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NOTE

Marine Mammal Science

Breeding and calving seasonality in the endangered Cook Inlet beluga whale population: Application of captive fetal growth curves to fetuses and newborns in the wild

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The Cook Inlet population of beluga whales (hereafter CIB) (*Delphinapterus leucas* Pallas 1776) was classified as Critically Endangered on the IUCN Red List in 2006 (Lowry, O'Corry-Crowe, & Goodman, 2012) and listed as Endangered under the U.S. Endangered Species Act as a Distinct Population Segment in 2008 (NOAA, 2008). CIB are managed as a discrete and genetically distinct stock (O'Corry-Crowe, Suydam, Rosenberg, Frost, & Dizon, 1997) that is isolated from other beluga stocks in Alaska (Laidre, Shelden, Rugh, & Mahoney, 2000). This population was estimated to number in the thousands in the late 1970s and early 1990s (Shelden et al., 2015), but after a period of unrestricted hunting by Alaska Natives in the 1990s (Mahoney & Shelden, 2000), abundance estimates remained under 400 with no sign of recovery (Hobbs, Shelden, Rugh, Sims, & Waite, 2015). The CIB summer range has steadily contracted to northern (upper) Cook Inlet (i.e., north of East and West Foreland) (Rugh, Shelden, & Hobbs, 2010; Shelden et al., 2015) despite a co-managed hunt since 1999 and no hunt permitted after 2006.

A lack of basic life-history information has hampered attempts to determine causes for this population's continued lack of recovery (Hobbs, Wade, & Shelden, 2015). Beluga whale carcasses reported to the Alaska stranding network provided morphometric data to construct sex-specific growth curves for CIBs (Vos, Shelden, Friday, & Mahoney, 2019) and data on reproductive status of mature females (Shelden et al., 2019). Necropsies occurred when logistics allowed access to remote sites, as the extreme tides in Cook Inlet (~11 m) often make it difficult to obtain tissue samples. This paper presents results from the youngest portion of this population, deceased fetuses and

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calves-of-the-year (Tables S1 and S2), to provide insights into breeding and calving seasonality for this endangered population.

Fetuses were collected from 10 deceased CIB females (Table 1, Figure 1). During the necropsy examination, another seven deceased adult females were found to be lactating (postpartum) or resting (not pregnant, a few ovulating) (Shelden et al., 2019). Four neonates (with fetal folds still present) and 14 calves-of-the-year were also examined (Table 1, Figure 1). Calves were assumed to have been born within the year they stranded based on length (<~180 cm straight length [SL] from rostrum to fluke notch, e.g., Hill, 2009), and, when possible, by examining any teeth in the mandible for the presence of prenatal lines or growth layer groups (Vos et al., 2019; also see Table S1 for examples of older calves). Per Robeck, Schmitt, and Osborn (2015), a fetus was classified as early stage (0–156 days in utero) if smaller than 50 cm in length from rostrum to fluke notch, mid-stage (157–313 days in utero) from 50 cm to 70 cm, and late-stage when >70 cm (314–470 days in utero). Of the 10 females with a fetus (Table 1), two had early stage fetuses, two had mid-stage, and six had fetuses that were approaching near-term (all >90 cm in length).

Fetuses were found in CIB females that died between late March and mid-October (Table 1). Stranded neonates occurred in mid-late July and early August (one of which was stillborn with uninflated lungs, another with meconium in the airway). Live neonates have been photographed in Cook Inlet as early as mid-July and as late as October (McGuire & Stephens, 2017; McGuire et al.[1]), during a field season that generally runs May through October. McGuire et al. (see Endnote 1) described live CIB neonates as (1) extremely small size relative to the associated adult, (2) wrinkled in appearance (i.e., prominent fetal folds), and (3) uncoordinated swimmers with erratic surfacing patterns. Within 1–3 weeks after observing prominent fetal folds, they noted folds were visible but diminishing. By 2 months old, fetal folds were not observed on most neonates, but were still faintly visible on some. Similar patterns were also observed in Russia's White Sea population (Krasnova et al., 2006), although after two months, fetal folds were no longer visible. Stranded calves-of-the-year (lacking prominent fetal folds, e.g., Figure S1) occurred from late June to mid-October (Table 1).

