



# Discriminating Canadian Arctic beluga management stocks using dentine oxygen and carbon isotopes

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**ABSTRACT:** In the eastern Canadian Arctic, belugas *Delphinapterus leucas* exhibit genetic and ecological differentiation across their distribution that forms the basis of management stocks for traditional Inuit hunts. Using oxygen and stable carbon isotope ratios in dentine phosphate ( $\delta^{18}\text{O}_p$ ) and structural carbonate ( $\delta^{13}\text{C}_{SC}$ ), respectively, we evaluated the spatial structure of 3 of these beluga stocks: Western Hudson Bay (WHB,  $n = 30$ ), Cumberland Sound (CS,  $n = 44$ ), and Eastern High Arctic–Baffin Bay (EHA-BB,  $n = 29$ ). Pairwise comparisons revealed significant differences in  $\delta^{18}\text{O}_p$  and Suess-adjusted  $\delta^{13}\text{C}_{SC}$  among all stocks, with the exception of similar  $\delta^{18}\text{O}_p$  between the WHB and CS stocks. A linear discriminant analysis (LDA) model fit to 60% of the data set (training data) successfully classified 84% of the remaining belugas (test data) to their respective stocks based on hunt location. Isotopic overlap among stocks could reflect (1) homogeneous baseline stable isotope (SI) composition between geographically adjacent stocks, (2) some degree of marginal geographic overlap in ranges or individual movements among stocks, perhaps during late spring, or (3) confounding dietary influences that increased within-stock SI variation. Some misclassifications consistent with individual movements among stocks were supported by limited genetic data, with a small number of belugas hunted from the CS stock exhibiting both isotopic and genetic similarity to WHB belugas. Geographic stock differentiation inferred from oxygen and carbon isotope proxies largely corroborates current eastern Canadian Arctic beluga stock definitions, which is relevant not only for management purposes but also for monitoring changing beluga distributions in response to ongoing climate-driven changes in Arctic marine ecosystems.

**KEY WORDS:** Biogeography · Bioapatite · *Delphinapterus leucas* · Distribution · Ecology · Isoscape · Stock assessment

## 1. INTRODUCTION

Effective management of exploited animal populations requires an understanding of underlying biological structure to avoid negative management outcomes. For example, abundance and productivity estimates of populations that are assumed to be closed will be inaccurate if mixing occurs (e.g. source–sink dynamics; Kerr et al. 2010, Secor 2014). On the other

hand, exploitation of heterogeneous populations (e.g. those that exhibit some type of spatial structure) can have a disproportionate impact on segregated portions of the population, particularly when removals concentrated in one area lead to local depletion (Reeves & Mitchell 1987, Hammill et al. 2004). Unlike biological units (i.e. populations; Waples & Gaggiotti 2006), management units (or stocks) correspond to groups of animals defined by genetic and/or ecological (e.g. dis-

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tribution) characteristics that allow them to be exploited and managed independently (NAMMCO 1999, IWC 2000, Clapham et al. 2008, Stewart 2008).

Throughout their near circumpolar distribution, belugas *Delphinapterus leucas* typically migrate from deep-water, offshore areas in winter to coastal areas and river estuaries in summer (Harwood et al. 2014, O'Corry-Crowe 2018). As for all Arctic marine mammals, prominent physical habitat features like extensive seasonal sea ice cover and convoluted terrestrial landscapes (e.g. the Canadian Archipelago) constrain the timing and locations of their seasonal movements (Barber et al. 2001, Hornby et al. 2016). Moreover, belugas exhibit site fidelity to certain summering areas and even specific estuaries (Caron & Smith 1990, Bailleul et al. 2012, Rioux et al. 2012), following distinct migration routes that are culturally maintained via stable matrilineal associations (Colbeck et al. 2013). As a result, beluga populations exhibit complex structure, comprised of geographically distinct aggregations with accompanying genetic (Brennin et al. 1997, Brown Gladden et al. 1997, Turgeon et al. 2012) and morphometric (Stewart 1994, Ferguson et al. 2020) differentiation.

Belugas are traditionally hunted throughout much of their range. In the eastern Canadian Arctic, hunt co-management by the federal government and Inuit organizations follows a stock system based largely on geographically discrete beluga aggregations during summer, when most hunting occurs (Hobbs et al. 2020). Three of these beluga management stocks, namely the Western Hudson Bay (WHB), Cumberland Sound (CS), and Eastern High Arctic–Baffin Bay (EHA-BB) stocks, are considered to be independent populations (Fig. 1). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the WHB, CS, and EHA-BB stocks as 'not at risk', 'endangered', and 'special concern', respectively, which reflects their estimated abundance (relatively large and stable for WHB [Matthews et al. 2017] to small and declining for CS [Watt et al. 2021]) (COSEWIC 2020). Previous studies using mitochondrial DNA have shown that each of the 3 stocks is genetically distinct (Brennin et al. 1997, Brown Gladden et al. 1997,

Turgeon et al. 2012, Postma 2017, Parent et al. 2023), and satellite telemetry (Smith & Martin 1994, Richard et al. 1998, 2001, Richard & Stewart 2008) and tissue microchemistry (Rioux et al. 2012) indicate that they have non-overlapping geographical ranges (Fig. 1). Inuit from Pangnirtung, Nunavut (NU), however, contend that belugas from different regions occupy CS, including residents as well as migratory belugas of unknown origins (Kilabuk 1998). Genetic differentiation among belugas hunted in CS based on thousands of nuclear DNA markers (Watt et al. 2023) supports this contention, but it remains unclear whether the individuals with admixed genetic composition are resident or temporary migrants to the area.

