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Seasonal Movements and Diving of Ringed Seals, *Pusa hispida*, in the Western Canadian Arctic, 1999–2001 and 2010–11

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ABSTRACT. Satellite-linked time-depth recorders were deployed on 17 ringed seals in early summer in 1999, 2000, and 2010, near the Inuvialuit community of Ulukhaktok, Northwest Territories, Canada. The main objective was to investigate movements and diving behaviour of ringed seals in the Prince Albert Sound (PAS) and eastern Amundsen Gulf (EAG) regions in relation to season, sex, and age-class. Tags performed well on 16 of 17 tagged seals, with average tracking periods of 256 d (SD 69, range: 134–352). Adult and subadult ringed seals traveled considerable distances throughout the open water period (mean = 5844 km, range = 1232–9473 km), using vast home ranges during this season, shown with 90 Percent Volume Contours (90 PVC) averaging 122 854 km^2 for subadults, 76 658 km^2 for adult females, and 21 649 km^2 for adult males**.** Overall, adults spent 69.5% of the observed open water days in foraging/resident mode and 22.8% in traveling mode. The majority (75%) of total observed foraging/resident time was spent in PAS and EAG. Eleven of 12 adults made forays outside EAG and PAS to distant areas, including Prince of Wales Strait (7 seals), Viscount Melville Sound (6), Minto Inlet (4), western Amundsen Gulf (4), and six other zones. During open water season, subadults spent 36.8% traveling and 51.4% foraging/resident, also mainly in EAG and PAS (61%), but they all traveled to distant zones, eight in total. During winter, all tagged adult females, five of seven adult males, and three of four subadults returned to PAS and EAG to occupy winter home ranges that were on average 15% of the size of the open water home range (mean winter ranges = 1299 km^2 for adult males, 3599 km^2 for adult females, and 30 499 km^2 for subadults). The mean size of the winter home ranges varied by as much as a factor of 10 among the three winters examined. Seal movements were most restricted during the winters with extensive fast ice (1999–2000 and 2010–11) and least restricted during the winter (2000–01) when fast ice did not form in EAG. In winter, adult females made more long, deep dives than either adult males or subadults.

Key words: ringed seal; satellite telemetry; Amundsen Gulf; Prince Albert Sound; Beaufort Sea; sea ice; diving; foraging

RÉSUMÉ. Des enregistreurs de profondeur temporelle en liaison avec un satellite ont été déployés sur 17 phoques annelés au début des étés 1999, 2000 et 2010 près de la collectivité inuvialuite d'Ulukhaktok, dans les Territoires du Nord-Ouest, au Canada. L'objectif principal consistait à étudier les déplacements et les comportements de plongée des phoques annelés des régions du détroit de Prince-Albert (DPA) et de la partie est du golfe Amundsen (EGA) en fonction de la saison, du sexe et de la classe d'âge. Les étiquettes ont donné des résultats valables dans le cas de 16 des 17 phoques étiquetés, les périodes moyennes de pistage ayant atteint 256 jours (SD 69, étendue : 134–352). Les phoques annelés adultes et jeunes adultes parcouraient des distances considérables pendant la période des eaux libres (moyenne = 5 844 km, étendue = 1 232–9 473 km), dans de vastes domaines vitaux au cours de la saison. Les pourcentages du volume des contours de 90 (90 PVC) s'établissaient en moyenne à 122 854 km^2 pour les jeunes adultes, à 76 658 km^2 pour les femelles adultes et à 21 649 km^2 pour les mâles adultes. Dans l'ensemble, les adultes ont passé 69,5 % des journées observées en eaux libres en mode d'alimentation et de résidence, et 22,8 % en mode de déplacement. La majorité (75 %) du temps total observé en mode d'alimentation et de résidence était dans le DPA et l'EGA. Onze adultes sur 12 se sont aventurés en dehors du DPA et de l'EGA pour atteindre des endroits éloignés, dont le détroit du Prince-de-Galles (7 phoques), le détroit du Vicomte de Melville (6), l'anse Mintot (4), l'ouest du golfe Amundsen (4) et six autres zones. Pendant la saison des eaux libres, les jeunes adultes ont passé 36,8 % du temps en mode de déplacement et 51,4 % du temps en mode d'alimentation ou de résidence, également principalement dans le DPG et l'EGA (61 %), mais ils se sont tous rendus dans des zones éloignées, huit en tout. Durant l'hiver, toutes les femelles adultes étiquetées, cinq mâles adultes sur sept et trois jeunes adultes sur quatre sont revenus dans le DPA et l'EGA pour occuper des domaines vitaux hivernaux qui correspondaient, en moyenne, à 15 % de la taille du domaine vital en eaux libres (étendues moyennes des domaines hivernaux = 1 299 km^2 pour les mâles adultes, 3 599 km^2 pour les femelles adultes et 30 499 km^2 pour les jeunes adultes). La taille moyenne des domaines vitaux hivernaux a varié en fonction d'un facteur de 10 au cours des trois hivers à

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l'étude. Le déplacement des phoques était plus restreint pendant les hivers où la glace était rapide (1999-2000 et 2010-2011) et moins restreint pendant l'hiver (2000-2001) où la glace rapide ne s'est pas formée dans l'EGA. L'hiver, les femelles adultes faisaient plus de plongées longues et profondes que les mâles adultes ou les jeunes adultes.

Mots clés : phoque annelé; télémesure satellitaire; golfe Amundsen; détroit de Prince-Albert; mer de Beaufort; glace de mer; plongée; alimentation

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INTRODUCTION

As apex predators, marine mammals provide a means to assess changes in the marine ecosystem (Moore et al., 2014). Knowledge of critical habitats used by marine mammals may help researchers to predict how seals will respond to climate change or other factors that alter habitat (Laidre et al., 2008). However, attempts to relate changes in the environment (Melling et al., 2005; Serreze et al., 2007; Walsh, 2008) to a marine mammal's responses to those changes, are often constrained by lack of baseline information about the species, its life history, prey, and critical habitats (Moore et al., 2014). Although the distribution, reproduction, and biology of the ringed seal (*Pusa hispida*) in the western Canadian Arctic have been the subject of scientific study for four decades (Stirling et al., 1977, 1982; Smith, 1987; Kingsley and Byers, 1998; Harwood et al., 2000, 2012b; Stirling, 2002), the seasonal movements and habitat use of ringed seals in Amundsen Gulf have not been explicitly examined to date.

The ringed seal is abundant throughout the circumpolar Arctic and feeds at several trophic levels (Dunbar, 1941; Lowry et al., 1978, 1980; Smith, 1987). Ringed seals are opportunistic predators, but adults prey mainly on Arctic cod, *Boreogadus saida*, throughout the Western Arctic at all times of the year (Johnson et al., 1966; Smith, 1987; Smith and Harwood, 2001). During the ice-free months, some adults travel considerable distances away from their fast ice breeding habitats in order to feed (Smith, 1987; Heide-Jørgensen et al., 1992; Teilmann et al., 1999; Freitas et al., 2008a), and ringed seals are well known to prey on zooplankton where they are abundant (e.g., Lowry et al., 1978, 1980; Harwood, 1989). There is growing evidence that adults are philopatric, returning annually to the same winter and breeding sites in the fast ice prior to freeze-up in the fall (Smith and Hammill, 1981; Kelly et al., 2010).

Subadult ringed seals in the Western Arctic population undertake extensive migrations during the fall, probably in response to food availability (Smith, 1987; Harwood et al., 2012a). In other areas, their migrations have been linked to advancing and retreating ice (e.g., Svalbard, Freitas et al., 2008a; Chukchi/Bering Seas, Crawford et al., 2011). Seasonal and age-specific prey preferences are known (Lowry et al., 1980; Thiemann et al., 2008; Young et al., 2010), as are patterns of habitat use, which differ within and among populations (Freitas et al., 2008a; Crawford et al., 2011; Carroll et al., 2013). In the Western Arctic, the less experienced subadults (< 6 y) appear to rely most heavily on invertebrates (Smith, 1987; Smith and Harwood, 2001; authors' unpubl. data), and occupy peripheral areas of the core breeding habitat in Prince Albert Sound (Smith, 1987).

