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WINTER FORAGING BY COMMON SEALS (*PHOCA VITULINA*) IN RELATION TO FOOD AVAILABILITY IN THE INNER MORAY FIRTH, N.E. SCOTLAND

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SUMMARY

(1) Parallel studies of fish distribution and the diet and activity of common seals were made to assess the relationship between the seals' winter feeding activity and the distribution and abundance of their prey. Echosounder and trawling surveys revealed that a large part of the fish biomass was sprat and small herring, while faecal analyses showed that >90% of common seal prey (by weight) were clupeoid fish.

(2) During the day, clupeoids concentrated in trenches and holes more than 12 m deep. Radio-tagged seals were located regularly over these areas. At night, clupeoid shoals rose in the water column and became more dispersed. Diel changes in seal activity patterns suggest that seals fed more often during the day.

(3) Prey sizes were estimated from the size of otoliths retrieved from seal faeces. Estimated sizes of clupeoids taken by seals were similar to the sizes of fish caught in trawls, even though estimates were not corrected to allow for partial digestion of otoliths. This suggests that the rapid otolith digestion rates previously reported from captive seals may have been artificially high, or that the Moray Firth seals selected fish larger than those caught in trawls.

INTRODUCTION

Common seals (*Phoca vitulina* L.) are coastal pinnipeds which haul-out regularly to rest, give birth and suckle their young. In most areas, they are seen at haul-out sites throughout the year, but their abundance varies in relation to factors such as season, time of day, tidal cycle and weather conditions (e.g. Boulva & McLaren 1979; Godsell 1988; Thompson 1989).

Because direct observations of foraging seals can rarely be made, changes in the abundance of seals at haul-out sites have sometimes been used to identify periods of foraging activity. For example, it has been suggested that diurnal peaks in abundance, or individual haul-out behaviour, are related to nocturnal foraging activity (Thompson *et al.* 1989). Nocturnal foraging activity is generally believed to occur because vertical migrations, or changes in fish schooling behaviour, may make prey more available to predators during the night. (Trillmich & Mohren 1981; Thompson *et al.* 1989). Common seals are catholic feeders and their diet can differ considerably between areas (Rae 1968; Brown & Mate 1983; Harkonen 1987). However, no published studies of activity patterns have been carried out in areas where the seals' diet, feeding areas and prey availability were also known. Consequently, the relationship between changes in the activity of common seals and the distribution and behaviour of their prey remains speculative.

This paper presents data from three parallel studies which were carried out in the inner Moray Firth during the winter of 1988–89. Common seal activity patterns were monitored using radio-telemetry and their diet determined by faecal sampling. The distribution and abundance of potential prey species were assessed using fishing and echosounder surveys. The combined results of these studies are used here to assess the relationship between spatial and temporal changes in common seal foraging activity and the availability of their prey.

METHODS

Study area

The study was carried out in the inner part of the Moray Firth, N.E. Scotland, between September 1988 and March 1989. This part of the Moray Firth is divided into two relatively narrow inlets, the Cromarty and Inverness Firths, the latter leading into the semi-estuarine Beauly Firth (Fig. 1). Throughout most of this area the water is shallow (<10 m) but it can be up to 50 m deep in channels and depressions. Common seals haul-out on sand banks in the Beauly and Cromarty Firths, a muddy shore in the upper Beauly Firth and a sandy shore near the mouth of the Inverness Firth (Fig. 1). These haul-out sites are completely covered at high water. The area uncovered at low water depends upon the height of the tide. Daily tidal range, and hence the degree to which the sites are exposed, is variable (1·5–5 m).

Distribution and availability of prey

During the period 4–15 November 1988, a combined echosounding and trawling survey was carried out by FRV 'Goldseeker' to assess the distribution and abundance of fish in the area. Further short surveys were carried out in January–February and March 1989.

