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Comparative Habitat Use and Foraging Behaviour of Harbour Seals and Grey Seals in Western Norway

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ABSTRACT

Adult harbour seals at Froan nature reserve, Central Norway, were tagged with VHF radio tags and depth-velocity, hart rate and stomach temperature sensors combined with ultrasonic transmitters. An automatic shore based VHF station received and logged information on surfacing intervals, surface times, and haul out periods. VHF signals were used to locate seals, and when seals were located at sea they were tracked at close proximity by inflatable boats with directional VHF receiver and hydrophones receiving ultrasonic transmitted behavioural and physiological data.

A combination of VHF and depth-velocity data was used to describe the activity of seals as transit-, foraging-, and resting behaviour. Swimming speed of about 1.1-1.6 m/sec and dive duration of 3.3 min (s.d. 1.9) were typically recorded for transit and foraging dives. There was no significant difference in dive times of transit dives and foraging dives. However, the dive profiles were clearly different, showing V-shaped transit dives and U-shaped foraging dives. Each seal used one or a few resting sites where seals typically congregated. However, solitary haul outs were also recorded.

Tracking free ranging seals at close proximity, made it possible to identify and describe their resting, foraging and display areas. When foraging, all tagged harbour seals operated solitarily, and they returned repeatedly to the same or approximately the same foraging sites. The radio tagged seals used different types of foraging habitats, ranging from shallow offshore kelp beds to 150-200 deep basins with muddy sea floor located few hundred meters off the respective haul out sites. Harbour seal foraging trips of up to 20 km were recorded.

Grey seals congregate at Froan in the breeding season. Towards the end of lactation, adult females were tagged with satellite linked transmitters. Shortly after end of lactation they dispersed and foraged at distances of up to 500 km from their breeding sites. After the first dispersal, grey seals settled (for an unknown period) and made repetitive short range trips at sea. These trips were interpreted as foraging movements. There was considerable overlap in the diet of harbour and grey seals in this area. Both seal species were foraging at or close to the sea floor. However, herring was the dominant species in the diet of harbour seals, while gadoids were more important in grey seals.

KEY WORDS: HARBOUR SEAL; GREY SEAL; HABITAT USE; DISPLAY BEHAVIOUR; FORAGING ECOLOGY

INTRODUCTION

The harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) are common, but not numerous at the west coast of Norway (Bjørge 1991; Wiig 1986). The harbour seal has typically been regarded as non-migratory and littoral in distribution (Bigg 1981), and exhibiting a diurnal haul out pattern (Stewart 1984; Roen and Bjørge 1995). Recent studies however, e.g. by Thompson and coworkers (Thompson 1981; Thompson and Miller 1990; Thompson et al. 1991), have revealed seasonal and year to year movements between a few haul out sites and between foraging locations. Thompson (1993) nevertheless concluded that harbour seals are resident in the same geographical area throughout the year. The diurnal haul out patterns and the limited traveling speed deployed, indicate that harbour seals forage within a few kilometers of their haul out sites. This is supported by studies of foraging movements of radio tagged seals where most foraging activity was less than 50 km from haul out sites (Stewart et al. 1989; Thompson and Miller 1990; Thompson et al. 1991; Thompson 1993). A typical harbour seal habitat should provide, therefore, suitable haul out sites, shelter during the parturition and lactation periods and sufficient food within reach of the haul out sites to sustain the population throughout the year.

Grey seals congregate in colonies in the breeding season. After breeding they disperse widely and their foraging movements may span hundreds of kilometers (McConnell et al. 1992). Although foraging may occur offshore, grey seal are frequently seen hauled out at exposed rocks along the west coast of Norway also outside the breeding season.

This paper is based on studies of seal behaviour and diet of seals at the west coast of Norway. The behavioural studies were organized as a joint project by the Norwegian Institute for Nature Research, NINA, Oslo, Norway, and the Sea Mammal Research Unit, SMRU, Cambridge, UK (Bjørge et al. 1995). Information on seal diet was generated by a project at NINA. Stomach samples were collected by the Institute of Marine Research, Bergen, Norway.

MATERIAL AND METHODS

The behavioural study was carried out in Froan Nature Reserve off the coast of Central Norway at 64° N 9° E. Samples for analysis of seals diet were collected between 62 and 66 degrees North. Froan is a coastal archipelago with a large number of small islands and islets on a shallow water plateau, and this area is used by both harbour and grey seals for breeding. Froan is separated from the mainland coast to the east by a 50 km wide and 500 m deep basin and separated from larger islands to the south by 300 m deep and about 5 km wide channels. To the north and west, Froan is exposed to the North Atlantic.

The harbour seals breed in the southern and central part of the archipelago in June and the number of animals in the area at the time of the study probably exceeded 200 animals (Bjørge 1991). Grey seal congregate in Froan in September - November to breed. Outside the breeding season grey seals are commonly seen but not numerous in the nature reserve.

Site fidelity and restricted foraging movements make the harbour seal suitable for studies of haul out and foraging distribution using short range VHF radio telemetry, and such studies have been carried out at several locations since late 1970's (e.g. Brown and Mate 1983; Pitcher 1981; Thompson and Miller 1990; Thompson et al. 1991). In this study, we conducted detailed investigations of the habitat use and at-sea behaviour of harbour seals before and during their breeding season, and after the moult. In order to obtain detailed real time information on the at-sea behaviour of individual seals, VHF telemetry was combined with underwater ultrasonic transmitter to collect data on dive depth and behaviour.

