Prey selection by harbour seals, *Phoca vitulina*, in relation to variations in prey abundance

Dominic J. Tollit, Simon P.R. Greenstreet, and Paul M. Thompson

Abstract: This study compared the composition of the diet of harbour seals (*Phoca vitulina*) feeding in the Moray Firth, Scotland, with the abundance of their fish prey estimated from dedicated fishery surveys in January 1992 and 1994 and June 1992. Prey-size selection was also examined in these three time periods and in January 1991. In each period, the most abundant fish species contributed most to the diet. However, the relative abundances of the remaining species in the sea showed little similarity to their contribution to the seals’ diet. Diet composition was almost totally dominated by either pelagic species or species dwelling on or strongly associated with the seabed, depending upon the relative abundance of pelagic schooling prey. Most fish consumed were 10–16 cm in length, although larger cod and herring were taken. With the exception of cod, the extent of size selection was dependent upon the use of correction factors that accounted for otolith erosion due to digestion.

[Traduit par la Rédaction]

Introduction

An understanding of a predator’s foraging ecology is important in assessing its impact on populations of its prey (Krebs and Davies 1981); however, there is a current lack of data on diet selection in pinnipeds. Although it has been suggested that most pinnipeds feed on the more abundant and, hence, probably more readily caught prey species within their geographical range (e.g., Rae 1973; Brown and Mate 1983; Härkönen 1987; Bowen and Harrison 1994), specialisation on particular prey may also occur (e.g., Ostfeld 1982; Lyons 1989). Factors that may influence prey selection include temporal changes in abundance (Bailey and Ainley 1982) as well as interspecific and age-related variations in prey size (Wanzenböck 1995), prey shape (Hoyle and Keast 1987), behaviour (Dipper 1987) or prey quality (Hislop et al. 1991).

Harbour seals feed on a wide variety of prey, yet their diet is often dominated by just a few key species (Pitcher 1980a, 1980b; Brown and Mate 1983; Payne and Selzer 1989; Härkönen and Heide-Jørgensen 1991). In a 7-year study in the Moray Firth, northeast Scotland, at least 40 different prey taxa have been identified in the diet of harbour seals, yet just 7 dominate by percent mass (Tollit and Thompson 1996). The importance of these key species has been shown to vary both seasonally (Pierce et al. 1991) and between years (Tollit and Thompson 1996), and the seasonal variation appears to be a result of probable changes in the availability of energy-rich prey (Pierce et al. 1990). Between-year differences in winter diet composition appeared to be due to fluctuations in the local abundance and distribution of the overwintering eluides herring (*Clupea harengus*) and sprats (*Sprattus sprattus*) (Thompson et al. 1996). However, the authors of none of these previous studies had access to data regarding the abundance of alternative non-eluid prey, such as whiting (*Merlangius merlangus*), cod (*Gadus morhua*), and lesser sandeels (*Ammodromus marinus*).

Alongside these dietary studies, VHF telemetry has been used to determine the foraging distribution of seals captured at haulout sites where faecal samples were collected (Thompson and Miller 1990; Thompson et al. 1991, 1996; Tollit 1996; University of Aberdeen, unpublished data). This allows us to define the area within the Moray Firth that is used by seals for feeding, and thus to assess the prey available to seals. Since 1991 the biomass and length-frequency distributions of the main fish species in this area have been assessed as part of several dedicated research vessel surveys. In this paper we examine the effect of variation in both the absolute and rela-
tive abundance of various prey on the species composition of the diet of harbour seals. We also determine whether the size range of fish in the seals’ diet is consistent with random or opportunistic sampling of the range of prey sizes available to them or provides evidence of prey-size selection.

**Methods**

**Study area**

This study was carried out in the inner Moray Firth. Results of radio-tracking studies of 47 harbour seals caught at haulout sites in the region suggested that seals from these sites fed in the area south of latitude 58°N and west of longitude 03°15'W (Fig. 1) (Thompson and Miller 1990; Thompson et al. 1991, 1996; Tollit 1996; University of Aberdeen, unpublished data). The data are from seals located during both summer and winter.

