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# The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland

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**Summary**

**1.** Almost 1000 faeces were collected in February, June, August and November 1985 in order to quantify the diet of grey seals around Orkney; 82% of these contained fish otoliths.
**2.** Diet composition, by weight, was assessed by identifying and measuring otoliths from the faecal material and correcting for reduction in otolith size as a result of digestion using experimentally derived species-specific digestion coefficients.
**3.** Sandeels accounted for almost half the fish consumed, by weight. The rest of the diet was composed mostly of gadids (particularly cod), flatfish (particularly plaice), and sculpins.
**4.** Sandeels were more prevalent in February and the summer than in November. They were found least often in the eastern area. No significant regional or seasonal differences were found in the number of cod, haddock or saithe consumed. Whiting featured strongly to the south in November. Ling occurred most frequently in the west. Of the flatfish, plaice were consumed more in February than in November and more in the east than in the north and west.
**5.** The largest sandeels and plaice were found when these species were also most prevalent in the diet, suggesting that seals may switch to these prey when and where they are larger. This was not found for other species.
**6.** Some flatfish and sculpins were important in the diet locally, perhaps reflecting their restricted habitat requirements and feeding by seals on locally abundant prey.
**7.** Mature fish of a number of species were more prominent in the diet in areas and at times of the year when spawning occurs, suggesting that grey seals take advantage of energy-rich prey when these are available.

*Key-words*: faecal analysis, fish otoliths, sandeels, regional and seasonal variation.

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## Introduction

It has been calculated that a grey seal, *Halichoerus grypus* (Fabricius) requires on average 5530 kcals (23 150 kjoules) per day; equivalent to about 7 kg of cod (*Gadus morhua* L.) or 4 kg of sandeels (Ammodytidae) (M.A. Fedak & L. Hiby, personal communication). These food requirements and the habit of some grey seals of damaging and taking salmon from nets have brought frequent demands by fishermen for grey seal numbers to be controlled.

In north-eastern Scotland, where seal–fisheries interactions have been a focus of attention for many years, there is limited information on grey seal diet. Rae (1960, 1968, 1973) looked at stomachs from seals taken mainly at or in the vicinity of fishing nets but the value of these data as an indication of grey seal diet as a whole is questionable. More recently, grey seal diet in Orkney and the Moray Firth has been investigated by Pierce, Boyle & Thompson (1990) but the range of sampling sites, the seasonal coverage and the number of samples examined was limited.

The grey seal population in British waters in 1991 was estimated to be 93 500 (Hiby, Duck & Thompson 1993). Most of the population breed during October/November off the north and west coasts of Scotland, including 29 000 associated with sites in Orkney. Grey seals are also present around Orkney during the rest of the year (Vaughan 1975).

The grey seal may be an important marine predator of fish in British waters and in this paper we provide a detailed quantitative description of the diet of grey seals from the Orkney Islands and other island and mainland sites in north-eastern Scotland, based on the identification and measurement of otoliths retrieved from faecal material collected in 1985.

The merits and weaknesses of faecal analysis to provide useful quantitative information on seal diet have been much discussed (e.g. DaSilva & Neilson 1985; Murie & Lavigne 1985; Jobling & Breiby 1986; Jobling 1987; Murie 1987; Prime & Hammond 1987; Harvey 1989; Hammond & Prime 1990; Pierce & Boyle 1991). Most criticisms are concerned with the loss of small otoliths and those that are easily damaged by digestion. All the available evidence indicates that grey seals feed on or near the sea bed (Thompson *et al.* 1991; Thompson & Fedak 1993) and are therefore unlikely to prey on fish such as herring and sprat which have small, fragile otoliths. Otoliths of sandeels, gadids and flatfish in particular are reasonably large and/or robust. For the purposes of obtaining representative quantitative information on the diet of grey seal populations around Britain, faecal analysis is probably the best single method available.

## Methods

Grey seal faeces were collected from haul-out sites on the Orkney Islands, Fair Isle, Sule Skerry and two Scottish mainland sites, Helmsdale and Whiten Head (Fig. 1) during February (January at Whiten Head), June, August and November in 1985.

Faeces were placed into individual plastic bags and stored at −20 °C. The methods for processing the material and the subsequent estimation of the percentage of each fish species in the diet by weight have been described fully in Prime & Hammond (1987, 1990). These can be summarized as follows.

Hard parts were extracted from the faecal material through four sieves, using mesh sizes from 4·0 mm to 0·25 mm, and stored in 70% alcohol. All otoliths were identified to species (except sandeels which were simply identified as such) using an extensive reference collection and identification guide (Härkönen 1986). Thickness, width and length of each otolith was measured to 0·01 mm with digital callipers. Thickness only was measured for sandeel otoliths; when more than 30 were found a subsample of 30 was measured.

