Evidence for Maternal Style Among Adult Female Dolphins When Sharing Pectoral Fin Contacts with Their Calves

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Abstract – Adult bottlenose dolphins share pectoral fin contacts (PFC) to manage their social relationships but less is known about how mothers share PFC with their calves. Using a dataset collected over 16 years, we analyzed how 10 matrilines, including three second generation female dolphins in a maternal role, used PFC with their pre-weaned calves. Mothers had different rates of initiation with their calves forming a continuum from those initiating few contacts (15%) to those initiating more (44%). For mothers with all-aged calves, the lateral side was contacted the most to start interactions with mothers contacting body parts at a similar rate. All mothers assumed the same posture regardless of their role as initiator or receiver, with horizontal the most prevalent posture. Two maternal styles were found for PFC: high and low use of PFC. Within the high PFC group, there was individual variation that was related to calf sex. Even though evidence of maternal style was confirmed in PFC exchanges between adult female dolphins and their calves, the number of PFC shared between these kin was only ~9% of all documented PFC contacts (*N* = 4,345) over 16 years, suggesting that other forms of tactile contact may be more important within the confines of the mother-offspring relationship in delphinids.

Keywords – Behavior, Bottlenose dolphins, Mother-calf dyads, Pectoral fin contact, Tactile contact

Most dolphin species are characterized by a fission-fusion social structure with smaller subgroups mingling and merging to form larger groups to forage or socialize and then dividing into smaller groups of same or different membership. Within these fluid societies, dolphins maintain complex relationships (Connor, 1992; Lusseau, 2003; Lusseau et al., 2006; Smolker et al., 1992). In some coastal delphinid populations, adult male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) form relationships that last their lifetimes with associations that rival the strength of the mother/calf bond (Connor et al., 1992). These male friendships facilitate increased breeding success when pairs compete with other male alliances (Connor, 1992; Connor et al., 1992; Wells et al., 1987), and alliances have been observed to coordinate their activity in competition with other male alliances for reproductive success (Connor, Smolker, et al., 2006). Some alliances can vary in duration, size, and stability, though first order alliances may persist for 20 years or more (Connor & Krützen, 2015). Young males will engage in much social-sexual activity, with pectoral fin contact (Dudzinski & Ribic, 2017) used as a social bonding tool that facilitates establishing and maintaining strong associations between individuals—this is a stage when young dolphins cultivate their social relationships and practice their social skills (Stanton & Mann, 2012). As adults, female dolphins coordinate with other adult females for a variety of reasons and have been recorded, in some groups, to babysit other females' calves (Dudzinski, 1996; Mann & Smuts, 1998), to coordinate behavior to fend off

harassment by adult males (Smolker et al., 1992), to develop foraging techniques and skills (Mann et al., 2007; Sargeant & Mann, 2009), and to protect calves (Mann et al., 2000). Still, one of the strongest bonds among dolphins is between a mother and her calf (e.g., Gubbins et al., 1999; Mann et al., 2000; Mann & Smuts, 1999).

Dolphin calves of most species are reared by their mothers for two to four years on average. The mother-calf bond is critical for survival and future social network success (Gibson & Mann, 2008). Calves depend on their mothers for protection, nutrition, resting opportunities, energy savings, and comfort or security (Mann et al., 2000; Mann & Smuts, 1999). Calves learn how to forage and navigate social networks from their mothers during their first few years of life (Gibson & Mann, 2008; Krzyszczyk et al., 2017). Even after weaning, juvenile dolphins may maintain their associations with their mother's social group until they form their own social group(s); when they become reproductively mature, females rejoin their natal pods and males begin to roam as dyads within and between larger networks (Mann et al., 2000; Mann & Smuts, 1999).

Dolphins in managed care demonstrate the same behavioral milestones and maternal care as wild dolphins (Gubbins et al., 1999; Hill et al., 2007). Mothers maintain continuous vigilance of their calves, especially early during the first year of life (Hill et al., 2008; Lyamin et al., 2005, 2007, 2008). Vigilance is monitored both visually and tactically by mothers but to different degrees; some mothers are extremely vigilant and protective of their calves, monitoring their calf's behavior by keeping the calf in close proximity and immediately retrieving a calf that has strayed too far, which may involve directed trajectory changes, including pushing or tossing the calf into the desired swim path (Hill et al., 2007). Many of these highly vigilant mothers were also more likely to discipline their calves for separations and, in some cases, exploration (Hill et al., 2007). In contrast, other mothers were more relaxed and allowed their calves to travel greater distances from her for longer periods, without frequent discipline (Hill et al., 2007). These quantitative and qualitative differences comprise evidence for different maternal styles. One area that has not been explored fully for dolphins is the role of contact in maternal styles. (Note: use of the word contact without a clarifying adjective will refer to any form of physical contact.) Although contact was a behavior that appeared to differ among mother-calf pairs, it was not systematically measured when maternal styles were investigated in these previous studies. Research with beluga (*Delphinaptera leucas*) calves has shown evidence for individual maternal styles (Hill, 2009; Hill et al., 2013), and contact between beluga mothers and calves was confirmed to significantly contribute to their bond formation (Hill et al., 2018). Still, the limited beluga sample size did not address if individual mother-calf pairs engaged in different types and amounts of contact (Hill et al., 2018), and it remains unclear if contact varies based on maternal style in odontocetes.