The water in much of the inner Moray Firth is too shallow to allow fish to be surveyed by either standard trawling methods or acoustic surveys. Consequently, survey effort was concentrated in those areas where radio-tagged seals were found to be feeding, and in similar areas identified from the characteristics of the sea bed (Fig 1). Transects were made over and between these areas using a Simrad Skipper 801 echosounder. Trawl hauls were made at a sample of points where fish shoals were detected by the echosounder. Previous surveys had indicated that most of the biomass in the area consisted of pelagic species. A pelagic trawl with a cod end mesh size of 12 mm was therefore chosen to identify the echotraces. On most occasions the trawl was fished in midwater to sample fish schools that were detected above the sea bed. However, in three of the four areas surveyed, the net was also fished on the

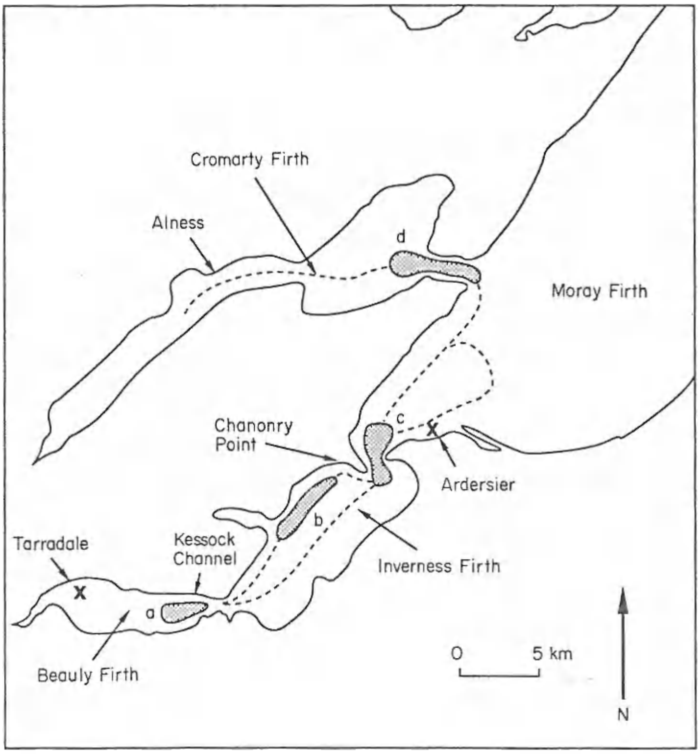

FIG. 1. A map of the study area showing the position of common seal haul-out sites (**X**) and the location of fishing survey areas. Area a = Kessock Channel, area b = *Inverness Firth*, area *c* = *Chanonry* Channel, area d = Sutors of Cromarty.

sea bed to sample demersal species. Species composition, size distribution and numbers of each species in the catch were calculated from a subsample of the catch.

Diet

Faeces were collected at haul-out sites in the Beauly, Cromarty and Inverness Firths (Fig. 1) between October 1988 and January 1989. Sampling was carried out at sites that seals were known to be using during this period. Sites were visited shortly after low tide by boat or, at one side (Tarradale), on foot. Any seals present were counted and identified to species. All faecal material present on the site was then collected and frozen.

Faeces were later thawed, washed through a 0·355-mm sieve and all sieve contents were retained. Otoliths were removed and identified using a reference collection and information in Harkonen (1986). Other fish skeletal elements were identified as far as possible using a reference collection. Otolith lengths or breadths were measured under a binocular microscope and used to estimate fish weight and length (regressions from Harkonen 1986 and G.J. Pierce, unpublished data). If more than thirty otoliths of a species were present in a sample, a random subsample of thirty otoliths was measured. No corrections were made for reduction in otolith size due to digestion.

Note that derived fish lengths and weights are not error free, so statistical tests utilizing the apparent variance in these parameters would not be meaningful.

Seal activity

In September 1988, two seals (an adult male and a subadult female) were caught at the haul-out site near the mouth of the Inverness Firth (Fig. 1), and VHF radio-tags glued to the hair on their head or back (Fedak, Anderson & Curry 1983; Thompson & Miller 1990).

