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Habitat Use of Ringed Seals (*Phoca hispida*) in the North Water Area (North Baffin Bay)

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ABSTRACT. In conjunction with the International North Water Polynya Study in Smith Sound (northern Baffin Bay) in 1997–99, we examined the area use and diving activity of 23 ringed seals (*Phoca hispida*) that had been equipped with satellite transmitters on the Greenland side of the North Water (NOW) area. The study covered the period 12 August 1996–30 June 1999. Contact with the seals was maintained for an average of 108 days (range: 8–332 days). Four seals emigrated from the NOW area. During all seasons, the seals that remained in the area spent about 90% of the time in coastal (< 100 m deep) waters in the eastern parts of the NOW area. The total area visited by the seals during the open-water season ranged between 10 300 km^2 (1996) and 18 500 km^2 (1998), corresponding to about 15% to 25% of the entire NOW area. In winter, the total area visited by the seals varied between 2500 km^2 (1996–97) and 7000 km^2 (1998–99), and in spring, between 800 km^2 (1999) and 2100 km^2 (1997). Individual movement was significantly greater during the open-water season than during winter and spring. Maximum dive depths recorded were over 500 m (maximum for the instrument) outside and 376 m inside the NOW, for a 96 kg male seal. Non-adult seals spent about 99% of the time in waters less than 100 m deep, and more than 92% of the time in the upper 50 m. In contrast, adults tended to spend more time at greater depths. The study indicated that (1) the ringed seals took advantage of the generally lighter ice conditions in the eastern NOW, and (2) that non-adults likely exploited ice-associated amphipods and young polar cod (*Boreogadus saida*), and adults, mainly older polar cod and cephalopods taken at greater depths.

Key words: ringed seal, *Phoca hispida*, North Water, polynya, satellite telemetry, habitat use, diving behaviour

RÉSUMÉ. Conjointement avec l'étude internationale sur la polynie de l'Eau du Nord dans le détroit de Smith (partie nord de la baie de Baffin) menée de 1997 à 1999, on a examiné l'utilisation de cette zone et l'activité de plongée de 23 phoques annelés (*Phoca hispida*) munis d'émetteurs-satellite du côté groenlandais de la région de l'Eau du Nord («NOW»). L'étude a couvert la période allant du 12 août 1996 au 30 juin 1999. Le contact avec les phoques a été maintenu pendant une moyenne de 108 jours (étendue: 8–332 jours). Quatre phoques ont émigré de la zone NOW. Durant toutes les saisons, les phoques qui restaient dans la zone passaient environ 90% du temps dans des eaux côtières (profondeur < 100 m) dans les secteurs orientaux de NOW. La superficie totale visitée par les phoques durant la saison d'eau libre allait de 10 300 km^2 (1996) à 18 500 km^2 (1998), correspondant à environ 15 à 25% de toute la zone NOW. En hiver, l'étendue totale fréquentée par les phoques allait de 2500 km^2 (1996–1997) à 7000 km^2 (1998–1999), et au printemps, de 800 km^2 (1999) à 2100 km^2 (1997). Les déplacements individuels étaient de beaucoup plus grands durant la saison d'eau libre qu'au cours de l'hiver et du printemps. Les profondeurs maximales de plongée enregistrées dépassaient 500 m (limite de l'instrument) à l'extérieur de la zone NOW et 376 m à l'intérieur, pour un phoque mâle de 96 kg. Les phoques non adultes passaient environ 99% du temps dans des eaux à une profondeur ne dépassant pas 100 m, et plus de 92% du temps dans les 50 m supérieurs. En revanche, les adultes avaient tendance à passer plus de temps à de plus grandes profondeurs. L'étude révèle 1) que les phoques annelés tiraient parti du fait qu'il y avait moins de glace dans la partie orientale de NOW, et 2) que, selon toute vraisemblance, les non-adultes exploitaient amphipodes et jeune morue polaire (*Boreogadus saida*) associés à la glace, les adultes se nourrissant surtout de morue polaire plus âgée et de céphalopodes prélevés à de plus grandes profondeurs.

Mots clés: phoque annelé, *Phoca hispida,* Eau du Nord, polynie, télémesure par satellite, utilisation de l'habitat, plongée

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INTRODUCTION

The North Water (NOW) of the Smith Sound–northern Baffin Bay region between Greenland and Ellesmere Island (Canada) is one of the largest recurrent polynyas (70 000 – 80 000 km^2) in the Arctic (e.g., Lewis et al., 1996; Barber et al., 2001a; Mundy and Barber, 2001). Polynyas remain open in winter and become ice-free early in spring; thus, they are areas of relatively high biological productivity, which begins earlier there than in ice-covered areas at the same latitudes (e.g., Stirling et al., 1981; Klein et al., 2002; Ringuette et al., 2002). Birds and marine mammals use polynyas for feeding and mating, and marine mammals use them as overwintering grounds as well (e.g., Vibe, 1950; Brown and Nettleship, 1981; Stirling et al., 1981; Stirling, 1997). Large colonies of dovekies (*Alle alle*) and thick-billed murres (*Uria lomvia*) in the North Water (e.g., Kampp, 1990; Boertmann and Mosbech, 1998; Kampp et al., 2000; Pedersen and Falk, 2001) testify to the area's great productivity, particularly on its eastern side. Vibe (1950) suggested that animal life was richer on the eastern versus the western side of the polynya due to earlier ice breakup and inflow of a nutrient rich and relatively warm current from southern Greenland (Kiilerich, 1933; Grøntved and Seidenfaden, 1938).

The International North Water Polynya Study was conducted from 1997 through 1999, with emphasis in 1998, to document physical and biological processes (Barber et al., 2001b; Deming et al., 2002). We examined the use of the NOW area by ringed seals (*Phoca hispida*) as one component of that international study.

Ringed Seal Ecology

Ringed seals are abundant year-round residents at both eastern and western margins of the NOW (Vibe, 1950; Born and Knutsen, 1989), as evidenced by large annual harvests by the Inuit living in Jones Sound, Canada (Reeves et al., 1998), and the Thule area, NW Greenland (Teilmann and Kapel, 1998).

