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Interannual variation in the summer diets of harbour seals *Phoca vitulina* at Mousa, Shetland (UK)

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The main prey species in the summer (July–September) diets of harbour seals (*Phoca vitulina*) on the Island of Mousa (Shetland, UK), 1994–1997, were whiting (*Merlangius merlangus*), herring (*Clupea harengus*), sandeel (Ammodytidae) and garfish (*Belone belone*). Norway pout (*Trisopterus esmarkii*) was numerically important but comprised no more than 11% of prey weight in any year. There were marked between-year fluctuations in the relative importance of these prey, with whiting comprising 16–34% (by weight) of the diet, herring 12–28%, sandeels 7–18% and garfish 7–22%. Additional data on spring (April–June) diet were available for 1995–1997: sandeels were the most important prey (% weight) in all three years (51–60% of the diet), while herring (8–48%) and gadids (2–22%) varied in importance. The average size of fish eaten was larger than that reported in comparable studies from other areas. Harbour seals appear to have selected larger sandeels, whiting and Norway pout than the average size available in the area, as indicated by survey trawls, although between-year changes in the size of Norway pout in the diet did to some extent reflect availability. Interannual variation in the importance of Norway pout in the diet appeared to track trends in abundance, although the short time series precluded detection of a statistically significant correlation. Thus, some of our results are consistent with harbour seals feeding opportunistically while others point to selectivity, particularly for prey size. Estimated consumption of fish by the 500 harbour seals on Mousa during summer ranged from 152–195 tonnes.

INTRODUCTION

Seals are important predators of commercially exploited fish in European waters and thus potentially compete with fisheries (e.g. Rae, 1968; SMRU, 1984, 1994; Harwood & Greenwood, 1985; Härkönen & Heide-Jørgensen, 1991; Harwood, 1992; Tollit & Thompson, 1996). This remains a contentious issue in the UK, with regular calls by fishermen to control the 'grey fleet'. While grey seals (*Halichoerus grypus* Fabricus), the population of which currently numbers over 110,000 in UK waters, are perceived as the more important threat to fisheries, harbour seals (*Phoca vitulina* L.) may also interact with fisheries in areas where they are abundant. Thus, harbour seals are the most numerous pinniped in the waters around Shetland, with a minimum population estimate of 6000 (C. Duck, personal communication).

Of interest as a general ecological question, and fundamental to understanding and predicting the impact of seals on fish stocks, is the question of whether seals are opportunistic predators or show fixed preferences. While seals are frequently referred to as generalist or opportunistic foragers (e.g. Härkönen & Heide-Jørgensen, 1991), previous evidence is equivocal. The occurrence of significant interannual and seasonal variation in diet is consistent with opportunistic predation on locally abundant prey and has been widely reported in harbour seals and other pinniped species. Pierce et al. (1991) demonstrated seasonal changes in the diet of harbour seals in the Moray Firth area of Scotland. Thompson et al. (1996) and Tollit & Thompson (1996) have shown that there is considerable between-year variation in the diet of harbour seals in the same area. Dedicated research vessel surveys in the areas used by radio-tagged harbour seals have related these changes in diet to changes in the abundance of fish prey (Tollit et al., 1997a).

Variations in diet may coincide with changes in the foraging movements of seals, which in turn could have implications for energy requirements and food consumption. For example, Boyd et al. (1994) reported behavioural changes in the foraging patterns of Antarctic fur seals (*Arctocephalus gazella* Peters, 1875) in response to changes in the abundance of key prey species. Furthermore, changes in diet may have consequences for individual health and, ultimately, population status. Thompson et al. (1996) showed that the body condition index of harbour seals in the Moray Firth was lower in years when the availability of clupeid fish was low, possibly reflecting both the consumption of prey of lower energy density and increased energetic costs of travelling further offshore to feed.

Understanding how and why diet changes from year to year is important to enable interactions with fisheries to be predicted. To date, most models of seal predation are based on a static picture of diet (e.g. Härkönen & Heide-Jørgensen, 1991; Olesiuk 1993; SMRU, 1994) and there are very few examples of studies in which it has been possible to construct dynamic models of seal predation. Bailey & Ainley (1982) produced one of the first models to explicitly consider a change in seal diet choice in response to shifts in prey abundance. However, in their model of fur seal predation on hake, Punt & Butterworth (1995) assumed that hake formed a fixed percentage of the diet. Field data on diet composition under different conditions of prey abundance are needed to construct empirical functional responses that can be used in models. Ultimately such models will need to predict the spatial pattern of predation by seals in relation to fish distribution and abundance, as has recently been attempted for seabirds (Ollason et al., 1997).

In previous studies, Brown & Pierce (1997, 1998) identified the fish species most commonly eaten by harbour seals at the island of Mousa in Shetland (Figure 1) and described seasonal variation in diet. On Mousa, harbour seal numbers reach a peak during August, coinciding with the annual moult, when up to 500 individuals may be present (Duck et al., 1993; E.G.B. unpublished data). Few harbour seals are present on Mousa during October–May. The present study focuses on interannual variation (1994–1997) in the diet of harbour seals in Shetland. Harbour seal diet composition at Mousa was quantified in four consecutive summers, to determine: (i) whether there was significant interannual variation; and (ii) if diet, and variation in diet, could be related to the size and abundance of fish available, as estimated from trawl catches, thus providing evidence for opportunistic foraging. Finally, the biomass of prey consumed by harbour seals on Mousa during summer is estimated, and the extent to which harbour seals may compete with local commercial fisheries in Shetland waters is discussed.

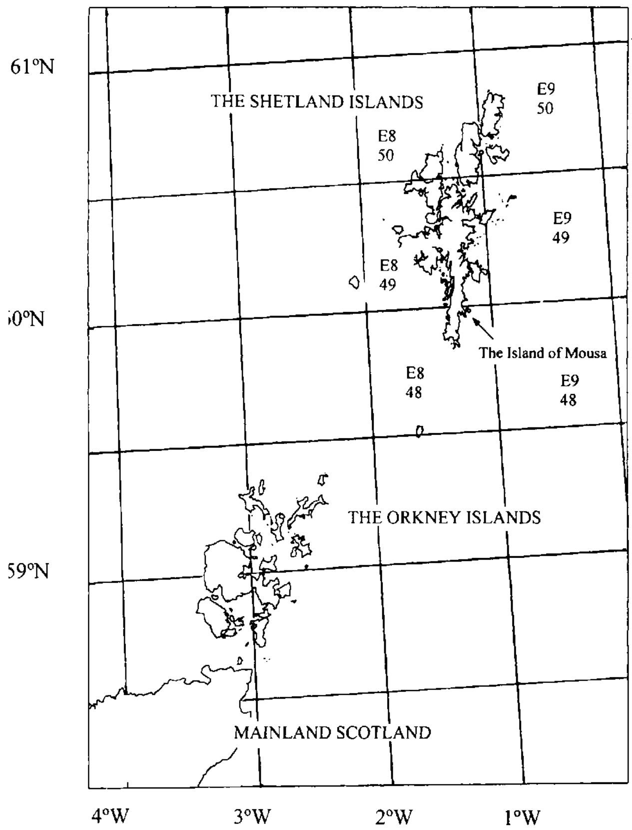

Figure 1. The Shetland Islands, with the location of the island of Mousa indicated.

