Fifty years of Cook Inlet beluga whale feeding ecology from isotopes in bone and teeth

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ABSTRACT: Beluga whales *Delphinapterus leucas* that reside in Cook Inlet (CIBW) are important to coastal Alaska Native culture and subsistence, tourism, and ecologically as a top-level predator. Due to a ~50% population decline in the 1990s, the distinct population segment in Cook Inlet was designated depleted under the Marine Mammal Protection Act in 2000 and listed as endangered under the Endangered Species Act in 2008. Diet changes are a concern in CIBW lack of recovery, but beluga feeding ecology is difficult to study. Skulls from 20 CIBW and tooth growth layer groups (GLGs) from 26 individual CIBW showed decreasing trends for both nitrogen and carbon stable isotope ratios (expressed as $\delta^{15}N$ and $\delta^{13}C$ values) from 1962 to 2007. The decline in $\delta^{15}N$ values (~1 to 2‰) could indicate a trophic level shift, but the magnitude of decline in $\delta^{13}C$ values (~3‰) is much greater (>5 times greater) than expected for a trophic level shift. A shifted baseline or increased use of freshwater prey could explain the decline in $\delta^{13}C$ values. We compared the strontium isotope composition ($^{87}Sr/^{86}Sr$ ratios) of GLGs with rivers that flow into Cook Inlet and used $\delta^{15}N$ values from the essential amino acid phenylalanine to determine that declining $\delta^{13}C$ values may be explained by 2 scenarios: (1) CIBW foraged in the same location while the environmental isotopic baseline changed, or (2) CIBW foraged in a different location with a different baseline. This study presents the first evidence for a long-term (~50 yr) change in CIBW feeding ecology.

KEY WORDS: Strontium · Carbon · Nitrogen · Dietary change · *Delphinapterus leucas* · Northern Gulf of Alaska

INTRODUCTION

The beluga whales *Delphinapterus leucas* in Cook Inlet (CIBW), Alaska, USA (Fig. 1), are isolated genetically (O'Corry-Crowe et al. 2002) and geographically (Hobbs et al. 2005, 2008, Rugh et al. 2010, Goetz et al. 2012, Shelden et al. 2015) from the other 4 beluga whale stocks in Alaska (Allen & Angliss 2015). Aerial surveys, including those conducted by the National Marine Fisheries Service (NMFS), revealed a decline in the CIBW population by ~50% between 1994 (653 belugas) and 1998 (347 belugas; Hobbs et al. 2015). This decline was attributed to an unsustainable harvest estimated between 287 and 406 for those 5 yr (Mahoney & Shelden 2000). In 1999, the harvest was greatly reduced, first by a temporary voluntary hunting moratorium and soon after by harvest regulations. CIBW were designated as depleted under the Marine Mammal Protection Act in 2000 (NOAA 2000) and listed as endangered under the

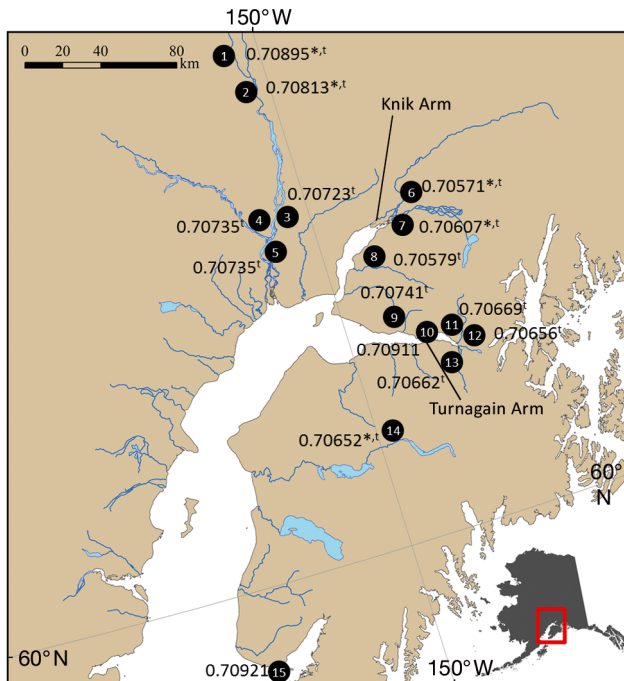*Corresponding author: mark.nelson@alaska.gov

Fig. 1. Cook Inlet, Alaska, USA, with ^{87}Sr/^{86}Sr ratios marked from this study. Numbers in black circles correspond to the IDs in Table 1. Data from Brennan et al. (2014) are indicated by '*', and superscript 't' denotes weighted average ratio derived from samples taken in triplicate. Inset shows the location of Cook Inlet within Alaska

Endangered Species Act in 2008 (NOAA 2008). Critical habitat was then designated in 2011 (NOAA 2011), and a recovery plan was published in 2016 (NMFS 2016). CIBW were also classified as Critically Endangered under the IUCN Red List of Threatened Species in 2012 (Lowry et al. 2012).

CIBW have been hunted throughout recorded history by coastal Alaska Natives for food and cultural purposes (Huntington 2000, Mahoney & Shelden 2000), and intermittently during the 20th century by non-Natives for commercial and sporting purposes. Marine mammals were protected in 1972 when the Marine Mammal Protection Act was passed by Congress; however, an exemption allows the taking of marine mammals by coastal Alaska Natives, provided such taking is for subsistence purposes and conducted in a non-wasteful manner.

Five CIBW have been harvested since 1999: 1 in 2001, 2002, and 2003, and 2 in 2005 (Mahoney & Shelden 2000). With the reduction in harvest, the CIBW population was predicted to increase, but instead, a slow (rate ± SE: −0.4 ± 1.3% yr^{-1}) decline occurred from 2004 to 2014 (NMFS 2016). During the documented population decline (1994–1999), the summer range of CIBW continued to contract into the upper reaches of Cook Inlet and shifted farther into the Knik and Turnagain Arms (Rugh et al. 2010, Shelden et al. 2015).

