

Differences in diving and movement patterns of two groups of beluga whales in a changing Arctic environment reveal discrete populations

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ABSTRACT: Harvest and global climate change are among the major ongoing threats to most Arctic marine mammal populations. Affected by commercial hunting in the past, beluga whales *Delphinapterus leucas* are still harvested for subsistence in many coastal areas of the Canadian Arctic, while ongoing climate changes are suspected to modify factors that may have determined the distribution and degree of interaction of the different populations. Although several populations have been clearly identified, the global discreteness of the Arctic metapopulation is not yet clearly established. In this study, seasonal diving activity and movement patterns of 46 belugas from 2 neighbouring groups in Hudson Bay (Canada) were analysed in relation to physical environmental characteristics and revealed significantly different migratory and habitat use patterns. Likely affected by local environmental conditions, the Eastern Hudson Bay beluga migrate, while the James Bay beluga remain resident, suggesting little overlap between the groups at all times of the year. This study provides useful baseline data for determining population interactions and habitat use. The information is also potentially useful in identifying critical habitat, which is an essential component to design and implement management and conservation policy, e.g. quota and harvesting regulations and the design of marine protected areas.

KEY WORDS: Conservation · Arctic changes · Bio-logging · Population mixing · Migration · *Delphinapterus leucas* · Marine mammals

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INTRODUCTION

Arctic systems are generally characterized by high seasonality in environmental characteristics (e.g. Svendsen et al. 2002). They have also been described as being partially resilient to climate variation because of the amplitude of seasonal fluctuations in environmental conditions, e.g. seasonally varying sea ice cover (Piepenburg 2005). However, the combined rate and magnitude of change expected in the future suggests that Arctic systems will nevertheless be vulnerable to climate change (Walsh 2008). Previous

studies have revealed trends over the past 20 to 30 yr of decreasing sea ice extent in the Arctic Ocean coincident with global warming (Maslanik et al. 1996). Such changes are expected to affect polar marine ecosystems (Smetacek & Nicol 2005).

More specifically, Hudson Bay (Canada) has experienced, and is predicted to further undergo, significant environmental changes that may affect the distribution of marine mammals (Petersen et al. 2010). Within this region, some species may become extirpated or isolated (e.g. southern Hudson Bay polar bears; Stirling et al. 2004), while others may expand

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their ranges (e.g. killer whales) as a result of warmer temperatures (Higdon & Ferguson 2009). Consequently, the greater Hudson Bay ecosystem may be viewed as an early warning system for the larger Arctic ecosystem. In parallel, the Hudson Bay ecosystem has also been strongly influenced by commercial hunting in the past, which has been responsible for the depletion of many resident marine mammal populations (Reeves 2000). Currently, in many locations within the bay, traditional harvest continues to maintain a negative pressure on especially small and depleted populations.

Beluga whales *Delphinapterus leucas* have a discontinuous circumpolar distribution in Arctic and sub-Arctic waters (Stewart & Stewart 1989) and are subdivided into at least 16 provisional management stocks, 11 of which exist in North America. Four of these stocks are currently recognized for management purposes in the Canadian Eastern Arctic (Donovan 1992). It is generally assumed that groups of belugas associated with particular summering areas constitute separate stocks (e.g. Reeves & Mitchell 1987), and to date, genetic studies have not disproven this postulate (Buchanan et al. 1996). The species undertakes seasonal migrations of varying extents, ranging from several hundreds of kilometres in the Beaufort Sea (Richard et al. 2001), to tens of kilometres in the St. Lawrence estuary (Lesage & Kingsley 1998). In other areas, e.g. Cook Inlet and Cumberland Sound, beluga populations reside in the same locale all year round (Moore et al. 2000). Although the variability among populations in the extent of seasonal movement is thought to be related to food availability and risks of ice entrapment or predation, the relative importance of these environmental factors in shaping population-specific habitat use and migration patterns is unknown. In a warming climate, a reduction in sea ice coverage might affect prey availability and entrapment risks, causing changes to existing population-specific migratory patterns (Walther et al. 2002). Therefore, climate change may lead to significant modifications in the geographic range and distribution of belugas and the degree of overlap among stocks.

Belugas in Hudson Bay are divided into a western population that may encompass more than 1 stock, and an eastern population centred on the Hudson Bay arc (hereafter referred to as EHB; Brennin et al. 1997). The western population is currently designated as being of special concern (COSEWIC 2004), while the eastern population, which declined from 4200 to 3100 individuals over the period 1985 to 2004 (Doniol-Valcroze et al. 2011), is designated as endan-

gered (COSEWIC 2004). Both populations undertake seasonal migrations through Hudson Strait, where their distribution likely overlaps (DeMarch & Postma 2003). Other congregations of belugas reported in areas in and adjacent to Hudson Bay include the Foxe Basin, south-western Hudson Bay, Belcher Islands and James Bay (Richard et al. 1990). The relationship of these stocks to the western and EHB stocks and their patterns of seasonal movement remain unclear.

Remote sensing and satellite telemetry have proven to be powerful tools for obtaining data on the seasonal movement patterns and habitat characteristics of wildlife, especially for large marine species, e.g. belugas, that would otherwise be difficult to observe *in situ* (Ropert-Coudert & Wilson 2005). Coupled with knowledge of environmental correlates now routinely available from satellites, telemetry data may enhance our understanding of the environmental factors that lead to seasonal migrations. In the present study, we have synthesized information on seasonal diving activity, movement patterns and associated environmental factors for belugas from 2 neighbouring geographical regions of the Hudson Bay complex in northern Canada, to investigate patterns of seasonal habitat use in relation to the physical environment available to belugas. In particular, we attempt to provide evidence of stock discreteness and to identify physical environmental features of beluga habitat that may help improve our ability to design and implement proactive conservation and management policies aimed at sustaining beluga populations confronted with combined harvest and environmental stressors.

MATERIALS AND METHODS

Characteristics of devices

Different satellite transmitters were used: SPOT tags (location and temperature recorders), SDR-T16 tags (satellite-linked time-depth recorders), both from Wildlife Computers, or temperature depth-satellite relayed data loggers (TD-SRDLs) from the Sea Mammal Research Unit (SMRU; St. Andrews, UK). TD-SRDLs were microprocessor-controlled recording units equipped with a pressure transducer (pressure ± 2 dbar), temperature probe (temperature $\pm 0.005^\circ\text{C}$) and real-time internal clock. All sensors were contained in a $105 \times 70 \times 40$ mm resin housing weighing about 500 g and operational to depths of 2000 m. Data from SPOT and SDR-T16 tags were

processed using the SATPAK and SATPAK2003 applications provided by Wildlife Computers, while data from TD-SRDLs were processed automatically by the SMRU applications and were made available in a standardized database format.

Whale capture and attachment of devices

From 1993 to 2009, 51 belugas were captured using 6 inch (~15 cm) square mesh, shore-anchored nets, and equipped with tags secured to the dorsal ridge (Richard et al. 1997, Kingsley et al. 2001). Thirty-seven animals (12 females, 18 males and 7 of unknown sex) were tagged in July or August between 1993 and 2004 in the EHB arc (32 at the Little Whale River and 5 at the Nastapoka River). From 2007 to 2009, an additional 14 (11 females and 3 males) were captured and equipped at Cape Hope Island, James Bay (JB). Five EHB belugas (hereafter referred to as EHBB) with less than 15 d of data were removed from the analyses, resulting in final sample of 32 EHBB (11 females, 17 males and 4 undetermined) and 14 belugas from JB (hereafter referred to as JBB; Table 1).