**Fish stocks**

Research vessel surveys were conducted throughout the Moray Firth during three winters (1991, 1992, and 1994) and one summer (1992) (Table 1). For this study, only acoustic and trawl data obtained from the area used by the foraging seals (Fig. 1) were analysed. The biomass of pelagic fish (herring, sprat, and sandeel) in the water column was determined using acoustic integration methods in conjunction with pelagic trawl sampling (for full details on acoustic integration methods see MacLennan and Simmonds 1991). Winter acoustic survey work was undertaken only during daylight hours. In summer, when sandeels were the principal acoustic target, acoustic survey work finished shortly after midday, since sandeels are particularly active in the water column during the morning (Macer 1966). Pelagic fish samples were taken using a pelagic trawl with a 6 mm mesh cod-end in areas of high fish abundance to obtain data on species and size composition. This allowed the numbers at length of each species to be estimated from the acoustic integrator data. Subsamples of each species were weighed to establish mass-length relationships, allowing biomass estimates to be made. The abundance of groundfish species was

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**Table 1. Details of samples used for fish survey and faecal analyses.**

<table>
<thead>
<tr>
<th>Survey</th>
<th>No. measured</th>
<th>Raised total</th>
<th>No. of fish from faecal samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cod</td>
<td>January 1992</td>
<td>44</td>
<td>46</td>
</tr>
<tr>
<td>Whiting</td>
<td>January 1992</td>
<td>1701</td>
<td>13460</td>
</tr>
<tr>
<td>Herring</td>
<td>January 1991</td>
<td>1379</td>
<td>24475</td>
</tr>
<tr>
<td></td>
<td>January 1992</td>
<td>1076</td>
<td>4403</td>
</tr>
<tr>
<td>Sprat</td>
<td>January 1991</td>
<td>488</td>
<td>16668</td>
</tr>
<tr>
<td></td>
<td>January 1994</td>
<td>1789</td>
<td>14118</td>
</tr>
<tr>
<td>Sandeel</td>
<td>June 1992</td>
<td>2055</td>
<td>1693167</td>
</tr>
<tr>
<td></td>
<td></td>
<td>590</td>
<td>73945</td>
</tr>
</tbody>
</table>

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assessed by demersal trawl survey using a Jackson Rockhopper bottom trawl with a 10 mm mesh cod-end. Net-monitoring equipment (SCANMAR, Norway) was attached to the net to record the area of seabed swept by the gear. The demersal samples were analysed to determine the number, species and length composition in each catch. Published (Coull et al. 1989) and unpublished (S.P.R. Greensstreet) mass–length relationships were used to determine the mass of each species in the catch. Dividing species’ catch masses by swept area provided density estimates (g/m²) at each sampling location. Multiplying these by the total area associated with each trawl station, then summing over all stations, provided estimates of total minimum trawlable biomass.

No catchability corrections were available for the particular demersal trawl used, so the effect of this on relative groundfish species density could not be evaluated. Since the greatest difference in groundfish catchability using this gear is likely to be between roundfish and flatfish, and since flatfish made only a minor contribution to the diet of seals, this will have had little effect on our results. Clearly, the largest difference in species catchability in demersal gear is found between pelagic and demersal species. We avoided these difficulties by using assessment techniques that were appropriate for the different types of fish (MacLennan and Simmonds 1991).

Seal diet

Between 1987 and 1995, faecal samples were collected regularly from intertidal haulout sites in the inner Moray Firth (Fig. 1) (Pierce et al. 1991; Thompson et al. 1991; Tollit and Thompson 1996). The analyses presented here are confined to samples collected within 2 weeks of fish surveys. Techniques for the collection, identification, and analysis of faecal samples are described in detail elsewhere (Pierce et al. 1991; Tollit and Thompson 1996). To summarise briefly, fish otoliths and cephalopod beaks extracted from faecal samples were identified and measured. We then estimated diet composition, as proportions by mass, by relating hard part size to total prey length (e.g., Härkönen 1986) and then prey length to prey mass (e.g., Coull et al. 1989). Sources for regressions used to calculate prey lengths from otolith and beak measurements and prey masses from length estimates are given in Tollit and Thompson (1996). The relative importance of fish prey was also expressed as the mean number of otoliths per faecal sample.

The proportion of the diet by mass is the most appropriate single measure to illustrate differences in the relative importance to seals of different prey species (Lavigne et al. 1982). However, many potential biases are involved in estimating diet from faecal samples in this way (for a comprehensive review see Pierce and Boyle 1991). In particular, captive feeding studies have demonstrated that otoliths of different species are eroded at different rates during passage through the digestive tract of pinnipeds (e.g., Harvey 1989). Recent captive feeding trials now allow us to take into account and correct for both inter- and intra-specific variations in otolith digestion (Tollit et al. 1997). Our dietary analyses also assume that seals eat the heads of prey. If this is not the case for larger fish, the number and size of these prey items will be underestimated. Harbour seals can and do occasionally eat large fish, including the head (Bowen and Harrison 1996), and only a few percent of faecal samples from this study contained large bones or vertebrae but no otoliths from larger fish (D.J. Tollit, unpublished data).

