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Reproductive Parameters for Female Beluga Whales (*Delphinapterus leucas*) of Baffin Bay and Hudson Bay, Canada

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ABSTRACT. Monitoring marine mammal populations and their habitats is crucial for assessing population status and defining realistic management and conservation goals. Environmental and anthropogenic changes in the Arctic have prompted the pursuit for improved understanding of female beluga whale (*Delphinapterus leucas*) spatial and temporal reproductive patterns. There are relatively few estimates for female reproductive parameters of beluga whale populations across the Arctic, and those few that are available are outdated. Here we summarize female reproductive data from samples collected through Inuit subsistence hunts of three eastern Canadian Arctic beluga populations: High Arctic/Baffin Bay (HA), Western Hudson Bay (HB), and Cumberland Sound (CS) from 1989 to 2014. We grouped the CS and HA populations into a Baffin Bay region (BB) population based on similar body growth patterns and genetic similarity. Asymptotic body length of BB beluga whales (370.9 cm) was greater than HB whales (354.4 cm) as established from Gompertz growth curves fitted for whales ranging in age from 1–89 y. We did not detect a significant difference in average number of pseudocervices (8.6) between regions. Differences in average age of sexual maturity (ASM) and length at sexual maturity (LSM) were identified, with evidence of BB females maturing earlier than females from HB (probability method BB = 9.9 y versus HB = 11.0 and logistic method ASM50% HB = 9.99 and BB unresolved). BB females were also longer than HB females at maturing age (logistic LSM50%: BB = 314.5 cm vs HB = 290.3). Total corpora counts were strongly correlated with age, although the number of corpora (≥ 10 mm) suggests reproductive senescence between 40 and 50 y. Improved understanding of female reproductive patterns and knowledge of changes in the spatial and temporal timing of reproductive processes are fundamental for effective conservation and sustainable management of beluga whale populations.

Key words: age of sexual maturity; body growth; vaginal folds; corpora lutea; pseudocervices; reproductive activity

RÉSUMÉ. La surveillance des populations de mammifères marins et de leurs habitats joue un rôle crucial dans l’évaluation de l’état d’une population ainsi que dans la formulation d’objectifs réalistes en matière de gestion et de conservation. Dans l’Arctique, les changements environnementaux et anthropiques incitent à mieux comprendre les tendances spatiales et temporelles de reproduction du béluga femelle (*Delphinapterus leucas*). Il existe relativement peu d’estimations des paramètres de reproduction des femelles au sein des populations de bélugas de l’Arctique, et celles qui existent ne sont plus à jour. Nous résumons ici les données de reproduction des femelles en fonction d’échantillons recueillis à partir des chasses de subsistance d’Inuits parmi trois populations de bélugas de l’est de l’Arctique canadien : Extrême-Arctique et baie de Baffin (HA), ouest de la baie d’Hudson (HB) et détroit de Cumberland (CS), de 1989 à 2014. Nous avons regroupé les populations de CS et de HA dans une population de la région de la baie de Baffin (BB) en fonction de tendances de croissance corporelle semblables et de similarité génétique. La longueur corporelle asymptotique des bélugas de BB (370,9 cm) était plus grande que celle des baleines de HB (354,4 cm), ainsi déterminée à l’aide des courbes de croissance de Gompertz adaptées aux baleines, dont l’âge varie de un an à 89 ans. Nous n’avons pas détecté de différence importante dans le nombre moyen de « pseudo-cols de l’utérus » (8,6) entre les régions. Des différences dans l’âge moyen de la maturité sexuelle (ASM) et dans la longueur à la maturité sexuelle (LSM) ont été décelées, avec preuve que les femelles de BB arrivaient plus vite à maturité que les femelles de HB (méthode de probabilité de BB = 9,9 ans par opposition à HB = 11,0 et une méthode de logistique d’ASM50% HB = 9,99 et de BB non résolue). Par ailleurs, les femelles de BB étaient plus longues que les femelles de HB à l’âge de la maturité (logistique LSM50% : BB = 314,5 cm par opposition à HB = 290,3). Le nombre total de corps jaunes était fortement corrélé à l’âge, bien que le nombre de corps jaunes (≥ 10 mm) suggère une sénescence reproductive variant entre 40 et 50 ans. Une meilleure compréhension des tendances de reproduction des femelles et de meilleures connaissances des changements spatiaux et temporels des processus de reproduction revêtent une importance fondamentale pour la conservation efficace et la gestion durable des populations de bélugas.

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Mots clés : âge de la maturité sexuelle; croissance corporelle; rides du vagin; corps jaune; pseudo-cols de l'utérus; activité reproductive

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INTRODUCTION

Marine mammals are typically apex predators in Arctic marine ecosystems, provide country food for Inuit communities, and function as indicators of ecosystem health and environmental change (Moore and Huntington, 2008). A warming Arctic poses serious threats for marine mammals that have a strong dependence on sea ice (Laidre et al., 2008; Kovacs et al., 2011) since a reduction in sea ice may have negative consequences on reproductive success and survival (Isaac, 2009; Molnár et al., 2010). The rate at which changes are occurring throughout the Arctic has accelerated for both abiotic (e.g., warming temperatures [Polyakov et al., 2010]) and biotic features (e.g., changing forage fish availability [Yurkowski et al., 2018] and increased presence of killer whales [Higdon and Ferguson, 2009]). The accelerated change provides impetus to update demographic parameters for Arctic marine mammal populations to ensure management, monitoring, and conservation programs are sustainable and effective. Assessment of female reproductive parameters and reproductive-related indices can be particularly helpful in detecting and monitoring temporal and spatial differences and trends in stock productivity and health of marine mammals (Stenseth et al., 2002; Burek et al., 2008). For example, monitoring the effects of climate variability and change on calving rates of North Atlantic right whales (*Eubalaena glacialis*) has shown demographic vulnerability that could negate conservation efforts attempting to ensure recovery of this whale population (Greene and Pershing, 2004).

To assess stock dynamics, Arctic cetacean populations are typically monitored using aerial surveys; however, due to their large distributions, logistical difficulties, and high costs of performing fieldwork (Mallory et al., 2018), abundance estimates have a large uncertainty and can be difficult to use in assessing population viability and demographic information (e.g., fecundity and survival). In contrast, community-based monitoring programs that rely on collaborations with Indigenous hunters can provide tissue samples, such as reproductive tracts, that can be used in gross anatomical analysis to provide detailed information on the reproductive condition of a population and on spatio-temporal variation in related indices across populations (Brodie, 1971; Sergeant, 1973; Stewart, 1994; Suydam, 2009; Harwood et al., 2015; Kelley et al., 2015).

In addition to management and conservation information, knowledge of reproductive morphology provides important biological information on species that are difficult to study. For example, the uterus in cetaceans is bicornuate and the vaginal channel is lined with longitudinal and transverse folds referred to as pseudocervices. Pseudocervices are a characteristic shared by artiodactyls and cetaceans and are thought to serve several functions, such as reducing contact with salt water and enabling post-copulatory choice (Pabst et al., 1998; Orbach et al., 2017). There is little description of the morphology of the cetacean uterus or pseudocervices in the literature, but this information is important to understand reproductive processes and population dynamics (Boyd et al., 1999; Rommel et al., 2007).