Ringed seals prefer annual landfast ice with good snow cover in fjords and bays with complex coastlines (e.g., McLaren, 1958a, b), but they also range widely in offshore pack ice (e.g., Finley et al., 1983). Adult ringed seals tend to winter under stable nearshore ice, whereas subadults are often found at the edges of the landfast ice (e.g., McLaren 1958a). In winter, ringed seals spend most of their time in the water or in subnivean lairs on the stable ice, but after the breeding season (March–early May), they haul out on the ice to molt until ice breakup (Vibe, 1950; McLaren, 1958a, b; Smith, 1973, 1987; Smith and Hammill, 1981). Ice breakup usually occurs in late July in the eastern areas of the NOW (Vibe, 1950; Born et al., 2002). Although the ringed seals feed relatively little (e.g., Smith, 1973, 1987) during the molt, they feed intensively during the open-water period (from late July until late October) in pelagic and demersal habitats (e.g., Smith, 1987; Weslawski et al.,

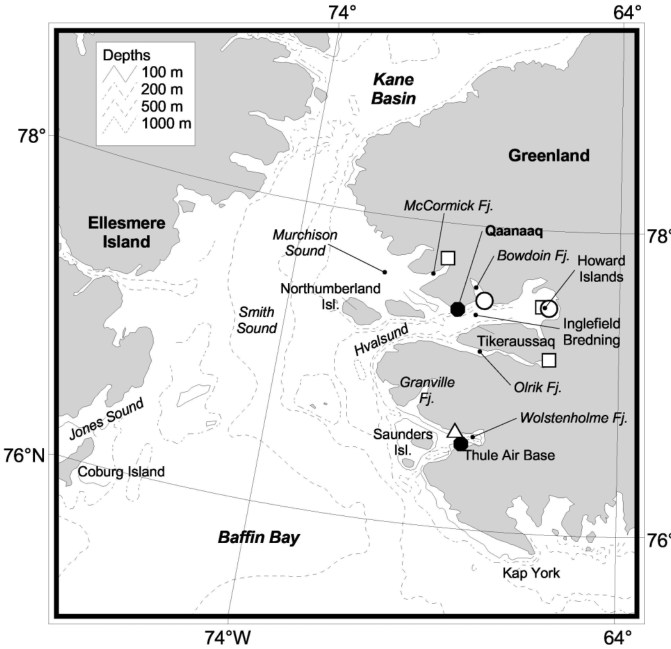

FIG. 1. Map with bathymetry of the North Water study area, indicating sites where 23 ringed seals were caught and equipped with satellite-linked radio transmitters in 1996 (squares), 1997 (open circles), and 1998 (triangle).

1994). They are euryphagous, eating a variety of crustaceans, mainly the hyperiid amphipod *Themisto* (*Parathemisto*) *libellula*, and fish, mainly polar cod, *Boreogadus saida*, and arctic cod, *Arctogadus glacialis* (e.g., McLaren, 1958a; Weslawski et al., 1994; Siegstad et al., 1998; Wathne et al., 2000; Holst et al., 2001). Some evidence suggests that juveniles and adults forage in different habitats (Holst et al., 2001).

Studies of Ringed Seal Movement and Distribution in the NOW

Previous studies of ringed seal movement in the NOW area included information on gross movement of some seals that were tagged between 1988 and 1997 (Kapel et al., 1998) and studies of movement, mainly during summer and fall, that used satellite transmitters (Heide-Jørgensen et al., 1992; Teilmann et al., 1999). To present an overall picture of habitat use by ringed seals in the NOW area, the seals tracked by Teilmann et al. (1999) are included in the present study. Holst and Stirling (2001) presented preliminary information, based on shipboard censuses, on the distribution and abundance of ringed seals in the NOW area during August 1997, April to July 1998, and September 1999.

Ringed seals have relatively great "ecological flexibility" (i.e., high mobility, ability to survive the winter in ice-covered waters, broad spectrum of food taken in all strata of the water column). Consequently, we assumed that ringed seals fitted with satellite transmitters could help identify geographical areas and water-column strata of

TABLE 1. Basic data on 23 ringed seals caught in the North Water area in 1996, 1997, and 1998 that were monitored via satellite telemetry between 12 August 1996 and 30 June 1999.

ID no.[1]	Date of Tagging	Tagging Site	Sex	Body Mass (kg)	Age Class[2]	Transmitter Type[3]	No. of Days with Contact
1858-96	12 August 1996	McCormick Fj.	m	26	S	A	137
3984-96	21 August 1996	Olrik Fj.	f	25	S	A	46
1857-96	22 August 1996	Olrik Fj.	f	24	S	A	134
4345-96	24 August 1996	Olrik Fj.	m	26	S	A	113
3985-96	25 August 1996	Olrik Fj.	m	82	A	A	58
4344-96	31 August 1996	Howard Isl.	m	34	S	A	146
1856-96	1 September 1996	Howard Isl.	m	29	S	A	127
1859-96	12 September 1996	Tikeraussat	f	25	S	A	29
1857-97	19 June 1997	Bowdoin Fj.	m	38	P	B	17
1856-97	21 June 1997	Bowdoin Fj.	m	39	P	B	31
1858-97	22 June 1997	Bowdoin Fj.	f	83	A	B	13
3984-97	27 June 1997	Bowdoin Fj.	m	47	A	B	8
11271-97	12 August 1997	Howard Isl.	m	96	A	B	253
11273-98	30 July 1998	Wolstenholme Fj.	m	24	S	C	8
4347-98	2 August 1998	Wolstenholme Fj.	m	33	S	D	98[4]
11272-98	2 August 1998	Wolstenholme Fj.	m	33	S	C	70
1857-98	3 August 1998	Wolstenholme Fj.	f	27	S	D	332
1859-98	5 August 1998	Wolstenholme Fj.	f	29	S	D	12
3985-98	10 August 1998	Wolstenholme Fj.	f	40	P	C	95[4]
11274-98	10 August 1998	Wolstenholme Fj.	f	22	S	C	12[4]
3984-98	11 August 1998	Wolstenholme Fj.	m	26	S	D	98
1858-98	11 August 1998	Wolstenholme Fj.	m	31	S	D	320
1856-98	13 August 1998	Wolstenholme Fj.	f	28	S	D	124

[1] Suffix indicates year of tagging.

[2] Age class (see Methods): S = Subadult; P = Pubescent; A = Adult.

[3] Types of satellite-linked radio transmitter: A = ST-6, continuous transmission; B = ST-10, transmission suspended after four hours of haul-out; C = same as "B" but with continuous transmission; D = SSC3, transmission suspended after four hours of haul-out. The units used in 1996 recorded dives only down to 250 m, whereas those deployed in 1997 and 1998 all recorded depths down to 500 m.

[4] Shot or netted by Inuit from the Thule area. Data not included in summary of system performance.

biological productivity. We studied the seasonal distribution of ringed seals and their diving behavior in the NOW area (i.e., the North Water polynya sensu stricto and adjacent fjords) by outfitting 23 seals with satellite transmitters in the Thule region from 1996 through 1998.

METHODS

Field Activities and Study Animals

We caught 23 ringed seals using modified drift gill nets (cf. Kapel et al., 1998; Teilmann et al., 1999) at different locations in the Thule region (76˚ to 78˚30' N, 66˚ to 73˚ W; Fig. 1), and then attached a satellite-linked radio transmitter to each seal (Table 1). All seals were handled and treated according to Greenland regulations and law concerning animal care.

The overall activity of subadult seals may differ from that of adult seals because the two groups usually occupy different coastal ice habitats, behave differently during the mating season, and may have different diving capability and diet (McLaren, 1958a; Teilmann et al., 1999; Holst et al., 2001). Therefore, the study animals were categorized at capture, on the basis of body length and mass, as subadults, pubescents, or adults (Born et al., 2002, and references therein; Table 1).

