

ORIGINAL PAPER

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Annual distribution of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas

Received: 3 August 1994/Accepted: 4 July 1995

Abstract Nineteen hooded seals (*Cystophora cristata*) were tagged with satellite-linked platform terminal transmitters (PTT) on the sea ice near Jan Mayen. Fifteen were instrumented after completion of the moult in July 1992 (five males, ten females, at 71°N, 12°W), and four during breeding in March 1993 (four females, at 69°N, 20°W). Sixteen of the seals were tagged with Satellite-Linked Time-Depth-Recorders (SLTDR), yielding location, dive depth and dive duration data. The average (\pm SD) longevity of all PTTs was 199 ± 84 days ($n = 19$; range: 43–340 days), and they yielded 12,834 location fixes. Between tagging in July 1992 and pupping in March 1993, two seals remained in or near the ice off the east coast of Greenland for most of the tracking period. However, most of the seals made one or several trips away from the ice edge, mostly to distant waters. These excursions had an average (\pm SD) duration of 47 ± 22 days ($n = 46$; range: 4–99 days). Eight seals travelled to waters off the Faeroe Islands, three to the continental shelf break south of Bear Island, and three to the Irminger Sea southwest of Iceland. Eleven seals were tracked in the period between breeding (March/April) and moulting (July). Several of these spent extended periods at sea west of the British Isles, or in the Norwegian Sea.

Jan Mayen (West Ice) stock of hooded seals gather along the drift ice edge to breed in late March, and then reappear in the drift ice to moult in July (e.g., Øritsland 1959; Rasmussen 1960). During the remainder of the year these seals disperse and are less accessible for studies. Therefore, their distribution, behaviour and diet outside the breeding and moulting periods are not well known. The size of the Jan Mayen (West Ice) stock of hooded seals is not known. Based on catch statistics and older estimates of the stock size (e.g. Rasmussen 1960), we believe that it must count at least 250,000 animals. A stock of this size may have important effects on fisheries resources in the central and northeast Atlantic Ocean. However, the extent of fish consumption by hooded seals is difficult to assess, since little is known both of their annual distribution and their prey selection at various times of the year. The present study addresses the first of these problems in dealing with data on the geographical distribution of hooded seals from the Jan Mayen (West Ice) stock at different times of the year. Due to the dispersal of these seals after breeding and moulting in remote areas of the North Atlantic, this type of information can only be obtained from this pelagic pinniped species by use of satellite telemetry and tracking.

Introduction

The hooded seal (*Cystophora cristata*) is a key pinniped species in the Greenland and Norwegian Seas. Hooded seals breed on the sea ice between the east coast of Greenland and Jan Mayen (the “West Ice”), off the west coast of Greenland (in the Davis Strait), in the Gulf of St. Lawrence, and off Newfoundland (the “Front”). The

Materials and methods

Catching and tagging

Subadult and adult hooded seals were caught and equipped with satellite-linked platform terminal transmitters (PTT) during two expeditions to the West Ice, one in July 1992 with the Norwegian sealing vessel M/V “Polarfangst” and one in March/April 1993 with the Norwegian Coastguard frigate “Senja”. The Jan Mayen (West Ice) stock of hooded seals moult in July and then spend much time hauled out on ice floes, often being reluctant to enter water. Moulting seals were caught on the ice by rapidly approaching them in a rubber boat with a 40 HP outboard engine, and throwing a large hoop net (opening diameter, 1.5 m; length, 3 m) over them. In March/April 1993, breeding hooded seals were found in relatively

dense and heavy ice and could not be reached with the boat. Instead, a helicopter based on board "Senja" was used to get investigators to the seals.

The seals were brought on board the ships where they were weighed with a Salter balance (Salterservice, Shropshire, UK) and placed in $1 \times 2 \text{ m}^2$ pens where they were kept until they were tagged and released.

We used three different types of PTTs: 0.5-W location-only PTTs, 0.5-W satellite-linked time-depth recorders (SLTDR) and 1.0-W SLTDRs. The 0.5-W location-only PTTs were $11 \times 7 \times 6 \text{ cm}$, 600-g, epoxy-casted Telonics ST-6 units (Telonics, Mesa, Ariz.), powered by 4 C-cells. They were equipped with conductivity sensors ("salt-water switches"), which ensured that the PTTs were turned off while the seals were diving, and they had an expected depth tolerance of at least 1,000 m. The 0.5-W SLTDRs (Wildlife Computers, Seattle, Wash.) were also cast in epoxy, but measured $14.5 \times 10 \times 3 \text{ cm}$ and weighed 700 g. They were powered by 4 C-cells, giving an expected transmission capacity of 100,000 transmissions, and had a depth tolerance of at least 1,000 m. The SLTDRs were equipped with a 0 to 1,000-m-range pressure transducer, and with conductivity sensors, which, in addition to turning off the SLTDR when submerged, also allowed collection of data on whether the transmitter was wet (at sea) or dry (hauled out). The 1.0-W SLTDRs (Wildlife Computers, Seattle, Wash.) were enclosed in a housing of anodized aluminium, having an anticipated depth tolerance of 1,300 m. They were slightly larger and heavier ($12 \times 10 \times 5 \text{ cm}$; 1,100 g) than the 0.5-W SLTDRs but had the same data collection and transmission characteristics. All PTTs transmitted with a transmission repetition rate of one transmission every 50 s. The SLTDRs all operated with a daily transmission allowance of 300 transmissions. Two of the Telonics ST-6 PTTs (#9872 and #9873) were continuously active while the third (#9874) operated with a duty cycle of 4 h on/24 h off. Data from the PTTs were processed by use of the Argos Data Collection and Location System (CLS/Service Argos 1989; Fancy et al. 1988).

The PTTs were attached by gluing them to the fur of the seals, using a quick-setting epoxy resin (Araldite Type AW 2104/HW2934, Ciba Geigy, Basel, Switzerland), as described by Fedak et al. (1983). Before gluing, the seals were lightly anaesthetized by an intramuscular injection ($1.0 \text{ mg} \cdot \text{kg}_{(\text{body mass})}^{-1}$) of tiletamine-zolazepam (Zoletil100, Reading, L'Hay-Les-Roses, France). Anaesthesia was maintained during the operation by giving additional intravenous doses of Zoletil ($0.3\text{--}0.5 \text{ mg} \cdot \text{kg}_{(\text{body mass})}^{-1}$), when necessary, using a 45-mm polyethylene catheter [16G (OD = 1.7 mm) Venflon, Viggo, Helsingborg, Sweden], which was inserted into the venous plexus of one of the hind flippers. In order to make sure that setting of the epoxy did not cause skin burns, the temperature of the setting epoxy was monitored with copper-constantan thermocouples, which were connected to a BAT-12 digital thermometer (Physitemp, Clifton, USA). After gluing (usually within 1.5 h), the seals were released on an ice floe and observed until they recovered and returned to sea.

Data treatment

CLS Argos provides location data with specified precision levels, or location classes (LC). The LC are based on the accuracy of the location determination. During the present study, four different LC, from LC 3 (68% of the calculated locations guaranteed to be within 150 m of true location), to LC 0 (no guarantee given as to the accuracy of the location) (CLS/Service Argos, 1989) were available. We considered LC 0 locations to be sufficiently accurate for a study of gross movements, provided that consecutive LC 0 locations were within an acceptable range. Acceptable distances between consecutive locations were judged to be those that the seals could cover if travelling at speeds of $3 \text{ m} \cdot \text{s}^{-1}$ or less, and if LC 0 locations were outside this range, the unrealistic ones were discarded. We plotted only one location per day. When locations of $\text{LC} > 0$ were obtained,

the location with the highest LC was plotted. When all locations for a particular day were of LC 0, the mean latitudinal and longitudinal values were calculated and plotted.