Activity patterns were monitored from 1 November 1988 to 30 January 1989 using permanent receiving stations which continuously recorded whether each individual was diving, hauled out or absent from the area (Thompson *et al.* 1989). Foraging ranges were determined during November and January. During these periods, seals were located once a day, at standardized times, on 6 days each week. Locations were made with a hand-held Yagi aerial from vantage points on coastal roads. At least three fixes were obtained from each of two vantage points using the null-average method (Springer 1979), and the mean bearing used to estimate the seal's position by triangulation.

From January 1988, weekly low-tide counts were made at haul-out sites in the Beauly, Cromarty and Inverness Firths (Fig. 1). Where possible, observations were also made in the feeding areas used by radio-tagged seals to assess whether other seals were also present in these areas.

RESULTS

Distribution and availability of prey

Seventeen species were caught during the fishing surveys (Table 1), of which two (herring, *Clupea harengus*, and sprat, *Sprattus sprattus*) are pelagic, three (whiting, *Merlangius merlangus*, cod, *Gadus morhua*, and sandeel, *Ammodytes marinus*) semi-pelagic and the remainder demersal. Catch rates were highest for herring, sprat and whiting, and these species were particularly abundant in deep water (20–40 m) in the Kessock channel at the eastern end of the Beauly Firth. The density of fish in this area was high during all surveys. For example, on 12 November 1988, a 5-min trawl haul through the upper part of an aggregation caught >1500 kg of fish, almost entirely herring and sprat. Smaller schools were also detected in many of the other areas surveyed, with most schools tending to occur in water deeper than 10 m. However, surveys were almost always carried out in daylight. Repeated transects of the eastern end of the Beauly Firth on 9 November showed that the vertical distribution of fish changed later in the day. During daylight, the fish were confined to the deeper part of the trench (>12 m) but with the onset of darkness they rose from the bottom, occupying the entire water column and spilling over into the shallow water surrounding the trench (Fig. 2).

The length–frequency distributions of the whiting and cod in the catch were usually unimodal and similar in all four areas surveyed. Virtually all of these fish were 0-group (1988 year-class). Length–frequency distributions for herring and sprat were bimodal, indicating the presence of fish which were spawned in both 1987 and 1988. Older clupeoids predominated in catches from the Beauly Firth (Fig. 3).

TABLE 1. Estimated numbers of fish per haul and size range (cm) for species caught in each of the four areas that trawling surveys were carried out in the inner Moray Firth: area 1 = Kessock channel (10 hauls); area 2 = Inverness Firth (5 hauls); area 3 = Chanonry Channel (6 hauls); area 4 = Sutors of Cromarty (3 hauls)

	Area			
	1 *n* (cm)	2 *n* (cm)	3 *n* (cm)	4 *n* (cm)
Pelagic sp.				
Sprattus sprattus L.	7927 (8–15)	141 (4–12)	72 (4–14)	45 (3–12)
Clupea harengus L.	11247 (7–25)	2134 (8–17)	1936 (9–19)	666 (8–19)
Semi-pelagic sp.				
Gadus morhua L.	30 (9–17)	19 (10–23)	8 (7–19)	
Merlangius merlangus L.	235 (10–19)	82 (10–27)	150 (10–21)	94 (11–20)
Ammodytes marinus Raitt				<1 (13)
Demersal/inshore sp.				
Raia clavata L.		<1 (28)		
Zoarces viviparus L.	18 (9–21)	1 (8–9)		
Spinachia spinachia L.	<1 (14)		<1 (10)	
Myoxocephalus scorpius L.	<1 (6)	<1 (7)	<1 (11–12)	
Agonus cataphractus L.	5 (3–13)	2 (5–11)	<1 (26)	
Liparis liparis L.			<1 (8–9)	
Pholis gunnelus L.	2 (15–17)	<1 (15)	<1 (12)	
Callionymus lyra L.		<1 (16)		
Pomatoschistus minutus Pallas		3 (7–8)	<1 (7–8)	
Pleuronectes platessa L.	<1 (6–8)	35 (6–12)	5 (7–19)	
Platichthys flesus L.	3 (7–18)		<1 (19–25)	
Limanda limanda L.	<1 (14)	14 (6–17)	1 (8–14)	

