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RESEARCH ARTICLE

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Playful mouth-to-mouth interactions of belugas (*Delphinapterus leucas*) in managed care

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Abstract

Belugas (*Delphinapterus leucas*) engage in many forms of play (e.g., object, water, locomotor), but no play is quite as curious as the unusual form of cooperative social play involving mouth-to-mouth interactions. These playful interactions are characterized by two belugas approaching each other head-to-head and interlocking their jaws, clasping one another, as if they were shaking hands. Observed in belugas both in the wild and in managed care, it is seemingly an important type of social play that offers a unique way of socializing with conspecifics. To describe this unusual behavior, a group of belugas in managed care was observed from 2007 to 2019. Although adults participated in mouth-to-mouth interactions, most were initiated and received by young belugas. Both males and females engaged in mouth-to-mouth interactions and did so at similar frequencies. Individual differences in how many mouth-to-mouth interactions were initiated among calves were also observed. Due to the unique, cooperative nature of mouth-to-mouth interactions, which require both social and motor skills, it is hypothesized that these interactions may be used to test social and motor competency.

KEYWORDS

cooperation, development, social networks, social play behavior, white whale

1 | INTRODUCTION

Physical contact is an important component of social interactions in mammals (Ewer, 1967). Social contact or touch includes affiliative contact (e.g., nuzzling, rubbing, holding), such as mother–infant contact, sociosexual or copulatory contact, social grooming, and aggressive contact (e.g., biting, scratching, aggressive wrestling) (Hill et al., 2016). While not mutually exclusive, these behaviors often differ in form. For example, sociosexual behavior resembles copulatory behavior (Hill et al., 2015; Lilley, Ham, & Manitzas Hill, 2022; Lilley, Ham, Miller, Kolodziej, et al., 2022; Manitzas Hill, et al., 2022) but can be considered affiliative or playful in certain contexts (Manitzas Hill, et al., 2023). The vast majority of affiliative social contact research has investigated mother-offspring contact and its role in the formation of social bonds and infant development (Harlow, 1958; Nakamura & Sakai, 2014). Touch is used to form bonds between mothers and their offspring as well as to facilitate the cognitive, physical, and social development of the young. For many

species, social contact continues to be important throughout their lifetime. For example, in primates, social contact often occurs through allogrooming, which strengthens bonds between individuals and is used to mediate postconflict interactions (Palagi et al., 2006; Romero et al., 2011). Similarly, juvenile Japanese macaques (*Macaca fuscata*) engage in social play that strengthens their social relationships with their conspecifics (Shimada & Sueur, 2018). Additionally, male juvenile bottlenose dolphins (*Tursiops* spp.) engage in sociosexual contact that can result in life-long bonds (Connor et al., 1992, 2001, 2006). Affiliative physical contact between conspecifics is important for many mammals (Dunbar, 2010; Pellis & Pellis, 2010), and this seems especially true for cetaceans.

Many species of Cetacea are very tactile (e.g., Dudzinski et al., 2010, 2012; Guarino et al., 2017; Jones & Swartz, 1984; Keener et al., 2018; Kraus & Hatch, 2001; Yeater, 2013). Observations of odontocetes in both managed care and the wild indicate that contact occurs relatively frequently between conspecifics during affiliative social interactions and often involves various forms of fin and body contact (Connor et al., 2006; Dudzinski, 1998; Dudzinski et al., 2009, 2010, 2012; Herman & Tavolga, 1980; Mann & Smuts, 1999). One common type of contact, pectoral fin rubbing, may reduce conflict and strengthen bonds similar to that of social grooming in primates (Dudzinski, 1998; Dudzinski et al., 2010; Mann & Smuts, 1998, 1999; Nakamura & Sakai, 2014; Norris, 1991). Odontocetes also use their mouths in both aggressive and affiliative tactile contexts (Dudzinski, 1998; Frick, 2018; Horback et al., 2010; Kuczaj II & Yeater, 2007; Overstrom, 1983). These interactions include raking with the teeth (aggressive; Ham, Lilley, & Manitzas Hill, 2021) and gentle mouthing (affiliative; Hill et al., 2015). The most unusual, and understudied, use of the mouth is in social interactions involving mouth-to-mouth contact.

Mouth-to-mouth contact has been observed in only a few species of Odontoceti. For example, killer whales (*Orcinus orca*) in managed care use mouth-to-mouth tongue touching during affiliative interactions (Bain, 1986; Martinez & Klinghammer, 1978; Nakamura & Sakai, 2014; Sánchez–Hernández et al., 2019). Although rare, mutual mouth contact has also been observed in Atlantic bottlenose dolphins (*T. truncatus*), in both managed care (Overstrom, 1983) and in the wild (Connor et al., 2000). Similarly, Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) and East-Asian finless porpoises (*N. a. sunameri*) living in managed care have been observed engaging in mouth-to-mouth interactions (MtMIs) (Serres et al., 2021). Young belugas (*Delphinapterus leucas*) also engage in mouth-to-mouth contact (Hill & Ramirez, 2014; Hill et al., 2019).

Despite the observation of MtMIs in a few species, a detailed study of such interactions has yet to be conducted. Beluga MtMIs satisfy Burghardt's (2005) five criteria for play as they are: (1) not completely functional in either form or context; (2) voluntary and pleasurable; (3) structurally or temporally different from the similar "serious" behavior; (4) performed repeatedly; and (5) are initiated by healthy animals. MtMIs have been reported in belugas in several groups in managed care (New York Aquarium, Connor & Peterson, 1994; MarineLand of Canada, Hill et al., 2019; Vancouver Aquarium,

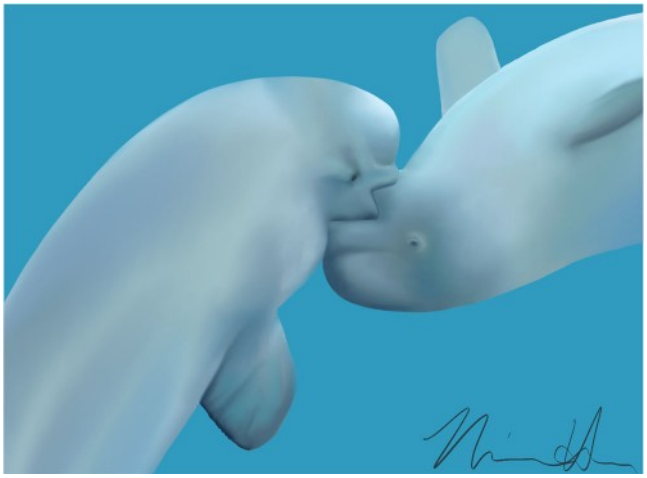

FIGURE 1 An illustration of a mouth-to-mouth interaction in which one animal interlocks their jaw with another, as if they were shaking hands with their mouths. Illustration by Nichole Ham.