Species-specific digestion coefficients, calculated from feeding experiments (Prime & Hammond 1987), were used to estimate undigested otolith thickness from partially digested otolith thickness. Fish weight was estimated from undigested otolith thickness using empirical relationships derived from samples of each species (Prime & Hammond 1987). Estimated fish weights were summed to give

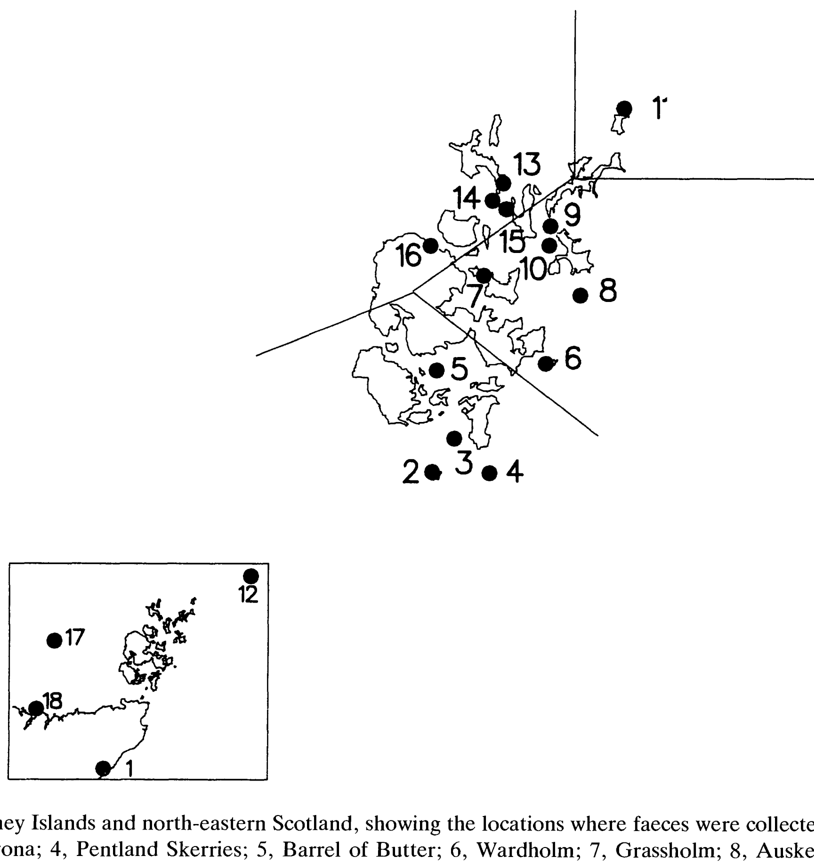


**Fig. 1.** The Orkney Islands and north-eastern Scotland, showing the locations where faeces were collected: 1, Helmsdale; 2, Stroma; 3, Swona; 4, Pentland Skerries; 5, Barrel of Butter; 6, Wardholm; 7, Grassholm; 8, Auskerry; 9, Holms of Spurness; 10, Little Linga; 11, Seal Skerry; 12, Fair Isle; 13, Westray; 14, Ruskholm; 15, Wartholm; 16, Eynhallow; 17, Sule Skerry; 18, Whiten Head.

mean weights for each species and estimates of the percentage of each species in the diet, by weight, for each combination of area and season.

Digestion coefficients and fish weight-otolith thickness relationships for cod, whiting (*Merlangius merlangus* L.), sandeels, plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.), bullrout (*Myoxocephalus scorpius* L.) and sea scorpion (*Taurulus bubalis* Euphrasen) are given in Prime & Hammond (1990). Those for other species found in this study are given in Table 1: haddock (*Melanogrammus aeglefinus* L.), saithe (*Pollachius virens* L.), ling (*Molva molva* L.), lemon sole (*Microstomus kitt* Walbaum), megrim (*Lepidorhombus whiffiagonis* Walbaum), witch (*Glyptocephalus cynoglossus* L.) and horse mackerel (*Trachurus trachurus* L.).

To investigate seasonal and regional differences in the diet, mean numbers of otoliths per faex were compared among seasons (February, June/August, November) and areas (north, west, east and south, see Fig. 1) for each species. This was done using the general linear model or analysis of variance facilities in the MINITAB statistical package (Minitab Inc. State College, Philadelphia, USA).

**Table 1.** Digestion coefficients and fish weight–otolith thickness relationships for fish species found in the diet of grey seals around Orkney, additional to those given in Prime & Hammond (1990). Fish weight ($W$) is in grams. Otolith thickness ($TH$) is in mm

| Species | Digestion coefficient | Relationship between fish weight and otolith thickness |
|---|---|---|
| Haddock | 1·54 | $W = (3{\cdot}1993 \times TH - 1{\cdot}0010)^3$ |
| Saithe | 1·55 | $W = (5{\cdot}2881 \times TH - 1{\cdot}7418)^3$ |
| Ling | 1·57 | $W = (20{\cdot}219 \times TH - 12{\cdot}072)^3$ |
| Lemon sole | 1·89 | $W = (96{\cdot}4583 \times TH + 2{\cdot}349)^3$ |
| Megrim | 1·89 | $W = (5{\cdot}946 \times TH + 0{\cdot}01)^3$ |
| Witch | 1·89 | $W = (5{\cdot}946 \times TH + 0{\cdot}01)^3$ |
| Horse mackerel | 1·57 | $W = 265{\cdot}0$* |

* For horse mackerel, insufficient data were available to fit a regression and a mean weight was calculated from available samples.

To investigate whether there were differences in the size of prey taken among seasons and areas, mean fish weights and distributions of fish length were estimated for each prey species. Fish lengths were calculated from weights using length–weight relationships from Bedford, Woolner & Jones (1986), Coull *et al.* (1989) and Prime & Hammond (1990).

## Results

The numbers of faeces collected from the Orkney Islands and other island and mainland sites in north-eastern Scotland in 1985 are shown in Table 2. It was not possible to obtain a balanced sample over seasons and regions. In particular, in June/August faeces were only found in the south, presumably because grey seals tend not to haul out in the other areas during the summer. The percentage of faeces containing no otoliths varied from 4% to 32%, the largest percentages were found in the east (Table 2).

