Vocalizations Associated with Pectoral Fin Contact in Bottlenose Dolphins (*Tursiops truncatus*)

Janan Evans-Wilent

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Members of Honors Committee:

Thesis Advisor: Dr. Robert Askins, Professor of Biology

Second Reader: Dr. Kathleen Dudzinski, Director of the Dolphin Communication Project

Third Reader: Dr. Stuart Vyse, Professor of Psychology

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Abstract

Pectoral fin contact in bottlenose dolphins is a form of tactile communication. Acoustic communication associated with pectoral fin contact is an additional level of communication that may change or enhance the tactile message between two individuals. In this study, we examine the types of vocalizations associated with pectoral fin contact in captive bottlenose dolphins (*Tursiops truncatus*). I examined 746 pectoral fin contact events from 2006-2009, and analyzed acoustic data using Raven acoustic software. The vocalizations associated with pectoral fin contact were whistles (WHS), click trains (ECC), overlap of whistles and click trains (WHS/ECC), and no vocalizations. The types of vocalizations during pectoral fin contact were compared for type of pectoral fin contact, vocalizer sex, how the contact is solicited, gender pair, and different individual vocalizers. Additional analyses of whistle parameters were also completed. Overall, vocalizations differed significantly for vocalizer role, vocalizer role as initiator, and individual vocalizers. Initiators and rubbers whistled more frequently, and receivers and rubbees clicked and used blended vocalizations more frequently. All except one adult female only whistled, while males were more vocal and used the different vocalization types more frequently. These results suggest that whistles may be used as a way to initiate pectoral fin contact or show preference for a particular partner, while click trains may be used to show disinterest in pectoral fin contact or to indicate the end of the contact. Examining vocalizations in conjunction with tactile contact may be useful for

analyzing dolphin social alliances and social preferences for various individuals within a population.

Introduction

The exchange of information via signals (i.e., communication) has been studied in many species of delphinids, including common bottlenose dolphins (*Tursiops truncatus*, Overstrom 1983), Indo-Pacific bottlenose dolphins (*Tursiops aduncas* Sakai et al. 2003, 2006a), Atlantic spotted dolphins (*Stenella frontalis*, Dudzinski 1996, 1998; Dudzinksi et al. 2009, 2010), and Hawaiian spinner dolphins (*Stenella longirostris,* Ostman 1994). Bottlenose dolphins use a variety of vocalizations, tactile behaviors, and postures to convey information. Non-vocal auditory signals may include jaw claps, tail slaps, breaches and leaps (Shane 1990; Norris et al.1994; Dudzinski et al. 2009b). Qualitative descriptions of behavior and associated vocalizations of dolphins were reported when systematic studies of captive dolphins commenced (Caldwell & Caldwell 1967). Details of dolphin behavior have most often been documented from surface observations with behavioral states categorized by group activity, including rest, socializing, feeding and travel (Shane 1990). Caldwell and Caldwell (1967) were first to examine the vocal repertoire of bottlenose dolphins; since the Caldwells' study, several researchers have examined the vocal behavior of various dolphin species (dos Santos et al. 1990; Smolker et al. 1993; Schultz et al. 1995; Connor & Smolker 1996). Information about individual vocalizers and their associated behaviors under water in wild studies is still difficult to obtain despite advanced technical methods (Dudzinski et al. 1995).

Types of Vocalizations

Dolphin vocalizations have been divided into two general categories: amplitude-modulated calls or clicks and frequency-modulated tones or whistles (Herman & Tavolga 1980; Tyack 1986a, 1986b; Au 1993). High-frequency clicks, with a fundamental frequency ranging from 120 to 140 kHz, are considered to be dolphin echolocation (sonar, Au 1993). The high frequency components of these clicks are highly directional, forming a narrow acoustic beam (Au 1993). This type of burst-pulsed sound has been qualitatively described for several delphinid species, including bottlenose dolphins (Caldwell et al. 1965; Tyack 1976; Herman & Tavolga 1980), common dolphins (*Delphinus delphis*, Caldwell & Caldwell 1968), Hawaiian spinners (Norris et al. 1985; Ostman 1994), killer whales (*Orcinas orca*, Bain 1986; Ford & Fisher 1986) and pilot whales (*Globicephala macrorhynchus*, Weilgart &Whitehead 1990).

Whistles present a lower fundamental frequency, typically less than 22 kHz, are omni-directional and produced by most, but not all, dolphin species. Dolphin whistles have been studied significantly more than pulsed calls for many species; these acoustic signals also lend themselves to quantitative measurement because of their narrow-band, frequency-modulated character and a fundamental frequency that resides within the range of most commercially-available recording gear (Caldwell & Caldwell 1965; Tyack 1976; Caldwell et al. 1990; Wang 1993). Whistles generally range from 0.5 to 2.5 s in duration, but length can vary considerably among species and individuals (Caldwell et al. 1990).

Caldwell and Caldwell (1965) suggested that individual dolphins might produce a different signal type from its conspecifics, called a “signature whistle”. Unique characteristics of the contour of a dolphin’s signature whistle allow visual representations on spectrograms to be distinguished from those of signature whistles of other dolphins (Janik & Slater 1998; Sayigh et al. 2007). Visual classification of vocal signals from spectrographic contours is a widely used methodology in the study of dolphin communication (Tyack 1986; Caldwell et al. 1990; Sayigh et al. 1990, 1995; Janik & Slater 1998; Janik 1999). Each dolphin may vary some features of its signature whistle, such as duration, but maintains the overall shape or contour (Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994; Sayigh et al. 2007).

In contrast to the signature whistle hypothesis, other researchers support the alternative whistle repertoire hypothesis, in which many individual dolphins share certain whistle types across different social groups (McCowan & Reiss 2001). McCowan and Reiss (2001) point out that captive dolphins may produce the same whistle types in all contexts studied, and that dolphins in isolation commonly produce a simple upsweep whistle (McCowan & Reiss 1995), refuting the signature whistle hypothesis. They highlight that differences in their research compared to other studies reporting signature whistles are based on difference in methods used for collecting and categorizing whistles (McCowan & Reiss 2001). This alternative to signature whistles suggests that all whistles produced by dolphins come from a common shared whistle repertoire and what appears to be imitation is simply repetition of similar whistle call-types (Watwood et al. 2004).

Shared calls are necessary for animals that maintain contact with individuals in changing social groups (Watwood et al. 2004). Individuals forming close associations may modify particular calls that are used for contact, or to coordinate group movements, protect resources, or form groups (Watwood et al. 2004). Bottlenose dolphins live in a fission-fusion society, in that the group is not consistent and different individuals may come and go frequently and do not remain in groups with the same members (Wells et al. 1987). This type of social system, in which different individuals are constantly coming and going, may utilize distinctive shared signals within a group for recognition and contact (Clark & Tyack 2000). In this case, the individual dolphins don't have distinctive identifying whistles, but rather the whole group shares specific calls that differ from those of other groups. As dolphins are both social and highly mobile, they may use shared whistle types as a means to maintain contact with other group members.

