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Behavioral Development in Beluga Whale (*Delphinapterus leucas*) and Pacific White-Sided Dolphin (*Aethalodelphis obliquidens*) Calves at the Shedd Aquarium

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Abstract – Knowledge of Odontocete developmental patterns is important for general comparative understanding and the implementation of informed husbandry policies. Although beluga whale (*Delphinapterus leucas*) calf behavioral development has previously been assessed in the literature, no previous studies have attempted to observe the behavioral development of Pacific white-sided dolphins (*Aethalodelphis obliquidens*). Seven beluga whale calves and four Pacific white-sided dolphin calves were observed for the first 30 days of life to determine the first occurrence and developmental trajectory of several typically monitored behaviors. Generalized linear mixed models (GLMMs) were used to evaluate the first 30 days for each behavior in successful calves. Beluga calves nursed for significantly longer duration (s/bout), but not frequencies (bouts/hr) compared to Pacific white-sided dolphins. Nursing duration was highest for belugas in the first 10 days of life, but otherwise nursing duration and frequency did not change significantly over time for belugas or Pacific white-sided dolphins. Overall respiration rates across the 30 days did not significantly differ between species, but beluga rates significantly increased over time while Pacific white-sided dolphin rates decreased. Pacific white-sided dolphins spent significantly more time associating with their dams and swimming in the slipstream position than belugas, and only Pacific white-sided dolphins saw significant decreases in these behaviors over time. The results of this study provide additional information regarding Odontocete developmental norms. Future research should continue to focus on calf behavioral development with the goal of increasing calf survival rates and promoting positive welfare in managed care.

Keywords – Odontocete, Behavioral development, Beluga whale, Pacific white-sided dolphin, Nursing, Neonate

Beluga whales (*Delphinapterus leucas*) and Pacific white-sided dolphins (*Aethalodelphis obliquidens*) are both members of the sub-order Odontoceti, or toothed whales. Belugas range throughout the Arctic, while Pacific white-sided dolphins can be found in the north Pacific Ocean. Both species seasonally migrate throughout their range, with both spending significant time in deeper offshore waters, though belugas tend to raise their young in warmer waters near the shore (Leatherwood & Walker, 1982; O'Corry-Crowe et al., 2018). Odontocetes (including belugas and Pacific white-sided dolphins) exhibit similar behavioral and physical developmental patterns to primates and ungulates (Karenina et al., 2013). Belugas calves nurse for approximately 2-3 years while Pacific white-sided dolphin calves nurse for approximately 18 months (Ferrero & Walker, 1996; Krasnova et al., 2006; 2009). While Odontocetes have

an extended nursing period, they physically develop rapidly, typically doubling their weight within the first week to the first few months of life and continue these rapid growth patterns during the first year (Russell et al., 1997). Calves must also begin swimming immediately after birth, relying heavily on maternal assistance before quickly increasing in independence with physical maturity. At one month of age, the average bottlenose dolphin (*Tursiops truncatus*) calf will reach 32% of adult swim speeds (Noren et al., 2006). Likewise, the behavioral changes that occur during the first month of life are typically more frequent and extreme when compared to the rest of the animal's lifespan. Additionally, one study found that early social interactions that occur within the first month of life were significant predictors of behavioral responses that persist into adult social relationships for beluga whales (Krasnova et al., 2009). Ultimately, these findings demonstrate how crucial the infancy period of Odontocete development can be, as early life experiences often influence survival and future development (Peddemors, 1990).

Research concerning the typical development of Odontocete calves is essential to answering some of the basic questions about each species' life history for conservation efforts in the wild, as well as for the continued success of conservation breeding programs in managed care. Importantly, developmental norms are important indicators of welfare that can be assessed alongside other indicators of sustainability, such as infant survival rates, fertility rates, and stillbirth rates (Hill, 2009; Hill et al., 2015). Studies focusing on measuring output variables of welfare, such as behavioral indicators, provide necessary information that can be used to assist facility personnel with assessing the welfare of animals under their care (Lauderdale, Mellen et al., 2021).

Currently, animal care personnel in accredited zoological facilities regularly monitor behavior such as social interactions, maternal care, nursing patterns, and respiratory patterns as indicators of physical health and normal calf development (Hill et al., 2007, 2016a; Robeck et al. 2005). However, estimating population averages and normal variance of each of these behaviors is also crucial for identifying both normal and abnormal development. Similar health reference intervals have been identified in large-scale studies assessing biological markers of health, such as hematology panels, plasma levels, and other biochemical variables (Lauderdale, Walsh, et al., 2021; Miller et al., 2021).

Once these developmental milestones have been established, animal care staff can better identify potential health concerns of young animals and enhance existing policies for interventions to increase survival rates of animals under their care. For instance, a study conducted on African elephants (*Loxodonta africana*) at one zoological facility found that one female calf that did not survive past the first 68 days of life significantly deviated from normal first occurrence of important developmental behaviors, such as nursing and standing (Miller & Andrews, 2013). In a study of bottlenose dolphin calves in one facility, calves that did not successfully survive past 30 days of age had significantly lower average total nursing performance and nursed for significantly shorter durations than successful calves (Ramont et al., 2024). Additionally, Hill (2009) reported increased rates of swimming in both echelon and infant positions, both of which reduce the physical demands of swimming alone, in an ill beluga whale calf at one managed care facility. Monitoring these deviations in normal developmental pattern allow facility staff to provide intervention when required and improve individual calf welfare.

Although the developmental trajectory of Odontocete species is an important area of study for both wild and managed care populations, it is a relatively understudied topic. Previous research has focused on development of beluga whale calves (e.g., Drinnan & Sadleir, 1981; George & Noonan, 2014; Hill, 2009; Hill et al., 2013, 2015; Krasnova et al., 2006; Robeck et al., 2005), while no such behavioral development studies have been conducted on Pacific white-sided dolphins. Therefore, the current study aims to describe the average developmental progression of calf behavior in both species for the first 30 days of life and to describe the developmental deviations of calves that did not survive the infancy period. Four main categories of behaviors were analyzed in both species: nursing, respiration, maternal association, and slipstream position. We expect that, consistent with the literature (Eastcott & Dickinson, 1987; Hill et al., 2013; Russell et al., 1997), both beluga whale calves and Pacific white-sided dolphin calves would decrease the frequency and duration of nursing, and respiration rates by the end of the 30-day observation period. Rates of maternal association were not expected to change, as calves are still largely dependent on their mothers at 30 days old. We did not expect there to be significant differences in any of the behaviors between

the two species, as research has suggested some behavioral similarities between the two such as eye gaze duration and laterality that may play a part in swim patterns and social behaviors (Hill et al., 2016b).