Faeces collected during February came from one site in the north (Seal Skerry), five sites in the west (Eynhallow, Westray, Wartholm, Ruskholm and Sule Skerry), three in the east (Auskerry, Grassholm and Holms of Spurness) and four in the south (Pentland Skerries, Swona, Stroma and Whiten Head), as shown in Fig. 1. Collections during the summer were all from the Pentland Skerries, Swona and Stroma in the south (Fig. 1). November collections were from Seal Skerry and Fair Isle in the north; Wardholm, Little Linga and Auskerry in the east; Eynhallow, Ruskholm, Wartholm, Westray and Sule Skerry in the west; and the Pentland Skerries, Swona, Stroma, Barrel of Butter and Helmsdale in the south (Fig. 1).

Table 3 shows the number of otoliths of each of the major fish prey species identified from the faecal material.

### PERCENTAGE DIET COMPOSITION BY WEIGHT

Table 4 shows the estimated percentage, by weight, of the major species of fish found in the diet. Figure 2

**Table 2.** Number of grey seal faeces collected from around the Orkney Islands in 1985

| Month | February | | | | June/Aug | November | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Area | N | W | E | S | S | N | W | E | S | Total |
| Total number of samples | 26 | 236 | 91 | 107 | 107 | 117 | 109 | 62 | 138 | 993 |
| Number of samples containing no otoliths (%) | 2 (4%) | 51 (22%) | 29 (32%) | 20 (19%) | 7 (7%) | 23 (20%) | 14 (13%) | 18 (29%) | 10 (7%) | 174 (18%) |
| Number of samples containing otoliths (%) | 24 (96%) | 185 (78%) | 62 (68%) | 87 (81%) | 100 (93%) | 94 (80%) | 95 (87%) | 44 (71%) | 128 (93%) | 819 (82%) |

**Table 3.** Number of otoliths from major fish prey species recovered from faeces. For sandeels, the number of otoliths measured from subsamples is also given

| Month | February | | | | June/Aug | November | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Area | N | W | E | S | S | N | W | E | S | Total |
| Cod | 5 | 44 | 29 | 53 | 34 | 20 | 42 | 15 | 57 | 299 |
| Whiting | 6 | 65 | 48 | 39 | 22 | 19 | 19 | 36 | 941 | 1195 |
| Haddock | 2 | 34 | 7 | 25 | 25 | 12 | 17 | 5 | 31 | 158 |
| Saithe | 3 | 8 | 17 | 35 | 2 | 16 | 22 | 1 | 21 | 125 |
| Ling | 12 | 63 | 6 | 10 | 8 | 9 | 73 | 16 | 36 | 233 |
| Plaice | 6 | 25 | 92 | 109 | 31 | 2 | 9 | 2 | 33 | 309 |
| Lemon sole | 5 | 37 | 5 | 6 | 10 | 13 | – | 15 | 7 | 98 |
| Megrim | 2 | 15 | 11 | 5 | – | – | 7 | 4 | 2 | 46 |
| Witch | 2 | 20 | 18 | 8 | 1 | 2 | 3 | 5 | 25 | 84 |
| Bullrout | – | 178 | 4 | 5 | – | 1 | 31 | 4 | 5 | 228 |
| Sea scorpion | – | 45 | 22 | 2 | – | 15 | 89 | 6 | 83 | 262 |
| Horse mackerel | – | – | 2 | 2 | – | 46 | 10 | 6 | 8 | 74 |
| Subtotal | 43 | 534 | 261 | 299 | 133 | 155 | 322 | 115 | 1249 | 3111 |
| Sandeels | 2518 | 17767 | 1424 | 12861 | 10709 | 4059 | 6941 | 2302 | 6640 | 65221 |
| (measured) | 386 | 2667 | 352 | 1444 | 2170 | 920 | 1212 | 346 | 1513 | 11010 |
| Total | 2561 | 18301 | 1685 | 13160 | 10842 | 4214 | 7263 | 2417 | 7889 | 68332 |

**Table 4.** Percentage, by weight, of the major fish prey in the diet of grey seals around Orkney

| Month | February | | | | June/Aug | November | | | |
|---|---|---|---|---|---|---|---|---|---|
| Area | N | W | E | S | S | N | W | E | S |
| Cod | 6 | 5 | 21 | 6 | 10 | 16 | 13 | 10 | 10 |
| Whiting | 2 | 3 | 4 | 2 | 1 | 3 | 1 | 4 | 35 |
| Haddock | – | 4 | 1 | 2 | 4 | 4 | 4 | 1 | 4 |
| Saithe | 2 | 1 | 5 | 13 | 1 | 11 | 7 | – | 3 |
| Ling | 34 | 12 | – | 1 | 7 | 5 | 16 | 11 | 4 |
| Gadids | 44 | 25 | 31 | 24 | 23 | 39 | 41 | 26 | 56 |
| Plaice | 1 | 1 | 37 | 17 | 5 | – | 2 | 4 | 2 |
| Lemon sole | 4 | 5 | 1 | 1 | 1 | 5 | 1 | 12 | 1 |
| Megrim | 2 | 1 | 2 | 1 | – | – | 3 | 5 | – |
| Witch | 1 | 3 | 11 | 3 | – | 2 | – | 7 | 5 |
| Flatfish | 8 | 10 | 51 | 22 | 6 | 7 | 6 | 28 | 8 |
| Bullrout | – | 3 | – | – | – | – | 2 | 2 | – |
| Sea scorpion | – | 2 | 1 | – | – | 1 | 3 | 1 | 4 |
| Sculpins | – | 5 | 1 | – | – | 1 | 5 | 3 | 4 |
| Horse mackerel | – | – | – | – | – | 11 | 2 | 2 | 1 |
| Subtotal | 52 | 40 | 83 | 46 | 29 | 58 | 54 | 59 | 69 |
| Sandeels | 48 | 54 | 8 | 54 | 68 | 38 | 44 | 38 | 28 |
| Total | 100 | 94 | 91 | 100 | 97 | 96 | 98 | 97 | 97 |

gives these results for groups of species (sandeels, gadids, flatfish, sculpins, others) shown as pie charts.