Deceased lactating CIB females occurred in late June, mid-July, mid-August, and late September (Table 1, see also Shelden et al., 2019). Two females appeared to have ovulated prior to dying. One in early April, the left ovary was slightly larger than the right and had two 10 mm (diameter) corpora lutea (CLs), and although not lactating, the mammary gland was developed. The other was in mid-July with a regressing CL on the ovary, no fetus present, and not lactating (Table 1; see also Shelden et al., 2019). For captive beluga whales (most from eastern Canadian populations), ovulations were observed from January through August, peaking from March to May, with conceptions from February through June (Robeck et al., 2005). On average, gestation period in captive beluga whales was 15.5 months (Robeck et al., 2015).

Assuming a 15.5 month gestation period, and using lengths obtained for CIB fetuses, neonates, and calves (Figure 2), data suggest calving in Cook Inlet occurs through the summer into late autumn (e.g., if the 92 cm fetus in early July is not an anomaly). CIB hunters reported calving in Cook Inlet from April through August (Huntington, 2000). Small, dark CIB were observed during aerial surveys in late May and early June (Hobbs, Sims, Shelden, VateBrattström, & Rugh, 2015), but it could not be established that these were neonates. The samples examined in this paper and a number of field studies of free-swimming CIBs, however, have not documented neonates before July (see Shelden et al., 2015 [appendices 1 and 2, pp. 10, 25–26, 32] and McGuire et al. [see Endnote 1]). To determine if fetal, neonatal, and calf length data could be used to further define seasonality of reproductive events in CIB, we applied the fetal growth formula developed for captive beluga whales (Robeck et al., 2015) to the length and girth data from CIB fetuses, neonates, and calves in the wild.

The fetal growth curves were developed from serial fetal growth measurements (total length [TL], biparietal diameter [BPD], thoracic circumference [TC] and diameter [TD]) as determined from transabdominal ultrasonography in pregnant beluga whales to predict both the day of conception and the day of parturition (Robeck et al., 2015). For CIBs, we applied the formula for TL to the 26 whales shown in Figure 2. Results of this analysis (Table S2), indicated that for the CIB sample, 58% (n = 15 of 26) of the predicted conception dates for TL and 88% (n = 23) of the

TABLE 1 Deceased Cook Inlet beluga whale neonates, calves-of-the-year, and adult females who were pregnant, lactating (postpartum), or resting (ovulating) examined between 1995 and 2017. Month-day = date stranded carcass was observed and reported to the Alaska stranding network (see Table S1). * = not included in growth analysis (length not given or suspect due to birth defects). CL = corpus luteum on ovary. ND = no data. SLC = SeaLife Center.

