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Predation by seals on salmonids in two Scottish estuaries

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Abstract Detailed observations of the behaviour of harbour seals, *Phoca vitulina* L., at sites within the estuaries of the Rivers Dee and Don, in north-eastern Scotland, were made over two full years between 1993 and 1996. Small numbers of grey seals, *Halichoerus grypus* Fab., were also present. The presence of seals within the estuaries was strongly related to season, with maximum numbers observed in winter and early spring; seals were virtually absent in June and July. The River Don was used largely as a haul-out site, while the River Dee was used predominantly as a foraging site, although it was not possible to determine whether the same seals were using the two estuaries. More seals were hauled-out on the River Don during twilight and dark than in daylight. The seals were observed to eat mostly salmonids, *Salmo salar* L. and *S. trutta* L., unidentified roundfish and flounder, *Pleuronectes flesus* L. The otoliths identified in scats collected at the mouth of the River Don belonged to marine species indicating that the seals were also feeding outside the estuaries. A minimum estimate is given of the numbers of large salmonids eaten in each river during the course of the year. Although no information was available on the numbers of salmonids using the rivers or the reproductive status of the fish eaten by the seals, as a cause of mortality, seal predation on large salmonids in estuaries is apparently an order of magnitude less important than mortality caused by angling within the river.

KEYWORDS: behaviour, estuaries, fisheries interactions, grey seals, harbour seals.

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Introduction

Grey seals, *Halichoerus grypus* Fab., and harbour seals, *Phoca vitulina* L., are abundant in Scottish waters. An estimated 110 200 grey seals were associated with breeding sites in Scotland in 1998, which represents >90% of the UK population, and at least one-third of the global population. The British grey seal population has been steadily increasing at a rate of ~6% per annum since 1984 (Sea Mammal Research Unit, personal communication). Although less is known about the status of harbour seals, the estimated minimum size of the Scottish population in 1998 was 29 600 (Sea Mammal Research Unit, personal communication).

For many years Scottish fishermen have expressed concern about the possible impact of seals on fish stocks and fisheries, and considerable effort has been devoted to investigate this 'problem'. Early studies, based mainly on the examination of the stomach contents of seals shot in the vicinity of inshore nets set for Atlantic salmon, *Salmo salar* L., and Atlantic cod, *Gadus morhua* L., concluded that much of the diet of Scottish seals consisted of valuable commercial fish and that seals were responsible for considerable economic loss to the fisheries (Rae 1960, 1968, 1973; Rae & Shearer 1965; Parrish & Shearer 1977). Later investigations of the diet of British seals were based mainly on the examination of fish otoliths extracted from seal faeces collected at haul-out sites (Prime & Hammond 1990; Pierce, Thompson, Miller, Diack, Miller & Boyle 1991; Hammond, Hall & Prime 1994; Thompson, McConnell, Tollit, MacKay, Hunter & Racey 1996; Tollit & Thompson 1996; Brown & Pierce 1997). Faecal analysis indicated that a large component of the diets of both grey and harbour seals in British waters consisted of sandeels (Ammodytidae), although there was considerable geographical and seasonal variation, and commercially valuable species such as cod and haddock, *Melanogrammus aeglefinus* (L.) were important constituents of the seals' diet in some areas and seasons.

Particular concern has been expressed over the possible impact of seals on salmon and sea trout, *Salmo trutta* L. Salmonid remains have seldom been detected in seals' faeces. This may be because salmonid bones and otoliths are friable and easily degraded (Boyle, Pierce & Diack 1990) and the heads of salmon may not always be eaten, so that the otoliths are not ingested. Another explanation for the scarcity of salmonid remains in random samples of seal faeces is that because salmonids are less abundant than many marine fish species they are, at best, a minor component of the diet of most seals. However, seals have been observed eating salmon, the basis for this and previous (e.g. Brown & Mate 1983) studies, and although salmonids may not be essential to the well-being of seals, seals might still have a significant impact on salmonid stocks that are already severely depleted. This appears to be the case in several British salmon rivers, including the Aberdeenshire River Dee, where the numbers of spring-running salmon are declining (Youngson 1995; Anonymous 1997).

The presence of harbour seals has been recorded in rivers and estuaries in many parts of the world (Fisher 1952; Brown & Mate 1983; Roffe & Mate 1984; Olesiuk 1993; Stanley & Shaffer 1995), including the British Isles (Vaughan 1978; Greenstreet, Morgan, Barnett & Redhead 1993; Gibb 1996; Thompson, Tollit, Wood, Corpe, Hammond & Mackay 1997). Many of the rivers frequented by seals are major salmon and sea trout rivers. Where seals occur in relatively confined waters used by pre- and post-spawning adults (kelts), the opportunity exists for seals to have a major impact on the numbers of fish entering and leaving the river.

The conclusion that seals are having a major impact on local salmon stocks is based on casual observations and anecdotal information, and a more objective assessment is needed. This study describes the behaviour of seals in the estuaries of two major salmon rivers in the north-east of Scotland; the River Dee and the River Don. The objectives were:

1. to document the spatial and temporal utilization of the lower reaches of the Rivers Dee and Don;
2. to estimate the minimum numbers of salmonids eaten by seals in each river during the course of a year.

Materials and methods

Study sites

The estuaries of the Rivers Don and Dee lie within the City of Aberdeen in north-eastern Scotland (Fig. 1a). Both rivers rise in the Cairngorm mountains and flow east towards the North Sea. The estuary of the River Don (Fig. 1b) is not navigable by commercial shipping and has a series of sand dunes at the mouth. The area around the estuary is part of a nature reserve and a city park, and is used by anglers and others. Downstream of the Bridge of Don (Fig. 1b) there are some houses on the north bank and a road runs along the south bank. Seals are regularly seen hauled out on an island just upstream of the Bridge of Don and sometimes on the sand dunes at the mouth of the river.

The River Dee enters the North Sea 4 km from the Don estuary, south of Aberdeen city centre (Fig. 1c). The last 2 km of the river are navigable and form part of the harbour. Aberdeen harbour has been used extensively for several hundred years, as both a major fishing and commercial port and, more recently, as a supply base for the offshore oil industry. Consequently, the estuary of the River Dee is subject to higher levels of disturbance than that of the River Don.

Observation protocol

The observations were made during two separate 12-month periods. The series of observations began in 1 July 1993, with most observations made by the same observer (JAH). The second period started in April 1995, with all observations being made by a single observer (TJC). During both periods, observations of seal behaviour were carried out from the banks of both rivers. There were two observation points on the River Don (the Bird Hide and the Bridge of Don) and one on the River Dee (Aberdeen Harbour) (Fig. 1b, c).

