

Migration phenology of beluga whales in a changing Arctic

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ABSTRACT: Global warming has been linked to dramatic environmental changes, particularly in polar marine environments, where water temperatures and sea-ice cover are especially affected. Using satellite telemetry, we investigated how local changes in sea-surface temperatures (2002–2004) affected the movement patterns of belugas *Delphinapterus leucas* in eastern Hudson Bay (EHB), Canada. Of 26 whales equipped with satellite transmitters, 17 had records that extended beyond the summer season and showed a fall migration pattern. During summer, foraging activity of individuals was either *aggregated*, at small spatial scales of <90 km (Strategy A), or *dispersed*, at larger spatial scales of >120 km (Strategy D). In 2002 and 2003, belugas preferentially selected cold water temperatures <4°C, while, in 2004, no selection occurred. In 2002–2003, the range of water temperatures was larger than in 2004. Moreover, while cold waters were found mainly to the north of the Belcher Islands in 2002–2003, cold waters were broadly scattered throughout the whole bay in 2004. Independent of year, animals employing Strategy A left their summer habitat late (31 October, ±14 d), while those using Strategy D left about 3 wk earlier (4 October, ±2 d). In 2002–2003, the range of water temperatures was larger than in 2004. Moreover, while cold waters were found mainly to the north of the Belcher Islands in 2002–2003, cold waters were broadly scattered throughout the whole bay in 2004. Therefore, it appeared that the strategy used in summer, and hence the migration timing among EHB belugas, was related to sea-surface temperature conditions. Although other factors may also trigger migration, the present study is among the first to reveal a relationship between environmental conditions and habitat use and the migration patterns of beluga whales. Consequently, this work indicates alterations in a well-established migration phenology due to longer term effects of climate change on this Arctic species.

KEY WORDS: Polar environment · Climate change · Biologging · Fall migration pattern · Marine mammal · *Delphinapterus leucas*

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1. INTRODUCTION

In polar regions, environmental conditions are largely affected by seasonal ice cover (Piepenburg 2005). Global warming is a long-term unidirectional change in the environment, as opposed to large-scale inter-annual variation, and has had measurable impacts on the environment, particularly in polar marine regions, where it has resulted in

changes in sea-ice cover, water temperature and ocean currents (Rothrock et al. 1999, Parkinson & Cavalieri 2002, Comiso & Parkinson 2004, Walsh 2008). Consequences on biological phenomena include changes in species distribution and abundance (Parmesan & Yohe 2003, Root et al. 2003), as well as in the phenology of basic characteristics such as reproduction and migration patterns (Walther et al. 2002). Sea-ice extent related to other phy-

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sical parameters, like water temperature, is predicted to change most rapidly in southern regions of the Arctic, along the marginal sea-ice zone (Walsh 2008), and impacts on marine populations are expected to be observed there first. Although Arctic marine mammals are adapted to a fluctuating environment and have an ability to endure drastic changes in environmental conditions (Harington 2008), long-term unidirectional changes (e.g. Johannessen et al. 1999, Vinnikov et al. 1999, Parkinson & Cavalieri 2002) present particularly difficult challenges to their survival. The way Arctic species will respond to ongoing climate change remains unclear (Wassmann et al. 2011).

Beluga whales *Delphinapterus leucas* are medium-sized, ice-adapted odontocetes, which are distributed in discrete populations around the Arctic (e.g. Stewart & Stewart 1989, IWC 1992). Although some beluga populations are relatively sedentary year round (e.g. Hobbs et al. 2005), many populations undertake large-scale annual migrations (e.g. Richard et al. 2001a,b). Migration is a special type of movement from one region to another, aimed at meeting energy requirements or responding to alternating favourable or unfavourable conditions in the environment. Therefore, migration is generally viewed as an adaptation to resource availability that fluctuates spatiotemporally, notably with seasons. For belugas potential effects of global warming include regional or seasonal shifts in prey availability (Tynan & DeMaster 1997) which in turn may alter the timing or patterns of their migration, although links between migratory behaviour and environmental variability and climate change have yet to be documented. Beluga whales have a varied diet (Hobbs et al. 2005, Kelley et al. 2010) and occupy a large range of habitats, from estuaries to deep ocean basins. These characteristics might somewhat reduce their vulnerability to climate change, although their tendency for site fidelity and low reproduction rate may counteract their capacity to respond to predicted climate changes (Laidre et al. 2008).

