

Reproduction, Growth and Development in Captive Beluga (*Delphinapterus leucas*)

Todd R. Robeck,^{1*} Steven L. Monfort,² Paul P. Calle,³ J. Lawrence Dunn,⁴ Eric Jensen,⁵ Jeffrey R. Boehm,⁶ Skip Young,⁷ and Steven T. Clark⁸

¹SeaWorld Texas, San Antonio, Texas

²Conservation and Research Center, National Zoological Park, Smithsonian Institution, Front Royal, Virginia

³Wildlife Conservation Society, Bronx, New York

⁴Mystic Aquarium, Mystic, Connecticut

⁵U.S. Navy Marine Mammal Program, San Diego, California

⁶John G. Shedd Aquarium, Chicago, Illinois

⁷Vancouver Aquarium Marine Science Centre, Vancouver, British Columbia

⁸Corporate Zoological Operations, Orlando, Florida

Recent success propagating captive beluga has resulted from combined efforts by North American zoos and aquariums to manage disparate collections as a single population. This success has provided a tremendous opportunity to increase our understanding of beluga reproductive biology. Blood samples were collected on a weekly to biweekly basis from 23 female and 12 male beluga, ranging in age from 2–15 years, for analysis of serum progesterone (P) and testosterone (T), respectively. Peri-parturient observational data, including food intake, duration and signs of labor, and nursing patterns were collected from 15 days prepartum to 30 days postpartum during 21 births. Total body lengths and weights were collected from 10 captive-born beluga. For female beluga, the mean (\pm SD) age, body length, and weight at first conceptions were 9.1 ± 2.8 years, 318.0 ± 9.1 cm, and 519 ± 84 kg. Thirty-five luteal phases and 13 conceptions were detected from January–June, and 70% of luteal phases and 80% conceptions occurred from March–May. The mean luteal phase and total estrous cycle lengths were 30.0 ± 6.5 days and 48.0 ± 4.6 days, respectively. For male beluga, the mean age that males sired their first calf was 13.3 ± 2.6 years. Compared to younger males (< 8 years of age, 0.95 ng/ml), levels of T secretion in older males (> 8 years of age, 5.0 ng/ml) were elevated significantly only during the interval from

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*Correspondence to: Todd R. Robeck, DVM, PhD; SeaWorld Texas, 10500 SeaWorld Drive, San Antonio TX 78251. E-mail: Todd.Robeck@SeaWorld.com

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January–April. Highest T concentrations (6.2 ± 4.9 ng/ml) were recorded from January–March, whereas nadir concentrations (1.1 ± 1.0 ng/ml) were detected from August–September. The mean gestation length was 475.0 ± 20.4 days ($n = 9$). For parturition, the mean time from the first appearance of fluke or rostrum to delivery, delivery to placental passage, and delivery to nursing were 4.4 ± 2.9 hr, 7.6 ± 1.8 hr, and 43 ± 45 hr, respectively. All cows had decreased food intake on the day of delivery, with 44% having zero intake. Peak 24-hr nursing activity occurred 3.9 ± 2.7 days post-partum. Growth (i.e., body weight and length) as a function of age were well described by the Gompertz model ($r^2 = 0.91, 0.93$). Based on the model, growth in body weight and length were significantly greater in males compared to females. Predicted birth weight (88.9 kg) was similar for both sexes, however, and male calves were predicted to be shorter (154.3 cm) than female calves (160.7 cm). The results provide the first descriptions of captive beluga reproductive physiology, including endocrinology, peri-parturient behavior, growth, and reproductive maturity. This knowledge is important for helping to maintain genetically diverse, self-sustaining populations of captive beluga whales. *Zoo Biol* 24:29–49, 2005. © 2005 Wiley-Liss, Inc.

Key words: monodontidae, cetacean age and growth, testosterone, progesterone, captive cetaceans

INTRODUCTION

Historically, beluga (*Delphinapterus leucas*) has been one of the most important food sources for Inuit's living in the arctic [Heide-Jørgensen, 1990]. Despite the continued reliance on this species, little information has been collected concerning their basic reproductive physiology. For the most part, existing information has been derived from observation of wild stocks or post-mortem analysis of animals collected during native harvests [Brodie, 1971; Braham, 1984; Burns and Seaman, 1986; Doidge, 1990; Heide-Jørgensen, 1990; Heide-Jørgensen and Teilmann, 1994; Høier and Heide-Jørgensen, 1994]. Assuming accurate methods exist for aging the animals harvested [Clark et al., 2000], and despite access restricted by season, this type of data has been used to document certain biological functions including reproductive seasonality, growth, and development. Free-ranging male and female beluga have been estimated to be reproductively mature between 4–7 and 6–9 years of age, respectively [Brodie, 1971; Braham, 1984; Heide-Jørgensen and Teilmann, 1994]. The species is believed to exhibit reproductive seasonality with breeding observed from April–May, although slight geographical variation exists [Brodie, 1971; Heide-Jørgensen and Teilmann, 1994]. Estimates of total gestation length range widely from 330 days (Western Greenland) [Heide-Jørgensen and Teilmann, 1994] to ~435 days (Canadian) [Brodie, 1971], and lactation is believed to last approximately 24 months [Brodie, 1971].

Høier and Heide-Jørgensen [1994] evaluated serum collected post mortem during May and September to describe mean serum testosterone (T) levels of 4.14 nmol/l (1.19 ng/ml) and 0.96 nmol/l (0.27 ng/ml) in mature and immature males, respectively. In addition, serum progesterone (P) in pregnant females was 27.9 nmol/l (9.15 ng/ml).

Thirty-two beluga currently reside in nine North American zoological institutions [L. Garibaldi, personal communication]. Since 1988, these facilities have been involved in a coordinated captive breeding management effort that has

resulted in the birth of 21 calves. The ready animal access inherent in zoological settings, combined with the high tractability of beluga, provides a unique opportunity to conduct systematic research to study the reproductive biology of this species. Nevertheless, the only beluga reproductive biology publications to date have been limited to descriptions of suckling behavior, nursing patterns, and preliminary data on gestational steroid hormones [Drinnan and Sadler, 1981; Calle et al., 1993, 1996; Russell et al., 1997]. Peak 24-hr nursing activity was described to occur at ~7–10 days of age, and suggested that abnormal nursing patterns could provide an early indicator of calf distress [Cook et al., 1992; Russell et al., 1997]. Peak gestational P (60–66 ng/ml) and estradiol (30–31 pg/ml) concentrations occurred by 4 months of pregnancy [Calle et al., 1993, 1996].

With known ages and the ability to collect accurate serial morphometric measurements and serum samples (for reproductive hormone assays), captive populations provide a unique opportunity to improve our understanding of reproductive biology in this species [Clark et al., 2000]. The objectives of our research with captive beluga were to quantify seasonal endocrine changes in females (serum P) and males (serum T); to establish the age of sexual maturity; to document behaviors during parturition and the peri-parturient interval; to compare and contrast nursing patterns in normal and clinically distressed calves, and; to characterize growth rates in captive born calves and compare these data to estimates of growth rates in wild beluga.

