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Observations of Adult–Calf Nonreproductive Copulatory Behavior in North Atlantic Right Whales (*Eubalaena glacialis*)

Gina L. Lonati,[1] Natasha J. Hynes,[1, 2] Kelsey R. Howe,[3]
Delphine Durette-Morin,[2, 4] Moira W. Brown,[2] and Kimberley T. A. Davies[1]

[1]*University of New Brunswick Saint John, Department of Biological Sciences, 100 Tucker Park Road, Saint John, NB E2K 5E2, Canada*
E-mail: gina.lonati@unb.ca
[2]*Canadian Whale Institute, 16 Herring Cove Road, Welshpool, NB E5E 1B6, Canada*
[3]*Anderson Cabot Center for Ocean Life, New England Aquarium, 1 Central Wharf, Boston, MA 02110, USA*
[4]*Dalhousie University, Department of Oceanography, 1355 Oxford Street, Halifax, NS B3H 4R2, Canada*

Nonreproductive copulatory behavior (NCB; also called nonreproductive, nonprocreative, nonconceptive, or socio-sexual behavior) refers to animals engaging in sexual behavior without the possibility of reproduction. This type of behavior includes interactions among same-sex, adult–immature, immature–immature, or interspecies individuals, as well as sexual activity that occurs outside of the conceptive season (reviewed in Bagemihl, 1999; Furuichi et al., 2014). NCBs, such as penile erection in the presence of conspecifics, genital-to-genital contact, or genital manipulation using various body parts, have been reported for several taxonomic groups, particularly primates (Bagemihl, 1999; Brown & Dixson, 2000; Sommer & Vasey, 2006; Li et al., 2007; Bailey & Zuk, 2009; Furuichi et al., 2014; Grueter & Stoinski, 2016). These behaviors may establish and strengthen social bonds or express dominance and could therefore be associated with complex social structures and intelligence (Sommer & Vasey, 2006; Bailey & Zuk, 2009; Furuichi et al., 2014). Alternatively, NCB may be a form of self-satisfaction, play, or practice for future procreation (Bailey & Zuk, 2009; Balcombe, 2009; Furuichi et al., 2014), or it may be maladaptive (Bailey & Zuk, 2009). These theories are not all mutually exclusive, and some or all may explain why these behaviors occur during a particular encounter within a particular species.

In Odontoceti, cases of same-sex, adult–calf, and interspecies copulatory behaviors have been reported for several small species that are capable of being observed in captivity or are relatively accessible in the wild (Spotte, 1967; Bagemihl, 1999; Mann, 2006; Xian et al., 2010; Hill et al., 2015; Harvey et al., 2017; Lilley et al., 2020; Serres et al., 2021). In Mysticeti, however, fewer cases of NCB have been documented. Specifically, four mysticete species—bowhead whales (*Balaena mysticetus*), gray whales (*Eschrichtius robustus*), humpback whales (*Megaptera novaeangliae*), and southern right whales (*Eubalaena australis*)—are known to engage in same-sex and adult–immature sexual behaviors (Rice, 1983; Würsig et al., 1993; Bagemihl, 1999; Pack et al., 2002; Sironi, 2004; D'Agostino et al., 2017). The first case of NCB between a mysticete adult and calf was documented in 2015 when researchers in Golfo San José off Península Valdes, Argentina, observed an adult male southern right whale pursuing a mother–calf pair (D'Agostino et al., 2017). During the pursuit, the calf became separated from its mother, at which point the male assumed a ventrum-up posture underneath the calf, positioning the calf between his flippers. Underwater video from a GoPro™ captured the male inserting his penis into the calf's genital slit (D'Agostino et al., 2017).

Similar to southern right whales, critically endangered North Atlantic right whales (*Eubalaena glacialis*, NARWs) engage in a promiscuous mating system in which individuals can have multiple mates (Brownell & Ralls, 1986; Kraus & Hatch, 2001; Kraus et al., 2007). Currently, the NARW species' sex ratio may be slightly male biased at approximately 3:2 (Hamilton et al., 2021), and while estimates of age at sexual maturity range between 5 to 21 y (average 9 y) for females and 10 to 15 y for males, it is likely females and males reach sexual maturity at similar ages (Frasier et al., 2007; Kraus et al., 2007). Observable mating behaviors take place in surface active groups (SAGs), defined as two or more whales at the surface less than one body length apart, with frequent physical contact (Kraus & Hatch, 2001; Kraus et al., 2007; Parks et al., 2007). A focal female will often roll, invert (i.e., flip ventrum-up), or swim horizontally during a SAG, presumably to select

the strongest, fittest, most agile mate. Meanwhile, males will jockey for what is called the "alpha" position closest to the female for a chance at copulation when she rolls upright. They will often place one or both flippers on her to maintain their position and possibly detect or predict her movements (Kraus & Hatch, 2001).