Comparison of the seal’s diet and prey abundance

Neither the acoustic nor the bottom trawl surveys adequately sampled squid (Loligo forbesi) or octopus (Eledone cirrhosa). These species were estimated to contribute only 0–10% of the seals’ diet at various times during the study period (D.J. Tollit, unpublished data), therefore we restricted our analyses to the fish component of the seals’ diet. However, the importance of cephalopods may be underestimated relative to that of fish, since it appears that cephalopod beaks are generally not passed through the digestive tract as readily as fish otoliths (Pitcher 1980b).

Biomass data for fish species were available for January 1992, January 1994, and June 1992. The rankings of species by percent mass in the diets of seals were compared with their rankings in the sea using a Spearman rank correlation. An odds ratio (Fleiss 1981) was calculated for each of 16 fish species to indicate the extent to which each species was being selected for by foraging seals (e.g., Sinclair et al. 1994). The odds ratio (O) is given by

\[ O = \frac{(p_1 - q_2)}{(p_2 - q_1)} \]

where \( p_1 \) is the proportion of the diet consisting of a particular prey item, \( p_2 \) is the relative abundance as a proportion of this prey item in the environment, \( q_1 \) is the proportion of the diet contributed by all other prey items and \( q_2 \) is the relative abundance as a proportion of all other prey items in the environment. Logarithms to the base 10 of the odds ratios were taken so that positive values indicate prey which were positively selected and negative values indicate potential prey which were ignored by seals. The numerical value of the index approximately indicates an order of magnitude difference between the level of representation in the diet and the sea. Thus, transformed odds ratios of +1 and −2 indicate prey occurring 10 or 100 times more frequently in the diet than would be expected given the species’ relative abundance in the food. Values of +1 and −2 indicate potential prey ignored by the predator, since the species’ relative abundance in the sea is 10 or 100 times greater than its frequency in the diet.

There are problems in estimating the biomass of fish both in the sea and in the diets of seals. In particular, we recognise that species with low relative abundance in either the sea or the diet will be most sensitive to potential errors when odds ratios are calculated, therefore the conclusions drawn from this study have concentrated primarily on those species with an odds ratio of greater or less than 1 and −1, respectively.

Comparison of prey size in seals’ diet and trawl samples

Tollit et al. (1997) demonstrated that the use of an average species-specific correction factor was probably unwise, owing to the level of intraspecific variation in the degree of otolith digestion. Instead, they provided a methodology that uses external morphological features such as location and shape to grade the degree of digestion of each otolith (low, medium, or high). They also showed that the size of fish influenced the degree of digestion, and therefore calculated grade-specific correction factors for a range of sizes of cod, whiting, and sandeels. We followed this methodology and graded herring, sprat, sandeel, cod, and whiting otoliths found in faecal samples to correct more reliably for the partial reduction in otolith size due to digestion. Appropriate grade-specific correction factors (from Tollit et al. 1997) were used for the size ranges of cod, whiting, and sandeels found in trawl samples (Table 2). Grade-specific correction factors were available for only one size range of herring and sprats (Table 2). Overall, these five fish species were the primary contributors, by mass, to the diet.

Sample sizes were sufficient to compare fish length frequency distributions in faecal and trawl samples for whiting and cod in January 1992, herring in January 1991, 1992, and 1994, sprats in January 1991 and 1994, and sandeels in June 1992. Two-centimetre size classes were chosen as a reasonable resolution of both data sets. In the case of herring-otoliths were also included from faecal samples collected in February 1992 and 1994 to improve the sample size for these comparisons. We consider that this would have little appreciable effect on any comparison with trawl sample data, since elupid growth is negligible in winter (Bryant et al. 1995).

Demersal trawl data were used for whiting and cod and pelagic trawl data for herring, sprats, and sandeels. Data sets were compared using Kolmogorov–Smirnov two-sample tests (Sokal and Rohlf 1981).
Table 2. Correction factors applied to key fish species graded for degree of digestion.

<table>
<thead>
<tr>
<th>Digestion grade</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring</td>
<td>1.05</td>
<td>1.23</td>
<td>1.41</td>
</tr>
<tr>
<td>Sprat</td>
<td>1.00</td>
<td>1.09</td>
<td>1.28</td>
</tr>
<tr>
<td>Cod</td>
<td>1.07</td>
<td>1.30</td>
<td>1.77</td>
</tr>
<tr>
<td>Whiting</td>
<td>1.04</td>
<td>1.25</td>
<td>1.92</td>
</tr>
<tr>
<td>Sandeel</td>
<td>1.12</td>
<td>1.30</td>
<td>1.52</td>
</tr>
</tbody>
</table>

Note: Numbers in parentheses show the number of otoliths characterised for each grade.