MATERIALS AND METHODS

Animals and Sample Collection

Blood samples were obtained by voluntary presentation or during routine venipuncture as part of medical or management procedures from 23 female and 12 male beluga for various intervals from 1983–1998. The animals were located at nine different facilities: John G. Shedd Aquarium, Chicago, IL; Mystic Aquarium, Mystic, CT; Point Defiance Zoo and Aquarium, Point Defiance, WA; SeaWorld of Texas, San Antonio, TX; SeaWorld of California, San Diego, CA; SeaWorld of Florida, Orlando, FL; US Navy Marine Mammal Program, San Diego, CA; Vancouver Aquarium Marine Science Centre, Vancouver, B.C.; and New York Aquarium, Wildlife Conservation Society, Brooklyn, NY. The US Navy Marine Mammal facility and the New York Aquarium are natural salt water systems ranging in temperature from 13–21°C and 1.7–28°C, respectively. All other facilities housed animals in manufactured salt water at temperatures ranging from 17–20°C.

The blood sampling periods for individual animals ranged from 2–15 years. Many of the samples or observational data were based on the availability of stored samples or animal records. During the main sampling period (1996–1998), 17 females ranging from 8–30 years were bled weekly to bi-weekly for 2 years (Table 1). In addition, 304 serum samples were collected from 10 males that were bled biweekly to quarterly over a maximum of 15 years (1983–1998). The males' ages ranged from 3–21 years at sampling onset (Table 2).

TABLE 1. Details of captive female beluga

Animal ID	EDOB ^a	Facility housed	Date range of serum samples	Samples (<i>n</i>)	Conceptions during sampling (<i>n</i>)	Calves with observational data (<i>n</i>)
Female 1	1983	Mys ^b	04/95–09/98	61	0	0
Female 2	1986	VC ^c	06/95–03/98	21	0	0
Female 3	1985	SWT ^d	No Samples	0	0	2
Female 4	1985	SWT	No Samples	0	0	0
Female 5	1986	SWT	No Samples	0	0	1
Female 6	1986	JGS ^e	02/95–06/98	25	1	1
Female 7	1970	WCS ^f	03/90–09/98	141	1	1
Female 8	1983	Mys	06/95–06/98	29	0	0
Female 9	1986	SWT	09/92–06/97	43	1	1
Female 10	1982	WCS	02/92–08/98	110	1	1
Female 11	1986	SWT	01/92–06/97	47	2	3
Female 12	1986	SWT	No Samples	0	0	4
Female 13	1967	Navy ^g	02/88–08/96	49	0	0
Female 14	1981	JGS	02/96–06/98	77	1	4
Female 15	1983	Mys	02/95–09/98	73	0	0
Female 16	1980	WCS	02/91–08/98	113	1	2
Female 17	1989	PtD ^h	03/97–12/98	48	0	0
Female 18	1985	SWT	No Samples	0	0	0
Female 19	1986	JGS	07/92–06/98	37	1	1
Female 20	1978	Navy	04/88–08/96	44	0	0
Female 21	1984	PtD	02/96–11/98	106	0	0
Female 22	1986	SWT	05/93–05/97	40	0	1
Female 23	1977	SWT	No Samples	0	0	2

^aEstimated date of birth.

^bMystic Aquarium

^cVancouver Aquarium.

^dSeaWorld of Texas.

^eJohn G. Shedd Aquarium.

^fNew York Aquarium, Wildlife Conservation Society.

^gUS Navy Marine Mammal Program.

^hPoint Defiance Zoo and Aquarium.

T Radioimmunoassay

Male beluga serum or heparinized plasma was analyzed in duplicate using a double-antibody [¹²⁵I] RIA (ICN, Costa Mesa, CA) for T according to the instructions provided except all reagent volumes were halved. The antiserum cross-reacts 100% with T, 3.4% with 5 α -dihydrotestosterone, 2.2% with 5 α -androstane-3 β -17 β -diol, 2.0% with 11-oxotestosterone, and <1% with all other steroids tested.

P Radioimmunoassay

Female beluga serum or heparinized plasma was analyzed in duplicate using a double-antibody [¹²⁵I] RIA that cross reacts with a wide variety of P metabolites. All female serum extracts were analyzed using [¹²⁵I] RIA described previously for P [Brown et al., 1994; Wasser et al., 1994]. The monoclonal antiserum cross-reacts 100% with P, 96% with 5 α -pregnane-3 β -ol-20-one, 36% with 5 α -pregnane- α -ol-20-one, 15%, with 17 α -hydroxyprogesterone, 13% with pregnenolone, 7% with

TABLE 2. Details of captive male beluga

Animal ID	EDOB ^a	Facility housed	Date range of serum samples	Samples (<i>n</i>)	Calves sired (<i>n</i>)	Age at first conception
Male 1	1985	SWT ^b	02/88–01/94	43	1	12
Male 2	1987 ^c	WCS ^d	02/91–09/94	45	0	NA
Male 3	1983	VC ^e	07/91–02/94	7	1	16
Male 4	1982	JGS ^f	01/94–06/94	15	3	9
Male 5	1985	SWT	05/86–04/81	12	1	13
Male 6	1986	JGS	09/90–03/11	6	0	NA
Male 7	1969	WCS	02/79–07/94	9	2	17
Male 8	1975	Navy ^g	03/84–08/92	48	0	NA
Male 9	1979	SWT	02/88–04/92	60	4	12
Male 10	1980	WCS	04/85–12/94	59	2	12

^aEstimated date of birth.

^bSeaWorld of Texas.

^cCaptive born.

^dNew York Aquarium, Wildlife Conservation Society.

^eVancouver Aquarium.

^fJohn G. Shedd Aquarium.

^gUS Navy Marine Mammal Program.

5 β -pregnane-3 α -ol-20-one, 5% with 5 β -pregane-3 α ,17 α -diol, 20 α -one, and <1% with pregnadiol-3 α -glucuronide and all other steroids tested.

Endocrine Data Analysis

Estimates of luteal phase and estrous cycle durations were limited to females that were blood sampled a minimum of every 2 weeks. For each individual female, P concentrations that exceeded 3 ng/ml and were at least $2.0 \times$ the mean non-pregnant P concentration for that particular individual were considered presumptive evidence of luteal activity. When a sample below this threshold was serially adjacent to a sample above the threshold, the beginning or end of a luteal phase was defined as median point between these two samples. The value with the highest concentration during a period of luteal activity was considered the peak. An estrous cycle was defined as the number of days between the beginning of two successive luteal phases. All of the cycle characteristics were calculated for each individual animal and then the data were pooled to determine mean values for the population. To determine seasonal estrous activity, any month(s) in which peak P of a luteal phase occurred was given a value of one. For analysis, all monthly data were combined across years to develop a composite 12-month period.

Peri-parturient Observations

Data were not available for all females for each set of observations. For peri-parturient food intake, values (kg/d) obtained from each animal's record (recorded as a standard husbandry practice) were utilized. For trend analysis, mean food intake was determined for all animals 15 days before and after parturition (Day 0). The date and time of the following events were recorded for each birth: first vaginal discharge, appearance of fluke or rostrum, delivery, and placental passage. For live calves, initial postpartum nursing time and total daily nursing were recorded.

Nursing data were collected with 24-hr observations beginning immediately postpartum and continuing for 30 days.

Age, Growth, and Morphometry

Total body length and weight were collected from 10 captive-born beluga (4 females, 6 males, 2 neonates) maintained at SeaWorld parks from August 1992 until January 2003. Total body length was assessed as per Norris [1961], whereas body weights were obtained using a hydraulic scale (Model 747-915-40; Emery Winslow Scale Company; Seymour, CT). Total body length (cm) and weight (kg) parameters were used to construct age-based growth models.