Ecological, as opposed to genetic, differentiation can occur over smaller spatial and much shorter temporal scales (i.e. within the lifetime of an organism vs. generational or evolutionary time scales). Animal distributions inferred from tissue stable isotope (SI) composition, which integrates underlying geographic char-

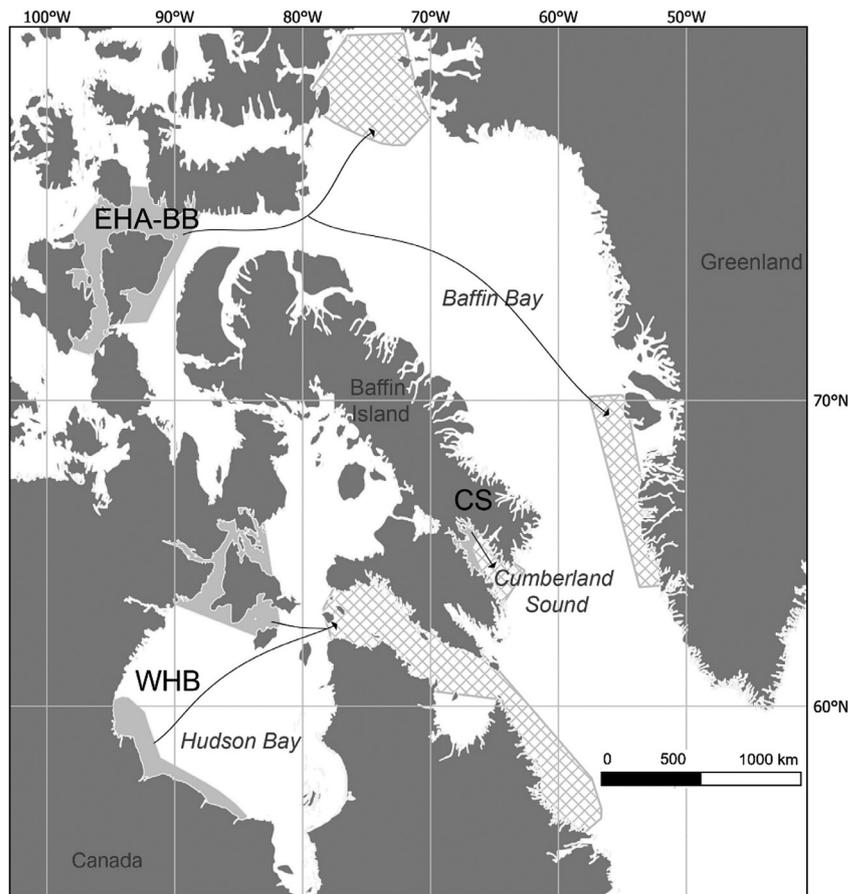


Fig. 1. Core summer (solid light grey) and winter (hatching) ranges of the Western Hudson Bay (WHB), Cumberland Sound (CS), and Eastern High Arctic–Baffin Bay (EHA-BB) beluga management units (stocks) sampled from Inuit hunts for this study. Arrows show connectivity between summer and winter ranges for each respective stock

acteristics over timeframes of tissue growth (Hobson 1999, Bowen et al. 2014), can thus be an informative marker for stock discrimination (e.g. Stewart 2008). The pronounced latitudinal  $\delta^{13}\text{C}$  gradient in marine surface water, which results indirectly from temperature-dependent  $\text{CO}_2$  solubility (Rau et al. 1982), is one of the most commonly utilized 'isoscapes' for inferring large-scale distributions of marine species (McMahon et al. 2013, Magozzi et al. 2017). Smaller latitudinal gradients in the oxygen isotope composition ( $\delta^{18}\text{O}$ ) of marine surface water also exist in both hemispheres, governed by relative rates of evaporation and precipitation (LeGrande & Schmidt 2006). Although not commonly used in this context, variation in phosphate oxygen  $\delta^{18}\text{O}$  ( $\delta^{18}\text{O}_\text{p}$ ) in whale bone and dentine compared to that of source marine water (Yoshida & Miyazaki 1991, Matthews et al. 2016) can also serve as a proxy for cetacean distributions across isotopically distinct marine regions (Matthews et al. 2021). While marine  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  gradients are not well-characterized at the scale of our study across the Eastern Canadian Arctic (McMahon et al. 2013), Matthews et al. (2016) showed that a small number of belugas from the WHB, CS, and EHA-BB management stocks (total  $n = 23$ ) could be differentiated based on  $\delta^{18}\text{O}_\text{p}$  in dentine, with highest values in EHA-BB belugas ( $17.9 \pm 0.56\text{‰}$ ; mean  $\pm$  SD), the most northerly distributed stock, followed by CS belugas ( $17.4 \pm 0.47\text{‰}$ ) and WHB belugas ( $16.7 \pm 0.54\text{‰}$ ), the most southerly distributed stock.

Distribution studies that form the basis for independent, geographically defined beluga management stocks have typically been limited to relatively short time frames, based either on telemetry data from temporary animal-borne satellite tags (e.g. Richard 2010, Bailleul et al. 2012) or microchemistry of tissues with relatively high turnover rates (e.g. skin; Rioux et al. 2012). Dentine, on the other hand, is deposited continually over the lifetime of belugas (Stewart et al. 2006) and is not remodeled (Goldberg et al. 2011), thus integrating average, long-term environmental exposure. Here, we build on the study of Matthews et al. (2016) with dentine  $\delta^{18}\text{O}_\text{p}$  and  $\delta^{13}\text{C}$  of structural carbonate ( $\delta^{13}\text{C}_\text{SC}$ ) measurements from a larger number of belugas ( $n = 103$ ) to evaluate the spatial structure of geographically adjacent beluga management stocks in the Canadian Arctic. Without a detailed, independent characterization of marine  $\delta^{18}\text{O}$  or  $\delta^{13}\text{C}$  baselines across the study area, we assumed underlying spatial variation in  $\delta^{18}\text{O}$  or  $\delta^{13}\text{C}$  exists and is sufficient to distinguish among stocks, given the decline in  $\delta^{18}\text{O}_\text{p}$  values with decreasing latitude observed in previous beluga dentine analyses (Matthews et al. 2016), along with evidence of latitudinal variation in marine  $\delta^{13}\text{C}$

across the broader study area (Pomerleau et al. 2011). To the extent our sample size allowed, we also evaluated hypotheses concerning the geographic origins of genetically differentiated belugas within CS; in particular, whether SI proxies provide evidence of residency or recent migration.

