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Article *in* Journal of Applied Ecology · December 1996

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Journal of Applied Ecology 1996, **33**, 1572–1584

Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N.E. Scotland

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Summary

1. The distribution, movements and foraging activity of harbour and grey seals from the inner Moray Firth, N.E. Scotland, were compared using a combination of observations at haul-out sites, VHF and satellite-link telemetry, and analyses of diet composition.

2. Terrestrial abundance of both grey and harbour seals was highest during the summer but there were marked differences in the extent to which the two species moved between different haul-out sites. Harbour seals showed local seasonal changes in distribution, but all 21 radio-tagged seals moved only to alternative haul-out sites within a range of 75 km. In contrast, four of the five grey seals tracked from the Moray Firth moved to haul-out sites 125–365 km away, and provided evidence of interchange between the Moray Firth and other grey seal breeding areas in Orkney, the Firth of Forth and the Farne Islands.

3. All harbour seals foraged within 60 km of their haul-out sites, but showed seasonal variation in their foraging areas which was related to changes in their terrestrial distribution. In contrast, those grey seals which foraged within the Moray Firth travelled up to 145 km from haul-out sites. Nevertheless, there was some overlap in the foraging areas used by harbour seals and grey seals in more inshore areas.

4. Sandeels, gadoids, flatfish and cephalopods formed over 95% of the diet of both species. However, dietary data, particularly for grey seals, may be biased toward those individuals which fed in more inshore areas.

5. These results suggest that Moray Firth harbour seals can be considered as a relatively discrete population, with clear links between breeding, feeding and resting areas, and little exchange of adults between this and adjacent breeding areas in Orkney and the Tay Estuary. In contrast, grey seals from several different breeding sites appear to move into the Moray Firth in summer and use the area primarily for foraging and non-breeding haul-out.

Key-words: fisheries interactions, foraging ecology, haul-out behaviour, pinnipeds, telemetry.

Journal of Applied Ecology (1996) **33**, 1572–1584

Introduction

Grey seals (*Halichoerus grypus* Fab.) and harbour seals (*Phoca vitulina* L.) are coastal phocids which are sympatric over much of their North Atlantic range. Throughout this area there are clear differences in the timing and nature of the two species' reproductive behaviour (Bonner 1972) but less is known of the extent of differences in their at-sea activity and movements away from breeding colonies.

Information on inter-specific differences in the distribution and behaviour of these two species is required for several current management issues. Both grey and harbour seals are involved in direct inter-

actions around both fishing and fish farming operations and more general ecological interactions may result in competition between seal populations and fisheries (Harwood 1983; Harwood & Greenwood 1985). However, information on the distribution, abundance and diet of seal populations is generally based on studies at terrestrial breeding or haul-out sites (Eberhard, Chapman & Gilbert 1979; Pierce & Boyle 1991; Hiby, Duck & Thompson 1993) whereas predatory interactions all occur while animals are at sea. Data on the movements and foraging distribution of seals from these sites are therefore required to identify which species or populations are involved in particular interactions. The identification of the foraging areas used by seals from major breeding colonies is also required for the implementation of the recent EC Habitats Directive, which aims to protect critical habitats for both grey and harbour seals in European waters.

Marking studies have shown that both grey and harbour seals may disperse widely from their natal sites in the post-weaning period (Bonner & Witthames 1974; Bonner 1981; SMRU 1984; Thompson, Kovacs & McConnell 1994). On the other hand, results from telemetric studies suggest that there could be inter-specific differences in the extent of adult movements away from breeding sites during the non-breeding season. For example, grey seals from the Firth of Forth and the east coast of England travelled extensively between different breeding areas (Thompson *et al.* 1991a; McConnell *et al.* 1992; Hammond, McConnell & Fedak 1993), whereas harbour seals from sites in Orkney and the Moray Firth made only relatively local movements around their breeding sites throughout the year (Thompson 1989; Thompson & Miller 1990; Thompson *et al.* 1991b). However, phocids may exhibit considerable intra-specific variations in behaviour in response to different environmental conditions such as haul-out or foraging habitats, or local variations in food supply. Comparative studies on populations of both grey and harbour seals from the same geographical area are therefore required to determine the extent of inter-specific differences in behaviour and their consequent effects as top marine predators.

In this paper, we compare the distribution, movements and diet of grey and harbour seals in north-east Scotland. In particular, we aim to use these data to compare the extent of movements between breeding and non-breeding haul-out sites, to determine whether the two species used similar foraging areas, and to assess whether there were differences in other aspects of their foraging activity.

Methods

STUDY AREA

This study was carried out in the Moray Firth, NE Scotland, here defined as the area of coast and sea to the west and south of a line from Duncansby Head to Rattray Head (Fig. 1.). The inner part of the Moray Firth consists of three sheltered estuaries; the Beauly, Cromarty and Dornoch Firths, each containing several inter-tidal sandbanks or muddy shores which were used as haul-out sites.

Harbour seal pups were born in the Beauly, Cromarty and Dornoch Firths during June and July. A fourth key harbour seal haul-out area was located at the mouth of the Inverness Firth but pups were only rarely observed at this site (Fig. 1). Other smaller non-breeding groups also occurred in Loch Fleet and Findhorn Bay (Fig. 1). Harbour seals were occasionally seen at rocky-shore sites further north and east, but the nearest breeding groups were found in Orkney and the Tay estuary, 130 km to the north and 325 km to the south, respectively (Hiby *et al.* 1993).

Inter-tidal haul-out sites in the inner Moray Firth were not suitable for grey seal mothers because they

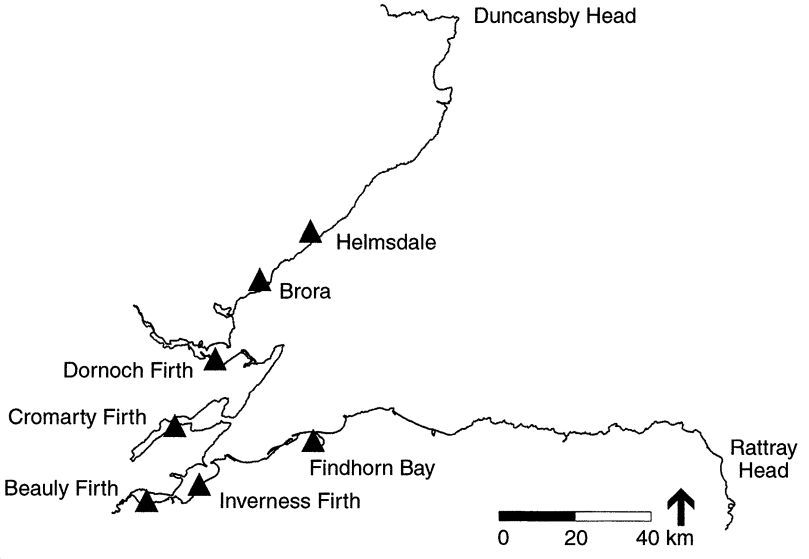

Fig. 1. A map of the Moray Firth showing the location of the haul-out areas (▲) and sites mentioned in the text.

must remain ashore with their pups throughout their 2–3 week lactation. Nevertheless, non-breeding grey seals did use some of these sites. Breeding grey seals were found on rocky beaches and in caves on the Moray Firth coast north of Helmsdale (Fig. 1). The nearest alternative grey seal breeding sites were in Orkney and 365 km to the south in the Firth of Forth (Hiby *et al.* 1993).