Methods

Ethics Statement

All data collected for this study were observational and did not require changes to animal care and husbandry. Observations were part of a routine monitoring protocol as part of management best practices, and Institutional Animal Care and Use Committee (IACUC) approval was not necessary.

Subjects and Facility

The subjects of this study are seven beluga whale calves and four Pacific white-sided dolphin calves born between 1999-2016 at the John G. Shedd Aquarium in Chicago, Illinois, USA (see Table 1 for demographic information). All animals were housed in the Abbot Oceanarium, an indoor facility comprised of six interconnected habitats. The larger two main habitats could hold either species at any time. Social groupings were flexible and changed often depending on husbandry needs. This includes the days leading up to and after birth in which most dams were usually secluded from the main social group. The Whale Harbor habitat is approximately 8790 sq. ft with a maximum depth of 31 ft, and the Secluded Bay habitat is approximately 2695 sq. ft with a maximum depth of 18 ft. Public viewing is accessible both above the water and in an underwater viewing area.

Table 1

Odontocete Calves Born Between 1999-2016 at the Shedd Aquarium

Species	CalfID	Date of Birth	Sex
Beluga	B1*	7/23/1999	Male
	B2	8/3/1999	Female
	B3	7/15/2000	Male
	B4	7/17/2006	Female
	B5	8/16/2007	Male
	B6	12/14/2009	Male
	B7	8/27/2012	Female
Pacific White-Sided Dolphin	D1*	6/3/2011	Female
	D2	5/28/2012	Male
	D3	6/1/2015	Male
	D4	4/18/2016	Male

Note. *Indicates an animal that did not live past the 30-day infancy period (D1, aged 7 days) or died shortly after (B1, aged 32 days).

Data Collection

All behaviors were recorded by staff members at the Shedd Aquarium during 24-h routine observation sessions. While interobserver reliability was not calculated, all staff members were experienced observers that were extensively trained using an established training protocol. The protocol involved first learning behavior definitions, shadowing a trained observer, training on each behavior individually, and finally a practice period in which the observer was not cleared to collect data until senior staff determined that the observer was fully trained. Over the course of the study, observers totaled approximately 720 h of observations across all 11 animals. Calves B1 and D1 were not observed nursing during the first few days of life; all other surviving calves except calf B2 began nursing within the first 24 h after birth.

Staff conducted focal-animal observations using a combination of all-occurrence continuous sampling for nursing behaviors and instantaneous sampling on the one-minute interval for calf associations and calf position (Altmann, 1974). Behavioral definitions were developed in an ethogram for in-house behavioral monitoring to capture changes in behavior that could be indicative of developing health concerns and monitor temporal variations in behavior. For every bout of nursing observed, the duration was recorded by starting a stopwatch when the calf successfully latched and stopping when the calf removed its rostrum from the mammary slit. The calf was recorded to be in association with its dam when it was located within one meter of her. The calf was recorded to be in the slipstream position when it was swimming no more than a few inches from the dam's side or touching her, and the front of the calf's head did not pass the dam's pectoral fins. Additionally, the trailing edge of the calf's tail could not overlap the dam's flukes, otherwise it was too far back for slipstreaming to occur. The calf could be in any position around the dam vertically; therefore, calves could be in either the echelon or infant positions while slipstreaming. Additionally, calf and dam respiration rates were recorded twice per hour (once in the first 15 min, and once in the last 15 min). Each respiration observation session consisted of a five-minute period in which the number of breaths for both the calf and dam was counted on a tally sheet.

Data Analysis

From staff observation sheets for each calf over the first 30 days of life, we calculated the daily average for nursing frequency (bouts/h), nursing duration (s/bout), maternal association (proportion of scans), slipstream (proportion of scans), and respiration rate (respirations/min). Observation day was binned into three time periods (days 1-10, 11-20, 21-30) for analysis. The calves that did not live past the 30-day infancy period (D1, aged 7 days) or died shortly after (B1, aged 32 days) were not included in the final dataset used in model selection and their behaviors were analyzed descriptively due to the small sample size.

To determine whether calf behaviors changed over time and whether belugas and white-sided dolphin behavior differed, we constructed linear mixed models (LMMs) and generalized linear mixed models (GLMM) in R using the *lme4* and *glmmTMB* packages in R (version 4.3.2; R Core Team, 2023). For nursing frequency, nursing duration, and respiration rate, we constructed LMMs with each of these behaviors as the response variable and calf ID as a random effect. Candidate models included time, species, and their interaction as fixed effects. The model with the lowest AIC was selected as our final model. Since maternal association and slipstream were both proportional response variables, we fitted GLMMs with a beta distribution and a log link function, with calf ID as a random effect. We constructed a full model including time, species, and their interaction as fixed effects. We created reduced models to isolate each effect and compared them to the full model using a likelihood ratio test using analysis of variance (ANOVA) and $\chi 2$ distribution to determine whether the excluded variable significantly affected model fit. We assessed model fit for all final models using plots to evaluate dispersion, residual distribution, zero-inflation, and multicollinearity and detected no violations of model assumptions. When applicable, post-hoc pairwise comparisons were made using the *emmeans* package in R to examine the effect of the interaction between species and time, with Bonferroni correction applied for multiple comparisons.