The large bays with stable fast ice in eastern Amundsen Gulf (EAG), including northwest Prince Albert Sound (PAS), where the present study was staged, provide prime habitat for ringed seals of the Western Arctic (Smith, 1987). The stable fast ice provides ringed seals with a substrate for pupping, lactation, haul-out, and protection from weather and predators (Smith and Stirling, 1975, 1978; Smith, 1976, 1987; Stirling et al., 1982; Lydersen and Gjertz, 1987; Hammill and Smith, 1989; Hammill et al., 1991; Smith and Lydersen, 1991; Furgal et al., 1996). The availability of food during the winter is also paramount to their reproductive success (Smith, 1987; Lydersen, 1991). The crucial combination of suitable sea ice and abundant winter prey is what makes eastern Amundsen Gulf and western Prince Albert Sound a core breeding habitat for ringed seals in Canada's Western Arctic (Smith, 1987).

Satellite tracking of ringed seals from other areas has revealed seasonal differences in habitat use strategies, which have included relatively restricted movements in winter and early spring (Harwood et al., 2007; Kelly et al., 2010), forays to distant areas in summer (Teilmann et al., 1999; Born et al., 2004), and extensive migrations during fall and winter (Freitas et al., 2008a; Crawford et al., 2011; Harwood et al., 2012a). Given the circumpolar range of ringed seals, which occupy areas as diverse as lakes, pack ice, and fast ice (Finley et al., 1983; Smith et al., 1991; Born et al., 2004), the annual feeding strategies of this species are clearly diverse and adaptable to a variety of habitat types.

The objectives of the present study were to investigate movements, habitat use, and diving behaviour of ringed seals in relation to season, age-class, and sex. We accomplished this through the use of satellite telemetry and with the assistance of local Inuvialuit harvesters.

METHODS

Capture and Tagging

In total, 17 ringed seals were captured, measured, weighed, and tagged with satellite-linked transmitters (SDR-10, SDR-16, SPLASH) in June and July of 1999, 2000, and 2010. The tags, manufactured by Wildlife Computers Ltd. (Redmond, Washington, USA), send data to polar orbiting satellites. Data are then retrieved via the Argos

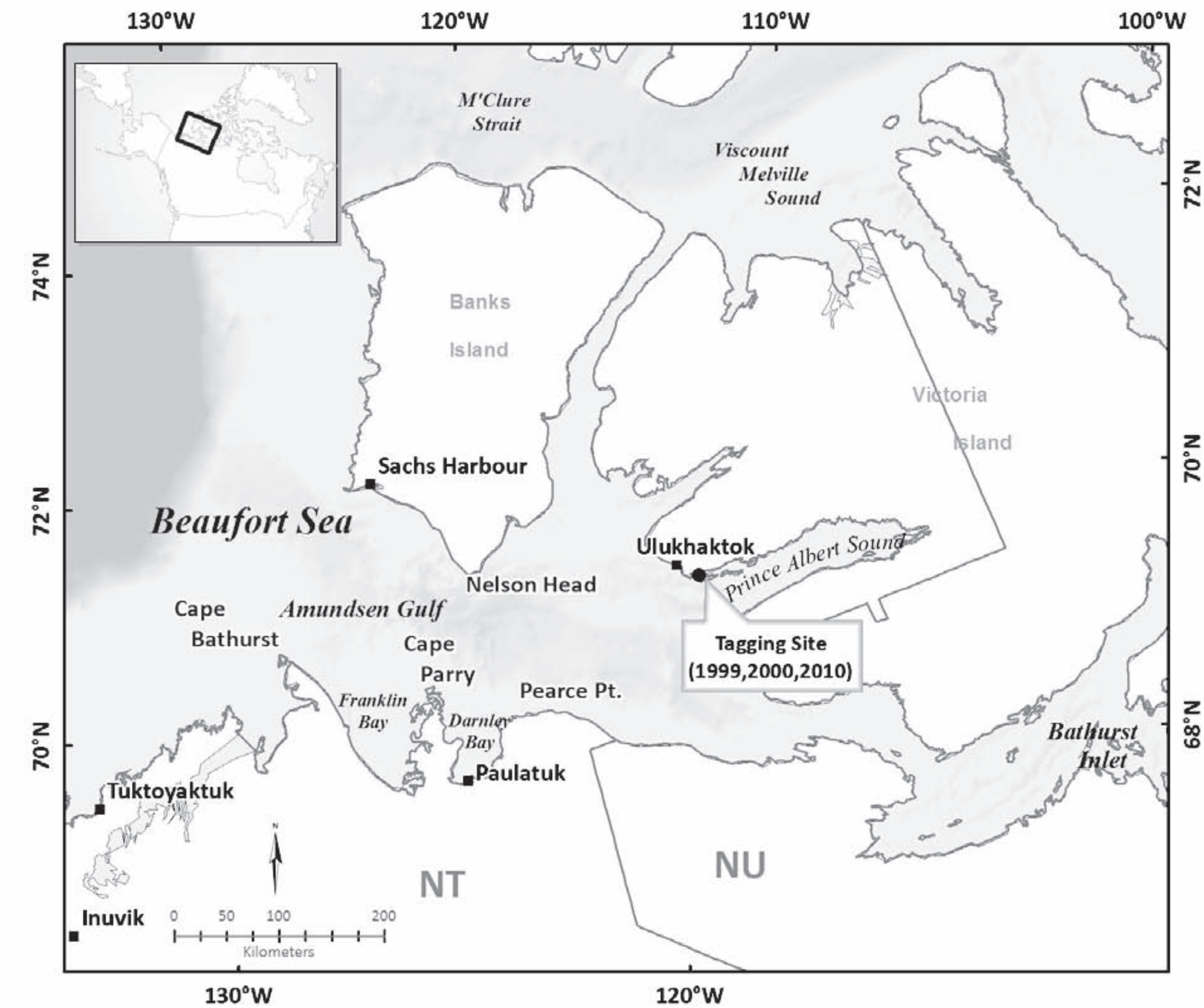

FIG. 1. Location of ringed seal satellite tag deployment site, northwest Prince Albert Sound, Northwest Territories, Canada.

system (Harris et al., 1990). Tags collected and relayed information on movement (geographic positions) and diving data of the instrumented animals. Tags were applied after the moult, 7–14 days prior to breakup of fast ice in NW Prince Albert Sound.

The seals were captured from shore at a site known locally as "Orhohivik" (70˚36′ N; 117˚18′ W), which is located in NW Prince Albert Sound, 17 km east of the seal monitoring site (Harwood et al., 2012b) and approximately 25 km southeast of Ulukhaktok, NT (Fig. 1). They were captured using 229 mm (9") mesh cotton seal nets set perpendicular to shore (Smith et al., 1973) and monitored continuously during deployment. When a seal became entangled, it was immediately removed from the net and transported to the workstation on shore. Covering their heads with a tarp calmed the seals, and only gentle restraint was necessary. The pelage was cleaned with rubbing alcohol, and a tag was applied using approximately 150 mL of five-minute epoxy glue (Christensen and Jensen, 1977; Priede and French, 1991; Heide-Jørgensen et al., 1992; McConnell et al., 1992; Testa, 1994; Burns and Castellini, 1998; Teilmann et al., 1999; Harwood et al., 2007). Tags were attached to the back between the two front flippers. Both the glue and transmitter were warmed with a hair dryer before deployment to initiate hardening of the glue, which took about 20 min. Standard length, sex, weight, and claw age were determined for all seals that were live-captured. Seals were classified as adults or subadults in the field by external examination and estimation of claw age. Seals were classified as adults if their claw age was greater than six (Smith, 1987; Harwood et al., 2012b).

After the tag application process was completed and the glue had dried, the seals were released at the capture site. The Animal Care Committee of Canada's Department of Fisheries and Oceans approved all animal handling procedures used in this study. The tag and epoxy attachment is shed when the animal next moults, in this case in May or June of the following year, and regeneration of the pelage has been noted in seals observed after the moult (Testa, 1994).

The transmitters were cast in epoxy. SDR tags (1999, 2000) measured 15 cm × 10 cm × 3.5 cm, and weighed 170 g in seawater and approximately 600 g in air. SPLASH tags (2010) were 78 mm × 51 mm × 25 mm and weighed 32 g in seawater and 114 g in air. The 1999 transmitters were programmed to transmit at a maximum of 500 transmissions per day, whereas the 2000 and 2010 tags transmitted for a maximum of 300 transmissions per day. Tags in 2010 were duty cycled to transmit every second day in order to conserve battery life.

