Received: 30 November 2019 | Accepted: 14 October 2020
DOI: 10.1111/mms.12766

ARTICLE

Marine Mammal Science

Patterns of mortality in endangered Cook Inlet beluga whales: Insights from pairing a long-term photo-identification study with stranding records

Tamara L. McGuire[1] | Kim E. W. Shelden[2] | Gina K. Himes Boor[3] | Amber D. Stephens[1] | John R. McClung[1] | Christopher Garner[4] | Caroline E. C. Goertz[5] | Kathleen A. Burek-Huntington[6] | Greg O'Corry-Crowe[7] | Bruce Wright[8]

[1]The Cook Inlet Beluga Whale Photo-ID Project, Anchorage, Alaska

[2]Marine Mammal Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, Seattle, Washington

[3]Ecology Department, Montana State University, Bozeman, Montana

[4]673d CES/CEIEC, Conservation Department, Joint Base Elmendorf Richardson, Alaska

[5]Alaska SeaLife Center, Seward, Alaska

[6]Alaska Veterinary Pathology Service, Eagle River, Alaska

[7]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, Florida

[8]Knik Tribe, Wasilla, Alaska

Correspondence
Tamara L. McGuire, The Cook Inlet Beluga Whale Photo-ID Project, 310 W 123rd Avenue, Anchorage, Alaska 99515.
Email: tamaracookinletbeluga@gmail.com

Funding information
Knik Tribe, Grant/Award Number: Species Recovery Grant NOAA-NMFS-PRPO-2017-2004972

Abstract

Mortality is a demographic metric crucial for understanding the dynamics of endangered populations such as Cook Inlet beluga whales (CIBWs, *Delphinapterus leucas*), but patterns of mortality are currently not well understood for CIBWs, making decisions about recovery actions challenging. We combined long-term photo-ID data from approximately 420 individual belugas identified during the period 2005–2017 with stranding data from 95 dead belugas to identify patterns of mortality with respect to age, sex, geographic range, cause of death, and to estimate minimum mortality rates. Reported mortality was greatest for adults of reproductive age, followed by calves, with fewer sub-adults and no adults older than 49 years in the stranding data set despite lifespans of 70+ years reported in other beluga populations. Dead females and males were evenly represented. Live stranding was the predominant assigned cause of death but represented only ~33% of deaths of known cause. Causal factors for the majority of deaths and live strandings are unknown. Annual mortality estimated from reported carcasses relative to total population size averaged 2.2%. Our analysis advances our current understanding of mortality patterns in CIBWs but linking a greater proportion of carcasses to photo-ID individuals would further improve our understanding; we conclude with recommendations for achieving this.

KEYWORDS
beluga whale, Cook Inlet, *Delphinapterus leucas*, mortality, photo-identification, stranding, survival

1 | INTRODUCTION

Rates and patterns of mortality are some of the fundamental metrics, along with reproduction, that allow us to understand the current status and future prospects of a species or population. When estimates of these parameters are unavailable or uncertain, especially for a declining population, resource managers are severely hampered in their efforts to address the true source(s) of the decline, and risk implementing ineffective protective measures. Such is the case with Cook Inlet beluga whales (hereafter CIBWs, *Delphinapterus leucas*; Figure 1), which have declined in recent decades, but for which rates and patterns of historic and current mortality and reproduction are uncertain. To provide additional information and further synthesize existing data on mortality in this endangered population, we combine long-term photo-identification data from individually identified whales with data from beluga carcasses and live strandings in order to discern any patterns in age, sex, geographic range, and cause of death (COD). We also use the carcass data to estimate minimum mortality rates that can be compared to the most-recent model-derived estimates of survival.

A geographically-(Laidre et al., 2000) and reproductively-isolated, small population (O'Corry-Crowe et al., 1997), CIBWs were listed as Critically Endangered on the IUCN Red List in 2006 (Lowry et al., 2019) and as an Endangered Distinct Population Segment (DPS) under the U.S. Endangered Species Act (ESA) in 2008 (U.S. Federal Register, 2008). The ESA listing decision noted over-harvest, destruction of habitat, predation by killer whales, and live strandings as factors in the population's decline (U.S. Federal Register, 2008), with the primary cause attributed to unsustainable levels of hunting (Hobbs et al., 2000; Mahoney & Shelden, 2000). This population was historically small, estimated to number over a thousand in the late 1970s and early 1990s (reviewed in Shelden et al., 2015). The most-recent population estimate, derived from aerial surveys in 2018, was 279 individuals (95% probability interval 250–317 belugas; Wade et al., 2019). Despite the protections of the ESA following the 2008 listing, and the regulation and eventual cessation of hunting (in 1999 and 2006, respectively), the CIBW population does not appear to be increasing in number (Wade et al., 2019). The CIBW Recovery Plan (National Marine Fisheries Service [NMFS], 2016) examined other possible threats, including: catastrophic events (i.e., natural disasters, oil spills, mass strandings), noise, disease, habitat loss/degradation, reduction in prey, unauthorized take, pollution, predation, and cumulative effects of multiple stressors, and concluded that while all of these possible threats are of concern, the reason(s) for the lack of recovery have not yet been identified.

Most research to-date has focused on estimating total population abundance and monitoring the distribution, movement, and habitat use of the population via aerial surveys (e.g., Goetz et al., 2007, 2012; Hobbs et al., 2000, 2015; Rugh et al., 2000, 2010; Shelden et al., 2015), satellite tagging (Ferrero et al., 2000; Hobbs et al., 2005; Shelden et al., 2018), photo-ID (McGuire & Stephens, 2017; McGuire, Himes Boor, et al., 2020), and passive acoustics (Castellote et al., 2016, 2020). More recent modeling efforts combining data from CIBW aerial surveys, hunting, and photo-ID in an integrated population model suggest that survival in CIBWs may be lower than other stable cetacean populations and thus, may be limiting their recovery (Jacobson et al., 2020). The model did not identify any specific factor(s) that may be reducing survival and did not include stranding data.

Given the declining population trend (Wade et al., 2019) and some indications of low survival (Jacobson et al., 2020), it is important to closely examine current CIBW patterns of mortality, to explore potential sources of

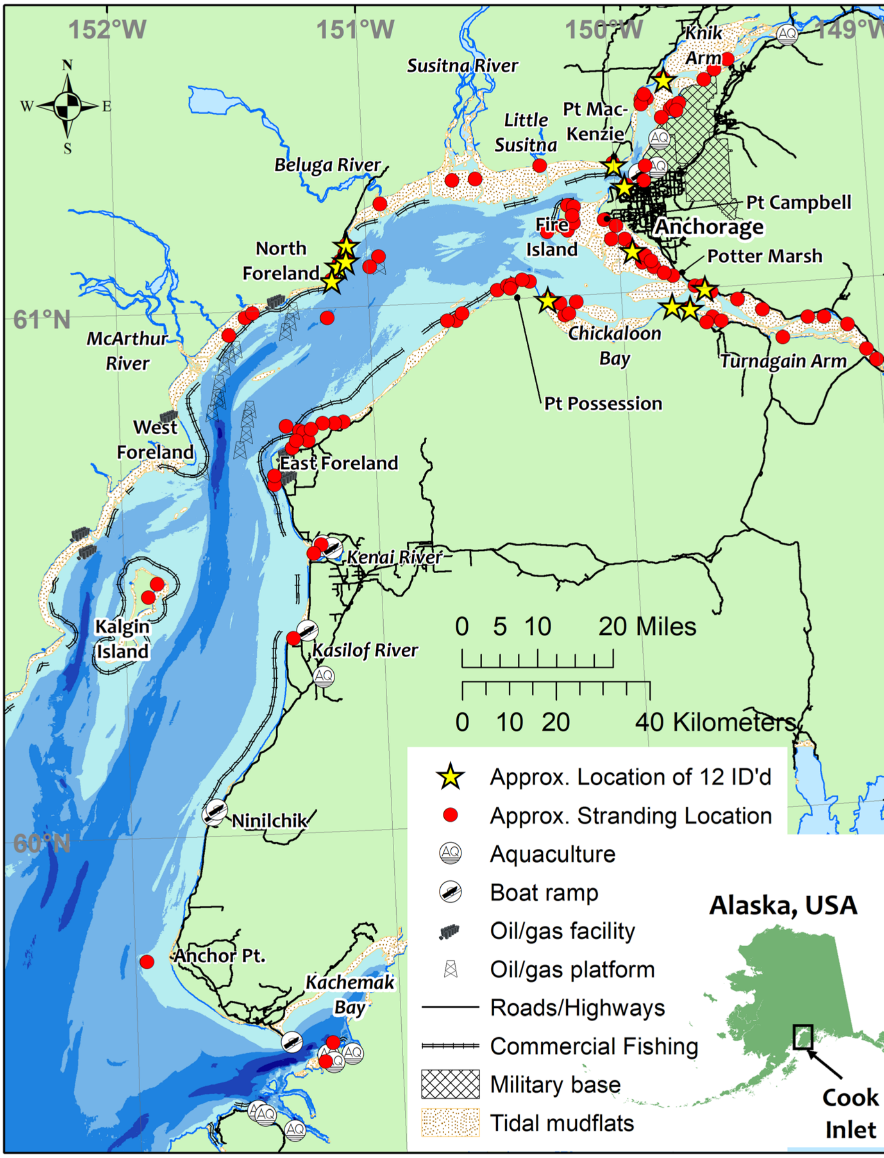

FIGURE 1 Cook Inlet, Alaska, with place names mentioned in the text and locations of all reported dead-stranded belugas, including 12 photo-identified individuals, 2005–2017.