Dolphins use tactile contact for both affiliative and agonistic reasons. Within dolphin dyads, physical contact has been shown to aid in the establishment, maintenance, and management of their relationships (Connor, Mann, et al., 2006; Dudzinski & Ribic, 2017), to be involved in both object and behavioral play (Greene et al., 2011; Kuczaj & Eskelinen, 2014; Paulos et al., 2010), and to allow for reconciliation after aggressive interactions (Tamaki et al., 2006) or for reconciliation more generally (Weaver, 2003). Physical contact has also been observed as a disciplinary action (Dudzinski, 1998; Hill et al., 2007), a perceived comforting action toward a conspecific (Dudzinski, 1998; Weaver, 2003), an affiliative action (Dudzinski, 1998; Harvey et al., 2017), and in more severe exchanges, contact has been recorded during aggressive interactions (e.g., rostrum rams, fluke kicks, etc., Dudzinski, 1998; Harvey et al., 2017). Although much has been examined with respect to how dolphins share physical contact, there is a paucity of data with regards to how touch (rubbing or static contact) is shared between mothers and their pre-weaned calves.

Current Study Objectives

We addressed two questions in this study: 1) How do adult female dolphins use pectoral fin contact with their calves? And, 2) are there individual differences among adult female dolphins (i.e., maternal style) in their use of pectoral fin contact, specifically with regards to younger and older calves and with regards to sex of the calves? To address these research questions, we examined the following variables from a 16-year

archive of video data collected using a focal follow sample protocol with all occurrence documentation of dolphin interactions and behavior, and event sampling of pectoral fin contacts (PFC) exchanged between two individuals from all video data. Previous research focused on PFC exchanges between dolphins in different settings (Dudzinski et al., 2009, 2010, 2013), PFC exchanges as compared with self-contact by individual dolphins (Dudzinski et al., 2012), and PFC as a tool for social bonding between non-kin (Dudzinski & Ribic, 2017); mother/calf pairs and sibling pairs are the final dyads in this dataset to examine with respect to the potential functional significance of PFC exchanges. To understand how kin might use PFC, we examined adult females as initiators of PFC with their calves, looking at variability by calf age and sex, as well as adult and calf postures and body parts contacted.

Method

We used data collected on 10 matrilines, including three second-generation females, to facilitate a multi-level examination into how adult females interact using PFC with their calves. Data specific to mother-calf interactions are part of long-term, comparative research into dolphin behavior by the Dolphin Communication Project (DCP; e.g., Dudzinski et al., 2009, 2010; Dudzinski & Ribic, 2017; Evans-Wilent & Dudzinski, 2013; Paulos et al., 2007). Permission to observe and collect data on the dolphins at The Roatan Institute for Marine Sciences (RIMS), Anthony's Key Resort (AKR), Roatan, Honduras, was granted by the facility; RIMS holds current permits from the Honduran government for housing dolphins.

Study Site and Population

Data were collected at RIMS annually for 16 years (~140 hr inclusive from 2003 to 2018, see Appendix). This common bottlenose dolphin (*Tursiops truncatus*) group is housed in coastal sea pens adjacent to Bailey's Key, along the NW side of Roatan. The sea pen, located inside Roatan's fringing reef, includes one large enclosure (~8,000 m^2 in surface area) and several smaller areas for training, research, and medical procedures. Video data were collected in the large enclosure. Dolphin ages in this study population ranged from neonate to 40+ years; the general social dynamic was similar to that observed for wild bottlenose dolphins (e.g., Connor, Smolker, et al., 2006; Kogi et al., 2004). The total number of dolphins per observation session varied depending on coordination with other facilities managed by RIMS, as well as by recorded deaths and births. Each adult female had a range of one to six offspring over the 16 years of observation (Table 1).

Data Collection

Dyadic interactions between dolphins and general dolphin behavior were recorded on video with concurrent stereo audio via a mobile video/acoustic system while underwater (Dudzinski et al., 1995). PFC exchanges were event sampled from video data that were collected using an all occurrence focal follow protocol; see Dudzinski et al. (2009) and Dudzinski and Ribic (2017) for details related to video data collection protocols. Each contact between one dolphin's pectoral fin and another dolphin's body (including the pectoral fin) was documented (see Dudzinski et al. (2009) for definitions and sampling protocol); for this study, focus was on mother/calf interactions.

Definitions

Because this paper extends our examination of PFC exchanges specifically to mother/calf dyads, our definitions for several terms (e.g., body parts, postures) were consistent with previously published work (e.g., Dudzinski et al., 2009, 2010, 2012, 2013; Dudzinski & Ribic, 2017). Kin relations were assessed based on maternal relatedness; paternity was being assessed via DNA sampling but was not complete for all dolphins in this study group and, thus, paternity was not used to define kin relations.

Four dolphin age classes [i.e., adult (~2 m long), subadult (~3/4 length of adult with less girth), juvenile (~½ adult length) and calf (less than ½ length of adult)] were used to categorize dolphins at RIMS

and were based on knowledge of year born (from RIMS records) or age estimation if wild-caught based on size and girth in comparison to literature for other bottlenose dolphin study populations (e.g., Connor, Smolker, et al., 2006; Kogi et al., 2004). Because this study focused on younger and older calves, the calf age class was further subdivided into three separate ages based on years: one-year-old calves (C1), two-year-old calves (C2), and three-year-old calves (C3). For all calves included in this study, date of birth was known. Thus, each calf was assigned to their age class category (C1, C2, C3) for each data collection session based on their birth date (Table 1).

