

Observations of Mating Practice by Non-Sexually Mature Male Belugas (*Delphinapterus leucas*)

Heather M. Manitzas Hill,¹ Jackson R. Ham,² and Malin K. Lilley³

¹Department of Psychology, St Mary's University, San Antonio, TX 78228, USA

E-mail: hhill1@stmarytx.edu

²Department of Neuroscience, University of Lethbridge, Lethbridge, Alberta, Canada T1K 3M4

³Department of Life Sciences, Texas A&M University, San Antonio, TX 78224, USA

Mating is critical to the propagation of cetaceans, and while much of this system is biologically hardwired or uses innate behavioral systems (see Hogan, 2001, for details on the development of behavior systems), there is evidence that learned behaviors contribute significantly to a species' success. However, the mechanisms by which cetaceans select their mates or develop the critical behaviors needed for mating success remain unknown. Whether females select male humpback whales (*Megaptera novaeangliae*) based on an intriguing song (see Herman, 2017), or female harbor porpoises (*Phocoena phocoena*) choose males that show the best aerial maneuvers (Keener et al., 2018), or female river dolphins (e.g., *Inia geoffrensis*) choose the male that presents the best stick (Martin et al., 2008; Araújo & Wang, 2012), or male bottlenose dolphins (*Tursiops truncatus*) choose previously successful breeders (Schaeff, 2007), we do not fully understand the roles of innate behaviors or learned behaviors within cetacean mating systems (reviewed by Orbach, 2019; Schaeff, 2007).

Belugas, or white whales (*Delphinapterus leucas*), are odontocetes that inhabit Arctic and subarctic waters, and live in a fission-fusion social system (Michaud, 2014; O'Corry-Crowe et al., 2020; Mayette et al., 2022), with seasonal migrations between winter hunting areas and summer socializing areas (Frost & Lowry, 1990; Lydersen et al., 2001; O'Corry-Crowe et al., 2018). There are 22 recognized beluga stocks, two of which are critically endangered: (1) the Cook Inlet stock and (2) the St. Lawrence River stock (Pippard, 1985; Lowry et al., 2012). One of the most important questions that remains is why these two stocks continue to decline in number. While many explanations include anthropogenic effects, such as noise, toxins, boat traffic, and strikes (Krasnova et al., 2015; Lesage, 2021; Vergara et al., 2021), there may also be an issue with mate selection. As a sexually dimorphic species with males about 1.5 times larger than females (Heide-Jørgensen &

Teilmann, 1994; Stewart, 1994), some scientists have suggested that females may choose their mating partners. Unfortunately, this suggestion remains speculative as a systematic study on mate selection has yet to be conducted, and the possible mechanisms have not been elucidated.

Socially, belugas are considered gregarious as they can be found in large social groupings, especially during the summer when hundreds or thousands of belugas converge on socialization areas (e.g., Cunningham Inlet; Sergeant & Brodie, 1975). While migrating to hunting grounds, some stocks of belugas are thought to split off into smaller, sex- and age-based social groups that appear to be related (O'Corry-Crowe et al., 2020). That is, adult males may be found in small social groups that travel separately from larger social groups that include females and their sexually immature offspring (O'Corry-Crowe et al., 2020). Curiously, despite the tendency to be found in large social groups that travel together, there appear to be limited social interactions indicative of bonded animals. Work with belugas in managed care has shown that adult and juvenile males appear to have partner preferences when provided opportunities for same age and sex companions (Hill et al., 2015a, 2015b, 2018; Mazikowski et al., 2018; Lilley et al., 2020), and this same-sex preference emerges early in development (Mazikowski et al., 2018; Ham et al., 2022). Adult females appear to be much more independent and bond primarily with their unweaned offspring (Krasnova et al., 2006, 2009, 2014). The frequent socio-sexual behavior observed in males and young females is very rarely observed in adult females (Hill et al., 2015b). As calves, females do appear to have partner preferences at times but are much more variable in their interactions with others (Ham et al., 2022).