The transmission repetition rate was 45 s at sea and 90 s when the seal was hauled out. The tag's saltwater switch ensured that transmissions occurred when the tag was in the air (when the seal surfaced to breathe or was hauled out). The pressure transducer had a resolution of ±1 m and an accuracy of +1% of the depth reading. Time and pressure (depth) were sampled every 42.5 s and stored in user-defined six-hour bins (n = 10 in 1999 and 2000, n = 14 in 2010). Data collected included maximum depth and duration of each dive (sensor capability to 500 m in 1999 and 2000 and to 1000 m in 2010).

Data Processing and Analysis

Data about locations, dives, and transmitter status were collected via the Argos Location Service Plus system (Fancy et al., 1988; Harris et al., 1990). We used Satpak 3.0 in 1999–2001 and DAP 3.00.0143 (Wildlife Computers) in 2010–11 to download data received from Argos into Excel. SAS V.8.0 (1990) and XLStat 13.6 were used for statistical analyses.

To remove locations with suspect accuracy, all locations (quality B, A, 0, 1, 2, 3) were filtered using the sdafilter developed by Freitas et al. (2008b) in the package Argosfilter in R version 2.5.1 (R Development Core Team, 2014). The filter has separate velocity and angular components. First, locations that indicated swim speeds exceeding 2 m/s were removed, since 3.3 km/h (approximately 0.91 m/s) is the upper limit of observed rate of movement for ringed seals (Teilmann et al., 1999). The angular component of the filter is used to remove locations with a high degree of location error that fall far from the line of travel, but are still within the above threshold velocity. Using default settings, locations with angles less than 15˚ within 2.5 km of the track line were removed. Within 2.5 and 5 km of the track line, locations were removed if they resulted in angles of less than 25˚. Finally, we removed any locations that fell on land.

Distance Traveled and Size of Seasonal Home Ranges

The minimum distance traveled was calculated as the distance between two successive filtered locations. The sum of these minimum distances was used to estimate distance traveled per seal and per season. A Kernel Density Estimator (KDE) was used to determine the spatial extent of home ranges used by adult and subadult seals in open water season and in winter (e.g., Silverman, 1986; Worton, 1989; Wand and Jones, 1995), and we refer to the 90 PVC as the "home range." The KDE is a non-parametric method for calculating the probability that an animal occurs within a defined area (Quakenbush et al., 2010). Smoothed cross-validation (SCV) was used for bandwidth selection (Quakenbush et al., 2010), separately for each seal and season, as described by Duong and Hazelton (2005) and using package "ks" (Duong, 2007) in R version 2.5.1. Percent Volume Contours (PVCs) used to visualize and compare the kernel densities (home ranges) of the tagged seals were derived from the KDE raster datasets (Sain et al., 1994; Seaman and Powell, 1996; Seaman et al., 1999; Gitzen and Millspaugh, 2003).

Since transmitters lasted different periods of time and did not transmit with equal frequency, we standardized the contributions made by individual seals over time for the kernel density estimation procedure. We did not want tags that contributed little information to have equal weight in the kernel densities; therefore, we weighted the contribution of individual seals according to the number of locations used to compute the kernel density for each seal. We selected the filtered location with the highest quality code from each of the four six-hour periods of each day. When multiple locations had the same location quality code, we selected the location that was transmitted the earliest within the time period. This procedure has the effect of spacing the accepted locations throughout the day and equalizing the contribution of information from tags that differed in transmission frequency.

Ice Conditions

The formation and persistence of fast ice is of particular interest in the study of ringed seals (Smith, 1987). The Canadian Ice Service maps fast ice weekly via satellite-image analysis to prepare regional ice charts (Environment Canada, 2013), on which fast ice is uniquely coded as 10/10 ice concentration. An area of ice is judged to be fast ice if the satellite reveals a flaw lead at its boundary with pack ice or no evidence of recently active leads. Correspondingly, we here judged breakup in the spring to have occurred when a lead (or area of generally light ice cover) at least 10 km wide persisted in EAG for one week or more. The number of days between the formation of fast ice in fall or winter, and the earliest date of breakup in spring was taken as the duration of the fast ice and referred to here as "winter." The (monthly) frequency of charting for the winters prior to 2004–05 would have the effect of negatively biasing these estimates of duration.

Using the annual estimated values of fast ice duration in EAG, we calculated the mean (±SD) duration of fast ice for two decades, from 1991–92 to 2010–11. To examine the relationship between fast ice and the size of home ranges used by the tagged adult seals, we prepared a scatterplot and used a Pearson product moment correlation to compare the duration of fast ice in the winters for which we had tagged seals (1999–2000, 2000–01, 2010–11) to the individual home ranges used by those seals in the corresponding winters.

Behavioural State during Open Water

To distinguish areas where seals were in apparent foraging/resident mode, as opposed to making sustained, directional migrations, Bayesian state-space models (BSSMs) were run using the filtered location data (Hoenner et al., 2012). This type of model is commonly applied to animal movement ecology in terrestrial and aquatic ecosystems as a correlated random walk (Jonsen et al., 2013). The BSSM is a time-series method that consists of two stochastic models: (1) the process model (i.e., transition equation), which estimates the individual's current state such as geographic location and behavioural state given its previous state, and (2) the observation model, which relates the unobserved states estimated by the process model to the observed locations obtained from Argos data (Jonsen et al., 2005). Here, we fit a two-state switching BSSM, which allows movement parameters to "switch" between two behavioural state modes (e.g., traveling and foraging/resident), within a hierarchical framework (hBSSM) which improves parameter and location estimation and overall model fit (see Jonsen et al., 2005, 2006, and Mills Flemming et al., 2010 for further details). Before running the models, we classified ringed seals into six distinct groupings by age-class (i.e., adult and subadult) and year captured (i.e., 1999, 2000, and 2010). The hBSSM runs in discrete and regular time intervals to mitigate irregularity over time of observations obtained via ARGOS transmissions (Jonsen et al., 2005). A time step of 12 h was used for each model, which is a common approach with duty-cycled transmitters and in animals inhabiting ice-covered environments (Jonsen et al., 2007; Bestley et al., 2012), and 24 h periods are referred to here as "observed days." The mean estimates of behavioural state are continuous values between 1 (traveling) and 2 (foraging/resident); values of 1.35 or less were considered to represent traveling, values of 1.65 or more were deemed to represent residence or foraging, and values between 1.35 and 1.65 were considered uncertain. This approach, similar to that used by Jonsen et al. (2007), is considered conservative.

The hBSSM was implemented using the package bsam v0.44 (Jonsen et al., 2013) in R v3.0.3 (R Development Core Team, 2014), which runs Markov Chain Monte Carlo (MCMC) methods using Just Another Gibbs Sampler (JAGS). Each ringed seal grouping was run in two MCMC chains for 30 000 iterations with a 20 000 sample burn-in and thinned every 10 samples. Thus, every 10th sample from the remaining 10 000 was used for parameter estimation and to reduce autocorrelation. Chain convergence and autocorrelation for all hBSSM model runs were assessed visually via trace and autocorrelation plots and then estimated by Gelman and Rubin's potential scale reduction factor, which was less than 1.1.

Filtered locations were grouped into 13 geographic zones: EAG, western Amundsen Gulf, PAS, Coronation Gulf, Dolphin and Union Strait, Darnley Bay, Franklin Bay, Minto Inlet, Eastern Beaufort Sea, Prince of Wales Strait, Viscount Melville Sound, M'Clure Strait, and McClintock Channel (Fig. 2). Using hBSSMs, we tallied the number of days and type of modeled activity during the open water period for adults and subadults in each zone. The model interpolates estimates of behaviour and location for each 12 h period in the tracking period (Jonsen et al., 2005). During winter, uplinks were too sporadic for interpolation using hBSSMs, so filtered locations were tallied and plotted.

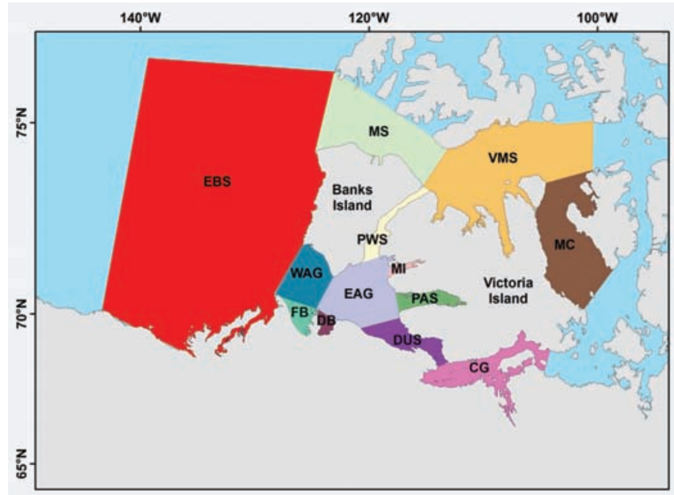

FIG. 2. Location of the 13 geographic zones used by satellite-tagged ringed seals in 1999–2000, 2000–01, and 2010–11 (EBS: eastern Beaufort Sea; WAG: western Amundsen Gulf; EAG: eastern Amundsen Gulf; MS: M'Clure Strait; MC: McClintock Channel; PAS: Prince Albert Sound; CG: Coronation Gulf; MI: Minto Inlet; PWS: Prince of Wales Strait; VMS: Viscount Melville Sound; DUS: Dolphin and Union Strait; FB: Franklin Bay; DB: Darnley Bay).