The dolphin body was divided into 11 sections (see Dudzinski et al., 2009) to characterize where on the body contact was made between one dolphin's pectoral fin and another dolphin's body. For this examination of mother-calf exchanges, because there were few contacts for some body parts, those body parts were put into a single category for analyses (Figure 1).

Table 1

Matrilines with Identified Offspring (calves) Available for Observation Across all Years (2003-2018) and the Number of Documented Pectoral Fin Contact Exchanges for Each Mother/calf Pair

Mother	Calf name (sex)	Calf ages observed	Pectoral fin contact exchanges observed *(regardless of Initiator)*
Alita	Fiona (F)	C1, C2, C3, J, S	0, 14, 2, 0, 0
	Anthony (M)	C1, C2, C3, J	7, 2, 0, 0
	Cortez (M)	C1, C2, J	nv, 0, nv
	Lenca (M)	C2, C3, J, S	1, 1, 0, 0
	Dory (F)	C1, C2	1, 30
Bailey*	Tank	C1	43
Carmella	Ritchie (M)	J, S, A	2, 0, 0
	Ken (M)	C1, C2, C3, J, S	0, 3, 1, 0, 0
	Dixon (M)	C1, C2, C3, J, S	0, 2, 0, 0, 0
	Elli (F)	C2, C3, J	0, 0, 0
	Stan (M)	C1, C2	0, 2
Cedeña	Bailey (F)	C1, C2, C3, J, S, A	0, 10, 0, 2, 0, 1
	Pigeon (F)	C1, C2, C3, J	0, 22, 2, 0
	Calli (F)	C2, C3, J	2, 0, nv
GeeGee**	Mika (F)	C3, J, S, A	2, nv, nv, nv
Gracie	Maury (F)	C2, C3, J, S, A	19, 1, 1, 1, 7
	Jack (M)	C1, C2, C3, J	0, 3, 23, 0
	Luna (F)	C1	20
	Tilly (F)	C1, C2, C3, J, S, A	0, nv, 8, 5, 0, 3
	Shawn (M)	C1, C2	3, 25
Maury*	Champ (M)	C2, C3, J	0, 1, 0
Mika*	Mickey (M)	C1, C2, C3, J	0, 17, 0, 0
	Poli (F)	C1, C2, C3, J, S	nv, nv, nv, 1, 0
	Mac (M)	C1, C2, C3, J	6, 5, 0, 0
Mrs. B.	French (M)	C1, C2, C3, J, S, A	8, 4, 2, 0, 0, 0
	Margarita (F)	C1, C2, C3, J, S	8, 6, 0, 2, 0
	Vin (M)	C1, C2, C3, J	0, 9, 2, 0
Rita	Tela (F)	J	0
	Ronnie (M)	C1, C2, C3, J, S, A	4, 0, 0, 0, nv, nv
	Osgood (M)	C1	9

Note. Abbreviations are: C1 is one-year-old calf; C2 is two-year-old calf; C3 is three-year-old calf; and F = female, M = male, A = adult, S = subadult, J = juvenile. Use of "nv" indicates no video collected for that calf at that age with mother; mother and calf were not observed or video-recorded together at the calf age indicated. A "0" in the Pectoral fin Contact exchanges column indicates the calf at the indicated age was available for observation and was video-recorded with the mother but that no PFC were documented on video. * indicates second generation adult female matrilines. ** GeeGee was present during observations only for Mika as a C3.

Figure 1

Diagram Presenting Labeled Body Parts for Analysis
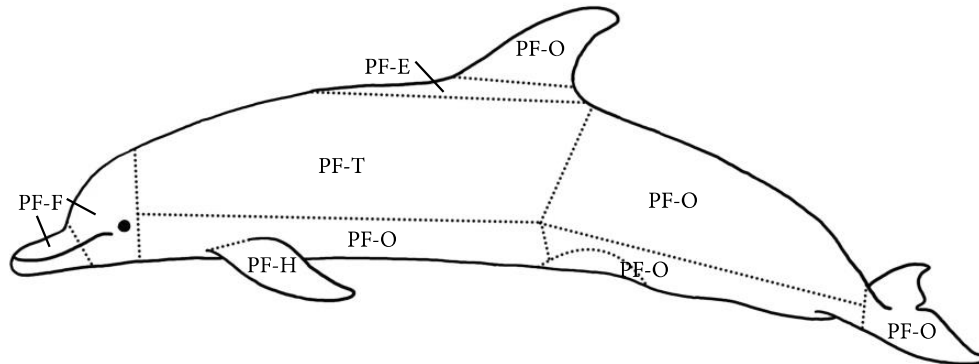
Note. PF-E is a dolphin's back. PF-F is the rostrum, face and melon. PH-H is the pectoral fin. PF-T is the lateral sides. PF-O includes the dorsal fin, belly, genital area, peduncle (dorsal and ventral) and the fluke. Sketch adapted from Dudzinski et al. (2009).

Statistical Analyses

The sampling unit was the identified initiating or receiving mother for each PFC exchange with her identified calves. Data were collated by mother (Table 2). Note that Table 1 contains all observations of PFC exchange between each adult female and each of her calves regardless of whether the initiator (INI) is known or not. Table 2 contains data for PFC exchanges between adult females and their calves for PFC exchanges only where the INI is known.