The percentage of sandeels in the diet was 38–68%, except in February in the east (8%) and November in the south (26%).

Large gadids were also important in the diet; the five major species contributed 23–52%. Cod were either the most or the second most important gadid prey in all seasons and regions, featuring most strongly in June/August and November, and in the east in February. Ling was the dominant gadid in the north and west in February, and in the west and east in November. Saithe were important in the south in February and in the north in November. Whiting and haddock made up a small percentage except in the south in November when an estimated 33% of the diet was whiting.

Flatfish (plaice, lemon sole, megrim and witch) contributed an estimated 6–12% in most months but made up a greater percentage of the diet than gadids in the east in both February and November. Plaice were the dominant flatfish in the east and south in February. Lemon sole were most important in the east in November, a result driven by a large

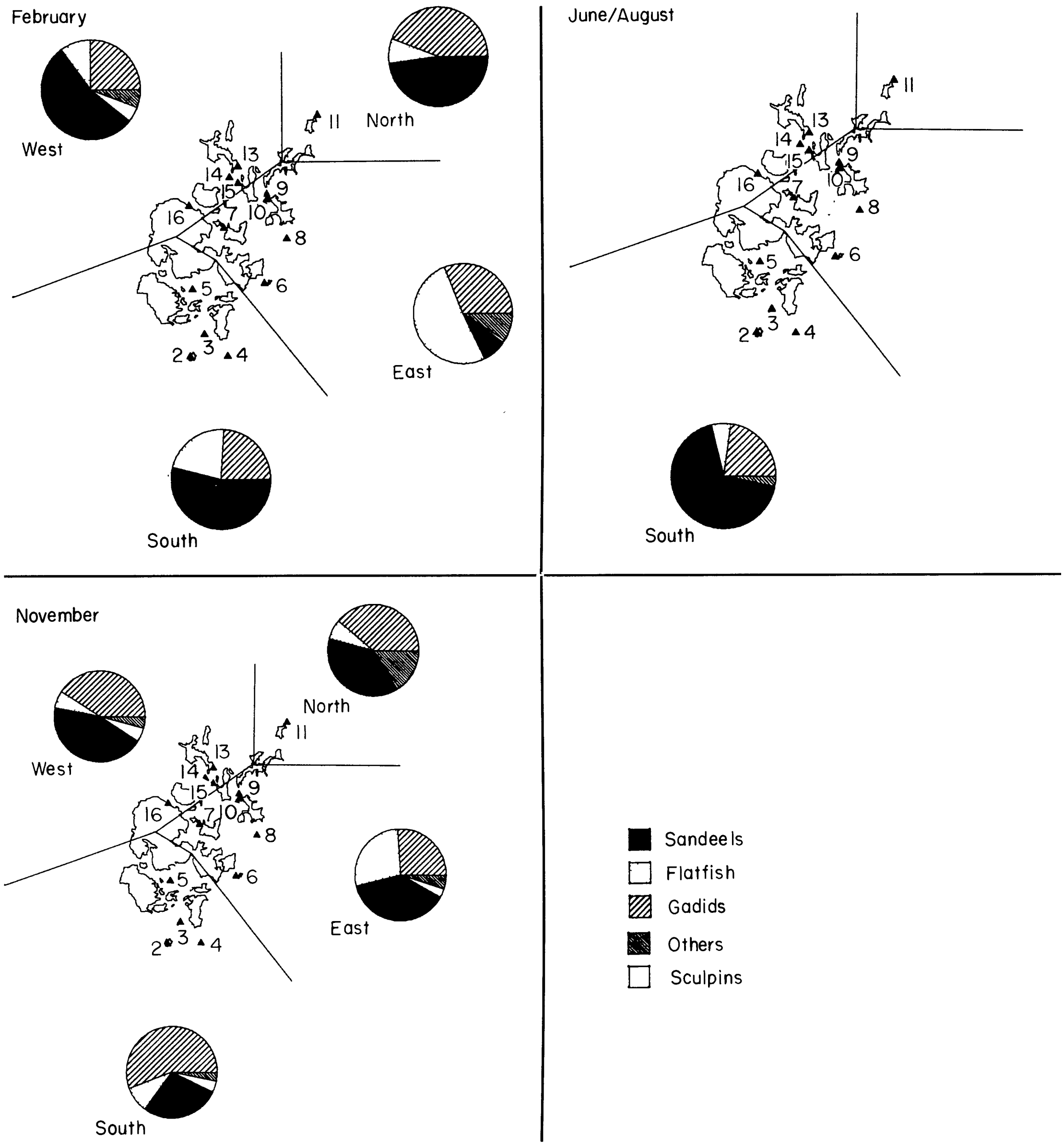


**Fig. 2.** Percentage by weight of sandeels, gadids, flatfish, sculpins and other fish in the diet of grey seals around the Orkney Islands, by area and season.

percentage contribution to the diet at the site of Auskerry (Fig. 1). Witch were found mostly at the site of Barrel of Butter (Fig. 1).

The other major fish prey in the diet were the sculpins, bullrout and sea scorpion, which occurred only at particular sites, mainly in the west and in November, and horse mackerel which occurred only in November, except in the north.