MATERIALS AND METHODS

Study site and sample collection

Regular visits were made to the island of Mousa (Figure 1) to collect faecal samples during summer (July–September) of the years 1994–1997. Data for 1994 are taken from Brown & Pierce (1997) and data for 1995 are a subset (i.e. data for Mousa) of the data included in Brown & Pierce (1998). In 1996 scats were collected from June through September and in 1995 and 1997 scats were collected from May through September. Thus, for 1995–1997 spring is also briefly described (i.e. May and June) diets.

As is usual in such dietary studies on seals, sample collection involved retrieval of all scats available at a site at a given time and it was not normally possible to identify the age and sex of the seals. It is assumed that the scats are representative of the seals using the haul-out site. For a detailed description of the study site and sampling protocol see Brown & Pierce (1997, 1998).

Processing of scats and identification of prey remains

Scats were washed through sieves with a minimum mesh size of 0.355 mm. Fish otoliths were stored dry and cephalopod beaks were stored in alcohol. Otoliths and cephalopod beaks were identified to the lowest possible taxon, normally to the species level, using published guides (Clarke, 1986; Härkönen, 1986) and reference material.

Quantification of the diet and comparison between years

Fish otoliths and cephalopod beaks were measured using a binocular-dissecting microscope fitted with an eyepiece graticule. For otoliths, the length was usually measured. Otolith width was measured whenever damage to the otolith prevented measurement of the length, as was commonly the case for cod (*Gadus morhua* L.) and mackerel (*Scomber scombrus* L.). Almost all whiting (*Merlangius merlangus* L.) otoliths were broken at the posterior end and width was therefore taken as the standard measurement for this species. Width is also the standard measurement taken on herring otoliths (Härkönen, 1986). Usually, all otoliths were measured but if large numbers of otoliths from one type of fish were present in the sample, a random subsample was measured. Subsampling was used for *Trisopterus* spp. (for which at least 50% of otoliths in each sample were measured) and sandeels (which occurred in even higher numbers and for which a minimum of 10% of otoliths in each sample were measured). For cephalopod beaks, the standard measurements are hood length or rostral length, depending on the species (see Clarke, 1986).

To correct for size reduction of the otoliths due to digestion, 'digestion coefficients' (Tollit et al., 1997b) were applied. These are experimentally derived ratios between original otolith length and the length of the otolith when it emerges in harbour seal faeces. Tollit et al. (1997b) derived: (a) average digestion coefficients for otoliths of all fish species; (b) species-specific coefficients for selected commonly eaten species; and (c) for a few species, 'grade-specific' coefficients for otoliths digested to

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different degrees, as identified from changes in morphological features of the otolith. Grade-specific digestion coefficients were available for cod, whiting and sandeels. The coefficient which best matched the degree to which the majority of the otoliths, recovered from seal scats, were eroded, was used. For cod and sandeels, coefficients for slightly eroded otoliths were thus used (1.070, 1.160, respectively) and for whiting the coefficient for moderately eroded otoliths (1.365). Species-specific digestion coefficients were available for herring and lemon sole (*Microstomus kitt* Walbaum, 1792). No species-specific coefficients were available for the other species and the average coefficient of 1.25 (or 1.24 for otolith width) was used. Cephalopod beaks pass through harbour seal digestive tracts virtually undigested (Tollit et al., 1997b) and the digestion coefficient is effectively 1.0.

The lengths and weights of fish in the seals' diet were estimated using previously established regression equations, as listed in Brown & Pierce (1998). Where possible, these otolith-size fish-size relationships were derived using fish caught in Shetland waters. Each otolith is assumed to represent 0.5 fish. Cephalopod weights were estimated using regressions from Clarke (1986) and from previously unpublished data. The new regressions are given in Appendix 1.

Considering only those scats that contained otoliths and/or beaks, for each prey category in each month and quarter of each year, the average number of otoliths per scat and the proportion (by estimated original weight) of the diet comprising that prey category were calculated.

Comparisons of diet composition between years were restricted to data for the third quarter (summer), during which samples were available in each month of each year. Insufficient data were available for the second quarter (spring) to permit a full analysis. The size and number of each prey category eaten in different years were compared.

Since neither the weight nor length of fish eaten is measured directly (being estimated from measurements on otoliths), when possible comparisons of the sizes of fish consumed were based on analysis of otolith size. For cod and mackerel estimated fish lengths were compared, because the otolith data available consisted of a mixture of otolith widths and lengths. For all fish species, size–frequency distributions were skewed or had polymodal distributions. Comparisons of size–frequency distributions were made using Kolmogorov–Smirnov (K–S) tests. It is assumed for this analysis that each otolith can be treated as an independent data point, although care is required in interpretation of statistically significant differences, since seals may prey on shoals of similarly sized fish. In addition to comparing the size distribution of fish eaten in different years, the size distribution of fish eaten by seals is also compared with the size of fish in trawl hauls (see below).

Frequency distributions of numbers of otoliths per scat were extremely right-skewed (for most prey categories, the most common frequency class was zero otoliths). Between-year comparisons for numbers of otoliths were therefore made using non-parametric Kruskal–Wallis tests and *post-hoc* pair-wise Mann–Whitney *U*-tests, including a Bonferroni correction of the accepted level of significance. (For the six pair-wise tests between data from four years, the appropriate value is $p=0.0083$.)

Comparison of fish eaten by seals with fish taken by trawling

Data on length–frequency distributions of demersal fish species in the Shetland area were available from standard trawl survey hauls made in August of each year. The length–frequency distributions used were composites of catches in the six International Council for the Exploration of the Sea (ICES) statistical rectangles closest to the Shetland Islands (Fisheries Research Services (FRS), unpublished data). Data for sandeels were available from surveys of commercial sandeel grounds in Mousa Sound in 1996 and 1997 (FRS, unpublished data, see Figure 1).

Formal statistical comparisons of fish length–frequency distributions, between dietary and trawl data, were made only for whiting, Norway pout and sandeels. Other fish species were insufficiently represented in the trawl catches and/or the faecal samples to permit comparison. Comparisons were made using two-sample K–S tests. For sandeels, only otoliths from faecal samples collected within two weeks before or after the trawl date were used in the comparison.

For the main demersal fish species eaten, interannual trends (1994–1997) in relative importance (% number) in the diet were compared with interannual trends in estimated stock size (FRS, unpublished data). Since the time-series is very short (4 y), only very high (almost perfect) correlations will be statistically significant. Nevertheless, it is considered to be of interest to examine these trends. For sandeels, data refer to the Shetland stock, whereas for the other species data refer to the North Sea.

Fish consumption by harbour seals on Mousa

Fish consumption by harbour seals on Mousa was estimated during the third quarter of each year. There are approximately 500 harbour seals present on Mousa during the summer months (Duck et al., 1993; E.G.B., unpublished data). The average daily energy requirements of free-living harbour seals are estimated to be $4680\,\mathrm{kcal\,d^{-1}}$ (Härkönen & Heide-Jørgensen, 1991). The population energy requirement (PER) of harbour seals on Mousa during quarter three of each year was thus estimated to be 213.5 million kcal ($91.25\,\mathrm{d}\times500$ seals$\times4680$ kcal).

