Patterns of mtDNA Variation in Relation to Currently Recognized Stocks of Beluga Whales, *Delphinapterus leucas*

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Introduction

Belugas (also known as white whales, *Delphinapterus leucas*) have a discontinuous circumpolar distribution and are one of only two toothed whale species found in the Arctic year round (O'Corry-Crowe, 2018). Belugas can migrate over vast distances—thousands of kilometres in some regions—between summering grounds (where they aggregate in shallow bays) and deeper wintering areas where they stay close to the sea ice fringe (Heide-Jørgensen et al., 2010; Citta et al., 2017). The size of beluga stocks differs markedly, from tens of thousands of individuals in western Hudson Bay and eastern Beaufort Sea to only hundreds in Cook Inlet, Svalbard, and St. Lawrence Estuary (Vacquié-Garcia et al., 2020; DFO[1]; Shelden and Wade[2]).

The Global Review of Monodontids (GROM) status review recently recognized 21 beluga stocks in addition to one extirpated stock in southwest Greenland, largely defined as separate summer aggregation sites across the species range (Hobbs et al., 2019). The GROM meeting took place in March 2017, and was the first of its kind in almost two decades. There, beluga researchers and stakeholders convened and combined data from telemetry, aerial surveys, traditional knowledge, and genetics to estimate the number of distinct beluga stocks. Based on the available information, the GROM panel reevaluated each previously recognized stock, in some cases merging old or recognizing new stocks. The previous GROM meeting in 1999 only included a review of Atlantic stocks, and in contrast to the 2017 meeting also included a review of wintering and mixed aggregations (NAMMCO[3]). The International Whaling Commission (IWC) has also published reviews of beluga stocks in 1993 and 2000, recognizing 16 and 29 stocks, respectively (IWC, 1993, 2000), while a more recent review recognized 19 stocks (Laidre et al., 2015). This clearly illustrates that although belugas have been studied for decades, delimiting stocks is not straightforward.

Technological advances in the field of genetics during the 1990's was readily adopted in beluga research to address questions regarding stock subdivision and connectivity. Several methodologies have been applied, including DNA fingerprinting (Patenaude et al., 1994), variation in the major histocompatibility complex locus DQβ (Murray, 1997), and restriction fragment length polymorphism (RFLP) (Brennin et al., 1997). The majority of studies published over the past two decades have analyzed regions of the maternally inherited mtDNA control region and microsatellites (Fig. 1, Table 1).

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[1]DFO. 2014. Status of beluga (*Delphinapterus leucas*) in the St. Lawrence river estuary. Sci. Advis. Sec. Sci. Advis. Rep. 2013/076. DFO Canada.

[2]Shelden, K. E. W., and P. R. Wade (Editors). 2019. Aerial surveys, distribution, abundance, and trend of belugas (*Delphinapterus leucas*) in Cook Inlet, Alaska, June 2018. AFSC Processed Rep. 2019-09, 93 p.

[3]NAMMCO. 1999. Scientific committee working group on the population status of beluga and narwhal in the North Atlantic, 36 p. (Avail. at http://nammco.wpengine.com/wp-content/uploads/2016/09/SC_7_4-WG-Report-1999.pdf).

ABSTRACT—Belugas, Delphinapterus leucas*, are one of only three whale species endemic to Arctic and sub-Arctic seas. They are found in both the Atlantic and Pacific Arctic and sub-Arctic, and are managed at a regional or national level within each of the five Arctic-range countries, along with international fora used to share information and management strategies. Genetic data—primarily mtDNA control region sequences and microsatellites—have played an important role in defining appropriate management units. Here, we review the genetic studies published to date and, for the first time, present a range-wide, circumpolar analysis of levels of mtDNA diversity and differentiation in beluga stocks. Our meta analysis is based on 302 bp of overlapping mtDNA control region sequence and includes 2,933 individuals spanning all 21 recognized beluga stocks. We find that all stocks are significantly differentiated from each other, except in five cases. Belugas in the St. Lawrence Estuary are the most distinct—the stock has the lowest range-wide level of genetic diversity and, with only two haplotypes present not found elsewhere, it is also the most well differentiated. Belugas in the Barents, Kara, and Laptev Seas stock have the highest level of diversity, supporting that this geographically far-ranging stock may harbor several distinct sub-units. Our study showcases insights gained from studying species at a range-wide level, while highlighting the challenges associated with compiling and comparing data from various publications with different study designs.*

