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RESEARCH ARTICLE

Spatiotemporal segregation among summer stocks of beluga (*Delphinapterus leucas*) despite nuclear gene flow: implication for the endangered belugas in eastern Hudson Bay (Canada)

Julie Turgeon · Pierre Duchesne · Gabriel J. Colbeck · Lianne D. Postma · Mike O. Hammill

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Abstract Migratory connectivity between areas frequented by wide-ranging animals provides crucial information for conservation and management. In and around Hudson Bay (Canada), three stocks of beluga whales (*Delphinapterus leucas*) are associated with distinct summering areas. We analyzed genetic variation at mtDNA and 13 microsatellite loci among individuals ($N > 1400$) harvested by 23 Inuit communities to identify mating units and assess temporal and spatial differences in the way stocks use common migratory pathways. Strong structure at mtDNA and a lack of convincing evidence for nuclear genetic differentiation indicate that both males and females adopt distinct migratory routes towards summering grounds while probably interbreeding on wintering grounds. Spatiotemporal variation in stock composition indicates that subsistence hunting targets all three stocks. While representing ca. 5% of belugas in Hudson Bay, the endangered Eastern Hudson Bay stock accounts for 17% of the overall subsistence harvest by Inuit communities of northern Nunavik (Quebec), and ca. 30% of the spring harvest along northeastern Hudson Bay. Despite interbreeding, cultural conservatism of maternally transmitted migration routes seems to prevent the re-establishment of stocks in previously frequented estuaries. This phenomenon supports the current use of demographic population models based on stock composition for developing behavior-based management strategies.

Keywords Beluga · Hudson Bay · Migratory connectivity · mtDNA · Microsatellites · Mixed stock analysis

Introduction

Population genetics often focuses on establishing the degree of differentiation among reproductive units, and on determining to which extent such units are demographically connected by gene flow (e.g., Waples and Gaggiotti 2006; Holsinger and Weir 2009). However, for mobile animals, genetic information can also provide crucial knowledge on how different groups of individuals occupy space for breeding, raising offspring, feeding, etc. over life cycles (Webster et al. 2002). Differences in space utilization can lead to behaviorally distinct population segments that may or may not form genetically differentiated mating units (e.g., Harrison et al. 2010). In cetaceans (dolphins and whales), differences in migratory routes or connectivity between breeding and non-breeding areas is common (Hoelzel 1998; Hoelzel et al. 2002). Social groups, often defining maternal lineages, have been associated with foraging resources or habitat specialization (Hoelzel et al.

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J. Turgeon (✉) · P. Duchesne · G. J. Colbeck
Département de Biologie, Université Laval, Quebec, QC G1V 0A6, Canada
e-mail: julie.turgeon@bio.ulaval.ca

G. J. Colbeck (✉)
College of Arts & Sciences, Maryville University, St. Louis, MO 63141, USA

L. D. Postma
Arctic Aquatic Research Division, Freshwater Institute, Fisheries and Oceans Canada, Winnipeg, MB R3T 2N6, Canada

M. O. Hammill
Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC G5H 3Z4, Canada

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1998a, b; Baird and Whitehead 2000; Whitehead and Rendell 2004; Natoli et al. 2005; Hoelzel et al. 2007; Foote et al. 2009; Valenzuela et al. 2009). Information on behavioral differentiation and migratory connectivity is highly relevant for conservation and management purposes (Hoelzel 1998, 2009; Webster et al. 2002; Whitehead et al. 2004; Berger-Tal et al. 2011). For example, strong site fidelity will affect time needed for the recolonization of extirpated population segments throughout historical ranges.

The beluga (*Delphinapterus leucas*) is a toothed whale with pan-Arctic distribution extending into Hudson Bay in sub-arctic eastern Canada (Donovan 1992; Richard and Pike 1993). Mating is thought to occur in late winter or early spring in off-shore waters; calves are born in late spring or early summer and they remain with their mother for up to 2 years (Heide-Jørgensen and Teilmann 1994). They are sexually mature at about 12 years of age and have a life span in the range of 50–80 years (Stewart et al. 2006). In the summer, belugas are strongly associated with coastal areas (Smith and Martin 1994; Kingsley et al. 2001; Lewis et al. 2009) and beluga stocks are distinguished by their tendency to home on a particular estuary or complex of estuarine embayments (Reeves and Mitchell 1987). The locations of these summering grounds, along with behavioral, morphometric, and genetic characteristics, have been used to define management stocks (Donovan 1992; COSEWIC 2004). In and around Hudson Bay (Fig. 1), four stocks are recognized: Western Hudson Bay (WHB), Eastern Hudson Bay (EHB), Ungava Bay (UB), and Cumberland Sound (CUM) stocks. Here, we use the term 'stock' to refer to the summering assemblages of belugas in specific areas.

Based on mtDNA, most summer aggregations of belugas from different regions of the Canadian Arctic are genetically differentiated (Brennin et al. 1997; Brown Gladden et al. 1997, 1999; de March et al. 2002; de March and Postma 2003). In eastern Canada, all studies have clearly demonstrated that the EHB stock is differentiated from the two main stocks in the vicinity, i.e., WHB and CUM stocks. There is little evidence, however, that the belugas recently captured in UB form a distinct stock. In addition, whales frequenting the Belcher Islands (SAN) and/or James Bay (JAM) may form distinct