Table 2

Total Number of PFC for Adult Females with her Calves, Regardless of Calf Sex and Age, Categorized by the Mother as Initiator and Mother as Receiver (i.e., Calf as Initiator)

		Pectoral Fin Contacts		
Mother	Number of calves	Mother as Initiator	Calf as Initiator	Total Known Initiator interactions
Gracie	5	36	64	100
Alita	4	19	39	58
Mrs. B.	3	6	33	39
Cedeña	3	16	20	36
Mika	2	5	23	28
Bailey	1	16	27	43
Carmella	3	4	5	9
Rita	1	3	6	9
GeeGee	1	1	1	2
Maury	1	0	1	1

Note: Number of calves are the number of the mother's calves with whom she interacted. The sample size and number of calves per female in this table can differ from the values in Table 1 because Table 2 includes only PFCs exchanged by confirmed initiators, whether adult female or her calf.

We first examined how mothers use PFCs with their calves, regardless of age and sex. We considered how mothers use PFCs overall to be a potential metric of maternal style. Specifically, we tested for whether mothers have the same probability of initiating contacts with their calves. We used data only from mothers interacting with multiple calves and where the interactions per calf was greater than 5. Using data from females that interact frequently with multiple calves gave us a better measure of maternal style (larger number of calves and larger number of interactions per calf) than one based on interactions with a single calf (sample size of 1) or low number of interactions/calf (low precision for probability estimates). To determine if the probability of initiating contact varied by mother, we used a generalized linear mixed effects model (McCullagh & Nelder, 1989). The response variable was coded as 1 if the mother was the initiator and 0 if the mother was the receiver (i.e., the calf was the initiator). The explanatory variable was mother ID as a fixed effect and we used a binomial error structure. Calf ID was the random effect. There were five females who interacted with multiple calves (i.e., multiple calf mothers; Alita, Cedeña, Gracie, Mika, Mrs. B.; Table 2). For females who only interacted with one calf (i.e., single calf mothers) and who had five or more PFC exchanges with their calf (Bailey, Rita) or who had low number of interactions/calf (Carmella; Table 2), we compared their patterns of initiation to possible maternal styles from the model of the five females. We identified potential maternal styles based on groups of mothers that had significantly different patterns of initiation. Specifically, we used the group average probability of the mother initiating contact to define the theoretical distributions against which to compare the patterns of the single calf mothers. We compared the patterns of the single calf mothers against each of the theoretical distributions using contingency tables and a simulation approach to determine significance of the test statistic; 20,000 simulations were conducted for each test (Rugg, 2003). In these tests, the null hypothesis is that single calf mother patterns follow the theoretical distributions. To control for using the same data in two separate tests, we used a p-value of .01 as a Bonferroni correction instead of .05 for significance for each test. Females were then assigned to the group where the null hypothesis was not rejected (i.e., the females' probabilities fit the theoretical distribution).

We next analyzed for differences in how the grouped mothers initiated PFC with younger and older calves, and then with respect to body part preference, posture(s) during exchanges, and duration of contacts. We used younger calves (C1) and older calves (C2 and C3) because sample sizes in the C3 age class were too low to allow for statistical examination. It is possible that any differences between these two older calf age classes might add variability in our final results but it was our assumption that potential developmental differences between C2 and C3 ages would not significantly impact our examination of younger (C1) versus older (C2 and C3) calves.

To determine if mothers in the different groups initiated contact differently by calf age, we fit models to see if there was an overall difference by calf age (i.e., a main effect of calf age) and then if the different groups of mothers had a different pattern of initiation by fitting an interaction between calf age and the group of the mother (i.e., an interaction term). We used generalized linear mixed effects models (McCullagh & Nelder, 1989). The response variable was coded as 1 if the mother was the initiator and 0 if the mother was the receiver (i.e., the calf was the initiator). Calf ID was a random effect and we used a binomial error structure.

To determine if mothers touched different body parts to initiate contact compared to when they received contact, we fit models to see if there was an overall difference by body part contacted (i.e., a main effect of body part). We included two interaction terms. The first interaction was to see if mothers in the different groups initiated an interaction by touching different body parts. The second interaction was to see if mothers initiated an interaction by touching a different body part depending on the age of the calf. We used a generalized linear mixed effects model (Pinheiro & Bates, 2009). The response variable was coded as 1 if the mother was the initiator and a 0 if the mother was the receiver (i.e., the calf was the initiator). Calf ID was a random effect and we used a binomial error structure.

Because the PF-O body part category was a mix of specific body parts, we looked within the PF-O body part category to see if mothers started an interaction by touching different body parts that fell within the PF-O category. We fit a model to see if the different groups of mothers had a different pattern of initiation by fitting an interaction between the PF-O body part contacted and the group of the mother. Due to small sample sizes, the random effects models did not converge and therefore we used generalized linear models.

The response variable was coded as 1 if the mother was the initiator and a 0 if the mother was the receiver (i.e., the calf was the initiator) and we used a binomial error structure.

We determined what postures the mothers assumed when initiating and receiving a contact. We used a generalized linear mixed effects model (Pinheiro & Bates, 2009) to determine if posture of the mother (the response variable) varied when the mother was the initiator or receiver dolphin, whether the mother was in the different initiator groups, and if the calf was younger or older. Due to small sample sizes in some of the postures used, we used two posture categories, the horizontal (HOR) posture and other postures (all postures except horizontal, including ventral up, tail up, head up, on right side, on left side; Dudzinski et al., 2009). The response variable was coded as 1 if the mother used HOR and a 0 if the mother used any other posture. Specifically, we modeled the probability of the mother using HOR as a function of the role of the mother (initiator or receiver), the initiator group of the mother, and calf age (younger, older), including interactions among the explanatory variables. Calf ID was a random effect and we used a binomial error structure. We used a similar approach for duration of PFC contact. We used a generalized linear mixed effects model (Pinheiro & Bates, 2009) to determine if duration of PFC (the response variable) was a function of the role of the mother, the initiator group, and calf age, including interactions. Calf ID was a random effect and, because duration of contact is a continuous variable, we used a Gaussian error structure.