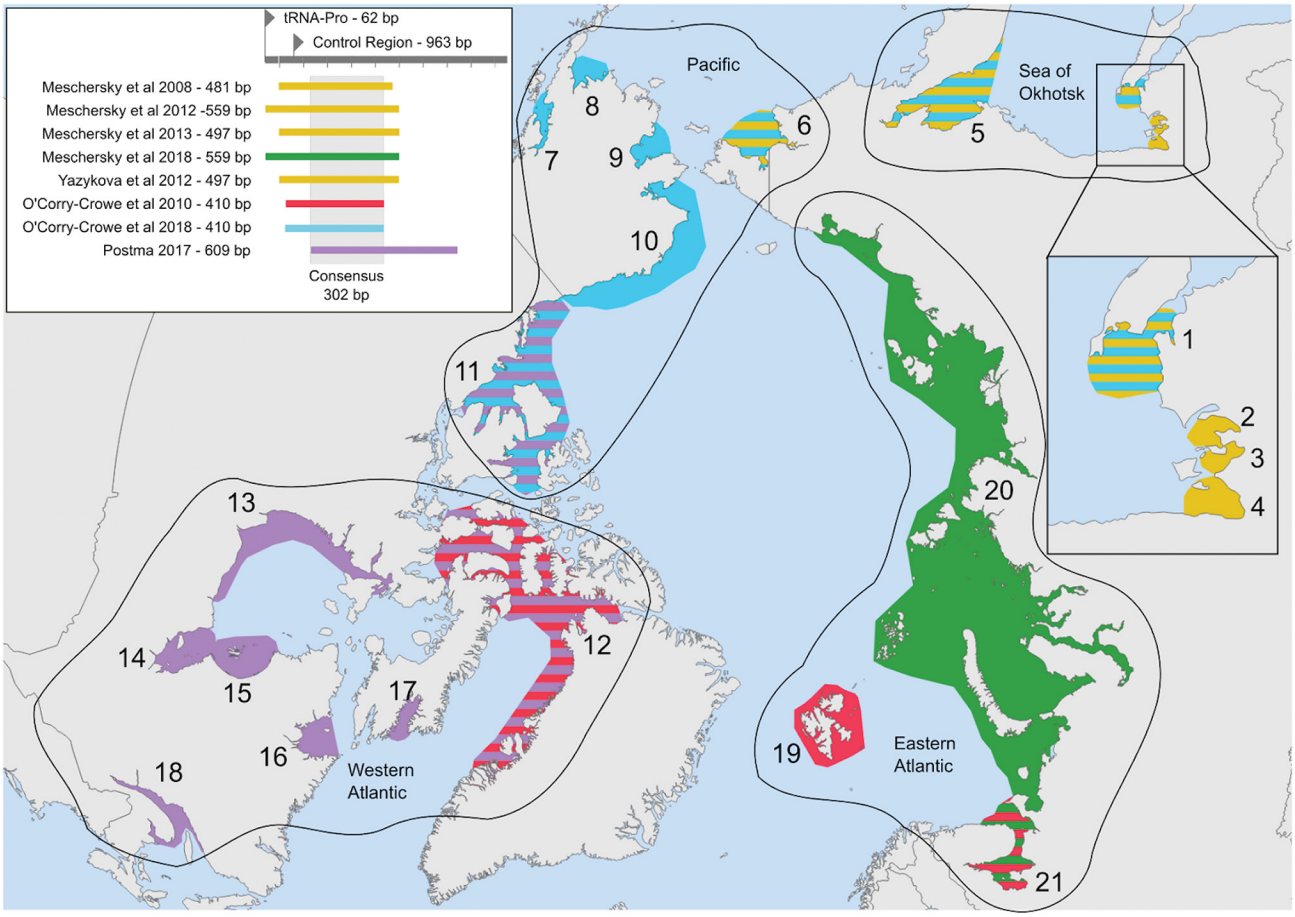


Figure 1.—Location of beluga whale stocks recognized by the Global Review of Monodontids (NAMMCO, 2018). Insert map: eastern Sea of Okhotsk. White insert (top left) shows the publications from which we retrieved mtDNA sequences for our circumpolar dataset, the mtDNA regions included in the original studies, and the position of the 302 bp overlapping sequence used in our analysis. Colors indicate the geographic range of the eight publications that contributed mtDNA squences to our study. The geographic extent of the four ad-hoc regions discussed in the main text are indicated by black lines.

Here, we review the population-level genetic data (mtDNA and microsatellites) published to date on the species. To test the genetic validity of the 21 beluga stocks presented in the GROM report (Hobbs et al., 2019), we compiled a pan-Arctic dataset of published mtDNA sequences. Because studies have not always sequenced the same region of the mitochondrial genome, we trimmed the available, aligned sequences to allow the most comprehensive dataset. Our analysis comprised 302 bp of overlapping control region sequence from 2,933 beluga individuals spanning the 21 GROM stocks. Because microsatellite data from different studies cannot be combined or compared when no standard reference sample has been included, we were unable to carry out a similar range-wide analysis of available microsatellite data and instead present an overview of the studies published.

Methods

Literature Review

We compiled the published population genetic literature on belugas based on mtDNA and microsatellites. We searched Google Scholar using the search terms: "Beluga whale," "*Delphinapterus leucas*," "population genetics," "population structure," "mtDNA," and "microsatellites". Furthermore, we looked through the refer-

Table 1.—Publications with population-level genetic data from belugas, including numbers of individuals analyzed and type of genetic marker used.

Publication	Genetic marker (n)	Stock in present study
Patenaude et al., 1994	DNA fingerprints	
Murray et al., 1995	Major Histocompatibility Complex (233)	
Buchanan et al., 1996	Microsatellites (100)	
O'Corry-Crowe et al., 1997	mtDNA (324)	
Brennin et al., 1997	RFLP (95)	
Brown Gladden et al., 1997	mtDNA (628)	
Brown Gladden et al., 1999	Microsatellites (640)	
O'Corry-Crowe et al., 2002	mtDNA (427)	
Palsböll et al., 2002	mtDNA (195)	
de March et al., 2002	mtDNA (481) Microsatellites (458)	
de March et al., 2003	mtDNA (714) Microsatellites (555)	
Meschersky et al., 2008	mtDNA (28)	
O'Corry-Crowe et al., 2010	mtDNA (122) Microsatellites (83)	White Sea
Borisova et al., 2012	Microsatellites (161)	
Yazykova et al., 2012	mtDNA (256) Microsatellites (209)	
Turgeon et al., 2012	mtDNA (1605) Microsatellites (1605)	
Colbeck et al., 2012	Microsatellites (1524)	
Meschersky et al., 2013	mtDNA (211) Microsatellites (175)	Anadyr and Shelikhov
O'Corry-Crowe et al., 2015	mtDNA (10) Microsatellites (10)	
O'Corry-Crowe et al., 2016	mtDNA (978) Microsatellites (816)	
Postma, 2017	mtDNA (2501) Microsatellites	Eastern Beaufort Sea, eastern Hudson Bay, western Hudson Bay, James Bay, Ungava Bay, Cumberland Sound, and St. Lawrence Estuary
Skovrind et al., 2017	mtDNA (2)	
Glazov et al.[1]	mtDNA	Barents, Kara, and Laptev Seas
Meschersky et al., 2018	mtDNA (58)	White Sea
Citta et al., 2018	Microsatellites (516)	
O'Corry-Crowe et al., 2018	mtDNA (1444) Microsatellites (1116)	Cook Inlet, Bristol Bay, eastern Chukchi Sea, eastern Bering Sea, eastern Beaufort Sea, Anadyr, Shelikhov, Sakhalin-Amur
Shpak et al., 2019	mtDNA (484)	Sakhalin-Amur, Ulbansky Bay, Tugursky Bay and Udskaya Bay