Beluga whales (*Delphinapterus leucas*) are medium-sized toothed whales that occupy Arctic and sub-Arctic regions, taking annual migrations from open-water areas (loose pack ice and polynyas) in wintering regions to open-water estuarine areas during spring and summer for calving, nursing, and feeding (Béland et al., 1990). The International Whaling Commission and the Global Review of Monodontids recognize 29 and 22 putative beluga stocks worldwide, respectively (IWC, 2000; NAMMCO, 2018). Eight beluga stocks (hereafter referred to as populations; see COSEWIC, 2016) reside in Canada (NAMMCO, 2018), and our study focuses on three that are part of subsistence hunts by Inuit in the eastern Canadian Arctic and provide a latitudinal range from 55˚ to 75˚ (Fig. 1). The Hudson Bay region includes different beluga stocks (i.e., Western Hudson Bay and Eastern Hudson Bay), which can aggregate and share common migratory routes, including mating areas in Hudson Strait (Brennin et al., 1997; de March and Postma, 2003; Turgeon et al., 2012; Mosnier et al., 2017). The abundance of Western Hudson Bay (HB) beluga whales is estimated at over 55 000 individuals (Matthews et al., 2017); these animals spend summers in western Hudson Bay and winter in Hudson Strait and southern Davis Strait (COSEWIC, 2004). The Eastern High Arctic-Baffin Bay (HA) beluga population is estimated at over 20 000 beluga whales (Innes et al., 2002) and is distributed around Somerset Island in summer, while spending the winter in the North Water and east Baffin Bay along the West Greenland coast (Richard et al., 2001). The Cumberland Sound (CS) beluga population is estimated at approximately 1380 individuals (DFO, 2019). It currently has a small distribution likely due to past overexploitation and remains in Cumberland Sound most of the year while spending the winter near the entrance of the sound in Baffin Bay (Richard and Stewart, 2008).

Despite the long history of aerial surveys of beluga populations in Canada (e.g., Smith and Hammill, 1986; Innes et al., 2002; Marcoux et al., 2016; DFO, 2017; Gosselin et al., 2017; Matthews et al., 2017), there is relatively little information on reproductive parameters for these populations. In Canada, potential biological removal

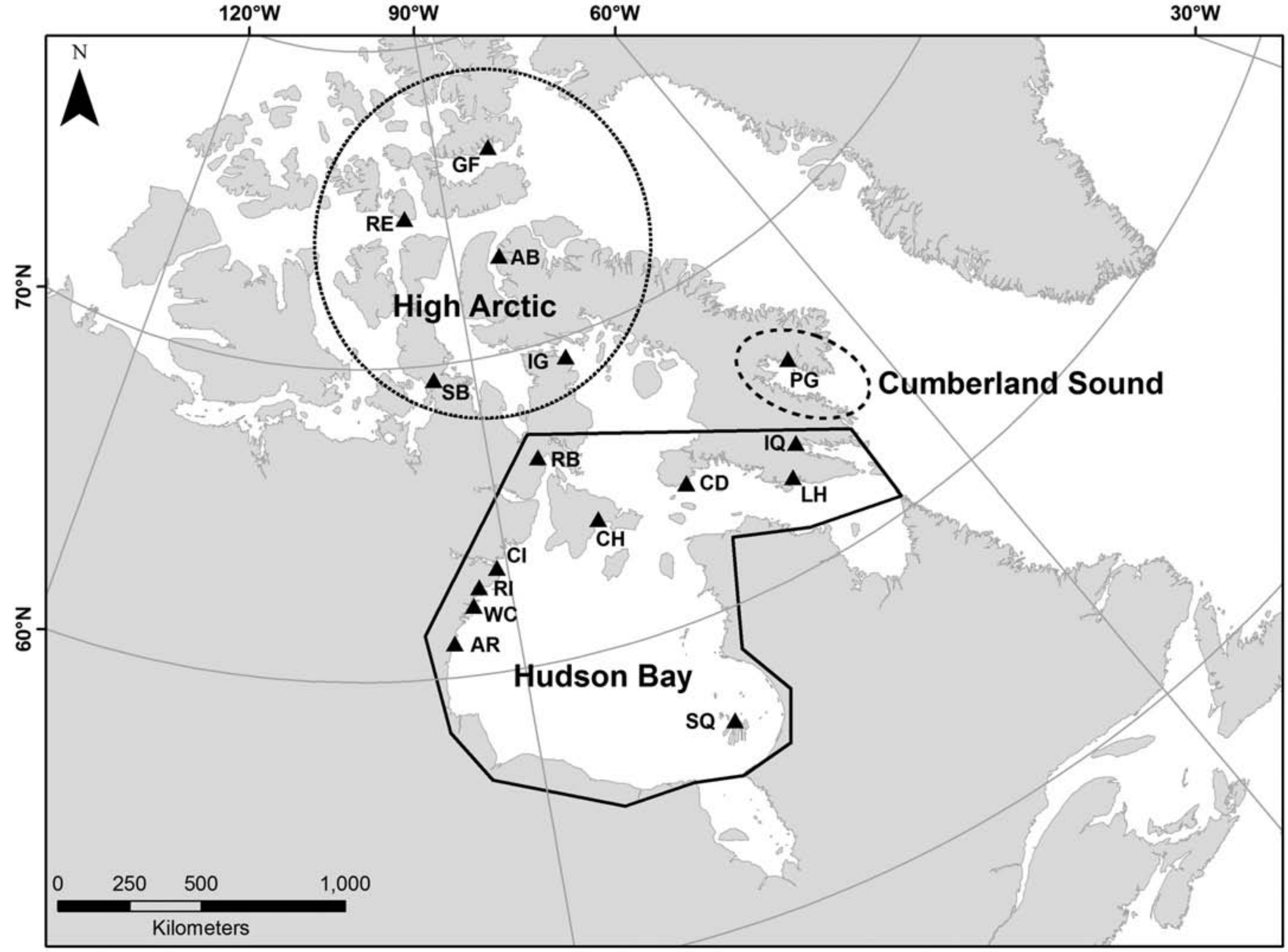

FIG. 1. Grouping of subsistence-harvest sample locations of three beluga whale populations (indicated areas) within the eastern Canadian Arctic from 1989 to 2014. High Arctic (dotted line): AB (Arctic Bay/Ikpiarjuk), GF (Grise Fiord/Ausuittuq), IG (Igloolik/Iglulik), RE (Resolute Bay/Qausuittuq), SB (Spence Bay/Taloyoak); Western Hudson Bay (solid line): AR (Arviat), CD (Cape Dorset/Kinngait), CH (Coral Harbour/Salliq), CI (Chesterfield Inlet/Igluligaarjuk), IQ (Iqaluit), LH (Lake Harbour/Kimmirut), RB (Repulse Bay/Naujaat), RI (Rankin Inlet/Kangiqliniq), SQ (Sanikiluaq), WC (Whale Cove/Tikirarjuaq); and Cumberland Sound (dashed line): PG (Pangnirtung).

estimates and population models to assess sustainability of beluga whale harvests have used an assumed reproductive rate for cetaceans of 4% (Wade, 1998; DFO, 2018, 2019); however, it is desirable to use a more informed estimate. Current knowledge of beluga whale reproduction originates from hunter and field staff observations and gross anatomical analyses of hunted specimens from studies of these eastern Canadian populations conducted over 40 years ago. Results of these studies estimated that females and males reach the age of sexual maturity (ASM) between 4 – 7 y of age and males between 6 – 7 y (Brodie, 1971; Sergeant, 1973; Seaman and Burns, 1981) based on two growth layer groups (GLGs)/y. Counts of GLGs in the dentine of marine mammal teeth are widely used as indicators of age and, as with most marine mammals, observations document that GLGs are deposited yearly. These estimates of ASM have proven to be underestimated because of the incorrect assumption that two GLGs equate to one year of age (Stewart et al., 2006; Lockyer et al., 2007; Luque et al., 2007). Annual mating occurs from late winter to early spring with a peak in early- to mid-April, followed by a gestation period of 12.8 – 14.5 months (Kleinenberg et al., 1969; Brodie, 1971; Sergeant, 1973; Burns and Seaman, 1985). Beluga whale interbirth interval is estimated to range from 2 – 4 y (Sergeant, 1973; Burns and Seaman, 1985; Doidge, 1990). More recent use of chemical tracers from beluga whale teeth has shown that weaning age varies between 1 and 3 y, which supports a 2 – 4 y interbirth interval (Matthews and Ferguson, 2015).

