Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water

A.M. Pagano, G.M. Durner, S.C. Amstrup, K.S. Simac, and G.S. York

Abstract: Polar bears (*Ursus maritimus* Phipps, 1774) depend on sea ice for catching marine mammal prey. Recent sea-ice declines have been linked to reductions in body condition, survival, and population size. Reduced foraging opportunity is hypothesized to be the primary cause of sea-ice-linked declines, but the costs of travel through a deteriorated sea-ice environment also may be a factor. We used movement data from 52 adult female polar bears wearing Global Positioning System (GPS) collars, including some with dependent young, to document long-distance swimming (>50 km) by polar bears in the southern Beaufort and Chukchi seas. During 6 years (2004–2009), we identified 50 long-distance swims by 20 bears. Swim duration and distance ranged from 0.7 to 9.7 days (mean = 3.4 days) and 53.7 to 687.1 km (mean = 154.2 km), respectively. Frequency of swimming appeared to increase over the course of the study. We show that adult female polar bears and their cubs are capable of swimming long distances during periods when extensive areas of open water are present. However, long-distance swimming appears to have higher energetic demands than moving over sea ice. Our observations suggest long-distance swimming is a behavioral response to declining summer sea-ice conditions.

Key words: polar bear, *Ursus maritimus*, sea ice, climate change, telemetry, swimming, behaviour, Beaufort Sea.

Résumé : L'ours blanc (*Ursus maritimus* Phipps, 1774) dépend de la banquise pour chasser les mammifères marins dont il se nourrit. Les diminutions récentes de la banquise ont été corrélées au déclin de l'état corporel, du taux de survie et de la taille de la population de cet animal. S'il est postulé que la réduction du nombre de possibilités d'alimentation constitue la principale cause du déclin de l'ours blanc associé à l'état de la banquise, les coûts de déplacements dans un contexte de banquise détériorée pourraient également être un facteur explicatif. Nous avons utilisé des données sur les déplacements de 52 ourses blanches adultes portant des colliers à système de localisation GPS, dont certaines accompagnées de jeunes dépendants, pour documenter leurs déplacements à la nage sur de longues distances (>50 km) dans la partie méridionale des mers de Beaufort et de Tchoukotka. En six ans (2004–2009), nous avons recensé 50 déplacements à la nage de longue distance par 20 ourses. La durée et la distance de ces déplacements allaient de 0,7 à 9,7 jours (moyenne de 3,4 jours) et de 53,7 à 687,1 km (moyenne de 154,2 km), respectivement. La fréquence des déplacements à la nage a semblé augmenter au cours de l'étude. Nous démontrons que les ourses blanches adultes et leurs oursons sont capables de parcourir de longues distances à la nage en périodes caractérisées par la présence de vastes étendues d'eaux libres. À ces déplacements de longue distance à la nage semble toutefois être associée une plus forte demande énergétique que pour les déplacements sur la banquise. Nos observations suggèrent que les déplacements de longue distance à la nage constituent un changement de comportement en réponse au déclin de l'état de la banquise estivale.

Mots-clés : ours blanc, *Ursus maritimus*, banquise, changements climatiques, télémétrie, nage, comportement, mer de Beaufort.

[Traduit par la Rédaction]

Introduction

Polar bears (*Ursus maritimus* Phipps, 1774) are a circumpolar Arctic species dependent on the sea ice for hunting ringed seals (*Pusa hispida* (Schreber, 1775)) and bearded seals (*Erignathus barbatus* (Erxleben, 1777)), resting, mating, and denning (Stirling and Archibald 1977; Stirling and Øritsland 1995; Amstrup 2003). Declines in body condition, survival, and population size of polar bears have been linked with changes in sea ice in western Hudson Bay and the southern Beaufort Sea (SB) (Stirling et al. 1999; Regehr et al. 2007, 2010; Rode et al. 2010). The recent extensive and prolonged retreat of summer and autumn sea ice has reduced the availability of preferred habitats over shelf waters (Durner

Received 7 October 2011. Accepted 28 February 2012. Published at www.nrcresearchpress.com/cjz on 27 April 2012.

A.M. Pagano, G.M. Durner, S.C. Amstrup,* K.S. Simac, and G.S. York.[†] US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA.

Corresponding author: Anthony Pagano (e-mail: apagano@usgs.gov).

*Present address: Polar Bears International, 810 North Wallace, Suite E, P.O. Box 3008, Bozeman, MT 59772, USA.
[†]Present address: WWF Global Arctic Programme, 30 Metcalfe Street, Suite 400, Ottawa, ON K1P 5L4, Canada.

doi:10.1139/Z2012-033

et al. 2009), which ultimately must lead to greater travel distances for bears that move from pack ice to denning areas on land or nearshore foraging habitats (Bergen et al. 2007).

Polar bears are adapted for swimming in marine waters and are considered strong swimmers (Øritsland 1969, 1970; Stirling 1974; DeMaster and Stirling 1981). DeMaster and Stirling (1981) reported polar bears swimming at least 64 km in a single event, and Stirling (1988) described a bear that possibly swam 100 km in a single event. Studies of Inuit traditional ecological knowledge in Foxe Basin indicate that polar bears are strong swimmers and are capable of swimming long distances (V. Sahanatien, University of Alberta, unpublished data). Most documented polar bear swims have been associated with bathing, escaping pursuit, or rarely, hunting (Øritsland 1969; Stirling 1974; Russell 1975; Furnell and Oolooyuk 1980; Smith and Sjare 1990; Aars and Plumb 2010). These swims generally were confined to relatively short open-water distances across small bays or leads in the ice. However, a swimming event >600 km was recently confirmed by radiotelemetry (Durner et al. 2011).

Polar bears are essentially a terrestrial mammal that filled a niche on the top surface of an ice-covered ocean (Ferguson et al. 2000; Amstrup 2003; Mauritzen et al. 2003*a*; Durner et al. 2004). Polar bears in the SB subpopulation occupy an extensive region of the Arctic Ocean (see Fig. 5 in Amstrup et al. 2004), and most polar bears in this subpopulation seldom come ashore (Amstrup et al. 2000; Schliebe et al. 2008). Stable sea ice provides suitable hunting habitat and a substrate for resting and travel (Mauritzen et al. 2003*a*). Long-distance swimming is likely more energy intensive than walking for polar bears, as swimming efficiencies are relatively low for nonaquatic mammals (Williams 1983; Fish 1996). Additionally, bears engaged in swimming are at risk of drowning from fatigue or rough seas (Monnett and Gleason 2006). Furthermore, young cubs may be unable to survive swims of even short duration (Blix and Lentfer 1979; Aars and Plumb 2010). During the melt season, polar bears using unconsolidated or low concentration sea ice far from the main pack ice are at risk of having to swim long distances to return to more stable habitats (e.g., sea ice or land).

Polar bears prefer sea ice over shallow seas and the continental shelves (Durner et al. 2004, 2009), where seal densities are thought to be highest (Stirling et al. 1982; Kingsley et al. 1985). Throughout the Arctic, the duration between melt and freeze onset has increased, the distance of summertime retreat of sea ice from the coast has increased, and sea-ice thickness has declined (Comiso 2002; Belchansky et al. 2004; Stroeve et al. 2006, 2007, 2011; Walsh 2008; Perovich and Richter-Menge 2009). In the Arctic basin, declines in sea-ice extent have placed most summer sea ice beyond the continental shelves, and in doing so have reduced the amount of optimal habitat for polar bears (Durner et al. 2009). In addition, reductions in sea-ice thickness have likely resulted in less predictable melting patterns (Amstrup et al. 2010). As a consequence, polar bears are likely forced to either hunt on remnant low concentration or unconsolidated sea ice over the continental shelf, follow the main pack ice as it recedes over deeper waters where there may be fewer seals (Stirling and Archibald 1977; Stirling et al. 1982; Durner et al. 2004; Frost et al. 2004), or move to land (Schliebe et al. 2008). On land, polar bears are usually food deprived (Ramsay and Hobson 1991), unless they find beach-cast marine mammals. In Alaska, polar bears are attracted to subsistence-harvested bowhead whales (*Balaena mysticetus* (L., 1758)) on land that are available at consistent times and locations (Miller et al. 2006; Bentzen et al. 2007; Gleason and Rode 2009).