To understand maternal differences with calves of different sex, we looked at the adult females who had both male and female calves. Although five matrilines had both male and female calves during this 16-year study (Table 1), only three adult females (Alita, Gracie, and Mrs. B.) were observed to exchange PFCs with both their male and female calves at all ages (C1, C2, C3) and thus, these three females were used for analysis. Over the years, Alita interacted with two female and two male calves, Gracie interacted with three female and two male claves, and Mrs. B. with one female and two male calves. We specifically were interested in testing whether the pattern of initiating and receiving depending on the sex of the calf was the same across the mothers. To do this, we used a three-dimensional contingency table analysis with the mothers being considered the third dimension (i.e., the strata). The analysis constructs a pooled table of the pattern of initiation by sex of the calves and then compares the three individual mother's patterns from the expected values based on the pooled table, using a simulation approach (see above) to determine significance of the test statistic. We used residual analyses (see above) to determine differences among the mothers.

We used the statistical package R (version 3.6.2) and used glm to run the generalized linear models and glmer for the mixed effects models. For all tests, we assessed significance at a p of .05, except where indicated above.

Results

How Mothers Use PFC with Their Calves

Over 16 years of observation of tactile exchanges within bottlenose dolphin dyads at RIMS, 4,345 PFC were documented between kin ($N = 766$) and non-kin pairs ($N = 3,579$). From the kin-exchanged PFC, 408 PFCs (53% of PFCs between kin) were within mother/calf dyads. For the five females that interacted with more than one calf (i.e., multiple-calf focal females; Table 2), there were 261 PFC within mother/calf dyads where the identity of both initiator and receiver were confirmed; for the remaining five adult females, there were 64 total PFC within these mother/calf dyads, with 43 from one mother/calf dyad (Table 2). Mothers initiated PFC with their calves at different rates ($c^2_4 = 11.6$, $p = .02$; from data for the five focal females, Table 2). Cedeña initiated the most contacts (.44) followed by Gracie (.36) and Alita (.33) while Mika and Mrs. B. initiated fewer (.18 and .15, respectively) with their calves (Table 2). Gracie (coefficient = -0.39, $SE = 0.46$, $p = .39$) and Alita (coefficient = -0.54, $SE = 0.66$, $p = .04$) were not different from Cedeña while Mika (coefficient = -1.34, $SE = 0.66$, $p = .04$) and Mrs. B. (coefficient = -1.53, $SE = 0.61$, $p = 0.01$) were, resulting in two groups of mothers (high and low PFC initiators).

The high PFC initiator group had an average probability of initiating PFC contact of .38 and the low PFC initiating group had an average probability of initiating PFC contact of .16. The two single-calf mothers (Bailey, Rita) and Carmella (low number of interactions) were more similar to the high PFC initiator group ($c^2_2 = 0.27$, $p = .98$) than the low PFC initiator group ($c^2_2 = 21.8$, $p < .001$).

Calf Age

There was no difference in the probability of initiating PFC contact with calves of different ages between the high and low PFC initiator groups of mothers (Calf Age-Mother Group interaction effect: $c^2_1 = 0.89$, $p = .34$). Overall, the probability of the mother initiating PFC contact was the same regardless of the age of the calf (Calf Age main effect: $c^2_1 = 0.77$, $p = .38$).

Body Parts Contacted

There was no difference in the probability of initiating PFC contact using different body parts between the high and low PFC initiator groups of mothers (Contact-Mother Group interaction term: $c^2_4 = 4.85$, $p = .30$). Mothers also initiated a PFC by touching similar body parts regardless of the calf's age (Contact-Calf Age interaction term: $c^2_4 = 7.07$, $p = .13$). Mothers and their calves did not contact different body parts to start an interaction (Contact main effect: $c^2_4 = 0.97$, $p > .50$) (Table 3). Both mothers and calves, regardless of calf age, contacted the lateral side (PF-T) and the group of other parts of the body (PF-O) the most to start interactions (Table 3).

Table 3

Probability of Starting an Interaction by Touching Specific Body Parts by Mothers and Their Calves

Population	Response Probabilities				
	The back (PF-E)	Rostrum, face, and melon (PF-F)	Pectoral fin (PF-H)	Other parts of the body (PF-O)	Lateral side (PF-T)
Mother Initiator	.077	.164	.067	.346	.346
Calves Initiator	.081	.153	.076	.345	.345
Combined	.079	.156	.073	.346	.346

Focusing on the body parts within the PF-O category, there was no difference for how mothers in the high and low PFC initiator groups started an interaction when touching a body part in the PF-O category (PF-O Contact-Mother Group Interaction term: $c^2_4 = 7.30$, $p = .12$). In addition, mothers and their calves did not contact different body parts to start PFC contact when starting an interaction touching a body part in the PF-O category (PF-O body part term: $c^2_5 = 8.30$, $p = .14$). Overall, mothers and calves touched the belly the most followed by the dorsal peduncle, the dorsal fin, and the ventral peduncle while the genital area and fluke were rarely contacted (Table 4).