Behaviorally, observations from both the natural habitat and managed care corroborate that belugas are extremely vocal and display oriented—whether the beluga stock inhabits the

muddy waters of the Cook Inlet or the clear waters of Cunningham Inlet (Horback et al., 2010; Hill et al., 2015b; Lomac-MacNair et al., 2016). One area of research that our laboratory has pursued is the development of socio-sexual behaviors and their relationship to non-conceptive behaviors and courtship-oriented mating behaviors. Since 2007, one beluga population in human care has been studied systematically using the same data collection protocols, creating a large behavioral dataset (Hill & Nollens, 2019). This longitudinal study has provided opportunities to follow the development of beluga behavior, with some animals followed since their birth and through their juvenile and subadult phases. In total, 20 different belugas (12 females and 8 males, ranging between birth and 35+ y) have been observed. Over the years, social composition has varied with respect to the adult males and sexually maturing subadult males present in this population and, occasionally, the number of sexually mature females. Animal care staff typically determine the daily social compositions but often group the belugas in compositions that are typical of wild populations (i.e., mothers and calves, mixed age and sex weaned immatures, and adult male and females without offspring).

Because breeding season occurs annually (usually February to May for this population, which is similar to wild populations; Heide-Jørgensen & Teilmann, 1994), social compositions are managed to simulate the breeding environments in the wild. After a number of years of study, it became clear that behavioral milestones existed and depended on social composition, especially with regard to the socio-sexual repertoire, which overlaps with and precedes the courtship/mating repertoire (see Ham, 2021; Ham et al., 2022). Ham et al. (2022) found these beluga calves (male and female) performed some elements of adult male courtship behavioral repertoire, but those behaviors were not well-formed and developed in a piecemeal fashion instead of emerging simultaneously. By the time the same male calves reached juvenile and subadult status (i.e., approximately 4 to 6 y and 7 to 10 y, respectively; sexual maturity is achieved by most males after 10 y; Robeck et al., 2005), many aspects of the courtship and mating repertoire were more fully developed (i.e., adult-like in topography) (Lilley et al., 2020). Together, these studies suggested that mating behavior, especially behaviors involved in courtship, by male belugas may have a learned, behavioral component that subsequently could affect their future success as a progenitor. These behavioral emergence trends were moderated by the presence or absence of adult male or immature male belugas. Ham et al. (2022) found that calves with older, mature males present during their pre-weaning years produced

socio-sexual behaviors at an earlier age than those who had not had older, mature males present, whereas weaned, immature males were more likely to display socio-sexual, courtship behaviors if young calves were present (Lilley et al., 2020). It is unclear if the presence of an adult male provides a model for adult male courtship behavior or enables immature animals to practice with the older males, while the presence of younger calves provides more opportunities to practice. It is likely a combination of both explanations given that immature animals occasionally displayed socio-sexual or future courtship behaviors toward inanimate or inappropriate stimuli such as environmental enrichment objects or humans (Ham et al., 2022). These trends suggest that emergence and mastery of some innate behaviors that are later exhibited in the adult male courtship/mating repertoire are influenced by the social composition and presence of older males, which could have long-term consequences on reproductive success. That is, if one male beluga is more socially adept due to previous exposure and practice (i.e., courtship behaviors) compared to another, future interactions with females may be affected, especially if female mate choice occurs.

In belugas, copulation is rarely observed. Glabicky et al. (2010) described the seasonal increase in pelvic thrusting for males that is correlated with the mating season, and Ham et al. (2021b) found that sexual play and other social behaviors fluctuate on a seasonal basis, peaking when mating and calving occurs in concert with hormones (Robeck et al., 2005; Richard et al., 2017). Despite many 24-h observations, few reproductive copulations were ever recorded for a breeding population of belugas with two adult males and seven adult females, but copulation had occurred as indicated indirectly by pregnancies. The adult male courtship sequence typically begins with directed gazes, follows at a distance, closer proximity lateral presentations, horizontal S-postures with the genital region thrust forward, and bubble trails with some open mouth displays (Lilley et al., 2022). In addition to visual displays, the adult male also produces a deep foghorn vocalization more frequently during the breeding season and may become more vocal (observations that need to be studied systematically). If a female is interested, she will swim with the male. In our experience, these sequences do correspond with follicular activity and can last up to a week (H. Manitzas Hill, pers. obs.).