A number of growth models have been used in the examination of size at age. For the present study, both the von Bertalanffy and Gompertz models were examined for fit. The Gompertz model provided an adequate fit as evidenced by an examination of the residuals. Additionally, due to the prevalence of this particular model in cetacean age and growth studies [Perrin and Henderson, 1984; Doidge, 1990; Read and Gaskin, 1990; Read et al., 1993; Ferrero and Walker, 1995; Fernandez and Hohn, 1998], we concluded its use for this dataset would be most appropriate because it would allow intraspecific comparison of growth parameters to those currently in the literature [Doide, 1990; Heide-Jørgensen and Teilmann, 1994]. The specific form of the Gompertz model used was taken from Fitzhugh [1975]

$$WT \text{ or } TL = W_{\text{inf}} \text{ or } L_{\text{inf}} \times [\exp(-b \times \exp(-k \times t))]$$

where WT or TL is the weight or total length of the animal at age, W_{inf} or L_{inf} is the asymptotic weight or length growth value for this particular dataset, b is the integration constant, k is the growth rate constant, and t is age (in years).

Expectedly, each animal's growth data were auto-correlated (runs test for trend data categorized by animal, P -values < 0.01). Therefore, the nonparametric statistical technique of bootstrapping, described in Clark and Odell [1999], was necessary to eliminate the problems associated with autocorrelation [Sokal and Rohlf, 1995]. The bootstrapping technique allowed calculation of parameter estimates, standard errors (SE), and 95% confidence intervals (CI). These calculations then provided the opportunity to analyze model parameter estimated gender and study-based differences.

Statistical Analysis

Descriptive statistics were applied to the data using Microsoft Excel (Microsoft, Redmond, WA). Kruskal-Wallis one-way ANOVA on ranks and Duncan's multiple comparison test were used to compare mean monthly serum T values for mature males and to compare mean serum T levels between adult and immature males during the breeding season. Student's t -tests were used to compare the time interval from flukes or rostrum presentation to parturition, and delivery to initial nursing in primiparous vs. multiparous animals. These data analyses were carried out using the SigmaStat for Windows (SPSS Statistical Software, San Rafael, CA). Morphometric statistical analyses were accomplished using the SYSTAT statistical package (version 8.0 for Windows, SPSS Statistical Software, 1998). Data are presented as mean \pm SD; $P < 0.05$ was considered significant.

RESULTS

Serum T

Parallel displacement curves were obtained by comparing serial dilutions (range = undiluted – 1:32) of pooled beluga serum and T standard preparations. Recovery of known amounts of unlabeled T (range = 0.05–5.0 ng/ml) added to a pool of diluted beluga serum was $123.4 \pm 11.9\%$ ($y = 0.06 + 1.0x$, $r^2 = 0.99$). RIA of elutes after HPLC [Monfort et al., 1991] showed that all immunoreactivity was associated with a single peak that co-eluted with T. Beluga serum was diluted (1:4–1:8) and assayed (25 μ l) in duplicate. Inter- and intra-assay variation were 8.5% and <10%, whereas assay sensitivity was 0.05 ng/ml.

Serum P

Parallel displacement curves were obtained by comparing serial dilutions (range = undiluted – 1:32) of pooled beluga serum and P standard preparations. Recovery of known amounts of unlabeled P (range = 3.75–240 pg/ml) added to a pool of diluted beluga serum was $106.8 \pm 13.3\%$ ($y = -1.09 + 1.1x$, $r^2 = 0.99$). RIA of elutes after HPLC [Monfort et al., 1991] showed that >80% of immunoreactivity was associated with a single peak that co-eluted with P. Beluga serum was diluted (neat–1:2) and assayed (100 μ l) in duplicate. Inter- and intra-assay variation were 12.0% and <10%, whereas assay sensitivity was 3.75 pg/ml.

Samples that had been collected before the study-sampling period were assayed for P by a commercial lab using RIA. Because different methods were used for sample analysis, only samples assayed by the same method were used to determine mean concentrations. Despite concentration differences, correlation between commercial lab results and the monoclonal P RIA during the luteal phase and early pregnancy was 0.73 ($P < 0.01$). Twenty of the 22 females (91%) sampled exhibited a total of 54 P peaks (34.4 ± 44.5 ng/ml), which were presumed to represent luteal phase activity or pregnancy. Two of the females did not secrete elevated P during the study. Thirteen conceptions and 10 births occurred during the serum P sampling period.

Female Reproductive Maturity

The mean age, length, and weight when luteal concentrations of serum P were first detected was 6.9 ± 1.5 year ($n = 9$), 318 ± 9 cm ($n = 6$), and 519 ± 83 kg ($n = 6$), respectively. The mean age, length, and weight at first conception were 9.1 ± 2.8 year ($n = 16$), 328 ± 17 cm ($n = 7$) and 561 ± 72 kg ($n = 7$), respectively. The mean age at first conception for animals ($n = 6$) housed with proven sires during the season when the first conception occurred was 8.0 ± 3.4 years. Of these females, 4 of 6 conceptions occurred during their first ovarian cycle at the age of 6 years. The oldest age for conception in a multiparous female was 20 years.

Seasonality

During periods when data were collected throughout the breeding season, all but two of the reproductively mature females exhibited at least one elevated serum P value indicative of luteal activity. The mean number of luteal events for each animal per season was 1.3 ± 0.4 ($n = 35$). All but two luteal events occurred between January and July, and 70.4% occurred in March, April, and May (Fig. 1). Conceptions