Locations were related to the average extension of the sea ice (based on data obtained from the Norwegian and Danish Meteorological Institutes) and to water depths (based on bathymetric data by Perry et al. 1980).

In cases where the time periods between consecutive location determinations were long, the following principles were followed: If both locations were in the same area, the seal was assumed to have stayed in that area during the gap period. When locations were from two different areas, one usually was in ice-covered waters, and the other at high sea. In such cases, the period between two locations was assumed to have been spent at sea, since seals in ice-covered areas proved to haul out frequently and were located almost every day.

Results

Fifteen hooded seals (five males and ten females) with a post-moulting body mass (BM) range of 68–171 kg were caught at about 72°N , 10°W in July 1992, while another four females (BM range: 170–195 kg) were caught and tagged at about 69°N , 20°W in March/April 1993. Three seals (1 male, 2 females) were tagged with Telonics ST-6 location-only PTTs, 11 (2 males, 9 females) with 0.5-W SLTDRs and 5 (2 males, 3 females) with 1.0-W SLTDRs. Detailed data about the seals, including their estimated age [based on length-age relationships presented by Rasmussen (1960)] are presented in Table 1. On average, each tag supplied data for 199 ± 84 (SD) days (range: 43–340 days). The 15 PTTs that were deployed in July 1992 were expected to last until the next moult, but had an average longevity of 229 ± 66 days. However, 1 tag stopped transmitting after only 76 days, and if this tag is excluded, the average longevity of the remaining 14 tags was 240 ± 52 days, with 1 tag being active for 340 days. The four PTTs that were deployed in late March (only 80–100 days before the moult) had an average longevity of 88 ± 33 days, with three tags remaining in operation until the moult started. A total of 12,834 locations were determined during an overall tracking period of 3,787 seal days, giving, on average, 3.39 locations per day. The majority (75% or 9,638) of these locations were of LC 0, and locations with $\text{LC} > 0$ (25%) were, with few exceptions, only obtained from seals that stayed in ice-covered waters where they regularly hauled out, as shown by the conductivity sensor data.

Between the moult in July 1992 and the breeding period in March/April 1993, the sea ice edge along the east coast of Greenland [from the Denmark Strait ($\sim 65^\circ\text{N}$) in the south and to the area between Jan Mayen and Greenland ($\sim 73^\circ\text{N}$) in the north], was an important area for these animals (Fig. 1). However, most of the seals performed long and often repeated journeys to distant waters. Thus, eight seals travelled to waters off the Faeroe Islands, some (two animals) via

Table 1 Argos PTT identity number, sex, body mass (BM), standard length (L), estimated age (*based on length-age relationship by Rasmussen 1960), tagging date, tagging position, type of PTT and PTT longevity and performance [number of location class 0 (LC = 0); location class 1–3 (LC > 0) and uplinks] for 19 satellite-tagged hooded seals

ID #	Sex	BM (kg)	L (cm)	Age* (yrs)	Date tagged	Position tagged	Type of PTT	Longevity (days)	LC = 0	LC > 0	Uplinks
9663	F	100	162	3	16.07.92	72°22'N 11°48'W	0.5 W SLTDR	192	415	163	1,214
9664	M	101	184	4	16.07.92	72°22'N 11°45'W	0.5 W SLTDR	265	607	290	1,662
9665	F	110	174	4–5	16.07.92	72°22'N 11°45'W	0.5 W SLTDR	294	595	227	1,703
9666	F	98	165	3–4	17.07.92	72°26'N 11°23'W	0.5 W SLTDR	265	670	168	1,934
9667	M	120	170	3	17.07.92	72°27'N 11°20'N	0.5 W SLTDR	275	726	170	1,789
9668	F	112	165	3	17.07.92	72°28'N 11°10'W	0.5 W SLTDR	296	490	226	1,229
9669	F	112	168	3–4	19.07.92	72°38'N 10°30'N	0.5 W SLTDR	267	893	214	2,208
9670	M	159	195	6	20.07.92	72°36'N 10°25'W	1.0 W SLTDR	188	1,401	202	2,533
9671	M	134	200	7	16.07.92	72°22'N 11°45'W	1.0 W SLTDR	201	796	259	1,676
9672	F	167	194	10	24.07.92	73°23'N 14°48'W	1.0 W SLTDR	215	733	221	1,747
9870	F	156	190	8	19.07.92	72°38'N 10°27'W	1.0 W SLTDR	197	638	288	1,377
9871	F	171	194	10	19.07.92	72°38'N 10°23'W	1.0 W SLTDR	194	486	210	1,099
9872	F	104	177	5	19.07.92	72°38'N 10°23'W	Telonics ST-6	76	44	41	242
9873	M	144	180	4	26.07.92	72°44'N 15°00'W	Telonics ST-6	169	137	130	590
9874	F	68	148	2	16.07.92	72°21'N 11°48'W	Telonics ST-6	340	40	29	206
17606	F	175	180	6	30.03.93	68°49'N 20°10'W	0.5 W SLTDR	43	59	13	294
17607	F	155	170	4	30.03.93	68°49'N 20°10'W	0.5 W SLTDR	110	277	125	789
17608	F	150	180	6	30.03.93	68°49'N 20°10'W	0.5 W SLTDR	116	436	124	1,080
17609	F	235	195	10	30.03.93	68°49'N 20°10'W	0.5 W SLTDR	84	195	96	485
Σ									9,638	3,196	23,849

a route south of Iceland, but most via the route on the north side of Iceland. Furthermore, three seals spent periods in the Irminger Sea southwest of Iceland, and three others travelled between the sea ice at about 73–78°N and to open sea areas at about 72–75°N, 12–15°E (between the Norwegian mainland and Bear Island). One week after tagging one male travelled to the west and north coast of Svalbard (not shown in Fig. 1; see Fig. 3), where he remained until the PTT stopped transmitting on 23 January 1993. None of the

seals were ever recorded to haul out on beaches or skerries during any of the excursions, even though they often operated close to coastal areas for several months.

