastern Scotland, harbour seal diet composition has been investigated as part of a broader study of the population and foraging ecology of seals in the Moray Firth. Studies carried out in this area in 1988 documented marked seasonal variations in diet, with herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) predominating in winter and sand eels (Ammodytidae) in summer (Pierce et al. 1991*c*). Furthermore, winter foraging behaviour and diet in 1988–1989 were related to a seasonal increase in the abundance of herring and sprat in inshore waters at this time (Thompson et al. 1991).

This paper presents data on the diet composition of Moray Firth harbour seals over the period 1989–1992. Using these data we aim, first, to assess whether diet composition changed between years and between seasons. Secondly, we combine these data with previously published data to determine whether changes in diet composition can be related to existing data on either seal distribution or prey availability.

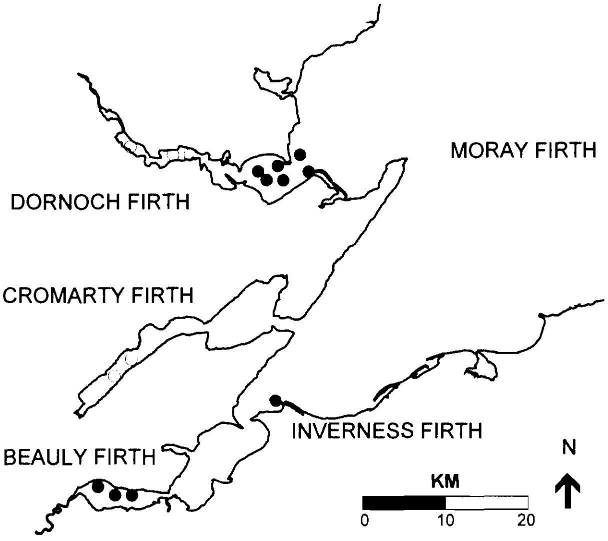
Methods

Study area and sampling

This study was carried out in the inner Moray Firth, northeastern Scotland (57°41′N, 4°W). In 1988 and 1989, visits to intertidal haulout sites were made throughout the year. Published data from faecal samples collected throughout 1988 indicated that the largest differences in diet composition occurred between summer (May–August) and winter (November–February) (Pierce et al. 1991*c*). Between 1990 and 1992, site visits were therefore confined to these two seasons and focused on three geographical areas: Dornoch Firth, Inverness Firth, and Beauly Firth (Fig. 1). In summer, visits were made at least twice per month to intertidal haulout sites in the Dornoch Firth and at the mouth of the Inverness Firth. In winter, monthly visits were made to haulout sites in the Inverness and Beauly firths and, in January and February, to haulout sites in the Dornoch Firth also. The geographical distribution of sampling effort reflected observed changes in harbour seal abundance and distribution (Thompson et al. 1992). Grey seals were also present at sites in the Inverness and Dornoch firths. Therefore, seals at these haulout sites were identified to species if possible, and if at least 90% of seals at a haulout site were of one species, faeces were classified to that species. Samples were collected separately in polythene bags and stored frozen (−20°C).

Techniques for analysing faecal samples were similar to those described by Pierce et al. (1991*c*). The following section summarizes the methods used in these analyses and provides details where the methodology differed from that outlined in Pierce et al. (1991*c*).

Fig. 1. Locations of harbour seal haulout sites in the inner Moray Firth, northeast Scotland. Faecal collections were made at haulout sites indicated by solid circles.



Analytical techniques

Prey hard parts were extracted from each faex through four sieves, using mesh sizes from 4.0 to 0.25 mm. Fish otoliths and cephalopod beaks were identified to species (except sand eels, of which only a small subsample were identified to species) using a reference collection and identification guides (Clarke 1986; Härkönen 1986). Other prey hard parts such as vertebrae, denticles, cephalopod eyes, and crustacean remains were also recorded, but were not included in further quantification of diet composition.

The number of individual fish consumed was estimated by dividing the total number of otoliths by 2. The total number of cephalopods consumed was assumed to be equal to the number of the more numerous beak halves. The length of intact otoliths was measured except in the case of six species, for which width was measured (Table 1), primarily because of the availability and accuracy of published regressions. For otoliths broken lengthways, the width was measured. Hood lengths of octopus beaks were measured and hood and rostral lengths of squid beaks were measured. All otoliths (except those of sand eels) and cephalopod beaks were measured to within 0.02 mm using a binocular microscope and eyepiece graticule. A video image analyser (Magiscan 2, Joyce-Loebl Ltd.) was used to measure sand eel otoliths, also to within 0.02 mm (Rankine and Cargill 1991). When >120 sand eel otoliths were present in a faex, a random subsample of at least 25% of the total number was measured. If samples contained <120 sand eel otoliths, a random subsample of at least 30 otoliths was measured.

Prey length and mass were estimated using published regressions (Bedford et al. 1986; Clarke 1986; Coull et al. 1989; Härkönen 1986; Pierce et al. 1991*c*, 1993) and unpublished data from J.R.G. Hislop (Scottish Office Agricultural and Fisheries Department (SOAFD) Marine Laboratory) and G.J. Pierce (University of Aberdeen). For each prey species, the scientific name, the dimension measured, and the source of the formulae and regression equations used in calculations are given in Table 1. An equal weighting factor was given to each individual otolith measurement (see Pierce et al. 1991*c*). However, if a single large individual was present in a faex that also contained a few small individuals, the resulting total estimated mass (using an equal weighting factor) could have been less than the mass of the largest individual. If this was the case, the mass of the largest individual was added to the sum of the minimum masses of the remaining individuals.

Table 1. Prey species identified in the faeces of harbour seals in the inner Moray Firth during 1989–1992.