Observations were made in 1-h blocks from a single observation point. The area was swept with binoculars for 3 min every 10 min. Whenever a seal was observed during an 'observation sweep' a 'seal sighting' was recorded. No attempt was made to identify individual seals. The behaviour of the seal was assigned to one of the following categories: out of the water (haul-out); in the water (other); or in the water with a prey item (feeding).

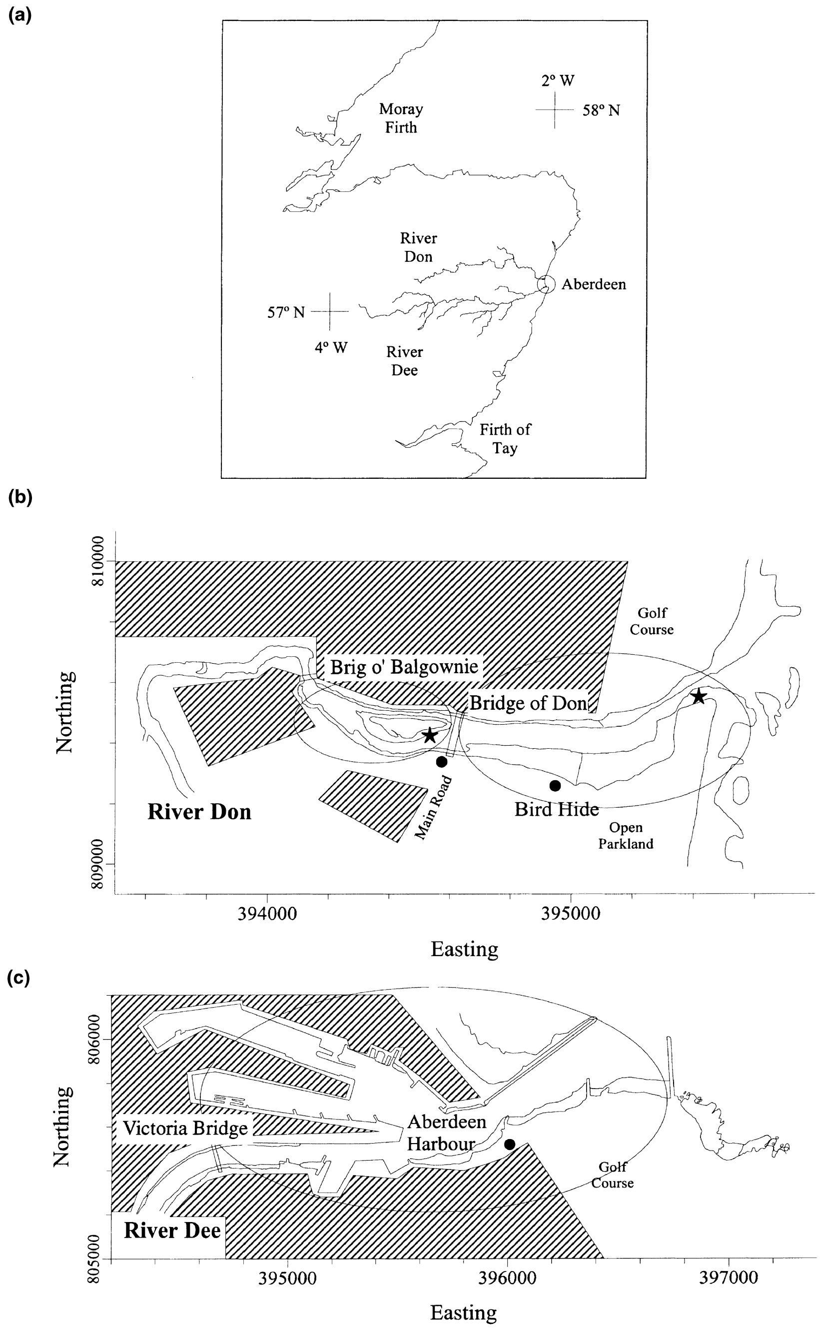


Figure 1. Location of Aberdeen in north-east Scotland (a) and the tidal limits of the River Don (b) and the lower 2.5 km of the tidal limits of the River Dee (c), showing the observation points (dots) and main haul-out sites (stars). Shading indicates built-up areas and the ellipses indicate the area covered from each observation point.

When the seal was seen at the surface with a prey item, the prey was classified as salmonid, unidentified roundfish (not a flatfish), flatfish (assumed to be flounder, *Pleuronectes flesus* L., the only flatfish species in the northern North Sea which occurs in brackish water) or 'other'. Prey items falling into the category 'other' were identified whenever possible. Seals may take many minutes to consume large prey, and on some occasions an individual seal eating a single large fish was logged as a 'feeding' event during successive 'observation sweeps' within an observation hour. This was taken into account when the monthly estimates of consumption were made, such multiple observations being recorded as single events.

During 1993–1994, all observations were made during daylight. In 1995–1996, observations were also made during the hours of darkness, to test whether extrapolation of observed behaviour from daytime to night could be justified. Night-time observations could be made at all three sites owing to the presence of artificial illumination. This comprised back-lighting from streetlights at the Don Bird Hide and from the harbour on the River Dee, while the Bridge of Don site was fairly well illuminated by lights on the bridge itself. Obviously, visibility of seals was reduced during twilight and dark and, although feeding events were readily detected, it is likely that the number of seals present was sometimes underestimated. For this reason, data collected during these periods were treated separately.

For each river, observations were classified according to the state of the tide (low, flood, high and ebb) and the phase of daylight (light, dusk, night and dawn). All sites were visited equally frequently and the number of visits for each combination of tidal state and daylight phase during each month was set to be proportional to the duration of each combination in that month.

Statistical analysis

Presence/absence data for seals were related to study year, month, river, phase of daylight (light or dark) and behaviour of seals (swimming or hauled-out) using multi-way frequency tables (MWF) as implemented in the BMDP© statistical package (Dixon, Brown, Engelman & Jennrich 1990). For these multi-way tests, a log-linear model was used and two different test statistics were calculated: partial association (which tests the significance of deleting a particular effect from the model) and marginal association (which tests the significance of deleting an effect from a model which contains all effects after summing over levels of categorical variables not included in the effect). If both tests gave significant results, the effect was assumed to be significant.

