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Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*)

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(With 5 figures in the text)

This study presents the first direct observations of the movements and behaviour of free-ranging grey seals at sea. Radio and ultrasonic transmitters were attached to three sub-adult male grey seals which were then tracked from a suitable vessel. Behaviour at sea fell into one of three categories: travelling between haul-outs, short duration trips, and resting adjacent to haul-out sites. Travelling was characterized by direct, relatively fast horizontal movement and by V-shaped dive profiles. During short duration trips the seals swam slower and invariably exhibited square-wave dive profiles, spending approximately 60% of total dive duration at the maximum depth. Resting involved shallow dives close to haul-out sites and an absence of directed lateral movement.

The excellent navigational abilities of grey seals are illustrated by the rapid, direct swimming between distant haul-out sites. It is proposed that short duration trips are specifically for foraging because of their association with other piscivores, and because swimming was slow and mostly on or near the sea bed (grey seals are known to feed almost exclusively on demersal and benthic fish). These trips accounted for only 14% of the nine days that seal 1 was tracked. It is also proposed that the habit of diving to the sea bed whilst travelling between distant haul-out sites is to allow opportunistic foraging with only a small increase in total swimming distance.

Contents

Introduction

The grey seal (*Halichoerus grypus*) is an important marine predator in British waters. It is both large (up to 365 kg) and abundant, with a current British population of around 88,000 animals

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(N.E.R.C., 1991). The reproductive biology and population dynamics of this species in the UK have been studied extensively (Hiby & Harwood, 1979; Fedak & Anderson, 1982; Anderson & Fedak, 1987; Ward, Thompson & Hiby, 1987) but, until recently, studies have been restricted to animals on shore. It is at sea, however, that seals spend most of their lives, feeding and displaying their physiological and behavioural adaptations to the marine environment.

Small, recoverable time-depth recorders (TDRs) developed in the early 1970s have facilitated studies of the diving behaviour of those pinniped species which can easily be recaptured, e.g. the Weddell seal (*Leptonychotes weddellii*) (Kooyman, 1975, 1981), northern elephant seal (*Mirounga angustirostris*) (Le Boeuf *et al.*, 1988) and various otariid species (Gentry & Kooyman, 1986). These devices produce a continuous record of dive depth and have proved to be efficient, cost-effective tools for studying diving in suitable species. However, the data are collected in isolation from other information such as location, environmental factors and interactions with other species, and the study animals must be recaptured to obtain the data.

Although it is possible to catch grey seals in the UK, the probability of recapturing the same animal is remote, so a recoverable device is an inappropriate method of data collection in this case. We have therefore developed a tracking and data gathering system based on radio and ultrasonic telemetry which allows us to follow seals at sea at relatively short range, accurately map their movements, and simultaneously collect behavioural data via the ultrasonic link. It also allows us to confirm visually the precise location and nature of the behaviour apparent in the diving records and relate it to local characteristics (such as bottom depth and topography and other oceanographic features) and the presence of other predators. During summer 1986, we used the combined VHF radio and ultrasonic telemetry system to track and study the movements and diving behaviour of free-ranging grey seals in the North Sea. This paper describes the methods used and the results obtained during this trial programme.

Methods

During August 1986, 3 sub-adult male grey seals were caught in tangle nets set on the sea bed, close to haul-out sites on the Farne Islands off the NE coast of England (Fig. 1). Each seal was immobilized using a Ketamine/Diazepam mixture (Baker, Anderson & Fedak, 1988). A VHF radio tag (Mariner Radar, UK) giving a 40 msec pulse at 173 MHz once every second was glued to the top of the head (Fedak, Anderson & Curry, 1983) ensuring that the aerial was clear of the water each time the animal surfaced. A purpose-built 100–120 KHz sonic tag was glued to the lower back ensuring that the transmitter remained submerged even when the seal was at the surface. The sonic tag incorporated a pressure transducer which controlled the pulse rate. Depth information was relayed as a linear function of pulse rate, varying between 0·3 Hz at the surface and 1 Hz at 100 m depth. All tags were calibrated in a pressure vessel before use and were accurate to $\pm 1{\cdot}5$ m.