Common name	Latin name	*n*	Tot%	Dimension	Source	
					FL	FM
Rays	*Raja* sp.	3+	—	—	—	—
Herring	*Clupea harengus*	67	2.1	W	Härkönen 1986	Coull et al. 1989
Sprat	*Sprattus sprattus*	53	0.2	W	J.R.G. Hislop (unpublished data)	Coull et al. 1989
Sea trout	*Salmo trutta*	1	<0.1	L	Härkönen 1986	Härkönen 1986
Cod	*Gadus morhua*	53	3.7	L	J.R.G. Hislop (unpublished data)	Coull et al. 1989
Haddock	*Melanogrammus aeglefinus*	11	<0.1	L	Härkönen 1986	Coull et al. 1989
Bib	*Trisopterus luscus*	1	<0.1	L	Härkönen 1986	Härkönen 1986
Poor cod	*Trisopterus minutus*	37	0.5	L	Härkönen 1986	Härkönen 1986
Whiting	*Merlangius merlangus*	845	5.8	W	J.R.G. Hislop (unpublished data)	Coull et al. 1989
Saithe	*Pollachius virens*	46	0.9	L	Härkönen 1986	Härkönen 1986
Ling	*Molva molva*	4	0.4	L	Härkönen 1986	Härkönen 1986
Four-bearded rockling	*Rhinonemus cimbrius*	6	<0.1	L	Härkönen 1986	Härkönen 1986
Cuckoo wrasse	*Labrus mixtus*	25	<0.1	L	Härkönen 1986	Härkönen 1986
Rock cook	*Centrolabrus exoletus*	2	<0.1	L	Härkönen 1986	Härkönen 1986
Sand eels	Ammodytidae	28 993	47.1	L	Härkönen 1986	Härkönen 1986
Greater weever	*Trachinus draco*	1	<0.1	L	Härkönen 1986*	Coull et al. 1989
Dragonet	*Callionymus lyra*	12	0.1	L	Pierce et al. 1991*c*	Coull et al. 1989†
Snake blenny	*Lumpenus lampretaeformis*	5	<0.1	L	Härkönen 1986*	Härkönen 1986*
Butterfish	*Pholis gunnellus*	11	<0.1	W	Härkönen 1986	Härkönen 1986
Catfish	*Anarhichas lupus*	1	0.4	L	Härkönen 1986	Coull et al. 1989
Eelpout	*Zoarces viviparus*	20	0.1	W	Härkönen 1986	Härkönen 1986
Sand goby	*Pomatoschistus minutus*	1	<0.1	W	Härkönen 1986	Härkönen 1986
Bullrout	*Myoxocephalus scorpius*	3	<0.1	L	Härkönen 1986	Coull et al. 1989
Sea scorpion	*Taurulus bubalis*	1	<0.1	L	Härkönen 1986	Härkönen 1986
Hooknose	*Agonus cataphractus*	3	<0.1	L	Härkönen 1986*	Coull et al. 1989
Turbot	*Scophthalmus maximus*	37	0.6	L	Härkönen 1986	Härkönen 1986
Norweg topknot	*Phrynorhombus norvegicus*	1	<0.1	L	Pierce et al. 1991*c*‡	Bedford et al. 1986‡
Topknot	*Zeugopterus punctatus*	4	<0.1	L	Pierce et al. 1991*c*‡	Bedford et al. 1986‡
Dab	*Limanda limanda*	13	0.2	L	Härkönen 1986	Bedford et al. 1986
Plaice	*Pleuronectes platessa*	22	0.8	L	Härkönen 1986	Coull et al. 1989
Flounder	*Platichthys flesus*	200	5.4	L	Härkönen 1986	Coull et al. 1989
Lemon sole	*Microstomus kitt*	12	1.1	L	Härkönen 1986	Härkönen 1986
Octopus	*Eledone cirrhosa*	195	26.8	HL	—	G.J. Pierce (unpublished data)
Cuttlefish	*Sepia* sp.	2	<0.1	HL	—	Clarke (1986)
Squid	*Loligo forbesi*	102	3.2	RL	—	Pierce et al. 1991*c*, 1993
Crustacean	Crustacea	55+	—	—	—	—
Polychaete	Polychaeta	17+	—	—	—	—

Note: Data from all years have been pooled to calculate the total number of fish or cephalopods (*n*) and the estimated percentage (Tot%), by mass, consumed. The otolith dimension measured (L, length; W, width) and source of regressions for fish length (FL) and fish mass (FM) are displayed. Cephalopod masses were derived from hood length and rostral length.

*Values were estimated.

†Regression corrected.

‡Combined data for Bothidae.

Table 2. Between-year fluctuations in harbour seal diet composition for winter and summer 1988–1989 to 1992: estimated biomass of major fish and cephalopod species represented by otoliths and beaks in faecal samples containing prey (n), expressed as a percentage of the total for all species at all sites in each season.

	Summer 1988* ($n = 102$)	Winter 1988–1989* ($n = 27$)	Summer 1989 ($n = 26$)	Winter 1989–1990 ($n = 23$)	Summer 1990 ($n = 97$)	Winter 1990–1991 ($n = 87$)	Summer 1991 ($n = 201$)	Winter 1991–1992 ($n = 187$)	Summer 1992 ($n = 382$)
Herring	1.7	6.9	11.9	0.8	<0.5	1.7	1.8	0.8	2.6
Sprat	<0.1	91.2	0.0	0.0	<0.1	1.0	<0.1	<0.1	<0.1
Cod	0.3	0.0	0.0	0.0	0.6	<0.1	1.3	13.7	3.1
Poor cod	0.0	0.0	0.0	0.0	0.0	0.5	0.0	3.1	0.0
Whiting	2.4	0.5	1.8	2.3	0.5	17.9	1.1	20.9	1.2
Saithe	0.0	0.0	0.0	0.0	0.0	0.0	0.4	4.6	<0.1
Other gadoids	0.0	0.0	0.0	0.5	1.1	1.7	0.0	0.8	0.7
Sand eels	68.1	1.4	86.3	90.5	44.4	59.9	20.3	48.8	64.7
Turbot	0.2	0.0	0.0	0.0	0.0	7.1	0.0	0.5	0.0
Plaice	4.6	0.0	0.0	0.9	0.0	0.0	1.1	1.2	0.8
Flounder	10.7	0.0	0.0	0.0	7.6	5.8	8.3	2.8	4.3
Lemon sole	0.0	0.0	0.0	0.0	1.4	0.2	1.7	0.0	1.3
Other flatfish	3.2	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.7
Octopus	3.9	0.0	0.0	3.4	40.0	4.4	62.0	2.4	9.6
Squid	0.0	0.0	0.1	0.0	0.5	0.0	1.7	<0.1	10.6
Other prey	4.9	0.0	0.0	1.5	3.6	0.2	0.3	0.4	0.3

*Data are from Pierce et al. (1991*c*) and Thompson et al. (1991).

The relative contribution of each prey species to the diet, for all years combined, was expressed both as the total number of each prey species and as a percentage of the total estimated mass of prey ingested (Table 1). The relative contribution of each major prey species in each year and season was also expressed as a percentage of the total estimated mass of prey ingested (Table 2) and all percentages in the text relate to this measure unless otherwise stated. It should be noted that these data have not been corrected for species-specific differences in otolith digestion rates (Prime and Hammond 1987; Harvey 1989) and cannot be used to provide a precise estimate of percent diet composition. Nevertheless, the percentage of the diet by mass remains the most appropriate single measure to illustrate differences in the relative importance of different prey species (Hammond et al. 1994). This assumes that for a particular species, the errors due to the digestion of otoliths remain similar through time and are normally distributed. However, it is difficult to estimate the variation around these figures, and one cannot determine the significance of apparent differences. Therefore, to investigate whether differences between years or between seasons were significant, we compared numbers of otoliths or beaks per faex for prey species making a >3.5% contribution to the overall diet. Together these key prey made up >89% of the total estimated mass of prey consumed (Table 1). Nonparametric tests were used because the data were skewed as a result of a large proportion of faecal samples containing no otoliths of most prey species. In addition, data sets were found to be heteroscedastic before and after log transformations were performed. All tests were carried out using the Unistat statistical package (Unistat Ltd., London, England, 1984).