The development of bio-logging technology, especially satellite telemetry, has provided a powerful tool for obtaining data on the long-distance movements, seasonal distributions and habitat use of marine species that are difficult to observe *in situ* (e.g. Costa 1993). In the present study, we used satellite telemetry in combination with dive recorders and remotely sensed sea-surface temperature (SST) data to show that SST conditions during the summer in eastern Hudson Bay (EHB), Canada, significantly influence the pre-migratory foraging behaviour and

migration timing of an endangered unit of belugas. Given the physical connexion between the atmosphere and the sea surface, water temperature is among the most intuitive indicators of physical change within the marine environment in the context of global warming. Although it is a reductive approach to consider a single parameter to estimate the impact of environmental changes on the behaviour of belugas, water temperature is a reliable parameter for measuring impacts of environmental change on this species given its cascading effects on sea-ice coverage and on local prey abundance (e.g. Heide-Jørgensen et al. 2011) and its importance for females and calves, feeding, moulting and predation avoidance (Kleinenberg et al. 1964, Sergeant 1973, Fraker et al. 1979, Finley et al. 1982, St. Aubin et al. 1990, Watts et al. 1991, Boily 1995, Richard et al. 2001a,b).

2. MATERIALS AND METHODS

2.1. Study area and whale capture

The present study focuses on the eastern Hudson Bay (EHB) (northern Quebec, Canada) bounded by latitudes 55–59°N and longitudes 76–81°W. The beluga stock has been defined as a distinct group on the basis of summering areas (e.g. Reeves & Mitchell 1987). To date, available genetic studies have not rejected the postulate (Buchanan et al. 1996), although the possibility of breeding with other populations remains. Satellite telemetry has shown that animals from the Hudson Bay complex overwinter together, and the absence of differences among microsatellite DNA analyses indicates that they interbreed. However, the satellite telemetry and mitochondrial DNA analyses show clear separations, particularly between EHB belugas and other belugas from the Hudson Bay complex, supporting the hypothesis that they form separate summering stocks (Gladden et al. 1999, DeMarch & Postma 2003, Turgeon et al. 2012).

From that EHB stock, a total of 26 belugas including 9 females and 17 males were captured in estuaries of the EHB in July 2002–2004. Animals were caught using 6-inch mesh, shore-anchored nets and were equipped with SPOT (location and temperature recorders), SDR-T16 tags (satellite-linked time-depth recorders), both from Wildlife Computers, or TD-SRDLs (time depth-satellite relayed data loggers) from the Sea Mammal Research Unit (SMRU, St. Andrews, UK) secured to the dorsal ridge (Richard et al. 1997, Kingsley et al. 2001).

2.2. Data processing

Data were processed using SATPAK and SATPAK2003 applications (Wildlife Computers) or automatically at the SMRU, which decodes the data and supplies a complete and exploitable database. Animal locations were provided via the ARGOS system. The theoretical accuracy of locations given by ARGOS varies from 150 m (Class 3 locations) through 350 m (Class 2), 1 km (Class 1), and >1 km (Class 0), to no calculated accuracy for Classes A, B and Z.

Tracks were filtered using a forward particle-filtering model (Tremblay et al. 2009). By this method, location accuracy was examined and unrealistic locations were rejected. The model assumes that each location corresponds to the geographic average of the many possible positions, the spread of which is a function of location accuracy. The first step of the filtering procedure consists of generating a number, here 50, of random locations (or 'particles') inside a circle around each received position of a radius that depends on the spatial error of the position. Each particle is weighted according to the likelihood of the speed needed to get there from a previous location. A maximum speed of 3 m s^{-1} is assumed based on the assumption that beluga rarely travel at speeds higher than this threshold (e.g. Richard et al. 1998). Information on local bathymetry (source: ETOPO 1) is used to eliminate particles identified as being on land. At each step, a new particle is randomly selected and used to create the next position. The output of this method is n complete tracks, each corresponding to 1 boot-strapped track iteration (here $n = 50$). The 'best track' can then be computed as the geographic average of the bootstrapped tracks (Tremblay et al. 2009).

A dive was defined as any excursion below 4 m. A summary record, including proportion of time spent diving, number of dives, mean, maximum and SD of maximum dive depth and mean, maximum and SD of dive duration was compiled for each 6 h period for each track. Compilation was processed directly by the SMRU and included in the database for the SMRU tags, while we developed a program in R 2.11 (R Development Core Team 2010) for the Wildlife Computer tags. Dive frequency was used as an index of foraging activity. The more the dive frequency increased, the more the individuals were considered to be foraging.

2.3. Environmental dataset

The AVHRR Oceans Pathfinder SST data were averaged within the boundaries of the study area

over 4 successive weeks at a 4 km grid scale and obtained through the online PO.DAAC Ocean ESIP Tool (POET) of the Physical Oceanography Distributed Active Archive Center (PO.DAAC), NASA Jet Propulsion Laboratory, Pasadena, California (<http://podaac.jpl.nasa.gov/poet>).

A time series of SST averaged over September and the corresponding variance ($V = SD^2$) within the study area were drawn up from 1985 to 2007.