Sonic and VHF signals and a commentary detailing visual observations, location, etc. were recorded on twin track magnetic tape. A 15-m catamaran capable of staying at sea for up to 14 days was used to track the seals and to collect data. A manually rotated 3 element Yagi aerial mounted 3 m above the deck of the boat received the VHF signals and was used to locate the seal at ranges up to 12 km, until they were within range of the acoustic transmitters. Sonic signals were detectable at ranges of up to 1 km using a steerable directional hydrophone mounted below the boat. Effective reception range was reduced when the seal surfaced or was close to shore in the surf. We attempted to keep the tracking boat 300–400 m away from the seal but depth data could be recorded at a range of up to 0·5 km. VHF signals were also monitored continuously using an omni-directional aerial mounted on the mast head, allowing activity patterns to be determined.

Good quality sonic recordings were decoded automatically using a purpose-built detector circuit. Low quality recordings were decoded by ear and entered manually into an event recorder. Depth data were smoothed by taking a 5-second moving average in order to remove variability introduced by the operator.

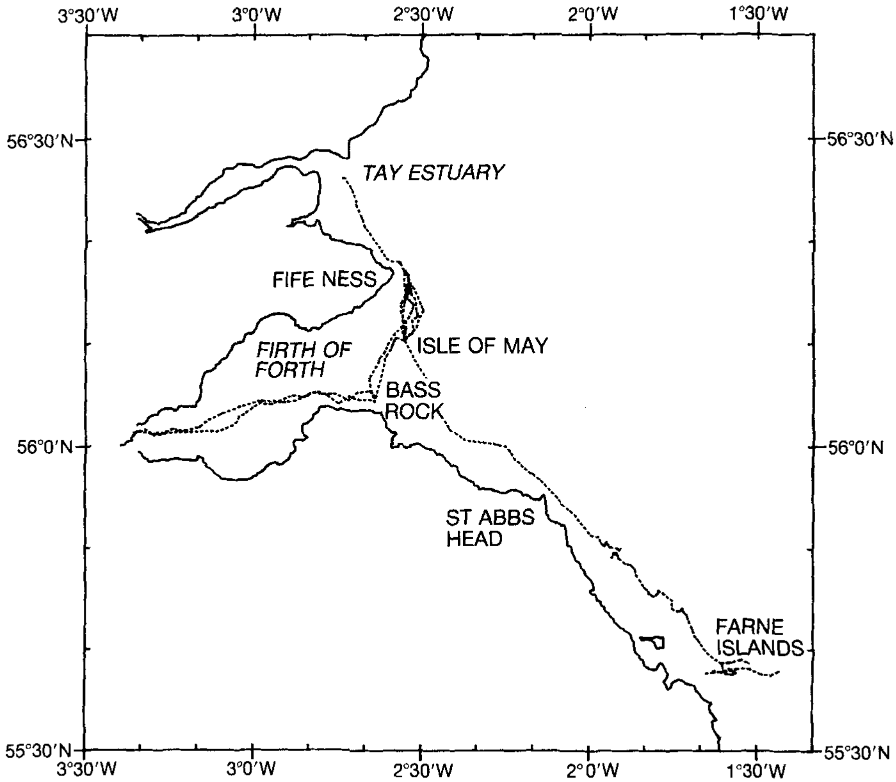

FIG. 1. Map of the east coast of northern England and southern Scotland showing the tracks of three male grey seals tagged at the Farne Islands. Two of the seals were only followed whilst in the vicinity of the Farne Islands.