Location data

Locations were obtained via the ARGOS satellite system. Locations were classified according to their estimated accuracy: 250, 500, 1500 and >1500 m for classes 3 through 0 (Argos). Classes A, B and Z had undetermined accuracies. Unrealistic locations were rejected using a forward particle-filtering model (Tremblay et al. 2009). 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 recorded position, of a radius that depends on its estimated accuracy. Each particle is weighted according to the likelihood of the speed needed to get there from the previous recorded location. A maximum speed of 3 m s^{-1} was considered, based on the assumption that belugas rarely travel at speeds faster than this (e.g. Richard et al. 1998). Information on local ocean depth (source: ETOPO 1, see 'Environmental features') is used to eliminate particles that are 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 boot-strapped tracks (Tremblay et al. 2009).

Diving behaviour

Belugas were considered to be diving when recorded depth exceeded 4 m, otherwise they were defined to be at the surface. A summary record, including proportion of time spent diving or at the surface, number of dives, and mean, maximum and standard deviation (SD) of maximum dive depth and 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 24 SMRU tags, while we developed an R program for the 22 Wildlife Computer tags.

For each dive, we extracted the local ocean depth (source: ETOPO 1, see 'Environmental features'). The ratio between the maximum dive depth and local ocean depth was used as an index of the position of the individual in the water column, with an index closed to 1 indicating a demersal activity.

Environmental features

Satellite remote sensing data were also used to complement the set of oceanographic data collected by the animals. Ocean depth was obtained from ETOPO1 (NOAA National Geophysical Data Center, <http://ngdc.noaa.gov/mgg/global/global.html>), a 1 arc-minute global relief model of the Earth's surface that integrates land topography and ocean bathymetry. Data on sea surface temperature (SST, $4 \times 4 \text{ km}$ resolution) used in the discussion and presented in Fig. 6 were gathered using the PO.DAAC Ocean ESIP Tool (POET, <http://poet.jpl.nasa.gov/>), while data for sea ice concentration ($1^\circ \times 1^\circ$) were collected via the Integrated Global Ocean Services System (IGOSS, <http://iridl.ldeo.columbia.edu/>).

Analyses of residency versus migration patterns

Seasons were defined using the traditional calendar for the northern hemisphere: summer from 21 June to 22 September, fall from 23 September to 21 December and winter from 22 December to 20 March. Spring was not considered in this study because all tags had failed by the end of March and, as a consequence, no data were available for that

Table 1. *Delphinapterus leucas*. Synthesis of deployments. Belugas were captured in 2 different locations, EHB: Eastern Hudson Bay and JB: James Bay. Colour of individuals is an index of their age from younger (G: gray, LG: light gray) to older (W: white) animals. Total number of locations is only indicated for the individuals included in the analyses. ?: unknown

ID_year	Tag type	Site of capture	Sex	Length (cm)	Colour	Deployment date (dd/mm)	Total locations	Record duration (d)	Total distance (km)
11747_1993	SDR-T16	EHB	?	280	G	12/08	–	30	1472
11748_1993	SDR-T16	EHB	?	?	W	15/08	–	19	592
5090_1993	SDR-T16	EHB	?	390	W	12/08	–	43	1855
17908_1999	SDR-T16	EHB	?	270	G	29/07	–	39	1639
1854_1999	SDR-T16	EHB	F	310	W	29/07	–	85	3976
2014_1999	SDR-T16	EHB	F	330	G	29/07	–	25	304
17905_2002	SPOT	EHB	M	375	W	28/07	307	122	5479
17906_2002	SPOT	EHB	M	394	W	28/07	325	136	4954
17911_2002	SPOT	EHB	M	290	LG	24/07	–	69	2374
1851_2002	SDR-T16	EHB	F	342	W	20/07	–	80	4131
1852_2002	SDR-T16	EHB	F	332	W	24/07	1389	165	10858
1853_2002	SDR-T16	EHB	M	353	LG	19/07	–	44	2396
1855_2002	SDR-T16	EHB	M	321	W	24/07	1667	175	10553
17905_2003	SDR-T16	EHB	M	294	G	22/07	1380	149	8818
17906_2003	SDR-T16	EHB	M	315	G/W	23/07	1229	153	9155
17911_2003	SDR-T16	EHB	M	360	W	27/07	1547	222	10538
1851_2003	SPOT	EHB	F	230	G	22/07	–	48	1492
1852_2003	SPOT	EHB	M	265	G	11/07	999	200	8449
1853_2003	SPOT	EHB	M	310	G	14/07	627	214	7644
1854_2003	SPOT	EHB	M	295	G	27/07	711	266	10252
1855_2003	SPOT	EHB	M	325	G	27/07	–	56	1515
3022_2003	SMRU	EHB	M	385	W	11/07	2711	220	14669
3415_2003	SMRU	EHB	F	335	W	22/07	3988	209	14057
5091_2003	SDR-T16	EHB	F	335	W	22/07	–	46	2184
9365_2004	SMRU	EHB	M	300	LG	09/07	–	71	4675
9366_2004	SMRU	EHB	F	350	W	04/07	–	105	4326
9367_2004	SMRU	EHB	F	361	W	18/07	2019	272	17433
9371_2004	SMRU	EHB	M	281	G/W	14/07	–	95	6688
9378_2004	SMRU	EHB	M	310	G/W	04/07	768	187	9790
9379_2004	SMRU	EHB	F	348	W	12/07	1073	156	8903
9390_2004	SMRU	EHB	M	370	W	17/07	2511	292	20407
9392_2004	SMRU	EHB	F	350	W	21/07	824	112	7664
44436_2007	SMRU	JB	F	304	W	14/08	696	83	2898
44485_2007	SMRU	JB	M	299	LG	20/08	558	84	3224
44436_2008	SMRU	JB	F	341	W	16/08	978	149	4500
44446_2008	SMRU	JB	F	353	W	06/08	219	115	694
44447_2008	SMRU	JB	F	275	LG	08/08	1132	137	6465
44451_2008	SMRU	JB	F	331	W	08/08	742	115	4337
44452_2008	SMRU	JB	F	333	W	10/08	293	47	2220
44477_2008	SMRU	JB	F	310	W	16/08	1035	210	6596
44478_2009	SMRU	JB	M	289	W	09/08	924	117	3354
44479_2009	SMRU	JB	F	366	W	30/07	2123	156	8283
44480_2009	SMRU	JB	F	344	W	31/07	1782	176	9081
44481_2009	SMRU	JB	F	288	LG	10/08	737	156	4761
44482_2009	SMRU	JB	F	310	LG	02/08	1496	193	8707
44483_2009	SMRU	JB	F	306	LG	01/08	299	58	1579

period. Areas of residency were identified using a first-passage time approach (FPT) as described by Fauchald & Tveraa (2003). The method was applied to the entire filtered track of each individual, which was fragmented and interpolated to obtain 1 location every 2 km. Each location was associated with a circle of a fixed radius r . The time required for

crossing the circle in the first passage (i.e. the FPT value) was calculated. The computational process was repeated for each location and for a range of r (here from 2 to 800 km). Over the entire track, the variance among the FPT values (log-transformed: see Fauchald & Tveraa 2003) was calculated as a function of r . The radius corresponding to the maxi-

mum peak in variance indicated the most relevant scale to differentiate the highest FPT values that revealed residency patterns from the lowest ones that revealed migration patterns. To spatially locate where an animal was resident and the time spent in that area, FPT values associated with the most relevant scale were plotted as a function of time since departure. The areas where tracks tended to be tortuous and movements repetitive yielded the highest FPT values and were defined as 'residency' areas (Fauchald & Tveraa 2003). In contrast, the lowest FPT values, especially those located between the end of summer and the beginning of fall, defined the fall migration period. The date of shift between high and low FPT states was defined as the date of departure for migration and validated by determining whether a route outside the residency area without return existed.