Although a range contraction may be the direct result of fewer animals requiring a smaller area, how it influences beluga feeding ecology is unknown. Increased concerns about CIBW susceptibility to potential threats within this restricted range (NMFS 2016) were summarized in the 2008 status review, which included catastrophic events, disease, predation, small population effects, noise, ship strikes, and decreased prey availability (Hobbs et al. 2008). The recovery plan examined these threats further and found that while the threat of a reduction in prey was of medium concern, little was known about prey availability and how availability has changed over time (NMFS 2016).

The diet of CIBW is mostly known from stomach contents of stranded and harvested animals (Quakenbush et al. 2015) and from subsistence hunter knowledge (Huntington 2000). CIBW summer prey is mainly seasonally available fish (e.g. eulachon *Thaleichthys pacificus*, Chinook salmon *Oncorhynchus tshawytscha*, chum salmon *O. keta*, and coho salmon *O. kisutch*) that enter Cook Inlet to spawn. Other fish prey available year-round include saffron cod *Eleginus gracilis*, walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, starry flounder *Platichthys stellatus*, and yellowfin sole *Limanda aspera.* Invertebrates are also eaten, primarily shrimp from the families Caridea and Crangonidae along with worms (Polychaeta), shrimp-like amphipods (Crustacea), and Oregoniidae crabs (Huntington 2000, Hobbs et al. 2008, Quakenbush et al. 2015). Stomach contents of CIBW provide prey identifiable to species, but content analysis is limited to whales that die shortly after eating that are available for sampling. Because of these limitations, there were not enough CIBW stomachs available throughout the year or annually to provide information about whether CIBW diet has changed over time.

An alternative to directly studying the diet of CIBW is examining changes in prey availability over time; but this approach also proved to be of limited use for understanding changes in diet. Prey assemblages in the Gulf of Alaska have changed among warm (1947–1976), cold (1977–1997), and warm regimes (1998 to present) at a multi-decadal scale (Anderson & Piatt 1999, Overland et al. 2008). Cold regimes produce more high-quality forage fish for birds and marine mammals than warm regimes (Anderson & Piatt 1999). Little is known about how Cook Inlet prey assemblages are influenced by regime shifts in the Gulf of Alaska, but extensive closures of commercial

shrimp, crab, and herring *Clupea pallasii* fisheries in lower Cook Inlet have occurred (Moore et al. 2000, Hollowell et al. 2016, Shields & Dupuis 2017). Between the 1980s and 1990s, the coho salmon escapement increased, while Chinook, chum, and pink salmon *O. gorbuscha* declined, and sockeye salmon *O. nerka* remained fairly stable in the Susitna River drainage (Moore et al. 2000). However, total salmon escapement may not be an appropriate estimator to determine the number of salmon available for CIBW because escapement in a particular river does not equate to fish available as CIBW prey (Moore et al. 2000, Citta et al. 2016).

Isotopic analyses of hard tissues from belugas can provide general diet information integrated over long periods (e.g. bone integrates diet over ≥10 yr) or short periods (e.g. a growth layer group from a tooth integrates an average diet of 1 yr), depending on how the tissue was formed and how it is maintained (turnover rate; Tieszen et al. 1983, Peterson & Fry 1987, Newsome et al. 2010, Rioux et al. 2012, Witteveen et al. 2012, Waugh et al. 2018). We examined changes in CIBW feeding ecology and foraging location using nitrogen, carbon, and strontium isotope ratio data (expressed as $\delta^{15}N$ and $\delta^{13}C$ values, and $^{87}Sr/^{86}Sr$ ratios) from bone ($\delta^{15}N$ and $\delta^{13}C$ values only), annual growth layer groups (GLGs) in teeth ($\delta^{15}N$ and $\delta^{13}C$ values, and $^{87}Sr/^{86}Sr$ ratios), and water ($^{87}Sr/^{86}Sr$ ratios) to determine if changes in CIBW feeding ecology had occurred during the last 50 yr. $\delta^{15}N$ and $\delta^{13}C$ values can be used to detect changes in trophic level; for example, when a whale feeds a full trophic level higher, the isotopic value of its tissues increases for both $\delta^{15}N$ and $\delta^{13}C$ by ~3 and 1‰, respectively (e.g. Peterson & Fry 1987, Hobson et al. 1996, Kelly 2000, Newsome et al. 2009). $\delta^{13}C$ values can also be used to determine if the carbon source of prey is marine or freshwater. For example, marine prey items often have higher $\delta^{13}C$ values than freshwater prey (e.g. Tieszen et al. 1983, Peterson & Fry 1987, Bentzen et al. 2007). $^{87}Sr/^{86}Sr$ ratios differ by geologic formation and influence the water in the rivers flowing through them (e.g. Brennan et al. 2014, 2015, Padilla et al. 2015), while marine waters are relatively uniform (Veizer 1989, Brennan et al. 2015), thus $^{87}Sr/^{86}Sr$ ratios can be used to determine the likely location within an estuarine system where prey or predators spent time. Another explanation to changing $\delta^{13}C$ and $\delta^{15}N$ values is a change in the environmental baseline. Previous research has shown that the $\delta^{15}N$ value of phenylalanine retains a record of the $\delta^{15}N$ value at the base of the food chain with little fractionation (Chikaraishi et al. 2014, Yamaguchi & McCarthy 2017). We therefore performed a pilot study to compare the $\delta^{15}N$ values of phenylalanine from individuals that died at the beginning of our record with those that died towards the end of the record. Through multiple lines of evidence, we will discuss how the feeding ecology of CIBW has changed over the past 50 yr.

