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Migratory response of polar bears to sea ice loss: to swim or not to swim

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Migratory responses to climate change may vary across and within populations, particularly for species with large geographic ranges. An increase in the frequency of long-distance swims (> 50 km) is one predicted consequence of climate change for polar bears *Ursus maritimus*. We examined GPS satellite-linked telemetry records of 58 adult females and 18 subadults from the Beaufort Sea (BS), and 59 adult females from Hudson Bay (HB), for evidence of long-distance swimming during seasonal migrations in 2007–2012. We identified 115 swims across both populations. Median swim duration was 3.4 d (range 1.3–9.3 d) and median swim distance was 92 km (range 51–404 km). Swims were significantly more frequent in the BS (n = 100) than HB (n = 15). In the BS, subadults swam as frequently as lone adult females, but more frequently than adult females with offspring. We modelled the likelihood of a polar bear engaging in swims using collar data from the BS. Swims were more likely for polar bears without offspring, with the distance of the pack ice edge from land, the rate at which the pack ice edge retreated, and the mean daily rate of open water gain between June–August. Coupled with an earlier study, the yearly proportions of BS adult females swimming in 2004–2012 were positively associated with the rate of open water gain. Results corroborate the hypothesis that long-distance swimming by polar bears is likely to occur more frequently as sea ice conditions change due to climate warming. However, results also suggest that the magnitude of the effect likely varies within and between populations.

Anthropogenic greenhouse gas emissions are the primary cause of global warming (Rosenzweig et al. 2008, Kokic et al. 2014), and the resulting climate effects are spatially heterogeneous, varying in scale, magnitude, and type (IPCC 2013). Habitat specific responses can alter the consequences of climate change for a species (Parn et al. 2012), and simultaneous changes to multiple types of abiotic conditions (e.g. temperature, precipitation, storm frequency) may interact to buffer or amplify the biotic response (Zvereva and Kozlov 2006, Tylianakis et al. 2008, Castro et al. 2010). As a result, biotic responses to climate change can vary in magnitude, and fluctuate across a species' range (Ackerly et al. 2010).

Animal migration is a behavioural response to local environmental conditions, triggered by exogenous cues that act as proxies for resource availability (Dingle 2014). Migration can be considered in a cost-benefit framework (Avgar et al. 2013), with the energetic costs of long-distance movements offset by access to temporal and spatial peaks in resources. The phenology and abundance of primary producers has been shifting as a consequence of climate change (Ji et al. 2013, CaraDonna et al. 2014), with cascading trophic impacts (Edwards and Richardson 2004, Donnelly et al. 2011). As a result, migration patterns are changing for many species (Cotton 2003, Singh et al. 2012, Otero et al. 2014). Studies on the impacts of climate change on migration have often focused on measuring the species-wide response, with few studies comparing differential migration, in which migratory behaviour varies between age and sex classes (Rainio et al. 2007, Hedlund et al. 2015). Ignoring individual and population variation may bias the estimates of the effect of climate change on migration, and fail to identify the ecological linkages that are sensitive to environmental change.

Several Arctic species use migration to mitigate the intense seasonality in resources, or to avoid unsuitable habitats. However, environmental change in the Arctic is occurring more rapidly than anywhere else, possibly due to climatic feedbacks tied to sea ice loss (Holland et al. 2006, Screen and Simmonds 2010, Stroeve et al. 2011). As such, the migratory dynamics of Arctic animals are likely to be affected (Sharma et al. 2009, Bailleul et al. 2012, Finstad and Hein 2012). Polar bears *Ursus maritimus* are an ice-obligate, apex predator, impacted by the effects of climate change (Stirling et al. 1999, Derocher et al. 2004, Regehr et al. 2007, 2010) that can vary in magnitude across their range (Rode et al. 2014). Polar bears prefer sea ice habitat on the continental shelf (Durner et al. 2009, McCall et al. 2014) where they hunt seals. Feeding intensifies in spring (Pilfold et al. 2012), when increased seal vulnerability allows polar bears to kill more frequently (Pilfold et al. 2015), and thus accumulate energetic stores (Ramsay and Stirling 1988). As the sea ice begins to melt in late spring, polar bears in seasonal-ice ecosystems move to refugia, migrating to land or offshore pack ice during the summer (Knudsen 1978, Derocher and Stirling 1990, Amstrup et al. 2000, Schliebe et al. 2008).

Laidre et al. (2008) suggested polar bear migration was moderately sensitive to climate change. In Hudson Bay (HB), polar bear migratory phenology is shifting with changing sea ice dynamics, with arrival dates on land correlated to sea-ice concentration and rate of loss (Stirling and Derocher 1993, Stirling et al. 1999, Cherry et al. 2013). In addition to changing sea-ice phenology, climatic forcing is resulting in a thinner, more fractured and mobile ice cover (Stroeve et al. 2011), which may affect migration because polar bears adjust movements and space use to drifting ice (Mauritzen et al. 2003, Auger-Méthé et al. 2016). Instead of walking on a consolidated sea ice surface, polar bears may be forced to undertake long-distance swims (hereafter: swims) to complete their migratory route. Although they are adept swimmers (Stirling 1974, Dyck and Romberg 2007, Pagano et al. 2012, Stirling and van Meurs 2015), swimming can be energetically costly (Durner et al. 2011), and may increase mortality risk (Monnett and Gleason 2006, Durner et al. 2011).

