Vol. 641: 227–240, 2020
https://doi.org/10.3354/meps13293

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 7

Patterns of sea ice drift and polar bear (*Ursus maritimus*) movement in Hudson Bay

Natasha J. Klappstein[1,*], Ron R. Togunov[1,2], Jody R. Reimer[1,3], Nicholas J. Lunn[4], Andrew E. Derocher[1]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada
[2]Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[3]Department of Mathematics, University of Utah, Salt Lake City, UT 84112, USA
[4]Wildlife Research Division, Science & Technology Branch, Environment and Climate Change Canada, CW-422 Biological Sciences Building, University of Alberta, Edmonton, AB T6G 2E9, Canada

ABSTRACT: Sea ice habitats are highly dynamic, and ice drift may affect the energy expenditure of travelling animals. Several studies in the high Arctic have reported increased ice drift speeds, and consequently, polar bears *Ursus maritimus* in these areas expended more energy on counter-ice movement for station-keeping. However, little is known about the spatiotemporal dynamics of ice drift in Hudson Bay (HB) and its implications for the declining Western Hudson Bay (WH) polar bear subpopulation. Using sea ice drift data from 1987–2015 and polar bear satellite telemetry location data from 2004–2015, we examined trends in drift speeds in HB, polar bear movement relative to drift, and assessed annual and individual variation. In contrast to other areas of the Arctic, we did not find an increase in ice drift speed over the period examined. However, variability in ice drift speed increased over time, which suggests reduced habitat predictability. Polar bear movement direction was not strongly counter to ice drift in any month, and ice drift speed and direction had little effect on bear movement rates and, thus, energy expenditure. On an annual scale, we found individuals varied in their exposure and response to ice drift, which may contribute to variability in body condition. However, the lack of a long-term increase in ice drift speed suggests this is unlikely to be the main factor affecting the body condition decline observed in the WH subpopulation. Our results contrast findings in other subpopulations and demonstrate the need for subpopulation-specific research and risk evaluation.

KEY WORDS: Polar bear · Sea ice drift · Remote sensing · Animal movement · Environmental variability · Interindividual variability · Hudson Bay

1. INTRODUCTION

Movement is a fundamental aspect of animal life, involved in migration, foraging, predator avoidance, dispersal, and mating (Greenwood 1980, Alerstam et al. 2003, Fahrig 2007, Holyoak et al. 2008). Optimal movement patterns should balance such processes with the energetic costs of locomotion, which vary among taxa, environments, and modes of transport (Tucker 1970, Dickinson et al. 2000, Nathan et al. 2008). Habitat heterogeneity in both time and space complicates movement decisions because physical features, such as topography, substrate or medium, and climate may affect the energetic costs of traversing the environment (Crête & Larivière 2003, Wilson et al. 2012, Shepard et al. 2013). Additionally, navigation may be confounded in variable environments if species evolved space use patterns based on predictable conditions (Amstrup et al. 2000, Fryxell et al. 2005, Mueller & Fagan 2008). It has been suggested

---

*Corresponding author: nklappst@ualberta.ca

that animal memory and learning may decrease energetic costs associated with exploratory movements, which may be necessary in highly variable environments where memory is confounded by a changing landscape (Sih & Del Giudice 2012, Fagan et al. 2013). Ultimately, environmental variability may be linked to lower survival and decreased times to extinction (Lande 1998, Inchausti & Halley 2003, Lande et al. 2003), but the exact mechanisms and severity are likely specific to the study system and species.

Animals that live in moving habitats face challenges associated with traversing their environment, as movement with or against the medium may be necessary, and therefore the velocity of the medium directly affects energy expenditure (Wikelski et al. 2006, Chapman et al. 2011, Shepard et al. 2013). However, there are also potential benefits in moving habitats: individuals may move with the habitat if it is directed towards preferred areas or they may use oppositional movement to cover more area and increase foraging opportunities (Auger-Méthé et al. 2016). Despite these benefits, counter-flow movement is often necessary for station-keeping (i.e. movement to remain within a home range or preferred habitat), migration, or other directional movement, and this may have energetic consequences (Mauritzen et al. 2003, Wikelski et al. 2006, Chapman et al. 2010, Auger-Méthé et al. 2016). There are 3 main moving environmental mediums: wind for volant animals (Wikelski et al. 2006, Chapman et al. 2010, Shepard et al. 2013), water currents for many aquatic species (Trump & Leggett 1980, Forward et al. 2003), and ice drift for pagophilic ('ice-loving') species (Ribic et al. 1991, Mauritzen et al. 2003, Nicol 2006). Therefore, animals must contend with the fluid's flow while flying or swimming (Chapman et al. 2011, Wilson et al. 2012, McLaren et al. 2014), while drifting sea ice acts as a moving platform that animals may walk against (Mauritzen et al. 2003). For all moving habitats, both the speed and direction of the environmental medium may affect energy expenditure.

Given the importance of sea ice drift speeds for pagophilic species' movement costs, understanding long-term ice dynamics can help in the assessment of the effects of environmental change. Ocean currents and winds cause sea ice drift, and drift speeds in much of the Arctic Basin are increasing due to climate change (Thorndike & Colony 1982, Rampal et al. 2009, Spreen et al. 2011, Kwok et al. 2013). Although increased ice speeds are linked to changes in wind forcing and major climate indices (e.g. Arctic Oscillation), ice characteristics, such as ice cover, compactness, and thickness have more pronounced effects on ice drift speeds (Hakkinen et al. 2008, Rampal et al. 2009, Spreen et al. 2011, Kwok et al. 2013). As ice thins, it is more likely to fracture into smaller, more labile ice floes, and this is exacerbated by ice melt, ice export, and decreased albedo associated with more open water (Rampal et al. 2009, Spreen et al. 2011). Changes in ice drift may present challenges for pagophilic species if counter-ice movement results in extra energy expenditure.

Polar bears *Ursus maritimus* evolved a life history dependent on sea ice (DeMaster & Stirling 1981). Although polar bears are a *K*-selected species and may be resilient to short-term perturbations (Derocher et al. 2004), they have specialized prey selection (Thiemann et al. 2011), migration (Mauritzen et al. 2001, Cherry et al. 2013), and denning (Richardson et al. 2005, Escajeda et al. 2018) behaviours, which make them less likely to withstand long-lasting environmental changes, particularly if these changes occur rapidly (Laidre et al. 2008, Derocher et al. 2013). Polar bears have high energetic costs due to high movement rates (Parks et al. 2006, Cherry et al. 2013), large home ranges (Mauritzen et al. 2001, McCall et al. 2015, Auger-Méthé et al. 2016), and high metabolic rates (Hurst et al. 1982, Pagano et al. 2018). In several High Arctic subpopulations, polar bears move against sea ice drift, which increases their realized home range size and may increase energetic loads due to increases in sea ice speeds (Mauritzen et al. 2003, Auger-Méthé et al. 2016, Durner et al. 2017). Durner et al. (2017) estimated that recent increases in counter-ice movement by polar bears in the Beaufort Sea and Chukchi Sea led to a 1.8–3.6% increase in energy expenditure between 1987–1998 and 1999–2013. To meet this demand, polar bears would need to consume an additional 1–3 seals yr^{-1}, a 2.0–6.1% increase in their foraging rate (Durner et al. 2017). Therefore, the amount of energy a bear uses for movement may not be reflected in the absolute displacement from telemetry data, and the energetic balance of these bears may be affected by changes in the lability of sea ice. However, ice drift may not always result in increased energetic demands, and its effects are likely specific to the system and the behavioural response to ice movement.

Hudson Bay (HB) is a seasonal system with no multi-year ice, and undergoes a complete cycle of ice formation and melt (Danielson 1971, Saucier et al. 2004). The Western Hudson Bay (WH) polar bear subpopulation migrates onto the sea ice in autumn–winter and returns to shore for the summer (Cherry et al. 2013). WH polar bears use the seasonal sea ice to acquire enough energy reserves during the on-ice period to last them through the on-land period, when they rely predominantly on their fat stores for energy (Ramsay & Hobson 1991, Hobson & Stirling 1997). Increased ice-free periods combined with shorter foraging times (Parkinson 2014, Stern & Laidre 2016) have altered the energy balance of the bears and lowered both survival and reproductive output (Stirling et al. 1999, Regehr et al. 2007). The WH polar bear subpopulation has declined by approximately 30% since the mid-1990s, which is linked to sea ice loss (Regehr et al. 2007, Lunn et al. 2016). Trends in ice speed and effects of ice drift on polar bear movement have been studied in higher latitude subpopulations (Mauritzen et al. 2003, Auger-Méthé et al. 2016, Durner et al. 2017), but have yet to be analyzed for the WH subpopulation where sea ice dynamics are different. Given that HB is a seasonal, largely enclosed system, it is unclear if trends in ice drift mirror other High Arctic areas where trends in drift are primarily driven by loss of multi-year ice (Spreen et al. 2011, Kwok 2018). While there is no perennial ice in HB, changes in ice concentration and fragmentation (Sahanatien & Derocher 2012), wind patterns (Steiner et al. 2015), and the timing of freeze-up and break-up (Parkinson 2014, Kowal et al. 2017) may cause long-term or seasonal changes in ice drift speeds. HB is a shallow, enclosed system, and station-keeping may be less prominent. Therefore, it is unknown whether WH polar bears interact with, and respond to, changes in the abiotic structure of their habitat in the same manner as High Arctic subpopulations.