MATERIALS AND METHODS

Bone collagen extraction and preparation

We extracted a small piece (1 cm × 5 cm × 5 cm) of bone from the zygomatic arch of 20 adult CIBW (8 males, 6 females, and 6 unknown) that died between 1964 and 2007 (Fig. 2a) and were archived at the University of Alaska Museum of the North (UAMN) in Fairbanks, Alaska, USA. The bone samples were cut out with a rotary tool and sanded to remove the outer cortex, and the clean solid bone was placed into a labeled glass culture tube. Each sample was then cleaned by: (1) rinsing twice with deionized water, (2) bathing for 1 min in a sonication bath, (3) soaking for 8 h in ethanol, (4) soaking for 8 h in methanol, (5) rinsing with deionized water, (6) soaking for 8 h in acetone, (7) rinsing with deionized water, (8) soaking twice for 8 h in chloroform and air drying under a fume hood, and (9) rinsing with deionized water (entire process modified from Matheus 1997). The cleaned bone was air-dried under a fume hood overnight and weighed. Demineralization occurred by covering the bone with water, adding 1.0 to 2.0 ml of
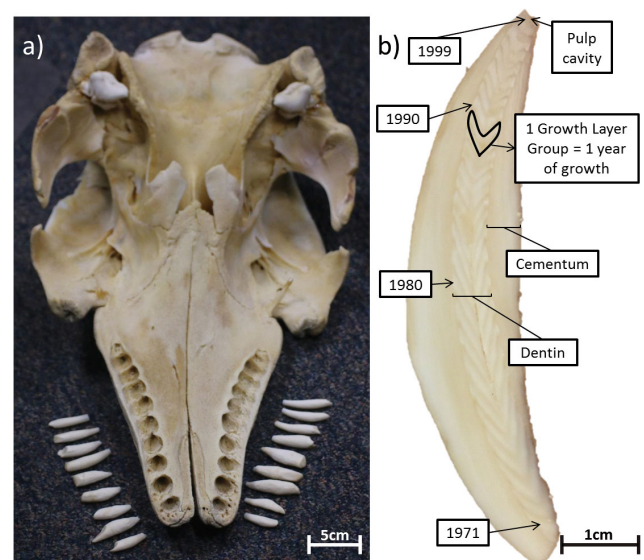

Fig. 2. (a) Skull of a Cook Inlet beluga whale (CIBW) and (b) CIBW tooth cut longitudinally to expose annual growth layer groups

6N hydrochloric acid (HCl), and refrigerating at 3°C for 12 to 24 h. Once the solution stopped bubbling, it was decanted and rinsed with fresh deionized water, then recharged with fresh HCl and repeated until bubbling ceased. Typically this step took 7–10 d to completely demineralize the bone samples. Once demineralized, the sample was gelatinized with HCl at a pH of 3 to 4 and capped with helium to displace the air. The samples were then placed in a heating block that was kept at 65°C until the collagen dissolved, at which point the samples were then centrifuged for 3 to 6 min at 626 × g. The supernatant was passed through a filter, 50 mm in diameter with a pore size of 0.45 μm, and the filtrate collected in a scintillation vial, which was covered with a glass filter disk and freeze-dried (lyophilized) until only dry collagen remained. A 0.2 to 0.5 mg sub-sample of each dried collagen sample was sealed in a tin capsule for stable carbon and nitrogen isotope analysis (described in the next subsection). A second sub-sample from 2 individuals that died in 1964 and 3 individuals that died after 2000 (see Table S6 in the Supplement at www.int-res.com/articles/suppl/n036p077_supp.pdf) were used for analysis of the δ15N values of phenylalanine following previously published protocols (Yamaguchi & McCarthy 2017).

Tooth collagen extraction and preparation

Beluga teeth (n = 26 teeth from individual whales: 14 males, 10 females, and 2 unknown; Fig. 2a), previously used to age the whales, were also analyzed for stable isotope composition. Bone from these 26 CIBW was analyzed for carbon and nitrogen isotope composition. A thin longitudinal section was cut from the center of each tooth, leaving 2 halves (Fig. 2b; Vos 2003). A micromill (ESI® New Wave™ Research) was used to remove dentin material along the selected GLG from one of the halves. A GLG was defined as a light and a dark layer of dentin (Vos 2003; our Fig. 2b) representing 1 yr of growth (Stewart et al. 2006, Waugh et al. 2018). GLGs integrating growth from whales 3 yr of age and younger were not used in this analysis to avoid diet signals associated with suckling (Newsome et al. 2010). Matthews & Ferguson (2015) showed that 17 of 18 (94%) belugas had been weaned during or before their third year.

The drilled powder from each GLG was collected with a small paintbrush into a microcentrifuge vial and demineralized by adding 0.25 N HCl to cover the powder, which was then left overnight in a refrigerator. Samples were centrifuged at 2236 × g for 5 min to concentrate the remaining powder at the bottom of the vial, and the liquid was pipetted off and discarded (Newsome et al. 2009). This was repeated until the white powder turned translucent, indicating that demineralization was complete. The samples were then rinsed with deionized water to remove HCl, frozen, and freeze-dried until dry fluffy collagen remained (~10 h). A 0.2 to 0.5 mg sub-sample of the isolated collagen was sealed into a tin cup for isotope analysis.