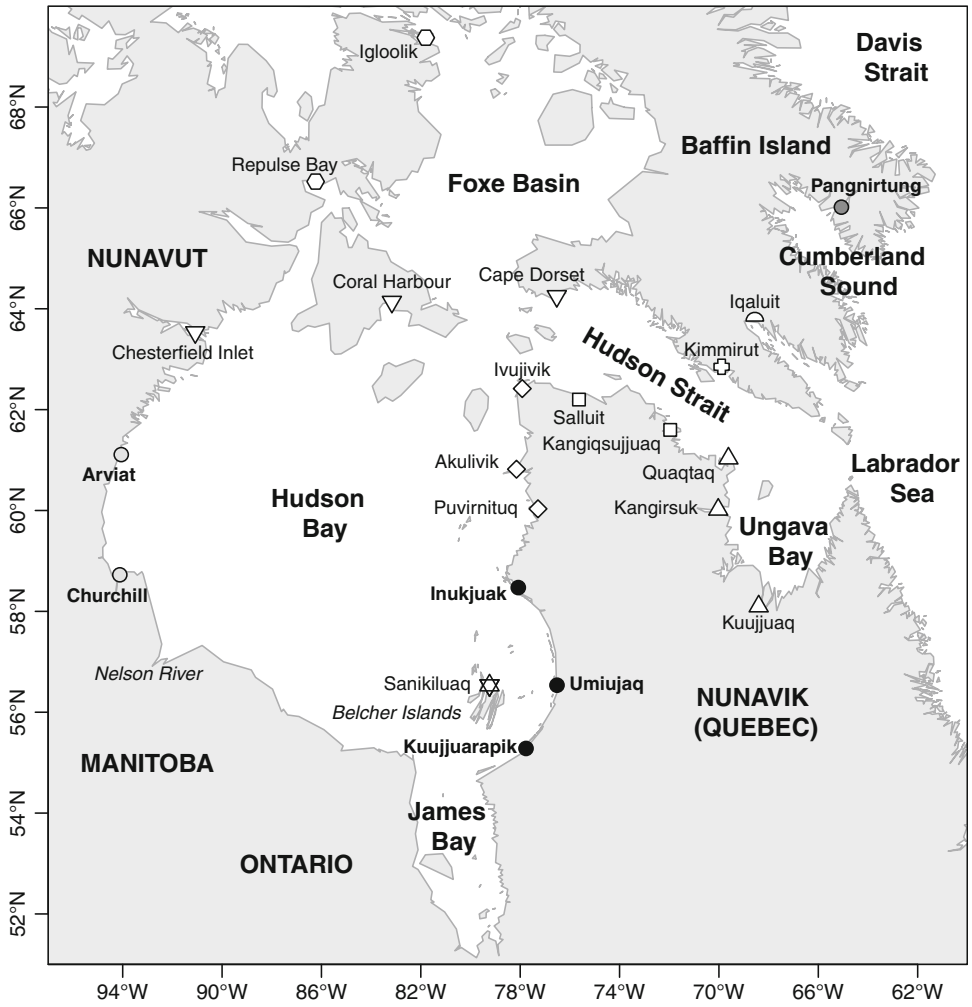

Fig. 1 General map showing important landmarks and main Sites reporting catch of belugas between 1982 and 2006. Main Areas are indicated by distinct *symbols*. Summer areas are shown with *filled circles*: Western Hudson Bay-WHB (*pale grey*), Eastern Hudson Bay-EHB (*black*), Cumberland Sound-CUM (*dark grey*). Other Main Areas are shown by symbols: Foxe Basin-FB (*hexagon*), Northern Hudson Bay-NHB (*triangle pointing down*), Sanikiluaq-SAN (*star*), Northeastern Hudson Bay-NeHB (*diamond*), Hudson Strait South-HSS (*square*), Ungava Bay-UB (*triangle pointing up*), Hudson Strait North-HSN (*cross*), and Iqaluit-IQA (*half circle*)

stock(s).Whales are observed very early in the season around the Belcher Islands and Inuit have long observed that large groups travel near the islands in the summer. In JAM, aerial surveys indicate that about 7,900 belugas were present in the area in the summer of 2004 (Hammill et al. 2004), where they may overwinter (Jonkel 1969; Lewis et al. 2009). However, genetic evidence for distinct stock(s) in these areas remains elusive (de March and Postma 2003).

Belugas are also highly mobile individuals and may swim considerable distances between summer and winter areas. In the winter, while Hudson Bay is frozen, belugas move towards the Labrador Sea, southwest Davis Strait, or stay in Hudson Strait and UB among the shifting pack-ice (Finley et al. 1982; Richard et al. 1990; Lewis et al. 2009; Luque and Ferguson 2010). In the spring and fall, there are clear seasonal migratory movements of belugas in and out of Hudson Bay. During these periods, the whereabouts of specific stocks are poorly understood. It is unknown whether stocks occupy separate breeding grounds during winter and early spring, when mating is thought to occur. At nuclear loci, there appears to be no significant structure among summering stocks in the Hudson Bay area in general (de March and Postma 2003), suggesting that they may form a single mating unit. During the spring and fall migration, these stocks may intermingle, especially in the Hudson Strait area. Possible differences in timing or migration routes during these periods are undocumented.

In the mid-nineteen century, heavy commercial harvesting in UB and along the EHB arc (Finley et al. 1982) initiated major demographic declines in the two Nunavik (Northern Quebec) stocks (EHB and UB). Demographic assessments in the early 1980s indicated that beluga numbers remained low, possibly due to the high subsistence harvests by Inuit at that time (Finley et al. 1982). Conservation concerns led to the implementation of management plans to limit subsistence harvests in 1986 and since then harvest levels have been limited by a management plan (e.g., Hammill et al. 2004). Recent assessments show that beluga numbers remain low in EHB and this stock is currently estimated at ca. 3,300 individuals (Hammill et al. 2009). Significant summer aggregations have not been seen in UB for decades, preventing any demographic population assessment (Smith and Hammill 1986; Kingsley 2000; Hammill et al. 2009). The Canadian Committee on Species of Endangered Wildlife in Canada (COSEWIC) has classified EHB and UB beluga stocks as 'Endangered' (COSEWIC 2004). By contrast, the WHB summer stock was estimated at 57,000 in 2004 (Richard 2005).

There are concerns that subsistence hunting by Inuit from northern Nunavik communities (i.e., UB, Hudson Strait South (HSS), and Northeastern Hudson Bay (NeHB), see Fig. 1) may harvest a disproportionate number of the endangered EHB belugas. Indeed, belugas from EHB are bound to be part of the hunting catch during the spring and fall migration along NeHB, southern Hudson Strait, and possibly UB. Previous analyses have indicated that the northern Nunavik beluga whale fishery probably comprises an important proportion (7–31%) of belugas from the EHB stock (de March and Postma 2003). However, the small sample sizes from many critical areas and the lack of seasonal information prevented firm conclusions on harvest stock composition.

In this article, we update the genetic characterization of belugas of the Hudson Bay area such that samples from both the summering areas and common migration corridors are well represented. Our analysis of both mtDNA and nuclear DNA aims to assess (1) the number of mating units present among all summer stocks in this region and (2) temporal and spatial differences in the way summering stocks use common migratory pathways. Given the endangered status of the EHB stock, we pay special attention to its contribution to the putative mixed harvest by Inuit communities in Nunavik, where specific management plans involve quotas.

Materials and methods

Biological material

Tissue samples (in general, skin) were obtained mostly from Inuit hunters from Hudson Bay and surrounding areas (Fig. 1). In all, 1605 individuals caught between 1982 and 2006 were analyzed (see Online Material 1 for details). Sex was determined genetically as per de March and Postma (2003) for 1327 samples (40% females, 60% males). Information about belugas is reported on a voluntary basis by Inuit hunters and varies through space and time. Samples are identified by hunters' community since the precise harvesting locations were seldom known. Thus, we pooled small localities with the closest important community into 23 Sites ($N = 22$–173 belugas per Site; mean: 71 ± 39, see Online Material 1). Inuit may also hunt a fair distance from where they reside, so these 23 Sites were further grouped into Main Areas comprising known Summering Areas (WHB, EHB, and CUM; de March et al. 2002; de March and Postma 2003; COSEWIC 2004) and distinct sectors along the common seasonal migratory corridor (Fig. 1). These are located in Northern Nunavik (Quebec) coastal sectors, i.e., HSS, UB, and NeHB, or in Nunavut, i.e., Iqaluit (IQA), Hudson Strait North (HSN, i.e., Kimmirut), Northern Hudson Bay (NHB), and Foxe Basin (FB). Belugas from Sanikiluaq (SAN, Belcher Is) and JAM were considered as two other Main Areas because observations about their seasonal whereabouts suggest that they may be part of distinct stock(s).

Samples from all years were pooled for each Main Area because sample sizes for a given year were rarely sufficient for analysis (see Online Material 1). Peak sampling periods vary across years within areas as well as across areas throughout the entire sampling period. While pooling all years may obscure some trends, it should not create spurious trends given that sampling periods are widely overlapping. Note that samples from 1982 to 1997 are those previously analyzed by de March and Postma (2003), including 721 individuals, of which 200 were from Northern Nunavik. With the addition of individuals captured between 1998 and 2006, the new dataset totals 1605 individuals, including 508 belugas from Northern Nunavik.

Genetic characterization

DNA extraction and sequencing of a 234 bp mtDNA D-loop segment were performed as per de March and Postma (2003). Three microsatellite datasets were pooled: (1) data from de March and Postma (2003), i.e., between 1983 and 1997 in and around Hudson Bay, (2) data from de March et al. (2002) for Pangnirtung (i.e., CUM) and IQA between 1982 and 1996 and (3) genotypes of 600 individuals, mostly from Nunavik and from more recent years in other locations. For these individuals, genotypes were determined for 13 microsatellite loci. Extractions were performed with Qiagen DNA easy spin columns, and PCR conditions were generally as per de March and Postma (2003). However, several loci were co-amplified (EV94-FCB2-FCB5-FCB11-FCB14, FCB10-FCB13, and EV37-FCB1-FCB17) using the Qiagen Multiplex PCR Kit and an annealing temperature of 57°C. FCB3, FCB4, and FCB8 were amplified apart using Qiagen Gold *Taq*. FCB8 was migrated with FCB10-13 and FCB3-4 were co-migrated on an ABI3100, and genotypes were scored using GeneMapper 3.7 (Applied Biosystems). The mean error rate per allele was estimated by retyping 89 of these 600 individuals at one or several loci (mean of 8 loci). In all, 495 individual loci were replicated (from extraction to PCR), i.e., 6.4% of all single locus genotypes (600 individuals $\times$ 13 loci $=$ 7800). Several individuals ($N = 50$) used in previous databases were also genotyped again to ensure that scoring was similarly performed and all databases compatible. Less than 2% of the allele scored by us did not match those from the existing database; this rate of allelic mismatch is lower than the genotyping error rate (2.5%, see "Results" section).