Month-day	Age (year)	Length (cm)	Status	Necropsy observations
March 31	23	365	Pregnant	130 cm female fetus
April 2	38	364	Resting	2 CLs, no fetus, developed mammary gland, not lactating
April 22	22	320	Pregnant	126 cm female fetus
May 27	41	386	Pregnant	150 cm male fetus
June 5	28	368	Pregnant	142.4 cm female fetus
June 11	16	305	Pregnant	~140 cm female fetus
June 18	23	367	Pregnant	2.5 cm fetus[a]
June 28	47	419	Lactating	Large, flaccid uterus (postpartum), no fetus, ND on mammary
July 4	32	391	Pregnant	92 cm male fetus
July 8		168	Calf	Skull not yet fused
July 14		*	Neonate	Congenital defect (caudal aplasia)
July 15	22	356	Resting	Regressing CL, no fetus, not lactating
July 20		136	Neonate	Female, meconium in airway
July 21	16	345	Lactating	CL present
July 23		128	Neonate	Male, prominent fetal folds
July 30		148.5	Calf	Possible scoliosis (male), age from tooth = 0
Aug. 4	20	~366	Pregnant	22 cm fetus[a]
Aug. 5		165	Calf	Advanced decomposition, no teeth erupted
Aug. 7		136	Neonate	Female, stillborn, uninflated lungs
Aug. 7		160	Calf	Male, umbilicus partially healed
Aug. 8	37	391	Lactating	Flaccid, thin-walled uterus
Aug. 11		172	Calf	Male, moderate decomposition
Aug. 17		162	Calf	Male, advanced decomposition
Aug. 22		*	Calf	Photos only (Figure S1), no necropsy
Sept. 11		135	Calf[b]	Female, mummified
Sept. 17		180	Calf	Female, fresh dead
Sept. 18		150	Calf	Female, advanced decomposition
Sept. 23		168	Calf	Male, advanced decomposition
Sept. 25	23	375	Lactating	No CL present
Sept. 28		137	Calf[b]	Mummified, age from tooth = 0
Sept. 30		162	Calf	Alive (male), transported to SLC
Oct. 7	14	305	Pregnant	55 cm female fetus
Oct. 12		166	Calf	Female, fresh dead
Oct. 15	27	363	Lactating	CL present
Oct. 11	29	370	Pregnant	61.4 cm fetus

[a]Total body length on stranding report was longer (3.8 cm and 23 cm) than laboratory measurement (2.5 cm and 22 cm) for these fetuses.
[b]Identified as a calf, too decomposed to determine if fetal folds were present.

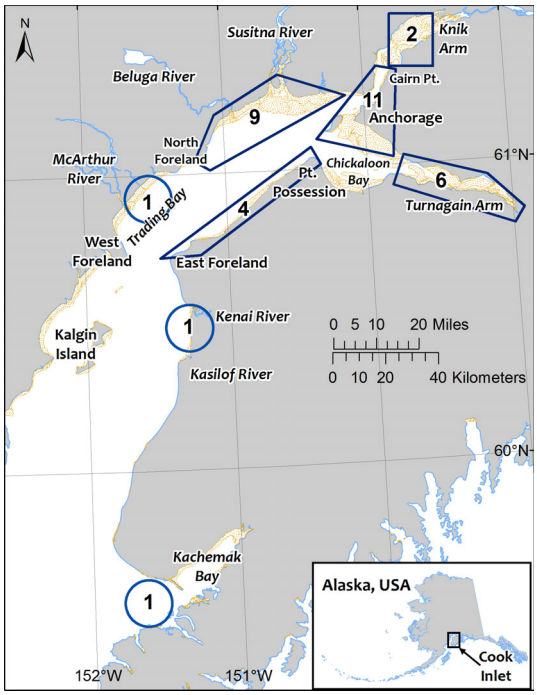

FIGURE 1 Areas in Cook Inlet, Alaska, where a total of 17 mature beluga whale females (pregnant, lactating, or resting), 4 neonates, and 14 calves-of-the-year (number of carcasses shown within each region boundary) were collected or examined over the period 1995–2018. Note: descriptive locations were often provided rather than latitude/longitude (see Table S1 for dates, regions, and morphological data).