Based on multiple observations across years and multiple facilities, it appears that adult males may vary in their mating success. Whether this mating success is related to body condition, vocalizations, behavior, or some other unidentified element, the mechanism remains unknown.

In this paper, we describe a series of observations that were categorized as courtship displays by two different immature males toward two different older, unrelated adult females. Both anecdotes have not been described before nor have they been included in previous work on understanding the emergence of behaviors represented initially in socio-sexual repertoires as immature males and later represented in courtship/mating repertoires.

Anecdote One

One observation occurred in May of 2012 in which an almost 5-y-old sexually immature male beluga initiated a sequence of social interactions that were perceived as courtship attempts toward a mature female. As shown in Supplemental Video A, the male initially presented to the mature female and swam alongside her (the Supplemental Videos for this paper are available in the “Supplemental Material” section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). In most other circumstances, the adult female would have ignored him and swam away or responded with agonistic behavior (e.g., Horback et al., 2010; Ham et al., 2021a). However, on this occasion, she continued to reciprocate the interaction with similar responses. The resulting interactions between the two belugas included bubble streams typically produced by the male, circle swimming around the adult female by the immature male, open mouths by both, mouthing along the female’s body by the male, and mouth-to-mouth interactions with each other (see Hill et al., 2019, for a description of mouth-to-mouth interactions between juveniles). The intriguing piece to this observation was that the social interaction was atypical for both animals. While tolerant to calves, the mature female either ignored or vocalized with a threat bark and head jerk when this male had previously swam too closely. Likewise, this immature male rarely attempted to swim with adult females as he spent more of his time interacting with younger animals or with the adult male (Hill & Ramirez, 2014; Lilley et al., 2020; Ham et al., 2022). Throughout this unusual social interaction, the male displayed many elements of the socio-sexual and courtship repertoires but did not do so in a typical adult behavioral sequence or form, and some behaviors such as an erection and thrust were missing (Glabicky et al., 2010; Hill et al., 2015b; Lilley et al., 2022). This social interaction lasted for approximately 3 min and was one of the first attempted courtship interactions observed for this immature male with an adult female.

Anecdote Two

A second set of observations occurred with a different 7- to 8-y-old male beluga and a different adult female between March and April 2020 (four observations), again in July 2020 (one observation), and then again between May and June 2021 (three observations). Like the other male beluga, this immature beluga also directed lateral presentations and pair swims toward the adult female. Unlike “Anecdote One,” in which the female engaged with the male and reciprocated some of the behaviors, in this set of observations, the adult female played a more active role. That is, this female actively solicited attention from the male by also displaying lateral presentations and bubble streams in addition to maintaining the social interaction through spatial proximity. Generally, the male displayed lateral presentations to the female, swam alongside her, exhibited sexual S-postures, bubble streamed, produced several open mouths, and had small erections several times (despite being capable of full erections and previously observed with penile erections). However, contact was minimal, no mouth-to-mouth interactions occurred, and only occasional pelvic thrusting was observed. Like the younger male in “Anecdote One,” these sequences were incomplete in comparison to previously recorded adult male courtship displays. On one occasion, the male opened his mouth at the surface and then, after submerging and beginning the presentation behavior, produced simultaneous bubbles from both his blowhole and his mouth. Following this behavior, the adult female also produced bubbles from the blowhole while reciprocating an S-posture toward the male (see Supplemental Video B).

