J. Zool., Lond. (1998) **244**, 209–222

Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat

D. J. Tollit, A. D. Black, P. M. Thompson*, A. Mackay, H. M. Corpe, B. Wilson, S. M. Van Parijs, K. Grellier and S. Parlane

Lighthouse Field Station, University of Aberdeen, Department of Zoology, Cromarty, Ross-shire, Scotland IV11 8YJ

(Accepted 4 June 1997)

Abstract

We use information on the at-sea distribution of radio-tagged seals to identify the summer foraging areas used by 31 harbour seals from two different haul-out sites in the Moray Firth, N.E. Scotland. We then determine whether seals tend to occur over particular sediment types or water depths as hypothesized by Härkönen (1987*b*), and assess whether local geographical variations in diet composition can be related to local differences in available foraging habitat.

The majority of seals foraged within 30 km of their haul-out site, consequently there was broad overlap between the foraging areas used by animals from the same site, but little overlap in the areas used by seals from different sites. Most seals foraged in water depths of 10–50 m with mainly sandy sea-bed sediments. Data on the distribution of dive depths of five seals which were fitted with time-depth-recorders indicated that seals were generally diving on, or close to, the sea-bed. Occasional pelagic dives between the more common benthic dives were also observed. Between-site differences in the seals' use of different water depths and sea-bed sediments suggest that local geographical variations in diet were related to local differences in foraging habitats, but that habitat use also differed between individual seals.

Key words: diving, habitat-use, pinnipeds, predation, telemetry

INTRODUCTION

The harbour seal (*Phoca vitulina* L.) is the most common species of seal present in the cold temperate waters of the North Atlantic and North Pacific. They come ashore to give birth, rest, and moult and are considered to be generalist predators in coastal waters, with fish and cephalopods forming the bulk of the diet (Bonner, 1972; Bigg, 1981; Brown & Mate, 1983). Populations of harbour seals are considered non-migratory but, as a species, use a wide range of habitats across their geographical distribution (Bigg, 1981). Usually they are found as concentrated colonies on sand and mudbanks in river estuaries, or as more dispersed groups along rocky shores (Bigg, 1981). The results of a number of studies (e.g. Härkönen, 1987*a*; Payne & Selzer, 1989; Bowen & Harrison, 1996) suggest that diet composition reflects differences in assemblages of prey species encountered in these different habitats. For example, Payne & Selzer (1989) documented that harbour seal diet, when estimated by faecal samples collected from haul-out sites surrounded by sandy sea-beds, was dominated by sand lance (also known as sandeels) (*Ammodytes americanus*), whereas when haul-outs were surrounded by rocky bottoms with deeper water, rockfish, gadoids, flounder, and herring were more commonly consumed. However, these studies presented no information on the foraging distribution of seals to substantiate suggestions of a relationship between foraging habitat and diet composition.

Several studies have investigated foraging activity and movements of harbour seals using conventional VHF radio-telemetry (e.g. Harvey, 1987; Allen, 1988; Stewart *et al.*, 1989; Thompson *et al.*, 1989; Thompson & Miller, 1990). Such studies indicate that the species generally forages within 50 km of haul-out sites (Stewart *et al.*, 1989; Thompson & Miller, 1990; Thompson *et al.*, 1991; Oxman, 1995). However, no empirical studies have yet determined whether seals tend to occur over particular habitat types or water depths within these areas. The potential importance of such studies is highlighted by Härkönen (1987*b*), who developed a model which hypothesized that differences in population size and haul-out patterns of harbour seals in European waters could be explained by the availability of suitable foraging habitats around haul-out sites. This model was based on

*All correspondence to: Dr P. M. Thompson, Lighthouse Field Station, University of Aberdeen, Department of Zoology, Cromarty, Ross-shire, Scotland IV11 8YJ.

three assumptions: first, that harbour seals are bottom feeders; second, that the profitability of taking different prey species is dependent on water depth; third, that the sizes of the feeding grounds available to seals are dependent on local bathymetrical conditions. He obtained indirect evidence of bottom feeding from analyses of faecal samples (Härkönen, 1987*a*, 1988) which, coupled with information on the habitat requirements of different prey, suggested that harbour seals fed mainly on soft sea-beds, shallower than 30 m, where vegetation was sparse or lacking.

The spatial distribution of fish can, in part, be influenced by a number of abiotic factors, in particular, bathymetry, temperature, salinity, currents and sea-bed sediment type (e.g. Gray, 1974; Lough *et al.*, 1989; Gray & Otway, 1994; Perry, Stocker & Fargo, 1994). Of these variables, water depth and bottom type stay relatively constant from year-to-year and are most easily quantified. The influence of interspecific sea-bed and depth requirements of certain prey have been previously suggested as a possible cause of geographical differences in harbour seal diet composition (e.g. Härkönen, 1987*a*; Payne & Selzer, 1989).

In this study, we use information on the at-sea distribution of radio-tagged seals to identify the foraging areas used by harbour seals from two different haul-out sites in the Moray Firth. We then use available information on sea-bed sediment characteristics and bathymetry to determine whether seals are more likely to occur over particular sediment types or water depths as predicted by Härkönen's (1987*b*) model. Finally, we compare the diet composition of the seals from the two sites, and use information on the biology of prey species to assess whether local geographical variations in diet composition can be related to local differences in available foraging habitat.

METHODS

Study area

The study was carried out in the Moray Firth, a large triangular embayment to the north-east of Inverness, Scotland (57°30′N, 4°14′W) (Fig. 1). The study area, defined as the region west of 03°10′W, contains 3 sheltered estuaries, the Beauly, Cromarty, and Dornoch Firths, where there are year-round harbour seal haul-out sites (Thompson *et al.*, 1997). The Beauly Firth is connected to the Inverness Firth, at the outer mouth of which lies another key haul-out site. These 4 firths make up what are known as the 'inner' firths.

The sea-bed of the south-west corner of the Moray Firth slopes gently from the coast to about 50 m in depth, approximately 15 km offshore (Fig. 1). A relatively deep channel, associated with the Great Glen fault, extends south-west to north-east from Inverness, ranging from 5–15 km off the south coast of the outer Moray Firth, and with a maximum depth of 76 m within the study area. The inner firths are all relatively shallow, with the exception of small deep basins (30–50 m) at tidal constrictions at the mouths of the Beauly Firth, the Inverness Firth, and the Cromarty Firth (Fig. 1). Several sub-tidal banks rise above the surrounding sea-bed, the largest of these being found 10 km SE of Helmsdale (Fig. 1). Sea-bed sediments are predominantly sand and muddy sand (Folk, 1954), but small discontinuous patches of sediments containing mainly gravel, mud, or rock are also apparent. In general, a close correlation exists between increased depths and decreasing sediment grain size. For example, the muddy bottoms of the fault-related deep water off the south-east coast contrast with the coarse sandy sediments of the relatively shallow areas in the northern part of the study area. The exception to this trend is the fine sediment which accumulates in the shallow sheltered waters of the inner firths (Reid & McManus, 1987).

Water depth and sea-bed sediment categories

The study area was divided into 1 km Ordnance Survey squares (OS square), each of which was assigned a 10 m depth category using Admiralty charts Nos. 223, 1077, 1708, 1889, and 1890 (Hydrographer for HM Navy, Taunton, Devon). Each OS square within the study area was also assigned a sediment category (Folk, 1954) based on data from Chesher (1984), Ruckley & Chesher (1987). Within the inner firths, only qualitative data were available on sediment type (EML, 1990; Julian Hunter, SEPA, pers. comm.) because the BGS surveys did not extend into these more inshore waters.

Identification of seal-foraging areas

Seal-foraging locations were determined by VHF radio-tracking during the summer (May–August) between 1988 and 1995. Seals were captured at haul-out sites in the Dornoch, Inverness, and Beauly Firths, and VHF radio-tags (173 MHz) were deployed on a total of 35 individuals. Further details of capture, handling, and tagging methods are found in Thompson & Miller (1990) and Thompson *et al.* (1992).

Seals were located by triangulating with hand-held directional aerials from coastal vantage points, and bearings were accurate to $\pm 7.5°$ (Thompson & Miller, 1990). Seals followed between 1988–1992 were located once each day on at least 6 days each week during June and July. Seals tagged between 1993 and 1995 were located less regularly, but we aimed to locate individuals when they were in the middle 80% of a foraging trip (between 2 haul-out bouts). Earlier studies had shown that seals generally travelled directly between haul-out and foraging areas (Thompson & Miller, 1990) and we assume, using published estimates of harbour seal swimming speed (Williams & Kooyman, 1985), that most travelling locations were avoided by excluding data from the first and last 10% of a trip.