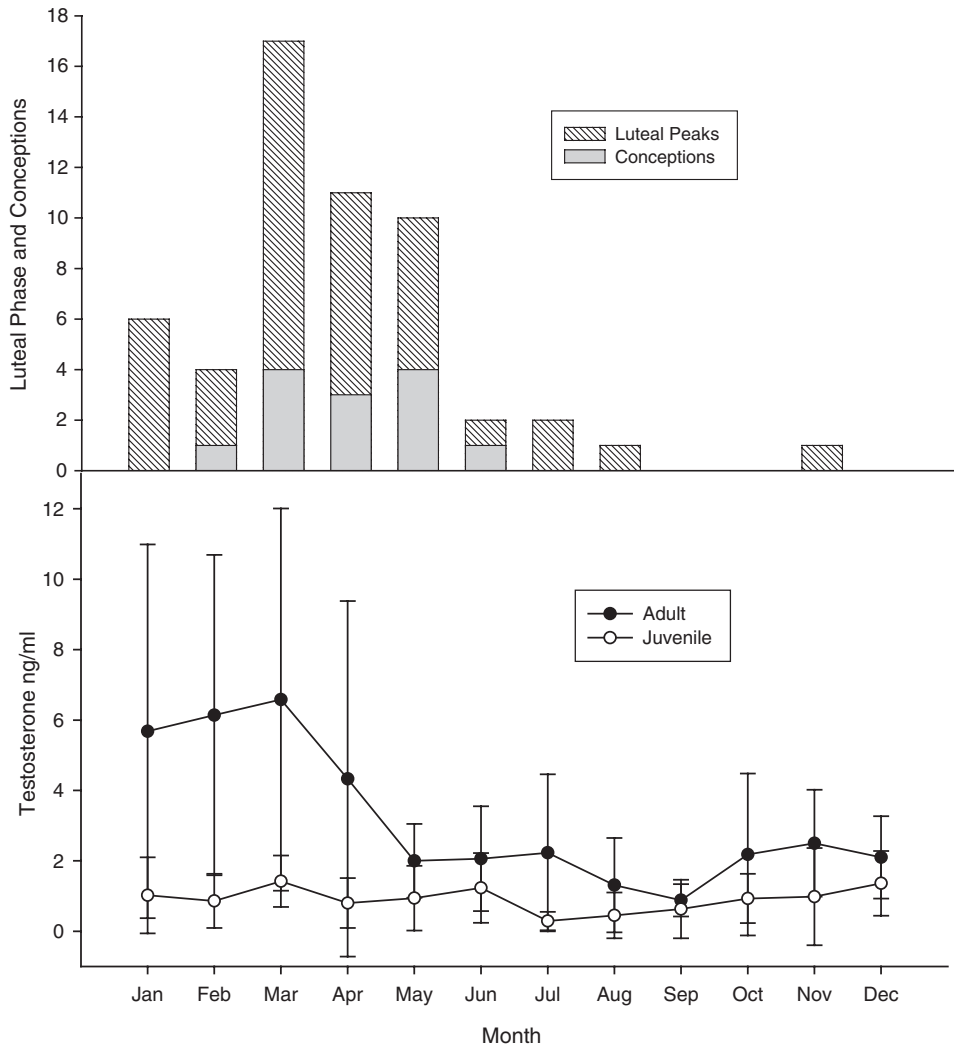


Fig. 1. Demonstrates seasonal variations in female (top graph) and male (lower graph) reproductive parameters. For the female, the bar charts illustrate frequency of luteal activity and conceptions. For the male the graph compares monthly mean values of T between adult (≥ 8 years) and juvenile (< 8 years) beluga. T -values were significantly different ($P < 0.05$) between adult and juvenile males during Jan–May, July, and August.

($n = 13$) occurred from February to June and 80.6% occurred in March, April, and May (Fig. 1).

Estrous Cycle and Pregnancy Characteristics

Mean luteal phase and estrous cycle durations were 30.0 ± 6.5 days ($n = 20$) and 47.8 ± 4.6 days ($n = 4$), respectively. The mean number of cycles that occurred before a conception was 0.6 ± 0.5 ($n = 10$). The mean gestation length was 475.0 ± 20.4 days ($n = 9$).

Male Sexual Maturity and Seasonality

The youngest male to sire a calf was 9 years old, and the mean age at which males first sired a calf was 13.3 ± 2.6 years ($n = 8$). Thus, all animals < 8 years of age were considered sexually immature. Based on this division, peak serum T production in adult males occurred from January–April (Fig. 1). The months of January, February, and March (mean = 6.2 ± 4.9 ng/ml) had significantly higher median (5 ng/ml) values ($P < 0.01$) than the nadir months of August and September (median = 0.9 ng/ml; mean = 1.1 ± 1.0 ng/ml). Comparisons between median serum T from mature and immature animals on a month-to-month basis show significant differences ($P < 0.05$) during January–May, July, and August (Fig 1).

Peri-parturient Observations

From 1990–1999, a total of 25 pregnancies resulted in 21 births. Fourteen of the pregnancies produced male calves (56%), nine were female (36%) and the sexes of two were undetermined. One female aborted twin male calves at approximately 11 months of gestation. Three cows experienced dystocia and calves were delivered with manual assistance. Of the 21 unassisted births, 18 were live births, two died shortly after birth, and one was stillborn. Two calves were born in a headfirst presentation (9.5%), and one of these calves died shortly after birth. The mean time from first observed vaginal discharge to appearance of flukes and the subsequent interval until birth was 3.2 ± 2.6 hr (range = 0.2–8 hr, $n = 17$) and 4.4 ± 2.9 hr (range = 0.4–12.4 hr, $n = 18$), respectively. The mean time from delivery to placental passage was 7.6 ± 1.8 hr (range = 4.6–11.8 hr, $n = 18$). The mean and median time from parturition until the onset of nursing was 43.0 ± 45.4 hr (range = 5.3–144.0 hr, $n = 15$) and 22.7 hr, respectively. The time period from first fluke appearance to birth and the subsequent interval until the first postpartum nursing tended to be longer in primiparous cows (4.4 ± 1.9 hr, $n = 5$; 52.3 ± 62.1 hr, $n = 4$, respectively) compared to cows delivering their second calf (2.7 ± 0.7 hr, $n = 5$; 19.1 ± 15.3 hr, $n = 4$, respectively).

For all animals with available data ($n = 16$), food intake decreased close to and on the day of parturition (Fig. 2). Seven of 16 (44%) beluga had zero food intake on the day of parturition. After parturition, first consumption of food by cows occurred at 1.8 ± 1.0 days (range = 1–4 days) and food intake returned to normal pre-parturient levels by 6.2 ± 3.4 days (range = 1–14 days, $n = 14$). Two of the animals were not included in this data set, however, because their food consumption had not returned to normal baseline levels by 15 days postpartum.

Age, Growth, and Morphometry

Of 18 live births, one died within 30 days from a congenital heart defect, and a second died within 60 days from an infection; another two animals died before the age of 2 years from infectious disease. Thus, 14 of 22 births (63.6 %) resulted in calves that reached 2 years of age. Mean 24-hr nursing time for normal calves (i.e., those surviving for > 2 years) is illustrated in Figure 3. In addition, nursing patterns of the four calves that died before the age of 1 year were compared to nursing profiles of normal calves (Fig. 3). Animal 1 had a period of increased nursing activity around Day 18; this animal was diagnosed with pulmonary nocardiosis and despite treatment died at 60 days [Robeck et al., 1994]. Animal 2 had prolonged elevations of nursing time from Day 6 to Day 12, but this animal died at Day 29 from a