mortality that may be contributing to this lower-than-expected survival rate, and to provide an independent estimate of known mortality from individual-level data to compare to model-based survival estimates. Examinations of beluga carcasses provided some information on causes of mortality (Burek-Huntington et al., 2015), but necropsy data alone from this population are insufficient to fully understand CIBW mortality patterns, particularly because the majority of dead CIBWs cannot be necropsied. Often carcasses are not accessible due to extreme tides (~11 m) and remote locations or are in advanced states of decomposition by the time they are reported. By combining our photo-ID data on individual belugas with reports of dead belugas and necropsy data, we can more fully explore the patterns and sources of mortality.

Studies of CIBWs using photo-ID methods have been ongoing since 2005 and have confirmed that most individuals possess distinct natural marks that persist across years. These marks can be identified and re-sighted using high-resolution digital photography (McGuire & Stephens, 2017). The CIBW photo-ID catalogs (left side, right side, and dual side) and associated survey data provide information about the distribution, movement patterns, and life-history characteristics of over 400 individually identified beluga whales, including individuals who have died during the 2005–2017 study period. The consistent monitoring of so many individually recognizable whales over such an extended period provides the most extensive data set available on the behavioral ecology and life history of this endangered population. Recent and ongoing work has focused on using these data in mark-recapture models to estimate population level demographic rates (e.g., Himes Boor & McGuire, 2020; Jacobson et al., 2020), but to date, no studies have provided a detailed assessment of mortality patterns for this population. Pairing our long-term data set with annual stranding reports allows us to examine demographic patterns in mortality. This work provides information to help address several of the objectives, criteria, and actions presented in the CIBW Recovery Plan, including the objective of "ensuring that prey, … human activities, … and disease … are not limiting recovery," the delisting criteria of ensuring that disease is not increasing mortality and reducing the rate of recovery, and the proposed action of determining annual mortality rates and improving CIBW stranding response (NMFS, 2016). Additionally, we provide information on minimum annual mortality rates and demographics that can be used in updated population viability analyses (PVA; see Hobbs et al., 2015). Based on our assessment and its limitations, we also make recommendations for improving future data collection to increase the value of carcass data by improving the possible links to photo-identified individuals.

2 | METHODS

2.1 | Stranding data set

Information on the numbers, encounter locations, and dates of dead CIBWs from 2005 to 2017 was compiled from stranding reports provided by the Alaska Marine Mammal Stranding Network and National Marine Fisheries Service (NMFS, the U.S. Federal agency with management authority for most marine mammals, including belugas). Necropsies of dead belugas were conducted by the Alaska Marine Mammal Stranding Network, under the authorization of NMFS (all permit numbers are listed in the Acknowledgments section of this paper). For each dead beluga examined, a veterinarian or other stranding responder assigned sex (male, female, or unknown), age-class (fetus, calf, subadult, or adult), and decomposition code (fresh, moderate decomposition, advanced decomposition, mummified/skeletal, unknown). We did not include in-utero fetuses as separate individuals in our analysis. Age-classes assigned at the time of the necropsy were determined based on total body length and skin color (belugas are dark when they are born and lighten as they age) following the methods described in Burek-Huntington et al. (2015). Sex was determined by genitalia and/or genital slits when visible and tissue was not too decomposed. Veterinarians also noted visible signs of reproductive status (pregnant, postpartum, or lactating) of adult females. When possible, they assigned probable proximate COD.

In some cases, laboratory analyses allowed for refinement of the field-assigned data about age, reproductive status, and sex. Tissues and teeth were collected from some individuals, and their ages were estimated from growth layers in the teeth, using one growth layer group (GLG) per year (Vos et al., 2019). A retrospective analysis of the reproductive status of dead females was conducted based on laboratory examination of their reproductive tracts (Shelden et al., 2019). The sex of necropsied individuals was assigned or confirmed using genetics methods for carcasses that were too decomposed or whose ventral sides were not exposed. Total DNA was extracted from tissue samples by established protocols (e.g., O'Corry-Crowe et al., 1997) and the genetic sex of each sample was determined by PCR-based methods (Fain & LeMay, 1995).

2.2 | Photo-identification data set

To create the photo-ID catalog, we conducted 477 photo-ID surveys over 13 consecutive field seasons (2005–2017) in Cook Inlet, an estuary in south-central Alaska (Figure 1). At the time of this study, the summer range of CIBWs had contracted to the area north of the East and West Foreland (Rugh et al., 2010; Shelden et al., 2015), hereafter, referred to as the Upper Inlet. Most of the photo-ID survey effort was concentrated in the Upper Inlet, with some effort in the Kenai River and its delta (Figure 1). Surveys were conducted during the ice-free season (April–October), with the most effort in August and September, and the least in April. Surveys were conducted from vessels (58%) and from shore (42%).

Free-swimming belugas were photographed with a digital SLR camera with a telephoto image-stabilized zoom lens (100–400 mm) with auto-focus. We also reviewed and cataloged photographs of live belugas shared with us from the public and colleagues. These shared photos were taken using a variety of cameras, cell phones, and other digital devices, and were held to the same quality standards as those collected during photo-ID surveys. Markings used for photo-ID of individual CIBWs consist of marks from conspecifics, pigmentation patterns, and scars from injury or disease. Details of the photo-ID methods are presented in McGuire and Stephens (2017). Because photographs taken from vessels or shore were lateral views of one side of a beluga's body, separate catalogs were created for right-side images, left-side images, and dual-side individuals. Photo-ID studies of other cetaceans, such as bottlenose dolphins (*Tursiops truncatus*), often use images of the dorsal fin to identify individuals, and these individuals can be recognized by fin shape and marks along the trailing edge that are visible from either side. Belugas do not have a dorsal fin, and therefore could only be classified as dual-side individuals if (1) they met the criteria to be classified as individuals in both right- and left-side catalogs, and (2) if marks that spanned both sides of the body could be seen and used to link the two sides.

Sighting histories (i.e., dates and locations of photographed sightings) were compiled for all identified belugas (n = 422 right-side individuals and n = 429 left-side individuals) in the 2005–2017 catalog. We augmented the photo-ID resight data of individual whales with biological data (e.g., sex, age, reproductive status) from identified whales that were photographed during necropsies (Burek-Huntington et al., 2015), satellite-tagging studies (McGuire & Stephens, 2016; Shelden et al., 2018), and biopsy collections (McGuire et al., 2017).

In addition to the photographs of live CIBWs taken during photo-ID surveys, photographs were taken when dead belugas were encountered (on shore or floating) during surveys, or when photo-ID team members were informed of a stranding event by NMFS. Photographs were also shared by the Alaska Marine Mammal Stranding Network, NMFS, colleagues, and members of the public. We compared these photographs of dead belugas to photographs in the photo-ID catalog, with the goal of identifying individual dead whales and learning more about their sighting histories. In cases where dead belugas were photographed but not necropsied or otherwise examined in the field, we evaluated the photographs for evidence of age-class (via skin color and approximate length in reference to other objects in the photographs), relative age (based on years of sightings for those in the photo-ID catalog), and sex (if genitalia were visible in the photographs).

2.3 | Minimum mortality rates

We estimated annual minimum mortality rates by dividing the reported number of dead whales by population size estimates derived from NMFS aerial surveys 2005–2017 (Wade et al., 2019). For those years when aerial surveys were not conducted, we estimated population size by interpolating between estimates derived for the year prior to and the year after the subject year. We calculated a mean annual rate by averaging the estimates across the 13 years of data and calculated the sample standard error.