The energy density of the prey species has a direct bearing on the estimated weight of food needed to satisfy a predator's energy demands. Härkönen & Heide-Jørgensen (1991) estimated that harbour seals require from 3.67 to 4.15 kg of fish per day, depending on the diet composition. Energy densities used for our calculations were taken from Murray & Burt (1977), Croxall & Prince (1982), Hislop et al. (1991) and SMRU (1994) (see Appendix 2).

For each prey category, the total energy represented by the otoliths in the scats (kcal, as estimated from the mass of fish and its energy density) was calculated and the individual values were expressed as a proportion of the total energy represented by all prey categories. The latter value was multiplied by the PER (see above) of the 500 harbour seals on Mousa during the quarter and converted to weight by dividing by the energy density of the prey category in question:

$$P_i = \frac{W_i E_i}{\sum_{i=1}^{n} W_i E_i} \text{ and } C_i = \frac{P_i \times PER}{E_i} \text{ Thus, } C_i = \frac{PER \times W_i}{\sum_{i=1}^{n} (W_i i)} \quad (1)$$

where: P_i=proportion (by energy) of prey type i in the diet, C_i=total weight of prey type i consumed by the seal population, PER=total energy requirements for the seal population on Mousa in the summer, W_i=total weight of prey type i in the set of samples, E_i=energy density of prey type i.

To estimate the mass of marketable fish eaten by seals on Mousa during the summer, the proportion by weight of the cod, haddock (*Melanogrammus aeglefinus* L.), whiting, saithe (*Pollachius virens* L.) and ling (*Molva molva* L.) that was above the respective minimum landing size (MLS) was calculated. The potential value was estimated by multiplying the weight eaten by the average quayside price per tonne. These results are compared with amounts caught by commercial fisheries from the six ICES rectangles in the Shetland area (FRS, unpublished data).

RESULTS

In total, 1620 scats were collected over the four years. Numbers of scats collected were highest in August of each year, coinciding with the annual moult (Table 1). A large proportion (70–100%) of the scats contained otoliths. Otoliths of sandeels (45,851 otoliths, 79.0% of the total) and Gadidae (8,965, 15.4%, including 6,368 *Trisopterus* spp.) were numerically the most abundant (Table 2). Of the *Trisopterus* spp. otoliths, the majority were Norway pout *Trisopterus esmarkii* (Nilsson, 1855). Cephalopod beaks were found in small numbers, mainly in the summer samples, the most frequently occurring species being the octopus (*Eledone cirrhosa* Lamarck, 1798) (remains of at least 62 individuals over the four years). Smaller numbers of sepiolids (mainly *Rossia macrosoma* (Delle Chiaje, 1830) but also *Sepiola* sp. and *Sepietta oweniana* (Orbigny, 1840)), ommastrephid squid (mainly *Todaropsis eblanae* (Ball, 1841) or *Illex coindetii* (Vérany, 1839)) and veined squid (*Loligo forbesi* Steenstrup, 1856) were also found.

Diet composition (by weight)

In summer, whiting, herring, garfish and sandeels were the most important prey categories, together accounting for 62–79% of the diet (Table 3). Over the four consecutive summers the contribution of gadids to the diet declined from 60% in 1994 to 37% in 1997. Over the same period, the contribution of pelagic fish increased from 21 to 44%. Sandeels were most important (18%) in 1994 and least important in 1996 (7%; Table 3). Cephalopods were a minor component of the diet in all years.

In spring, sandeels made up 49–61% of the diet and herring were also important (8–48%), especially in 1996. Herring were most important in the spring diet in 1996, the year in which gadids dropped to 2% of the spring diet.

Between year variation in diet: numbers of otoliths per scat

In the summer (quarter 3), there were statistically significant between-year differences in the numbers of otoliths per scat for the majority of prey categories (Table 4). Significant differences identified by post-hoc pair-wise tests were as follows: haddock were found more frequently in 1994 than in 1996 and 1997. Saithe were found least frequently in 1997. Ling were more common in 1996 than in 1995. Norway pout and herring were found least frequently in 1994. Herring were more common in 1996 than in 1995 and 1997. Garfish were found most frequently in 1997 and were more common in 1995 than 1994 and 1996. Sandeels were found more frequently in 1994 and 1995 than in 1996 and 1997.

In the spring (quarter 2, 1995–1997 only), sandeels were the numerically dominant prey in all years and *Trisopterus* spp. were markedly more numerous in 1997 than the other two years.

Between year variation in diet: sizes of fish consumed by harbour seals in summer

Size distributions are compared, between years, for those species occurring sufficiently frequently in the

Table 1. *Numbers of harbour seal,* Phoca vitulina *scats collected on Mousa during spring (quarter 2) and summer (quarter 3) 1994–1997, with the percentage containing otoliths given in parentheses. Data for 1994 are taken from Brown & Pierce (1997) and data for 1995 are a subset (i.e. data for Mousa) of the data included in Brown & Pierce (1998).*

Year	May	June	ΣQtr 2	July	August	Sept	ΣQtr 3	ΣQtrs2+3
1994	0	0	0	38 (89.5)	95 (82.1)	67 (70.1)	200 (79.5)	200
1995	18 (94.4)	50 (90.0)	68 (91.2)	31 (96.8)	158 (89.9)	134 (77.6)	323 (85.4)	391
1996	0	57 (89.5)	57 (89.5)	91 (80.2)	237* (82.1)	156 (88.5)	484 (84.0)	541
1997	8 (100)	89 (95.5)	97 (95.9)	73† (92.3)	198 (87.9)	120 (88.3)	391 (88.6)	488
Totals	26	196	222	233	688	477	1398	1620

*, only 184 were processed; †, only 52 were processed.

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Table 2. *Numbers of otoliths recovered for the main fish prey categories during each spring (quarter 2) and summer (quarter 3). The mean number of otoliths per scat is given in parentheses. Data for 1994 are taken from Brown & Pierce (1997) and data for 1995 are a subset (i.e. data for Mousa) of the data included in Brown & Pierce (1998). Only the main prey categories are listed individually and totals (boldface) are provided for major groups of species.*