Results

Successful Calves

Nursing Behaviors

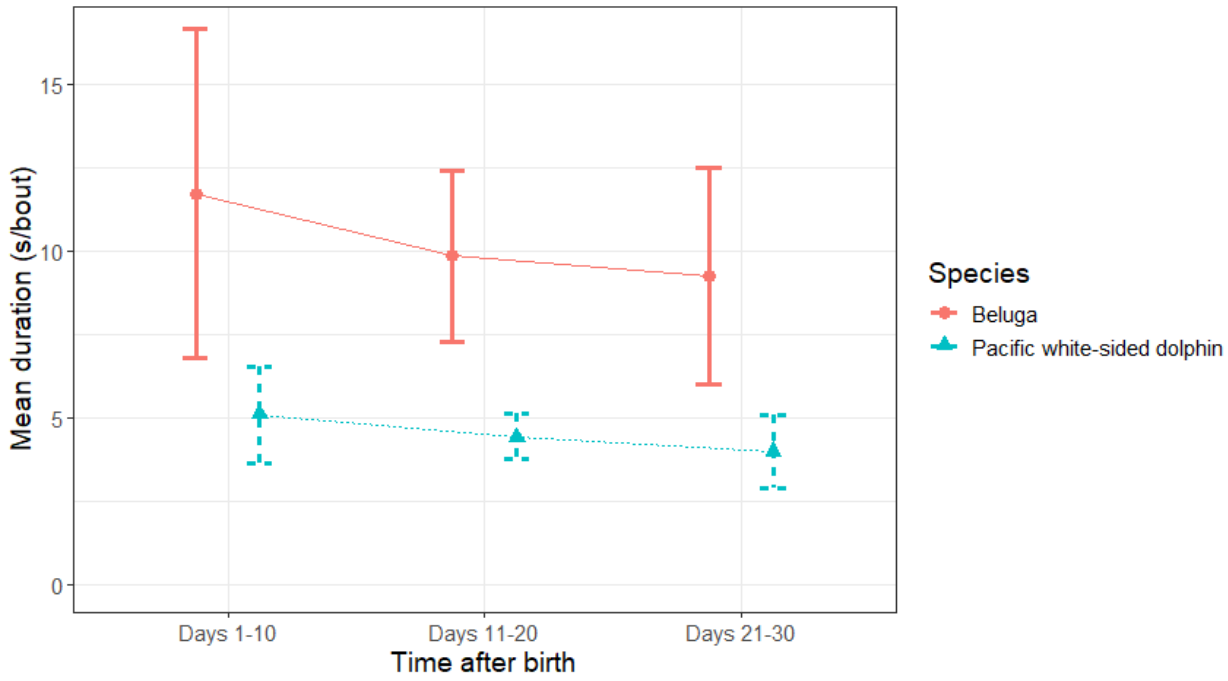
The best fitting model for average nursing duration (seconds/bout) included time, species, and their interaction as fixed effects and calf ID as a random effect. On average, beluga calves nursed for significantly longer durations than Pacific white-sided dolphin calves (β = -6.64, SE = 1.37, t = -4.86, $p < .001$). Post hoc comparisons show that for belugas, nursing duration significantly decreased between time 1 to time 2

(β = 1.90, SE = 0.49, t = 3.85, $p < .001$) and time 1 to time 3 (β = 2.48, SE = 0.48, t = 5.03, $p = < .001$), but not between time 2 to time 3 (β = 0.58, SE = 0.49, t =1.19, $p = .70$). For Pacific white-sided dolphins, nursing duration was not significantly different between time periods ($p > .05$ for all comparisons; Figure 1). Beluga calves nursed an average of 11.7 (SD = 4.93) s/bout during time 1, 9.85 (SD = 2.57) s/bout during time 2, and 9.23 (SD = 3.24) s/bout during time 3. Pacific white-sided dolphin calves nursed an average of 5.10 (SD = 1.45) s/bout during time 1, 4.43 (SD = 0.68) s/bout during time 2, and 4.00 (SD = 1.08) s/bout during time 3.

The best fitting model for average nursing frequency (bouts/hour) included species as a fixed effect and calf ID as a random effect. Time was not included in the model; consequently, average nursing frequency did not vary over time. Additionally, there was no significant difference between the average nursing frequency between species (β = -2.57, SE = 1.47, t = -1.74, $p = .125$). Beluga calves nursed an average of 8.60 (SD = 3.50) bouts/hour, and Pacific white-sided dolphin calves nursed an average of 6.04 (SD = 2.68) bouts/hour.

Figure 1

Average Calf Nursing Duration (s/bout) by Species over Time



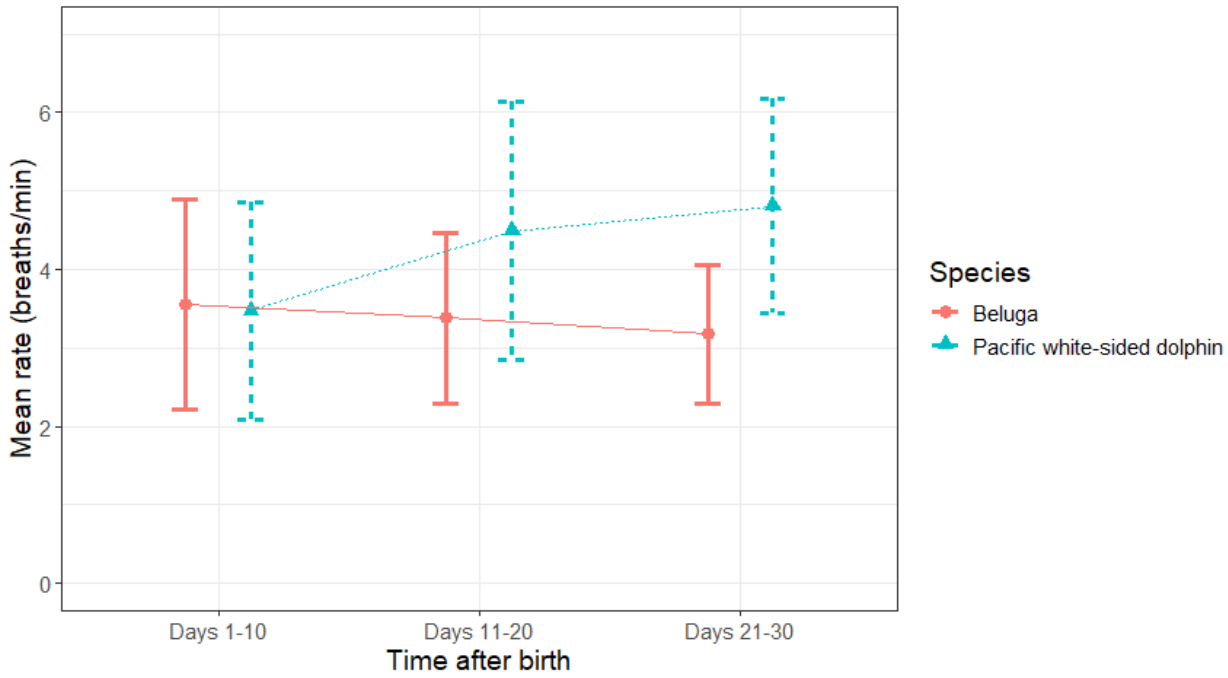
Note. Error bars represent the standard deviation.