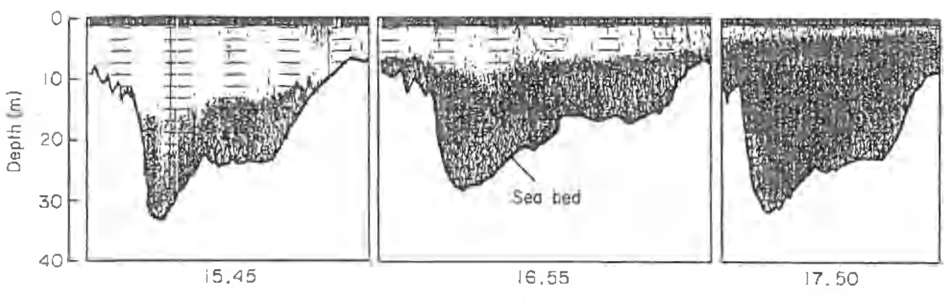

FIG. 2. Echotraces recorded by FRV 'Goldseeker' during east–west transects of the Kessock Channel on 9 November 1988. Recordings were made at 15.45 h, 16.55 h, and 17.50 h, and show fish rising with the onset of darkness. Bottom profiles differ slightly because of slight variations in the course and speed of the vessel.

Diet

A total of forty faecal samples were collected, most of them from Tarradale in the Beauly Firth. All faeces are believed to be from common seals; the Tarradale haul-out site appeared to be used only by common seals and no grey seals *Halichoerus grypus* (Fabricius) were present when samples were collected at other sites. Although

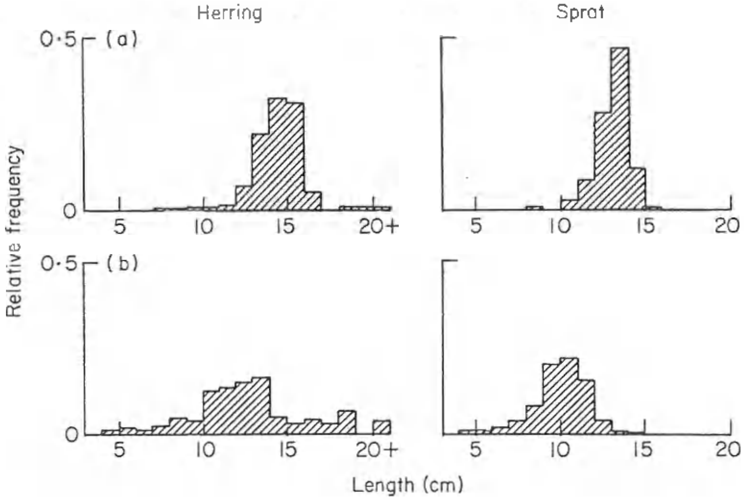

FIG. 3. Length–frequency composition of herring and sprat (a) from trawl catches in the Kessock Channel, and (b) from the faeces of common seals.

some faecal material may remain on the haul-out sites over a high-tide, most samples are believed to have been fresh.

The samples collected contained remains of at least 491 individual fish representing four species and three higher taxa (Table 2). One small otolith remained completely unidentified. Estimated fish sizes are also given in Table 2; the largest fish represented by an otolith was a herring estimated to have been 27 cm long and to have weighed 158 g.