Diving

Because of the potential for sensor error in the upper 2 m of the water column, descents were considered dives only if they exceeded 4 m in depth and 1 min in duration. Data from the dive depth bins were pooled into five intervals (> 4–10 m, > 10–40 m, > 40–100 m, > 100–200, and > 200 m), as were data from the dive duration bins (> 1–5, > 5–10, > 10–18, > 18–24, and > 24 min). The mean (±SD) proportion of dives in each interval for each six-hour diving record was calculated and plotted separately for open water and winter, and for adult males, adult females, and subadults, and presented in bar graphs. The mean proportion of dives in each time/depth interval of each six-hour record was compared among age/sex classes and seasons, using PROC GLM and a Duncan's Multiple Range test in SAS V.8 (1990).

RESULTS

Tag Performance and Sample Size

Seventeen seals were tagged near Ulukhaktok, NT (Fig. 1) during 28 June–1 July in 1999 (n = 4), 16–19 July in 2000 (n = 4), and 6–10 July 2010 (n = 9), immediately following breakup of the fast ice in EAG in those years

TABLE 1. Identifiers and platform transmitter terminal (PTT) numbers, and biological and deployment data, for 17 ringed seals instrumented with satellite-linked tags near Ulukhaktok following breakup of the fast ice in 1999, 2000, and 2010.

Seal id no.	PTT number	Sex	Relative age	Estimated age (claw bands)	Weight (kg)	Standard length (cm)	Axillary girth (cm)	Year tag deployed	Type of tag	Release date MDT
12	5056	male	adult	7++	100.91	127	129	1999	SDR-10	20 June 1999
13	5092	male	adult	7++	84.55	132	122	1999	SDR-10	08 June 1999
14	11747	female	subadult	5	36.36	104	101	1999	SDR-10	01 July 1999
15	21212	female	adult	6++	52.27	102	115	1999	SDR-10	28 June 1999
16	23526	female	adult	6++	79.55	120	120	2000	SDR-16	19 July 2000
17	23527	male	adult	8	50.00	110	97	2000	SDR-16	17 July 2000
18	23528	male	subadult	2.5	36.36	100	91	2000	SDR-16	16 July 2000
19	23529	female	adult	6	50.45	111	100	2000	SDR-16	16 July 2000
41	44391	male	adult	6++	87.27	121	126	2010	SPLASH	09 July 2010
42	44392	female	adult	6++	74.09	130	117	2010	SPLASH	06 July 2010
43	44393	male	subadult	4+	41.36	104	61	2010	SPLASH	04 July 2010
44	44395	female	subadult	4+	47.73	116	95	2010	SPLASH	10 July 2010
45	44396	male	adult	6++	63.64	126	115	2010	SPLASH	06 July 2010
46	44397	female	adult	6++	61.82	136	101	2010	SPLASH	06 July 2010
47	44399	male	adult	6++	78.18	134	113	2010	SPLASH	06 July 2010
48	44400	female	adult	6++	69.09	126	113	2010	SPLASH	10 July 2010
49	44402	male	adult	6++	50.91	117	102	2010	SPLASH	05 July 2010

TABLE 1. – *continued*:

Seal id no.	Last transmission date	Days from first to last inclusive	Days with filtered positions	No. of filtered positions	Distance tracked (km)	% filtered location	Maximum recorded dive depth (m)	Distance between first and last signal (km)	Farthest distance from tagging site (km)
12	05 March 2000	251	105	338	1232	11	82	34	150
13	10 November 2000	136	106	421	3707	14	465	79	900
14	02 February 2000	217	132	453	4391	13	443	16	330
15	07 July 2000	10	5	na[1]	74	na	na	48	60
16	02 June 2001	319	170	840	6547	21	491	167	480
17	15 June 2001	334	202	1287	6946	26	497	166	400
18	21 February 2001	221	142	1454	4506	31	472	457	560
19	26 October 2000	103	90	701	4693	23	307	95	720
41	01 March 2011	236	158	1750	5401	67	466	85	710
42	10 April 2011	279	182	1478	6415	67	366	248	1251
43	26 April 2011	297	184	2033	8182	73	508	245	1344
44	26 June 2011	352	224	1706	9473	65	524	102	1812
45	17 June 2011	347	221	2489	8738	77	542	280	1653
46	15 February 2011	225	146	1820	7653	78	490	82	2383
47	11 March 2011	249	161	1291	4045	75	156	702	995
48	27 March 2011	261	170	1603	6399	67	392	61	676
49	23 March 2011	262	161	1709	5179	70	318	378	845
	Mean[2]	256	160	1336	5844				
	Total[2]			21373	93507				

[1] na = not available.

[2] Does not include seal 15 (PTT 21212).

(Table 1). Thirteen adults (6 females, 7 males) and 4 subadults (2 males and 2 females) were tagged and released. Tags performed well on 16 of 17 instrumented seals, and they were tracked during all four seasons. Fourteen tags transmitted for more than 200 days, and four of these transmitted for more than 300 days (Table 1). Battery voltages reported in the last transmissions indicated that battery power was not the reason for tag failure in any of the deployments (Kevin Ng, Wildlife Computers, pers. comm. 2013).

Animals were tracked from the time of tagging in June or July until October (no. of tags transmitting = 16), November (15), February (12), March (7), April (5), May (4) and June (3). We received only 13 transmissions from one of the adult females tagged (seal ID 15; Table 1), and those results are not included in any analyses (Table 1).

We obtained a total of 21 373 filtered positions, representing a minimum tracking distance of 93 507 km, from the 16 tagged seals (Table 1); the average was 1336 filtered locations per seal (range 338–2489). The proportion of all received locations accepted by the filtering procedure averaged 13% for the SDR tags (range 11%–31%) and 71% for the SPLASH tags (range 65%–78%; Table 1). Seals were tracked for an average of 256 days (SD 69, range 134–352). Overall, 81.5% of the filtered positions and 83.4% of the minimum distances tracked were in the open water period (Table 2). On average, open water locations were seven

TABLE 2. Filtered locations and size of individual 90 PVC for adult females, adult males, and subadults during open water and ice-covered periods.

Year tagged	Seal id no.	Date ice formed in east Amundson Gulf	Open water			Winter		
			No. filtered locations	Distance tracked (km)	90 PVC (km^2)	No. filtered locations	Distance tracked (km)	90 PVC (km^2)
Adult females:								
2000	16	23 October	510	4349	11729	330	2198	3745
2000	19	23 October	701	4787	15819	nd	nd	nd
2010	42	15 November	1265	5448	89736	213	956	10055
2010	46	15 November	1698	7503	215770	122	140	257
2010	48	15 November	1368	5795	50238	235	597	338
Adult males:								
1999	12	25 October	301	1182	954	37	50	178
1999	13	25 October	381	3466	11795	40	241	686
2000	17	23 October	630	3708	9382	657	3238	4647
2010	41	15 November	1619	5257	8847	131	141	16
2010	45	15 November	1729	7582	54049	760	1127	509
2010	47	15 November	1015	3192	30026	276	850	3009
2010	49	15 November	1612	5015	36492	97	141	46
Subadults:								
1999	14	25 October	377	3667	14632	76	878	5003
2000	18	23 October	1319	4227	18853	135	314	842
2010	44	15 November	1078	6136	298620	628	3302	87640
2010	43	15 November	1809	6738	159312	224	1379	28512

times as numerous as locations during periods of ice cover (range 1–17 times among individual tagged seals).

Movements and Size of Home Range, by Season

All but one of the tagged seals moved out of the capture area within days of tagging (Fig. 3a, b). The farthest distance that individual seals traveled from the tagging site ranged from 150 to 2383 km (average = 951 km; Table 1), and the minimum distance traveled during deployment averaged 5844 km (range = 1232–9473 km).