Respiration Rate

The best fitting model for average respiration rate (breaths/minute) included time, species, and their interaction as fixed effects and calf ID as a random effect. Species alone did not have a significant effect (β = -0.12, SE = 0.40, t = -0.29, $p = .783$), but there was a significant interaction effect between day and species. Post hoc comparisons show that for belugas, all time points were significantly different from each other ($p < .001$), with respiration rate decreasing over time. For Pacific white-sided dolphins, all time points were significantly different from each other ($p < .001$), with respiration rate increasing over time (Figure 2).

Figure 2

Average Calf Respiration Rate (breaths/min) by Species over Time



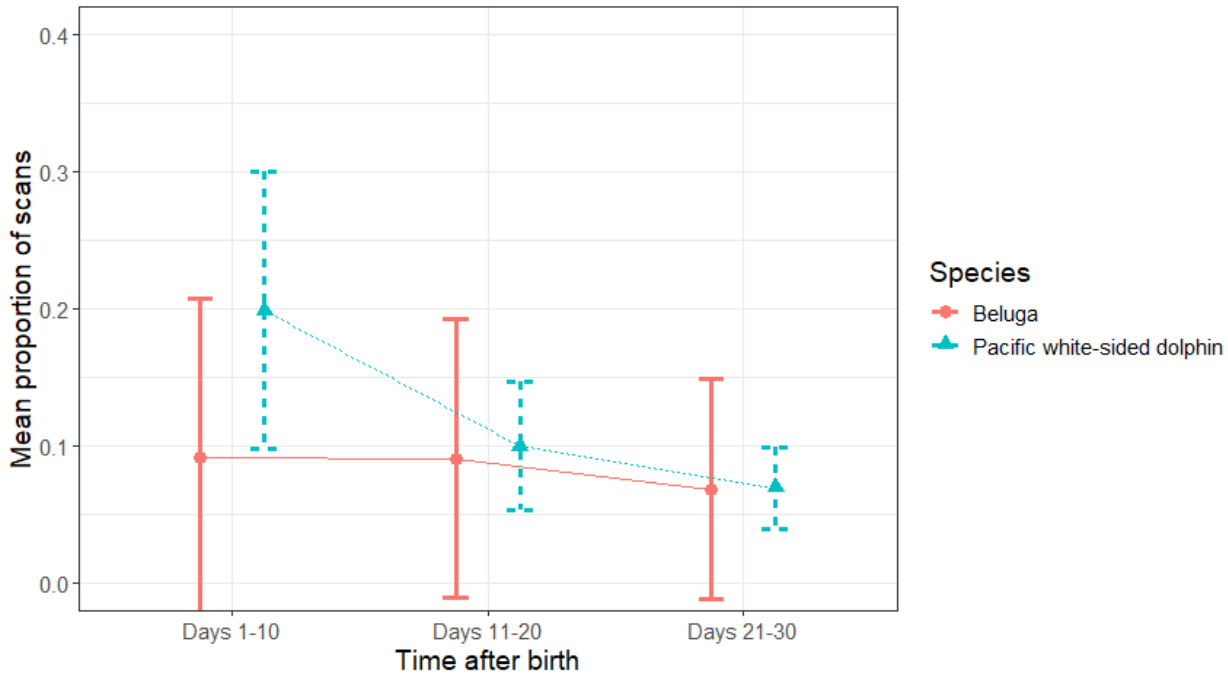
Note. Error bars represent the standard deviation.

Slipstream Position

Full-reduced model comparisons showed that including the interaction between species and time significantly improved fit ($\chi^2 = 34.23$, $p < .001$). The final model included time, species, and their interaction as fixed effects and calf ID as a random effect. On average, beluga calves spent a significantly lower proportion of scans in the slipstream position compared to Pacific white-sided dolphin calves ($\beta = 1.26$, SE = 0.54, z = 2.34, $p = .02$). Post hoc comparisons show that for belugas, the average proportion of scans in slipstream in time 1 did not significantly differ from time 2 ($\beta = -0.08$, SE = 0.10, z = -0.80, $p = 1.00$) and time 3 ($\beta = 0.25$, SE = 0.11, z = 2.32, $p = 0.06$). However, the average proportion of scans in slipstream was significantly lower in time 3 compared to time 2 ($\beta = 0.33$, SE = 0.11, z = 3.12, $p = .005$). For Pacific white-sided dolphins, post hoc comparisons show all time points significantly different from one another ($p < .05$), with the average proportion of scans in slipstream deceasing over time (Figure 3).

Figure 3

Average Proportion of Scans Spent in Slipstream by Species over Time



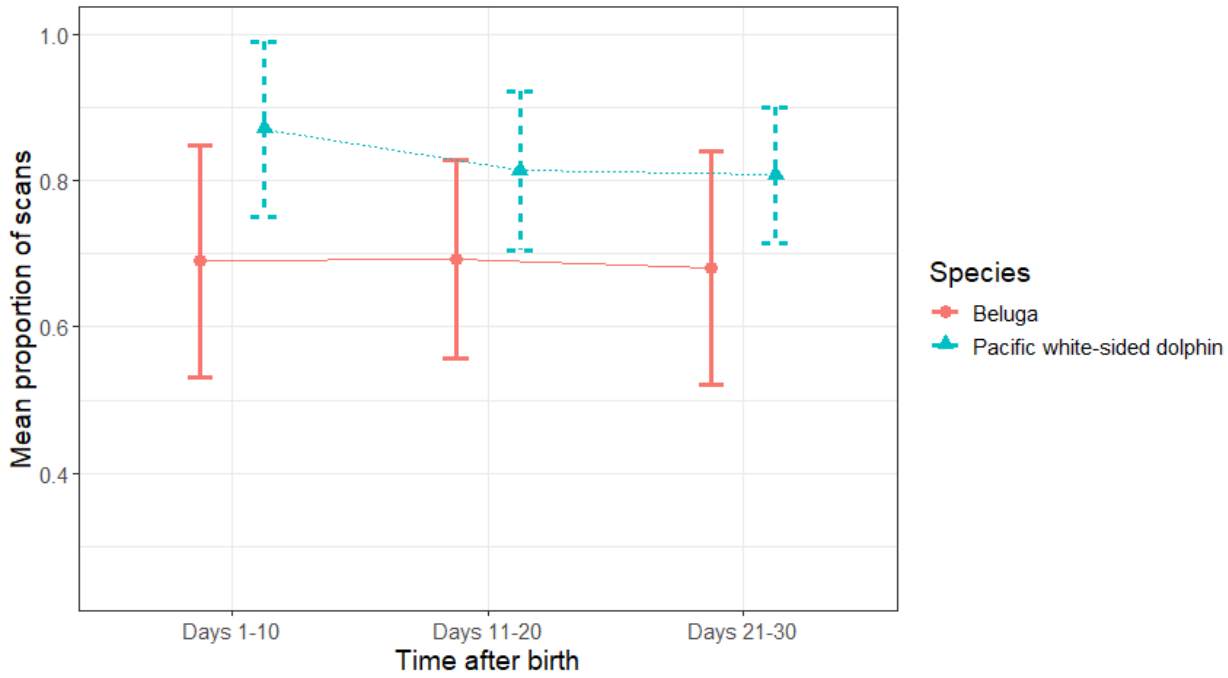
Note. Error bars represent the standard deviation.