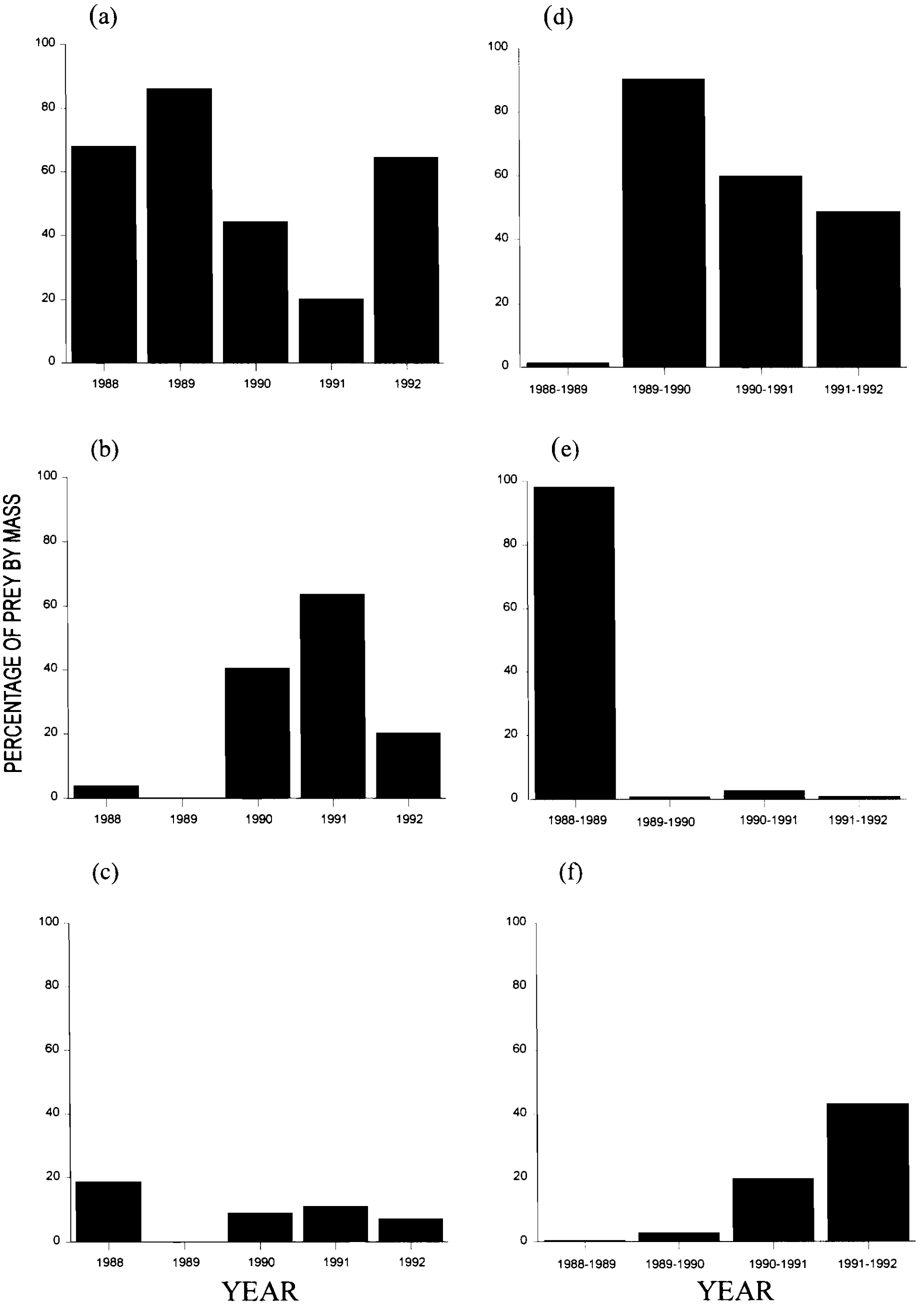
Initially, faecal samples from all three geographical areas were combined to allow an overall between-year comparison for a period of four summers (1989–1992) and three winters (1989–1990 to 1991–1992). For each year–season combination, the number of otoliths or beaks in each faecal sample was divided by the number of faecal samples (excluding those with no otoliths or beaks) in order to take account of differences in sample sizes between data sets. The Kruskal–Wallis one-way analysis of variance (ANOVA) test was then used to derive a statistic, for each species separately, that described between-year differences in the numbers of prey per faex. However, spatial variation in diet composition and differences in the number of faecal samples collected in each haulout area may have contributed to an apparent between-year difference in any overall comparison. Therefore, between-year differences were also compared (ANOVA) for each geographical area separately. Where significant differences were found, Mann–Whitney U tests were used to ascertain the years between which significant differences occurred. This test was also used when data from an area were collected in only 2 years and for comparing winter and summer data.

In any one data set, both the frequency of occurrence of a species and the number of prey of that particular species in each faex could affect any comparison that included the number of that species per faex. Therefore, for each season, using data from all areas combined, we also made between-year comparisons (ANOVA) of the number of otoliths or beaks per faex in those faecal samples that contained the prey species in question.

Sand eels are a major prey item for predatory fish (Daan 1989) and therefore may be found in faecal samples, owing to secondary ingestion. Prime and Hammond (1987) and Pierce et al. (1991*c*) both found that when large numbers of sand eels were identified in a faecal sample, they were generally the only species present. In contrast, when other predatory species were present, the number of sand eels was small, consequently these may have been of secondary origin. The extent of this potential bias was therefore assessed by excluding from samples containing sand eels, first, all sand eels from samples containing large predatory fish and second, all samples containing <30 sand eels.

To investigate between-year and between-season differences in the relative size range of prey consumed, mean masses were calculated for those key prey species for which >30 otoliths or >15 beaks were found in a season. In addition, length-frequency distributions were constructed for comparison with data collected from fishery surveys in the area. It is at present difficult to estimate the variation in the amount of digestion of otoliths and beaks, therefore the apparent significance of any observed differences in mean prey size was not tested.

Fig. 2. The between-year fluctuations of major prey groups in harbour seal diet composition in summer (1988–1992) and winter (1988/1989–1991/1992), expressed as a percentage of the total estimated biomass consumed for sand eels in summer (*a*), cephalopods in summer (*b*), flatfish in summer (*c*), sand eels in winter (*d*), clupeids in winter (*e*), and gadoids in winter (*f*).



Results

One hundred and twelve visits were made to haulout sites in the Moray Firth between 1 May 1989 and 31 August 1992. These yielded 1704 faecal samples, of which 1129 were of certain or probable harbour seal origin. Only these latter samples were analysed and of these, 1003 (89%) contained identifiable hard prey remains. Typically, samples generally included only one or two ($\bar{x} = 1.61$; $n = 1003$) different prey species, but occasionally contained as many as seven. Otoliths from 31 species of teleost fish, the beaks from 3 cephalopod species, and skate (*Raja* sp.) denticles were identified. The total estimated numbers of each prey species are presented in Table 1.

Of the 248 faecal samples containing >30 sand eels, only 12 (5%) contained large predatory fish. The sand eels from these 12 samples accounted for <4% of the total number of sand eels overall, whilst the remaining 80 samples (containing <30 sand eels) accounted for <20% of the total number of sand eels.