2.4. Residency versus migration patterns

Residency was distinguished from more directional movements such as migration using first-passage time (FPT) analysis performed over the entire track of each individual, following Fauchald & Tveraa (2003), using the programming language R 2.11 (R Development Core Team 2010). FPT was defined as the time required for crossing a circle of radius r , with a long transit time indicating residency and a short transit time corresponding to more directional movements such as migration. Beluga paths at the surface were interpolated to obtain a position every 2 km. Each location was associated with a circle of a given radius (r). FPT was calculated every 2 km for r values varying from 2 to 800 km. The relative variance among FPT values, obtained from log-transformed FPT (Fauchald & Tveraa 2003), was calculated as a function of r . The corresponding plot [variance in $\log(\text{FPT})$ vs. r] allowed us to identify the area-restricted search (ARS) scales (i.e. the size of areas of residency) by peaks in the variance (Fig. 1a). To locate where animals entered an ARS zone and the time spent in a specific area, FPT values where a variance peak occurred were plotted as a function of time since departure (Fig. 1b). The time of shift between long and near-zero FPT at the end of summer was defined as the date of departure for migration (Fig. 1b,c).

A second FPT analysis was conducted only on track portions corresponding to the period before migration to determine, from the ARS scales, areas of higher residency within the summer habitat. Broken-stick analyses, i.e. analyses for estimating the location of breaks in the slope of fitted regression lines, were conducted with the function 'segmented' (package 'segmented' in R Development Core Team 2010) to reveal changes in cumulative ordered values of ARS scales for each individual (Muggeo 2003). The break was used to distinguish between 2 movement strategies: Strategy A was defined as an *aggregated* strategy, where movement occurred

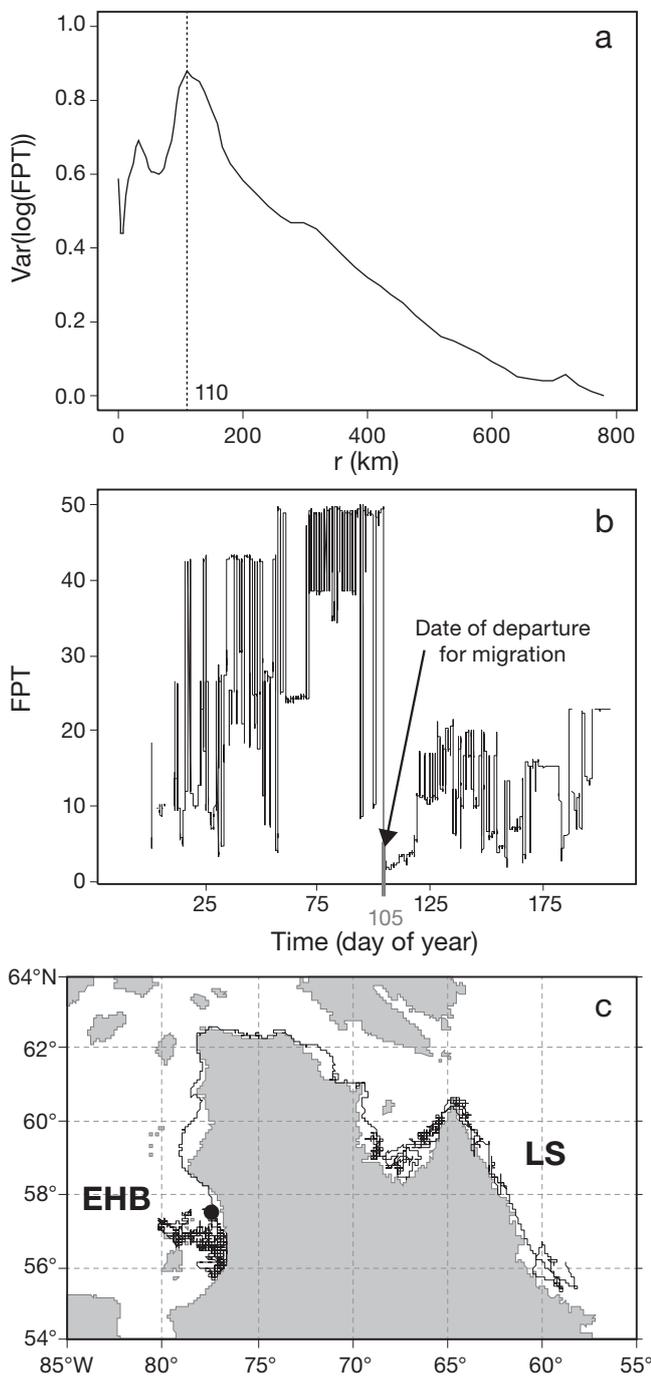


Fig. 1. *Delphinapterus leucas*. First passage time (FPT) analysis for a typical track of 1 beluga from eastern Hudson Bay (EHB) to the Labrador Sea (LS). (a) The higher peak in variance indicates the most relevant scale (dotted line) of area restricted search (ARS) behaviour (i.e. the size of the residency areas). (b) Plot of FPT values corresponding to the higher peak in variance as a function of time since departure. The time of shift between long and near-zero FPT at the end of summer (gray) was defined as the date of departure for migration. (c) Track of the animal with the location of departure (black dot)

over small spatial scales, and Strategy D was defined as a *dispersed* strategy, where movement patterns occurred over larger spatial scales (Fig. 2, Table 1).