3 | RESULTS

3.1 | Mortality of individual belugas

Between 2005 and 2017, 95 dead CIBWs were reported to NMFS, and photographs were taken of 41 of these (Table 1). Necropsies were performed on 33 of the 41 individuals that were photographed. For eight dead belugas that were not necropsied but were photographed, we determined age-class (via skin color and approximate length in reference to other objects in the photographs) for all individuals, and the sex of two individuals whose genitalia were visible in photos. Photographs of 12 dead belugas were matched to individuals in the 2005–2017 photo-ID catalog (hereafter, identified dead; Table 2).

3.1.1 | Sex

Sex was unknown for approximately half of the 95 reported dead belugas, with the remaining divided equally between females and males (Table 1). Six of the 12 identified dead belugas were males and six were females (Table 2).

3.1.2 | Age

The predominant age-class of the 95 reported dead belugas was adult, followed by calf, then adult/subadult (Table 1). Eleven of the 12 identified dead belugas were classified as adults based on length (and age, if available) and color (Table 2). The 12th identified dead beluga was a 10-year-old female classified as adult/subadult because it fell on the border of age-class categories based on age and undetermined reproductive status (Shelden et al., 2019; Vos et al., 2019).

From the sample of 95 dead belugas reported in 2005–2017, male ages ranged between 0 and 49 years old, and female ages between 0 and 41 years old (ages estimated by counting GLGs in the teeth; Vos et al., 2019). Ten of the identified dead individuals were necropsied, and ages of identified males ranged between 15 and 40 years and ages of identified females between 10 and 39 years (Table 2). Two of the identified females were not necropsied, and therefore did not have teeth removed for aging. We estimated their minimum age (based on skin color and size) at the time they were first photographed and counted the number of years they were photographed up until their deaths. At the time of death, both females were estimated to be over 13 years old (Table 2).

3.1.3 | Reproductive status

The age of first reproduction for belugas as a species has been reported as 8–13 years for females and 8–15 years for males (Burns & Seaman, 1986; Suydam, 2009), which suggests that at least 11 of the 12 identified dead CIBWs were of reproductive age. Ovaries from the 10-year-old identified female were not examined to confirm reproductive status. No 8–12-year-old whales were in the data set of necropsied females whose reproductive tracts were examined (Shelden et al., 2019), therefore we could not use these data to determine if the age of sexual maturity for CIBWs is similar to other beluga populations. One of the six identified dead females was pregnant at the time of death, one was lactating, one was sexually mature but neither pregnant nor lactating (Table 2), and one was sexually mature but of undetermined reproductive status. The remaining two females were not necropsied and their reproductive status at the time of death was, therefore, unknown. Additional details (i.e., calving interval, length of

TABLE 1 Annual minimum mortality estimates of Cook Inlet belugas whales 2005–2017, based on estimated total population size from National Marine Fisheries Service (NMFS) aerial surveys (Wade et al., 2019) and dead strandings reported to NMFS. Details of strandings reported to NMFS are presented in Supplemental Table 1. Probability intervals (PIs) around NMFS population estimates provide the basis for the estimated ranges on the minimum mortality estimates.

				Age class of dead belugas					Sex of dead belugas				
Year	NMFS population estimate (95% PIs)	# Dead belugas reported to NMFS[a]	Estimated % annual minimum mortality (range from 95% PI)	# Adult	# Adult/ subadult	# Subadult	# Calves	# Unknown age class	# Females	# Males	# Unknown sex	# Reported dead with photos	# Matched to photo-ID catalog
2005	287(269–312)	6	2.1(1.9–2.2)	3	1	1	1	0	2	2	2	1	0
2006	289(269–314)	9	3.1(2.9–3.3)	4	1	2	2	0	2	1	6	0	0
2007	318(295–343)	15	4.7(4.4–5.1)	6	0	5	2	2	3	5	7	1	0
2008	323(304–344)	11	3.4(3.2–3.6)	4	2	1	4	0	6	3	2	2	2
2009	346(323–373)	4	1.2(1.1–1.2)	3	0	0	1	0	3	1	0	4	1
2010	369(339–400)	5	1.4(1.3–1.5)	2	0	0	2	1	2	0	3	1	0
2011	361(336–388)[b]	3	0.8(0.8–0.9)	1	1	0	0	1	0	0	3	0	0
2012	353(333–376)	3	0.8(0.8–0.9)	1	0	1	1	0	0	2	1	2	1
2013	346(325–368)[b]	5	1.4(1.4–1.5)	3	1	0	0	1	1	1	3	3	2
2014	338(317–360)	11	3.3(3.1–3.5)	8	1	1	1	0	3	3	5	10	5
2015	316(294–339)[b]	3	0.9(0.9–1.0)	1	0	0	2	0	0	1	2	1	1
2016	293(271–318)	8	2.7(2.5–3.0)	2	1	0	4	1	2	2	4	4	0
2017	286(260–317)[b]	12	4.1(3.8–4.6)	4	4	1	3	0	3	6	3	12	0
Total		95		42	12	12	23	6	27	27	41	41	12
% of total				44%	13%	13%	24%	6%	28%	28%	44%	43%	13%
Mean	325	7	2.2 (SE = 0.36)[c]										
Range	286–369	3–15	0.8–4.7										

[a]Some numbers differ from those presented in the 2016 CIBW Recovery Plan (NMFS, 2016). We have checked those numbers against original stranding reports and believe the numbers presented here are accurate; [b]Linear interpolation between the two years on either side given surveys were not conducted that year (or in the case of 2011, results were compromised and removed from the abundance time series, see Wade et al., 2019); [c]Sample standard error was calculated as the square root of the sample variance divided by the sample size.

TABLE 2 Summary of 12 photo-identified dead-stranded Cook Inlet beluga whales from the 2005–2017 study period. Information on age class, sex, reproductive status, and cause of death (COD) of necropsied whales are courtesy of NMFS and the Alaska Marine Mammal Stranding Network, with additional information on reproductive status from Shelden et al. (2019a). Information on COD is from Burek-Huntington et al. (2015) and NMFS unpublished data. Information on age at death is from Vos et al. (2019) for those necropsied whales from which a tooth was collected or estimated from photo-ID sightings histories.

Year	Date	Necropsy	Age class	Sex	Length (cm)	Reproductive status of females at death	Probable COD	Age at death[a] (years)	Photo-id catalog number
2008	Aug 8	Yes	Adult	F	391	Lactating	Undetermined (died one day after mass live stranding in same area)	37	R16
2008	Aug 8	Yes	Adult/ subadult	F	318	Undetermined	Undetermined (died one day after mass live stranding in same area)	10	R197
2009	Oct 8	Yes	Adult	F	305	Pregnant	Undetermined (possible death post-live single stranding, had aspirated sand in lungs)	14	D157
2012	Oct 4	Yes	Adult	M	423	n/a	Blunt trauma (possible ship strike)	15	D7244
2013	Aug 30	No	Adult	F	n/a	Unknown (not examined)	Unknown (not examined); no obvious sign in photos	Estimated >13 years[b]	L2634
2013	Oct 7	Yes	Adult	M	450	n/a	Trauma (choked on large flatfish)	40	D106
2014	May 26	Yes	Adult	M	410	n/a	Asphyxia (glacial silt in airways during live stranding)	23	D115[c]
2014	Aug 1	Yes	Adult	M	447	n/a	Undetermined	40	L2294
2014	Sep 2	Yes	Adult	F	419	Not pregnant, not lactating	Undetermined	39	L1849
2014	Sep 8	Yes	Adult	M	417	n/a	Undetermined	20	L496
2014	Sep 27	No	Adult	F	~366	Unknown (not examined)	Unknown (not examined; no obvious signs in photos	Estimated >13 years[c]	L265
2015	Jun 12	Yes	Adult	M	428	n/a	Infection	20	D2303[d]

[a]Ages from tooth, assuming one growth layer group per year (Vos et al. 2019); [b]First photographed in 2008 with a calf, so at least eight years old in 2008, based on 8 years minimum age of first reproduction; [c]First photographed in 2005 and appeared to be four or more years old, based on color and size; [d]Satellite-tagged in 2002.

association with calves, calving rate) about the reproductive histories of these and other photo-identified female CIBWs can be found in McGuire, Stephens, et al. (2020).

3.1.4 | Cause of death of identified individuals

Veterinarians examined 10 identified individuals and assigned probable proximate COD for 5 of them (Table 2). One was attributed to blunt trauma (possibly ship strike; Burek-Huntington et al., 2015), one to choking on a large flatfish (Rouse et al., 2017), two to aspirating mud/sand following possible live-stranding events (Shelden et al., 2019), and one to pneumonia.