The Satellite Transmitters

Different types of satellite transmitters were used (Table 1), but the configuration, battery capacity, and mass of the transmitters were similar to those described in Teilmann et al. (1999). All transmitters were manufactured by Wildlife Computers (Seattle, U.S.A.). The sampling protocol of the transmitters was described in Teilmann et al. (1999) and Born et al. (2002). On all seals except three, the unit was positioned with the antenna pointing backward. On seals 1859-98, 3984-98, and 1856-98 (Table 1), the antenna pointed forward.

Sampling of Dive Activity

The transmitters sampled "time" and "pressure" (depth) every 10 seconds. These data were stored in six-hour blocks and then relayed to the satellite during the following 24 hours. Three types of dive data were used to describe the vertical use of the NOW area by the seals: (1) Daily maximum dive depth (MDD), (2) number of dives per day, and (3) time spent in each depth interval (Time At Depth, or TAD). Dive data were stored in 10 user-defined intervals that were organized as follows for analysis: 0–50 m, 51–100 m, 101–200 m, ≥ 201 m. Haul-out periods (Born et al., 2002) were extracted from the activity data before analyses and presentation of diving activity.

Organization of Data and Statistical Analyses

Data on movements and dive behavior were collected via the Argos Location Service Plus system (Toulouse, France; cf. Harris et al., 1990; www.cls.fr). The software program Satpak 3.14 (Wildlife Computers, 1997) was used to validate locations and dive data received.

In analyzing the activity of the study animals, we defined three "ecological seasons" based on ice and light conditions and the basic life history of ringed seals: (1) "Summer" or the "open-water season" (1 August–31 October), the time between breakup of the landfast ice and its formation in the fall; (2) "Winter" (1 November–31 March), when the fjords are covered with fast ice and darkness prevails for most of the time; and (3) "Spring" (1 April–31 July), when the seals are breeding and spend progressively more time hauling out. The spring season ends with the breakup of the fast ice.

Information on ice formation, ice coverage, and ice type was determined from ice charts provided by the Canadian Ice Services (Environment Canada) and from National Oceanic and Atmospheric Administration (NOAA) infrared satellite images. In addition, information on ice formation and ice breakup was obtained from people living in the Thule area. In 1996, a dense layer of fast ice formed in the Inglefield Bredning by 1 November (Teilmann et al., 1999). Fast ice formed in the fjords of the Thule area by 10 November in 1997 and by 9 November in 1998 (Born et al., 2002). Local residents reported that in 1998, breakup of the landfast ice occurred on 17 July in Wolstenholme Fjord and around 28 July in Inglefield Bredning.

At 77˚ N, there is 24-hour daylight between 22 April and 21 August, and darkness prevails from 1 November until 12 February.

We produced digital maps of the North Water area, with the permission of the Canadian Hydrographic Service, from Bathymetric Map 817-A (scale 1:2 000 000; Canadian Hydrographic Service). In some cases, the existing bathymetric contours were refined and corrected on the basis of soundings made during the NOW cruises (courtesy: L. Fortier, Département de Biologie, Université Laval, Québec, Canada).

The extension of the North Water polynya varies annually and seasonally (e.g., Barber et al., 2001a). However, in the present paper, the NOW area was defined as the waters (including adjacent fjords) between ca. 75˚45' N (southern entrance to Jones Sound, Ellesmere Island) and ca. 79˚ N (position in some years of the "ice bridge" between Canada and Greenland in northern Smith Sound and southern Kane Basin).

We used ArcView 3.0a to map seal movement and calculate distances and rates of movement. Except for one seal, we used only location classes 1, 2, and 3, for which theoretical radial precision has been specified by Argos as less than 1000 m (cf. Harris et al., 1990; Anon., 1996). Because of a general lack of good-quality locations from an adult male (11271-97), class 0 locations (for which accuracy is not specified by Argos) were included in the analyses.

The areas visited by the seals ("ranges") were mapped using the locations from all seals that transmitted during the season in question. A daily location for each seal was selected using the highest quality class available. Total seasonal ranges for all seals combined were calculated using the fixed-kernel method (Seaman and Powell, 1996) using the ArcView extension "Animal Movement v. 2.04" (Hooge et al., 1999) and "ArcGIS Spatial Analyst 1.1" (ESRI, http://www.esri.com/software/arcgis/arcgisxtensions/spatialanalyst/index.html). The 95% probability contours of the seasonal ranges were depicted (Figs. 2 and 3).

Monthly gross movement of a seal was determined by summing all linear distances (km) between consecutive locations received for an individual during a month. Monthly net movement, or shift in geographic position, of each animal was defined as the linear distance (km) between first and last locations recorded each month. Following Amstrup et al. (2001), these estimators of movement or displacement were calculated only if 20 or more days had elapsed between the first and last locations recorded during a month.

To minimize uncertainty in determining swimming speed from distance between locations and time, we included only cases for which (1) the combined theoretical uncertainty was less than 10% of the "point" distance between the two positions, (2) time elapsed between the two locations was between 0.5 and 6 hours (Teilmann et al., 1999), and (3) at least five estimates of speed were available per season.

We used analysis of variance (ANOVA) to test the influence of four factors—sex, age class, season of deployment, and position of the transmitter (i.e., antenna pointing backward or forward)—on the performance of the transmitters (i.e., number of days of contact with the transmitters). The data on duration were $\log_{10}$-transformed to obtain normality and homoscedasticity.

Movement data were ln-transformed and ANOVA (factors: sex, age, season, and the interaction between sex and season) was applied to test for differences in gross movement, net movement, and swimming speed during the three seasons. Seasonal differences in range size were tested with ANOVA (and Tukey post hoc test) weighted with number of seals.

ANOVA was also used to test differences in diving behavior. For analyses of MDD, ANOVA and Tukey-Kramer post hoc tests were made, whereas Wilcoxon Signed Rank analyses were used to test for differences among age groups in time spent at various depths (TAD).

Pearson's correlations were used to analyze the relationships between MDD and the deepest map depth in areas visited by a seal during the same day. This analysis included only seals that remained in the NOW area and were equipped with transmitters able to record depths down to 500 m (Table 1) and for which at least 45 pairs of MDD and map readings were available.

TABLE 2. The number of ringed seals, by age group, that provided dive data in each of the 12 months during 1996–98. Data are given in this format: Number of individual seals transmitting dive data in the month/average number of hours with dive data per seal (standard deviation of the average number of hours).

	No.	Jan	Feb	Mar	Apr	May	Jun
Adult	4	1/474	1/216	1/108	1/174		2/69(13)
Pubescent	3						2/159(38)
Subadult	16	3/68(35)	2/111(55)	2/177(30)	2/165(89)	2/228(85)	2/369(13)
		Jul	Aug	Sep	Oct	Nov	Dec
Adult	-	1/84	2/237(225)	2/327(412)	1/426	1/420	1/474
Pubescent	-	2/240(221)	1/498	1/732	1/606	1/150	
Subadult	-		13/423(218)	14/648(93)	14/475(188)	9/263(170)	7/226(145)

To detect whether there was a relationship between total body mass and the tendency of the seals to use different strata of the water column, a weighted (1/variance) regression was made of daily MDD regressed on total body mass (TBM).