Seven (2 males, 5 females) of the 15 PTTs that were deployed in July 1992 were still active during parts of the period between breeding (March/April) and moulting (July) in 1993. Six of these (two males, four females) were attached to animals estimated to be 3–5 years old (Table 1) and some of these may have reached sexual

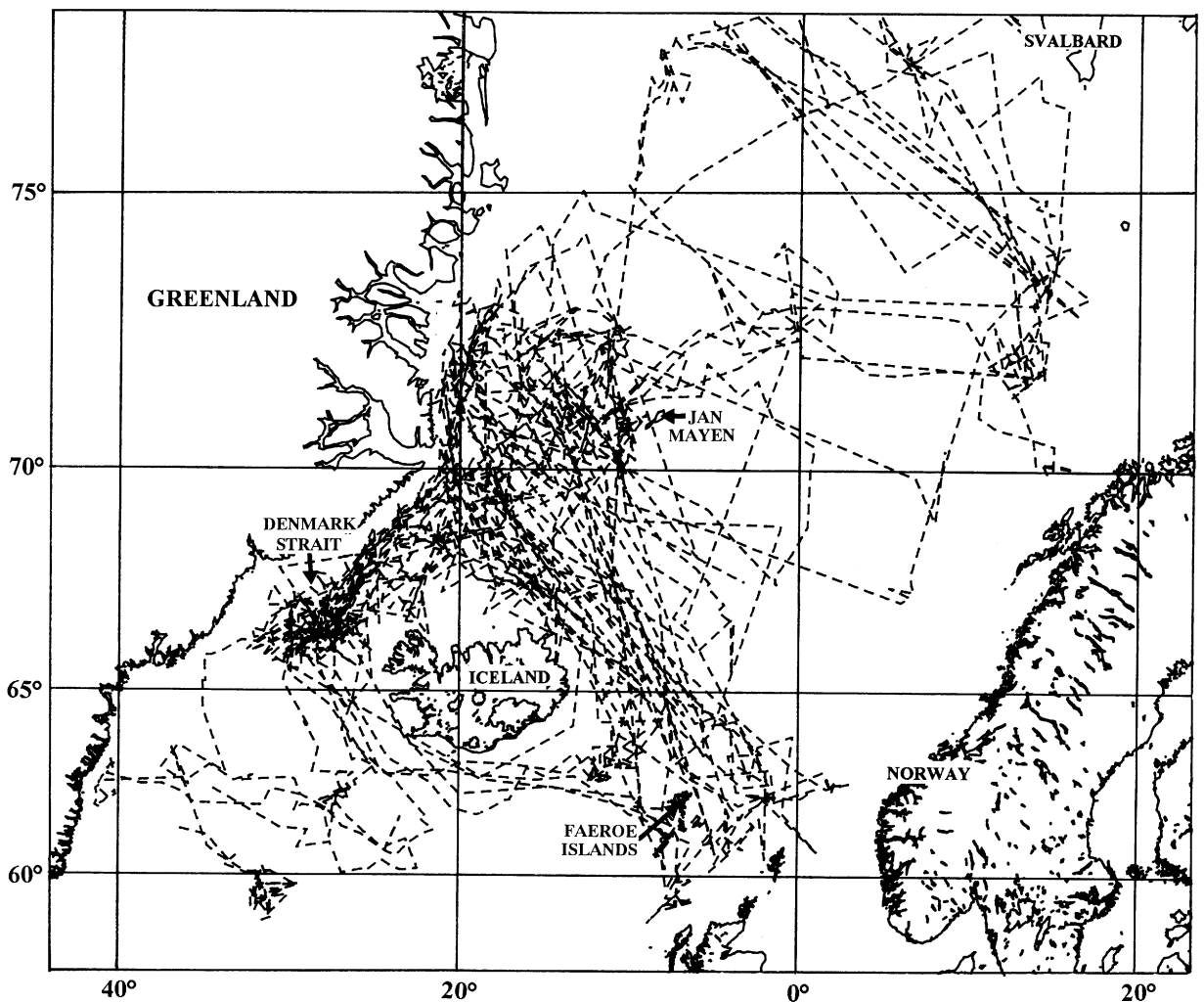


Fig. 1 Distribution and overall movements of 15 hooded seals between tagging in July 1992 and breeding in March 1993. Not shown is the major part of the track of 1 male, which travelled and spent the rest of the tracking period near Svalbard. Note that the *track lines* do

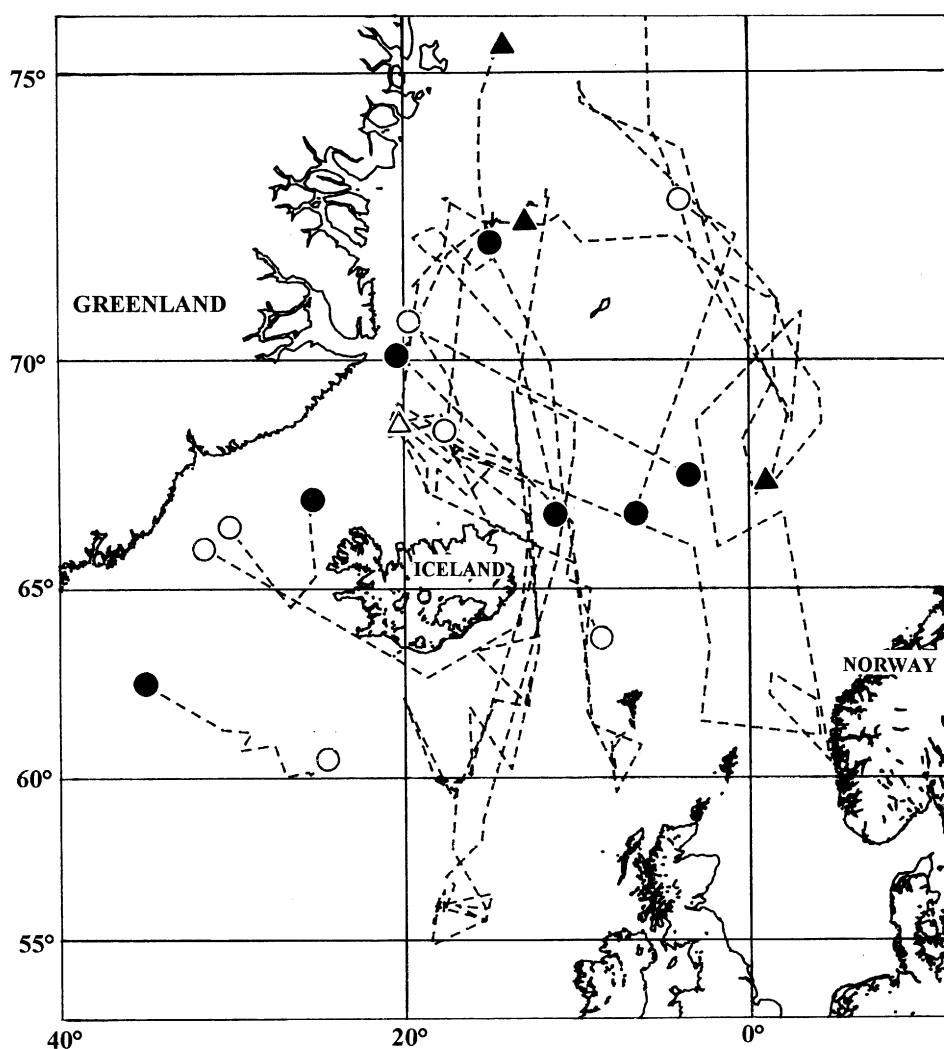
not correctly reflect the frequency distribution of seals in different areas, since location fixes from hauled-out seals in sea ice were obtained much more frequently than from seals diving at high sea

maturity [which according to Rasmussen (1960) is reached at 4 years of age for females]. One of these females (#9665) returned to and spent 6 days (22–27 March) on the ice during the breeding season (20 March–10 April). Also one male (#9667) returned to the same area at the end of the breeding season (around 6 April), while the remaining animals stayed in open sea during this time period (Fig. 2). The four mature females (with pups) that were tagged during breeding in April 1993, dispersed at high sea between breeding and moulting. Two of them left the breeding area 2–4 days after tagging and travelled to waters south of Iceland and west of the British Isles, while the other two ventured into the Norwegian Sea (Fig. 2). Four PTTs were active until June/July, when moulting started. These PTTs presumably stopped transmitting because they fell off when the animals shed their fur. At that time, three seals were in the ice at about 72–75°N,

14°W, while the last animal had travelled way north, to about 83°N, 3°W (Figs. 2, 3L, 3M).