From 2005 to 2017, there were 14 confirmed live-strandings with group sizes ranging from 1 to 76 whales. Although the majority of live-stranded belugas were observed alive in the water immediately following the live-stranding, 3 of these live-stranding events had known associated mortalities (Table S1). There was one instance in which a CIBW was photographically documented to survive a live-stranding event. An identified female that had been annually photographed was documented to have live-stranded with a calf in 2015 and was later photographed with a calf in 2017 (it was unclear if this was the same calf or a younger one, as little of the calf body was visible in the photograph in 2017). Two identified female carcasses were found in August 2008, days after a mass live-stranding event of around 30 belugas in the same area; the freshness of the photographed carcasses suggested that the time of death was during or after the stranding (e.g., Burek-Huntington et al., 2015; Vos & Shelden, 2005). The COD of these two identified females could not be determined because they were not necropsied. High-quality photographs taken at close-range by shore-based photographers show the length of the left side and dorsal surface of each whale and did not show obvious indications of ship strikes, predation marks, or net entanglements on the photographed surfaces. We include the information about the timing and location of these two carcasses with respect to the live-stranding, because although it is inconclusive, the close association in time and space of the carcasses and the live-stranding may be relevant.

3.1.5 | Seasonal and spatial patterns of reported dead belugas

Of the 95 CIBW carcasses reported during 2005–2017, 96% were reported during the April–October ice-free season (Figure 2), and 87% were reported in the Upper Inlet (Figure 1). All of the 12 identified dead whales died between May and October (Table 2), and all were found dead in the Upper Inlet (Table 3). All of the fresh carcasses were reported April–October, and all of the moderate decomposition carcasses were reported April through November. Carcasses reported in December and January were in a state of advanced decomposition or mummified (Figure 2).

3.1.6 | Previous sighting histories of dead individuals

The interval between when each of the 12 identified dead individuals was photographed alive and when it was reported dead ranged between 3 days and 4 years, with most (67%) reported dead within a year of when they were last photographed alive (Table 3). In comparison, an average of 50% of all identified whales in the catalog are photographed alive in any given year, although this varies annually depending on the survey effort, field conditions, and cumulative catalog size of any given year. All 12 of the dead identified individuals had been photographed in Knik Arm (Figure 1) when they were alive, and all but one had also been photographed alive in other photo-ID survey areas of the Upper Inlet. Two of the identified males had scars from satellite tags that had been attached to them by

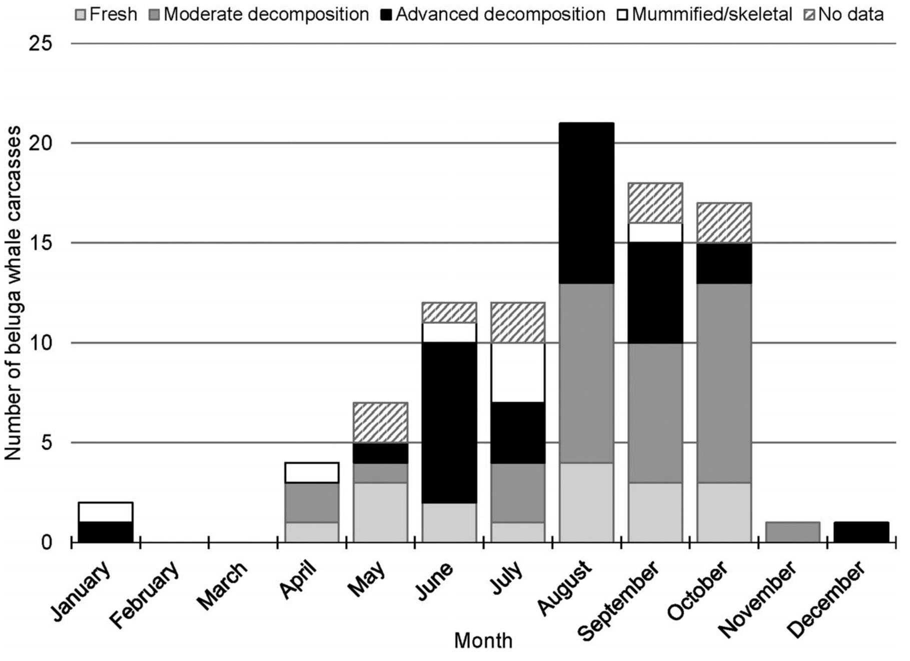

FIGURE 2 Number of beluga whale carcasses per month in Cook Inlet, Alaska, reported to the Alaska Marine Mammal Stranding Network during the period 2005–2017 (n = 95). Carcasses are recovered during months with ice (November–March) if they have come ashore or if they are in open-water leads. Ice-free months are April through October.

NMFS in 2002 (McGuire & Stephens, 2016; Shelden et al., 2018). Tag transmissions from these males in 2002 showed they moved extensively around the Upper Inlet (Shelden et al., 2018).

3.2 | Minimum mortality estimates

The percent of dead individuals reported annually relative to the annual population estimates from NMFS aerial surveys of free-swimming CIBWs varied between 0.8% and 4.7% from 2005 to 2017, with a mean reported annual mortality of 2.2% (SE = 0.36%; Table 1).

4 | DISCUSSION

Our analyses provide important information on mortality patterns and minimum rates that can be used in future population modeling efforts to better understand why the CIBW population continues to decline. Mortality appears to be equal between males and females, but our data shows some unexpected patterns in the ages of reported dead individuals. We found no distinctive spatial-use patterns of the photo-identified dead whales that would suggest that whales using particular areas of Cook Inlet are at an elevated risk of mortality. Below we discuss these findings in the context of existing knowledge about CIBWs and compare our results with patterns observed in other cetacean populations. We also suggest how future data collection on reported dead belugas could be improved to provide critical additional information that would aid CIBW conservation.

4.1 | Minimum mortality estimates

Our analysis suggests a minimum mean annual mortality estimate of 2.2% (*SE* = 0.36%) based on the ratio of reported dead CIBWs to aerial survey-based estimates of population size. This is a minimum estimate because reported dead CIBWs are a subset of the total number that died (Faerber & Baird, 2010; Williams et al., 2011). As Mosnier et al. (2015) caution for Canada's St. Lawrence Estuary (SLE) beluga population, the "number of reported deaths cannot be interpreted as a direct index of population mortality rates because they could also reflect variations in population size or in the probability that carcasses are found in a given year." Our minimum mortality estimate suggests that the population has an average annual survival rate less than 0.978, which is consistent with recent survival estimates and the nature of Cook Inlet. Jacobson et al. (2020) estimated adult/subadult survival for the CIBW population based in part on photo-ID data to be 0.93–0.94, and calf and juvenile survival to be somewhat less than that (but estimates were imprecise for calves and confounded with fecundity estimates). Most of Cook Inlet is considered remote, uninhabited wilderness, where beluga carcasses would not be detected. In addition, there is some evidence that floating carcasses may be swept out of Cook Inlet with the tides (Shelden et al., 2018; Table S1: Kodiak Is. stranding). While the vast majority of the dead belugas in this study were reported during the ice-free season and in the Upper Inlet (Table S1), belugas die year-round and throughout their range (Moore et al., 2000). Therefore, with strandings primarily reported for only half of the year and in only part of the CIBW range (mainly parts of Cook Inlet where human use is highest and carcasses are therefore most likely to be seen), we would expect the true number of dead CIBWs to be much higher than is reported annually.

Underreporting of cetacean mortality is common and not unique to Cook Inlet. For example, the rate of detection of cetacean carcasses has been estimated at only 0%–6% in the Gulf of Mexico (Williams et al., 2011), and 8% along the French coast based on known bycaught common dolphins (*Delphinus delphis)* that were set adrift in the Atlantic (Peltier et al., 2012), suggesting that true mortality for these populations could be on the order of 12–17 (or more) times the number of detected carcasses. In Canada's SLE, dead adult belugas were estimated to have only a 14.5%–27.2% probability of detection (Mosnier et al., 2015), indicating true mortality between four and seven times higher than the number of reported carcasses. Assuming true CIBW population survival is at most 0.93 (based on estimates of 0.93–0.94 adult/subadult survival and lower estimates for calves and juveniles from Jacobson et al. 2020), the mean number of reported CIBW carcasses represents less than one third of the total number of dead belugas each year.