RESULTS

Seasonal movements

Of the 46 belugas with data records for ≥ 15 d, 29 individuals, including 17 EHBB and 12 JBB (all tagged in 2002 or later), had records that extended beyond the summer season (Table 1). Belugas from these 2 neighbouring regions differed markedly in their seasonal movements. The 17 EHBB still transmitting in the winter had migrated out of Hudson Bay by mid-November, while all 12 JBB still transmitting on that date were still in JB and remained there until their last day of transmission (mid-November to mid-March; Fig. 1).

The analysis of FPT identified 3 seasonally-dependent residency areas for EHBB, i.e. EHB, Ungava Bay (UB) and the Labrador Sea (LS; Fig. 1). The mean scale of restricted search decreased from 158 ± 61 km

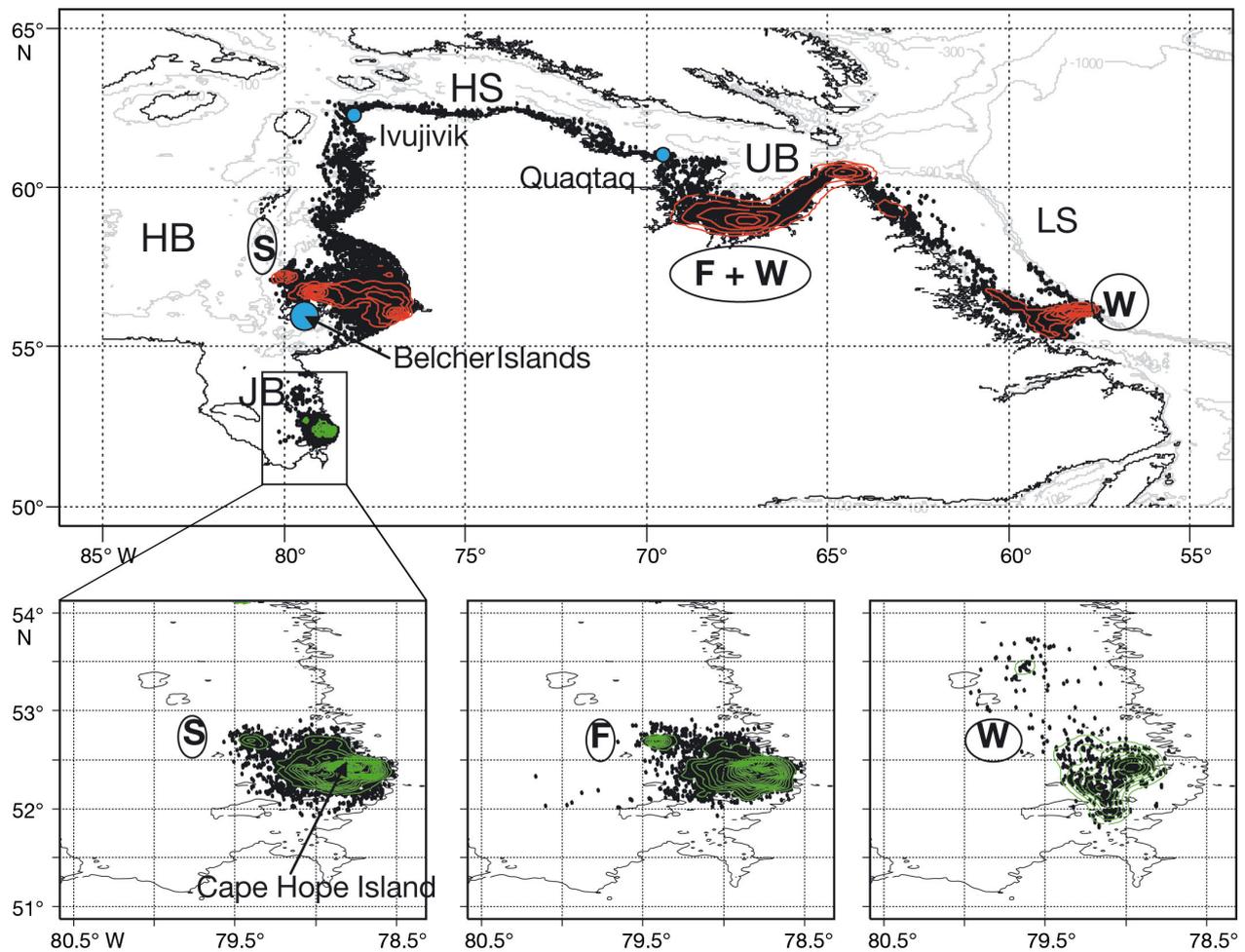


Fig. 1. *Delphinapterus leucas*. Hudson Bay beluga complex showing all locations recorded during the study (black dots). Density curves (95%) in red indicate the main residency areas of eastern Hudson Bay (HB) belugas in summer (S), fall (F) and winter (W). Density curves (95%) in green indicate the same for belugas in James Bay (JB). HS: Hudson Strait, UB: Ungava Bay, LS: Labrador Sea

in the summering area (EHB) to 104 ± 65 km in UB and 67 ± 68 km in the wintering area (LS; Table 2). At the beginning of summer, tracks of EHBB indicated regular inshore–offshore movements of an average 119 ± 74 km (max: 425 km) from their tagging site. Although all animals immediately left the capture site after being tagged, 28 individuals (i.e. 87.5%) returned to it at least once during the summer. The first time was on average less than 10 d after capture. Starting in September, all individuals moved offshore, with 23 belugas (i.e. 72%) moving closer to the northern coast of the Belcher Islands (Fig. 1).

The shift from high to low FPT values indicated a departure from EHB between 19 September and 26 November, depending on the individual (mean \pm SD: 16 October \pm 18 d). Animals moved to the Hudson Strait and Ivujivik area, approximately 400 km north of the EHB arc, and reached the strait on average 10 ± 12 d after departure. During the migration phase,

Table 2. *Delphinapterus leucas*. Spatial scale of restricted movement of Eastern Hudson Bay (EHB) and James Bay (JB) belugas within their summer, fall and winter residency areas as determined by the first-passage time (FPT) analysis. –: no scale was identified

ID_year	Site of capture	Scale of restricted movement (km)		
		Summer	Fall	Winter
17905_2002	EHB	190	240	50
17906_2002	EHB	200	100	25
1852_2002	EHB	170	110	–
1855_2002	EHB	85	25	–
17905_2003	EHB	–	90	15
17906_2003	EHB	200	85	20
17911_2003	EHB	170	55	–
1852_2003	EHB	55	110	–
1853_2003	EHB	120	90	100
1854_2003	EHB	65	220	–
3022_2003	EHB	200	220	20
3415_2003	EHB	280	45	35
9367_2004	EHB	140	70	–
9378_2004	EHB	110	90	–
9379_2004	EHB	190	70	220
9390_2004	EHB	220	–	120
9392_2004	EHB	140	50	–
44436_2007	JB	20	10	–
44485_2007	JB	25	15	–
44436_2008	JB	25	15	–
44446_2008	JB	–	–	–
44447_2008	JB	35	20	–
44451_2008	JB	–	10	–
44477_2008	JB	25	35	–
44478_2009	JB	10	6	–
44479_2009	JB	25	40	–
44480_2009	JB	8	30	20
44481_2009	JB	40	20	20
44482_2009	JB	25	20	–

animals remained 15 ± 12 km from shore (range: 0.05 to 61.5 km). EHBB continued eastward through Hudson Strait towards Quartaq and the UB, while remaining within 14 ± 11 km (range: 0.57 to 50 km) from shore (Fig. 1). On average, it took animals 7 ± 4 d to cover the 500 km distance separating Ivujivik and Quartaq at the entrance of UB, resulting in a mean total migration time of 22 ± 9 d and a mean swimming speed of 2.0 ± 0.6 km h⁻¹.