Recchia, 1994) and for one group in the wild (Krasnova et al., 2014). This behavior involves two belugas approaching one another in a face-to-face orientation and interlocking their mouths together, as if shaking hands with their mouths (Figure 1). A preliminary study on the development of calf MtMIs found that this playful social behavior emerges within the first few months of life and occurs sporadically among calves in their first year (Hill et al., 2019). Successful mouth-to-mouth contact would seem to require considerable interanimal coordination, and for this reason, it was suggested that the experience of MtMIs could be important in the development of physical and social skills (Hill et al., 2019).

MtMIs resemble the play fighting reported in many mammals in which partners compete to gain an advantage over one another (Aldis, 1975). But for playful fighting to remain playful, both partners have to have the opportunity to gain that advantage at least sometimes, and this requires that the animals also cooperate (Pellis & Pellis, 2017). Balancing competition and cooperation requires considerable interanimal coordination of movements, and it is the experiences derived from such coordination, in play, that appear to be critical in training social skills (Pellis et al., 2017, 2019). Therefore, it is not unreasonable to hypothesize that the cooperation needed to coordinate movements during MtMIs in beluga calves provides comparable opportunities to improve social skills. Given how little is known about MtMIs, an important starting point is to understand their developmental milestones, including partner preferences and how these may change with age.

Recent reports on sociosexual play of belugas in managed care has revealed that belugas prefer to engage in sexual play with older and larger individuals, when given a choice (Lilley et al., 2020). This is a rather peculiar finding as nearly all animals studied to date, that engage in social play, prefer to play with same-age, same-size individuals (e.g., Byers, 1980; Gomendio, 1988; Mackey et al., 2014; Maestripieri & Ross, 2004; Palagi, 2006). To determine if this unusual

social preference in sexual play is true of other forms of social play in belugas, a detailed investigation of MtMIs was conducted. As an exploratory descriptive study of mouth-to-mouth play behaviors in a group of belugas observed over a 12-year study period, this study expanded on the initial report by Hill et al. (2019). We explored the frequency of behaviors, age and sex biases, partner preferences, seasonality and correlation with social behavior, and the developmental time course to better understand the possible functions of MtMIs.

2 | MATERIALS AND METHODS

2.1 | Subjects

The animals included in this study were belugas housed at SeaWorld Texas (SWT). The subjects consisted of 9 (4 females, 5 males) juveniles born at SWT and 10 (7 females, 3 males) adults. Animals were observed from 2007 to 2019. All the animals were housed with several other individuals with social groupings changing daily based on facility activities and staff decisions. Table 1 summarizes the date of birth and dates of data collection, as some animals were not at the facility for the whole 12-year study period. In addition, when two juveniles were transferred to Georgia Aquarium (GA), we continued recording their behavior at the new facility for a limited time (Table 1).

The animals at SWT were housed in a series of seven, connected pools that hold approximately 2,000,000 gal of water. Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) were also housed within this facility and usually occupied the pools adjacent to the belugas at any given time. At GA, subjects were housed in an approximately 800,000 gal habitat comprised of three interconnected pools along with a few other belugas and harbor seals (*Phoca vitulina*).

2.2 | Data collection

Data were collected via video recordings from 2007 to 2019 at SWT and from 2013 to 2015 at GA. Video recordings included following focal animals and scan samples (Martin & Bateson, 2007), with some recordings taken from above the water and some below the water through a viewing window. Scan samples typically lasted 20 min and aimed to capture the behavior of several individuals at 1-min intervals. Focal follows lasted 15 min and followed the behavior of one individual for the entirety of the video. The same focal follow protocol was implemented at GA. The Institutional Animal Care and Use Committee at St. Mary's University approved the data collection (StMU2018-3). Observations were conducted primarily at SWT, and several of these subjects were genetically related to one another to some degree.

Video recordings were sampled for the presence of MtMIs, based upon recorded notes provided in an archived log or notes collected during the scoring of archived videos for other behaviors. Additional videos were randomly selected for social interactions in an attempt to examine at least three videos per month during our 12-year sample period. This additional video selection process enabled the sample to be evaluated for both the occurrence of MtMIs and overall social behavior. Out of the 144 months examined, 77 months had more than three videos available, and for 7 months, only two videos were available. Videos were recorded between 0600 and 1800 when trainers were absent. The sample included video recordings spread across the day. In total, the present study consisted of 555 videos, which represented 142 h.

2.3 | Video analysis

Video recordings were scored for social behaviors (excluding mother–calf social swims) and MtMIs (as described in Appendix A) for belugas of all ages. MtMIs were identified according to the

TABLE 1 Demographics on juvenile belugas followed in this study.