The first objective of our study was to examine spatiotemporal patterns of ice drift across HB. Using ice drift data from 1987–2015, we examined ice drift speed at 2 temporal scales (across years and within years) and spatially as a function of the distance to coast. As habitat predictability may affect how polar bears make movement decisions, we also examined long-term temporal trends in ice speed variability. The energetic consequences of ice drift are dependent on the behavioural response to drift conditions; therefore, our second objective was to examine the effects of ice drift on polar bear movement. We quantified ice drift at locations of satellite-collared polar bears (2004–2015) and compared the directionality and speed of polar bear movement and ice drift vectors. We also examined how ice speed and direction affected polar bear movement rates (used as a proxy for energy expenditure). We explored monthly and annual temporal scales, as bears may not actively compensate for drift immediately at the scale of GPS relocations, and effects may be cumulative throughout the season. We also examined inter-individual variability in the exposure and response to ice drift, which has yet to be examined in any polar bear subpopulation.

2. MATERIALS AND METHODS

2.1. Study area and data acquisition

HB, Canada (Fig. 1), is a large, shallow inland sea with a mean depth of 150 m that is ice-covered in winter and ice-free in summer (Danielson 1971). Ice drift circulation is predominantly counter-clockwise, but also responds to wind-forcing, particularly when the ice is thin (Saucier et al. 2004). Freeze-up occurs in November–December, reaching maximum ice concentration in January–February, while break-up typically begins in May, and the Bay is ice-free by August (Danielson 1971, Saucier et al. 2004).

We acquired daily gridded ice drift data (Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors) from 1987–2015 from the National Snow and Ice Data Center (NSIDC), which was processed into netCDF format by the Integrated Climate Data Centre (Tschudi et al. 2016) and analyzed in R v.3.5.1

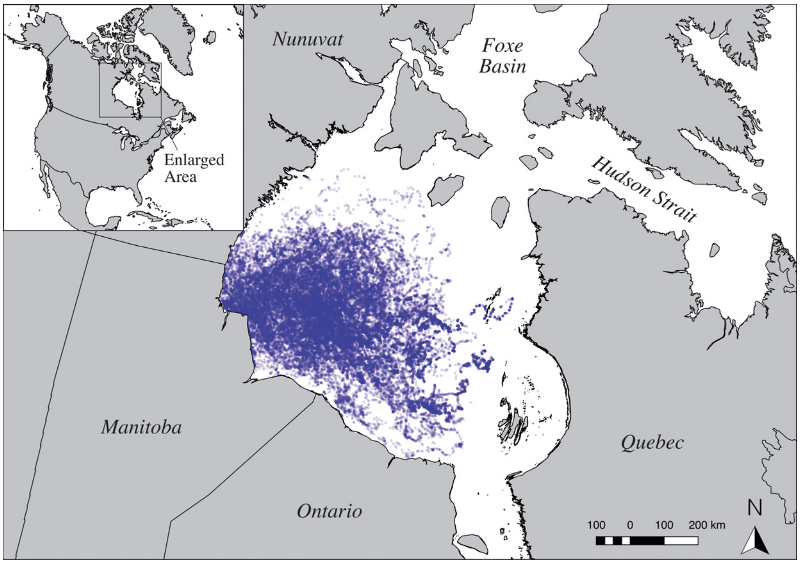

Fig. 1. Adult female polar bear satellite telemetry locations from 2004–2015 in Hudson Bay, Canada (locations on land are excluded)

(R Core Team 2018; used for all subsequent analyses). The data comes as a 25 × 25 km Equal-Area Scalable Earth (EASE) grid of horizontal and vertical movement, and speed fields of ice drift. We projected the gridded ice drift into UTM (NAD83 Teranet Ontario Lambert, EPSG: 5321) for analysis. We defined a 'year' as the 9 consecutive months from November–July (e.g. '1987' denotes November 1987 to July 1988). Although ice concentration can be low in November and July, polar bears in WH leave shore at only 10% ice concentration and return when it reaches approximately 30% in break-up (Cherry et al. 2013). Therefore, these 9 mo represent the period in which bears are most likely to be on the sea ice. We also assigned each gridded ice point a unique identification number (gridID) and removed estimates over open water (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m641p227_supp.pdf).

Adult female polar bears (≥5 yr old) accompanied by offspring were captured in WH in August–September 2004–2015 using standard protocols (Stirling et al. 1989). They were assigned unique identification numbers (bearID) and fitted with satellite-linked (CLS Argos) global positioning system (GPS) collars with a timed-release mechanism (Telonics). Collars provided locations every 4 h for 2 yr, after which the collars dropped or were removed. Before analysis, we excluded telemetry locations on land, those without a corresponding daily ice drift estimate, and those locations from collars that were determined to be drifting with sea ice (i.e. from dropped collars or mortality). We rarefied telemetry GPS locations to a 24 h resolution to match the ice drift data. Starting with the first GPS fix, we first removed any fixes <24 h apart from that fix. Next, we calculated the speed and bearing between consecutive fixes and removed any fixes >24 h from prior fix. This procedure resulted in estimates of drift and bearing at 24 h intervals, with no overlap, and which were not standardized to any particular time of day. Capture and handling protocols were reviewed and approved by the University of Alberta Animal Care and Use Committee for Biosciences and the Environment and Climate Change Canada Prairie and Northern Region Animal Care Committee and were consistent with the Canadian Council on Animal Care.

2.2. Spatial and temporal trends in ice drift

Due to spatial correlation of the ice drift data, we increased the independence of the gridded estimates by removing highly autocorrelated points before statistical analyses. To determine the scale of autocorrelation, we calculated Moran's *I* coefficient using the R package 'pgirmess' (Giraudoux 2018). Moran's test evaluates spatial autocorrelation by examining spatial clustering at different distance classes ($I = 1$ represents perfect clustering/correlation; $I = 0$ represents randomness; and $I = -1$ represents perfect dispersion) (Moran 1950). We calculated Moran's *I* on a subset of 100 randomly sampled days of ice drift in HB. We averaged the *I* coefficients from the 100 d to find the mean minimum distance between grid points at which $I < 0.6$, above which we considered a strong correlation. We determined the distance between grid points should be 150 km to reduce spatial autocorrelation and we rarefied to this resolution. This rarefication was a random process by which we randomly selected a grid point and removed all points within 150 km. We repeated this process on the remaining grid points until there were no grid points left to sample. As this is a random process, the first iteration may be overly conservative and remove more points than necessary. To maximize the amount of grid points used in our analyses, we used 10 000 iterations of the rarefication process and selected the rarefied data set with the most remaining grid points (Fig. S2). This process is explained in more detail in the section 'Gridded ice drift rarefication' in the Supplement. We used this rarefied data set to conduct all analyses of spatial and temporal trends in ice drift across HB.