After the breeding season the grey seals range widely and it is difficult to decide which breeding colony they may belong to. Due to the short range of VHF radio tags, these tags are not suitable for tracking grey seal movements. Satellite linked tags were therefore used on adult grey seals at Froan to study the post breeding dispersal and thereby the range of this breeding population.

Seal capture and handling
Seals were captured in nets with mesh size of 17 - 19 cm (stretched mesh). The nets were set close to haul out sites and watched continuously to minimize the risk of drowning seals. A total of 13 harbour seals were tagged: 2 males and 2 females in June-July 1990; 3 males in June 1991; 1 female and 5 males in August -September 1993 (not all seals had a complete set of transmitters). Four female grey seals captured towards the end of the lactation period, and one female was tagged in September just before the breeding season.

When necessary, seals were tranquilized by Zoletil 100 (Laboratories Reading, Z.A.C. 17 Rue des Marronniers, 94240 L' Hay-les-Roses) before further handling. After handling seals were left on land until they voluntarily entered the water.

Tags and tagging
Small VHF radio tags transmitting on frequencies between 142.0 and 142.5 MHz (produced by Marine Radar Ltd, UK) were attached to the head of the seals. This position was chosen to ensure that the aerial was exposed when seals were at the surface.

Depth-velocity tags were attached behind and above the right fore flipper. These tags were composed of a pressure sensor, paddle wheel, alkaline battery and an ultrasonic transmitter. Components were made by VEMCO Ltd, Halifax, Canada, and assembled at SMRU. A temperature tag (produced for this project by SINTEF, Trondheim, Norway) composed of a temperature sensor, alkaline battery and an ultrasonic transmitter was lowered though the oesophagus and placed in the stomach of the seal. Experiments on captive harbour seals at NINA-University of Oslo, showed that the temperature tags would remain in stomachs from two to about 14 days. Ultrasonic tags transmitted on frequencies between 60 and 99.9 KHz and all external tags were glued to the fur using an epoxy resin as described by Fedak et al.(1983).

The satellite tags were produced by TOYACOM and transmitting at frequency 401 MHz. In addition to generating information on the seals horizontal movements, the tags were recording dive depth and swim speed. The final analysis of grey seal movements is not yet completed.

Data recording and tracking
An automatic land based VHF radio receiving station received and stored radio signals from the harbour seals when they were hauled out or at the surface. The VHF radio station is described by Nicholas et al. (1992) and was composed of a set of aerials covering 360 degrees, a YAESU VHF/UHF Communication Receiver FRG-9600, and a SANYO 16LT portable computer used as datalogger. The station could be programmed to switch from one frequency to another and thus record information from more than one animal.

Tracking seals at sea was conducted by a directional VHF radio (a purpose built directional aerial and display unit and a YAESU VHF/UHF Communication Receiver FRG-9600) mounted onboard an inflatable boat, type Zodiac MK IV with twin 30 hp Johnson outboard engines. The VHF signals were used to locate and close in on seals at sea. Information on dive duration and dive intervals and positions of the tracking boat were automatically logged on a SANYO 16LT portable computer. Position of the tracking boat was obtained by a GARMIN GPS 65 Personal Navigator.

When tracking seals at close proximity, detailed behavioural and physiological data from the ultrasonic transmitters were received by hydrophone and logged on VEMCO VR60 Ultrasonic Receivers (Manufactured and marketed by VEMCO Ltd, Halifax, Canada).

RESULTS

Harbour seal haul out patterns and haul out sites

We considered that continuous VHF signals for 8 minutes or more indicated that seals were hauled out. Although haul out bouts were recorded both during day and night and at high and low tide, there was a tendency for seals to haul out more frequently during the day and at low tide. After a trip to sea, seals regularly returned to the same haul out rock or to adjacent rocks in the same area. The radio tagged seals typically hauled out among other seals on intertidal rocks in clusters of small islands (e.g. at Hestvær, Sandskjær and Måsskjær in Fig. 1). One seal (91M2) tagged at Hestvær however, regularly hauled out alone just outside the harbour of Sørburøy (Fig. 1).