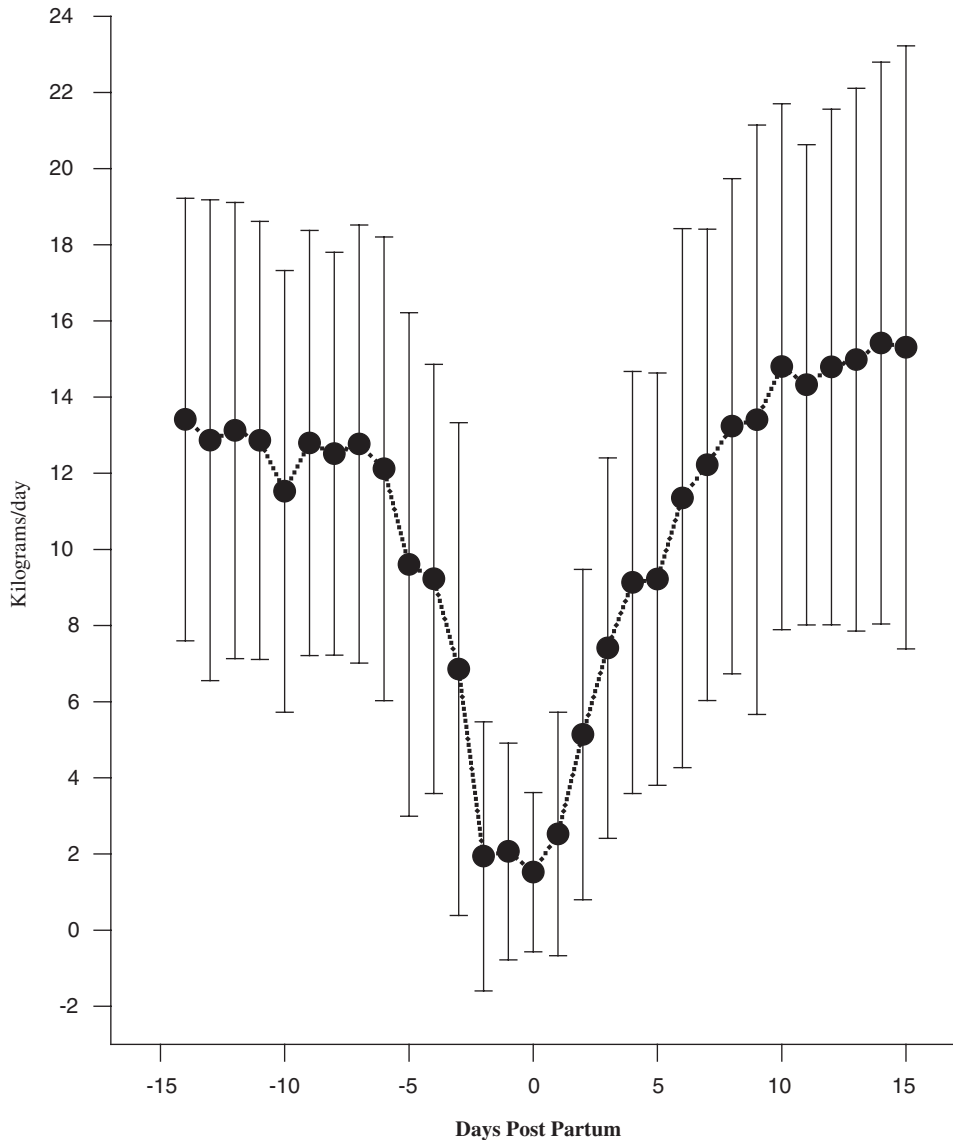


Fig. 2. Pre- and post-partum food consumption in captive beluga ($n = 16$).

congenital heart defect [L. Dalton, unpublished data]. Animal 3 consistently exhibited a below-average nursing pattern and died by 6 weeks of age from a bacterial infection. Animal 4 did not nurse initially, was administered supportive care and antibiotics on Day 5, began nursing by Day 10, but eventually died from a bacterial infection. For normal calves, the period from parturition to peak nursing time was 3.9 ± 2.7 d (range = 1–10 days, $n = 13$), but for calves that died before the age of 1 year, peak nursing occurred 5.0 ± 2.4 days post-partum (range = 3–8 days, $n = 4$). The mean body weight and length of beluga calves up to 5 days of age was 61.8 ± 4.5 kg ($n = 5$) and 148.0 ± 6.2 cm ($n = 3$), respectively.

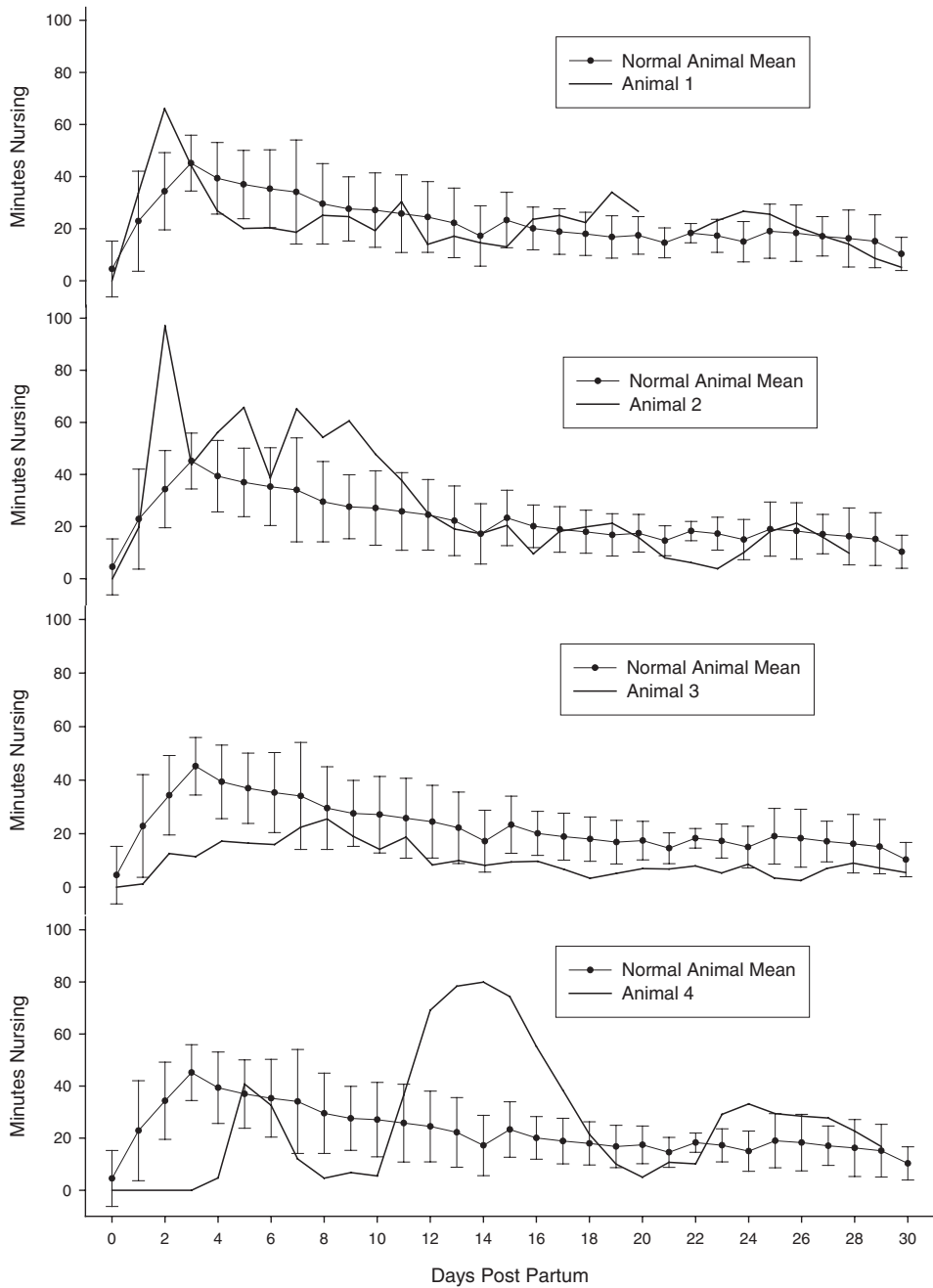


Fig. 3. Nursing profiles (minutes of nursing/day) for calves surviving after (pooled mean data = normal animal mean) or dying before (individual data = Animals 1-4) 1 year of age.

Total body length and weight

The relationship between body weight and total length was exponential ($r^2=0.94$; Fig. 4). The overlap of the 95% CI for male and female parameter

estimates (Table 3) indicated a lack of sexual dimorphism at this age, which permitted analyses to be conducted on combined sex data. Present study parameter estimates differed from those reported in the literature (Table 4).

Age and body weight

Weight at age was described by a Gompertz model ($r^2=0.91$ for the sexes combined dataset) and was sexually dimorphic (Fig. 5). Sexual dimorphism was more apparent than in the total length model. The predicted growth curves for males and females were clearly different in shape and there was an absence of overlap between the parameter estimates 95% CI for both maximum predicted length (WT_{∞}) and growth rate constant (k) (Table 3). Model-estimated weights at birth for the combined sexes data was 88.9 kg, whereas gender-specific models returned estimated birth weights of 70.7 kg and 107.8 kg for males and females, respectively. Present study parameter estimates were significantly different to those reported by Heide-Jorgensen and Teilmann [1994] (Table 4).