Data on the at-sea distribution of seals from the

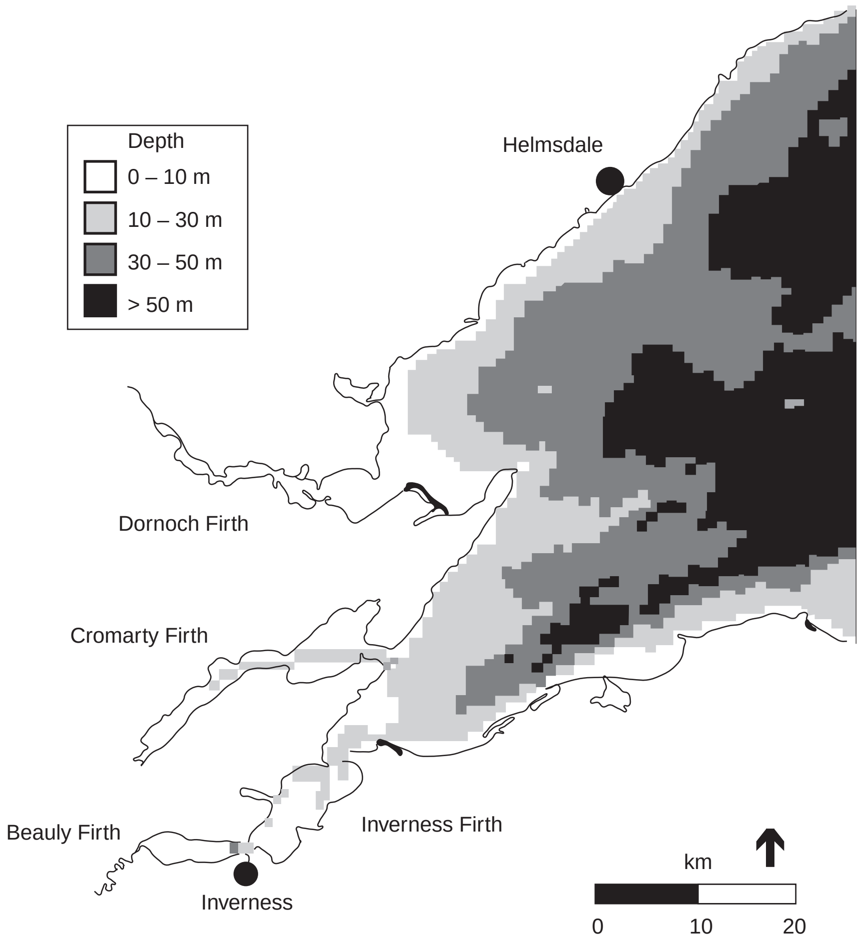

Fig. 1. Bathymetry of each 1 km OS square within the Moray Firth study area.

Dornoch Firth ($n = 16$) have already been presented (Thompson *et al.*, 1996). Habitat characteristics of the foraging areas of these seals were compared with those seals which were captured in the Inverness and Beauly Firths ($n = 15$), the more southern part of the study area. Data from these 2 firths were combined as all 3 seals captured in the Beauly Firth subsequently used the Inverness haul-out site.

To avoid misidentification of foraging areas, we excluded certain at-sea foraging locations. First, we assumed that any locations within 2 km of haul-out sites may have been associated with haul-out activity and these data were excluded from further analyses (Thompson *et al.*, 1994). Second, for those males known to be involved in display behaviour during July (Van Parijs *et al.*, 1997), we used only data collected prior to the breeding season (1 July). Finally, we excluded all locations where the error polygon (Heezen & Tester, 1967) around our estimated at-sea locations exceeded 100 km^2 ($n = 23$).

The foraging areas used by each individual were then identified by carrying out harmonic mean analyses (Dixon & Chapman, 1980) using MCPAAL (National Zoological Park, Smithsonian Institution, Washington, U.S.A.) to assess the area within which 75% and 50% of the remaining locations occurred. Harmonic analyses could not be carried out for all animals owing to intermittent tag failure or insufficient sample sizes of at-sea locations ($n < 5$). For the remaining 31 seals (Table 1), we recorded the co-ordinates of each OS square which was within, or at least 50% covered by, each seal's 75% harmonic mean isopleth. This method permitted the main seal foraging areas to be identified, displayed and analysed between sites on the basis of the relative use of each OS square by different individuals (Thompson *et al.*, 1996). The 50% harmonic mean isopleth was considered to be equivalent to each individual's 'core area' of activity and was used in our analyses of each seal at an individual level. Using this lower value isopleth restricted the inclusion of areas not visited by each animal, but necessarily excluded some areas used only occasionally (Harris *et al.*, 1990).

Determination of seal foraging depths

For 8 seals, recoverable time-depth recorders (TDR Mk. 3 & 5, Wildlife Computers, Woodinville, WA, U.S.A.) were used in conjunction with VHF telemetry to ascertain whether harbour seals dived to the sea-bed when foraging. Such analyses are required before further analyses of depth and sediment type are justifiable.

A VHF radio transmitter was embedded into a pressure resistant flotation matrix and attached to each TDR. Epoxy glue was used to attach the package (approx. 200 g) between the shoulders of the seal, with the antenna pointing backwards close to the back of the animal. The design and positioning of tags were chosen to minimize cross-sectional area, and the combined weight of the TDR and head tag did not exceed 0.5% of total body weight. Transmitters were therefore considerably less than the maximum 5% of body weight recommended for radio-telemetry studies (Cuthill, 1991). The package was positively buoyant in sea-water and balanced to float with the VHF antenna upright to permit recovery once it became detached when the animal moulted in late summer.

The TDRs recorded hydrostatic pressure from a pre-calibrated pressure transducer at sampling intervals of either 5 or 10 sec. After recovery, data were downloaded to a PC and analysed using default settings on the purpose-written software (Wildlife Computers). These allowed individual dive profiles to be examined graphically and also provided estimates of key dive parameters, such as maximum dive depths (Boness, Bowen & Oftedal, 1994).

To determine the distribution of dive depths while seals were in foraging areas, we selected data from complete foraging trips which were associated with at least one foraging location. Only dives in the middle 80% of each of these bouts were analysed in an attempt to exclude travelling dives and dives immediately before and after bouts of haul-out. The resolution of the pressure sensor was 0.5 m and only dives deeper than 1 m were included. The distribution of dive depths recorded by each individual's TDR was then compared with the distribution of water depths encompassed within each individual's 50% harmonic mean isopleth.

Between-site comparison of foraging area characteristics and habitat use

Foraging areas used by the 16 seals caught at haul-out sites in the Dornoch Firth were compared with those used by the 15 seals which used the Inverness Firth haul-out site. To identify the areas available to seals from different sites, we compared the distances which seals travelled from each site to their respective foraging areas using a χ^2 contingency table. This analysis compared the mean number of seals in each OS square within 10 km concentric bands from the 2 haul-out sites. As the majority of seals foraged within 30 km of their haul-out sites, we restricted comparison of depths and sediment categories to areas within 30 km of each haul-out site. To determine if there were between-site differences in the use of different water depths, we compared the number of seals using those OS squares which fell within each of 4 depth categories (<10 m, 10–30 m, 30–50 m, >50 m) using a Mann–Whitney U-test. Seals in this study generally used water depths of 10–50 m and therefore comparison of the sediment categories was confined to OS squares within this range. The 3 most abundant sediment categories were also compared at water depths of 10–30 m and 30–50 m separately.

Individual use of particular water depths and sediments

The relative use (P) of different water depths or sediment categories by individual seals was investigated using a conventional index of preference (e.g. Hunter, 1962; Duncan, 1983).

$$P_{1i} = U_i / A_i$$

where A_i = the percentage of the study area covered by category 'i' and where use U_i = the percentage of observations which were recorded in the category 'i'. This index varies from 0 (total avoidance) through 1.0 (no preference) to higher values indicating increasing use in relation to availability. An arbitrary value of 2.0 was chosen to indicate a 'preference' for a particular category, as this indicates that seals used these areas twice as much as would be expected by their relative availability. Because individual seals foraged at different ranges from their haul-out site, the habitat available to each individual differed. Therefore, A_i was adjusted for each individual to include only those 10 km concentric bands within that seal's maximum foraging range (i.e. to the outer boundary of its 75% harmonic mean isopleth). Use (U_i) was calculated as the area covered by that seal's 50% harmonic mean isopleth. Thus, for each seal, we compared the overall extent of each habitat category within each seal's estimated range with the extent of that habitat category in the area in which the seal was most consistently located. The area of each water depth and sediment category in both the seal's foraging areas and each of the 10 km concentric bands was measured using a digitizing tablit (SummaSketch II, Seymour, CT, USA) and purpose-written software.