	Quarter 2				Quarter 3						
Prey category	1995	1996	1997	Σ Qtr2	1994	1995	1996	1997	Σ Qtr3	Σ 2+3	% of Total
Cod	1	0	3	4	5	36	35	40	116	119	0.2
	(0.02)	(0)	(0.03)		(0.03)	(0.13)	(0.10)	(0.12)			
Haddock	1	0	0	1	34	10	6	9	59	60	0.1
	(0.02)	(0)	(0)		(0.21)	(0.04)	(0.02)	(0.03)			
Saithe	3	1	2	6	25	80	63	6	174	179	0.3
	(0.05)	(0.02)	(0.02)		(0.16)	(0.29)	(0.17)	(0.02)			
Ling	10	0	4	14	25	16	78	48	167	181	0.3
	(0.16)	(0)	(0.04)		(0.16)	(0.06)	(0.22)	(0.15)			
Whiting	19	1	3	23	190	474	423	359	1446	1469	2.5
	(0.31)	(0.02)	(0.03)		(1.19)	(1.72)	(1.17)	(1.09)			
T. esmarkii	42	18	1402	1462	143	1021	498	2234	3896	5358	9.2
	(0.68)	(0.35)	(15.1)		(0.90)	(3.70)	(1.38)	(6.81)			
Σ Gadidae	**116**	**24**	**1488**	**1628**	**793**	**2084**	**1553**	**2907**	**7337**	**8965**	**15.4**
	(1.87)	**(0.47)**	**(16.0)**		**(4.99)**	**(7.55)**	**(4.29)**	**(8.86)**			
Herring	112	101	104	317	122	423	767	468	1780	2097	3.6
	(1.81)	(1.98)	(1.12)		(0.77)	(1.53)	(2.12)	(1.43)			
Garfish	1	0	0	1	15	145	84	289	533	534	0.9
	(0.02)	(0)	(0)		(0.09)	(0.53)	(0.23)	(0.88)			
Σ Pelagic	**113**	**101**	**105**	**319**	**144**	**593**	**928**	**800**	**2465**	**2784**	**4.8**
	(1.82)	**(1.98)**	**(1.13)**		**(0.91)**	**(2.15)**	**(2.56)**	**(2.44)**			
Σ Flatfish	**13**	**1**	**3**	**17**	**10**	**12**	**67**	**50**	**139**	**156**	**0.3**
	(0.21)	**(0.02)**	**(0.03)**		**(0.06)**	**(0.04)**	**(0.19)**	**(0.15)**			
Σ Sandeels	**5655**	**4525**	**7792**	**17,772**	**4579**	**9706**	**5703**	**8091**	**28,079**	**45,851**	**79.0**
	(91.2)	**(88.7)**	**(83.8)**		**(28.8)**	**(35.2)**	**(15.8)**	**(24.7)**			
Σ All fish categories	**5901**	**4652**	**9388**	**19,941**	**5531**	**12,421**	**8251**	**11,884**	**38,087**	**58,028**	**100.0**
	(95.2)	**(91.2)**	**(101)**		**(34.8)**	**(45.0)**	**(22.8)**	**(36.2)**			

Table 3. *Harbour seal,* Phoca vitulina *spring (quarter 2) and summer (quarter 3) diet on Mousa: percentage contribution by weight of the main prey categories in each year of the study.*

	Quarter 2				Quarter 3				
Prey category	1995	1996	1997	Average	1994	1995	1996	1997	Average
Cod	0.33	0.00	1.15	0.49	1.65	1.33	1.79	2.00	1.69
Haddock	0.15	0.00	0.00	0.05	2.92	0.23	0.21	0.68	1.01
Saithe	2.82	0.70	4.20	2.57	5.27	5.86	6.64	0.51	4.57
Ling	9.93	0.00	2.20	4.04	13.5	3.33	11.1	6.59	8.63
Whiting	5.96	0.25	0.31	2.17	24.7	33.5	23.7	16.3	24.6
Σ *Trisopterus*	**2.86**	**0.70**	**22.3**	**8.62**	**8.00**	**5.38**	**0.95**	**10.8**	**6.28**
Σ Gadidae	**22.1**	**1.65**	**30.0**	**17.9**	**60.0**	**50.0**	**46.7**	**37.2**	**48.5**
Herring	19.9	47.9	7.86	25.2	12.3	19.4	27.7	18.3	19.4
Garfish	0.20	0.00	0.00	0.00	7.14	13.7	6.48	22.0	12.3
Σ Pelagic	**20.1**	**47.9**	**7.86**	**25.3**	**20.6**	**34.7**	**38.6**	**43.4**	**34.3**
Σ Flatfish	**4.00**	**0.03**	**0.58**	**1.54**	**0.81**	**0.33**	**2.08**	**3.23**	**1.61**
Σ Sandeels	**51.3**	**49.3**	**60.3**	**53.6**	**17.6**	**12.8**	**6.88**	**10.6**	**12.0**
Σ other fish	**1.75**	**0.00**	**0.00**	**0.00**	**0.00**	**1.28**	**2.24**	**3.64**	**1.79**
Σ Cephalopods	**0.83**	**1.17**	**1.29**	**1.10**	**1.04**	**0.91**	**3.23**	**1.94**	**1.78**

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Table 4. *Results of Kruskal–Wallis tests for between-year differences in summer diet of harbour seals,* Phoca vitulina *on Mousa. The tests compared the average numbers of otoliths per scat in each year for each of the main prey categories in the diet. Note: significant differences are in boldface.*

Prey category	*H*	*P*
Cod	5.46	0.1412
Haddock	16.91	**0.0007**
Saithe	16.54	**0.0009**
Ling	8.94	**0.0301**
Whiting	3.52	0.3184
T. esmarkii	25.29	**<0.0001**
Σ Gadid fish	2.16	0.5404
Herring	43.55	**<0.0001**
Mackerel	6.74	0.0806
Garfish	69.36	**<0.0001**
Σ Pelagic fish	60.37	**<0.0001**
Σ Flatfish	7.88	**0.0487**
Sandeels	23.73	**<0.0001**
Σ All Categories	25.68	**<0.0001**

H, value of Kruskal–Wallis statistic; *P*, probability.

summer diet to allow statistical analysis. The size distribution of whiting (based on direct analysis of otolith width data) shows a bimodal distribution in each summer. The distribution in 1997 differed significantly from those in the other years (K–S tests, $P<0.05$) but there were no significant differences among the distributions for 1994–1996. The smaller (and less abundant) size mode was relatively more important in 1997 than in the other three years (Figure 2).

The size distributions of both sandeels and *Trisopterus* in the summer diet differed significantly between every pair of years (K–S tests, $P<0.05$). Sandeels eaten in 1994 were generally larger than those eaten in other years, while the highest proportion of smaller sandeels was seen in the 1997 diet (Figure 2). The highest proportion of larger *Trisopterus* was eaten in 1997 whereas only smaller fish were eaten in 1996 (Figure 2).

The size–frequency distributions for herring in the summer diet differed between all pairs of years except 1996 and 1997 (K–S tests, $P<0.05$). All the distributions are poly-modal and it is difficult to pick out any clear patterns from visual inspection (Figure 2). The size–frequency distributions for saithe in the summer diet in 1994–1996 differed for each pair of years (K–S tests, $P<0.05$). The main difference apparent is that the saithe eaten in 1995 were smaller than those taken in 1994 and 1996. There were too few saithe in the 1997 diet to allow comparison of sizes. The size–frequency distributions for garfish in seal diets did not differ significantly between years: distributions in 1995 and 1997 looked very similar, while sample sizes for 1994 and 1996 were small (Figure 2).