We assessed spatial and temporal trends in ice drift speeds using generalized linear mixed effect models (GLMMs). Drift speeds can only be positive values and consequently are right-skewed. Using GLMMs enabled us to examine a non-normally distributed response variable with corresponding non-normal error structures. Our telemetry and satellite data are inherently autocorrelated due to repeat sampling (by collar or grid cell). Incorporating gridID in the GLMMs controls for the effect of repeat sampling and decreases the probability of a Type I error. For the modelling procedure, we first visually inspected the response data to identify possible error distributions, then used Akaike's information criterion to identify the most appropriate distribution (determined to be a gamma distribution with a log link function) for modelling ice drift speeds (Table S1). Next, we fitted GLMMs with the R package 'lme4' (Bates et al. 2015) to assess long-term temporal and spatial trends in ice drift speeds from 1987–2015. We fitted separate models for each month because assessing an overall trend (pooling months) has the risk of masking any trends within months, and increasing ice drift has potentially different consequences between months (i.e. it may be more important during periods of highly directional polar bear movement). We included year and distance to coast as fixed effects, with gridID as a random effect, and set significance to a Bonferroni-corrected $\alpha = 0.006$ to account for multiple tests (one test for each of 9 mo) (Holm 1979). We also assessed a seasonal trend across months with a single GLMM with month as a fixed effect and gridID and year as random effects ($\alpha = 0.05$). For all models, we calculated the marginal pseudo-R^2 of the fixed effects with the R package 'piecewiseSEM' (Lefcheck 2016), and calculated the intra-class correlation as a measure of repeatability (R) of random effects (Nakagawa et al. 2017). R is a measure of the variation explained by repeatable differences between the random effect levels with multiple observations. Lastly, we calculated the coefficient of variation (CV) for each month and each year. We fitted a linear regression model to test for a trend in CV over time (years) with $\alpha = 0.05$. For all preceding analyses, we analyzed ice drift over the entire HB, which assumes that this was representative of the habitat used by WH bears. To test this assumption, we conducted all GLMMs and CV analyses on ice drift within the 100% minimum convex polygon (MCP) of the polar bear telemetry data (R package 'adehabitatHR'; Calenge 2006) to compare to full HB results.

2.3. Polar bear movement data

We estimated the amount of drift polar bears were exposed to by calculating an ice drift velocity for each polar bear location. We used Shepherd's method of inverse distance weighting with a weighting of 3 ('idw' function of the R package 'gstat') to spatially interpolate ice drift estimates to GPS location coordinates (Pebesma 2004, Auger-Méthé et al. 2016), which we then temporally interpolated to match the time of the GPS location (Dodge et al. 2013). Ice drift estimates represent the mean displacement between consecutive days: for locations before 12:00 h (UTC) we used ice drift estimates from the same day and the previous day, and for locations after 12:00 h we used same day and next day ice drift estimates. We interpolated ice drift from the entire NSIDC data set (i.e. not the rarefied data set described in the previous section). Due to ice drift, the distance between GPS locations is a combination of both ice and bear movement, and is therefore an indirect measure of how much bears actually moved (i.e. bear movements counter to ice drift are underestimated and bear movements with ice drift are overestimated by GPS displacement). Therefore, we differentiated ice drift-corrected bear movements (hereafter 'bear movement') and the observed GPS displacement. We calculated bear movements by subtracting northings and eastings of ice drift estimates from those of GPS locations (Mauritzen et al. 2003, Auger-Méthé et al. 2016, Durner et al. 2017). We excluded bear movement steps within the top 2.5% of the data (>50 km d^{-1}) as we considered these to be unrealistic. Directionality of polar bear movement was calculated as the clockwise angle relative to north, following $\theta_{b,t} = \text{atan2}(\Delta x, \Delta y)$ where atan2 refers to a 2 argument arctangent, Δx and Δy are the changes in the longitude (x) and latitude (y) between GPS location $t+1$ and t, where t is the GPS fix for which bearing is being calculated. Directionality of ice drift was similarly calculated following $\theta_{i,t} = \text{atan2}(u_t, v_t)$ where u_t and v_t are the horizontal and vertical components of sea ice drift at GPS fix t, respectively. Mean monthly directions of bear movement and sea ice drift were calculated as the monthly mean of $\theta_{b,t}$ and $\theta_{i,t}$, respectively. We then calculated angular concentration, κ, as a metric of the tortuosity of mean movement direction following $\kappa = \sqrt{\text{mean}(\sin\theta_t)^2 + \text{mean}(\cos\theta_t)^2}$, where θ_t is either $\theta_{b,t}$ for bear movement or $\theta_{i,t}$ for ice drift. Values of κ range from 0–1, with higher numbers indicating higher directionality/concentration and lower dispersion (Bovet & Benhamou 1988, Estevez & Christman 2006). We tested the significance of angle directions using a Rayleigh's test (R package 'CircStats'; Lund & Agostinelli 2001), with a Bonferroni-corrected $\alpha = 0.006$.

2.4. Energetic consequences of sea ice drift

To assess how ice drift velocity affects polar bear energy expenditure in each month, we used a series of GLMMs. As a proxy for energy expenditure, we used bear speed (S, km d^{-1}) as the response variable. The effects of ice drift on energetic expenditure depend on both the speed and direction of drift relative to bear motion. We therefore modelled S as a function of drift speed (km d^{-1}), the component of 'bear orientation' along the same axis of drift (hereafter, angular co-directionality, C_θ), as well as an interaction term between them. Angular co-directionality was calculated following:

$$C_{\theta,t} = \cos[\text{atan2}\,(\Delta x \times v_t - \Delta y \times u_t, \Delta x \times u_t + \Delta y \times v_t)] \quad (1)$$

Values of angular co-directionality range from −1 to 1; −1 indicating counter-ice movement (i.e. 180° relative to the direction of ice drift) and 1 indicating movement in the same direction as ice drift (i.e. 0°). Finally, we included bearID as a random effect to account for inter-individual variation. We used a gamma error distribution following pre-model protocols described in Section 2.2 and Table S2. Significance threshold was set to a Bonferroni-corrected $\alpha = 0.006$ for 9 tests.

2.5. Inter-individual and inter-annual variation

The above analysis explored an immediate behavioural response (i.e. at each step), but effects of ice drift may be cumulative throughout the season and thus not reflected in short-term movements. To address this point, we summed the ice drift exposure and total movement with or counter to ice drift for bears with ≥5 locations mo^{-1} from December–May (November, June, and July were excluded due to low sample sizes). We limited our analysis to bears with ≥5 locations mo^{-1} because we needed representative samples to reduce temporal bias in the yearly sum. For each bear, we calculated the total seasonal ice drift speed across the 6 mo and the total annual component of 'bear velocity' along the same axis of drift (hereafter, total vector co-directionality, C_v). We calculated vector co-directionality following:

$$C_v = \sum_{m=1}^{6} \frac{\sum_{j=1}^{n_m} C_{\theta,\,j} \times S_j}{n_m} \times d_m \qquad (2)$$

where j is a bear step, n_m is the total number of steps in month m, S_j is the bear speed for step j, and d_m is the number of days in month m. Values of C_v increase as mean bear angle to ice drift direction approach 0° and as mean bear speeds increase. Conversely, negative C_v values increase in magnitude as mean bear speeds increase and mean relative angle to drift approaches 180°.

Table 1. Mean ice drift (km d^{-1}) and coefficients of variation (CV) by month from 1987–2015 and results from generalized linear mixed effect models with ice drift speed as the response variable. R^2: marginal pseudo-R^2 of the fixed effects; R: repeatability of the random effect (gridID). ***p < 0.001

Month	Ice drift speed Mean ± SD (km d^{-1})	CV %	Coefficient Intercept	Year	Distance to coast (km)	R^2	R
November	5.0 ± 2.5	51.3	1.60	−0.02	0.03	0.004	0.11
December	4.6 ± 2.9	62.3	1.51	−0.005	0.11***	0.03	0.14
January	4.3 ± 3.1	71.2	1.44	−0.03***	0.16***	0.04	0.21
February	3.9 ± 2.8	71.2	1.35	−0.06***	0.15***	0.04	0.22
March	3.9 ± 2.7	68.7	1.35	−0.08***	0.14***	0.05	0.18
April	4.0 ± 2.6	65.8	1.36	−0.02***	0.12***	0.03	0.16
May	3.9 ± 2.2	57.0	1.36	−0.007	0.08***	0.02	0.11
June	3.5 ± 1.9	52.5	1.26	−0.009	0.07***	0.01	0.12
July	3.3 ± 1.8	56.5	1.17	−0.01	0.08***	0.02	0.12