Knowledge of the courtship and mating process in belugas would benefit beluga populations in their natural habitat as well as beluga populations in managed care (see Manitzas Hill et al., 2021). While some behaviors of the courtship repertoire emerge as part of the developmental process of calves, other behavioral aspects of the repertoire may benefit from socially appropriate models, like the presence of older male subadults and adults to observe and potential adult females with whom to practice. This idea is supported by research with bottlenose dolphin juvenile males that have been observed to practice socio-sexual behavior with adult females, age-matched conspecifics, and adult males (Mann, 2006; Harvey et al., 2017). Based on the timing of the seasonal breeding in wild populations and gestation length, it seems plausible that the summer gatherings of belugas, where animals of both sexes and all ages are present (O’Corry-Crowe et al., 2018, 2020), is a time that immature calves may be able to observe how

subadult and adult males court the adult females and potentially even participate in a more playful manner (Lilley et al., 2020; Ham et al., 2022). If male competition is present in belugas (see Kelley et al., 2015), most likely in subtle forms, and female choice occurs, then observation of successful males (i.e., able to copulate with a receptive female) could influence future reproductive success for the immature males.

The two sets of observations described herein provide additional insight to the development of courtship in belugas. Based on our longitudinal work, socio-sexual behavior, which is often playful, emerges early (in the first month of life) and is directed first toward the calf's mother and similar-aged calves for both male and female calves (Ham et al., 2022). These behaviors subsequently become more refined and complex over time with practice, especially when exposed to older immature males and adult males (Hill et al., 2015b; Lilley et al., 2020; Ham et al., 2022). Same-sex, socio-sexual behaviors become more frequent for males as they mature, whereas these behaviors drop off for females (Lilley et al., 2020). Although immature females may be the recipient of attempted pelvic thrusts and courtship maneuvers by immature and mature males, the females do not practice the same behaviors as frequently as they mature. Clearly, more observations are needed to better understand the mating system of belugas. However, it seems reasonable that practice with specific courtship behaviors and its adult sequence is needed to develop the repertoire fully, and this process can be facilitated by the presence of appropriate male models and potential adult female partners as males near sexual maturity. For example, with different observations that could be categorized as mating practice for immature male belugas, the adult male that was present in the social composition was observed to intervene between the interacting immature male and adult female at times while making no response other times; no pattern was observed depending on current group composition (H. Manitzas Hill & M. Lilley, pers. obs.). Future studies should attempt to correlate frequency and/or refinement of socio-sexual behavior and mating success (i.e., number of successful pregnancies, number of calves sired). This knowledge can inform animal management processes for both captive and wild populations, especially beluga stocks that are critically endangered, and should continue to be studied systematically in both settings.

Acknowledgments

The authors thank SeaWorld of Texas for generously giving us access to observe the animals (SeaWorld Parks & Entertainment Technical Contribution Number 2022-8), the numerous research assistants who have helped with this long-term study, and two anonymous reviewers whose feedback helped to improve the paper.