Non-Acoustic Communication

Dolphins use many physical and visual behavioral signals for communication; Pryor (1990) suggests that all social behavior, whether it is physical, vocal, or visual, constitutes a form of communication. Visual cues employed by dolphins include different postures or physical orientation in the water column, as well as coloration patterns (Herman & Tavolga 1980; Würsig et al. 1990). Dolphins may also use eye contact to communicate, especially during synchronized displays (Pryor 1990; Sakai et al. 2006b). Elaborate color patterns could enable individuals to recognize conspecifics, especially in the open sea or with murky visibility (Pryor 1990; Würsig & Kieckhefer 1990). Gestures and postural displays by dolphins have been observed in many different social situations, including aggression or affiliative displays (Tavolga 1966; Norris et al. 1985; Pryor 1990).

Tactile contact is frequently observed between dolphins, and involves, for example, rubbing bodies, rubbing against a surface in the environment, or rubbing a part of the body on another individual (Pryor 1990). Pectoral fin contact is an affilative behavior involving touching or rubbing part of one dolphin's body and another dolphin's pectoral fin (Sakai et al. 2006a; Dudzinski et al. 2009, 2010). Pectoral fin contact has been studied in Indo-Pacific bottlenose dolphins (Mann & Smuts 1998, 1999; Sakai et al. 2003, 2006a; Dudzinski et al. 2009), bottlenose dolphins (Tavolga & Essapian 1957; Samuels et al. 1989; Tamaki et al. 2006; Dudzinski et al. 2010), Commerson's dolphins (*Cephalorhynchus commersoni*, Johnson & Moewe 1999), spinner dolphins (Norris et al. 1994), Atlantic spotted dolphins (Dudzinski 1996, 1998; Dudzinski et al. 2009), belugas (*Delphinapterus leucas*, Smith et al. 1992), and sperm whales (*Physeter macrohynchus*, Whitehead & Weilgart 2000). Pectoral fin contact is often observed during play, sexual contexts, maternal interactions, or general social contexts, and may strengthen social bonds between individuals (Dudzinski et al. 2009, 2010).

Association of Dolphin Behavior with Vocalizations

Although much research has been conducted to document and understand cetacean vocalizations, there has been less information gathered on vocalizations that might be produced in association with particular individual behaviors. This scarcity of detail is primarily related to the difficulties of conducting behavioral studies on highly mobile animals in a marine environment while synchronously recording sound. Clark (1982) found an association between certain types of pulsed calls and close, physical social interactions in southern right whales (*Eubalaena australis*). Sjare and Smith (1986) examined vocalizations and behavioral activity in belugas using the broad behavioral categories of feeding, resting, and socializing. Vocalizations included clicks and whistles, and vocalization rates were generally higher during social interaction than during directive swimming, resting behavior, or alarm situations (Sjare & Smith 1986).

In North Atlantic pilot whales, greater click activity was associated with feeding and surface active behavior (Weilgart &Whitehead 1990); whistles seemed to function as calls to maintain contact with group members and coordinate movements of the herd (Weilgart & Whitehead 1990). Hector's dolphins (*Cephalorhynchus hectori)* use complex sounds more commonly in large groups, suggesting that they have a social communicative function (Dawson 1991); high pulse rate sounds were more common in aerial and aggressive contexts than in more restful activity states (Dawson 1991).

Some studies examined the association between a particular sound with behavior as expressed by an individual dolphin. Caldwell et al. (1962) observed a high-energy sound associated with fright in captive bottlenose dolphins; they observed that the "crack" sound occurred when the animals were displaying flight, tight schooling and hyper-excitability. Overstrom (1983) described pulsed emissions that accompanied aggressive displays in bottlenose dolphins. He found that dolphins displayed an open-mouthed posture accompanied by violent head motions and pulse-type vocalizations, often accompanied by jaw claps. Additionally, increased aggression was accompanied by longer, stronger burst-pulse sounds (Overstrom 1983). A "thunk" vocalization has been linked to mother-infant aggression in captive bottlenose dolphins (McCowan & Reiss 1995). Thunks are produced by mothers or alloparental aunts when infants swim more than 1.5 m away from the mother and infants respond by returning closer to the mother (McCowan & Reiss 1995).

Herzing (1996) examined vocalizations associated with general behaviors of Atlantic spotted dolphins and bottlenose dolphins: 10 types of vocalizations (including signature whistle, excitement vocalization, genital buzz, squawk, synchronized squawk, scream, and bark) were generally associated with underwater behaviors. Particular vocalizations were linked to various behaviors, including foraging and feeding behavior, excitement or anxiety, courtship, aggressive behavior, and sexual play. Connor and Smolker (1996) examined a male vocalization called a “pop”, a narrow-band low frequency pulse associated with female consortship in the bottlenose dolphin population in Monkey Mia, Australia.

Although progress has been made in understanding the basic acoustic behavior of many delphinid species, associating vocalizations with specific underwater behaviors has been difficult primarily because of the lack of access to dolphins in the underwater venue with clear visibility, and to details related to individual and group life history, sex, and relationships between individuals (Herzing, 2000). Most current research has focused on associations between general vocalizations and group behaviors, such as socializing, feeding, or resting. Few studies have examined the relationship between specific, non-vocal interactions and potentially linked acoustics.

Goals of this Study

This study examines the vocalizations potentially associated with pectoral fin contact exchanges between individual bottlenose dolphins. The goals are to examine whether particular vocalizations are commonly associated with pectoral fin contact and to examine whether different vocalizations are associated with different vocalizer categories, such as sex, role, or individual identity, or with different combinations of dolphin pairs, such as sex or age-classes. Understanding the role of specific vocalizations within the context of this particular behavior may reveal more information about dolphin relationships and social structure. Examining the role of tactile and acoustic communication could reveal more details about the role of these signals in securing relationships in a fission-fusion society. Because individuals in this study population can be readily identified and viewed for extended periods under water, it provides an excellent opportunity to examine specific behavioral interactions that might be associated with distinct vocalizations in order to understand how signals might be used jointly by dolphins within their social relationships.

Methods

Study Site and Population

Data analyzed for this thesis were collected as part of a long-term, longitudinal examination of dolphin communication and signal exchange (Dolphin Communication Project (DCP) Archive, K.M. Dudzinski, personal communication, 2010; Dudzinski et al. 2010). Four years of data were analyzed (2006-2009) from the longitudinal data archive collected at the Roatan Institute for Marine Science (RIMS), located at Anthony Key Resort, Roatan, Honduras (DCP Data Archive 2006 – 2009). Founded in 1989, RIMS is on the northwestern coast of Roatan, the center island of three Bay Islands approximately 27 miles north of Honduras. The dolphin facility is located inside a fringing reef in a natural lagoon that encloses about 300 m^2 in surface area. The sea floor is covered with sand, seagrass beds and natural coral. Bottlenose dolphins in this captive population range in age from neonate to 30+ years; the social dynamic is similar to that observed for wild bottlenose dolphins (Kogi et al. 2004; Connor et al. 2006). Accordingly, age and sex distribution for the group matches most coastal wild bottlenose dolphin study groups, with this particular population ranging annually between 18 and 24 dolphins (with the total number of dolphins varying depending on distribution between other facilities managed by RIMS) (K.M. Dudzinski, personal communication, 2010).