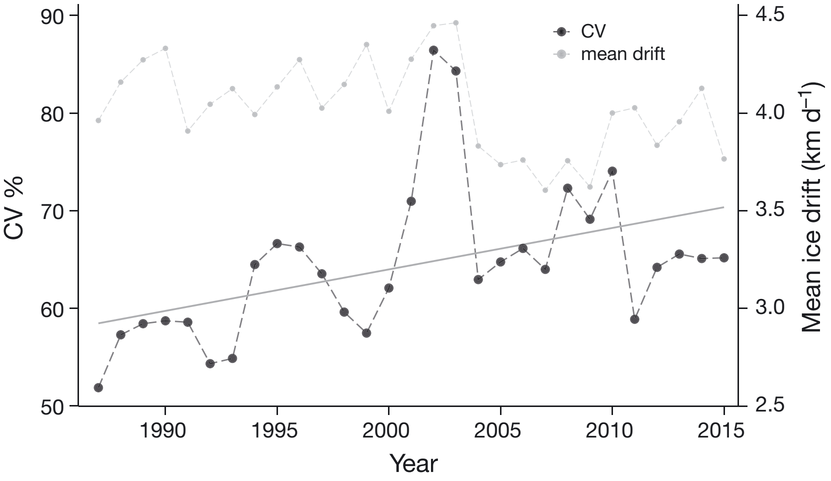

Fig. 2. Annual coefficients of variation (CV %) from 1987–2015 in Hudson Bay. Mean annual ice drift is included for reference (km d^{-1}). Ice drift estimates from Polar Pathfinder 25 km EASE-Grid Sea Ice Motion Vectors (Tschudi et al 2016). Line shows the significant trend of increasing CV across years (R^2 = 0.18, df = 27, p = 0.01)

3. RESULTS

3.1. Spatiotemporal patterns in sea ice drift

Monthly mean (±SD) ice drift speeds ranged from 3.3 ± 1.8 km d^{-1} (July) to 5.0 ± 2.5 km d^{-1} (November), and CVs ranged from 51.3% (November) to 71.2% (January and February; Table 1). The GLMMs for January–April revealed a significant decrease in ice drift speed in HB from 1987–2015, but the remaining months showed no significant trend (Table 1). Annual CV of ice drift ranged from 51.7% (in 1987) to 86.4% (in 2002), and significantly increased from 1987–2015 (R^2 = 0.18, df = 27, p = 0.01; Fig. 2). The intra-annual GLMM revealed a significant negative trend in ice drift speed from November to July (R^2 = 0.02, p < 0.001). Spatially, ice drift was significantly faster farther from the coast in all months except November, in which there was no significant trend (Table 1, Fig. 3). All results for the entire HB (Table 1,

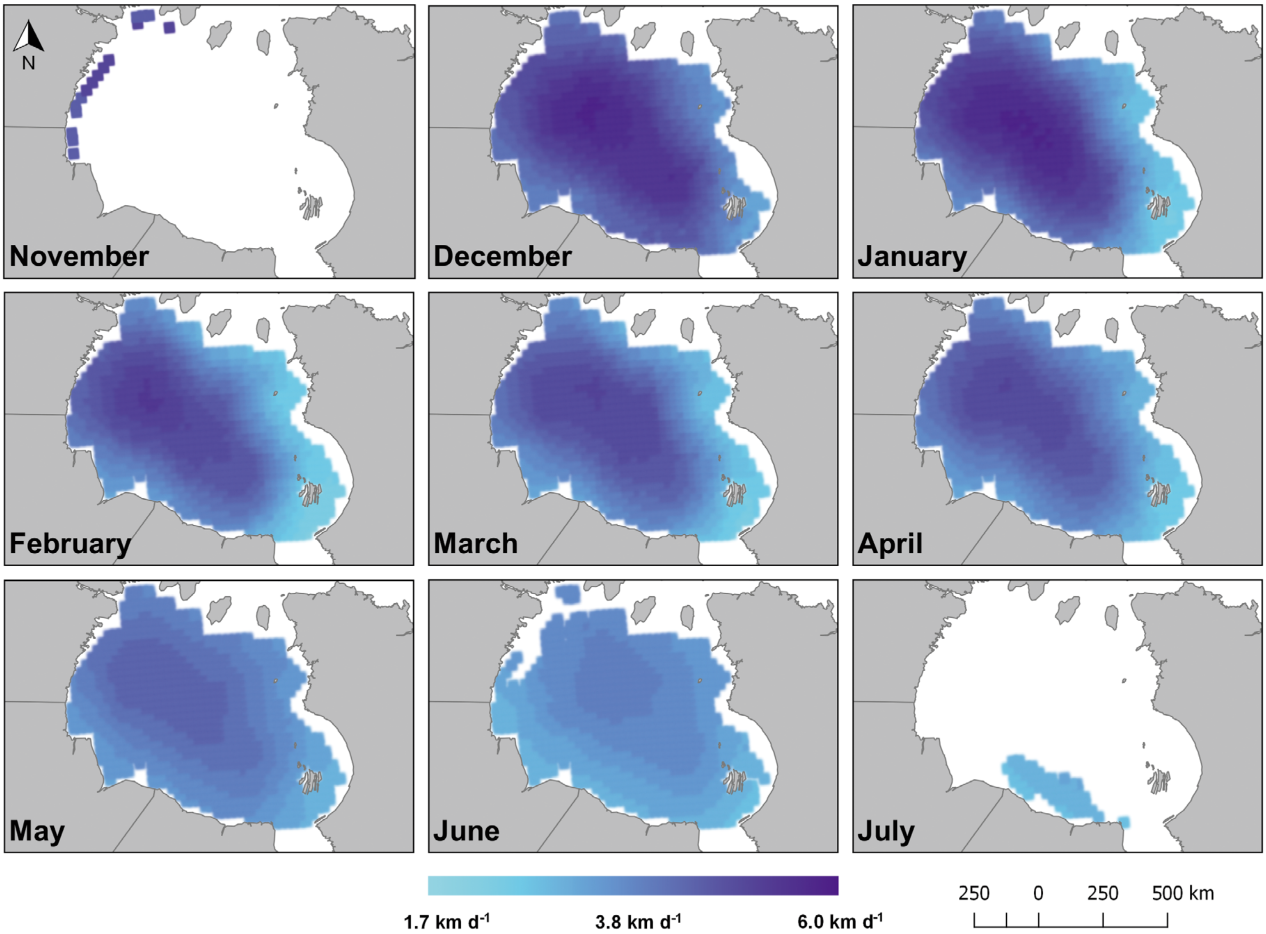

Fig. 3. Mean sea ice drift derived from Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors (Tschudi et al 2016) in Hudson Bay, Canada, 1987–2015. Mean estimates only included coordinates where ice drift estimates were available (speed > 0) for more than 50 % of the days examined

Fig. 2) were similar to those of the 100 % MCP, except for no significant trend over time in January and April (Table S3, Fig. S3).

3.2. Directionality and speed of bear and ice movements

Collars were deployed on 101 adult females from 2004–2015. In total, 9 bears were collared twice, in 2 separate years, while the remaining bears (n = 92) were collared once. After rarefying the data to a 24 h resolution, we analyzed 10 009 daily GPS locations. Bears were exposed to monthly mean ice drift ranging from 2.8 ± 1.7 km d^{-1} in July to 4.6 ± 2.9 km d^{-1} in December (Table 2), with an overall mean of 3.9 ± 2.4 km d^{-1}. Mean GPS displacement was 17.4 ± 11.3 km d^{-1} and ranged from 13.3 ± 9.2 km d^{-1} (July) to 23.1 ± 12.5 km d^{-1} (December). Mean polar bear movement was 16.5 ± 10.8 km d^{-1} and ranged from 12.6 ± 8.8 km d^{-1} in July to 21.9 ± 12.3 km d^{-1} in November (Table 2). Mean GPS displacement was higher than mean bear movement rates in all months,

Table 2. Mean (km d^{-1}) ice drift at polar bear locations, GPS displacement, and ice-corrected polar bear movements in November–July. Ice drift from Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors and bear locations from GPS-collared adult female polar bears (2004–2015)

Month	Mean speed ± 1 SD (km d^{-1})			n
	Ice	GPS	Bear	
November	4.2 ± 1.8	22.4 ± 113.5	21.9 ± 12.3	521
December	4.6 ± 3.0	23.1 ± 12.5	21.3 ± 11.8	1527
January	4.3 ± 2.6	17.9 ± 11.4	16.6 ± 11.0	1452
February	3.8 ± 2.6	14.0 ± 10.3	13.2 ± 9.9	1324
March	3.5 ± 2.2	16.2 ± 10.6	15.4 ± 10.4	1497
April	3.7 ± 2.3	15.9 ± 9.8	15.1 ± 9.6	1441
May	3.5 ± 2.0	16.4 ± 9.6	16.0 ± 9.5	1212
June	3.0 ± 1.7	16.1 ± 10.1	15.4 ± 9.7	906
July	2.8 ± 1.7	13.3 ± 9.2	12.6 ± 8.8	149