Between-site comparison of diet composition

Faecal samples have been collected regularly in the study area since 1987 (Pierce *et al.*, 1991; Tollit & Thompson, 1996). To compare the diet of seals from the Dornoch and Inverness sites, samples from June and July 1991–1993, the period which coincided with the radio-tracking studies, were selected. The weight of each prey species, as a percentage of the total reconstructed weight of all prey in each year, was calculated using measurements of hard prey remains (see Tollit & Thompson, 1996). An overall combined result for each site was calculated by equally weighting each year. A percentage modified frequency of occurrence (frequency of occurrence down weighted so that the sum of all prey frequencies totalled 100%, Bigg & Perez (1985)) was calculated. Comparison of these 2 indices between haul-out sites was made using the percentage similarity index (PSI, Krebs, 1989)

$$PSI = \Sigma \text{ minimum } p_1i\ p_2i$$

Table 1. Summary data for the 31 harbour seals used in this study. These include: the identification numbers used for each seal (M = Male; F = Female); site and year of capture and weight at capture; the number of daily locations used to calculate each individual's harmonic mean isoclines; the maximum distance from the haul-out site to the outer limit of the 75% harmonic mean isocline; and the total area within each seal's 50% harmonic mean isocline. Also presented are the water depth and sea-bed sediment categories where the index of preference (P) ≥ 2.0

ID no.	Capture site	Year	Weight (kg)	At-sea locs	Maximum distance (km)	Total area (km^2)	Water depth (m)	Sea-bed sediment*
M1	Inverness	1988	87.5	49	17.5	67.7	20–30	gS, sG
M2	Inverness	1988	81	19	21.0	60.9	10–20	mS, (g)mS
M28	Beauly	1994	55.5	19	20.0	38.6	20–30	–
M30	Beauly	1994	96.6	11	72.5	90.8	40–50	(g)S, gS, sG
M32	Beauly	1994	94	19	28.0	15.4	0–10	mS
M34	Inverness	1995	116	10	40.0	72.5	30–40	G
M35	Inverness	1995	104	9	28.0	58.2	20–30	gS
M36	Inverness	1995	103	14	33.0	11.0	20–30	mS
M37	Inverness	1995	47	10	10.0	43.5	0–10	–
M39	Inverness	1995	85	11	19.0	40.8	50–70	mS, gS
F1	Inverness	1988	106	20	21.0	34.7	30–60	gS
F17	Inverness	1992	80	10	24.0	22.6	20–30	gS
F18	Inverness	1992	81	20	40.5	85.8	–	mG
F19	Inverness	1992	94	20	16.5	24.8	–	–
F20	Inverness	1992	82	10	16.5	10.5	10–20	–
M10	Dornoch	1991	55.5	15	30.0	71.9	40–50	gM, gmS
M11	Dornoch	1991	85	19	29.5	66.9	40–50	gM
M12	Dornoch	1991	88.5	10	21.5	38.8	30–40	gmS, sG
M13	Dornoch	1991	55.5	16	26.0	54.5	30–50	sG
M14	Dornoch	1991	58.5	19	23.0	29.4	30–40	–
M15	Dornoch	1991	56	14	27.0	42.5	30–40	gM, gmS, sG
M16	Dornoch	1991	81.7	38	20.5	30.8	–	gmS, mG
M17	Dornoch	1991	88	10	35.0	65.1	40–50	gM
M18	Dornoch	1991	57	17	22.0	43.3	30–40	gmS
F4	Dornoch	1989	90.5	18	21.5	37.4	30–40	gmS
F5	Dornoch	1989	93.5	20	25.0	16.2	0–10	–
F6	Dornoch	1989	89.5	24	21.0	40.0	30–40	gmS
F7	Dornoch	1989	74.5	16	19.0	28.0	10–20	–
F8	Dornoch	1989	89.5	20	25.0	39.4	30–40	gM
F9	Dornoch	1989	79	25	26.0	31.5	30–40	gmS, mG
F15	Dornoch	1991	95	23	25.0	45.6	> 30–40	–

* Sediment codes follow those used throughout all U.K. waters by the British Geological Survey (Chesher, 1984); i.e. muddy sand [mS], sand [S], gravelly sand [gS], gravel [G], sandy mud [sM], sandy gravel [sG], muddy gravel [mG], gravelly muddy sand [gmS], slightly gravelly muddy sand [(g)mS], slightly gravelly sand [(g)S], gravelly mud [gM] and rock [R].

where p_1i and p_2i are the percentages of species i from community samples '1' and '2', respectively. The index ranges from zero (no similarity) to 1.00 (complete similarity). Last, we used a Mann–Whitney U-test to make a between site comparison of mean number of fish otoliths and cephalopod beaks per faecal sample (Hammond, Hall & Prime, 1994). Information on the biology, depth and habitat preferences of prey species was collated from a variety of sources (Raitt, 1934; Müus & Dählstrøm, 1964; Macer, 1965, 1966; Reay, 1970; Langham, 1971; Wheeler, 1978; Hopkins, 1986; Dipper, 1987; Storey, 1993).

RESULTS

Characteristics of foraging areas

The maximum distance travelled by individual seals from their respective haul-out sites to the outer edge of their foraging areas (75% harmonic mean isopleth) varied from 10–73 km (Table 1). However, the majority of seals foraged in an area 30 km or less from their haul-out site, with a strong modal distance of 10–20 km (Fig. 2). Overall, the distance to respective foraging areas was similar for Inverness and Dornoch animals (Chi-square contingency analysis, $\chi^2 = 2.5$, $d.f. = 4$, $P > 0.5$). Consequently, there was broad overlap between the foraging areas used by animals from the same site, but little overlap in the areas used by seals from the Inverness and Beauly Firths (Fig. 3a) with those from the Dornoch Firth (Fig. 3b). Overall, seals in this study area foraged over an area exceeding 1000 km^2. Within this range, however, individual seals returned consistently to the same areas, as highlighted by the size of their 'core' foraging areas which varied from only 10 to 91 km^2 (Table 1). The majority (95%) of OS squares in the

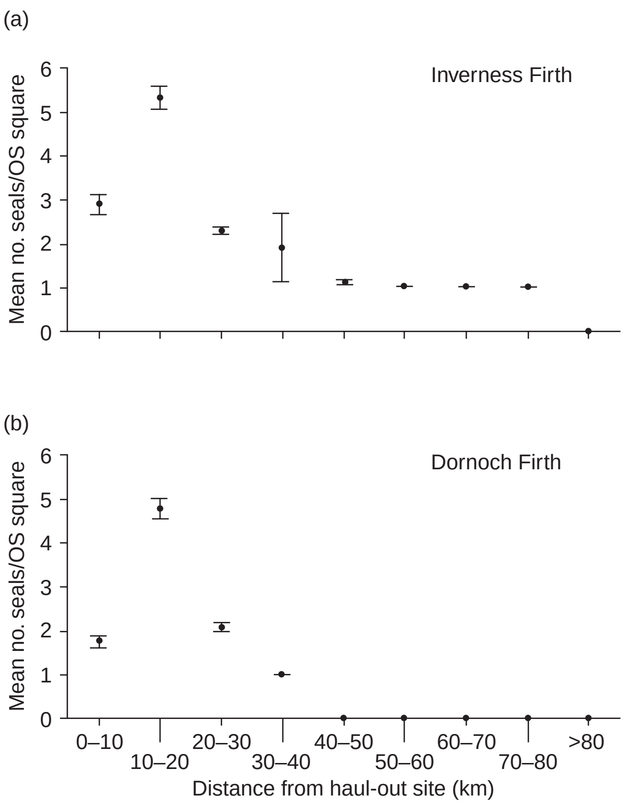

Fig. 2. Comparison of the distance from haul-out site to the outer bounds of foraging areas used by seals from (a) Inverness Firth and (b) Dornoch Firth, using the mean number of seals (± 1 standard deviation) based on OS squares within each 10 km concentric band.

areas used by seals were of water depths of <60 m and over soft sea-beds (Figs 1 & 3).

