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NOTE

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Reproductive status of female beluga whales from the endangered Cook Inlet population

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The Cook Inlet population (hereafter CIB) of beluga whales (*Delphinapterus leucas*) is a discrete and genetically distinct stock (O'Corry-Crowe, Suydam, Rosenberg, Frost, & Dizon, 1997) that is geographically isolated from other beluga stocks in Alaska (Laidre, Shelden, Rugh, & Mahoney, 2000). The CIB population was classified as Critically Endangered on the IUCN Red List in 2006 (Lowry, O'Corry-Crowe, & Goodman, 2012) and was listed as Endangered under the U.S. Endangered Species Act (ESA) as a Distinct Population Segment in 2008 (NOAA, 2008). Population estimates since listing have ranged from 284 to 375 CIB (Hobbs, Shelden, Rugh, Sims, & Waite, 2015; Shelden et al., 2017), down from estimates of over 1,000 whales in the late 1970s and early 1990s (Shelden et al., 2015). This decline was attributed to unrestricted hunting by Alaska Natives in the 1990s (Mahoney and Shelden, 2000; Hobbs et al., 2015).

Following a moratorium on hunting in 1999, comanagement agreements between the National Marine Fisheries Service (NMFS) and two Alaska Native hunting cooperatives allowed takes of only one whale per cooperative per year. However, the population has not shown signs of recovery (Hobbs et al., 2015), and hunting was not permitted after 2006. The seasonal range of the population has steadily contracted from all of Cook Inlet to the point that it is now almost entirely limited to the northern (upper) part (i.e., north of East and West Foreland) during the summer and autumn (Rugh, Shelden, & Hobbs, 2010; Shelden et al., 2015). A lack of basic life-history information has hampered

attempts to determine causes for this population's continued decline (Hobbs, Wade, & Shelden, 2015). The primary objectives of this study are to determine reproductive status of CIB females by (1) examining ovaries and uteri collected from carcasses reported by subsistence hunters or the NMFS stranding network; (2) supplementing these findings by reviewing necropsy records of carcasses that were examined, but for which organs were not collected; and (3) comparing necropsy photographs to images of live whales in the Cook Inlet Beluga Whale Photo-ID Project's (http://www.cookinletbelugas.com) catalog for possible matches and additional information on calf production.

The extreme tides in Cook Inlet (~11 m), frequent high winds, and remote locations often make it difficult to conduct a thorough necropsy and obtain tissue samples. Morphological data recorded on the stranding form (example form available at https://www.fisheries.noaa.gov/national/marine-life-distress/national-stranding-database-public-access) included sex (male, female, unknown), estimated age class (adult, subadult, yearling, calf, unknown), total body length (straight length from rostrum to fluke notch), and weight. At the time of necropsy, age class was usually assigned based on total body length and skin color. At birth, beluga whales have dark gray skin that becomes lighter with increasing age, eventually becoming white. White skin color usually indicates the whale is a sexually mature adult. However, some light gray whales have been observed with calves, and some white whales have been found to be sexually immature after examination of reproductive tracts. Therefore, in addition to age class, we only included females from the necropsy data set that had a chronological age. Chronological age was obtained by examination of teeth following methods described in Vos (2003), and Vos, Shelden, Friday, and Mahoney (2019). Teeth were cut into thin sections that were viewed, wet or dry, on a dissecting microscope. Age is defined by the presence of one growth layer group (GLG) per year (Hohn, Lockyer, & Acquarone, 2016; Lockyer, Hohn, Hobbs, & Stewart, 2016; Matthews & Ferguson, 2014; Vos et al., 2019). Females of known-age were included in subsequent analyses only when the stranding form and/or necropsy report included a description of the reproductive tract, if ovaries/uteri were collected, if mammary glands were examined, or if carcass photographs matched to photo-ID records showing the live female with an associated calf.

The data set of known-age whales included 48 females (Figure 1, Table S1). Of these, reproductive status could not be determined for 16 whales that were too decomposed (n = 9), had stranded on their stomach (n = 2), were already partially submerged (n = 1), submerged part way through the necropsy by the incoming tide (n = 2), or hunters did not provide reproductive information (n = 2) (Table S1). For two whales, we were unable to make a definitive determination (Table 1). The remaining 30 whales were assigned to a reproductive status category (Table 1, Figure 2). Categories included sexually immature; resting (neither pregnant nor lactating; i.e., no fetus present, mammary glands examined, and ovulating if corpus luteum present), pregnant (fetus present), and lactating (engorged mammary and/or enlarged, distended uterus with no fetus).