Subject	Sex	Location	Birthdate	Data start date	Data end date
OLI	Male	SWT	06/23/2007	06/24/2007	01/08/2019
GRA	Male	SWT	06/26/2007	07/25/2007	11/08/2010
		GA		04/30/2013	02/18/2015
QIN	Female	SWT	07/31/2008	08/26/2008	11/15/2010
		GA		11/12/2013	03/04/2015
BEL	Female	SWT	06/12/2009	06/08/2009	06/14/2013
ATL	Female	SWT	06/23/2010	06/29/2010	02/12/2014
SAM	Male	SWT	07/09/2013	07/19/2013	07/29/2019
STL	Female	SWT	07/26/2013	08/10/2013	11/03/2015
KEN	Male	SWT	08/11/2016	08/15/2016	07/29/2019
INK	Male	SWT	09/17/2017	09/18/2017	07/04/2019

Abbreviations: GA, Georgia Aquarium; SWT, SeaWorld Texas.

description provided by Hill et al. (2019). All the MtMIs were considered to be a type of play fighting, rather than aggression, as they satisfied Smith's (1997) criteria for distinguishing play fighting from serious fighting. These are that (1) the play is not over access to resources; (2) the animal invited to engage in play fighting could refuse and not engage; (3) there are often two involved; (4) there is little interest from nonparticipants; (5) a stronger or older animal will often self-handicap and not use their full strength and restraint is shown by participants; (6) participants may take turns; and (7) participants often stay together in another activity following a play fight. One criterion described by Smith (1997) that could not be verified for belugas was if there are facial and/or vocal expressions made by the animals during the play fighting encounter as neither of these were observable in the data collection method (i.e., no hydrophone present, facial expressions not visible). Most occurrences of MtMIs occurred without play behaviors preceding or following them (Ham, 2021), though, other play behaviors (e.g., sexual play, object play) occurred at other points in a given observation.

J. Ham scored most of the videos, with additional videos scored by M. Lilley, R. Wincheski, J. Lelekach, J. Miranda, and Á. Dediós. To assess interrater reliability, videos scored by the other scorers were reanalyzed by J. Ham. In all cases, MtMI events were reliably reported in the reanalyzed videos as indicated by using the Bland–Altman plot (Bland & Altman, 1986), which showed that 92% ($n = 35$ videos) of the repeated observations fell within the statistical limits of agreement ($x \pm 1.96$ s,−0.47 ± 1.96 (1.35), upper limit = 0.08, lower limit = −0.03), suggesting that there was substantial reliability among coders. Interactions were evaluated for duration, initiator and receiver, and the type of interaction. Belugas were identified via individual physical characteristics by the observer recording the video. Information regarding the ages of the initiator and receiver and the identity of all other subjects present in the same pool was also recorded. The ages of the belugas were grouped into three categories: calf (0–36 months old), juvenile (37–96 months old), and subadult/adult (97+ months old). Animals were considered to be age-matched if they were born within 24 months of each other.

2.4 | Statistical analysis

To determine if age in months was correlated with the occurrence of MtMIs (for both animals initiating and receiving the behavior), Kendall rank correlation test was used after finding that the data were nonnormally distributed using a Shapiro–Wilk test ($p < 0.05$). The data were then plotted in R (R Core Team, 2020) using the package *igraph* (Csardi & Nepusz, 2006). Kendall's τ was also used to determine if there were correlations between the age of the initiator and the age of the receiver. To determine if there was a correlation between the age of onset of MtMIs and the age of onset of other social behaviors, the Kendall correlation test was also used, given that all of the behaviors were nonnormally distributed (Shapiro–Wilk $p < 0.05$). The p values were corrected using a Bonferroni correction using the *FSA* package (Ogle et al., 2021).

Partner preferences for each age category were visualized using egocentric, unidirectional social networks. These social networks were created for both males and females. Because there was day-to-day fluctuation regarding which animals were housed together, partnerships were evaluated by considering the age and sex of the other partners housed in the same pool with the initiating animal. These networks are used simply to visualize the overall preference in play partners for each age and sex category. Dyads were categorized by sex and age categories: calf, juvenile, and adult. Age categories were only used in determining partner preferences. The social networks were created in R (R Core Team, 2020) using the package *igraph* (Csardi & Nepusz, 2006). To determine if there were individual differences in the rate of initiating MtMIs, the total number of MtMIs initiated by an individual was divided by the total months observed.

To determine the average frequency of social behavior over the course of the year, we divided the total number of social bouts in a month by the total observation time of the corresponding month, combining the whole 12-year observation period. The frequency of social behavior was calculated for both male and female belugas and was then plotted against the number of MtMIs per month. To determine if MtMIs were an artifact of an overall increase in social behavior throughout the year, we looked at all other social interactions (sociosexual, aggressive, affiliative, and play), excluding mother–calf interactions. To determine if there was a correlation between overall female sociality, as measured by average frequency of any social interactions, and the occurrence of MtMIs, we used the Kendall correlation test after finding the data to be nonnormally distributed (Shapiro–Wilk $p < 0.05$). The same procedure was conducted with overall male sociality and male MtMIs but using a Pearson's correlation test as the data were normally distributed (Shapiro–Wilk $p > 0.05$). Finally, the number of MtMIs initiated by each calf was plotted against the total number of months observed to compare the rate at which animals initiate MtMIs. This was plotted with R using the package *ggplot2* (Wickham, 2016). In addition, we used a linear mixed effects model, using the *lmerTest* package (Kuznetsova et al., 2017) in R, to model the correlations between age and the occurrence of MtMIs of both participants. The age of the initiator and the age of receiver was also modeled along with the age onset of MtMIs and the age onset of other social behaviors. In all models, the initiator's ID and the date of the interaction were considered as random factors. To replicate the correlations between sociality and the number of MtMIs per month for both males and females, and the number of MtMIs initiated by each calf against the total number of months observed. The initiator's ID was considered as a random factor. As the results of the linear mixed effects model were the same as the other models, only the correlation results are reported.

3 | RESULTS

3.1 | Frequency

A total of 155 MtMIs were observed over the 12 years of observation initiated by 11 different individuals. Due to unclear

video footage and issues with partner identification, six MtMIs were removed from the partner preference analyses. MtMIs made up 13.8% of all social play bouts ($n = 1120$) that were observed in this study.

3.2 | MtMIs participants

3.2.1 | Age

The age of the belugas was plotted against the number of MtMIs observed by all of the animals (Figure 2). Most of the animals initiating MtMIs were calves (75.4%, $n = 117$, Table 2), with juveniles (10.3%, $n = 16$) and adults (14.3%, $n = 22$) initiating a similar amount. Most of the receivers were also calves (68.5%, $n = 102$), followed by juveniles (22.1%, $n = 33$), then adults (9.4%, $n = 14$). MtMIs significantly declined with age for both initiators ($r_\tau = -0.40$, $p = 0.007$) and receivers ($r_\tau = -0.50$, $p = 0.0001$).