Determination of seal foraging depths

Five TDRs deployed on seals were recovered. No significant difference was found between the distribution of dive depths recorded and the distribution of water depths within each individual's 50% harmonic mean isopleth (Student's *t*-test on arcsine transformed data, all tests $P > 0.6$) (Fig. 4). Three seals (M28, M35, & M39) had modal dive depths of 20–30 m. In each case, this corresponded with the modal depth category within the foraging area. Greater than 82% of M34's dives were to depths of 20–40 m and 75% of M30's dives were to depths of 50–60 m. The depths of these dives indicated that the seals generally dived to the deepest waters available within their foraging area. Although, this suggests that most dives were to the bottom, our results indicate that this was not always the case. For example, whilst the majority of dives by M30 were between 50–60 m, approximately 15% were of <20 m, even though the area covered by the 50% harmonic mean isopleth (or indeed the 75% isopleth) contained no water of these depths. Examination of dive profiles indicated that all but one seal (M28) appeared to be making occasional mid-water pelagic dives in between the more common benthic dives.

Between-site comparison of habitat use

The relative use of water depths used by seals differed between sites (Table 2). Those from the Inverness Firth used water of 10–30 m in depth, while seals from the Dornoch sites used water of 30–50 m in depth (Table 2). Overall, seals were unlikely to be found in water depths of 10 m or less or more than 50 m (Table 2, Fig. 5).

The clearest between-site differences in the use of sea-bed sediments were found for gravelly sand (Table 3). Availability of this sediment was similar within 30 km of both sites, but relative use of these areas was significantly higher for seals from the Inverness Firth ($P < 0.0001$, Table 3). Seals from the Inverness Firth were also more likely to use waters over muddy sand (Table 3). In contrast, seals from the Dornoch Firth tended to be found over some of the rarer sediments (e.g. slightly gravelly sand) which were not available to seals from the Inverness Firth site (Table 3).

Individual use of particular water depths and sediments

Twenty-eight seals ($>90\%$) exhibited a high relative use ($P \geq 2.0$) of at least one depth category (Table 1). For most seals (80%) from the Dornoch Firth, this was in depths of 30–50 m. Individuals from the Inverness Firth were found in wider range of depths, but $>30\%$ tended to be found in depths of 20–30 m. Overall, only three seals ($<10\%$) showed a relatively high use of the most shallow water category (<10 m), and only two (6%) used deeper waters (>50 m).

Most seals ($>75\%$) also exhibited a relatively high use ($P \geq 2.0$) of areas over at least one sediment category (Table 1). In general, these were mixed sediments, with $>50\%$ of seals from the Inverness Firth showing a relatively high use of areas over gravelly sand. Seals from the Dornoch Firth, in contrast, were more likely to be found over gravelly muddy sand and gravelly mud.

Between-site comparison of diet composition

Overall, sandeels were the predominant prey by weight and by number at both sites, but these prey accounted for a higher proportion of the diet of seals from the Inverness Firth (Table 4). Lesser octopus were also taken at both sites, but pelagic species such as herring, sprat, and squid were poorly represented over this period (Table 4). Between site PSI values for percentage weight were 0.74, with significant between-site differences in diet composition resulting primarily from higher numbers of flounder, plaice and dab in samples from the Dornoch Firth (Table 4).

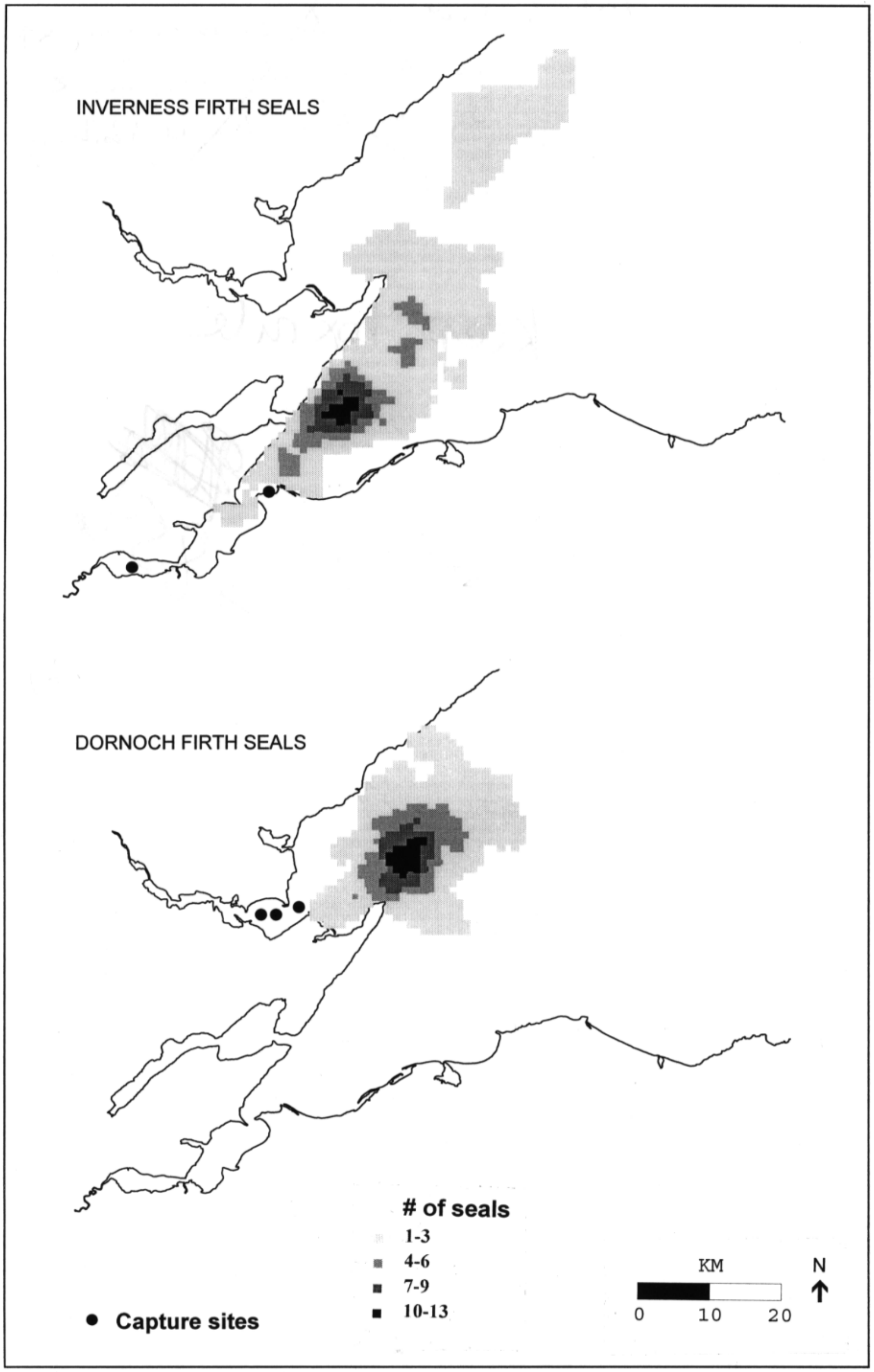

Fig. 3. Foraging areas of harbour seals from: (a) the Inverness Firth and (b) the Dornoch Firth. Relative use was described by the number of individual 75% mean harmonic isopleth which covered each 1 km OS square.

DISCUSSION

Although one individual seal travelled over 70 km to forage, most seals used areas within 30 km of their respective haul-out sites, with most foraging occurring within distances of between 10–20 km (Fig. 2). All foraging areas were also less than 20 km from land (Fig. 3). Such limited foraging ranges resulted in broad overlap of areas used by seals from the same haul-out site, but little overlap of areas used by seals from the two different haul-out sites studied (Fig. 3).