Overall, 5 prey species accounted for >89% of the total mass, with 13 prey species totalling >98% (Table 1). The

Table 3. Mean numbers of fish otoliths and cephalopod beaks per faex containing prey (*n*) for each geographical area (I, Inverness Firth; D, Dornoch Firth; B, Beauly Firth) in summer and winter for those prey species contributing >3.5% to the overall diet composition, by mass.

(A) Summer

	1989		1990		1991		1992	
	I (*n* = 17)	D (*n* = 9)	I (*n* = 29)	D (*n* = 68)	I (*n* = 84)	D (*n* = 117)	I (*n* = 194)	D (*n* = 188)
Cod	0	0	0	0.014	0.07	0.034	0.05	0.12
Whiting	0.06	0	0.103	0.014	0.07	0.154	0.592	0.548
Sand eels	98.8	16.3	75.0	70.0	26.8	38.4	47.7	68.0
Flounder	0	0	1.03	0.29	0.43	0.517	0.08	0.484
Octopus	0	0	0.07	0.662	0.535	0.641	0.005	0.074

(B) Winter

	1989–1990	1990–1991			1991–1992		
	I (*n* = 23)	I (*n* = 22)	D (*n* = 40)	B (*n* = 25)	I (*n* = 93)	D (*n* = 71)	B (*n* = 23)
Cod	0	0.45	0	0	0.15	0.24	1.26
Whiting	1.74	4.73	5.70	5.56	1.67	4.62	15.8
Sand eels	190.7	65.3	81.2	25.3	59.3	62.6	2.83
Flounder	0	0.05	0.10	0.17	0.02	0.25	2.22
Octopus	0.22	0	0.05	0	0	0.08	0.35

most important prey were sand eels (47%), lesser octopus (27%), whiting (6%), flounder (5%), and cod (4%). The remaining major prey species (squid, herring, lemon sole, saithe, plaice, turbot, poor cod, and ling, in decreasing order of importance) made up 3% or less of the total estimated mass, whilst sprat contributed only 0.2% (Table 1).

Between-year and seasonal variation in the diet

Percent diet composition by mass

Distinct between-year differences in the estimated percent mass of a number of species were apparent (Table 2). In summer, the proportion of sand eels in the diet declined from 86 to 20% between 1989 and 1991. Over the same period the proportion of lesser octopus increased from 0 to 62%. In summer 1992, sand eels increased to 65% and lesser octopus decreased to 10%. The proportion of sand eels in the winter diet also declined between 1989–1990 (91%) and 1991–1992 (49%), whilst both whiting and cod increased (from 2 to 21% and from 0 to 14%, respectively) over the same period. Herring and sprat were relatively unimportant in the diet throughout this study. Sprat never exceeded 1% in any single season, whilst herring never exceeded 3%, except in summer 1989 (12%). The contribution of flatfish, mainly flounder, fluctuated between years in both summer (0–11%) and winter (0–13%). Between-year fluctuations of the estimated percent mass of the major prey groups in each season are presented in Fig. 2. This includes comparable data for summer 1988 and winter 1988–1989 (Pierce et al. 1991*c*; Thompson et al. 1991).

Seasonal differences in diet composition were clearest when the contributions of cephalopods and gadoids were compared. The estimated percent mass of cephalopods did not exceed 5% in any winter, whilst gadoids did not exceed 5% in any summer (Table 2).

Numbers of prey per faex

These apparent between-year differences in estimated percent mass were analysed, first, by comparing numbers of prey per faex for the five key species that made up >3.5% of the overall diet by mass since 1989. Mean numbers per faex are given in Table 3. In the between-year comparison of summer data, significant differences were found for sand eels and lesser octopus between the Inverness and Dornoch firths when the data were both pooled and analysed separately (Table 4). However, the two areas differed with respect to the years in which differences occurred. In the Inverness Firth, values were high for sand eels in 1989 and 1990 and for lesser octopus in 1991. In the Dornoch Firth, values were high for sand eels in 1990 and 1992 and for lesser octopus in 1990 and 1991 (Table 3). Overall, no significant differences were found for numbers of flounder. However, there were significant differences in the contribution of this species in the Inverness Firth (Table 4), where they were high in 1990.

Over all areas combined, between-year differences were found in winter in numbers of sand eels and cod per faex (Table 5). Values for sand eels were low in 1991–1992 in all areas. For cod, differences were primarily due to high values in 1991–1992 compared with 1990–1991 in both the Dornoch and Beauly firths (Table 3). High values for whiting in 1991–1992 were also found in the Beauly Firth whilst, in the Inverness Firth, differences were found for flounder (high in 1990–1991) and lesser octopus (high in 1989–1990) (Table 5).

In the comparison of numbers of prey per faex between seasons, significant differences were found for sand eels, cod, and whiting (high in winter), in addition to lesser

Table 4. Results of one-way Kruskal–Wallis ANOVAs (df = 3) to test for between-year differences in summer diet composition in 1989–1992, measured by numbers of otoliths or beaks per faex (see the text for details).

	Inverness and Dornoch firths		Inverness Firth		Dornoch Firth	
	χ^2	P	χ^2	P	χ^2	P
Cod	2.89	0.41	4.89	0.18	1.28	0.73
Whiting	5.38	0.15	0.95	0.81	7.13	0.16
Sand eels	**67.1**	**<0.001**	**41.7**	**<0.001**	**25.8**	**<0.001**
Flounder	6.33	0.96	**11.7**	**0.003**	2.89	0.41
Octopus	**94.8**	**<0.001**	**74.8**	**<0.001**	**37.6**	**<0.001**

Note: Values that are significantly different are in boldface type.

Table 5. Results of tests for between-year differences in winter diet composition measured by numbers of otoliths or beaks per faex (see the text for details).

	Inverness, Dornoch, and Beauly firths*		Inverness Firth*		Dornoch Firth†		Beauly Firth†	
	χ^2	P	χ^2	P	Z	P	Z	P
Cod	**11.09**	**<0.001**	2.62	0.27	**2.31**	**0.021**	**2.83**	**0.005**
Whiting	3.61	0.16	2.07	0.36	0.92	0.36	**1.99**	**0.045**
Sand eels	**41.4**	**<0.001**	**28.2**	**<0.001**	**1.99**	**0.045**	**2.39**	**0.017**
Flounder	2.10	0.35	**103.1**	**<0.001**	0.57	0.57	0.93	0.35
Octopus	3.61	0.16	**10.07**	**0.006**	0.43	0.67	**1.77**	**0.08**

Note: Values that are significantly different are in boldface type.

*One-way Kruskal–Wallis ANOVA (df = 2) for 1989–1990, 1990–1991, and 1991–1992.

†Mann–Whitney *U* test for 1990–1991 and 1991–1992.

Table 6. Results of Mann–Whitney *U* tests for differences in diet composition between summer and winter, in all years (1989–1992), measured by numbers of otoliths or beaks per faex (see the text for details).