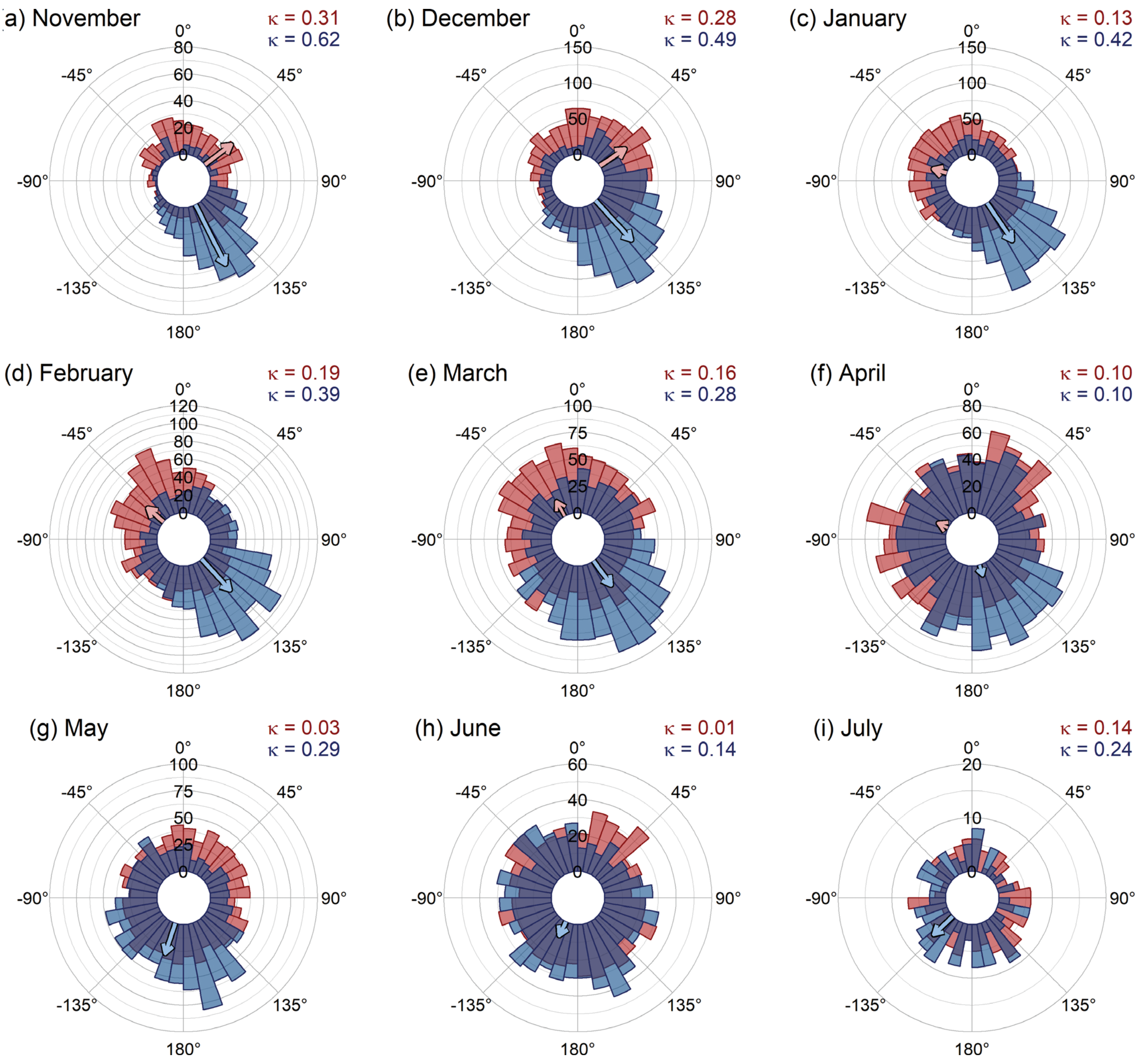

Fig. 4. Frequency of monthly adult female polar bear (ice-corrected) movement directions (0° = north) calculated from telemetry locations and ice drift data (red) and ice drift directions from Polar Pathfinder 25 km EASE-Grid Sea Ice Motion Vectors (blue; Tschudi et al. 2016) from November to July 2004–2015. Arrow direction corresponds to mean angle of bear movement or ice drift; arrow length represents angular concentration (κ). Polar bear directions are not shown for May–July, as they were not significant (Rayleigh's tests, p > 0.006)

ranging from 2.3% greater in November to 8.3% greater in December. Overall, mean GPS displacement was 5.5% greater than mean bear movement. Polar bear directionality was greatest in November (northeast, θ = 53° relative to north, κ = 0.31) and December (northeast, θ = 56°, κ = 0.28), during which ice drift was towards the southeast (θ = 153°, κ = 0.62 and θ = 138°, κ = 0.49; Fig. 4). There was lower angular concentration of polar bear movement in the remaining months: κ values were ≤0.19 and were not significant in May–June (Rayleigh's test: p > 0.006). Ice drift had higher directionality than polar bear movement in every month and was lowest in April (θ = 164°, κ = 0.10). The GLMMs that assessed polar bear movement speed as a function of ice drift speed and directionality showed a significant trend of increasing bear speed with increasing ice drift speeds in all months, except December, March, and July (Table 3). There was a significant positive relationship between the angular co-directionality of bear

Table 3. Monthly generalized mixed effect models with ice speed, angular co-directionality (C_θ) of polar bear and ice angles, and an interaction term as fixed effects and bear movement speed as the response. R^2: marginal pseudo-R^2 of the fixed effects; R: repeatability of the random effect (bearID). $^{***}p < 0.001$; ** $p < 0.005$

Month	Coefficient				R^2	R
	Intercept	Ice speed	C_θ	Ice speed × C_θ		
November	−1.44	0.12***	0.14***	−0.02	0.08	0.23
December	−1.40	0.03	0.07***	−0.01	0.02	0.10
January	−1.69	0.06***	0.02	0.02	0.01	0.16
February	−1.96	0.03***	0.02	−0.04	0.004	0.24
March	−1.76	0.03	0.0001	0.02	0.003	0.20
April	−1.76	0.05**	0.004	0.04	0.008	0.16
May	−1.70	0.07***	0.002	0.03	0.01	0.14
June	−1.76	0.11***	0.06**	0.07**	0.05	0.16
July	−1.96	0.13	0.12	0.06	0.08	0.29

movement relative to ice drift (C_θ) and bear movement speed in November, December, and June. The interaction between ice speed and C_θ was only significant in June. All pseudo-R^2 estimates were low (≤0.08) and R estimates were low to moderate (≤0.24).

3.3. Inter-annual and inter-individual variability

After removing individuals with insufficient data for the entire year, we assessed 5302 locations for 39 individuals. Sample size (N; total individuals), ranged from 0 in 2013 and 2014 to 9 in 2006. In 2011 and 2015, we had a sample size of only one bear in each year. Total ice drift over the entire year per individual (excluding 2013 and 2014, due to N = 0) ranged from 575–922 km, with a mean of 712 km (Fig. 5). The annual mean ice drift experienced by all bears (only including years with ≥3 individuals) ranged from 626 km in 2006 to 819 km in 2008. Total vector co-directional movement (C_v) per individual ranged from −232 km (i.e. 232 km counter to ice drift) to 1011 km (i.e. 1011 km in the same direction as ice drift), with a mean of 310 km. Annual mean C_v ranged from 110 km in 2005 to 673 km in 2009.