In this spatial and temporal comparative study, we examine beluga whale age-size reproductive parameters, Specifically, we compare (1) female body length growth among populations to assess whether grouping populations into a north (Baffin Bay) and south (Hudson Bay) region is warranted, (2) number of vaginal folds or pseudocervices, (3) total corpora counts as a measure of reproductive activity, and (4) age and length at sexual maturity. We test whether population samples could be combined based on similar body growth patterns to provide for a north-south comparison between those whales residing in Baffin Bay in winter (BB) and those residing in Hudson Bay in summer (HB). However, we also provide pooled results from all of our samples since some of our measurements are unique and can be used for interspecific comparisons that require species-specific information. Our results provide baseline female reproductive data that can be used to assess changes associated with environmental variation in reproductive productivity and health of managed populations, including changes in beluga whale age at sexual maturity and birth rate.

MATERIALS AND METHODS

Sample Collection

Female beluga whale tissue samples were collected by Inuit during seasonal subsistence hunts throughout eastern Canadian Arctic communities from 1989 to 2014 from three populations that are unlikely to interbreed (COSEWIC, 2016; Fig. 1). HA whales were hunted in Arctic Bay, Grise Fiord, Igloolik, Resolute, and Taloyoak (Spence Bay), Nunavut. Beluga whales were collected from HB hunts in Arviat, Cape Dorset, Coral Harbour, Chesterfield Inlet, Iqaluit, Kimmirut, Naujaat, Rankin Inlet, Sanikiluaq, and Whale Cove, Nunavut, and include primarily Western Hudson Bay whales but may also include some Eastern Hudson Bay whales. Whales from CS were hunted in Pangnirtung. As part of community-based marine mammal monitoring programs co-managed by Fisheries and Oceans Canada (DFO) and hunters and trappers associations and organizations across Nunavut, participating communities were sent sampling kits, and hunters collected tissues (jaws and reproductive tracts) that were shipped frozen to the Freshwater Institute in Winnipeg, Manitoba, Canada, along with a data sheet containing recorded bio-data on standard length (tip of rostrum to notch in tail; Committee on Marine Mammals American Society of Mammalogists, 1961), sex, date and location of kill.

Ageing

Age was estimated from GLG (IWC, 1980) counts from median, longitudinal sections of the left-sided second and fifth mandibular tooth according to previously established and described protocols (e.g., Sergeant, 1959; Stewart and Stewart, 2014). Briefly, jaws were boiled and teeth extracted from the lower mandible and mounted onto wooden blocks in preparation for sectioning and GLG counting. We infer one GLG per y as evidenced from radiocarbon marking (Stewart et al., 2006), captive-held individuals (Robeck et al., 2005), and life-history correlations (Luque et al., 2007) that support the deposition of one dentinal GLG per annum in beluga whales. Most dentine counts were performed by one reader and age determined after three independent viewing sessions (Barbara Stewart, Sila Consultants, Howden, Manitoba, Canada).

Body Size Growth

We first tested whether the relative size of whales differs among and between populations as this would support grouping of populations into regions that would allow for more robust comparisons of reproductive morphometrics. We used analysis of covariance (ANCOVA) to test for differences in body growth patterns (effect of age on length) among the three populations, including the interaction term age*population (slope), to determine whether regional comparisons of reproductive measurements require controlling for body size effects. Length measures were non-normal (Shapiro-Wilks test); therefore, both length and age were log-transformed. Homogeneity of variance was assessed using Levene's test ($p = 0.53$). Specifically, we used ANCOVA results to assess whether HA and CS populations could be combined into a BB region. A Tukey honestly significant difference (HSD) post hoc test was performed on each ANCOVA to determine differences among populations. T-test analyses (independent two-sample assuming equal variances) and graphics were performed for reproductive tract morphometrics and sexual maturity (ASM and LSM) using R statistical software (v. 3.6.1). Results were assessed relative to whether populations could be grouped because of similar body growth patterns and other considerations (see Discussion).

A Gompertz growth model was used to graph the differences among populations and visually assess the success of grouping populations. The indeterminate growth trajectory of marine mammals is usually modelled using a three-parameter logarithmic function, the Gompertz growth function (Winsor, 1932), to describe the length of the average individual at any given age. The growth parameters among regions were estimated by fitting the Gompertz growth curve to the length-at-age data as follows:

$$-k(t-I)$$

$$lt = L_\infty e^e$$

where lt is the estimated length at age (t), L_∞ is the asymptotic maximum length reached by individuals in the study population, e is Euler's Number ($e = 2.71828...$), k is a growth coefficient that describes how quickly the maximum length is attained, t is an extrapolation of data to fix the position of the curve along the x-axis, and I is the age at the inflection point (Quist et al., 2012). Data were fit using nonlinear least squares regression (nls function in the nlstools Package [Baty et al., 2015]) in R. Approximate 95% confidence intervals (CI) of parameter estimates for each model were obtained by calling to a bootstrap function (nlsBoot in R) with 10 000 iterations providing robust estimates for nonlinear regression (Motulsky and Ransnas, 1987; Ogle, 2013). Residuals were plotted to examine variability among the models (i.e., homoscedasticity), data distribution, and outliers.

TABLE 1. Number of examined female reproductive tract samples, ovary presence, and reproductive status categories (R-Status) and observed pathologies by population and year.[1]