Published observations are few, but they suggest that long-distance swimming could be costly for polar bears. Monnett and Gleason (2006) observed four drowned polar bears in the SB, floating, on average, 54 km offshore after a storm event in September 2004. They roughly approximated this one storm event could have drowned up to 27 polar bears. Durner et al. (2011) described a 687 km swim by one radio-collared female in the SB during the fall of 2008. This bear lost 22% of her body mass and her yearling offspring as a possible consequence from 9 days of continuous swimming and the subsequent 53 days of walking on pack ice over deep water.

Changes in sea ice have been linked to declining survival rates (Regehr et al. 2007, 2010) and population size (Regehr et al. 2007). Additionally, anecdotal observations of cannibalism, long-distance swimming, and unusual hunting behavior in polar bears suggest that the SB subpopulation may be nutritionally stressed (Amstrup et al. 2006; Stirling et al. 2008; Durner et al. 2011). Reduced foraging ability, caused by the combination of spatial and temporal reductions in availability of sea-ice habitats, has been suggested to be one mechanism in this linkage (Regehr et al. 2007, 2010; Cherry et al. 2009; Molnár et al. 2010). The direct impacts on energy balance, as well as the impacts of long-distance swimming on survival of adults and young, remain unexamined mechanisms.

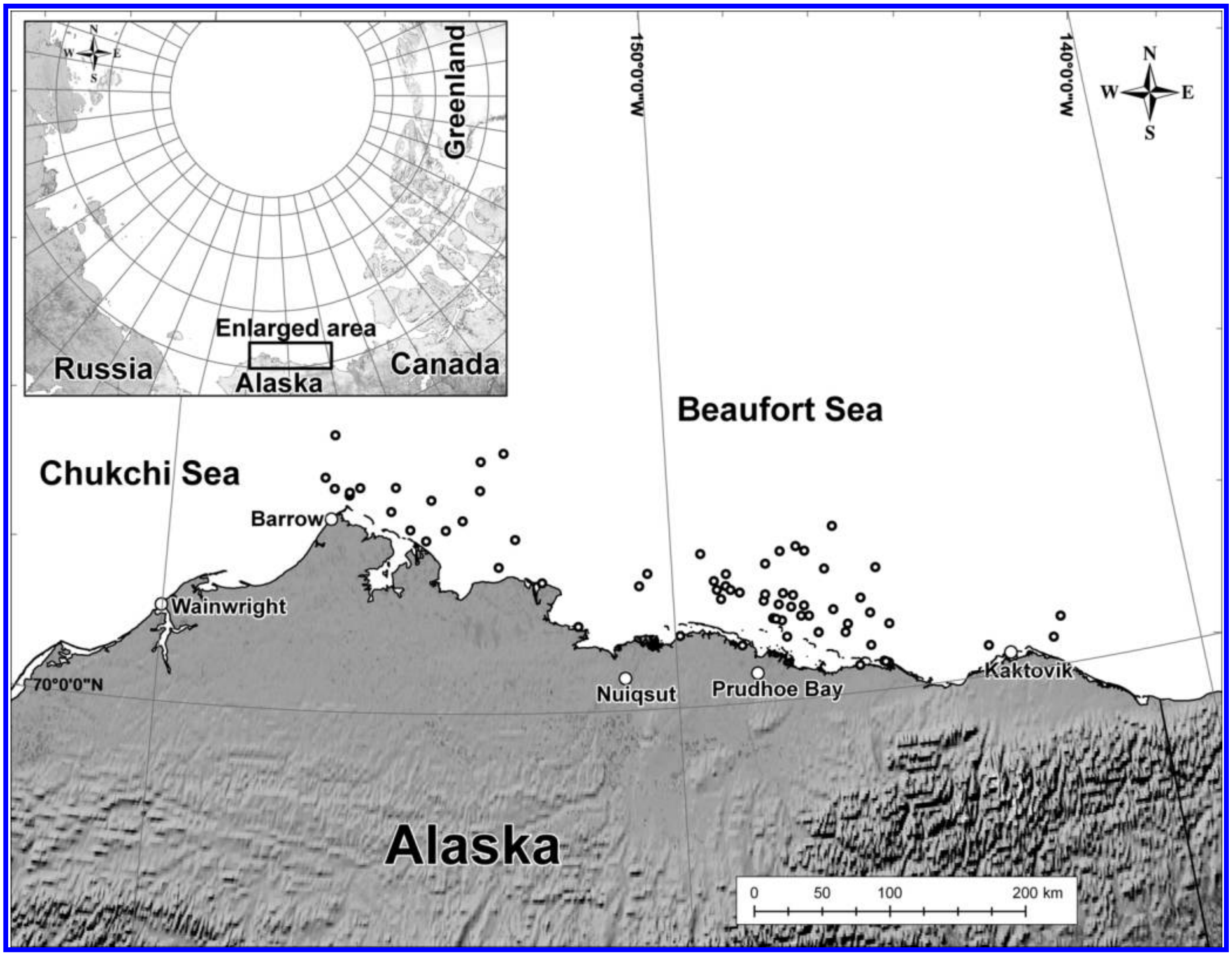
GPS satellite transmitters provide the opportunity to examine swimming behavior through highly accurate location data combined with multiple locations per day (Andersen et al. 2008; Durner et al. 2011). We use data from adult female polar bears equipped with GPS satellite radio collars in the SB and satellite images of sea ice to provide the first quantitative evaluation of long-distance swimming by polar bears. In addition, we use 25 years of satellite radio-collar data (Argos transmission data) from polar bears captured in the SB to examine premature cessation of radio-collar transmission data. We hypothesized that transmission cessation during open-water periods from collars worn by bears that were never resighted may be indicative of swimming-related drowning events.

Materials and methods

Our study area included the SB and Chukchi Sea (CS) adjacent to northern Alaska (Fig. 1). We captured polar bears in the SB each spring (March–May) from 2004 to 2009, and in August of 2008, from logistic bases in Barrow, Prudhoe Bay, and Kaktovik, Alaska (Fig. 1). We captured polar bears by injecting them with immobilizing drugs (tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®); Warner-Lambert Co., Fort Dodge, Iowa, USA) through projectile syringes (Palmer Cap-Chur Equipment, Douglasville, Georgia, USA) fired from a helicopter (Stirling et al. 1989).

We attached GPS radio collars (Telonics Inc., Mesa, Arizona, USA) on many of the adult female polar bears that we captured during 2004–2009. We did not collar adult male polar bears because their muscular necks are larger than their

Fig. 1. Study area and locations where 68 polar bears (*Ursus maritimus*) were captured and fitted with GPS-equipped satellite radio collars in the southern Beaufort Sea from 2004 to 2009.



heads and they do not retain radio collars. The GPS radio collars transmitted data to polar-orbiting satellites through the Argos Data Collection and Location System (ADCLS; Fancy et al. 1988). The transmitted data included high-accuracy locations (≤31 m) obtained with the GPS (D'Eon et al. 2002). The GPS radio collars also stored all location fixes in nonvolatile memory and these data were recoverable if the collar was retrieved.

The number of programmed GPS location fixes per day varied among years and ranged from 3 to 24 (Appendix A, Table A1) spaced evenly throughout the day. Argos transmission schedules varied by year and ranged from 4 to 8 h daily or every other day (Appendix A, Table A1). For the collars deployed in 2004–2008, transmissions relayed up to six previous GPS locations to the Argos satellites. For the collars deployed in 2009, transmissions relayed up to 24 previous GPS location fixes to Argos satellites. We obtained location data using the ADCLS or by downloading data directly from the collar if it was recovered. We postprocessed the raw transmission data using the Argos Data Converter – T03 (ADC–T03) version 4.03.0010 software (Telonics, Inc.) or the Telonics Data Converter version 1.35 (Telonics, Inc.) to reconstruct the GPS-tracking time series, which we analyzed with SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA) and ArcInfo version 9.3 (Environmental Systems Research Institute (ESRI) Inc., Redlands, California, USA). Only GPS locations assigned a "Good" or "Succeeded" fix status were included in analyses.