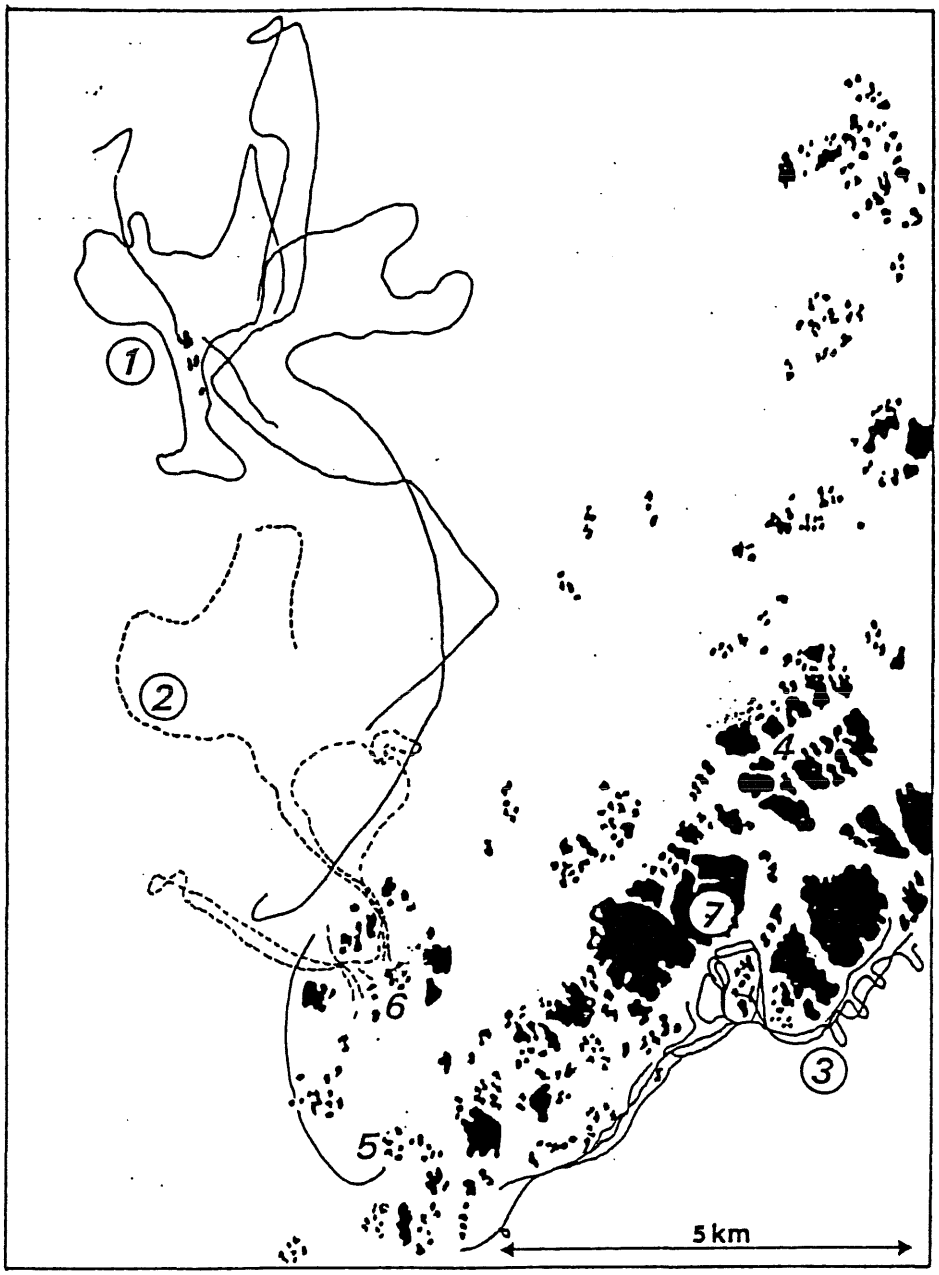

Fig. 1. The southern part of the archipelago of Froan, Norway. 1, 2 and 3 are examples of foraging movements of three adult male seals (seals 91M3, 90M2 and 91M2, respectively). 4, 5 and 6 are haul-out sites frequently used by harbour seals at Hestvær, Sandskjær and Måsskjær; 7 is the island of Sørburøy.

Harbour seal dive profiles as indicators of transit and foraging activity
When the seals were at sea, we used dive profiles to characterize their behaviour. Travelling to and from the foraging grounds, the seals moved in typical V-shaped dives (Fig. 2). Usually we observed several consecutive V-shaped dives in a constant direction, and we defined these dives as transit dives. These dives did not always reach to the sea floor.

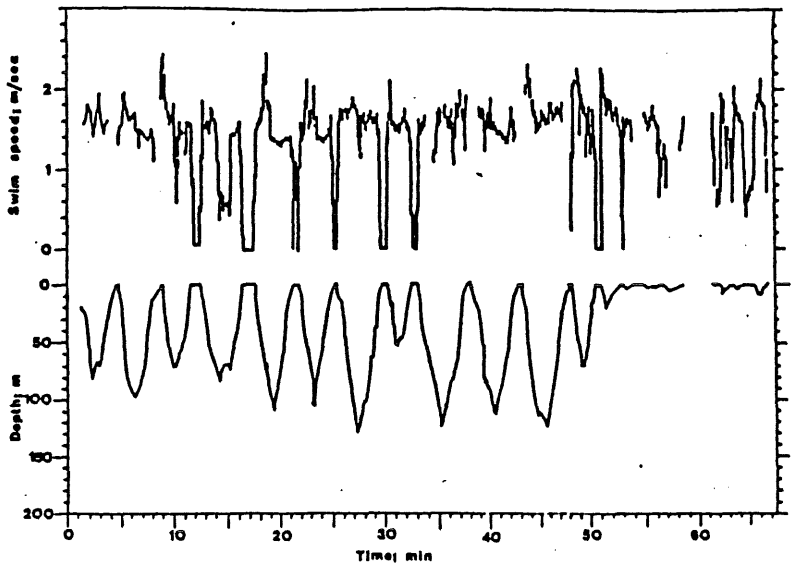

Fig. 2. Swim speed and V-shaped dive profiles of an adult male harbour seal. The V-shaped dives were defined as transit dives.