4. DISCUSSION

We examined sea ice drift in HB in the context of polar bear ecology. There was no long-term increase in ice speed over the entire Bay from 1987–2015. Polar bears did not walk against drift, which indicates that ice drift is unlikely to be a significant factor in the WH subpopulation decline. However, we observed an increasing trend of habitat (i.e. drift) variability along with variability in ice drift conditions experienced by individuals. This complex spatiotemporal variability may have important, yet varied impacts on individuals. Further, many of our findings contrast observations in other High Arctic polar bear

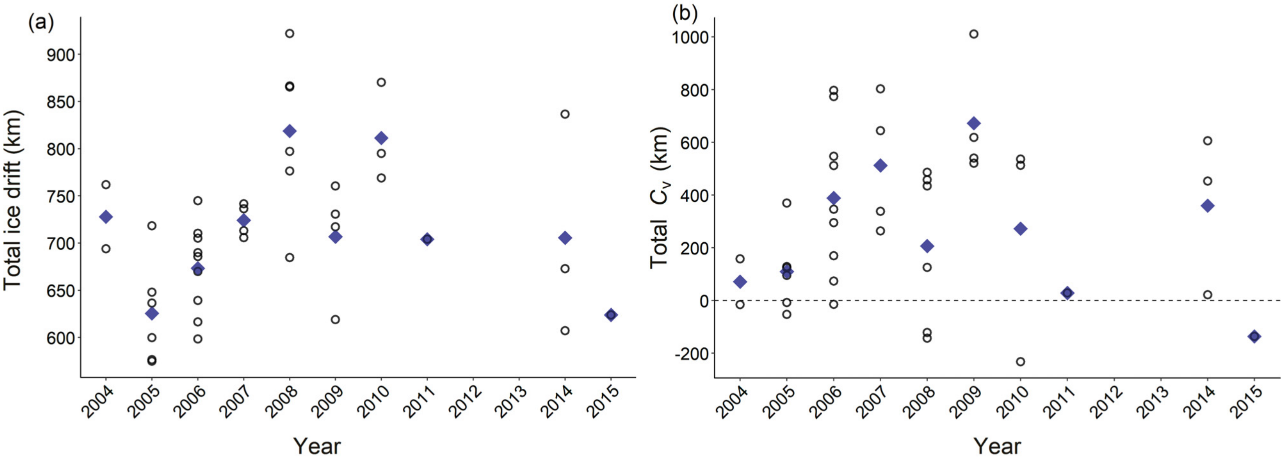

Fig. 5. Individual and annual variation in (a) total ice drift experienced and (b) total vector co-directionality (C_v). In (b), positive values represent movement with ice drift, and negative values represent movement counter to ice. Dashed lined = 0 represents movement with no net distance with or against drift. In both (a) and (b), drift and movement were calculated over an entire ice season (December–May). Open circles: total/mean for a single individual for an entire year; blue diamonds: mean of all individuals within that year

subpopulations, and therefore suggests intraspecific and geographic variation in responses to climate change.

In nearly half of the months examined (January–April), we observed a long-term negative trend in ice drift speeds across years (1987–2015), while November, December, May, June, and July had no significant trend (Table 1). However, even models with significant trends had low effect sizes, which may not be biologically meaningful. In all months but November, ice drift was faster with increasing distance from the HB coastline, which contributes to a spatially variable habitat. Based on varying space-use strategies, this may lead to inter-individual differences in the exposure to and consequences of ice drift. We did not observe this spatial trend in November, likely due to low spatial coverage and variability during sea ice formation (Danielson 1971, Saucier et al. 2004). Despite recent changes in the melt season and ice concentration throughout the year (Sahanatien & Derocher 2012, Parkinson 2014, Kowal et al. 2017), HB ice drift rates have remained somewhat stable, indicating that the loss of multi-year ice (i.e. in High Arctic systems) is an important factor causing greater increases in ice speed (Spreen et al. 2011, Kwok et al. 2013, Kwok 2018). These trends in ice drift speed in conjunction with inter-annual variation indicate that the effects of ice drift speed may be independent among years and may not contribute to a long-term energy deficit in WH bears. However, polar bears may also be affected by long-term changes in the variability of their environment. We observed a significant increase in the CV of sea ice drift speed over time, which suggests a potential change in the predictability of their habitat. CV varied by as much as 34.7% between years and there was some evidence of a cyclic pattern (observed in Fig. 2). However, our focus was long-term shifts in environmental conditions due to climate change, as variable habitats have been linked to decreased population viability and time to extinction (Inchausti & Halley 2003, Lande et al. 2003). In this case, sea ice drift variability may be a risk factor for the declining WH polar bear subpopulation (Regehr et al. 2007, Lunn et al. 2016). Within-year, there was a trend of decreasing ice drift speeds and variability throughout the season (November–July), when we pooled all data from 1987–2015. Ice drift was fastest during freeze-up, which is likely due to thin ice paired with strong external wind forcing in autumn and early winter (Saucier et al. 2004, Yu et al. preprint doi:10.5194/tc-2019-183). Therefore, storm-driven drift may explain why ice speeds are faster during freeze-up than in break-up, despite similarly low ice concentrations (Saucier et al. 2004). Overall, sea ice drift speed was seasonally, spatially, and annually variable, with decreased habitat predictability. Although long-term trends in ice drift speed would not solely suggest an energetic effect, the lack of a long-term change indicates that ice drift speed cannot account for trends of decreased body condition (Stirling et al. 1999, Stirling & Parkinson 2006), although variability may play a role at the annual and individual levels.

Although temporal trends in ice drift provide important information on climate change-driven shifts in the physical structure of polar bear habitats, they were not directly reflective of energetic consequences. These energetic effects are dependent on individual and population-level interactions with abiotic factors. Therefore, we assessed polar bear movement rates and direction relative to ice drift and polar bear responses at the scale of the movement step and at an annual scale. Mean daily movement rates in WH bears (16.5 km d^{-1}) were higher than polar bears in the Beaufort Sea (11.74 km d^{-1}; Durner et al. 2017) and the Chukchi Sea (5.14 km d^{-1}; Durner et al. 2017). However, polar bear movement rates were not comparable across all ice drift studies, due to differences in GPS resolution and methodology (Mauritzen et al. 2003, Auger-Méthé et al. 2016). Mean ice drift speeds in WH (3.9 km d^{-1}) were similar to those in the Beaufort Sea (2.3–4.92 km d^{-1}; Auger-Méthé et al. 2016, Durner et al. 2017), but were slower than ice drift rates found in the Chukchi Sea (4.34–5.96 km d^{-1}; Durner et al. 2017) and Barents Sea (4.28 km d^{-1}; Mauritzen et al. 2003). However, Mauritzen et al. (2003) used different ice drift data, and it is therefore uncertain if ice drift rates are comparable to studies using ice motion vectors from the NSIDC (Auger-Méthé et al. 2016, Durner et al. 2017, this study). On average, GPS displacement was 5.5% greater than bear movement, indicating WH polar bears did not move substantially counter to ice drift. This is contrary to the Beaufort Sea subpopulation, where incorporating ice drift positively affected bear movement rates and home range size (Auger-Méthé et al. 2016). Bear movement was greatest during freeze-up, and bears moved approximately perpendicular (predominately northeast) to ice drift (predominately southeast). During freeze-up, adult female bears may move >300 km by January as they disperse throughout the Bay (Parks et al. 2006). Directional movement to the northeast has been noted in this subpopulation both on land and on the sea ice (Ramsay & Andriashek 1986, Parks et al. 2006, Togunov et al. 2017, 2018), and likely reflects population-level migration. Due to the circular gyre in HB, dispersal from shore into the Bay would tend to be perpendicular to drift on the onset of migration. Migratory behaviour during freeze-up was supported by our results of high movement rates and angular concentration. In November, bear movement speed increased as ice drift speeds increased, and in both freeze-up months (November, December), bear movement was highest when they were moving with ice drift. This suggests that in this time of directional movement, bears may be using ice drift to their advantage to save energy. Ice drift was slower during winter than freeze-up but exhibited the highest degree of variability among the 3 ice seasons. Bear movement was generally opposite ice drift, which could reflect station-keeping, as bears often show fidelity to areas on the sea ice (Mauritzen et al. 2001, McCall et al. 2016). However, station-keeping was not obviously reflected in movements at a 24 h time interval, as bear movement was not greater when in opposition to ice drift. Lower angular concentration of polar bear movements during winter and break-up may indicate that area-restricted search (i.e. foraging) was prioritized (Stirling & Parkinson 2006, Togunov et al. 2017, 2018). It may also reflect higher inter-individual variation in space-use, contrary to freeze-up when directional movement from land is similar throughout the subpopulation (Parks et al. 2006, Cherry et al. 2013, Castro de la Guardia et al. 2017). Further, directional movements during spring may be masked by increased rates of swimming (Pilfold et al. 2017) and fewer locations (collars cannot transmit while submerged in water). During spring, WH bears may swim >3 d and >200 km from the southward retreating pack ice to the west coast of HB (Saucier et al. 2004, Pilfold et al. 2017). As part of their migration back to land, these swims are directional, but locations are not transmitted by the collars and were therefore not part of our analysis. Bear movement increased as ice speeds increased in much of the break-up season. Ice speeds tend to be positively correlated to wind speeds, and therefore, high ice speeds may represent unfavourable olfactory foraging conditions, at which time bears may prioritize travelling behaviours or wait for weather conditions to improve (Harington 1968, Togunov et al. 2017, 2018). The results of the GLMM examining bear movement rates should be interpreted with caution, as low effect sizes indicated weak trends. Further, these results may be influenced by inaccuracies in the ice drift data used; for example, if modelled ice speeds tended to be underestimated, it would lead to underestimating speed of counter-ice movements. Several studies quantifying the accuracy of satellite-based sea ice drift suggest that estimates tend to underestimate drift (Rozman et al. 2011, Schwegmann et al. 2011, Johansson & Berg 2016, Durner et al. 2017, May 2018, but see Hwang 2013, Sumata et al. 2014, Lavergne 2016). Further, the accuracy of drift estimates also varied by region, distance to shore, ice concentration, ice thickness, and time of year (Sumata et al. 2015, Mahoney et al. 2019, Togunov et al. preprint doi:10.5194/tc-2020-26).