Distances travelled by the seals and swimming speeds were calculated using latitude and longitude fixes from the boat's *Decca* navigator. This assumes that: (1) the boat's track coincided with the seal's and (2) that the seal swam in straight lines between position fixes. Violation of assumption (1) will result in an overestimate of distance and speed, violation of (2) in an underestimate.

In all cases where both VHF records and depth profiles were received, the apparent timing of surfacing and submergence from depth records coincided with the first and last pulses received from the VHF transmitters. Consequently, overall estimates of surface and dive times were derived from the VHF data which provided a more continuous record of events.

Activity was determined from direct observations and by interpretation of the diving behaviour and VHF records, and assigned to 1 of 4 categories: (1) hauled out of the water, (2) resting in the water adjacent to haul-out sites, (3) short duration trips, usually returning to the same haul-out site, and (4) travelling between distant haul-out sites.

Results

Movements and activity

All three animals were observed hauled-out; dive depth data were collected from each animal during rest and short duration trips away from land and while resting in the water close to land.

Detailed descriptions of the behaviour and diving patterns observed in each category are given below.

Seal number 1 was the only one observed travelling between distant haul-out sites and the only one monitored continuously for an extended period. Its activity over nine consecutive days can be summarized as:

	%
Hauled-out	13
Resting in water adjacent to haul-outs	41
Short duration trips	14
Travelling between haul-outs	32

Immediately after release, seal 1 swam amongst the Farne Islands for approximately 2 h, possibly in an attempt to escape the attentions of the tracking vessel (at that time, a small inflatable boat). This entailed navigating through narrow channels while submerged and in apparent darkness. We were therefore concerned that the presence of a tracking vessel may have influenced the behaviour of seal 1. Attempts were made to spot the seal at each surfacing and, after the initial 2-h period at the Farne Islands, it showed no obvious reaction to the tracking vessel, even at ranges of less than 20 m. On several occasions the catamaran overtook the seal, but each time it continued on track swimming beneath the boat, sometimes surfacing within a few metres of it.

After leaving the Farne Islands, seal 1 was tracked for a continuous period of nine days during which it swam a minimum distance of 270 km, ignoring small deviations from the track. It visited and rested at three widely separated haul-out sites: the Isle of May, the upper Firth of Forth, and the Tay Estuary (Fig. 1).

Seals 2 and 3 were tracked only for short periods in the vicinity of the Farne Islands.

Travelling between haul-out sites

Swimming between haul-out areas was characteristically direct; e.g. when travelling from the Farne Islands to St Abbs Head (Fig. 1), seal 1 swam continuously for 11 h through the night, maintaining an almost constant heading of 340°. On reaching the Isle of May, it had swum continuously for 20 h at a mean horizontal velocity of $1{\cdot}25\ \mathrm{m{\cdot}s^{-1}}$, a total distance of 90 km.

During transit, seal 1 dived continuously but spent very little time at the maximum depth, giving the dives a characteristic V-shape in profile (Fig. 2). The depths attained on most dives were consistent with diving to, or very close to, the sea bed, which varied between 30 and 70 m. The mean dive duration, mean surface duration, and mean proportion of time submerged during transit dives are given in Table I. The distribution of surface and dive times are given in Fig. 3a.

Infrequently interspersed with these long sequences of V-shaped dives were occasional longer dives during which the seal spent a significant proportion of the dive at the maximum depth giving the profile a square-wave shape. One such dive is shown in Fig. 2. Of a total of 399 transit dives recorded, only eight were longer than eight minutes. Depth profiles were obtained for five of these and all were square-wave dives. Six of these long dives occurred during the initial transit from the Farne Islands to the Isle of May and on each occasion the seal appeared to remain over a particular spot for the duration of the dive. For example, two hours after leaving the Farne Islands the seal made two consecutive dives of 15·5 min and 9·5 min duration during which his position did not change.