Advancements in aerial imagery via remotely piloted aircraft systems (RPAS; commonly called drones) have allowed for more photo-documentation of free-swimming large whales *in situ* (Torres et al., 2018; Fiori et al., 2020; Orbach et al., 2020). Herein, we present two cases of adult–calf NCB in NARWs, both recorded using RPAS in the Shediac Valley in the southwestern Gulf of St. Lawrence (GSL), Canada. Observation #1 was made by colleagues (N. Hawkins & A. Tapia, Nick Hawkins Photography) on 26 July 2020 from the R/V *Calanus* and included an adult male, a female calf, and the calf's mother. Observation #2 was made on 18 July 2021 during a NARW research expedition on the F/V *Jean-Denis Martin* and included an adult male and a presumed female calf. Both observations were opportunistic—that is, not the focus of the RPAS flights. After reviewing these videos, we consulted the literature and NARW behavioral experts (P. Hamilton & A. Knowlton, New England Aquarium; M. Moore, Woods Hole Oceanographic Institution; S. Parks, Syracuse University) to help characterize both observations.

Observation #1 – 26 July 2020

At ~1300 h ADT, three NARWs were observed exhibiting SAG-like behavior at 47.7308° N, -64.0519° W. An Inspire 2 RPAS (DJI, Shenzhen, China) carrying a DJI Zenmuse X7 visible-spectrum camera (4K video at 4,096 × 2,160 pixel resolution) with a circular polarizing filter was launched. The RPAS provided live-stream, first-person-view video to the pilot. At first, the RPAS flew directly over two NARWs that were later photo-identified as NARW Catalog #1429 (a 38-y-old adult male) and the 2020 female calf of NARW Catalog #2642 (a 24-y-old adult female).

Between 1305 and 1314 h, RPAS video was recorded (Supplemental Video 1, timestamps 00:05 to 07:10; the supplemental video for this paper is 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). Initially, #1429 was observed ventrum-up and aligned head-to-head and ventrum-to-ventrum with the calf, with his flippers positioned on either side of the calf. This posture resembled that of the male southern right whale reported in D'Agostino et al. (2017) and was similar to a behavior sometimes observed between mothers and their calves called "cradling" (Zani & Hamilton, 2017). Since subsurface water visibility was poor and the dark coloration of #1429's ventrum provided poor contrast, we were unable to observe the adult male's genitalia and thoroughly assess his subsurface behaviors and positions. Occasionally, #1429 rolled upright and separated from the calf to breathe; at this point the calf inverted or rolled with its dorsum toward #1429 (e.g., timestamps 01:18 to 01:34 and 02:54 to 04:02). The calf also performed two tail slashes (i.e., lateral movements of the tail) near #1429 when both whales were upright (i.e., dorsum-up) at the surface (timestamps 01:03 to 01:21).

At 1309 h, #2642 ascended from beneath #1429 and began swimming around her calf at the surface (timestamp 04:20). When #1429 resumed a ventrum-up, cradling-like position beneath the calf, #2642 turned and swam toward the calf's right midsection (timestamp 05:06). Then, #2642 appeared to push her calf off #1429 with her rostrum and chin (timestamp 05:18). The calf remained mostly upright during this time. At 1311 h, #2642 and her calf swam away from #1429 together.

At 1313 h, during a separate video from the same RPAS flight, #1429 was observed ventrum-up underneath the upright calf once more (timestamp 05:51). The mother pushed her calf off #1429 again, causing the calf to roll ventrum-up (timestamps 06:00 to 06:38; Figure 1). The calf remained in this position for ~30 s while #1429 surfaced upright and the mother performed a ~15 s dive. The pilot terminated the video shortly thereafter and flew the RPAS back to the vessel due to low battery.

In total, 7 min of RPAS video at an altitude of ~20 m was recorded of these three whales. Post-flight behavioral observations were not conducted. #1429 was observed on three other occasions between 20 June and 31 July 2020, and in each sighting, he was alone. In this same time period, the mother–calf pair was observed seven times. Specifically, on 23 July 2020, #2642 and her calf were observed in a SAG with another adult female and adult male. Later that day, the Aerial Survey Team from Fisheries and Oceans Canada (DFO) sighted the calf of #2642 with a 6-y-old juvenile male (NARW Catalog #4446). The male was photographed in a ventrum-up, cradling-like position beneath the calf, and #2642 was also observed interacting with the two whales. NCB could not be confirmed as the male's genital area was not visible from the plane. The other five sightings were of #2642 and her calf by themselves.