ABUNDANCE AND DISTRIBUTION OF SEALS AT HAUL-OUT SITES

Seasonal changes in terrestrial distribution and abundance were assessed by making regular counts of both grey and harbour seals at haul-out sites in the inner Moray Firth (Fig. 1). In the Beauly, Inverness & Cromarty Firths, counts were made at least once each week between January 1988 and August 1990. Sites in the Dornoch Firth and Loch Fleet were visited at least twice each month over the same period. Additional counts were made at all sites in June–August of 1991 and 1992. Groups of seals were observed from the shore at distances of 0·5–4·0 km using binoculars or a 30 × 75 telescope. All counts were made within ±2 h of low tide, and were abandoned in poor weather conditions, particularly in persistent rain, fog or strong winds.

Because seasonal changes in haul-out frequency could mask local variations in terrestrial distribution, we produced a monthly measure of the relative abundance of seals for different haul-out areas within the Moray Firth. This was calculated by dividing the maximum monthly count for each haul-out area by the combined maximum monthly count for all sites. Between-year comparisons of seasonal trends at each site were then made using Spearman's Rank Correlation by comparing the relative abundance for each month in different years.

DISTRIBUTION AND MOVEMENTS AT SEA

The at-sea distribution and movements of individual harbour and grey seals were compared by radio-tracking the seals which were caught at haul-out sites in the Dornoch Firth.

Twenty-one harbour seals were tracked during the summers (May–July) of 1989 and 1991 and the winter (November and January) of 1989/90. Seals were captured at haul-out sites in either May or early autumn, and VHF radio-tags were attached as described in Thompson & Miller (1990) and Thompson *et al.* (1992). Radio-tags remained on the seals for up to 6 months or until their annual moult in July or August (Table 4). Searches were made for tagged seals from coastal vantage points on 6 days of each week. Seventeen of the 21 individuals were located on 100% of these days (Table 4) and radio-signals were 'lost' only at around the time that radio-tags were expected to have fallen off. A further two seals (F8 & F9) were not located on the first day's tracking but, once their regular foraging areas had been discovered, were then located every day. Of the remaining two individuals, one was discovered to have a faulty VHF transmitter.

Once a signal had been heard, a daily location for each seal was obtained by triangulating with directional aerials from at least two coastal vantage points. Three estimates of each seal's position were obtained from each vantage point, resulting in 95% confidence limits of ±7·5° around the mean bearing (Thompson & Miller 1990). These earlier studies had also indicated that locations tended to be clustered either around haul-out sites or at sea, over what were presumed to be foraging areas. All locations which were >2km from haul-out sites were therefore considered to be foraging locations. The foraging areas used by each individual were then identified by carrying out harmonic mean analyses (Dixon & Chapman 1980) to identify the area within which 75% of foraging locations occurred. Because of the difficulty of displaying many overlapping ranges, we recorded the coordinates of each 1 km Ordnance Survey square which was within, or at least 50% covered by, each individual's foraging area. This method permitted key foraging areas to be identified and displayed on the basis of the relative use of each 1 km square by different individuals. Comparisons of the areas used by different groups of seals or in different seasons and years were made using Spearman's Rank Correlation. First, we selected only those 1 km squares which were covered by at least one individual foraging area during the study, thus excluding those areas of sea which were never used by seals. For different paired groups (e.g. males vs. females; winter vs. summer) we then compared the number of individual foraging areas which overlapped each 1 km square. Where Spearman Rank Correlations were significant ($P < 0{\cdot}05$) and positive, we concluded that seals in the two groups were using similar foraging areas. Where significant correlations were negative, we concluded that seals in the two groups were using different foraging areas.

Grey seal movements and distribution were recorded using satellite-link UHF telemetry. In August 1992, five grey seals were captured at inter-tidal haul-out sites and a 1300 g package consisting of a data logger, which recorded the start and end of haul-out periods, and satellite-link transmitter (McConnell, Chambers & Fedak 1992) was glued to the hair at the base of the neck. The start of a haul-out period was identified when the submergence sensor was continuously dry for >240 s. The haul-out period ended when the submergence sensor was continuously wet for >40 s. Periods between haul-out bouts were considered to be 'foraging trips'. System Argos provided information on the location and quality of transmitted signals and their related data values (Argos 1989). Locations with a large error were rejected by a filter described by McConnell *et al.* (1992) using a maximum travel rate of 2·0 m s^{-1}. On average, accept-

able locations were obtained between 3·6 (SE = 1·9) and 6·3 (SE = 3·5) times per day for each individual for periods of 2–22 weeks (Table 5).

Differences in data collection techniques prevented the use of identical analytical methods for both species. In order to compare the use of foraging areas as directly as possible, we first determined whether the locations obtained during a grey seal's 'foraging trip' were in the vicinity of haul-out sites. Because individual 'wet' locations were rarely of guaranteed accuracy, we calculated the mean of locations obtained during the mid-80% of each 'foraging trip', and determined whether these mean locations were within 2 km of haul-out areas. Locations at the beginning and end of each trip were not used to avoid locations from seals in transit between foraging and haul-out areas. Key foraging areas within the Moray Firth were then identified using harmonic mean analyses, using all the original location values from those 'foraging trips' which occurred away from haul-out areas. Because there was almost no overlap between the ranges of different grey seals, 75% harmonic mean isoclines are presented for each individual's foraging range.

DIET

Diet composition was determined from the analyses of faeces collected at haul-out sites in the Dornoch Firth during the summer of 1992 (May–August). Sites were visited at least twice each month, shortly after low-tide, and any seals present were identified to species. Grey and harbour seals were generally segregated at haul-out sites, and only those faeces collected in parts of the site where one species predominated (>95% of seals present) were used for this study. All faeces collected in these areas were collected and frozen at −20°C.