### SEASONAL AND REGIONAL VARIATION IN THE DIET

We believe that estimates of the percentage of each species in the diet, by weight, are the most appropriate measures of diet composition. But the estimation of variability about these estimates is problematic so that we could not use percentage by weight to test for seasonal or regional differences in diet. Instead, we compared the average number of fish of a given species consumed in each area in each month, measured by the mean number of otoliths per faex (excluding those with no otoliths). Table 5 gives these mean values for the major prey species.

Two analyses were carried out for each species. In the first, data were compared between two months (February and November) and among all areas (N, W, E, S) in a two-way analysis of variance. In the second, data from the southern area only were compared among all three seasons (February, June/August, November) in a one-way analysis. Table 6 gives the results for those species where there are significant differences.

In the comparison between February and November across all areas, there were no significant seasonal or regional differences in the mean number of otoliths per faex for cod, haddock, saithe, lemon

**Table 5.** Mean number of otoliths per faeces for major fish prey species

| Month | February | | | | June/Aug | November | | | |
|---|---|---|---|---|---|---|---|---|---|
| Area | N | W | E | S | S | N | W | E | S |
| Cod | 0·208 | 0·238 | 0·468 | 0·609 | 0·340 | 0·213 | 0·442 | 0·364 | 0·445 |
| Whiting | 0·250 | 0·351 | 0·774 | 0·448 | 0·022 | 0·202 | 0·200 | 0·818 | 7·35 |
| Haddock | 0·083 | 0·184 | 0·113 | 0·287 | 0·250 | 0·128 | 0·179 | 0·114 | 0·242 |
| Saithe | 0·125 | 0·043 | 0·274 | 0·402 | 0·020 | 0·170 | 0·232 | 0·023 | 0·164 |
| Ling | 0·500 | 0·341 | 0·097 | 0·115 | 0·080 | 0·096 | 0·768 | 0·364 | 0·281 |
| Plaice | 0·250 | 0·135 | 1·48 | 1·25 | 0·310 | 0·021 | 0·095 | 0·046 | 0·258 |
| Lemon sole | 0·208 | 0·200 | 0·081 | 0·069 | 0·100 | 0·138 | 0·021 | 0·341 | 0·055 |
| Megrim | 0·083 | 0·081 | 0·177 | 0·057 | 0 | 0 | 0·074 | 0·091 | 0·016 |
| Witch | 0·083 | 0·108 | 0·290 | 0·092 | 0·010 | 0·021 | 0·032 | 0·114 | 0·195 |
| Bullrout | 0 | 0·962 | 0·065 | 0·058 | 0 | 0·011 | 0·326 | 0·091 | 0·039 |
| Sea scorpion | 0 | 0·243 | 0·355 | 0·023 | 0 | 0·160 | 0·937 | 0·136 | 0·648 |
| Horse mackerel | 0 | 0 | 0·032 | 0·023 | 0 | 0·489 | 0·105 | 0·136 | 0·063 |
| Sandeels | 104·9 | 96·0 | 23·0 | 147·8 | 107·1 | 43·2 | 73·1 | 52·3 | 51·9 |

**Table 6.** Results of the ANOVAS to test for seasonal and regional differences in diet measured by mean number of otoliths per faex

| | GLM: Month = Feb, Nov Area = N, W, E, S | | | One way ANOVA: Area = *S* Month = Feb, Jun/Aug, Nov | |
|---|---|---|---|---|---|
| | Month *F* (*P*) | Area *F* (*P*) | Interaction of month with area *F* (*P*) | *F* | (*P*) |
| Whiting | 23·9 (<0·001)*** | 44·4 (<0·001)*** | 31·6 (<0·001)*** | 69·3 | (<0·001)*** |
| Ling | 3·67 (0·056) | 5·70 (0·001)*** | 2·13 (0·095) | 4·28 | (0·015)* |
| Plaice | 36·9 (<0·001)*** | 12·0 (<0·001)*** | 9·45 (<0·001)*** | 10·8 | (<0·001)*** |
| Witch | 2·14 (0·144) | 2·61 (0·050)* | 1·80 (0·145) | 3·41 | (0·034)* |
| Bullrout | 0·05 (0·820) | 3·31 (0·020)* | 0·05 (0·986) | 0·91 | (0·406) |
| Sea scorpion | 2·87 (0·090) | 1·49 (0·216) | 0·72 (0·542) | 4·68 | (0·010)** |
| Horse mackerel | 18·2 (<0·001)** | 2·51 (0·058) | 3·22 (0·022)* | 3·17 | (0·043)* |
| Sandeels | 6·39 (0·012)* | 9·79 (0·001)*** | 3·51 (0·015)* | 21·2 | (<0·001)*** |

sole, megrim or sea scorpion. There was a slight difference among areas for witch and bullrout (caused by high values in the east and west, respectively) and a strong regional difference for ling (high in the west). There were significant differences in the mean number of otoliths per faex between months and among areas and a significant month by area interaction term for several species. These were whiting (low in February, high in November; low in the north and west, very high in the south), plaice (high in February, low in November; low in the north and west, high in the east and south), and sandeels (high in February, low in November; low in the east). For horse mackerel, the difference between months (low in February, high in November) and the month by area interaction term (high in the north in November) were significant.

In the comparison among seasons in the southern area, significant differences were found for whiting (high in November), ling (high in November), plaice (high in February), witch (low in February, high in November), sea scorpion (high in November), horse mackerel (none in June/August, high in November) and sandeels (low in November).

### SIZE OF FISH IN THE DIET

#### *Mean weight*

Analysing the data on mean number of otoliths per faex provides information on seasonal and regional differences in the number of fish consumed but does not take into account the size of these fish. For example, the mean number of otoliths for a given prey species in one area may be twice that in another but the mean weight of the fish in the first area could be less than half that in the second, so that a greater biomass was consumed in the second area.