3.2.2 | Sex

When excluding adults from the sex comparisons, as only adult males initiated MtMIs ($n = 22$), immature females initiated a similar amount of MtMIs as immature males (female $n = 62$, male $n = 71$). The mean individual initiation between males ($M = 14.40$, SD = 7.44) and

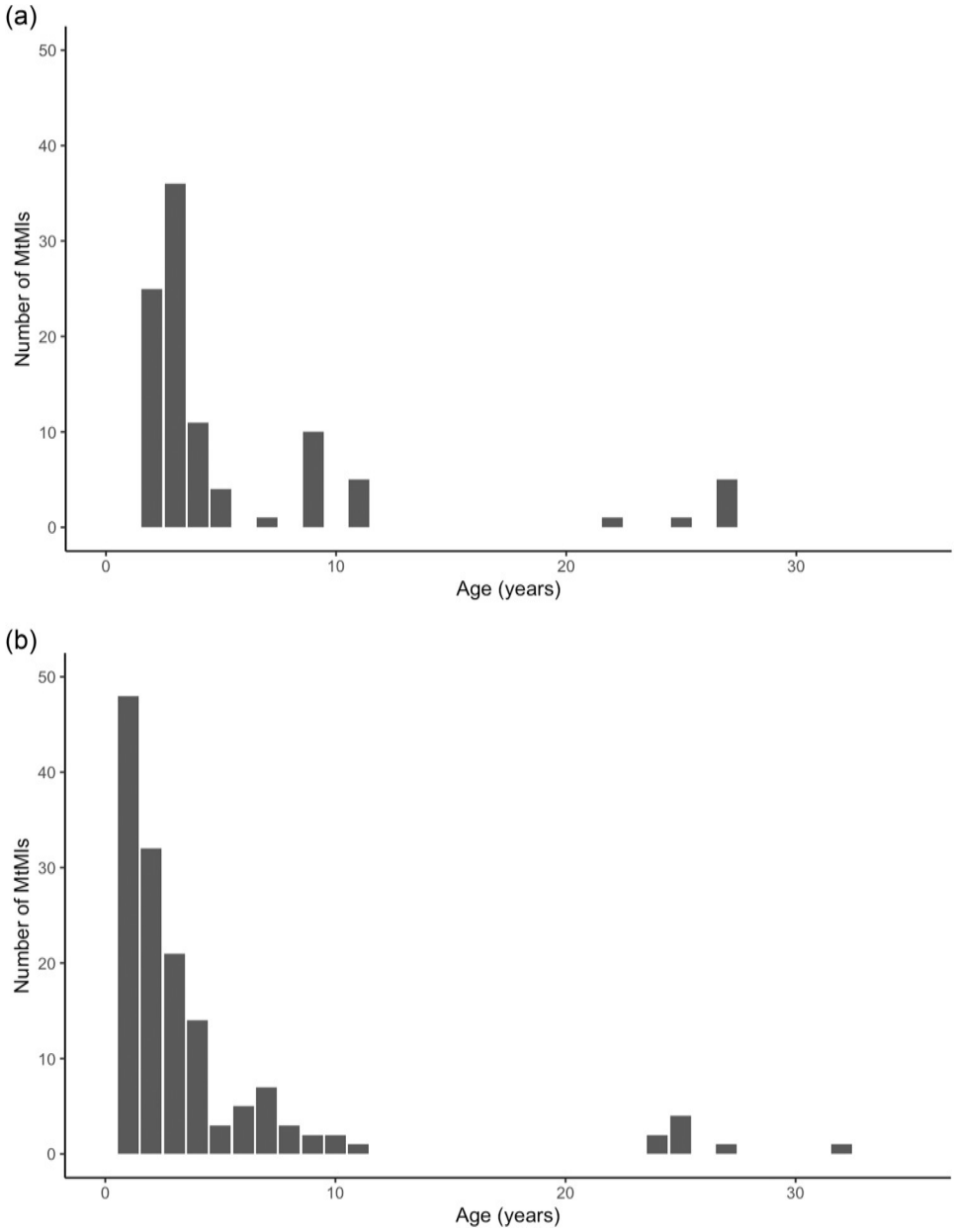

FIGURE 2 Age (in years) when mouth-to-mouth interactions were initiated (a) and received (b).

females ($M = 15.50$, $SD = 7.55$) was not significantly different ($t(7) = 0.22$, $p = 0.83$). With regard to receiving MtMIs, immature females received fewer ($n = 56$) than did immature males ($n = 79$); however, this was not statistically significant ($t(7) = 0.30$, $p = 0.77$) between the mean initiation of males ($M = 15.80$, $SD = 8.84$) and females ($M = 14.00$, $SD = 8.76$). Although adult females did not initiate MtMIs, they did receive MtMIs ($n = 5$) similar to adult males ($n = 9$).

TABLE 2 Summary of mouth-to-mouth interactions (MtMIs) seen in calves.

Subject	Sex	MtMI total	Age of first MtMI (months)
OLI	Male	31	3
GRA	Male	20	3[#]
QIN	Female	9	5
BEL	Female	23	2
ATL	Female	21	11
SAM	Male	22	3
STL	Female	9	6
KEN	Male	7	19
INK	Male	6	6

Note: [#]Age rounded to the nearest month as the first recorded MtMI for OLI and GRA occurred 2 days before GRA turned 3 months and 1 day after OLI turned 3 months.

3.3 | Partnerships

3.3.1 | Age

The majority of MtMIs (71.1%, $n = 106$) occurred between age-matched partners (Figure 3). However, for adults, only 27.3% ($n = 6$) of the 22 MtMIs initiated were directed to age-matched adults. Only 6.5% ($n = 7$) of immature initiated MtMIs were between nonage-matched partners when age-match partners were available. When immature interactions were not between age-matched partners, 23.8% ($n = 5$) were with younger individuals and 76.2% ($n = 16$) were with older partners. Immature animals that were engaging in MtMIs with older animals were doing so mostly with adults ($n = 14$), and most of these were directed to animals other than their mother (78.6%, $n = 11$). A significant Kendall correlation ($r_\tau = 0.45$, $p < 0.0001$) was found between the age of the initiator and the age of the receiver, indicating that belugas prefer to perform MtMIs with age-matched partners.