Sagittal otoliths and cephalopod beaks were later extracted from faecal remains and used to identify and measure prey as described in Pierce *et al.* (1991a) and Tollit & Thompson (1996). All otoliths and beaks were measured to within 0·02 mm using a binocular microscope and eyepiece graticule, with the exception of sandeels (*Ammodytidae*). A video image analyser (Magiscan 2, Joyce-Loebel Ltd) was used to measure sandeel otoliths. When >120 sandeel otoliths were present in a faecal sample, a random subsample of >10% of the total were measured. If samples contained <120 sandeel otoliths, a random subsample of >30 otoliths were measured.

The importance of each prey species was quantified using three approaches. First, each was expressed as the mean number of otoliths or beaks per sample (that contained prey remains). Secondly, as a modified frequency of occurrence, in which occurrence values are down-weighted so that, summed across all prey types, they total 100% (Bigg & Perez 1985). Lastly, diet composition was expressed as a percentage of the total estimated weight of prey ingested.

Results

ABUNDANCE

Regular counts through 1988 until August 1990 indicated that harbour seals were present at haul-out sites in the inner Moray Firths throughout the year, although their abundance peaked during June, July and August during the breeding season and moult (Fig. 2a). Grey seal abundance also peaked during the late summer, but few grey seals continued to use haul-out sites in the inner Moray Firth during the winter (Fig. 2b). Less frequent counts in subsequent years indicated that the relative abundance of the two species remained similar in each of the summers between 1988 and 1992 (Table 1).

Harbour seals were seen at haul-out sites throughout the study area but there were both seasonal and between-year differences in their distribution within the Moray Firth. Seasonal patterns were similar in the first 2 years of the study, when the Beauly and Cromarty Firths and Loch Fleet contained a higher proportion of the population in winter (Fig. 3; Table 2). In contrast, the Dornoch and Inverness Firths were used most intensively in summer (Fig. 3; Table 2). These patterns were consistent in 1988 and 1989 and, for each area, relative abundances in each month were significantly correlated in the 2 years (Table 3). However, a similar seasonal trend was not seen at most sites in 1990. When data from 1990 were compared with those from either 1988 or 1989, seasonal trends were only significantly correlated between years at Loch Fleet in 1989 and 1990. To ensure that these comparisons were not affected by the smaller sample size in 1990, comparisons between 1988 and 1989 were repeated using only data from months when sites were monitored in all 3 years (January to August). Relationships for all four areas remained significant (Table 3). The most marked between-year difference in haul-out distribution was seen in the Inverness Firth, which was used more intensively during January of 1990 than in the winter of previous years. Over the same period, there was a drop in the relative abundance of seals in the Beauly and Cromarty Firths (Fig. 3).

Grey seals, in contrast, were only seen in large numbers (>10) at five sites within the inner Moray Firth; four around the mouth of the Dornoch Firth and one at the mouth of the Inverness Firth (Fig. 4). Between May and September, when peak numbers were

Table 1. Maximum summer haul-out counts for grey and harbour seals at haul-out sites in the inner Moray Firth, 1988–92

	1988	1989	1990	1991	1992
Harbour seals	1249	1118	1103	1166	1308
Grey seals	479	322	486	356	443

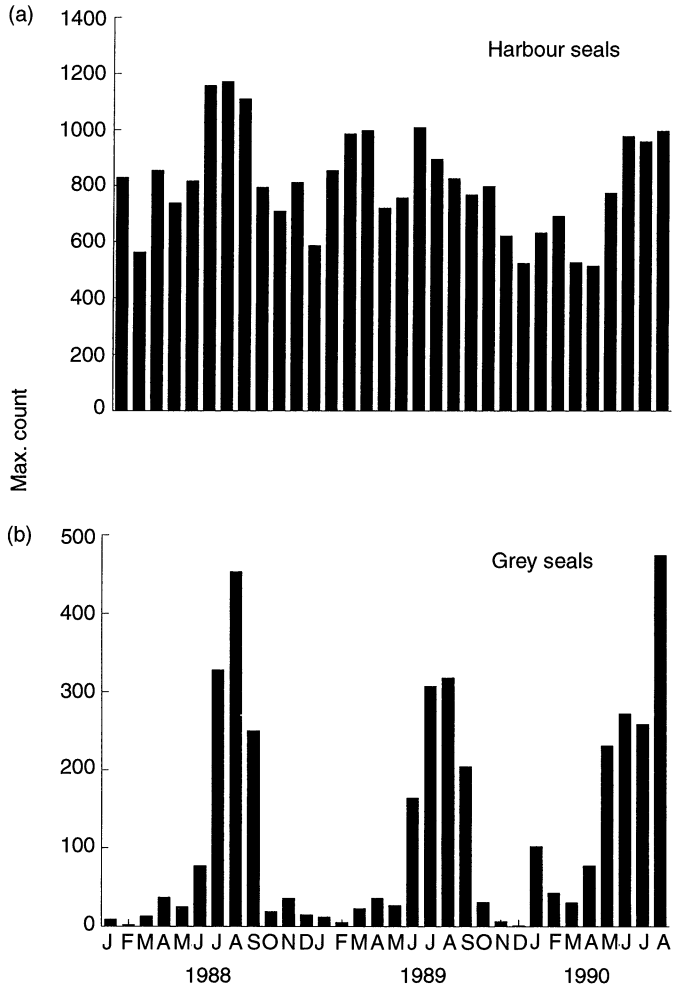

Fig. 2. Maximum monthly counts of harbour seals and grey seals at haul-out sites in the inner Moray Firth. Data are from January 1988 to August 1990.

observed (Fig. 2), the Dornoch Firth sites held the majority of grey seals in the area; an average of 87% (SD = 9·7) of the maximum monthly count for the whole Moray Firth. When large numbers of both species occurred at these sites grey seals tended to form tighter groups at the waters' edge, whereas harbour seals were spaced more widely over larger areas of sandbank. Small numbers (< 10) of grey seals could be found at other sites during the winter and one larger group (of 35) was also observed in the Beauly Firth in January 1989.

MOVEMENTS BETWEEN HAUL-OUT SITES

There were marked differences in the extent to which the two species moved to alternative haul-out sites. Of 16 harbour seals captured during the summer, all except one continued to use sites within the Dornoch Firth. The one individual which did use a different site moved only 20 km north from the Dornoch Firth to Brora (Fig. 1). Even though seals regularly travelled out of the Dornoch Firth on what we assume were foraging trips, they did not necessarily use those haul-out sites at the mouth of the firth (Fig. 4). Harbour seals tagged in the autumn exhibited greater movements, with three of the five individuals moving to sites outwith the Dornoch Firth. However, all were relatively local movements (< 75 km) to alternative sites within the Moray Firth; two to the Beauly Firth and one to the Inverness Firth (Table 4).