Samples were collected between 1995 and 2016 and spanned the months from March to November (Table 1). Sexually immature females included two calves-of-the-year and likely a 2-year-old calf (reproductive tract not examined); it was not possible to determine reproductive status of a 10-year-old (Table 1, Figure 2). Sexually mature females ranged in age from 14 to 47 years old and were categorized as resting (neither pregnant nor lactating, n = 5; ovulating, n = 2), pregnant (n = 10), or lactating (n = 11) (Table 1, Figure 2). Most of the sexually mature females were in their 20s (n = 19, Table 1, Figure 2). Stranding teams were able to obtain ovaries from 23 whales (Table 2).

Reproductive tracts including ovaries were preserved in 10% buffered formalin. Ovarian analyses were primarily performed by JJB; some were also examined at other laboratories, mainly at the University of Illinois, Laboratory of Veterinary Diagnostic Medicine. Procedures used during reexamination of these samples and subsequent samples provided to the analyst (JJB) are reported in Burns and Seaman (1986). Females were classified as sexually immature or mature based on examination of ovaries and presence of corpora lutea (CLs) or corpora albicantia (CAs). A CL forms in the ovary during ovulation at the site where the follicle ruptured and released the ovum, and is sometimes visible as a prominent reddish-yellow bulge. If the egg is not fertilized, a CL will become inactive (usually within a week or two) and will rapidly degenerate becoming a much smaller nonluteinized body referred to as CA (white body). Fully developed CLs are prominent endocrine features evident in ovaries of pregnant beluga whales from the time of conception to either loss of a fetus (either by resorption or abortion) or until shortly after giving birth, after