*Data from Tollit (1996).
*Data from Tollit et al. (1997).

Results

Prey species selection
Eleven fish species made up 99% of the fish component of the seals’ diet during the study. However, just five prey species, sandeel, cod, whiting, herring, and sprat, made up most (>85%) of this total (Table 3). A further five species occurred frequently in our trawl samples (Table 4). Hence, just 16 species contributed over 99% of both the total fish biomass in the area used for foraging by harbour seals and the fish component of the seals’ diet. The most abundant fish species differed in each of the three periods examined (Table 4). Our analysis of faecal samples indicated that in each case this species was the dominant or one of the dominant species in the diet (Table 3). However, the relative abundance of the remaining fish species showed little similarity to their frequency in the seals’ diet. In none of the three periods was the rank of each species in the diet of seals correlated with its rank in the sea (Spearman rank correlation, $P > 0.31$ for all tests). The diet tended to be dominated by either demersal species closely associated with the seabed or by pelagic species, which tend to occupy higher levels of the water column (Fig. 2). In any one time period, only one to three prey species dominated (>80%) the diet, by mass (Table 3).

Calculated odds ratio selection index values indicate that cod were strongly selected in January 1992 (Table 5) but not in January 1994, when they were 4.5 times more abundant in absolute terms (Table 4). Whiting were taken in approximately the same proportion as their relative abundance in the sea in January 1992 but not in January 1994, when they were twice as abundant in absolute terms. In contrast, herring, ignored in January 1992, were selected in January 1994 despite a fivefold decrease in their absolute abundance in the latter year. The situation in June 1992 was similar to that described for January 1992: cod were again selected, whiting were taken in roughly the same proportion as their relative abundance in the sea, and herring were not selected (Table 5).

Sprints were most abundant in January 1994, making up over half the total fish biomass in the area (Table 4). The odds ratio suggested that sprats were consumed by the seals in approximately the same proportion as their relative abundance in the sea and they contributed nearly 50% of the seals’ diet. In January 1992 the absolute abundance of sprats was more than two orders of magnitude lower than in January 1994, while in June 1992 it was half the January 1994 level. The odds ratios for sprats in January 1992 and June 1992 suggested that seals were not selecting sprats to an extent which could not be accounted for simply by these reduced absolute abundance levels; sprats were almost completely excluded from the seals’ diet in 1992 (Table 5).

In January 1992, sandeels contributed nearly a third of the seals’ diet, but their absolute abundance was least. The resulting high odds ratio is clearly likely to be an artefact of the problem of accurately sampling sandeels, which are known to bury themselves in the sediment for much of the winter (Winslade 1974a, 1974b). In January 1994, sandeels were apparently four orders of magnitude more abundant in the water column, yet they contributed less than 10% of the diet and the odds ratio suggested that they were taken by seals in approximately the same proportion as their relative abundance in the sea. In June 1992, sandeels were a further order of magnitude more abundant; they were the most abundant species in the water column, making up nearly half the fish biomass in the area. The odds ratio suggested a degree of preferential selection by seals, and during this period sandeels constituted over 80% of their diet in total.

Prey-size selection
The length-frequency distributions of the five key fish species eaten by harbour seals were compared with the length-frequency distributions of these prey present in the sea. Two comparisons were made: the first used estimates of the lengths of fish eaten that were not corrected to account for otolith erosion during passage through the seals’ guts (Fig. 3) and the second used corrected estimates that allowed for the effects of differential digestion (Fig. 4). In all cases, correcting length estimates had the effect of making the frequency distribution more leptokurtic and increasing the modal length size class of prey in the diet. For sandeels, whiting, and


<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Sandeel</td>
<td>29.3%</td>
<td>8.1%</td>
<td>0.458%</td>
</tr>
<tr>
<td>Herring</td>
<td>1.1%</td>
<td>0.02%</td>
<td>0.396%</td>
</tr>
<tr>
<td>Sprat</td>
<td>0.01%</td>
<td>48.6%</td>
<td>2.458%</td>
</tr>
<tr>
<td>Whiting</td>
<td>28.9%</td>
<td>9.1%</td>
<td>0.042%</td>
</tr>
<tr>
<td>Haddock</td>
<td>0.1%</td>
<td>0.016%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Cod</td>
<td>22.4%</td>
<td>0.72%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Lemon sole</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Plaice</td>
<td>11.6%</td>
<td>0.049%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Flounder</td>
<td>3.8%</td>
<td>0.279%</td>
<td>0.083%</td>
</tr>
<tr>
<td>Turbot</td>
<td>0.5%</td>
<td>0.082%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Eelpout</td>
<td>0.1%</td>
<td>0.016%</td>
<td>0.125%</td>
</tr>
<tr>
<td>Other species</td>
<td>1.3%</td>
<td>0.213%</td>
<td>0.0%</td>
</tr>
</tbody>
</table>

Note: The importance of each species is given in terms of percent biomass (%) and the mean number of otoliths per faecal sample (No.).