Table 2. Results of Mann–Whitney U-tests comparing the relative use of available water depths between the Inverness (Inv) and Dornoch (Dorn) Firth. (n^1 and n^2 are respective sample sizes, significant results have been highlighted in boldface type)

Site and water depth comparison					n^1	n^2	Z statistic	*P* value
Inv	**< 10 m**	**vs.**	**Inv**	**10–30 m**	**95**	**224**	**10.2**	**< 0.001**
Inv	**< 10 m**	**vs.**	**Inv**	**30–50 m**	**95**	**107**	**9.1**	**< 0.001**
Inv	**< 10 m**	**vs.**	**Inv**	**> 50 m**	**95**	**32**	**3.6**	**< 0.001**
Inv	**10–30 m**	**vs.**	**Inv**	**30–50 m**	**224**	**107**	**3.7**	**< 0.001**
Inv	**10–30 m**	**vs.**	**Inv**	**> 50 m**	**224**	**32**	**5.6**	**< 0.001**
Inv	**30–50 m**	**vs.**	**Inv**	**> 50 m**	**107**	**32**	**4.7**	**< 0.001**
Dorn	< 10 m	vs.	Dorn	10–30 m	118	304	0.9	0.35
Dorn	**< 10 m**	**vs.**	**Dorn**	**30–50 m**	**118**	**419**	**7.6**	**< 0.001**
Dorn	< 10 m	vs.	Dorn	> 50 m	118	107	1.9	0.06
Dorn	**10–30 m**	**vs.**	**Dorn**	**30–50 m**	**304**	**419**	**8.8**	**< 0.001**
Dorn	10–30 m	vs.	Dorn	30–50 m	304	107	0.9	0.37
Dorn	**30–50 m**	**vs.**	**Dorn**	**> 50 m**	**419**	**107**	**5.8**	**< 0.001**
Inv	< 10 m	vs.	Dorn	< 10 m	95	118	1.5	0.14
Inv	**10–30 m**	**vs.**	**Dorn**	**10–30 m**	**224**	**304**	**12.9**	**< 0.001**
Inv	30–50 m	vs.	Dorn	30–50 m	107	419	1.9	0.05
Inv	> 50 m	vs.	Dorn	> 50 m	32	107	1.6	0.12
All	**< 10 m**	**vs.**	**All**	**10–30 m**	**213**	**528**	**7.7**	**< 0.001**
All	**< 10 m**	**vs.**	**All**	**30–50 m**	**213**	**526**	**11.2**	**< 0.001**
All	**< 10 m**	**vs.**	**All**	**> 50 m**	**213**	**139**	**3.6**	**< 0.001**
All	**10–30 m**	**vs.**	**All**	**30–50 m**	**528**	**526**	**4.8**	**< 0.001**
All	**10–30 m**	**vs.**	**All**	**> 50 m**	**528**	**139**	**3.8**	**< 0.001**
All	**30–50 m**	**vs.**	**All**	**> 50 m**	**526**	**139**	**7.2**	**< 0.001**

Table 3. A comparison of the sea-bed sediments available to seals from the Inverness and Dornoch Firths. The median number of seals (and inter-quartile ranges) using OS squares within 30 km of each site. (n^a = OS squares available, n^u = OS squares used by seals). Results for the three main sediment categories are also given for different water-depth categories. Between-firth differences in sea-bed sediment use relative to availability were tested with the Mann–Whitney U-test, *** = $P < 0.0001$, * = $P < 0.05$, nt = not tested due to insufficient samples

			Inverness Firth			Dornoch Firth		
Sea-bed sediment category	Code	Water Depth (m)	n^a	n^u	No. seals	n^a	n^u	No. seals
Muddy sand	Ms	10–30	91	85	5 (3–8)***	79	32	0 (0–2)
		30–50	78	71	2 (1–3)	210	114	1 (0–5)
Sand	S	10–30	105	71	2 (0–3)***	168	57	0 (0–1)
		30–50	15	9	1 (0–1)	180	134	2 (0–4)*
Gravelly sand	gS	10–30	23	23	3 (3–5)***	27	3	0 (0–0)
		30–50	0	0	–	0	0	–
Gravel	G	10–50	0	0	–	6	2	0 (0–1)
Sandy mud	sM	10–50	12	12	2 (2–2.5)	3	0	–
Sandy gravel	sG	10–50	2	2	3 (3–3)	11	2	0 (0–0)nt
Muddy gravel	mG	10–50	2	2	3 (3–3)	8	6	2.5 (1–3)nt
Gravelly muddy sand	gmS	10–50	0	0	–	3	3	7 (7–10)
Slightly gravelly muddy sand	(g)	10–50	3	3	5 (4–5)	-	0	–
Slightly gravelly sand	(g)S	10–50	0	0	–	18	12	1 (0–1)
Gravelly mud	Gm	10–50	0	0	–	2	2	6.5 (6–7)
Rock	R	10–50	2	1	2 (0–4)	6	3	0.5 (0–1)nt

Foraging depth characteristics

Our comparison of estimated dive depths from the TDRs and the depths available within each seal's core foraging area, suggest that a large proportion of foraging dives were to the sea-bed. These data support the findings of Bjørge *et al.* (1995) who, using a combination of acoustic and VHF telemetry, found that most harbour seal foraging activity in their Norwegian study occurred at or near to the sea-bed. However, examination of dive profiles from this study also indicate that seals made occasional mid-water pelagic dives between these benthic dives. Mixed diving has also been observed in male northern elephant seals (*Mirounga angustirostris*) (Le Boeuf *et al.*, 1993) and harbour porpoises (*Phocoena phocoena*) (Westgate *et al.*, 1995) and may be linked with encounters with pelagic prey.

Despite the fact that they foraged in relatively inshore areas, seals tended not to use shallow water of less than 10 m in depth (Table 2; Fig. 5). Instead, most seals were found in moderate water depths of between 10 and 50 m, and only three large males had water depths of

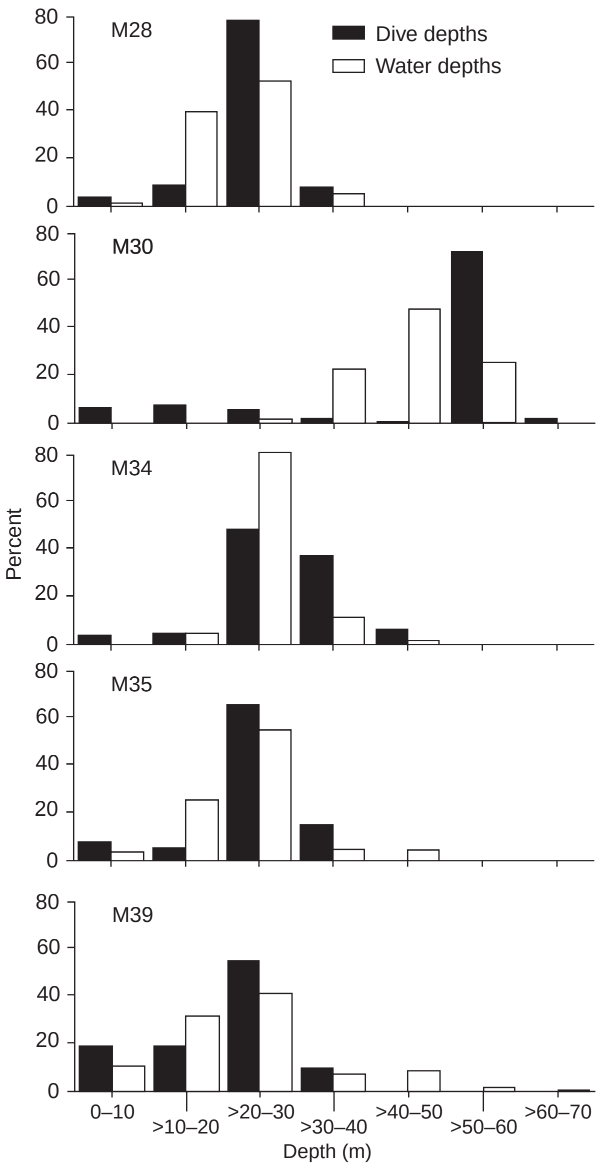

Fig. 4. The distribution of dive depths recorded from the time-depth recorders of five harbour seals compared with the distribution of water depths encompassed within each seal's 50% harmonic mean isopleth. (Number of dives, M28 $n = 6850$, M30 $n = 2354$, M34 $n = 4111$, M35 $n = 2266$, M39 $n = 3198$).