To investigate whether there were seasonal or regional differences in the estimated size of fish

**Table 7.** Estimated mean weight of fish (kg) from otoliths of the major fish prey species

| Month | February | | | | June/Aug | November | | | |
|---|---|---|---|---|---|---|---|---|---|
| Area | N | W | E | S | S | N | W | E | S |
| Cod | 0·477 | 0·377 | 1·32 | 0·420 | 0·748 | 0·884 | 0·505 | 0·418 | 0·386 |
| Whiting | 0·165 | 0·151 | 0·161 | 0·151 | 0·105 | 0·171 | 0·108 | 0·079 | 0·083 |
| Haddock | 0·012 | 0·353 | 0·328 | 0·333 | 0·408 | 0·339 | 0·366 | 0·088 | 0·259 |
| Saithe | 0·216 | 0·562 | 0·500 | 1·26 | 0·932 | 0·767 | 0·521 | 0·086 | 0·334 |
| Ling | 1·17 | 0·622 | 0·175 | 0·190 | 2·32 | 0·672 | 0·349 | 0·436 | 0·231 |
| Plaice | 0·068 | 0·179 | 0·726 | 0·517 | 0·382 | 0·035 | 0·287 | 1·26 | 0·124 |
| Lemon sole | 0·338 | 0·420 | 0·532 | 0·573 | 0·332 | 0·472 | 0·438 | 0·548 | 0·326 |
| Megrim | 0·446 | 0·287 | 0·328 | 0·455 | – | – | 0·790 | 0·776 | 0·102 |
| Bullrout | – | 0·061 | 0·253 | 0·111 | – | 0·142 | 0·123 | 0·376 | 0·066 |
| Sea scorpion | – | 0·146 | 0·097 | 0·128 | – | – | 0·051 | 0·116 | 0·104 |
| Sandeels | 0·0080 | 0·0101 | 0·0097 | 0·0143 | 0·0168 | 0·0107 | 0·0101 | 0·0108 | 0·0094 |

consumed, we calculated the mean weight of each prey species in each area/month combination. Table 7 gives these mean weights.

For the gadids, the mean estimated weight of fish consumed was significantly greater in November than in February for cod in the east ($d = 2{\cdot}76$, $P < 0{\cdot}01$), whiting in the east ($d = 3{\cdot}49$, $P < 0{\cdot}001$) and in the south ($d = 2{\cdot}46$, $P < 0{\cdot}05$), haddock in the east ($d = 2{\cdot}305$, $P < 0{\cdot}05$) and saithe in the south ($d = 5{\cdot}21$, $P < 0{\cdot}001$).

Plaice were bigger in both February ($d = 5{\cdot}10$, $P < 0{\cdot}001$) and June/August ($d = 2{\cdot}39$, $P < 0{\cdot}05$) than in November in the south. Thus, the significantly greater numbers taken in February in the south were also larger fish.

In the west, bullrout were smaller in February than in November ($d = 2{\cdot}86$, $P < 0{\cdot}01$) but sea scorpions were bigger in the same comparison ($d = 3{\cdot}65$, $P < 0{\cdot}001$). Table 4 shows that the estimated percentage by weight of these two species in the diet in this area was similar in February and November. So, where there was a significantly greater number of fish taken this was balanced by the fish being smaller.

Table 8 gives the results of the tests for seasonal and regional differences in mean weight of sandeels. In the south, they were bigger in February and June/August than in November. In the north, they were smaller in February than in November. In February they were bigger in the south than in the east and west, and bigger in the east and west than in the north. But in November, they were bigger in the north and east than in the south. Thus, the greater number of sandeels taken in the south in February and June/August than in November were also bigger fish. The same is true for differences among areas in February where higher numbers of larger fish were taken in the south.

### *Length frequencies*

To investigate the size range of fish consumed, length–frequency distributions were constructed for the major species of fish in the diet, where sufficient data were available (Fig. 3). Data were pooled over all areas but not over months (except for ling).

During February most cod eaten were less than 50 cm (Fig. 3a); the few large fish were from samples collected in the east. In November there were three clear modes in the length distribution (Fig. 3b) at about 20, 43 and 60 cm. Almost half the fish taken were less than 25 cm in length but the proportion of fish over 55 cm in length was greater than in February.

**Table 8.** Significant seasonal and regional differences in mean weight of sandeels. Mean weights are given in the last row of Table 7

| | | |
|---|---|---|
| *Seasonal* | | |
| In the north: | smaller in Feb than Nov | $d = 233$, $P < 0{\cdot}001$ |
| In the south: | bigger in Jun/Aug than Feb | $d = 5{\cdot}89$, $P < 0{\cdot}001$ |
| | bigger in Feb than Nov | $d = 17{\cdot}3$, $P < 0{\cdot}001$ |
| *Regional* | | |
| In Feb: | bigger in S than W | $d = 13{\cdot}3$, $P < 0{\cdot}001$ |
| | bigger in S than E | $d = 9{\cdot}20$, $P < 0{\cdot}001$ |
| | bigger in W than N | $d = 6{\cdot}65$, $P < 0{\cdot}001$ |
| | bigger in E than N | $d = 2{\cdot}92$, $P < 0{\cdot}01$ |
| In Nov: | bigger in N than S | $d = 3{\cdot}61$, $P < 0{\cdot}001$ |
| | bigger in E than S | $d = 2{\cdot}21$, $P < 0{\cdot}05$ |