The 17 EHBB then entered UB, where they spent time in the southeastern part of the bay (Fig. 1). Tags from 8 whales failed after spending 44 ± 28 d there (range: 12 to 107 d). The last transmission from a tag in this area was in late February, indicating that at least 1 individual spent a substantial portion of the winter in the bay. The other 9 individuals left UB between 1 and 25 December, after spending on average 40 ± 17 d there (range: 6 to 55 d). EHBB then migrated approximately 570 km along the coast to an area of deep troughs along the Labrador shelf in the LS, where they arrived between 31 December and 23 January and remained until tag failure 61 ± 46 d later (Fig. 1). All transmitters had ceased functioning by 5 March.

In contrast with EHBB, JBB had a distribution which varied seasonally little. All animals remained within JB as long as the tags transmitted (mean \pm SD: 144 ± 68 d, median: 140 d, range: 45 to 299 d). With the exception of 3 individuals that moved to the northern part of the bay in January, JBB generally did not venture far from their tagging site (Cape Hope Island) where they returned regularly until tag failure (5 November to 10 February; Fig. 1). The mean scale of restricted search in JB did not vary seasonally (summer: 23.8 ± 9.7 km; fall: 20.1 ± 10.8 km, $t_{18,99} = 0.83$, $p = 0.42$; small sample size for winter prevented inclusion in the analysis; Table 2).

Diving activity

In EHB, diving activity markedly increased when belugas were located to the north of the Belcher Islands and was maintained at a maximum, around 80% of total time, for the 1 to 2 mo preceding the fall migration (Fig. 2a). While the EHBB used the entire water column when close to the mainland coast, most dives in the vicinity of the Belcher Islands were closer to the sea floor (Fig. 3a). With the onset of migration, diving activity decreased compared to the end of summer, although it still represented between 60 and 70% of their time (Fig. 2a). Diving activity increased again to about 80% of total time when animals reached the UB fall residency area (Fig. 2a), although

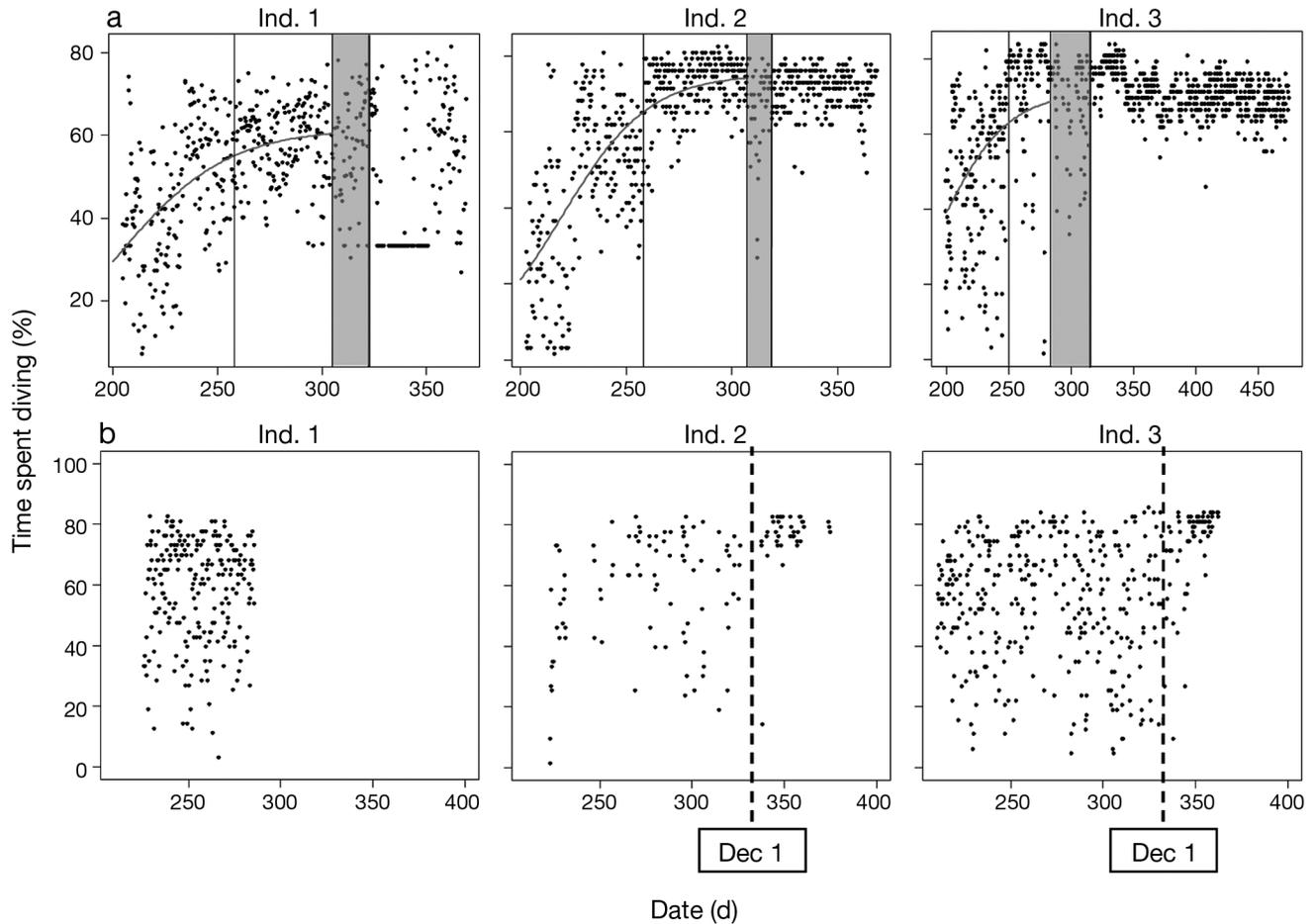


Fig. 2. Proportion of time spent diving according to date for (a) 3 individuals from Eastern Hudson Bay (EHB) that showed a progressive increase in diving activity to reach a maximum in September, about 1 or 2 mo before migration (in gray) (as illustrated by the curve), and (b) 3 individuals from James Bay (JB) that showed an increase in diving activity only from December

no specific depth seemed to be preferred during their stay in this area (Fig. 3b). Belugas wintering in the LS continued to spend a large proportion (80%) of their time diving (Fig. 2a). There, individuals either remained close to the surface or dived close to the sea floor, spending little time in between (Fig. 3c).

In JB, diving activity was highly variable until December (Fig. 2b), when it increased substantially and was maintained at a high level (around 80% of time) until the tags failed (Fig. 2b). Although JBB tended to use the entire water column (Fig. 3d), they dived significantly deeper during winter (from December; 29 ± 18 m) than during summer and fall (16 ± 13 m; $t = 37.4$, $p < 0.001$).

Environmental correlates

EHBB preferentially used relatively shallow waters (58 ± 28 m; Fig. 4). The habitat was characterized by

strong thermal stratification of the water column (range: -1.5 to 13.5°C), with a thermocline located at around 40 m. EHBB dived mainly around the thermocline during summer (Fig. 5a). Diving activity increased in September, when belugas occupied areas to the north of the Belcher Islands where the water column was more homogeneous in temperature, at around 3°C (Fig. 5a). In UB, EHBB generally used deeper waters (119 ± 84 m). Although there were clear indications from some tracking positions that individuals entered river estuaries in UB, no particular depth was favoured (Fig. 4) within the well-mixed water column ($\approx 1^\circ\text{C}$). In the LS, EHBB preferentially selected an area on the continental plateau characterized by a deep trough (353 ± 171 m; Fig. 4). In this region, most of the water column had temperatures of $\approx 0^\circ\text{C}$, with a minimum of -1.8°C . The one exception was a deep zone where EHBB systematically dove to depths where temperatures were between 3 and 4°C .