The month-by-month plots of all daily location fixes in relation to the monthly average extension of the drift ice edge (Fig. 3A–M) indicate that the seals stayed in close association with the ice edge for most of the month of July, but that some dispersal occurred after the moult at the end of this month (Fig. 3A). In August, the dispersal from the ice edge was more pronounced (Fig. 3B), while the extent of inhabitation of ice-covered waters again appeared to be higher in September and October (Fig. 3C, D). The months November to June (Fig. 3F–L) were all characterized by a large proportion of at-sea locations, while the two remaining seals with operational PTTs largely stayed within the ice edge in July (Fig. 3M), when hooded seals moult. Hooded seals were found to be present in waters off the Faeroe Islands during all months of the year, except

Fig. 2 Distribution and overall movements of 11 hooded seals (2 males, 9 females) in the period between 1 April (breeding) and July (moulting) 1993. *Unfilled and filled circles*, start and end locations, respectively, of continuation tracks for seven seals that were tagged in July 1992. *Unfilled and filled triangles*, tagging location and end locations, respectively, for four breeding females that were tagged on 1 April 1993. Not shown is the end track of one female that travelled to 84°N, 5°W and presumably moulted there in July 1993



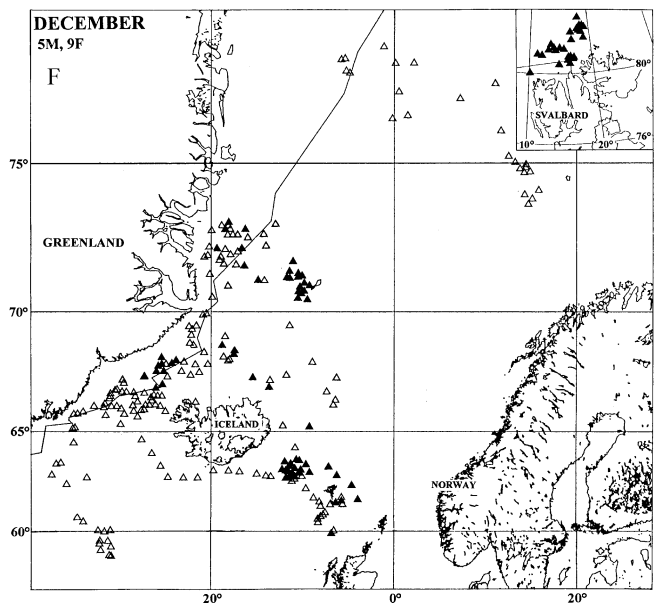
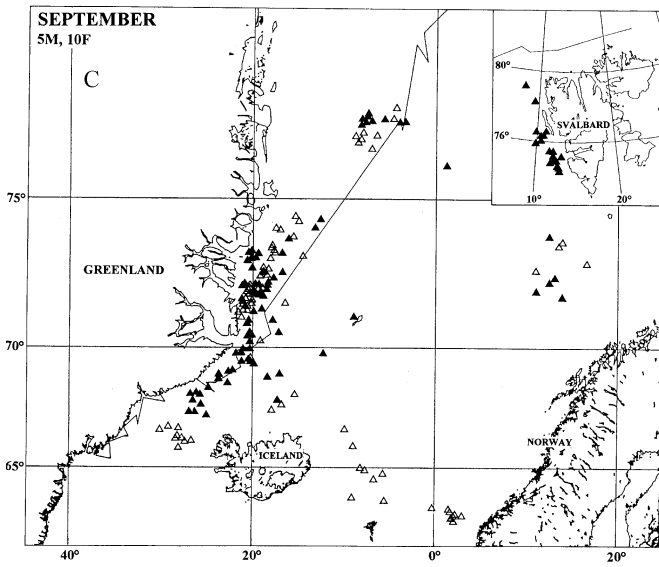
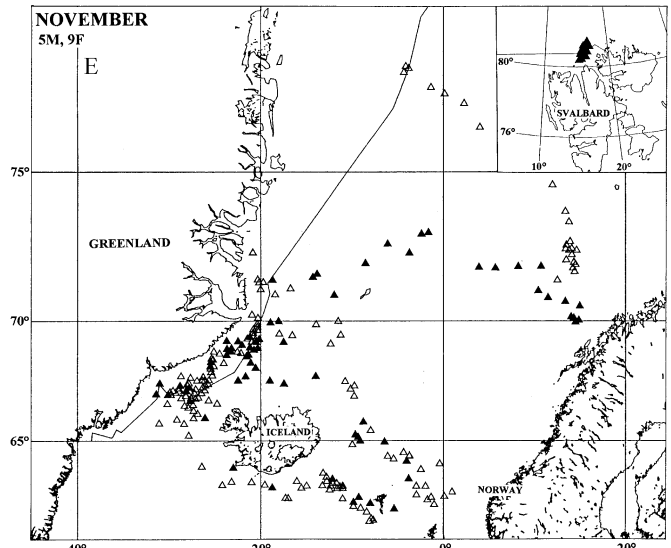
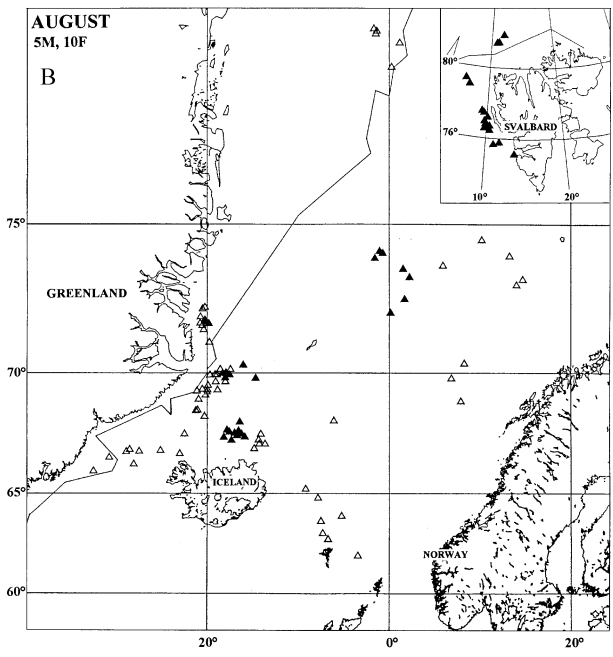
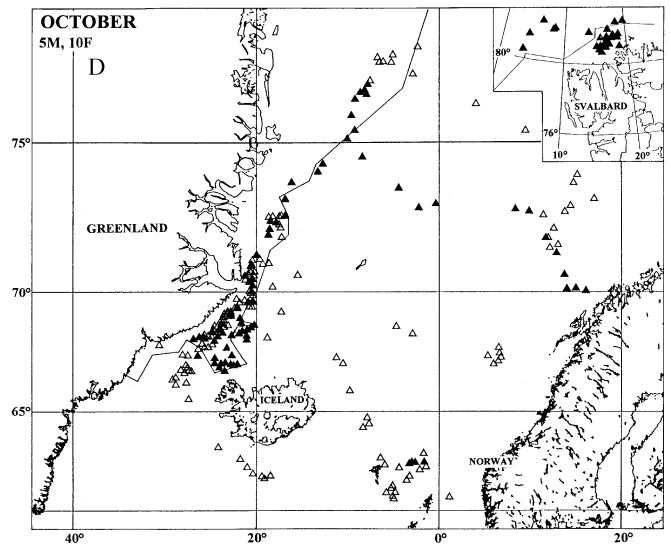
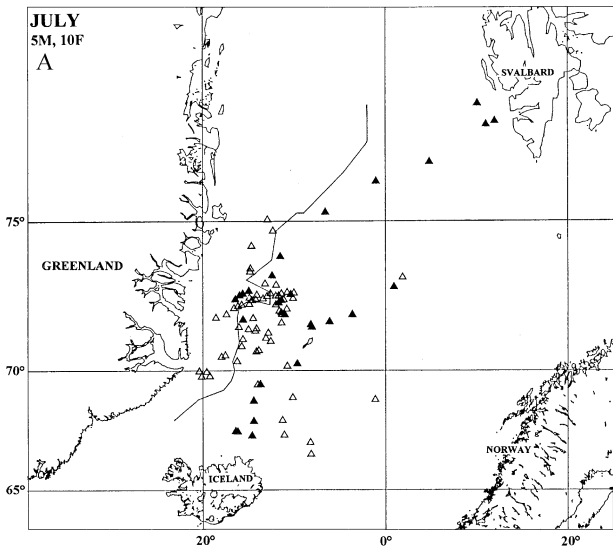
May, June and July (Fig. 3B–J). Males and females generally appeared to be similarly distributed, except for March (Fig. 3I), when two males stayed further north than the five females that still carried operational PTTs at that time. Another obvious exception is the single male, which was responsible for all locations from the waters off Svalbard (Fig. 3A–G).