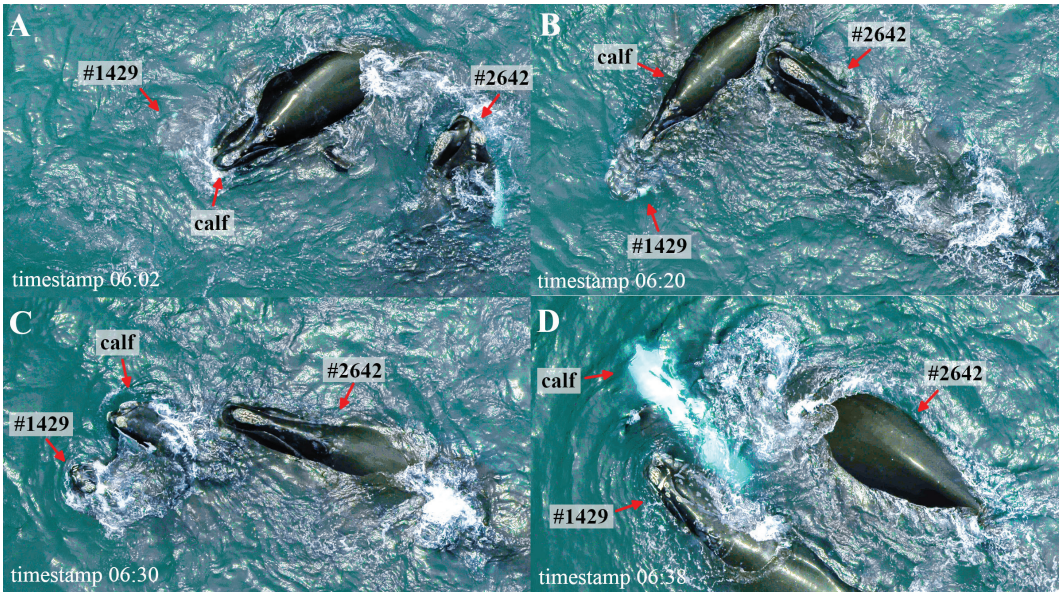

Figure 1. A series of video still images (Supplemental Video 1, timestamps 06:02 to 06:38) taken with a remotely piloted aircraft system (RPAS)-mounted camera at 1313 h on 26 July 2020 in the Gulf of St. Lawrence, Canada, of three North Atlantic right whales (*Eubalaena glacialis*, NARWs)—an adult female (#2642), her 2020 calf, and an adult male (#1429): (A) #1429 was submerged in a ventrum-up, cradling-like position underneath the calf and #2642 was turning toward her calf; (B) #2642 contacted the left mid-section of her calf with her rostrum as she swam forward and over #1429; (C) the calf rolled sideways off #1429 as #2642 continued to push the calf with her chin; and (D) the calf (white belly) inverted as #1429 surfaced and #2642 began to dive. (Photos provided by Nick Hawkins Photography)