Daily number of dives summed per month by the three age classes were not all normally distributed (Shapiro-Wilk test; adults: $p = 0.047$; pubescents: $p = 0.555$; subadults: $p = 0.018$); therefore, a Wilcoxon Signed Rank test was used to explore for differences among age classes in dive activity. A Kruskal-Wallis test was used to test for differences in dive activity among seasons (winter, summer, spring).

Statistical analyses were conducted using the software Statview for Windows 4.5 (1992–97, Abacus Concepts), Systat 9.0 (1999, SPSS Inc.), and SAS (1990, SAS Inst. Inc.).

RESULTS

Seals Studied and Performance of the Transmitters

Sixteen (70%) of the seals that we monitored were subadults, three were pubescent, and four were adults. Fourteen were males and nine were females. Total body mass ranged between 22 and 96 kg (Table 1).

Contact with the transmitters was maintained for an average of 108 days (SD = 96, range: 8 to 332 d, $n = 20$; three seals killed by hunters were not included; Table 1). Season of deployment was the only variable that significantly influenced the number of days of contact with the seals ($F = 5.54$, $p = 0.03$, $df = 4/1$). Contact was maintained longer with the transmitters that were deployed during the open-water season (mean = 130 d, SD = 95, range: 12–332 d, $n = 16$) than with those deployed during spring (mean = 17 d, SD = 10, range: 8–31 d, $n = 4$). Among transmitter types, the direction of the antenna was the only factor that was statistically significant ($F = 7.35$, $p = 0.02$, $df = 3/1$). The units with the antenna pointing backward transmitted longer (mean = 113 d, SD = 102, range: 8–332 d, $n = 17$) than those with the antenna pointing forward (mean = 78 d, SD = 59, range: 12–124 d, $n = 3$).

The satellite-transmitted data from all years combined allowed us to map the ringed seals' spatial use of the NOW for nearly an entire annual cycle (Table 2).

Horizontal Use of the NOW Area

Nineteen of the seals remained in the North Water area throughout the study period, and four seals left the area.

Two subadult seals (3985-96, 1858-96) emigrated from the NOW area in August 1996 (Teilmann et al., 1999), and one adult seal (11271-97) moved offshore around 15 August 1997. After the formation of landfast ice in the Thule area around 10 November 1997, the adult remained offshore in the polynya (Fig. 2B) until 2 December, when it moved south. This seal stayed at ca. 73˚30' N, 58˚50' W in NE Baffin Bay until transmission stopped on 11 April 1998 (Fig. 3B). The fourth emigrant was a subadult (1859-98) that left the tagging site in Wolstenholme Fjord on 5 August 1998 and moved south along the Greenland coast, where contact was lost on 16 August 1998 at 74˚23' N, 64˚26' W (Fig. 2C).

The seasonal variation in spatial use of the NOW area by the 19 seals that remained there was reflected in the distribution of relocations, in the monthly gross and net movement, and in individual swimming speed. Gross and net movement (Table 3) and speed did not differ between months, sexes, or age groups within any of the seasons (ANOVAs, $p > 0.05$), and this activity is therefore summarized for all seals, by season, from summer to spring:

Summer: During summer or the open-water season, the six seals that were monitored in 1996 stayed along the eastern shores of the NOW, primarily between 77˚ and 78˚30' N (Fig. 2A).

Before seal 11271-97 emigrated from the North Water area, it stayed on the eastern side of the NOW area and in southern Kane Basin. Maximum dive depth readings down to 376 m and the relocations indicated that this seal visited the central parts of the NOW area, where the depths are greater than 500 m (Fig. 2B).

Of nine seals that stayed in the NOW area in 1998, six remained near the tagging site in Wolstenholme Fjord. The majority of the relocations from these "inshore" seals came from areas where water depths are less than 100 m (Fig. 2C). Three 1998 seals made excursions offshore into the central parts of the NOW area (Fig. 2D).

The four seals that left coastal areas in 1997 and 1998 spent widely different fractions of their total offshore time