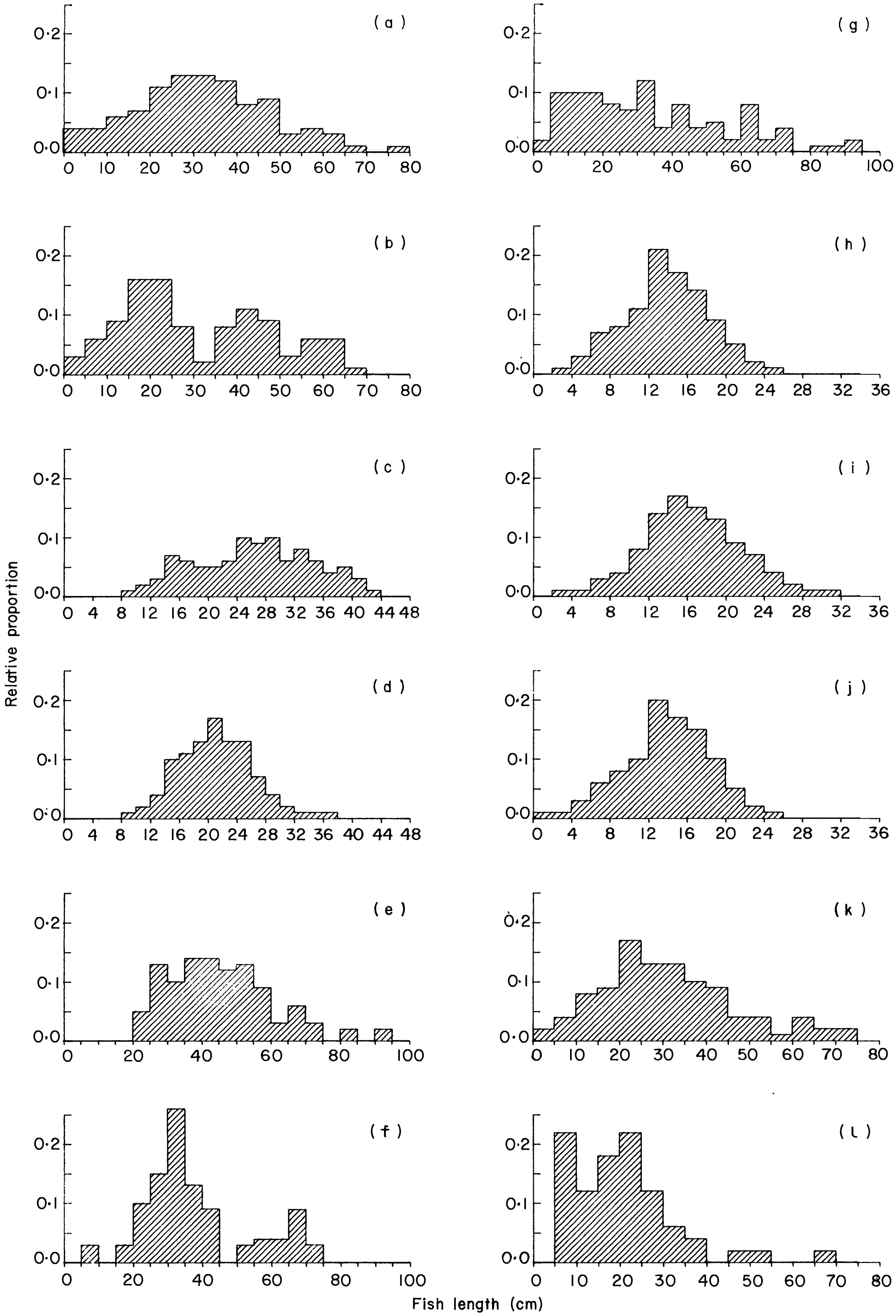


**Fig. 3.** Length–frequency distributions, shown as a proportion of total sample, for the major fish prey in the diet of grey seals around Orkney: (a) cod in February, $n = 145$; (b) cod in November, $n = 172$; (c) whiting in February, $n = 203$; (d) whiting in November, $n = 1318$; (e) saithe in February, $n = 63$; (f) saithe in November, $n = 79$; (g) ling in February and November, $n = 256$; (h) sandeels in February, $n = 6752$; (i) sandeels in June/August, $n = 1536$; (j) sandeels in November, $n = 5943$; (k) plaice in February, $n = 247$; (l) plaice in November, $n = 51$.

During February a wide range of sizes of whiting was taken (Fig. 3c). A similar distribution was seen in the summer data (not plotted). In November, however, few fish longer than 30 cm were consumed (Fig. 3d).

The February diet of saithe was composed mainly of 25–60 cm fish with no obvious mode (Fig. 3e). In November, the distribution had strong modes at 30–35 cm and 65–70 cm (Fig. 3f).

Length–frequency distributions for ling were pooled over all samples. Over 60% of fish taken were less than 40 cm in length (Fig. 3g).

Length–frequency distributions for sandeels are shown for February (Fig. 3h). June/August (Fig. 3i) and November (Fig. 3j). Those for February and November were practically identical with a single mode at 12–14 cm. The distribution during the summer was skewed towards larger fish with about 15% longer than 22 cm.

The length distributions for plaice during February (Fig. 3k) and November (Fig. 3l) were very different. During February the estimated size ranged widely up to 75 cm. During November, the distribution was strongly skewed toward small fish, mostly less than 30 cm long.

## Discussion

Our results show that grey seals feed on a wide variety of fish prey in the Orkney area and that there is both seasonal and regional variation in the diet.