It has been hypothesized that as seasonal periods of open water extend spatially and temporally, the frequency of swims by polar bears will increase (Derocher et al. 2004, Monnett and Gleason 2006, Pagano et al. 2012, Stirling and Derocher 2012). However, empirical assessment of swimming has been hampered by small sample sizes and short study durations. We examined location data of polar bears fitted with satellite collars in the Beaufort Sea (BS) and HB to compare the frequency of swims within and between populations, and infer whether behavioural responses during migration were associated with changes to sea ice. In addition, we combine our results with Pagano et al. (2012) to evaluate temporal trends in the frequency of swims relative to climate-induced sea ice changes in the BS.

Methods

Study area

In HB, sea ice begins to form in mid-October, radiating outward from the western coast until the Bay is fully frozen by the end of December (Saucier et al. 2004, Joly et al. 2010). Breakup begins in May, and the last remaining ice melts out along the southern coast in July. Polar bears begin migrating to land when sea ice concentrations reach 30–50% (Stirling et al. 1999, Cherry et al. 2013), and spend the open water season along the western coast (Derocher and Stirling 1990, Stirling et al. 2004). In the BS, sea ice forms both as shorefast ice along the coast in late-September (Barry et al. 1979), and as pack ice expanding southward off of multiyear ice in the Canada Basin (Galley et al. 2008). The shorefast ice and pack ice meet over the continental shelf by late October. Breakup begins in May, with the initial open water forming along the shorefast ice boundary and Cape Bathurst polynya (Barber and Hanesiak 2004, Galley et al. 2008). Pack ice retreats northward, while the last remaining shorefast ice melts out in July. The majority of BS polar bears migrate north with the pack ice, with some moving to land during the open water season (Amstrup et al. 2000, Schliebe et al. 2008).

Data collection

Polar bears were captured (Stirling et al. 1989) in April–May and in August–September in BS and HB, respectively (Fig. 1). The sex of each bear was determined in the field, whereas

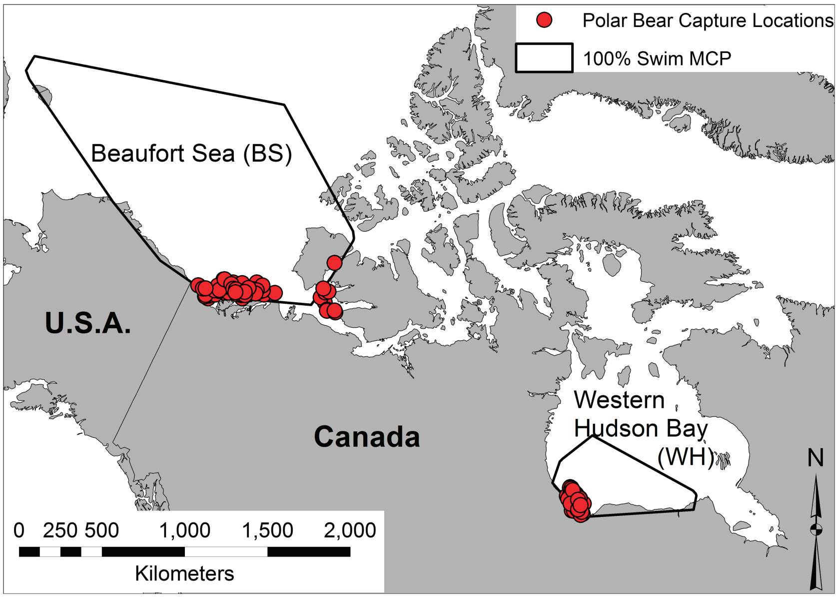

Figure 1. Map of Beaufort Sea (BS) and Hudson Bay (HB) study areas. Symbols indicate capture locations for polar bears that had active collars during the study (2007–2012). Polygons represent the 100% minimum convex polygon (MCP) for all long-distance swims in each population.

age was determined by extracting a vestigial premolar and subsequently counting cementum growth layer groups (Calvert and Ramsay 1998). Subadults (3–5 yr old) of both sexes (BS only) and adult female polar bears (>5 yr old) with and without offspring (≤ 2 yr old) were fitted with collars (Telonics, Mesa, AZ) equipped with a geographic position system (GPS) receiver. GPS locations (accuracy 31 m; Tomkiewicz et al. 2010) were collected every 4 h and relayed daily to an Argos satellite (CLS America, Lanham, MD). All collars were equipped with a timed-release mechanism (CR-2a, Telonics, Mesa, AZ) to drop 1 or 2 yr after deployment. Collars were deployed as part of ongoing research programs in the BS and HB, and study duration (2007–2012) was limited to the years that collars were deployed in both regions.

Potential swims were identified by examining Argos transmission reports from collars active between 1 May and 31 December, 2007–2012, which covered the open water and migratory period for BS and HB. Only data from collars that functioned for ≥ 3 months during the period of interest were retained. Because the Argos transmission antenna is located laterally on the collar, it is submerged during swimming and will result in a failed connection. Transmission gaps were identified and the GPS paths during this period were examined against satellite-derived sea ice imagery (Supplementary material Appendix 1, Table A1; Spreen et al. 2008). We retained only paths that fell in open water, with no option for travelling the same route via sea ice or land. Following Pagano et al. (2012), we defined 'long-distance' as any swim >50 km, and included instances when a polar bear may have rested briefly (≤ 16 h) on non-detectable ice floes during a swim as a single event.

Swim characteristics

We examined three characteristics of swims: distance, duration, and speed. Swim distance was measured as the minimum great-circle length between successive GPS locations over open water. Swim duration was defined as the amount of time between the last location on sea ice or land before the start of the swim and the first location on sea ice or land at the end of the swim. Swim speed was calculated as the distance travelled divided by the duration of the swim.