[1]Glazov, D. M., I. G. Meschersky, D. M. Kuznetsova, V. V. Krasnova, M. V. Gavrilo, D. A. Udovik, and O. V. Shpak. Review of current knowledge on beluga whale of the Russian northern seas. Unpubl. ms.

ence lists of the publications retrieved via Google Scholar for any publications that had not been retrieved in our original search. We also went through the recent GROM status review to ensure that we included all relevant papers used to define the 21 beluga stocks (Hobbs, et al., 2019). For each publication, we compiled information on genetic markers used, sample sites, and any sample overlap among studies.

Our Use of the Term "Stock"

Several terms have been used in the literature to delimit distinct beluga units, including "population," "subpopulation," "management unit," and "stock". Although they have at times been used interchangeably, their meanings differ. "Population" and "subpopulation" indicate different levels of reproductively isolated groups. "Management unit" indicates that each unit is being managed separately, and "stock" is a term implying that a natural resource is harvested as a single unit. None of these accurately describe distinct beluga units. We adopt the use of "stocks" as it is defined in the GROM report, which is to identify distinct beluga summering grounds (NAMMCO, 2018).

mtDNA Data Compilation

The main objectives of this study were to compile a range-wide dataset of beluga mtDNA sequences, to test the genetic validity of the GROM stocks, and to further our understanding of pan-Arctic patterns of structuring and variation in the species. When generating our dataset, we wanted to 1) maximize the length of overlapping mtDNA sequence, while also maximizing the number of individuals analyzed, 2) ensure our dataset included individuals from all 21 stocks, and 3) avoid duplicate sequences from individuals sequenced in multiple studies. This was achieved using data from eight publications (Fig. 1), including five peer-reviewed publications (Meschersky et al., 2008, 2013, 2018; O'Corry-Crowe et al., 2010, 2018), two conference papers (Meschersky et al., 2012; Yazykova et al., 2012) and a Ph.D. thesis (Postma, 2017). Information on haplotype frequencies within stocks and DNA sequence accession numbers from Meschersky et al. (2008, 2012, 2013, 2018) and Yazykova et al. (2012) were kindly provided by the authors. Two publications (O'Corry-Crowe et al., 2010, 2018) presented tables of haplotype frequencies and haplotype GenBank accession numbers, from which we reconstructed the original datasets. Haplotype frequencies from Postma (2017) were presented in the thesis, and the corresponding sequences were provided by the author. Sequences were assigned to the 21 GROM stocks using sample site information from the original publications. In cases where the same individuals were analyzed in multiple studies, only the sequence from the most recent publication was used. Sequences collected outside recognized GROM stocks, e.g., from migrating individuals or individuals with insufficient information, were omitted from further analysis.

mtDNA Data Analysis

The mtDNA sequences were aligned using ClustalW (Larking et al., 2007) with default settings and trimmed in the 5' and 3' end to only include genetic regions covered by all individuals. This resulted in a final dataset of 2,933 individuals with 302 bp of overlapping control region sequence. Haplotypes were named GROM_XX, with XX representing a two-digit sequential number starting at 01 (Supplementary Table 1)[4]. Due to the reduced sequence length, some previously unique

[4]Haplotypes found in our meta dataset and their frequencies in each of the 21 stocks recognized by GROM (NAMMCO, 2018) (provided as .xlsx file available at https://doi.org/10.7755/MFR.81.3-4.4s1).

Table 2.—Publications with population-level microsatellite data from belugas, including number of individuals and loci analyzed.

Publication	*n*	No. of loci	Markers
Buchanan et al., 1996	100	15	DlrFCB1, DlrFCB2, DlrFCB3, DlrFCB4, DlrFCB5, DlrFCB6, DlrFCB7, DlrFCB8, DlrFCB10, DlrFCB11, DlrFCB12, DlrFCB13, DlrFCB14, DlrFCB16, DlrFCB17
Brown Gladden et al., 1999	640	5	DlrFCB4b, DlrFCB5b, 464/465-1, EV37Mna, EV94Mnb
de March et al., 2002	458	15	DlrFCB1, DlrFCB2, DlrFCB3, DlrFCB4, DlrFCB5, DlrFCB8, DlrFCB10, DlrFCB11 DlrFCB13, DlrFCB14, DlrFCB16, DlrFCB17, Gme464/465, MnoEV37Mn, MnoEV94Mn
de March et al., 2003	555	15	DlrFCB1, DlrFCB2, DlrFCB3, DlrFCB4, DlrFCB5, DlrFCB8, DlrFCB10, DlrFCB11, DlrFCB13, DlrFCB14, DlrFCB16, DlrFCB17, Gme464/465, MnoEV37Mn, MnoEV94Mn
O'Corry-Crowe et al., 2010	83	8	CS415,CS417, CS468, EV37, EV94, DlrFCB3, DlrFCB5, DlrFCB17
Turgeon et al., 2012	1,605	13	EV37, EV94, FCB1, FCB2, FCB3, FCB4, FCB5, FCB8, FCB10, FCB11, FCB13, FCB14, FCB17
Yazykova et al., 2012	209	19	DlrFCB1, DlrFCB2, DlrFCB3, DlrFCB4, DlrFCB5, DlrFCB6, DlrFCB8, DlrFCB10, DlrFCB11, DlrFCB13, DlrFCB14, DlrFCB16 DlrFCB17, EV37Mn, EV94Mn, 415/416, 417/418, 464/465, 468/469
Colbeck et al., 2012	1,524	13	EV37, EV94, FCB1, FCB2, FCB3, FCB4, FCB5, FCB8, FCB10, FCB11, FCB13, FCB14, FCB17
Borisova et al., 2012	161	8	DlrFCB4, DlrFCB5, DlrFCB17, EV94Mn, 415/416, 417/418, 464/465, 468/469
Meschersky et al., 2013	175	9	DlrFCB4, DlrFCB5, DlrFCB17, EV37Mn, EV94Mn, 415/416, 417/418, 464/465, 468/469
O'Corry-Crowe et al., 2015	10	8	CS415, CS417, CS468, EV37, EV94, DlrFCB3, DlrFCB5, DlrFCB17
O'Corry-Crowe et al., 2016	816	8	CS415, CS417, CS468, EV37, EV94, DlrFCB3, DlrFCB5, DlrFCB17
O'Corry-Crowe et al., 2018	1,116	8	CS415, CS417, CS468, EV37, EV94, DlrFCB3, DlrFCB5, DlrFCB17
Citta et al., 2018	516	7	CS415, CS417, EV37, EV94, DlrFCB3, DlrFCB5, DlrFCB17