An index of the probability of seeing a seal at any month/site was derived as the number of observation hours during which at least one seal sighting was made (either seal species), expressed as a proportion of the total number of observation hours in that month and at that site. Separate indices were also calculated for seals in the water and seals hauled-out, and for daylight and night (twilight and dark). For this analysis, all sightings of seals in the water were included, regardless of whether they were feeding. Indices of seal abundance were also calculated as the average number of sightings occurring during an observation hour for a given month/site combination. Seasonal trends in these monthly indices were compared (between rivers and between years) using Spearman's rank correlation coefficient. Comparisons of median values of monthly indices (between rivers, between years, between day and night, between seals in the water and hauled-out seals) were made using Mann–Whitney *U*-tests (M-WU).

Predation on salmonids

Estimates of the number of salmonids eaten by seals were based only on those direct observations of feeding when the prey could be positively identified as a (large) salmonid, on the basis of its size, shape and the characteristic pink or orange colour of its flesh. Estimates of the numbers of salmonids eaten each month by seals in the two study areas were derived from the average number of salmonids seen to be eaten per hour:

$$N_m = F_m \times (H_m / O_m) \tag{1}$$

where N_m is the minimum estimate of the number of salmonids taken by seals during month m, F_m the average observed number of feeding events on salmonids per hour during month m, H_m the total hours in month m and O_m the number of hours of observation during month m.

Estimates of the numbers of unidentified roundfish (potential salmonid prey) eaten each month by seals were also calculated. Adding these values to those for the estimates of positively identified salmonids eaten provides a less conservative estimate for the numbers of salmonids eaten.

Sampling errors in estimates of salmonid and unidentified roundfish consumption were quantified using bootstrap simulations (Reynolds & Aebischer 1991). For each river in each month of the study, the set of observations ('observation sweeps') was taken to be the sampled population. Individual observation scores were set to 1 if one salmonid was seen to be eaten or 0 if no salmonids were eaten. For the bootstrap simulation the population of *N* observations was sampled with replacement 1000 times, each time taking a sample of *N* observations and scoring the numbers of salmonids seen to be eaten. The resulting set of sample scores was sorted and the 25th and 975th scores (the 2.5 and 97.5% points of the distribution) define the 95% confidence limits. Finally, confidence limits were scaled up by the ratio of the number of possible observations in the month to the actual number of observations. The procedure was repeated for each month's data in both rivers and the whole exercise repeated for consumption of unidentified roundfish. Overall annual confidence limits were calculated by sampling, with replacement, from the sets of observations from all of the 12 months, again repeating the process 1000 times.

Faecal collection and analysis

During the study periods, attempts were made to collect harbour seal faeces (scats) at the main seal haul-out site (Don Island). These attempts were largely unsuccessful, reflecting the relative inaccessibility of the site (it could be visited only during spring low tides) and the small number of seals present. Only one sample was collected at this site, in November 1993. During October/November 1996, after the end of the second observation period, eight scats were collected from the sand dunes at the mouth of the river. All scats were sieved and identifiable hard parts were removed, identified and measured following the standard methodology (see Pierce & Boyle 1991). Fish otoliths and cephalopod beaks were identified using reference material and guides (Clarke 1986; Härkönen 1986).

Results

Seal numbers and frequency of occurrence

Although both harbour seals and grey seals were observed in both estuaries, the overwhelming majority of the sightings in the two study areas were of harbour seals. On the River Dee, 91.4% of sightings ($N = 1169$) were of harbour seals while on the river Don, only one grey seal was seen among a total of 4905 sightings. Hauled-out seals were recorded only within the estuary of the River Don. There were, however, anecdotal reports of seals hauled-out on the River Dee several kilometres upstream of the tidal limits (I.P. Smith, personal communication).

On both rivers, the probability of seeing a seal followed a clear seasonal pattern, with a minimum between June and August and a maximum between October and February (Fig. 2). The monthly indices of seal presence in the two rivers and the two years were significantly correlated (Spearman rank correlation, $r_s = 0.658$, $P < 0.05$).

On the River Don, during the second period, haul-out behaviour was more commonly observed (in relation to the total number of observations) at night than during the day (U-test, $P < 0.05$), although this trend was mainly evident in the winter months (Fig. 2a). In both rivers, during the second period, seals were seen in the water more often (in relation to the total number of observations) during the day than at night (twilight and dark) (U-test, $P < 0.001$). During daylight observations in the River Don activity in the water was seen more often than haul-out behaviour in both periods (M-WU, $P < 0.001$).

With the exception of June–August, the mean number of seals in the water in both rivers stayed relatively constant throughout the year (Fig. 3b, c). In winter, the mean number of seals observed hauled out on the River Don was greater during night (twilight and dark) than during the day (Fig. 3a), and the numbers of seals observed in the water at night were generally lower than during daylight. The variation (indicated by the SE bars) in observed numbers of hauled-out seals was greater than for numbers of seals in the water.

The study areas are not the only parts of the two rivers used by seals. On the River Dee, harbour seals have often been seen up to 4 km above the mouth of the river. A small group of seals, probably harbour seals, has been observed hauled-out just upstream of a non-operational fish counter situated ~2 km above tidal limits and seals have also been observed 'surfing' on the weir of this counter (I.P. Smith, personal communication). Seals are occasionally seen much farther upstream on the Dee. An unidentified seal was sighted 19 km upriver (Williamson 1988) and another at Banchory, ~35 km above the tidal limits of the Dee (J. Massie, personal communication). A young male harbour seal was shot 13 km from the mouth of the Dee in August 1988 (J.R.G. Hislop, personal observation). On the River Don, seals are frequently seen within the boundaries of a public park, just above the tidal limits ~2.5 km upstream (G.J. Pierce, personal observation) and have been