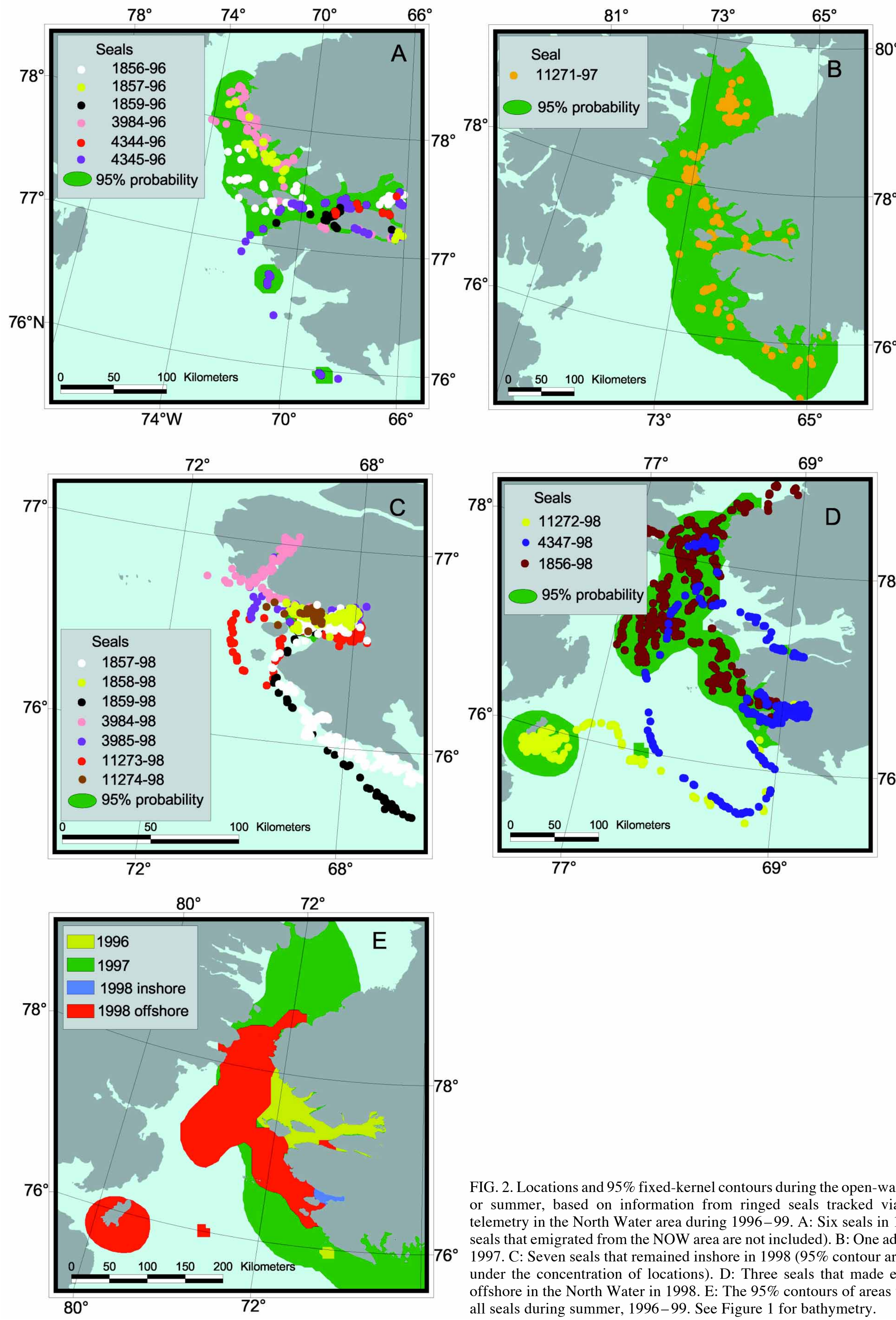

FIG. 2. Locations and 95% fixed-kernel contours during the open-water season or summer, based on information from ringed seals tracked via satellite telemetry in the North Water area during 1996–99. A: Six seals in 1996 (two seals that emigrated from the NOW area are not included). B: One adult seal in 1997. C: Seven seals that remained inshore in 1998 (95% contour area hidden under the concentration of locations). D: Three seals that made excursions offshore in the North Water in 1998. E: The 95% contours of areas visited by all seals during summer, 1996–99. See Figure 1 for bathymetry.

TABLE 3. Monthly gross and net movement distances (cf. Methods), by season, of ringed seals tagged with satellite transmitters in the NOW area, 1996–99.

Season	Open water		Winter		Spring	
	Gross	Net	Gross	Net	Gross	Net
Mean (km/month)	407	61	75	14	91	22
SD (km/month)	245	64	74	15	79	27
Seals (n)	13	13	3	3	3	3
Months (n)	28	28	4	4	6	6
Min (km/month)	49	2	4	0	12	1
Max (km/month)	940	222	164	31	201	68

TABLE 4. Fixed-kernel contour ranges, by season, of ringed seals that were tracked via satellite telemetry in the NOW area, 1996–99.

Year	Season	Number of Seals	95% Contour Area (km^2)
1996	Open-water	7	10292
	Winter (1996/97)	3	7097
1997	Spring	4	2104
	Open water	1	48950
1998	Open water (inshore)	6	569
	Open water (offshore)	3	17924
	Winter (1998/99)	2	2535
1999	Spring	2	815

in the central parts of the NOW area. (Time used offshore = % of days (n) in the NOW area: 11271-97: 97% (n = 99); 4347-98: 19% (n = 98); 1856-98: 50% (n = 124); 11272-98: 14% (n = 70).)

Overall, the distribution of locations received from all the seals during the open-water seasons of 1996, 1997, and 1998 clearly reflects their preference for the eastern parts of the NOW area (Fig. 2E).

Monthly mean gross movement (407 km/month) and mean net movement (61 km/month) were significantly higher during the summer open-water season than during winter and spring ($p < 0.01$; Table 3). Mean swimming speed during summer was 1.6 km/h (SD = 0.5, range: 1.0–2.8 km/h, $n = 14$ seals). Although the seals tended to travel faster during summer than during winter and spring, this tendency was not significant ($p = 0.79$).

Winter: During winter, the seals remained on the eastern side of the polynya, in areas that are covered with first-year fast ice during this season, or at the edge of this ice (Figs. 3A and 3D). Two subadult seals (1857-98, tracked for 332 days, and 1858-98, tracked for 320 days) were remarkably stationary during the entire survey period. Between 15 November and 6 June, seal 1857-98 transmitted regularly from a shallow-water location close to the coast (76˚02' N, 67˚34' W; Fig. 3D), probably in the shear zone between fast ice and moving pack ice. The monthly net movement of this seal during winter was only 0.03 km/month. Seal 1858-98 stayed for the entire period in Wolstenholme Fjord, where it wintered in fast ice at eastern Saunders Island (Fig. 3D). Monthly net movement of this seal during winter averaged 2.2 km/month.

For all seals during winter, mean gross movement was 75 km/month and mean net movement 14 km/month (Table 3), and swimming speed averaged 1.3 km/h (SD = 0.9, range: 0.9–2.7, $n = 4$ seals). These three estimators of movement did not differ between winter and spring ($p > 0.05$).

Spring: Seals were monitored during spring in 1997 and 1999. The four pubescent and adult seals that were monitored from late June 1997 (Table 1) remained in the fast ice–covered Bowdoin Fjord and Inglefield Bredning until transmissions stopped on 21 July (Fig. 3C).

The two subadult seals (1857-98; 1858-98) that transmitted during the spring of 1999 stayed close to their wintering sites (Fig. 3E). On 6 June, however, 1857-98 moved from the area where it had wintered north along the coast, and by 24 June, it had returned to the area where it was originally captured (Fig. 3E). The monthly net movements indicated increased movements of both seals during spring (km/month; seal 1857-98: April = 0.7, May = 68; seal 1858-98: April = 1.6, May = 1.4, June = 32).

Mean gross movement and net movement of all seals during spring were 91 and 22 km/month, respectively (Table 3), and mean traveling speed was 1.5 km/h (SD = 0.5, range: 1.1–2.2, $n = 4$ seals).

Total Ranges: The tendency of the seals to expand their use of the NOW area during summer was also reflected in the seasonal variation in the size of total areas visited. The ranges of the animals during the open-water seasons 1996 and 1998 were ca. 10 300 km^2 and 18 500 km^2, respectively (Table 4). The area visited by the single adult male that was tracked during summer in 1997 was ca. 49 000 km^2 (Table 4). The ranges of movement varied from ca. 2500–7100 km^2 during winter to ca. 800–2100 km^2 in spring (Table 4). Total ranges during the open-water season (inshore range in 1998 not included) were significantly larger (ANOVA, $p = 0.04$), than ranges during winter and spring (no difference between the two latter seasons; $p > 0.05$).

Vertical Use of the NOW Area

Generally, the dive data indicated that while non-adult seals occasionally explored the water column down to the sea floor, they spent much of their time foraging at depths shallower than 50 m. Adults, in contrast, spent much more time at greater depths.

The daily maximum dive depth reflects the vertical exploratory activity of the seals in a general way. The mean MDD of the 15 seals (TBM: 22–96 kg) with transmitters that recorded dives down to 500 m was positively correlated with TBM (MDD in m = 1.27 • (TBM in kg) + 85.52, $p = 0.002$, $r^2 = 0.398$). While moving around offshore in the eastern parts of the NOW area until early December, the 96 kg adult male (11271-98) dove regularly to between 300 and 376 m depth. This seal made the deepest dive recorded in this study—beyond the 500 m depth-reading capability of the instrument—on 28 January 1999 at 73˚25' N, 58˚55' W (i.e., in NE Baffin Bay south of the North Water area).