### REGIONAL AND SEASONAL VARIATION

The dominant prey by number (and by weight) in the diet of grey seals around the Orkneys were sandeels. They were more prevalent in February and the summer, and least prevalent in November. This pattern is similar to that found in the diet of grey seals from the south-western North Sea where sandeels were important from January to March and from June to October, but rare in April/May and in November/December (Prime & Hammond 1990).

During February and November, the length distributions of sandeels in the diet indicated that the seals were feeding on the smaller species, *Ammodytes marinus* (Raitt) and *Gymnammodytes semisquamatus* (Jourdain), found by Langham (1971) to be the most abundant sandeel species in the area and/or on young fish of the greater sandeel (*Hyperoplus lanceolatus* Le Sauvage). In the summer, however, the presence of sandeels in the diet greater than 24 cm indicates that they must also have been taking adult greater sandeels.

Of the gadids, cod were important in the diet in all areas and seasons. Age–length data provided by the Ministry of Agriculture, Fisheries and Food (MAFF), indicate that the three modes in the length distribution of cod in the diet in November roughly correspond to 1-group, 2- and 3-group, and 4-group fish. There is a spawning ground for cod at this time in the Moray Firth (Hopkins 1986) and the larger fish in the November sample could be a result of an increased abundance of mature fish at that time.

Ling were important in the diet of seals from the northerly (in February) and westerly areas. It is typically an open water species (Wheeler 1978) indicating that seals from these areas may have been feeding some way from the islands. However, the seals took a high percentage of small ling (<40 cm) which are often found inshore and sometimes in very shallow water (Dipper 1987).

Whiting were particularly important in the south during November. The fish taken in this month were all small, probably no older than 2-group based on MAFF age–length data. Large whiting were seen in the diet in February. Whiting spawn from January to July off the east coast of Scotland in an area which extends at least as far north as the Moray Firth (MAFF 1981).

Flatfish were generally more important in the east and south. Plaice spawn in this area from January to March (MAFF 1981); our results show more large plaice in the diet in February than at other times of the year. In November, almost all the fish were less than 30 cm and probably mostly immature (Rijnsdorp 1989).

There are some similarities between our results and those presented by Pierce *et al.* (1990) who reported the frequency of occurrence of prey types in faeces collected on the island of Eynhallow (see Fig. 1). In February, our results from the west (which included faeces from Eynhallow) were dominated by sandeels and gadids, as were Pierce *et al.*'s (1990) results in the period January–March. At the end of the year, both studies showed a greater domination by gadids and a reduction in sandeels in the diet.

Rae's (1973) sample of grey seal stomachs from Orkney was very small but he did note that salmon were of relatively minor importance to seals in Orkney, a view confirmed by our results which failed to find any evidence of salmon in the diet. Grey seals have been observed around fishing nets consuming large fish at the surface but not eating the heads. It is possible, therefore, that salmon were taken but not detected.

### IMPLICATIONS FOR SEAL–FISHERIES INTERACTIONS

According to Mason *et al.* (1985), the main demersal fisheries in the Orkney area from 1972 to 1983 were for cod, haddock, whiting and saithe. Of these species, haddock was by far the most important. Plaice, lemon sole, ling, angler (*Lophius piscatorius*, L.) and skates (Rajidae) were also caught incidentally. Most of these species formed part of grey seal diet in Orkney in 1985, especially cod, ling and whiting. There were also pelagic fisheries in the area for herring (*Clupea harengus*, L.) and mackerel (*Scomber scombrus*, L.) (Mason *et al.* 1985) but, according to our results, these species did not feature in the diet of grey seals in 1985.

#### FOOD AVAILABILITY, FEEDING STRATEGIES AND PREY SELECTION

A wide variety of prey is available to grey seals in the Orkney area throughout the year; our results show that they exploit these prey fully using a variety of strategies. Some species (such as cod and whiting) appear to be taken indiscriminantly. At particular sites, other species (such as sculpins) seem to form a constant proportion by weight in the diet. However, greater numbers of some species (such as plaice and sandeels) are consumed when and where they are larger, indicating that some seals may deliberately switch to these prey at particular times.

Spawning fish occur in the area at certain times (cod in November, whiting in January–July, plaice in January–March) and the seals seem to take advantage of this. Such fish are higher than usual in energy content and would be expected to be preferred prey.

Fish which have restricted habitat requirements featured strongly at certain sites at certain times. Our results show a larger percentage of lemon sole, which can be a locally common species (Wheeler 1978), in the diet at one particular site in November but not elsewhere. Similarly witch, which have a requirement for muddy bottoms, were found mostly at one site. Sea scorpion and bullrout, which live on rocky bottoms, were also only found in the diet at particular sites. These restricted contributions to the diet may reflect feeding, perhaps by specific individuals, on locally abundant prey.

A species which feeds on many prey species, seemingly using a variety of strategies, would be expected to display behaviour patterns at sea to facilitate this. Indeed, telemetry studies have shown that individual grey seals can move long distances but also display specific repeated patterns of movement at sea, sometimes over periods of several months (Thompson *et al.* 1991; McConnell *et al.* 1992; Hammond *et al.* 1992; Hammond, McConnell & Fedak 1993).

Telemetry studies have also provided information on the feeding habits of grey seals (Thompson *et al.* 1991; Thompson & Fedak 1993). They usually dive to the sea bed and there is very little evidence for any pelagic activity. The slow swimming speeds recorded for grey seals are indicative of gathering or sitting in wait for prey rather than chasing it. These strategies would maximize the time the seals were able to spend feeding at the bottom by making best use of the limited oxygen supply. These results corroborate the results presented here that grey seals are bottom feeders and do not normally feed on pelagic species.

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