haplotypes collapsed into the same GROM_XX haplotype (Supplementary Table 2)[5]. To visualize the relationships among mtDNA haplotypes, we used the sequence alignment to construct a median spanning haplotype network (Bandelt et al., 1999) using Popart 1.7[6].

We used two parameters to estimate levels of diversity within stocks (H and π), both calculated using Arlequin (Excoffier and Lischer, 2010). These estimators have been widely used in beluga genetics, and report levels of diversity in different ways. Haplotype diversity (H) delimits the proportion of unique haplotypes within each stock, whereas nucleotide diversity (π) uses the average number of nucleotide differences between all possible pairs of sequences within each stock. Thus, stocks with a high proportion of unique haplotypes will have a high level of H, without consideration of how different the haplotypes are, while stocks with many variable sites will have a high level of π, ignoring the number of unique haplotypes. Levels of differentiation among all stock pairs was estimated by the fixation index F_{ST} using Arlequin 3.5 (Excoffier and Lischer, 2010). Levels of significance were corrected for multiple testing by dividing 0.05 by the number of tests (210), yielding a corrected p value of 0.00024.

To assess the broad-scale, macrogeographic patterns of mtDNA diversity across the species range, and to assist readers less familiar with Arctic geography, we divided the 21 stocks into four geographic regions ad hoc (Fig. 1):

1. Sea of Okhotsk, including Sakhalin-Amur, Ulbansky Bay, Tugursky Bay, Udskaya Bay, and Shelikov Bay stocks; these stocks all exclusively inhabit the Sea of Okhotsk during winter.
2. Pacific, including Anadyr Estuary, Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chukchi Sea, and eastern Beaufort Sea stocks, which all inhabit the Bering Sea and adjacent waters during winter.
3. Western Atlantic, including eastern High Arctic, western Hudson Bay, James Bay, eastern Hudson Bay, Ungava Bay, Cumberland Sound, and St. Lawrence Estuary stocks, which spend winters in Baffin Bay, Labrador Sea, and Hudson Strait, or remain resident in adjacent bays.
4. Eastern Atlantic, including Svalbard, Barents, Kara, and Laptev Seas, and White Sea stocks. These three stocks are assumed to inhabit separate geographic regions during winter but are all located in waters connected to the north-eastern Atlantic Ocean.

Results

Literature Review

We retrieved 27 beluga publications with population-level genetic data (Table 1). In total, >4,500 beluga individuals have been sequenced for part of their mitochondrial genome. Twenty-one publications are based on the analysis of mtDNA sequences, while 13 of the 27 publications include microsatellite data. Ten publications analyze both mtDNA sequences and microsatellite data (Table 1).

Our literature review revealed a regional publication bias, with some geographic regions more intensely studied than others. Only three of the 27 publications identified in this review include samples from the eastern Atlantic region (Fig. 1), by far the least-studied region. The Sea of Okhotsk is included in seven publications. The Pacific and western Atlantic regions are the most studied regions, and have been included in 16 and 14 publications, respectively. The eastern Atlantic region is covered by fewer genetic studies, although the Svalbard and White Sea stocks have been inves-

[5]GROM_XX haplotype numbers and the corresponding NCBI accession numbers of sequences included in our 302 bp dataset (provided as .xlsx file available at https://doi.org/10.7755/MFR.81.3-4.4s2).

[6]Available from http://popart.otago.ac.nz.

tigated using other non-genetic methodologies including telemetry and aerial surveys (Lydersen et al., 2001; Glazov et al., 2010). The Barents, Kara, and Laptev Seas stock has only been analyzed genetically in Meschersky et al. (2018).

Microsatellites

Microsatellites have played an important role in providing valuable information regarding the subdivision of beluga stocks (Brown Gladden et al., 1999; de March and Postma, 2003; O'Corry-Crowe et al., 2010, 2015; Turgeon et al., 2012; Meschersky et al., 2013). Microsatellites are long repeats of short motifs (<10 bp sequences) that can be found throughout the nuclear genome. The variation in microsatellites is captured by the length of the repetitive sequences (allele size), reflecting the varying number of times the short motifs are repeated (Vieira et al., 2016).

Microsatellites evolve at an elevated rate compared to other nuclear markers making them suitable for investigations of recent evolutionary changes (Ellegren, 2004). They have been used in local and regional studies to investigate kinship in pods (Colbeck et al., 2013), genetic mark-recapture (Citta et al., 2018), stock assignment (O'Corry-Crowe et al., 2018), and impacts of changing sea ice conditions (O'Corry-Crowe et al., 2016).