Comparisons of sizes of fish eaten by seals and caught by trawls in summer

Trawl data on sandeel abundance were available only for 1996–1997. In both years, distributions of sizes in

Table 5. *Estimates of the quantities of fish consumed by harbour seals,* Phoca vitulina *on Mousa during quarter 3 of each year. Figures tabulated are the percentage contribution to total energy intake (%E) and total weight consumed (C, tonnes).*

	1994		1995		1996		1997	
Species	%E	C	%E	C	%E	C	%E	C
Cod	0.7	2.10	1.0	2.82	1.0	2.96	1.4	4.10
Haddock	1.9	5.70	0.4	1.21	0.2	0.45	0.4	1.19
Saithe	2.5	6.67	3.2	8.55	4.3	11.55	0.4	1.11
Whiting	14.1	38.95	15.2	42.14	13.9	38.07	9.1	25.24
Ling	8.7	21.06	2.4	5.81	7.5	17.90	4.9	13.04
Σ All *Trisopterus*	**5.0**	**9.67**	**5.1**	**9.77**	**0.7**	**1.53**	**7.6**	**14.71**
Σ All Gadidae	**36.6**	**93.54**	**27.6**	**71.22**	**29.5**	**76.83**	**24.1**	**60.14**
Herring	21.2	24.55	31.7	36.65	37.1	42.66	20.07	23.22
Garfish	10.2	13.82	16.0	21.67	11.4	15.28	36.05	49.00
Σ Pelagic fish	**33.0**	**40.65**	**50.4**	**62.20**	**55.7**	**68.27**	**60.2**	**79.40**
Σ Sandeels	**29.4**	**53.70**	**20.5**	**37.33**	**10.5**	**19.04**	**10.1**	**18.47**
Σ Flatfish	**0.6**	**1.72**	**0.2**	**0.50**	**1.4**	**3.82**	**1.4**	**3.80**
Σ Others	**0.3**	**1.01**	**1.4**	**3.19**	**4.0**	**9.75**	**4.2**	**9.67**
Total C (tonnes)		190.6		174.5		177.5		171.5
C per seal per day (kg)		4.178		3.824		3.897		3.759

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trawls and seal diet were significantly different (K–S tests, $P<0.05$). The modal size of sandeels in trawls was around 7 cm. In 1996, only around 7% of sandeels from the survey trawls in Mousa Sound were 1-group or older fish with lengths greater than 11 cm compared with 54% of sandeels eaten by seals. The pattern was similar in 1997 (Figure 3).

There were also significant differences between the sizes of whiting in trawls and in summer diets (K–S tests, $P<0.05$), with seals taking a substantial proportion of whiting above the modal size taken in the trawls (Figure 3).

Comparisons with trawl data for Norway pout (*Trisopterus esmarkii*) indicate that fish in the summer diet tended to be larger than those in trawls. Each year's size distribution in trawls differs statistically from the respective dietary size distribution (K–S tests, $P<0.05$). However, the data also suggest that inter-annual changes in the sizes eaten to some extent track available size-classes. Thus, in 1995 and 1997 there was a single size mode in trawl catches around 15–16 cm whereas in 1996 there were two modes, at 8 cm (0-group fish) and 15–17 cm. This change is reflected in the diet (Figure 3).

Interannual trends in indices of fish abundance and seal diet in summer

Norway pout was the most commonly occurring gadid both in the seals' summer diet and in the August trawl catches. The interannual changes in the numerical importance (mean number of otoliths per scat) of *Trisopterus* spp. in seal diet appear to track changes in Norway pout abundance. However, the correlation ($R=0.516$, $P=0.484$) is clearly not statistically significant (see Figure 4).

The numerical importance of whiting in the diet was (non-significantly) negatively correlated with abundance ($R=-0.567$, $P=0.433$). The numerical importance of sandeels in the seals' diet was uncorrelated with abundance ($R=-0.209$). The importance of cod in the diet followed a similar (but non-significant) trend to stock size ($R=0.656$, $P=0.344$) whereas the importance of haddock and saithe appeared to be unrelated to stock sizes ($R=-0.214$ and 0.316 respectively).

Estimated fish consumption by seals during summer

Estimates of the amount of fish consumed by harbour seals on Mousa each summer ranged from 172 tonnes in 1997 to 191 tonnes in 1994. The estimated decrease in per capita fish consumption between 1994 and 1997, from 4.2 to 3.8 kg per seal per day (Table 5), reflected an increasing contribution of energy-dense pelagic species to the seals' diet.

Estimated consumption of whiting, the most important gadid species in the diet, ranged from 25 tonnes in 1997 to 42 tonnes in 1995. Overall, the contribution of gadids to energy requirements declined from over one-third (94 tonnes) in 1994 to less than a quarter (60 tonnes) in 1997. Consumption of pelagic species showed a corresponding increase, from 33% (41 tonnes) to 60% (79 tonnes). Between 1994 and 1996, herring was the main pelagic species eaten (21–37%). However, in 1997 garfish

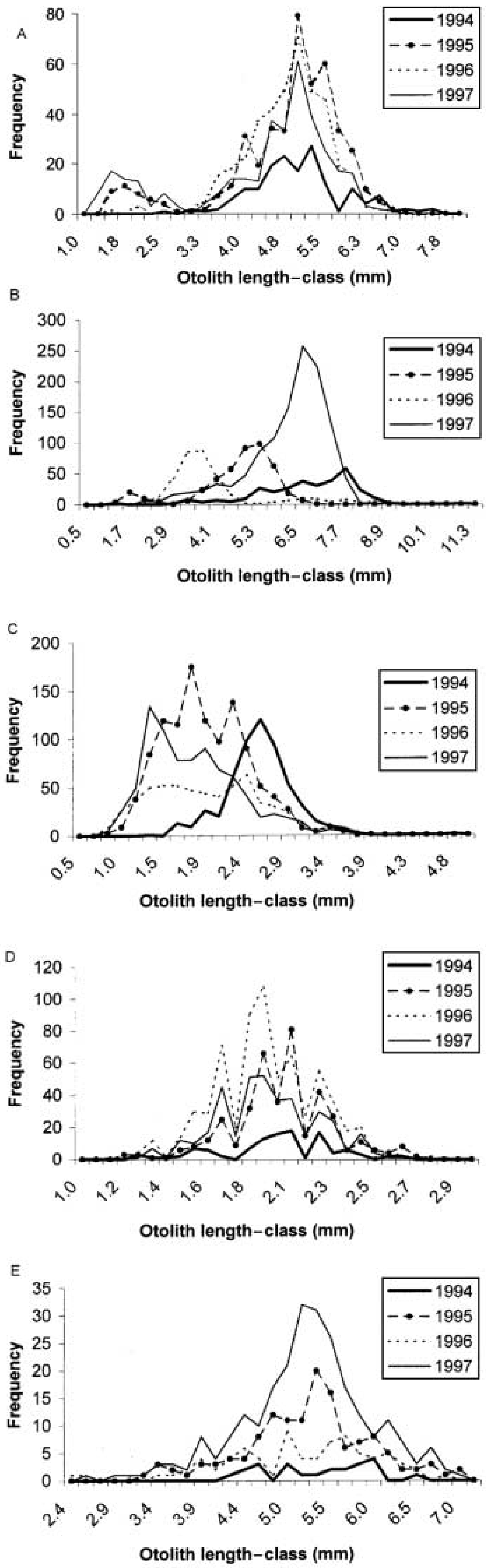

Figure 2. Size–frequency distributions for otoliths of (A) whiting, (B) Norway pout, (C) sandeels, (D) herring, and (E) garfish in the summer diet of *Phoca vitulina* on Mousa, 1994–1997.