2.5. Resource selection analyses

Resource selection analyses were conducted according to Design II with Sampling Protocol A of Manly et al. (2002). Individual belugas were identified, and the use of resources was measured for each. Availability was estimated at the population level and corresponded to a random sample of unused temperature values, averaged over the pre-migration period, within the entire study area; 3 classes of temperatures were defined as potential habitat.

Two χ^2 tests provide useful information about selection. In the first test the null hypothesis is that animals are using resource categories in the same proportions, irrespective of whether this is selective or not. The χ^2 statistic was computed as:

$$\chi^2_{L1} = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e [u_{ij} / E(u_{ij})] \quad (1)$$

where $E(u_{ij}) = u_{i+} u_{+j} / u_{++}$ is the expected number of units of type i used by the j th animal if that animal uses the resources in the same way as the other animals (Manly et al. 2002).

The second is an overall test of the null hypothesis of selection in proportion to availability. This test

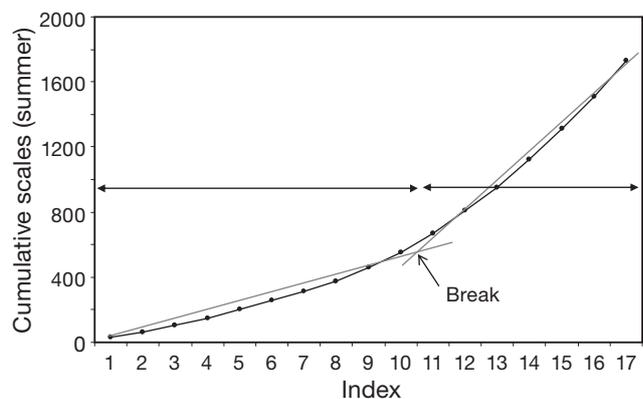


Fig. 2. *Delphinapterus leucas*. Cumulative ordered values of scales obtained by the second first passage time analysis conducted only on data obtained prior to migration for each individual. The index refers to Table 1. Gray lines illustrate the 'broken-stick' analysis. The break occurring between index values 10 and 11 allowed determination of 2 different movement strategies: Strategy A, an *aggregated* strategy for index values ≤ 10 (i.e. spatial scales ≤ 90 km, cf. Table 1), and Strategy D, a *dispersed* strategy for index values ≥ 11 (i.e. spatial scales ≥ 120 km, cf. Table 1) depending on the individual

Table 1. *Delphinapterus leucas*. Results of the first passage time analysis applied to the summer period, showing that the most relevant scale (r) of area restricted search behaviour was larger on average in 2004 than in 2002 and 2003. Departure date of migration was significantly dependent on the strategy used. Animals employing Strategy A (*aggregated*) left their summer habitat later than those using Strategy D (*dispersed*). The mean date of departure seemed to be earlier in 2004 than in other years, but the small sample size prevented relevant statistical analyses

No. of ind.	Scale of movement		Strategy	Migration departure date (day of year)
	Index (cf. Fig. 2)	Scales r (km) (summer period)		
2002				
1852	6	55	A	302
1855	7	60	A	300
17905	9	85	A	296
17906	14	170	D	276
Mean \pm SD		92.5 \pm 53.3		21 Oct. \pm 12 d
Conf. interval (95%)				281–306
2003				
1852	16	200	D	258
1853	3	45	A	282
1854	11	120	D	279
3022	4	45	A	291
3415	1	30	A	305
17905	5	50	A	306
17906	8	60	A	315
17911	2	30	A	312
Mean \pm SD		72.5 \pm 58.9		21 Oct. \pm 20 d
Conf. interval (95%)				279–308
2004				
45723	17	220	D	276
45724 ^a	10	90	A	334
45729	12	140	D	276
45730	13	140	D	274
45731	15	190	D	280
Mean \pm SD		156 \pm 50.3		4 Oct. \pm 3 d
Conf. interval (95%)				263–310
^a This individual represents an atypical case and was not included in the calculation				

involves comparing the observed frequencies with which different resource categories are used by different animals, with expected frequencies calculated from the resources available. The test statistic was:

$$\chi^2_{L2} = 2 \sum_{j=1}^n \sum_{i=1}^I u_{ij} \log_e [u_{ij} / E(u_{ij})] \quad (2)$$

where $E(u_{ij}) = \pi_i u_{+j}$ is the expected number of resource type i units used by the j th animal if use is proportional to availability ($\pi_i = a_i / a_+$, with a_i the number of available resource units in category i and

a_+ the total sample size of available unused units) (Manly et al. 2002).