Association with Dam

Full-reduced model comparisons showed that including the interaction between species and time significantly improved fit ($\chi^2 = 11.94$, $p < .001$). The final model included time, species, and their interaction as fixed effects and calf ID as a random effect. There was a significant effect of species on the model, with Pacific white-sided dolphin calves spending more time in association with their dam than beluga calves ($\beta = 1.22$, SE = 0.42, z = 2.93, $p = .003$). Post hoc analysis found that beluga calves did not significantly change the average proportion of scans spent in association with the dam over all time points ($p > .05$ for all). In contrast, Pacific white-sided dolphin calves spend lower proportions of scans in association with the dam as time went on, with significant differences between time 1 to time 2 ($\beta = 0.55$, SE = 0.15, z = 3.55, $p = .001$) and time 1 to time 3 ($\beta = 0.66$, SE = 0.15, z = 4.26, $p < .001$), but not between times 2 and 3 ($\beta = 0.11$, SE = 0.14, z = 0.75, $p = 1.0$; Figure 4).

Figure 4

Average Proportion of Scans Spent in Association with the Dam by Species over Time



Note. Error bars represent the standard deviation.

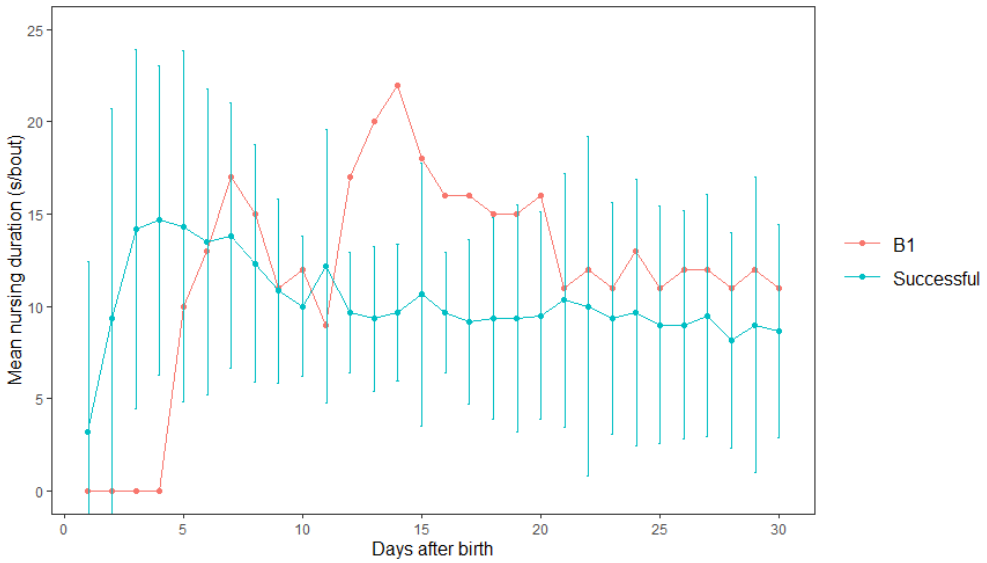
Unsuccessful Calves

Nursing Behaviors

Unsuccessful beluga calf B1's overall average nursing duration across the first 30 days of life (mean = 13.8 s/bout, SD = 3.3) was similar to calves that successfully survived (mean = 10.3 s/bout, SD = 3.8). However, for several days between days 10-20 after birth, calf B1's average nursing duration was over 2 SD higher than successful calves (Figure 5). Unsuccessful Pacific white-sided dolphin calf D1's average nursing duration (mean = 3.4 s/bout, SD = 2.2) was similar to calves that successfully survived (mean = 4.5 s/bout, SD = 1.2). D1's average daily nursing duration for the last 3 days of its life was over 2 SD lower than successful calves (Figure 6).

Figure 5

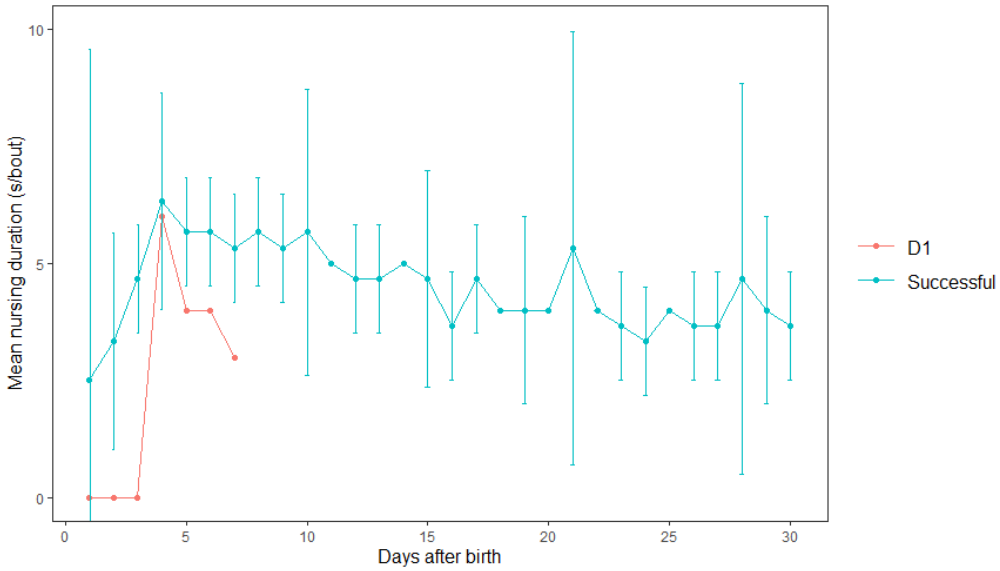
Comparison of Average Daily Nursing Duration Between Successfully Surviving Beluga Calves and Unsuccessful Calf B1 over the First 30 Days of Life



Note. Error bars represent two standard deviations from the mean.