Video Data Collection

A mobile video/acoustic (MVA) system that permits real-time synchronous video and audio recordings under water was used to record dolphin behaviors and sounds at RIMS (Dudzinski et al. 1995). Underwater swims were video-documented opportunistically with limiting factors including visibility conditions, weather, sea state, and facility schedule and availability. Behavioral data were collected using focal animal and all-occurrence sampling (Altmann, 1974; Mann 1999). Individuals were opportunistically observed, based upon which dolphin(s) were readily in view of the camera and the observer. Follows (in which the researcher follows a single dolphin or group of dolphins with the camera until they are out of view and/or are no longer visible) and recordings of dolphins began as soon as the video camera and observer were in position under water and subgroup composition was assessed. An individual was selected and recorded until it was no longer within the field of view.

Event sampled pectoral fin contacts between dolphins were examined for 2006-2009 from video data gathered over these years (pectoral fin contact data are described in Dudzinski et al. 2010). Each contact event between one dolphin's pectoral fin and another dolphin's body (including the pectoral fin) was documented. Other relevant, recorded information included: date, "real" time; initiating dolphin identification, age and sex; receiving dolphin identification, age and sex; each dolphin's posture, duration of contact; and whether contact was a touch or rub. In addition, whether the initiating and receiving dolphins were the rubber or rubbee and which body part was contacted on the rubbee were documented. (For more detailed information on the pectoral fin contact data collection, see the methods of Dudzinski et al. 2009; Dudzinski et al. 2010.)

Acoustic Data Collection

Acoustic data were digitized by transferring audio files via an iMic directly from videotape to iMac computer using RAVEN 1.4 software (Charif et al. 2008). Using previously collected data on pectoral fin contact for the selected four-year study period (Dudzinski et al. 2010), audio segments with vocalizations potentially associated with each pectoral fin contact event for 2006-2009 were examined; if sounds were not audible or visually detected on a spectrogram with a pectoral fin contact, this was indicated on the data sheets. Audio segments were digitized in 20 s intervals, beginning 10 s prior to the time of the start of the pectoral fin contact and ending 10 s after the start of the contact. If several pectoral fin contact events occurred in succession within the 20 s interval, they were included in the same recording, starting 10 s before the first contact and 10 s after the final pectoral fin contact.

The Raven record buffer was set at 20 s with a 44100 Hz sample rate. The update rate was 10 Hz, using AIFF file format and a 16-bit sampling size. The spectrogram FFT was 512 pts. Each 20-s interval was examined for presence of vocalizations – whistles (WHS) and click trains (ECC). If both whistles and click trains were present during a pectoral fin contact event, they were called overlap sounds (ECC/WHS). The vocalizer was identified when possible. If the vocalizer could not be specifically identified, opportunistic information including the sex and age were noted when possible. The duration of each sound and the presence of bubbles or a bubble stream (BBS) were documented. Pectoral fin contacts in which the vocalizer was unknown or could not be indentified were not included in data analyses.

Definitions

Rubbing behavior or contact between pectoral fins or a pectoral fin and the body of a second dolphin are defined in various ways in the published literature (see Sakai et al. 2006a for an overview on various definitions of pectoral fin contact). Specific pectoral fin contact definitions presented in Dudzinski et al. (2009) have been followed during the course of this study. Pectoral fin tactile exchanges were begun by one dolphin, the initiator, approaching and physically contacting another dolphin, the receiver, and were ended by one of the dolphins departing from the other (Dudzinski et al. 2009). In the role of initiator, the dolphin was either the rubber or rubbee. The rubber is the dolphin whose pectoral fin is in contact with the body of a second dolphin, the rubbee. Dolphin pectoral fin contacts were classified by gender pairs as male-male, female-male, or female-female.

Data Analysis

For whistles, the following measurements were taken: duration, beginning and ending frequencies, maximum and minimum frequencies, and the number of inflections. Click trains were defined as a sequence of clicks longer than 0.075 s, and a click train ended when the interval between clicks was greater than 0.025 s. The number of click trains per recording was reported, as well as the range of click train durations from shortest to longest. The repetition rate was calculated by counting the number of clicks in three one-second samples from the 20-second recording: one sample was taken during the pectoral contact at 10 s into the recording; the second one-second sample was randomly chosen in the 10 s before the pectoral fin contact; and the third was randomly chosen from the 10 s after the pectoral fin contact. These counts were averaged to obtain an average click train repetition rate per recording. Additionally, whether the click train was continuous or discontinuous was noted.

Statistical Analyses

Acoustic information was analyzed using SPSS version 19 software. Chi-square tests were used to compare frequencies of different types of vocalizations associated with the following variables: vocalizer as rubber or rubbee, vocalizer as initiator or receiver, rub or touch, sex of vocalizer, type of interaction, and individual identity of vocalizer. Fisher's exact test was used when sample sizes were less than 5. Independent sample t-tests were used to compare the means for the vocalizer variables (rubber/rubbee, initiator/receiver, rub/touch, male/female) and whistle parameters, including whistle duration, beginning frequency, end frequency, maximum frequency, minimum frequency, and the number of inflections. One-way analysis of variance (ANOVA) tests were used to examine gender-pair type on whistle parameters, because there were more than two categories within gender pairs (male-male, male-female, and female-female).

Results

A total of 748 pectoral fin contact events were examined from 12.43 hours of video data from 2006 to 2009 (*n* = 354 contacts in 2009, *n* = 99 in 2008, *n* = 54 in 2007, and *n* = 241 in 2006). In 2007 there were fewer pectoral fin contacts because the data collection trip was significantly shorter. In association with pectoral fin contacts, there were 175 contacts associated with whistles, 19 contacts associated with click trains, 10 contacts associated with overlapped sounds, and 349 pectoral contact events with no vocalizations (Table 1). There were an additional 195 click train events that did not fit the parameters for analysis. In most cases, the click train frequency was too low (i.e., less than 1.0 ku) and thus deemed to be produced too far away from the hydrophone (and the behavior in the viewfinder) to be considered for analysis. In total, there were 204 vocalizations associated with pectoral fin contact events used for analysis (Figure 1).

Table 1. Frequency of pectoral fin contacts and the number of associated vocalizations (and no vocalization) for each year of data. An additional 195 pectoral fin contacts had click trains present but they did not have the correct parameters for measurement or analysis inclusion (see text for a description of parameters).