A subadult female (Fig. 3b, ID 44; Table 1) covered the longest distance between July 2010 and June 2011 by traveling north through Prince of Wales Strait, then circling Banks Island to the west, and eventually returning to overwinter less than 60 km from the tagging site (Fig. 3b). One adult female (2010, ID 46; Fig. 3a) followed a relatively linear track, starting in EAG. The seal moved in a northwestward direction for approximately 1000 km far into the offshore Beaufort Sea and then returned to EAG along an essentially identical route prior to freeze-up. At the end of the open water period, 13 tagged seals (10 of 12 adults and 3 of 4 subadults) eventually returned to PAS and EAG for wintering. The average distance between the tagging site and the last location in winter was 191 km (range 16–702 km; Table 1; Fig. 4a, b). Among all tagged individuals, the total distance tracked was lower during winter (average = 1037 km; range = 140–3302 km) than during the open water period (average = 4878 km; range = 1182–7503 km; Table 2).

During the open water season, tagged ringed seals used home ranges that were 6.6 times as large as winter home ranges (Table 2; mean 90 PVC winter = 9699 km^2; mean 90 PVC open water = 64 141 km^2). Open water home ranges were largest for subadults (n = 4, mean 90 PVC 122 854 km^2), followed by adult females (n = 5, mean 90 PVC = 76 658 km^2), and smallest for adult males (n = 7; mean 90 PVC = 21 649 km^2). In winter, the home ranges (mean 90 PVC) were smaller for every sex/age class (30 499 km^2 for subadults, 3599 km^2 for adult females, and 1299 km^2 for adult males; Table 2).

The duration of the fast ice in eastern Amundsen Gulf averaged 51.4 d (61.8 SD; range 0–163 d) for the 20 winters between 1991–92 and 2010–11. Ice conditions in eastern Amundsen Gulf were variable during our three study years; fast ice persisted for 133 d in 1999–2000 and 98 d in 2010–11, but did not form at all in 2000–01. The size of winter 90 PVCs was negatively correlated with number of days of fast ice in winter ($R^2 = -0.87094$, df = 9, $p < 0.05$): seals used the smallest ranges in winters with persistent fast ice (Fig. 5) and the largest in 2000–01, when fast ice did not form.

During 1999–2000 and 2010–11, mean 90 PVCs were 432 km^2 and 695 km^2, respectively (Table 2). These figures contrast with those for the winter of 2000–01, when the mean 90 PVC was 4196 km^2, 10 times as large as in winter 1999–2000 and six times as large as in winter 2010–11. Ice was present in Amundsen Gulf in 2000–01, but never reached a solid sheet of 10/10 concentration. A shear zone remained active between Cape Parry and Cape Bathurst throughout the winter, and by 1 April, a large lead had formed off Ulukhaktok, which persisted until June. During that winter, two of the tagged seals (IDs 17 and 47) were tracked regularly within this lead.

Examining the behavioural mode of adults and subadults during the open water season revealed that adults spent 69.5% of the 1625 days observed in foraging/resident mode and 22.8% in traveling mode. Adults spent the majority

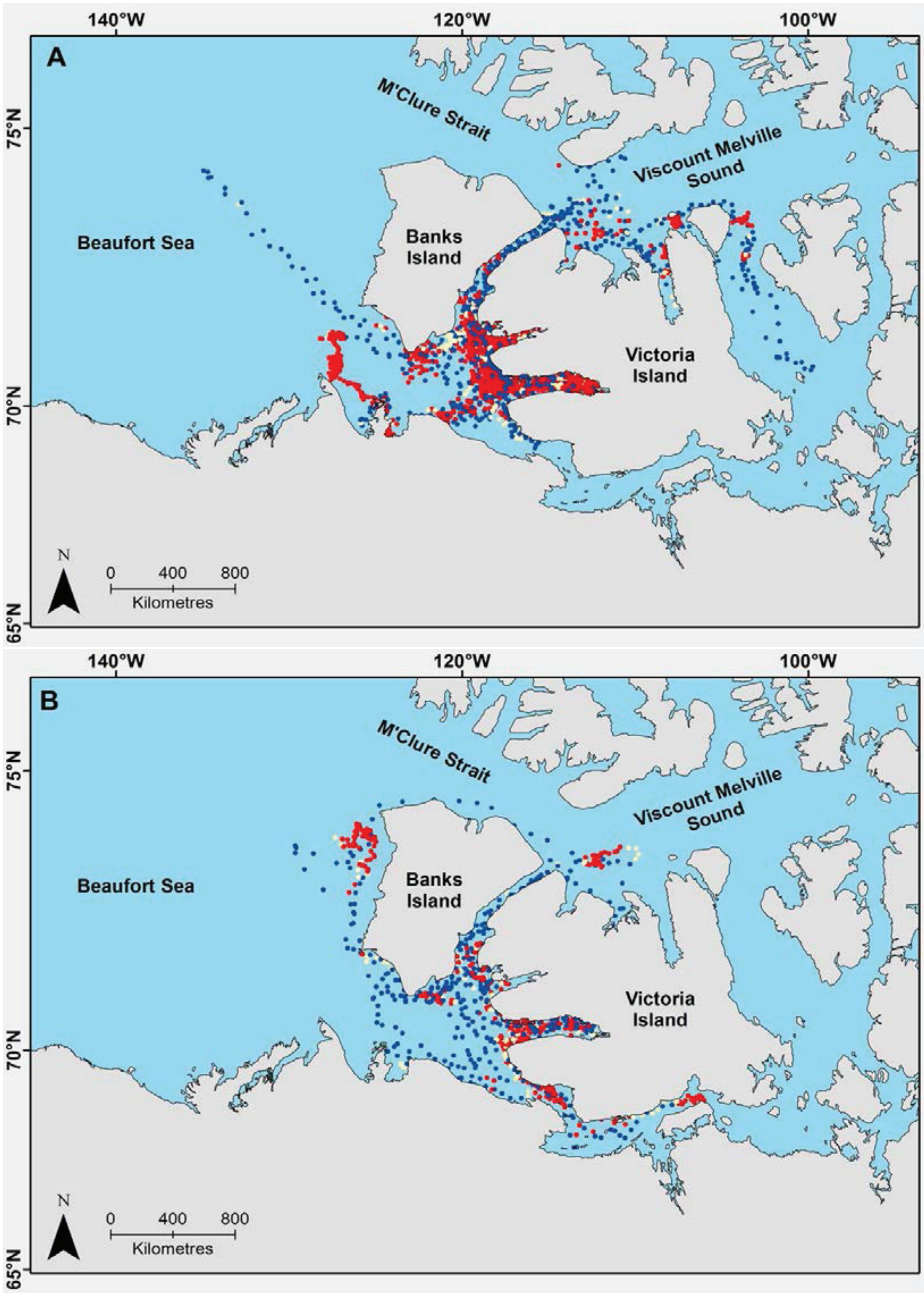

FIG. 3. Location estimates for (A) adult and (B) subadult ringed seals during the open water period. Each location represents a 12 h time step and is associated with a behavioural state estimation (blue = traveling, red = foraging/resident, and yellow = uncertain).

(75%) of foraging/resident days in PAS and EAG (Fig. 3a, Table 3). Similarly, subadults spent 51.4% of 555 observed days foraging/resident, also mainly (61%) in PAS and EAG, and 36.8% of observed days traveling (Fig. 3b, Table 3). Eleven of 12 adults made forays to other zones during summer, traveling to distant areas most notably Viscount Melville Sound (6 of 12 seals) and the southern end of Prince of Wales Strait (7 of 12). There were also indications of seals in foraging/resident mode in McClintock Channel (1 of 12), Minto Inlet (4 of 12), Amundsen Gulf near Nelson Head (2 of 12), Darnley Bay (1 of 12), Dolphin and Union Strait (4 of 12), and offshore of Cape Bathurst (1 of 12) (Fig. 3a; Table 3). Subadults also used open water foraging areas located in Viscount Melville Sound (2 of 4 seals), offshore of the NW coast of Banks Island (1 of 4), southern Prince of Wales Strait (4 of 4), the Nelson Head area (3 of 4), Dolphin