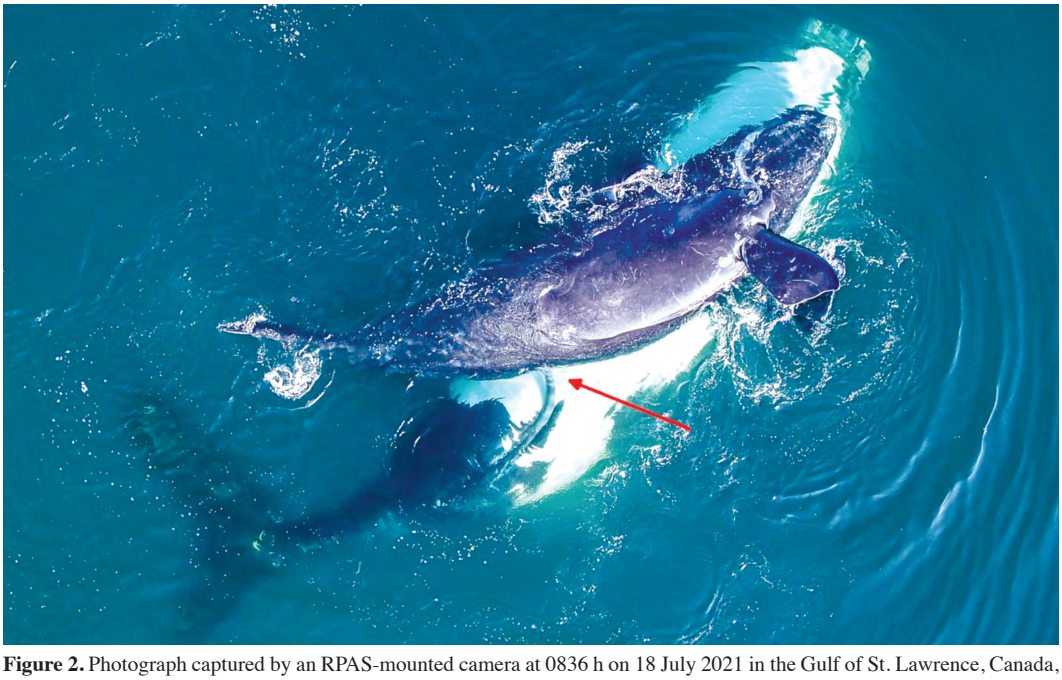

Figure 2. Photograph captured by an RPAS-mounted camera at 0836 h on 18 July 2021 in the Gulf of St. Lawrence, Canada, showing likely intromission (red arrow) between an adult male NARW (#3442, ventrum-up, white belly) and the 2021 presumed female calf (rolled right side up) of #3720 (*Photo credit:* Gina Lonati, University of New Brunswick Saint John)

Observation #2 – 18 July 2021

At 0736 h ADT, a NARW mother–calf pair was sighted at 47.9054° N, -63.9348° W and identified in real time as NARW Catalog #3720 (a 14-y-old adult female) and her 2021 calf, her first known offspring. Based on genital morphology that was partially observed that day, the calf was presumed female, with confirmation pending from molecular sexing analyses (Frasier et al., 2006).

The vessel approached the pair to facilitate photo-identification and visual health assessment. At 0833 h, a DJI Matrice 210 V2 RPAS was launched. The RPAS carried a DJI Zenmuse XT2 for collecting simultaneous long-wave thermal infrared video and visible-spectrum video (12 megapixels, 4K Ultra HD), a PEN E-PM2 camera (Olympus, Tokyo, Japan) for collecting visible-spectrum photographs (16.1 megapixels), and a laser altimeter (modified from Dawson et al., 2017). The RPAS provided live-stream, first-person-view video to the pilot. For the purposes of this paper, we only reviewed visible-spectrum imagery.

Between 0834 and 0847 h, continuous video (Supplemental Video 1, timestamps 07:11 to 20:06) and sequential still images (at 1 Hz) were collected with the RPAS. At first, the calf was observed rolling laterally at the surface with its right side up; the white ventrum of a larger NARW was present underneath it. Initially, we thought the larger whale was #3720 cradling her calf; however, once the RPAS was directly overhead, the male genitalia of the larger whale could be seen. Visibility was facilitated by very light winds (1 to 3 kts), low wave heights (< 0.2 m), and contrast between the whale's gray penis and white ventrum. The larger whale was later identified as NARW Catalog #3442, a 17-y-old male.

For ~10 min, #3442 and #3720's calf interacted at the surface. Specifically, #3442 was aligned head-to-head and ventrum-to-ventrum with the calf and had his flippers positioned vertically on either side of the calf, resembling #1429 from Observation #1. He also appeared to probe the calf's genital region with his extended penis underwater. Meanwhile, the calf rolled, thrashed side to side, and arched often at the surface. Occasionally, #3442 surfaced to breathe, but then returned to a ventrum-up, cradling-like position beneath the calf. Intromission could not be confirmed, although we suspect it occurred for a maximum of 1 min, 15 s between 0835 and 0836 h (timestamps 07:55 to 09:10; Figure 2). Near the end of this suspected intromission, the calf defecated (timestamp 09:05) and then rolled away from the adult.

Starting at 0844 h (timestamp 16:25), #3442 rolled upright to breathe, and the calf rolled laterally and swam in a clockwise circle. As the calf's head neared the peduncle of #3442, the adult male performed a horizontal tail slash that nearly contacted the calf's head (timestamp 16:55). The adult male performed another tail slash ~8 s later as he turned and swam away from the calf. We continued to record RPAS video of #3442 for 3 min as he swam subsurface. At 0847 h, the pilot terminated the video and flew the RPAS back to the vessel due to low battery.