Figure 6

Comparison of Average Daily Nursing Duration Between Successfully Surviving Pacific White-Sided Dolphin Calves and Unsuccessful Calf D1 over the First 30 Days of Life



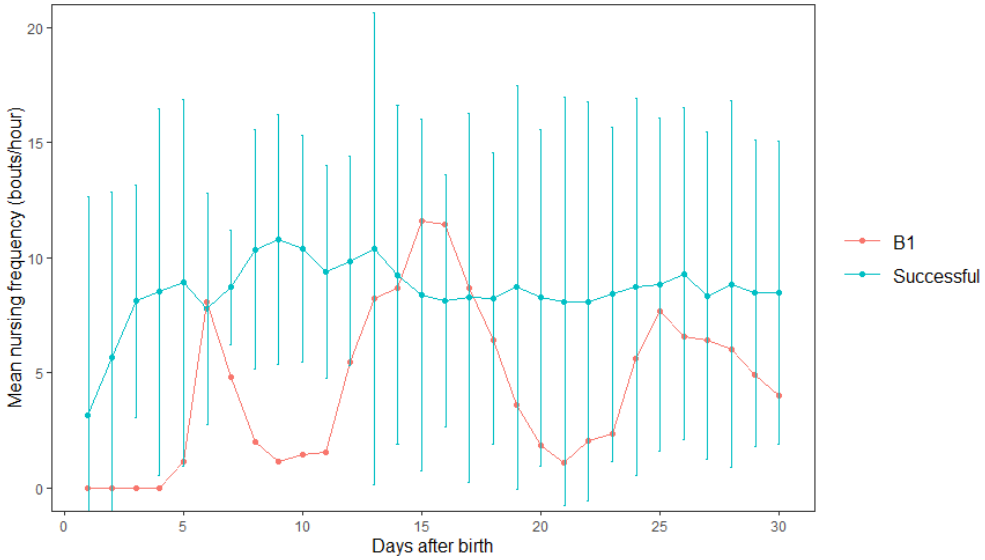
Note. Error bars represent two standard deviations from the mean.

Unsuccessful beluga calf B1's overall average nursing frequency across the first 30 days of life (mean = 5.1 bouts/h, SD = 3.2) was similar to calves that successfully survived (mean = 8.6 bouts/h, SD = 3.5). However, on days 7-11, calf B1's daily average nursing frequency was over 2 SD lower than successful calves (Figure 7). Unsuccessful Pacific white-sided dolphin calf D1's overall average nursing frequency (mean = 1.9 bouts/h, SD = 3.4) was similar to the nursing frequency of calves that successfully

survived (mean = 6.0 bouts/h, SD = 2.7). Unsuccessful Pacific white-sided dolphin calf D1's daily average nursing frequency was within 2 SD of successful calves but was generally lower (Figure 8).

Figure 7

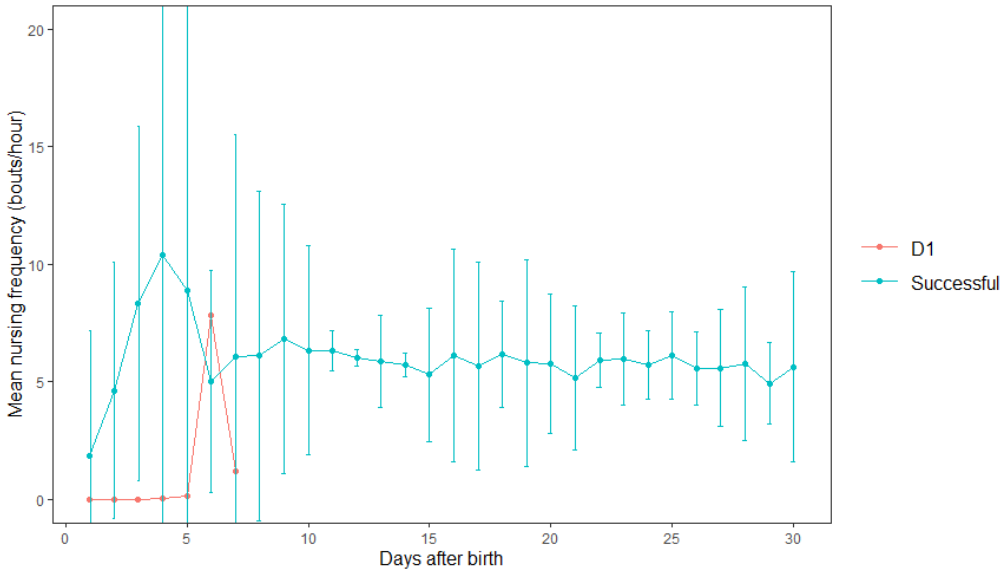
Comparison of Average Daily Nursing Frequency Between Successfully Surviving Beluga Calves and Calf B1 over the First 30 Days of Life



Note. Error bars represent two standard deviations from the mean.

Figure 8

Comparison of Average Daily Nursing Duration Between Successfully Surviving Pacific White-Sided Dolphin Calves and Unsuccessful Calf D1 over the First 30 Days of Life



Note. Error bars represent two standard deviations from the mean.

Respiration Rate

Unsuccessful beluga calf B1's overall average respiration rate across the first 30 days of life (mean = 2.6 resp/min, SD = 0.9) was similar to calves that successfully survived (mean = 3.4 resp/min, SD = 1.1). In addition, B1's average daily respiration rate fell within 2 SD of surviving calves for all 30 days. Unsuccessful Pacific white-sided calf D1's overall average respiration rate (mean = 6.1 resp/min, SD = 2.3) was similar to calves that successfully survived (mean = 4.2 resp/min, SD = 1.6). Unsuccessful Pacific white-sided dolphin calf D1's daily average respiration rates were within 2 SD of successful calves.