Category	**2009**	**2008**	**2007**	**2006**	**Total**
Whistles	70	34	17	54	**175**
Click trains	3	0	1	15	**19**
Overlap vocals	1	1	0	8	**10**
Total Vocalizations	74	35	18	77	**204**
No Vocalization	189	47	39	83	**349**
Associated Pectoral Contact Events	353	99	53	241	**748**

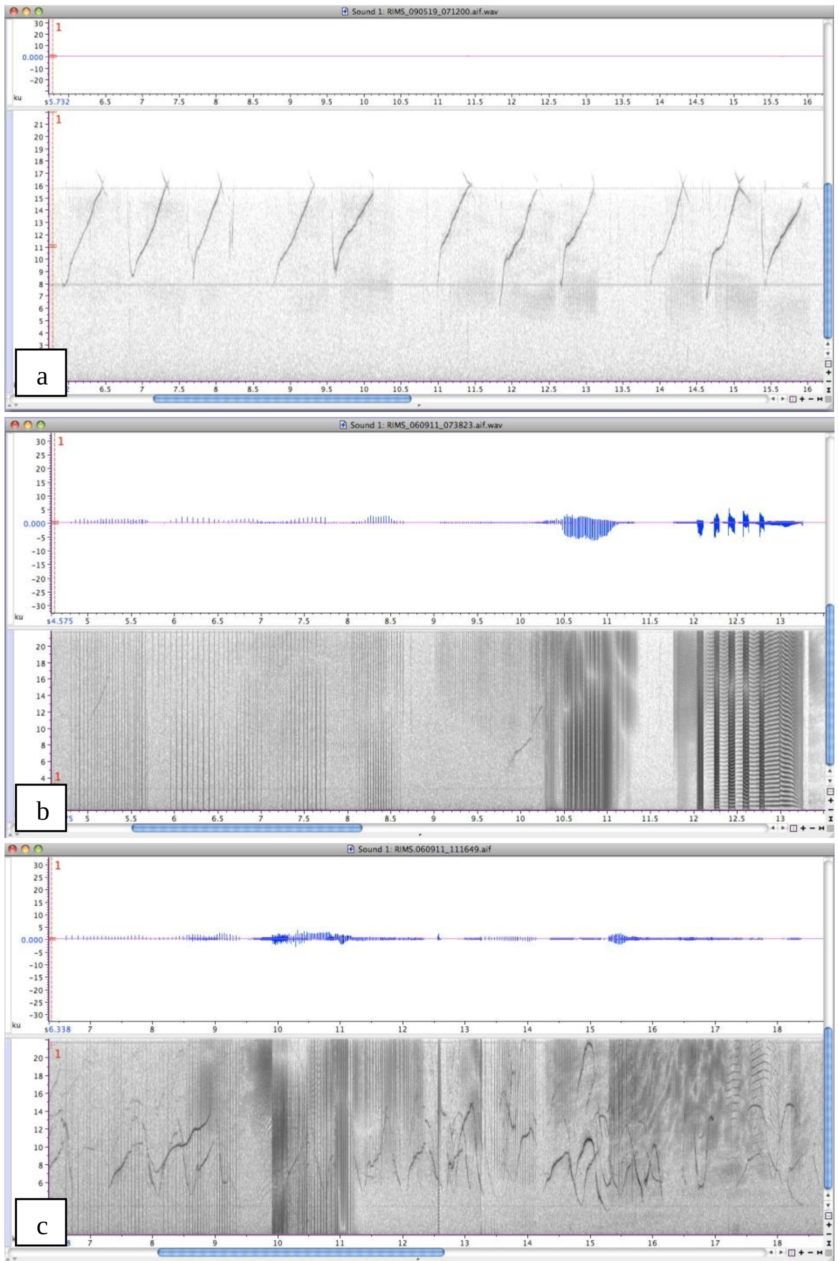

Figure 1. Spectrogram examples of the three types of dolphin vocalizations associated with pectoral fin contact. Each image presents the waveform on top, and spectrogram on the bottom. Waveform analysis was only used for amplitude-modulated calls (click trains). a.) Whistle (WHS), b.) Click trains (ECC), and c.) Overlap (WHS/ECC).

Vocalizer Sex

While exchanging pectoral fin contact, there was no significant difference between the sexes with respect to production of vocalization types (χ^2 (DF = 2, N = 119) = 3.977, p = 0.147). However, males tended to be the vocalizer more frequently during pectoral fin contact that had associated vocalizations as compared to females (males vocalized during 36% of pectoral fin contacts with vocalizations compared to 30% for females). Males produced 72.2% of click trains and 88.9% of overlap (ECC/WHS) vocalizations produced in association with pectoral fin contact. Yet the frequency of click trains for males was not significantly greater than for females (χ^2 (DF = 1, N = 119) = 0.770, p = 0.380), with males clicking during 6% of pectoral fin contacts and females 3%. The frequency of WHS for males as compared to that of females emitted during pectoral fin contact was also not significantly different (χ^2 (DF = 1, N = 119) = 3.262, p = 0.071), with males and females whistling during 25% and 26% of pectoral fin contacts, respectively.

Additional analyses of the sex of the vocalizer were examined for touch versus rub, vocalizer role, and vocalizer role as the initiator. For rubs or touches, the sex of the vocalizer was not significantly different during pectoral fin contacts (χ^2 (DF= 1, N = 111) = 0.262, p = 0.609). Male vocalizers touched 31.4% and rubbed 68.6%, while females touched 26.8% and rubbed 73.2%, respectively, during pectoral fin contact. The sex of the vocalizer compared to the vocalizer role was also not significantly different (χ^2 (DF = 1, N = 60) = 0.235, p = 0.628) during pectoral fin contact. Initiators vocalized over 60% for both males and females of the time during pectoral fin contacts (60.6% for males, 66.7% for females), and, similarly, both sexes of receivers vocalized less than 40% (39.4% for males, 33.3% for females).

The sex of the vocalizer as rubber or rubbee was also not significantly different (χ^2 (DF = 1, N = 76) = 0.12, p = 0.912). Females were rubbers for 55.9% of pectoral fin contacts, and males were rubbers for 55.9% of these contacts. Females were rubbees 44.1% while males were rubbees during 42.9% of pectoral fin contacts.

Vocalizer Role

Vocalization type was significantly related to the vocalizer role as either the contact initiator or contact receiver (χ^2 (DF = 2, N = 62) = 8.685, p = 0.009). Almost twice as many initiators produced WHS (65.2%) as did receivers (34.8%) during pectoral fin contact; however, the receiver produced twice as many ECC calls (69.2%) and all overlap calls (100%) as compared to the initiating dolphin (30.8% and 0%, respectively) (Figure 2).