Spatial genetic structure

All analyses were performed using both sexes, and with each sex separately to investigate if sexes participated equally in generating spatial structure. We first used GENEPOP v. 4.0 (Rousset 2008) to test for Hardy–Weinberg equilibrium (HWE) within each Main Area. We performed exact HW tests as well as tests for heterozygote excess and deficit. We also tested for the presence of null alleles within each Main Area using MICROCHEKER 2.3.3 (Van Oosterhout et al. 2004).

Genetic structure was tested using two types of analyses. First, we performed analysis of molecular variance (AMOVA) with Arlequin 3.5 (Excoffier and Lischer 2010) to test whether population structure relates to the spatial structure of harvest sites. We used Sites nested within Main Areas, as well as Sites within Summering Areas. These analyses were performed with mtDNA haplotypes and with microsatellite genotypes. As a complement, pairwise differentiation (F_{st}) between Sites and between Summering Areas was estimated based on haplotype frequencies for mtDNA and θ_{ST} for microsatellites.

Second, we used clustering methods with microsatellite data to investigate whether genotypes form distinct groups that may or may not reflect spatial structure. First, we used the Bayesian clustering method implemented in STRUCTURE 2.3.1 (Pritchard et al. 2000; Hubisz et al. 2009) to estimate the most likely number of genetic populations (K). Given that low genetic structure was apparent, Sites and Main Area were used to inform LocPrior in two distinct analyses; no LocPrior was used in another analysis. In addition, given the strong structure among Summering Areas for mtDNA, we performed an analysis using only those individuals harvested in these areas, and using Summering Areas as LocPrior. For all analyses, we performed 500,000 iterations, following a burn-in of 50,000 iterations, with 5 runs per K value ($K = 1$–12 with the entire dataset, and $K = 1$–5 with only the three Summering Areas). The most likely value of K was evaluated using the criteria of Pritchard et al. (2000) and Evanno et al. (2005). Given the very weak evidence for population structure (see "Results" section), we applied another method that did not rely on a priori information on individual group membership to define such groups. We used FLOCK v.2.0 (Duchesne and Turgeon 2009). This algorithm uses maximum-likelihood iterative allocation to form K genetic groups. For each value of K, a χ^2 test examined how individuals from Sites, Main Areas or Summering Areas were allocated among $K = 2$ to $K = 5$ groups formed by FLOCK.

Genetic Mixture Analysis (GMA)

Based on mtDNA haplotypes, we performed GMA to estimate the proportion of individuals contributed by the different stocks (defined by Summering Areas) in areas and periods with potentially mixed stock composition, i.e., all other Main Areas. This equates to estimating seasonal stock composition in areas of putative mixed-fishery by Inuit communities. First we used the genetic stock

identification method implemented in the software SPAM version 3.7b (Debevec et al. 2000). SPAM employs maximum likelihood methods to estimate relative contributions of discrete stocks in a mixture of several stocks. The contribution estimates for each stock are computed as those that result in the largest likelihood of obtaining the observed mixture sample. SPAM was run with the following parameter values: maximum number of iterations = 300, number of resamplings = 500, estimate tolerance = 0.001. We also ran BAYES, another computer program for stock-mixture analysis but based on Bayesian methods (Pella and Masuda 2001). BAYES outputs a Markov chain Monte Carlo (MCMC) sample of stock proportions and genetic parameters. Values for genetic prior parameters are determined from the method described in Pella and Masuda (2001). For each analysis, three chains were run. The starting relative contributions for the three stocks (WHB, EHB, CUM) were (0.95, 0.25, 0.25) for the first chain, (0.25, 0.95, 0.25) for the second chain and (0.25, 0.25, 0.95) for the third chain. The values of the prior parameters of the Dirichlet distribution were 0.33, 0.33, and 0.33. The length of chains varied according to the recommendations of the program. For each chain, the size of the burn-in sample was half the length of the chain.

Baseline samples (sources) included belugas hunted in summering areas during summer, i.e., in July or August. Belugas hunted outside Summering Areas were considered as potentially mixed samples whose composition was to be determined. Belugas from SAN (Belcher Is, $N = 152$) were analyzed separately given the uncertain status of whales from this area. Month of capture was known for 80% of the individuals from the putatively mixed samples. Seasons were defined based on long term observation of belugas in the study area (Finley et al. 1982; Lewis et al. 2009). May and June were considered spring, July and August summer, September to November fall, and December to April winter. GMA were conducted on mixed samples from each Main Area and season with a minimal sample size of ten individuals. Samples from winter, from JAM, and from Summering Areas outside the defined summer period, were insufficient for analyses ($N < 10$).

Results

MtDNA and microsatellite datasets

Mitochondrial DNA D-loop haplotypes were defined for 1432 belugas hunted from 1982 to 2006 (Online Resource 2).There were 37 haplotypes; half of the individuals (54%) bore the same haplotype (H02) and 27 haplotypes were represented by two or more individuals.

Microsatellite genotypes were determined at 13 loci for 1605 individuals, with a mean of 12.6 loci successfully scored per individual. For the new data, the mean error rate per allele was estimated at 2.5%. Polymorphism level was moderate with a mean of 15.7 alleles per locus (range: 9–27), and mean heterozygosity of 0.678 (range: 0.209–0.876).

Genetic structure

When performing HW tests with both sexes, most Main Areas displayed significant disequilibrium caused by significant heterozygote deficits (Table 1). These results were not consistently associated with any particular loci. Results

Table 1 Summary of tests on Hardy–Weinberg expectations performed with Genepop 4.0 on belugas from 12 Main Areas (see Fig. 1)

Main Area	Males and females			Females only			Males only		
	HWD	*N* loci	Het. def.	HWD	*N* loci	Het. def.	HWD	*N* loci	Het. def.
FB	***	3	**	n.s.	0	n.s.	**	1	*
NHB	***	2	**	n.s.	0	n.s.	***	3	*
NeHB	n.s.	0	n.s.	n.s.	0	n.s.	n.s.	0	n.s.
HSS	*	2	*	n.s.	0	n.s.	***	1	n.s.
UB	n.s.	0	*	n.s.	0	n.s.	n.s.	0	n.s.
HSN	n.s.	0	n.s.	n.s.	0	n.s.	***	1	n.s.
IQA	n.s.	0	**	n.s.	0	n.s.	n.s.	0	*
SAN	***	5	**	n.s.	0	n.s.	***	2	**
JAM	n.s.	0	n.s.	n.s.	0	n.s.	n.s.	0	n.s.
WHB	***	3	**	*	1	n.s.	n.s.	0	n.s.
EHB	***	2	**	*	1	n.s.	n.s.	0	n.s.
CUM	***	1	**	n.s.	0	n.s.	**	1	**

Significance levels are reported for global tests on disequilibrium (HWD. along with the number of loci in HWD) and for tests on heterozygote deficit (Het. def.). *P*-values categories are indicated as follows: *n.s.* $P \geq 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

were clearly different when males and females were analyzed separately. For males, there was significant HW disequilibrium and heterozygote deficit in several Main Areas. Again, there was no evidence that any particular locus was causing this pattern. In contrast, female genotypes were in proportions respecting HW expectations in all but two Main Areas. Deviations from equilibrium were modest ($0.01 < P < 0.05$) and caused by different loci in each of these Main Areas. There was no evidence of heterozygote deficit in any of the Main Areas for females. Thus, deviation from HW equilibrium is mainly associated with the genotypic composition of males in several of the Main Areas. There was no evidence of null alleles.