Table 4

Frequency of Contacts for Body Parts Included in the PF-O Section from Mother-initiated and Calf-initiated Contacts

	Dorsal fin	Belly	Genital area	Dorsal peduncle	Ventral peduncle	Fluke	Total PF-O
Mother Initiator	4	13	0	12	4	3	36
Calf Initiator	15	19	4	17	15	3	73
All Initiators (Mother-Calf)	19	32	4	29	19	6	109
Proportions	0.174	0.293	0.037	0.266	0.174	0.056	

Postures Used by Mothers

Mothers in both high and low PFC initiator groups used the horizontal (HOR) position when they initiated or received PFC (Mother role-Mother group interaction term: $c^2_1 = 0.34$, $p = .56$). Mothers also initiated or received PFC using the HOR position regardless of age of calf (Mother role-Calf Age interaction term: $c^2_1 = 0.56$, $p = .45$). The strongest effect was the age of the calf; the use of the HOR position declined when the mothers interacted with their older calves (older calf coefficient = -1.07, SE = 0.49, $p = .03$); mothers used the HOR position 68.9% with the older calves compared to 87.4% with younger calves (Table 5). Mothers used the HOR posture regardless of role (Mother INI coefficient = -0.53, SE = 0.30, $p = .08$) and regardless of mother high or low PFC initiator group (Low INI group coefficient = 0.61, $SE = 0.62$, $p = .32$).

Table 5

Frequency of Horizontal (HOR) and Other Postures Assumed by Mothers When Initiating and Receiving PFC by Calf Age

Mother Role	HOR	Other	Proportion (HOR)	Total
Initiator	74	32	.698	106
with young calves	28	8		36
with older calves	46	24		70
Receiver	172	47	.785	219
with young calves	76	7		83
with older calves	96	40		136
Total	246	79	.757	325

Contact Durations

Duration of contact did not differ regardless of whether the mother was the initiator or receiver of a PFC with their calves (mother INI coefficient = -0.10, $SE = 0.26$, $p = .67$) nor between the mother high and low PFC initiator groups (mother group coefficient = -0.06, $SE = 0.31$, $p = .75$). Contact duration differed with age of the calf with older calves having a shorter duration of contact (older calf age coefficient = -0.61, $SE = 0.25$, $p = .016$). Average contact duration for mothers and younger calves was 2.3 sec ($SD = 2.8$ s, $N = 119$ PFCs). Average contact duration for mothers with older calves was 1.7 s ($SD = 1.7$ s, $N = 203$ PFCs).

Differences in PFC Exchanges between Adult Females with Female and Male Calves

There were differences among the three females (Alita, Gracie, and Mrs. B.) in how they interacted with their female and male calves (regardless of age) ($c^2_2 = 32.0$, $p < .001$; Table 6). Alita had a higher probability of receiving contact from her female calves than from her male calves. Gracie and her calves initiated the same proportion of PFC as expected under the pooled distribution. Mrs. B. had a higher probability of receiving contact from her male calves than from her female calves.

Table 6

Frequency of Contact for Three Dolphin Mothers and Their Female and Male Calves in the Role of Initiator of Pectoral Fin Contacts

	Mother initiates with CF	Mother initiates with CM	CF initiates	CM initiates
Pooled pattern	0.17	0.14	0.38	0.31
Counts				
Alita	13	6	34	5
Gracie	18	18	29	35
Mrs. B.	2	4	12	21
Chi Residuals				
Alita	1.05	-0.78	**2.54**	-3.06
Gracie	0.31	1	-1.47	0.73
Mrs. B.	-1.77	-0.66	-0.74	**2.57**

Note. CF is female calf. CM is male calf. Bold font in the residual tables indicates significance.

Discussion

Our previous research on pectoral fin contacts (PFC) exchanged between dolphins established that PFC is exchanged at similar overall rates and within same-aged and sexed dyads than mixed-aged and sex pairs regardless of environmental setting (Dudzinski et al., 2009, 2010, 2013). We also found PFC is a tool to establish and maintain social bonds between non-kin male bottlenose dolphins (Dudzinski & Ribic, 2017). This study extends these findings by examining the functional role of PFC within mother-calf dyads. Overall, only 17.6% of all documented PFC exchanges were shared between kin, including mother/calf dyads who shared about 9% of the total PFC exchanges. This quantity of documented PFC is much lower than that found for interactions of unrelated animals (Dudzinski & Ribic, 2017) and indicates that PFC is primarily used by unrelated dolphins to build and maintain bonds or mitigate social interactions (Dudzinski & Ribic, 2017).

Even though our sample of PFC exchanges was small for kin and suggestive that other tactile behaviors might be used more frequently within mother/calf dyads, we were able to identify patterns that indicate functional use and maybe developmental (or maturation-related) factors in how PFC are used when shared by these kin. As a calf ages and matures, less time is spent with the mother, which may be directly reflected in decreased durations between mother-calf PFC from the first year to the next two years combined. PFC might be used as a teaching tool (either actively from the mother or passively through observation of the mother by the calf) that provides offspring with the fundamental meaning underlying the different uses of PFC that also could be modified by individual (maternal) style. Krzyszczyk et al. (2017) identified sex differences in social and behavioral development of juvenile bottlenose dolphins; for example, juvenile same-sex social bonds seemed to foreshadow adult patterns and observed increased foraging rates by juvenile females but not males could be related to future energetic demands of gestation and lactation.