Multiday transmission gaps created satellite-transmitted GPS location gaps because the collars were programmed to send only the last six locations (previous 24 h) upon a successful connection. As the GPS receiver is on the dorsal side of the collar and exposed during swims, collars continue to record and store locations in non-volatile memory. If the collar is recovered, GPS positions can be downloaded directly, retrieving the non-transmitted locations. To examine the effect of transmission gaps on swim distance and speed, we compared the distances travelled during swims from recovered collars to the distances calculated from the satellite-transmitted locations using a related-samples Wilcoxon sign ranked test. We also examined the downloaded locations as a confirmation of the method to identify swims. If the method was accurate, downloaded GPS locations from the transmission gaps should be in open water rather than on sea ice or land.

Intra-population comparisons

In 2007–2009, subadults and adult females in the BS were collared, thus allowing examination of age-related differences in swimming. We retained data from the first year of collar activity only, to reflect demographic status recorded the same spring. The frequency, distance, duration and speed of swims were compared between subadults of both sexes, lone adult females, and adult females with offspring. Frequency was defined as the total number of swims per collar month (2007–2009), and totals were examined across age-classes using a Pearson χ^2, with null expectation that the frequency of swims would be proportional to collar activity. Collar activity was defined as the total number of collar months, where one collar month equalled 30 d of active collar transmission, during the period of interest (May–December). Distance, duration and speed of swims were compared between age-classes using an independent samples Kruskal–Wallis test.

Inter-population comparison

The frequency, distance, duration, seasonal timing, and starting and ending habitats of swims by adult females with offspring were compared between HB and the BS, for 2007–2012. Nearly all (58/59) of the collars in HB were deployed on adult females with offspring. As swim frequency may be influenced by the presence of offspring, we limited the inter-population comparison to adults with offspring only. Frequency of swims were compared using a Pearson χ^2, with null expectation that the frequency of swims would be proportional to collar activity in each population. Inter-population swim distance and duration were compared using an independent samples Mann–Whitney U-test reported with a Z-test statistic. Seasonal timing was examined by counting the frequency of swims by month. Finally, we analysed the starting and ending habitats of swims, classified as either offshore pack ice or land together with fast ice to match seasonal refugia preferences (Knudsen 1978, Derocher and Stirling 1990, Amstrup et al. 2000, Schliebe et al. 2008). Seasonal timing and starting and ending habitats were compared between populations using the Marascuilo procedure for proportional data, reported with a χ^2 (Marascuilo 1966).

HB sea ice dynamics

We compared onshore dates of collared HB polar bears in 2007–2012 with sea ice dynamics as a post-hoc investigation of patterns in migration. The objective was to determine whether HB polar bears avoided swims, or if the distance from shore of the melting ice limited the occurrence of swims >50 km in length. Each day we calculated the mean and minimum distance of the pack ice edge from land as well as the ice concentration within the 95% minimum convex polygon home range for HB (McCall et al. 2014). Pack ice edge was the margin of consolidated ice concentration greater than 15%, with the edge defined using the boundary clean tool in ArcGIS ver. 10.1 (Environmental Systems Research Inst., Redlands, CA). Onshore dates were determined as the date on which the first location occurred on land without a subsequent return to the sea ice until autumn (Cherry et al. 2013). We excluded onshore dates when > 7 previous days of telemetry data were missing (i.e. bears appearing on land after a large temporal gap in locations). We then matched the onshore date with the mean sea ice conditions of the previous 7 d, as well as calculated the number days between the onshore date and when the 50 and 30% ice concentration thresholds had been reached.

BS swimming model

We used collar data from the BS to examine the influence of sea ice, open water, climate, and demographic factors on the frequency of swims using a count model. HB data was excluded due to the limited number of swims. We retained data from the first year of collar activity only, to reflect demographic status and body condition of polar bears collared the same spring. We modelled the monthly frequency of swims, counting the number of swims for each collared individual over the open water period (June–October; 2007–2012). We used a mixed-effect Poisson regression as the data model, and Akaike information criterion for small samples (AIC_C) as a measure of model fit (Burnham and Anderson 2002). We used a Bear ID random intercept to account for repeated observations from the same individuals, and models were run using the 'glmmADMB' package in R Studio (Fournier et al. 2012). Overdispersion of the top model was examined by dividing the Pearson χ^2 for the model by the degrees of freedom.

We examined variables that we hypothesized would influence swims, broadly classified into four groups: demographic, sea ice conditions, open water conditions, and climate (Table 1). Demographic variables were used to assess individual variation in the likelihood of a swim. As offspring are at risk of hypothermia if exposed to water for extended periods (Blix and Lentfer 1979, Aars and Plumb 2010), and adult females with cubs-of-the-year tend to avoid habitats with open water (Stirling et al. 1993, Pilfold et al. 2014), we hypothesized that females with offspring would be less likely to swim. Additionally, we used body condition metrics to assess how individual condition may influence the likelihood of a potentially energetically costly movement strategy (Durner et al. 2011). Polar bear fatness was estimated in the field using a subjective five-category index (Stirling et al. 2008). A relative index of weight was derived from length and girth measurements using an established body-dimension to mass relationship for the BS (Durner and Amstrup 1996).

Sea ice conditions between the summer breakup and autumn reformation were described with several variables. Distance to the edge of the main pack ice from land was hypothesized as an important driver of swims in the BS (Pagano et al. 2012), and was derived using the same process as for HB. Additionally, because Pagano et al. (2012) reported that a high proportion of swims started from unconsolidated sea ice, we examined pack ice heterogeneity as a factor. We used the region-group tool in ArcGIS to examine sea ice imagery and isolate and count giant floes greater than 150 km in size. The rate at which sea ice changes during the summer melt was associated with polar bear migration phenology (Cherry et al. 2013). Because swims depend on open water, we included a variable measuring the mean rate of daily open water gain during the summer months (June–August). Open water area was estimated as the proportion of the study area with 0% sea ice concentration.