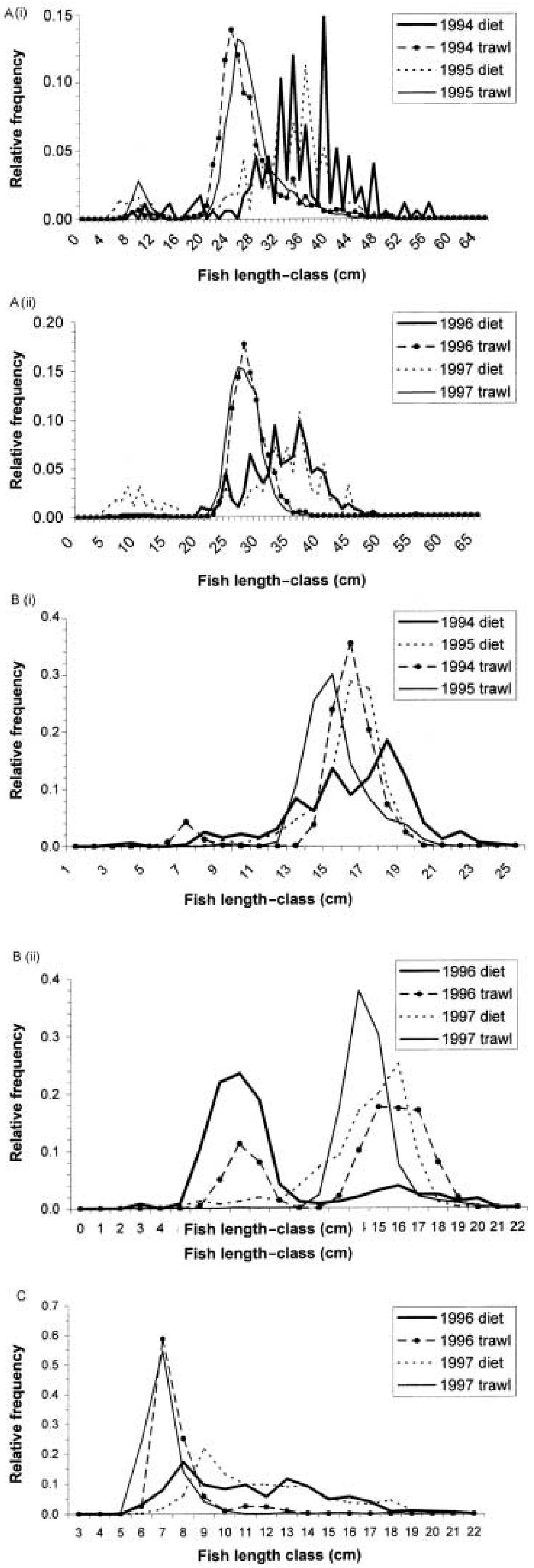

Figure 3. Length–frequency distributions for (A) whiting, (B) Norway pout and (C) sandeels consumed by seals and caught in survey trawls during the summers of 1994–1997. All frequencies are expressed as proportions of the total sample.

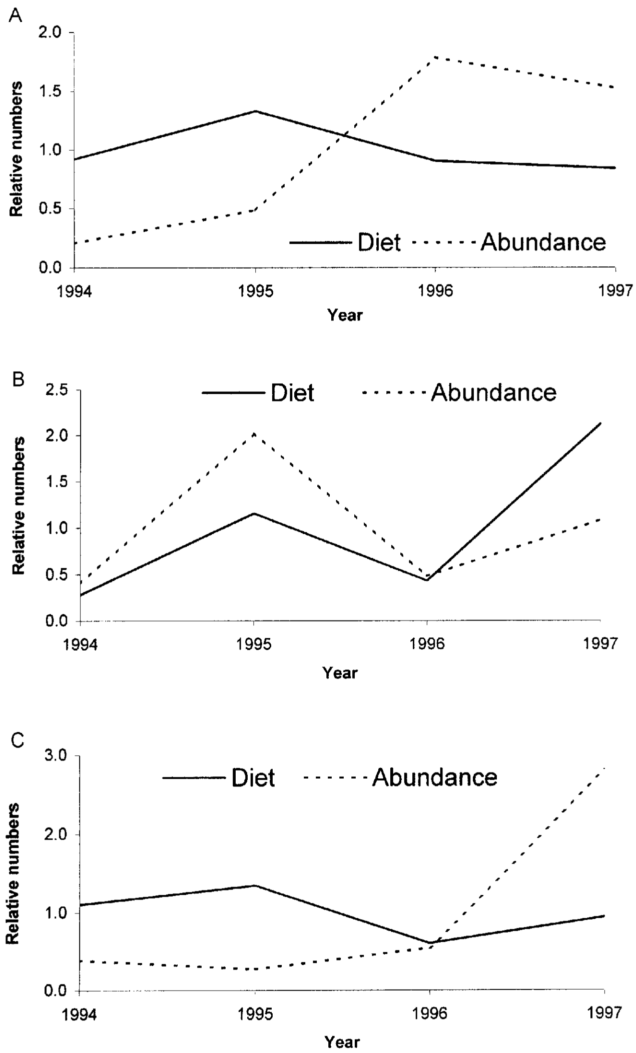

Figure 4. Changes in numeric importance of abundance of (A) whiting 1994–1997, (B) Norway pout 1994–1997, and (C) sandeel 1996–1997, in relation to trends in abundance. To provide comparable scales, all data are expressed as a proportion of the mean values for 1994–1997.

replaced herring as the main pelagic species (32%). Consumption and importance of sandeels declined over the study period from 30% (54 tonnes) to 12% (18 tonnes) (Table 5).

The estimated amounts of the main commercial gadid species (cod, haddock, ling, saithe, whiting) consumed by seals in summer, including only fish that were over the minimum landing size (in January 2000, (minimum landing size) MLS for ling was increased from 46 to 63 cm. The calculations are based on the earlier value) declined from 74 tonnes (approx. £43,000) in 1994 to 36 tonnes (approx. £21,000) in 1997 (Table 6). Seal predation on cod and haddock was negligible compared to amounts landed by fisheries in the area. The amount of whiting eaten by seals at Mousa was equivalent to 2–4% of commercial landings from Shetland waters during summer, while amounts for saithe ($\leqslant$9%) and ling ($\leqslant$12%) were higher in some years (Table 7). In making this comparison, it should be borne in mind that harbour seals on Mousa represent only around 12% of the Shetland population.