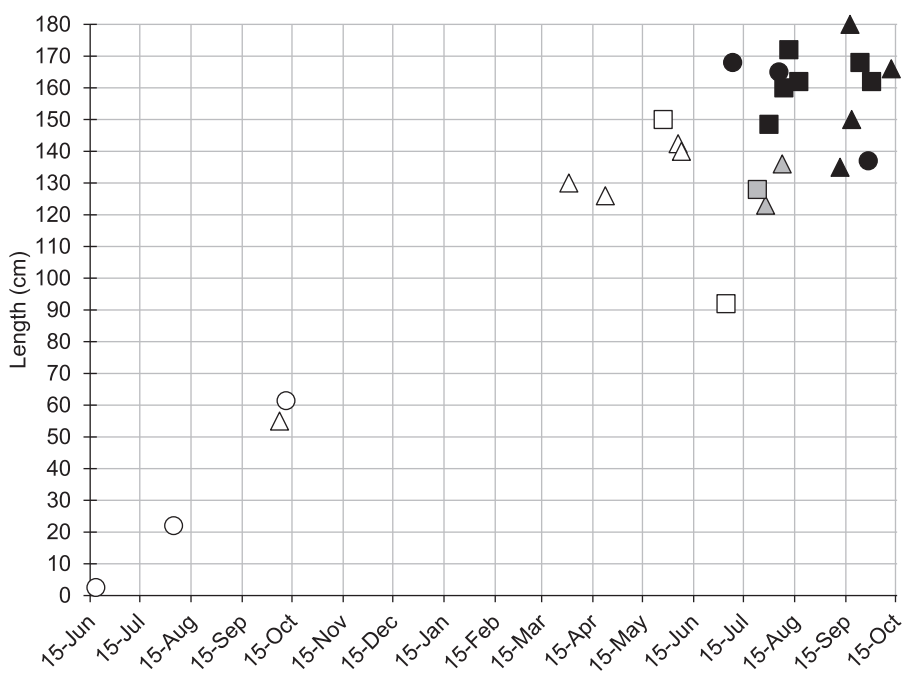

FIGURE 2 Length (straight length in centimeters) and date of collection of beluga whale fetuses (white symbols, n = 10), neonates (gray symbols, n = 3), and calves-of-the-year (black symbols, n = 13) from Cook Inlet, Alaska. Males = squares, females = triangles, unknown sex = circles.

predicted range of conception dates (based on Robeck et al. (2015) estimates of accuracy) fell within the period of March–May (Figure 3a, Table S2). Axillary girth measurements were obtained from 16 of the 26 whales. Applying the formula for TC, 69% (n = 11) of the conception dates (94% (n = 15) when including predicted variation) were

within the March–May time period (Figure 3b). These rates are comparable to those observed from captive beluga whales whereby 70% of ovulations and 80% of conceptions occurred from March through May.

The analysis of these data is the first application of fetal growth curves developed from captive animals for the estimation of reproductive parameters in wild beluga whales. The results indicate that similar to captive beluga whales, CIB experience a seasonal trend of peak reproductive activity from March through May. This would support the visual observations of possible CIB mating activity recorded on two occasions; once in late April and the other in early May (Lomac-MacNair, Smultea, Cotter, Thissen, & Parker, 2015). While the majority of predicted CIB conceptions occurred during this period, as has been observed for captive animals, females exhibit a wide period of up to seven months during which conception can occur (Robeck et al., 2005; e.g., the CIB female in mid-July with a regressing CL).

Despite these similarities with the reproductive patterns observed in captive beluga whales, and because the sampling occurred over a 23-year interval, we cannot definitively determine if the females that conceived outside of the peak periods represent normal seasonal variation or if they are indicative of annual shifts in peak fertility that may occur in wild populations. Captive male beluga whales are also known to have annual periods of peak fertility (i.e., higher ejaculate volumes, total spermatozoa, and increased testis size) from February to May (O'Brien, Steinman, Schmitt, & Robeck, 2008; Richard et al., 2017), a period which overlaps the peak ovulation period observed within this population of wild animals. Therefore, a changing availability of breeding males during the protracted period of female seasonal reproduction may be an important factor that helps define months of peak fertility. From May to October, photo-identification studies found no evidence of sexual segregation or segregation by age class, males and females were in the same groups (McGuire & Stephens, 2017; McGuire et al.[2]), however, this effort began near the end (May) of what appears to be the peak ovulation period for CIB.