	HA R–Status							HB R–Status							CS R–Status						
Year	n^t	n^{bOV}	R	A	J	$A^{\%}$	P_n	n^t	n^{bOV}	R	A	J	$A^{\%}$	P_n	n^t	n^{bOV}	R	A	J	A%	P_n
1989	–	–	–	–	–	–	–	11	3	3	–	3	0	3	1	1	1	–	–	n/a	–
1990	–	–	–	–	–	–	–	1	–	–	–	–	n/a	–	–	–	–	–	–	–	–
1991	–	–	–	–	–	–	–	5	1	1	–	–	n/a	2	3	3	–	1	2	33.3	–
1992	–	–	–	–	–	–	–	20	6	3	7	1	35.0	3	7	–	–	2	1	14.3	1
1993	–	–	–	–	–	–	–	14	6	4	3	–	21.4	3	5	–	–	1	–	20.0	–
1994	–	–	–	–	–	–	–	18	3	2	4	–	22.2	2	12	1	–	2	2	16.7	–
1995	9	1	2	3	–	33.3	1	12	3	1	2	–	16.6	3	7	3	–	1	3	14.3	1
1996	1	–	1	–	–	n/a	–	25	13	13	10	5	40.0	2	9	2	2	6	–	66.7	1
1997	9	5	4	3	–	33.3	1	49	18	7	27	3	55.1	13	5	1	–	4	–	80.0	–
1998	–	–	–	–	–	–	–	10	3	1	4	–	40.0	–	–	–	–	–	–	–	–
1999	3	–	–	–	–	n/a	1	19	–	–	2	–	10.5	1	–	–	–	–	–	–	–
2000	6	2	–	2	1	33.3	–	13	–	–	3	–	23.1	1	1	–	–	–	1	n/a	–
2001	4	1	–	2	–	50.0	–	13	–	–	5	–	38.5	5	1	–	–	1	–	n/a	–
2002	–	–	–	–	–	–	–	3	–	–	1	–	33.3	–	6	–	–	–	–	n/a	–
2003	–	–	–	–	–	–	–	13	3	2	1	1	7.7	1	–	–	–	–	–	–	–
2004	–	–	–	–	–	–	–	16	6	5	3	1	18.8	3	–	–	–	–	–	–	–
2005	–	–	–	–	–	–	–	5	–	–	–	–	n/a	2	–	–	–	–	–	–	–
2006	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2007	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2008	1	–	–	–	–	n/a	–	17	8	6	6	–	35.3	2	1	–	–	–	–	–	–
2009	–	–	–	–	–	–	–	4	1	1	–	–	n/a	1	–	–	–	–	–	–	–
2010	–	–	–	–	–	–	–	1	–	–	1	–	n/a	–	–		–	–	–	–	–
2011	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2012	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–
2013	–	–	–	–	–	–	–	2	–	–	–	–	n/a	–	–	–	–	–	–	–	–
2014	3	1	–	1	–	33.3	1	11	5	4	3	–	27.3	3	–	–	–	–	–	–	–

[1] HA: High Arctic/Baffin Bay, HB: Western Hudson Bay, CS: Cumberland Sound; n^T: total number of female reproductive tract samples, n^{bOV}: number of samples with both ovaries provided, R: resting females (with corpus albicans, non-gravid), A: active females (with corpus luteum (CL ≥ 10 mm), gravid, placental remains within uterus or postpartum), J: juvenile, $A^{\%}$: percent active females, P_n: number of pathological cases (observed reproductive tracts with abnormalities including ovaries), n/a: not applicable.

Reproductive Morphology

Following the results from analyzing female beluga whale length with age, we combined reproductive morphology data for CS and HA into a BB region. We conducted post-mortem gross examinations of 375 female reproductive organs (Table 1), collected from three beluga populations (HA: n = 36, HB: n = 282, and CS: n = 57) across 17 northern communities within the Eastern Canadian Arctic from 1989 to 2014 (Fig. 1). Not all whales had matching information on age (HB: 271 of 282, CS: 55 of 57, and HA: 33 of 36), length (HB: n = 240, CS: n = 56, and HA: n = 29), and ovaries [HB: n = 79, CS: n = 11, and HA: n = 9).

All measurements (to 1.0 mm) were taken by tape measure or ruler and weights were recorded in grams (to 0.01 g) using an electronic balance (Denver Instruments, Bohemia, New York), and digital photographs were taken of all reproductive organs. Individuals were examined for evidence of conception (an embryo, foetus, placenta, or thickened and heavily vascularised endometrium). Endometrial colour and form, as well as the presence of placental material, were recorded. Ovaries were excised, wet weight and dimensions (length, height, width, and any unusual features) recorded and thereafter preserved in 10% neutral-buffered formalin for subsequent ovary sectioning and corpora readings. We recorded the presence of pseudocervices within the elongated vaginal tract, as well as width and height of existing pseudocervices. Additionally, reproductive tracts were macroscopically assessed for any abnormalities within external or internal parts of the female reproductive tracts (e.g., stenosis, occlusions, endometriotic lesions, genital warts, leiomyoma, cysts or growths, and calcifications) that may impede ovulation, fertilization, or implantation and possibly affect the reproductive health of individuals. Raw data are available on the Government of Canada's Open Data website.

For each ovary, we recorded the presence of the site of the ruptured follicle, a yellow body or corpus luteum (CL), and the regressed CL as a pale corpus albicans (CA) (Best, 1968; Perrin et al., 1976; Marsh and Kasuya, 1984). In cetaceans, CLs and CAs form distinct and persistent features that accumulate within the ovary (Harrison, 1969; Perrin and Donovan, 1984) and provide a record of a female's reproductive history (Slijper, 1962; Collet and Saint Girons, 1984).

For ovarian examination, tissue fixative for each excised ovary was replaced by distilled water at least 24 h before sectioning and corpora reading. Formalin-fixed ovaries were weighed and cross-sectioned by hand in approximately 2–3 mm intervals longitudinally to the excision axis, resulting in a fan-like ovary profile. Each section was inspected for ovarian structures and any observed feature was measured for length, width and height (to the nearest mm) and classified into corpus luteum, corpus albicans, follicle, or accessory corpora. Any unusual features (e.g., calcifications, discolorations) were recorded. Sexual maturity was confirmed by the presence of at least one corpus luteum or albicans as in Perrin and Donovan (1984) and by the presence of a conceptus or equally of placental material within the uterine horns, as often fetuses were removed by hunters. Corpora assessments were performed by one reader (C. Willing) to minimize bias in the subjective determination of atretic or accessory corpora that can be confused as CLs or older CAs (Harrison, 1977; Beckmen, 1986); therefore, these features were not included in total corpora counts.

We followed similar classifications of females into reproductive status categories as previously described (Read, 1990; Lanyon and Burgess, 2014; Orbach et al., 2016; Corkeron et al., 2017). As an alternative to pregnancy and ovulation status, we use the terms "active" female (with corpus luteum in one ovary or conceptus/placental material present in the uterus or both), "resting" female (no corpus luteum and no conceptus but at least one corpus albicans present in one ovary) and "juvenile" female (no corpora lutea or albicantia present). This allowed us to include in our analyses single ovaries, containing a corpus luteum (CL $\geq$ 10 mm), which indicates a gravid or postpartum/lactating female and displays an individual with high reproductive capacity compared to their resting counterparts without a CL. All statistical comparisons of reproductive morphology were conducted using Welch's t-test, which adjusts the number of degrees of freedom when the variances are thought to be unequal.

Total Corpora (Reproductive Activity)

In addition to reproductive status and given that paired ovaries were provided, total corpora counts of each beluga whale were assessed by counting all existing corpora lutea and albicantia within the ovaries (hereafter referred to as reproductive activity). Thus, reproductive activity reflected a female's past and present ovarian potential to reproduce. Reproductive activity was then compared over age and time for regions using ANOVA and t-tests.

We assessed possible reproductive senescence in beluga whales by testing model fit for three possible patterns of reproductive activity over time: (1) linear ($Y = b_0 + b_1X$), (2) curvilinear (quadratic: $Y = b_0 + b_1X + b_2X^2$), and (3) sigmoidal (polynomial: $\mathrm{Y} = \mathrm{b}_0 + \mathrm{b}_1\mathrm{X} + \mathrm{b}_2\mathrm{X}^2 + \mathrm{b}_2\mathrm{X}^3$). We assumed a sigmoidal fit would be indicative of an asymptote in reproductive activity suggesting possible occurrence of post-reproductive females (Marsh and Kasuya, 1986). Model fit was assessed using adjusted R^2, and the process was run for each of the pooled samples by region and all samples together.