The difference $\chi^2_{L1} - \chi^2_{L2}$ with $I - 1$ df is a test of the null hypothesis that animals are, on average, using resources in proportion to availability, irrespective of whether they are selecting the same or not. If this test statistics is significantly large when compared to the χ^2 distribution with $I - 1$ df then there is evidence that the average selection is not in proportion to availability of resources (Manly et al. 2002).

As our interest is primarily in the selection ratios for resource categories regardless of which animals in the population are doing the selection, the estimator of the overall selection ratio of the i th category for the population is:

$$\hat{w}_i = (u_{i+} / u_{++}) / \pi_i \quad (3)$$

The standard error can be estimated as follows:

$$SE(w_i) = w_i \sqrt{1 / u_{i+} - 1 / u_{++} + 1 / a_i - 1 / a_+} \quad (4)$$

and thus the confidence intervals

$$w_i \pm z_{\alpha/(2I)} SE(w_i) \quad (5)$$

can be considered, for i from 1 to I , where $z_{\alpha/(2I)}$ is the upper $100\alpha/(2I)$ percentage point for the standard normal distribution (Manly et al. 2002). The selection coefficient w_i differs significantly from 1 (no selection) if the confidence interval associated with w_i excludes 1. Thus, if $1 < w_i \pm z_{\alpha/(2I)} SE(w_i) < \infty$ then selection is positive and if $0 < w_i \pm z_{\alpha/(2I)} SE(w_i) < 1$ then selection is negative (Manly et al. 2002).

2.6. Statistical analyses

To test the difference in the migration timing of belugas according to the strategy used, we conducted a linear mixed effect model including year as a random factor. The model was structured as follows with the function 'lme' (package 'nlme' in R Development Core Team 2010):

$$\text{test} = \text{lme}(\text{date of migration} \sim \text{strategy used}, \text{random} = \sim 1\text{years of study})$$

3. RESULTS

Of the 26 belugas equipped with satellite transmitters, 17 individuals had records that extended beyond the summer season. The analysis of FPT applied over the entire record identified 3 seasonally dependent residency areas for these individuals. The EHB arc, including waters north of the Belcher Islands, constituted the summer residency area for the 26 whales, and we focused our analyses on this summer habitat and the subsequent migration from the summer habitat.

A plot of cumulative ordered values of ARS scales obtained from the FPT analysis for each individual indicated that belugas used either of 2 movement strategies: Strategy A for the movements occurring at small spatial scales ≤ 90 km (mean \pm SD: 55 ± 20 km) and Strategy D for movements occurring at larger spatial scales ≥ 120 km (168 ± 37 km) (Table 1, Fig. 2). Independent of the year, animals employing Strategy A left their summer habitat late in October (31 October, ± 14 d), while those using Strategy D left about 3 wk earlier (4 October, ± 2 d) (linear mixed-effect model with year as a random factor, $F_{1,13} = 5.72$, $p < 0.001$) (Table 1). Although the low sample sizes each year prevented relevant statistical analyses, we observed that the average date of departure for migration seemed to occur earlier in 2004 than in other years (Table 1). This latter comparison was made while excluding 1 individual in 2004, which departed exceptionally late in the fall (Calendar Day 334, i.e. > 2 wk [17 d] after any other tagged whales)

and moved rapidly throughout migration (mean swimming speed = 3.1 km h^{-1} while mean swimming speed for the other individuals never exceeded 2.3 km h^{-1}).

The use of one or the other strategy was related to SST. The χ^2 statistics for the resource selection analyses (RSA) were significant in 2002 ($\chi^2_{L1} - \chi^2_{L2} = 213.2$, $df = 2$) and 2003 ($\chi^2_{L1} - \chi^2_{L2} = 11215.7$, $df = 2$) and showed that belugas preferentially selected SSTs $< 4^\circ\text{C}$ (Tables 2 & 3). Higher temperatures were avoided. In 2004, the difference was not significant ($\chi^2_{L1} - \chi^2_{L2} = 0.3$, $df = 2$) revealing no clear selection for a class of temperature (Tables 2 & 3).