Literature Cited

- Araújo, C. C., & Wang, J. Y. (2012). Botos (*Inia geoffrensis*) in the upper reaches of the Tocantins River (Central Brazil) with observations of unusual behavior, including object carrying. *Aquatic Mammals*, 38(4), 435-440. <https://doi.org/10.1578/AM.38.4.2012.435>
- Frost, K., & Lowry, L. (1990). Distribution, abundance and movements of beluga whales, *Delphinapterus leucas*, in coastal waters of western Alaska. *Canadian Bulletin of Fisheries and Aquatic Sciences*, 224, 39-57.
- Glabicky, N., DuBrava, A., & Noonan, M. (2010). Social-sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). *Polar Biology*, 33(8), 1145-1147. <https://doi.org/10.1007/s00300-010-0790-3>
- Ham, J. R. (2021). *Social and non-social play in beluga whales* (*Delphinapterus leucas*) (Master's thesis). University of Lethbridge, Lethbridge, Alberta, Canada. <https://hdl.handle.net/10133/6087>
- Ham, J. R., Lilley, M. K., & Manitzas Hill, H. M. (2021a). Conspecific scarring on wild belugas (*Delphinapterus leucas*) in Cunningham Inlet. *Behaviour*, 158(8-9), 663-683. <https://doi.org/10.1163/1568539X-bja10086>
- Ham, J. R., Lilley, M. K., Miller, M. R., & Manitzas Hill, H. M. (2021b). Seasonality of social behaviour among immature belugas (*Delphinapterus leucas*) in managed care. *Polar Research*, 40, 5498. <https://doi.org/10.33265/polar.v40.5498>
- Ham, J. R., Lilley, M. K., Lelekach, J., Miller, M. R., Robeck, T. R., Pellis, S. M., & Manitzas Hill, H. M. (2022). The emergence and early development of socio-sexual behavior in beluga calves (*Delphinapterus leucas*). *Behavioural Processes*, 200, 104695. <https://doi.org/10.1016/j.beproc.2022.104695>
- Harvey, B. S., Dudzinski, K. M., & Kuczaj, S. A. (2017). Associations and the role of affiliative, agonistic, and socio-sexual behaviors among common bottlenose dolphins (*Tursiops truncatus*). *Behavioural Processes*, 135, 145-156. <https://doi.org/10.1016/j.beproc.2016.12.013>
- Heide-Jørgensen, M. P., & Teilmann, J. (1994). Growth, reproduction, age structure, and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. *Meddelelser Om Grønland, Bioscience*, 39, 195-212.
- Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews*, 92(3), 1795-1818. <https://doi.org/10.1111/brv.12309>