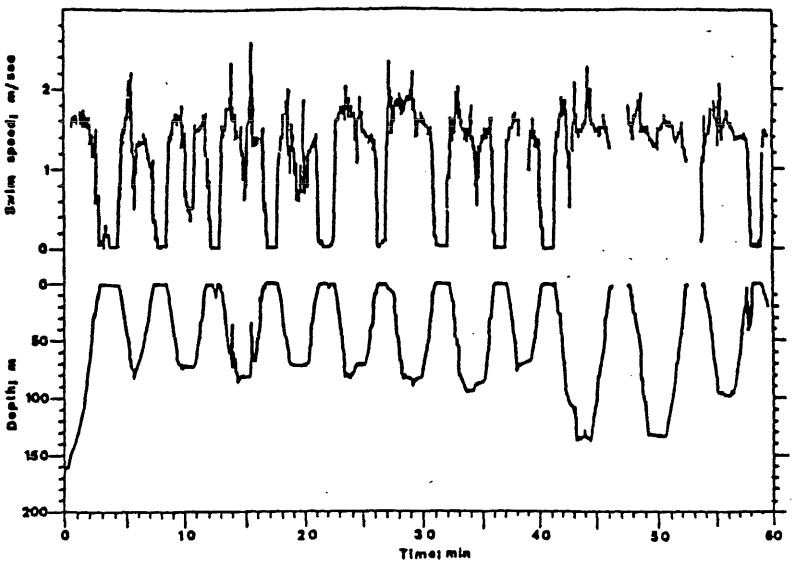

Fig. 3. Swim speed and U-shaped dive profiles of an adult male harbour seal. The U-shaped dives were defined as foraging dives.

When seals ceased directed travel at sea, a different type of dives was observed. The dive profile was U-shaped (Fig. 3), the dives usually reached the sea floor and the swimming direction frequently changed during and between dives. We defined these dives as foraging dives. The stomach temperature was used as further support in identification of foraging activity. Significant drops in temperature were interpreted as ingestion of food. An example is given in Fig. 4. On

this occasion the stomach temperature of seal 93M3 was lowered stepwise from about 37°C to about 30°C over a period of 30 minutes during a trip at sea. The temperature gradually returned to about 37°C over a longer period of time (Bekkby and Bjørge 1995).

In a few occasions, in particular when seals foraged in areas with complex topography, transit and foraging type dives may be mingled.

Dive durations of transit and foraging dives were not significantly different, and the average dive duration was 3.3 minutes (s.d. 1.9 minutes). The longest dive recorded was 14.3 minutes. For both transit and foraging dives the swimming speed was typically between 1.1 and 1.6 m/sec.

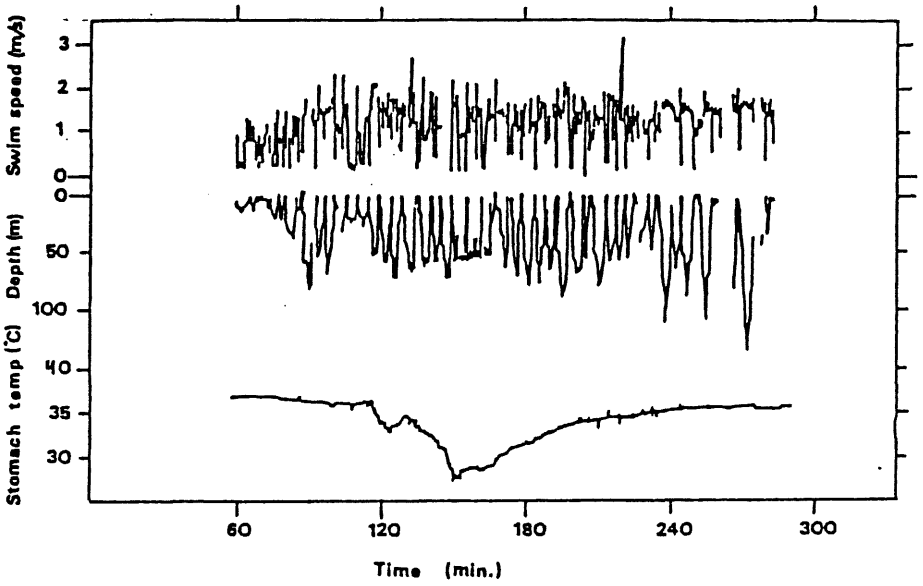

Fig 4. Swim speed, dive profiles and stomach temperature of an adult male harbour seal foraging at sea.

Examples of harbour seal foraging trips

All recorded harbour seal foraging activity was at or close to the sea floor. At the sea floor, the seals continued swimming, presumably searching for food, at their usual swim speed. The seals foraged at water depths between 15 and 200 meters and in areas with different substrate. Examples of foraging behaviour of typical seals are given below.

One male seal tagged June 22, 1991 (91M3) travelled regularly about 20 km from his haul out site at Sandskjær to feed at some shallow offshore rocks (Fig. 1). He fed predominantly at depths between 15 and 50 meters. Between his haul out site and foraging grounds he passed through a 200 meter deep basin where other radio tagged seals were foraging (see below). Seal 91M3 however, showed no sign of foraging activity until he reached the shallow rocks. His foraging trips were approximately 8 to 22 hours long and most of his foraging activity was during night hours (between 18:00 and 06:00). The seal remained in water until he was back at his haul out site. However, during the longer foraging trips, periods of little movement were recorded. We interpreted these periods as periods with resting in water.