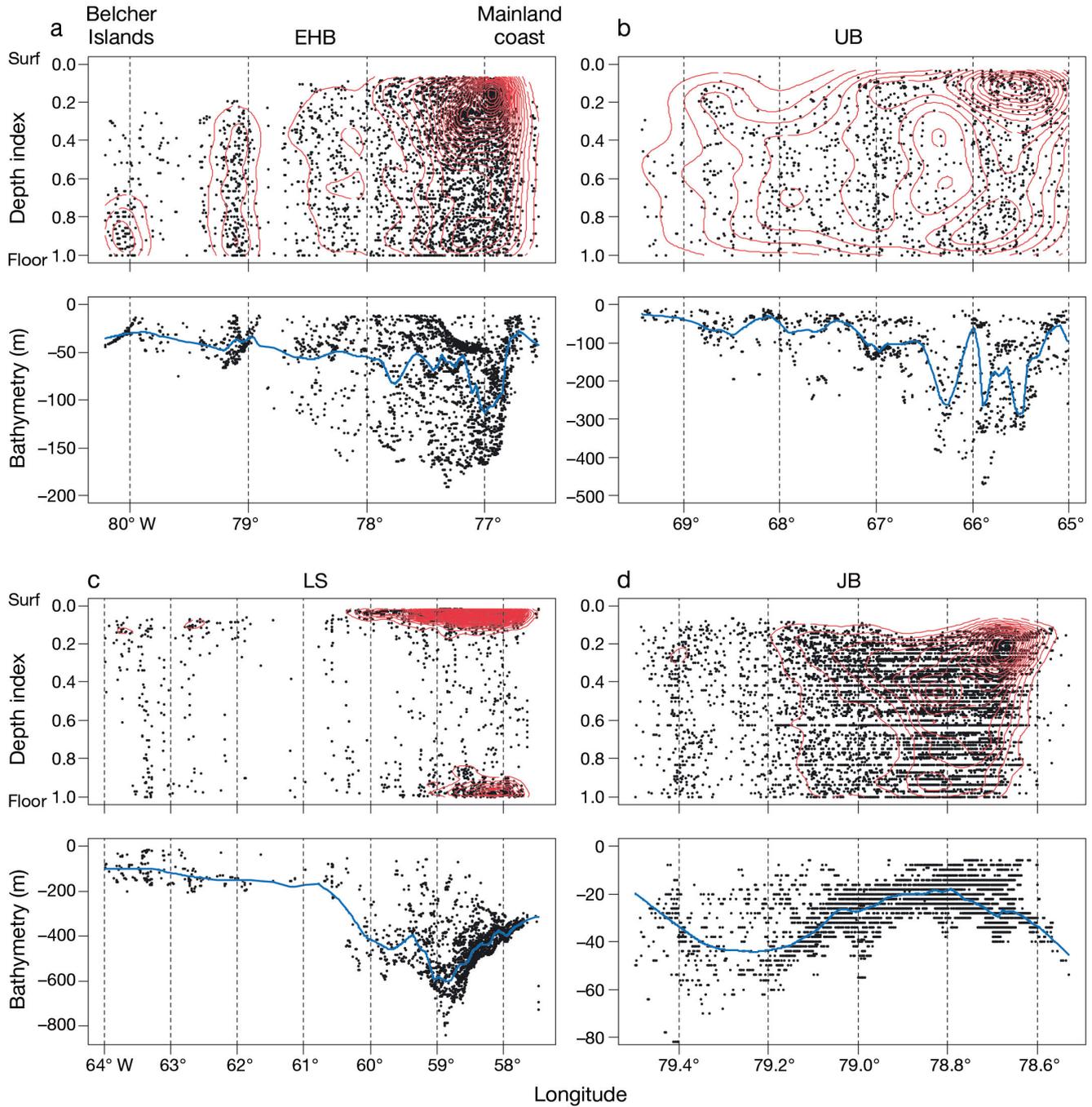


Fig. 3. *Delphinapterus leucas*. Density (red curves, external curve = 95%) of diving activity through the water column. Depth index is the ratio between maximum dive depth and corresponding bathymetry: 0 corresponds to the sea surface (surf), and proximity to the sea floor increases as the index approaches 1. Bathymetry corresponding to each dive is also shown, and a smooth curve (in blue) shows the relative shape of the sea floor. (a) Eastern Hudson Bay, EHB; (b) Ungava Bay, UB; (c) Labrador Sea, LS; (d) James Bay, JB

The habitat preferentially used by JBB was shallow (25 ± 10 m) and generally warm, with a strong thermal stratification (range: 2.5 to 15°C) during summer (Fig. 5b). Starting in October, water temperatures

began to homogenize and progressively decreased to reach negative values in December (range: -1.3 to 3.6°C; Fig. 5b). An intensification of JBB diving activity was observed at this time (Fig. 5b).