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Table 6. *Commercially important gadid fish above minimum landing size (MLS) eaten by harbour seals* Phoca vitulina *on Mousa during summer: estimated percentages by weight (%W), quantities (W, tonnes) and value (£). Price per tonne is based on average prices on Shetland markets during 1995, 1996 and 1997 (J.H. Black, Fishery Officer, Scottish Fisheries Protection Agency, personal communication).*

		Seal Consumption											
	Price per tonne	1994			1995			1996			1997		
Species	(£)	%W	W	£	%W	W	£	%W	W	£	%W	W	£
Cod	877	93.5	2.0	1747	68.0	2.0	1720	60.9	1.8	1603	71.0	2.6	2271
Haddock	568	88.6	5.1	2910	60.8	0.7	419	69.8	0.4	218	64.1	0.7	404
Ling	689	98.2	23.0	15,875	92.5	5.9	4087	85.3	17.0	11,722	89.8	10.4	7160
Saithe	365	84.6	5.7	2085	69.1	5.9	2164	92.0	10.8	3932	96.0	0.9	345
Whiting	519	97.8	38.6	20,031	95.0	40.1	20,850	96.4	37.2	19,299	96.0	21.6	11,190
Σ			74.4	42,648		54.6	29,239		67.2	36,774		36.2	21369

Table 7. *Amounts of five commercially important gadid species landed (L, tonnes) from the fishery in Shetland waters in summer (July–September) 1994–97. Amounts of fish over the MLS consumed by seals on Mousa during summer are expressed as a percentage (%C) of the previous figure.*

	1994		1995		1996		1997	
	L	% C	L	% C	L	% C	L	% C
Cod	1083	0.2	1107	0.2	1171	0.2	752	0.3
Haddock	2531	0.2	1549	0.0	1953	0.0	1969	0.0
Ling	198	11.6	233	2.5	210	8.1	167	6.2
Saithe	151	3.8	155	3.8	127	8.5	125	0.7
Whiting	1750	2.2	1400	2.9	1164	3.2	532	4.1
Total	5713	1.3	4444	1.2	4625	1.5	3545	1.0

DISCUSSION

Diet composition

The main prey in the summer diet of harbour seals in Shetland were whiting, herring, sandeels and garfish. The spring diet was dominated by sandeels, with gadids and herring also being important. Some of the main prey species are also important in the diet of harbour seals in other areas, notably sandeels and whiting. Thus, in the Moray Firth, sandeels and whiting were among the main species eaten by harbour seals (Pierce et al., 1990, 1991; Tollit & Thompson, 1996; Tollit et al., 1997a) and whiting is also among the main prey in the south-western North Sea (Hall et al., 1998). In the present study, *Trisopterus* spp., mainly Norway pout (*Trisopterus esmarkii*), contributed up to 11% by weight of the summer diet (and up to 22% of the spring diet). This species is also important in harbour seal diet in Norway (Olsen & Bjørge, 1995) although not in Orkney or the Moray Firth (Pierce et al., 1990, 1991; Tollit & Thompson, 1996; Tollit et al., 1997a). In Danish waters, flatfish and cod have been reported to be the most important components of harbour seal diet (Härkönen, 1987).

One fish species in the harbour seal diet in Shetland that does not feature prominently in the diet in other areas is the garfish. A surface living species of shallow inshore waters of Northern Europe (Wheeler, 1969), it is not commercially exploited in the North Sea and little is known about its abundance or biology. According to Muus & Dahlstøm (1977) garfish follow a migratory pattern similar to Atlantic mackerel, i.e. entering the North Sea in March–April and, towards the end of the year, migrating to the west and south of the British Isles. It is presumed that their migration takes them into areas frequented by harbour seals in Shetland during the summer.

Interannual variation in diet

The results of the present study provide clear evidence of substantial interannual changes in harbour seal diets, as might be expected in an opportunistic predator. In the summer diet, gadids declined markedly in importance from 1994 to 1997, whilst pelagic fish (herring or garfish) increased in importance. In spring, the importance of herring peaked in 1996, a year in which gadids almost disappeared from the spring diet. Tollit & Thompson (1996) also found considerable between-year variation in the diet of harbour seals in the Moray Firth between 1989 and 1992, mainly in the contributions of clupeids, sandeels and octopus.

Examining the results of the present study in more detail, however, there is evidence both for interannual

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variation in diet that apparently matches changes in prey abundance and some distinct dietary preferences. The obvious caveat to the former observation is that our main source of independent evidence on abundance, trawling surveys, is of course also subject to various well-known biases—certainly pelagic shoaling species are underrepresented in demersal trawl hauls and seals may well forage in specific areas unsampled by trawls. However, even if comparisons of abundance between fish species may be invalid, it is expected that trawl catch per unit effort will provide a consistent abundance index for individual species, consistent with our approach of examining trends in different prey species separately.

The most interesting trends were seen for Norway pout, for which year to year changes in abundance, and size–frequency distribution in trawls during the summer months, appear to be, at least in part, reflected in the seal diet, as expected if the seals were feeding opportunistically. Thus, when abundance of Norway pout increased in 1995 and 1997, the importance of the species in the diet also increased. Furthermore, there was a single main size mode at 14–20 cm in both trawl hauls and diet in 1995 and 1997, whereas in 1996 a smaller size mode (6–11 cm) increased in relative importance in both trawl samples and the diet. Having said this, differences between trawl and dietary size–frequency distributions were significant in each year (with seals tending to take larger fish than in the trawls) and the time-series is too short to detect a statistically significant correlation between abundance and importance in the diet. The importance of cod in the diet was also positively (but non-significantly) correlated with annual abundance estimates. For other prey species, there was less evidence that interannual trends in importance in the diet tracked abundance, although there was clearer evidence of size selection.

Evidence for opportunistic predation has been found in other studies on harbour seals. Tollit et al. (1997a) showed that the most abundant species in fishery surveys in the Moray Firth contributed the most to the diet of harbour seals. Bowen & Harrison (1994) reported that the rank order of importance of prey species in the diet of grey seals on Sable Island (Canada) was correlated with the order of abundance of prey species in trawl catches. Olsen & Bjørge (1995) reported similar results for harbour seals in Norway.

Seals in the present study apparently preyed selectively on whiting and sandeels that were larger than the modal size in the trawl hauls. A preference for larger sandeels could be explained by behavioural differences between small and large sandeels, with large ones being more easily exploited. However, foraging for 7–8 cm sandeels may simply be uneconomic for seals. Both the energy density and the total energy content of sandeels increase with length (Hislop et al., 1991). Some degree of size selectivity is also reported in other studies on harbour seal diet (e.g. Tollit et al., 1997a), although not usually for larger fish (Tollit & Thompson, 1996; Tollit et al., 1997a; Hall et al., 1998). Hall et al. (1998) found that, for the larger prey species eaten by harbour seals in the south-western North Sea, i.e. cod, whiting and sole, a large proportion of the fish eaten by seals were small individuals. They hypothesised that there is a maximum preferred limit on the size of fish taken by harbour seals.

The fish consumed by harbour seals on Mousa in summer (this study) were generally larger than those taken in the Moray Firth (Tollit & Thompson, 1996). The mean mass of whiting eaten by harbour seals in the Moray Firth was 11.9 g as compared with 324 g at Mousa. Seals in the Moray Firth took mainly 8–12 cm sandeels in both summer and winter, whereas seal in Shetland took sandeels up to 20 cm in length. Similarly, the average size of herring eaten in summer in Shetland varied from 27–32 cm in length while harbour seals in the Moray Firth appeared to have a preference for herring 14–16 cm in length. Tollit & Thompson (1996) suggested that the seals' preference for small herring was due to size related differences in (herring) swimming speed and handling time: juvenile herring were easier to catch and consume. However, the size of fish available to seals is also likely to be important. The Moray Firth is a nursery ground for juvenile herring, sprat and gadids (Hopkins, 1986) and it is not surprising that harbour seals exploit this small and abundant prey. Herring migrating past Shetland tend to be adult fish and our results show that harbour seals on Mousa are capable of catching these large herring.