However, in a pan-Arctic context, the methodology is limited by the fact that allele sizes are influenced by lab-specific practices, and the data generated by different labs are therefore not directly comparable, unless they are calibrated by one or more reference samples. These difficulties have been overcome in work on other species by the inclusion of reference samples by all labs that contribute to the compiled data (Ellis et al., 2011). However, this requires coordinated efforts among research groups prior to the onset of the work, and is perhaps a more realistic approach for the investigation of commercially important species. Nevertheless, to provide an overview of the microsatellite literature, we compiled an exhaustive list of the studies published to date and present details of the specific microsatellite markers used in each study in Table 2.

mtDNA Data Analysis

Aligning and trimming of mtDNA sequences resulted in 302 bp overlapping sequence of the control region (Fig. 1), representing 2,933 individuals and all 21 GROM stocks (Supplementary Table 1). Sample sizes of individual stocks ranged from 22 (Barents, Kara, and Laptev Seas) to 579 (eastern Chukchi Sea). Our dataset included 71 haplotypes defined by 16 variable sites. The median-spanning network revealed two major haplogroups differentiated by four variable sites (Fig. 2). Haplogroup A harbors samples from all four geographic regions, while Haplogroup B only includes samples from the western Atlantic region. Within Haplogroup A, all haplotypes are differentiated from neighboring haplotypes by only one variable site. This is also the case for all haplotypes within haplogroup B, except for haplotypes found in the St. Lawrence Estuary, which are separated from other haplogroup B haplotypes by two variable sites (Fig. 2).

Haplotypes GROM_01, GROM_02, and GROM_23 are found at the highest frequencies in our trimmed dataset and result from the collapse of 43, 11, and 7 haplotypes, respectively, from the published, longer sequences that were trimmed in our analysis (Supplementary Table 1). GROM_01 is found in 809 individuals from 19 stocks, GROM_02 is found in 365 individuals from 10 stocks, and GROM_23 is found in 461 individuals from 11 stocks. Twenty-four haplotypes are found in less than five individuals.

Levels of haplotype diversity (H) across the 21 beluga stocks range from 0.19 in St. Lawrence Estuary and Bristol Bay, to 0.87 in Barents, Kara, and Laptev Seas (Fig. 3a). Nucleotide diversity (π) ranges from 0.001 in Ulbansky Bay to 0.014 in eastern Hudson Bay (Fig. 3b). Five stocks have $\pi < 0.002$ (White Sea, Bristol Bay, Ulbansky Bay, Shelikov Bay, and Anadyr Estuary), and two stocks have $\pi > 0.01$ (James Bay and eastern Hudson Bay). The remaining 15 stocks have π between 0.002 and 0.007.

The fixation index F_{ST} shows large variation and ranges from 0.00 to 0.93 (Table 3). All but five F_{ST} values are significant. Pairwise comparisons between (Tugursky Bay/Udskaya Bay), (Ulbansky Bay/Bristol Bay), (Ungava Bay/western Hudson Bay), (Ulbansky Bay/western Hudson Bay), and (Svalbard/Anadyr) are not significant after Bonferroni correction for multiple testing ($\alpha = 0.00024$).

Discussion

The mitochondrial genome is a non-recombining, independently evolving genome, which is passed on from mother to offspring (Hutchison et al., 1974). The development of easy-to-use, highly conserved primers that amplify targeted mtDNA fragments, coupled with high levels of intraspecific diversity, has made the control region the marker of choice in population genetics and phylogeography (Kocher et al., 1989; Ballard and Whitlock, 2004). Mitochondrial DNA analysis has been applied frequently in beluga research and has revealed high levels of diversity and differentiation across the belugas' range, establishing it as a valuable tool in beluga conservation and management (Brown Gladden et al., 1997; O'Corry-Crowe et al., 1997, 2002; Palsbøll et al., 2002; Meschersky et al., 2008, 2013, 2018).

However, mtDNA has inherent limitations (Balloux, 2010). The lack of recombination and the small size of the mitochondrial genome (16,386 bp (Kim et al., 2017)) makes it susceptible to stochastic events, and intraspecific patterns of mtDNA variability may not accurately reflect the evolutionary history of a population (Toews and Brelsford, 2012). Further, the maternal inheritance means that only the female lineage is reflected in mtDNA. Nevertheless, as long as these limitations are recognized, mtDNA remains a valuable resource for investigating phylogeographic patterns across a species range.