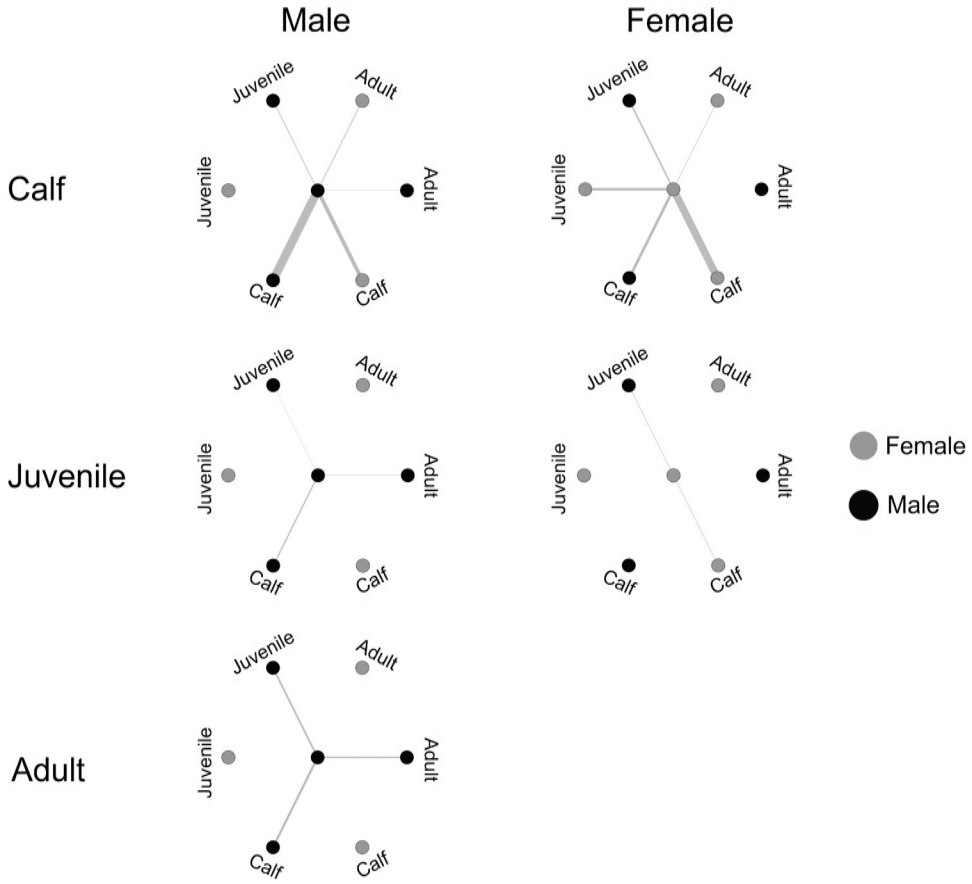

FIGURE 3 Unidirectional egocentric social networks of male and female MtMIs through development. Adult females are not included as they did not initiate any MtMIs. MtMI, mouth-to-mouth interaction.

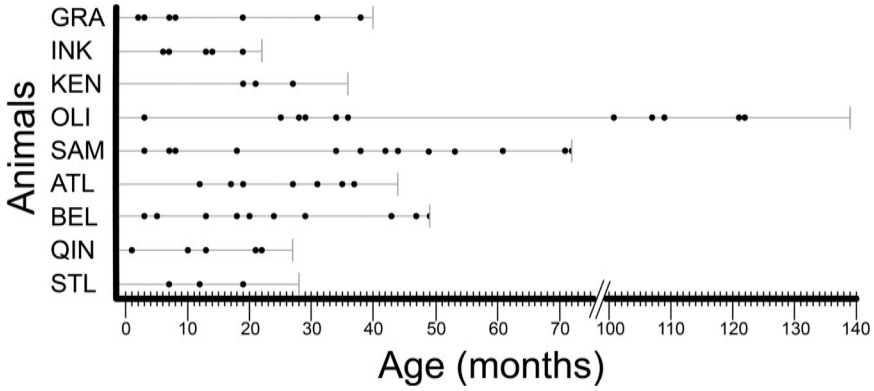

FIGURE 4 Presence of mouth-to-mouth interactions (MtMIs) for each month of life for all nine calves born at SeaWorld Texas. This graph illustrates the sporadic nature of these interactions and the variation in the age of onset. The light gray lines reflect the observation period of each animal while the black dots represent the occurrence of MtMIs (one black dot could be just one MtMI or multiple for any given month of life). Please note that as the animals were born from 2007 to 2017, this graph does not accurately reflect the conspecifics to which each beluga had access.

TABLE 3 The age of onset of mouth-to-mouth interactions used to predict the age of onset of other social behaviors.

Factors	Social category	Test (r_τ)	*p*
Open mouth	Aggressive	0.58	1.00
Ventral presents	Sexual	0.58	0.28
Pelvic thrusts	Sexual	−0.21	1.00
Horizontal S-posture	Sexual	−0.32	1.00
Genital rub	Sexual	0.34	1.00
Social play	Affiliative	0.42	0.91
Locomotor play	N/A	0.30	1.00

3.3.2 | Sex

Most of the MtMIs occurred between female–female pairs (46.3%, $n = 69$), with the remaining interactions distributed between male–male pairs (28.9%, $n = 43$) and mixed-sex pairs (24.8%, $n = 37$).

3.3.3 | Same-sex and same-age

MtMIs between same-sex and same-age partners occurred more often (32.9%, $n = 49$) than between opposite-sex and same-age partners (20.1%, $n = 30$).