We may thus suggest that harbour seals use a mixed diet selection strategy, taking some fish species in proportion to their abundance and actively selecting or avoiding other species (or size-classes). Tollit et al. (1997a) suggested that harbour seals in the Moray Firth switched between two foraging strategies, foraging pelagically when clupeids were abundant and switching to demersal forging when clupeids were scarce.

Potential for interactions with fisheries

To date much of the work on interactions between seals and fisheries in British waters has been carried out on grey seals because of their possible impact on commercial fish stocks (SMRU, 1984, 1994; Hammond et al., 1994a,b). Few other published studies have estimated the quantity and numbers of fish of commercial size consumed by harbour seal populations in the UK.

We estimate that harbour seals at Mousa could consumed between 152–195 tonnes of fish each summer, including gadid fish worth (had they been available to fisheries) between £21,400–£42,600 each summer during the study period—whiting and ling accounting for most of the value (see Table 6). However, these figures relate only to one quarter of the year and to only 12% of the total Shetland population of harbour seals. The total amount and value of fish consumed by Shetland's harbour seal population is therefore likely to be much higher. However, it is also important to put predation by seals into the context of estimated fish stock sizes (in comparison to which numbers eaten by seals may seem small) and to recognise that fish eaten by seals are not necessarily otherwise available to fishermen—certainly not in a fishery managed by quotas.

It is important to know whether the fish eaten are of a size that may be legally landed by fishermen. Hall et al. (1998) reported that most of the fish consumed by harbour seals in the south-western North Sea were small and Des Clers & Prime (1996) reported that around 70% of cod eaten in the Clyde area of Scotland were below the MLS of 35 cm. However, because of the power relationship between fish length and weight, even if most fish consumed by harbour seals are under the MLS, fish of commercial size may still represent a significant proportion of the total weight of fish consumed. Thus we found that 60–68%, by number, of the cod eaten by harbour seals on Mousa had estimated lengths below 35 cm. However, in terms of total weight consumed, 61–94% of the cod was above the MLS. For both whiting and ling, a large proportion of the estimated fish lengths were above the respective MLS, 82% for whiting and 70% for ling. The MLS for ling was increased to 63 cm in January 2000. Only around 30% of ling eaten by seals were bigger than the new MLS.

Our work thus indicates that harbour seals eat the same sizes of fish as taken by commercial fishermen and consume substantial quantities of commercially valuable fish. Given that harbour seals forage in inshore waters, whereas the grey seals tend to forage offshore, the possible impact of harbour seal predation on inshore fisheries could be substantial and is in need of further study.

It is not possible at this stage to recommend management actions. Understanding of the dynamics of predation is important to enable prediction of the consequences of different management scenarios. Although this four-year study provides some evidence about how seals responded to changing prey abundance, a longer time-series will be needed to construct empirical models of diet selection. Another necessary precursor to management is completion of a full cost–benefit analysis of different management options, taking into account economic, ecological and political considerations. Thus, under certain circumstances, reduced abundance of seals could lead to lower abundance of commercially important fish species due to reduced consumption of competitors or predators (Punt & Butterworth, 1995; Woodley & Lavigne, 1995). The economic impact of reduced seal predation is also difficult to predict. It is uncertain whether increased fish abundance could be detected or whether managers could then increase quotas. Even if this were so, increased landings at local fish markets could produce little economic benefit due to decreased demand and lower prices at auction.

Methodology

Our calculations of total amounts of fish eaten by the harbour seals around Mousa are necessarily simplistic and all the figures used in our calculations are subject to various uncertainties, briefly summarized below.

Errors due to using otoliths to assess the diet composition of seals have been thoroughly reviewed (e.g. Jobling, 1987; Dellinger & Trillmich, 1988; Harvey, 1989; Pierce & Boyle, 1991; Harvey & Antonelis, 1994; Brown & Pierce, 1998). Among the most important errors are those due to erosion and loss of otoliths as they pass though the gut, which can to some extent be accounted for by applying 'correction factors' (Harvey, 1989; Cottrell et al., 1996; Tollit et al., 1997b).

Harbour seal population size is usually estimated from counts at haul-out sites. However, at all stages of the annual cycle, the proportion of seals using a haul-out site may be variable, e.g. Ries et al. (1998) found that between 60–70% of seals hauled out during moult. The energy budget of harbour seals referred to an 'average' individual seal and was based on seals in Danish waters (Härkönen & Heide-Jørgensen, 1990, 1991).

A final point, since we have based our calculations on energy values rather than weight, is that the energy density (kcal kg^{-1}) of several fish species (e.g. herring, mackerel, sandeel and sprat) exhibits marked seasonal changes (Hislop et al., 1991; Mårtennson et al., 1996) related to the size and reproductive condition of the fish. For example clupeid and scrombrid fish have extremely high energy densities when mature and prior to spawning but when spent or immature, the energy densities of these fish are no higher than those of gadid fish, which are amongst the least energy rich species. The total energy content of sandeels of a given length may vary by a factor of two, between spring and summer (Hislop et al., 1991). In this study we have used the most appropriate energy values that were available in the literature.

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Appendix 1. *Previously unpublished regression equations used to predict cephalopods weights from beak measurements.*

Species	Estimated squid weight (g)	S
Todarodes sagittatus	$FW = 4.039615 \times (URL^{2.576})$	MC
Todaropsis eblanae	$FW = 1.641637 \times (URL^{2.773})$	MR
	$FW = 1.635867 \times (LRL^{3.011})$	MR
Ommastrephidae	$FW = 1.992457 \times (LRL^{2.927})$	MC/MR
	$FW = 1.075333 \times (URL^{3.153})$	MC/MR

Sources (S) are: MR, Mario Rasero, unpublished data; MC, Martin Collins, unpublished data; MC/MR, combined data from both sources.

Appendix 2. *Energy densities (kcal kg^{-1}) used in the estimation of fish and cephalopod consumption.*

Species	Energy Density	Source
Cod	739	1
Haddock	728	1
Whiting	772	1
Haddock/Saithe	761	Average for these species
Saithe	794	1
Pollack (Lythe)	794	1
Haddock/Saithe/Pollock	772	Average for these species
Gadidae	836	Average for gadids
Ling	882	1
Tusk (Torsk)	882	Used value for ling
Trisopterus spp.	1102	1
Herring	1850	1
Mackerel	1839	1
Horse mackerel (scad)	1036	2
Garfish	1575	Average for pelagic species
Lemon sole	772	1
Witch	882	1
Dab	716	1
Plaice	937	1
Argentine	1080	1
Catfish	1036	1
Eledone cirrhosa	688	3
Squid (*Illex*/*Todaropsis*)	865	3
Sandeels	1173	4

Sources are given: 1, Murray & Burt (1977); 2, SMRU (1994); 3, Croxall & Prince (1982); 4, Hislop et al. (1991).