In contrast, four of the five grey seals moved outside the Moray Firth (Fig. 5). Two adult females travelled to Orkney, one immediately after capture, the other after continuing to use sites in the Dornoch Firth for 4 months. Both females subsequently spent extended periods of 16–17 days ashore at known grey seal breeding sites (Stroma and Swona) and were assumed to have produced pups while in Orkney. One sub-adult male travelled to the Farne Islands, and a sub-adult female moved first to the Tay estuary and subsequently to a small skerry in the Firth of Forth. In all cases, the long distance movements between haul-out sites were direct and fast (Table 5).

FORAGING AREAS

All of the radio-tagged harbour seals regularly moved out of the Dornoch Firth to forage, but travelled no

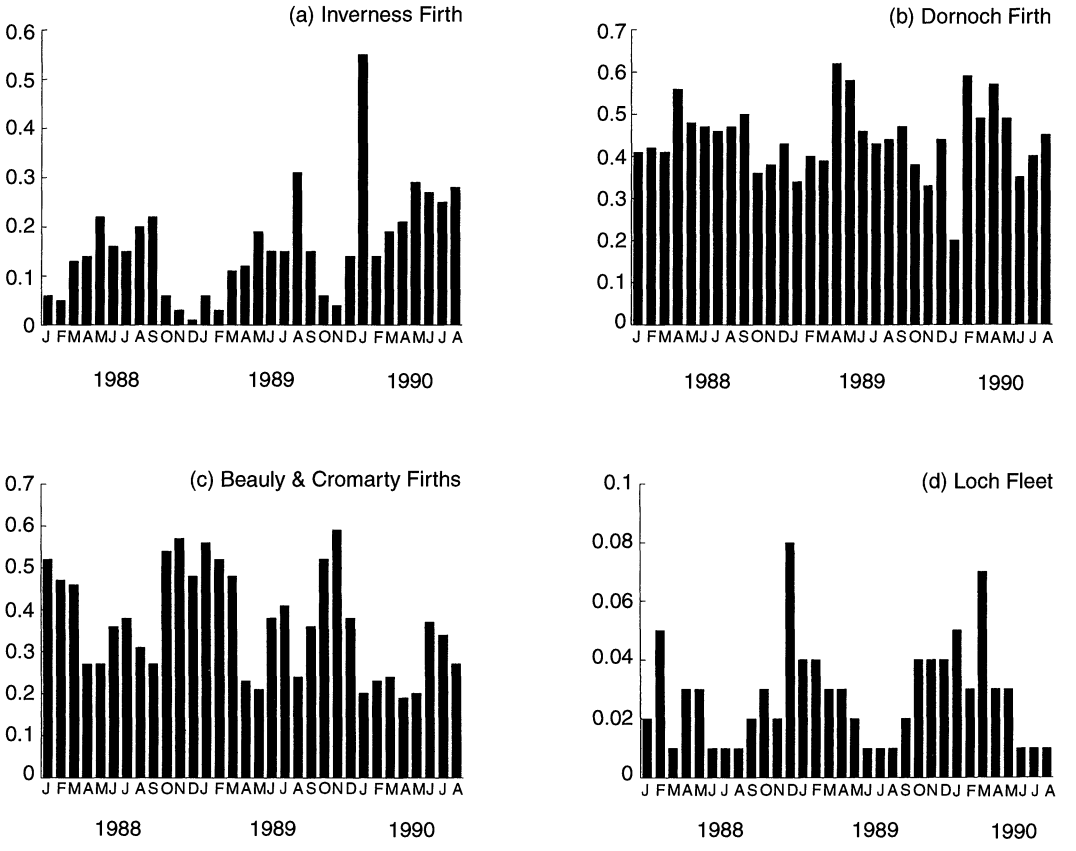

Fig. 3. Changes in the relative distribution of harbour seals in the Inverness, Dornoch, Beauly & Cromarty Firths and Loch Fleet (January 1988 to August 1990). Seal abundance in each area is expressed as a proportion of the maximum count for the entire Moray Firth for that month.

Table 2. Results of Mann–Whitney U tests to assess the significance of seasonal trends in the relative abundance of harbour seals. Data for 1988 and 1989 were pooled and the relative abundance of seals in each area in the summer months (May, June, July, August) was compared with that for winter months (January, February, November, December)

Site	Season of highest relative abundance	*n*	*U*	*P*
Beauly & Cromarty Firths	Winter	16	1·5	<0·01
Inverness Firth	Summer	16	0	<0·001
Dornoch Firth	Summer	16	2	<0·01
Loch Fleet	Winter	16	3	<0·01

Table 3. Results of Spearman's rank correlations to determine the consistency of seasonal trends in relative abundance at haul-out sites in 1988, 1989 and 1990

	1988 vs. 1989 (Jan–Dec) d.f. = 10	1988 vs. 1989 (Jan–Aug) d.f. = 6	1988 vs. 1990 (Jan–Aug) d.f. = 6	1989 vs. 1990 (Jan–Aug) d.f. = 6
Beauly & Cromarty Firths	$r = 0{\cdot}901$	$r = 0{\cdot}994$	$r = 0{\cdot}15$	$r = 0{\cdot}13$
	$P < 0{\cdot}001$	$P < 0{\cdot}001$	NS	NS
Inverness Firth	$r = 0{\cdot}803$	$r = 0{\cdot}97$	$r = 0{\cdot}5$	$r = 0{\cdot}467$
	$P < 0{\cdot}001$	$P < 0{\cdot}001$	NS	NS
Dornoch Firth	$r = 0{\cdot}945$	$r = 0{\cdot}98$	$r = 0{\cdot}258$	$r = 0{\cdot}361$
	$P < 0{\cdot}001$	$P < 0{\cdot}001$	NS	NS
Loch Fleet	$r = 0{\cdot}684$	$r = 0{\cdot}689$	$r = 0{\cdot}349$	$r = 0{\cdot}818$
	$P < 0{\cdot}01$	$P < 0{\cdot}05$	NS	$P < 0{\cdot}01$