In total, the flight lasted 16.5 min, during which ~13 min of video and 427 still images were collected. Altitude above the two whales ranged from 13 to 36 m. The calf's mother was not observed from the RPAS, and observations of post-flight behaviors were not conducted. This mother–calf pair was not sighted for the remainder of the summer. However, #3442 was observed the following day (19 July 2021) in a SAG, which included one adult female, three adult males, one juvenile female, and one juvenile male. #3442 was also observed on 16 August 2021 engaging in a SAG with one other adult male. In RPAS videos of both of these SAGs, #3442's extended penis was often visible.

Interpretations and Discussion

Observations of copulatory behavior in wild cetaceans are rare because mating activity usually occurs underwater. However, NARWs regularly engage in copulatory behaviors near the surface, which offers a unique opportunity to study the sexual behaviors of this species. Our observations represent the first documented cases of adult–calf NCB in NARWs, and, to the best of our knowledge, they are the first RPAS-based observations of these behaviors in any cetacean (but see Orbach et al., 2020, for the use of RPAS to study mating patterns in free-ranging dolphins). The RPAS provided a useful, minimally invasive vantage point to collect minutes-long, high-resolution video of these near-surface behaviors, specifically allowing us to observe the genitalia of one of the males underwater, which would not have been possible from a vessel.

There are many theories, both adaptive and maladaptive, to explain the prevalence of NCBs in nature (summarized in Bailey & Zuk, 2009); therefore, we can only speculate about this behavior in NARWs and other mysticetes. For example, it could be important for immature individuals to learn successful mating behaviors (Sironi, 2004; Mann, 2006; Furuichi et al., 2014). Both calves in the cases presented here exhibited a lot of rolling, and the calf of #2642 maintained

a ventrum-up posture for up to 30 s at a time, possibly trying to invert as adult females do in SAGs to incite male competition for access to their genital area (Kraus & Hatch, 2001). Right whale calves are also known to engage in "play" behaviors (e.g., rolling, turning, touching) with their mothers, which may help calves develop motor skills and coordination for future socializing, mating, and feeding (Thomas & Taber, 1984). Therefore, adult–calf NCB may also be a form of play that facilitates calf development. In addition, these interactions may establish or strengthen social bonds as Mann (2006) hypothesized for bottlenose dolphins (*Tursiops truncatus*). This could be especially important for species that live in vast aquatic environments where establishing and maintaining connections between conspecifics is difficult. Furthermore, NCB could be a means of self-satisfaction, although we could not confirm whether ejaculation took place in either case presented here, and we have no way of knowing any of the whales' physiological responses (e.g., sexual arousal) to these interactions.

Alternatively, it is possible that NCBs do not serve to benefit the population or are aberrant. It may simply be a case of mistaken identity or an indicator of the species' small population size. With only 336 NARWs estimated to remain in 2020 and only ~20% of those being adult females (Pettis et al., 2022), there is some support for the "mate deprivation hypothesis," which states that males with limited access to females may exhibit more forced or deviant copulatory behavior (Thornhill & Thornhill, 1983, 1992; Lalumière et al., 1996; Haddad et al., 2015). Ultimately, NARW reproductive rates have declined in the last decade due to increased anthropogenic stressors and a declining and shifting food source (Meyer-Gutbrod et al., 2015, 2021; Pettis et al., 2017; van der Hoop et al., 2017; Moore et al., 2021; Stewart et al., 2021), and the connection between NCBs and successful or unsuccessful reproduction—if any—remains poorly understood.

While reviewing these videos, we questioned whether the calves were being harassed by the adult males, and, in the case of #2642, if the mother was trying to protect her calf by separating it from #1429. Such speculations, however, would be largely based on an assumption that the males' sexual advances were unwanted, unsolicited, or harmful to the calves. Currently, we do not have sufficient insight into the behavioural biology of this species to know whether NCB is beneficial or detrimental to calves.

In summary, these two observations represent the first documented cases of adult–calf NCB in NARWs. While we do not know the frequency or purpose(s) of these interactions among right whales, further observations of whales with RPAS will provide more insight. Without the ability to observe postures and genitalia underwater, researchers on vessels and land could easily overlook or misidentify these behaviors, especially given the resemblance to mother–calf cradling (Zani & Hamilton, 2017). RPAS technology offers a unique opportunity to study and interpret the behavioral ecology and reproductive strategies of these large, cryptic animals (Torres et al., 2018; Fiori et al., 2020; Orbach et al., 2020).

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