Age and Length at Sexual Maturity

There is some discrepancy as to how immature and mature stages should be defined in odontocetes. Here we use immature whales as those having no corpora lutea or corpora albicantia, were not lactating, were not pregnant,

TABLE 2. Results of ANCOVA explaining log body length due to whale age, population, and interaction (slope), including the relevant *p*-values of post hoc Tukey pairwise comparison tests among beluga whale populations. ANCOVA$_1$ assessed differences among three populations whereas ANCOVA$_2$ tested for differences between the HB population and BB (the combined CS and HA populations). Significance is set at α = 0.05 and bolded values are considered significant.[1]

	ANCOVA$_1$			ANCOVA$_2$		
Variables	DF	F	*p*-value	DF	t-value	*p*-value
Log(age)	1	177.7	**< 0.001**	1	5.77	**< 0.001**
Population	2	16.5	**< 0.001**	1	−2.31	**0.02**
Age*Pop	2	0.79	0.45	1	0.98	0.33
	Tukey test		*p*-values	Tukey test		*p*-values
	HA vs. CS		0.71	BB vs. HB		**< 0.001**
	HB vs. CS		**< 0.001**			
	HB vs. HA		**0.006**			

[1] DF = degree of freedom, F = F statistics, t-value = t statistics; CS = Cumberland Sound, HA = High Arctic, BB = Baffin Bay, and HB = Hudson Bay.

and had small uteri (Hohn et al., 1985; Sørensen and Kinze, 1994). Age of sexual maturity (ASM) can be estimated using a number of approaches (DeMaster, 1984). One technique for discrete breeders that we apply here uses age-specific reproductive data that allow for the probability estimation of variation and can be used statistically to assess differences between regions (DeMaster, 1978). Another technique commonly used in fisheries assessments is to run a logistic regression on the binary dependent variable (mature or immature), allowing for the interpolation of the median age at which 50% of the females mature (also referred to as LD50). The median age can then be incorporated into the ANOVA to compare populations or regions (Perrin et al., 1976; Ferrero and Walker, 1995). Similarly, we used logistic regression to estimate length at age of maturity (LSM) when half of the whales at a particular length were mature (Suydam, 2009). Last, we compared the ratios of mature whales (e.g., 12 of 17 whales aged at 13 were sexually mature) at 8, 9, 10, 11, 12, 13, 14 years-of-age, which covers a period when beluga whales mature, as a further check on our results.

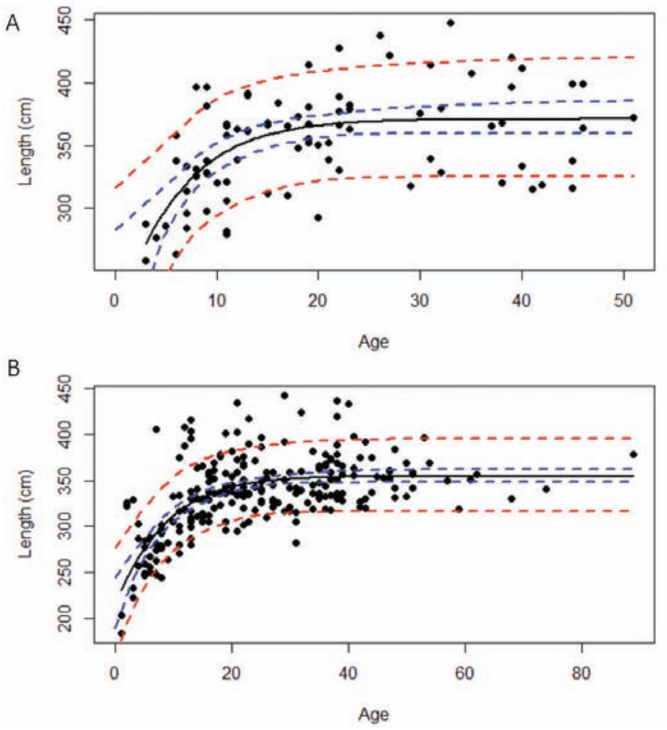

FIG. 2. Fitted line plot of length at age for female (A) BB and (B) HB beluga using the Gompertz growth model with approximate 95% bootstrap confidence bounds shown as blue dashed lines and 95% bootstrap prediction bounds shown as red dashed lines. For BB, asymptotic maximum length L_∞ = 370.9 ± 6.2 cm (mean ± SE), growth coefficient k = 0.732, t0 = 1.044 (n = 86) and for HB L_∞ = 354.4 ± 3.6, k = 0.722, t0 = −0.1560 (n = 235).

RESULTS

Body Size Growth

The average age of beluga whales for CS was 18.6 ± 12.3 (mean ± SD; range 3-51; n = 55), 23.5 ± 12.3 (6-46; n = 31) for HA, 20.4 ± 12.6 (3-51; n = 86) for BB, 25.3 ± 15.1 (1-89; n = 235) for HB, and 24.0 ± 14.6 (-89; n = 321) when pooled. For beluga whales greater than 20 years of age, average length for CS was 335.2 ± 38.1 cm (range 264–396; n = 13), for HA was 346.4 ± 42.1 (279-396; n =10), for BB was 340.1 ± 39.3 (264–396; n = 23), for HB was 303.6 ± 49.2 (184–401; n = 60), and when pooled was 313.7 ± 49.2 (184–401; n = 83). ANCOVA results indicated that HA and CS beluga whales did not differ significantly in regards to body length (Table 2). The HA and CS beluga whales were subsequently combined as a BB region. Accordingly, subsequent ANCOVA between BB and HB resulted in significantly different body lengths (Table 2). Beluga whale asymptotic maximum body length was greater in BB (370.9 ± 6.2 cm; mean ± SE; n = 86) than in HB (354.4 ± 3.6; n = 235) based on Gompertz growth models (Fig. 2).

Pseudocervices/Vaginal Folds

No significant differences in average number of pseudocervices (vaginal folds) were observed among

TABLE 3. Summary statistics from pooled left and right mature female beluga whale reproductive tract and tissues. CS = Cumberland Sound, HA = High Arctic, and HB = Hudson Bay; Mean ± SD (Min-Max).