## 2. MATERIALS AND METHODS

### 2.1. Specimen collection and sampling

Mandibles were collected from belugas hunted by Inuit during the 1980s to 2010s in Arviat, NU ( $n = 30$ ), Pangnirtung, NU ( $n = 44$ ), and both Resolute Bay and Grise Fiord, NU ( $n = 29$ ), representing, respectively, the WHB, CS, and EHA-BB management stocks (Fig. 1). Relevant biological data were collected in the field (body length) or determined later (genetic sex, age estimation). Mandibles were stored frozen at  $-20^\circ\text{C}$  until teeth with minimal wear, typically from positions 2 and 5, were extracted and sectioned longitudinally using a water-cooled diamond saw blade. The entire exposed central core of dentine (effectively, a 'whole-tooth' dentine sample) was then sampled using a high-resolution micromill fitted with a 1 mm diameter drill bit at a depth of 0.5 mm to avoid nicking underlying cementum.

### 2.2. Oxygen and carbon isotope analysis

Dentine  $\delta^{18}\text{O}_\text{p}$  and  $\delta^{13}\text{C}_\text{SC}$  were analyzed at the University of Western Ontario's Laboratory for Stable Isotope Science (LSIS) following procedures described by Matthews et al. (2016). For isotopic analysis of phosphate oxygen, 25 to 35 mg of each powdered dentine sample were dissolved in 3 M acetic acid, followed by precipitation of silver phosphate ( $\text{Ag}_3\text{PO}_4$ ) using the ammonia volatilization method (Firsching 1961, Stuart-Williams & Schwarcz 1995). Approximately 0.2 mg of powdered  $\text{Ag}_3\text{PO}_4$  were then weighed into silver capsules and introduced into a Thermo Scientific<sup>TM</sup> High Temperature Conversion Elemental Analyzer (TC/EA). The resulting carbon monoxide (CO) was purified on a GC column packed with a 5 Å molecular sieve and carried in a continuous helium stream to a Thermo Scientific<sup>TM</sup> Delta<sup>PLUSXL</sup><sup>TM</sup> isotope-ratio mass spectrometer (IRMS) for isotopic analysis.

Oxygen isotope ratios are reported in  $\delta$ -notation relative to Vienna Standard Mean Ocean Water (VSMOW), calibrated using accepted  $\delta^{18}\text{O}$  values for standards IAEA-CH-6 (sucrose, 36.40‰; Flanagan &

Farquhar 2014) and Aldrich Silver Phosphate—98%, Batch 03610EH (silver phosphate, 11.2‰; Webb et al. 2014). Precision (standard deviation; SD) of these standard analyses ranged from 0.36‰ (IAEA-CH-6,  $n = 27$ ) to 0.39‰ (Aldrich,  $n = 36$ ) during this project's analytical sessions. Duplicate sample  $\delta^{18}\text{O}_p$  analyses ( $n = 29$ ) produced an average SD of 0.27‰ (range 0 to 0.74‰).

We measured  $\delta^{13}\text{C}_{\text{SC}}$  of untreated dentine, because pretreatment of bioapatite with sodium hypochlorite and acetic acid to remove secondary carbonate and organic matter has been demonstrated to have inconsistent effects (Snoeck & Pellegrini 2015, Matthews et al. 2016, Pellegrini & Snoeck 2016, Chung et al. 2023). Approximately 0.8 mg of each powdered sample was dried overnight at 80°C in a reaction vial including a small amount of steel wool to remove any sulfurous compounds released during subsequent reactions. Each vial was then septa-sealed, capped, and evacuated using an automated sampler (Micromass Multi-Prep). Carbon dioxide gas ( $\text{CO}_2$ ) was generated by reaction with ortho-phosphoric acid at 90°C for 10 min, and then cryogenically scrubbed and automatically transferred to an IRMS (Fisons Optima) for analysis in dual-inlet mode.

$\delta^{13}\text{C}_{\text{SC}}$  values were calibrated relative to Vienne Pee-Dee belemnite (VPDB) using accepted values for NBS 19 (calcite; 1.95‰) and LSVEC (Li-carbonate; -46.6‰). During this project's analytical sessions, the precision (SD) of these standard analyses ranged from 0.05‰ (NBS 19,  $n = 14$ ) to 0.08‰ (LSVEC,  $n = 12$ ). Accuracy and precision (SD) were assessed via replicate measurements of international standards and laboratory reference materials not included in calibration: NBS 18 (calcite;  $\delta^{13}\text{C}$  measured =  $-5.02 \pm 0.07\text{‰}$ ,  $n = 11$ ; accepted =  $-5.01\text{‰}$ ), WS-1 (calcite;  $\delta^{13}\text{C}$  measured =  $0.81 \pm 0.03\text{‰}$ ,  $n = 21$ ; accepted =  $0.77\text{‰}$ ), and Suprapur (calcite;  $\delta^{13}\text{C}$  measured =  $-35.64 \pm 0.06\text{‰}$ ,  $n = 8$ ; accepted =  $-35.48\text{‰}$ ). Duplicate sample analyses ( $n = 20$ ) produced an average SD of 0.06‰ (range 0 to 0.31‰).

### 2.3. Data analysis

Given that the teeth used in this study were collected over several decades, we adjusted all  $\delta^{13}\text{C}_{\text{SC}}$  values to the year of the most recent sample (2008) by  $-0.023\text{‰ yr}^{-1}$ , the magnitude of the Suess effect in the North Atlantic (45–60°N) during years encompassed by this study (1973–1990) (Sonnerup et al. 1999). Calendar year of dentine deposition was calculated by subtracting half the whale's estimated age

from its year of death to represent the midpoint of whole-tooth deposition. All  $\delta^{13}\text{C}_{\text{SC}}$  values presented and analyzed in this study have been adjusted to account for the Suess effect.