- Hill, H. M., & Nollens, H. (2019). Providing belugas (*Delphinapterus leucas*) in controlled environments opportunities to thrive: Health, self-maintenance, species-specific behavior, and choice and control. *Frontiers in Psychology*, *10*(1), 52-71. <https://doi.org/10.3389/fpsyg.2019.01776>
- Hill, H., & Ramirez, D. (2014). Adults play but not like their young: The frequency and types of play by belugas (*Delphinapterus leucas*) in human care. *Animal Behavior and Cognition*, *1*(2), 166-185. <https://doi.org/10.12966/abc.05.07.2014>
- Hill, H. M., Garcia de Oliveira Silva-Gruber, D., & Noonan, M. (2018). Sex-specific social affiliation in captive beluga whales (*Delphinapterus leucas*). *Aquatic Mammals*, *44*(3), 250-255. <https://doi.org/10.1578/AM.44.3.2018.250>
- Hill, H. M., Dietrich, S., Guarino, S., Banda, M., & Lacy, K. (2019). Preliminary observations of an unusual mouth interaction between beluga calves (*Delphinapterus leucas*). *Zoo Biology*, *38*, 149-156. <https://doi.org/10.1002/zoo.21463>
- Hill, H., Guarino, S., Crandall, S., Lenhart, E., & Dietrich, S. (2015a). Young belugas diversify adult beluga (*Delphinapterus leucas*) behavior. *Animal Behavior and Cognition*, *2*(3), 267-284. <https://doi.org/10.12966/abc.08.06.2015>
- Hill, H. M., Dietrich, S., Yeater, D., McKinnon, M., Miller, M., Aibel, S., & Dove, A. (2015b). Developing a catalog of socio-sexual behaviors of beluga whales (*Delphinapterus leucas*). *Animal Behavior and Cognition*, *2*(2), 105-123. <https://doi.org/10.12966/abc.05.01.2015>
- Hogan, J. A. (2001). Structure and development of behavior systems. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology* (Vol. 13, pp. 229-279). Kluwer Academic/Plenum Press. <https://doi.org/10.3758/BF03210948>
- Horback, K. M., Friedman, W. R., & Johnson, C. M. (2010). The occurrence and context of S-posture display by captive belugas (*Delphinapterus leucas*). *International Journal of Comparative Psychology*, *23*, 689-700.
- Keener, W., Webber, M. A., Szczepaniak, I. D., Markowitz, T. M., & Orbach, D. N. (2018). The sex life of harbor porpoises (*Phocoena phocoena*): Lateralized and aerial behavior. *Aquatic Mammals*, *44*(6), 620-632. <https://doi.org/10.1578/AM.44.6.2018.620>
- Kelley, T. C., Stewart, R. E. A., Yurkowski, D. J., Ryan, A., & Ferguson, S. H. (2015). Mating ecology of beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) as estimated by reproductive tract metrics. *Marine Mammal Science*, *31*(2), 479-500. <https://doi.org/10.1111/mms.12165>
- Krasnova, V. V., Bel'kovich, V. M., & Chernetsky, A. D. (2006). Mother-infant spatial relations in wild beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. *Biology Bulletin*, *33*(1), 53-58. <https://doi.org/10.1134/S1062359006010079>
- Krasnova, V. V., Bel'kovich, V. M., & Chernetsky, A. D. (2009). Formation of behavior in the White Sea beluga calf, *Delphinapterus leucas*, during early postnatal ontogenesis. *Russian Journal of Marine Biology*, *35*(1), 53-59. <https://doi.org/10.1134/S1063074009010088>
- Krasnova, V. V., Chernetsky, A. D., & Russkova, O. V. (2015). Skin defects in the beluga whale *Delphinapterus leucas* (Pallas, 1776) from the Solovetsky gathering, as revealed by photo-identification analysis. *Russian Journal of Marine Biology*, *41*(5), 372-383. <https://doi.org/10.1134/S1063074015050077>
- Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., & Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (*Delphinapterus leucas*) in natural environment. *Biology Bulletin*, *41*(4), 349-356. <https://doi.org/10.1134/S1062359014040062>
- Lesage, V. (2021). The challenges of a small population exposed to multiple anthropogenic stressors and a changing climate: The St. Lawrence Estuary beluga. *Polar Research*, *40*, 1-18. <https://doi.org/10.33265/polar.v40.5523>
- Lilley, M. K., Ham, J. R., & Hill, H. M. (2020). The development of socio-sexual behavior in belugas (*Delphinapterus leucas*) under human care. *Behavioural Processes*, *171*, 104025. <https://doi.org/10.1016/j.beproc.2019.104025>
- Lilley, M. K., Ham, J. R., Miller, M. R., Kolodziej, K., & Manitzas Hill, H. M. (2022). Investigation of lateralization of socio-sexual behavior in belugas (*Delphinapterus leucas*). *Behavioural Processes*, *201*, 104718. <https://doi.org/10.1016/j.beproc.2022.104718>
- Lomac-MacNair, K. S., Smultea, M. A., Cotter, M. P., Thissen, C., & Parker, L. (2016). Socio-sexual and probable mating behavior of Cook Inlet beluga whales, *Delphinapterus leucas*, observed from an aircraft. *Marine Fisheries Review*, *77*(2), 32-39. <https://doi.org/10.7755/MFR.77.2.2>
- Lowry, L., O'Corry-Crowe, G., & Goodman, D. (2012). *Delphinapterus leucas* (Cook Inlet subpopulation). In International Union for Conservation of Nature (Ed.), *The IUCN red list of threatened species 2012* (e. T61442A17691385). IUCN. <https://doi.org/10.2305/IUCN.UK.2012.RLTS.T61442A17691385.en>
- Lydersen, C., Martin, A. R., Kovacs, K. M., & Gjertz, I. (2001). Summer and autumn movements of white whales *Delphinapterus leucas* in Svalbard, Norway. *Marine Ecology Progress Series*, *219*, 265-274. <https://doi.org/10.3354/meps219265>
- Manitzas Hill, H. M., Yeater, D. B., & Noonan, M. (2021). Synergy between behavioural research on beluga whales (*Delphinapterus leucas*) conducted in zoological and wild settings. *Polar Research*, *40*, 5508. <https://doi.org/10.33265/polar.v40.5508>
- Mann, J. (2006). Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In V. Sommer & P. L. Vasey (Eds.), *Homosexual behaviour in animals* (pp. 107-130). Cambridge University Press.
- Martin, A. R., da Silva, V. M. F., & Rothery, P. (2008). Object carrying as socio-sexual display in an aquatic mammal. *Biology Letters*, *4*(3), 243-245. <https://doi.org/10.1098/rsbl.2008.0067>
- Mayette, A., Loseto, L., Pearce, T., Hornby, C., & Marcoux, M. (2022). Group characteristics and spatial organization