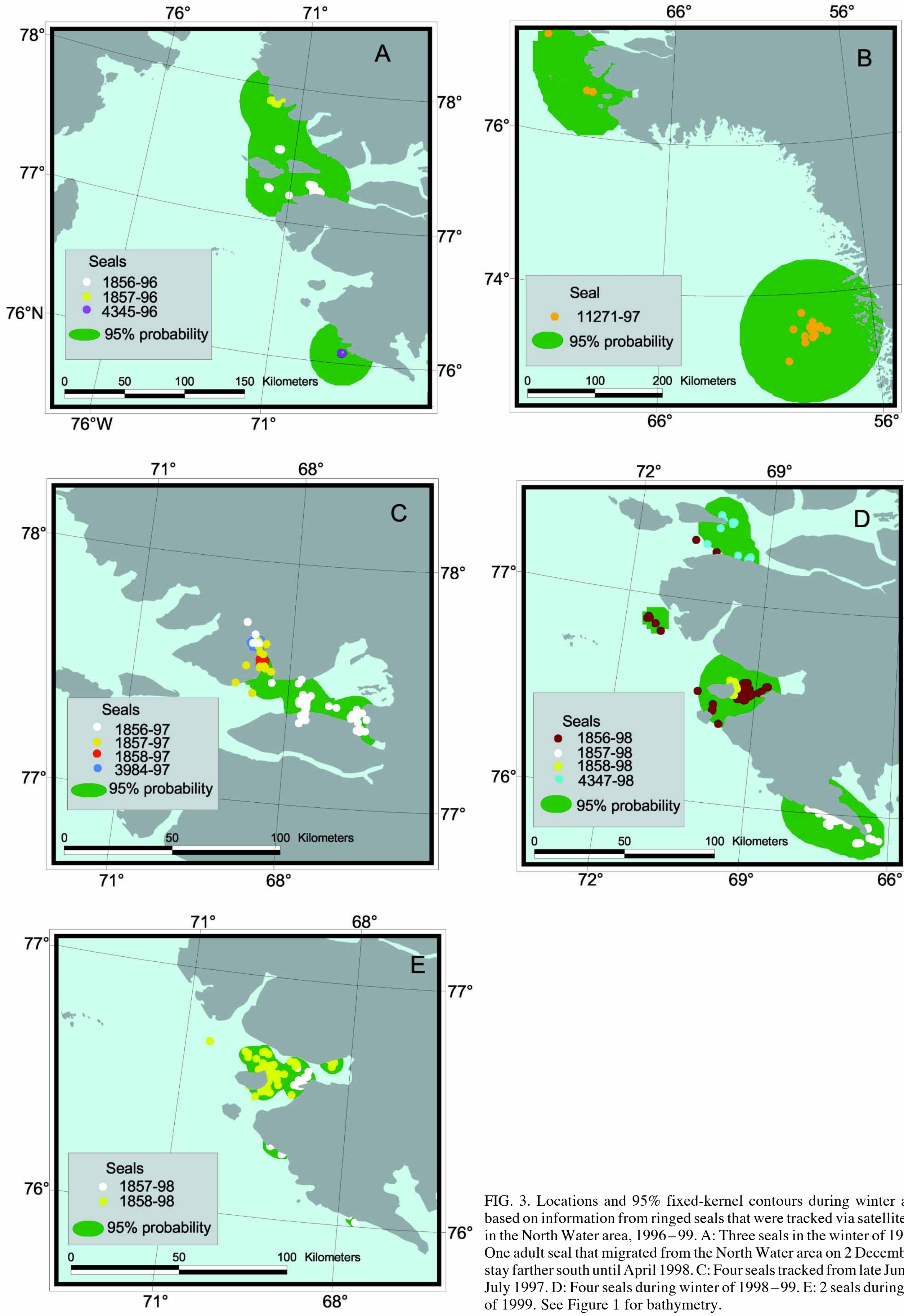

FIG. 3. Locations and 95% fixed-kernel contours during winter and spring based on information from ringed seals that were tracked via satellite telemetry in the North Water area, 1996–99. A: Three seals in the winter of 1996–97. B: One adult seal that migrated from the North Water area on 2 December 1997 to stay farther south until April 1998. C: Four seals tracked from late June until late July 1997. D: Four seals during winter of 1998–99. E: 2 seals during the spring of 1999. See Figure 1 for bathymetry.

TABLE 5. Correlations between daily maximum dive depth (MDD) and water depth in North Water areas visited by a seal the same day, as inferred from location data of seven seals.

Seal ID	*r*	*p*	No. of records of MDD with Map Depths (*n*)	No. of records of MDD > 100 m (% of all records *n*)	Highest daily MDD on Days with a Map Depth (m)	Highest Daily MDD on *all* days (m)
11273-98	0.40	**0.001**	73	16 (22)	156	156
3985-98	0.14	0.38	45	21 (47)	224	232
1857-98	0.40	**< 0.001**	101	23 (23)	252	252
3984-98	0.16	0.19	70	20 (29)	184	184
1856-98	-0.20	0.07	80	70 (88)	340	360
1858-98	0.63	**< 0.001**	80	23 (29)	320	320
4347-98	0.41	**< 0.001**	87	70 (80)	288	288

The four pubescent and adult seals that transmitted during June–July from Inglefield Bredning and Bowdoin Fjord, where water depths exceed 600 m (Fig. 1; Fig. 3C), did not dive deeper than about 250 m.

The seals that stayed in the NOW area in 1998 dove to MDD of approximately 156–360 m (Table 5). For some of these animals, the MDD was correlated with the maximum depth in the area visited during the same day (Table 5), indicating a tendency to explore the entire water column down to the seafloor.

Three subadult seals that made offshore excursions into the central parts of the NOW area (Fig. 2D), where water depths exceed 500 m, did not dive deeper than about 300 m while there (maximum depths recorded 220, 328, and 288 m, respectively).

There were no trends with time in MDD ($p > 0.05$) for 11 of the 15 seals equipped with transmitters that recorded dives down to 500 m. However, MDD did decrease with time for three seals, and increased for one. The MDD of seals 11272-98, 1857-98, and 1858-98 decreased gradually (r^2 between 0.13 and 0.50; p between < 0.001 and 0.06), indicating that they made shallower dives as time progressed. This was particularly pronounced in 1857-98 and 1858-98, which stayed in shallow coastal waters until late June 1999. During winter and spring, the MDD of seal 1857-98 averaged 15.2 m (SD = 7.3, range: 4–36 m, $n = 35$ days with MDD), and the MDD of 1858-98 averaged 19.6 m (SD = 13.5, range: 8–72 m, $n = 19$). The MDD of seal 3984-98 increased with time ($r^2 = 0.16$, $p = 0.008$) from 13 August to 27 October 1998. During August, this seal moved from shallow waters in Wolstenholme Fjord into Granville Fjord, where it spent September and most of October (until transmission stopped) in front of a glacier at the head of this fjord.

Adult seals generally made fewer dives than pubescent seals, and pubescents made fewer dives than the subadults (Wilcoxon Signed Rank tests, $p < 0.05$; Fig. 4). Overall, the average number of dives per day of adults was 182 (SD = 61.4, range: 120–312 dives/day, $n = 11$ months). Pubescent seals made an average of 324 dives per day (SD = 44.9, range: 264–384 dives/day, $n = 6$ months), whereas subadults dove 409 times per day on average (SD = 55.0, range: 336–528 dives/day, $n = 11$ months). In adults, the number of dives per day differed significantly with season (winter lower than summer and spring; $p = 0.026$). The other two age groups showed no seasonal trend in the daily number of dives (subadults, $p = 0.69$; pubescent seals: $p = 0.39$).