	Inverness, Dornoch, and Beauly firths		Inverness Firth		Dornoch Firth	
	Z	P	Z	P	Z	P
Cod	**4.65**	**<0.001**	**2.54**	**0.004**	**2.57**	**0.01**
Whiting	**12.35**	**<0.001**	**6.60**	**<0.001**	**9.68**	**<0.001**
Sand eels	**67.7**	**<0.001**	**5.85**	**<0.001**	**7.17**	**<0.001**
Flounder	0.27	0.87	1.33	0.18	0.13	0.89
Octopus	**4.60**	**<0.001**	**3.19**	**0.001**	**3.16**	**0.002**

Note: Values that are significantly different are in boldface type.

Table 7. Mean masses of prey (in grams), estimated from otoliths and cephalopod beaks of key prey species.

	Summer 1989	Winter 1989–1990	Summer 1990	Winter 1990–1991	Summer 1991	Winter 1991–1992	Summer 1992
Cod	—	—	—	—	—	99.4 (19.43)	64.3 (16.00)
Whiting	—	8.7 (1.33)	—	9.0 (0.30)	—	11.9 (0.34)	4.5 (0.49)
Sand eels	2.9 (0.04)	3.3 (0.05)	2.8 (0.03)	2.6 (0.02)	2.6 (0.03)	2.5 (0.02)	3.0 (0.02)
Flounder	—	—	51.6 (8.07)	—	66.7 (9.19)	15.4 (3.03)	29.3 (4.33)
Octopus	—	—	182 (9.90)	—	245 (12.92)	—	278 (44.20)

Note: Values in parentheses are standard errors. Mean masses were only calculated when at least 30 otoliths or 15 beaks were found in any one season.

octopus (high in summer). These results were consistent for all areas combined and when the Inverness and Dornoch firths were analysed separately (Table 6).

When the numbers of prey per faex containing that prey were analysed, between-year comparisons for all areas combined were not significant for all species but one. The exception was whiting, where significantly more fish were found in samples containing whiting in winter 1991–1992 ($\bar{x}$ = 12.4; n = 846) than in 1990–1991 ($\bar{x}$ = 5.06; n = 471) and 1989–1990 ($\bar{x}$ = 6.6; n = 40) (ANOVA: χ^2 = 15.9, df = 3, $p < 0.001$).

Size of prey in the diet

The mean mass of sand eels ranged between 2.5 and 3.3 g (Table 7). Length-frequency distributions for each season all show >93% of sand eels in the 7.5 to 12.5-cm range. Figures 3*a* and 3*b* show distributions of sand eel length in pooled summer and winter samples, with modes at 10 and 9 cm, respectively.

In winters 1989–1990 and 1990–1991, the mean mass of whiting ranged from 8.7 to 9.0 g (n = 511), but there was a mean mass of 11.9 g (n = 831) in winter 1991–1992 (Table 7). The length-frequency distribution pooled for winter seasons (Fig. 3*c*) was similar to that of sand eels, with >75% of fish in the 7.5- to 12.5-cm range and a mode at 9 cm. Whiting from summer 1992 had a mean mass of 4.5 g (n = 219) (Table 7).

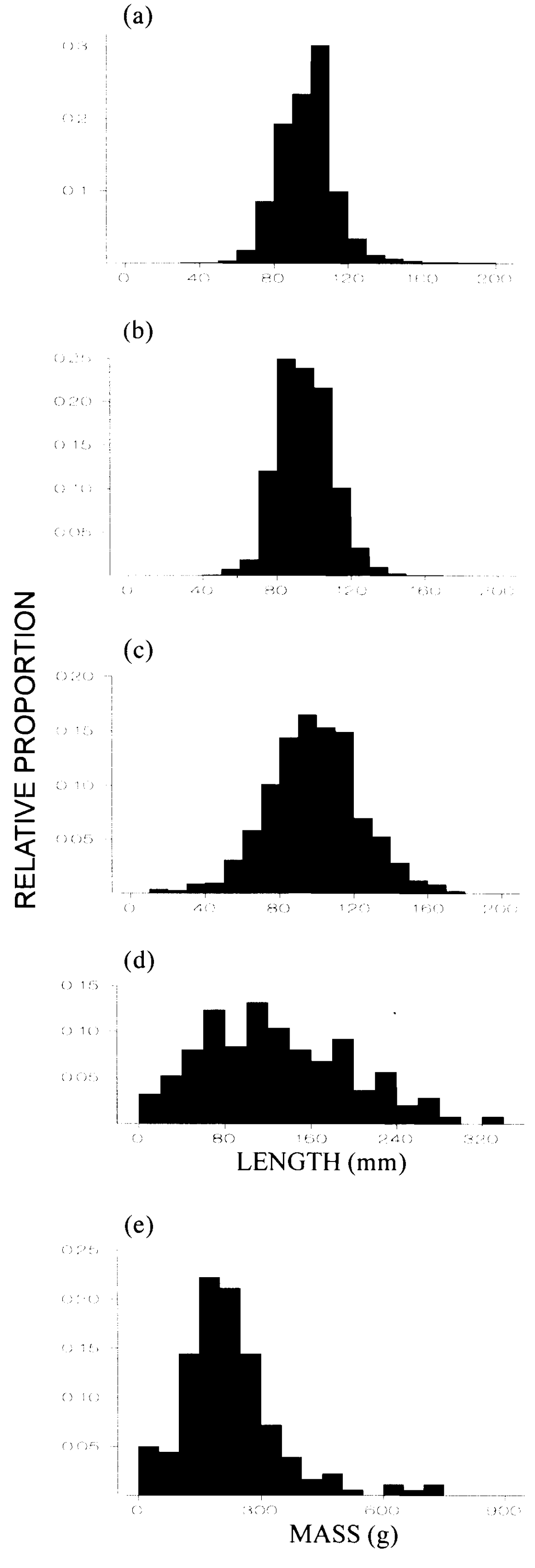
The mean mass of cod was 99.4 g (n = 60) in winter 1991–1992 and 64.3 g (n = 31) in summer 1992. Fish lengths ranged between 3 and 42 cm. In summer, the mean mass of flounder ranged from 29.3 to 66.7 g (n = 254), with a length-frequency distribution pooled for summer seasons (Fig. 3*d*) that ranged between 1 and 33 cm, but with no clear mode. The mean mass of lesser octopus in summer was 182 g (n = 47) in 1990, 245 g (n = 118) in 1991, and 276 g (n = 16) in 1992 (Table 7). The overall mean mass of lesser octopus found in summer was 231 g (n = 181; Fig. 3*e*), whilst those found in winter were 79 g (n = 16).

Discussion

The errors involved in analyses of pinniped diets are reviewed comprehensively by Jobling and Brieby (1986), Jobling (1987), and Pierce and Boyle (1991). A major problem is that the otoliths of different species have been found to erode at different rates during their passage through the gut (Prime and Hammond 1987) and some are completely digested (da Silva and Neilson 1985; Dellinger and Trillmich 1988; Harvey 1989). However, the aim of this study was not to estimate diet composition in order to quantify the annual consumption of prey by harbour seals in the Moray Firth, but to investigate the extent of variations in the relative contributions of key prey species between years and between seasons. The percentage of each prey species, by mass, was used primarily to highlight the key prey species and the extent of observed temporal variations.