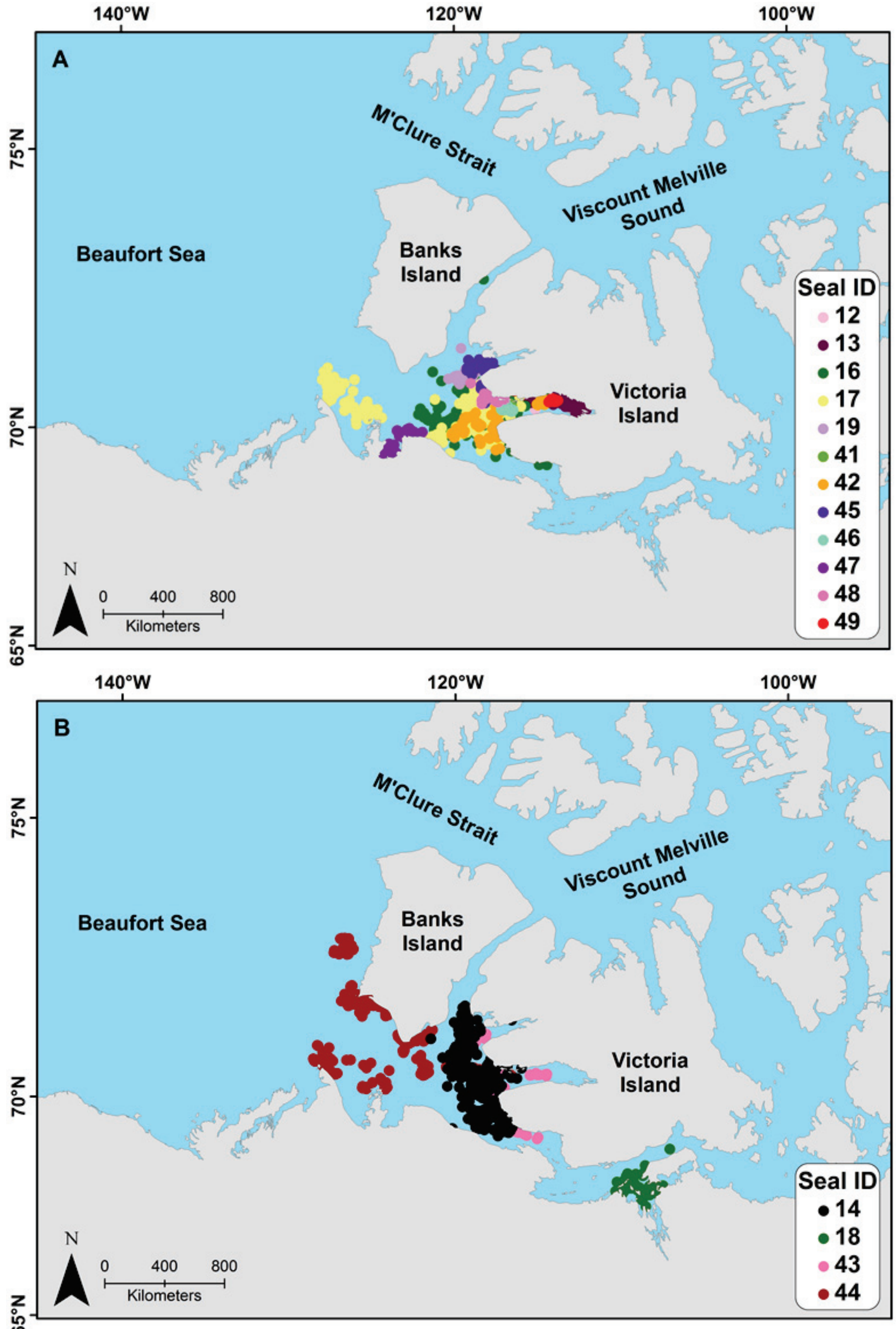

FIG. 4. All filtered location estimates for (A) adult and (B) subadult ringed seals during winter in 1999–2000, 2000–01, and 2010–11. Behavioural state estimates could not be modeled because of intermittent transmission frequency.

and Union Strait (4 of 4), and Coronation Gulf (2 of 4) (Fig. 3b, Table 3).

Most adults (12/14) overwintered in EAG and PAS (83% of all observed days, Fig. 6). They also used five other zones in winter, but the proportion of days in other areas was minor (16% in total). Three of four tagged subadults ultimately overwintered in EAG/PAS (31% of all observed days), but they also used six other zones during winter (28% in Coronation Gulf, and 40% in the other areas combined, Fig. 6).

Diving

Dive depth and duration records were available for 16 seals (> 10 892 records), each record representing a six-hour interval with 6–10 bins of diving data. The diving records

TABLE 3. Number of days (% of total tracking days) in open water period on which adult and subadult ringed seals were observed foraging/resident (F/R) or traveling in each of 13 geographic zones. No. of seals = number of seals contributing to all behaviour states indicated for each zone. See Figure 2 caption for geographic area abbreviations.

	Adults (n = 12)				Subadults (n = 4)			
Location	F/R	Traveling	Uncertain	No. seals	F/R	Traveling	Uncertain	No. seals
EBS	13 (1%)	13 (4%)	2 (1%)	2	42 (15%)	15 (7%)	3 (5%)	1
MS	1 (0%)	0 (0%)	0 (0%)	1	0 (0%)	4 (2%)	0 (0%)	1
MC	11 (1%)	24 (7%)	1 (1%)	2	0 (0%)	0 (0%)	0 (0%)	0
VMS	37 (3%)	67 (19%)	16 (12%)	6	12 (4%)	11 (5%)	5 (8%)	2
PWS	19 (2%)	53 (15%)	7 (5%)	7	7 (2%)	33 (16%)	6 (8%)	4
CG	0 (0%)	0 (0%)	6 (4%)	1	20 (7%)	12 (6%)	5 (8%)	2
DUS	3 (0%)	12 (3%)	31 (24%)	4	27 (10%)	22 (11%)	10 (15%)	4
MI	62 (6%)	10 (3%)	4 (3%)	4	4 (1%)	1 (0%)	1 (2%)	2
PAS	539 (48%)	63 (18%)	32 (24%)	12	111 (39%)	29 (14%)	16 (24%)	4
EAG	305 (27%)	104 (29%)	31 (24%)	12	61 (22%)	61 (30%)	14 (22%)	4
WAG	49 (4%)	9 (2%)	2 (1%)	4	1 (0%)	14 (7%)	4 (6%)	2
FB	37 (3%)	4 (1%)	1 (1%)	2	0 (0%)	0 (0%)	0 (0%)	0
DB	53 (5%)	3 (0%)	1 (1%)	1	0 (0%)	2 (1%)	2 (3%)	1
Total	1129 (100%)	362 (100%)	134 (100%)		285 (100%)	204 (100%)	66 (100%)	

represented 239 041 dives, 84% during the open water period and 16% during the winter. Approximately half of the records were obtained from seven SDR tags deployed in 1999 and 2000 (113 015 dives) and half from the nine SPLASH tags deployed in 2010 (126 026 dives). The deepest dives recorded ranged from 82 to 497 m for the SDR-tagged seals and from 156 to 542 m for those with SPLASH tags (Table 1). Three of nine 2010 tagged seals had recorded dives deeper than 500 m, although this involved very few records (< 0.7%).

Adult females dove to all depth intervals, but compared to adult males and subadults (Fig. 7), they had a significantly greater proportion of their dives in the 200–500 m depth interval in winter (32.7%; df = 2, 254, F = 20.33, $p < 0.0001$). There were no statistical differences detected between the dive depth patterns of adult males and subadults during the winter (df = 2, 770, F = 0.0582, $p > 0.9511$). In the open water period, however, subadults had a greater proportion of dives in the shallower (< 100 m) intervals (30.7% 10–40 m, df = 2, 4046; F = 35.58, $p < 0.0001$; 31.1% in 40–100 m, df = 2, 4046; F = 9.28, $p < 0.0001$) than either adult males or adult females, as well as the fewest dives in the 200–500 m interval (13.6%, df = 2, 1644, F = 42.21, $p < 0.0001$).

Durations of adult female dives were mainly in the 1–5 min (36% open water, 26.7% winter) or 5–10 min intervals (50%, open water, 30.7% winter), with some dives in the 10–18 min interval (9.8% open water), but most often (16.8%) in winter (Fig. 8). The proportion of dives in the 10–18 min interval was significantly greater for adult females than for adult males (6.6%) or subadults (6.0%) during winter (df = 2, 539, F = 20.31, $p < 0.0001$). Adult males showed the same pattern as adult females in open water dive durations, which fell mainly in the 1–5 min (39.3%) and 5–10 min (27.3%) intervals. Subadults had statistically shorter dives than adult males or adult females during the open water period, with 49.2% in the 1–5 min interval (df = 2, 3982, F = 58.31 $p < 0.0001$) and 53.3 % in the 5–10 min interval (df = 2, 3089, F = 58.64, $p < 0.0001$).