Stable nitrogen and carbon isotope analysis

The δ15N (n = 343 GLGs) and δ13C (n = 296 GLGs) values for bone collagen and tooth dentin samples were measured using a Costech® Elemental Analyzer coupled to a ThermoFisher Scientific™ Delta V™ Isotope Ratio Mass Spectrometer. Stable isotope ratios are presented in delta (δ) notation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \qquad (1)$$

where R_{sample} is the ratio of the heavy to light isotope of the sample, and R_{standard} is the ratio of the heavy to light isotope of the standards (i.e. atmospheric N_2 for nitrogen and Vienna Pee Dee Belemnite for carbon). Analytical precision was validated by running a laboratory standard (peptone) after every 10 samples, and the standard deviation of these 71 analyses was ≤0.2‰ for both δ13C and δ15N values. Increased burning of fossil fuels since the industrial revolution continues to alter the isotopic composition of CO_2 in the atmosphere and the ocean, a phenomenon known as the Suess effect, which gradually lowers the baseline δ13C value over time (Francey et al. 1999). The baseline δ13C values decreased by ~0.8‰ from 1960 to 2010, and all δ13C values in this study were corrected for this effect following the approach described by Misarti et al. (2009). A 2-sample t-test was used to determine if δ13C and δ15N values changed before and after 1995, and linear regression was used to determine how δ13C and δ15N values trended over the entire study period.

Collagen quality

The quality of collagen from bone and teeth was evaluated by the atomic carbon to nitrogen ratio (C:N) calculated by the formula:

$$\text{C:N} = \left(\frac{14}{12} \right) \times \left(\frac{\text{Concentration (\%) Carbon}}{\text{Concentration (\%) Nitrogen}} \right) \qquad (2)$$

All C:N ratios for bone were between 3.1 and 3.5 (Table S1 in the Supplement at www.int-res.com/articles/suppl/n036p077_supp.pdf), indicating the collagen was of good quality (i.e. between 2.9 and 3.6; DeNiro et al. 1985, Ambrose 1990, Tatsch et al. 2016). C:N ratios from CIBW tooth dentin GLGs were between 3.1 and 5.7 (Table S2 in the Supplement). When a sample had a C:N ratio ≥ 3.6, only its $\delta^{15}N$ data were used in further data analyses because C:N ratios higher than 3.6 indicate possibly compromised $\delta^{13}C$ values (DeNiro et al. 1985, Ambrose 1990, Tatsch et al. 2016).

Tooth dentin preparation and strontium isotope analysis

A subset of GLGs (n = 44) from teeth analyzed for $\delta^{15}N$ and $\delta^{13}C$ values in this study were selected for strontium isotope ratio ($^{87}Sr/^{86}Sr$) analyses using approximately 20 mg of powdered dentin. GLGs that spanned 1968 to 2005 from 3 males and 2 females were analyzed (Table S5 in the Supplement). Of the 44 GLGs analyzed, 34 matched the GLGs (same GLG on same tooth) analyzed for $\delta^{15}N$ and $\delta^{13}C$ values.

A ThermoFisher Scientific™, High Resolution Neptune™ Multicollector-Inductively Coupled Plasma Mass Spectrometer housed at the University of Utah was used to analyze strontium samples, which had been purified for the $^{87}Sr/^{86}Sr$ analysis via an introduction system of aqueous solution using an inline chromatographic column (Mackey & Fernandez 2011, Brennan et al. 2014). This solution method was also used to measure the $^{87}Sr/^{86}Sr$ ratios of water samples collected from the Cook Inlet region. Blanks or NIST standard reference material SRM987 were run between samples, and the mean 1 SE was <0.00001 for all standard reference samples.

Water collection and strontium isotope analysis

Water samples were collected (in triplicate) from 8 freshwater rivers and 1 marine location (Turnagain Arm) in upper Cook Inlet and 1 marine location (Kachemak Bay) in the lower inlet during 27 May to 5 June 2016. Freshwater river samples were either collected above tidal influence (Susitna River, Yentna River, and Eagle River), or at low tide when access to areas above tidal influence was more difficult (Bird Creek, 20 Mile River, Portage Creek, and Placer River). Samples were collected for strontium isotope analysis following field collection methods described

by Brennan et al. (2014), and sent via 2 d FedEx® to the Geochemistry Laboratory at the University of Utah, Salt Lake.

Mean $^{87}Sr/^{86}Sr$ ratios from water samples collected in triplicate were calculated by weighting each individual of the 3 values by their respective measurement error (ME):

$$\text{Weighted triplicate mean (TM)} = \frac{\sum_{i=1}^{3}\left(\frac{1}{ME_i^2} \times Sr_i\right)}{\sum_{i=1}^{3}\frac{1}{ME_i^2}} \quad (3)$$

where Sr_i is the $^{87}Sr/^{86}Sr$ ratio from sample i and ME_i is the analytical ME from sample analysis from sample i.

Weighted SE of the triplicate was calculated as:

$$SE = \sqrt{\frac{\sum_{i=1}^{3}\left(\frac{1}{ME_i^2} \times (Sr_i - TM)^2\right)}{2\sum_{i=1}^{3}\frac{1}{ME_i^2}}} / 3 \quad (4)$$

$^{87}Sr/^{86}Sr$ ratios are presented as triplicate mean ± 2 SE, where SE is calculated as above for samples collected in triplicate. Samples not collected in triplicate are presented as $^{87}Sr/^{86}Sr$ ratios ± 2 ME.