To test for differences between time periods, we compared the numbers of otoliths and beaks per faex (Hammond et al. 1994) for key prey species. This method was considered most appropriate, firstly, because it is not affected by otoliths and beaks having been eroded by different amounts and, secondly, it allows sample sets of unequal sizes to be com-

Fig. 3. Length-frequency distributions, shown as a proportion of the total sample, for sand eels in pooled summers (n = 13,394) (*a*), sand eels in pooled winters (n = 6331) (*b*), whiting in pooled winters (n = 1343) (*c*), flounder in pooled summers (n = 251) (*d*), and mass-frequency distribution for lesser octopus in pooled summers (n = 181).



pared. However, this analysis does not take account of the size of prey. Prey masses were therefore calculated (although uncorrected) to provide information on relative differences in size. This type of comparison is valid if the associated errors due to digestion remain consistent between samples for each prey species and data sets are large, i.e., only frequently occurring prey are analysed.

Potential bias due to the presence of secondary prey (e.g., sand eels) is an unresolved problem when using faeces to determine the diet of marine mammals (Pierce and Boyle 1991). However, in this study, a large proportion of all sand eels (>75% numerically) were found in samples containing >30 sand eels and no other large predatory fish.

At least 35 species of prey were identified in the faeces of harbour seals in the Moray Firth, but just five key species (sand eels, lesser octopus, whiting, flounder, and cod) accounted for >89% of the overall diet by mass (Table 1).

Sand eels were the dominant prey by number (and by mass) in the diet (Table 1). The predominance of sand eels in summer (Fig. 2) corresponds well to earlier dietary studies in the inner Moray Firth (Pierce et al. 1991*c*). In contrast to the findings of other harbour seal dietary studies (e.g., Härkönen 1987, 1988; Pierce et al. 1990, 1991*c*; Härkönen and Heide-Jørgensen 1991), sand eels were also predominant in winter (Fig. 2). These results indicate that harbour seals, as well as grey seals (Prime and Hammond 1990), have the ability to prey on sand eels at a time when they are relatively unavailable to fisheries and other predators because they overwinter in the substratum (Reay 1970).

The majority of sand eels (>93%) were between 7.5 and 12.5 cm in length (Figs. 3*a* and 3*b*). Based on sand eel age–length data in Macer (1966) and Dann (1986), and the potential underestimate in size due to digestion (Harvey 1989), seals appeared to be feeding predominantly on the younger age-classes (0-, 1-, and 2-group fish) of the smaller species *Ammodytes marinus*, *Gymnammodytes semisquamatus*, and *Ammodytes tobianus*. These age groups also occur most frequently in the diet of many fish and birds (e.g., Harris and Wanless 1985, 1986; Fraser 1987; Daan 1989). In summer, a small proportion of otoliths of the greater sand eel, *Hyperoplus lanceolatus* (<0.002% numerically), were identified. These results are in contrast to studies of grey seals in British waters which reported that both lesser and greater sand eels ranging widely in size were eaten (Hammond and Prime 1990; Prime and Hammond 1990; Hammond et al. 1994). Our study confirms the view that sand eels, particularly juvenile lesser sand eels, play an important trophic role for a wide range of marine predators in Scottish waters.

The contribution of cephalopods was generally confined to samples collected in summer (Table 2). Because of the relative robustness of cephalopod beaks, they tend, if not regurgitated, to be overrepresented in the diet (Harvey 1989). Nevertheless, their contribution, by mass, in 1990 (40%) and 1991 (62%) exceeds that reported in all known published studies of harbour and grey seal diets (e.g., Prime and Hammond 1987, 1990; Härkönen 1987, 1988; Harvey 1988; Benoit and Bowen 1990; Härkönen and Heide-Jørgensen 1991; Pierce et al. 1991*a*, 1991*b*, 1991*c*; Bowen et al. 1993; Hammond et al. 1994).

In contrast, the gadoids (mainly whiting and cod) contributed to the diet predominantly in winter (Table 2). The occurrence of gadoids in the diet of harbour seals has been well documented in Scottish (Pierce et al. 1990), Swedish (Härkönen 1987; Härkönen and Heide-Jørgensen 1991), and Icelandic waters (Hauksson 1984). Flatfish, especially flounder, contributed to the diet in both summer and winter (Table 2) and have also been previously recorded (see earlier references).

Between-year and seasonal variations in the diet

Our results also suggest that there were significant between-year and seasonal differences in the importance of the key species (Table 3). These differences were most apparent for sand eels and lesser octopus in summer (Table 4) and sand eels and cod in winter (Table 5).

Overall, sand eels were more prevalent in summer 1989 and winter 1989–1990 (Table 3). In the following 2 years, there was a significant decrease in numbers of sand eels per faex in all areas and both seasons (Tables 4 and 5). On the other hand, there were no significant between-year differences in numbers of fish present in those samples containing sand eels. The decrease in the contribution of sand eels therefore appears to be due to fewer seals preying on sand eels rather than fewer sand eels being taken by a similar number of seals. This pattern may be expected if changes in prey availability led to a decrease in seals' encounter rate with patchy prey such as schooling sand eels, or if some seals switched to alternative prey that were more abundant or easier to capture.

This observed decrease in the importance of sand eels in summer coincided with a significant increase in numbers of lesser octopus found in both the Inverness and Dornoch firths (Table 3). The foraging areas used by radio-tagged harbour seals in the Moray Firth in the summers of 1988–1991 appeared to be similar (Thompson and Miller 1990; Aberdeen University, unpublished data). Observed between-year differences in diet therefore appear to reflect seals exploiting changes in prey availability in the same local area. The factors that affect prey choice, however, remain unclear. Although small shoaling fish are apparently important to harbour seals in the Moray Firth (Pierce et al. 1990), larger prey with a lower calorific value, such as octopus and flatfish (Murray and Burt 1977), were also taken (Fig. 2). There are few data on temporal or spatial changes in the abundance of sand eels in the Moray Firth over the period in question. However, figures for commercial landings of lesser octopus in north-eastern Scotland (International Council for the Exploration of the Sea (ICES) area 4A) in 1990 and 1991 were two and half times those in 1989 and 1992 (Scottish Sea Fisheries Statistical Tables, 1989–1992; figures provided by SOAFD).

Whilst the contribution of sand eels in successive winters decreased in all areas, the contribution of gadoids appeared to increase from 0.5 to 43% (Fig. 2). In contrast to sand eels, the interannual contributions of cod and whiting per faex also appeared to vary between geographical areas. A significant between-year increase in numbers of cod was apparent in the Beauly and Dornoch firths, whilst numbers of whiting increased in the Beauly Firth only (Table 5). These between-year differences may be linked to recently improved years of recruitment in the North Sea for whiting in 1990 and 1991 and for cod in 1991 (Anonymous 1992), but Härkönen (1988) also suggests that smaller gadoids are preyed upon more heavily when preferred prey such as herring (and presumably sand eels) are unavailable. Consequently, the observed increase in the contribution of gadoids in the Moray Firth may be related to decreased availability of clupeids and sand eels. Switching to alternative prey when the availability of a favoured prey species decreases has also been documented for Californian sea lions, *Zalophus californianus* (Bailey and Ainley 1982), and for southern sea otters, *Enhydra lutris nereis* (Ostfeld 1982).