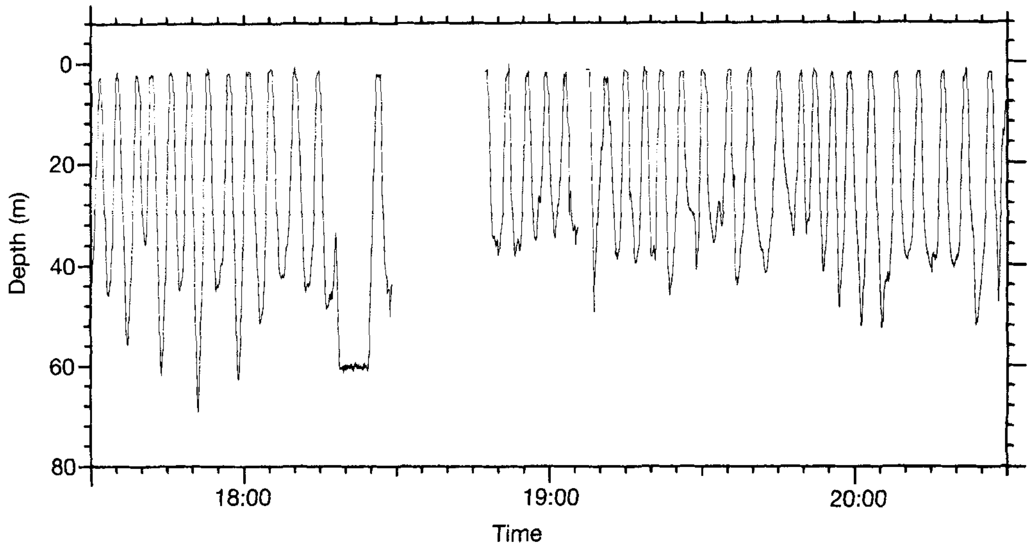

FIG. 2. Dive profiles for a male grey seal travelling from the Farne Islands to the Isle of May. The plot shows the typical V-shaped dive profiles of travelling and one extended square-wave dive.

Short duration trips

All three study animals were tracked whilst making short duration trips. Seal 1 made two return trips to the north of the Isle of May of about 4 h duration. It also made two other short trips from the Isle of May, one ending at the Bass Rock and the other ending at Fife Ness (Fig. 1). Seals 2 and 3 made one return trip each to the east of the Farne Islands covering 8·5 km and 10·3 km, respectively.

All three seals displayed very similar diving behaviour during these trips. Dive profiles were invariably of the uniform square-wave shape (Fig. 4), with the animals spending approximately 60% of the total dive duration at the maximum depth. As with transit dives, the depths attained suggested that the seal always dived to the bottom. Swimming speed in short duration trips was characteristically slow with a mean horizontal velocity of 0·8 $m \cdot s^{-1}$. Square-wave diving began with the first dive (Fig. 5) and continued until the seal returned to shallow water adjacent to the haul-out site.

TABLE I

Mean dive duration, mean surface interval (sec) and mean percentage time submerged for different diving behaviour

	Number of dives	Mean (S.E.) dive duration	Mean (S.E.) surface interval	Mean % time submerged
Travelling	399	206 (4·41)	38·5 (0·73)	84·3
Short duration trips	161	243 (7·27)	48·0 (1·27)	83·5
Resting (all)	187	321 (12·1)	58·8 (2·74)	84·5
Resting (sleeping only)	50	491 (7·53)	54·6 (1·73)	90·0