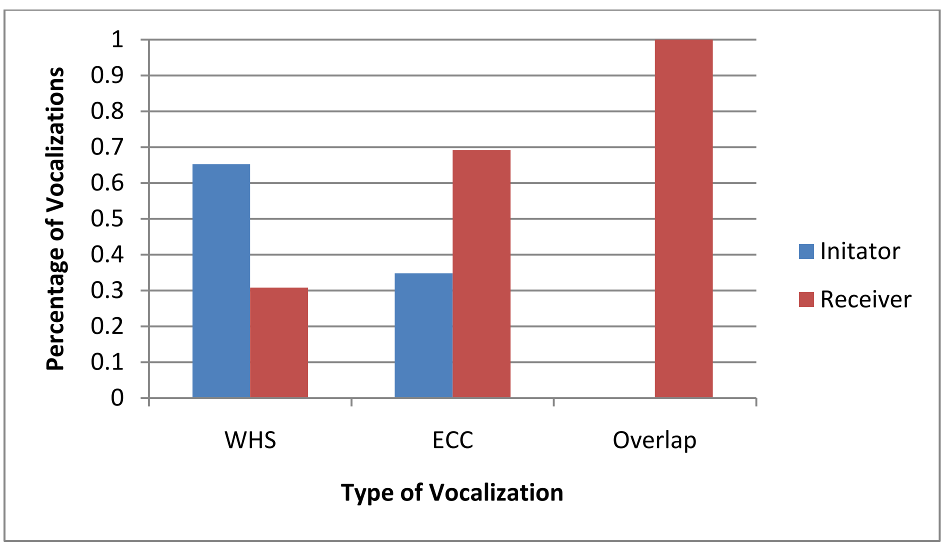

Figure 2. Percentage of different vocalizations emitted by initiator versus receiver during pectoral fin contact exchanges from 2006 to 2009 in total.

Similarly, vocalization type was significantly related to the vocalizer role as initiator (χ^2 (DF = 2, N = 77) = 7.103, p = 0.03). Rubbers produced vocalizations during pectoral fin contact 57.1% the time while rubbees vocalized 42.9% (Figure 3). During pectoral fin contact, almost twice as many rubbers (65.5%) produced WHS as did rubbees (34.5%), whereas the rubber produced twice as many (64.3%) ECC and three times as many overlap calls (80%) as compared to the rubbee (35.7% and 20% respectively).

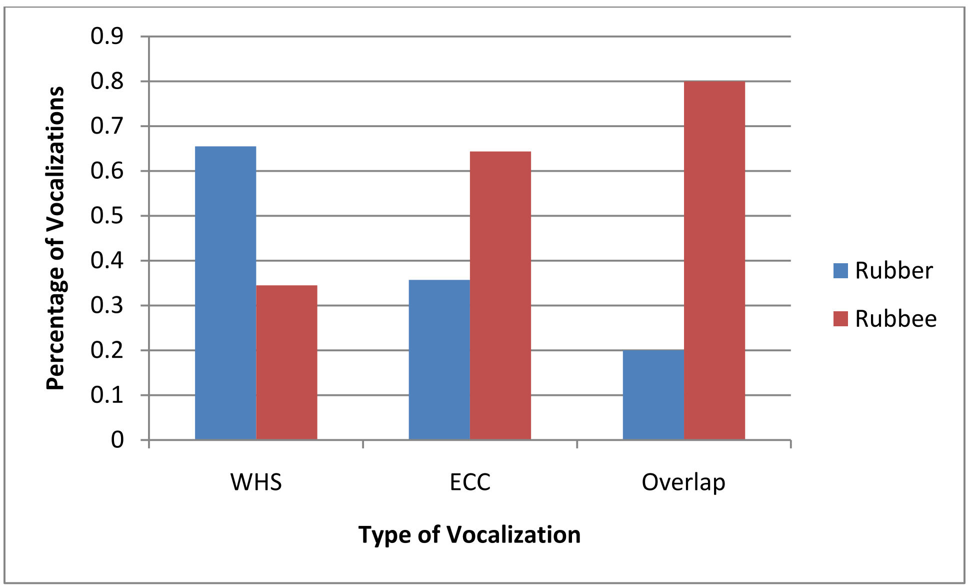

Figure 3. Percentage of the three different vocalizations emitted by rubber versus rubbee during pectoral fin contact from 2006-2009.

Touch vs. Rub

There was no significant difference between rub or touch and type of vocalization associated with pectoral fin contact (χ^2 (DF = 3, N = 559) = 1.887, p = 0.596). Still, a trend exists such that for all three vocalization types were more frequently associated with rubs than with touches (Figure 4). Whistles were associated with rubs and touches during 87.9% of rubs compared to 80.8% of touches. During pectoral contact, ECC was associated with 15.4% of touches and 7.4% of rubs, and overlap sounds were associated with touches and rubs were 3.8% and 4.7% respectively. Additionally for pectoral fin contacts with no associated vocalizations, 73.5% were rubs and 27.3% were touches. Because there were so many more rubs than touches in pectoral fin contact events, they did not vary by vocalization type over the four years.

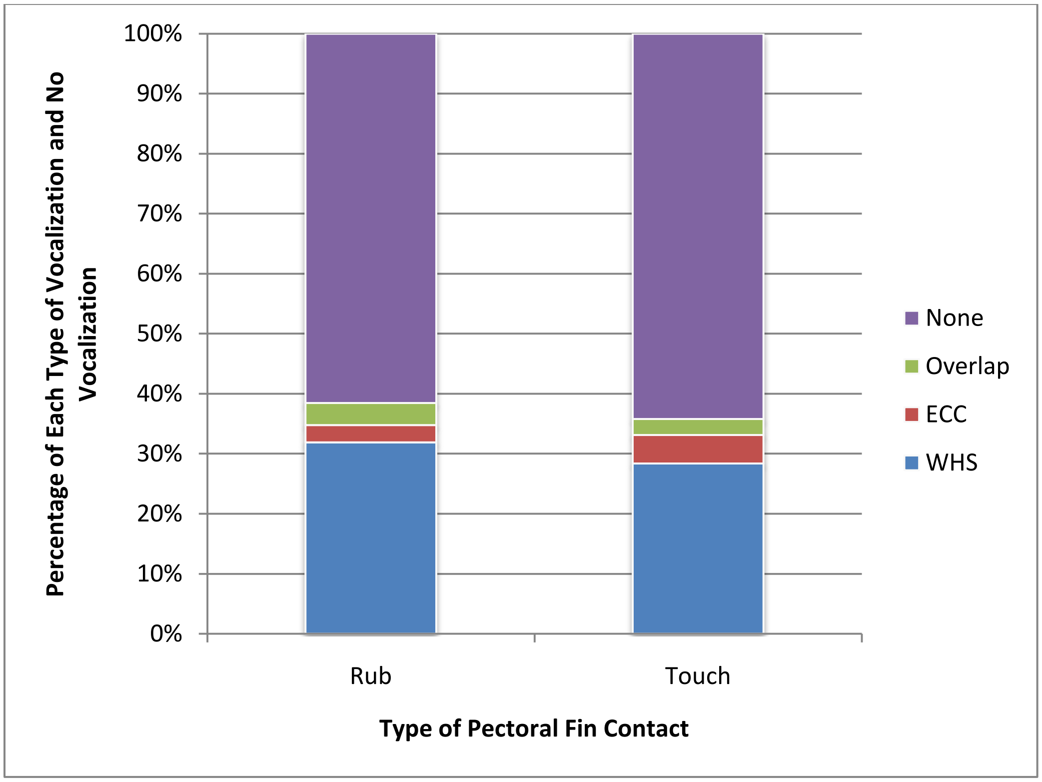

Figure 4. Percentage of type of vocalization or no vocalization (none) associated with touches or rubs during pectoral fin contact, from 2006- 2009.