As open water conditions associated with surface roughness may be linked to drowning events (Monnett and Gleason 2006), we examined wave height and wind speed measured across the study area using ICOADS data (<http://icoads.noaa.gov/>). We also examined regional climate variability using two climate indices: Arctic Oscillation Index (AOI)

Table 1. Initial set of covariates used to model the frequency of long distance swims by polar bears in the Beaufort Sea, June–October, 2007–2012, post-removal of highly correlated variables (Supplementary material Appendix 1, Table A2).

Covariate	Acronym	Range	Description and source
Demographic variables			
Family status[1]	Offspring	1/0	Field observation in spring (April–May)
Fatness[1]	Poor	1/0	Field measurement in spring (April–May), condition ranked 1–5[3], with 1–2 coded as 'poor'
Weight[1]	FIELD_WGT	120–306 kg	Field measurement in spring (April–May), tape conversion following Durner and Amstrup (1996)
Sea ice variables			
Distance to pack ice[2]	EDGE_DIST	38–385 km	Mean distance of pack ice–open water boundary from land
Change in distance to pack ice[2]	EDGE_CHNG	–9.4–6.3 km d^{-1}	Mean daily rate of change in distance to pack ice–open water boundary from land
Pack ice heterogeneity[2]	FLOE_COUNT	3–14	Number of giant pack ice floes (> 150 km^2)
Open water variables			
Rate of open water gain[1]	OW_CHNG	0.32–0.91% d^{-1}	Mean daily rate of open water gain between June–August, measured as % area
Wind speed[2]	WIND	4.1–8.6 m s^{-1}	Mean wind speed, ICOADS 2° enhanced data[4]
Wave height[2]	WAVE	0.2–1.3 m	Mean wave height, ICOADS 2° enhanced data[4]
Climate variables			
Arctic Ocean Oscillation[1]	AOO	0.8–4.6	Proshutinsky and Johnson (1997)
Arctic Oscillation[1]	AOI	–2.0–1.9	Thompson and Wallace (1998)

[1]Yearly scale; [2]monthly scale; [3]Stirling et al. (2008); [4]International Comprehensive Ocean-Atmosphere Data Set – release 2.5 available from CISL Climate Data Archive (<http://rda.ucar.edu/>).

and the Arctic Ocean Oscillation (AOO) because both can influence sea ice conditions in the BS (Proshutinsky 2002, Rigor et al. 2002). The AOI is an index of sea level pressure anomalies north of 20°N (Thompson and Wallace 1998), whereas the AOO is an index of Arctic wind-driven circulation regimes (Proshutinsky and Johnson 1997).

A priori covariates were measured either at monthly or yearly scales (Table 1), but spatially constrained to the 100% minimum convex polygon in which all swims occurred (Fig. 1). Before modelling, we tested all continuous covariates for non-linearity using transformations (e.g. quadratic, natural log) and assessed fit with AIC_C. We also examined correlation between covariates. Covariates with a correlation coefficient of $r \geq 0.6$ were screened using univariate log-likelihood scores, retaining the covariate with best fit for modelling (see Supplementary material Appendix 1, Table A2 for list of removed variables). Continuous covariates were examined for biologically meaningful interactions. Covariates were mean-centered to minimize multi-collinearity arising from interaction terms, and the resulting variance inflation factors for all covariates were ≤ 3.3. For model selection, we built a set of candidate models and used AIC_C model selection to determine a top model. We report the unstandardized beta coefficients for the top model.

BS temporal trends

We counted the number of collared adult female polar bears that made at least one swim for each year of collar data in the BS, and combined the results with the data from Table 1 of Pagano et al. (2012) to assess trends in swim frequency between 2004–2012. We excluded subadults from the trend analysis because Pagano et al. (2012) only tracked adult females. We assessed the association between the proportions of swimming polar bears to the top yearly abiotic variable from the swim model using a Spearman's rho. Data on Arctic sea ice extent and dates of annual September sea-ice minimums were obtained from the National Snow and Ice Data Center (nsidc.org). Statistical tests were conducted in SPSS 21.0 (IBM, Chicago, IL). For all significance tests, alpha was 0.05.

Results

Swim characteristics

We identified 115 swims (100 BS; 15 HB) from the telemetry records of 135 individually collared bears active in the BS and HB, 2007–2012. Overall, 45% (61/135) of the bears tracked recorded at least one swim. Swims all occurred from June to November (Fig. 2). Swims in HB occurred predominately in July, and 91% (91/100) of the swims in the BS occurred before the annual September minimum sea ice extent had been reached. From Argos-transmitted GPS locations, median swim duration was 3.4 d (range: 1.3–9.3 d) and median distance was 92 km (range: 51–404 km). The median swim speed was 1.4 km h^{-1} (range: 0.4–2.6 km h^{-1}). From recovered collars, 12 swims were directly downloaded. All GPS locations (n = 311) from recovered collars that occurred during Argos transmission gaps were located in open water. The distance swam as recorded by the GPS collar was a median of 1.4 × longer (range: 1.2–2.3×) than the distance measured with Argos transmitted GPS points (n = 12, $Z = -3.06$, p = 0.002, Fig. 3). Adjusting all swims with a median correction factor of 1.4×, the adjusted median distance was 125 km (range: 71–566 km) and adjusted median swim speed was 2.0 km h^{-1} (range: 0.5–3.7 km h^{-1}).