DISCUSSION

This study brings together local expertise and knowledge with modern scientific methods to provide new information on the wide-ranging seasonal movements and diving behaviour of ringed seals in the Western Arctic. The extent of movements and the range of locations used by adult and subadult ringed seals during the open water season were much greater than had been previously thought for this population. The study also confirmed strong fidelity to core winter habitats for adults, and also to some extent for subadults. Our finding that adult females dive deeper and for longer periods than either males or subadults during winter suggests there are seasonal differences among sex/age classes. Although our sample size was not robust, particularly for subadults, and had temporal gaps in tag deployment years, the data collected in this study are unique and increase our understanding of the habitats used by this species in the western Canadian Arctic.

Movements and Diving: Open Water

Ringed seals fast during the annual spring moult, which occurs for several weeks during May-June or early July before the sea ice melts or degrades (Smith, 1987). During the open water period, which follows their moult, the seals do extensive foraging while they regain condition prior to the onset of winter and the next breeding season (Smith, 1987; Harwood and Stirling, 1992). In this study, all but one of the tagged seals used vast and variable ranges in the Western Arctic during the open water period, some making forays for thousands of kilometres to a multitude of geographic areas. Other studies have demonstrated the use of

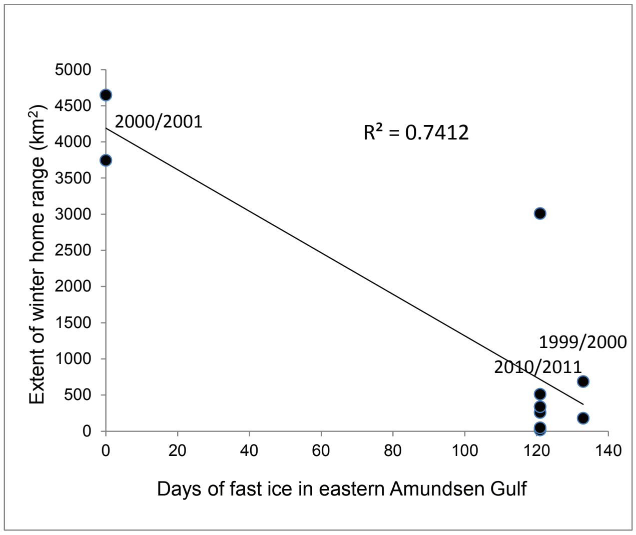

FIG. 5. Scatterplot of the size of the 90 PVC used by tagged adult ringed seals in relation to days of fast ice in eastern Amundsen Gulf during winter in 1999–2000, 2000–01 and 2010–11.

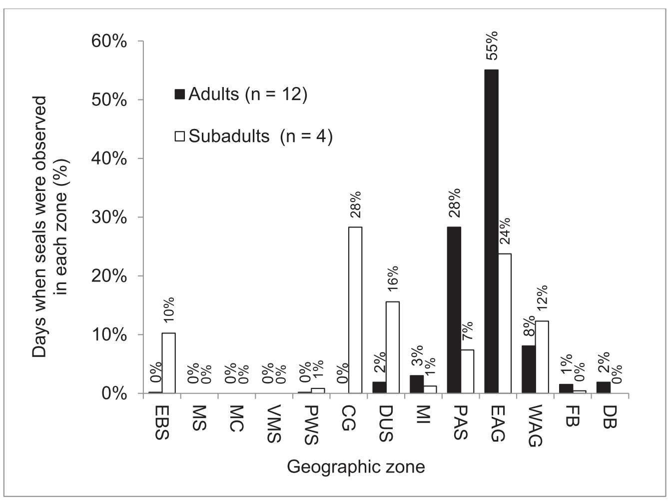

FIG. 6. Percentage of tracking days when adult and subadult seals were observed in each zone during the winters of 1999–2000, 2000–01 and 2010–11.

an extensive summer range by ringed seal adults (Teilmann et al., 1999; Gjertz et al., 2000; Born et al., 2004; Freitas et al., 2008a; Kelly et al., 2010), and our results show a similar pattern of habitat use in the Western Arctic.

During open water, PAS and EAG had the greatest proportion of observed days for both adults (75%) and subadults (61%), and both zones had indications that seals were mainly in foraging/resident mode. Tagged seals were also in foraging/resident mode in several other zones during open water (Fig. 2a, b). The diving activity of ringed seals in this and other studies was concentrated in the upper 200 m of the water column, with most dives lasting less than 10 minutes (e.g., Lydersen, 1991; Kelly and Wartzok, 1996; Gjertz et al., 2000; Born et al., 2004; Crawford et al., 2011).

We note that the tagged seals favoured some of the same geographic locations that bowhead whales (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*) use for feeding during late summer. Coincidence of bowhead whales and ringed seals has been documented previously for the Beaufort Sea (Harwood, 1989; Harwood and Stirling, 1992). Bowhead whales are well known for aggregating in later summer to feed on dense patches of zooplankton (Laidre et al., 2007; Walkusz et al., 2012), and in the present study, we observed adult and subadult ringed seals in foraging/resident mode in at least five of the same areas that bowheads use. These included Viscount Melville Sound (Heide-Jørgensen et al., 2011; ADFG, 2014), offshore of the NW coast of Banks Island (Harris et al., 2008), north of Cape Parry (Paulic et al., 2012), south of Nelson Head (Davis et al., 1982), and north of Cape Bathurst (Walkusz et al., 2012).

Tagged belugas, major consumers of Arctic cod (Quakenbush et al., in press), also made sustained and directional migrations to Viscount Melville Sound in late summer (Richard et al., 2001), remaining there for more than three weeks and making deep dives that indicated foraging. The coincidence of ringed seals, bowhead whales, and beluga whales in specific locations in this region contributes to an emerging picture of distant, offshore foraging habitats used by at least these three species. We urge further research and monitoring in such areas to identify oceanographic processes that produce and possibly sustain these habitats, so that regulators and managers are well positioned to ensure their protection given pending offshore developments (AANDC, 2012).

Movements and Diving: Winter

Following the open water period, 12 of 14 of our tagged adults and 3 of 4 of our tagged subadults returned to EAG and PAS areas, just prior to freeze-up. Fidelity to wintering areas has been indicated for adults in other populations (Smith and Hammill, 1981; Krafft et al., 2007; Kelly et al., 2010), although generally not to the same extent for subadults. While our sample size of subadults was small, those subadults tagged in the core habitats of EAG and PAS (Smith, 1987) did not disperse in fall to the same extent as has been observed in other studies (Bering/Chukchi, Crawford et al., 2011; Svalbard, Freitas et al., 2008a; Cape Parry, Harwood et al., 2012b). This finding may reflect the exceptionally productive character of EAG and PAS, which makes it a core habitat that is attractive to and capable of supporting subadults, as well as the breeding adults.

Within the wintering areas in EAG and PAS, the more restrictive movements of ringed seals appear moderated by the constraints of sea ice, a situation that has also been observed in other locations across the circumpolar Arctic (Teilmann et al., 1999; Gjertz et al., 2000; Born et al., 2004; Freitas et al., 2008a; Kelly et al., 2010). During winter 2000–01, the year when our tagged seals used the largest winter home ranges, persistent southeasterly winds pushed ice out of Amundsen Gulf and into the Beaufort Sea, and fast ice did not form. Our tagged seals used a feeding area