4.2 | Demographic patterns in mortality

Almost all of the photo-identified dead belugas (*n* = 11 of 12) were reproductive-age adults of both sexes, and none were in the last 20 years of the species' expected lifespan (i.e., greater than 40 years old; Burns & Seaman, 1986; Vos et al., 2019). Due to the nature of the photo-ID catalog, which requires whales to acquire distinguishing marks over time before they can be identified as individuals, we would not expect to have a large sample of very young whales, but we would expect to see whales in the oldest age classes in the photo-ID sample and therefore among the identified dead. To ensure the patterns detected with respect to sex, age-class, sexual maturity, location, and COD were not merely artifacts of the small sample size of photo-identified carcasses, below we discuss these patterns and our assumptions about them in the broader context of the 95 dead individuals reported in 2005–2017.

4.2.1 | Adult mortality

If the CIBW population was robust, we would have expected the mortality patterns to be similar to other healthy mammal populations, with relatively higher mortality of the very old and the very young compared to other age

TABLE 3 Summary of photo-ID resighting histories of 12 dead identified Cook Inlet beluga whales in the 2005–2017 photo-ID catalog.

Photo-ID catalog number[a]	Year photographed 2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Interval live/dead[b]	Span of years photographed	# Days photographed	Photographed with a calf	Sex	Susitna River Delta[c]	Knik Arm	Turnagain Arm	Chickaloon Bay	Location of dead-stranded belugas (Figure 1)
D157	P	P	P	P	P									3 days	5	17	Y	F	P	P	0	0	Knik Arm
L1849		P	x	x	x	x	P	P	x					2 years	9	4	Y	F	P	P	0	0	SW of Susitna River Delta
R16	P	P	P											1 year	4	10	N	F	0	P	0	0	Knik Arm
R197	P	P	x											2 years	4	5	N	F	0	P	0	P	Knik Arm
L265	P	P	P	P	P	P	P	P	P	P				2 months	10	20	Y	F	P	P	P	P	Chickaloon Bay
L2634				P	x	P	x	P	P					1.5 months	6	6	Y	F	P	P	P	0	Turnagain Arm
D7244			P	P	P	P	x							2 years	6	11	N	M	P	P	0	0	SW of Susitna River Delta
D106	P	P	P	P	P	P	P	P	P					2.5 months	9	48	N	M	P	P	P	0	Turnagain Arm
D115*	P	P	P	P	P	P	P	P	P					10 months	10	74	N	M	P	P	P	P	Turnagain Arm
L2294	P	x	P	x	x	P	P	P	P	P				8 days	10	13	N	M	P	P	P	0	SW of Susitna River Delta
L496	P	x	x	x	x	P	x	x	x					4 years	10	6	N	M	P	P	P	0	Turnagain Arm
D2303[b]		P	P	P	P	P	P	P	P	P				10 months	10	39	N	M	P	P	P	0	SW of Susitna River Delta

Note. P = individual photographed; x = individual not photographed. Blank cells indicate an individual could not be sighted in a given year because it was not yet in the catalog, or because it had died in previous years. Shaded cells indicate year of death.
[a]The letter at the beginning of the catalog number indicates which photo-ID subcatalog: D = dual, L = left-side, R = right-side. Note, whales in the dual-catalog also appear in the right- and left-side catalogs; [b]Previously satellite-tagged [c]Interval between last day an individual was photographed alive and first day it was reported dead; [d]Little Susitna River to Beluga River.

classes. For example, mortality in killer whale (*Orcinus orca*) populations has been described as a U-shaped curve, in which mortality is high for calves under six months, relatively low for subadults and young adults, and high for older adults (NMFS, 2008). In addition, mortality rates for female killer whales of reproductive age are low, then increases sharply in old age, while mortality rates for adult males increase steadily with age (summarized in NMFS, 2008). In contrast, the sample of photo-identified dead CIBWs was composed of relatively young (10–15 years old) and middle-aged (15–40 years old) adults, but not older adults (>40 years old).

Our sample, consistent with Vos et al. (2019), suggests that adult CIBWs are dying (of as-yet unknown causes) at relatively younger but still reproductive ages, and few survive to reach the full extent of the potential lifespan of the species (i.e., 70+ years; Burns & Seaman, 1986; Stewart et al., 2006; Suydam, 2009). Taking the inverse of our estimated minimum mortality rates yields a mean age at death between 42 and 45 years old. Considering our estimates are minimal, mean age at death is likely younger. Survival estimates by Jacobson et al. (2020) would put mean age at death closer to 14–17 years old (i.e., 1/1-survival).

The calving histories of the oldest photo-identified females suggest that the oldest whales in our sample are still reproductively active. One female was estimated to be 39 years old at the time of its death in 2014 and was last photographed with an accompanying calf when it would have been 31 years old. Another photo-identified female was 37 years old and lactating at the time of its death and had been last photographed with a possible calf at age 34. Shelden et al. (2019) documented a pregnant CIBW female who was estimated to be 41 years old using the methods in Vos et al. (2019). Menopause in belugas is estimated to begin at around 35 years old (Ellis et al., 2018) and may occur over a broad span of individual ages (Burns & Seaman, 1986). The lack of any animals older than 40 years old in our photo-ID sample, and the lack of belugas older than 49 in previous analyses of stranded animals (Vos et al., 2019) suggests that the oldest members of the CIBW population are in their 40s and still of reproductive age. Future work should focus on understanding why adult mortality appears to be falling heavily on adults of reproductive age and if postreproductive adults are truly absent from this population.

4.2.2 | Calf mortality

Of the 95 stranded dead belugas reported to NMFS, 24% were identified as calves (defined as 180 cm or smaller and includes neonates and aborted fetuses). This proportion is not unexpected based on other marine mammals, such as killer whales (NMFS, 2008) and subarctic fur seals (Beauplet et al., 2005). In Canada's SLE beluga population, calf and adult female mortality relative to other age classes of SLE belugas sharply increased around 2008–2010 and has remained high (Lair et al., 2016; Lesage et al., 2014), with mortality from labor and postpartum complications attributed to endocrine disruption from environmental contaminants (Lair et al., 2016). No similar trends were discernible in reported CIBW deaths. Burek-Huntington et al. (2015) examined demographic trends in 38 CIBWs necropsied during the period 1998–2013 (some of which were also in our sample of 95) and found a peak in calf mortality in 2008 (of unknown cause), but not in the other years.

4.2.3 | Subadult mortality

The integrated population model developed by Jacobson et al. (2020) used to estimate the current and historical population dynamics of CIBWs found a combined subadult/adult survival rate that was lower than in other healthy cetacean populations, but the model was unable to differentiate subadults from adults, and therefore cannot determine if the higher-than-expected mortality was for adults, subadults, or both age-classes. Assignment of age-class and the rationale behind the assignment were not always clear in the stranding data and, as a result, we were unable to consistently separate subadult and adult mortality in our data set. In addition, an apparent under-reporting of dead subadults has been noted for SLE belugas (Lair et al., 2016) and is attributed to a lower probability of detection of younger dead belugas because of their reduced buoyancy, smaller size, and gray coloration (in contrast to the larger, fatter, whiter adults). It seems likely that small, gray belugas would be even harder to detect in the highly turbid waters and on the mudflats of Cook Inlet than in the relatively clear waters of the SLE. We would therefore expect an even more extreme detection and reporting bias for subadults in Cook Inlet, but the data do not currently allow us to estimate the degree of this bias.

4.3 | Cause of death

We examined the stranding data for COD capable of affecting adults of both sexes in their prime reproductive years. Because COD has not been assigned to all of the 95 belugas reported dead 2005–2017, we reviewed other data sets to help address this question. Burek-Huntington et al. (2015) assigned a single primary COD for 38 CIBWs necropsied between 1998 and 2013 as follows: unknown (29%), trauma (18%), perinatal mortality (13%), mass stranding (13%), single-animal stranding (11%), malnutrition (8%), and disease (8%), with other disease processes coded as contributory or incidental to COD. If single strandings and mass strandings are combined, then live-stranding was the COD for 33% of these necropsied whales with known COD (n = 27) and was the most-commonly known COD. Vos and Shelden (2005) examined the unusually high number (n = 20) of dead CIBWs in 2003 relative to deaths reported in the previous decade, and listed COD for this year as live strandings (25%), trauma marks possible from killer whale attack (5%), emaciation (5%), and the rest unknown (hunted belugas had been excluded from the sample). A number of possible causes have been proposed for both live and dead CIBW strandings, including avoidance of killer whales; disorientation or trauma caused by sound from seismic exploration, military detonations, ship strikes, or pile driving; changes in bathymetry; pathogens; contaminants; malnutrition due to reduction in quality, quantity, or availability of prey; and the cumulative effects of multiple stressors (Burek-Huntington et al., 2015; NMFS, 2016; Vos & Shelden, 2005). It is often not possible to discern if a live-stranding was the result of an unhealthy animal with other morbidity factors becoming weakened and stranding, or a live, healthy animal becoming stranded and dying as a result. However, if the carcass was relatively fresh and had signs consistent with a fatal live-stranding (such as silt deep in the airways and/or of sufficient quantity as to preclude respiration), and there was a lack of other findings consistent with disease or debilitation, then the examining veterinarians attributed the proximate COD to live-stranding. Live-strandings of CIBWs are relatively common, with such events reported nearly every year since records began in 1998 (NMFS, 2016; Vos & Shelden, 2005; Table S1). Reported live-stranding events involved anywhere from 1 to 184 individuals per event, with no indication of the incidence of live-stranding increasing over time.