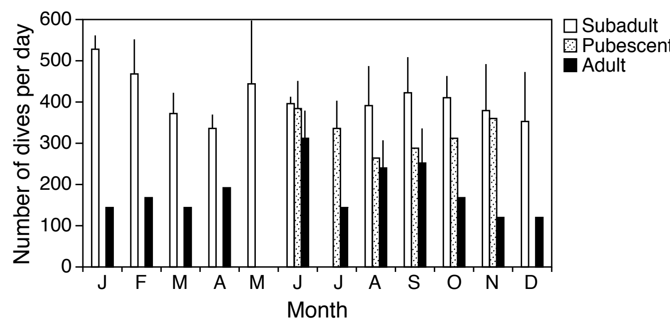

FIG. 4. Seasonal variation in number of dives per day of subadult, pubescent, and adult ringed seals in the North Water area (1996–99). For each seal, we calculated the monthly mean of number of dives per day. Bars represent the mean dive activity of all seals, and lines the standard deviations. For number of seals per month, see Table 2.

The time-at-depth (TAD) data indicated that all age groups except for adults spent the majority of time in the upper 50 m of the water column, with limited seasonal variation. During the open-water season, subadult seals spent an average of 92% and pubescents 90% of the time between 0 and 50 m, whereas adults spent an average of only 66% of the time in this depth range (Fig. 5). During winter, subadults used 96% and pubescent seals spent 93% of the time in depths shallower than 50 m, whereas adults averaged only 47% of the time at depths shallower than 50 m. The single adult (11271-97) that was monitored during winter and early spring used progressively more time deeper than 50 m (Fig. 5). All seals foraged at similar depths in June and July (i.e., time of maximum haul-out on the ice) spending about 90% of their time at depths less than 50 m (Fig. 5).

The three subadult “offshore” seals (Fig. 2D) spent an average of 94% (SD = 1.62) of the time in the upper 50 m of the water column while visiting the central parts of the NOW. Overall, these seals spent only 0.5% of the time (SD = 0.20) deeper than 100 m. In contrast, the adult seal (Fig. 2B) spent an average of about 17.5% (SD = 3.1) of the time below 100 m while in the central parts of the NOW area (Fig. 5).

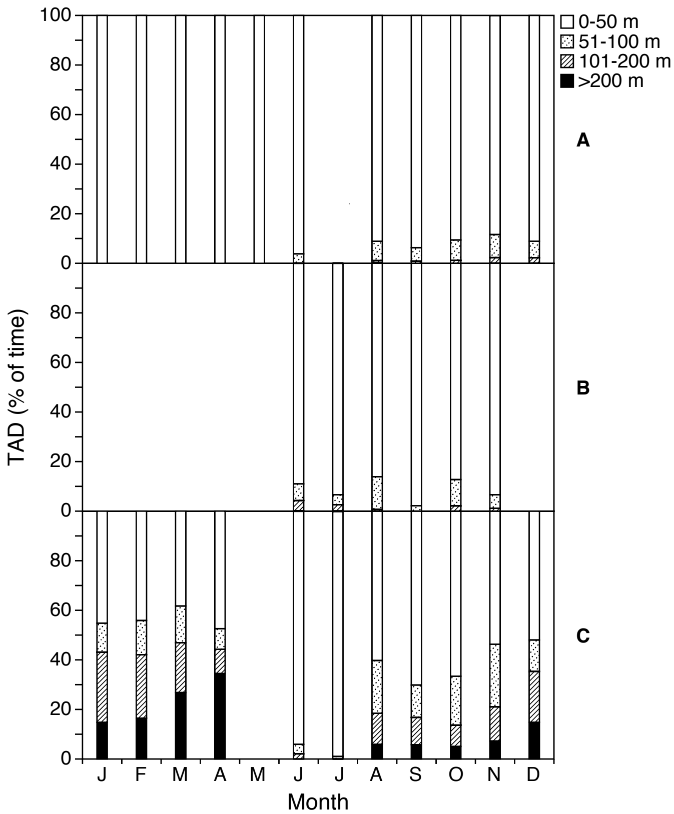

FIG. 5. Time allocation (% of total time monitored) to specified depth categories (Time-At-Depth, or TAD), by month and age group, in ringed seals in the North Water area, 1996–99. A: Subadults, B: Pubescent seals, C: Adults. Note that the depth intervals are not of equal size. The TAD per month was determined for each seal. A bar represents the average TAD for all individual seals in that month (for number of seals per month, see Table 2).

DISCUSSION

Limitations of the Study

The NOW study focused on the physical and biological processes, particularly during 1998, when an extensive, multidisciplinary icebreaker-based study was conducted (reviewed in Deming et al., 2002). We had hoped to be able to monitor the ringed seals during all of 1998. However, because the satellite transmitters did not operate long enough in 1997, and because seals were more difficult to catch then, our study overlapped with only the latter half of the NOW emphasis period. About 70% of the 23 study animals were immature seals (likely less than three years old at capture), and 14 (61%) were males. Thus the age composition of the study animals was representative of the catch of ringed seals in NW Greenland, which has a surplus of young seals and a sex ratio that is skewed towards males (cf. Teilmann and Kapel, 1998), and likely also of the ringed seal population, which generally has a high proportion of young individuals (e.g., Smith, 1973, 1987). However, because the transmitters on pubescent and adult animals generally performed less reliably, the present study mainly addresses the use of habitat by subadult seals.

We decided to catch the seals as close to the polynya area as possible and therefore operated in the populated Thule area that borders the North Water to the east. The effects of tracking seals that had been caught on only one side of the polynya area could not be assessed a priori, but it is possible that the picture of their movement patterns was influenced by a tendency of the seals to show fidelity to the area where they were caught. Although some long-distance movements of ringed seals have been reported (e.g., Heide-Jørgensen et al., 1992; Kapel et al., 1998; Teilmann et al., 1999), there are indications that ringed seals may show site tenacity both within and between years (Smith and Hammill, 1981; Kapel et al., 1998; Gjertz et al., 2000).

However, despite these limitations, we believe that the behavior of the seals monitored in this study allows for some general inferences about the spatial use of the NOW area by ringed seals.

Horizontal Use of the NOW Area

Our data indicated that the ringed seals tagged in the eastern part of the NOW area stayed in the eastern areas with relatively shallow water (< 100 m) and spent little time in the central polynya area in Smith Sound.

The icebreaker-based NOW study confirmed that the earlier ice breakup in the eastern parts of the NOW area favors marine production and animal abundance in general along the Greenland coast (Holst and Stirling, 2001; Klein et al., 2002; Ringuette et al., 2002 and references therein).