Another male seal (90M2) tagged July 6, 1990 foraged in a deep basin 3-6 km from his haul out sites during July (Fig. 1). His foraging trips were 3 to 8 hours long, predominantly during day hours, and he repeatedly returned to his haul out site or to a site were he remained stationary in water for several hours (see description of display sites below).

A male seal tagged June 13, 1991 (91M2) foraged off the east side of the archipelago. This seal often hauled out outside the harbour of Sørburøy and was foraging within distances of 5 km from his haul out site (Fig. 1). Most of his foraging activity was at depths of about 100 m. This particular seal started or finished his foraging trips in shallow sandy bays (depth of 15-30 m), where he caught flatfish, as verified by visual observation when he brought his catch to the surface. This seal foraged predominantly during night hours, and the swimming speeds and dive profiles of his nocturnal foraging trip from June 17 to June 18 are shown in Fig. 5.

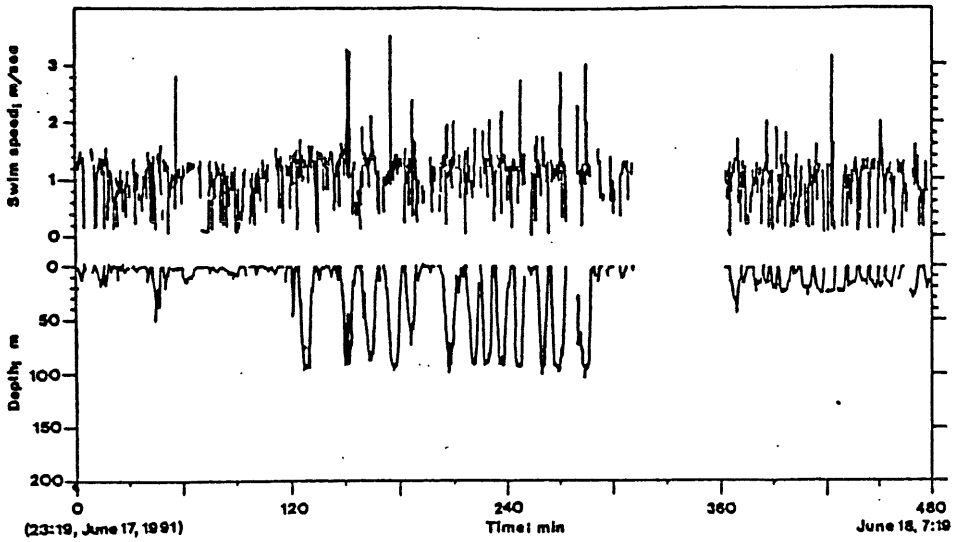

Fig. 5. Swim speed and dive profiles of an adult male harbour seal (91M2) during a nocturnal foraging trip from June 17 to June 18, 1991. The X-axis is time in minutes from start tracking. From 0 to 120 min the seal moved at the surface close to the islands. Between 120 and 248 min he foraged at about 100 m depth about 0.5 km from shore. From 248 min he moved into shallow water where he foraged between 362 and 480 min. The pause in tracking between 253 and 260 min was due to echo-sounding the first foraging grounds which prevented receiving ultrasonic transmitted data from the seal.

One male seal (93M3) tagged at Hestvær August 28, 1993 foraged on slopes, mostly at depths between 30 and 150 m in the waters mainly north of the haul out site. He foraged predominantly during the day and regularly returned to Hestvær to haul out. However, on September 2, when he foraged on the east side of the archipelago about 5-8 km from Hestvær, he hauled out about 5 km east of his usual haul out site. On September 4 he foraged about 15 km northeast of Hestvær and he hauled out about 10 km from his normal haul out site.

Harbour seal foraging habitats

Using the dive profiles as indicators of foraging activity, we were able to identify the foraging grounds of the individual seals. Foraging was recorded at or close to the sea floor at depths ranging from 15 to 200 m and on different substrate. The complex topography at Froan creates a diversity of habitats and the harbour seals used a variety of these for foraging.

The foraging grounds of seal 91M3 can be described as shallow rocks, 15 to 50 m below surface. At depths of less than 35 m the rocks were covered by kelp forest. The main kelp species was *Laminaria hyperborea* where adult plants may have a stipes of 2 meter and a leaf of 1-1.5 meter. The behavioural data did not provide information on whether the seal was foraging within or just above the kelp forest. Echo-surveys showed concentrations of fish surrounding the top of these shallow rocks. The fish were thought to be young saithe *Pollachius virens*.

Seal 93M3 foraged on slopes from the deeper part of the kelp forest to depths of about 120 meters. The substrate was characterized by rocks and stones in the kelp zone and stones, gravel, shells, sand and mud as the depth increased. The foraging grounds of seal 93M3 were not echo-surveyed, but concentrations of fish and single fishes were recorded at similar habitat types in 1991. The recorded concentrations of fish were probably young saithe.

In shallow bays and narrows between islands, the substrate consisted of shells, crushed shells, sand and clay. In shallow parts, such bays and narrows were often dominated by sea grass *Zostera marina*. No concentrations of fish were recorded when echo-surveying this habitat type. Seal 91M2 used this habitat type for parts of his foraging activity. However, during most of his foraging, seal 91M2 searched for food at depths of about 100 m on substrate of gravel, sand and mud where the sea floor was gently sloping down into the 500 m deep basin east of the archipelago. Echo surveys showed dense schools of fish at these foraging grounds of seal 91M2, and based on the characteristics of the echogram the fish species was thought to be herring *Clupea harengus*.