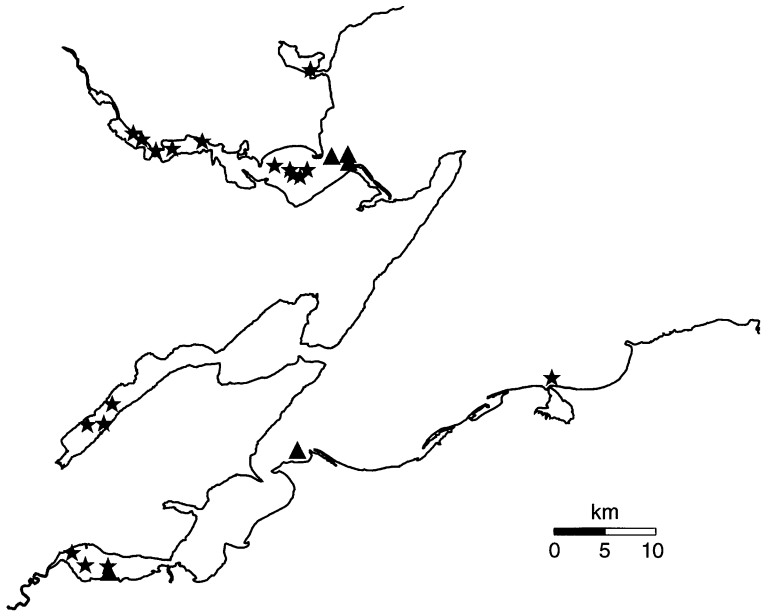

Fig. 4. A map showing the locations of haul-out sites in the inner Moray Firth which were used by predominantly harbour seals (★) and by both grey and harbour seals (▲). Sites where grey seals were recorded in groups of < 10 are not included.

Table 4. Details of the sex, weight and period of study for harbour seals captured from the Dornoch Firth. Data are also presented on the number of different haul-out sites used during the period of study and the maximum distance travelled between haul-out sites

Seal number	Sex	Weight (kg)	Dates followed	% of days located	No. of sites	Max. dist. between sites (km)
F4	F	90·5	29 May 89–29 Jul 89	100	3	5
F5	F	93·5	29 May 89–29 Jul 89	100	3	4
F6	F	89·5	29 May 89–29 Jul 89	100	6	7·5
F7	F	74·5	29 May 89–8 Jul 89	100	4	7
F8	F	89·5	29 May 89–29 Jul 89	98	6	41·5
F9	F	79·0	29 May 89–29 Jul 89	98	6	18·5
F13	F	59·0	30 Oct 89–30 Nov 89	66	3	72
F14	F	66·0	30 Oct 89–6 Feb 90	100	4	3·5
F15	F	95	28 May 91–31 Jul 91	100	4	5·0
M7	M	66	30 Oct 89–18 Jan 90	100	3	44
M8	M	77·5	30 Oct 89–30 Jan 90	100	3	73
M9	M	73·0	30 Oct 89–6 Feb 90	100	2	1·5
M10	M	55·5	28 May 91–5 Jul 91	100	4	15·25
M11	M	85·0	28 May 91–31 Jul 91	100	4	15·25
M12	M	88·5	28 May 91–17 Jul 91	100	5	7·5
M13	M	55·5	28 May 91–6 Jul 91	100	5	15·25
M14	M	58·5	28 May 91–29 Jun 91	100	6	15·25
M15	M	56·0	28 May 91–6 Jul 91	100	4	14·0
M16	M	81·75	28 May 91–27 Jul 91	100	3	6·5
M17	M	88·0	28 May 91–8 Jul 91	73	5	18·5
M18	M	57·0	28 May 91–8 Jul 91	100	3	14

more than 60 km from haul-out sites. There was also considerable overlap in the foraging ranges of different individuals. In summer, the key foraging areas used by harbour seals were similar for both males and females and for animals tracked in the two different years (Table 6; Fig. 6a). Sample sizes in winter were too small to compare the behaviour of the two sexes but, in general, seals tended to forage slightly further from haul-out sites. Their foraging areas also covered a different area to that used during summer, with animals spending more time in the southern part of the study area (Table 6; Fig. 6b).

Three grey seals spent a minimum of 125 days within the Moray Firth. At least 71 of these were spent at sea and they were assumed to have been foraging during at least part of this time. Compared with the harbour seals, grey seals foraged more widely over the Moray Firth. One female, which moved to Orkney soon after tagging, made two long trips of 13 and 15 days, travelling 130 km to the S.E. corner of the

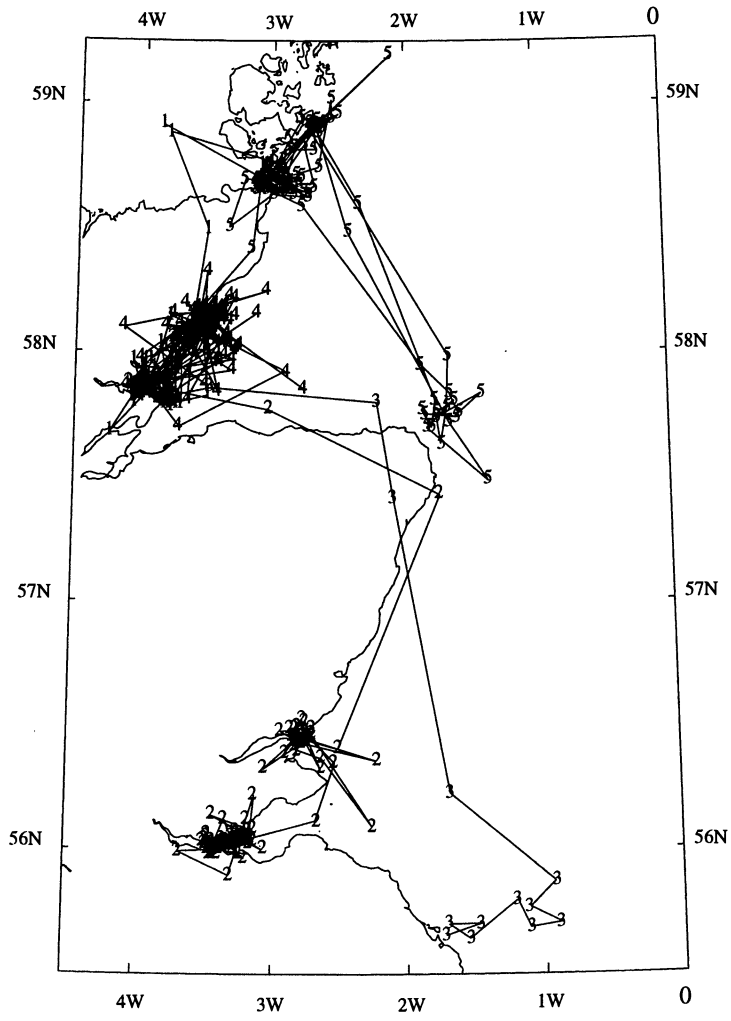

Fig. 5. Mean daily locations of the five satellite tagged grey seals, illustrating the long-range movements made by four individuals: 1 = HG 344; 2 = HG337; 3 = HG 345; 4 = HG 346; 5 = HG 371.