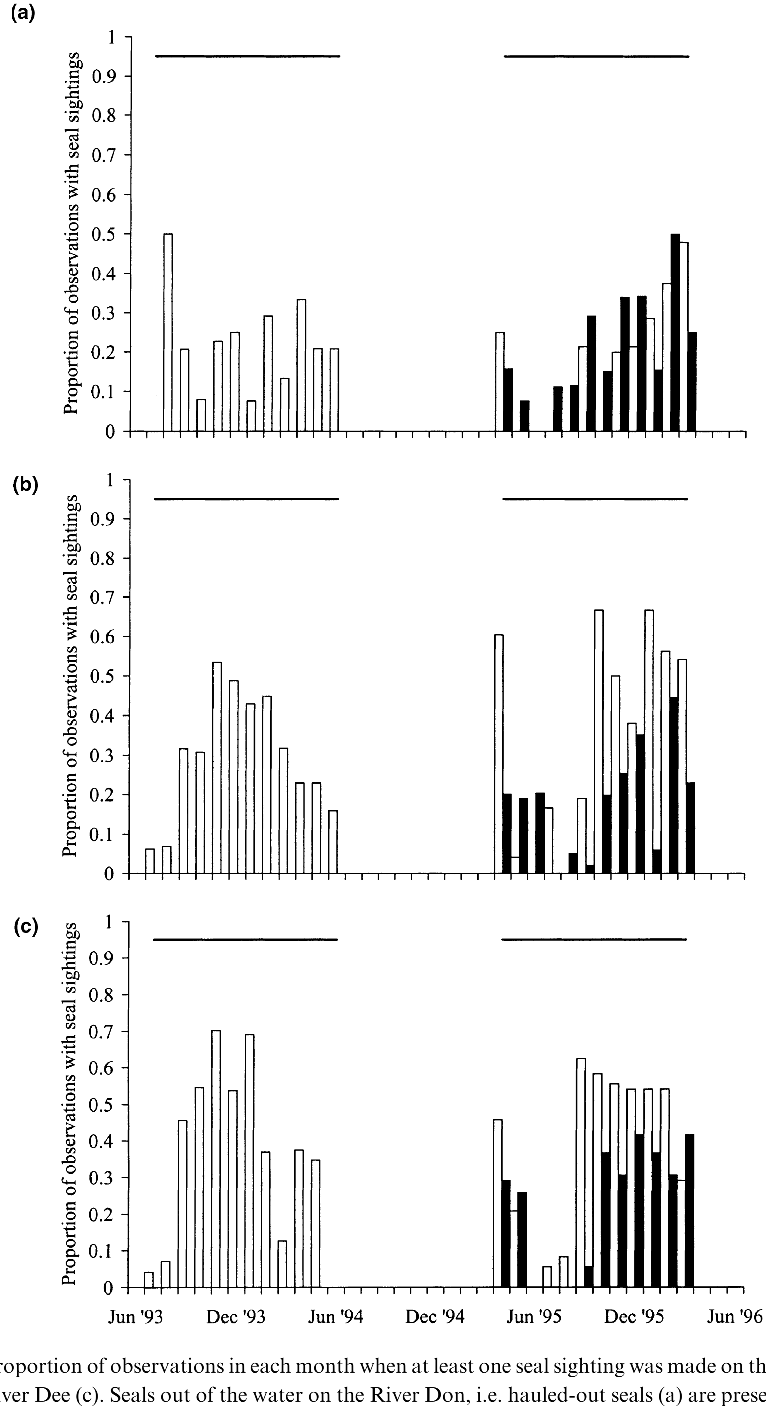


Figure 2. Proportion of observations in each month when at least one seal sighting was made on the River Don (a, b) and the River Dee (c). Seals out of the water on the River Don, i.e. hauled-out seals (a) are presented separately from those exhibiting all other types of behaviour (b). Observations for two seasons are shown with daylight (clear) and twilight and dark (black) observations separated. Lines show the duration of the observation periods.

observed at a bridge ~4 km above tidal limits (newspaper report – Aberdeen Press and Journal).

Observed feeding events

Relatively few feeding events were recorded during both periods. In the majority of cases the prey seen to be taken by seals were fish but there were also single observations of seals taking starfish and crabs. Most observed feeding events were of seals eating salmonids and flounders (Fig. 4). Predation on salmonids was observed more frequently on the Dee than the Don, while the reverse was true for predation on flounder. The highest number of observed feeding events occurred in September through January and in May. During 1993–1994, all four records of predation on salmonids on the Don involved harbour seals, whereas four out of 26 instances of salmonids being eaten on the Dee involved grey seals. During 1995–1996, all but one recorded feeding events involved harbour seals. The grey seal was observed to eat an unidentified roundfish. For the purpose of the calculations below, the four salmonids and one unidentified roundfish eaten by grey seals were included. Predation on salmonids was seen equally frequently at day and at night (five times each) in the Dee, and more frequently at night (five out of six times) in the Don.

Estimates of predation on salmonids

The monthly estimates of numbers of large salmonids and unidentified roundfish eaten by seals, with bootstrapped 95% confidence limits, showed that they ate more salmonids in the River Dee than in the River Don, and that several hundred salmonids were taken in both years (Tables 1 and 2, Fig. 5). Substantial numbers of unidentified roundfish were also eaten. The minimum estimates of the numbers of large salmonids eaten by seals were an order of magnitude less than the numbers of salmon and sea trout caught by anglers (Table 3).

Faecal analysis

The single sample collected in November 1993 contained unidentifiable fish bones. The eight seal scats collected at the mouth of the River Don in November and December 1996 yielded 608 fish otoliths, all from marine fish: 480 from whiting, *Merlangius merlangus* (L.) 99 from sandeels, Ammodytidae, six from cod, 13 from *Trisopterus* spp., six from haddock and one each from plaice, *Pleuronectes platessa* L., and lemon sole, *Microstomus kitt* (Walbaum). Three octopus, *Eledone cirrhosa* Lamarck, beaks were also found. Apart from cod, sandeels and whiting, all the other species recorded came from a single scat.

Discussion

The presence of seals in the Rivers Dee and Don was highly seasonal. Maximum numbers were observed in winter and early spring, and seals were virtually absent from the study areas in June and July. The scarcity of harbour seals during summer might be explained in