There was clear evidence for spatial genetic structure based on mtDNA (Table 2). When considering Sites nested in all Main Areas, a significant portion of the genetic variance was associated with differences among areas (17.4%, $P = 0.024$, Table 2A). A much larger proportion of the variance was explained by differences among summering areas (42%, $P = 0.005$, Table 2A). These summering areas were significantly differentiated (pairwise F_{st}: CUM–EHB: 0.514; CUM–WHB: 0.065, EHB–WHB: 0.417, all $P < 0.\ 001$). In addition, pairwise F_{st} among Sites clearly revealed that EHB Sites were very strongly differentiated from all other Sites (Table 3). Interestingly, animals from SAN were significantly differentiated from other Sites in EHB (F_{st}: 0.217–0.517, $P < 0.001$) as well as from CUM and Churchill, the main Site in WHB (F_{st}: = 0.07–0.09, $P < 0.001$). Belugas from CUM were significantly different from many Sites, including other Sites in South Baffin (i.e., HSN and IQA, F_{st}: = 0.05, $P < 0.001$, Table 3). In general, WHB Sites were not individually differentiated from other Sites. Results for analyses conducted separately for males and females harvested in the three Summering Areas were highly similar to those for pooled samples, although there was a higher proportion of variance explained by Summer Areas for females than males (57%, $P = 0.005$ vs. 49%, $P = 0.007$). Also, indices of differentiation were higher for females than males (significant pairwise F_{st} (all $P < 0.001$): EHB–WHB: 0.617 vs. 0.574; EHB–CUM: 0.634 vs. 0.570; WHB–CUM: 0.055 vs. 0.040).

Table 2 Analyses of molecular variance partitioning genetic variation at (A) mtDNA and (B) microsatellites among belugas harvested from Main Areas (Main) or Summering Areas (Summer) in and around Hudson Bay, Canada

Source of variation	d.f.	% Variation	*P* value
(A) mtDNA			
Among areas			
Main	11	17.4	0.024
Summer	2	42.0	0.005
Among sites within area			
Main	12	6.4	<0.0001
Summer	3	3.9	<0.0001
Within sites			
Main	1,432	74.9	<0.0001
Summer	439	54.1	<0.0001
(B) Microsatellites			
Among areas			
Main	11	0.23	0.13
Summer	2	0.29	0.01
Among sites within area			
Main	12	0.13	<0.0001
Summer	3	0.24	0.004
Within sites			
Main	3,187	99.6	<0.0001
Summer	1,044	99.5	<0.0001

See "Materials and methods" section and Fig. 1 for description of these areas

Differences among Summering Areas were clearly reflected in the different haplotype arrays comprised in each group (Table 4). EHB had, by far, the most distinct set of haplotypes. Haplotypes H07, H17 and H18 made up 78% of all EHB haplotypes and were either absent or rare in WHB and CUM. Haplotype H02 was largely dominant in both WHB (66%) and CUM (43%) while much less common in EHB (15%). In CUM, the sum of haplotypes H06, H11, H13, H22 amounted to 44% while these haplotypes were either very rare or absent from WHB and EHB, respectively. For WHB, the most discriminative haplotype was H20, contributing 8% while entirely absent from the two other summer grounds. The haplotype composition of whales caught at SAN was also unusual (Online Resource 2). Although dominated by haplotype H02, it comprised six haplotypes not seen elsewhere, totaling 7% of individuals. Also somewhat unexpected was the high proportion of H06 (11%), a haplotype found almost exclusively in CUM, and extremely rare in the samples from the Nunavik hunters. Many whales (14%) also bear haplotypes typical of EHB.

In contrast, we found very weak evidence for significant genetic structure based on nuclear genotypes (Tables 2B, 3). Indeed, a very small proportion of genetic variation was explained by differences among Main Areas, or among Summering Areas (<1%, $P = 0.13$ and $P = 0.01$, respectively, Table 2B). For both types of grouping, variation among Sites was significant, but again, explained less than 1% of the variation (Table 2B). Pairwise θ_{ST} between Summering Areas were very low, but CUM was significantly differentiated from EHB and WBH (pairwise θ_{ST}: CUM–EHB and CUM–WHB: 0.006, $P < 0.\ 0.001$; EHB–WHB: 0.002, $P = 0.16$). Pairwise θ_{ST} values between Sites also indicated that only the belugas from CUM were slightly, but significantly different from many other Sites,

Table 3 Pairwise F_{st} ($\times 10^2$) between Sites (from ARLEQUIN 3.5)

Main Area	FB		WHB		NHB			EHB				SAN	NeHB			HSS		UB			HSN	IQA	CUM
Site	Igl	Rep	Arv	Chu	Che	Cor	Dor	Inu	Kup	Umi	Jam	San	Aku	Ivu	Puv	Kaq	Sal	Kar	Kuj	Qua	Kim	Iqa	Pan
Igloolik (Igl)	*	0.2	0.7	0.3	–	–	0.1	0.5	0.5	0.3	0.6	0.3	0.6	0.4	0.2	0.3	0.4	0.3	0.3	0.7	1.3	0.6	1.4
Repulse Bay (Rep)	4.0	*	0.5	0.1	–	0.1	–	**0.3**	0.2	0.1	–	–	0.2	–	0.2	0.9	0.1	0.5	0.1	0.6	**0.9**	0.4	**1.8**
Arviat (Arv)	2.2	0.6	*	–	0.2	0.2	−0.1	0.5	**0.9**	0.3	**0.9**	0.4	0.2	0.3	0.3	–	0.4	0.2	0.2	0.7	**0.6**	0.1	**2.1**
Churchill (Chu)	**10.7**	15.7	4.7	*	–	–	–	–	0.5	–	0.1	0.1	–	–	–	0.3	–	–	–	–	0.3	–	**1.3**
Chesterfield Inlet (Che)	0.5	–	–	11.3	*	0.1	–	0.3	0.7	0.2	0.3	0.1	0.8	0.3	0.7	1.0	0.2	0.1	–	0.4	**1.4**	0.6	1.3
Coral Harbour (Cor)	**7.7**	**9.2**	1.4	1.5	4.9	*	–	–	0.5	–	0.3	0.1	–	–	–	–	–	–	–	0.3	**0.6**	–	**1.4**
Cape Dorset (Dor)	**9.1**	10.8	2.2	0.2	6.7	–	*	–	0.1	–	–	–	–	–	–	–	–	–	–	–	0.8	–	1.8
Inukjuak (Inu)	**68.9**	**54.1**	**61.3**	**75.7**	**58.4**	**70.1**	**71.0**	*	0.5	–	0.4	0.3	0.1	–	–	–	–	0.3	0.1	0.3	**0.6**	–	–
Kuujjuarapik (Kup)	**35.3**	**18.6**	**28.4**	**44.0**	**21.7**	**39.3**	**36.9**	**19.2**	*	0.6	**0.7**	0.3	0.5	0.5	0.4	0.6	0.1	0.7	0.2	**0.8**	**0.9**	0.5	1.4
Umiujaq (Umi)	**50.8**	**33.4**	**44.0**	**58.9**	**37.5**	**54.4**	**52.5**	4.0	5.2	*	0.4	0.4	0.1	0.1	–	–	–	0.4	–	0.4	**0.8**	0.2	**1.6**
James Bay (Jam)	**21.7**	5.9	7.5	**30.4**	6.4	**15.2**	**16.7**	**52.8**	14.1	**30.3**	*	0.3	0.3	–	0.2	–	0.1	0.6	0.2	0.3	**1.1**	0.2	**1.8**
Sanikiluaq (San)	6.3	–	1.9	**9.1**	–	6.9	7.8	**52.7**	**21.7**	**36.8**	6.3	*	0.5	0.2	0.3	0.4	0.0	0.0	0.2	0.5	**1.3**	0.4	**1.9**
Akulivik (Aku)	5.3	4.2	0.1	1.5	1.5	0.4	1.2	**67.0**	**32.0**	**47.7**	14.1	3.1	*	–	–	–	–	0.3	0.1	0.2	0.3	0.2	**2.6**
Ivujivik (Ivu)	4.6	0.3	–	6.2	–	3.1	4.7	**61.9**	**27.1**	**43.2**	9.3	0.6	–	*	–	–	–	–	0.1	0.4	0.4	–	**1.8**
Puvirnituq (Puv)	5.6	0.3	–	7.6	–	3.6	4.9	**58.9**	**24.1**	**40.6**	4.9	0.4	1.0	−1.0	*	–	–	0.1	–	–	0.3	–	**1.8**
Kangiqsujjuaq (Kaq)	6.1	–	0.5	9.3	–	5.0	6.3	**54.3**	**20.6**	**36.5**	2.3	0.5	2.8	0.0	−0.7	*	–	–	–	–	0.2	–	**2.1**
Salluit (Sal)	8.8	–	1.5	**15.6**	–	8.5	9.8	**50.7**	**15.0**	**30.4**	–	0.3	5.3	1.3	–	–	*	–	–	–	0.1	–	**2.0**
Kangirsuk (Kar)	9.0	4.8	0.1	6.2	2.3	0.3	1.9	**65.1**	**28.8**	**45.6**	6.8	2.9	0.1	0.2	–	0.9	2.7	*	0.2	0.6	0.7	0.1	**2.1**
Kuujjuaq (Kuj)	3.4	–	–	7.6	–	1.4	3.1	**58.9**	**22.3**	**38.3**	3.1	–	–	–	–	–	–	–	*	0.2	0.5	0.1	**1.6**
Quaqtaq (Qua)	6.3	1.4	0.1	7.2	–	3.2	4.7	**60.1**	**25.7**	**42.3**	5.5	1.0	1.1	–	–	–	0.3	–	–	*	0.7	–	**2.0**
Kimmirut (Kim)	**10.7**	**13.4**	4.0	1.4	8.6	0.2	–	**73.1**	**42.7**	**57.6**	**19.9**	**9.2**	2.7	5.5	6.3	**7.3**	**12.4**	3.0	4.3	5.9	*	0.4	2.8
Iqaluit (Iqa)	**9.4**	12.0	3.6	0.7	7.7	0.1	–	**72.7**	**42.5**	**57.3**	**20.1**	**8.3**	1.1	4.4	5.6	**6.9**	**11.9**	2.6	3.4	5.4	–	*	1.8
Pangnirtung (Pan)	**12.3**	**12.5**	**5.6**	**6.6**	**9.7**	**4.0**	3.8	**69.8**	**41.0**	**55.9**	**17.0**	**7.2**	3.6	**6.2**	**6.2**	**7.8**	**11.6**	3.3	4.9	**6.0**	**5.6**	**4.3**	*