The time periods that were spent at high sea differed among individuals, ranging from only a few days up to 99 days (Fig. 4). The average duration (\pm SD) of excursions at high sea (time from leaving the ice edge until return back to it) was 47 ± 22 days for $n = 46$ recorded excursions by all animals. These time periods were usually spent in transit to and from some remote location, where most of the time period was spent, presumably feeding. A few excursions, however, had the character of a reconnaissance in which the seal appeared to be on the move all the time. At-sea excursions occurred at all times of the year (Fig. 4).

During periods at sea, time periods without reception of location data occurred, usually including periods

of transit between at-sea locations and the ice edge. Generally such periods lasted for only a few days, but for 11 of the seals at least one period of > 15 days without a location was recorded (Fig. 4). Most of these long duration data gaps were of less than 1 month [range: 15–32 days; average (\pm SD): 22 ± 5 , $n = 13$], but three examples of very long gaps were noted for three seals (62, 58 and 39 days for #9872, #9873 and #9874, respectively), which, incidentally, all carried Telonics ST-6 PTTs.

In most cases the duration of transits could be determined with great accuracy. For example, transits of 400–700 nautical miles (nm) between the ice edge and waters off the Faeroe Islands took 6–15 days, the record being held by seal #9665, which travelled 430 nm in 7 days, which gives an average minimum (straight line, at surface) travelling speed of 2.6 knots ($1.3 \text{ m}\cdot\text{s}^{-1}$). Male #9670 travelled even faster, and covered 415 nm in 6 days during his journey to Svalbard, which gives a speed of 2.9 knots ($1.5 \text{ m}\cdot\text{s}^{-1}$). Transit travelling speeds calculated in this way ranged between 1.0 and



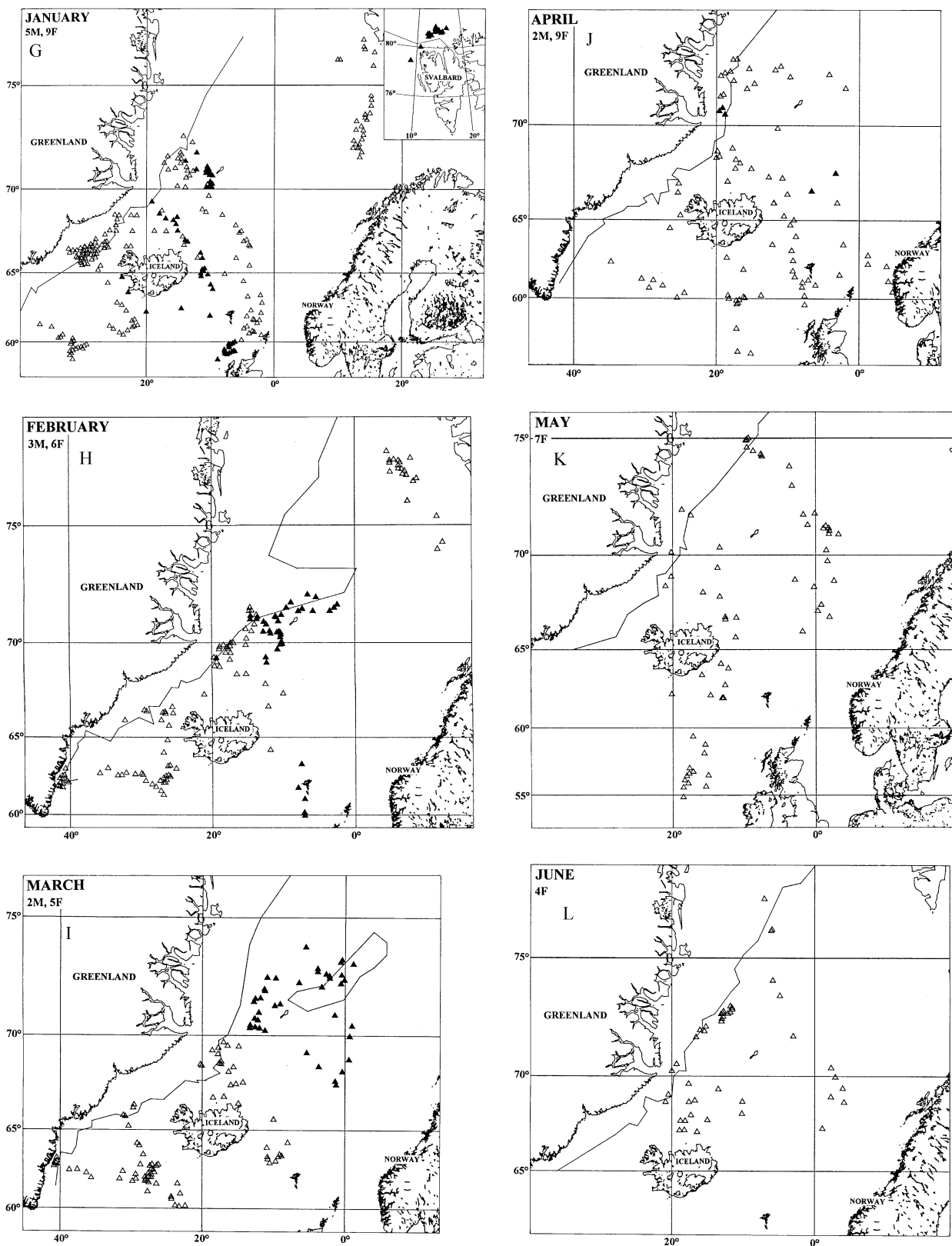


Fig. 3A–M Average daily locations of 19 tagged hooded seals by month, from July 1992 to July 1993. Filled triangles represent males, unfilled triangles represent females, solid lines represent the monthly

average sea ice extension. The month and the number of tagged males (M) and females (F) in each plot are shown in the upper left-hand corner of each map