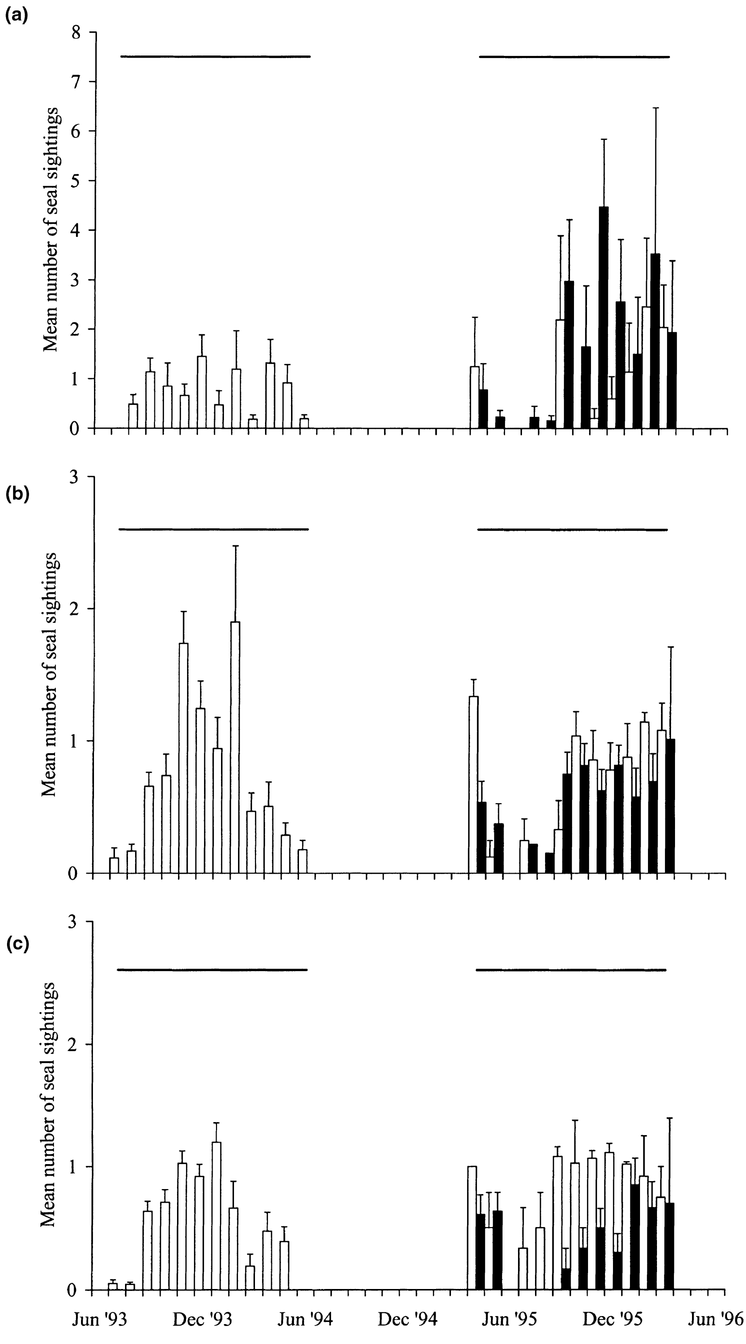


Figure 3. The hourly mean (±SE) number of seal sightings made in each month on the River Don (a, b) and the River Dee (c). Seals out of the water on the River Don, i.e. hauled-out seals (a) are presented separately from those exhibiting all other types of behaviour (b). Observations for two seasons are shown with daylight (clear) and twilight and dark (black) observations separated. Lines show the duration of the observation periods.

terms of their migration to pupping and/or moulting sites elsewhere on the coast. The nearest known breeding sites are in the inner Moray Firth, ~200 km to the north (Thompson, Miller, Cooper & Hammond 1994) and the estuary of the River Tay, ~100 km to the south (Gibb 1996). However, it is not known which, if either, of these sites is used by the seals observed on the Rivers Dee and Don. In other areas, changes in the seasonal abundance of harbour seals have been related to differences in habitat quality and prey abundance (Pierce *et al.* 1991; Olesiuk 1993; Tollit & Thompson 1996). Brown & Mate (1983) showed that the peak abundance of Pacific harbour seals, *P. vitulina richardsi* Gray, in Netarts Bay on the Oregon coast, in October and November, coincided with the return of chum salmon, *Oncorhynchus keta* (Walbaum), to spawn. In contrast, peak abundance in Tillamook Bay, 15–20 km north of Netarts Bay, was in May and June (pupping season) and August (moulting season).

The River Don is used mainly as a rest and haul-out site, although some feeding was observed, while the River Dee is apparently predominantly a feeding site. Harbour seals from other populations in north-east Scotland may forage tens of kilometres from their haul-out sites (Thompson *et al.* 1994, 1996) so it cannot be assumed that the seals observed resting at haul-outs on the River Don are the same individuals that were observed feeding on the River Dee. Seals were seen feeding both during daylight hours and during twilight and dark.

More seals were observed hauled-out on the River Don during twilight and dark than during daylight. This is the reverse of the haul-out patterns observed in open water areas in British Columbia (Watts 1996) and during the pupping and moulting season in the Moray Firth (Thompson, Fedak, McConnell & Nicholas 1989). The difference may be because seals hauling out in an urban area, such as the Don estuary, suffer more disturbance during the hours of daylight.

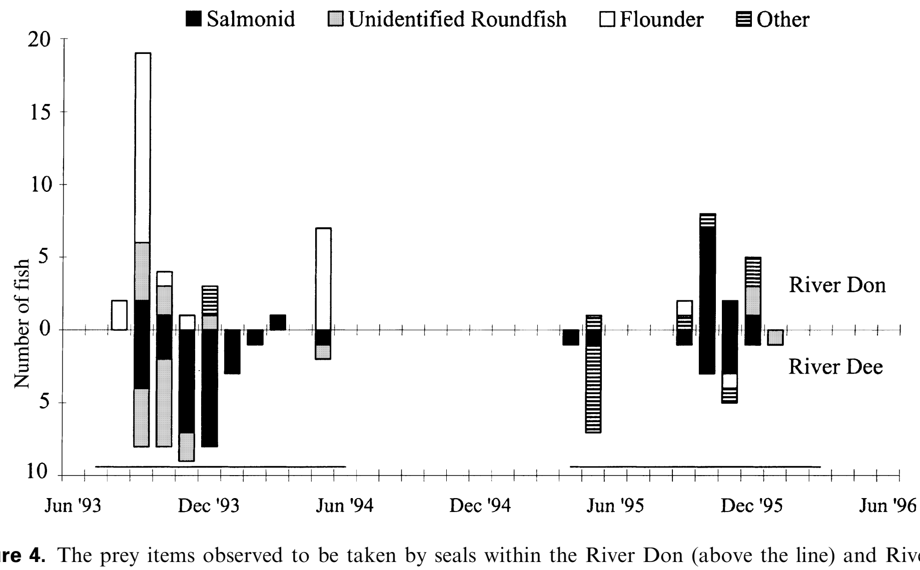


Figure 4. The prey items observed to be taken by seals within the River Don (above the line) and River Dee (below the line) during the two studies. The lines indicate the duration of the two studies.