Differences in  $\delta^{18}\text{O}_p$  and  $\delta^{13}\text{C}_{\text{SC}}$  among management stocks were assessed using multivariate ANOVA (MANOVA) followed by univariate ANOVA with pairwise comparisons using Tukey's honestly significant difference (HSD) post hoc tests. MANOVA and ANOVA tests were conducted using base functions in R, version 4.0.5 (R Core Team 2021).

Following MANOVA, a linear discriminant analysis (LDA) was conducted to determine how well beluga stocks could be classified based on their  $\delta^{18}\text{O}_p$  and  $\delta^{13}\text{C}_{\text{SC}}$  values. After scaling each variable to zero mean and unit variance, an LDA model fit to a randomly chosen training subset comprising 60% of the entire data set was used to classify the remaining 40% not used in model fitting (test subset). The LDA was conducted using the 'MASS' package, version 7.3.53.1 (Venables & Ripley 2002) in R version 4.0.5 (R Core Team 2021).

Samples from each stock comprised belugas of different sex, age, and body length, all factors known to influence beluga distribution and/or tissue SI composition (Lesage et al. 2001, Loseto et al. 2006, 2009, Marcoux et al. 2012). To better understand potential contributions of these factors to within-stock SI variation, we used multivariate linear regression to model variation in  $\delta^{18}\text{O}_p$  and  $\delta^{13}\text{C}_{\text{SC}}$  (dependent variables) with respect to sex (determined genetically), age (estimated as the median of 3 counts of annual growth layer groups observed under reflected light conducted over several weeks), body length (measured in the field as the distance from the tip of the rostrum to the tail notch), and calendar year of deposition (calculated as described above). For the CS stock, regression models also included mitochondrial DNA haplotype (from Watt et al. 2023) as an independent variable, with the values 'private' (exist only in CS) and 'shared' (common with at least 1 other population; Parent et al. 2023). The R package 'nlme', version 3.1.152 (Pinheiro et al. 2021) was used to fit regression models, ranging from the full model including all independent variables without interactions, reduced models with different combinations of independent variables, and the null model.  $\delta^{18}\text{O}_p$  and  $\delta^{13}\text{C}_{\text{SC}}$  were modeled separately for each of the 3 stocks, and model selection was based on Akaike's information criterion (AIC; Akaike 1973).

For all analyses, model fits and assumptions were assessed via visual inspection and statistical tests of residuals for deviations from normality (Shapiro-Wilk test) and homoscedasticity (Levene test).

Table 1. Oxygen and stable carbon isotope ratios (mean  $\pm$  SD) of dentine phosphate ( $\delta^{18}\text{O}_\text{P}$ ) and structural carbonate ( $\delta^{13}\text{C}_\text{SC}$ ; Suess-adjusted) of beluga from 3 eastern Canadian Arctic management stocks. VSMOW: Vienna Standard Mean Ocean Water; VPDB: Vienna PeeDee Belemnite

	$\delta^{18}\text{O}_\text{P}$ (‰) VSMOW	$\delta^{13}\text{C}_\text{SC}$ (‰) VPDB
Western Hudson Bay (WHB) (n = 30)	16.30 $\pm$ 0.75	-11.77 $\pm$ 0.40
Cumberland Sound (CS) (n = 44)	16.03 $\pm$ 0.91	-12.48 $\pm$ 0.37
Eastern High Arctic–Baffin Bay (EHA-BB) (n = 29)	17.77 $\pm$ 0.91	-12.20 $\pm$ 0.35

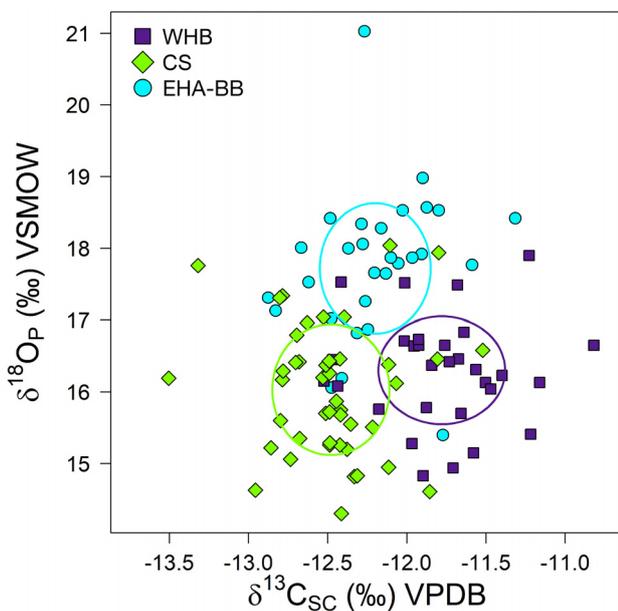


Fig. 2. Beluga dentine  $\delta^{18}\text{O}_\text{P}$  vs. Suess-adjusted  $\delta^{13}\text{C}_\text{SC}$  from 3 eastern Canadian Arctic beluga management stocks: WHB, CS, and EHA-BB. Ellipses (width and height = 2 standard deviations) indicate geographic separation among the 3 management stocks. See Table 1 for definitions

### 3. RESULTS

MANOVA indicated significant  $\delta^{18}\text{O}_\text{P}$  and  $\delta^{13}\text{C}_\text{SC}$  differences among beluga stocks ( $F_{4,200} = 32.87$ ,  $p < 0.0001$ ; Table 1, Fig. 2). Subsequent univariate ANOVA indicated significant differences in  $\delta^{18}\text{O}_\text{P}$  among stocks ( $F_{2,100} = 34.68$ ,  $p < 0.0001$ ), with Tukey HSD indicating significant differences between the WHB and EHA-BB stocks ( $p < 0.0001$ ) and between the CS and EHA-BB stocks ( $p < 0.0001$ ), but not between the WHB and CS stocks ( $p = 0.42$ ; Table 1, Fig. 2). Significant differences in  $\delta^{13}\text{C}_\text{SC}$  occurred

among all stocks ( $F_{2,100} = 31.75$ ,  $p < 0.0001$ ); between the WHB and CS stocks ( $p = 0.0001$ ); between the WHB and EHA-BB stocks ( $p < 0.0001$ ), and between the CS and EHA-BB stocks ( $p < 0.01$ ; Table 1, Fig. 2).