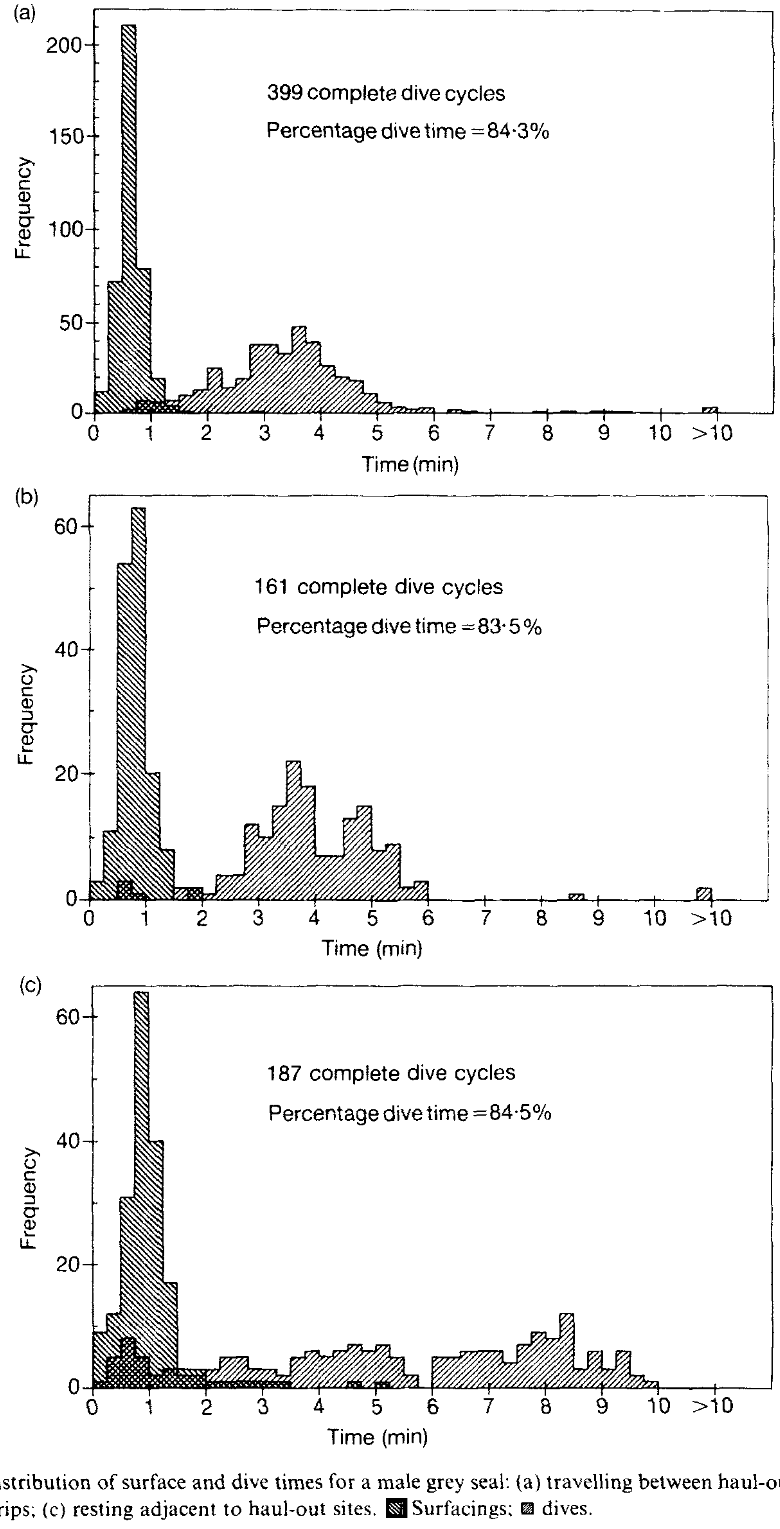

FIG. 3. The distribution of surface and dive times for a male grey seal: (a) travelling between haul-out sites; (b) during short duration trips; (c) resting adjacent to haul-out sites. ▧ Surfacings; ▨ dives.

The mean dive duration and mean surface interval for short duration trips were significantly longer (at the 1% level) than for transit dives but the proportion of time spent submerged was about the same (Table I). Distributions of surface and dive times are shown in Fig. 3b.