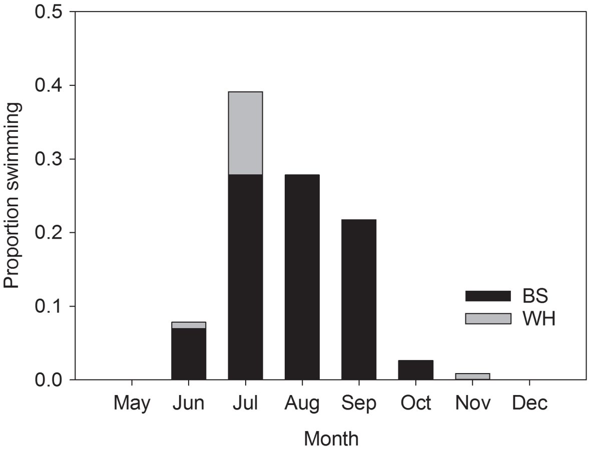

Figure 2. Monthly frequency distribution of long-distance swims (>50 km) by adult female polar bears in Hudson Bay (HB) and Beaufort Sea (BS), 2007–2012.

Intra-population comparison

The distribution of swims across age-classes was significantly different than expected from collar activity ($\chi^2 = 23.8$, DF = 3, $p < 0.001$; Table 2). Adult females with offspring swam less frequently than each of the other three demographic classes ($\chi^2 \geq 11.0$, DF = 1, $p \leq 0.001$). Median swim distance and duration differed significantly across age-classes ($H_{dis} = 11.7$, $H_{dur} = 12.2$, DF = 3, $p < 0.01$), with subadult females having shorter swims both in terms of distance and duration than lone adult females ($H_{dis} = 20.1$, $H_{dur} = 19.8$, DF = 1, $p < 0.01$). There was no significant difference in median swim speeds across age-classes ($H = 3.3$, DF = 3, p = 0.35).

Inter-population comparison

In 2007–2012, we detected 36 swims in the BS and 15 in HB by adult females with offspring. In total, 49% (18/37) of BS and 22% (13/58) of HB adult females with offspring swam at least once in 2007–2012. Frequency of swims was significantly different between populations ($\chi^2 = 10.6$, DF = 1, $p < 0.001$), with more swims occurring in the BS. Significantly different proportions of swims occurred between populations in July, August, and September ($\chi^2 \geq 12.6$, DF = 1, p = 0.001).

Median swim duration in BS was 3.9 d (range: 1.5–8.5 d) and was not significantly different ($Z = -0.46$, p = 0.64) than the median duration of 3.3 d (range: 1.6–7.0 d) for HB.

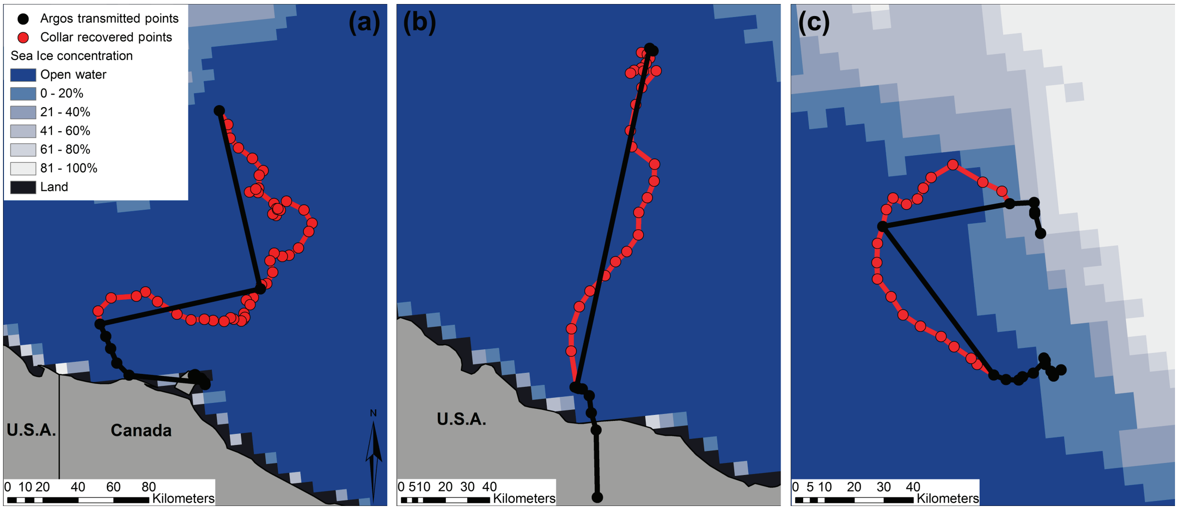

Figure 3. Swim distances of three polar bears calculated from both Argos-transmitted GPS locations (black), which include transmission gaps, and from locations downloaded directly from the collars when recovered (red). (a) Argos = 196 km; collar = 302 km, (b) Argos = 68 km; collar = 86 km, (c) Argos = 107 km; collar = 139 km.

Median swim distance in the BS was 97 km (range: 52–340 km) and was not significantly different ($Z = -0.51$, $p = 0.61$) from the mean distance of 113 km (range: 51–269 km) for HB. The most frequent habitats in which swims started and ended were significantly different between populations ($\chi^2 \geq 12.8$, DF = 1, $p < 0.001$). In the BS, 81% (29/36) of swims started and ended in pack ice whereas in HB, 60% (9/15) started on pack ice and ended on land.

HB sea ice dynamics

We recorded 26 onshore dates for HB adult female polar bears in 2007–2012. The median onshore date was July 13 (range: 25 June–6 August), which corresponded to a median ice concentration of 3.2% (range: 0.1–44.4%). Onshore dates occurred a median of 23 d (range: 5–43 d) after 50% sea ice concentration was reached, and 17 d (range: 1–35 d) after 30%. Median ice edge distance from land was 113 km (range: 20–219 km), and median minimum ice edge distance from land was 37 km (range: 2–155 km).