Age and total body length

A Gompertz function adequately described the relationship between age and total body length ($r^2=0.93$ for the sexes combined dataset) and suggested growth dynamics in total length were sexually specific (Fig. 6). Body length at birth for both

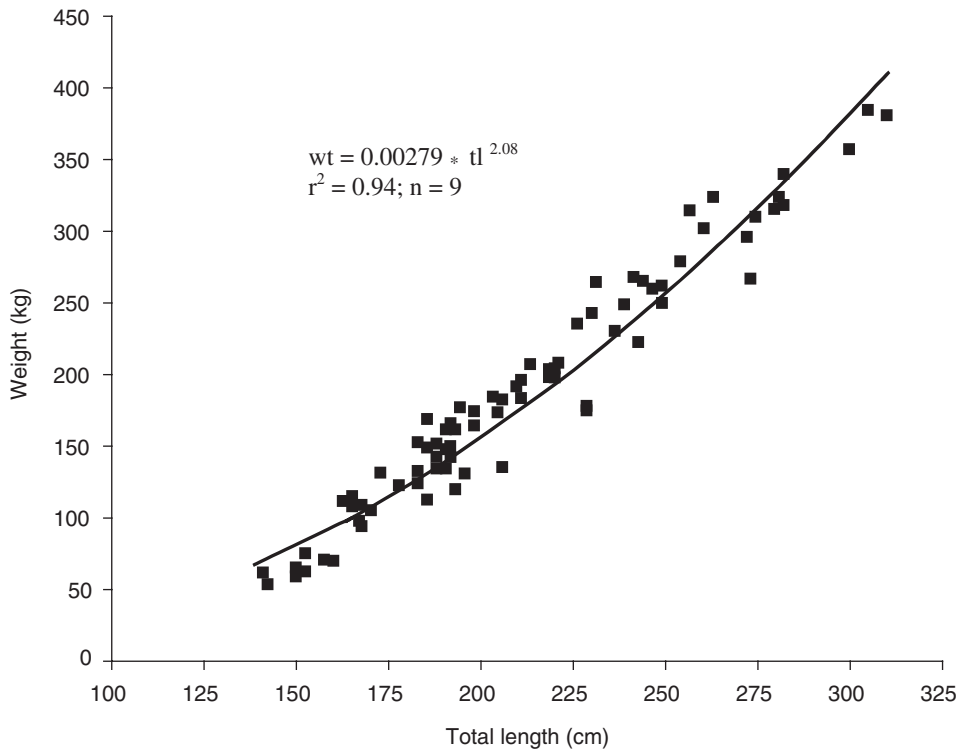


Fig. 4. Exponential relationship between body weight (kg) and total length (cm) in captive beluga. Data combined for sex (males: $n = 5$; females: $n = 4$).

TABLE 3. Parameter estimates with associated 95% CI of the weight and total length morphometric relationship for captive belugas at SeaWorld parks with comparisons to data from previous studies^a

	A			B		
	This study	Heide-Jørgensen and Teilmann [1994]	Doidge [1990]	This study	Heide-Jørgensen and Teilmann [1994]	Doidge [1990]
Both genders	0.002794	0.000514	0.000031	2.080	2.37	2.85
95% CI	0.001339–0.004249			1.983–2.177		
Males	0.002224	0.000295	0.000002	2.132	2.47	3.37
95% CI	0.000778–0.003670			2.013–2.252		
Female	0.004750	0.000137	0.003515	2.0000	2.21	2.03
95% CI	0.000051–0.009448			1.812–2.188		

^aWeight in kg, length in cm. Males: $n = 5$; Females: $n = 4$. Length Morphometric relationship $\text{weight} = A * \text{total length}^B$, where A was the initial value of weight when total length was 0 and B was the exponential growth factor.

sexes combined was predicted by the model to be 158.7 cm. The predicted body length of females at birth was slightly greater than that for males (160.7 and 154.3, respectively). Theoretical maximum body length was greater for males (333.2 cm) than females (284.1 cm). The steeper incline of the male growth curve derived from the model-predicted growth curve (Fig. 6) provided visual evidence of support for gender differences in asymptotic length. The male growth rate constant (k) was less than the female, whereas growth rate constants of either sex were substantially greater than those reported in the literature (Table 5).

DISCUSSION

Similar to findings for age at first pregnancy for wild beluga [Heide-Jørgensen and Teilmann, 1994; Braham, 1984], we found the mean age of first ovulation was 6.9 years for captive females. The mean age for first pregnancies in captive beluga was 9.1 years, however, which is later than their wild counterparts that apparently conceive during their first estrous cycles. In captive populations, the inconsistent availability of breeding males may artificially lengthen the period between the first estrous cycle and first pregnancy. This is supported by the observation that 67% of captive females ($n = 6$) maintained in the presence of a proven breeding male became pregnant at 6 years of age. These data support previous speculation [Heide-Jørgensen and Teilmann, 1994] that given the right social environment, beluga can conceive during their first season of cyclic ovarian activity. Similar to the maximum age of reproduction for wild female beluga (21 years) [Brodie, 1971] the maximum age of reproduction for captive females was 20 years. Although this may be due to reproductive senescence [Brodie, 1971], the captive population of female beluga is too young to establish if or when senescence occurs.

The ability to serially collect hormonal data enabled us to begin to describe the reproductive biology of captive beluga. We estimated a luteal phase of 30 days and a

TABLE 4. Parameter estimates with associated 95% CI of the Gompertz non-linear relationship between total length and age for captive belugas from SeaWorld parks with comparisons to data from previous studies.^a

	TL _∞				b				k			
	This study	Burns and Seaman [1985]	Doidge [1990]	Heide-Jorgensen and Teilmann [1994]	This study	Burns and Seaman [1985]	Doidge [1990]	Heide-Jorgensen and Teilmann [1994]	This study	Burns and Seaman [1985]	Doidge [1990]	Heide-Jorgensen and Teilmann [1994]
Both genders	330				0.73				0.43			
95% CI	320–340				0.66–0.80				0.33–0.53			
Males	333	427	349	483 ^b /434 ^c	0.77	0.74	0.71	0.95 ^b /0.75 ^c	0.47	0.14	0.28	0.22 ^b /0.21 ^c
95% CI	322–344				0.71–0.82				0.38–0.56			
Females	284	359	330	385 ^b /375 ^c	0.57	0.68	0.60	0.62 ^b /0.65 ^c	0.71	0.30	0.27	0.27 ^b /0.31 ^c
95% CI	273–295				0.46–0.67				0.50–0.91			

^aLength in cm, age in years. Males: $n = 5$; females: $n = 4$ Gompertz non-linear relationship: $TL = TL_{inf} \times [\exp(-b \times \exp(-k \times t))]$; where TL was the total length of the animal at age, TL_{inf} was the asymptotic total length growth value, b was the integration constant, k was the growth rate constant, and t was age (in years).

^bWest Greenland.

^cWhite and Kara Seas.