	CS	HA	HB	Pooled
Corpora albicantia (Left ovary):				
N	29	69	457	555
Horizontal length (mm)	8.1 ± 4.1 (1–16)	8.6 ± 5.1 (2–22)	8.1 ± 4.7 (1–25)	8.2 ± 4.7 (1–25)
Horizontal diameter (mm)	8.4 ± 4.3 (1–16)	8.6 ± 5.0 (1–20)	8.1 ± 4.7 (1–20)	8.2 ± 4.7 (1–20)
Vertical diameter (mm)	5.9 ± 3.0 (1–14)	6.6 ± 3.5 (1–17)	5.8 ± 3.1 (1–16)	5.9 ± 3.2 (1–17)
Corpora albicantia (Right ovary):				
N	64	67	567	698
Horizontal length (mm)	9.9 ± 5.3 (1.5–20)	9.0 ± 4.6 (1–23)	7.8 ± 4.4 (1–28)	8.1 ± 4.5 (1–28)
Horizontal diameter (mm)	10.4 ± 5.2 (1–25)	9.3 ± 4.8 (1–20)	8.1 ± 4.5 (1–25)	8.4 ± 4.7 (1–25)
Vertical diameter (mm)	6.9 ± 3.1 (2–13)	7.0 ± 3.0 (2–14)	5.7 ± 2.9 (1–17)	5.9 ± 2.9 (1–17)
Corpora albicantia (ovaries combined[1]):				
N	93	136	1024	1253
Horizontal length (mm)	9.3 ± 5.0 (1–20)	8.8 ± 4.8 (1–23)	7.9 ± 4.5 (1–28)	8.1 ± 4.6 (1–28)
Horizontal diameter (mm)	9.8 ± 5.1 (1–25)	9.0 ± 4.9 (1–20)	8.1 ± 4.6 (1–25)	8.3 ± 4.7 (1–25)
Vertical diameter (mm)	6.6 ± 3.1 (1–14)	6.8 ± 3.3 (1–17)	5.7 ± 3.0 (1–17)	5.9 ± 3.0 (1–17)
Ovary:				
N	33	33	203	269
Weight (g)	36.8 ± 25.4 (6.4–95.3)	32.5 ± 14.4 (11.4–57.5)	25.7 ± 13.8 (6.0–90.3)	27.5 ± 15.9 (6.0–95.3)
Length (mm)	88.5 ± 21.0 (48.0–140.0)	83.0 ± 13.7 (60.0–122.0)	78.7 ± 13.9 (44.0–120.0)	80.4 ± 15.3 (44.0–140.0)
Width (mm)	55.9 ± 21.5 (23.0–131.0)	50.4 ± 9.8 (33.0–76.0)	45.7 ± 8.1 (28.0–78.0)	47.5 ± 11.4 (23.0–131.0)
Height (mm)	22.5 ± 15.7 (7.0–55.0)	20.1 ± 12.2 (8.0–53.0)	17.9 ± 10.4 (5.0–55.0)	18.7 ± 11.5 (5.0–55.0)
Corpora lutea:				
N	12	8	52	72
Horizontal length (mm)	42.6 ± 12.7 (18.0–67.0)	37.0 ± 9.4 (14.0–48.0)	35.9 ± 9.9 (10.0–51.0)	37.1 ± 10.7 (10.0–67.0)
Horizontal diameter (mm)	26.5 ± 4.8 (17.0–35.0)	30.3 ± 6.1 (22.0–40.0)	30.5 ± 10.1 (7.0–50.0)	29.8 ± 9.2 (7.0–50.0)
Vertical diameter (mm)	33.8 ± 13.5 (11.0–53.0)	31.9 ± 8.3 (13.0–40.0)	28.2 ± 10.5 (8.0–47.0)	29.5 ± 11.1 (8.0–53.0)
Accessory corpora lutea:				
N	1	1	4	6
Horizontal length (mm)	7.0 ± 0.0 (7.0–7.0)	9.0 ± 0.0 (9.0–9.0)	5.5 ± 4.4 (2.0–13.0)	6.3 ± 3.8 (2.0–13.0)
Horizontal diameter (mm)	10.0 ± 0.0 (10.0–10.0)	10.0 ± 0.0 (10.0–10.0)	6.3 ± 4.6 (2.0–14.0)	7.5 ± 4.2 (2.0–14.0)
Vertical diameter (mm)	5.0 ± 0.0 (5.0–5.0)	5.0 ± 0.0 (5.0–5.0)	4.8 ± 2.2 (2.0–8.0)	4.8 ± 1.8 (2.0–8.0)
Follicles:				
N	7	9	60	76
Horizontal length (mm)	11.9 ± 4.8 (7.0–22.0)	8.0 ± 3.0 (3.0–13.0)	10.0 ± 5.7 (3.0–30.0)	10.0 ± 5.5 (3.0–30.0)
Horizontal diameter (mm)	11.6 ± 4.8 (5.0–22.0)	7.1 ± 3.9 (2.5–13.0)	10.2 ± 5.4 (2.0–30.0)	9.9 ± 5.3 (2.0–30.0)
Vertical diameter (mm)	10.5 ± 5.4 (5.0–22.0)	5.9 ± 2.7 (2.0–11.0)	7.4 ± 4.9 (0.5–30.0)	7.5 ± 4.9 (0.5–30.0)
Pseudocervices:				
N	13	17	137	167
Number	8.7 ± 3.6 (3–13)	9.1 ± 2.6 (2–12)	8.5 ± 3.8 (0–16)	8.6 ± 3.6 (0–16)

[1] not necessarily including complementary ovary.

populations (ANOVA: $F_{2,164} = 0.21$, $p = 0.81$; overall mean of 8.6 ± 3.6) (Table 3). No significant differences in average number of pseudocervices were observed among mature and immature females ($t = -0.230$, df = 23.8, $p = 0.82$), and there was no significant increase with age ($F_{1,58} = 1.33$, $p = 0.25$).

Total Corpora/Reproductive Activity

Reproductive status was determined for 235 female beluga whales from the three populations over the collection periods (CS: 1989–2002; HA: 1995–2013; HB: 1989–2014; Table 1). Total corpora counts (10-60 y) from HB (79 paired ovaries) and BB (n = 21) beluga whales increased with age (ANOVA: $F_{2,87} = 55.26$, $R^2 = 0.55$, $p < 0.001$) with BB having a greater rate of additional corpora counts with age (slope differed: $t = 2.05$, $p = 0.044$). Comparing model fit indicated that for HB and the pooled data a logistic pattern best represented reproductive activity over age, which suggests that an asymptote in reproduction occurred for older individuals (Fig. 3). For BB whales, an exponential model best fit the data, which suggests that reproductive activity was reduced with age but an asymptote was not supported (Table 4). Estimated total corpora counts at age 30 for HB was 10.7 ± 5.0 SD compared to 13.1 ± 11.5 SD for BB. High numbers of large corpora (> 10 mm) suggest an onset of reproductive senescence between the ages of 40 and 50 y (Fig. 3). Age-matched corpora counts of HB females (n = 65) and BB (19) beluga whales over two decades did not show a significant trend (ANOVA: $F_{2,87} = 1.65$, $R^2 = 0.036$, $p = 0.20$) nor differ between regions ($t = 1.70$, $p = 0.093$).

TABLE 4. Comparing linear, exponential, and polynomial model fits for beluga whales residing in Baffin Bay (BB), Hudson Bay (HB), and pooled eastern Canadian Arctic to assess the best representation of reproductive activity over age. Results suggest that an asymptote in reproduction occurred for older females for the HB and pooled data (best model bolded).