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Table 4. Biomass (tonnes) and relative abundance (\%, in parentheses) of 11 fish species frequently occurring in the diets of harbour seals, together with five additional abundant fish species (indicated by an asterisk), in the inner Moray Firth.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandeel</td>
<td>0.04 (0.002)</td>
<td>645.89 (5.097)</td>
<td>8433.74 (46.765)</td>
</tr>
<tr>
<td>Herring</td>
<td>1035.89 (40.463)</td>
<td>193.45 (1.527)</td>
<td>5742.38 (31.804)</td>
</tr>
<tr>
<td>Sprat</td>
<td>53.33 (2.092)</td>
<td>7671.87 (60.547)</td>
<td>2082.80 (11.535)</td>
</tr>
<tr>
<td>Whiting</td>
<td>1278.67 (50.168)</td>
<td>2575.66 (20.327)</td>
<td>437.87 (2.425)</td>
</tr>
<tr>
<td>Haddock</td>
<td>0.51 (0.020)</td>
<td>1184.54 (9.348)</td>
<td>29.14 (0.161)</td>
</tr>
<tr>
<td>Cod</td>
<td>11.64 (0.457)</td>
<td>47.80 (0.377)</td>
<td>15.18 (0.084)</td>
</tr>
<tr>
<td>Saithe*</td>
<td>61.35 (2.407)</td>
<td>0.00 (0.000)</td>
<td>76.12 (0.422)</td>
</tr>
<tr>
<td>Lemon sole</td>
<td>8.02 (0.315)</td>
<td>25.75 (0.203)</td>
<td>335.18 (1.856)</td>
</tr>
<tr>
<td>Common dab*</td>
<td>30.28 (1.188)</td>
<td>158.47 (1.251)</td>
<td>312.84 (1.733)</td>
</tr>
<tr>
<td>Long rough dab*</td>
<td>10.62 (0.417)</td>
<td>40.06 (0.316)</td>
<td>70.80 (0.392)</td>
</tr>
<tr>
<td>Plaice</td>
<td>16.89 (0.662)</td>
<td>26.28 (0.207)</td>
<td>243.00 (1.346)</td>
</tr>
<tr>
<td>Flounder</td>
<td>11.43 (0.449)</td>
<td>3.04 (0.024)</td>
<td>65.53 (0.363)</td>
</tr>
<tr>
<td>Turbot</td>
<td>0.00 (0.000)</td>
<td>0.00 (0.000)</td>
<td>4.90 (0.027)</td>
</tr>
<tr>
<td>Norway pout*</td>
<td>13.56 (0.532)</td>
<td>61.06 (0.481)</td>
<td>0.48 (0.003)</td>
</tr>
<tr>
<td>Poor cod*</td>
<td>8.51 (0.334)</td>
<td>2.87 (0.023)</td>
<td>84.70 (0.469)</td>
</tr>
<tr>
<td>Eelpout</td>
<td>0.00 (0.000)</td>
<td>0.00 (0.000)</td>
<td>0.00 (0.000)</td>
</tr>
<tr>
<td><strong>Subtotal</strong></td>
<td>2540.73 (99.685)</td>
<td>12636.75 (99.731)</td>
<td>17944.66 (99.385)</td>
</tr>
<tr>
<td>Minor species (24)</td>
<td>8.02 (0.315)</td>
<td>34.15 (0.269)</td>
<td>110.99 (0.615)</td>
</tr>
<tr>
<td><strong>Total biomass</strong></td>
<td>2548.75 (100.00)</td>
<td>12670.90 (100.00)</td>
<td>18055.65 (100.00)</td>
</tr>
</tbody>
</table>

Table 5. Log_{10} odds ratio selection index values calculated for 16 species of potential fish prey of harbour seals in the inner Moray Firth in January 1992, January 1994, and June 1992.