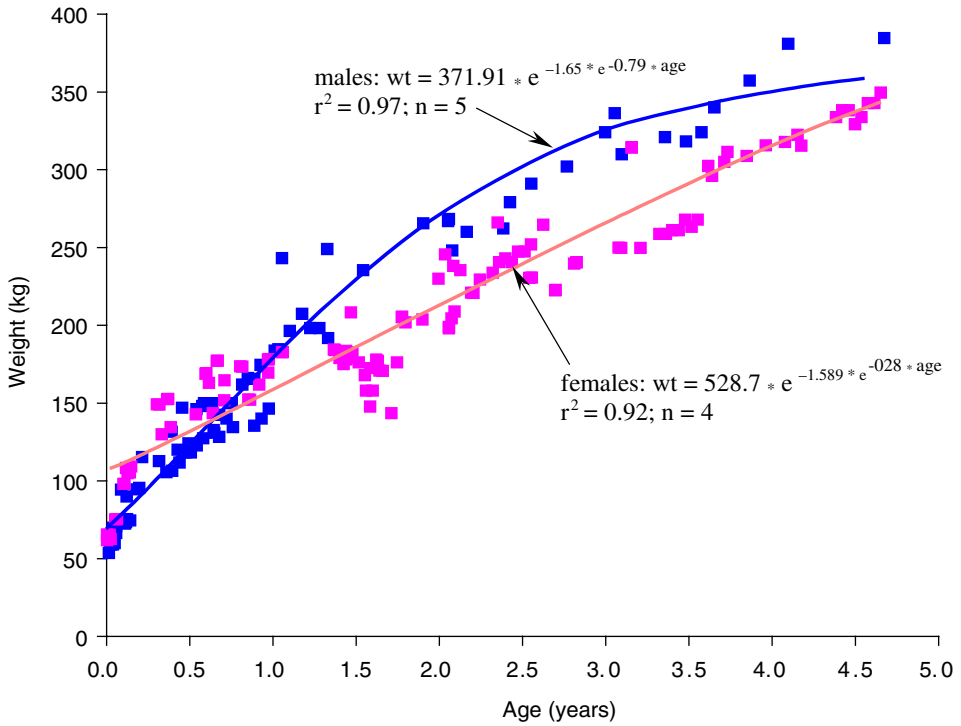


Fig. 5. Gompertz non-linear relationship between weight (kg) and age (years) by sex for captive beluga (males: $n = 5$; females: $n = 4$).

total estrous cycle length of 47 days, which is longer than the bottlenose dolphin (30 days) [Brook, 2000] and the killer whale (40 days) [Walker et al., 1988]. Future efforts should be directed toward conditioning beluga for daily urine sample collections, which will permit more detailed analysis of the various components of the estrous cycle.

Similar to most populations of wild beluga, our peak conception period occurred in March, April, and May [Brodie, 1971; Heide-Jørgensen and Teilmann, 1994]. Using hormone data, however, we were able to demonstrate that female beluga are seasonally polyestrous, with animals exhibiting up to two ovulations per season. For animals that conceived during the breeding season, approximately 50% conceived during the second estrous cycle. This suggests that in the wild there would be more than one opportunity for female beluga to conceive during the breeding season.

Gestation estimates of wild beluga have varied from 330 days to a maximum of 441 days [Brodie, 1971; Sergeant, 1973; Heide-Jørgensen and Teilmann, 1994]. This variation seems to depend on population location and methodology used to extrapolate conception dates. Relying on hormone data, we were able to estimate conception within a 2-week period and determined a longer mean gestation period of 475 ± 20 days. The reason that captive animals seem to have a longer gestation than wild animals is unknown, but may reflect the inaccuracy of methodologies employed previously.

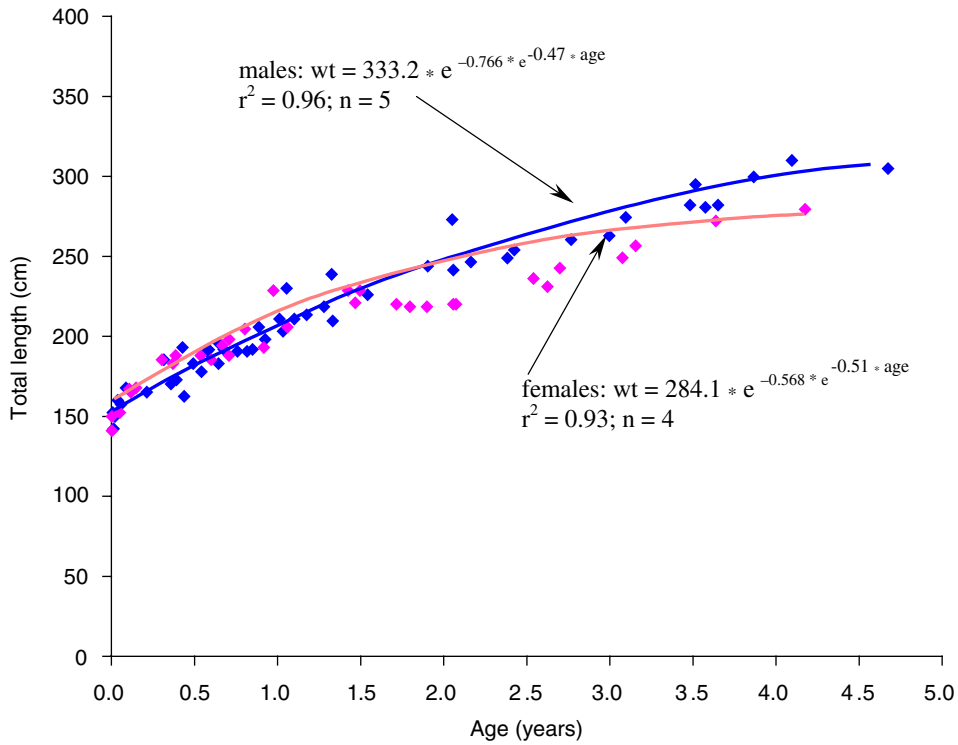


Fig. 6. Gompertz non-linear relationship between total length (cm) and age (years) by sex for captive beluga (males: $n = 5$; females: $n = 4$).

TABLE 5. Gompertz non-linear relationship between weight and age by sex parameter estimates for captive belugas from SeaWorld parks with comparisons to data from previous studies^a

	WT _∞		<i>b</i>		<i>k</i>	
	This study	Heide-Jorgensen and Teilmann [1994]	This study	Heide-Jorgensen and Teilmann [1994]	This study	Heide-Jorgensen and Teilmann [1994]
Both genders	383		1.46		0.53	
95% CI	375–391		1.39–1.53		0.45–0.60	
Males	372	483 ^b /434 ^c	1.66	0.95 ^b /0.75 ^c	0.79	0.22 ^b /0.21 ^c
95% CI	357–387		1.60–1.72		0.71–0.87	
Female	529	385 ^b /375 ^c	1.59	0.62 ^b /0.65 ^c	0.28	0.27 ^b /0.31 ^c
95% CI	273–295		1.34–1.84		0.20–0.35	

^aLength in cm. age in years. Males: $n = 5$; females: $n = 4$. Gompertz non-linear relationship: $TL = TL_{inf} \times [\exp(-b \times \exp(-k \times t))]$; where TL was the total length of the animal at age, TL_{inf} was the asymptotic total length growth value, b was the integration constant, k was the growth rate constant, and t was age (in years).

^bWest Greenland.

^cWhite and Kara Seas.

The present study is the first to demonstrate seasonal differences in serum T levels in mature beluga males. In contrast to T concentrations observed in other seasonally reproductive cetaceans spinner dolphin (*Stenella longirostris*) [T. Robeck, 1984], Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) [M. Yoshioka, unpublished], and similar to cetaceans that produce spermatozoa throughout the year (e.g., bottlenose dolphins [*Tursiops truncatus*] and killer whales [*Orcinus orca*]) [Schroeder and Keller, 1989; Robeck et al., 1995], mean monthly T concentrations never dropped below 1 ng/ml. Although minimum T levels required to maintain sperm production are unknown for this species, the observed minimum mean of 1 ng/ml suggests that some degree of spermatogenesis may occur throughout the year. This would agree with the observation of Heide-Jørgenson and Teilmann [1994] that although epididymal spermatozoa concentrations are higher in May, spermatozoa are still present in October. In bottlenose dolphins, peak sperm production occurs approximately 60 days after peak serum T levels [Schroeder and Keller, 1989]. Although further study is required to determine the timing of spermatogenesis, based on a 60-day interval, the occurrence of peak T from January–March in captive beluga suggests that peak sperm output may occur from March–May. This is a logical suggestion because the timing of peak sperm production in the male would coincide with the occurrence of estrous cycles in the female.