One fetus, (length 61 cm) was predicted to have been conceived in late December and a second during mid-January (length 55 cm). While at least one conception (and an ovulation in a second animal) has been documented in captive beluga whales in January, none were observed as early as December. However, if we apply the known accuracy for the first half of gestation, we find that the predicted range in which these two animals may have conceived was from 5 December to 23 January and 22 December to 9 February (Figure 3), potentially placing both females within the known range of conception in captive animals. If we included the girth measurements (Figure 3b, Table S2), conception dates for these fetuses were predicted within the peak ovulation period of March to May.

The major limitation of using beluga whale fetal growth curves acquired via ultrasonography is that as the fetus increases in size the accuracy of the predictive power of the curves decreases because of curvature of the body within the womb (Robeck et al., 2015). Because of this limitation, the accuracy of TL growth curves during the second half of gestation is unknown and we had to rely on the combined accuracy of the other fetal measurements (BPD, TD, and TC) to predict the accuracy range for predicted conception dates (see tables 2 and 3 in Robeck et al., 2015). This limitation illustrates the need for clinicians working in captive settings to obtain more data on in utero total fetal length and for field biologists collecting fetal morphometric data to include thoracic circumference (at the level of the heart) as a standard measurement, although this may prove difficult if the carcass is not fresh. Advanced decomposition of some carcasses made it impossible to obtain TC measurements.

For predicted birth dates we found that 65% of predicted births (n = 17 of 26) based on TL occurred within the July–October period (Figure 4a, 81% when including predicted variation). The TC formula predicted 44% (n = 7 of 16, 69% when including variation) of births within the observed calving period (Figure 4b). Predicted gestation lengths when compared to estimated age suggest that all neonates and one calf were premature, while one fetus appeared to be past due (Table S2). However, all were within the predicted variation of birth dates (Figure 4). The formula, when applied to a live-stranded CIB calf named Tyonek (now in residence at SeaWorld San Antonio), returned an estimated birth date ~12 days prior to stranding. This was consistent with the age estimates made by veterinarians based on morphological observations and physiological analyses (e.g., length, weight, fetal folds, skin color, umbilicus healing, behavior, and physiological parameters from hematology and serum chemistry analyses).

Burns and Seaman (1986) noted that for some Alaska beluga whale populations breeding "probably begins in midwinter and extends to June" while births occur "over a prolonged period from April to late July or early August."