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Sandeel</td>
<td>+4.3</td>
<td>+0.2</td>
<td>+0.7</td>
</tr>
<tr>
<td>Herring</td>
<td>-1.8</td>
<td>+1.5</td>
<td>-1.9</td>
</tr>
<tr>
<td>Sprat</td>
<td>-2.3</td>
<td>-0.2</td>
<td>-</td>
</tr>
<tr>
<td>Whiting</td>
<td>-0.4</td>
<td>-1.9</td>
<td>-0.5</td>
</tr>
<tr>
<td>Haddock</td>
<td>-0.6</td>
<td></td>
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</tr>
<tr>
<td>Cod</td>
<td>+1.8</td>
<td></td>
<td>+1.4</td>
</tr>
<tr>
<td>Saithe</td>
<td>-1.4</td>
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</tr>
<tr>
<td>Lemon sole</td>
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<td>-0.4</td>
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</tr>
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<td>Common dab</td>
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</tr>
<tr>
<td>Long rough dab</td>
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<tr>
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<td>+0.3</td>
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<tr>
<td>Flounder</td>
<td>+0.9</td>
<td>+2.3</td>
<td>+1.2</td>
</tr>
<tr>
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<td>+</td>
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<tr>
<td>Norway pout</td>
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</tr>
<tr>
<td>Poor cod</td>
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</tr>
<tr>
<td>Eelpout</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Note: Where no value is shown, log_{10} odds ratio could not be calculated, either because the species was recorded as present in the sea but not in the seals' diet (+), it was present in the seals' diet but not recorded in the sea (+), or it was not recorded in either the sea or the seals' diet (cell left blank).

Sprats the corrected modal length class increased by 2 cm, whilst for herring it increased by approximately 4 cm. Most of the fish of these species consumed by seals were estimated after correction to be 8-16 cm. Cod were larger at 20-30 cm. Calculated $D_{max}$ values for Kolmogorov-Smirnov comparisons of the length-frequency distributions of prey estimated from faecal samples and fish from trawls, together with the $D_{critical}$ values at three different levels of significance, are given (Table 6). Only 2 of the 16 comparisons were not significant at $P < 0.05$; when uncorrected sprat lengths in the diet in January 1991 and corrected sprat lengths in January 1994 were used. All the remaining comparisons were significant at $P < 0.001$. When corrected prey-size estimates were used, the results of six of our eight comparisons indicated that seals were selecting larger individuals, whilst when uncorrected prey-size estimates were used, six of our eight comparisons suggested selection of smaller individuals. For whiting, sandeels, and herring in 1992 and 1994, the application of correction factors profoundly affects the conclusions drawn from the data; use of correction factors suggests that seals are selecting larger than average prey, while the opposite appears to be the case if the prey-length estimates are not corrected. Only in the case of cod did both sets of comparisons indicate selection of larger individuals, while in the case of herring in January 1991, both sets of comparisons suggested selection of smaller individuals.

Discussion

Five fish species, sandeel, herring, sprat, whiting, and cod, were the key prey of harbour seals in the Moray Firth. However, in any one time period, only one to three of these species dominated (>80%) the diet. The prevalence of elvers and gadoids in the diet of harbour seals in the Moray Firth in winter and sandeels in summer has been noted in previous studies (Pierce et al. 1991; Thompson et al. 1991). In all three time periods, the most abundant fish species in the sea was the dominant or one of the dominant species in the diet of seals. Taken on its own, this result sug-
Fig. 2. The relative abundance in the sea of the eight major fish species in the inner Moray Firth and their proportion (by mass) in the diet of common seals. HER, herring; SPR, sprat; WHI, whiting; HAD, haddock; PLA, plaice; FLO, flounder. Total biomass estimates for each survey period are presented in Table 4.

JANUARY 1992

PROPORTION OF TOTAL BIOMASS

JANUARY 1994

JUNE 1992

PELAGIC

DEMERSAL

FISHERY SURVEYS

SEAL DIET

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Fig. 3. Comparisons of the length-frequency distributions of key species in the diet of Moray Firth common seals (histograms) with the length-frequency distributions of these fish observed in the sea (curves). The length-frequency distributions of prey are not corrected to account for otolith erosion due to digestion during passage through the seals' guts.
Fig. 4. Comparisons of the length-frequency distributions of key species in the diet of Moray Firth common seals (histograms) with the length-frequency distributions of these fish observed in the sea (curves). The prey length-frequency distributions are corrected to account for otolith erosion due to digestion during passage through the seals’ guts.
Table 6. Kolmogorov–Smirnov two-sample test results comparing length-frequency distributions of prey in the diet of Moray Firth harbour seals with length-frequency distributions of these prey in the sea.