Gender-Pairs

There was no significant difference between the gender pair engaged in pectoral fin contact (i.e., male-male, male-female, or female-female) and the type of vocalization (χ^2 (DF = 6, N = 521) = 5.965, p = 0.4414). For pectoral fin contacts in which both initiator and receiver were identified, 38.6% of interactions were male-male, 29.4% were male-female, and 32.0% were female-female. Male-male interactions have more overlap vocalizations associated with pectoral fin contact than male-female and female-female interactions, and male-female interactions have more ECC associated with pectoral fin contact than do the other gender pairs (Figure 5). Overall, the percentages of each type of vocalization and no vocalization are quite similar for each of the different gender pairs when engaging in pectoral fin contact.

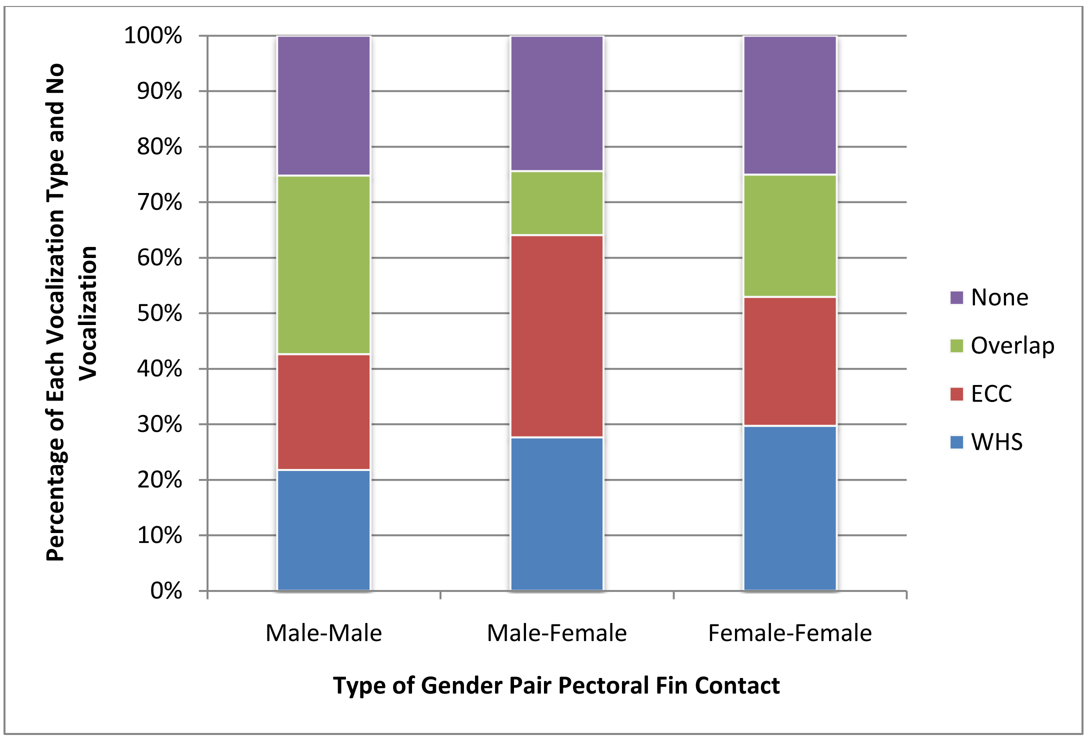

Figure 5. Distribution of gender pairs engaged in pectoral fin contact in association with each vocalization type and no vocalization (none) documented from 2006 to 2009.

Individual Vocalizing Dolphins

The individual identity of a vocalizing dolphin during pectoral fin contact events was significantly related to vocalization type (χ^2 (DF = 36, N = 210) = 49.571, p= 0.025). Certain members of the RIMS population assumed the role of vocalizer more frequently than did others (Figure 6): Ken, Fiona, and Maury whistled during the most interactions, Jack was the most frequent producer of click trains, and also vocalized the most frequently for overlap vocalizations. A number of the individuals (e.g., Carmella, Cedena, and Paya) were in pectoral fin contact with other RIMS dolphins but were not documented to have vocalized in association with pectoral fin contact.

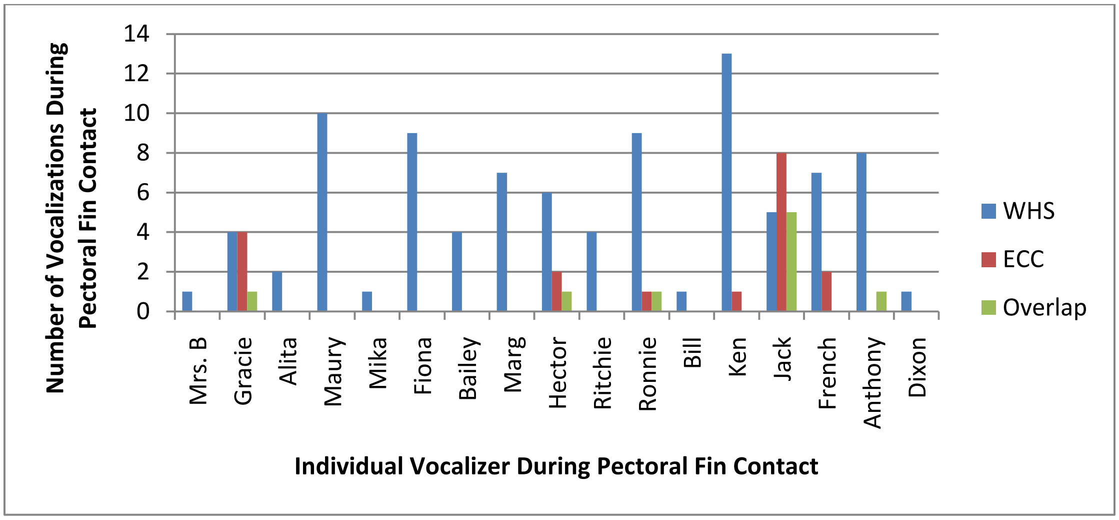

Figure 6. Number of each type of vocalization produced by individually identified RIMS dolphins involved in pectoral fin contact from 2006 to 2009.