greater than 70 m within their 75% foraging area. In general, these results support the second assumption of Härkönen's (1987*b*) model. He predicted that low prey densities in shallow waters, and the increased energetic costs of diving in deeper waters, result in maximum energy gains being obtained by foraging at intermediate water depths. Based on information on habitat preferences of the key prey species (Härkönen, 1988), Härkönen (1987*b*) concluded that this depth was less than 30 m in the Kattegat–Skagerrak area. Our data on foraging distribution suggests that many seals in the Moray Firth use deeper waters, in the region of 50 m. Furthermore, TDR records confirm that some individuals consistently made benthic dives to depths greater than 50 m. However, even the deepest recorded dives of around 70 m (Fig. 4) were well within the maximum dive capabilities of harbour seals. For example, Bjørge *et al.* (1995) recorded several individuals diving to depths of 100–200 m, while harbour seals from coastal California have been recorded at depths in excess of 450 m (Kolb & Norris, 1982; T. Eguchi, Moss Landing Marine Laboratory, CA, U.S.A., pers. comm.). In these other study areas, such deep waters occur relatively close to haul-out sites. The shallow sloping nature of the Moray Firth basin means that seals would have to increase their foraging range considerably to reach deep waters (Fig. 1), and energetic constraints on the duration or range of foraging trips may prevent the use of these areas. Thus, while our data appear at first to support Härkönen's (1987*b*) model, comparison with these other studies suggests that observed dive depths may largely depend on the range of water depths available within close range of haul-out sites. Similarly, the between-site differences in the depths of water used by seals from the Dornoch and Inverness Firths (Table 2; Fig. 5) may largely reflect differences in the relative availability of each depth category (Fig. 1). Ultimately, the choice of an optimal dive depth is likely to be influenced by a combination of local bathymetric conditions, the ability to maximize the proportion of time spent foraging (Houston & Carbone, 1992), the availability of prey both geographically and at different depths in the water column (Dolphin, 1988), and the cost and benefits of feeding on different species (e.g. Stephens & Krebs, 1986; Wanzenböck, 1995).

Relationships between characteristics of foraging areas and diet

This study shows that harbour seals in the Moray Firth feed on species that are found at a variety of depths and habitats (Table 4). Few pelagic prey items were consumed and the majority of prey species found in faeces were strongly associated with (e.g. sandeels) or live on (e.g. flatfishes and octopus) the sea-bed (Table 4). These data further support our findings of the animals deployed with TDRs, that seals forage benthically during this period.

Analyses of the seals' foraging habitats were constrained by the broad spatial scale at which data on the distribution of both sediment types and foraging seals were collected. Nevertheless, they do provide a first quantitative description of the foraging habitats used by harbour seals, and highlight patterns which deserve further investigation at a finer spatial scale. In particular, between-site comparison of the sea-bed sediments and water depths used by seals suggest that local geographical variations in diet may be related to local differences in foraging habitats. Seals from the Inverness Firth, for example, were more likely to be found over pockets of gravelly sand at 10–30 m (Table 3). Sandeels, known to favour clean, coarse, sandy substrata (Reay, 1970), were the dominant prey item found at this site, contributing > 67%, by weight, overall (Table 4), and as much as 92% in some years. Sandeels contributed far

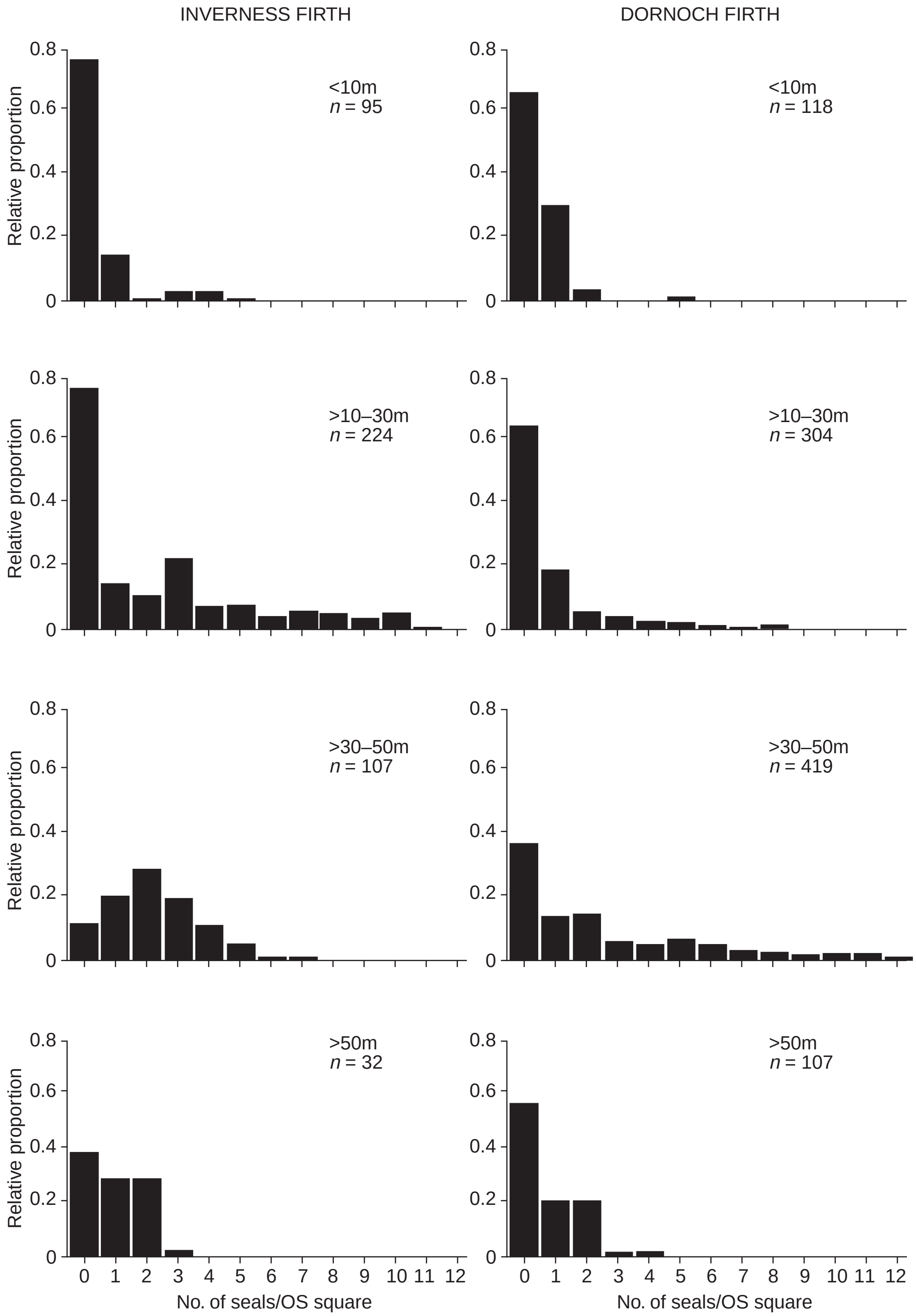

Fig. 5. Frequency histogram of the number of seals per OS square using four different water depth categories within 30 km of a) Inverness Firth site and b) Dornoch Firth sites (n denotes the number of OS squares available).

less to the diet of seals in the Dornoch Firth, where patches of gravelly sand were rarely used (Table 3). A similar relationship was suggested by a qualitative study off the east coast of England. At-sea locations of grey seals (*Halichoerus grypus*) estimated from satellite transmitters were clustered over sea-beds composed of gravelly sand (McConnell *et al.*, 1995) and the diet of grey seals in the area had previously been shown to be principally sandeels (Hammond & Prime, 1990; Hammond & Hall, 1994). While harbour seal dietary investigations in most other study areas have presented no information on foraging distribution and habitat use, the influence of available habitat in the waters surrounding seal haul-out sites on seals' diet has been

Table 4. Between-site comparison of harbour seal diet estimated from faecal samples collected in June and July (1991–1993) from a site in the Inverness (Inv) Firth ($n = 178$) and sites in the Dornoch (Dorn) Firth ($n = 178$). The importance of each prey species has been expressed first as estimated weight as a percentage (% Wt) of the total reconstructed weight of all prey and second, as the percentage modified frequency of occurrence (% MFO) of each prey (equally weighted across years). The mean number of otoliths or beaks per faecal sample (No.) in all years was compared using a Mann–Whitney U-test and significant results highlighted ($P < 0.001$). The distribution of the prey species is indicated with a depth range (preferred depths single spaced), preferred sea-bed sediments and benthic (B) or pelagic (P) occurrence (see text for details and references)