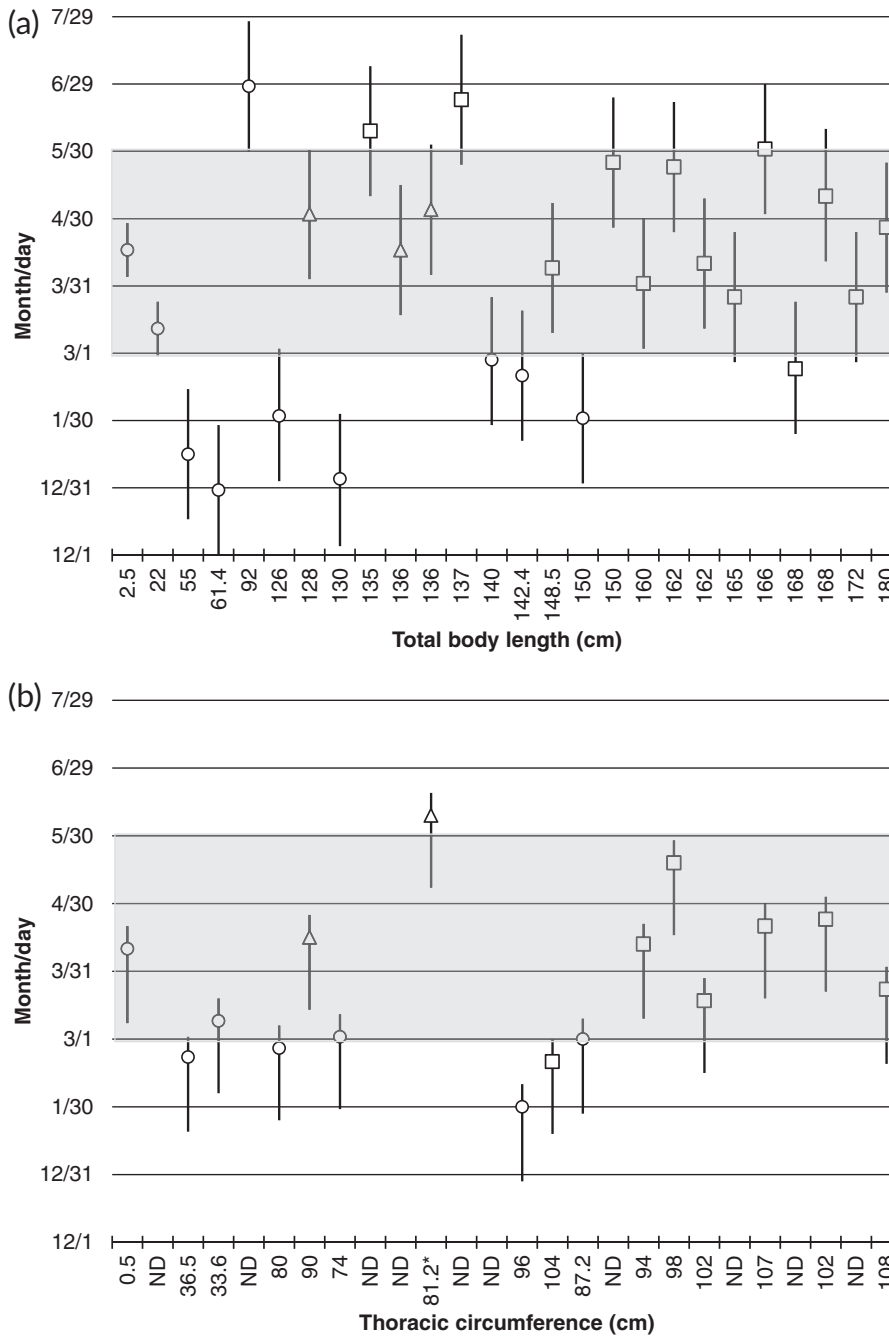

FIGURE 3 Predicted conception dates (symbols), and variation (black lines), for deceased Cook Inlet beluga whale fetuses (circles), neonates (triangles), and calves-of-the-year (squares) (1995–2018) based on total body length (a) and thoracic circumference (b). * = estimated from xiphoid girth measurement. Calculations are provided in Table S2. Shaded area shows months (March–May) when peak ovulation activity was observed in captive beluga whales.

Although we did not observe stranded neonates or calves-of-the-year during April–June, nor have live neonates and calves been documented during this period, the predicted birth dates suggest calving could occur throughout the entire ice-free period from April to November (Figure 4, Table S2). As with predicting conception dates, the accuracy