Values below and above diagonal are based on mtDNA haplotype frequencies and 13 microsatellite loci (θ_{st}), respectively. Sites are grouped within Main Areas, and Summering Areas are underlined. $F_{st} < 0.0001$ are indicated as '–'. Bold values are significant at $P < 0.05$ after Bonferroni correction

Table 4 Distribution of mitochondrial haplotypes among beluga samples from Summering Areas (*WHB* Western Hudson Bay, *EHB* Eastern Hudson Bay, *CUM* Cumberland sound)

Haplotype	WHB	EHB	CUM	Total
H01	0	0	1	1
H02	88 (0.66)	29 (0.15)	66 (0.43)	183 (0.38)
H03	0	0	4 (0.03)	4 (0.01)
H05	12 (0.09)	2	5 (0.03)	19 (0.04)
H06	2 (0.01)	1	18 (0.12)	21 (0.04)
H07	2 (0.01)	17 (0.09)	5 (0.03)	24 (0.05)
H11	0	0	11 (0.07)	11 (0.02)
H13	0	0	19 (0.13)	19 (0.03)
H17	0	24 (0.12)	0	24 (0.04)
H18	6 (0.04)	113 (0.57)	0	119 (0.24)
H19	0	2	0	2
H20	11 (0.08)	0	0	11 (0.02)
H21	1	0	0	1
H22	3 (0.02)	0	18 (0.12)	21 (0.04)
H23	3 (0.02)	0	0	3 (0.01)
H24	0	0	4 (0.03)	4 (0.01)
H26	0	2	0	2
H32	1	3 (0.02)	0	4 (0.01)
H35	0	0	1	1
H44	1	0	0	1
H45	0	1	0	1
H56	1	0	0	1
H59	2 (0.01)	0	0	2
H61	0	4 (0.02)	0	4 (0.01)
H63	0	1	0	1
H64	1	0	0	1
H67	0	1	0	1
Total	134	199	152	485

Frequencies larger than 0.01 are given in parentheses. Haplotypes are labelled as per de March and Postma (2003)

but notably not from IQA (Table 3). Analyses conducted for each sex provided very similar results, and the very small proportion of variation attributed to differences among Summering Areas was not significant for both sexes ($P > 0.18$). Both males and females from CUM were significantly differentiated from the other Summering Areas (females pairwise θ_{ST}: CUM–EHB: 0.007 and CUM–WHB: 0.006, $P < 0.01$; EHB–WHB: 0.002, $P = 0.13$; males pairwise θ_{ST}: CUM–EHB and CUM–WHB: 0.004, $P < 0.01$; EHB–WHB: <0.001, $P = 0.41$).

When the entire dataset was analyzed, neither clustering analyses provided evidence that two or more genetic groups existed. Results from STRUCTURE indicated that the most likely value of K is 1. Applying Pritchard et al. (2000) or Evanno et al. (2005) criteria suggested that there might be three or four clusters, respectively. However, for $K = 2$–4, nearly 95% of the 1605 individuals had coefficients of ancestry clearly associating them to a single cluster ($q > 0.8$). Clearly, this indicates that all but one cluster comprises nearly all individuals and makes biological sense (Pritchard et al. 2000). This was found whether Main Area, Sites, or no LocPrior was used. Also $K = 1$ is the last value for which subsequent K values do not show an improved likelihood after penalization of 1/2 the variance. Likewise, FLOCK provided no support for two or more clusters, whether Sites or Main Areas were used in χ^2 tests (all $P > 0.1$).

When only the animals from the three Summering Areas were considered, the analyses using LocPrior offered weak support $K = 3$ when applying Evanno's method (Online Material 3). However, based on individual q values, most individuals (88%) were clearly assigned to the same cluster. In fact, ancestry in the two other clusters, although higher for individuals from CUM or WHB, was nevertheless very low (CUM: mean: 0.46, range: 0.22–0.76; WHB: mean: 0.22, range: 0.12–0.39). As a result, only 36% of the individuals from CUM could be assigned to a cluster seemingly typical of this Summering Area. Evidence for $K = 3$ was also challenged by applying Pritchard's criterion, which indicated that a single cluster existed (penalized likelihood highest for $K = 1$). Moreover, it is worth nothing that Evanno's method, by definition, cannot select $K = 1$ as a most likely number of clusters given that it is based on the rate of change in the log probability of data between successive K values. Using FLOCK with $K = 3$ also resulted in belugas from CUM being more frequent in one of the three clusters, but the contingency table was not significant. All results were qualitatively identical when males and females were analyzed separately.

Thus, it appears that nuclear genetic differentiation between Summering Areas, as estimated with these 13 microsatellites, is extremely small. Attempts at using these summering areas (with sexes pooled or separate) to classify individuals from the other Main Areas with GENECLASS (Piry et al. 2004) yielded inconclusive results and are not presented.