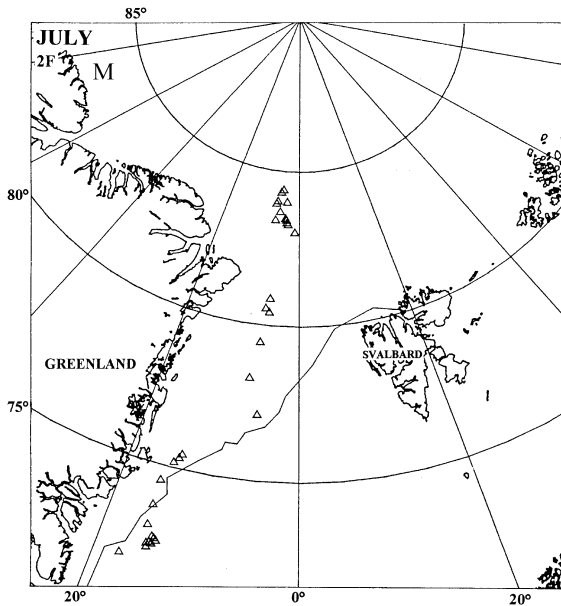


Fig. 3M (Continued)

2.9 knots with an average (\pm SD) at-surface speed of 1.9 ± 0.5 knots ($n = 42$ analysed transits).

The relative importance of different areas as habitats for hooded seals is not evident from the distribution plots (Figs. 1–3), since the probability of obtaining (good) location fixes is much higher when the seals can haul out on the ice than when they dive at high sea. To overcome this problem, the total number of tracking days (3,787 “seal days”) was distributed between different geographical areas, which were selected and delineated based on geographical and bathymetrical considerations, as well as on the distribution pattern of the seals (Fig. 5). The areas with the highest number of seal days were those which were covered with drift ice, off the east coast of Greenland (Fig. 5, areas 1 and 2), while the most frequented open water areas were those near the Faeroe Islands (Fig. 5, areas 4 and 5), where 14.5% of all seal days were spent. The areas south-west of Iceland, north/north-east of Iceland, in the Norwegian Sea, and in waters over the continental shelf break between Bear Island and the Norwegian mainland, all had approximately equal weighting (3.8, 4.9, 3.7 and 4.3% of all seal days, respectively).

Also, the number of seal days spent in transit between different areas, or in known or unknown areas

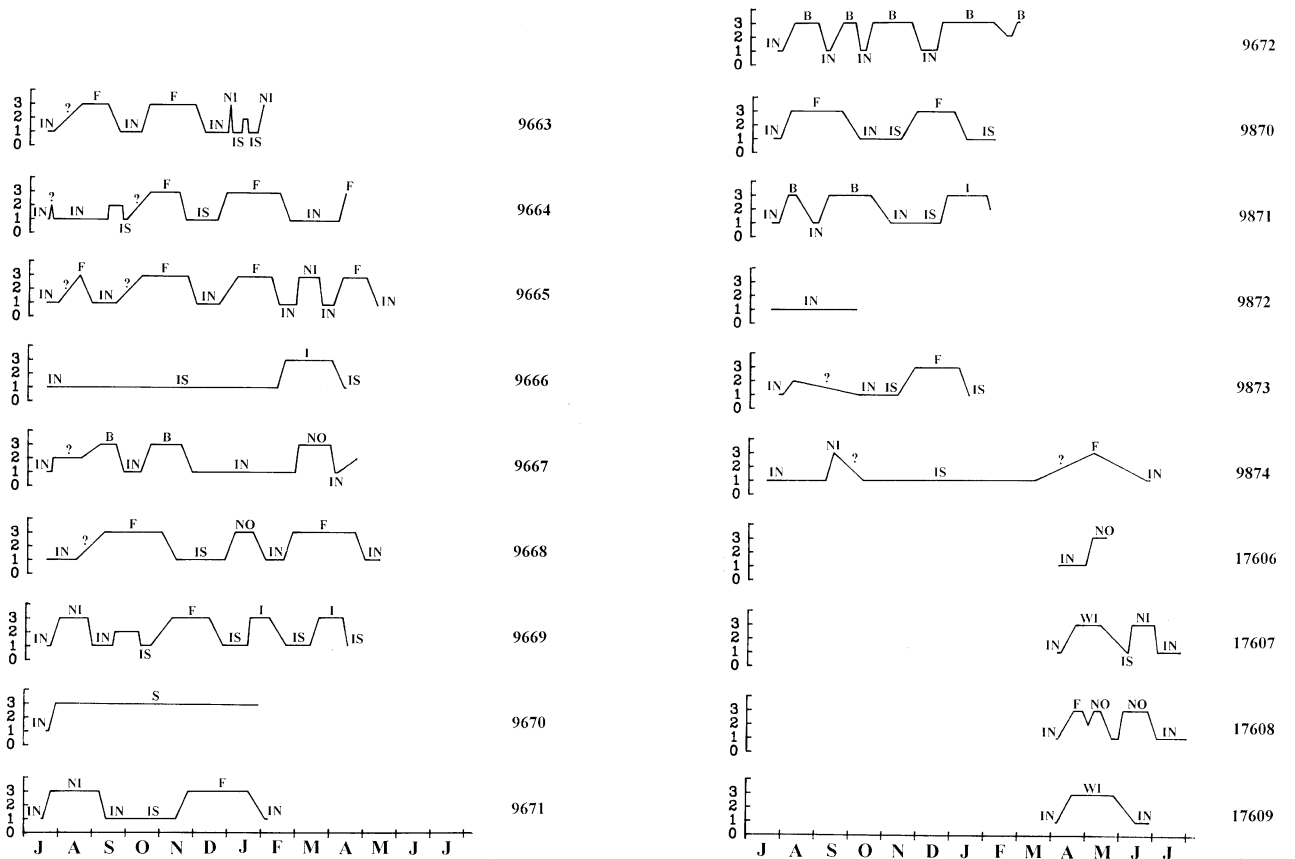


Fig. 4 Activity diagram for 19 hooded seals. The ordinate indicates where the seal stayed: *I* ice edge off Greenland (*IN* ice north of 70°N and east of 20°W; *IS* ice south of 70°N and west of 20°W); *2* at sea off but near ice edge; *3* at high sea (*F* off the Faeroe Islands; *I* in

Irminger Sea; *B* southwest of Bear Island; *NI* north of Iceland; *NO* in Norwegian Sea; *S* off Svalbard; *WI* northwest of Ireland; ? transit periods of > 15 days without location data). Vertical (tilted) lines indicate true or apparent times in transit between areas