Both whiting and cod were preyed upon more frequently in winter than in summer (Table 6), and estimated sizes of both species (Fig. 3*c*, Table 7) suggest that these were young fish. Although immature whiting are often found around inshore wrecks and rocks (Dipper 1987), there is also a general offshore movement towards cooler water in summer (SOAFD, unpublished data). Seasonal changes in the contribution of gadoids in the diet of coastal species such as harbour seals may result from such spatial changes in fish distribution. Seasonal differences in the number (Table 6) and size of lesser octopus found in the diet were most likely due to the postspawning die-off of mature animals in the autumn (Muus and Dahlstrom 1964), whilst the low numbers of sand eels per faex observed in samples from the Beauly Firth (Table 3) may be due to the lack of the sand eels' preferred sea bed type (smooth areas of gravelly sand) in the Beauly Firth (Reid and McManus 1987). These points serve to show the potential influence of both restricted habitat preferences and life-history strategies on the selection of prey by harbour seals.

The between-year differences in diet composition observed in this study highlight the importance of long-term studies for understanding the dynamics of seal prey interactions. In winter 1988–1989 clupeids formed >90% of the diet by mass (Fig. 2). At this time seals tended to use more inshore haulout and foraging sites, apparently in relation to the local availability of overwintering clupeid prey (Thompson et al. 1991). In contrast, during the following three winters we found little evidence of predation on clupeids, with sand eels and gadoids forming the bulk of the diet (Figs. 2*d*, 2*e*, and 2*f*). Data on haulout site use and foraging behaviour indicated that the observed differences in diet also reflected a change in foraging area, in contrast to the situation occurring in summer. Furthermore, the available fisheries data suggest that clupeids were less abundant in the inner firths during these winters (Thompson et al. 1996).

Together, these results suggest that harbour seals' diet choice is consistent with "sensible" foraging strategies (Pyke 1984) and that they adjust their foraging patterns and find alternative prey when food conditions change. Given the large interannual variations in the recruitment rates of many of their potential prey (e.g., Cushing 1988), we suggest that similar changes in composition will be found in the diet of other coastal marine mammals. To date, assessment of interactions between seals and fisheries have focused on improving estimates of seals' prey consumption. These results suggest that such parameters are highly variable and influenced by prey availability. Consequently, predictions concerning future predator–prey interactions should also take account of the predicted availability of different potential prey species. As seen in a number of other studies, it appeared that clupeids were a favoured prey when conditions were suitable (Härkönen and Heide-Jørgensen 1991; Thompson et al. 1991), with sand eels and (or) small gadoids becoming more important only in winters when clupeids were less available (Härkönen 1988). Such temporal changes in diet also highlight the need for more dynamic models to estimate the impact of seal populations upon stocks of their prey.

Acknowledgements

We thank John Prime for processing samples, everyone at the Lighthouse Field Station who helped with sample collections, especially D. Miller and S. Reddy, also Dr. D.G. Raffaelli and Dr. P.W. Rankine for assistance with the image analyser, Dr. G.J. Pierce, Dr. J.R.G. Hislop, and Dr. S.P.R. Greenstreet for advice and access to unpublished data and Prof. P.A. Racey, Dr. A. Hall, Dr. P.H. Hammond, and Dr. J. Watt for advice on an earlier version of the manuscript. We thank three anonymous reviewers for constructive comments. The work was funded by a series of contracts from the SOAFD to Prof. P.A. Racey and Dr. P.M. Thompson.

References

Anonymous. 1992. Co-operative research report No. 193. International Council for the Exploration of the Sea, Copenhagen.

Bailey, K.M., and Ainley, D.G. 1982. The dynamics of Californian sea lion predation on Pacific hake. Fish. Res. **1**: 163–176.

Beck, G.G., Hammill, M.O., and Smith, T.G. 1993. Seasonal variation in the diet of harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence and western Hudson Strait. Can. J. Fish. Aquat. Sci. **50**: 1363–1371.

Bedford, B.C., Woolner, L.E., and Jones, B.W. 1986. Length–weight relationships for commercial fish species and conversion factors for various presentations. Fish. Res. Data Rep. No. 10, Lowestoft, U.K. pp. 1–41.

Benoit, D., and Bowen, W.D. 1990. Seasonal and geographical variation in the diet of grey seals (*Halichoerus grypus*) in eastern Canada. Can. Bull. Fish. Aquat. Sci. No. 222. pp. 215–226.

Bowen, W.D., Lawson, J.W., and Beck, B. 1993. Seasonal and geographical variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on Scotian Shelf. Can. J. Fish. Aquat. Sci. **50**: 1768–1778.

Brown, R.F., and Mate, B.R. 1983. Abundance, movements, and feeding habits of harbour seals (*Phoca vitulina*), at Netarts and Tillamook Bays, Oregon. Fish. Bull. **81**: 291–301.

Clarke, M.R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford.

Costa, D.P., Croxall, J.P., and Duck, C.D. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology, **70**: 596–606.

Coull, K.A., Jermyn, A.S., Newton, A.W., Henderson, G.I., and Hall, W.B. 1989. Length/weight relationships for 88 species of fish encountered in the north east Atlantic. Scottish Fisheries Res. Rep. No. 43, Department of Agriculture and Fisheries for Scotland.

Cushing, D.H. 1988. The study of stock and recruitment. *In* Fish population dynamics. *Edited by* J.A. Gulland. John Wiley & Sons, New York. pp. 105–128.

Daan, N. 1989. Data base report of the stomach sampling project 1981. Co-operative Res. Rep. No. 164, International Council for the Exploration of the Sea, Copenhagen.

Dann, J. 1986. The fishery for sandeels off the English coast 1978–1983. Ann. Biol. (Copenhagen), **40**: 179–181.

da Silva, J., and Neilson, J.D. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. **42**: 1439–1442.

Dellinger, T., and Trillmich, F. 1988. Estimating diet consumption from scat analysis in otariid seals (Otariidae): is it reliable? Can. J. Zool. **66**: 1865–1870.

Dipper, F. 1987. British sea fishes. Underwater World Publications Ltd., Ipswich. U.K.

Fraser, P.J. 1987. Atlantic salmon (*Salmo salmar* L.) feed in Scottish coastal waters. Aquacult. Fish. Manage. **18**: 243–248.

Hammond, P.S., Hall, A.J., and Prime, J.H. 1994. The diet of grey seals around Orkney and other islands and mainland sites in north-eastern Scotland. J. Appl. Ecol. **31**: 240–250.

Hammond, P.S., and Prime, J.H. 1990. The diet of British grey seals (*Halichoerus grypus*). Can. Bull. Fish. Aquat. Sci. No. 222. pp. 243–254.

Härkönen, T.J. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu ApS, Biological consultants, Hellerup, Denmark.

Härkönen, T.J. 1987. Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. J. Zool. (Lond.), **213**: 535–543.

Härkönen, T.J. 1988. Food habitat relationship of harbour seals and black cormorants in Skagerrak and Kattegat. J. Zool. (Lond.), **214**: 673–681.