To evaluate long-distance swimming events, we analyzed GPS data between 1 June and 31 October. Generally this, is the time of year when open water was present in the SB and CS. We excluded transmission data from collars that did not transmit at least 2 months during our 5-month period of interest (June through October). We first identified potential extended swimming events by searching for time gaps in the record of Argos Doppler-derived transmissions that were ≥3 days. To minimize mechanical failure, the Argos antennae on radio collars were connected to the transmitter with a short cable. This design places the antenna lateral to the neck and below the waterline when bears were swimming. Collars were programmed to transmit at least once every 2 days. Because a submerged antenna prevents signal transmission, a gap of ≥3 days in Argos signal reception may indicate submersion of the Argos antenna in water and hence a bear that was swimming.

After data gaps were identified, we compared GPS location data with available satellite imagery of sea-ice presence, concentration, and extent using GIS software (ArcMap version 9.3.1; ESRI). Sea-ice concentration refers to the percentage of a given area covered with sea ice (Spreen et al. 2008). GPS locations or paths that led over open water with little to no opportunity to rest on sea ice or land were defined as swimming events. We treated instances where GPS data suggested that a bear may have rested briefly (≤16 h) on nondetectable ice floes during a swim as a single event because the resumption of swimming was predicated on the initial swimming event and there was no clear evidence that the bear was walking on land or sea ice. We defined a long-distance swimming event as being >50 km. Potential swimming events <50 km were excluded because it became difficult to confidently identify bears as swimming at shorter distances and because shorter distance swimming events are generally considered normal behavior for polar bears (Stirling 1974).

We used Advanced Microwave Scanning Radiometer for the Earth Observing System (AMSR-E) passive microwave raster imagery (Spreen et al. 2008) obtained from the Institute of Environmental Physics, University of Bremen (available from http://iup.physik.uni-bremen.de:8084/amsr/amsre.html, accessed 1 October 2010) to examine sea-ice presence, concentration, and extent. AMSR-E data provide raster-cell-specific estimates of sea-ice concentration on a 6.25 km grid resolution. AMSR-E is neither limited to the visual spectrum nor limited by clouds, so it provides a nearly consistent daily record of sea ice. We also used Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery at 250 m resolution (NASA–GSFC, MODIS Rapid Response; available from http://earthdata.nasa.gov/data/nrt-data/rapid-response, accessed 22 October 2010). MODIS imagery is limited by clouds, but when available, provides a higher resolution daily record of sea-ice presence and extent. Lastly, we used ice analysis charts provided by the National Ice Center (NIC; available from http://www.natice.noaa.gov/, accessed 11 February 2011) to further identify sea-ice presence, concentration, and extent. NIC charts are only available weekly, but provide another estimate of sea ice when concentrations are below the detection abilities of passive microwave sensors (Partington et al. 2003). When available and not obscured by cloud cover, we used all three of these satellite images to identify sea-ice presence, concentration, and extent. Because sea-ice conditions could change rapidly, we primarily used AMSR-E and MODIS images to obtain daily images of sea-ice presence and extent. We then overlaid polar bear GPS movement paths, including their respective data gaps, on these satellite images and sea-ice charts within ArcMap. The cumulative evidence from Argos transmission gaps, GPS locations and paths, and sea-ice imagery allowed us to identify locations of polar bears that coincided temporally and spatially with open water and unconsolidated ice.

We based swimming distances and durations on the GPS data in comparison with sea-ice images. We calculated the minimum distance travelled between two successive locations as the great-circle distance between locations. We calculated time spent swimming by subtracting the time that GPS locations resumed over sea ice or land from the time at the beginning of the swimming event (the GPS location just prior to locations or paths that occurred over open water). We calculated hourly movement rates by dividing the total distance by the total duration from the start of the event to its conclusion. We defined the main pack ice based on the AMSR-E data to be adjoining grid cells with >50% concentration that were contiguous with sea ice over the polar basin.

We compared movement rates (km/h) of swimming bears to movement rates by the same individuals while located on sea ice (when bears were assumed to be walking). To quantify movement rates over sea ice, we identified travel that clearly occurred over grid cells composed of >50% sea-ice concentration, based on AMSR-E data. For comparison to swimming events, we used the equivalent time duration for assumed walking bouts. We chose dates at random during the period of interest (June through October) and excluded dates 1 week following the conclusion of the swimming event because we hypothesized that the swimming event could influence subsequent movement patterns. We tested our prediction that mean movement rates during swimming events varied from mean movement rates over sea ice using a paired *t* test.

We examined temporal trends in the mean straight-line distance swam per year using linear regression. We used a two-sample Welch's *t* test assuming unequal variances to test whether survival of young of GPS-collared adult females that swam differed from survival of young of GPS-collared adult females that did not swim.

We quantified changes in the distance to the sea-ice edge in September during the years 1979–2010 to examine how summer sea-ice habitat has changed and whether it would have been possible for polar bears in the SB to swim long distances in years prior to our study. We estimated the extent of open water in the SB from passive microwave monthly averaged sea-ice data (National Snow and Ice Data Center (NISDC), Boulder, Colorado, USA; available from ftp://sidads.colorado.edu/pub/DATASETS/nsidc0051_gsfc_nasateam_seaice/final-gsfc/north/monthly/, accessed 4 January 2012). We measured the distance between 30 fixed points along the Canada and Alaska mainland coast of the SB to the nearest sea-ice edge for each year. Coastal points were set at 1° increments from 128°W (Cape Bathurst, Canada) to 157°W (near Barrow, Alaska). We used the 15% sea-ice concentration threshold for the main ice pack of the SB and CS as the sea-ice edge for each year (Durner et al. 2009). We defined the continental shelf as waters <300 m deep (Regehr et al. 2010). Distance measures between coastal points and the ice edge were made with the ARC/INFO NEAR command version 10.0 (ESRI). We report annual distances as mean ±1 SD and estimated annual trend from mean values with a second-order polynomial regression in SigmaPlot version 11.0 (Systat Software, Inc., San Jose, California, USA).

We also used Argos transmission data from satellite radio collars deployed in the spring (March to May) between 1985 and 2009 in the SB to examine whether premature cessation of radio-collar transmission data (Argos) could be indicative of drowning events. Collars submerged in water would be unable to transmit, and thus, cease transmitting before their anticipated end of battery life. If premature cessation coincided with open-water periods and the bears wearing these collars were never subsequently resighted, we hypothesized this could be indicative of swimming-related drowning events. We identified the last transmission date for all satellite radio

Table 1. Number and proportion (mean (95% CI, based on binomial distributions)) of polar bears (*Ursus maritimus*) identified as having at least one long-distance swimming event (>50 km) between June and October detected with GPS-equipped satellite radio collars deployed in the southern Beaufort Sea from 2004 to 2009.

Year	No. of swimming bears	No. of bears that did not swim	Total no. monitored	Proportion swimming
2004	2	6	8	0.25 (0–0.57)
2005	3	8	11	0.27 (0–0.55)
2006	4	11	15	0.27 (0.04–0.50)
2007	0	1	1	0
2008				
Spring	2	2	4	0.50 (0–1)
August	2	3	5	0.40 (0–0.88)
2009	8	5	13	0.62 (0.34–0.89)

collars that prematurely ceased transmitting during July, August, or September of the first year of deployment, excluding records from bears whose collars had been identified as shucked and excluding locations that occurred on land. In combination with our capture records, we performed two analyses. The first analysis examined last transmission dates for bears that were never subsequently resighted and compared this with the last transmission dates for bears that were subsequently resighted. If premature cessation occurred more frequently for bears that have never been resighted, then this might suggest drowning events. Secondly, we also hypothesized that if premature cessation was indicative of drowning events, then we would expect last transmission dates to occur more frequently in recent years when greater amounts of open water would be present. To test this, we regressed the percentage of collars that prematurely ceased each year against our September mean estimate of the distance to the sea-ice edge in the SB using linear regression.