Despite the apparent site tenacity, we think that the distribution of the seals in our study was influenced by the general distribution and availability of prey, and we suggest that a key factor influencing the spatial use by the seals was the occurrence of polar cod (*B. saida*). In the Thule area, polar cod constituted 80% to 90% by mass of the diet of ringed seals (all age classes) in 1985 and 1998 (Siegstad et al., 1998). In Jones Sound, adult ringed seals mainly consumed arctic cod (*A. glacialis*), and polar cod comprised only about 16% of the diet by mass in 1998. In this area, subadults foraged mainly on the hyperiid amphipod *T. libellula* (Holst, 2000, cited in Hobson et al., 2002a; Holst et al., 2001). However, a study of stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) that likely represent dietary integrations over one to two months indicated that during late spring to early summer (1998), the diet of ringed seals on both sides of the NOW consisted primarily of polar cod (Hobson et al., 2002a).

Polar cod sometimes move in large shoals during the open-water season (Falk-Petersen et al., 1986; Born and Knutsen, 1988; Finley et al., 1990; Crawford and Jorgenson, 1996). Most polar cod ingested by ringed seals in Thule were young (age inferred from length; Gjøsæter and Ajiad, 1994; Siegstad et al., 1998), indicating that the seals fed on shoaling polar cod of uniform age class.

The crustacean *T. libellula* can also occur in swarms during summer and winter (Cross, 1982; Percy, 1993;

Wathne et al., 2000; Auel et al., 2002). A patchy distribution of crustaceans (including *T. libellula*) in the NOW was indicated in a study of the diet of dovekies (Pedersen and Falk, 2001).

The occurrence of their principal prey in localized shoals and swarms may govern the movements of predatory ringed seals during the open-water season, when they move around more to detect concentrations of food. Furthermore, during winter and spring, ringed seals are associated with their breeding holes in the fast ice and subnivean lairs, which in itself may reduce their horizontal mobility (Kelly and Quakenbush, 1990).

During the open-water season, harp seals (*P. groenlandica*) , narwhals (*Monodon monoceros*), dovekies, and thick-billed murres migrate in substantial numbers to the coastal areas and fjords of the Thule area to exploit the same prey as ringed seals (Vibe, 1950; Born, 1986; Kampp, 1990; Born et al., 1994; Heide-Jørgensen et al., 1994; Kampp et al., 2000; Pedersen and Falk, 2001; Hobson et al., 2002b). However, despite increased competition for food during summer from other marine mammals and sea birds, the ringed seals in our study stayed near the coast of the Thule area.

One seal moved from Thule to spend September and the first half of October at Coburg Island at the entrance to Jones Sound (Fig. 2D), where there is a large colony of thick-billed murres. The enhanced marine productivity in this area (Hobson et al., 2002b) was probably the reason that the seal stayed there.

Vertical Use of the NOW Area

The upper water layers in the NOW area are relatively active biologically (e.g., Ringuette et al., 2002). We found that ringed seals foraged in the upper 100 m of the water column almost exclusively, with a clear preference for the upper 50 m. Our findings were similar to those of Gjertz et al. (2000) at Svalbard, where about 50% of all dives between July and May were to depths less than 20 m, and about 90% to depths less than 100 m. For two seals that visited offshore pack ice areas, diving was significantly shallower there than in coastal areas (Gjertz et al., 2000).

There is probably no real need for ringed seals to use time at greater depths in the NOW area. First-year polar cod generally occur between 0 and 80 m, typically associated with ice (Craig et al., 1981; Bradstreet et al., 1986; Falk-Petersen et al., 1986; Lønne and Gulliksen, 1989), whereas older and larger polar cod can be found between 200 and 400 m depth (Falk-Petersen et al., 1986; Wathne et al., 2000). Like the polar cod, the crustacean *T. libellula* occurs in concentrations in the upper 100 m of the water column (Cross, 1982; Percy, 1993; Wathne et al., 2000; Auel et al., 2002). In the northeastern Barents Sea, at latitudes comparable to those of the NOW (about 77˚ and 79˚ N), about 80% of the standing biomass (including important ringed seal food) was distributed in the upper 200 m, while less than 1% was below 300 m (Wathne et al., 2000). The fact that huge concentrations of thick-billed murres find food in the upper layers of the water column in the North Water (Falk et al., 2002) reflects the high productivity of those strata, particularly on the eastern side.

The dives in the NOW by subadult, pubescent, and adult seals were very shallow during June and July, when the seals also spend a greater proportion of time on the ice (Born et al., 2002). The two subadults that were studied in the fast ice habitat during winter and spring dove only to shallow depths. This may reflect the fact that during these periods, the seals prey upon polar cod and crustaceans directly under the ice. In contrast, the 96 kg adult continued to make deep dives during winter.

Records of the daily maximum dive depth indicated that the seals occasionally dove to the sea floor. Lydersen and Hammill (1993) found a similar positive correlation between MDD and bottom depths for three ringed seal pups that were monitored with time-depth recorders at Svalbard. These excursions to the bottom may be in search of benthic prey. Ringed seals are known to take benthic food in the NOW area (Siegstad et al., 1998; Holst et al., 2001). In Thule, the third most important prey by weight was the bottom-living sea snail, *Liparis* spp. (Siegstad et al., 1998).

Dive duration and depth are positively correlated with body mass in ringed seals (Kelly and Wartzok, 1996; Teilmann et al., 1999; Kunnasranta, 2001). Hence, the MDD may reflect the physical limits of the diving capability of the individual seals (Teilmann et al., 1999). In the present study as well, daily maximum dive depth was correlated with total body mass. The diving capability of ringed seals increases with age (synonymous with total body mass), so older and larger seals can dive deeper than smaller seals and consume more fish (e.g., older polar cod), as indicated by the studies of Bradstreet and Cross (1982) and Holst et al. (2001). Adult 11271-97 spent more time at depths beyond 200 m during winter and early spring, when located in NE Baffin Bay at about 73˚30' N, 58˚50' W. Bottom-trawling in October 2001 at 73˚41' N, 58˚59' W, close to where 11271-97 wintered, showed that polar cod of 8.5–21.0 cm length made up ca. 40% of the biomass at 150 m. At another trawling station in NE Baffin Bay (73˚46' N, 59˚40' W), polar cod made up ca. 80% of the biomass at 350 m (O. Ankjær Jørgensen, pers. comm. 2002). Although this survey did not get farther north (Jørgensen, 2002), it indicated that polar cod is available as ringed seal prey at greater depth in northern Baffin Bay and probably also in the NOW area.

Cephalopods have also been reported in the diet of ringed seals from the North Water. Holst et al. (2001) reported finding *Bathypolypus arcticus* in the stomachs of ringed seals from the Thule area. This species is typically found between 200 and 600 m depth (O'Dor and Macalaster, 1983). Another cephalopod, *Gonatus fabricii*, which is widely distributed around Greenland (Kristensen, 1984) and can occur at great depths (Lu and Clarke, 1975), has been found in stomachs of ringed seals in NW Greenland

(Siegstad et al., 1998). We think that cephalopods are also likely prey of ringed seals — probably adult seals — at greater depths in the NOW area.

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