Different patterns of initiating PFC were observed for the adult female bottlenose dolphins in this study group. The five multiple-calf mothers initiated PFC differently; three adult females (Gracie, Alita, Cedeña) initiated PFC more than twice as much with their calves as did the other two multiple-calf mothers (Mika and Mrs. B.). Bailey, Carmella, and Rita, the single-calf mothers group, had similar PFC initiation rates with their calves to the high PFC initiator group, which includes Gracie, Alita, and Cedeña. In addition, there is variation in the amount of contact observed between mother-calf dyads with some pairs having few interactions (e.g., Cedeña/Calli, GeeGee/Mika) or none (e.g., Mika/Poli) while others had many (e.g., Alita or Gracie and their calves). These findings support the notion of maternal style for adult female dolphins using PFC as one characteristic used to distinguish different styles (Hill et al., 2007; Mann & Smuts, 1998).

In our study, the three adult females (Alita, Gracie, Mrs. B.) that comprised the high PFC initiator group shared contact as initiator and receiver with both female and male calves. Because Gracie and her calves presented the largest sample size of documented PFC, she is driving the common pattern. Thus, our analyses investigated whether Alita and Mrs. B. were more similar to Gracie or not. All three of these females presented different patterns of interaction for their shared PFC with their calves, which further supports the hypothesis that these dolphins have distinct maternal styles (Hill et al., 2007). Gracie shared the most PFC with her calves – both younger and older individuals, though she initiated more with her older calves. Alita received more PFC from her older calves but initiated more with her younger offspring. And, Mrs. B. rarely initiated with her calves, even though she was a very protective and attentive mother, and received more PFC from her younger than older calves.

Even though the other adult females in this study had calves of both sexes, the PFC dataset for these mother/calf dyads represented only one calf sex (e.g., PFC for Mika and Carmella were only with their male calves). We were not able to document each adult female with all of her calves at each pre-weaning age (i.e., C1, C2, C3). This variation in recording may reflect each female's individuality as well as data collection opportunities (i.e., time of year when data were collected versus calf births). Although the dolphin calf personalities in our study group have not been assessed and may not yet have become stable (Highfill & Kuczaj, 2007), the adult females in this social group have documented distinct personalities (Macgregor, 2018; Moreno et al., 2017), which likely directly contribute to the maternal differences observed in this study. For example, Gracie routinely presented her calves to trainers and observers both at the surface and underwater whereas Carmella and Mrs. B. tended to be more protective and guarded with their calves, hovering in the background even when their older calves were playing with peers. Second, because data were collected in short (1 to 3 weeks) field sessions once or twice a year, our observation dates may not have overlapped with some ages for all calves from each adult female (see Limitations and Future Directions section below).

In most mammals, mother-infant interactions are typically measured by spatial proximity (Hinde, 1970), which includes the frequency with which a mother-infant dyad is in contact and who is responsible for this contact (e.g., Japanese monkeys (*Macaca fuscata*), Schino et al., 1995; macaques (*Macaca mulatta*), Fairbanks, 1996; bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), DeLathowres & Eslacker, 2004). Emphasis is placed on describing who initiated the contact and who received it, which is very successful in showing how contact is a variable that plays an important role in differentiating different mother-infant dyads. These distinct patterns of directed PFC (i.e., initiator versus receiver role) by the three adult female dolphins (Alita, Gracie, Mrs. B.) for whom large enough PFC samples were available are similar to documented contacts among chimpanzees in their first few months of life. Chimpanzee infants mostly solicit contact with or from their mothers within their first few months of life (Botero et al., 2013, 2017), with individual differences observed among chimpanzee mothers and also between different infants of the same mother.

Previous PFC research on dolphins identified a body part preference for the rubber and rubbee as initiators (Dudzinski et al., 2010). In this study, mothers contacted calf body parts differentially with the lateral side being the most preferred body part. This tendency may be driven by the observation that horizontal postures were assumed more frequently than all other postures by all observed adult female dolphins when sharing PFC with their calves. However, it is unclear whether the preference for the lateral side is a true preference, especially for the younger calves, or simply an artifact of the echelon swim position (Noren, 2008; Noren et al., 2008), when calves gain hydrodynamic benefits at an energetic cost to the mother (Noren, 2008; Noren & Edwards, 2011). Other physiological development markers (e.g., breath-holding and stroke rate increases; Noren et al., 2002) also correlate with maturity as a calf approaches independence from the mother; thus, changes in PFC exchanges between mothers and calves associated with calf age would not be unexpected. Use of the echelon swim position decreases as a calf matures and develops musculature that allows for more independent swimming (Gubbins et al., 1999; Xian et al., 2012). A transition to social independence, not only physical maturity, was documented for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) as calves aged into juvenility (Krzyszczyk et al., 2017). Mothers (in the role of rubbee with a calf as rubber) in our study also showed more contact with the belly, after the lateral side, which could be associated with the infant swim position (Gubbins et al., 1999). The infant swim position

places the calf below the mother's genital and mammary gland area. This position also affords energetic swim benefits as well as close proximity to the mammary glands for more efficient nursing. As a calf develops, it shifts from the echelon to the infant swim position with mother (Gubbins et al., 1999; Xian et al., 2012). Thus, for younger calves the two primary body parts contacted could be related to swim position that has other survival benefits for the calf, rather than a selection of body part per se. An alternative is that the calves might simply not yet be discriminatory in their body awareness or selection until they have gained more maturity.