<table>
<thead>
<tr>
<th>Date</th>
<th>(D_{\text{max}}) Not corrected</th>
<th>(D_{\text{max}}) Corrected</th>
<th>(P = 0.05)</th>
<th>(P = 0.01)</th>
<th>(P = 0.001)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whiting</td>
<td>June 1992</td>
<td>-0.289</td>
<td>+0.338</td>
<td>0.061</td>
<td>0.073</td>
</tr>
<tr>
<td>Cod</td>
<td>Jan. 1992</td>
<td>+0.479</td>
<td>+0.911</td>
<td>0.290</td>
<td>0.347</td>
</tr>
<tr>
<td>Sandeel</td>
<td>June 1992</td>
<td>-0.404</td>
<td>+0.223</td>
<td>0.085</td>
<td>0.102</td>
</tr>
<tr>
<td>Sprat</td>
<td>Jan. 1991</td>
<td>-0.127</td>
<td>+0.339</td>
<td>0.153</td>
<td>0.184</td>
</tr>
<tr>
<td>Herring</td>
<td>Jan. 1991</td>
<td>-0.307</td>
<td>-0.103</td>
<td>0.129</td>
<td>0.154</td>
</tr>
<tr>
<td></td>
<td>Jan. 1994</td>
<td>-0.793</td>
<td>-0.583</td>
<td>0.210</td>
<td>0.252</td>
</tr>
<tr>
<td></td>
<td>Jan. 1992</td>
<td>-0.542</td>
<td>+0.481</td>
<td>0.204</td>
<td>0.245</td>
</tr>
<tr>
<td></td>
<td>Jan. 1994</td>
<td>-0.445</td>
<td>+0.425</td>
<td>0.273</td>
<td>0.328</td>
</tr>
</tbody>
</table>

Note: Data for two comparisons are presented, one using uncorrected prey-length estimates and the second using prey-length estimates that have been corrected to allow for the effect of digestion on otoliths during their passage through the seals’ guts. Positive values indicate a tendency for seals to select larger prey than the average available; negative values indicate selection of small prey. Critical values of \(D\) for three probability levels are also given; sample sizes are given in Table 1 (see the text for details). All comparisons are significant at \(P < 0.001\), except for the two values in boldface type, which are not significant.

suggests that seals were consuming prey species roughly in proportion to their abundance in the sea. However, when one examines the log odds ratios the situation is more complicated.

In winter, the local abundance of clupeids appears to strongly influence not only the seals’ diet but also their foraging and haulout behaviour (Thompson et al. 1996). We suggest that these differences in seal diet and behaviour indicate the pursuit of different foraging strategies by the seals, which, in common with many other predators (Kreb and Davies 1981; Krebs and McCleery 1984; Stephens and Krebs 1986), they adopt to suit different prevailing feeding conditions. The evidence on which we base this suggestion is not so much the level of selection of the most common prey species by the seals at any one time, but in the extent to which other potential prey species were not consumed (Fig. 2).

For example, whiting and cod contributed over 52% of the diet of harbour seals in January 1992 but less than 1% in January 1994. This decrease cannot be attributed to changes in the absolute abundance of whiting or cod, since the biomass of both species was higher, by a factor of 2 and 4.5, respectively, when predation on these species was lowest. Conversely, 32% of the seals’ diet consisted of herring in January 1994, but the herring fraction was only 1% in January 1992, despite the absolute abundance of herring in the sea being approximately 5 times higher (Tables 3 and 4). Clearly, the prey choices made by seals were not dependent upon the absolute abundance of these species. In contrast, Bailey and Ainley (1982) documented Californian sea lions (Zalophus californianus) switching to alternative prey when the abundance of 2- to 4-year-old Pacific hake (Merluccius productus) declined. In addition, Bowen and Harrison (1994) reported a correlation between the rank of abundance of prey in the sea around Sable Island and their corresponding rank of importance in the diet of grey seals (Halichoerus grypus).

The results of our study indicate that the diet tended to be dominated by either pelagic or demersal species (Fig. 2). These results are most easily explained if one accepts that harbour seals in the Moray Firth adopt one of two foraging strategies in their efforts to find and capture prey in winter.

When clupeid availability is relatively high, seals adopt a “pelagic foraging strategy.” When clupeid availability is low, seals follow a “demersal foraging strategy.” A consequence of adopting either strategy appears to be a strongly negative odds ratio selection index for alternative prey types. Thus, we speculate that these strategies may involve different foraging behaviours. Clearly, data comparing dive profiles and swim speeds (Croxall et al. 1985; Boyd et al. 1994) during periods of contrasting food availability are required to test this hypothesis.