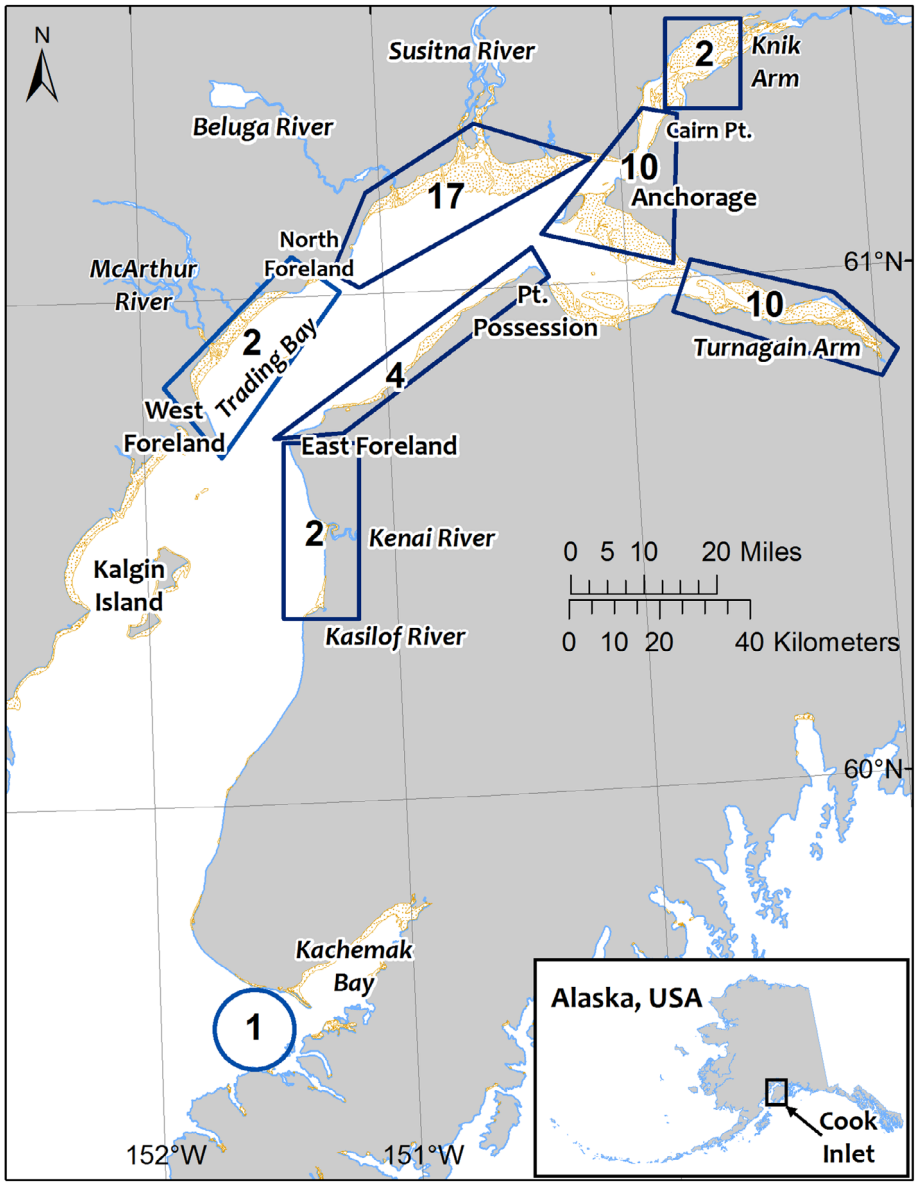

FIGURE 1 Areas in Cook Inlet, Alaska, where a total of 48 female beluga whales (number of carcasses shown within each region boundary) were examined over the period 1995–2016. Note: descriptive locations were often provided rather than latitude/longitude (see Table S1 for dates, regions, and morphological data).

which they rapidly regress to CAs (Slijper, 1966). Dominance was assigned to an ovary based on corpora counts when both ovaries were collected and examined (Table 2).

The youngest (at 14 years old) and the oldest (at 41) sexually mature females were pregnant (Table 2). The only immature whales (i.e., those lacking any CAs or CLs in both ovaries) were calves-of-the-year (Table 2). Only two females were between the ages of a calf-of-the-year and 14 years old, but ovaries were not obtained from either whale (Table 1). Dominance was almost evenly split between right and left ovaries of a pair (n = 13 pairs), with one instance of a lactating 29-year-old with one ovary only slightly heavier but with one fewer CA (43.2 g, 6 CAs) than the other (42.2 g, 7 CAs) (Table 2). Left-ovary dominance has been reported in other cetacean species (Steinmen,

TABLE 1 Reproductive status of known-age female beluga whales necropsied between 1995 and 2016 in Cook Inlet, Alaska. Reproductive status categories = sexually immature, resting (neither pregnant nor lactating, ovulating if corpus luteum (CL) present), pregnant (fetus present), and lactating (mammary examined and/or enlarged, distended uterus with no fetus). In the column "Ovaries collected": (a) = at least one ovary was collected/examined, (b) = all samples were not available to lead investigator (JJB) for examination but necropsy or laboratory notes were consulted, (c) = not weighed, and (d) = necropsy photographs matched to Cook Inlet Beluga Whale Photo-ID Project database. N/R = not reported on stranding form or other records. ? = could not make a definitive determination.

Whale ID	Month	Age (year)	Length (cm)	Reproductive status	Necropsy observations	Ovaries collected
67	March	23	365	Pregnant	130 cm female fetus	Both (a,b)
9	April	2	240	Immature?	Uterine tract not collected	None
122	April	38	364	Resting	2 CLs, no fetus, not lactating	Both (a,b)
36	April	22	320	Pregnant	126 cm female fetus	Right (a)
39	May	26	~320	Lactating	Uterine tract collected (b)	N/R (b)
111	May	41	386	Pregnant	150 cm male fetus	Both (a)
105	June	16	305	Pregnant	140 cm female fetus	None
41	June	20	350	Lactating	No CL present	Both (a)
20	June	23	367	Pregnant	3.8 cm fetus	Both (a)
13	June	28	368	Pregnant	142.4 cm female fetus	Left (a)
68	June	47	419	Lactating	Uterus distended, no fetus	None
57	July	16	345	Lactating	CL present, no fetus	Both (a)
22	July	22	356	Resting	Large CL, no fetus, not lactating	Both (a)
23	July	29	359	Lactating	No CL present	Both (a)
101	July	32	391	Pregnant	92 cm male fetus	None
102	August	10	318	Immature?	Small, thick-walled uterus	None
79	August	20	~365	Pregnant	23 cm fetus	Both (a)
28	August	22	377	Lactating	Regressing CL present	Both (a)
103	August	37	391	Lactating	Flaccid, thin-walled uterus	One (a,d)
119	September	<1	180	Immature	Calf-of-the-year	Both (a)
75	September	22	372	Resting	No CL present	Both (a,c)
55	September	23	375	Lactating	No CL present	Both (a)
56	September	22	364	Lactating	No internal exam	None
84	September	26	353	Resting	No CL present	Both (a,b,c)
113	September	39	419	Resting	Uterus examined	None (d)
61	October	<1	166	Immature	Calf-of-the-year	Both (a)
107	October	14	305	Pregnant	55 cm female fetus	Both (b,d)
62	October	21	396	Resting	No CL present	Left (a,c)
97	October	27	363	Lactating	CL present, no fetus	Both (b,c)
92	October	29	370	Pregnant	61.4 cm fetus	Both (a)
66	October	29	372	Lactating	No internal exam	None
81	November	23	369	Resting	No CL present	Both (a,c)