Slipstream Position

Unsuccessful beluga calf B1's overall average proportion of scans in slipstream position across the first 30 days of life (mean = .14, SD = 0.10) was similar to calves that successfully survived (mean = .08, SD = 0.10). In addition, B1's average daily proportion of scans in slipstream position fell within 2 SD of surviving calves for all days except for days 4-6, where B1 spent a higher proportion of time in slipstream position (approximately 38% of scans). Unsuccessful Pacific white-sided calf D1's overall average proportion of scans in slipstream position (mean = .06, SD = 0.04) was similar to calves that successfully survived (mean = .12, SD = 0.09). Unsuccessful Pacific white-sided dolphin calf D1's daily average proportion of scans in slipstream positions was within 2 SD of successful calves.

Association with Dam

Unsuccessful beluga calf B1's overall average proportion of scans in association with the dam across the first 30 days of life (mean = .59, SD = 0.14) was similar to calves that successfully survived (mean = .69, SD = 0.15). In addition, B1's average daily proportion of scans in association with the dam fell within 2 SD of surviving calves for all days. Unsuccessful Pacific white-sided calf D1's overall average proportion of scans in association with the dam (mean = .83, SD = 0.18) was similar to calves that successfully survived (mean = .83, SD = 0.11). Unsuccessful Pacific white-sided dolphin calf D1's daily average proportion of scans in association with the dams was within 2 SD of successful calves except for a steep decline on its last day of life (prop = .49).

Discussion

Overall, behavioral development of these zoo-housed beluga and Pacific white-sided dolphin calves was similar, but notable differences highlight the importance of comparative studies to understand general biology and improve the health and welfare of Odontocete calves in managed care. Beluga calves in the present study exhibited a similar nursing duration and frequency to other beluga calves (Russell et al., 1997; Robeck et al., 2005), although the total daily nursing time on average (2024 s/day) was higher compared to calves studied by Drinnan and Sadleir (1981; < 1000 s/day), likely due to methodological differences in defining successful/unsuccessful nursing events. Beluga calves demonstrated the highest average nursing duration during the first 10 days of life but decreased to a similar average duration for the rest of the observation period, a pattern seen in other beluga calves (Drinnan & Sadleir, 1981; Russell et al., 1997; Roebeck et al., 2005), false killer whales (*Pseudorca crassidens;* Clark & Odell, 1999a), killer whales (*Orcinus orca*; Clark & Odell, 1999b), and bottlenose dolphins (Reid et al., 1995).

In contrast, Pacific white-sided dolphin average nursing duration did not significantly differ between the three time periods, and the average nursing frequency remained relatively constant. While little information has been published on this species in managed care, bottlenose dolphins maintained a relatively constant average nursing duration during the same time period, though average nursing frequency decreased (Peddemores et al., 1992; Ramont et al., 2024). Beluga calves in our study also did not demonstrate significantly different average nursing frequency over the first 30 days. Both beluga and Pacific white-sided dolphin calves did not immediately begin nursing, and peak average nursing duration and frequency did

not occur until around four to five days after birth, likely due to the time needed for the calf to learn to nurse. This has been observed in many Odontocete species and has been suggested that calves need the first few days after birth to develop the strength and skills necessary to develop efficient nursing behavior (Robeck et al., 2005; Sweeney et al., 2010; Venn-Watson et al., 2011).

These results suggest that both beluga and Pacific white-sided dolphin calves develop nursing behaviors following similar overall patterns to other Odontocete species in managed care. However, comparisons between species suggest that there may be some slight differences across taxonomic groups. For example, our model found that beluga calves exhibited a longer average nursing duration than Pacific white-sided dolphin calves but did not differ in nursing frequency. Beluga average nursing duration was around 8.6 s/bout, while Pacific white-sided dolphins averaged around 6.0 s/bout. In one study, bottlenose dolphins averaged around 7.2 s/bout during the first 30 days of life (Ramont et al., 2024). False killer whales demonstrated a similar mean duration during the same time period (approximately 8.4 s/suckle; Clark & Odell, 1999a). These species differences are likely tied to differences in life history and habitat and the speed at which the different species mature. Future research should focus on documenting species differences in nursing to understand the evolution of these behaviors in Odontocetes.

In general, Odontocete calf respiration rates are higher than in adults (George & Noonan 2014; Mortola & Limoges, 2006). Calves need time to build the strength and coordination to hold their breath for longer dive times (Cockroft & Ross, 1989). During the first 30 days, we did not find any significant differences in respiration rate between belugas and Pacific white-sided dolphins in this short time period, and both species' respiration rates were similar to calves in the newborn period for belugas (2.05 breaths/min; George & Noonan 2014; 3.0 breaths/min; Mortola & Limoges 2006) and bottlenose dolphins (approximately 3.0 breaths/min; Kastelein et al., 1990; Mann & Smuts, 1999; Sweeney et al., 2010). However, over the three time periods beluga calves significantly decreased their mean respiration rate while Pacific white-sided dolphin calves significantly increased their mean respiration rate. This difference in pattern suggests that as these species mature, they develop different respiratory behavior patterns. In adult Odontocetes at rest, belugas have a lower breathing rate than bottlenose dolphins (Mortola & Limoges, 2006). It is likely that these different respiratory patterns evolved based on the different niches occupied by these species, as belugas must hold their breath for longer when navigating under ice floes on the ocean surface, while most dolphins do not have this constraint. Additionally, Pacific white-sided dolphins have a reputation for being a very high energy species and thus may need to breathe more frequently due to increased activity (Stacey & Baird, 1991).

Both beluga and Pacific white-sided dolphin calves spent the majority of their time located near their mothers. However, Pacific white-sided dolphins spent a significantly greater proportion of scans in association with their dam than belugas. This may be due to social/developmental factors that differ between belugas and dolphins such as rate of growth and social group composition (Hill et al., 2013; Mann & Smuts, 1999). Additionally, only Pacific white-sided dolphin calves saw significant changes over time. Calves spent the highest proportion of time associating with their dam during the first 10 days, which decreased and then plateaued for the rest of the 30-day period. This pattern of maternal association is similar to what has been observed in bottlenose dolphins in managed care, where there was a gradual decrease in the time spent with mothers from birth to one year (Gubbins et al., 1999). In wild bottlenose dolphins, mother-infant proximity also gradually decreased between the first and second months of life (Mann & Smuts 1999). In contrast, beluga calves did not have any significant changes in the proportion of time spent associating with their dam over the first thirty days of life. Similar patterns of association have been seen in other studies of beluga calves in managed care (Hill et al., 2013, 2017) and in the wild (Krasnova et al., 2006), suggesting that successful beluga and Pacific white-sided dolphin calves in this study followed developmentally normal patterns of dam association.