Statistical analysis

Linear regressions were used to evaluate the isotopic signatures of CIBW bone collagen for temporal trends. The isotopic signatures ($\delta^{13}C$, $\delta^{15}N$, and $^{87}Sr/^{86}Sr$) of GLGs were also evaluated for temporal trends and the effect of sex using mixed-effects models appropriate for analyzing these repeated measures data. The random effect, or grouping variable, in these models is the individual beluga. Mixed-effects models were also used to explore the relationship between these isotopic signatures while controlling for the effect of sex. A set of candidate models was developed to test each hypothesis, and model selection was performed using likelihood ratio tests and Akaike's information criterion (AIC) for small sample sizes (AICc; Sugiura 1978, Hurvich & Tsai 1989). Diagnostic tests were performed to evaluate model assumptions. R^2 values were obtained using the r.squaredGLMM function in the R-package MuMIn (Bartoń 2018). This function is based on Nakagawa & Schielzeth (2013), and its extension by Johnson (2014); marginal values are reported. In addition, an ANOVA was performed on the results from our pilot study to compare the $\delta^{15}N$ signature of phenylalanine between whales that died near the beginning of our study

period with those that died toward the end. All analyses were carried out using Program R (R Core Team 2017).

RESULTS

The δ^{15}N and δ^{13}C values of CIBW bone collagen generally declined over time (Fig. 3, Table S1 in the Supplement). Simple linear regressions indicated that δ^{15}N values declined at a rate ± SE of 0.028 ± 0.005‰ yr^{-1} (R^2 = 0.66, p < 0.001) and δ^{13}C values declined at a rate ± SE of 0.06 ± 0.009‰ yr^{-1} (R^2 = 0.79, p < 0.001; Fig. 3).

The mean δ^{15}N value of phenylalanine from bones of CIBW that died in 1964 (13.6 ± 0.3‰) was significantly higher than from those that died after 2000 (8.4 ± 1.5‰) at the 92% confidence level (p = 0.08; Table S6). Therefore, the δ^{15}N value of the base of the food chain appears to have changed over the duration of this record.

Annual GLGs from CIBW teeth showed significant declines in δ^{15}N and δ^{13}C values over time. The top mixed effects model in both cases included a random intercept term and correlated random slope for each animal. Random intercept and slope models allow for a separate line, each with its unique intercept and slope, to be fit to the data from each beluga. The top model is preferred over alternative models that call for either a common slope for all belugas or a common intercept. The effect of sex was not significant in either case (p = 0.13 for δ^{15}N and 0.28 for δ^{13}C). At the population level, δ^{15}N values (n = 343 GLGs) decreased by 0.035 ± 0.005‰ each year (p < 0.0001, R^2 = 0.28; Fig. 4a, Tables S2 & S3 and Fig. S1), and δ^{13}C values (n = 296 GLGs) decreased by 0.072 ± 0.05‰ each year (p < 0.0001, R^2 = 0.63; Fig. 4b, Tables S2 & S3, Fig. S2). Individual CIBW random effects for slope and intercept are listed in Table S3. Autocorrelation and partial autocorrelation functions applied to the residuals from simple linear regressions on individual whales showed no significant correlation, and we did not need to account for autocorrelation in the top model. ^{87}Sr/^{86}Sr (±2 SE) ratios varied across the sample locations in the Cook Inlet watershed (Fig. 1, Table 1, Table S4). The highest ^{87}Sr/^{86}Sr ratio was found in Kachemak Bay (near Homer Spit), in lower Cook Inlet (site 15, Fig. 1, Table 1, Table S4) and was equivalent to the global marine ratio (0.70918 ± 0.00006; Brennan et al. 2015). The second highest ^{87}Sr/^{86}Sr ratio was also from marine waters in Turnagain Arm in upper Cook Inlet (site 10, Fig. 1, Table 1, Table S4).

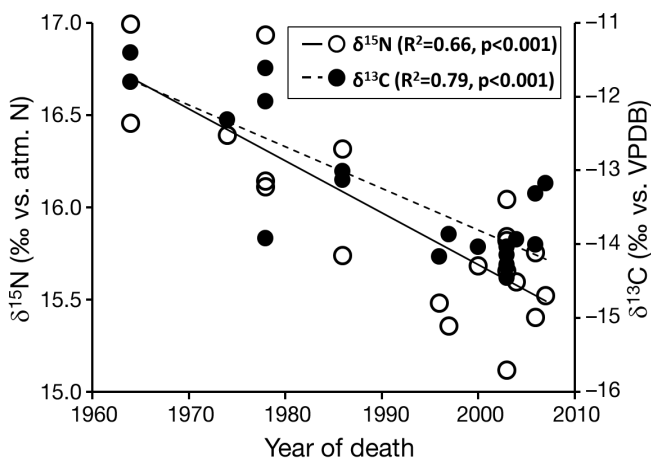Fig. 3. δ^{15}N and δ^{13}C values from Cook Inlet beluga bone collagen (skulls) plotted against year, showing regression (linear) lines for both; atm. N: atmospheric nitrogen, VPDB: Vienna Pee Dee belemnite
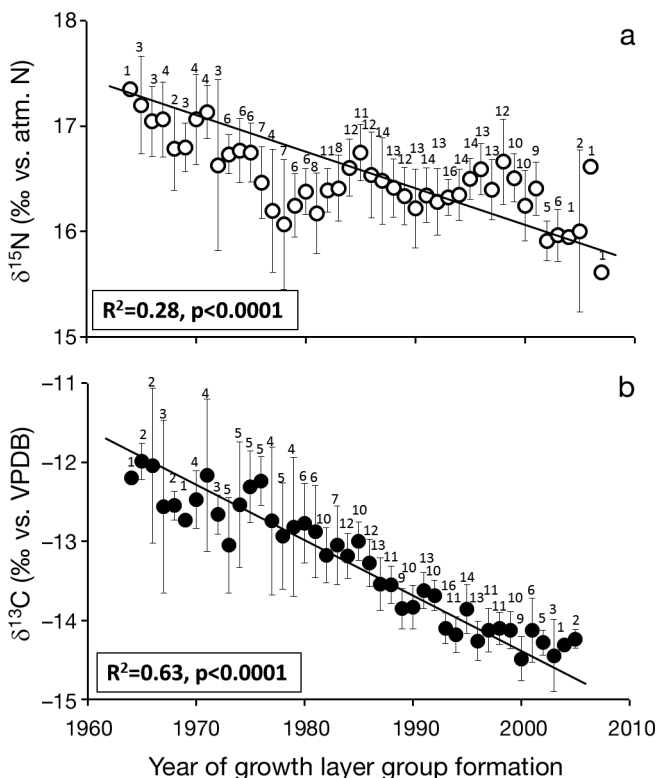