Table 1. Results of bootstrap simulations of foraging observations on Salmonids. Monthly means, upper ($U_{95\%}$) and lower ($L_{95\%}$) 95% confidence limits are shown

		Salmonids			
		1993–1994		1995–1996	
	Month	Mean	($L_{95\%}$–$U_{95\%}$)	Mean	($L_{95\%}$–$U_{95\%}$)
River Don	January	0		0	
	February	0		0	
	March	51	(0–154)	0	
	April	0		0	
	May	0		0	
	June	0		0	
	July	0		0	
	August	0		0	
	September	24	(0–61)	0	
	October	22	(0–65)	180	(77–334)
	November	0		48	(0–120)
	December	0		30	(0–89)
	Totals	97	(12–229)	258	(124–434)
River Dee	January	197	(0–460)	0	
	February	62	(0–186)	0	
	March	0		0	
	April	0		45	(0–135)
	May	62	(0–248)	50	(0–149)
	June	0		0	
	July	0		0	
	August	0		0	
	September	58	(15–130)	72	(0–216)
	October	59	(0–147)	172	(0–401)
	November	155	(44–288)	135	(0–315)
	December	271	(101–473)	57	(0–172)
	Totals	864	(517–1267)	531	(242–887)

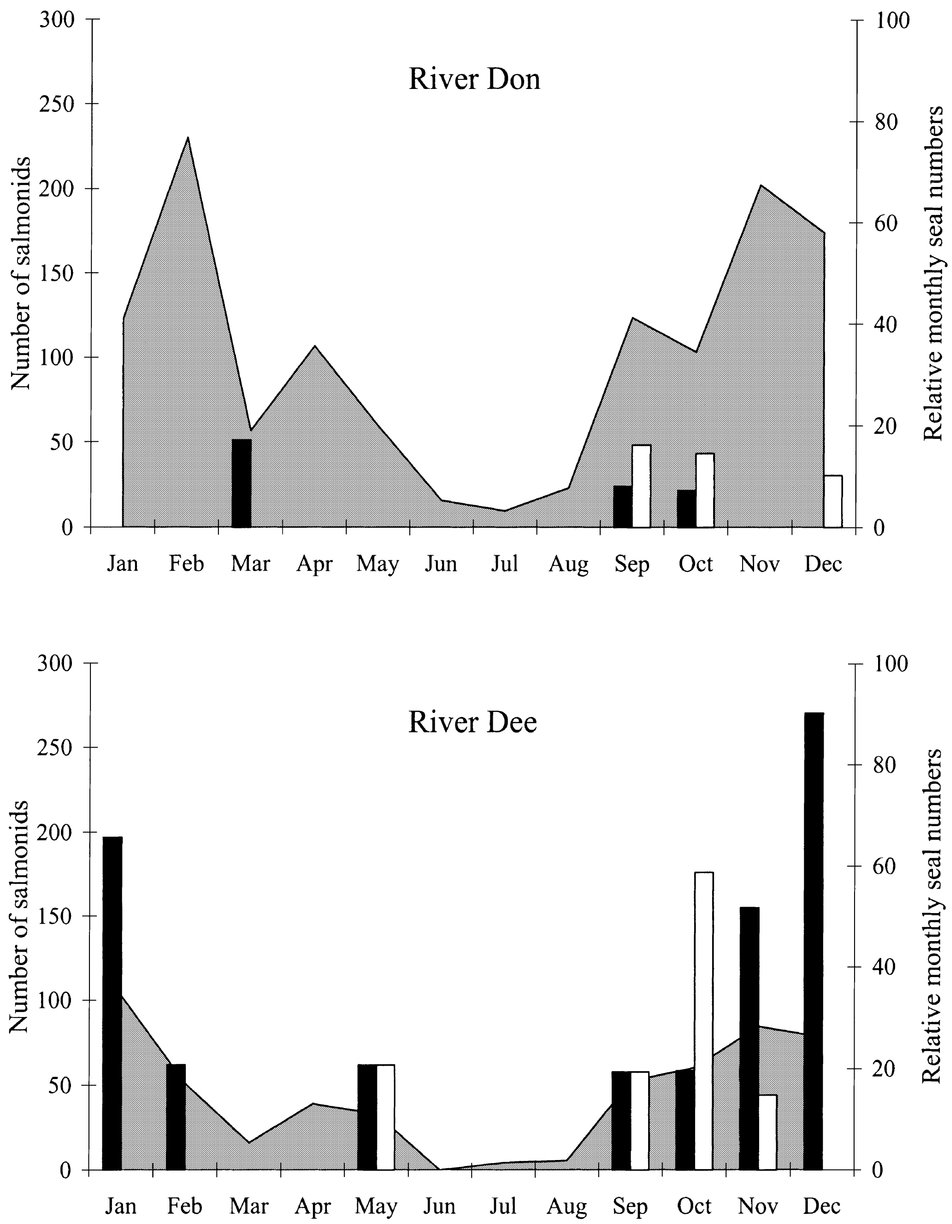
The estimate of the quantities of salmonids eaten by seals was based entirely on field observations of fish being eaten at the surface. This method provides a biased estimate of the composition of the seals' diet (Roffe & Mate 1984) because only large and awkward prey items, such as adult salmon and flatfishes, are brought to the surface to be broken up and consumed; smaller prey are eaten whole under water, out of sight. Observations of predation on salmonids by Pacific harbour seals in California suggest that fish measuring more than 35 cm are brought to the surface at least once by a feeding seal (Stanley & Shaffer 1995). The present study therefore provides no information on the occurrence or importance of small prey items in the diet of the seals in the Dee and the Don. However, the presence of otoliths of a wide variety of marine species in the small sample of seal scats collected at the mouth of the Don indicates that the prey items observed to be eaten during the two study periods (salmonids, flounders and large unidentified roundfish) do not

Table 2. Results of bootstrap simulations of foraging observations on unidentified roundfish. Monthly means, upper ($U_{95\%}$) and lower ($L_{95\%}$) 95% confidence limits are shown

		Unidentified roundfish			
		1993–1994		1995–1996	
	Month	Mean	($L_{95\%}$–$U_{95\%}$)	Mean	($L_{95\%}$–$U_{95\%}$)
River Don	January	0		0	
	February	0		0	
	March	0		0	
	April	0		0	
	May	0		0	
	June	0		0	
	July	0		0	
	August	0		0	
	September	48	(0–109)	0	
	October	43	(0–109)	0	
	November	0		0	
	December	30	(0–92)	60	(0–149)
	Totals	121	(24–239)	60	(0–149)
River Dee	January	0		83	(0–248)
	February	0		0	
	March	0		0	
	April	0		0	
	May	62	(0–186)	0	
	June	0		0	
	July	0		0	
	August	0		0	
	September	58	(15–116)	0	
	October	176	(59–323)	0	
	November	44	(0–111)	0	
	December	0		0	
	Totals	340	(154–556)	83	(0–248)