3.4 | Individual differences

A beluga's age at first participation in MtMIs varied greatly. Some animals were observed initiating MtMIs at 2 months old while others were not observed initiating them until 19 months old (Figure 4). The age of onset of MtMIs was not correlated with the age of onset of any other behaviors (Table 3). Individual differences were found in the rate of initiating MtMIs with some animals initiating more than double the MtMIs than others (e.g., KEN vs. BEL) (Figure 5).

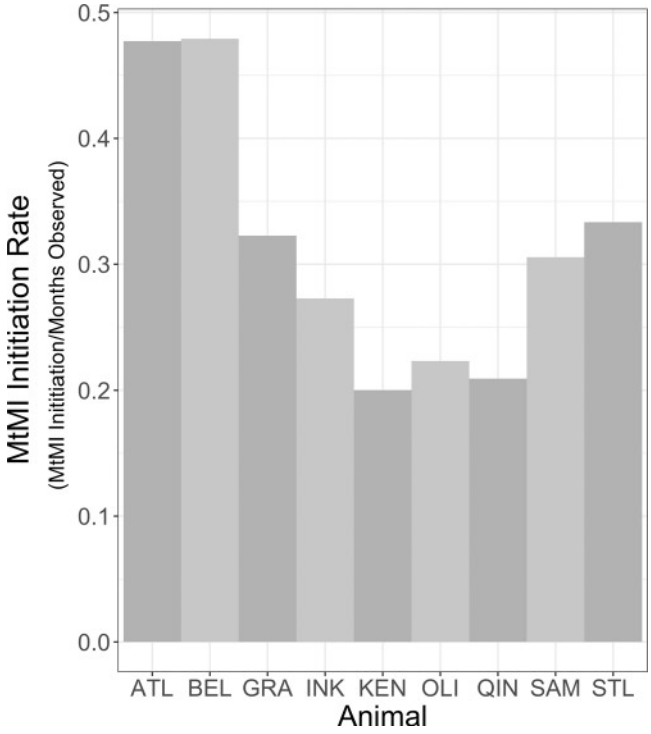

FIGURE 5 A comparison of how many mouth-to-mouth interactions (MtMIs) were initiated by each calf when standardized by the number of months they were observed.

3.5 | Seasonality of MtMIs

Initiation of MtMIs was observed year-round, but peaked in the summer (Figure 6), with an apparent sex difference as females peaked

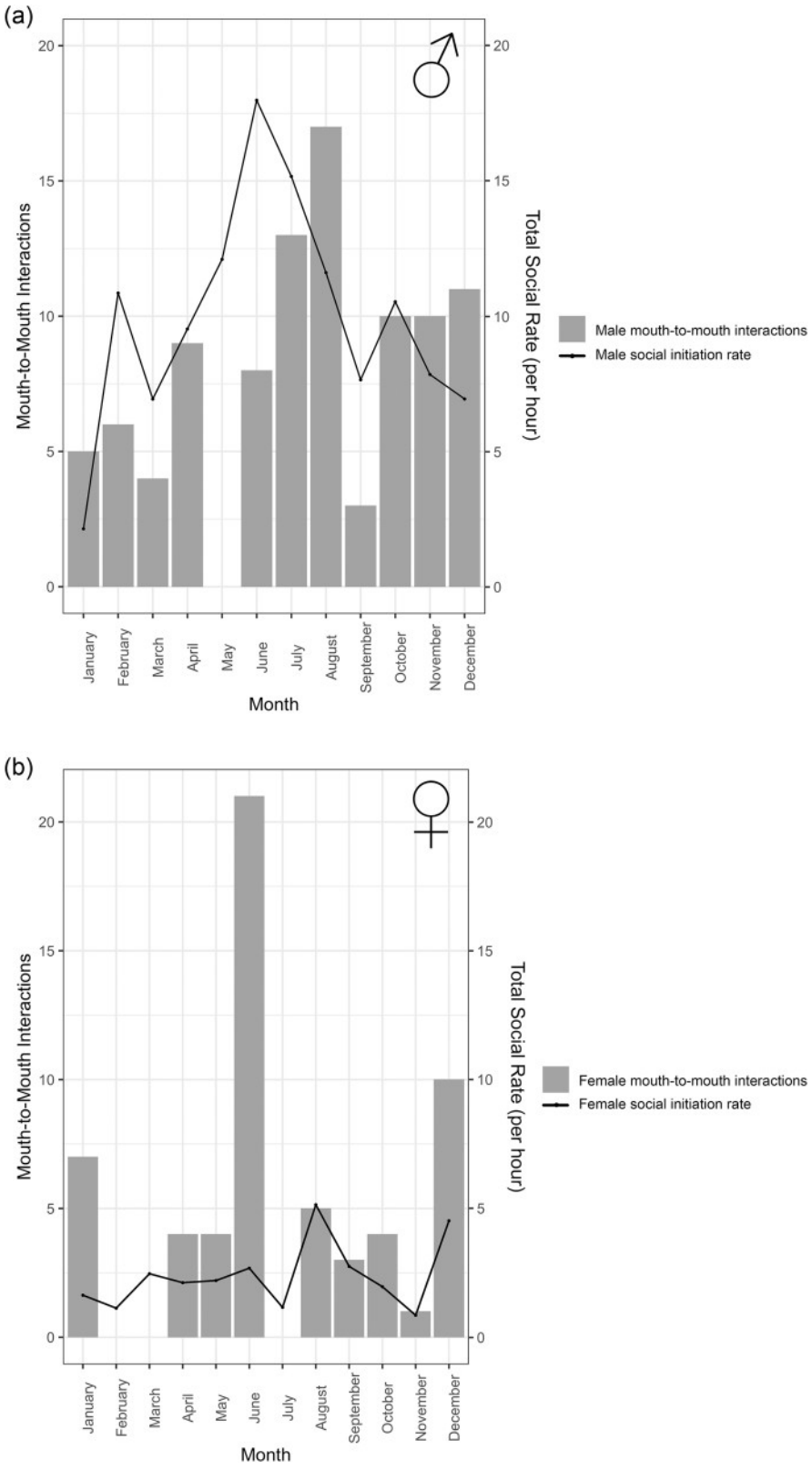

FIGURE 6 Both male (a) and female (b) mouth-to-mouth interactions and social frequency as a function of month.

early in summer (June), and males peaked later (August). The initiation of overall social behavior was also seasonal (Figure 6). The overall sociality of females was not significantly correlated to MtMIs ($r_\tau = 0.35$, $p = 0.125$). The same was true for males ($r(10) = 0.26$, $p = 0.407$).