On five occasions during short duration trips, seal 1 was observed to be diving directly beneath dense assemblies of feeding seabirds, mostly gannets (*Sula bassana*), kittiwakes (*Rissa tridactyla*), puffins (*Fratercula arctica*), guillemots (*Uria aalge*), and shags (*Phalacrocorax aristoteles*). When directly beneath these assemblies, the seal continued to dive to the bottom at depths of 30–50 m.

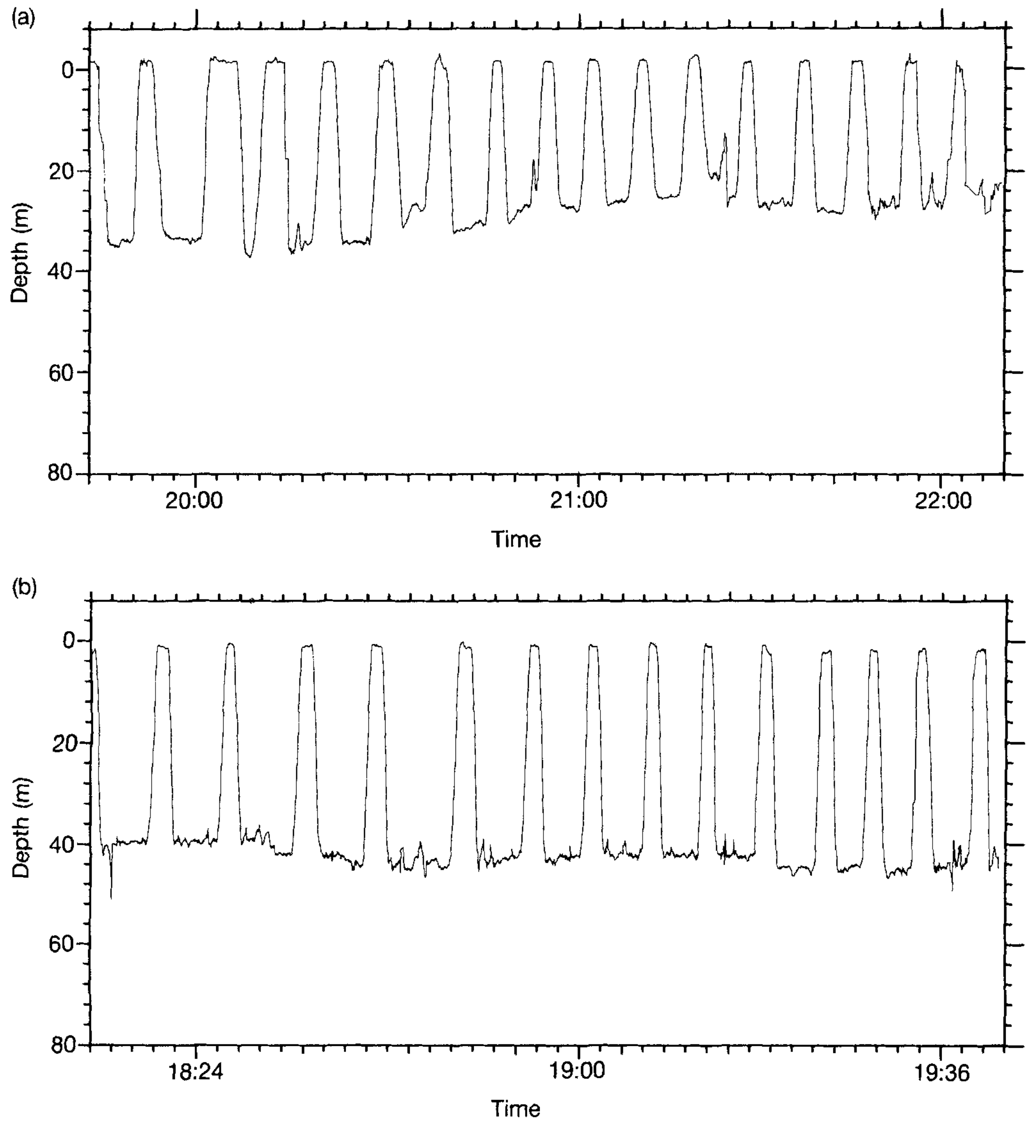

FIG. 4. Dive profiles for two male grey seals during short duration trips. (a) Seal 1 near the Isle of May; (b) seal 2 near the Farne Islands. Both plots show the typical square-wave dives seen during short duration trips. Note the different time scales in (a) and (b).