Belugas in Canada's SLE have experienced high mortality, with demographic patterns and COD appearing to have changed in recent decades (Lair et al., 2016). Previously, gastrointestinal cancer attributed to environmental contamination was more prevalent, with no significant difference in occurrence between males and females (Lair et al., 2016). As noted above, endocrine disruption attributed to environmental contaminants was linked to an increase in calf and maternal mortality starting between 2008 and 2010 (Lair et al., 2016; Lesage et al., 2014). Despite similarities between the SLE and CIBW populations (e.g., endangered status, geographic isolation, proximity to urban areas, historic overharvest, and high mortality), we found no evidence to support similar patterns in COD between the two populations.

4.4 | Geographic patterns in mortality

We reviewed photo-ID resight movement records and locations of dead belugas for insight into COD. If individuals had exhibited strong site fidelity to areas in which they were also found dead, then this might point to localized environmental features or human activities in these areas that caused or contributed to stranding. Data from satellite-tagging (Shelden et al., 2018) and photo-ID (McGuire & Stephens, 2017) indicate individual CIBWs move extensively and often throughout their range and the photo-identified dead whales were no exception. The range of identified individuals was not limited to areas in which they stranded, making it challenging to associate stranding location with COD. It is far more probable that the geographic patterns of stranded animals primarily reflect locations where stranded whales were more likely to be detected, such as coastal areas bordered by the road system, recreational areas with coastal access for hiking, biking, or off-road vehicles, established flight paths, routes for vessel operations, and in-water platforms used for oil and gas extraction (Figure 1). Circulation patterns and bathymetry of some areas may also increase the likelihood of live-stranding, and/or of carcasses coming ashore. For example, in 37 live-stranding events reported between 1998 and 2016 (NMFS, 2016; Vos & Shelden, 2005), 62% were in Turnagain Arm, 27% were in Knik Arm, while only 5% were in the Susitna Delta, 3% in the Kenai River, and one (3%) was in an unknown location (NMFS, 2016). It may be the shallow waters, extensive mudflats, and strong currents of the upper arms of Cook Inlet result in more strandings (live and dead) in these locations. However, Turnagain Arm is also one of the few places in Cook Inlet with both road access and reliable cell-phone coverage, and it is therefore difficult to separate likelihood of strandings occurring here from the likelihood of strandings being detected and reported. It may also be important to separate the number of stranding events from the number of whales per event. For example, while only two live-stranding events have been documented in the Susitna Delta, they involved large numbers of whales (186 and 63), which combined, make the Susitna region second behind Turnagain Arm in terms of total numbers of belugas stranded.

4.5 | Trends in abundance and mortality

There is some recent evidence that the trend in population size may have changed during the 2005–2017 period we examined, with an increasing trend until around 2010 after which the population began declining once again (Wade et al., 2019). Despite this apparent population decline, mean mortality estimates from reported strandings did not increase during this time (mean reported minimum mortality was 2.6% for 2005–2010; and 2.0% for 2011–2017; Table 1). Unfortunately, our methods are not able to estimate the level of true mortality in the population or detailed interannual patterns, and more complex models are required. Analyses utilizing our photo-ID catalog and including carcasses of identified individuals are currently in development to provide estimates of reproduction and mortality based on Bayesian state-space mark-recapture models (Himes Boor & McGuire, 2020).

4.6 | Recommendations

Our recommendations to fill remaining data gaps around CIBW mortality largely echo those made previously by other investigators (Burek-Huntington et al., 2015; NMFS, 2016; U.S. Federal Register, 2008; Vos & Shelden, 2005), but we believe they are worth repeating and amplifying here given the failure of this species to recover despite legal protections and the cessation of hunting. In addition, the photo-ID data set offers a unique opportunity to gain additional insight into mortality patterns. Being able to consistently link mortality information from a carcass with information from the whale's life history could provide important clues to the population's failure to recover, thus making our recommendations particularly urgent given the continued decline of this population. In the previously mentioned integrated population model developed for the SLE beluga population, the carcass data were an essential data source for enabling Mosnier et al. (2015) to identify a mechanism for the population's declining abundance. Increasing the effort to detect CIBW carcasses and to appropriately photo-document their dorsal and lateral surfaces to enable linking carcasses to known individuals has the potential to provide important information on why the CIBW population continues to decline. Specifically, when necropsies are completed and/or tissue and teeth samples are collected, carcass data can yield ages of identified whales (contributing to a better understanding of the proportion of subadults in our sample), sex of individuals (contributing to data on the sex ratio in the population and in our sample), pregnancy rates (providing more information to compare to our fecundity estimates), and body condition and contaminant levels (contributing to our understanding of mortality causes).

We summarize our recommendations here and provide more details in Supplementary Information 2.

- Increase the levels of carcass detection, reporting, and response.
- Increase the amount of information obtained from dead belugas and live strandings.
- Decrease the uncertainty and variability of stranding information obtained during field examinations. (Demographic patterns in age-class and sex of stranded animals might have been obscured by high numbers of "unknowns" in the current database.)
- Increase the capacity of the stranding network to retrieve carcasses from the field and transfer them to a dedicated laboratory for full necropsy, removed from the challenging and often dangerous field conditions of Cook Inlet, as is done with the SLE belugas (Lair et al., 2016).
- Conduct a systematic health determination (i.e., signs of disease, trauma, malnutrition) for all identified whales in the photo-ID catalog, after first standardizing categories and methods with veterinarians and researchers who study other beluga populations, including in aquaria.
- Develop and maintain a single CIBW stranding database, with a single designated manager for quality control, and make this database accessible to relevant agencies (including Alaska Tribal agencies), stranding network members, researchers, and the public.
- Better integrate all data sets and modeling efforts.

4.7 | Summary

We found that CIBW mortality rates have been at least 2.2% per year since cessation of hunting and implementation of ESA protective measures and are likely many times higher. Mortality rates seemed to be especially high for adults of reproductive age, followed by calves. Very old adults were not in the stranding data set and all available evidence suggests individual CIBWs are living only into their 40s at most. Dead females and males were reported at the same rates. The predominant cause of mortality, when it can be assigned, was attributed to complications from live-stranding, but this only explains about one third of the examined deaths. It is unknown what is causing the majority of deaths, and it is unknown what is causing the live-strandings. A better understanding of how many CIBWs are dying annually, and why, may be the key to understanding the population's lack of recovery. Policy makers and managers would benefit from implementation of our seven data-collection recommendations, all of which are relatively easy to implement and will vastly increase our knowledge about mortality causes and patterns for this Critically Endangered population.

ACKNOWLEDGMENTS

This manuscript was developed through Species Recovery Grant NOAA-NMFS-PRPO-2017-2004972 to the Knik Tribe. The authors are grateful to the Knik Tribe for their foresight and perseverance in promoting the dissemination of results from this long-term photo-ID study, and to the reviewers of the manuscript for their input. The CIBW Photo-ID Project represents work conducted by numerous people and with the support of several organizations, all of whom are sincerely thanked for support of this project. Project Skippers: Henry Hershberger, Brad Goetz, Dave McKay, Gary Kernan, Geoffrey Hershberger, Bob Cellers, Page Herring, and Nathan McKay, Jr. Financial Support for Photo-ID Research: The National Fish and Wildlife Foundation; ConocoPhillips Alaska, Inc.; The North Pacific Research Board; The Alaska Department of Fish and Game; The Kenai Peninsula Borough; LGL Alaska Research Associates, Inc.; Chevron; The U.S. Fish and Wildlife Service; Joint Base Elmendorf Richardson; and the National Marine Fisheries Service, Alaska Region and Marine Mammal Laboratory. Research Coordination: NMFS Alaska