GMA

Given the significant mtDNA differentiation among the three summering areas, these can be used as source samples for the GMA (Tables 2, 3, 4). Moreover, it seems that the stock definition can be extended to include the few individuals that are caught within summering areas but not during the summer. Indeed, when the total catch within Summering Areas (including non-summer samples) are used as mixed samples, neither SPAM nor BAYES revealed any contribution from any other stocks (>99% of each stock is attributed to itself, results not shown). This provides additional evidence that the delineation of the

summering areas is biologically meaningful and that these areas are uniquely occupied by each of the three mitochondrial assemblages.

SPAM and BAYES yielded estimates that were largely consistent with one another. The only notable differences were for estimates when all Main Areas were pooled, where BAYES yielded slightly lower estimates for the contribution from the CUM stock. We report the results from SPAM in Table 5 and those from BAYES in Online Material 4. When all individuals from potentially mixed stock samples are considered, the relative contribution of each stock is estimated with confidence at 79% (±2%) for WHB, 11% (±1%) for EHB, and 7% (±2%) for CUM (Table 5). However, compositions are highly heterogeneous among sectors (Table 5; Fig. 2a). The WHB stock contributes the greatest proportion of whales in all sectors, including HSN and IQA, and is overtly dominant in areas closer to this summering ground, i.e., FB (97 ± 4%) and NHB (96 ± 3%). A contribution from the CUM stock is apparent in Hudson Strait, including HSS (15 ± 6%), HSN (24 ± 10%), as well as in IQA (19 ± 9%), where the estimate is imprecise. The EHB stock is observed in significant proportion only in northern Nunavik, where its contribution varies between 15% (±4%) in NeHB and UB and 21% (±4%) in Hudson Strait. Overall, the stock composition is polarized in sectors near summering grounds and mixed in areas near Hudson Strait.

The estimated contribution of summering stocks is seasonally heterogeneous (Table 5; Fig. 2b–d). In spring, the general dominance of WHB belugas is less pronounced because the estimated contribution of the CUM stock is rather high (24 ± 8%; Fig. 2b). Animals bearing haplotypes typical of this stock are harvested on both sides of Hudson Strait, while this stock is notably absent from

Table 5 Results of GMA with SPAM based on mtDNA haplotype distribution among belugas from Hudson Bay and surrounding areas (see also Fig. 2)

Season	Source	Main Areas								Sanikiluaq
		FB	NHB	NeHB	HSS	UB	HSN	IQA	All areas[a]	
Spring	WHB	*	*	69 (13)	51 (5)	72 (16)	64 (21)	40 (12)	65 (4)	40 (12)
	EHB	*	*	31 (13)	10 (7)	2 (6)	0	4 (13)	9 (4)	4 (3)
	CUM	*	*	0	32 (14)	26 (15)	36 (21)	56 (12)	24 (8)	56 (12)
	Unknown			0	0	0	0	0	3	0
	N	*	*	23	43	28	19	14	113	69
	H	*	*	4	10	6	5	4	12	10
Summer	WHB	81 (10)	93 (6)	*	74 (12)	80 (35)	*	78 (12)	80 (5)	45 (20)
	EHB	19 (10)	0	*	11 (7)	2 (8)	*	0	9 (3)	42 (15)
	CUM	0	7 (6)	*	12 (10)	12 (22)	*	22 (12)	9 (4)	8 (15)
	Unknown	0.7	0		3	7		0	2	6
	N	26	54	*	39	15	*	54	147	18
	H	5	8	*	8	5		6	14	6
Fall	WHB	100 (<0.2)	98 (4)	75 (7)	*	67 (9)	90 (11)	*	85 (3)	100
	EHB	0	0	18 (6)	*	28 (9)	0	*	12 (2)	0
	CUM	0	0	4 (4)	*	0	10 (11)	*	2 (2)	0
	Unknown	0	2	3		5	0		2	0
	N	40	59	73	*	40	50	*	274	14
	H	5	11	10		6	4	*	14	2
All seasons[a]	WHB	97 (4)	96 (3)	79 (5)	59 (7)	73 (6)	76 (10)	80 (19)	79 (2)	14 (17)
	EHB	3 (4)	0	15 (4)	21 (4)	15 (4)	0	0	11 (1)	24 (8)
	CUM	0	3 (3)	3 (3)	15 (6)	7 (4)	24 (10)	19 (9)	7 (2)	52 (16)
	Unknown	0	1	3	4	5	0	1	3	10
	N	73	129	151	145	117	81	89	696	152
	H	7	14	13	13	12	6	9	26	16

Given are the estimated proportion (± s.e.m.) of each stock of beluga (Source: WHB, EHB, CUM, and 'unknown') in potentially mixed samples from different Main Areas (FB, NHB, NeHB, HSS, UB, HSN, IQA). Estimates for SAN are provided separately. *N* and H give sample size and number of haplotypes, respectively; estimates <0.1% are given a null (0). Results with BAYES are shown in the Online Material 4

[a] Sample sizes of 'All Areas'/'All Seasons' may exceed the sum of sample sizes per are/season because some haplotypes were too few within sector/season to use in GMA calculations