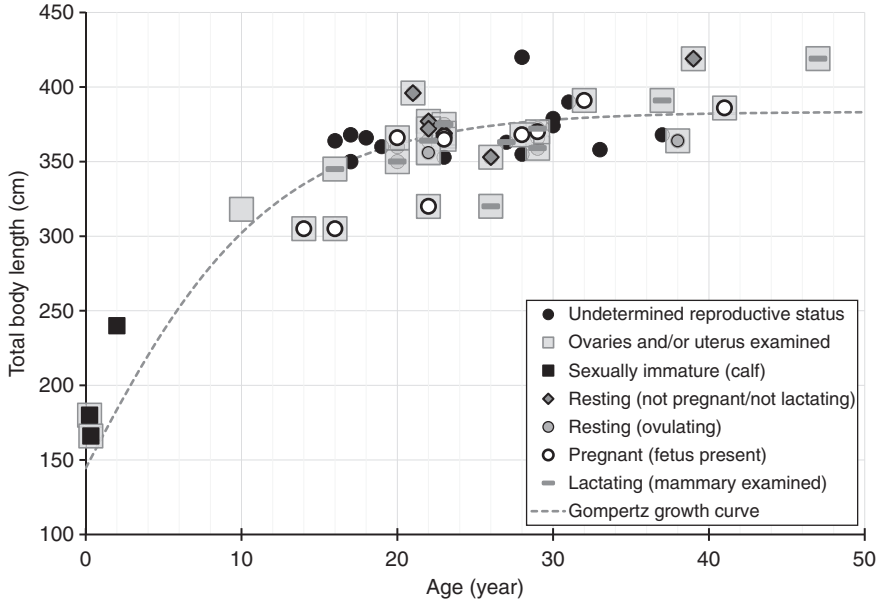

FIGURE 2 Age, total body length (straight length from rostrum to fluke notch), and reproductive status of 48 female beluga whales from Cook Inlet, Alaska. Note: lengths for four females were estimated (Table S1). Growth curve (dashed line) is described in detail in Vos et al. (2019).

O'Brien, Monfort, & Robeck, 2012), whereas captive beluga whale females, as well as those from other wild populations showed a similar pattern of equal distribution of CAs (Robeck et al., 2010) and CLs (Brodie, 1971; Kleinenberg, Yabokov, Bel'kovich & Tarasevich, 1964) in both ovaries. Ovarian structures counted and measured included CLs and CAs (Table 2).

The number of CAs in paired ovaries from beluga whales, especially from older whales, was not a good estimator of the number of past ovulations or pregnancies (see Brodie, 1971; Burns & Seaman, 1986). Two unusual examples were evident in our findings. The first example is that of a newly pregnant 23-year-old (ID 20 in Table 2) supporting a 3.8 cm fetus. Ovaries of this whale showed several unusual features. First was that both ovaries were very large, weighing 74.9 g and 64.7 g. The second was that each ovary contained a very large, fully formed CL and much smaller luteinized accessory CL (Figure S1). This seemed unusual, given when accessory CLs do occur, they form in the ovary of pregnancy (Stewart & Stewart, 2014). Those four structures would have eventually become or resembled a CA. The third was the combined presence of eight CAs, which together with the CLs, far exceeds the possible number of pregnancies for a 23-year-old beluga whale. The second example is that of a lactating 22-year-old (ID 22 in Table 2). The right ovary was 45.6 g and contained no CAs. All of the activity had been in the left ovary, which weighed 71.6 g. Of note was the formation of two CAs apparently developing at two nodes or loci within what was a single CL (Figure S2).