Sandeels spend much of the winter buried in the sediment, although they do emerge occasionally, around the spawning period in December (Winslade 1974a, 1974b) and in response to local disturbance (Hain et al. 1995). Since buried sandeels would have been missed by the acoustic survey and thus not included in the biomass estimate, this would account for their exceptionally high and biased odds ratio selection index in January 1992. However, the extent of sandeels’ contribution to the diet in this period suggests that seals may consume sandeels which they disturb in the sediment. In June 1992, sandeels made up over half of the total fish biomass and contributed over 80% of the seals’ diet. The positive odds ratio selection indices for demersal species such as cod, lemon sole (Microstomus kitt), plaice (Pleuronectes platessa), and flounder (Platichthys flesus), and the negative indices for herring and sprats, suggest that the seals were using a foraging strategy similar to the winter demersal technique. Evidence from time–depth recorders in conjunction with conventional VHF radiotelemetry indicates that the Moray Firth harbour seals generally forage on or close to the bottom in summer (Tollit 1996).

We recognise that the comparison of seal diet and prey abundance has certain limitations. We have previously highlighted the imprecise nature of estimating fish abundance, owing to the problems of assessing species such as the sandeel and estimating diet composition because of biases such as the differential erosion of otoliths. Additionally, seals might have utilised some habitats that were not, or could not be, adequately sampled by demersal trawling (Tollit 1996). It is
also possible that coastal and estuarine species were taken by
seals as they returned to their haulout sites. The frequent
presence of eelpout (Zoarces viviparus) in faecal samples but
never in the trawl samples, and the higher representation
of cod and flounder in the seals’ diet than their relative
abundance estimates, may be evidence of this. However,
these problems do not apply to any great extent to herring,
sprats, or whiting, and our conclusions concerning harbour
seed prey selection draw primarily on the magnitude of the
observed differences in selection of these three species. It is
also unlikely that faecal samples reflect a random sample of
the population; for example, animals making short foraging
trips are more likely to be represented in our dietary analysis
than those making longer trips. However, most harbour seals
in the Moray Firth forage relatively close to their haulout
sites in both summer (Thompson and Miller 1990; Thompson
et al. 1994; Tollit 1996) and winter (Thompson et al. 1991,
1996). Finally, because harbour seals forage from a central
place, the relative availability of these prey as perceived by
seals will also depend upon their spatial distribution.

Odds ratio selection indices suggest further selectivity for
the larger species within a prey group, i.e., cod when seals
are foraging demersally or herring when they are foraging
pelagically. In addition, the data we present suggest a general
preference by seals for larger individuals within a prey species.
These conclusions are, however, dependent upon the
application and validity of correction factors which take into
account the reduction in the size of otoliths that occurs as
a result of digestion during passage through a seal’s gut.
The generally accepted conclusion is that failure to correct
for the effect of digestion on otolith size results in serious
underestimation of prey size (Harvey 1989). We have used
the best correction factors that are available (see also Tollit
et al. 1997).

It would appear that Moray Firth harbour seals have a
strong preference for herring around 14–16 cm in length,
although larger sizes were also taken. The average size of
herring available in January 1991 was much greater than
in other years, but the larger herring were rarer in the seals’
diet than expected, given their relative abundance in the sea.
A combination of factors such as higher swim burst speeds
and longer handling times may make larger herring less opti-
mal prey. Preferential selection of juvenile valiexe pollock
(Theragra chalcogramma) over adults by northern fur seals
(Callorhinus ursinus) has previously been reported by Sinclair
et al. (1994). Alternatively, as other populations of harbour
seals are known to eat large herring (e.g., Olesiuk et al.
1990), shoal size, depth, and spatial distribution relative to
haulout sites are likely to be important factors influencing
prey-size selection.

Analysis of the cost effectiveness of feeding on certain
prey has often concentrated on their energy content (e.g.,
Harris and Hislop 1978). If seals do generally concentrate on
fish between 10 and 16 cm in length (the exception being
when they feed on cod), then a diet of herring and sprats may
well be energetically advantageous compared with one con-
sisting of sandeels and whiting (Hislop et al. 1991). In the
Moray Firth, Thompson et al. (1996) showed that indices of
body condition of harbour seals of all ages were higher, and
Corpe (1996) documented that yearlings of both sexes were
heavier, following winters when clupeids had been the pre-
dominant prey than following winters when seals had fed
primarily on gadoids and sandeels.

If our foraging strategies hypothesis is correct, one of its
consequences is that the predatory impact of seals on cod and
whiting in the inner Moray Firth is dependent not on vari-
ation in the abundance of these gadoid species but on the
abundance of herring and sprats. This has clear conse-
quencies if the impact of seals on their prey stocks is to be
accurately predicted. Further investigations of prey selection
by pinnipeds on a more detailed spatial scale and dietary
analyses at the individual level (see Reed et al. 1997) are
key requirements for determining the underlying mechanisms.

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