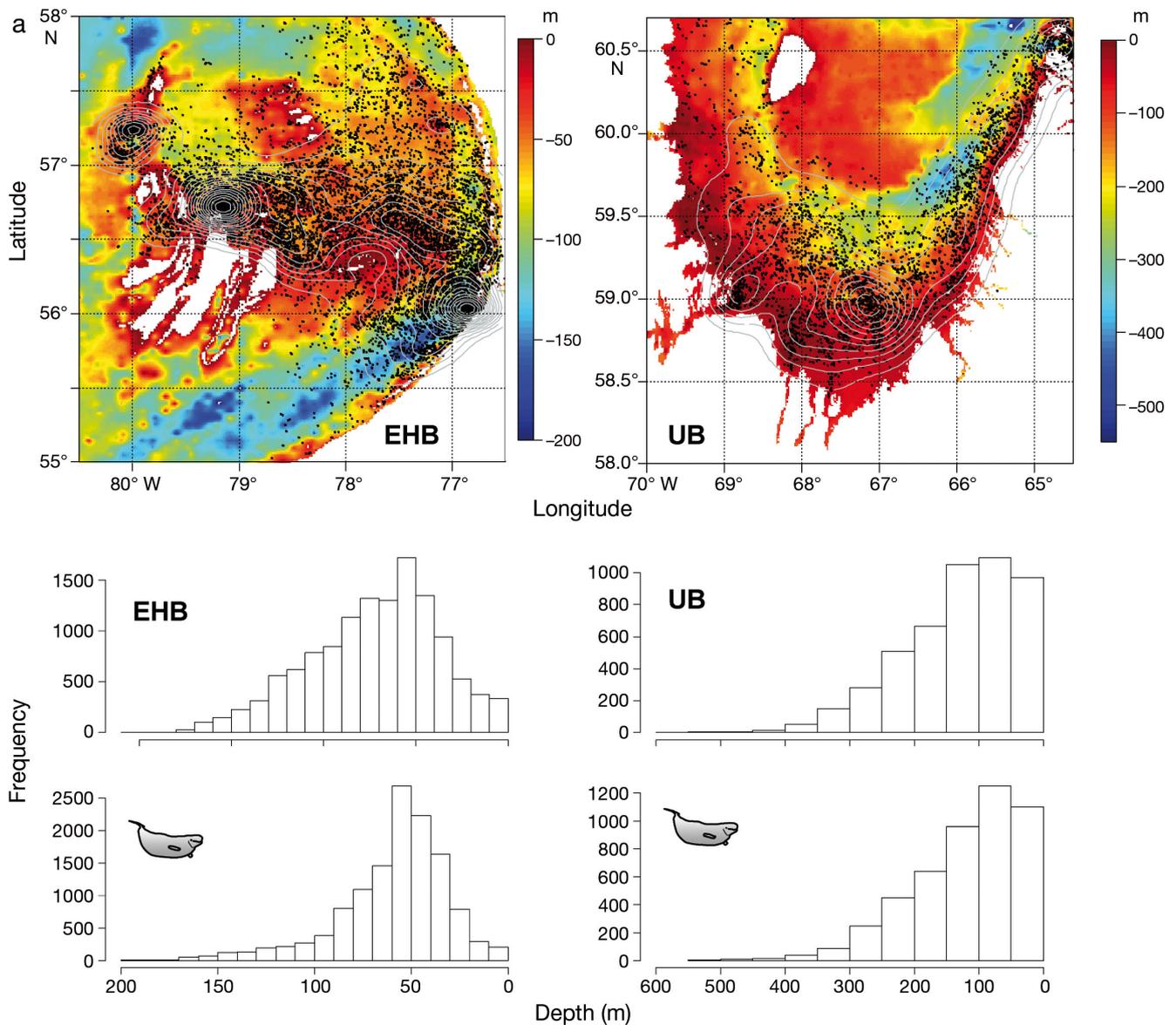


Fig. 4 (continued over page). *Delphinapterus leucas*. Bathymetry in each residency area associated with position (black dots) of all individuals (density curves in gray, external curve = 95%). Histograms represent values of bathymetry extracted under random locations (top graphs) in each area in comparison with values extracted using known beluga positions (bottom graphs); n = number of beluga positions. (a) Eastern Hudson Bay, EHB, and Ungava Bay, UB; (b) (next page) Labrador Sea, LS, and James Bay, JB

DISCUSSION

The analysis of seasonal diving activity, movements and associated measures of the physical environment for 2 neighbouring groups of belugas from the Hudson Bay complex revealed significant between- and within-population differences in movement patterns and diving activity. Movement patterns within JB were limited to a few tens of kilometres regardless of season, and there is a

strong probability that JBB reside year round in the bay. However, this cannot be confirmed because of loss of tags over time. In contrast, EHBB migrate thousands of kilometres between distinct summer and winter residency areas. Although the tagged individuals in our study may not demonstrate the complete range of variation in movements for the 2 groups, the consistency in movement patterns and habitat use among individuals from the same region suggests that our samples were statistically

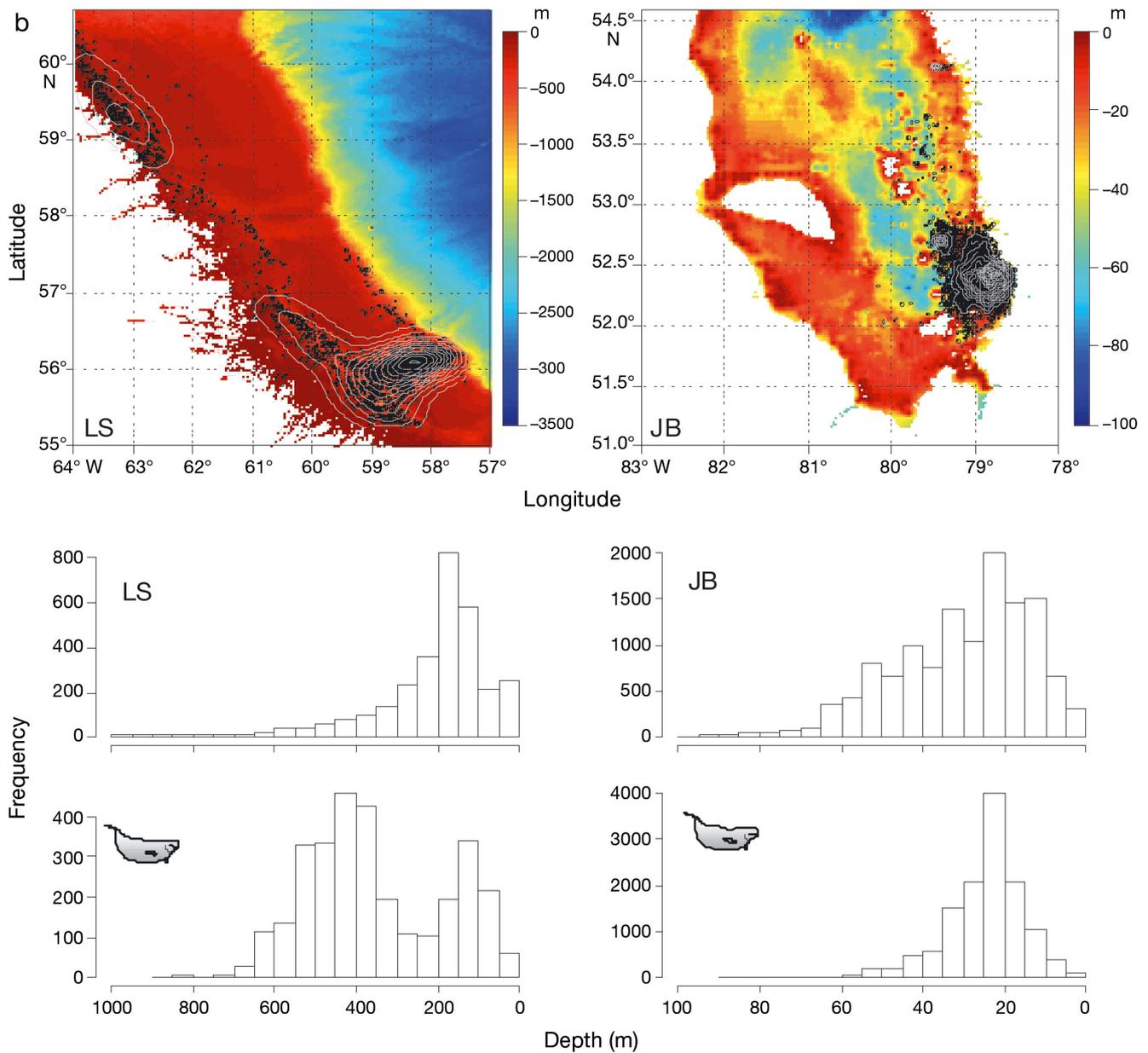


Fig. 4. (continued)

representative of the 2 populations. Although tag battery life was insufficient to document the spring migration, reports from Inuit hunters suggest a westward movement of beluga back into EHB along the south coast of Hudson Strait from late May through July (Lewis et al. 2009). These reports, when combined with previous studies documenting re-sightings of individuals identifiable by scars in the same estuary over successive years, suggest a certain degree of site fidelity, at least in EHB (Caron & Smith 1990).

Belugas from Eastern Hudson Bay

During summer, belugas from several populations are known to consistently congregate in shallow coastal waters or river estuaries. The life-history functions of these areas are unknown and may vary among sites, but might include thermal advantages for females and calves, feeding, moulting and predator avoidance (St. Aubin et al. 1990, Watts et al. 1991, Boily 1995, Richard et al. 2001). Arctic estuaries, in particular, are known to have some of the world's

highest concentrations of dissolved organic matter (DOM) and, thus, to be highly productive (Hessen et al. 2010). In EHB, where belugas undertake frequent inshore (estuaries) to offshore movements, the movements may represent multiple foraging trips influenced by the cyclicity of tidally-driven prey accessibility (Ezer et al. 2008).