4 | DISCUSSION

MtMIs have been reported in belugas at several facilities (e.g., Connor & Peterson, 1994; Hill et al., 2019; Recchia, 1994) and in the wild (e.g., Krasnova et al., 2014), suggesting that MtMIs are species-

typical. As previously reported for the belugas housed at SWT (Hill et al., 2019), MtMIs are mostly performed by immature animals, but unlike the earlier preliminary study, we found that MtMIs continue into adulthood, albeit at a much lower frequency. MtMIs emerge within the first few months of life and occur sporadically over the preweaning and juvenile periods, gradually declining in frequency thereafter. Our results also show that immature animals initiated most MtMIs, and most animals partnered in MtMIs were also immature. In contrast, MtMIs involving adults most frequently involved immature animals and were exclusively initiated by adult males. All nine of the immature belugas studied initiated MtMIs, as did all three adult males. These patterns provide insights into the potential functions of MtMIs, which will be discussed below.

4.1 | Do belugas prefer to play with different-aged animals?

Considering that most of the MtMIs by immature animals involved age-matched partners, it might be that, at earlier ages, this form of social play, like play fighting more generally (e.g., Biben, 1986; Cheney, 1978; Koyama, 1985; Meaney & Stewart, 1981; Pellis & Pellis, 2016), is involved in the social and physical development of belugas. In many species, play fighting preferentially involves same-age peers and often same-sex peers. Previous investigations into the sociosexual play of belugas revealed that calves prefer to play with older animals (Ham et al., 2022), while juvenile and subadult animals prefer to play with calves (Lilley et al., 2020). This pattern is different from other animals which prefer to play with same-age and same-sex partners (e.g., Byers, 1980; Gomendio, 1988; Mackey et al., 2014; Maestripieri & Ross, 2004; Palagi, 2006). Belugas prefer different-aged peers for sociosexual play but exhibit the typical pattern of same-aged peers in MtMIs. Controlling for availability of partners diminished the possibility that the divergent partner preferences between sociosexual interactions and MtMIs were a product of the group composition at the time of observation (present study; Ham et al., 2022; Lilley et al., 2020). Perhaps these differences between types of play are accounted for by differences in the degree of competition involved. MtMIs are more competitive, involving a test of strength, so partners with similar skill levels are preferred. In contrast, sociosexual play, involves more interanimal coordination, so a more skilled partner may be preferred. These differences in play partner preference suggest that the adaptive functions of sociosexual play and those of MtMI may differ.

4.2 | Are MtMIs used to facilitate motor skill development?

MtMIs may be a way for belugas to train motor skills, as appropriately positioning the body to make mouth-to-mouth contact requires fine motor control. The motor training hypothesis could explain both the early and varied onset of MtMIs. If suitable partners are available, MtMIs can emerge in their first few months of life (Hill et al., 2016, 2018). As shown in the present paper, if no suitable partners are available, the onset of MtMIs can be delayed until later in the first or second year of life. However, whether the onset is early or late, MtMIs provide an opportunity for training motor skills. By engaging with partners that have only small differences in skill advantage, it has been hypothesized that these interactions provide optimal opportunity for training cognitive and physical skills (e.g., Biben, 1998; Fagen, 1981; Thompson, 1998).

Consistent with the motor training hypothesis, most MtMIs involved immature animals (85.7% of those initiated and 90.6% of those received), and most bouts occurred between age-matched partners (71.1%). Indeed, when age-matched partners were available, only 6.5% of MtMIs were observed between nonage-matched partners. Further, immature female belugas preferred to play with same-sex partners more than males (46.3% vs. 28.9%), however, females did not initiate more MtMIs than males overall. As males engage in sociosexual play primarily with same-sex partners, while females play with males more than same-sex partners (Ham, Lilley, Miller, & Hill, 2021; Hill et al., 2015; Lilley et al., 2020), perhaps males and females compensate this partner sex discrepancy by engaging in more MtMIs. In other words, males are the desirable partner in sociosexual play, but females are more desirable in MtMIs. In addition, the same-sex preference exhibited by young females engaging in MtMIs may further enhance motor training, as they are playing with partners with a similar level of skill (Biben, 1998; Thompson, 1998). As already noted, MtMIs require as much physical and social coordination as do some of the more complex actions performed during sociosexual play. Even though MtMIs are less frequent than sociosexual play (Ham et al., 2022; Ham, Lilley, Miller, & Hill, 2021; Lilley et al., 2020), they may provide similar training benefits.

4.3 | Are MtMIs used to facilitate social relationships?

Although it is unlikely that MtMIs are sufficient in themselves to promote the development of social skills in immature belugas, due to their rarity and sporadic occurrence (making up less than 15% of all social play), MtMIs may still provide unique opportunities with which to develop social relationships (Palagi, 2011; Pellis, 2002). By engaging in social play, some animals explore the type and strength of social connections with conspecifics (Kohn, 2019; Pellis, 2002). While most adult-initiated MtMIs were directed toward juveniles (72.7%), all adult–adult MtMIs occurred between male pairs. Adult males engage in social behavior frequently; however, it is primarily sociosexual (Hill et al., 2015). In contrast, adult females did not initiate MtMIs, but they were partnered in MtMIs. The finding that such play is rare in adults, and mostly arises from being initiated by immature whales, suggests that MtMIs may not serve this function for adults. This low incidence of MtMIs found in this study may be related to the small number of adults in this stable social group, but

observations of another social group with adult males corroborate that MtMIs are not a common behavior (M. Noonan, personal communication).