We performed statistical analyses using the R programming language (R Foundation for Statistical Computing, Vienna, Austria; available from http://cran.r-project.org/). We considered $P \leq 0.05$ to be significant and report means with 95% confidence intervals (CIs) when sample sizes are ≥10. Samples sizes <10 are reported as means with range values.

Results

From 2004 to 2009, we deployed 68 GPS radio collars on 62 different adult female polar bears (Fig. 1). The number of GPS collars deployed and the number that successfully operated varied among years (Appendix A, Table A2). Excluding collars that failed to transmit during the period of interest, we monitored 52 different adult female polar bears. Only 1 of the 2 GPS collars deployed in 2007 transmitted during the June through October period, so we excluded this year from analyses.

We identified 50 swimming events by 20 different adult female polar bears over the 6 years of this study (Table 1). We found five instances (10%) where it appeared that bears may have had a brief (≤16 h) opportunity to rest on small non-detectable ice floes during the swim (e.g., Fig. 2; 25–26 June 2005). The annual proportion of polar bears that took long-distance swims increased over the course of this study, but confidence intervals overlapped (Table 1). Overall, 3 swimming events occurred in June, 15 in July, 13 in August, 18 in September, and 1 in October (mean = 31 August, 95% CI = 31 July – 1 October). Swimming distances ranged from 53.7 to 687.1 km (mean = 154.2 km, 95% CI = 121.4–187.0 km; Table 2) with a duration of 0.7–9.7 days (mean = 3.4 days, 95% CI = 2.8–4.0 days; Table 2). We found no relationship between mean straight-line distance swam and year ($\beta = -0.10$, $r^2 < 0.01$, $P = 0.996$).

Swimming movement rates ranged from 0.7 to 3.7 km/h (mean = 2.0 km/h, 95% CI = 1.8–3.8 km/h) and were 2.3 times higher than movement rates on sea ice of >50% concentration (mean = 0.9 km/h, 95% CI = 0.8–1.0 km/h; paired *t* test, $t = 11.2$, $P < 0.0001$; Fig. 3).

Most swimming events were from unconsolidated sea ice (ice concentration <50%) to the main pack ice (mean distance = 155.9 km, 95% CI = 114.5–197.4 km, $N = 25$; Fig. 2), from land to another area of land (mean distance = 106.2 km, range = 53.7–288.3 km, $N = 7$; Fig. 4), or from unconsolidated sea ice to land (mean distance = 169.1 km, range = 69.9–302.6 km, $N = 6$; Fig. 5). Other swimming events were from unconsolidated sea ice to unconsolidated sea ice (mean distance = 120.6 km, range = 59.5–195.7 km, $N = 5$), from land to unconsolidated sea ice (mean distance = 102.3, range = 68.3–113.7 km, $N = 3$), from the main pack ice to land (mean distance = 176.7, range = 151.3–202.1 km, $N = 2$), or from land to the main pack ice (mean distance = 402.5, range = 117.9–687.1 km, $N = 2$). Twelve of the 20 bears (60%) that made long-distance swims had multiple long swims in the same year. Of the 20 bears, 5 (25%) were monitored over multiple years of interest, but only 1 bear made long swims in more than 1 year.

At the time of collar deployment, 12 of the 20 adult female polar bears that later swam had cubs of the year (COY) or yearlings. Of these 12, we recaptured or resighted 10 bears 64–386 days following collar deployment. Based on these records, 6 of the 10 bears (60%) still had their dependent cubs, indicating that they survived long-distance swims. Four of 7 bears (57%) had COY that survived long-distance swims, swimming a mean of 141.4 km (95% CI = 109.3–173.4 km, $N = 11$). Two of 3 bears (67%) had yearlings that survived long-distance swims, swimming a mean of 125.4 km (range = 55.0–204.9 km, $N = 4$).

Of the 32 bears we monitored that did not swim long distances, 21 had dependent offspring (COY or yearlings) at the time of collar deployment. We re-observed seven of these bears 50–349 days later. Five of these seven bears (71%) still had dependent cubs since the time of the initial collar deploy-

Fig. 2. Swimming event by polar bear (*Ursus maritimus*) 20797 wearing a GPS-equipped satellite radio collar swimming from unconsolidated sea ice just west of Point Hope, Alaska, on 20 June 2005 toward the Chukchi Sea pack ice ending on 30 June 2005. GPS location data are shown over National Ice Center chart data from 20 June 2005. Sea-ice concentration refers to the percentage of area covered with sea ice. National Ice Center charts reproduced with permission of the National Ice Center, Suitland, Maryland, USA.

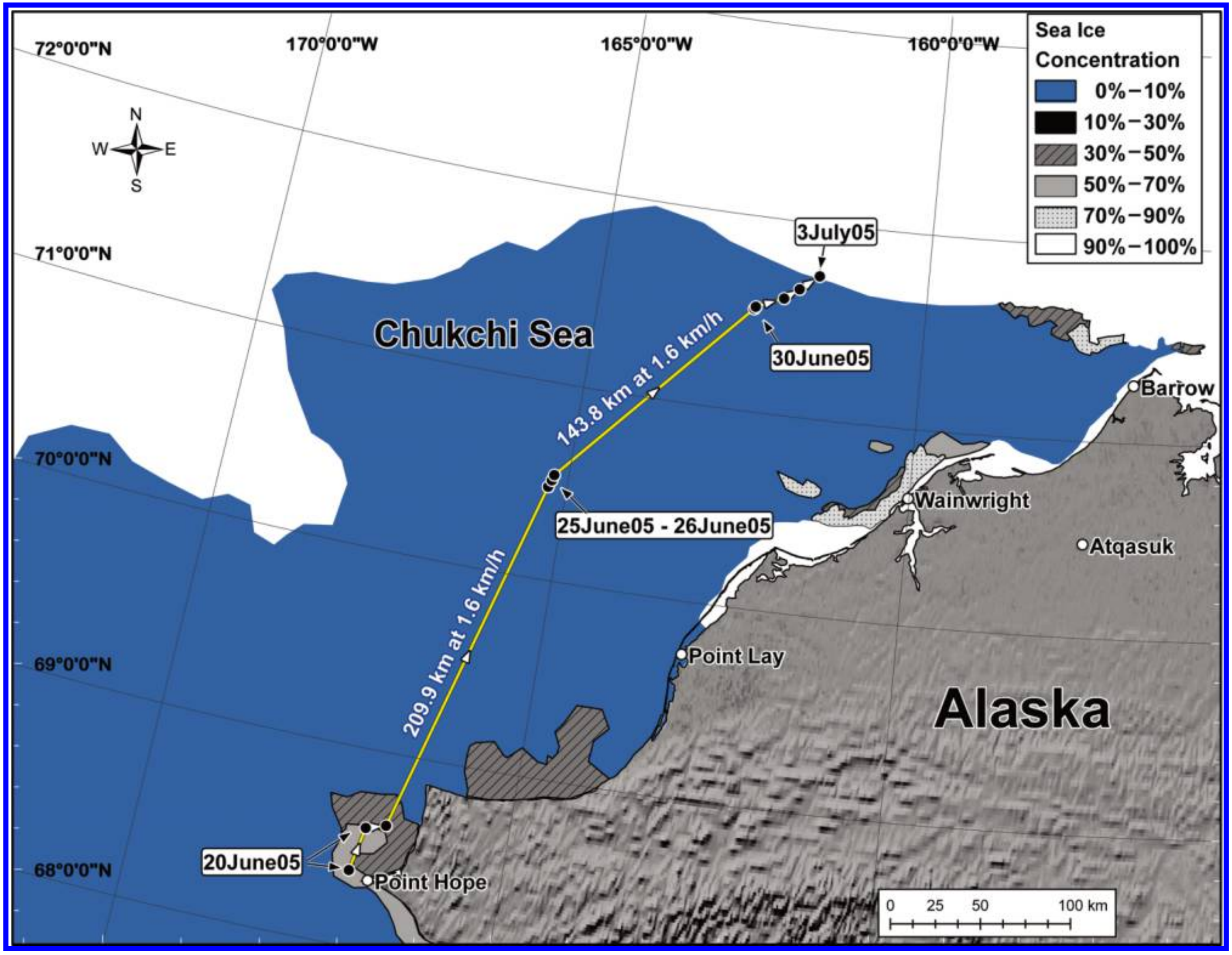


Table 2. Annual summaries (mean (range)) of long-distance swimming events (>50 km) of polar bears (*Ursus maritimus*) detected with GPS-equipped satellite radio collars in the southern Beaufort and Chukchi seas, 2004–2009.