The range of water temperatures varied from 2.9 to 9.7°C in 2002 and from 3.3 to 9.5°C in 2003, with cold waters being found primarily to the north of the Belcher Islands (Fig. 3a,b). In 2004, the range was marginally lower from 2.8 to 8.4°C and cold waters were broadly dispersed throughout EHB (Fig. 3c). Consequently, average water temperatures were lower in 2004 ($4.8 \pm 1.1^\circ\text{C}$) than in 2002 and 2003 ($6.0 \pm 1.6^\circ\text{C}$ and $6.0 \pm 1.1^\circ\text{C}$, respectively; ANOVA: $F_{2,7497} = 736.24$, $p < 0.001$ with computation of Tukey's 'honestly significant differences').

4. DISCUSSION

Although the deployment of satellite tags on 27 belugas represents a considerable field effort, sample size and time span for tag deployment are small for examining inter-annual differences and effects

Table 2. *Delphinapterus leucas*. Habitat (temperature) classes, proportion of study area in each type and number of occasions a given beluga was observed in class. x]: x is included in the class; [x: x is excluded from the class; dashes: no data

Temp. class ($^\circ\text{C}$)	Available proportion	Ind. 1	Ind. 2	Ind. 3	Ind. 4	Ind. 5	Ind. 6	Ind. 7	Ind. 8	Total
2002										
≤ 4	0.320	258	204	38	31	–	–	–	–	531
]4; 6]	0.350	26	94	119	21	–	–	–	–	260
> 6	0.330	2	2	24	20	–	–	–	–	48
Total	1	286	300	181	72	–	–	–	–	839
2003										
≤ 4	0.170	1	20	407	28	26	156	20	303	961
]4; 6]	0.580	70	350	383	67	273	154	61	80	1438
> 6	0.250	0	2	1	4	0	14	12	0	33
Total	1	71	372	791	99	299	324	93	383	2432
2004										
≤ 4	0.496	108	112	158	105	95	–	–	–	578
]4; 6]	0.501	60	217	69	119	111	–	–	–	576
> 6	0.004	0	4	1	0	1	–	–	–	6
Total	1	168	333	228	224	207	–	–	–	1160

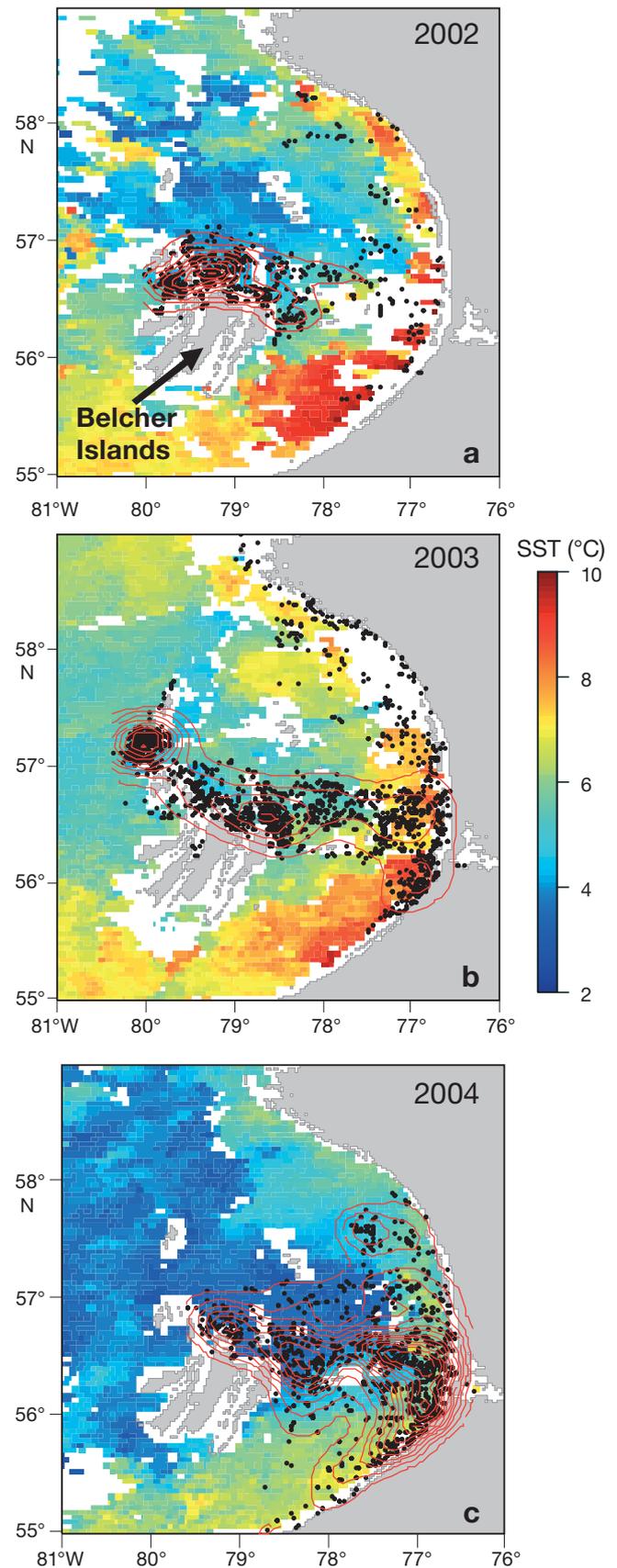
Table 3. *Delphinapterus leucas*. Estimated relative probabilities of selection for different habitats by overall belugas, with lower and upper simultaneous 90% confidence limits computed using Bonferroni inequality. u_{i+} is the number of units of type i used by all the animals and u_{++} is the total number of units used by all the animals. $\pi_i = a_i / a_+$ with a_i the number of available resource units in category i and a_+ the total sample size of available unused units. x_j : x is included in the class; $|x$: x is excluded from the class; CL: confidence limit