Table 5. Details of the size and sex of the five grey seals which were satellite-tracked from the Dornoch Firth. Data are also presented on the maximum distance which they travelled between haul-out sites

Seal number	Weight (kg)	Sex	Dates followed	Max. distance travelled between sites (km)
HG337	76·0	F	6 Aug 92–28 Nov 92	365
HG344	193·0	F	8 Aug 92–16 Jan 93	125
HG345	94·0	M	9 Aug 92–23 Aug 92	360
HG346	105·0	M	9 Aug 92–20 Dec 92	40
HG371	114·0	F	22 Aug 92–14 Jan 93	144

Moray Firth and returning to haul out in Orkney after each trip. Overall, grey seals showed considerable individual variation in their use of foraging areas within the Moray Firth and there was almost no overlap in their 75% foraging ranges (Fig. 7). On the other hand, there was overlap between the foraging area used by another female grey seal and those of some harbour seals from the Dornoch Firth (Figs 6 & 7).

DIET COMPOSITION

A total of 308 faecal samples was collected from Dornoch Firth haul-out sites during the summer of 1992.

Table 6. Results of Spearman's Rank Correlations which were used to compare the foraging areas of seals captured at different haul-out sites or followed in different time periods. Significant positive *r*-values indicate that similar foraging areas were used whereas significant negative values indicate that foraging areas differed. The comparison of males vs. females and between years is for summer data only

	r	*P*
Winter vs. summer	−0·71	<0·0001
Males vs. females	0·36	<0·0001
1989 vs. 1991	0·32	<0·0001

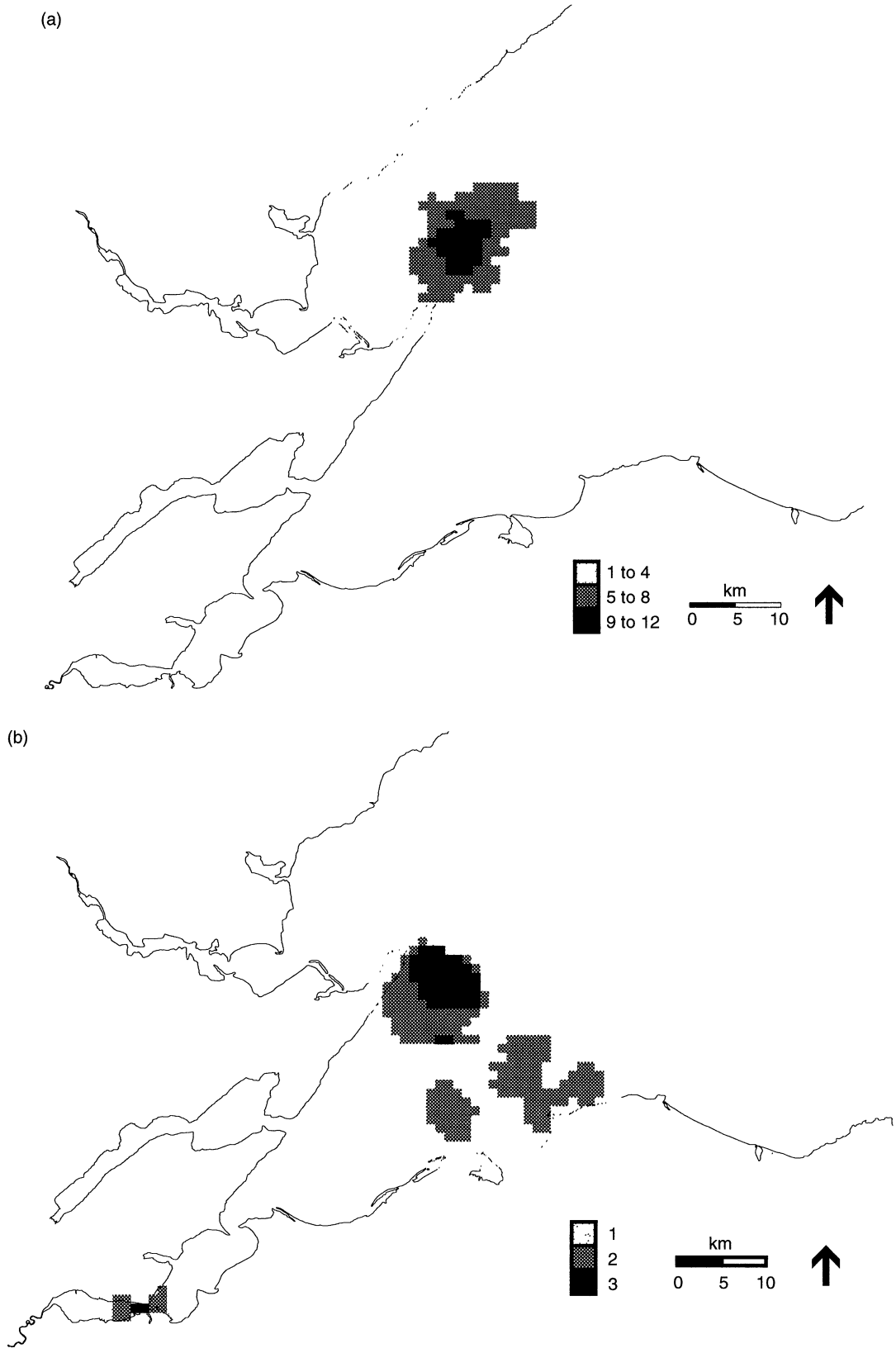

Fig. 6. Foraging areas used by radio-tagged harbour seals from the Dornoch Firth (a) in summer and (b) in winter. The shading on these maps is related to the number of different individuals whose 75% foraging areas overlapped each 1 km square.