Clupeoid otoliths were found in 75% of samples, and clupeoid bones were present in 90% of samples. Herring and sprat thus formed the bulk of the diet in terms of both numbers of fish and ingested weight, as estimated from otoliths (Table 2). The frequency distributions of estimated lengths of herring and sprat from faecal material were similar to those of trawl-caught herring and sprat from the Beauly Firth, the area from which most faecal material originated (Fig. 3). However, although differences in sampling techniques prevented formal statistical comparison of these two distributions, mean estimated lengths of fish from faecal samples were slightly lower (herring $\bar{x}$ = 12·9 cm; sprat $\bar{x}$ = 11·6 cm) than those from trawls (herring $\bar{x}$ = 14·6 cm; sprat $\bar{x}$ = 13·0 cm). Of the other species present in the diet, the cod, other gadoids (possibly haddock, *Melanogrammus aeglefinus* L.), gobies, flounder (*Platichthys flesus*) and most of the sandeels (*Ammodytidae*) were present in December samples from the Cromarty Firth.

Invertebrate remains were also found in three of the samples from the Cromarty Firth in December (crustacean and polychaete remains each occurring twice).

Seal activity

Activity patterns for both tagged individuals indicated that there was one peak of haul-out activity in the early morning with a second, higher, peak in the early evening (Fig. 4). Similarly, morning low-tide haul-out counts were significantly lower

TABLE 2. Estimated winter diet composition for common seals in the inner Moray Firth, together with lengths (mm) and weights (g) of prey species estimated from otoliths found in faecal samples. The relative importance of each prey species in the faecal samples is expressed in terms of (a) frequency of occurrence, (b) percentage of total number of fish in the sample, and (c) percentage of total estimated ingested weight (g) in the sample

Prey species	(a)	Number of fish	(b)	Estimated weight (g)	(c)	Estimated length			Estimated weights		
						Min	Max	Mean	Min	Max	Mean
Sprattus sprattus	75·0	356	72·5	4329·3	76·6	52·9	155·9	115·7	0·7	35·8	12·2
Clupea harengus	37·5	55	11·2	883·5	15·6	34·2	272·1	129·1	0·6	157·5	16·1
Gadus morhua	5·0	3	0·6	109·0	1·9	59·0	183·6	121·7	12·1	68·4	36·3
Other Gadidae	2·5	2	0·4	6·3	0·1	46·8	123·1	81·2	0·1	8·5	3·1
Ammodytidae	10·0	70	14·3	175·7	3·1	64·8	131·8	92·7	0·8	6·3	2·5
Gobidae	5·0	4	0·8	4·5	0·1	27·9	72·3	51·7	0·1	2·7	1·1
Platichthys flesus	2·5	1	0·2	144·5	2·6	247·7	247·7	247·7	144·5	144·5	144·5

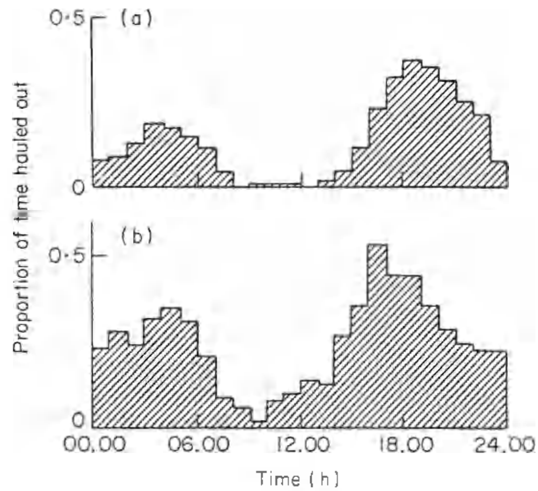

FIG. 4. Diel variations in the haul-out activity of (a) the male and (b) the female radio-tagged common seals during the period 1 November 1988–31 January 1989.

than those made on afternoon low-tides in both the Cromarty Firth ($\bar{x}$ a.m. = 39, $\bar{x}$ p.m. = 92: $t = 3{\cdot}3$, 17 d.f., $p < 0{\cdot}01$) and the Beauly Firth ($\bar{x}$ a.m. = 96, $\bar{x}$ p.m. = 249: $t = 5{\cdot}9$, 23 d.f. $p < 0{\cdot}001$). Peak counts for the Cromarty and Beauly Firths over this period were 152 and 355, respectively.