The earliest age that a captive male sired a calf was 9 years (mean = 13 years) is in agreement with the estimate for wild beluga of 8–9 years of age [Brodie, 1971], but is contrary to the 6–7 years of age estimate for Greenland beluga [Heide-Jørgenson and Teilmann, 1994].

Peri-parturient behaviors exhibited by beluga during Stage 1 and Stage 2 of labor were similar to those reported for other cetaceans, but there were differences in the timing and duration of these events. For example, beluga remain in Stage 2 labor longer (range = 0.4–12.4 hr) than killer whales (range = 1–4 hr) [Robeck et al., 2001], and bottlenose dolphins (range = 0.8–4.0 hr) [Joseph et al., 2000]. Because it is not uncommon for beluga to experience dystocia, it is important to consider normal delivery times when evaluating the progression of labor.

Most peri-parturient reproductive problems of captive cetaceans (e.g., dystocia, stillbirth, weak calf, poor maternal care) occur during labor and within a few hours of birth [Robeck et al., 2001]. Thus, being able to accurately predict the timing of parturition is an important management tool. Although some species of cetaceans have been noted to inconsistently exhibit reduced food intake before birth, food intake in beluga is consistently decreased on the day of parturition. Killer whales [Katsumata et al., 1998] and bottlenose dolphins [Terasawa et al., 1999] exhibit a consistent decline in rectal temperature on the day of parturition, but the predictive value of this approach has not been evaluated in beluga.

Within individual animals, we saw differences in the time from delivery to nursing for their first (53 hr) compared to their second calf (19 hr). This finding supports the hypothesis proposed by Russell et al. [1997], stating that cows are able to reduce the time it takes to first nurse their newborn calf as they become more experienced. This implies that the cow, to a large degree, is responsible for providing the calf with the best opportunity to learn to nurse.

Nursing patterns among normal calves were similar, with an initial peak total nursing time around Day 4, after which they gradually decreased reaching

a plateau around 20 days after parturition. Russell et al. [1997] observed a slightly longer time to peak postpartum nursing time of 7–10 days. A similar nursing pattern has been observed in killer whales [Asper et al., 1988; Clark and Odell, 1999], bottlenose dolphins [Read et al., 1995], and Pacific white-sided dolphins [Dalton et al., 1995]. Although some authors attribute this early peak in nursing to a need for increased caloric intake [Russell et al., 1997], we speculate that it is related to the learning curve required for the calf to become efficient at obtaining milk. Normal calves are born with fat reserves that provide a caloric buffer during this learning process. As the calf grows, it is reasonable to assume its caloric demand will rise accordingly. Reduced nursing time may actually reflect more efficient nursing by the calf, as well as possible changes in milk quality during lactation. In addition, a neonatal calf does not have the ability to handle large volumes of milk during any one feeding. Thus, as the animal's nursing efficiency improves and the digestive functional capacity increases, total nursing time decreases.

In support of the hypothesis of Russell et al. [1997] that total nursing time can serve as an indicator of clinical stress in calves, we saw abnormal nursing patterns in four calves that were clinically ill (Fig. 3). Nursing patterns have proven diagnostically useful for evaluating the health of calves from all cetaceans bred in captivity [Cook et al., 1992; Robeck et al., 1994; Dalton and Robeck, 1995; Robeck and Dalton, 2002]. Once normal nursing patterns have been determined for a species, they may be useful indicators of the health of the calf or cow [Amundin, 1986].

Our indications of sexual dimorphism corroborate results reported from wild beluga [Burns and Seaman, 1986; Heide-Jorgensen and Teilmann, 1994], although Doidge [1990] found little, if any, gender-based bias in growth in length. Indeed, sexually dimorphic growth patterns in cetaceans are not lacking from the literature [Best, 1970; Christensen, 1984; Cockcroft and Ross, 1990; Read et al., 1993]. Analyses of growth in total body length in the present study were consistent with those seen in wild beluga [Burns and Seaman, 1986; Doidge, 1990; Heide-Jorgensen and Teilmann, 1994] in that adult males were larger than females, but grow at a slower rate. Yet, our data suggested that male beluga reach lighter asymptotic weights than females while growing faster in this regard, and this contrasts to what has been reported for wild animals [Heide-Jorgensen and Teilmann, 1994]. Captive beluga seem to follow similar body length, but not body weight growth patterns, compared to their wild counterparts. Because adult male beluga are both larger and heavier than females, this discrepancy warrants further discussion.

Previous investigators describing growth in other cetacean species have experienced similar paradoxes, albeit when describing body length and not weight [Best, 1970; Christensen, 1984; Duffield and Miller, 1988; Cockcroft and Ross, 1990; Read et al., 1993; Read and Tolley, 1997]. In general, two hypotheses are presented to explain this disparity. One theory is that adolescent male cetaceans may experience a rapid growth spurt. This would answer the question of how young male beluga end up heavier than females upon reaching adulthood, whereas our model suggests otherwise. It is possible that we failed to capture this growth spurt simply because many of the animals had not yet achieved this milestone within the study period. The other hypothesis discounts the growth spurt and presents the argument

that males end up larger (or in this case, heavier) than females simply because they continue to grow after the females have reached asymptotic weight. If either of these hypotheses holds true for growth in body weight, as well as length, then it may explain our observed data. Similarities and differences notwithstanding, the results from the present study must be viewed cautiously due to the restrictive nature of the range of the data set and the obvious environmental differences between captive and wild beluga.

Results from further captive studies may provide useful tools for assessing baseline life history information pertaining to age and growth dynamics of not only captive, but also wild beluga. As our animals continue to mature, continued monitoring of growth and subsequent analyzes should permit more definitive conclusions on attributes of sexual dimorphism and differences between growth in captive-born and wild beluga.

CONCLUSIONS

In conclusion, we have found that for female beluga, the mean age, length, and weight at first conception were 9.1 ± 2.8 years, 318.0 ± 9.1 cm, 519 ± 84 kg. Beluga are seasonally polyestrous with 80% of conceptions occurring in March–May. The mean luteal phase and total estrous cycle length were 30.0 ± 6.5 days and 48.0 ± 4.6 days, respectively. The mean gestation length was 475.0 ± 20.4 days. For beluga males, the highest serum T values (6.2 ± 4.9 ng/ml) were recorded from January–March with the lowest from August–September (1.1 ± 1.0 ng/ml). At parturition, times of first appearance of flukes or rostrum to delivery, delivery to placental passage, and delivery to nursing were 4.4 ± 2.9 hr, 7.6 ± 1.8 hr, and 43 ± 45 hr, respectively. Food intake decreased consistently on the day of labor with 44% of parturient females exhibiting zero intake. Mean 24-hr peak nursing occurred on Day 3.9 ± 2.7 days, and nursing patterns, as compared to mean ‘normal’ consumption, can be used as an indicator of calf or cow stress or health. Based on the models, captive beluga exhibited gender-biased differences in growth in body length and weight. Predicted body weight at birth for either sex and body length at birth for male and female calves was 88.9 kg, and 154.3 and 160.7 cm, respectively.

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