Year	GPS positions	Duration (days)	Straight-line distance (km)	Movement rates (km/h)	*N*
2004	3 (2–6)	4.1 (2.3–6.9)	149.7 (55.0–305.7)	1.3 (1.0–1.8)	3
2005	4 (2–8)	4.5 (0.9–9.7)	188.8 (64.3–366.0)	1.9 (0.7–2.9)	6
2006	3 (2–6)	4.2 (0.7–7.0)	119.0 (55.0–182.2)	1.6 (0.9–3.4)	5
2008	38 (2–135)	3.9 (1.7–9.7)	216.6 (55.3–687.1)	2.1 (1.4–3.0)	11
2009	36 (2–130)	2.6 (0.7–6.0)	126.0 (53.7–302.6)	2.2 (0.7–3.7)	25

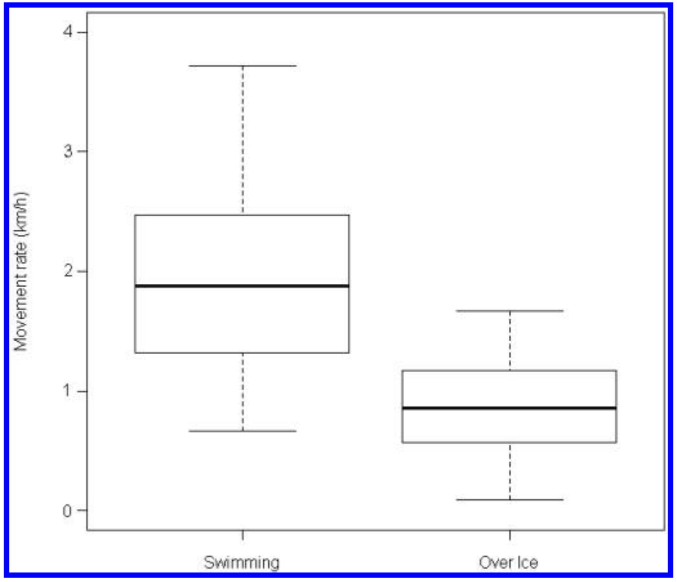
ment. Although the rate of cub mortality for mothers that made long swims was higher than the cub mortality rate for mothers that did not swim, the difference was not significant (Welch's *t* test, $t = 0.70$, $P = 0.50$).

We found an increasing and significant trend in the distance between the mainland coast and the sea-ice edge during September over the years of the passive microwave record of sea ice from 1979 to 2010 ($r^2 = 0.37$, $P = 0.001$; Fig. 6). Additionally, it appeared that the passive microwave record could be divided into an "early" and "late" period (Fig. 6). After 1996, the lowest mean distance was 168 km in 2001. Prior to 1997, however, the mean distance from land to the sea-ice edge was ≤168 km in 11 of 18 years. During the early period (1979–1996), the greatest mean distance from land to the sea-ice edge was 274 km in 1993. After 1996, however, 6 of 14 years exceeded 274 km (Fig. 6). Furthermore, during the early period, the September median sea-ice edge for all years (1979–1996) was largely concordant with the 300 m depth contour (continental shelf) in the SB, or extended >200 km south of the 300 m depth contour in the CS

(Fig. 7). During the late period (1997–2010), the September median sea-ice edge was largely >200 km farther north of the early period ice edge, and the 300 m depth contour, especially in the western SB and CS (Fig. 7).

Premature cessation of radio-collar transmission data was not clearly indicative of a drowning event. We identified 15 radio collars that prematurely ceased from bears that were never subsequently resighted compared with 12 radio collars that prematurely ceased from bears that were later resighted (Table 3). Mean last transmission date was 2 August (95% CI = 21 July – 13 August) for bears that were never resighted following transmission cessation. Mean last transmission date was 24 August (95% CI = 7 August – 10 September) for bears that were later resighted following transmission cessation. However, we found a significant correlation in the percentage of premature cessation for bears that we never resighted and the mean distance to the sea-ice edge in September ($\beta = 0.0003$, $r^2 = 0.37$, $P = 0.005$; Table 3), but not for resighted bears ($\beta = -0.0002$, $r^2 = 0.12$, $P = 0.15$; Table 3).

Fig. 3. Movement rates from 20 adult female polar bears (*Ursus maritimus*) wearing GPS-equipped satellite radio collars while swimming ($N = 50$) compared with their movement rates while on ice of >50% concentration ($N = 50$). Box plots show the median, first and third quartiles, and maximum and minimum values.