The dynamic nature of HB ice drift was reflected in the variation between years and individuals. Mean yearly ice drift for all polar bears varied by as much as 193 km, and mean ice drift per individual varied by nearly 350 km. This variation was likely due to the temporally variable nature of HB ice drift, and to individual differences in space-use patterns — particularly regarding distance to coastline, as we found faster drift farther from land. However, despite this variation in ice drift, bear movement was generally in the same direction as drift, which supports the GLMM results indicating that the bears' movements are higher when they are moving with ice drift. However, 8 bears did have negative vector co-directional (C_v), ranging from 7–232 km counter to ice, indicating individuals differ in their response to ice drift and energetic challenges. These findings suggest that small differences in ice drift exposure and individual responses to ice drift can accumulate into larger differences over an entire season. However, we were unable to compare years with <3 bears (2011–2013, 2015), which limits our inferences on inter-annual variability. In contrast to much of the Arctic where ice drift rates are increasing (Rampal et al. 2009, Spreen et al. 2011, Kwok et al. 2013, Durner et al. 2017), we observed stable or decreasing ice drift speeds in HB. Although ice drift may not explain long-term WH subpopulation decline, it may be important at the individual level and may contribute to variation in condition and survival.

Although our findings are limited by the accuracy and precision of the ice drift data, these are the best estimates available. Further, our analyses used the same ice drift data used in studies of both the Beaufort Sea and Chukchi Sea polar bears (Auger-Méthé et al. 2016, Durner et al. 2017). Another potential limitation is the mismatch in the spatial resolution of the data. The bear movement data is spatially continuous, whereas the ice drift data is at a 25 km resolution. If ice drift heterogeneity is significant at scales <25 km, interpolated estimates may be spurious. However, ice drift in HB appears to be relatively homogenous across large spatial scales (>25 km), even during periods of low ice concentrations (Togunov et al. pre-print doi:10.5194/tc-2020-26, video supplement available at https://av.tib.eu/media/45186). Therefore, error due to the mismatched resolution was likely not significant in our system.

Although sea ice drift in the HB was inter-annually variable, there was no long-term increase in drift speeds. Further, none of our results suggested a substantial amount of bear movement counter to ice drift, which suggests that WH bears were not subjected to increased energetic demands from ice drift. This is contrary to other subpopulations (Barents, Beaufort, and Chukchi Seas) with increased rates of ice drift (Rampal et al. 2009, Kwok et al. 2013), and oppositional polar bear movement (Mauritzen et al. 2003, Auger-Méthé et al. 2016, Durner et al. 2017). Inter-individual and inter-annual variation in ice drift exposure and response to ice drift may play a role in intra-population body condition variability, and habitat variability increased over time, which may alter polar bear movement and navigation. Therefore, our study highlights the need for subpopulation-specific risk evaluation, as threats vary geographically. Risk factors may be largely based on the rate of environmental change, biogeographic relationships, and subpopulation-specific behaviours, such as movement rates and foraging periods.

Acknowledgements. We thank members of the Derocher lab and others who assisted with field work, as well as the Churchill Northern Studies Centre for their support. We thank Dr. Kimberley Mathot for input on statistical analysis during project development. We acknowledge and thank our funders: Canadian Association of Zoos and Aquariums, Canadian Wildlife Federation, Care for the Wild International, Earth Rangers Foundation, Environment and Climate Change Canada, Hauser Bears, the Isdell Family Foundation, Manitoba Sustainable Development, Natural Sciences and Engineering Research Council of Canada, Parks Canada, Polar Bears International, Polar Continental Shelf Project of Natural Resources Canada, Quark Expeditions, Wildlife Media Inc., and World Wildlife Fund Canada. Finally, we thank the editors and 3 anonymous reviewers, whose input greatly improved the manuscript.

LITERATURE CITED

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260

Amstrup SC, Durner GM, Stirling I, Lunn NJ, Messier F (2000) Movements and distribution of polar bears in the Beaufort Sea. Can J Zool 78:948–966

Auger-Méthé M, Lewis MA, Derocher AE (2016) Home ranges in moving habitats: polar bears and sea ice. Ecography 39:26–35

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1–48

Bovet P, Benhamou S (1988) Spatial analysis of animals' movements using a correlated random walk model. J Theor Biol 131:419–433

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Castro de la Guardia L, Myers PG, Derocher AE, Lunn NJ, Terwisscha van Scheltinga AD (2017) Sea ice cycle in western Hudson Bay, Canada, from a polar bear perspective. Mar Ecol Prog Ser 564:225–233

Chapman JW, Nesbit RL, Burgin LE, Reynolds DR, Smith AD, Middleton DR, Hill JK (2010) Flight orientation behaviors promote optimal migration trajectories in high-flying insects. Science 327:682–685

Chapman JW, Klaassen RHG, Drake VA, Fossette S and others (2011) Animal orientation strategies for movement in flows. Curr Biol 21:R861–R870

Cherry SG, Derocher AE, Thiemann GW, Lunn NJ (2013) Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. J Anim Ecol 82:912–921

Crête M, Larivière S (2003) Estimating the costs of locomotion in snow for coyotes. Can J Zool 81:1808–1814

Danielson EW Jr (1971) Hudson Bay ice conditions. Arctic 24:90–107

DeMaster DP, Stirling I (1981) *Ursus maritimus*. Mamm Species 145:1–7

Derocher AE, Lunn NJ, Stirling I (2004) Polar bears in a warming climate. Integr Comp Biol 44:163–176

Derocher AE, Aars J, Amstrup SC, Cutting A and others (2013) Rapid ecosystem change and polar bear conservation. Conserv Lett 6:368–375

Dickinson MH, Farley CT, Full RJ, Koehl MAR, Lehman S (2000) How animals move: an integrative approach. Science 288:100–106

Dodge S, Bohrer G, Weinzierl R, Davidson SC and others (2013) The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. Mov Ecol 1:3

Durner GM, Douglas DC, Albeke SE, Whiteman JP and others (2017) Increased Arctic sea ice drift alters adult female polar bear movements and energetics. Glob Change Biol 23:3460–3473

Escajeda E, Laidre KL, Born EW, Wiig Ø and others (2018) Identifying shifts in maternity den phenology and habitat characteristics of polar bears (*Ursus maritimus*) in Baffin Bay and Kane Basin. Polar Biol 41:87–100

Estevez I, Christman MC (2006) Analysis of the movement and use of space of animals in confinement: the effect of sampling effort. Appl Anim Behav Sci 97:221–240

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T and others (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Funct Ecol 21:1003–1015

Forward RB, Tankersley RA, Welch JM (2003) Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. Bull Mar Sci 72:347–365

Fryxell JM, Wilmshurst JF, Sinclair ARE, Haydon DT, Holt RD, Abrams PA (2005) Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecol Lett 8: 328–335

Giraudoux P (2018) pgirmess: spatial analysis and data mining for field ecologists. R package version 1.6.9. https://CRAN.R-project.org/package=pgirmess

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28: 1140–1162

Hakkinen S, Proshutinsky A, Ashik I (2008) Sea ice drift in the Arctic since the 1950s. Geophys Res Lett 35:L19704

Harington RC (1968) Denning habits of the polar bear (*Ursus maritimus* Phipps.). Canadian Wildlife Service Report Series No. 5, Canadian Wildlife Service, Ottawa

Hobson KA, Stirling I (1997) Low variation in blood $\delta^{13}C$ among Hudson Bay polar bears: implications for metabolism and tracing terrestrial feeding. Mar Mamm Sci 13: 359–367

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O (2008) Trends and missing parts in the study of movement ecology. Proc Natl Acad Sci USA 105:19060–19065

Hurst RJ, Leonard ML, Watts PD, Beckerton P, Øritsland NA (1982) Polar bear locomotion: body temperature and energetic cost. Can J Zool 60:40–44