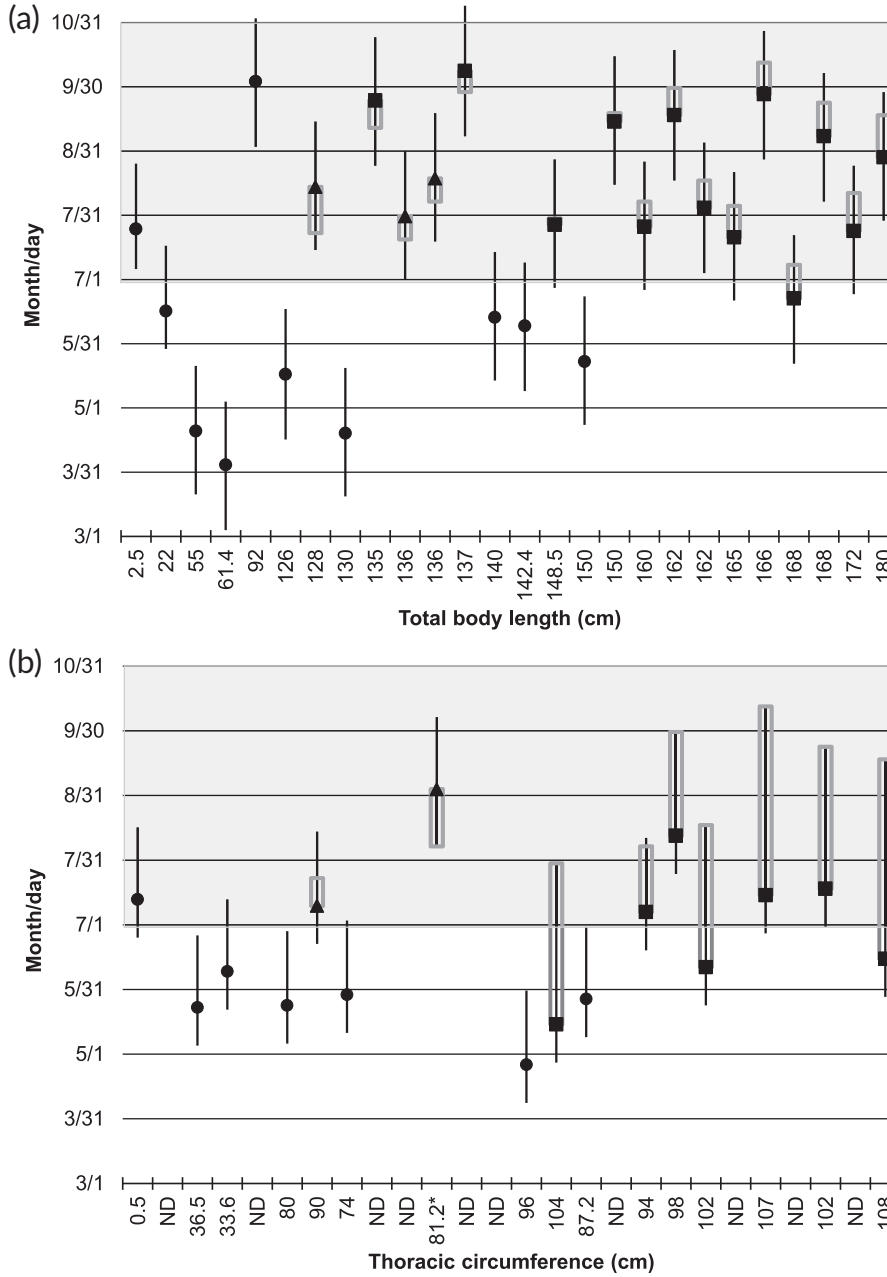

FIGURE 4 Predicted birth dates (symbols), and variation (black lines), for deceased Cook Inlet beluga whale fetuses (circles), neonates (triangles), and calves-of-the-year (squares) (1995–2018) based on total body length (a) and thoracic circumference (b). * = estimated from xiphoid girth measurement. Calculations are provided in Table S2. Shaded area shows months (July–October) when neonates were observed during photo-identification surveys conducted between 2005 and 2017. The time from the reported stranding date (Table S2) to the predicted birth date (symbol) is shown within the dark, gray box.

of predicting birth dates for the second half of gestation is unknown based solely on TL data, but using other metrics (BPD, TD, TC) can range over a period of two months (Figure 4, Table S2). This is, in part, due to the difficulty in getting accurate measurements of large beluga whale fetuses in utero and that the last trimester of fetal growth can

naturally vary considerably between pregnant females (see Robeck et al., 2015 for discussion). While more data are needed to both evaluate and improve the accuracy of these models, they still provide a necessary template for understanding and validating the wide potential range of seasonal reproductive events and can be used to help target population management periods during these critical life-history events.

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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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