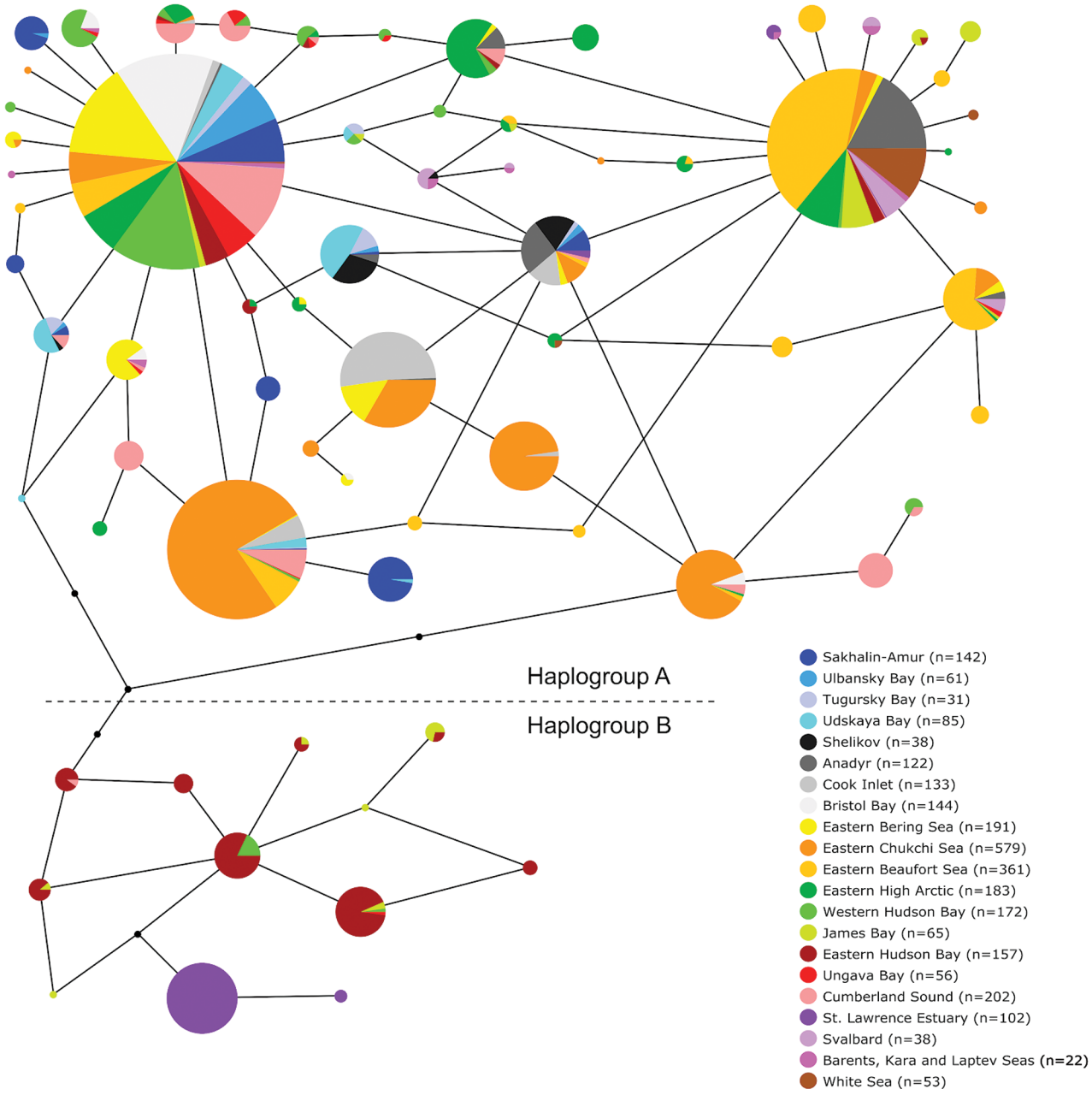


Figure 2.—Median-spanning network of 71 haplotypes across 2,933 mtDNA sequences from 21 beluga stocks. Each haplotype is represented by a circle colored according to the stocks where the specific haplotype was found. Black dots indicate haplotypes not sampled in the data. Circle size indicates relative haplotype frequency.

Circumpolar Insights

To carry out a pan-Arctic meta analysis that allowed the direct comparison of stock diversity and differentiation across the beluga range, the complexity of the original data was necessarily reduced, as our analysis included 302 bp of overlapping sequences from 2,933 individuals and all 21 GROM stocks.

We found 71 haplotypes defined by 16 variable sites. Our haplotype network revealed two major haplogroups, A and B (Fig. 2). Haplogroup A included individuals from 20 of the 21 GROM stocks, excluding St. Lawrence Estuary, individuals from which were exclusively found in Haplogroup B. Our results lack the genetic structure reported in a previous analyses of 609 bp sequences (n=2,501) and complete mitochondrial genomes (n=106) from Canadian belugas (Postma,