All the adult females who vocalized (Mrs. B., Alita, Maury, and Mika) only produced whistles during pectoral fin contacts documented from 2006 to 2009. Bailey, Marg and Fiona, who were either calves or juveniles depending on the year, also were only documented to produce whistles during these pectoral fin contacts. Gracie is the only female who produced all three types of vocalizations (WHS, ECC and Overlap) in association with pectoral fin contact. Jack, Ronnie and Hector were the only males who produced all three vocalizations during pectoral fin contact. Ritchie, Bill, and Dixon only produced whistles during pectoral fin contact; however, these observations of preference for certain vocal behaviors by some individual dolphins could be a result of low sample sizes of ECC and overlap vocalizations as compared to the sample size for WHS.

The frequency of vocalizations associated with pectoral fin contact varied considerably among individuals. For females it ranged from 3% to 100% (Figure 7), with Mrs. B vocalizing during only 3% of her pectoral fin contacts, and Mika whistling during all of her pectoral fin contact events. The frequency of vocalizations associated with pectoral fin contact for males varied from 9% to 85% (Figure 8). Ronnie was the most frequent vocalizer during pectoral fin contacts (85%), followed by Jack (56%) with Dixon and Bill vocalizing the least frequently (9%). Females vocalized on average during 45% of pectoral fin contacts, while males vocalized during pectoral fin contacts 36%. Unidentified or unknown vocalizers were not included.

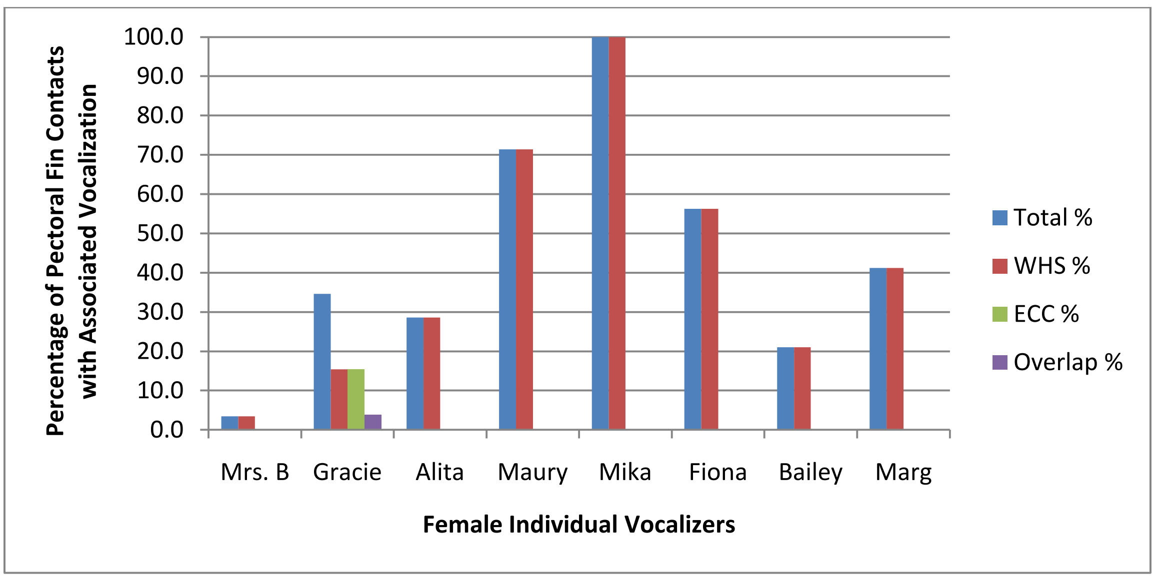

Figure 7. Percentage of female pectoral fin contacts with associated vocalizations. Total percentage refers to the total percentage of pectoral fin contacts in which the individual was the vocalizer. WHS % refers to the percentage of pectoral fin contact events in which the individual was whistling. ECC % refers to the percentage of pectoral fin contact events in which the individual was producing click trains, and Overlap % refers to the percentage of pectoral fin contact events in which the individual was producing overlap calls.

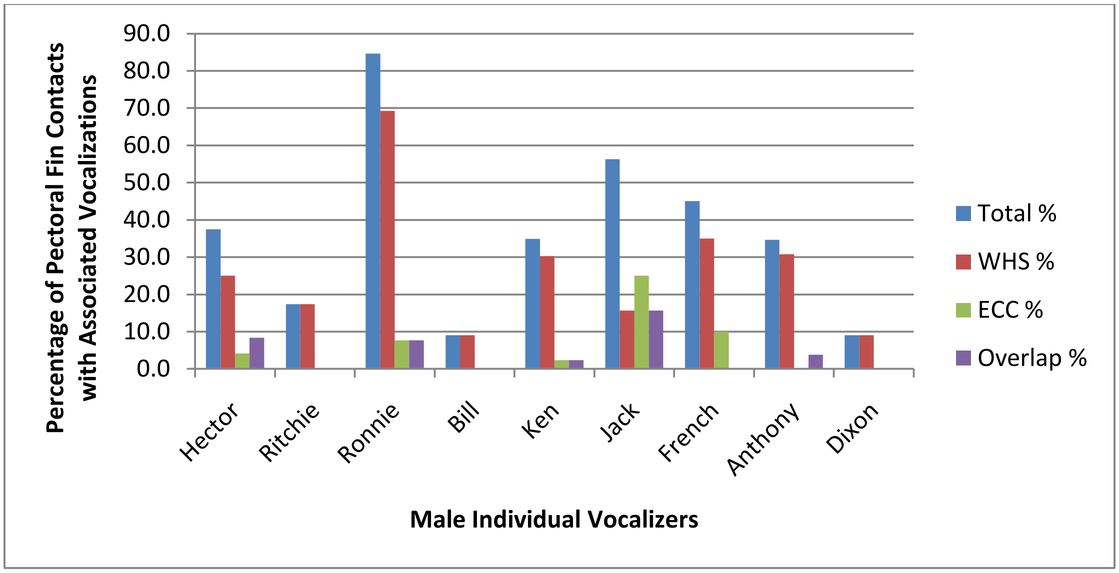

Figure 8. Percentage of male pectoral fin contacts with associated vocalizations. Total percentage refers to the total percentage of pectoral fin contacts in which the individual was the vocalizer. WHS % refers to the percentage of pectoral fin contact events in which the individual was whistling. ECC % refers to the percentage of pectoral fin contat events in which the individual was producing click trains, and Overlap % refers to the percentage of pectoral fin contact events in which the individual was producing overlap calls.

Whistle Parameters

Several vocalizer categories were significantly related to whistle parameters during pectoral fin contact. However, given the number of separate statistical tests that were run, there is the possibility of Type I error in this study. Whistle duration during pectoral fin contact is significantly related to whether the interaction is a touch or a rub ($t = 2.110$, $p = 0.037$, Table 2), with longer whistles during rubs than touches. The type of pectoral fin contact, touch or rub, is also significantly related to the beginning frequency of the whistles emitted ($t = 2.290$, $p = 0.023$), with higher beginning frequencies for rubs than touches.