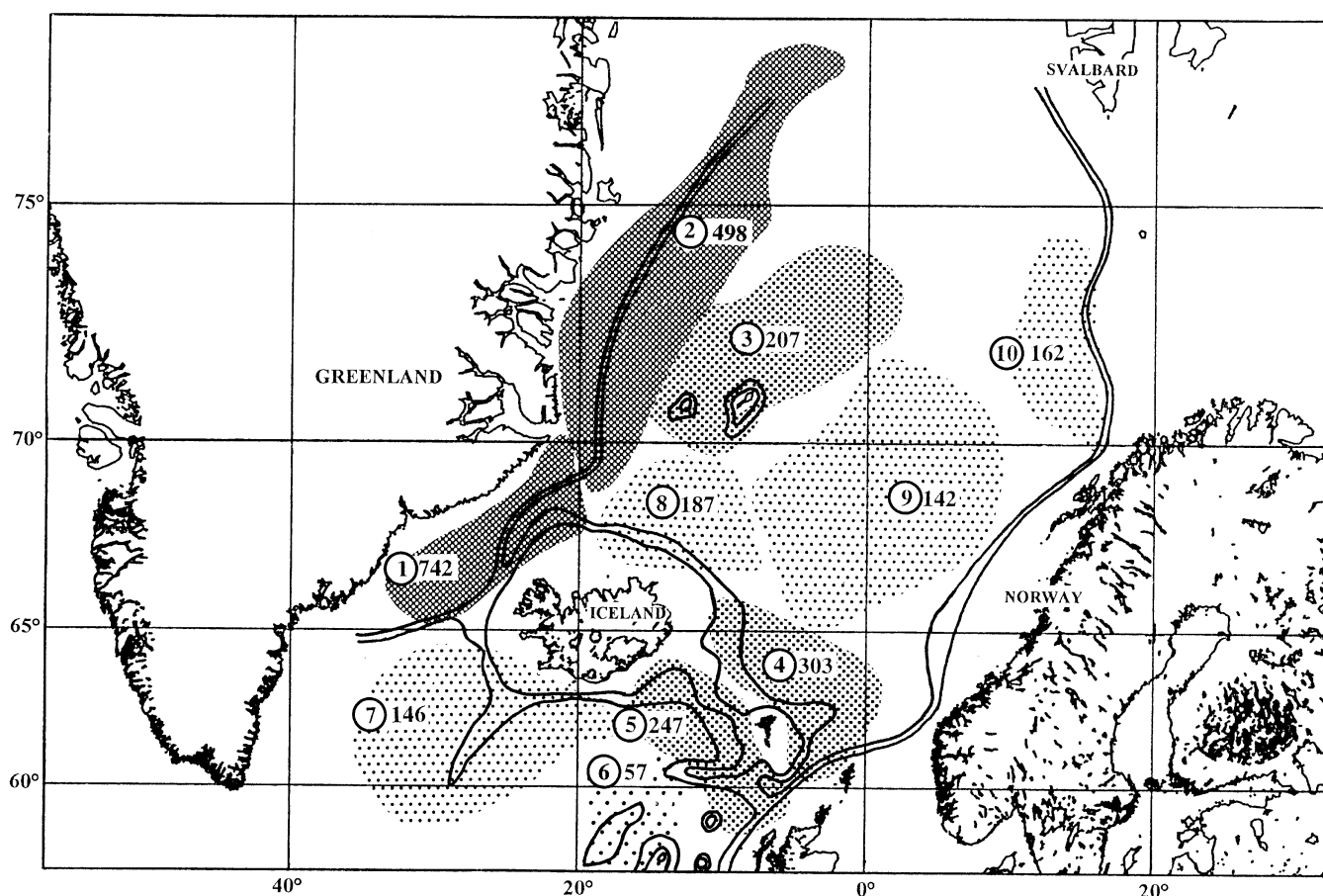


Fig. 5 The extension of ten key areas that were inhabited by tagged hooded seals: **1** in or near sea ice in the Denmark Strait (south of 70°N and west of 20°W); **2** in or near sea ice north of 70°N and east of 20°W; **3** near ice patches or in open (deep) water north of Jan Mayen; **4** northeast of the Faeroe Islands; **5** southwest of the Faeroe Islands; **6** northwest of Ireland; **7** Irminger Sea (southwest of Ice-

land); **8** north of Iceland; **9** Norwegian Sea; **10** south of Bear Island. Numbers in areas and densities of dots reflect area use by hooded seals (dot scale, from high to low density: I 400–800 seal days; II 200–400 seal days; III 100–200 seal days; IV < 100 seal days). Lines describe 500-m and 1,000-m depth contours (from Perry et al. 1980)

outside those identified, were calculated (Fig. 6). Here, time periods without locations (gaps in data) were either assigned to the “unknown location” category, or, when involving transits between areas, were split in two between the area in question and the “transit” category. In all, the seals spent 38% (1,447 seal days) of their time in ice-covered areas off Greenland, and 5% (207 seal days) mostly in ice-covered waters off Svalbard (one male), while 52% (1,964 seal days) was spent at high sea, in different areas or in transit (Fig. 6).

Sixteen of the seals were equipped with SLTDRs carrying pressure transducers that enabled us to collect dive depth and duration data. A detailed presentation of these data is not possible within the scope of this text, and this material will be published separately.

Discussion

This study has shown that hooded seals may swim large distances and operate over vast areas. In fact, location

fixes obtained during the present study range from 54°N to 84°N, and from 41°W to 16°E. Such a wide distribution of hooded seals from the Jan Mayen (West Ice) stock has hitherto not been documented. Previous reports (e.g. Øritsland 1959) and records of sporadic sightings ($n = 37$) of the species over the last 24 years [Torger Øritsland, Marine Research Institute, Bergen, Norway (personal communication)] have shown that hooded seals may venture both into the Barents Sea and to the coasts of Svalbard, and Gjertz (1991) reported that hooded seals are, in fact, frequent visitors to Svalbard. Though hooded seals have previously been reported off the Faeroe Islands (Mohr 1955), the high incidence of excursions to these waters that was demonstrated by several of our seals was previously unknown.

The tagged seals displayed an interesting migration pattern in that they appeared to be based in ice-covered waters off the coast of Greenland, from where they made long excursions to distant waters, presumably to feed, before returning to the ice edge again. During

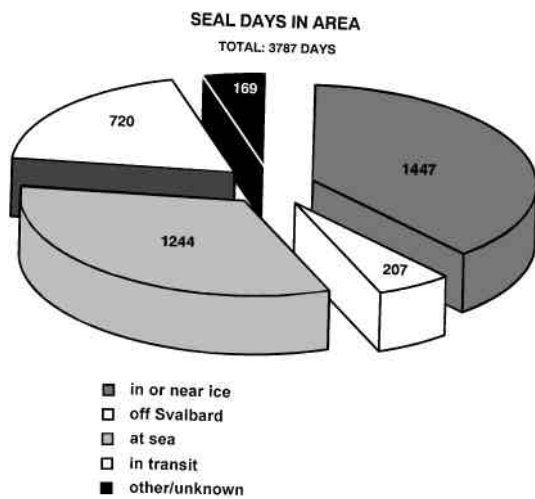


Fig. 6 Number of seal days in different areas: *in or near ice* in areas 1, 2 and 3 (see Fig. 5) off the east coast of Greenland; *off Svalbard* in ice or open water west and north of Svalbard (Spitzbergen); *at sea* in open water in areas 4–10 (see Fig. 5); *in transit* time spent travelling from one area to another; *other/unknown* in other, known or unknown, areas

excursions, which could last for more than 3 months, the seals apparently never hauled out, even if they sometimes stayed very close to coastal areas, either the Faeroe Islands or along the coast of Norway or Iceland. Transit to such remote areas appears to have been quite fast, since the seals generally travelled with at-surface speeds of almost 2 knots at the same time as they were diving repeatedly and often quite deeply (L.P. Folkow and A.S. Blix, unpublished observation).