Model	Regression fit	*p*-value	Adjusted R^2	AIC
Linear:				
BB	$F_{1,18}$ = 224.5	< 0.0001	0.921	83.02
HB	$F_{1,74}$ = 103.8	< 0.0001	0.578	404.9
Pooled	$F_{2,93}$ = 95.15	< 0.0001	0.665	498.4
Exponential:				
BB	**$F_{1,18}$ = 106.2**	**< 0.0001**	**0.917**	**84.99**
HB	$F_{1,74}$ =51.34	< 0.0001	0.573	406.9
Pooled	$F_{2,93}$ = 93.62	< 0.0001	0.661	499.4
Polynomial:				
BB	$F_{1,18}$ = 77.84	< 0.0001	0.924	84.10
HB	**$F_{1,74}$ =34.15**	**< 0.0001**	**0.570**	**408.3**
Pooled	**$F_{2,93}$ = 63.02**	**< 0.0001**	**0.662**	**500.1**

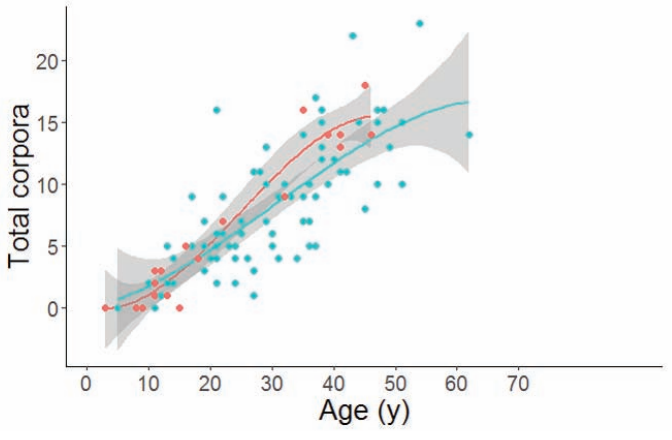

FIG. 3. Reproductive activity (total counts of corpora lutea and albicantia (> 9 mm) in paired ovaries) of Hudson Bay (blue) and Baffin Bay (red) female beluga whales by age.

Sexual Maturity

Using the probability method (DeMaster, 1978), average age of sexual maturity was not significantly greater for Hudson Bay (10.97 ± 0.52, n = 68) than for Baffin Bay (9.92 ± 0.71, n = 37), with a pooled ASM of 9.52 ± 0.63 (n = 103). Using logistic regression and restricting age classes between 3 and 30 y of age (n = 32 immature and 171 mature), we estimated an ASM of 9.12 ± 0.60 y (n = 130) for the pooled data and 9.93 ± 0.69 (n = 98) for HB, while the BB model (n = 31) was not significant (Table 5). Using whales aged 8-14 y, which covers a period when beluga whales typically mature, the BB whales had proportionately more mature females (11 of 19; 58.0%) than the HB population (21 of 43; 48.9%; $\chi^2 = 7.56$, $p = 0.006$). The first indication of maturity (with CL/CA ≥ 10 mm) was at age 8 (1 mature of 9 whales inspected), and full maturity status (all females with CL/CA ≥ 10 mm) was attained between 13 and 14 y (12 of 17 whales aged at 13 were sexually mature, and all five 14-year-old whales were mature). Based on all three approaches, the overall pattern was for later ASM for HB versus BB whales.

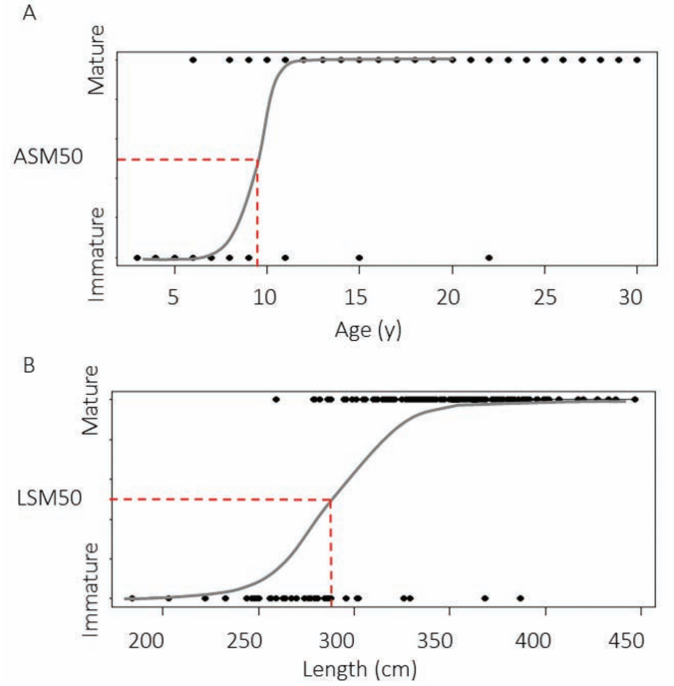

FIG. 4. Age (A) and body length (B) at which 50% of females reached sexual maturity status (ASM50% and LSM50% represented by dashed line) for beluga whales from eastern Canadian Arctic populations. The pooled estimated age of sexual maturity was 9.1 y at 298.1 cm (see Table 5).

Length of sexual maturity (LSM) was assessed using nonlinear logistic regression that estimated lengths at which half of females were sexually mature (LSM50% = 314.5 ± 19.78 cm for BB (n = 33); and 290.3 ± 5.52 for HB (n = 88) and 298.1 ± 5.27 (n = 121) for pooled; Table 5; Fig. 4A and 4B).

DISCUSSION

Little is known about beluga whale reproduction from field studies largely because of the logistical challenges in studying Arctic marine mammals living in areas with low human density and limited infrastructure (Heide-Jørgensen

TABLE 5. Summary of age (ASM) and length (LSM) at female sexual maturity for Hudson Bay (HB) and Baffin Bay (BB = HA + CS), Nunavut, Canada, estimated using logistic regression on 3 – 30 y-old whales.

Variable	n	Ratio (Immature/Mature)	LD50[1]	SD	*p*	z-value	Residual deviance	df	AIC
ASM:									
HB	99	24/75	9.93	0.69	0.0003	3.59	72.5	97	33.0
BB	32	4/28	5.11	3.01	0.037	2.08	33.8	30	22.3
Pooled	131	28/103	9.12	0.60	< 0.001	4.25	107.2	129	58.0
LSM:									
HB	88	25/63	290.3	5.52	< 0.001	4.39	44.2	86	48.2
BB	33	7/26	314.5	19.78	0.015	2.42	25.8	31	29.8
Pooled	121	32/89	298.1	5.27	< 0.001	5.23	75.8	119	79.8

[1] Median age or length at which 50% of females mature.

and Teilmann, 1994; O'Corry-Crowe, 2009; Suydam, 2009). Although research on captive beluga whale reproduction is available (Robeck et al., 2005; Katsumata, 2010), results may not represent natural fitness situations (Schmitt et al., 2010). Here, using a large dataset of female reproductive tracts and morphometrics from beluga whales, we were able to test for population differences in female body growth and reproductive parameters, including age and length of sexual maturity, and confirm that beluga whale body size differed among regions with a general trend of larger whales at higher latitudes (Stewart, 1994; Luque and Ferguson, 2010). How body size differences relate to spatial differences in reproductive morphology is largely unknown (Lockyer, 1986). Therefore, we have provided population-specific basic morphological measurement data on a government open-data website and here summarize female whale beluga reproductive parameters including number of pseudocervices and reproductive activity (corpora counts). This study is one of the first to detail morphological reproductive measurements for wild-caught female beluga whales across multiple populations (Suydam, 2009; Kelley et al., 2015). Our results confirm that belugas are characterized by late maturation, long interbirth intervals, and extreme longevity relative to body mass (Connor et al., 1998; Ferguson and Higdon, 2013).