Fig. 4. Mean (±2 SE) (a) δ^{15}N and (b) δ^{13}C values from Cook Inlet beluga tooth growth layer groups (GLGs) plotted by year of formation. The fitted line in each case is the population level trend from the top mixed-effects model. (Refer to Tables S2 & S3 and Figs. S1 & S2 in the Supplement for time series data and trend lines for individual belugas in addition to the population level trend line.) The number above each mean value represents the number of GLGs that make up that mean value; atm. N: atmospheric nitrogen, VPDB: Vienna Pee Dee belemnite

Table 1. Summary of ^{87}Sr/^{86}Sr ratios from Cook Inlet rivers and marine waters, including date and location of sampling sites. ID matches the ID used in Fig. 1. Data from Brennan et al. (2014) are indicated by *; average ratios and the standard error (SE) from triplicate samples, indicated by a superscript 't,' are weighted by the SE from analysis in the present study

ID	Date collected	Waterbody	Latitude (°N)	Longitude (°W)	^{87}Sr/^{86}Sr	±2 SE
1 *,t	11-Sep-10	Chulitna R.	62.568	150.236	0.708948	0.000042
2 *,t	11-Sep-10	Susitna R.	62.178	150.172	0.708127	0.000057
3 t	27-May-16	Susitna R.	61.588	150.410	0.707232	0.000039
4 t	27-May-16	Yentna R.	61.608	150.508	0.707349	0.000011
5 t	27-May-16	Susitna R.	61.533	150.545	0.707353	0.000074
6 *,t	14-Sep-10	Matanuska R.	61.734	148.765	0.705711	0.000013
7 *,t	14-Sep-10	Knik R.	61.476	148.876	0.706074	0.000075
8 t	2-Jun-16	Eagle R.	61.309	149.574	0.705793	0.000020
9 t	2-Jun-16	Bird Cr.	60.973	149.467	0.707406	0.000050
10	5-Jun-16	Turnagain Arm	60.937	149.265	0.709110	0.000021
11 t	2-Jun-16	20 Mile R.	60.845	148.989	0.706692	0.000014
12 t	2-Jun-16	Portage Cr.	60.827	148.977	0.706558	0.000041
13 t	2-Jun-16	Placer R.	60.817	148.988	0.706623	0.000005
14 *,t	12-Sep-10	Kenai R.	60.487	149.935	0.706517	0.000012
15	2-Jun-16	Lower Cook Inlet	59.606	151.436	0.709206	0.000028

The ^{87}Sr/^{86}Sr ratios of all rivers tested in this study were lower than the marine values; the highest was from Bird Creek (site 9, Fig. 1) and the lowest was from Eagle River (site 8, Fig. 1, Table 1, Table S4).

^{87}Sr/^{86}Sr ratios of 44 GLGs in teeth from 5 CIBW teeth (3 males, 2 females) trended away from the marine signature in Lower Cook Inlet (0.70921) toward the more freshwater signature of Turnagain Arm (0.70911; Fig. 5). The top model included a random intercept term for each animal, the variable sex, and the interaction of sex and year. Two of the 3 males were displaced to lower ^{87}Sr/^{86}Sr ratios than the waters of Lower Cook Inlet, while the 2 females not only had lower mean ^{87}Sr/^{86}Sr values, but they also showed a trend of decreasing values with time (1982 to 1997 and 1991 to 2005). For males, the slope ± SE which was $-1.749 \times 10^{-7} \pm 7.507 \times 10^{-7}$ was not significantly different from 0, while that for females ($-2.258 \times 10^{-6} \pm 4.728 \times 10^{-7}$) was significant and had $R^2 = 0.63$.

We also examined the correlation between ^{87}Sr/^{86}Sr ratios with δ^{15}N and δ^{13}C values from the same GLGs on the same tooth (n = 34 GLGs), and neither pairing was significantly correlated (p = 0.10 for δ^{15}N and p = 0.95 for δ^{13}C). However, sex was significant in both cases (p = 0.0001 for δ^{15}N and p = 0.0008 for δ^{13}C). In addition to sex, the top models included a random intercept for each animal and a common slope.