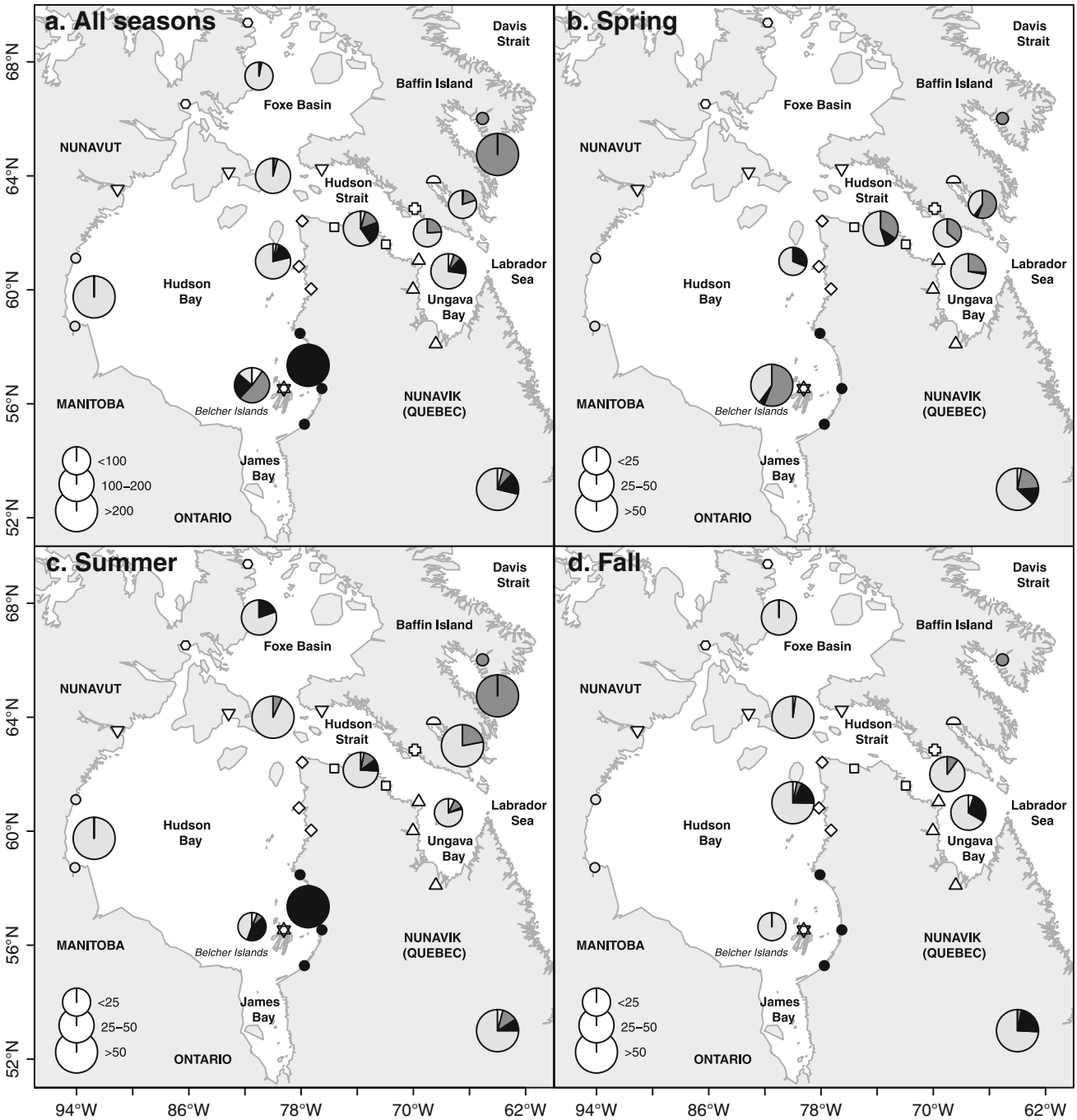

Fig. 2 Results of GMA based on mtDNA haplotypes for 1,432 belugas. *Pie diagrams* indicate estimated proportions of belugas originating from each summer stock in each Main Area for: **a** all seasons, **b** spring, **c** summer and **d** fall. *Black*, *pale grey*, *dark grey* and *white fillings* indicate proportions from EHB, WHB, CUM summer stocks, and unknown origin, respectively. *Pies* on the lower right corner give the proportion for Nunavik only. *Symbols* for Main Areas are as per Fig. 1

NeHB, NHB and FB. EHB belugas were detected only along the coasts of Nunavik, where they accounted for 13% (±5%) of the harvest. Heterogeneity within Nunavik was high; EHB whales accounted for 31% (±13%) of the harvest along NeHB, while representing only 10% (±7%) in Hudson Strait, and were largely absent from UB (2% ± 6%; Table 5; Fig. 2b).

In summer, samples caught outside recognized Summering Areas were all dominated by WHB (>74%, Table 5; Fig. 2c). Estimates for the contribution of the CUM stock are low, but this stock may still be present in IQA during the summer (22 ± 12%). Few Nunavik belugas appear to originate from the EHB stock (9 ± 3%), with most of them in Hudson Strait South (11 ± 7%).The

contribution of EHB belugas to UB during summer was based on only 15 individuals and is probably close to null (2 ± 8%). Surprisingly, although EHB does not contribute to NHB, an estimated 19% (±10%) of FB specimens consist of haplotypes from the EHB group.

During the fall, the WHB stock still dominates in all sectors (Table 5; Fig. 2d), and the CUM stock is practically absent in the harvest. The EHB stock is well represented in northern Nunavik (22 ± 9%), and especially so in UB (28 ± 9%) relative to NeHB (18 ± 6%).

The composition of the SAN harvest was unusual (Table 5; Fig. 2). Overall, contributions of WHB, EHB and CUM stocks to SAN harvest are estimated at 14% (±17%), 24% (±8%), and 52% (±16%). Unlike other sectors, the mixture analysis identifies the contribution of an 'unknown' source for 10% of the specimens which is also detected during the summer (6%). Composition estimates vary with season and are estimated at 40% (±12%), 4% (±3%) and 56% (±12%) in the spring for the WHB, EHB and CUM components, respectively. Summer estimates support the presence of the EHB stock at SAN during this season (42 ± 15%), along with that of WHB (45 ± 20%), while the contribution of CUM is probably null (8 ± 15%). In the fall, all whales are from WHB.

Discussion

Beluga whales from Hudson Bay and surrounding areas form at least three distinct summering stocks that are genetically distinct using mitochondrial DNA. The extensive dataset analyzed in this study firmly confirms that belugas summering along the EHB coast form a distinct biological unit (de March and Postma 2003). Whales summering in the other two summering zones (CUM and WHB) are also distinct, forming stocks that may serve as valid references for ecological studies and management purposes (Brennin et al. 1997; Brown Gladden et al. 1997, 1999; de March et al. 2002; de March and Postma 2003). A distinct stock of belugas may exist in the vicinity of SAN, but it is likely intermingling with other components during the summer (see below).

In sharp contrast, we found no convincing evidence that Hudson Bay belugas are genetically structured at nuclear loci. Belugas from the EHB and WHB stocks were not differentiated. Belugas from CUM were slightly differentiated from most other Sites, but not from the two other Sites in South Baffin Island (i.e., HSN and IQA) where a significant CUM component was detected in the spring by the GMA. This supports the recognition of CUM as a distinct management unit on the basis of a persistent summer aggregation in the area, Inuit Traditional Ecological Knowledge (TEK) and tagging (Richard 2010). However, it also suggests that belugas of the CUM stock, or animals bearing haplotypes typical of this stock, are present in northern Hudson Strait during the spring. In general, there was no evidence for nuclear genetic structure among sites in areas where mtDNA stocks intermingle. This confirms previous results that were based on much fewer samples (de March and Postma 2003). It is improbable that the absence of differentiation is due to the lack of power of the microsatellite markers. Evidence of intraspecific genetic differentiation has been detected with very similar sets of microsatellite markers between western and eastern Canadian Arctic belugas (Brown Gladden et al. 1997), between West Greenland and Svalbard belugas (O'Corry-Crowe et al. 2010) as well as in other whale species (e.g., Engelhaupt et al. 2009). Moreover, we found small but significant differentiation of the CUM belugas.

Given the undisputable evidence for structure at mtDNA, the lack of structure at nuclear DNA loci strongly indicates that the EHB and WHB stocks, while occupying different areas in the summer, probably experience considerable gene flow. This contention fits with the life cycle and the spatiotemporal distribution of belugas in eastern Arctic Canada. Indeed, it is thought that Hudson Bay belugas mate during winter or early spring while they are in Hudson Strait and UB, and also in the North Labrador Sea and southwest Davis Strait (Richard et al. 1990; Lewis et al. 2009). Certainly, our mixed stock analysis shows that belugas of three mtDNA types (WHB, EHB and CUM) are found together in various sectors close to Hudson Strait during spring time. However, interbreeding between CUM and WHB or EHB animals may be more limited, as is suggested by the small but significant differentiation at microsatellite loci and clustering analyses with Summering Areas indicating some differentiation of the CUM stock. Traditional knowledge, contaminant information and movement data from tagged belugas in CUM (Pangnirtung) suggests that some animals stay in this area all year round, a behavior that may account for this slight differentiation (De March et al. 2004; Richard 2010). Also, whales caught in CUM early in the season have a distinct isotopic signature suggesting they feed in a different wintering area (Rioux 2011). However, winter and offshore samples are needed to examine this further.

Altogether, these results strongly suggest that the mtDNA differences among different summering stocks are maintained by maternally directed site fidelity, while (nearly) random mating occurs among summer stocks, probably in areas commonly occupied by migrating animals. As such, there seems to be strong migratory connectivity between the areas where belugas of the eastern Canadian Arctic summer and where they breed. However, assuming a single general breeding area for all matrilineages, interbreeding apparently prevents genetic