Life-history traits are strongly associated with body size (Dobson and Oli, 2008), and therefore we expected to find differences in body growth among the beluga populations that relate to reproduction. A general pattern of greater body size with latitude, which was first described for beluga whales by Luque and Ferguson (2010), was corroborated by our data, which showed a larger size of BB beluga whales relative to HB whales. Similar body lengths that we estimated with the Gompertz growth model for BB (370.9 ± 6.2 cm; n = 86 average female asymptotic length) and HB (354.4 ± 13.6 cm) were found by Sergeant and Brodie (1969) who calculated lengths of 350 cm for CS and 310 cm for HB; Stewart (1994) who calculated lengths of 321.3 ± 15.3 cm (n = 12) for HA, 337.6 ± 22.2 (n = 7) for CS, and 283.5 ± 41.5 cm (n = 51) for HB; and Luque and Ferguson (2010) provided lengths of 385.7 ± 9.24 cm (n = 55) for CS and 360.5 ± 5.25 cm (n = 151) for HB belugas. Justification for combining HA and CS into a BB region based on body size similarities is supported by genetics (Postma, 2017), winter range use (at least historically; Watt et al., 2016), and similar demographic history due to severe depletion following commercial whaling activity in the early 20th century (NAMMCO, 2018). Adult body size is related to mobility, feeding strategy, and home range (McNab, 1963). Luque and Ferguson (2010) speculated that larger body size may be correlated with greater migration distances in beluga whales as it would assist with maintaining physiological processes over a period of limited foraging. Although greater body size is thought to correlate with later age of first reproduction (Wootton, 1987), our results suggest later age of reproduction for the smaller HB whales.

A large corpus typically indicates pregnancy and confirms sexual maturity (Mann, 2009). The first evidence of this occurred at 8 y of age for beluga whales across all populations, while full maturity status (all females with corpus ≥ 10 mm) was achieved by age 13 – 14 y. Previous studies, using 2 GLG ageing, have found that female beluga whales have their first pregnancy between 4 – 7 y of age (Brodie, 1971; Sergeant, 1973; Doidge, 1990; Heide-Jørgensen and Tielmann, 1994). We found that sexual maturity was attained at double that age (13 – 14 y) using 1 GLG ageing. However, first conception in captive beluga whale was found to be between 6 and 12 y of age (Robeck et al., 2005), suggesting a slightly earlier ASM under aquarium conditions. Delayed onset of sexual maturity in females in eastern Canadian Arctic beluga whale populations may have repercussions on population demography. While most studies agree that population growth is limited more by adult survival than by reproduction in long-lived mammals like cetaceans (Crone, 2001; Oli and Dobson, 2003), Manlik et al. (2016) found that reproduction is considerably more important in dolphins (*Tursiops* cf *aduncus*). They argued that conservation efforts should focus on raising reproductive rates to reverse population decline, while reducing adult survival would be less effective (Manlik et al., 2016). Delayed onset of sexual maturity may be one factor that has played a role in listing the CS beluga whales as threatened.

Beluga whales in the northern region (BB) grew to a larger body size and matured earlier compared to southern HB (Western Hudson Bay) beluga whales. This pattern is at odds with interspecific theory, which suggests that larger-bodied species grow slower and mature later (Western, 1979; Harvey and Purvis, 1999), as well as with intraspecific theory, whereby larger populations of smaller-sized mammals show earlier maturation (Christian, 1971; Clutton-Brock and Harvey, 1978), and stable populations often have higher reproductive output (Manlik et al., 2016). The HB beluga population is the largest in Canada (Matthews et al., 2017) and with a smaller body size, we would have anticipated that they would have earlier maturation. However, in being such a large population, HB beluga whales may be at or near carrying capacity and are starting to see a density-dependent decrease in reproduction (Sergeant and Brodie, 1969). Alternatively, it is possible that the HA and CS beluga whales have an earlier maturation because of their lower density and possible higher population growth rate associated with recovery from past depletion by commercial whaling (Kemper, 1980; Brodie et al., 1981; Mitchell and Reeves, 1981). Besides, earlier maturation does not necessarily translate into greater reproductive output. An understanding of the interbirth interval and weaning duration is needed to evaluate total reproductive output. Matthews and Ferguson (2015) found there was variability in weaning duration among individual beluga whales, although due to small sample sizes, they did not detect significant differences among populations of beluga whales.

Cetaceans exhibit complex foldings of the vaginal wall, sometimes referred to as vaginal folds or pseudocervices (Orbach et al., 2017). We found that beluga whales had an average of approximately nine pseudocervices, and there was no variation among populations suggesting species-level adaptation. The presence and morphology of pseudocervices have been used to assess mating systems in whales (Orbach et al., 2016), and the number of pseudocervices has varied across species from one in common bottlenose dolphins (*T. truncatus*), long-beaked common dolphins (*Delphinus capensis*), and short-beaked common dolphins (*D. delphis*) to 13 in harbor porpoises (*Phocoena phocoena*). Thus, the number of pseudocervices in beluga whales is at the higher end of this range. Although the exact function of pseudocervices is unknown, two hypotheses include a functional mechanism for preventing seawater from entering, and for post-copulatory sexual selection (Orbach et al., 2017). Beluga whales have a promiscuous mating system (Kelley et al., 2014), and promiscuity may support the need for post-copulatory sexual selection and result in more pseudocervices. Future studies may want to compare the number of pseudocervices in beluga whales to that in narwhal (*Monodon monoceros*), which is considered to be polygynous (Kelly et al., 2015). Recording morphological data on pseudocervices for more whale species, in conjunction with studies of social structure and mating system, will help in evaluating their function.

Total corpora found within the ovaries increased with age for female beluga whales, which suggests that corpora counts may provide approximate estimates of the lifetime reproductive success of individuals (Danil and Chivers, 2007). We provide preliminary evidence that whales in this study reproduced up to age 40–50 y, which corresponds to the upper range of their mean reported lifespan (COSEWIC, 2004). The number of corpora reached an asymptote between 40 and 50 y, which may suggest a reduction in reproductive activity, but with few animals older than 50 in this study, it is difficult to make any conclusions about beluga whale senescence. Reproductive senescence in mammals is rare (Croft et al., 2015), but in whales it has been found in at least two species: killer whales (*Orcinus orca*) and short-finned pilot whales (*Globicephala macrorhynchus*) (Foote, 2008). Clear confirmation in other social cetaceans remains elusive. Field studies of killer whales have shown that no female older than 48 y has given birth, yet the maximum lifespan of killer whales is approximately 90 y (Olesiuk and Bigg, 1990). No clear evidence of senescence in beluga whales has been found (Suydam, 2009). Although we do not have a high proportion of beluga whales older than age 50 in our study, it is estimated that beluga whales can live up to 80–90 y (Stewart et al., 2006; Luque and Ferguson, 2010 reported a maximum age of 77 for HB). If so, the asymptote at age 40–50 may be indicative of a period of reproductive senescence. More information on reproduction in the oldest cohort of beluga whales is needed.

To ensure monitoring and conservation programs for beluga whales are sustainable and effective, information on demographic parameters such as abundance and reproduction is needed. Our study provides the first step to using species, and even population-specific, reproductive parameters. This study also provides baseline information for comparison in the future as populations adapt and deal with environmental changes. Further work to evaluate the implications of later maturation and to define the interbirth interval across populations is needed. Overall, an improved understanding of beluga reproductive strategies would facilitate adequate management and conservation of this species (Hunt et al., 2013).

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