Hwang B (2013) Inter-comparison of satellite sea ice motion with drifting buoy data. Int J Remote Sens 34:8741–8763

Inchausti P, Halley J (2003) On the relation between temporal variability and persistence time in animal populations. J Anim Ecol 72:899–908

Johansson AM, Berg A (2016) Agreement and complementarity of sea ice drift products. IEEE J Sel Top Appl Earth Obs Remote Sens 9:369–380

Kowal S, Gough WA, Butler K (2017) Temporal evolution of Hudson Bay sea ice (1971-2011). Theor Appl Climatol 127:753–760

Kwok R (2018) Arctic sea ice thickness, volume, and multiyear ice coverage: losses and coupled variability (1958-2018). Environ Res Lett 13:105005

Kwok R, Spreen G, Pang S (2013) Arctic sea ice circulation and drift speed: decadal trends and ocean currents. J Geophys Res Oceans 118:2408–2425

Laidre KL, Stirling I, Lowry LF, Wiig Ø, Heide-Jørgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18:S97–S125

Lande R (1998) Demographic stochasticity and Allee effect on a scale with isotropic noise. Oikos 83:353–358

Lande R, Engen S, Saether BE (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford

Lavergne T (2016) Validation and monitoring of the OSI SAF low resolution sea ice drift product. http://osisaf.met.no/docs/osisaf_cdop2_ss2_valrep_sea-ice-drift-lr_v5p0.pdf

Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7:573–579

Lund U, Agostinelli C (2001) CircStats: circular statistics, from 'topics in circular statistics'. R package version 0.2.6. https://CRAN-R.project.org/package=CircStats

Lunn NJ, Servanty S, Regehr EV, Converse SJ, Richardson ES, Stirling I (2016) Demography of an apex predator at the edge of its range: impacts of changing sea ice on polar bears in Hudson Bay. Ecol Appl 26:1302–1320

Mahoney AR, Hutchings JK, Eicken H, Haas C (2019) Changes in the thickness and circulation of multiyear ice in the Beaufort Gyre determined from pseudo Lagrangian methods from 2003–2015. J Geophys Res Oceans 124: 5618–5633

Mauritzen M, Derocher AE, Wiig Ø (2001) Space-use strategies of female polar bears in a dynamic sea ice habitat. Can J Zool 79:1704–1713

Mauritzen M, Derocher AE, Pavlova O, Wiig Ø, Wiig O (2003) Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. Anim Behav 66: 107–113

May RI (2018) Verification of sea ice drift data obtained from remote sensing information. In: IGARSS 2018: Proc IEEE Int Geosci Remote Sens Symp, 22–27 July 2018, Valencia, p 7344–7347

McCall AG, Derocher AE, Lunn NJ (2015) Home range distribution of polar bears in western Hudson Bay. Polar Biol 38:343–355

McCall AG, Pilfold NW, Derocher AE, Lunn NJ (2016) Seasonal habitat selection by adult female polar bears in western Hudson Bay. Popul Ecol 58:407–419

McLaren JD, Shamoun-Baranes J, Dokter AM, Klaassen RHG, Bouten W (2014) Optimal orientation in flows: providing a benchmark for animal movement strategies. J R Soc Interface 11:20140588

Moran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37:17–23

Mueller T, Fagan WF (2008) Search and navigation in dynamic environments — from individual behaviors to population distributions. Oikos 117:654–664

Nakagawa S, Johnson PCD, Schielzeth H (2017) The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J R Soc Interface 14:20170213

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059

Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56: 111–120

Pagano AM, Durner GM, Rode KD, Atwood TC and others (2018) High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. Science 359:568–572

Parkinson CL (2014) Spatially mapped reductions in the length of the Arctic sea ice season. Geophys Res Lett 41: 4316–4322

Parks EK, Derocher AE, Lunn NJ (2006) Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. Can J Zool 84:1281–1294

Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. Comput Geosci 30:683–691

Pilfold NW, McCall AG, Derocher AE, Lunn NJ, Richardson ES (2017) Migratory response of polar bears to sea ice loss: to swim or not to swim. Ecography 40:189–199

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rampal P, Weiss J, Marsan D (2009) Positive trend in the mean speed and deformation rate of Arctic sea ice, 1979-2007. J Geophys Res Oceans 114:C05013

Ramsay MA, Andriashek DS (1986) Long distance route orientation of female polar bears (*Ursus maritimus*) in spring. J Zool 208:63–72

Ramsay MA, Hobson KA (1991) Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. Oecologia 86:598–600

Regehr EV, Lunn NJ, Amstrup SC, Stirling I (2007) Effects of earlier sea ice breakup on survival and population size of polar bears in Western Hudson Bay. J Wildl Manag 71: 2673–2683

Ribic CA, Ainley DG, Fraser WR (1991) Habitat selection by marine mammals in the marginal ice zone. Antarct Sci 3: 181–186

Richardson E, Stirling I, Hik DS (2005) Polar bear (*Ursus maritimus*) maternity denning habitat in western Hudson Bay: a bottom-up approach to resource selection functions. Can J Zool 83:860–870

Rozman P, Hölemann JA, Krumpen T, Gerdes R and others (2011) Validating satellite derived and modelled sea-ice drift in the Laptev Sea with in situ measurements from the winter of 2007/2008. Polar Res 30:7218

Sahanatien V, Derocher AE (2012) Monitoring sea ice habitat fragmentation for polar bear conservation. Anim Conserv 15:397–406

Saucier FJ, Senneville S, Prinsenberg S, Roy F and others (2004) Modelling the sea ice-ocean seasonal cycle in Hudson Bay, Foxe Basin and Hudson Strait, Canada. Clim Dyn 23:303–326

Schwegmann S, Haas C, Fowler CW, Gerdes R and others (2011) A comparison of satellite-derived sea-ice motion with drifting-buoy data in the Weddell Sea, Antarctica. Ann Glaciol 52:103–110

Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. Am Nat 182:298–312

Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc B 367:2762–2772

Spreen G, Kwok R, Menemenlis D (2011) Trends in Arctic sea ice drift and role of wind forcing: 1992–2009. Geophys Res Lett 38:L19501

Steiner N, Azetsu-Scott K, Hamilton J, Hedges K and others (2015) Observed trends and climate projections affecting marine ecosystems in the Canadian Arctic. Environ Rev 23:191–239

Stern HL, Laidre KL (2016) Sea-ice indicators of polar bear habitat. Cryosphere 10:2027–2041

Stirling I, Parkinson CL (2006) Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic 3:261–275

Stirling I, Spencer C, Andriashek D (1989) Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. J Wildl Dis 25:159–168

Stirling I, Lunn NJ, Iacozza J (1999) Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climatic change. Arctic 52:294–306

Sumata H, Lavergne T, Girard-Ardhuin F, Kimura N and others (2014) An intercomparison of Arctic ice drift products to deduce uncertainty estimates. J Geophys Res Oceans 119:4887–4921

Sumata H, Gerdes R, Kauker F, Karcher M (2015) Empirical error functions for monthly mean Arctic sea-ice drift. J Geophys Res C Oceans 120:7450–7475

Thiemann GW, Iverson SJ, Stirling I, Obbard ME (2011) Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. Oikos 120: 1469–1478

Thorndike AS, Colony R (1982) Sea ice motion in response to geostrophic winds. J Geophys Res 87:5845–5852

Togunov RR, Derocher AE, Lunn NJ (2017) Windscapes and olfactory foraging in a large carnivore. Sci Rep 7: 46332

Togunov RR, Derocher AE, Lunn NJ (2018) Corrigendum: Windscapes and olfactory foraging in a large carnivore. Sci Rep 8:46968

Trump CL, Leggett WC (1980) Optimum swimming speeds in fish: the problem of currents. Can J Fish Aquat Sci 37: 1086–1092

Tschudi M, Fowler C, Maslanik J, Stewart S, Meier WN (2016) Polar Pathfinder Daily 25 km EASE-Grid Sea Ice Motion Vectors, version 3. USA National Snow and Ice Data Center, Boulder, CO

Tucker VA (1970) Energetic cost of locomotion animals. Comp Biochem Physiol 34:841–846

Wikelski M, Moskowitz D, Adelman JS, Cochran J, Wilcove DS, May ML (2006) Simple rules guide dragonfly migration. Biol Lett 2:325–329

Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. Proc R Soc B 279:975–980

Editorial responsibility: Kyle Elliott,
Sainte-Anne-de-Bellevue, Québec, Canada

Submitted: October 24, 2019; Accepted: March 10, 2020
Proofs received from author(s): April 18, 2020