Common name	Species	Category: Site: Index: Inv % Wt	Dorn % Wt	Inv % MFO	Dorn % MFO	Inv No. (S.D.)	Dorn No. (S.D.)	B	P	Sediment	Depth (m) 0 10 20 30 40 50 100+
Herring	*Clupea harengus*	1.81	0.10	3.44	1.06	0.06 (0.31)	0.03 (0.20)		+		- - - - - - - - - - - - - - - - -
Sprat	*Sprattus sprattus*	0.01	0.05	0.52	1.32	0.01 (0.07)	0.13 (1.07)		+		———————— - - - -
Cod	*Gadus morhua*	3.65	2.44	2.59	0.88	0.03 (0.17)	0.02 (0.18)	+	+	S R	- - - - - - - - - - - - - - - - -
Whiting	*Merlangius merlangus*	2.59	1.07	4.42	3.34	0.11 (0.60)	0.10 (0.56)	+	+	S M R	- - - - - - - ———————
Saithe	*Pollachius virens*	0.0	1.69	0.0	0.83	0.0	0.01 (0.15)		+	R	- - - - - - - - - - - - - - - - -
Rockling	*Rhinonemus cimbrius*	0.10	0.0	1.04	0	0.03 (0.30)	0.0	+		S M	- - - - - - - - - - - -
Sandeel	*Ammodytidae*	67.48	44.58	75.83	61.23	48.04 (77.65)	49.79 (97.61)	+	+	S Gs	- - —————— - -
Dab	*Limanda limanda*	0.0	2.24	0.0	4.27	0.0	**0.53 (2.39)**	+		S	- - - - - ———— - - - - - -
Flounder	*Platichthys flesus*	4.05	8.97	2.42	8.73	0.21 (1.99)	**0.87 (4.20)**	+		M	———— - - - - -
Lemon sole	*Microstomus kitt*	2.09	1.83	0.52	1.14	0.01 (0.07)	0.03 (0.26)	+		G R	- - - - - - - - - - - -
Plaice	*Pleuronectes platessa*	0.0	5.52	0.0	2.42	0.0	**0.29 (1.48)**	+		S M	- - - - - - ————— - - -
Turbot	*Scophthalmus maximus*	0.0	0.80	0.0	0.53	0.0	0.04 (0.46)	+		S R G	- - - - - - ————— - -
Lesser octopus	*Eledone cirrhosa*	17.05	28.71	6.25	7.71	0.12 (0.53)	0.13 (0.49)	+		R	- - - - - - - - - - - - - - - - -
Northern squid	*Lologo forbesi*	1.14	1.25	2.11	2.77	0.05 (1.43)	0.02 (0.13)		+		- - - - - - - - - - - - - - - - -
Ballan wrasse	*Labrus berggyylta*	0.04	0.18	0.85	0.92	0.02 (0.21)	0.26 (0.18)	+		R Kelp	——— - -
Rock cook	*Centrolabrus mixttus*	0.0	0.02	0.0	0.26	0.0	0.01 (0.07)	+		R Kelp	- - - - - - -
Eelpout	*Zoarces viviparus*	0.0	0.22	0.0	1.10	0.0	0.03 (0.20)	+		M S	——— - - -
Snake blenny	*Lumpenus lampretaeformis*	0.0	0.05	0.0	0.31	0.0	0.05 (0.07)	+		M S	- - - - -
Bullrout	*Myoxocephalus scorpius*	0.0	0.05	0.0	0.31	0.0	0.02 (0.22)	+		M S	- - - - - - - - - - - - - - -
Sea scorpion	*Taurulus bubalis*	0.0	0.01	0.0	0.31	0.0	0.01 (0.07)	+		R	- - - - - - -
Catfish	*Anarchichas lupus*	0.0	0.34	0.0	0.53	0.0	0.01 (0.11)	+		R G M	- - - - -

noted. For example, Payne & Selzer (1989) found that the diet of harbour seals using haul-out sites surrounded by sandy sea-beds was dominated by sand lance, whereas seals from haul-out sites surrounded by rocky habitats were more likely to consume rockfish, gadoids, flounders, and herring. Härkönen (1987*a*) also showed wide-scale geographical variations in diet when comparing prey taken at a rocky shore site with those taken from a sandy shore. In our own study, the potential influence of habitat differences on a local scale was further illustrated by dab and plaice which were only found in the diet of Dornoch Firth seals. Both these prey are found on sandy sediments and in water depths of 20–50 m (Table 4), which were more commonly used by seals from the Dornoch Firth (Table 3).

The variety of different foraging habitats used by individual seals (Table 1) may be an indication of individual specialization for particular prey or foraging techniques. Alternatively, the tendency to use one particular area repeatedly may be related to previous foraging experience, where individuals return to exploit prey patches where they were previously successful. Individual foraging specializations have been found in other marine mammals (see Ostefeld, 1982; Hoelzel, Dorsey & Stern, 1989; Lyons, 1989). However, whilst individual habitat specialization indirectly suggests that individual seals may also specialize on certain prey, the lack of information on the source of a faecal sample currently prevents more detailed analyses of individual variations in diet composition. Recent developments using genetic (Reed *et al.*, 1997) and biochemical (Iverson, 1993; Hobson *et al.*, 1996) techniques may soon provide opportunities to combine telemetric studies of individual foraging patterns with information on the diet composition of instrumented individuals.

Acknowledgements

We thank all the colleagues who have assisted in the capture and radio-tracking of seals and the collection and analyses of faecal samples, especially M. Froome, B. Greig, G. Mackay, D. Miller, L. Porter, J. Prime, S. Reddy and D. Wood. We are indebted to S. Greenstreet, J. Hislop, B. McConnell, P. A. Racey and an anonymous referee for constructive criticism on earlier drafts. Capture was conducted under licence from the Scottish Office and Home Office. The work was funded by a series of contracts from the Scottish Office Agriculture Environment and Fisheries Department to Professor P. A. Racey and Dr P. M. Thompson.

REFERENCES

Allen, S. G. (1988). *Movement and activity patterns of harbor seals at the Point Reyes Peninsula, California*. MSc thesis, University of California, Berkeley, U.S.A.

Bigg, M. A. (1981). Harbour seal, *Phoca vitulina* and *Phoca largha*. In *Handbook of marine mammals* **2:** 1–28. Ridgway, S. H. & Harrison, R. J. (Eds). New York: Academic Press.

Bigg, M. A. & Perez, M. A. (1985). Modified volume; a frequency-volume method to assess marine mammal food habits. In *Interactions between marine mammals and fisheries*: 277–283. Beddington, J. R., Beverton, R. J. H. & Lavigne, D. M. (Eds). London: George Allen & Unwin.

Bjørge, A., Thompson, D., Hammond, P., Fedak, M., Bryant, E., Aarefjord, H., Roen, R. & Olsen, M. (1995). Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In *Whales, seals, fish and man*: 211–223. Walløe, I. & Ulltang, Ø. (Eds). Norway: Elsevier.

Bonner, W. N. (1972). The grey seal and common seal in European waters. *Oceanogr. Mar. Biol. Annu. Rev.* **10:** 461–507.

Boness, D. J., Bowen, W. D. & Oftedal, O. T. (1994). Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav. Ecol. Sociobiol.* **34:** 95–104.

Bowen, W. D. & Harrison, G. D. (1996). Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Can. J. Zool.* **74:** 125–135.

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

Chesher, J. A. (1984). *Moray–Buchan sea bed sediments and Quaternary geology*. 1:250,000 Sheet 57°N 04°W. British Geological Survey, Natural Environment Research Council, Swindon.

Cuthill, I. (1991). Field experiments in animal behaviour: methods and ethics. *Anim. Behav.* **42:** 1007–1014.

Dipper, F. (1987). *British sea fishes*. 1st edn. Ipswich: Underwater World Publications Ltd.

Dixon, K. R. & Chapman, J. A. (1980). Harmonic mean measure of animal activity areas. *Ecology* **61:** 1040–1044.

Dolphin, W. F. (1988). Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. *Can. J. Zool.* **65:** 83–90.

Duncan, P. (1983). Determinants of the use of habitat by horses in a Mediterranean wetland. *J. Anim. Ecol.* **52:** 93–109.

Environmental Management Ltd. (1990). *Inverness Main Drainage Scheme, Environmental Assessment*. Final Study Report, University of Strathclyde, Glasgow.

Folk, R. L. (1954). The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *J. Geol.* **62:** 344–359.

Gray, J. S. (1974). Animal-sediment relationships. *Oceanogr. Mar. Biol. Ann. Rev.* **12:** 223–261.