differentiation at the nuclear markers used in this study. This pattern has also been observed in North Atlantic humpback whales (*Megaptera novaeanliae*) using a single breeding ground in the Caribbean, but distinct feeding grounds in the north Atlantic (Stevick et al. 2002; Hoelzel 2009). Likewise, southern right whales (*Eubalaena australis*) sampled on the same nursery ground form maternal groups employing distinct feeding areas (Valenzuela et al. 2009). The lack of differentiation at nuclear markers could also be due to higher male dispersal among several breeding units, as has been proposed for sperm whales in the North Atlantic (Engelhaupt et al. 2009). In that species, there are clear differences in male and female seasonal movements (Rice 1989; Whitehead and Weilgart 2000). Mature males roam far away from groups of females and juveniles that are spatially segregated and generally differentiated at mitochondrial DNA (Engelhaupt et al. 2009). In belugas, however, males clearly contribute to the differentiation of summer stocks. In EHB, there are more males harvested in summer areas, most being mature males of ages similar to females (females: 16.4 years, $N = 64$; males: 17.8 years, $N = 80$, t-test: $P = 0.32$, unpublished data). Males may disperse slightly more within summer areas, but are certainly not disrupting the genetic differences observed among the summer stocks. The possibility remains that males are heavily dispersing among distinct breeding areas to which females of each summer stock are faithful. Indeed, the more pronounced deficit in heterozygotes observed for males in several of the Main Areas may result from the more frequent mixing of males from yet unidentified mating units, and/or indicate that males are less consistently associated with family members through space and time. Finally, as per many other cetaceans, it is highly probable that the homing behavior to specific summering area is culturally and vertically transmitted in belugas (Connor et al. 1998; Whitehead 1998; Whitehead et al. 2004). Lactation is estimated to last between 20 and 32 months in this species (Doidge 1990), thus calves are dependent upon and accompany their mother for one to two migration cycles in and out of the Hudson Bay area. Moreover, there are reports that older calves stay close to adult females, possibly a kin, after weaning (Sergeant 1962; Doidge 1990). This long lasting association favors vertical transmission and learning of migration routes (Hoelzel 1998) and translates into genetic differences between summering areas.

The three summer stocks use common migratory pathways differently. Indeed, variations in harvest composition indicate seasonal differences in the whereabouts of beluga stocks in spring and fall. The WHB stock dominates the composition of most mixed samples around Hudson Bay, as would be expected from the larger estimated size of this summering stock (ca. 57,000 individuals; Richard 2005). During both the spring and fall migrations, WHB belugas are present on both sides of Hudson Strait, and swim along the coast of NeHB. In contrast, CUM belugas do not seem to venture much into Hudson Bay, but they intermingle with other stocks in and near Hudson Strait and South Baffin, especially during spring. The presence of CUM belugas along the Nunavik coast of Hudson Strait was previously undocumented, although earlier studies concluded that some whales seen around Kimmirut (HSN) and Frobisher Bay (IQA) in the summer belonged to the stock centered in CUM (Richard and Orr 1986; de March et al. 2004). Given some evidence that CUM animals do not move far from CUM in winter, this result raises the possibility that another mtDNA stock(s), similar to CUM, exist(s) in the area (de March et al. 2004) but this hypothesis must await further sampling and analyses.

The endangered EHB stock also displays migratory specificities. First, unlike the WHB stock, it is found mainly along the south shore of Hudson Strait. Second, in the spring, EHB belugas contribute a third of the harvest along the northeastern coast of Hudson Bay while representing only ca. 5% of the census population of Hudson Bay (Richard 2005; Hammill et al. 2004). This result suggests a particularly early entrance of EHB belugas into Hudson Bay. Also, EHB belugas may follow a migration route closer to the coast than that of WHB belugas, the latter moving offshore to cross Hudson Bay towards their summering grounds. As a result, Nunavik hunters may unintentionally target EHB belugas simply because they tend to hunt closer to shore. This could also explain why the EHB stock tends to be overrepresented in other areas (e.g., UB in the fall). However, the route of EHB relative to other stocks, in both spring and fall, remains undocumented. Third, in summer, when not along the coastal areas, EHB belugas are hunted near SAN, accounting for nearly half of the catch. This corroborates recent findings showing that whales tagged along the EHB arc frequently swim to the Belcher Islands during the summer, a behavior previously unsuspected by TEK (Lewis et al. 2009). Finally, some belugas with haplotypes typical of EHB are also reported in the summer catch of FB. This could suggest that some EHB specimens may wander into remote waters; alternatively, perhaps some migrants changed their migration route at some time in the past, and this result is a historical genetic signal.

The peculiar haplotype assemblage observed at SAN suggests that a distinct stock may intermingle with EHB and WHB stocks in the Belcher Islands area. The high proportion (20%) of unique or unusual haplotypes points to a distinct group of individuals frequenting this area. Also, the presence of haplotypes typical of the CUM stock is unlikely to truly reflect the presence of that stock so far south into Hudson Bay. Indeed, CUM belugas are detected

in Hudson Strait, but they are restricted to this area. It is thus very improbable that genuine representatives of the CUM stock are present at SAN. This is especially true in the spring season, when haplotype H06, typical of CUM, accounts for 18% of the available samples in SAN. This group of belugas may have originated in part from northern whales and now is demographically disconnected from the current CUM stock. The seasonal variation in estimated contributions of the other two stocks clearly shows that EHB and WHB whales are also hunted in SAN during the summer and fall, respectively. Thus, whales frequenting the Belcher Islands area likely represent a variable mixture of stocks, which may include some animals that overwinter in this area (Richard 1993; Lewis et al. 2009). However, more genetic data is needed to explore this further.

Impact on beluga conservation and management

The strong contrast between structure at mitochondrial and nuclear DNA, coupled with knowledge on seasonal migration patterns and reproductive timing, indicate that groups of individuals summering in distinct areas are likely maintained by cultural inheritance whereby maternal lineages define migration routes along coastal areas where whales are hunted. While these summering stocks are likely interbreeding, the maintenance of aggregations in these summering areas is therefore dependent upon the existence of these lineages. This validates the current conservation strategy and management plans focusing on these summering stocks (Reeves and Mitchell 1987; Donovan 1992; COSEWIC 2004).

This study establishes that subsistence harvests in Northern Nunavik targets all three summering stocks, including a substantial proportion of the endangered EHB stock (17% overall). Our estimates are close to those of de March and Postma (2003; HS and UB: 19%, NeHB: 15%). More importantly, our analysis reveals that the EHB catch varies seasonally. Overall, the proportion of the EHB stock in the total Nunavik catch is higher in the fall (22%) than in the spring (12%), and particularly high along NeHB in the spring (31%). This information may be very important in establishing seasonal hunting quotas for that region. Unlike past studies, we found no evidence for a contribution of EHB to the NHB or HSN catch, previously estimated at ca. 10% by de March and Postma (2003). We feel that our estimates are more reliable because they are based on a larger dataset that included all potential sources, and, more importantly, on a method overcoming the problems associated with the unreliable assignment of individual haplotypes shared among summering areas (Manel et al. 2005).

Our results underscore the pertinence of protecting the EHB stock, where a small and declining population size is well established (Hammill et al. 2004, 2009). While only representing about 5% of the overall number of beluga in Hudson Bay, the EHB stock comprise about 17% of the annual harvest. Management actions have succeeded in reducing the reported harvest from approximately 100 animals per year during the 1990s, to around 50 animals per year. However, EHB belugas are not managed within a Precautionary Approach framework and such levels are still associated with a 50% probability of a population decline. Given the culturally-transmitted site fidelity to summering grounds, a disproportionately high harvest directly threatens the persistence of the EHB summer aggregation. Should these animals disappear, cultural conservatism would probably limit recolonization, as has been observed in parts of Nunavik, among beluga elsewhere, and in other species. In the southern sperm whale, extirpated populations failed to reestablish because of fidelity to feeding grounds and the loss of cultural memory of these grounds (Valenzuela et al. 2009). Among beluga whales, significant areas of summer abundance in river estuaries which were extensively hunted, particularly by net or drive fisheries, are no longer occupied by large numbers of belugas. Such areas include the Mucalic River (UB), Nowliapik River (EHB), and Great Whale River (EHB) in Nunavik and other beluga populations further south, e.g., Manicougan Bank in the St Lawrence Estuary (Reeves and Mitchell 1987; Sergeant and Hoek 1988; Hammill et al. 2004).

The distinct nature of the EHB stock is currently recognized in population models guiding recommendations for hunting quotas (e.g., Doniol-Valcroze et al. 2010). This practice should be continued to protect the groups of beluga whales frequenting the EHB arc that support culturally important subsistence hunting activities by Nunavik Inuit communities.

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