Migrations to distant waters were not synchronized in time. On the contrary, different seals made excursions, e.g. to the Faeroe Islands, at different times of the year (Figs. 3, 4). In that sense, hooded seals do not display any general seasonal migration pattern. The dispersal pattern after the moult agrees with that indicated in a previous pilot study (Folkow and Blix 1992), and appears at first sight to be random. When the locations are related to the bathymetry of the oceans, however, their distribution makes more sense. A large proportion of the at-sea locations is confined to waters along the continental shelf break, submarine ridges or near sea mounts (Fig. 5), where upwelling presumably causes high biological productivity. This pattern is clearly seen around the Faeroe Islands, where the highest proportion of at-sea locations was obtained, but is even more conspicuous for the seals that operated along the shelf break between Bear Island and the Norwegian mainland. It is worth noticing, moreover, that none of these seals ever entered into the Barents Sea, perhaps because hooded seals mainly feed on deep-water fish that are not found in the shallower waters of the Barents Sea. The wide dispersal suggests that different parts of the hooded seal population pursue different types of prey in different areas and at different times of the year. The dive behaviour of the

seals varied from area to area within the same season, and also within one and the same area between seasons (L.P. Folkow and A.S. Blix, unpublished data). Thus, seasonal, diurnal and geographical differences in diving depths at different locations may reflect which species of prey the seals are feeding on. This rather complex matter will be discussed with the presentation of our data on the dive behaviour of these animals in another paper.

Seven out of the 15 PTTs that were deployed in July 1992 were still transmitting in late March, when pupping and subsequently mating takes place. Based on length-age relationships presented by Rasmussen (1960), six of these seals (two males, four females) were judged to be 3–5 years old, and one female only 2 years old. According to Rasmussen (1960), female hooded seals attain sexual maturity at 4 years of age, and give birth to their first pup at age 5 years. At least some of the tagged animals may therefore have been sexually mature and should be expected to visit the breeding area. One of the females hauled out for 6 days (22–27 March) on ice [as judged from data from the conductivity sensors, and, further confirmed by the location of the seal relative to the ice edge, the high quality of locations (LC 2), and the high frequency of uplinks] in a potential breeding area (Fig. 2). Given the short nursing period of hooded seals (4–6 days; Bowen et al. 1985), this female may have given birth and nursed a pup before returning to sea. One of the males arrived in the same area a bit later and spent 3 days (6–8 April) there, probably in time to participate in breeding, which continues in early April in this area (L.P. Folkow and A.S. Blix, unpublished observation). The remaining seals were dispersed at high sea in different areas at the time of breeding (Fig. 2), which suggests that none of these were sexually mature.

Our data show that hooded seals then again disperse widely at high sea immediately after breeding (Fig. 2). This observation contrasts with previous views stating that hooded seals migrate southwards along the east coast of Greenland between breeding and moulting (Sivertsen, 1936).

During moulting in June/July, hooded seals have been known to congregate in the Denmark Strait, where animals both from the Jan Mayen (West Ice) stock and from Newfoundland have been assumed to moult (e.g. Øritsland 1959; Rasmussen 1960). Another moulting area north of Jan Mayen was reported by Nansen (1890). We observed vast numbers of moulting hooded seals northwest of Jan Mayen during tagging operations in 1990 (Folkow and Blix 1992) and 1992 (this study) (Fig. 7). Three of four seals whose PTTs were still functioning during the moult period in June/July 1993 were located in the same general area northwest of Jan Mayen (Fig. 7). The fourth animal made a remarkable excursion northwards to 84°N where contact was lost on 24 July 1993, presumably because the tag moulted off. Although the sample size is

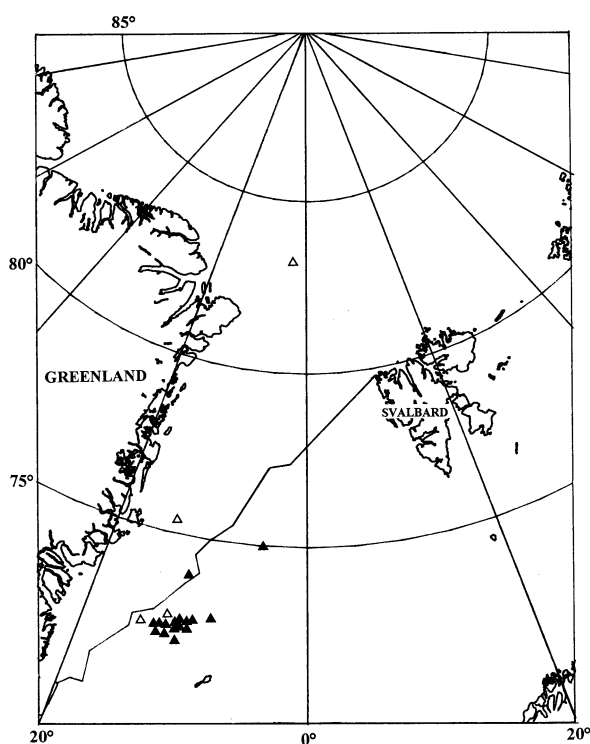


Fig. 7 Locations of moulting hooded seals in the West Ice area. *Filled triangles*, moulting animals observed during tagging expeditions in 1990 and 1992. *Unfilled triangles*, locations of four tagged animals in June/July, when moulting starts. *Solid line*, average extension of sea-ice edge in June 1993

small, these data suggest that hooded seals that moult in the Denmark Strait belong to the Newfoundland stock, while the moulting grounds of the Jan Mayen (West Ice) stock are located much further north. This conclusion agrees with that of the ICES Working Group on harp and hooded seals, which was based on data from unpublished Russian studies and results from previous mark-recapture studies (Anonymous 1990).

The majority of our at-sea locations were of location class (LC) 0. We consider these to be sufficiently accurate to describe the movements of hooded seals at sea, since the present study is concerned with the gross movements of this species. In addition, most of the presented at-sea locations represent the daily average of several consecutive LC 0 fixes, which were all close to each other. Finally, if consecutive (average daily) locations were separated by distances that hooded seals could not cover at travelling speeds of $3 \text{ m} \cdot \text{s}^{-1}$ or less, the unrealistic location was discarded. The reliability of our LC 0 data is demonstrated by the fact that the transit route of individual seals that were travelling at relatively high speed from one area to another, could often be followed from the string of LC 0 fixes that were obtained.

The reason why most of the tags did not last until moulting is not known. Status messages from the PTTs indicated that the batteries were not exhausted at the time when tags stopped transmitting. Tag damage due

to high water pressure at depth might explain some of the failures, since several of the seals appear to have dived repeatedly to depths beyond 1,000 m (L.P. Folkow and A.S. Blix, unpublished observation). The third, and perhaps most likely reason for failure, is that the tags for some reason just fell off. One factor that could cause premature tag release is skin burns that may develop during setting of the epoxy. We monitored the temperature of the setting glue, but never recorded temperatures higher than 42°C , which excludes skin burns as a cause for loss of tags in the present study. Perhaps additional growth of fur after deployment of the tag, resulting in increased shear forces on the fur, with subsequent rupture, may explain some of the tag losses. In any case, as far as we know, the overall longevity of the tags used in the present study was superior to that in any other previously published satellite tracking study on any marine mammal.

Acknowledgements The authors wish to thank Anne R. Lager for assistance in the field, and the crews of M/V "Polarfangst" and CGV "Senja" for their helpful cooperation. This study was financed by the Norwegian Research Council, grants no. 408.006 and 104503/110.

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