- of the Eastern Beaufort Sea beluga whale (*Delphinapterus leucas*) population using aerial photographs. *Canadian Journal of Zoology*, 100(6). <https://doi.org/10.1139/cjz-2021-0232>
- Mazikowski, L., Hill, H. M., & Noonan, M. (2018). Young belugas (*Delphinapterus leucas*) exhibit sex-specific social affiliations. *Aquatic Mammals*, 44(5), 500-505. <https://doi.org/10.1578/AM.44.5.2018.500>
- Michaud, R. (2014). *St. Lawrence Estuary beluga (Delphinapterus leucas) population parameters based on photo-identification surveys, 1989-2012* (DFO Canadian Science Advisory Secretariat Research Document 2013/130). iv + 27 pp. www.dfo-mpo.gc.ca/csas-sccs
- O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D., & Ferrer, T. (2020). Group structure and kinship in beluga whale societies. *Scientific Reports*, 10(1), 11462. <https://doi.org/10.1038/s41598-020-67314-w>
- O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K., & Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLOS ONE*, 13(3), e0194201. <https://doi.org/10.1371/journal.pone.0194201>
- Orbach, D. N. (2019). Sexual strategies: Male and female mating tactics. In B. Würsig (Ed.), *Ethology and behavioral ecology of odontocetes* (pp. 75-93). Springer International Publishing. https://doi.org/10.1007/978-3-030-16663-2_4
- Pippard, L. (1985). Status of the St. Lawrence River population of beluga, *Delphinapterus leucas*. *Canadian Field-Naturalist*, 99(3), 438-450.
- Richard, J. T., Robeck, T. R., Osborn, S. D., Naples, L., McDermott, A., LaForge, R., Romano, T. A., & Sartini, B. L. (2017). Testosterone and progesterone concentrations in blow samples are biologically relevant in belugas (*Delphinapterus leucas*). *General and Comparative Endocrinology*, 246, 183-193. <https://doi.org/10.1016/j.ygcen.2016.12.006>
- Robeck, T. R., Monfort, S. L., Calle, P. P., Dunn, J. L., Jensen, E., Boehm, J. R., Young, S., & Clark, S. T. (2005). Reproduction, growth and development in captive beluga (*Delphinapterus leucas*). *Zoo Biology*, 24(1), 29-49. <https://doi.org/10.1002/zoo.20037>
- Schaeff, C. M. (2007). Courtship and mating behavior. In D. L. Miller (Ed.), *Reproductive biology and phylogeny of Cetacea* (pp. 349-370). Science Publishers. <https://doi.org/10.1201/b11001-14>
- Sergeant, D. E., & Brodie, P. F. (1975). Identity, abundance, and present status of populations of white whales, *Delphinapterus leucas*, in North America. *Journal of the Fisheries Research Board of Canada*, 32(7), 1047-1054. <https://doi.org/10.1139/f75-123>
- Stewart, R. E. A. (1994). Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. *Meddelelser Om Grønland, Bioscience*, 39, 217-225.
- Vergara, V., Wood, J., Lesage, V., Ames, A., Mikus, M-A., & Michaud, R. (2021). Can you hear me? Impacts of underwater noise on communication space of adult, sub-adult and calf contact calls of endangered St. Lawrence belugas (*Delphinapterus leucas*). *Polar Research*, 40, 1-19. <https://doi.org/10.33265/polar.v40.5521>