Starting in September, animals stopped the inshore–offshore pattern of movements and most moved to a small area to the north of the Belcher Islands where they increased the frequency of demersal diving activity. Aggregations of marine mammals and seabirds are often associated with abundant prey resources constituted by fish schools (Welch et al. 1993). EHBB probably have, as many other beluga populations do, a diverse diet (e.g. Hobbs et al. 2008). Although their diet has not been well described, it is likely to include both capelin *Mallotus villosus* and Arctic cod *Boreogadus saida*, which are important components of Arctic marine food webs and form dense aggregations during the open-water season (Welch et al. 1993, Kelley et al. 2010). Accordingly, belugas may be congregating north of the Belcher Islands to exploit aggregations of these, or other, prey species.

During their seasonal migration, EHBB remained close to the coastline, a migration strategy that may allow them to benefit from the northward-flowing current that prevails along the east side of Hudson Bay (Saucier et al. 2004). Along the Labrador coast, beluga diving activity suggests repeated movement between partially ice-covered sea surface habitats and warmer, deep-sea areas. Such activity may be associated with foraging.

Belugas from James Bay

JBB displayed markedly different seasonal movements and habitat use characteristics from EHBB, which suggests that they likely represent a distinct population that is unlikely to overlap with EHBB regardless of season. JBB occupied smaller areas, re-

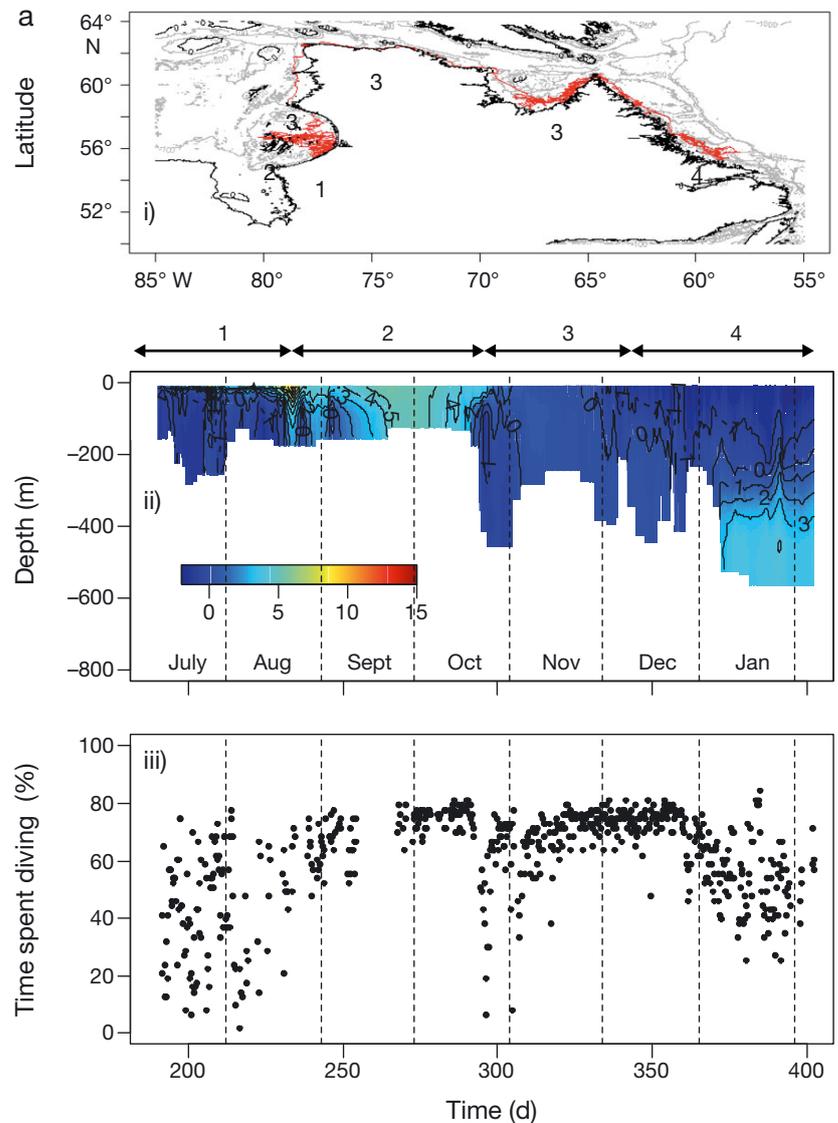


Fig. 5 (continued over page). *Delphinapterus leucas*. (i) Track of 1 representative individual (red line) associated with (ii) the vertical section of temperature (°C) it recorded and (iii) its diving activity according to the time in (a) Eastern Hudson Bay (EHB) and (b) (next page) James Bay (JB)

mained closer to their capture site and did not undertake any significant fall/winter migration. Although some small-scale movements to the northern part of the bay were observed, the majority of JBB movements were suggestive of localized overwintering. The lack of data on diet, fish abundance and distribution in JB limits our understanding of the proximate causes of the non-migratory behaviour of JBB. However, in contrast to EHBB, JBB appear able to find favourable thermal and feeding conditions year-round. The increase in diving activity in December prior to freeze-up may reflect a change in the distri-

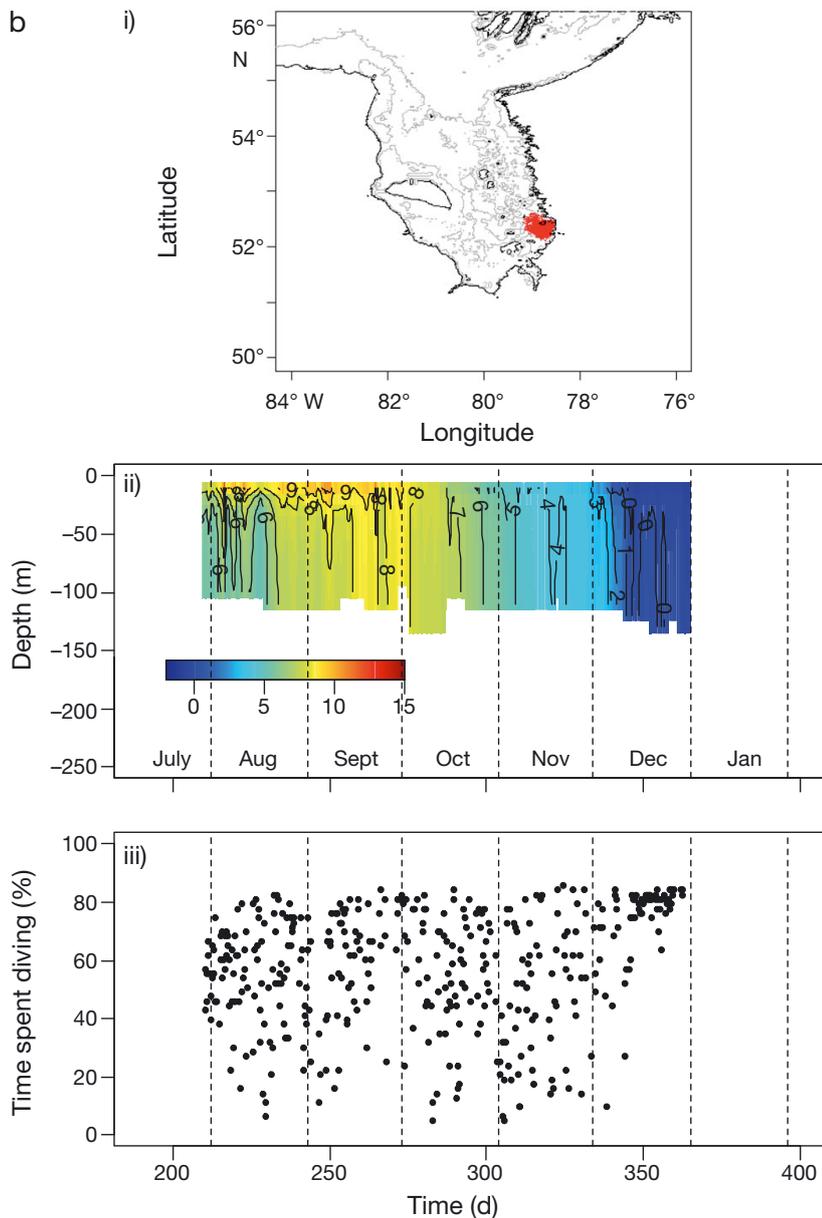


Fig. 5. (continued)

butional ecology of their main prey or a shift in diet. If sea ice represents an entrapment risk, then available JBB movement data indicate that sea-ice conditions in JB are generally conducive to successful over-wintering.