In a detailed study of CAs in *Delphinus delphis*, the persistence of CAs was attributed to incorporation of elastoid material, and smaller (older) CAs had a higher proportion of elastin (Takahashi et al., 2006). Earlier, Collet and Harrison (1981) had noted numbers of CAs in *Delphinus* ovaries that greatly exceeded the probable number of actual pregnancies. They theorized that during attainment of sexual maturity, successive estrous cycles (ovulations) that do not result in pregnancy can produce CAs. The situation was more complicated for CIB, although there were instances of more than one CL per pregnancy and regression of a single CL into what appeared to be multiple CAs, it seems that CAs become so small they are not recognized, or that resorption or disintegration is occurring (e.g., Dabin, Cossais, Pierce, & Ridoux, 2008). For example, a 23-year-old CIB female had more corpora scars than a 41-year-old (Table 2).

TABLE 2 Ovary weights (in grams) and number of corpora lutea (CLs) and corpora albicantia (CAs) found in each ovary for Cook Inlet beluga whales (1995–2016). If ovary position (left, right) was not documented, ovaries were labeled 1 and 2. N/C = ovary not collected, N/R = information not reported, ? = too decomposed to make definitive assessment. Status = SI (sexually immature), R (resting), P (pregnant), L (lactating).

	Whale ID																						
	107	57	41	79	62	22	28	36	75	20	55	67	81	84	97	13	23	92	103	111	122	119	61
Age (year)	14	16	20	20	21	22	22	22	22	23	23	23	23	26	27	28	29	29	37	41	38	<1	<1
Body length (cm)	305	345	350	~366	396	356	377	320	372	367	375	365	369	353	363	368	359	370	391	386	364	180	166
Status	P	L	L	P	R	R	L	P	R	P	L	P	R	R	L	P	L	P	L	P	R	SI	SI
Ovary Wt. (left)	N/R	61.6	a	41.0	N/R	71.6	45.1	N/C	N/R	74.9	a	N/R	46.5	N/R	N/R	98.7	42.2	43.0	a	30.6		a	a
#CL (left)	b	1		0	0	1e	1e		0	2		1e	0d	?d	1c	1	0	0		0	2c		
#CA (left)	b	2		2	?	5	5		1	5		2	3d	?d	c	3	7	1		4			
Ovary Wt. (right)	N/R	29.8	a	73.1	N/C	45.6	40.7	75.4	N/R	64.7	a	N/R	N/R	N/R	N/R	N/C	43.2	100.2	a	82.2		a	a
#CL (right)	1c	0		1		0	0	1	0	1		0	0	d	b		0	1		1			
#CA (right)	1c	0		4		0	3	1	2	4		0	0	d	b		6	3		3			
Ovary Wt. (1)			28.0								38.3								59.2			2.1	1.5
#CL			0								0								1			0	0
#CA			3								1								0			0	0
Ovary Wt. (2)			38.7								60.6											1.7	2.0
#CL			0								0											0	0
#CA			3								3											0	0
Dominant ovary	Right	Left		Right		Left	Left		Right	Left		Left	Left		Left		L=R	Right		Right	Left		

a = ovaries were collected but not identified as from the left or right side, see rows Ovary Wt (1) or (2).

b = gross morphology was smooth/oval (ovary not yet sectioned).

c = structure identified during necropsy (ovary not yet sectioned).

d = analyses conducted by University of Illinois, sample examined by JJB included only one ovary and ID 81 & 84 were mislabeled, left ovary of ID 84 was too decomposed to evaluate, right ovary was completely effaced by parasitic granulomas, uterus was normal.

e = University of Illinois laboratory report differed from JJB reexamination of available tissues (large, regressing CL identified as CA, dimensions suggest regressing CL).