BS swimming model

From first-year BS collar data, we tracked 76 individuals from which 86 swims were recorded and used for modelling. In total, 43% (33/76) of the individuals tracked engaged in at least one swim. The Poisson distribution showed no signs of overdispersion on the top model ($\hat{c} = 0.88$). The top model included four covariates and one interaction term: presence of offspring; rate of daily open water change in June–August; mean distance from land to the edge of the consolidated pack ice; daily mean rate of change of the distance from land to pack ice edge; and an interaction term between the last two variables (Supplementary material Appendix 1, Table A3). For polar bears without offspring, the likelihood of a swim increased with the rate of open water gain between June–August, with the distance from land to the pack ice edge and the rate at which it retreated, as well as the interaction term (Table 3). Body condition metrics, including indices of weight and fatness, were not in the top model.

BS temporal trends

In 2004–2012, the daily rate of open water gain between June–August in the BS was positively correlated with year ($r_s = 0.85$, n = 9, $p < 0.01$) and negatively correlated with the minimum ice extent in September ($r_s = -0.76$, n = 9, $p = 0.02$). Combining our data with Pagano et al. 2012, 115 swims by adult females were recorded in 2004–2012 in the BS (Table 4). The proportion of adult females swimming each year was positively associated with the rate of open

Table 2. Swims by polar bears in the Beaufort Sea, 2007–2009, by age-class. Results are constrained to the years that collars were deployed on subadults in addition to adult females. Swim characteristics are reported as medians with ranges in parentheses.

	Age-class			
	Subadult male[1]	Subadult female[1]	Lone adult females[2]	Adult females[2] with offspring
Number of collars	8	9	10	24
Collar activity (months)[3]	64.0	66.1	91.3	135.2
Swims	20	12	16	5
Distance (km)	88 (51–310)	74 (51–404)	156 (59–217)	101 (52–147)
Duration (days)	2.8 (1.3–8.0)	1.7 (1.3–9.0)	3.8 (2.2–8.3)	3.5 (3.4–3.8)
Speed (km h^{-1})	1.5 (0.5–2.4)	1.6 (0.7–2.5)	1.4 (0.7–2.7)	1.1 (0.6–1.7)

[1]3–5 yr of age; [2]> 5 yr of age; [3]total sum of time collars were active during study period.

Table 3. Parameter estimates for coefficients of the top long-distance swim model for the Beaufort Sea, June–October, 2007–2012.

Parameter[1]	$\mathrm{AIC}_C w_i$	Beta	95% CI Lower	95% CI Upper	*Z*-value	p-value
INTERCEPT	–	–2.169	–2.749	–1.589	–7.33	< 0.01
Offspring	0.70	–0.677	–1.262	–0.092	–2.27	0.02
EDGE_DIST	1.00	0.009	0.006	0.012	4.69	< 0.01
EDGE_CHNG	1.00	0.246	0.143	0.349	4.70	< 0.01
EDGE_DIST × EDGE_CHNG	1.00	–0.002	–0.003	–0.001	–3.20	< 0.01
OW_CHNG	0.91	5.000	1.090	8.910	2.51	0.01

[1] Offspring: females with cubs < 2 yr old; EDGE_DIST: distance to the pack ice edge; EDGE_CHNG: change in the daily distance of pack ice edge from land; OW_CHNG: change in the daily percentage of open water in the study area.

water gain between June–August ($r_s = 0.73$, n = 9, p = 0.02; Fig. 4), as well as year ($r_s = 0.68$, n = 9, p = 0.04).

Discussion

The sensitivity of migratory animals to climate change has become an early warning sign of the biotic effects that may occur (Cotton 2003, Newson et al. 2009, Anderson et al. 2013). However, the variation inherent to climate change is often overlooked or simplified in ecological analyses. Polar bears have an expansive, circumpolar range, and it is likely that their response to climate change will vary in space and time. Additionally, differentiation in migratory strategy as a function of age and sex class may alter the effect of climate change within polar bear populations. Here, we documented variation in the migratory response of polar bears to changing sea ice conditions between and within populations.

Polar bears are a solitary species, and compared with group-living species, migratory behaviour is more likely to exhibit strong individual variation to changing conditions. We found support for within-population variation in the migratory response of polar bears to changing sea ice conditions, suggesting differential migration. For lone polar bears, results suggest body size may influence the distance and duration of swims during migration. Body size has been suggested to influence migration patterns in other species (Williams 1999, Hein et al. 2012). Williams (1999) suggested that larger animals have a lower energetic transportation cost per unit body mass, and our results lend some support to this relationship. Lone adult females swam longer in both median distance and duration than smaller subadult females. However, subadults of both sexes swam as frequently as lone adult females, and a subadult female recorded the longest swim in our study (Fig. 5a). Body size and condition metrics were also not included in the top model for swim frequency. However, because body metrics were observed in spring, the data may not have accurately reflected the condition of polar bears when swims occurred in summer.

Table 4. Number and proportions of adult female polar bears engaging in at least one long-distance swim (> 50 km) in the Beaufort Sea, 2004–2012. Data combined from Pagano et al. (2012) and this study. Numbers in parentheses are from Pagano et al. (2012).