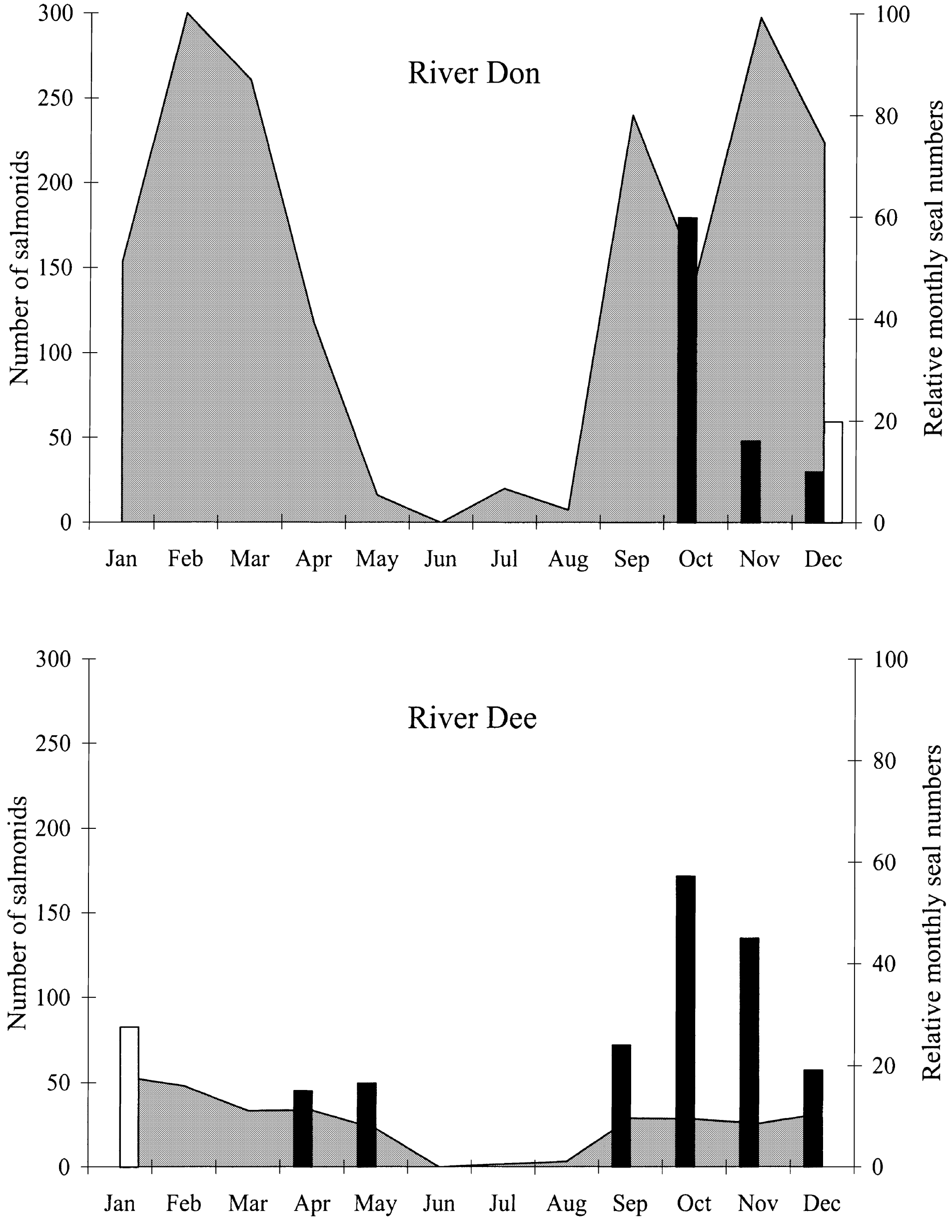
represent the seals' entire diet, and that the seals forage in the sea as well as in the estuaries.

Highest levels of predation on salmonids occurred over the winter months when water temperatures are lower, which may make poikilothermic species such as salmon easier prey for the seals. During the summer, and when the river level is low, salmon tend to move through the estuary of the Dee and into the river at night and during the ebb tide (Smith & Smith 1997). At other times of the year, and at higher river flows, salmon also migrate into and up rivers during the day. It has been suggested that salmon movement during low visibility conditions such as at night or during high river flows may minimize their vulnerability to predation (Smith & Smith 1997). Predation on salmon by seals was observed at night during the second study period. However, this was at a site where there was artificial illumination.



(a) July 1993–June 1994

Figure 5. Estimated number of salmonids (solid bar) and unidentified roundfish (clear bar) eaten monthly by seals on the Rivers Don and Dee for both studies. The shaded area gives an indication of the estimated monthly abundance of potentially foraging seals, i.e. seals in the water, relative to the maximum estimate recorded in February 1996 on the River Don.



(b) **April 1995–March 1996**

Figure 5. (Contd.)

Table 3. Numbers of wild salmon, grilse and sea trout caught by rod and line in 1993–1995. The figures for 1994 and 1995 include fish caught and then released in compliance with a voluntary stock conservation scheme (Source: Fisheries Research Services, Freshwater Fisheries Laboratory, Montrose Field Station, unpublished data)

District	Year	Salmon and grilse *a*	Sea trout *b*	All salmonids *c*	Eaten by seals *d*	*d*/*c* (%)
Don	1993	1408	379	1787	97	
	1994	1332	353	1685	–	
	1995	2110	482	2592	258	
	Mean	1617	405	2021	178	8.8
Dee	1993	5022	2061	7083	864	
	1994	4086	1915	6001	–	
	1995	4991	1584	6575	531	
	Mean	4700	1853	6553	698	10.7

The relatively frequent observations of seals in the river Don eating flounder could well be related to their abundance. Raffaelli, Richner, Summers & Northcott (1990) reported that flounder are present in the Ythan estuary at Newburgh, ~12 km north of Aberdeen, from late spring (April–May) until late winter (December–January).

The assessment of predation on salmon based on direct observations almost certainly overestimated the proportional contribution made by adult salmonids to the diet of seals in the study areas. However, there is no *a priori* reason to suppose that it overestimated the absolute numbers of adult salmonids eaten by seals. Indeed, these studies probably provided only minimum estimates of the numbers of salmonids eaten in the two rivers. First, although the estimates were based solely on formal observations within the study areas, seals were seen feeding on salmonids at other sites on the two rivers (T.J. Carter & J.R.G. Hislop, personal observations). Secondly, some of the 'unidentified roundfish', which were analysed separately, may have been adult salmonids. Thirdly, some small or juvenile (smolts, parr) salmonids may have been consumed under water. Finally, indirect indications of feeding, including sightings of seals being mobbed by gulls, a patch of oil appearing on the water close to where a seal had been seen to dive (probably indicating that an oily fish had been captured) and sightings of seals manoeuvring rapidly just below the surface, presumably in pursuit of a prey item (Stanley & Shaffer 1995) were not taken into account.