Habitat class (°C)	u_{i+}	$\pi_i u_{++}$	w_i	SE(w_i)	Bonferroni CL	
					Lower	Upper
2002						
≤4	531	267.81	1.98	0.08	1.87	2.09
]4; 6]	260	296.67	0.88	0.03	0.83	0.92
>6	48	274.52	0.17	0.01	0.16	0.18
2003						
≤4	961	419.28	2.29	0.16	2.12	2.46
]4; 6]	1438	1405.70	1.02	0.02	0.98	1.05
>6	33	607.03	0.05	0.01	0.04	0.07
2004						
≤4	578	102.59	1.00	0.04	0.95	1.06
]4; 6]	576	103.66	0.99	0.04	0.94	1.04
>6	6	0.74	1.44	0.75	0.35	2.52

of climate change. Although SST was related to the movement of belugas and appears to be a good proxy for predicting migration timing, the atypical behaviour of one of the whales suggests that other environmental characteristics or features intrinsic to the animals might also trigger migration. Nonetheless, the present study is among the first to reveal a mechanism by which environmental conditions determine habitat use and migration patterns of beluga whales, and this work indicates possible alteration of well-established migration phenology by longer term effects of climate change on this Arctic species.

Migration can be viewed as an adaptation to areas in which changes in habitat quality occur asynchronously, so that movement allows a succession of temporary resources to be exploited as they arise. One notable feature of the marine Arctic environment is

Fig. 3. *Delphinapterus leucas*. (a) Sea-surface temperatures (SST) in eastern Hudson Bay (EHB) during the pre-migratory period (September). Red density curves are based on the locations of all individuals (black dots) and illustrate that the main strategy in (a) 2002 and (b) 2003 was Strategy A (*aggregated*), while in (c) 2004 it was Strategy D (*dispersed*). Strategy A: diving activity occurs in a restricted area of cold waters located north of the Belcher Islands (2002 and 2003); Strategy D: diving activity occurs over a broad area within the arc of EHB (2004)



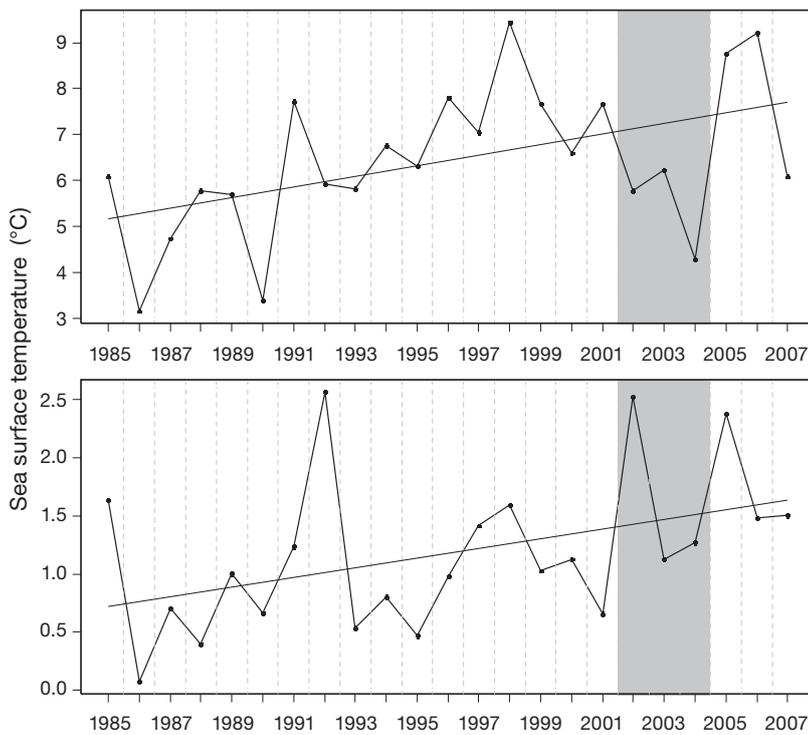


Fig. 4. (a) Time series of sea-surface temperature (SST) in eastern Hudson Bay (EHB) (continuous black line) averaged over September from 1985 to 2007, showing an increase in mean temperature (regression line; $y = 0.11x + 5.04$; $R^2 = 0.23$; $p = 0.02$). The gray shading represents the study period. (b) Spatial variance in SST (continuous black line), showing a significant increase in temperature heterogeneity within EHB (regression line; $y = 0.04x + 0.68$; $R^2 = 0.18$; $p = 0.04$)