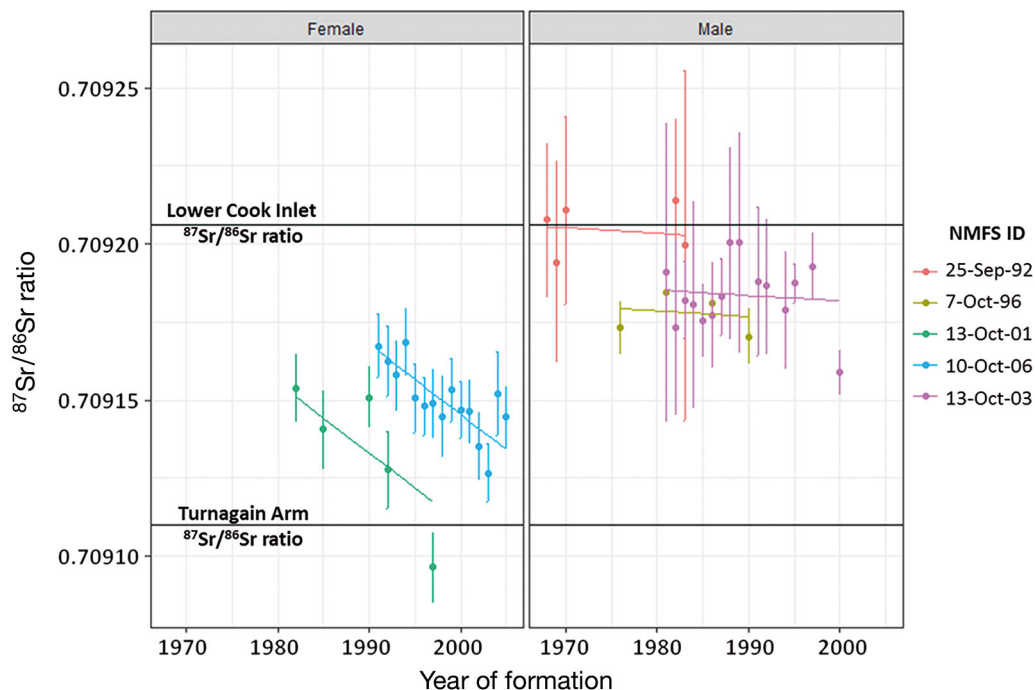Fig. 5. ^{87}Sr/^{86}Sr ratios from Cook Inlet beluga growth layer groups (GLGs) by year of formation

DISCUSSION

Stable isotope ratios preserved in CIBW bone and GLGs from CIBW teeth integrate the isotopic composition of beluga diet. In this study, we analyzed samples representing the period from the 1950s to 2007. Bone metabolism involves removing old material (made with diet items of the past) by osteoclasts and secreting new material (made with diet items available currently) via osteoblasts at a very slow rate (2 to 3% yr^{-1}), such that bone integrates dietary isotopes for at least 10 yr and possibly for the lifetime (Clarke 2008). In contrast, GLGs remain biochemically unchanged after they are formed and, because belugas form 1 GLG yr^{-1}, the isotopes in each GLG integrated diet for 1 yr of a beluga's life (Stewart et al. 2006, Luque et al. 2007). Both $\delta^{15}N$ and $\delta^{13}C$ values from CIBW declined during our study period (1950s to 2007) in both bone and teeth, providing definitive evidence that a change in CIBW feeding ecology occurred. For a full decrease in trophic level we would expect $\delta^{15}N$ values to decline by ~3‰ and $\delta^{13}C$ values to decline by ~1‰ (Peterson & Fry 1987). However, our data showed less than a full trophic level decline for $\delta^{15}N$ (~1 to 2‰) and more than a trophic level decline for $\delta^{13}C$ (~3‰; Fig. 4).

Declining $\delta^{15}N$ and $\delta^{13}C$ values could represent a change in prey source (Peterson & Fry 1987). However, a change in $\delta^{15}N$ and $\delta^{13}C$ values of the baseline, primary production in the environment can also occur over time (Schell 2000, Post 2002, Christensen & Richardson 2008, Casey & Post 2011, Marcoux et al. 2012). Because of the documented range contraction from more marine areas, middle and lower Cook Inlet, to more freshwater-influenced areas in upper Cook Inlet (Rugh et al. 2010), we suspected the decline in $\delta^{13}C$ values indicated a change from a marine prey base to a more freshwater-influenced prey base.

To test if the declining $\delta^{13}C$ values indicated a change to more freshwater prey, we used isotopes of a third element, strontium. Fish exchange water passively over gills, and their internal $^{87}Sr/^{86}Sr$ ratio reflects their surroundings (Brennan et al. 2014, Padilla et al. 2015). Beluga whales are not known to drink water, but rather receive their metabolic water, and thus strontium, from their prey. When prey is consumed, strontium is incorporated into hard structures, such as bone and teeth, because of its similarity to calcium (Britton et al. 2009). Because $^{87}Sr/^{86}Sr$ ratios are driven by geologic processes, the ratio of $^{87}Sr/^{86}Sr$ in a river's water remains relatively unchanged at a specific site through time, but varies

along the length of the river as a result of the geologic formation the river flows through. The magnitude of variation in terms of $^{87}Sr/^{86}Sr$ in ocean waters is considerably lower compared to the $^{87}Sr/^{86}Sr$ variation exhibited by the rivers and estuaries in Alaska (Bataille et al. 2014, Brennan et al. 2014, 2015). Therefore, $^{87}Sr/^{86}Sr$ ratios measured in the hard structures of an organism can be compared to the $^{87}Sr/^{86}Sr$ ratios of various estuarine and freshwater sources, and used to determine when an organism switches from a marine-influenced prey to a more freshwater-influenced prey. In some cases, the $^{87}Sr/^{86}Sr$ ratio can identify the source (river) of freshwater prey.

We compared $^{87}Sr/^{86}Sr$ ratios and $\delta^{13}C$ values from the same GLG on the same tooth for 5 whales (representing diet from 1968 to 2005) to determine whether a change in CIBW diet to a more freshwater-influenced prey was indicated. Although we found no correlation between $^{87}Sr/^{86}Sr$ ratios and $\delta^{13}C$ values (p = 0.78), we did find that $^{87}Sr/^{86}Sr$ ratios trended away from the global marine ratio towards a more freshwater signal. Fig. 5 shows a significant declining trend of $^{87}Sr/^{86}Sr$ values in the 2 females sampled, but not in the 3 males sampled. The declining trend in females and displacement in males most likely represent a dietary change from marine to more freshwater prey. Although this analysis is sufficient for proposing a hypothesis regarding differences between the sexes, the sample size is too small to draw conclusive population-level inferences. It is notable that these changes in foraging ecology occurred while the range of CIBW continued to contract into the upper reaches of Cook Inlet (Rugh et al. 2010), where freshwater prey items are available. To determine which freshwater input was most influential, we compared the $^{87}Sr/^{86}Sr$ ratio from GLGs to known ratios in river systems flowing into Cook Inlet available from Brennan et al. (2014) and from the present study (Fig. 1). Although we were not able to definitively identify which river(s) influenced CIBW the most, the recent lower $^{87}Sr/^{86}Sr$ ratios indicate that CIBW are now feeding on prey that is more influenced by freshwater.