Year	Bears swimming	Total swims	Bears monitored	Proportion swimming
2004	2 (2)	3 (3)	8 (8)	0.25
2005	3 (3)	6 (6)	11 (11)	0.27
2006	4 (4)	5 (5)	15 (15)	0.27
2007	2 (0)	2 (0)	10 (1)	0.20
2008	7 (4)	14 (11)	13 (9)	0.54
2009	14 (8)	43 (25)	30 (13)	0.47
2010	6	9	22	0.27
2011	6	14	16	0.38
2012	9	19	13	0.69

In spring, subadults select for active ice that is near areas of open water (Stirling et al. 1993, Pilfold et al. 2014), which may increase the need for short-distance swims. Stirling (1974) observed subadults swimming more frequently than other age-classes in summer in the High Arctic. Our results support the suggestion that subadults are capable swimmers, and demonstrate their ability to complete long-distance swims, some of extreme length. Given that polar bear fur has little insulative capacity when wet (Scholander et al. 1950), these results may reflect an adaptation to protect against hypothermia via regional hetereothermy (Whiteman et al. 2015). However, the survival implications of long-distance swims for subadults remain unknown, and further study on swimming energetics is warranted.

Adult females with offspring were less likely to swim than other age-classes. Studies have suggested that prolonged exposure to frigid water may have negative consequences for offspring survival (Blix and Lentfer 1979, Durner et al. 2011, Pagano et al. 2012). Females with offspring-of-the-year avoid habitats with open water in spring (Stirling et al. 1993, Freitas et al. 2012, Pilfold et al. 2014) and may swim

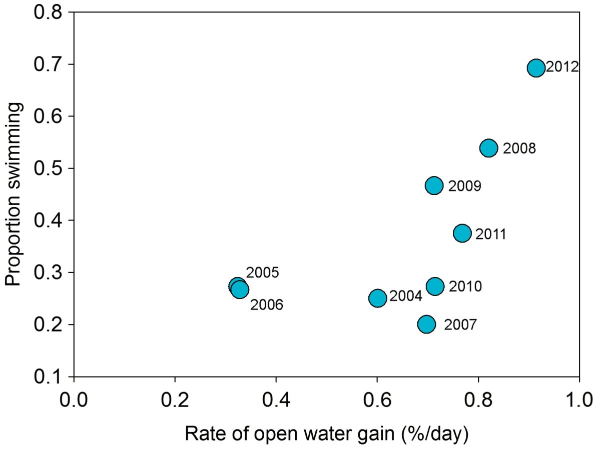

Figure 4. Relationship between the proportion of polar bears swimming and the daily rate of open water gain June–August in the Beaufort Sea, 2004–2012.

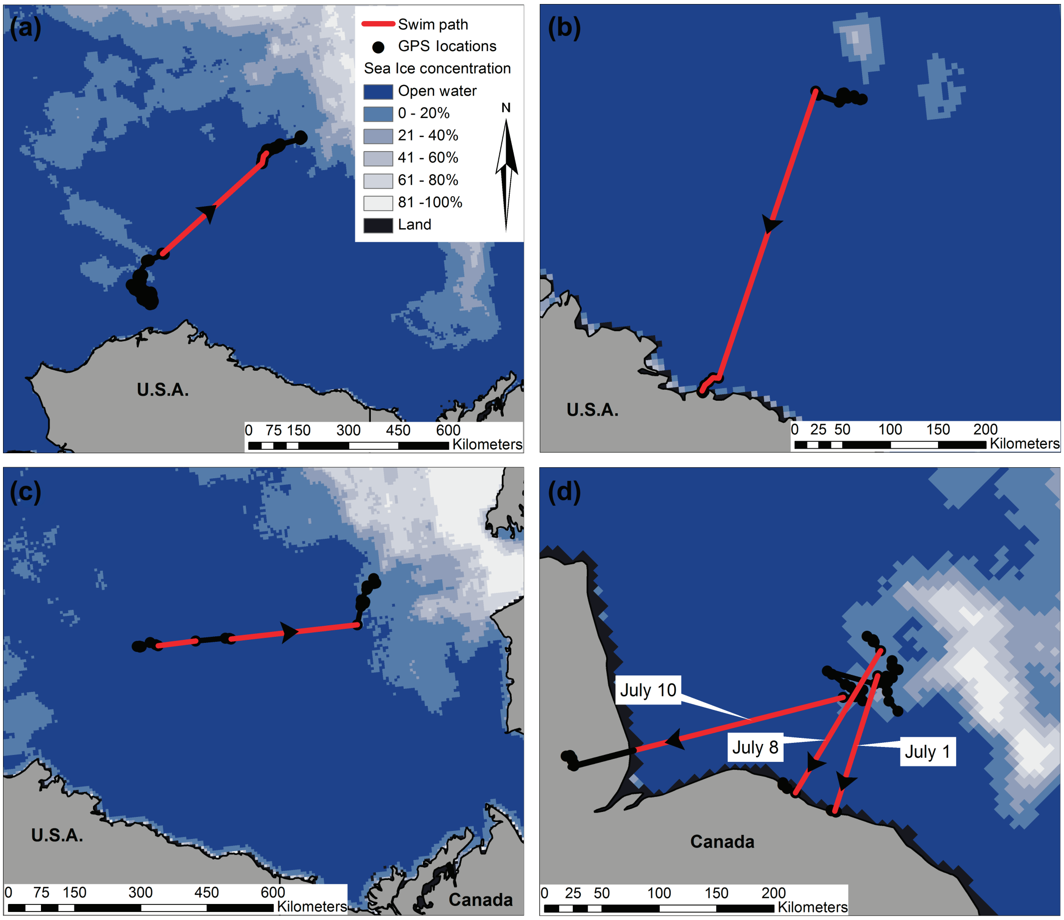

Figure 5. Examples of long-distance swims (> 50 km) by polar bears in the Beaufort Sea (BS) and Hudson Bay (HB), with mean sea ice concentration and location for the swim duration. (a) BS subadult female, 5–14 September, 2009, 404 km. (b) BS adult female, 7–14 September, 2011, 340 km. (c) BS adult female, 8–10 August, 2012, 86 km, 12–20 August, 2012, 288 km. (d) HB adult female A, 1–5 July, 2011, 124 km; HB adult female B, 8–14 July, 2011, 145 km; HB adult female C, 10–18 July, 2011, 185 km.

with cubs on their back to reduce offspring immersion (Aars and Plumb 2010). Reducing the frequency of swims is likely the main mechanism adult females use to protect their offspring from the high energetic cost associated with submergence in water.