This is the first attempt to estimate the numbers of salmonids eaten by seals in a UK estuary. It was not possible to estimate the impact of this predation on the salmon population because data on the numbers of fish entering and leaving the Rivers Dee and Don are not available. The minimum estimates of the numbers of large salmonids eaten by seals are an order of magnitude less than the numbers of salmon and sea trout caught by anglers within the rivers. However, this latter total includes fish of all sizes and no data on the number of small salmonids taken by seals was available.

It is also important to know whether the seals are feeding mainly on fresh-run fish that have entered the rivers to spawn, or spent fish (kelts) returning to the sea after spawning, which may return in future years to spawn again. The fresh-run fish have greater monetary value and, because they have survived the marine phase of the salmon life cycle and only have to survive until spawning time in the river, may be considered to have a greater biological value. Peak feeding on salmonids and unidentified roundfish in the Dee was observed during the period September–January. This period covers the inward migration of salmon that will spawn in the current year, the beginning of the migration of spring salmon (which will not spawn until the following autumn and winter), and the start of the kelts' post-spawning seaward migration. It was not possible to determine, on the basis of the field observations, which class of fish was being eaten. Some adult salmonids were taken in April and May. These may have been late spring-run fish. April and May are also the months when most smolts leave the Dee, but no smolts were seen to be eaten, possibly because they are usually less than 20 cm in length and as such can be eaten whole under water. Either the seals were eating smolts under water or their presence was not related to the smolt migration but to other factors such as changes in the abundance of other fish species (Greenstreet *et al.* 1993). The period when seals were less abundant on the rivers corresponds to the time when grilse (salmon returning after one winter at sea) begin to enter the River Dee. This suggests that factors other than the availability of salmon, such as the need to move to breeding and moulting sites, may influence the presence of seals.

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References

Anonymous (1997) *Report of the Scottish Salmon Strategy Task Force*. Edinburgh: The Scottish Office Agriculture, Environment and Fisheries Department, 86 pp.

Boyle P.R., Pierce G.J. & Diack J.S.W. (1990) Sources of evidence for salmon in the diet of seals. *Fisheries Research* **10,** 137–150.

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

Brown E.G. & Pierce G.J. (1997) Diet of Harbour seals at Mousa, Scotland, during the third quarter of 1994. *Journal of the Marine Biological Association, UK* **77,** 539–555.

Clarke M.R. (ed.) (1986) *A Handbook for the Identification of Cephalopod Beaks*. Oxford: Clarendon Press, 273 pp.

Dixon W.J., Brown M.B., Engelman L. & Jennrich R.I. (eds) (1990) *BMDP Statistical Software Manual*, Vol. I. Berkeley, Los Angeles, Oxford: University of California Press, 629 pp.

Fisher H.D. (1952) The status of the harbour seal in British Columbia, with particular reference to the Skeena River. *Bulletin of the Fisheries Research Board of Canada* **93,** 1–58.

Gibb G.M. (1996) Tay estuary seal count. *Salmon Net* **27,** 41–44.

Greenstreet S.P.R., Morgan R.I.G., Barnett S. & Redhead P. (1993) Variation in the numbers of shags *Phalacrocorax aristotelis* and common seals *Phoca vitulina* near the mouth of an Atlantic salmon *Salmo salar* river at the time of the smolt run. *Journal of Animal Ecology* **62,** 565–576.

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. *Journal of Applied Ecology* **31,** 340–350.

Härkönen T. (1986) *Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic*. Hellerup, Denmark: Danbiu ApS, 256 pp.

Olesiuk P.F. (1993) Annual prey consumption by harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin* **91,** 491–515.

Parrish B.B. & Shearer W.M. (1977) *Effects of Seals on Fisheries*. International Council for the Exploration of the Sea, Council Meeting 1977. Document CM, 1977/M: 14 (mimeo).

Pierce G.J. & Boyle P.R. (1991) A review of methods for diet analysis in piscivorous marine mammals. *Oceanography and Marine Biology: An Annual Review* **29,** 409–486.

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. *Journal of Zoology, London* **223,** 641–652.

Prime J.H. & Hammond P.S. (1990) The diet of grey seals from the south-west North Sea assessed from analyses of hard parts found in faeces. *Journal of Applied Ecology* **27,** 435–447.

Rae B.B. (1960) Seals and Scottish fisheries. *Marine Research* **2,** 1–39.

Rae B.B. (1968) The food of seals in Scottish waters. *Marine Research* **2,** 1–23.

Rae B.B. (1973) Further observations on the food of seals. *Journal of Zoology, London* **169,** 287–297.

Rae B.B. & Shearer W.M. (1965) Seal damage to salmon fisheries. *Marine Research* **2,** 1–39.

Raffaelli D., Richner H., Summers R. & Northcott S. (1990) Tidal migrations in the flounder (*Platichthys flesus*). *Marine Behaviour and Physiology* **16,** 249–260.

Reynolds J.C. & Aebischer N.J. (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the red fox *Vulpes vulpes*. *Mammal Review* **21,** 97–122.

Roffe T.J. & Mate B.R. (1984) Abundancies and feeding habits of pinnipeds in the Rogue River, Oregon. *Journal of Wildlife Management* **48,** 1262–1274.

Smith I.P. & Smith G.W. (1997) Tidal and diel timing of river entry by adult Atlantic salmon returning to the Aberdeenshire Dee. *Journal of Fish Biology* **50,** 463–474.

Stanley W.T. & Shaffer K.E. (1995) Harbour seal (*Phoca vitulina*) predation on seined salmonids in the lower Klamath River, California. *Marine Mammal Science* **11,** 376–385.

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. *Journal of Applied Ecology* **26,** 521–535.

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. *Journal of Animal Ecology* **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. *Journal of Applied Ecology* **33,** 1572–1584.

Thompson P.M., Tollit D.J., Wood D., Corpe H.M., Hammond P. & Mackay I. (1997) Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology* **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. *Canadian Journal of Zoology* **74,** 1110–1121.

Vaughan R.W. (1978) A study of common seals in the Wash. *Mammal Review* **8,** 25–34.

Watts P. (1996) The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. *Journal of Zoology, London* **240,** 175–200.

Williamson G.R. (1988) Seals in Loch Ness. *Scientific Reports of the Whales Research Institute* **39,** 151–157.

Youngson A. (1995) *Spring Salmon*. 1994 Bensinger Liddell Memorial Atlantic Salmon Fellowship. Pitlochry: Atlantic Salmon Trust 52 pp.