Origin of differences between populations

Predation by killer whales and ice entrapment are important causes of mortality in Arctic beluga populations (Shelden et al. 2003). Habitat selection should

therefore reflect a trade-off between accumulation of energy stores and avoidance of direct mortality. Food abundance and accessibility might be affected by physical environmental conditions, including SST and sea ice. The observed differences in environmental conditions and predation risks between regions might therefore explain the observed differences in the seasonal distribution and movement patterns among beluga populations. The precise role of each factor, particularly sea ice and risks of entrapment, in shaping seasonal movement patterns of EHBB and JBB remains unclear.

Belugas generally prefer sea ice cover of 70% or less, although they also use areas with multi-year ice and ice concentrations of up to 90% (Barber et al. 2001, Asselin et al. 2011). The EHB and JB regions both begin to freeze in early December and are normally ice-covered 15 d later (Canadian Ice Service, www.ec.gc.ca/glaces-ice/). From the long time series of temperatures and sea ice concentrations illustrated in Fig. 6, we observed that SSTs during the ice-free period appreciably increased within the last 25 yr, both in EHB and in JB (Fig. 6a). Concomitantly, a decrease in winter sea ice concentration seemed to occur in JB, while no clear tendency appeared in EHB sea ice conditions (Fig. 6b).

The evolution, distribution and ecology of belugas are greatly influenced by the dynamic nature of seasonal pack ice (Harington 2008). One could argue that the recent decrease in sea ice concentrations in JB may have provided suitable conditions for this group of animals to remain in the bay throughout the year. Although ice data were too coarse to permit detection of small bodies of open water, beluga sightings in JB suggest the occurrence of polynyas, or unconsolidated ice, and suitable and sufficient food resources in the region throughout the year. Such conditions would obviate the need for movement to winter feeding grounds (Lewis et al. 2009). In contrast, unfavourable environmental conditions and a mismatch between resource availability and demand provide likely

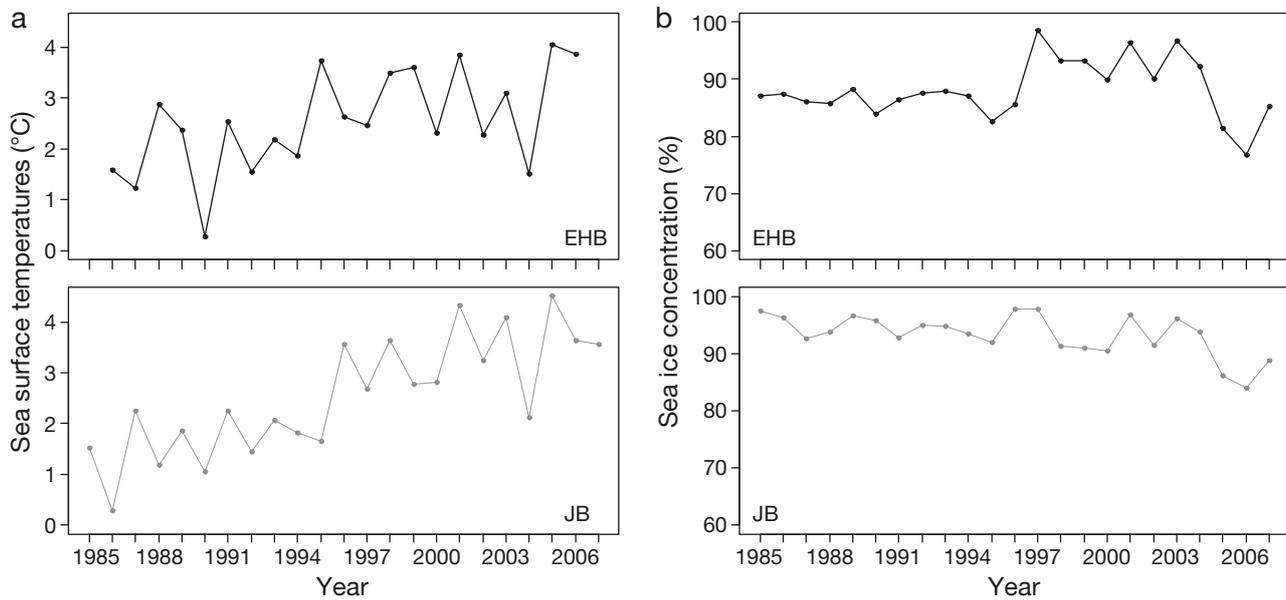


Fig. 6. Time series of (a) sea surface temperatures averaged during the ice-free period (April to November) in Eastern Hudson Bay (EHB, black) and in James Bay (JB, grey) and of (b) sea ice concentration averaged from December to March for a grid spatially limited by the maximum and minimum latitudes and longitudes reached by belugas within their summer residency areas

ecological drivers for the development of the migratory behaviour in EHBB.

The beluga is believed to be a relative generalist predator, preying upon a large number of different species, and able to occupy many different habitat types (Laidre et al. 2008). Given these characteristics, belugas might be able to exploit new ecosystems as sea ice loss opens new areas within their range (Laidre et al. 2008), as is suspected to have happened in JB. However, previous work based on early spring aerial survey observations (Jonkel 1969) and Inuit traditional ecological knowledge (Lewis et al. 2009) indicate that belugas have overwintered in JB for decades. Accordingly, environmental changes observed within the past 25 yr may have been too recent to have appreciably impacted beluga migratory movements at coarser temporal scales.

Implications for management and conservation

By improving knowledge of complex movement patterns and periods of aggregation and mixing among beluga populations, we have clarified animal assignment to 1 stock or another. Improved assignment information is fundamental for preventing excessive removal of animals from the endangered EHB population that might have cascading effects on the local food chain and lead to marked shifts in

ecosystem structure (Smetacek & Nicol 2005). Nevertheless, results must be interpreted with caution in the absence of corroborating genetic evidence. We have also determined the spatial scale of restricted movements within each residency area, which is an important precursor to improving our understanding of critical habitat. Moreover, the physical characterization of habitat is a necessary requirement to assess current determinants of beluga distribution. For instance, a temperature around 3°C, which might be the ecological signature of prey, seems to be targeted by EHBB for presumed foraging activity during both summer and winter periods. In contrast, JBB increased what is presumed to be foraging activity in colder waters during the freeze-up period. In the context of current Arctic climate change, such observations may be an initial point for the development of a dynamic approach that may predict future distribution of populations under plausible environmental scenarios. Although this work provides the first detailed information on the behaviour of belugas in relation to their environment in the eastern sub-Arctic, further investigation of the ecology, population interactions and genetics of the Hudson Bay beluga stock complex is needed to complement conservation policies already in place (DFO 2010) and to maintain beluga abundance and genetic diversity within the Arctic.

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