Seal 90M2 and several of the tagged seals not described here, foraged at the sea bed in 100-200 m deep basins, 2 -15 km from their haul out sites. The substrate in these basins was soft, consisting of mud and ooze. No concentrations of fish were recorded at these sites.

Harbour seal display behaviour and breeding habitats

In June 1991 three adult males were tagged (91M1 on June 6; 91M2 on June 13; 91M3 on June 22). Until about June 27 they alternated between foraging trips and hauling out. From June 28 and July 3 seals 91M1 and 91M2, respectively, changed their activity patterns. Between foraging trips they spent much of their time in water at particular sites with repetitive dives uniform in both profile and duration (Fig. 6). The mean duration of these dives was 3.34 minutes (sd 0.34) and mean surface interval was 0.53 minutes (sd 0.16). The seals vocalized at 45-60 second intervals during each dive giving 3 to 5 calls per dive. One seal was monitored for periods of 3 hours but VHF reception indicated that he performed similar dive patterns for up to 7 hours continuously. The characteristics of these calls are described in detail by Thompson et al. (in press). We interpreted this behaviour as sexual display activity.

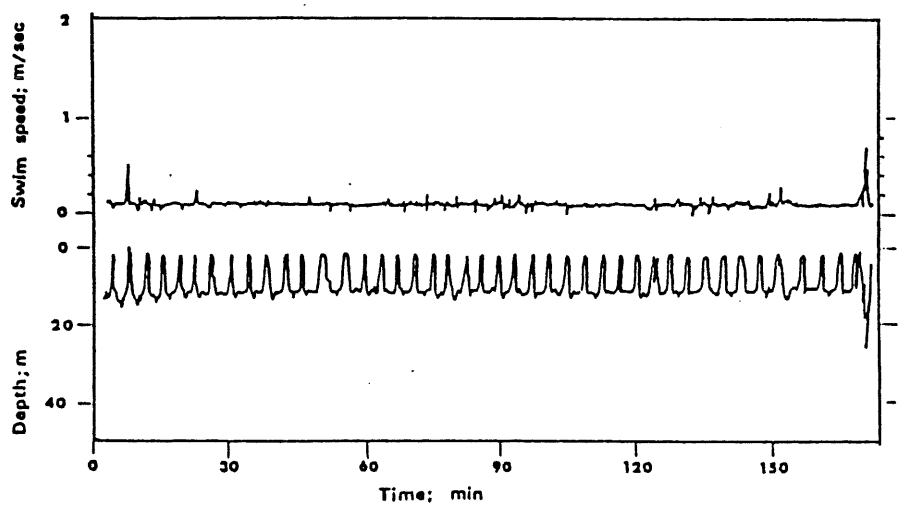

Fig. 6. Swim speed and dive profiles of an adult male harbour seal (91M1) displaying and vocalizing, July 3, 1991 at Froan, Norway.

Similar calls were recorded over large areas in Froan. At some sites, we heard calling at rates up to 6 calls per minute. Dividing the call detection rates by the calling rate of our tagged seals indicates that between five and nine seals were calling within the audible distance of our hydrophone at some sites. These sites were mainly in the deeper channels penetrating into the shallow water plateau between the haul-out sites which were used by females with pups and other seals (Fig.7). Harbour seals breed on intertidal and small islets in sheltered locations the central and southern part of Froan.

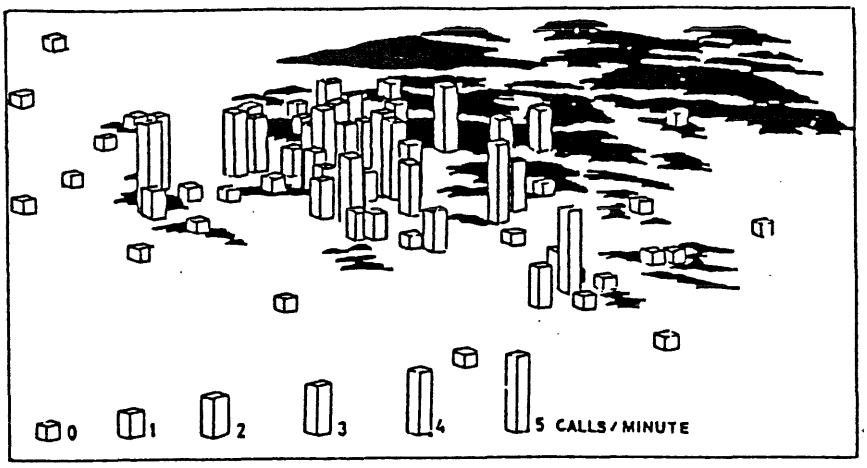

Fig. 7. Display vocalization by male harbour seals at southern Froan in late June early July 1991. The height of bars indicates number of calls per minute.

Grey seal breeding habitats
Grey seals breed in the northern part of Froan in October, and they choose larger and more exposed islets for their breeding. There is no (or very little) terrestrial macro-vegetation on these islets, and some of them may be washed over in extreme weather.