Resting adjacent to haul-out sites

Resting behaviour was characterized by an absence of directed lateral movement. It always occurred adjacent to haul-out sites used by other grey seals, mostly within a few metres of the emergent rocks. Two types of diving behaviour were observed at rest. The first was composed of a long series of long dives, the seal sinking to a constant shallow depth, probably the bottom, and remaining stationary at this depth until just before surfacing. Surface intervals were relatively short and the seals appeared to be asleep when observed at the surface. The second type comprised series of shorter, much less regular, shallow dives, with variable length surface intervals during which the seal appeared to be alert. Figure 5 shows some typical resting dive profiles.

The resting dive and surface durations were significantly longer and more variable (at the 1% level) than during other activities (Table I, Fig. 3c). Table I also gives mean dive duration, mean surface interval and mean percentage of time submerged for a subset of resting dives where the seal appeared to be asleep. In these sleeping dives, the mean dive duration and the mean percentage time submerged were significantly longer (at the 1% level) than in all other activities.

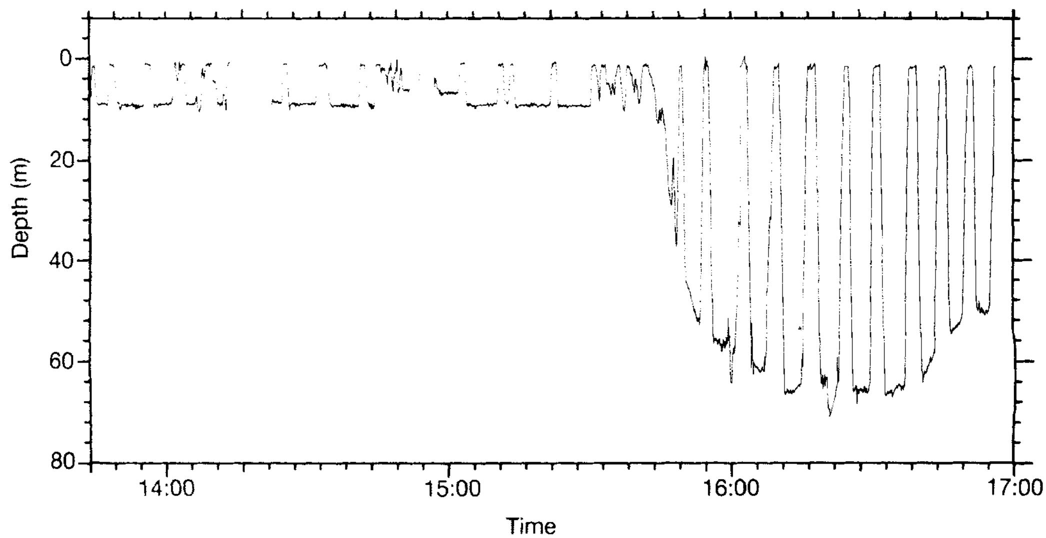

FIG. 5. Dive profiles of seal 1 initially at rest at the Isle of May then moving off on a short duration trip.

Discussion

Navigation

The observations of seal 1 swimming, at night, through very narrow channels at the Farne Islands in order to swim directly to particular haul-out rocks, suggest that the seal had an intimate knowledge of the topography of the area. The rapid, direct swimming between distant haul-out sites suggests that the seal 'knew' these destinations and had presumably visited them previously. This, together with records of several grey seals branded or radio-tagged at the Farne Islands subsequently being recorded at the Isle of May (SMRU, unpubl. data), suggests that there may be frequent interchange of seals between these sites during the summer.