Daily radio-locations indicated that both seals remained in the inner firths and used restricted areas throughout the winter (Fig. 5). The male moved into the Cromarty Firth by 9 October and remained there until 16 February when he returned to his capture site. During November and January he was located every day, either around a deep channel off Alness (Fig. 1) or on or nearby the haul-out sites *c.* 8 km south-west of Alness. Over this period, the female was located each day until her radio-tag failed on 21 January. She continued to haul-out at the capture site until the end of November. When at sea during this period she was located around the Chanonry Channel. She moved into the Beauly Firth on 30 November and continued to use haul-out sites there until here radio-tag failed. When not hauled out, she was regularly located at the eastern end of the Beauly Firth, in the vicinity of the Kessock Channel.

Although only opportunistic observations were made, it was clear that the Kessock Channel was used as a feeding area by many other common seals. During echo surveys of the area on both 12 and 15 November, up to forty-four actively diving common seals were seen at the surface around FRV 'Goldseeker' at any one time. Only two or three seals were ever seen at once while carrying out similar surveys at Chanonry and in the Cromarty Firth.

DISCUSSION

Fishing surveys showed that a wide variety of potential prey species were present for seals in the area examined. Other species may have been present but not caught in the survey gear. For example, demersal and intertidal species were probably sampled

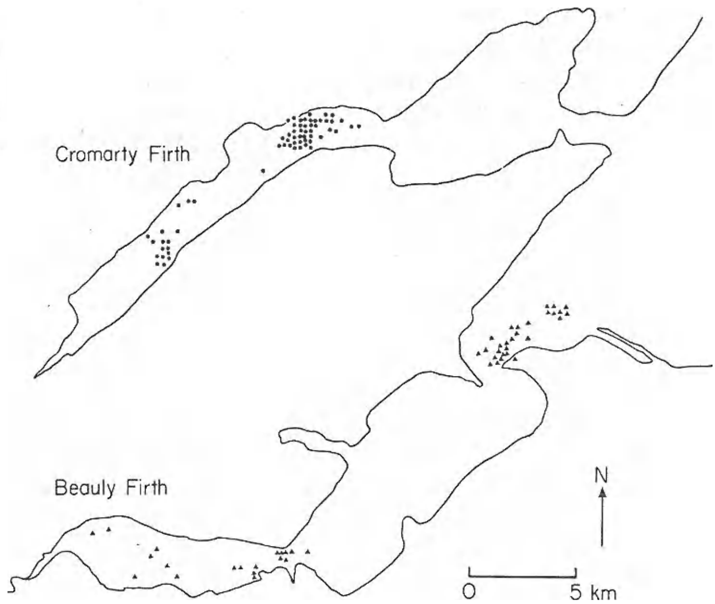

FIG. 5. Daily locations of radio-tagged seals during November 1988 and January 1989: (●) male, (▲) female.

less effectively than pelagic species by the pelagic trawl. For this reason, catch rates in Table 1 cannot be used as reliable indices of relative abundance. Nonetheless, it seems reasonable to infer from the echosounder traces that a large part of the fish biomass in the inner Moray Firth consisted of clupeoids. The area is known as an important overwintering ground for sprat and juvenile herring, and these stocks were intensively exploited by Scottish fishermen until the fishery was closed in the early 1980s (Saville 1971; Hopkins 1986).

Analyses of faecal samples indicated that clupeoids formed the most important component of the diet of common seals over the study period, although other prey species (e.g. sandeels) are more important at other times of year (Pierce *et al.*, in press). The use of otoliths to assess the diet of seals is known to involve certain biases but these will tend to under-represent species such as clupeoids which have small or fragile otoliths (da Silva & Neilson 1985; Jobling & Breiby 1986; Murie & Lavigne 1986; Jobling 1987). Had species such as whiting and flatfish, which fish surveys had shown to be present, been taken by seals we would have expected to detect their remains in faecal samples. Consequently, clupeoids may have constituted an even more important component of the diet than our analyses indicated.