We found support for variation in the migratory response to sea ice conditions between-populations. Polar bears in HB swam infrequently during migration compared to the BS, and primarily from pack ice to land in July. During breakup, the last sea ice in Hudson Bay generally melts along the southern coast (Saucier et al. 2004, Stirling et al. 2004). However, HB polar bears show fidelity to the western coast of Hudson Bay as summer refuge (Derocher and Stirling 1990, Stirling et al. 2004). Stirling et al. (1999) and Cherry et al. (2013) suggested polar bear migratory phenology was correlated to sea ice concentration thresholds of 50 and 30% respectively, and that a temporal lag of 3 to 4 weeks existed between thresholds and arrival of polar bears on land. Our results corroborate the temporal lag, as onshore dates occurred when nearly all the ice in Hudson Bay had melted, indicating that most polar bears are maximizing their time on the sea ice. In most years, sea ice conditions in Hudson Bay did not require long-distance swims to complete the migratory route. The minimum median distance that the consolidated pack ice was from land in the week previous to polar bears coming ashore was < 50 km, which is below the minimum distance of a swim used in our study. However, in years when the sea ice melts out towards the centre of the Bay, polar bears that remain on the ice may have no other option but a long-distance swim to shore (e.g. Fig. 5d).

During the open water period in the BS, some polar bears take refuge on land, while the majority follow the retreating pack ice (Amstrup et al. 2000, Schliebe et al. 2008). In the BS, swims were more frequent than HB, and most started and ended in the pack ice. Results suggest that swims in the BS are primarily related to polar bears following the pack ice edge as it retreats. During spring, polar bears of the BS preferentially hunt seals in active ice, selecting for areas near the shorefast ice boundary (Pilfold et al. 2014). As sea ice begins to breakup, polar bears may try to extend their time over the continental shelf where seal densities are highest (Stirling et al. 1982, Frost et al. 2004). During breakup, sea ice becomes more fractured and mobile, and polar bears likely have to swim between floes more frequently. Remaining on the sea ice throughout the summer months may yield positive energetic benefits for BS polar bears, either through increased encounters with seals resulting in kills during summer (Derocher et al. 2002), or by gaining earlier access to seals in autumn when the pack ice moves back over the continental shelf.

We found support for the hypothesis that swims in the BS were related to the dynamics of the pack ice in the Arctic Basin (Monnett and Gleason 2006, Pagano et al. 2012). The frequency of swims was positively related to the distance the pack ice edge was from land and the rate at which it retreated. The interaction between the two variables suggests that the direction of movement (retreat vs expansion) of the pack ice edge influences the frequency of swims as much as its distance from land. Most swims in the BS were recorded before the annual minimum sea ice extent had been reached, suggesting that swims are part of the migratory strategy to stay with the pack ice edge as it retreats. When the pack ice expands again, polar bears likely stay on the sea ice and track its movement toward the continental shelf.

We found support for the hypothesis that increased expanses of open water influence the frequency of swims in the BS, and that swim frequency is increasing temporally in association with sea ice change (Derocher et al. 2004, Monnett and Gleason 2006, Pagano et al. 2012, Stirling and Derocher 2012). Results suggest that as the rate of open water formation increases, adult female polar bears are more likely to swim long distances during migration. The rate at which open water increased across the summer months in our study area was correlated with September minimum sea ice extent for the Arctic, suggesting similar underlying climatic drivers. The largest proportion of individuals participating in at least one swim was in 2012, which was associated with the highest rate of open water gain during the summer, and a record low September sea ice extent. The record low in 2012 was aided by a strong storm in early August, which sheered off a large portion of the ice pack that melted in the Bering Strait (Parkinson and Comiso 2013, Zhang et al. 2013). Any polar bears on the portion of pack ice heading for the Bering Strait would have had to cross a large body of open water to return to the main pack ice (e.g. Fig. 5c).

We document variation in the migratory response to changing sea ice conditions between two polar bear populations, suggesting a region-specific response to climate change. Timing of sea ice breakup is changing in both the BS and HB (Parkinson 2014), and will likely lead to the earlier onset of migration to summer refugia (Stirling et al. 1999, Gleason and Rode 2009, Cherry et al. 2013). However, the spatial dynamics of sea ice breakup differs between regions, leading to variation in movement behaviour. Polar bears in HB swam less frequently than bears from the BS, which was likely a reflection of the sea ice melting out in close proximity to land, as it has done historically. In the BS, the distance between land and sea ice and rate of open water formation necessitated swims. These results emphasize how spatial habitat heterogeneity can vary the impact of climate change on species' response. Variation in movement dynamics during migration, and therefore energy expenditure, may alter the rate at which climate change affects polar bear populations. Process-based and population specific energetic modelling may provide greater insight into future climate change scenarios, and reveal overall plasticity to change.

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Supplementary material (Appendix ECOG-02109 at <www.ecography.org/appendix/ecog-02109>). Appendix 1.