While MtMIs may serve as tools for building social relationships, it may also be that these interactions are practice for other aspects of their behavioral repertoire, such as sociosexual or courtship behavior. The seasonal trend in MtMIs, with both males and females peaking in summer months, found in the present paper, supports the possibility of this behavior having a sociosexual or courtship component. Not only does mating (Doan & Douglas, 1953; Heide-Jørgensen & Teilmann, 1994; Krasnova et al., 2009; Robeck et al., 2005; Shelden et al., 2020) and calving vary seasonally (Sergeant, 1973), peaking in the summer months, so does sociosexual behavior and other affiliative behavior (Ham, Lilley, Miller, & Hill, 2021). This heightened social arousal during the summer months could also account for the seasonal trend of MtMIs. Closer attention to the presence and context of MtMIs in belugas in managed care could elucidate if these MtMIs are influenced by different social compositions.

4.4 | Could MtMIs be dominance or aggression?

Earlier reports suggested that MtMIs may be used to establish dominance relationships (Krasnova et al., 2014; Serres et al., 2021). However, close examination of the topography of this behavior does not indicate that there is a "winner" or "loser" and both participants actively participated in the behavior, suggesting that MtMIs are a mutually cooperative behavior (Hill et al., 2019). Our current observations of MtMIs suggest that this is a form of social play rather than being related to dominance or aggression, fitting the criteria for play in general (Burghardt, 2005) and play fighting in particular (Smith, 1997). Tactile aggressive behaviors in belugas often result in tooth rakes on the skin (Ham, Lilley, & Manitzas Hill, 2021). If MtMIs were a form of aggression, then tooth raking, whether teeth are present or not (Stewart, 2012), should occur occasionally, and the mouth-lock should be broken by one of the partners who then bites or mouths the other's body. However, this was never observed in any of the instances of MtMIs.

4.5 | Are MtMIs similar to jaw sparring in other species?

The jaw wrestling or jaw sparring that has been described in several species of Carnivora appears similar to the MtMIs observed in belugas. For example, black bears (*Ursus americanus*; Burghardt, 1975; Henry & Herrero, 1974), coyotes (*Canis latrans*; Fox, 1969), wolves (*C. lupus*; Fox, 1969), and domesticated dogs (*C. familiaris*; Coppinger et al., 1987; Smuts, 2014), have all been described engaging in the mutual interlocking of their jaws during play. In the jaw sparring of dogs, the partners move their heads in such a way as to avoid their teeth contacting the other dog's face, further supporting the view that this is a playful, not aggressive, behavior (Smuts, 2014). Nonetheless, jaw wrestling is rare, with most species orienting toward other body targets during play fighting (Aldis, 1975; Pellis, 1988). One proposed function of this unusual behavior, at least in some species, is that it used for play-invitation or play-solicitation (Burghardt, 1975). This is unlikely to account for MtMIs in belugas, as most social play, such as sociosexual play (Ham et al., 2022), most often occurs without MtMIs preceding interactions. Similarly, sociosexual play does not often directly precede MtMIs. The scarcity of playful mouth-to-mouth contact in the animal kingdom may be due to the opportunities afforded by body morphology.

Mammals with fins or flippers rely more heavily on their mouths to manipulate the world, and so may be more likely to use their mouth more in playful contact, like jaw sparring or MtMIs (e.g., see Gentry, 1974 and Llamazares-Martín & Palagi, 2021, which includes photographs of Steller sea lion, *Eumetopias jubatus*, and California sea lion pups, *Zalophus californianus*, respectively, engaging in jaw sparring). Killer whales engage in affiliative gentle tongue biting, in which two animals face each other making gentle contact with their rostrum, followed by one animal opening its mouth and the other lightly holding its partner's tongue in its teeth (Bain, 1986; Martinez & Klinghammer, 1978; Nakamura & Sakai, 2014; Sánchez–Hernández et al., 2019). Irrawaddy dolphins (*Orcaella brevirostris*), a much smaller euryhaline delphinid, often form groups of individuals that face each other and engage in head-to-head contact after bouts of chasing and mating (see Sutaria et al., 2019). Similarly, bottlenose dolphins will face each other, often with their mouths open, during bouts of sociosexual behavior and engage in head-to-head contact while emitting vocalizations and blowing bubbles (Connor et al., 2000; Overstrom, 1983). Bottlenose dolphins also engage in mouth-to-rostrum mouthing, in which one animal places its mouth around the rostrum or beak of another (see Hill et al., 2019). In these cases, however, there is no mention of interlocking jaw contact, even though killer whale tongue touching does require the rostrum of one whale to be inside the mouth of the other. Although not frequently reported among cetaceans or other aquatic mammals, mouth-to-mouth contact may be widespread and should be studied more systematically.

5 | CONCLUSIONS

Our results indicate that MtMIs are a form of play behavior that occurs sporadically, and most frequently performed by immature animals. Despite other toothed whales reportedly engaging in head-to-head interactions or MtMIs, the topography of beluga MtMIs is unique. Further, our findings are consistent with two functional hypotheses: immature belugas may engage in MtMIs to train motor and social coordination skills, and both adults and immature animals may use MtMIs to facilitate social bonds. While these hypotheses remain to be tested, the present study should inspire comparative studies in other cetaceans to ascertain whether comparable patterns of interaction are present and if they have comparable age and partner preferences.,

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This study was a purely observational study of animals housed in a long-term managed care setting. No invasive procedures were conducted. Animal care was provided by the zoological facilities housing the animals, and animals remained at the zoological facilities upon completion of this study. The St. Mary's University IACUC number is StMU2018-3.

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APPENDIX A

Behaviors	
Mouth-to-mouth interaction (MtMI)	Two individuals gently clasp each other's mouth and then pull in opposite directions (i.e., like a handshake but with the mouth).
Social behavior	Including sociosexual behavior (an actor displays sexual posturing, thrusts, penile erections, see Hill et al., 2015), affiliative behavior (social swims and play), and agonistic behavior (an actor chases, bites another, as well as head jerks, or open mouths at another). For the purposes of this paper, we excluded mother–calf interactions from overall social behavior.

Note: Adapted from Hill et al. (2019) and Lilley et al. (2020).