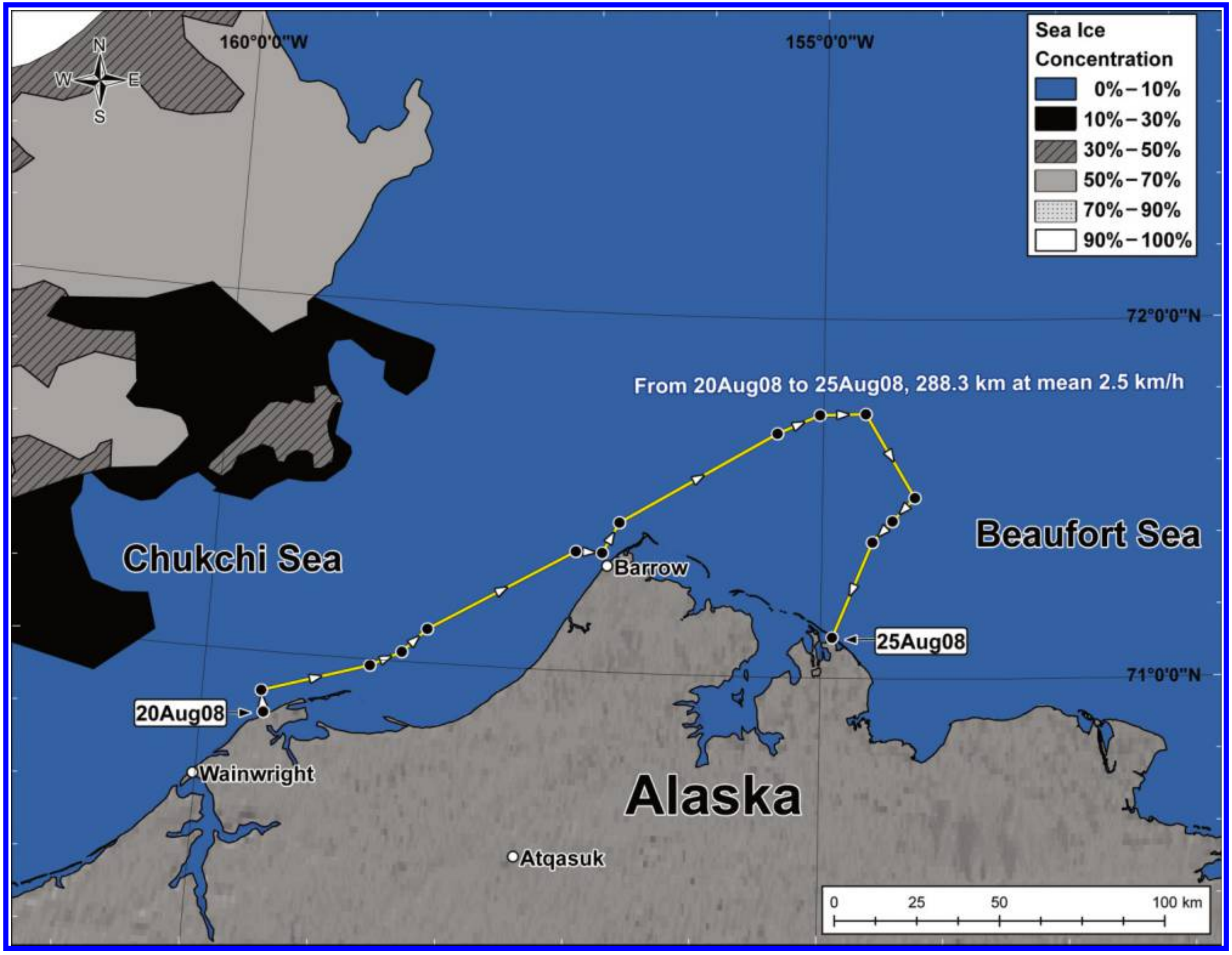
Discussion

We show that both adult female polar bears and their dependent young possess an ability to swim long distances. Prior to the development of GPS radio collars, Argos positioning radio collars (Doppler-derived) generally provided infrequent locations of low precision (Andersen et al. 2008). Although we lack a historical quantification of long-distance swimming by SB polar bears, summer and fall sea-ice extent and thickness in the SB and CS during 2004 to 2009 were much lower than historical conditions and the extent of open-water continues to increase (Comiso et al. 2008; Walsh 2008; Perovich and Richter-Menge 2009; Stroeve et al. 2011; Fig. 7). Summer sea ice remained over the continental shelf off the Alaska coast up to the late 1980s (Comiso 2002; Fig. 7). Since then, the SB and CS have experienced some of the greatest sea-ice loss in the entire Arctic (Comiso 2002; Walsh 2008). The decrease of multiyear ice (Comiso 2002; Comiso et al. 2008; Maslanik et al. 2011) and the summer retreat of the pack ice far beyond the continental shelf has likely resulted in polar bears using unconsolidated and low-concentration sea ice (Durner et al. 2009). These habitats would be more vulnerable to rapid and complete melt than the main pack ice (Amstrup et al. 2010) and melting of marginal ice areas would force bears to swim long distances to reach stable pack ice or land. The majority of the long-distance swimming events that we identified occurred in August and September, especially near the September sea-ice minimum. Historically, the persistence of sea-ice habitat over the continental shelves (Durner et al. 2009) would have required polar bears to swim tens of kilometres between floes, instead of the hundreds of kilometres that we have observed in recent years (Fig. 7).

Despite a demonstrated ability to swim long distances, swimming can place both adults and dependent young at risk of drowning (Monnett and Gleason 2006; Durner et al. 2011). Also, swimming is likely more energetically intensive than walking on the sea ice or land (Williams 1983; Fish 1996). Bears in this study swam significantly faster than they moved while on sea ice. Swimming movement rates also exceeded previously reported movement rates for bears moving on the pack ice in the SB (Amstrup et al. 2001). Although our estimates of movement rates for bears on sea ice may have had some bias as a result of ice drift (Mauritzen et al. 2003*b*), the high frequency of GPS location data in our study likely reduced this bias. Our estimates of swimming rates may have been biased low because transmissions generally would not resume until the bear was out of the water. In addition, we identified five instances where bears appeared to have brief opportunities to use nondetectable ice floes during their swims. As a result, our swimming rates likely incorporated some nonswimming-related behavior either during or after the swim had ended. Thus, the actual swimming movement rates may have been even higher than we calculated. However, swimming movement rates also would have incorporated ocean currents, which likely introduced some bias in our estimates. Nevertheless, the high rate of speed we observed suggested that bears making long swims were traveling as directly as possible from one location to another. In contrast, bears on sea ice alternately spend time traveling, hunting, and resting (Mauritzen et al. 2003*a*).

Exposure to cold water and rough sea conditions could cause swimming bears to expend additional resources or potentially drown (Blix and Lentfer 1979; Monnett and Gleason 2006; Aars and Plumb 2010). The longest swim that we quantified was examined in detail by Durner et al. (2011). They documented a 22% loss in body mass for this bear, as well as the loss of her yearling cub, over the course of 9 days of continuous swimming and another 54 days of walking across the pack ice (Durner et al. 2011). Durner et al. (2011) indicated that the adult bear in their study made its swim during relatively benign sea states. We found 60% of the dependent cubs survived long-distance swims, indicating that in many instances cubs can survive swims of extended dis-

Fig. 4. Swimming event by polar bear (*Ursus maritimus*) 20333 wearing a GPS-equipped satellite radio collar swimming from land northeast of Wainwright, Alaska, on 20 August 2008 to land on 25 August 2008. We retrieved this bear's collar, which allowed us to recover the GPS location data during the swimming event. GPS location data at 4 h intervals are shown over National Ice Center chart data from 22 August 2008. Sea-ice concentration refers to the percentage of area covered with sea ice. National Ice Center charts reproduced with permission from the National Ice Center, Suitland, Maryland, USA.



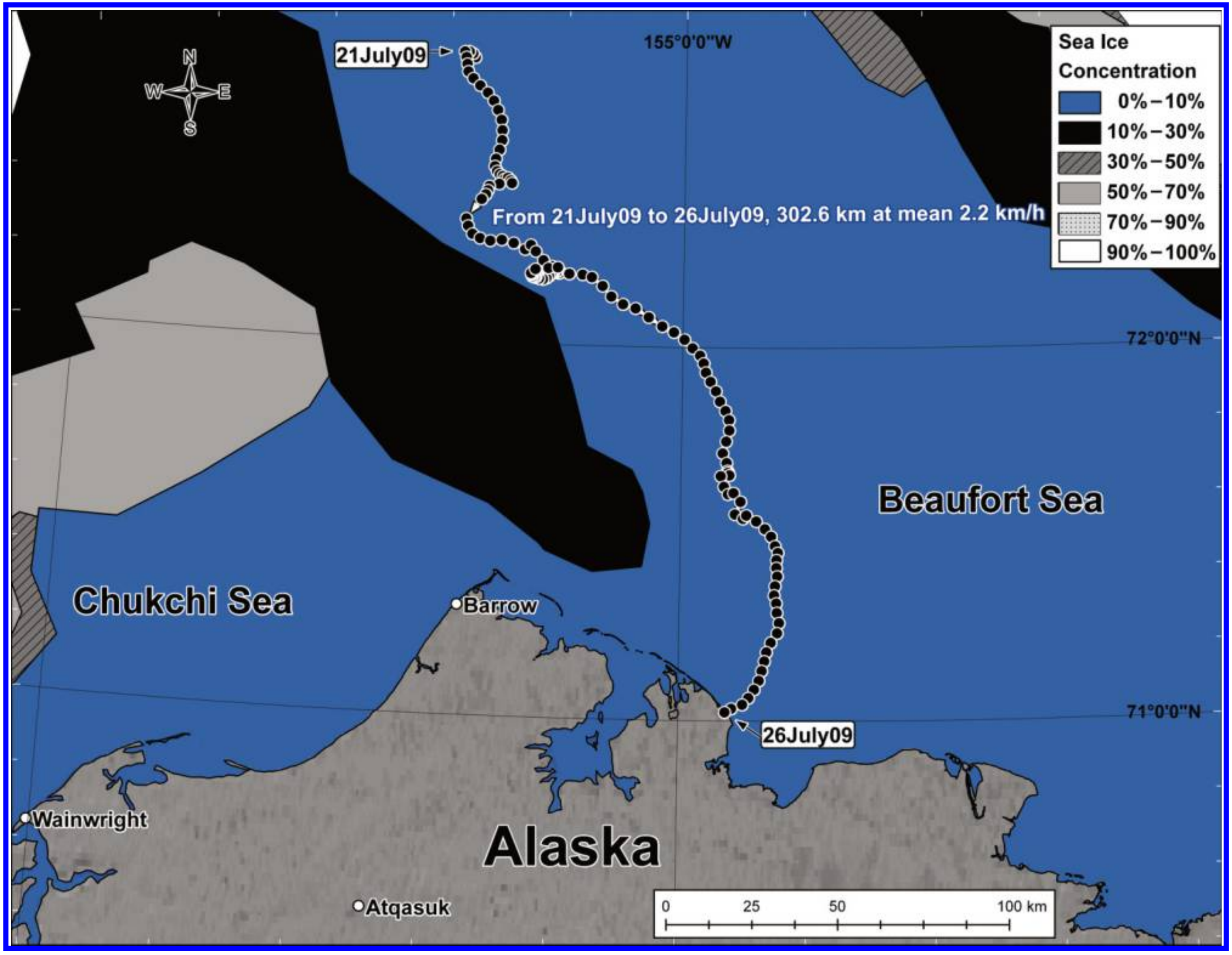
tances and durations. The rate of cub loss for adult bears that made long-distance swims was 11% higher, but was not significant compared with adults with young that did not swim long distances. Other studies have suggested that long-distance swimming could place dependent young at greater risk of mortality (Blix and Lentfer 1979; Aars and Plumb 2010; Durner et al. 2011) and this is an important topic for future investigation.