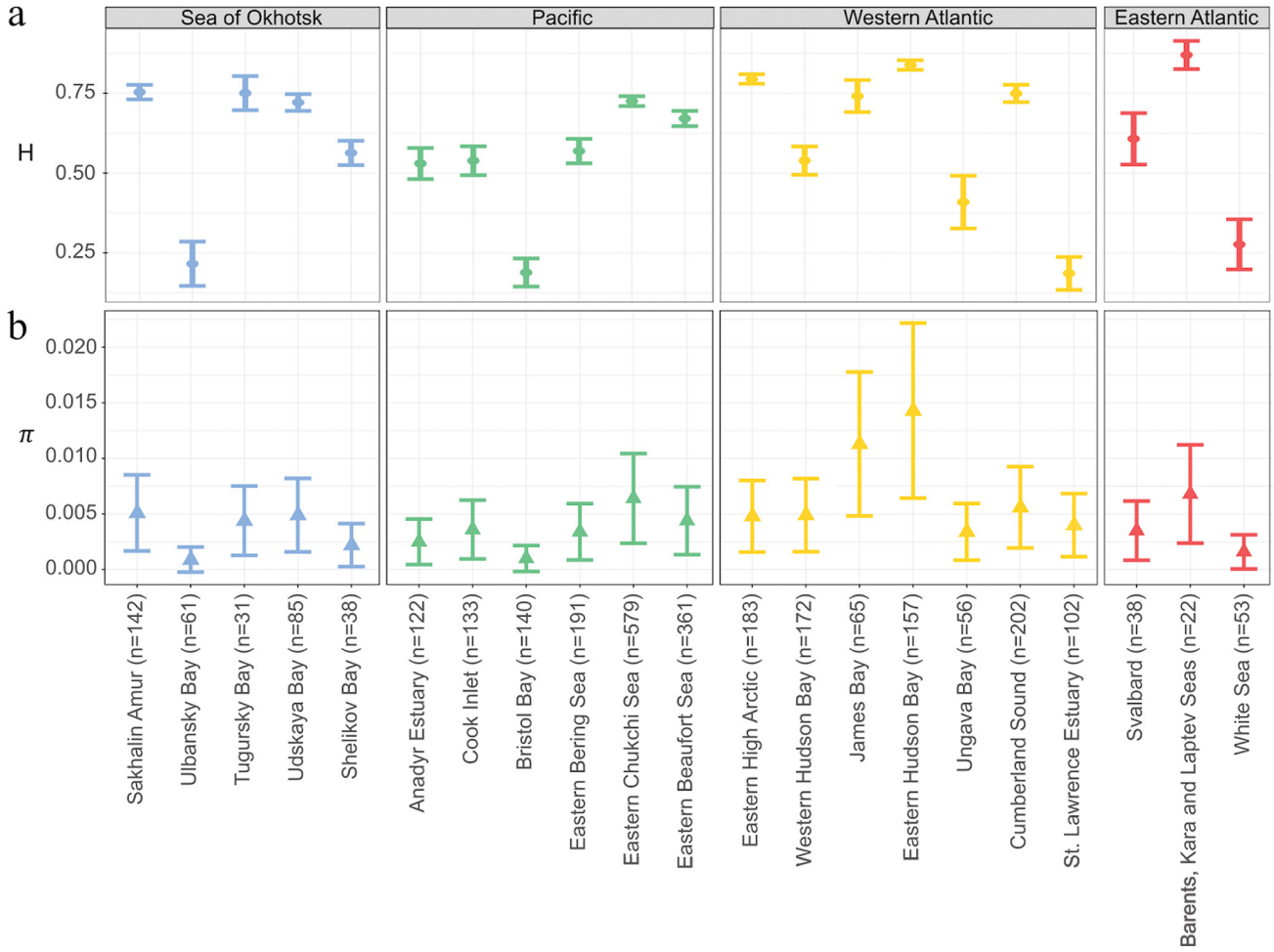


Figure 3.—Levels of genetic diversity in the 21 beluga stocks. a) Haplotype diversity (H) and, (b) Nucleotide diversity (π).

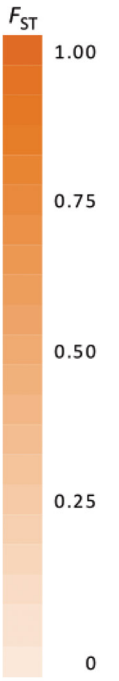
2017), which in our analysis cluster together with no apparent structuring in Haplogroup A. The analysis of the longer sequences revealed two well-differentiated haplogroups, highlighting the limited resolution of our 302 bp mtDNA dataset, and hence caution should be exercised when interpreting results.

Our diversity estimates show large variation among beluga stocks both in haplotype diversity (H), which counts the proportion of unique haplotypes in each stock, and nucleotide diversity (π), which describes how different the sequences are. The lowest H was found in Bristol Bay (0.19), St. Lawrence Estuary (0.19), Ulbansky Bay (0.22), and White Sea (0.28) (Fig. 3a). This is supported by corresponding low levels of π in these stocks (Bristol Bay and Ulbansky Bay (0.001), White Sea (0.002) (Fig. 3b)). However, we find relatively high π in St. Lawrence Estuary (0.004), which reflects that this stock has only two unique, but more diverse haplotypes (Fig. 2). The low levels of mtDNA diversity in the former beluga stocks could have arisen from several evolutionary processes, including 1) low levels of diversity in the founding individuals, 2) insufficient time since establishment of the stock to accumulate new mutations, 3) low levels of females migrating into the stock, and 4) genetic drift—a stochastic mechanism removing rare haplotypes—which affects small populations to a higher degree than larger populations. The St. Lawrence Estuary stock is less than half the size of the three other low-diversity stocks, which suggests that it is shaped by genetic drift to a larger degree (Hobbs, et al., 2019).

The Barents, Kara, and Laptev Seas stock has the highest level of H (0.87) and π (0.14) (Fig. 3). This could reflect the stock harboring multiple distinct, but as-yet undefined stocks, as has been suggested (Hobbs, et al., 2019). Substructuring within the stock would result in inflated diversity estimates. This is likely, as the Barents, Kara, and Laptev Seas stock has an extensive geographic range (Fig. 1) yet has only been included in one genetic study (Meschersky et al., 2018).

Table 3.—Levels of differentiation F_{ST} between the 21 beluga stocks recognized by GROM (NAMMCO, 2018). Values in bold are insignificant with p > 0.00024.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Sea of Okhotsk	1 Sakhalin-Amur		0.14	0.15	0.16	0.46	0.55	0.45	0.18	0.17	0.18	0.48	0.29	**0.14**	0.41	0.55	0.13	0.10	0.86	0.54	0.27	0.61
	2 Ulbanskiy Bay			0.16	0.17	0.70	0.68	0.53	**0.01**	0.05	0.22	0.49	0.26	0.03	0.41	0.52	0.03	0.07	0.91	0.72	0.36	0.83
	3 Tugurskiy Bay				**0.00**	0.33	0.53	0.39	0.25	0.11	0.18	0.40	0.23	0.10	0.27	0.45	0.13	0.10	0.86	0.49	0.13	0.65
	4 Udskaya Bay					0.25	0.49	0.38	0.25	0.15	0.19	0.41	0.26	0.14	0.31	0.48	0.16	0.13	0.85	0.47	0.17	0.58
	5 Shelikov Bay						0.52	0.43	0.74	0.47	0.32	0.41	0.44	0.44	0.28	0.47	0.56	0.39	0.87	0.52	0.34	0.68
	6 Anadyr Estuary							0.53	0.72	0.52	0.38	0.03	0.25	0.50	0.11	0.56	0.60	0.47	0.88	**0.04**	0.23	0.09
Pacific	7 Cook Inlet								0.59	0.38	0.20	0.46	0.44	0.43	0.39	0.55	0.48	0.38	0.88	0.53	0.37	0.62
	8 Bristol Bay									0.07	0.24	0.53	0.31	0.03	0.51	0.59	0.03	0.08	0.93	0.77	0.46	0.84
	9 Eastern Bering Sea										0.18	0.42	0.20	0.06	0.39	0.56	0.06	0.07	0.88	0.54	0.19	0.61
	10 Eastern Chukchi Sea											0.33	0.27	0.21	0.34	0.56	0.21	0.13	0.81	0.38	0.21	0.45
	11 Eastern Beaufort Sea												0.18	0.43	0.10	0.59	0.46	0.40	0.83	0.04	0.16	0.09
Western Atlantic	12 Eastern High Arctic													0.21	0.21	0.56	0.22	0.21	0.85	0.28	0.07	0.33
	13 Western Hudson Bay														0.36	0.51	**0.01**	0.05	0.85	0.50	0.18	0.58
	14 James Bay															0.35	0.34	0.35	0.71	0.06	0.08	0.12
	15 Eastern Hudson Bay																0.49	0.53	0.43	0.47	0.41	0.53
	16 Ungava Bay																	0.04	0.88	0.58	0.23	0.70
	17 Cumberland Sound																		0.84	0.46	0.18	0.53
	18 St. Lawrence Estuary																			0.85	0.84	0.88
Eastern Atlantic	19 Svalbard																				0.19	0.09
	20 Barents, Kara and Laptev Seas																					0.37
	21 White Sea																					