Region, NMFS Office of Protected Resources, NMFS Office of Law Enforcement (especially Les Cockreham and Noah Messenheimer), NMFS Marine Mammal Laboratory, the Alaska Marine Mammal Stranding Network (especially Barbara Mahoney and Mandy Migura); Department of Defense (JBER, Rich Graham, Christie Osburn, Kori Blakely, and observers), the Marine Mammal Commission, and the Group for Research and Education on Marine Mammals (GREMM). Photo-ID Database Development: Axiom Consulting and Design. A list of frequent contributors of incidental sightings and photographs, as well as a list of former project colleagues, can be found in McGuire and Stephens (2017), available at https://www.cookinletbelugas.com. Biological samples from stranding, tagging and biopsy were collected under NMFS permits #932-1905/MA-009526 (stranding), #957 and 782-1438 (Amendment 3; satellite tagging), #14245-04 (biopsy), and samples were analyzed by Nick Kellar (hormones from 2016 biopsy), Greg O-Corry Crowe (genetics from 1999–2002 satellite tagging), tooth aging (Dan Vos), and necropsy (Kathy Burek-Huntington and Carrie Goertz). We are grateful to the Alaska Native hunters who reported and shared samples with NMFS. Special thanks to Kate Savage for pulling together initial NMFS stranding records. CIBW photo-ID surveys were conducted under General Authorization, Letter of Confirmation No. 481-1759, and NMFS Scientific Research Permits #14210 and #18016. All CIBW Photo-ID Project reports are publicly available at https://www.cookinletbelugas.org. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce. Mention of trade names and commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

AUTHOR CONTRIBUTIONS

Tamara McGuire: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review and editing. **Kim Shelden:** Data curation; formal analysis; investigation; validation; writing-review and editing. **Gina Himes Boor:** Formal analysis; methodology; writing-original draft; writing-review and editing. **Amber Stephens:** Data curation; formal analysis; investigation; validation; writing-review and editing. **John McClung:** Data curation; formal analysis; investigation; software; visualization; writing-review and editing. **Christopher Garner:** Data curation; formal analysis; investigation; writing-review and editing. **Carrie Goertz:** Data curation; formal analysis; investigation; methodology; writing-review and editing. **Kathleen Burek-Huntington:** Data curation; formal analysis; funding acquisition; investigation; methodology; writing-review and editing. **Greg O-Corry-Crowe:** Data curation; formal analysis; investigation; methodology; writing-review and editing. **Bruce Wright:** Conceptualization; funding acquisition; project administration; writing-review and editing.

ORCID

Tamara L. McGuire https://orcid.org/0000-0003-4536-007X
Kim E. W. Shelden https://orcid.org/0000-0002-9831-0933
Gina K. Himes Boor https://orcid.org/0000-0003-3924-5198
John R. McClung https://orcid.org/0000-0003-3486-6710
Christopher Garner https://orcid.org/0000-0002-7487-0442
Caroline E. C. Goertz https://orcid.org/0000-0002-1282-5654
Kathleen A. Burek-Huntington https://orcid.org/0000-0002-6903-735X
Greg O'Corry-Crowe https://orcid.org/0000-0001-9077-1340
Bruce Wright https://orcid.org/0000-0003-3465-9316

REFERENCES

Beauplet, G., Barbraud, C., Chambellant, M., & Guinet, C. (2005). Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: Influence of pup sex, growth rate and oceanographic conditions. *Journal of Animal Ecology*, *74*, 1160–1172.

Burek-Huntington, K. A., Dushane, J. L., Goertz, C. E., Romero, C. H., & Raverty, S. A. (2015). Morbidity and mortality in stranded Cook Inlet beluga whales *Delphinapterus leucas*. *Diseases of Aquatic Organisms*, *114*, 45–60.

Burns, J. J., & Seaman, G. A. (1986). *Investigations of belukha whales in coastal waters of western and northern Alaska. II. Biology and ecology* (Final report U.S. Department of Commerce, NOAA, Outer Continental Shelf Assessment Program NA 81 RAC 00049). Alaska Department of Fish and Game, Fairbanks. (Available from the lead author).

Castellote, M., Small, R. J., Lammers, M. O., Jenniges, J., Mondragon, J., & Atkinson, S. (2016). Dual instrument passive acoustic monitoring of belugas in Cook Inlet, Alaska. *Journal of the Acoustical Society of America*, *139*, 2697–2707.

Castellote, M., Small, R. J., Lammers, M. O., Jenniges, J., Mondragon, J., Garner, C. D., Atkinson, S., Delevaux, J. M. S., Graham, R., & Westerholt, D. (2020). Seasonal distribution and foraging occurrence of Cook Inlet beluga whales based on passive acoustic monitoring. *Endangered Species Research*, *41*, 336–343. https://doi.org/10.3354/esr01023

Ellis, S., Franks, D. W., Nattrass, S., Currie, T. E., Cant, M. A., Giles, D., Balcomb, K. C., & Croft, D. P. (2018). Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Scientific Reports*, *8*, 12833.

Faerber, M. M., & Baird, R. W. (2010). Does the lack of observed beaked whale strandings in military exercise areas mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and main Hawaiian Islands. *Marine Mammal Science*, *26*, 602–613.

Fain, S. R., & LeMay, J. P. (1995). Does the lack of observed beaked whale strandings in military exercise areas mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and main Hawaiian Islands. *Proceedings of the American Academy Forensic Science*, *1*, 34.

Ferrero, R. C., Moore, S. E., & Hobbs, R. C. (2000). Development of beluga, *Delphinapterus leucas*, capture and satellite tagging protocol in Cook Inlet, *Alaska*. *Marine Fisheries Review*, *62*(3), 112–123. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr623/mfr62310.pdf

Goetz, K. T., Montgomery, R. A., Ver Hoef, J. M., Hobbs, R. C., & Johnson, D. S. (2012). Identifying essential summer habitat of the endangered beluga whale *Delphinapterus leucas* in Cook Inlet, Alaska. *Endangered Species Research*, *16*, 135–147.

Goetz, K. T., Rugh, D. J., Read, A. J., & Hobbs, R. C. (2007). Habitat use in a marine ecosystem: Beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Marine Ecology Progress Series*, *330*, 247–256.

Himes Boor, G. K., & McGuire, T. L. (2020). *Estimating Cook Inlet beluga whale* (Delphinapterus leucas) *reproductive rates from photo-ID data, 2005–2017*. (North Pacific Research Board Core Research Program Final Report). https://www.nprb.org/nprb/about-the-science/#publications

Hobbs, R. C., Laidre, K. L., Vos, D. J., Mahoney, B. A., & Eagleton, M. (2005). Movements and area use of belugas, *Delphinapterus leucas*, in a subarctic Alaskan estuary. *Arctic*, *58*, 331–340.

Hobbs, R. C., Rugh, D. J., & DeMaster, D. P. (2000). Abundance of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska, 1994–2000. *Marine Fisheries Review*, *62*, 37–45. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr623/mfr6235.pdf

Hobbs, R. C., Shelden, K. E. W., Rugh, D. J., Sims, C. L., & Waite, J. M. (2015a). Estimated abundance and trend in aerial counts of beluga whales, *Delphinapterus leucas*, in Cook Inlet, Alaska, 1994–2012. *Marine Fisheries Review*, *77*, 11–31.

Hobbs, R. C., Wade, P. R., & Shelden, K. E. W. (2015b). Viability of a small, geographically-isolated population of beluga whale, *Delphinapterus leucas*: Effects of hunting, predation, and mortality events in Cook Inlet, Alaska. *Marine Fisheries Review*, *77*(2), 59–88. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/mfr7724.pdf

Jacobson, E. K., Boyd, C., McGuire, T. L., Shelden, K. E. W., Himes Boor, G. K., & Punt, A. E. (2020). Assessing cetacean populations using integrated population models: An example with Cook Inlet beluga whales. *Ecological Applications*, *30*, e02114. https://doi.org/10.1002/EAP.2114

Laidre, K. L., Shelden, K. E. W., Rugh, D. J., & Mahoney, B. A. (2000). Beluga, *Delphinapterus leucas*, distribution and survey effort in the Gulf of Alaska. *Marine Fisheries Review*, *62*(3), 27–36. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr623/mfr6234.pdf

Lair, S., Measures, L. N., & Martineau, D. (2016). Pathologic findings and trends in mortality in the beluga (*Delphinapterus leucas*) population of the St. Lawrence Estuary, Quebec, Canada, from 1983 to 2012. *Veterinary Pathology*, *53*, 22–36.