Limitations in collar technology and the coarse resolution of sea-ice imagery prevented us from examining swimming events <50 km. Although short-distance swims are considered normal behavior for polar bears (Øritsland 1969; Stirling 1974), short-distance swims also could have conservation implications if they are occurring more frequently as a result of declining summer sea-ice conditions. Some bears in our study may have avoided long-distance swims by making multiple shorter distance swims. We would not have detected such events, but these swims could potentially have similar energetic demands as long-distance swims. Higher frequency GPS location data is needed to examine the frequency of shorter distance swims and this is an important topic for future investigation.

Most of the long-distance swimming events that we identified involved bears swimming from unconsolidated sea ice to the main pack ice or to land. Bears that use unconsolidated sea ice would likely be forced to swim to reach more stable habitats as the ice continues to melt. However, we also identified swimming events where bears swam from unconsolidated sea ice to other areas of unconsolidated sea ice or swam from land to unconsolidated sea ice. These could be instances where bears were attempting to locate the main pack ice but terminated their swim within the marginal ice zone or they may have been selecting this habitat. We also identified swimming events where bears swam from land to the main pack ice, from one land area to another, or from the main pack ice to land. Hence, the motivation for swimming was not always clear.

Polar bears that summer on land are generally either food-deprived during the open-water season (Ramsay and Hobson 1991) or use beach-cast or subsistence-harvested marine

Fig. 5. Swimming event by polar bear (*Ursus maritimus*) 20735 wearing a GPS-equipped satellite radio collar swimming from unconsolidated sea ice on 21 July 2009 to the Alaska coast on 26 July 2009. We retrieved this bear's collar, which allowed us to recover the GPS location data during the swimming event. GPS location data at 1 h intervals are shown over National Ice Center chart data from 24 July 2009. Sea-ice concentration refers to the percentage of area covered with sea ice. National Ice Center charts reproduced with permission from the National Ice Center, Suitland, Maryland, USA.



mammals (Miller et al. 2006; Bentzen et al. 2007; Gleason and Rode 2009). Polar bears that use the pack ice over deep waters during summer also may experience reduced feeding opportunities. Polar bears are largely dependent on ringed and bearded seals. These seals are thought to be primarily pelagic during the summer (Harwood and Stirling 1992; Gjertz et al. 2000; Freitas et al. 2008*a*; Kelly et al. 2010; but see Härkönen et al. 1998; Sipilä and Hyvärinen 1998) and movement patterns of ringed seals are expected to change with changing ice conditions if offshore migrations become energetically costly (Laidre et al. 2008; Freitas et al. 2008*b*). Hence, ringed and bearded seals would generally be unavailable to polar bears on land and it is not known if they would be available from the pack ice when it retreats over the deep polar basin water. In addition, although polar bears may occasionally catch ringed seals in open water (Furnell and Oolooyuk 1980), we found no evidence in any of the long-distance swims we documented that polar bears were hunting. Swims appeared to be point to point, travel rates were high, and deviations necessary for hunting prey or other activities were not observed. Consequently, we suggest that

Fig. 6. Distance of 30 fixed locations along the Canada and Alaska mainland coast of the Beaufort Sea to the edge of September sea ice from 1979 to 2010. Trend (broken line) was estimated with a second-order polynomial ($r^2 = 0.37$, $P = 0.001$).

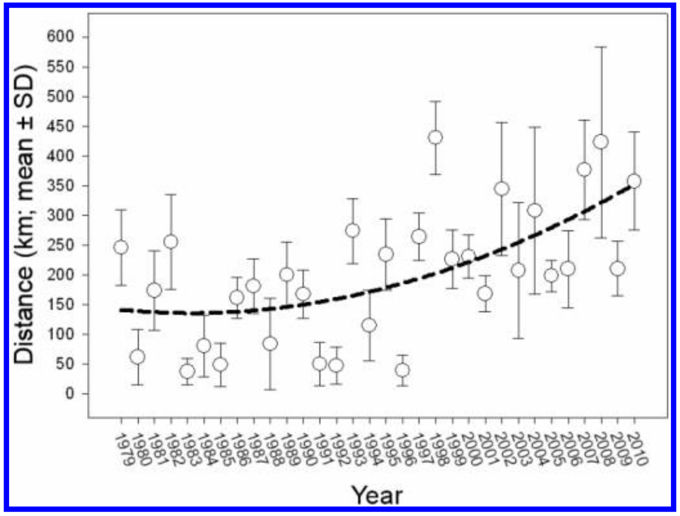


Fig. 7. Median estimates of September sea-ice extent based on passive microwave sea-ice data in the Beaufort and Chukchi seas during 1979–1996 (solid line) and 1997–2010 (broken line). The 300 m depth contour (dotted line) is provided to show the spatial relationship of sea-ice extent to the continental shelf. Xs represent locations where we measured the distance from land to the edge of the September sea ice.