Of these, 214 were categorized as being from harbour seals and 94 from grey seals. Samples were collected in each month, but sample sizes were greater later in the summer. The diet composition of the two species of seals was remarkably similar with sandeels being the major prey item for harbour and grey seals (Table

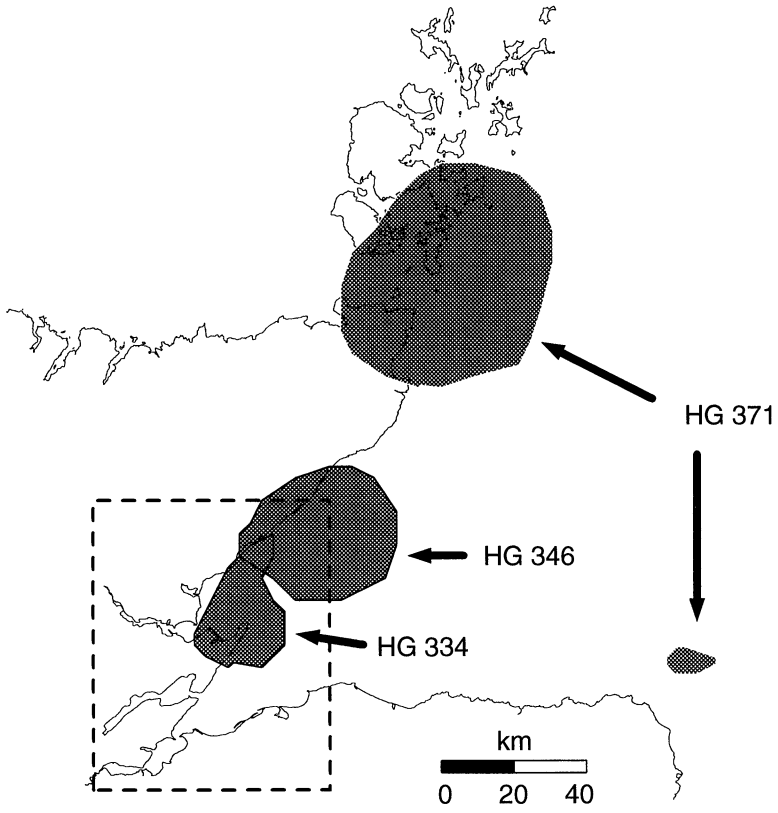

Fig. 7. 75% harmonic mean isoclines around the foraging locations of the three satellite-tagged grey seals which spent at least 125 days within the Moray Firth. The dashed line represents the area encompassed by Fig. 6.

7). The remainder of the diet of both species was comprised almost entirely of gadoids, flatfish and cephalopods.

Discussion

ABUNDANCE AT HAUL-OUT SITES AND MOVEMENTS BETWEEN SITES

Both harbour and grey seals showed a summer peak in abundance at Moray Firth haul-out sites but telemetric studies indicated that there were marked differences in the extent to which the two species moved away from these sites. Harbour seals were present at haul-out sites in the inner firths throughout the year and VHF-tagged individuals were located within the inner Moray Firth on almost all days that we searched for them (Table 2). Whilst we cannot rule out the possibility that a seal may have travelled beyond our confirmed maximum distance (Table 4), most movements of harbour seals from the Dornoch Firth were relatively local. Similar studies of the foraging behaviour of a further 16 seals captured at other sites within the inner Moray Firth have recorded only one long-distance movement; an adult female who travelled to Orkney from the Inverness Firth (unpublished data). Telemetric studies in other areas have shown that individual harbour seals spend more time ashore during the summer breeding season and moult (Thompson *et al.* 1989), and the observed summer increase in abundance at haul-out sites in this study seems likely to have resulted from such a change in behaviour.

The summer peak in grey seal abundance was more marked, with grey seals being virtually absent during the winter and spring (Fig. 2b). While this could partly have been due to local movements to breeding beaches in the northern part of the Moray Firth, the results of the satellite-telemetry suggest that wider-scale movements may be common in this species. Observed changes in abundance at Moray Firth haul-out sites are therefore likely to be the result of larger-scale movements between different breeding and foraging areas around the UK coast, and may indicate that the Moray Firth is a preferred foraging area in summer. Although the sample of animals studied was small, we found evidence of interchange between the Dornoch Firth and almost all major grey seal breeding groups on the east coast of the United Kingdom. Furthermore, the two adult females came ashore for long periods while in Orkney are likely to have given birth there; the local breeding site on the Helmsdale coast being used regularly by only one (sub-adult) seal. These results support studies carried out at other UK breeding sites (McConnell *et al.* 1992; Hammond *et al.* 1993) which have suggested that adult grey seals may make more extensive movements than harbour seals. Our comparison of the two species' behaviour at single site

Table 7. Comparison of the diet composition of harbour seals (P.v.) and grey seals (H.g.) in the Dornoch Firth in summer 1992. Diet is expressed in terms of the number of otoliths (or beaks) per sample containing hard remains (*n*), modified frequency of occurrence and percentage of the total weight of prey ingested

	Mean number of prey items per sample		Modified frequency of occurrence (%)		Percentage of the total weight of prey ingested	
Seal species	P.v.	H.g.	P.v.	H.g.	P.v.	H.g.
n	190	85	190	85	190	85
Prey species						
Herring	0·09	0·02	1·1	1·7	4·1	0·8
CLUPEIDS	0·09	0·02	1·1	1·7	4·1	0·8
Cod	0·12	0·11	2·5	4·1	3·0	2·1
Whiting	0·54	0·61	5·4	7·3	0·7	1·3
Saithe	–	0·02	–	1·7	–	3·3
Ling	<0·01	0·04	0·3	2·4	0·7	0·3
GADOIDS	0·66	0·78	8·2	15·5	4·4	7·0
SANDEELS	67·26	109·38	65·3	62·5	64·3	69·1
Dab	0·10	0·46	2·2	2·4	1·3	3·0
Flounder	0·48	0·68	7·2	4·9	6·6	6·9
Lemon sole	0·03	0·05	1·1	1·7	2·1	1·0
Plaice	0·05	0·26	1·4	3·2	1·4	3·4
FLATFISH	0·66	1·45	11·9	12·2	11·4	14·3
Octopus	0·07	0·06	3·6	4·1	14·5	8·0
Squid	0·06	–	3·6	–	0·9	–
CEPHALOPODS	0·13	0·06	7·2	4·1	15·4	8·0
Others*	0·37	0·05	6·0	4·1	0·3	0·7

* Other prey species include eelpout, cuckoo wrasse, snake blenny, bullrout and long spined sea scorpion, Raja species, crustaceans and polychaetes.

suggest that this is a genuine inter-specific difference, and not the result of variations in environmental conditions in different study areas. This difference may have consequences for the dynamics of these populations, both in relation to patterns of disease transfer and in the extent to which the two species may be affected by local changes in food availability (Trillmich 1992).