If it is assumed that the diet composition reported here indicates the preferred prey species for common seals in winter, data from the fish surveys, together with historical fishery data, can be used to make a preliminary assessment of spatial and temporal variations in the distribution of the seals' main winter prey resource in this area. Data on the winter activity and distribution of seals can then be used to assess how these predators respond to variations in their food supply during this period.

Clupeoids arrive in the Moray Firth as 0-group fish in autumn and remain there for about 2 years, concentrating in the inner firths in most winters and dispersing out to sea in spring and summer (Saville 1971; Jones 1976; Hopkins 1986). Between 1960 and 1980, landings from the Moray Firth fishery ranged from a few hundred to tens of thousands of tonnes year^{-1}, of which a variable percentage was caught in the inner firths. The annual variations in the catch were due largely to fluctuations in the strength of the year-classes recruiting to the fishery (Saville 1971; Hopkins 1986), but there were also variations in the degree to which they concentrated in the inner firths. The location of the fishery within the inner firths also varied, with boats working the Beauly, Cromarty or Inverness Firths depending upon where the densest shoals were located (DAFS, unpublished data). Fishery data therefore suggest that clupeoid movements into the inner firths each winter are predictable, but that the size of the stock and its precise distribution can vary from year to year.

In the winter of 1988–89, our survey data suggest that the densest shoals of fish were located in the Kessock Channel, in the Beauly Firth. In addition, smaller shoals were found in similar deep holes or trenches in other firths and in the outer approaches to the firth, areas where the fishery is known to have operated in the past. When not hauled-out, the locations of both radio-tagged seals (Fig. 5) were clustered over and around these areas of deeper water, suggesting that the seals were feeding there. Observations of large numbers of unmarked seals diving in the Kessock Channel during the study period suggested that this behaviour was commonplace. In contrast, three common seals which had been caught at the same site in the Inverness Firth and tracked between May and August 1988 spent little time in the inner firths, travelling up to 45 km out to sea to feed (Thompson & Miller 1990). These data suggest that common seals feed closer inshore in winter, probably in response to the movements of clupeoids into the inner firths.

Activity patterns of the two radio-tagged seals show that they spent least time hauled-out during daylight. Determining whether or not this indicates a preference for feeding during daylight is difficult. In particular, the tidal cycle in this area is such that the time of low water during periods of neap tides is in the middle of the day or the middle of the night, leading to a reduction in haul-out site availability at this time. This would not, however, explain why seals hauled out more in the afternoon than in the morning (Fig. 4). Furthermore, the overall pattern was similar for the female when she hauled out at Ardersier (Fig. 1), a site which was available on all low-tides. We suggest, therefore, that the observed activity patterns reflect a preference towards daylight feeding, with seals tending to haul-out soon after a feeding bout in the late afternoon, rather than immediately prior to a feeding bout in the morning. Echo surveys showed that the schooling behaviour of clupeoids also varied in relation to levels of light intensity, with fish forming dense schools in the bottoms of deep holes during the day (Fig. 2). Thus, preferences for daytime feeding among seals could be related to variations in the success with which they can capture fish in different types of schools, or at different heights in the water column.

Published relationships between otolith size and fish length and weight (e.g. Harkonen 1986) do not allow the accurate estimation of the sizes of fish taken by seals because suitable data on rates of digestion of otoliths from clupeoids eaten by common seals are not available. Our estimates of fish size (Table 2) are therefore uncorrected and are underestimated by an unknown amount. Estimated fish sizes may also vary according to the regression used (see Pierce *et al.*, in press). Nevertheless, it is worth noting both the high number of clupeoid otoliths recovered and the similarity between the fish sizes from the faeces and from fishing surveys (Fig. 3).

Previous studies using captive fed seals have reported very low recovery rates for clupeoid otoliths in pinniped scats (e.g. da Silva & Neilson 1985). Our results therefore suggest either that the seals in the inner Moray Firth were selecting larger fish which were not captured in the trawls, or that digestion rates reported previously from relatively inactive captive seals may have been artificially high, a suggestion that has also been made by Harvey (1987).

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