Ten females in the sample were alive when a photo-identification project began in 2005. Of these, three were matched from their necropsy photographs to photographs in the catalog (Table 1; McGuire & Stephens, 2017). One pregnant 14-year-old whale had been photographed with an associated smaller, grayer beluga (possibly an older calf) when about 10 years old (in 2005). It could not be determined if this was her calf or simply a nearby juvenile that was not her offspring. The next two years she was photographed without a calf. In 2008, at 13 years old, she was photographed with a small calf that was presumed to be hers. Another female was 39 years old at the time of her death in September 2014. There were no obvious signs of lactation, and she was not pregnant, the bowel had herniated through the abdominal cavity, and the ovaries were not found. She had been photographed with a calf at 31 years old (in 2006), without a calf at 36 (in 2011), and again without a calf at 37 years old (in 2012), but was not photographed during any other years before her death (Table 1). The third female, 37 years old at the time of her death in August 2008, was lactating and the uterus was described as large, flaccid, and thin-walled (Table 1). This whale, at 34 years old, was photographed in 2005 with what appeared to be a calf.

The photo-ID data indicate 13 is the youngest age of confirmed reproduction, with some suggestion that it may be a few years younger if the calf associated with this individual when 10 years old was hers. We could not confirm age of first reproduction based on the current necropsy data set, which does not include any known-age females between the ages 2 and 10, nor ovaries from the 2- and 10-year-old whales in the sample. Age 13 aligns with age of first birth of 8–13 years old (based on GLG totals) in other wild beluga populations (Brodie, 1971; Burns & Seaman, 1986; Heide-Jørgensen & Teilmann, 1994; Suydam, 2009) as well as captive whales (Robeck et al., 2005).

Reproductive senescence was not evident in our current sample. The pregnant 41-year-old whale was alive when she stranded with her full-term fetus in late May, alongside an adult male beluga (previously satellite-tagged; McGuire & Stephen, 2016; Shelden et al., 2018). The cause of their subsequent deaths was attributed to stranding in a shallow area and not illness or injury. Another older individual appeared to have recently given birth (at 37 years old: lactating and enlarged uterus) and had been observed with a calf 3 years earlier. A 47-year-old female may have recently given birth as well. On necropsy, the uterus was considerably distended, measuring 50 × 45 cm (KAB-H, personal observation). Beluga whales may live to >60 years (Brodie, 1969; Burns & Seaman, 1986; Khuzin, 1961); therefore, our samples may be "too young" to detect age-related cessation or decline in ovulation rate in the CIB population. Ellis et al. (2018) estimated a significant post-reproductive lifespan for beluga whales that appears to begin about age 35. Their analysis was based on samples collected from beluga whales of the eastern Chukchi Sea (Suydam, 2009) and eastern Beaufort Sea (Harwood, Kingsley, & Pokiak, 2015) populations, and northwest Alaska (Burns & Seaman, 1986). Pregnancy rates showed signs of decline after age 40 in the eastern Chukchi Sea sample and around 46 in the northwest Alaska sample. It is notable, however, that the oldest female in the northwest Alaska sample, at age 70, was carrying a near-term fetus (Burns & Seaman, 1986).

From our limited data, corpora counts between paired ovaries do not indicate left-ovary dominance as observed in some other cetacean species (with the exception of ID 22 in Table 2). Reproductive tracts from younger (<14 years old), possibly reproductively mature females, are not present in the current data set and will be necessary to determine age of first ovulation and conception. Currently, photo-identification data suggest age of first reproduction around 13 years old. Priority should be given to collecting entire reproductive tracts and teeth during future necropsies, particularly from animals that are in good condition, and especially for younger whales as these are also necessary to refine growth curve estimates (Vos et al., 2019).

Because sampling occurred over a 20-year interval, determining if changes have occurred in reproductive health of the CIB population may not be possible. Often the condition of the carcass (e.g., advanced decomposition) compromised any attempt to determine cause of death (Burek-Huntington et al., 2015). Beluga whales in Cook Inlet are exposed to a number of potential natural and anthropogenic causes of death (Norman et al., 2015). Our assessment of female reproductive status indicates hunted and stranded carcasses are coming from a reproductively mature population that is calving between the ages of 14 and 41, and possibly at younger and older ages. Additional analyses of this data set examining breeding and calving seasonality (Shelden et al., in press), will provide information necessary for policy makers and managers tasked with the protection and recovery of this Critically Endangered population.

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SUPPORTING INFORMATION

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

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