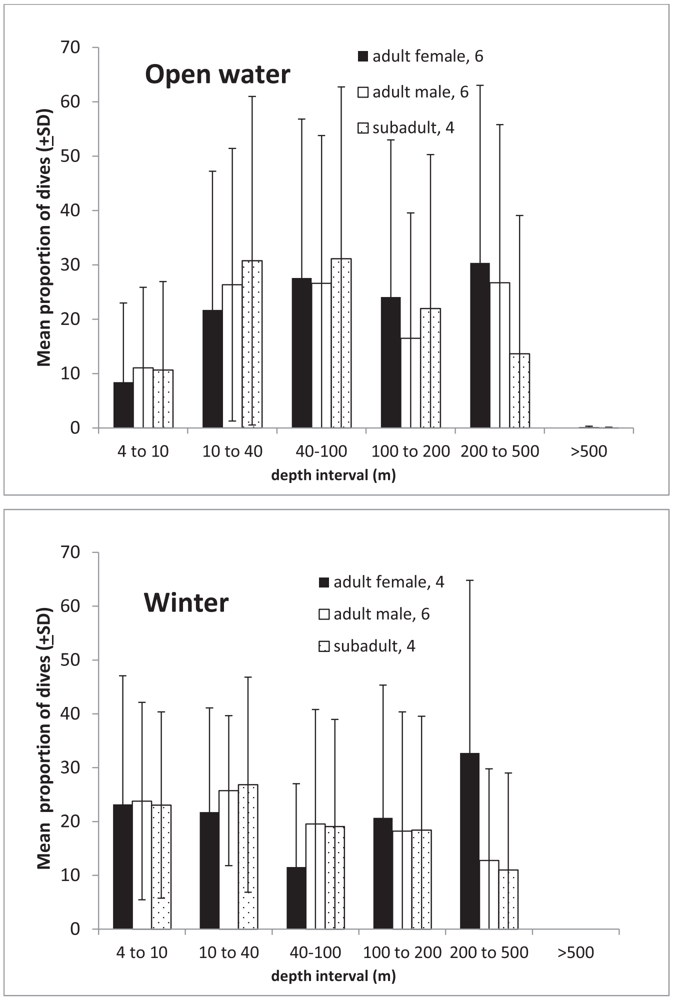

FIG. 7. Depth distribution (proportion ± SD at each depth interval) of 239 041 dives recorded for adult and subadult ringed seals during open water and winter periods in the three study years.

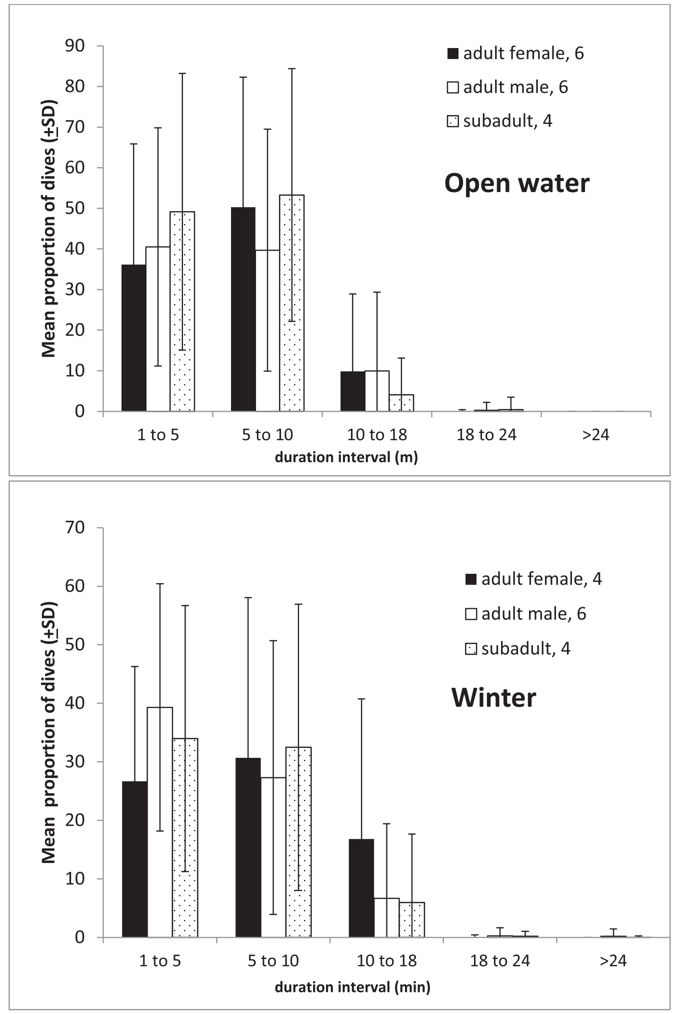

FIG. 8. Duration distribution (proportion ± SD at each duration interval) of 206 296 dives recorded for adult and subadult ringed seals during open water and winter periods in the three study years.

that was approximately 10 times larger than that of the previous year and six times as large as in 2010–11. The winter conditions in 2000–01 indicated a tendency for open leads along the shear line on the southern side of Amundsen Gulf. This westward movement of pack ice would also have forced upwelling of nutrient-rich water from greater depth along the southern side of Amundsen Gulf, as discussed by Williams et al. (2006, 2008). Upwelling would be further strengthened to the east of Cape Bathurst because of the steep bottom gradient on the west side of Franklin Bay (Williams and Carmack, 2008). The consequent likelihood of higher primary and secondary productivity, combined with warm Atlantic-derived water here below 250 m depth, may have encouraged aggregations of Arctic cod near the seabed in Franklin Bay, such as the one observed during winter 2003–04 (Benoit et al., 2008). Born et al. (2004) also found the size of the winter home range varied among winters, in their case by a factor of three. The relationship of ice cover and its interaction with oceanographic features and bottom topography in governing the distribution of seal prey in winter is not understood. However, the ice apparently had a direct influence on the movements and distribution of ringed seals as evidenced by our variable results over three winters.

As long-lived and wide-ranging oceanic predators, marine mammals can provide clues to explain changes in the food web and ecosystem structure (Boyd, 2002; Moore, 2008; Williams et al., 2013; Moore et al., 2014). Since they respond to ecosystem variation with changes in body condition (Moore, 2008; Moore et al., 2014), trends in seal body condition are a direct and useful link to the year-to-year availability and quality of the seals' prey. More than 2500 harvested ringed seals were sampled from this area during 1971–79 (Smith, 1987) and 1992–2011 (Harwood et al., 2012b). That monitoring study found a significant and sustained temporal trend of decreasing body condition of ringed seals since 1994, occurring in all age/sex classes and measured in spring just after breakup. The results of the present tagging study allow the general inference that seals sampled in the Harwood et al. (2012b) monitoring study used winter habitats mainly in EAG and PAS. The present results, and spatial and temporal linkages between the tagging and monitoring studies, point to changes having occurred in the winter prey base of ringed seals in the EAG/PAS area.

In our study, dives deeper than 200 m were infrequent in males and subadults during winter, although they occurred 33% of the time in adult females in winter. This pattern may represent the female's foraging efforts towards aggregations of Arctic cod in mid-water and demersal habitats and reflect the greater energetic demands of breeding females prior to pupping and nursing. Arctic cod are found in demersal, mid-water, and under-ice habitats (Dunbar, 1941; Gulliksen, 1984; Bradstreet et al., 1986; Mundy et al., 2009; Crawford et al., 2012). They can occur both as dense near-surface shoals (Welch et al., 1993; Benoit et al., 2008) and as non-schooling individuals (Bradstreet et al., 1986; Hop et al., 1997). The summer distribution of Arctic cod is not well documented in this or other regions, although two recent studies have advanced our knowledge of cod distribution in summer for the Beaufort and Chukchi Seas (Crawford et al., 2012; J. Reist, DFO, pers. comm, 2013). In August 2012, a near-bottom aggregation of Arctic cod was found at approximately 200–400 m depth, spanning the slope along the entire southern Canadian Beaufort Shelf (J. Reist, pers. comm. 2013). Also during late summer sampling, Crawford et al. (2012) report cod were abundant in the Beaufort and Chukchi Seas at 200–375 m depths, in demersal habitats, as well as in the upper 75 m of the water column.

Predicted and contemporary oceanographic and sea ice changes will influence the availability of seal prey and structuring of the food web (Tynan and DeMaster, 1997; Serreze et al., 2007; Bluhm and Gradinger, 2008; Comiso et al., 2008; Laidre et al., 2008; Walsh, 2008; Kovacs et al., 2011). Knowledge of habitats that the seals use for feeding in winter may contribute to our understanding of contemporary, sustained declines in seal body condition that have been observed in this area over the past two decades (Harwood et al., 2012b). We have as yet no detailed information about the distribution of Arctic cod in winter or the factors that control this distribution. The opportunity now exists, however, using satellite tags deployed on seals, to refine our understanding of the seasonal distribution of seals (Smith, 2001; Fedak, 2004; Lydersen et al., 2004), and at the same time study water masses that influence the distribution of cod. CTDs (recorders that measure conductivity, temperature, and depth) deployed on marine mammals have shown enormous potential for cost-effective, in situ oceanographic sampling in important foraging habitats used by the marine mammals (Lydersen et al., 2002). Well-funded, long-term research programs using ringed seals and other marine mammals as "educated oceanographic sampling platforms" could be a key to understanding the changes that are occurring in the Arctic marine ecosystem.

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