the seasonal sea-ice cover, which has effects on habitat quality. For instance, sea ice, particularly in marginal zones, creates conditions for a seasonal primary production bloom (Bluhm & Gradinger 2008), which favours the aggregation of copepod grazers and other zooplankton species and is attractive for species from higher trophic levels (Pershing et al. 2004, Bluhm & Gradinger 2008). In such a changing habitat, predators like belugas might use environmental cues, e.g. ocean temperature or prey distribution and/or availability, to adjust the timing of their migration so as to maximize the gain from habitat occupancy. Arctic cetaceans are well-adapted to a life in ice-covered waters, breaking through thin ice to breathe and using ice-associated biological resources for feeding or exploiting ice properties for predator avoidance. At the same time, beluga may also be constrained by ice, as it entails risk of mortality by entrapment through reduced access to air and/or the availability of suitable habitat (Ivashin & Shevlyagin 1987). The increase in the risks of ice entrapment as the fall progresses, coupled with a possible reduc-

tion in feeding opportunities compared to other locations, probably influence beluga decisions in regard to migration timing.

Beluga migration patterns are relatively stable from year to year (Barber et al. 2001, Richard et al. 2001a,b, Suydam et al. 2001, Laidre et al. 2008). Given that calves accompany their mothers closely for 1 to 2 annual cycles, learned migratory behaviour is likely matrilineal. Our study has demonstrated how whales can make annual adjustments to the timing of migration on the basis of variations in the prevailing environmental conditions. While the degree of flexibility in migratory route is unknown, it is possible that flexible traditions have been developed through centuries of matrilineal culture that is adapted to changes in local conditions.

Long-term changes in temperature and sea-ice regimes linked to global warming affect the functioning of many Arctic systems (Hinzman et al. 2005). Habitat change is particularly critical when a species is highly specialized in its resource use. Although beluga whales are feeding generalists, they remain vulnerable to climate-induced food web cascades that may be triggered by rapid shifts in environmental conditions (Hansen et al. 2003). For instance, reduced sea-ice cover

results in a premature phytoplankton bloom, with the potential to disrupt connectivity between phytoplankton and copepod grazers ascending from depth at specific times of the year (Hunt et al. 2002, Hansen et al. 2003, Bluhm & Gradinger 2008). Such a trophic decoupling could affect the abundance of prey, resulting in reduced energy availability for belugas. Temperature-induced delays in migration might also reduce the period spent within winter areas, where EHB belugas are thought to acquire most of their energy reserves, and have the potential to alter their energy balance. Predator–prey relationships at higher trophic levels may also be altered, as reduced ice cover may negatively affect polar bears, while being favourable to predators of belugas such as killer whales (Higdon & Ferguson 2009). Consequently, a modification in migration phenology might affect individual survival and population demography (Both et al. 2006).

The year 2004 was the coldest summer in the past 15 yr (Fig. 4a), but had SSTs similar to those observed prior to 1991. Since the mid-1990s, SST and its spatial

variability have generally increased, i.e. EHB has become warmer and more heterogeneous (Fig. 4a,b). The later departure of belugas for migration observed in 2002 and 2003, when warmer and spatially more heterogeneous temperatures prevailed in EHB during summer, may become more typical of the migration pattern of belugas as temperatures continue to increase. However, more information on prey distribution and abundance and on the migratory behaviour of belugas over a longer time series is required before definitive conclusions can be drawn on the risks posed by rapid environmental changes in the Arctic.

The EHB stock of beluga has declined sharply as a result of past commercial and continued subsistence harvest and is currently designated as endangered in Canada (COSEWIC 2004). The importance of beluga for Inuit culture and subsistence place a premium on the preservation of the resource, as it represents a key element linking aboriginal communities to the Arctic ecosystem (Kemper 1980). A later departure for fall migration might decrease accessibility to hunters because of shorter daylight periods later in the season, possibly reducing harvesting pressure on the population. Combined with knowledge of possible changes in marine mammal assemblages and changes in the condition of belugas, which could result from a trophic decoupling, our observation of a climate-driven change in migration phenology provides important information for the conservation of belugas.

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