The first discriminant function (LD1) of the LDA explained 54.3% of the between-group variance, and LD2 explained 45.7% (Fig. 3). The coefficients were 0.35 ( $\delta^{13}\text{C}_\text{SC}$ ) and  $-1.24$  ( $\delta^{18}\text{O}_\text{P}$ ) for LD1, and  $-1.31$  and  $-0.11$  for LD2. Model accuracy on the training data set (n = 59) was 71.2% (Table 2, Fig. 3;

Table S1 in the Supplement at [www.int-res.com/articles/suppl/n054p093\\_supp.pdf](http://www.int-res.com/articles/suppl/n054p093_supp.pdf)). Of the 44 samples in the test subset, 37 were classified correctly, yielding an overall classification success rate of 84.1% (Table 2, Fig. 3). Misclassification rates were 14% for the WHB stock, 10% for the CS stock, and 30% for the EHA-BB stock (Table 2; Table S1). Overall, when misclassifications occurred, the WHB and EHA-BB stocks were generally misclassified as CS, while CS misclassifications were split evenly between the WHB and EHA-BB stocks (Table 2).

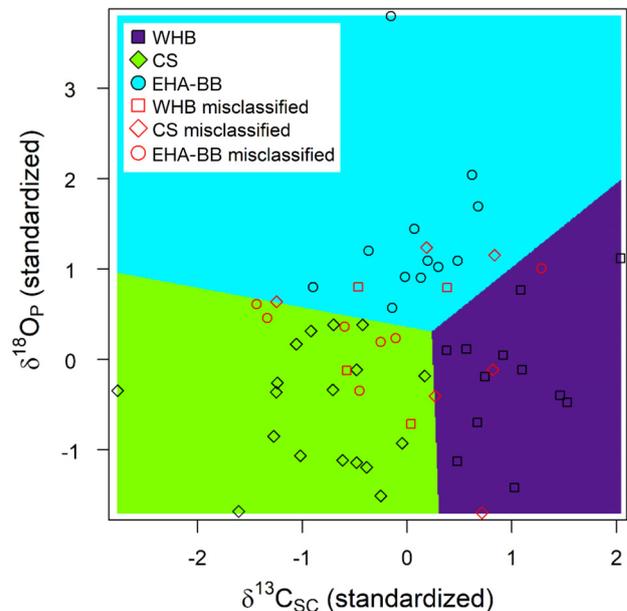


Fig. 3. Classification borders/decision boundaries from the linear discriminant analysis (LDA) of  $\delta^{18}\text{O}_\text{P}$  and Suess-adjusted  $\delta^{13}\text{C}_\text{SC}$  of the training subset comprising 60% of the entire data set. Correctly assigned whales match the background colors for the WHB, CS, and EHA-BB beluga management stocks, while misclassified whales are indicated by mismatched (red) symbols and background colors. Figure made using the 'klaR' package (Weihs et al. 2005) in the statistical software R (R Core Team 2021)

Table 2. Linear discrimination analysis (LDA) model classifications of 103 belugas from 3 management stocks in the eastern Canadian Arctic based on whole-tooth dentine  $\delta^{18}\text{O}_\text{P}$  and Suess-adjusted  $\delta^{13}\text{C}_\text{SC}$  values. The LDA model was fit to a training subset of 59 whales (see Fig. 3) and then used to predict the management stock of the remaining 44 whales (test data set). Overall classification success of the training and test data sets were 71.2 and 84.1%, respectively

Management stock	Training data set (n = 59)			Test data set (n = 44)		
	WHB	WHB	WHB	WHB	CS	EHA-BB
Western Hudson Bay (WHB)	12	2	2	12	2	0
Cumberland Sound (CS)	3	18	3	1	18	1
Eastern High Arctic–Baffin Bay (EHA-BB)	1	6	12	2	1	7

The null model was the optimal multivariate linear regression model of  $\delta^{18}\text{O}_\text{P}$  for the WHB and EHA-BB stocks, while  $\delta^{18}\text{O}_\text{P}$  increased significantly at a rate of  $0.041 \pm 0.018\% \text{ yr}^{-1}$  in the CS stock (Table 3; Fig. S1). The null model was the optimal model of  $\delta^{13}\text{C}_\text{SC}$  for the EHA-BB stock, while  $\delta^{13}\text{C}_\text{SC}$  decreased with age in

WHB belugas, and decreased with whale length and increased with calendar year in the CS stock (Table 3). This means that for the CS stock, which included genetic stock identification as an explanatory variable, neither  $\delta^{18}\text{O}_\text{P}$  nor  $\delta^{13}\text{C}_\text{SC}$  were related to mitochondrial DNA haplotype (Fig. 4).