RELATIONSHIP BETWEEN HAUL-OUT DISTRIBUTION AND FORAGING DISTRIBUTION

Although harbour seals were present in the study area throughout the year, the importance of different haul-out areas varied seasonally. Changes in the relative abundance of seals suggest that haul-out sites in the Inverness and Dornoch Firths were used most intensively during summer, while those in the Beauly & Cromarty Firth were favoured during winter. The relative abundance of seals in Loch Fleet was also high in winter, although the number of seals using this site was low. Studies of other harbour seal populations have also reported seasonal shifts in haul-out distribution. In some cases seasonal changes in site-use were believed to be related to the sites' physical characteristics; for example, because they were particularly suitable for use by breeding females during pupping (Fancher & Alcorn 1982; Slater & Markowitz 1983) or by groups undergoing their annual moult (Jeffries 1986; Thompson 1989). In other cases, seals were believed to have switched haul-out sites in order to move closer to seasonally abundant food supplies (Brown & Mate 1983; Roffe & Mate 1984; Jeffries 1986; Greenstreet *et al.* 1993). However, in none of these studies were there data available on the at-sea distribution of seals using different haul-out sites.

In the present study, changes in harbour seal abundance at haul-out sites (Fig. 3) and data on the foraging distribution of radio-tagged harbour seals (Fig. 6) suggest that both proximity to foraging area and site characteristics may influence their haul-out site choice. In summer, all radio-tagged seals foraged outside the Dornoch Firth, but individual seals did not necessarily use haul-out sites closest to their foraging areas. Several of these animals were females with pups, and their use of sites in the upper part of the Dornoch Firth may have been related to the suitability of these sites for pupping. In contrast, the haul-out sites used by grey seals were those closest to the mouths of the firths (Fig. 4) and, thus, closest to those offshore areas in which we assume they were foraging. Our data also suggest that, outside the summer breeding season, harbour seal haul-out distribution is more closely related to their foraging distribution. Three of the five seals caught in the Dornoch Firth and tracked during winter moved to sites in the Beauly Firth. Studies in previous winters suggested that harbour seals preyed heavily upon clupeids which overwintered in the Beauly and Cromarty Firths (Pierce *et al.* 1991a; Thompson *et al.* 1991b). Together, these data suggest

that the increase in the relative abundance of seals in these haul-out areas reflects a change in foraging distribution during winter. However, the winter foraging distribution observed in the present study (Fig. 6b) suggests that animals were foraging further offshore than two seals that we had tracked in the previous 1988/89 season (Thompson *et al.* 1991b). Although, sample sizes were small, related data suggest that this change in behaviour may have been typical. First, the relative abundance of seals in the Inverness Firth, a site closer to offshore foraging areas, increased during the winter of 1989/90 when those seals foraged further offshore in winter (Fig. 3). Secondly, the relative distribution of seals in the Beauly and Cromarty Firths and the Inverness Firth remained similar in the winters of 1989/90–1992/93, and the clupeids found in the harbour seal's winter diet in earlier years (Pierce *et al.* 1991a; Thompson *et al.* 1991b) were virtually absent during these years (Thompson *et al.* 1996). Finally, both the relative abundance of harbour seals in the Inverness Firth in January and the proportion of clupeids in their winter diet have been shown to be related to the relative abundance of clupeids overwintering in the inner Moray Firth (Thompson *et al.* 1996).

COMPARISON OF HARBOUR SEAL AND GREY SEAL FORAGING AREAS

Of the five grey seals studied, three individuals spent much of their time at sea in the Moray Firth and were presumed to be foraging locally. Sample sizes were clearly too small to provide an overall picture of key grey seal foraging areas within the Moray Firth, but comparison with the larger data set from harbour seals does provide some indication of differences in the behaviour of the two species. In particular, these data suggest that grey seals not only make longer distance movements between haul-out sites, but that they also make longer distance foraging trips from their haul-out sites than harbour seals. As a consequence, grey seals could utilize a much broader area within the Moray Firth and a wider range of foraging habitats may be available to them. Individuals of both species consistently used favoured areas through the study and the harbour seals also showed considerable individual overlap in their use of foraging areas. In particular, one area to the east of the mouth of the Dornoch Firth was used consistently by both male and female harbour seals in both years of the study (Fig. 6), despite marked between-year differences in diet composition in these two years (Tollit & Thompson 1996). Although we studied grey and harbour seals in different years, the consistency of these harbour seal foraging areas between years suggests that the observed between-species differences are real.

In contrast to the harbour seals, there was little overlap in the foraging areas used by the three grey seals. However, one grey seal did use an inshore foraging area which overlapped with those used by harbour seals (Figs 6 & 7). Because seals which forage further offshore may be more likely to defaecate at sea, our estimates of the diet composition of Dornoch Firth grey seals may therefore be biased towards those individuals that use more inshore foraging areas. Nevertheless, these comparative data on diet composition suggest that, at least in these inshore areas in a single year, the diet of harbour and grey seals was remarkably similar. These data reflect previous studies of grey seal diet composition in the Moray Firth (which included samples from the breeding site at Helmsdale) and Orkney, particularly in the importance of sandeels (Pierce *et al.* 1991b; Hammond, Hall & Prime 1994). Longer-term studies of harbour seal diet composition in the Moray Firth have shown that seasonal and between-year intra-specific differences in diet composition (Pierce *et al.* 1991b; Tollit & Thompson 1996) can be greater than the inter-specific differences seen in this study (Table 7). These between-year differences in harbour seal diet, again, reflect how the behaviour of this species may be more strongly influenced by local changes in food availability.

In conclusion, this study confirms previous work that indicated that grey and harbour seals differ in the extent to which they move between terrestrial breeding and haul-out sites and in the extent to which they travel from these sites to feed. The harbour seal population in the inner Moray Firth appears to be resident, and animals using haul-out sites in the area used distinct local foraging areas. Thus, the population of harbour seals in the inner Moray Firth can be considered as a single management unit with clear links between breeding, resting and foraging sites. In contrast, grey seals using these same haul-out sites travelled extensively outside the Moray Firth and mixed with seals from several other UK breeding sites. This suggests that, despite evidence for genetic differences between grey seals at different breeding colonies (Allen *et al.* 1995), there is considerable overlap between the foraging ranges of seals from different UK breeding sites. As suggested by Hammond *et al.* (1993), grey seals on the east coast of Britain should therefore be treated as a single ecological management unit, within which discrete breeding populations may exist.

Acknowledgements

We would like to thank the many colleagues and friends who assisted with the capture and handling of seals, radio-tracking and haul-out counts. Particular thanks are due to Richard Cooper, Heather Corpe, Karen Gardiner, Rohan Holt, Gordon Liddle, David Miller, Morton Mitchell, Simon Reddy, Sean Twiss, Ben Wilson and David Wood. Sarah Curran, John Harwood, John Hislop, Shelagh Parlane and Ben Wilson all provided constructive criticism of earlier drafts of this manuscript. The work was carried out under a

series of contracts from the Scottish Office Agriculture Environment and Fisheries Department. Capture and handling were carried out under licences from the Scottish Office and the Home Office, respectively.

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Received 4 November 1994; revision received 5 October 1995