Our carbon and nitrogen isotope data could indicate a change in CIBW feeding ecology, and the strontium data indicate a change towards a more freshwater-influenced diet; however, whether these changes could also be explained by an environmental change in baseline was unknown. Therefore, we analyzed the $\delta^{15}N$ values of the amino acid phenylalanine from 5 bone collagen samples from CIBW that died during 1964 (2 whales) and after 2000 (3 whales).

Phenylalanine is an essential amino acid (i.e. not manufactured by organisms other than primary producers or altered along the food chain) and the δ^{15}N values of this amino acid have been used to identify the δ^{15}N value at the base of food chains (e.g. Chikaraishi et al. 2014). Because the mean δ^{15}N value of phenylalanine from beluga whales that died more recently (after 2000) was lower than those that died at the beginning of our study period (during 1964; Table S6), the δ^{15}N value of the base of the food chain sustaining CIBW has changed over the duration of this record. Further analyses would be beneficial to strengthen this compound-specific analysis; however, a change in the isotopic (N) composition of the base of their food chain could result from 3 scenarios: (1) CIBW have foraged in a similar location through time and the δ^{15}N value of the base of the food chain decreased at that location, (2) CIBW now forage in a different location that has a δ^{15}N value at the base of the food chain that is lower than at the prior location, or (3) a combination of the first 2 scenarios.

The ^{87}Sr/^{86}Sr results, especially when interpreted in the context of range contraction, indicate a change in foraging to areas with fresher water, thus ruling out scenario 1 in favor of scenarios 2 or 3. A change in CIBW distribution to greater use of the upper inlet was documented over 3 periods: 1978–1979, 1993–1997, and 1998–2008 (Rugh et al. 2010). This change in location puts CIBW in closer proximity to freshwater and likely to prey influenced by freshwater. Indeed, we suspect the decline in δ^{13}C values indicates a change from a marine prey base to a more freshwater-influenced prey base. Lower ^{87}Sr/^{86}Sr ratios demonstrate greater freshwater influence in foraging ecology, and the change in isotopic (N) composition of the amino acid phenylalanine also supports a shifted baseline that could be explained by a shift towards more freshwater prey. Based on our complete data set (including declining δ^{15}N and δ^{13}C values in bone and teeth, lower ^{87}Sr/^{86}Sr ratios in teeth, and lower δ^{15}N values in phenylalanine from teeth) and previous survey findings (Rugh et al. 2010), we consider the most likely explanation to be scenario 2 from above or scenario 3, a combination of both scenarios, that CIBW now forage in a different location (upper Cook Inlet) with a different δ^{15}N value at the base of the food chain than in the base at the previous forage location. Our isotope data are consistent with more freshwater-influenced prey through time, the δ^{13}C data (bone and GLGs) indicate that the change in foraging behavior began at least as far back as the 1950s, and the ^{87}Sr/^{86}Sr ratio data indicate that the change in females has occurred since at least 1982 (Figs. 4 & 5). More data are necessary to better determine when these changes began and if they are continuing, but both data sets indicate that the shift began long before the documented population decline in the 1990s. Therefore, if this change in habitat and prey is related to the decline in CIBW abundance, then we must look farther back in time (i.e. before the documented decline in the 1990s) to determine what was responsible for the greater freshwater influence in CIBW feeding ecology.

If changes in prey populations are responsible for the change in feeding ecology, we could evaluate changes in prey availability. Decreases in shrimp, crab, and some fish including herring and salmon (chinook, chum, and pink) over the last few decades have been documented, but determining whether declines in prey abundance correspond to declining CIBW foraging opportunities is difficult to measure (Moore et al. 2000, Hollowell et al. 2016, Shields & Dupuis 2017).

The ^{87}Sr/^{86}Sr ratio data from GLGs indicate that female CIBW were increasingly feeding on more freshwater-influenced prey through their lifetime, while the males, although displaced towards a more freshwater signature, showed no trend through time (Fig. 5). This difference in ^{87}Sr/^{86}Sr ratios between sexes was not seen in the δ^{15}N and δ^{13}C values, but could indicate a sex-specific foraging strategy. Citta et al. (2016) found that female beluga whales in Bristol Bay spent more time in areas where pink salmon were more abundant, possibly to allow more foraging opportunities for their calves. Beluga whales do not break apart or chew their prey; therefore, prey size is limited by what they can swallow whole, which likely makes larger salmon unavailable to smaller female belugas and their calves. If CIBW exhibit a similar sex-specific foraging strategy, this could explain the differences detected in ^{87}Sr/^{86}Sr ratios between males and females. It is still unclear, however, why the difference in foraging was detected in ^{87}Sr/^{86}Sr ratios but not in the δ^{15}N and δ^{13}C values.

Additional research using strontium isotopes (e.g. more water sample locations, GLGs representing more recent years) and carbon and nitrogen isotopes are necessary to better understand the changes we identified in this study. Additionally, further study of phenylalanine would be beneficial to better determine how the baseline has changed and to better understand the different behaviors between males and females. Our data provide evidence of a long-term shift to more freshwater-influenced feeding habitat and ecology. How this behavior relates to the continued decline in CIBW or their possible recovery, however, remains unknown.

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