Lesage, V., Measures, L., Mosnier, A., Lair, S., Michaud, R., & Béland, P. (2014). *Mortality patterns in St. Lawrence Estuary beluga* (Delphinapterus leucas), *inferred from the carcass recovery data, 1983–2012* (DFO Canadian Science Advisory Secretariat, Research Document 2013/118). http://www.dfo-mpo.gc.ca/csas-sccs/index-eng.htm

Lowry, L., Hobbs, R., & O'Corry-Crowe, G. (2019). *Delphinapterus leucas* (Cook Inlet subpopulation). The IUCN Red List of Threatened Species 2019: e.T61442A50384653. https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T61442A50384653.en

Mahoney, B. A. & Shelden, K. E. W. (2000). Harvest history of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska. *Marine Fisheries Review*, *62*(3), 124–133. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr623/mfr62311.pdf

McGuire, T., & Stephens, A. (2016). *Summary Report: Status of previously satellite-tagged Cook Inlet beluga whales* (Report prepared for National Marine Fisheries Service, Alaska Region). LGL Alaska Research Associates, Inc. https://www.cookinletbelugas.com/reports-and-publications

McGuire, T., & Stephens, A. (2017). *Photo-identification of beluga whales in Cook Inlet, Alaska: summary and synthesis of 2005–2015 data* (Report prepared for National Marine Fisheries Service, Alaska Region). LGL Alaska Research Associates, Inc. https://www.cookinletbelugas.com/reports-and-publications

McGuire, T. L., Himes Boor, G. K., McClung, J. R., Stephens, A. D., Garner, C., Shelden, K., & Wright, B. (2020). Distribution and habitat use by endangered Cook Inlet beluga whales: Patterns observed during a photo-identification study 2005–2017. *Aquatic Conservation: Marine and Freshwater Ecosystems*. Advance online publication. https://doi.org/10.1002/aqc.3378

McGuire, T., Michaud, R., Moisan, M., & Garner, C. (2017). *Cook Inlet beluga whale biopsy: Field report for 2016 feasibility study* (Report prepared for National Marine Fisheries Service, Marine Mammal Laboratory, Alaska Fisheries Science Center and Alaska Region, Protected Resources Division). LGL Alaska Research Associates, Inc. https://www.cookinletbelugas.com/reports-and-publications

McGuire, T. L., Stephens, A. D., McClung, J. R., Garner, C., Shelden, K. E. W., Himes Boor, G. K., & Wright, B. A. (2020). Reproductive natural history of endangered Cook Inlet beluga whales: Insights from a long-term photo-identification study. *Polar Biology*, 43(11), 1851–1871. https://doi.org/10.1007/s00300-020-02750-y

Moore, S. E., Shelden, K. E. W., Litzky, L. K., Mahoney, B. A., & Rugh, D. J. (2000). Beluga, *Delphinapterus leucas*, habitat associations in Cook Inlet, Alaska. *Marine Fisheries Review*, *62*(3), 60–80. http://aquaticcommons.org/9771/1/mfr6237.pdf

Mosnier, A., Doniol-Valcroze, T., Gosselin, J. F., Lesage, V., Measures, L. N., & Hammill, M. O. (2015). Insights into processes of population decline using an integrated population model: The case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). *Ecological Modelling*, *314*, 15–31.

National Marine Fisheries Service (NMFS). (2008). *Recovery plan for the southern resident killer whale* (Orcinus orca). National Marine Fisheries Service, Northwest Region. https://repository.library.noaa.gov/view/noaa/15975

National Marine Fisheries Service (NMFS). (2016). *Recovery plan for the Cook Inlet beluga whale* (Delphinapterus leucas). National Marine Fisheries Service, Alaska Region, Protected Resources Division. https://repository.library.noaa.gov/view/noaa/15979

O'Corry Crowe, G. M., Suydam, R. S., Rosenberg, A., Frost, K. J., & Dizon, A. E. (1997). Phylogeography, population structure and dispersal patterns of the beluga whale *Delphinapterus leucas* in the western Nearctic revealed by mitochondrial DNA. *Molecular Ecology*, *6*, 955–970.

Peltier, H., Dabin, W. Daniel, P. Van Canneyt, O. Doremus, G. Huon, M. & Ridoux, V. (2012). The significance of stranding data as indicators of cetacean populations at sea: Modelling the drift of cetacean carcasses. *Ecological Indicators 18*, 278–290.

Rouse, N., Burek-Huntington, K. A., & Shelden, K. E. W. (2017). Asphyxiation of an endangered Cook Inlet beluga whale, *Delphinapterus leucas*. *Marine Fisheries Review*, *79*(2), 38–43. https://doi.org/10.7755/MFR.79.2.3

Rugh, D. J., Shelden, K. E. W., & Hobbs, R. C. (2010). Range contraction in a beluga whale population. *Endangered Species Research*, *12*, 69–75. https://doi.org/10.3354/esr00293

Rugh, D. J., Shelden, K. E. W., & Mahoney, B. A. 2000. Distribution of belugas, *Delphinapterus leucas*, in Cook Inlet, Alaska, during June and July 1993–2000. *Marine Fisheries Review*, *62*(3), 6–21. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr623/mfr6232.pdf

Shelden, K. E. W., Burns, J. J., McGuire, T. L., Burek-Huntington, K. A., Vos, D. J., Goertz, C. E. C., O'Corry-Crowe, G., & Mahoney, B. A. (2019). Reproductive status of female beluga whales from the endangered Cook Inlet population. *Marine Mammal Science*, *36*, 690–699. https://doi.org/10.1111/mms.12648

Shelden, K. E. W., Goetz, K. T., Hobbs, R. C., Hoberecht, L. K., Laidre, K. L., Mahoney, B. A., Barbara, A., Norman, S. A., O'Corry-Crowe, G., Vos, D. J., Ylitalo, G. M., Mizroch, S. A.; Atkinson, S. K. C., Burek-Huntington, K. A., & Garner, C. (2018). *Beluga whale*, Delphinapterus leucas, *satellite-tagging and health assessments in Cook Inlet, Alaska, 1999 to 2002*. U.S. Department of Commerce. https://repository.library.noaa.gov/view/noaa/17856

Shelden, K. E. W., Goetz, K. T., Rugh, D. J., Calkins, D. G., Mahoney, B. A., & Hobbs, R. C. (2015). Spatio-temporal changes in beluga whale, *Delphinapterus leucas*, distribution: Results from aerial surveys (1977–2014), opportunistic sightings (1975–2014), and satellite tagging (1999-2003) in Cook Inlet, Alaska. *Marine Fisheries Review*, *77*(2), 1–31. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/mfr7721_0.pdf

Stewart, R. E. A., Campana, S. E., Jones, C. M., & Stewart, B. E. (2006). Bomb radiocarbon dating calibrates beluga (*Delphinapterus leucas*) age estimates. *Canadian Journal of Zoology*, *84*, 1840–1852.

Suydam, R. S. (2009). *Age, growth, reproduction, and movements of beluga whales* (Delphinapterus leucas) *from the eastern Chukchi Sea* (Ph.D. dissertation). University of Washington, Seattle, WA). http://www.north-slope.org/assets/images/uploads/suydam_dissertation2009.pdf

U.S. Federal Register. 2008. *Endangered and threatened species; endangered status for the Cook Inlet beluga whale*. FR 73: 62919–62930 (22 October 2008). National Marine Fisheries Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. https://federalregister.gov/a/E8-25100

Vos, D. J. & Shelden, K. E. W. (2005). Unusual mortality in the depleted Cook Inlet beluga (*Delphinapterus leucas*) population. *Northwestern Naturalist*, *86*, 59–65. https://doi.org/10.1898/1051-1733(2005)086[0059:UMITDC]2.0.CO;2

Vos, D. J., Shelden, K. E. W., Friday, N. A., and Mahoney, B. A. (2019). Age and growth analyses for the endangered belugas in Cook Inlet, Alaska. *Marine Mammal Science*, *36*, 293–304. https://doi.org/10.1111/mms.12630

Wade, P. R., Boyd, C., Shelden, K. E. W., & Sims, C. L. (2019). Group size estimates and revised abundance estimates and trend for the Cook Inlet beluga population. In K. E. W. Shelden & P. R. Wade (Eds.), *Aerial surveys, distribution, and trend of belugas* (Delphinapterus leucas) *in Cook Inlet, Alaska, June 2018* (AFSC Processed Report 2019–09). https://repository.library.noaa.gov/view/noaa/22918

Williams, R., Gero, S., Bejder, L., Calambokidis, J., Kraus, S.D., Lusseau, D., Read, A. J., & Robbins, J. (2011). Underestimating the damage: Interpreting cetacean carcass recoveries in the context of the Deepwater Horizon/BP incident. *Conservation Letters*, *4*, 228–233.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: McGuire TL, Shelden KEW, Himes Boor GK, et al. Patterns of mortality in endangered Cook Inlet beluga whales: Insights from pairing a long-term photo-identification study with stranding records. *Mar Mam Sci*. 2020;1–20. https://doi.org/10.1111/mms.12766