The ability of seals to navigate has not been explained. On several occasions seal 1 appeared to be following a constant heading while swimming between haul-out sites. During these transits, the seal spent little time at the surface or at the bottom, hence the majority of swimming was in mid-water. The topography of the sea bed could provide some indication of location. However, at night information would be reduced to tactile or audible cues and it is difficult to envisage how such limited data could allow the seal to navigate as accurately as was demonstrated. At the surface, visual cues such as lighthouses or prominent landmarks may be used. In mid-water, however, where almost all swimming occurred, there would be no such information and at least a short-term, accurate sense of direction would be required.

Foraging behaviour

We propose that short duration trips were specifically for foraging for the following reasons: the seals were frequently associated with other piscivores; movement over the ground was very slow; and the majority of the dive time was spent at or near the sea bed. Grey seal diet is composed almost exclusively of benthic and demersal prey at all sites around northern Britain (Hammond & Prime, 1990). Seal diet at the Farne Islands was found to consist mainly of sandeel (*Ammodytes* spp.), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*), and at the Isle of May it consisted mainly of cod and sandeel. The main food taken by gannets, puffins, guillemots and shags in the Firth of Forth is sandeel, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Nelson, 1978; Harris, 1983; Bradstreet & Brown, 1985). When diving repeatedly beneath feeding seabirds, seals may be feeding on the deeper parts of the shoals being preyed upon by the shallow feeding birds, or on predatory fish which were themselves feeding on the smaller shoaling fish.

All three seals spent all the time whilst they were being tracked in inshore waters, and all feeding forays were made close to haul-out sites. They appeared to spend very little time actively foraging; e.g. seal 1 spent only 14% of his time on four short-duration trips with square-wave dive patterns. This low level of foraging activity and the presence of many other grey seals in these areas throughout the summer suggests that food was readily available at each site. It is unclear, therefore, why seal 1 spent so much time moving between haul-out areas. Why should a seal leave one apparently suitable, productive feeding area for another?

Bottom diving during transit

Seal 1's habit of diving to the bottom during every transit dive is an interesting result. Continual diving can be explained as the result of the seal avoiding surface drag effects, which decrease with depth. However, this surface effect is trivial below a depth equivalent to a few body diameters, in this case only a few metres, and it is not clear why a seal should dive to the sea bed each time, often at depths of over 60 m. We propose that the purpose of this behaviour is opportunistic foraging. By maintaining continuous V-shaped dive profiles a seal is able to sample the sea bed for potential foraging sites on every dive with an increase of only 3–6% in total swimming distance. This idea is reinforced by the occurrence of prolonged square-wave 'foraging' dives at irregular intervals during transit.

Similar V-shaped dives are performed by northern elephant seals leaving breeding sites on Año Nuevo Island, California (Le Boeuf *et al.*, 1988). These seals approach the sea bed on each dive until reaching the continental shelf when they immediately begin very deep diving. It is possible that these are also exploratory dives, allowing the animal to swim rapidly out to deep water while frequently testing for the shelf edge and hence to begin foraging as soon as possible.

Resting

All three seals spent long periods resting in the water next to haul-out sites. They were submerged, and hence invisible, for over 80% of this time. Estimation techniques relying on direct counts of seals to indicate local abundance clearly need to account for this behaviour.

It is known that diving bradycardia in pinnipeds is associated with a general metabolic depression (Kooyman *et al*., 1980; Fedak, 1986), i.e. the animal has a lower overall metabolic rate when breathing periodically. Thus, an undisturbed seal which is able to commit itself to periods of resting dives may use less energy than when resting on land or at the surface. The implications of this for long-term energy requirements are intriguing.

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