Dispersal of adult grey seals after breeding season
After the lactation finished, four of the five tagged female grey seals left Froan. The average duration of the tags were about 60 days. In the period we received signals from the tags, one seal remained in the area; two seals moved east to the mainland coast; one moved about 100km to the south and one moved about 500 km northward along the coast to Værøy in Lofoten. Examples of adult female grey seal dispersal from Froan after breeding are shown on Fig. 8.

Grey seal foraging habitats
When seals settled in an area they had repetitive local movements withing that area at distances of few km to few tens of kilometers. These local movements were interpreted as foraging trips. The depth range were the seals may have been foraging varied from shallows to about four hundred meters. A full analysis of the satellite transmitted data will provide information on foraging depths.

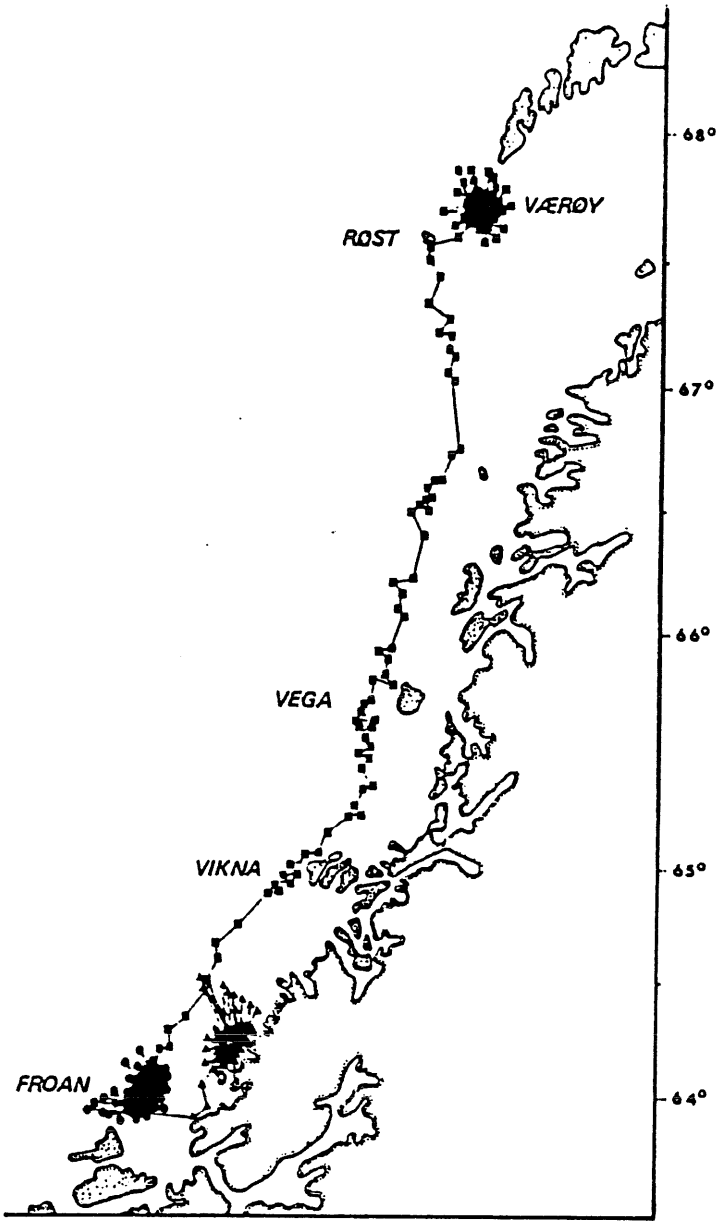

Fig. 8. Dispersal of three satellite tracked adult grey seal females from Froan after breeding.

Differences in harbour and grey seal diet composition

Fish species recorded in stomach contents from 236 harbour seals and 21 grey seals sampled between 62 and 66 degrees North in the period 1978-1982 are shown in Table 1. There is considerable overlap in diet composition between the two seal species with regard to fish species present in the diet. However, herring, *Clupea harengus*, which was the most frequently occurring fish species in the harbour seal (about 40 % by volume of stomach content) constituted less than 1% by volume in grey seal stomach content. Codfishes (Gadidae) are important in both seal species, but more so for the grey seals then in harbour seals. Haddock, *Melanogrammus aeglefinus*, was important in grey seals (15% by volume in stomach content) but not occurring in harbour seals.

Table 1. Occurrence of fish species in the diet of harbour seal (*Phoca vitulina*) and gery seal (*Halichoerus grypus*) between 62 and 66 degrees north at the Norwegian west coast. The depth range, benthic (B) or pelagic (P) occurrence in fish species are indicated (Pethon 1989).

	P.v. N=236	*H.g.* N=21	B	P	Depth range 0 50 100 150 200 250 300
Clupeidae					
Herring *Clupea harengus*	+	+			----------
Sprat *Sprattus sprattus*	+				-------
Salmonidae					
Salmon *Salmo salar*	+			+	-----
Argentinidae					
Greater argentine *Argentina silus*	+	+		+	----------
Gadidae					
Cod *Gadus morhua*	+	+	+	+	----------
Saithe *Pollachius virens*	+	+		+	----------
Pollach *Pollachius pollachius*	+	+	+	+	----------
Whiting *Merlangius merlangus*	+	+	+	+	----------
Haddock *Melanogrammus aeglefinus*		+	+		----------
Norway pout *Trisopterus esmarkii*	+	+	+		----------
Poor cod *Trisopterus minutus*	+		+		-------
Wolf fish *Anarchichas lupus*		+			
Lumpsucker *Cyclopterus lumpus*		+	+	+	----------
Libridae					
Ballan wrasse *Ctenolabrus rupestris*	+		+		-----
Scombridae					
Mackerel *Scomber scombrus*	+			+	----------
Cottidae					
Sculpin *Myoxocephalus scorpius*	+		+		-----
Scorpaenidae					
Red fish *Sebastes marinus*	+	+	+		----------
Red fish *Sebastes viviparus*	+	+	+		----------
Ammodytidae		+	+	+	----------
Pleuronectidae					
Lemon sole *Microstomus kitt*	+		+		----------
Unidetified flatfish species	+	+			