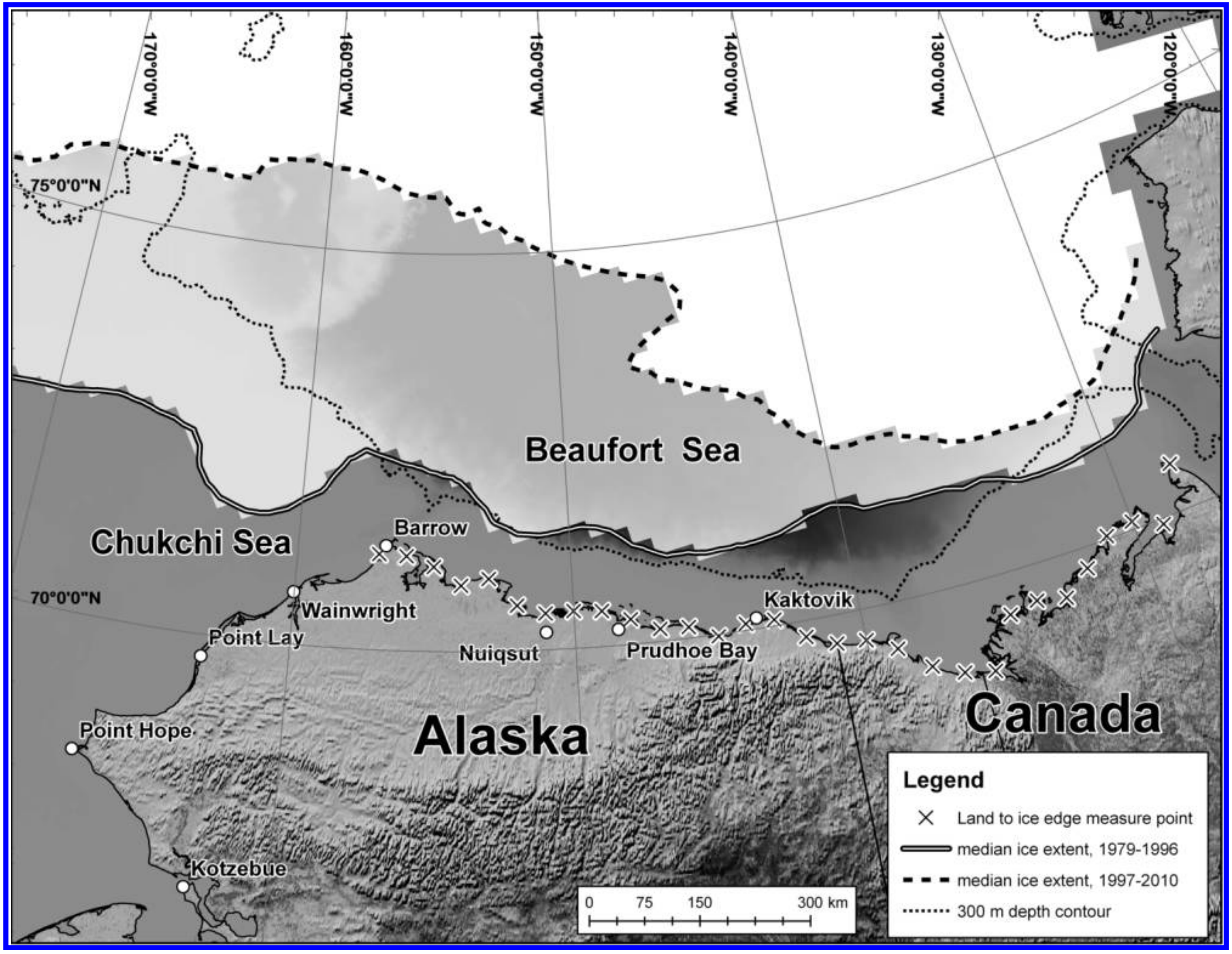


Table 3. Last transmission dates (mean (range)) of GPS-equipped satellite radio collars that prematurely failed in July, August, or September during the first year of deployment on polar bears (*Ursus maritimus*) in the southern Beaufort Sea from 1985 to 2009.

	Bears that were not later resighted		Bears that were later resighted	
Year	Last transmission date	*N*	Last transmission date	*N*
1986			7 Sept. (17 Aug. – 29 Sept.)	2
1987			10 Sept.	1
1988			14 Sept. (1–28 Sept.)	2
1991			21 Sept.	1
1992	15 Aug. (28 July – 11 Sept.)	3	26 Aug.	1
1998	16 Aug.	1		0
2001			9 Aug.	1
2005	28 July	1		
2006	22 July (12 July – 1 Aug.)	2		
2007	13 July (6 July – 21 July)	2		
2008	28 July (3 July – 4 Sept.)	5	17 July	1
2009	10 Sept.	1	2 Aug. (2 July – 16 Sept.)	3

when ice conditions are inadequate for walking, long-distance swimming is primarily a relocation behavior that polar bears use to find suitable or superior habitat. Provisioning of bowhead whale carcasses at villages and hunting camps (Miller et al. 2006) also could be a strong incentive for some bears to swim from distant sea-ice habitats to land.

We do not have data to indicate why 38% of the adult female bears that we collared swam long distances, while the remaining 62% did not. Long-distance swimming may be related to body condition and foraging success. Bears in better body condition may be more apt to follow the receding pack ice, whereas bears in poorer body condition may attempt to continue hunting among deteriorating sea ice or more readily abandon a stable substrate (Mauritzen et al. 2003*a*). However, Durner et al. (2011) did not believe body condition was a factor in the 687 km swim that they documented. Instead, they speculated this swim was indicative of a preference for sea ice over land (Durner et al. 2011), which also could explain a number of the long-distance swims that we identified. We do not have enough data immediately prior to and immediately following swimming events to evaluate the potential mechanisms behind long-distance swimming.

Minimum Arctic sea-ice extent in September 2007 reached a record low based on the start of satellite measurements in 1979 and minimum sea-ice extent in September 2008 and September 2009 were the second and third lowest recorded, respectively (Stroeve et al. 2011). We observed an increase in the proportion of GPS-collared polar bears that swam long distances over the course of this research (with the greatest number of swimming events occurring in 2009, the last year of our study). However, the number of GPS collars that were successfully deployed and transmitted varied considerably among years. These sampling differences among years preclude us from fully evaluating what appears to be an increasing trend in the number of long-distance swimming events since 2004.

We hypothesized that premature cessation of radio-collar transmission data during the open-water season from bears that were never later resighted could be indicative of swimming-related drowning events. If this was the case, we would expect a higher rate of premature cessation for bears that have never been resighted and we would expect to observe a greater percentage of collars to prematurely cease in years when greater amounts of open water were present in the SB. We found similar numbers of premature cessations for both resighted and non-resighted bears. However, we found a significant correlation between the percentage of premature cessations per year for bears that were never resighted and the mean distance to the sea-ice edge in September. This suggests that the cause of some transmission failures may be related to the amount of open water in the summer. We cannot rule out the possibility that some of these events could be indicative of drowning. Other possible explanations for these prematurely failing collars could be mechanical problems with the collar, shucking of the collar by the bear, or unrelated mortality. Of the 15 records of prematurely ceasing collars on bears that we did not later resight, 6 bears (40%) had not been previously captured before the collar deployment in which their collars failed. This may indicate that these individuals had low recapture probabilities.

Our observations suggest that long-distance swimming is a behavioral response to declining summer sea-ice conditions. Adult female polar bears and their cubs are capable of swimming long distances during periods when extensive areas of open water are present. However, long-distance swimming appears to have higher energetic demands than moving over sea ice and other studies suggest that long-distance swimming can be life threatening (Monnett and Gleason 2006; Durner et al. 2011). Reduced availability of sea ice has been associated with novel polar bear behavior (e.g., Monnett and Gleason 2006; Stirling et al. 2008; Durner et al. 2011), reduced stature and survival (Stirling et al. 1999; Regehr et al. 2007, 2010; Rode et al. 2010), and population decline (Regehr et al. 2007). With decreasing sea-ice extent expected in the future (Overland and Wang 2007; Walsh 2008) and continued declines in sea-ice thickness resulting in less predictable melting patterns (Amstrup et al. 2010), long-distance swimming behavior is likely to increase.

Acknowledgements

Primary funding for this research was provided by the US Geological Survey (USGS), Climate and Land Use Change Research and Development Program. Additional support was provided through a National Science Foundation grant (OPP 0732713) to the University of Wyoming, and by the US Fish and Wildlife Service, Marine Mammals Management. Captures of polar bear were made possible under US Fish and Wildlife marine mammal research permit 690038 granted to the USGS, Alaska Science Center. Capture procedures were conducted under the approval of the Alaska Science Center Institutional Animal Care and Use Committee (IACUC) protocols (assurance no. 2010-3). We thank the US Fish and Wildlife Service, Arctic National Wildlife Refuge, and the North Slope Borough Department of Wildlife Management for logistical support. We thank M. Lockhart and E. Regehr for assistance in the field. The following individuals are recognized for valuable input on earlier versions of the manuscript: C. Amundson, T. DeGange, D. Douglas, K. Oakley, L. Peacock, and two anonymous reviewers. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

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Appendix A

Appendix tables appear on the next page.

Table A1. GPS programming and Argos transmission schedules for GPS-equipped satellite radio collars deployed on adult female polar bears (*Ursus maritimus*) in the southern Beaufort Sea.

Year	No. of GPS location fixes per day	Argos transmission schedule
2004	6	4 h daily
2005	3	4 h every 2nd day
2006	3	4 h every 2nd day
2007	3	4 h every 2nd day
2008		
Spring	4	4 h daily
August	24	8 h daily
2009	24	4 h daily

Table A2. Number of GPS-equipped satellite radio collars that were successfully deployed (excluding collars that were immediately shucked) and transmitted on adult female polar bears (*Ursus maritimus*) in the southern Beaufort Sea.

Year	No. of GPS collars deployed	No. of GPS collars transmitted[a]
2004	10	8
2005	12	11
2006	16	15
2007	2	1
2008		
Spring	4	4
August	8	5
2009	16	13

[a] Limited to collars that transmitted >2 months during June to October.

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