Härkönen, T.J., and Heide-Jørgensen, M.-P. 1991. The harbour seal *Phoca vitulina* as a predator in the Skagerrak. Ophelia, **34**: 191–207.

Harris, M.P., and Wanless, S. 1985. Fish fed to young guillemots (*Uria aalge*) and used in display on the Isle of May, Scotland. J. Zool. (Lond.), **207**: 441–458.

Harris, M.P., and Wanless, S. 1986. Food of young razorbills (*Alca torda*) on the Isle of May, Scotland and a comparison with that of young guillemots (*Uria aalge*) and puffin (*Fratercula arctica*). Ornis Scand. **17**: 41–46.

Harvey, J.T. 1988. Population dynamics, annual food consumption, movements and dive behaviours of harbour seals, *Phoca vitulina richardsi* in Oregon. Ph.D. thesis, University of Oregon, Portland.

Harvey, J.T. 1989. Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. J. Zool. (Lond.), **219**: 101–111.

Harwood, J. 1987. Competition between seals and fisheries. Sci. Progr. **71**: 429–437.

Harwood, J., and Croxall, J.P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Mar. Mammal Sci. **4**: 13–33.

Harwood, J., and Greenwood, J.J.D. 1985. Competition between British grey seals and fisheries. *In* Marine mammals and fisheries. *Edited by* J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen and Unwin, London. pp. 153–169.

Hauksson, E. 1984. Food of the common seal (*Phoca vitulina* L.) and grey seal (*Halichoerus grypus* Fabr.) in Icelandic waters. Hafrannsoknir, **30**: 27–55.

Jobling, M. 1987. Marine mammal faeces samples as indicators of prey importance—A source of error in bioenergetics models. Sarsia, **72**: 255–260.

Jobling, M., and Breiby, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia, **71**: 265–274.

Lavigne, D.M., Innes, S., Stewart, R.E.A., and Worthy, G.A.J. 1985. An annual energy budget for north-west Atlantic harp seals. *In* Marine mammals and fisheries. *Edited by* J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen and Unwin, London. pp. 319–336.

Macer, C.T. 1966. Sand eels (*Ammodytidae*) in the south-western North Sea: their biology and fishery. Fishery Investigation Ser. No. 24(6), Ministry of Agriculture, Fisheries and Food, U.K.

Markussen, N.H., and Øritsland, N.A. 1991. Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents and White Seas. Polar Res. **10**(2): 603–608.

Murray, J., and Burt, J.R. 1977. The composition of fish. Torry Advisory Note No. 38, Ministry of Agriculture, Fisheries and Food, U.K.

Muus, B.J., and Dahlstrom, P. 1964. Sea fishes of Britain and N.W. Europe. Collins, Glasgow.

North, A.W., Croxall, J.P., and Doidge, D.W. 1983. Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. Br. Antarct. Surv. Bull. No. 61. pp. 27–37.

Olesiuk, P.F. 1993. Annual prey consumption by harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish. Bull. **91**(3): 491–515.

Ostfeld, R.S. 1982. Foraging strategy and prey switching in California sea otter. Oecologia (Berl.), **53**: 170–178.

Pierce, G.J., and Boyle, P.R. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanogr. Mar. Biol. Annu. Rev. **29**: 409–486.

Pierce, G.J., Boyle, P.R., and Thompson, P.M. 1990. Diet selection in seals. *In* Trophic relationships in the marine environment. *Edited by* M. Barnes and R.N. Gibson. Aberdeen University Press, Aberdeen. pp. 222–238.

Pierce, G.J., Boyle, P.R., and Diack, J.S.W. 1991*a*. Identification of fish otoliths and bones in faeces and digestive tracts of seals. J. Zool. (Lond.), **224**: 320–328.

Pierce, G.J., Miller, A., Thompson, P.M., and Hislop, J.R.G. 1991*b*. Prey remains in grey seal (*Halichoerus grypus*) faeces from the Northeast coast of Scotland. J. Zool. (Lond.), **224**: 337–341.

Pierce, G.J., Thompson, P.M., Miller, A., Diack, J.S.W., Miller, D., and Boyle, P.R. 1991*c*. Seasonal variation in the diet of harbour seals (*Phoca vitulina*) in the Moray Firths area of Scotland. J. Zool. (Lond.), **223**: 641–652.

Pierce, G.J., Boyle, P.R., Watt, J., and Grisley, M. 1993. Recent advances in diet analysis of marine mammals. Symp. Zool. Soc. Lond. No. 66. pp. 241–261.

Prime, J.H., and Hammond, P.S. 1987. Quantitative assessment of grey seal diet from faecal analysis. *In* Approaches to marine mammal energetics. *Edited by* A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini. Allen Press, Lawrence, Kans. pp. 161–181.

Prime, J.H., and Hammond, P.S. 1990. The diet of grey seals from the south-western North Sea assessed from analyses of hard parts found in faeces. J. Appl. Ecol. **27**: 435–447.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. **15**: 523–575.

Rae, B.B. 1968. The food of seals in Scottish waters. Mar. Res. **2**: 1–23.

Reay, P.J. 1970. Synopsis of biological data on the North Atlantic sand eels of the genus *Ammodytes*. FAO Fish. Synop. No. 82.

Rankine, P.W., and Cargill, L.H. 1991. The automated measurement of growth increments of larval fish otoliths using image analysis enhancement procedures. Scottish Fisheries Working Pap. No. 25, Scottish Office Agriculture and Fisheries Department, Aberdeen.

Reid, G.L., and McManus, J. 1987. Sediment exchanges along the coastal margin of the Moray Firths, Eastern Scotland. J. Geol. Soc. (Lond.), **144**: 179–185.

Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

Thompson, P.M., and Miller, D. 1990. Summer foraging activity and movements of radio-tagged harbour seals (*Phoca vitulina* L.) in the Moray Firths, Scotland. J. Appl. Ecol. **27**: 492–501.

Thompson, P.M., Pierce, G.J., Hislop, J.R.G., Miller, D., and Diack, J.S.W. 1991. Winter foraging by harbour seals (*Phoca vitulina*) in relation to food availability in the inner Moray Firths, N.E. Scotland. J. Anim. Ecol. **60**: 283–294.

Thompson, P.M., Wood, D., Tollit, D.J., and Miller, D.M. 1992. Seasonal and between-year differences in harbour seal *Phoca vitulina* foraging activity. Int. Coun. Explor. Sea CM 1992 N:15.

Thompson, P.M., Tollit, D.J., Greenstreet, S.P.R., Mackay, A., and Corpe, H.M. 1996. Between year variations in the diet and behaviour of harbour seals *Phoca vitulina* in the Moray Firth: causes and consequences. *In* Aquatic predators and their prey. *Edited by* S.P.R. Greenstreet and M. Tasker. Blackwells Science, Oxford. pp. 44–52.

Trillmich, F., and Dellinger, T. 1991. The effects of El Niño on Galapagos Pinnipeds. *In* Pinnipeds and El Niño responses to environmental stress. *Edited by* F. Trillmich and K.A. Ono. Springer-Verlag, Germany. pp. 66–74.