Table 3. Multiple linear regression of dentine  $\delta^{18}\text{O}_\text{P}$  and Suess-adjusted  $\delta^{13}\text{C}_\text{SC}$  of belugas from 3 eastern Canadian Arctic management stocks against sex, age, length, and calendar year. Models were evaluated based on differences in Akaike's information criterion corrected for small sample size ( $\Delta\text{AICc}$ ). Note that additional models including mitochondrial DNA haplotype were run for the Cumberland Sound stock, including  $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{haplotype})$

Models tested	Full	[1] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{age} + \text{year} + \text{length} + \text{sex})$					
		[2] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{year} + \text{length} + \text{sex})$					
		[3] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{length} + \text{sex})$					
		[4] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{length} + \text{year})$					
		[5] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{sex})$					
		[6] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{age})$					
		[7] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{length})$					
		[8] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim \text{year})$					
	Null	[9] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \text{ or } \delta^{13}\text{C}_\text{SC} \sim 1)$					
			Estimate	SE	t	p	Adj. r <sup>2</sup>
<b>Western Hudson Bay (WHB) (n = 30)</b>							
$\delta^{18}\text{O}_\text{P}$							
Model [9] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \sim 1)$							
	Intercept		16.28	0.141	115.4	<0.0001	
$\delta^{13}\text{C}_\text{SC}$							
Model [6] <- $\text{lm}(\delta^{13}\text{C}_\text{SC} \sim \text{age})$							
	Intercept		-11.32	0.166	-68.14	<0.0001	0.216
	Age		-0.0186	0.0063	-2.955	0.0064	
<b>Cumberland Sound (CS) (n = 44)</b>							
$\delta^{18}\text{O}_\text{P}$							
Model [8] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \sim \text{year})$							
	Intercept		-65.1	36.0	-1.806	0.0784	0.109
	Calendar year		0.0408	0.0182	2.25	0.0300	
$\delta^{13}\text{C}_\text{SC}$							
Model [4] <- $\text{lm}(\delta^{13}\text{C}_\text{SC} \sim \text{length} + \text{year})$							
	Intercept		-46.04	14.18	-3.24	<0.003	0.128
	Length		-0.00145	0.00087	-1.67	0.106	
	Calendar year		0.0017	0.0072	2.39	0.020	
<b>Eastern High Arctic–Baffin Bay (EHA-BB) (n = 29)</b>							
$\delta^{18}\text{O}_\text{P}$							
Model [9] <- $\text{lm}(\delta^{18}\text{O}_\text{P} \sim 1)$							
	Intercept		17.75	0.206	86.25	<0.0001	
$\delta^{13}\text{C}_\text{SC}$							
Model [9] <- $\text{lm}(\delta^{13}\text{C}_\text{SC} \sim 1)$							
	Intercept		-12.19	0.0674	-180.9	<0.0001	

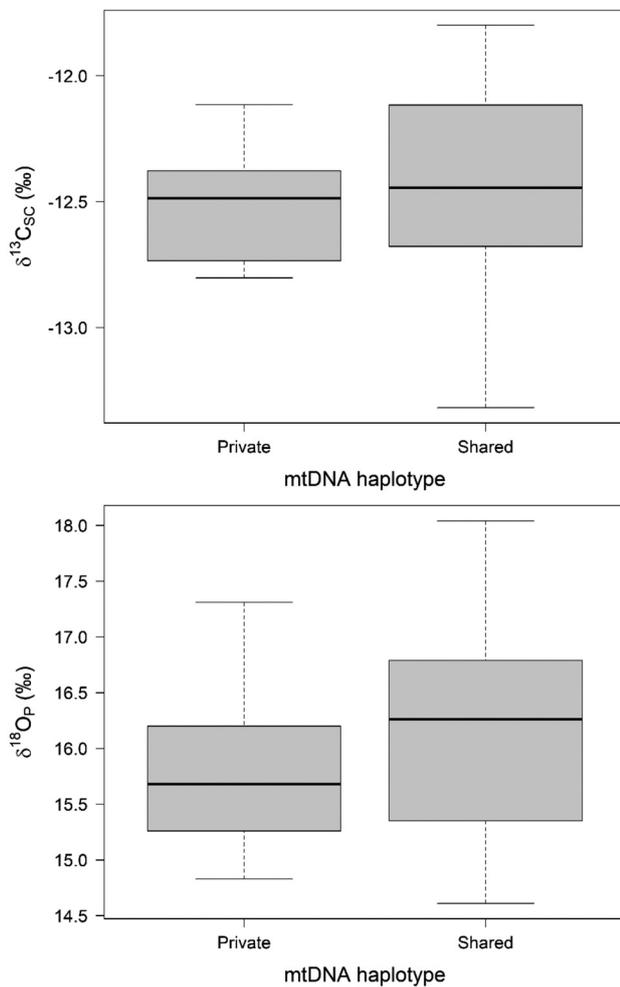


Fig. 4. Dentine Suess-adjusted  $\delta^{13}\text{C}_{\text{SC}}$  and  $\delta^{18}\text{O}_{\text{P}}$  are unrelated to genetic identification of Cumberland Sound (CS) beluga whales based on mitochondrial DNA (mtDNA), with similar mean values and ranges of private (unique to CS;  $n = 13$ ) and shared (common to other stocks;  $n = 21$ ) haplotypes. Boxplots indicate median (band within box) and the lower (25<sup>th</sup>) and upper (75<sup>th</sup>) quartiles (bottom and top of box, respectively). Whiskers represent 1.5 times the quartile range in either direction

#### 4. DISCUSSION

Ensuring that management units accurately reflect underlying population structure has proven particularly relevant for belugas, which have failed to recolonize areas after local depletion due to extensive hunting (Reeves & Mitchell 1987, Hammill et al. 2004, DFO 2005). Distribution differences inferred here using  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  proxies support current beluga stock definitions based on discrete summer aggregations (see Fig. 1), consistent with other studies that have shown that the WHB, CS, and EHA-BB beluga

stocks differ genetically (Brennin et al. 1997, Brown Gladden et al. 1997, Turgeon et al. 2012), ecologically (Richard & Stewart 2008, Rioux et al. 2012), and morphometrically (Stewart 1994, Ferguson et al. 2020). While isotopic separation among the 3 stocks was sufficient to produce rather good classification results, some degree of overlap (and subsequent classification errors) likely reflected (1) uniform baseline variation across adjacent stock boundaries, (2) marginal geographic overlap in ranges or individual movements among stocks, and/or (3) potential diet influences that increased within-stock SI variation.