Given the paucity of PFC within mother/calf dyads as compared with PFC shared between non-kin individuals in this study group, it is not likely that contact via the pectoral fin is a behavioral tool used by kin to establish or maintain their relationships, though siblings might share PFC differently compared to how each offspring might share PFC with their mother (Dudzinski et al., in press). Though human researchers might not know how, it is likely that dolphins recognize kin without aid of behavioral contact or overt signal use. Bruck et al. (2013) demonstrated that dolphins possess long-term social memory for conspecifics with whom a strong relationship was once shared. Dolphins possess a large, complex brain that facilitates recognition of the ever-changing relationships within a complex fission-fusion society (Marino et al., 2007). While pectoral fin contact is probably not important within the confines of the mother-calf relationship, other forms of tactile contact (e.g., body-body rubbing) likely are more socially essential to the developing relationships between both kin and non-kin.

Limitations and Future Directions

These data are part of a longitudinal study to assess dolphin communication, behavior, and social structure among several study populations: data were (and are) collected in a non-invasive manner from the underwater perspective. Data collection was (and is) conducted during short field sessions (observational periods) ranging from one to several weeks in length. Because this study population resides in managed care, we know the birth dates of all individuals born at the facility (75% of the group). As such, we were able to confirm each calf's age (C1, C2, C3, etc.) during each field session. Two data collection limitations were encountered that affected our observations: 1) not observing some calves at specific ages (i.e., not observing the calf at a given age), and 2) collecting data for each calf's age but not recording any PFC between a mother and calf for a particular calf age. These two limitations are quite different in that the first represented no data possible for a particular calf at a given age category while the second could actually be related to personality or style differences. That is, for the data collection second limitation, observations of the calf at each age were conducted but there were no PFC documented.

While we found maternal differences studying only a small number of mothers, personality may be an important factor explaining why we found these differences. Five-factor personality surveys have been applied to dolphins with results indicating that stable and distinct personalities are present (see Highfill & Kuczaj, 2007). Even though surveys have been completed for each dolphin in this study population (Macgregor, 2018; Moreno et al., 2017), a comparative discussion of personality differences between individuals has not been formalized. Based on ad libitum and anecdotal reports of approach proximity by training staff and authors of the study, some adult females are considered more shy or aloof while others are more bold or confident. Thus, due to individual differences in approach proximity, we likely have more video data of females and their calves who would be categorized as more confident or bolder as compared to the females who would be rated as shy and aloof. Additionally, as related to potential personality differences, some adult females will be frequent (i.e., high) initiators of shared interaction and behavioral exchange while others will be less likely to initiate contact. These differences between individuals could be related to variation in established dyadic relationships (e.g., Themelin, 2019) or to other factors (e.g., environmental or habitat differences or human-dolphin interactions during swim-with programs). More research is required to better understand maternal differences in other dolphin groups and how these different profiles emerge.

Dolphins use tactile behavior to share a variety of messages depending on the context. Dudzinski et al. (2010) and Dudzinski et al. (2013) confirmed that PFC is a conserved behavior shared between dolphins consistently regardless of the environment (e.g., substrate or habitat). Dudzinski and Ribic (2017) clarified

that PFC is one tool in the dolphin cognitive box that allows individuals within a dyad to establish and maintain their social relationships. The functional aspects of PFC as a tool to manage dolphin relationships is further supported by the results related to the paucity of PFC exchanges within mother/calf dyads, indeed the overall lack of PFC among kin. Social behavior and developing relationships are mediated by a variety of complex, coordinated signals. The current paper only describes the maternal role in PFC. To understand the development and use of PFC by young dolphins, PFC must also be examined from the calf perspective (Dudzinski et al., in press).

An evaluation of other forms of contact, not only PFC, between mothers and calves will elucidate better the role of tactile contact in a dolphin's life, from neonate through weaning and into adulthood. Touch is a valuable tool that helps mediate social relationships through a variety of functional roles: as an affiliative contact, a disciplinary action, for aggressive intent, and possibly as a learning platform. Future research should continue to examine the role of touch in all animals.

Acknowledgments

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Appendix

Effort, population demographics, and pectoral fin contacts documented per year of data collection at RIMS, AKR, on Roatan, Honduras. Data summarized for 2003-2013, with data details available in Dudzinski and Ribic (2017). Abbreviations include F = female, M = male, A = adult, S = subadult, J = juvenile, C = calf. Sessions ranged from one week (2006 – 2011, 2013 – 2015), two weeks (2016), and a mix of one- and two-week sessions (2017-2018).

Year	Effort (min.)	Group (N)	F:M	F: A, S, J, C M: A, S, J, C	Pectoral Fin Contact (N)
2003-2013	6,494	16 - 26	*See Dudzinski & Ribic (2017) for details.*		3,022
2014	115	22	12:10	F: 8, 0, 2, 2 M: 6, 1, 0, 3	76
2015	335	20	10:10	F: 6, 0, 4, 0 M: 7, 0, 2, 1	284
2016	324	23	11:12	F: 6, 0, 4, 0/1* M: 7, 0, 2/3*, 3/2*	255
2017	482	22	11:11	F: 6/7*, 2/3*, 2/0*, 1 M: 7/6*, 0, 3/2*, 2/3*	382
2018	649	20	11:9	F: 7, 3, 0, 1 M: 5/4, 2, 0, 2	326
Totals:	8,399	16-26			4,345

Note. * indicates that one or two dolphins were different ages between sessions within one year.