DISCUSSION

At Froan, seals haul out on rocks and apparently suitable rocks are available throughout the tidal cycle. However, the haul out pattern of harbour seals in this area was influenced by the diel cycle and tidal cycle. The number of hauled out seals peaked at low tide, but according to Roen and Bjørge (1995), the peaks were higher during the day than during the night. This may indicate a preference for foraging at night and a tendency to skip one haul out bout at low tide during the night. The radio tagged seals had different timing to their foraging trips, but at least two seals (91M2 and 91M3) showed preference for foraging at night. The number of successfully tracked seals was too limited to evaluate the 24 hour distribution of foraging activity. In a sample of 17 radio tagged seals in California, 6 seals hauled out most often during day, 7 hauled out most frequently during night and for the rest of the tagged seals, no preference were recorded (Yochem et al. 1987). In most studies, the predominant diurnal pattern indicates that seal are foraging at night. However, Thompson (1993) found that harbour seals in the Moray Firth fed more often during the day when feeding on wintering clupeids. At Froan, hauled out grey seals were observed on exposed, offshore rocks in May-July. However, there was no systematic recording of grey seal haul out pattern.

During May, June and July the tracked harbour seals normally returned to their usual haul out (or display) sites after a foraging trip. Tracking of seal 93M3 after moult in September 1993 indicated that this seal frequently hauled out at alternative sites, e.g. after a period of active foraging and before returning to the usual site. The present data provide, however, no basis to conclude whether this was due to individual behaviour, or if it reflects a change in behaviour and site fidelity after moult. However, Thompson (1993) stated that breeding may influence movement patterns of harbour seals.

In June and July the seals showed strong site fidelity towards haul out sites and also towards display sites in sexually mature males. Seals tracked during this period were solitary when foraging and they regularly returned to the same or approximately the same feeding grounds for several trips during the period of tracking. Most of the foraging activity was within few kilometers of the haul out sites. Under such conditions, intraspecific competition for food and feeding grounds may develop. The variety of different types of foraging habitats utilized by the harbour seals and the pattern of returning to the same feeding grounds may be indication of individual specialization and a means to minimize intraspecific competition and optimize foraging in periods of the year when site fidelity may cause constrains on the foraging movements of these seals.

Are harbour and grey seals specialists or opportunistic feeders?
According to Härkönen (1987), the harbour seal is an opportunistic feeder within some groups of fish, but it does not feed on all abundant species available. The methods used in the present study are not sufficient to determine whether individual seals are opportunistic or specialized in their foraging behaviour. They cannot reveal whether individual seals vary their diet from day to day (as is most likely with opportunistic feeding), or if they forage persistently on a narrow range of species of prey (as is the case with specialized foraging).

The considerable overlap in diet composition of harbour and grey seals may indicate that both seal species are opportunistic and forage on the available resources. The individual specialization with regard to foraging habitat as indicated in this study, may be a result of intraspecific competition between harbour seals. However, within their particular habitat, harbour seals may be opportunistic predators. The grey seals seem to be opportunistic both with regard to foraging area and prey species. However, the difference in diet composition may indicate that grey seals are more confined to demersal fish than is the harbour seal.

Foraging depths
The radio tagged harbour seals at Froan were foraging close to the sea floor. Several fish species do migrate vertically and are distributed deeper or closer to the sea floor during the day. Foraging during the day may be advantageous if seals are feeding on species which are more easily caught when they are concentrated on the sea bed and this limits the range of escape routes. However, some deep water fish, such as the greater argentine, may be available to the seals only during their nocturnal vertical migrations, indicating that seals may benefit of nocturnal foraging.

Knowledge of the distribution and biology of the prey species may provide information on what depth and in which fish community the seals have been feeding. The present study shows that harbour seals in Norwegian waters had been feeding on species that are found in a variety of depths and habitats (Table 3). The diet contained fish species that are normally found at depths of more than 100m (e.g. redfish *Sebastes marinus*, greater argentine *Argentina silus*), as well as demersal species found in shallow waters (poor cod *Trisopterus minutus*, ballan wrasse *Ctenolabrus rupestris*, and sculpin *Myoxocephalus scorpius*). Of demersal fish species preferring water deeper than 100m, red fish prefers hard sea floors while Norway pout *Trisopterus esmarkii* prefers soft sea beds. In shallow water, ballan wrasse and sculpin prefer areas covered by sea weed; and the flat-fishes (Pleuronectidae) are primarily found on sandy sea floors. Some of the species recorded in the diet of harbour seals are pelagic species. Greater argentine are often found in mesopelagic waters deeper than 100m, while salmon and sprat are normally found near the surface.

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