Our primary assumption in using dentine  $\delta^{18}\text{O}_{\text{P}}$  and  $\delta^{13}\text{C}_{\text{SC}}$  to assess beluga management stock structure was that baseline values of both isotopes varied sufficiently across the ranges of each stock to differentiate among them. The separation of all stocks based on both isotope measures indicates this is generally the case. However, similar  $\delta^{18}\text{O}_{\text{P}}$  of the WHB and CS stocks suggests the marine  $\delta^{18}\text{O}$  isoscape is relatively uniform across adjacent stock boundaries (significantly different  $\delta^{13}\text{C}_{\text{SC}}$  values between these 2 stocks rule out geographically overlapping distributions; see below). Our understanding of baseline oxygen isotope variation across the Canadian Arctic is based on relatively few measurements (LeGrande & Schmidt 2006, McMahon et al. 2013) and is therefore limited. Similar  $\delta^{18}\text{O}_{\text{P}}$  between the geographically adjacent WHB and CS stocks may reflect uniform  $^{18}\text{O}$  depletion of coastal, high-latitude waters (LeGrande & Schmidt 2006). Significantly higher  $\delta^{18}\text{O}_{\text{P}}$  of the EHA-BB stock, the most northerly distributed of the 3 stocks, relative to the WHB and CS stocks is inconsistent with the decline in marine  $\delta^{18}\text{O}$  with latitude in the North Atlantic (LeGrande & Schmidt 2006), possibly reflecting other factors (e.g. seasonal freeze and melt cycles) that contribute to spatial variation in Arctic seawater  $\delta^{18}\text{O}$  (Tan & Strain 1980).

Overlapping geographic distributions could also explain isotopic similarities among stocks. However, we rule out anything more than marginal overlap, as stocks distributed across the same area would be expected to exhibit similarities in both isotopes, which was not observed between any of the stocks. The bulk of beluga dentine is thought to be deposited during summer (Matthews & Ferguson 2015), but the whole-tooth samples also comprised dentine deposited during winter. The closer geographic proximity of the 3 stocks during winter (Fig. 1) may therefore have diluted isotopic differences among them. Alternatively, movements of individuals among otherwise discrete stocks could account for observed LDA misclassifications (i.e. a beluga migrated from its resident stock,

which is reflected in its dentine isotope composition, to an adjacent stock with different isotopic baselines, where it was then hunted). Hudson Strait and Hudson Bay are the most plausible source locations for putative migrants into CS due to their geographic proximity, and the large population size of the WHB stock (Matthews et al. 2017). Belugas from WHB are known to migrate and overwinter in Hudson Strait and off southeast Baffin Island (Finley et al. 1982, Richard et al. 1990, Lewis et al. 2009), potentially overlapping the winter/late spring distribution of CS whales at the mouth of CS (Richard & Stewart 2008). This could explain the 4 belugas that were hunted in CS but were isotopically similar to WHB whales (3 of which were also genetically similar to WHB whales; see below). The remaining 4 LDA misclassifications between WHB and CS occurred in the opposite direction (i.e. belugas hunted in WHB being classified as CS belugas). EHA-BB belugas migrate to areas in Baffin Bay and Davis Strait during winter, primarily along the west coast of Greenland (Finley & Renaud 1980, Heide-Jørgensen et al. 1993, Richard et al. 1998). EHA-BB whales overwintering in Davis Strait could conceivably enter the mouth of CS, where much of the hunting occurs at the floe edge over just a few days in late spring, and could thereby account for EHA-BB whales being taken in CS (4 CS whales misclassified to EHA-BB stock). There is no evidence, either from Inuit Qaujimagatuqangit or scientific studies, however, of movements of CS whales to Grise Fiord or Resolute Bay that would explain the relatively large number of misclassifications (7) in the opposite direction.

Inuit Qaujimagatuqangit from Pangnirtung, NU, states that several different types of belugas are regularly present in CS during the seasonal hunt, including smaller animals with behavioral differences (Kilabuk 1998). While the relatively low overall misclassification rate suggests that most whales in our study were resident to their assigned stock areas (i.e. where they were hunted), we can focus more specifically on the 34 CS whales which were classified using available mitochondrial DNA data as belonging either to the CS population (private haplotype;  $n = 13$ ) or to an unknown population (shared haplotype;  $n = 21$ ; Watt et al. 2023; Table S1). Haplotype was not a significant predictor of SI composition, suggesting that these 34 whales hunted in CS occupied a similar long-term distribution. This result is consistent with telemetry results showing that small numbers of belugas having either haplotype ( $n$  total = 7) remained in CS year-round, as well as hunt location data that indicate belugas having private or shared haplotypes are

taken from the same areas within CS (Watt et al. 2023). Interestingly, however, isotopic variation was larger for the subset of belugas having the shared mitochondrial haplotype (Fig. 4), which would be expected given that this group can include belugas from CS and other populations (Parent et al. 2023), and thus merits further study.