All but five pairs of beluga stocks are significantly differentiated ($p < 0.00024$) indicating that this dataset of only 302 bp in most cases supports the 21 stocks recognized by GROM (Table 3). The lack of significant differentiation between western Hudson Bay and Ungava Bay is a result of shared haplotypes (Fig. 2). Although western Hudson Bay has 15 haplotypes and Ungava Bay has 10 haplotypes, 201 out of 228 individuals (88%) found in the two stocks belong to seven shared haplotypes (Supplementary Table 1). Haplotype sharing may be explained by their close geographic proximity (Fig. 1), or reflect that individuals from western Hudson Bay were sampled as they migrate through the Hudson Strait just outside Ungava Bay (Lewis et al., 2009; Hobbs, et al., 2019).

Tugursky Bay and Udskaya Bay, which are adjacent stocks in the Sea of Okhotsk, are not differentiated in our F_{ST} analysis; 95% of individuals from the two stocks belong to one of four shared haplotypes (Fig. 2, Supplementary Table 1). This could reflect that a single genetic unit is distributed across the two bays, which is further supported by similar H and π levels (Fig. 3). A previous study using longer mtDNA fragments and 19 microsatellite loci was also unable to differentiate between them (Yazykova et al., 2012). However, GROM evaluations are based on a composite of data, and Tugursky Bay and Udskaya Bay belugas use separate summering grounds and show behavioral differences towards motorized boats (Hobbs, et al., 2019).

Our analysis was unable to differentiate between several stocks that are otherwise separated by large geographic distances, in large part reflecting the low resolution in our data. The pattern could also be explained by shared recent demographic histories, or the colonization of one area from the other, but we consider this less likely. For example, Ulbansky Bay and Bristol Bay are separated by more than 3,000 km (Fig. 1). Both stocks harbor haplotype GROM_01 at ~90% frequency (Supplementary Table 1), and additional haplotypes are closely related to GROM_01, resulting in low levels of both H and π (Fig. 3). During the trimming of the sequence alignment to 302 bp, a number of informative sites were lost; GROM_01 includes 43 collapsed haplotypes from the original studies (Supplementary Table 2). This could indicate that longer sequences might enable us to distinguish Ulbansky Bay and Bristol Bay, although when we analyzed the available 410 bp mtDNA sequence shared by the two stocks, they remain indistinguishable.

Our F_{ST} analysis supports that St. Lawrence Estuary is the most divergent, underscoring the uniqueness of this stock (Gladden et al., 1999; de March and Postma, 2003; Postma, 2017). This is in agreement with the haplotype network in which the two St. Lawrence haplotypes are not shared with any other stock and are differentiated from their nearest neighbor by two variable sites (Fig. 2).

Limitations of mtDNA

Our meta analysis of 302 bp pan-Arctic sequences from 2,933 indi-

viduals highlights that, even with large sample sizes and range-wide sampling, inferences based on short control region mtDNA fragments are limited. In the light of this, short mtDNA markers may still have a role to play in future genetic work in belugas, providing an accessible initial exploratory tool to help form hypotheses for further testing. Full mitochondrial genomes offer more information and higher resolution (Postma, 2017; Skovrind et al., 2017). Mitochondrial genome analyses have been used in a number of other whale species to make a wide variety of inferences, including historic female population size, detailed phylogeographic structuring, and the existence of subspecies (Morin et al., 2010, 2018; Van Cise et al., 2019), illustrating the potential of mitogenomes in beluga research in providing a clearer picture of the history and structuring of maternal lineages. However, mitochondrial data is not able to elucidate the demography and history of both sexes, including levels of male migration and patterns of gene flow among stocks, which require insights from the nuclear genome. Hence, mtDNA should not be used as a stand-alone tool with which to differentiate stocks, but should be used, with caution, as a component in a multidisciplinary effort including other methodologies, e.g. telemetrics, aerial surveys, and behavioral studies, where available, as has been applied in the GROM stock evaluation (Hobbs, et al., 2019). For example, behavior, social bonds, migration routes, site fidelity, and possibly other traits might delineate stocks, even in the absence of genetic differentiation, as is the case for Tugursky Bay and Udskaya Bay in the Sea of Okhotsk.

Perspectives

The redistribution of belugas in the face of Arctic climate change is of high conservation concern and will require cooperation and coordination across the circumpolar range of the species (Laidre et al., 2015). Our review highlights that obtaining genetic insights across the species range is a challenge with the available data. This severely limits range-wide inferences, which is vital for understanding widely distributed species, such as belugas. Facing this challenge, a natural next step in informing the management and conservation of belugas with genetics is the transition to genome-wide sequencing methodologies, which analyze tens of thousands to millions of genetic markers across the nuclear genome. This will enable high-resolution insights into levels of differentiation and diversity, which will aid our understanding of current demographic processes in species.

Future range-wide genetic beluga studies could 1) identify evolutionary lineages and their divergence times to better understand the demographic history of the species, 2) estimate gene flow between populations to determine their current connectivity and enable tracking of future changes in gene flow patterns, and 3) identify genes under selection to inform managers of local populations with unique adaptations to their specific habitats. Such work will benefit from the recent release of a high-quality beluga reference nuclear genome (Jones et al., 2017), which offers a valuable resource for future genomic studies of the species (Allendorf, 2017). However, with new methods come new challenges. The transition from mtDNA and microsatellites to genome-wide sequencing requires appropriate lab and computational facilities and can be, despite ever-declining sequencing costs, prohibitively expensive to implement compared with methodologies that are already in wide use in beluga genetic research.

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