Gray, C. A. & Otway, N. M. (1994). Spatial and temporal differences in assemblages of demersal fishes on the inner continental shelf off Sydney, south-eastern Australia. *Aust. J. Freshwat. Res.* **45**(40): 665–676.

Hammond, P. S. & Prime, J. H. (1990). The diet of British grey seals (*Halichoerus grypus*). *Can. Bull. Fish. Aquat. Sci.* **222:** 243–254.

Hammond, P. S. & Hall, A. J. (1994). The summer diet of grey seals at the Farne Islands. In *Grey seals in the North Sea and their interactions with fisheries*: 23–27. Hammond, P. S. & Fedak, M. A. (Eds). Final report to MAFF. Contract MF 0503. Sea Mammal Research Unit, Natural Environment Council, Cambridge.

Hammond, P. S., Hall, A. J. & Prime, J. H. (1994). The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *J. Appl. Ecol.* **31:** 340–350.

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

Härkönen, T. J. (1987*b*). Influence of feeding on haul-out patterns and sizes of sub-populations in harbour seals. *Neth. J. Sea Res.* **21**(4): 331–339.

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

Harris, S., Cresswell, W. J., Forde, P. J., Trewhella, W. J., Woollard, T. H. & Wray, S. (1990). Home range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mamm. Rev.* **20:** 97–123.

Harvey, J. T. (1987). *Population dynamics, annual food consumption, movements and dive behaviours of harbor seals (**Phoca vitulina richardsi**) in Oregon*. PhD thesis, Oregon State University, U.S.A.

Heezen, K. L. & Tester, J. R. (1967). Evaluation of radio-tracking by triangulation with special reference to deer movements. *J. Wildl. Manag.* **31:** 124–141.

Hobson, K. A., Schell, D. M., Renouf, D. & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can. J. Fish. Aquat. Sci.* **53:** 528–533.

Hoelzel, A. R., Dorsey, E. M. & Stern, S. J. (1989). The foraging specialization of individual minke whales. *Anim. Behav.* **38:** 786–794.

Hopkins, P. J. (1986). Exploited fish and shellfish populations in the Moray Firth. *Proc. R. Soc. Edinb. (B)* **91:** 57–72.

Houston, A. I. & Carbone, C. (1992). The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3:** 255–265.

Hunter, R. F. (1962). Hill sheep and their pasture; a study of sheep grazing in South East Scotland. *J. Ecol.* **50:** 651–680.

Iverson, S. J. (1993). Milk secretion in marine mammals in relation to foraging: can milk fatty acids predict diet? *Symp. zool. Soc. Lond.* No. 66: 263–291.

Kolb, P. M. & Norris, K. S. (1982). A harbour seal, *Phoca vitulina richardsi*, taken from a sable fish trap. *Calif. Fish Game* **68:** 123–124.

Krebs, C. J. (1989). *Ecological methodology*. New York: Harper & Row.

Langham, N. P. E. (1971). The distribution and abundance of larval sandeels (Ammodytidae) in Scottish waters. *J. Mar. Biol. Assoc. U.K.* **51:** 697–707.

Le Boeuf, B. J., Crocker, D. E., Blackwell, S. B., Morris, P. A. & Thorson, P. H. (1993). Sex differences in diving and foraging behaviour of northern elephant seals. *Symp. zool. Soc. Lond.* No. 66: 148–178.

Lough, R. A. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Nielson, J. D. & Perry, R. I. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Mar. Ecol. Prog. Ser.* **56**(1–2): 1–12.

Lyons, K. J. (1989). *Individual variation in diet of the female Californian sea otter, **Enhydra lutris***. MA thesis, University of California, Santa Cruz. pp. 40.

Macer, C. T. (1965). The distribution of larval sandeels (Ammodytidae) in the southern North Sea. *J. Mar. Biol. Assoc. U.K.* **45:** 187–207.

Macer, C. T. (1966). Sandeels (Ammodytidae) in the south-western North Sea; their biology and fishery. *MAFF, Fishery Investigation Series II* **24:** 1–55.

McConnell, B. J., Fedak, M. A., Lovell, P. & Hammond, P. S. (1995). The movements and foraging behaviour of grey seals. In *Grey seals in the North Sea and their interactions with fisheries*: 88–100. Hammond, P. S. & Fedak, M. A. (Eds). Final report to MAFF. Contract MF 0503. Sea Mammal Research Unit, Natural Environment Council, Cambridge.

Müus, B. J. & Dählstrøm, P. (1964). *Sea fishes of Britain and N.W. Europe*. Glasgow: Collins.

Ostefeld, R. S. (1982). Foraging strategies and prey switching in California sea otters. *Oecologia* **53:** 170–178.

Oxman, D. A. (1995). *Seasonal abundance, movements, and food habits of harbor seals (**Phoca vitulina richardsi**) in Elkhorn Slough, California*. MSc thesis, California State University, Stanislaus.

Payne, P. M. & Selzer, L. A. (1989). The distribution, abundance and selected prey of the harbour seal *Phoca vitulina concolor*, in S. New England. *Mar. Mamm. Sci.* **5:** 173–192.

Perry, I., Stocker, M. & Fargo, J. (1994). Environmental effects on the distributions of groundfish in Hecate Strait, British Columbia. *Can. J. Fish. Aquat. Sci.* **51**(6): 1401–1409.

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

Raitt, D. S. (1934). A preliminary account of the sandeels in Scottish waters. *J. Cons. Perm. Int. Explor. Mer.* **9:** 365–372.

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

Reed, J. Z., Tollit, D. J., Thompson, P. M. & Amos, W. (1997). Molecular scatology, the use of molecular analysis to assign species, sex and individual identity to seal faeces. *Mol. Ecol.* **6:** 225–234.

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

Ruckley, N. A. & Chesher, J. A. (1987). *Caithness sea bed sediments and Quaternary geology*. 1:250,000 Sheet 58°N 04°W British Geological Survey, Natural Environment Research Council, Swindon.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory*. Guildford: Princeton University Press.

Stewart, B. S., Leatherwood, S., Yochem, P. K. & Heide-Jørgensen, M. P. (1989). Harbor seal tracking and telemetry by satellite. *Mar. Mamm. Sci.* **5:** 361–375.

Storey, G. (1993). *The trophic ecology of the sandeel, **Ammodytes tobianus** (L). and other planktivorous fish species from Aberdeen Bay*. PhD thesis, University of Aberdeen, Scotland.

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

Thompson, P. M., Cornwell, H. J. C., Ross, H. M. & Miller, D. (1992). Serologic study of phocine distemper in a population of harbour seals in Scotland. *J. Wildl. Dis.* **28:** 21–27.

Thompson, P. M., Fedak, M. A., McConnell, B. J. & Nicholas, K. S. (1989). Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* **26:** 521–535.

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

Thompson, P. M., Miller, D., Cooper, R. & Hammond, P. S. (1994). Changes in the distribution and activity of female harbour seals during the breeding season; implications for their lactation strategy and mating patterns. *J. Anim. Ecol.* **63:** 24–30.

Thompson, P. M., McConnell, B. J., Tollit, D. J., Mackay, A., Hunter, C. & Racey, P. A. (1996). Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N.E. Scotland. *J. Appl. Ecol.* **33:** 1572–1584.

Thompson, P. M., Tollit, D. J., Wood, D. G., Corpe, H. M., Hammond, P. S. & Mackay, A. (1997). Estimating harbour seal abundance and status in an estuarine habitat in N.E. Scotland. *J. Appl. Ecol.* **34:** 43–52.

Tollit, D. J. & Thompson, P. M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Can. J. Zool.* **74:** 1110–1121.

Van Parijs, S. M., Thompson, P. M., Tollit, D. J. & Mackay, A. (1997). Changes in the distribution and activity of male harbour seals during the mating season. *Anim. Behav.* **54**: 35–43.

Wanzenböck, J. (1995). Changing handling times during feeding and consequences for prey size selection of 0+ zooplanktivorous fish. *Oecologia* **104:** 372–378.

Westgate, A. J., Read, A. J., Berggren, P., Koopman, H. N. & Gaskin, D. E. (1995). Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Can. J. Fish. Aquat. Sci.* **52:** 1064–1073.

Wheeler, A. (1978). *Key to the fishes of Northern Europe*. 2nd edn. London: Frederick Warne Ltd.

Williams, T. M. & Kooyman, G. L. (1985). Swimming performance and hydrodynamic characteristics of harbor seals, *Phoca vitulina*. *Physiol. Zool.* **58:** 576–589.