Alternatively, we can also focus on the 14 CS animals common to our study and that of Watt et al. (2023) that can be classified to either the CS stock ( $n = 10$ ) or an unknown population resembling the WHB stock ( $n = 4$ ) using nuclear DNA (Table S1). Three out of 4 belugas hunted in CS were both genetically and isotopically more similar to the WHB stock (Table S1), which is consistent with temporary or recent migration into CS. The remaining whale that was genetically similar to WHB belugas was isotopically similar to CS belugas, suggesting it was resident to CS. Possible dispersal of animals at a young age, particularly males (see Turgeon et al. 2012, Colbeck et al. 2013), would not be apparent in our data since whole-tooth dentine sampled from adults would obscure the isotopic composition of the earliest deposited dentine. However, the similar proportions of males among misclassified whales (74%) and the entire sample (65%), as well as similar proportions of misclassified females (19%) and males (26%), provide little support for male dispersal. Similar mean ages of correctly classified ( $20.8 \pm 10$  yr) and misclassified ( $22.7 \pm 13$  yr) belugas also lends little support for dispersal of younger belugas. Although the relatively large sample requirements of  $\delta^{18}\text{O}_p$  analysis dictated the whole-tooth sampling design of this study, longitudinal isotope profiles constructed from within-tooth sampling (e.g. Matthews et al. 2021) would provide a more refined assessment of the frequency of potential movements among stocks, as well as potential ontogenetic links (e.g. dispersal at sexual maturation).

We based our study on the assumption that variation in dentine  $\delta^{18}\text{O}_p$  and  $\delta^{13}\text{C}_{\text{SC}}$  primarily reflected underlying baseline variation; however, other factors such as diet likely contributed to within-stock isotopic variation, thus reducing among-stock variation and negatively impacting our ability to discern among them. Previous studies have attributed higher  $\delta^{13}\text{C}$  in adult male belugas to their greater diving ability and offshore habitat, which allows them to access  $^{13}\text{C}$ -enriched benthic prey (see Schreer & Kovacs 1997, Mori 2002). Decreasing  $\delta^{13}\text{C}_{\text{SC}}$  with age and length in the WHB and CS stocks, respectively, in this study is therefore inconsistent with the findings and interpretations of previous studies. While decreasing  $\delta^{13}\text{C}_{\text{SC}}$  with age and length could reflect more offshore or

pelagic foraging of adult belugas, neither of these effects were pronounced in magnitude or strongly significant (Table 3), and could instead be an artefact of our 'whole-tooth' sampling design that is weighted towards younger ages given the compression of annual growth layers with age. Matthews (2015) measured  $\delta^{13}\text{C}$  (and  $\delta^{15}\text{N}$ ) of collagen in annual dentine growth layers and observed differences in both isotope ratios on the order of several ‰ among individuals within each of the WHB, CS, and EHA-BB beluga stocks. Individual dietary differences unrelated to sex, age, or length could therefore have contributed to within-stock  $\delta^{13}\text{C}_{\text{SC}}$  variation also observed in this study.

Metabolic water, produced as a by-product of cellular respiration, can represent a large component of total oxygen fluxes in terrestrial animals (Luz & Kolodny 1985, Kohn 1996). Diet, however, is not expected to strongly influence  $\delta^{18}\text{O}_\text{p}$  of cetaceans, as diffusion of water across cetacean skin is thought to greatly exceed other oxygen fluxes (Hui 1981, Andersen & Nielsen 1983). This assumption is supported by similar dentine  $\delta^{18}\text{O}_\text{p}$  between sympatric fish- and mammal-eating killer whales *Orcinus orca* (16.75 vs. 16.87‰, respectively; Matthews et al. 2016), along with linear relationships between bone or dentine  $\delta^{18}\text{O}$  of various whale species and environmental water, regardless of their trophic position (Yoshida & Miyazaki 1991, Matthews et al. 2016). However, the 2–3‰ range of  $\delta^{18}\text{O}_\text{p}$  we measured across each beluga stock exceeds the <1‰ range typical of other cetacean populations (Clementz & Koch 2001, Borrell et al. 2013, Vighi et al. 2016), suggesting other contributing sources of variation. If metabolic water represents a more prominent oxygen source than assumed, it could explain not only the relatively large within-stock  $\delta^{18}\text{O}_\text{p}$  variation, but potentially also the increasing  $\delta^{18}\text{O}_\text{p}$  in CS belugas over the duration of the study (Fig. S1). CS beluga diet had historically been dominated by Arctic cod *Boreogadus saida*, but shifted gradually over the last ~40 yr to include capelin *Mallotus villosus* (Marcoux et al. 2012, Watt et al. 2016, Yurkowski et al. 2018). Arctic marine surface water is relatively  $^{18}\text{O}$ -depleted due to inputs of meteoric water (Tan & Strain 1980), so gradual replacement of a surface/sea ice-associated species like Arctic cod (Hop & Gjøsaeter 2013, Majewski et al. 2016) with an upper water column species like capelin (Brown 2002, Hop & Gjøsaeter 2013) could have driven the positive trend in  $\delta^{18}\text{O}_\text{p}$ . The significant increase in Suess-adjusted  $\delta^{13}\text{C}_{\text{SC}}$  of CS belugas with calendar year over the study period would also be consistent with this diet shift, as the  $\delta^{13}\text{C}$  of capelin ( $-19.5 \pm 0.3\text{‰}$ ) is higher than that of Arctic cod ( $-20.5 \pm 0.3\text{‰}$ ) in

Davis Strait/CS (Marcoux et al. 2012). Declines in relative contributions of meteoric water (e.g. river runoff) could also cause  $\delta^{18}\text{O}$  to increase in the estuarine habitat of belugas, although to our knowledge, no long-term trends specific to CS have been reported.

Defining management stocks at the appropriate spatial and temporal scales is critical to the conservation of exploited animal populations (Clapham et al. 2008). Beluga population sub-structure inferred here using isotope proxies corroborates the current definition of management stocks in the eastern Canadian Arctic. Regarding groups of genetically differentiated belugas within CS (DFO 2022) that also exhibited isotopic evidence of temporary movement into CS, our comparison of different CS beluga haplotypes and genotypes should be repeated using a larger sample given the stock's endangered status (COSEWIC 2020) and uncertainty surrounding its management (DFO 2022). Sound management of all beluga stocks in the future will require not only continued assessment of beluga population structure, but also an understanding of underlying mechanisms to predict population-level responses in the face of climate change. The persistence of beluga population structure, along with geographic patterns in SI baselines from which it was inferred, should therefore be regularly re-visited.

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