In addition, Pacific white-sided dolphin calves spent a significantly higher proportion of time swimming in the slipstream position than beluga calves. Since swimming in the dam's slipstream reduces the energy requirement of swimming, younger calves spend more time in this position. Both the echelon position taken by neonates and the infant position taken by slightly older calves confer hydrodynamic benefits to the calf (Noren & Edwards, 2011). The Pacific white-sided dolphin is specifically known for its

agile swimming and acrobatic nature (Stacey & Baird, 1991). As a result, Pacific white-sided dolphin calves may utilize slipstream swimming positions more frequently to better keep up with their fast-swimming dams while slower swimming beluga calves do not necessarily need this extra boost. Future research should explore the swim speeds of mother-calf dyads of multiple odontocete species throughout their development to elucidate potential relationships between swim speed and calf swimming position.

Pacific white-sided dolphin calves displayed a significant decrease in the proportion of slipstream behaviors over the first 30 days. Some bottlenose dolphin calves follow a similar trend (Reid et al., 1995; Von Streit et al., 2013), while others only saw a difference in the type of slipstream position (e.g., echelon position decreased, infant position increased; Gubbins et al., 1999; Mann & Smuts, 1999). However, our study did not distinguish between the two positions and thus we cannot make direct comparisons. In contrast, Beluga calves stayed relatively consistent in the proportion of time spent in the slipstream position, with a significant difference observed only between days 11-20 and days 21-30. Hill et al. (2013) found that for two female beluga calves, the proportion of time swimming with the dam stayed relatively consistent across the first year of life. It is possible that species differences in the consistency of swimming behaviors is due to the faster growth rate of Pacific white-sided dolphins compared to beluga whales.

Comparing the behavior of calves that did not successfully survive to successful calves can help determine deviations from normal patterns of behavior for animal care staff to identify early warning signs of illness or other complications. For example, some bottlenose dolphin calves that did not successfully survive past 30 days of age struggled to develop appropriate nursing patterns from birth (Ramont et al., 2024; Von Streit et al., 2013). In the current study, both unsuccessful calves took several days to begin nursing after birth. While surviving Pacific white-sided dolphin calves took the first few days of life to develop nursing competency, calf D1 did not seem to develop normal patterns of nursing at all during its lifetime, despite the dam's normal levels of maternal care and additional support from animal care staff. Similarly, beluga calf B1 was given supportive care and antibiotics on day 5, and nursing duration rose to higher than developmentally normal calves between days 12-17. Additionally, when calf B1 first established nursing at day 5, average daily nursing frequencies were comparatively low. Calf B1 also had more variable nursing behavior over the first 30 days of life compared to calves that survived. These comparisons provide further evidence that in beluga and Pacific white-sided dolphin calves nursing behavior over the first 30 days can inform animal care staff about a calf's current health status to determine whether further care or intervention is necessary.

Respiration rate is an easily observed indicator of animal health and welfare (George & Noonan, 2014). Like terrestrial mammals, young marine mammals generally have higher respiration rates compared to adults (Kastelein et al., 1990; George & Noonan 2014; Peddemors, 1990; Mann & Smuts, 1999; Mortola & Limoges, 2006). However, sudden elevated respiration rates in calves can be an indicator of stress and rapidly declining health in bottlenose dolphin calves (Thurman & Williams 1986). Neither of the unsuccessful calves in this study demonstrated dramatic differences in respiration rates compared to developmentally normal calves. However, animal activity, time of day, and seasonality can affect respiration rates (George & Noonan, 2014; Mortola & Limoges, 2006). Our methods did not control for these factors; therefore, it is possible that the unsuccessful calves may have experienced elevated respiratory rates during the first 30 days that were masked by the calf's activity or other confounding factors. Future research should aim to record respiratory rates only during periods of rest.

Previous research has suggested that the proportion of time spent near the dam can be influenced by calf health (Hill et al., 2013; Reid et al., 1995). Both unsuccessful calves spent similar proportions of their time in proximity to their dam in comparison to successful calves, though calf D1 dramatically decreased the proportion of time spent in proximity to its dam on the last day of life due to the intensive veterinary care provided during this time. While this decrease was due to husbandry interventions, it is likely that the calf would have struggled to maintain proximity during this time. While dam proximity is an important behavior, swimming in the dam's slipstream additionally provides a hydrodynamic boost and energy savings to young calves, which some individuals may take advantage of when in poor health (Hill, 2009). Calf B1 had a peak in the average proportion of time specifically spent in the slipstream position with the dam on days four to six, which coincided with delayed nursing development and the administration

of antibiotics; it is likely the calf relied on its dam's slipstream to conserve energy during this period. Consequently, the calf's ability to remain close by its dam and to take advantage of slipstreaming benefits can be an important indicator of calf health in belugas and Pacific white-sided dolphins.

While this research provides essential data on the growth and development of two less-studied cetacean species, we encountered several limitations. First, our small sample size, particularly for calves that did not survive, prevents us from generalizing our data to the population as a whole. Future research should attempt to recruit as many individuals as possible from multiple institutions. Second, while both the beluga and Pacific white-sided dolphins spent time in either habitat, we did not factor in which calves spent time in which habitat. It is possible that the different habitat or social groupings could have an impact on behaviors such as calf position and respiration rate. Third, because of our small sample size, we were unable to evaluate the effect of maternal experience on calf survivability. Maternal experience has been shown to affect calf behaviors, including nursing. In bottlenose dolphins, one comparison of two mother-calf pairs found that the primiparous pair needed more time to develop normal swimming and nursing behaviors than the calf of the experienced mother (von Streit et al., 2013). Additionally, bottlenose dolphin mothers can have different maternal styles, with some mothers more likely to actively keep their calf close by, which can change swimming behaviors in the calf (Hill et al., 2007). Consequently, future research should investigate maternal experience and maternal style in the context of the development of calf behavior.

This research confirms developmental norms for belugas over the first 30 days and provides novel information about the development of Pacific white-sided dolphin calves in managed care. Comparing unsuccessful calves to those that successfully survived provides additional information regarding what parameters should be considered "normal" for each species. A comparative method is helpful to ensure that animal care staff has as much information as possible to inform their management decisions for future Odontocete calves to promote peak animal health and welfare and continue to add to our knowledge about their general biology and behavior.

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