Table 2. Results of t-tests comparing the effect of the type of pectoral fin contact (touch or rub) on whistle parameters for all whistles associated with pectoral fin contact from 2006-2009. Data in **bold** are significant (<0.05).

Dependent Variable	Mean Touch	Mean Rub	t[1]	p
WHS Duration (s)	1.226	1.6	2.11	**0.037**
Beginning Frequency (kHz)	8498	9750	2.29	**0.023**
End Frequency (kHz)	10657	10127	0.246	0.806
Maximum Frequency (kHz)	13900	14645	1.227	0.222
Minimum Frequency (kHz)	5619	5537	0.281	0.779
Number of Inflections	4.89	6.17	1.534	0.127

[1.] Degrees of freedom = 161.0, N touch = 131, N rub = 42

No whistle parameters were significantly related to the sex of the whistling dolphin (Table 3). The vocalizer role was significantly related to minimum WHS frequency during pectoral fin contact (t = 2.445, p = 0.019, Table 4) with initiators starting whistles at a lower frequency than receivers. The vocalizer role as initiator was also significantly related to minimum whistle frequency when dolphins were in pectoral fin contact (t = 2.481, p = 0.016 Table 5), with rubbers starting whistles at a lower frequency than rubbees.

Table 3. Results of t-tests comparing whistle parameters for males and females for all whistles associated with pectoral fin contact from 2006-2009. Data in **bold** are significant (<0.05).

Dependent Variable	Mean Male	Mean Female	t[1]	p
WHS Duration (s)	1.48	1.41	0.316	0.753
Beginning Frequency (kHz)	8812	8558	1.065	0.29
End Frequency (kHz)	9178	9729	0.675	0.109
Maximum Frequency (kHz)	14218	14589	0.5	0.618
Minimum Frequency (kHz)	5356	5156	0.65	0.518
Number of Inflections	5.44	6.47	0.931	0.354

1. Degrees of freedom = 90.0, N male =54, N female = 38

Table 4. Results of t-tests comparing whistle parameters for initiators and receivers of pectoral fin contact for all whistles associated with pectoral fin contact from 2006-2009. Data in **bold** are significant (<0.05).

Dependent Variable	Mean Initiator	Mean Receiver	t[1]	p
WHS Duration (s)	1.24	1.25	0.026	0.979
Beginning Frequency (kHz)	8976	8361	0.572	0.57
End Frequency (kHz)	8885	9909	0.903	0.371
Maximum Frequency (kHz)	13468	13923	0.381	0.705
Minimum Frequency (kHz)	5016	6006	2.445	**0.019**
Number of Inflections (kHz)	5.4	5.2	0.314	0.755

1. Degrees of freedom = 44.0, N initiator = 30, N receiver = 16

Table 5. Results of t-tests comparing whistle parameters for the vocalizer role as initiator (rubber or rubbee) for all whistles associated with pectoral fin contact from 2006-2009. Data in **bold** are significant (<0.05).

Dependent Variable	Mean Rubber	Mean Rubbee	t[1]	p
WHS Duration (s)	1.23	1.6	1.206	0.233
Beginning Frequency (kHz)	8812	9144	0.307	0.76
End Frequency (kHz)	8725	10344	1.628	0.109
Maximum Frequency (kHz)	13902	14488	0.548	0.586
Minimum Frequency (kHz)	4920	5996	2.481	**0.016**
Number of Inflections (kHz)	5.21	7.1	1.256	0.214

[1.] Degrees of freedom = 56.0, N rubber = 38, N rubbee = 20

Whistle parameters were also compared to the gender-pairing during the pectoral fin contact (male-male, female-male, female-female, Table 6). Whistle duration during pectoral fin contact was significantly different for different gender pairs (F = 4.64, p = 0.004) with a significant difference between male-female interactions and female-female. Male-female interactions had the shortest whistles, and female-female interactions had the longest whistles. The type of gender pairing also had a significant effect on maximum whistle frequency during pectoral fin contact (F = 3.237, p = 0.042), with a significant difference between male-female and female-female interactions. Male-female interactions had the lowest maximum frequency of whistles, while female-female interactions had the highest maximum whistle frequency during pectoral fin contact. Lastly, the number of whistle inflections was significantly different between female-female and male-female dolphin pairs in pectoral fin contact (F = 4.384, p = 0.005). Male-female whistles had the fewest inflections, while female-female interactions had the greatest number of inflections during pectoral fin contact.

Table 6. Results of independent-sample ANOVA examining whistle parameters for gender-pair interactions during pectoral fin contact from 2006-2009. Values in **bold font** are significant (<0.05).

Dependent Variable	Mean Male-Male	Mean Male-Female	Mean Female-Female	f[1]	p
WHS Duration (s)	1.37	1.02	1.59	4.64	**0.004**
Beginning (kHz)	8892	8050	9463	2.198	0.114
End Frequency (kHz)	11831	9580	9603	0.647	0.525
Maximum Frequency (kHz)	14371	13176	14962	3.337	**0.042**
Minimum Frequency (kHz)	5695	5565	5477	0.246	0.782
Number of Inflections	5.31	3.8	6.76	4.384	**0.005**

1. Degrees of freedom = 2, 159; N male-male = 75, N male-female = 41, N female-female = 46

Discussion

In this study, most pectoral fin contact events had no associated vocalization. Dolphins are highly vocal, often communicating with each other under water using acoustic signals because they are frequently too distant to see each other or to share tactile interaction. Within this study, dolphins that were in tactile contact with their pectoral fins may not have used associated acoustic signals because the contact provided the signal vehicle for communication. Gentle contact behavior between conspecifics is common in many cetacean species, especially among mothers and calves (Dudzinski et al. 2009b). In captivity, many trainers report that tactile stimulation is reinforcing, and rubbing between dolphins might also be rewarding (Dudzinski et al. 2009b; Dudzinski 2010).

Following the expression of no vocalizations, whistles were the most common vocal behavior associated with pectoral fin contact for the dolphins at RIMS. For these dolphins, whistles often accompanied pectoral fin contact, especially rubs. Although the frequency of vocalizations associated with touches and rubs was not significantly different, pectoral contact is more frequently a rub than a touch, and the WHS with rubs were longer. Many studies have examined the role of whistles, especially signature whistles, for dolphin-to-dolphin communication (Caldwell et al. 1990; Sayigh et al. 1990; Janik 1998; Janik & Slater 1998; Harley 2008). Because the RIMS dolphins are in a captive location and thus always together, it is unlikely that they would need to identify themselves regularly using a signature whistle. Perhaps the RIMS dolphins use whistles in association with tactile communication to convey different types of messages. More whistles may be emitted during more gentle interactions, i.e., rubbing which occurs over longer duration rather than a brief touch, and so these longer duration interactions might have more concurrent vocal behavior. If so, this detail would have been missed within the scope of this study, because only 20 s segments were examined for physical contact and associated vocalization.

Rubber/Rubbee and Initiator/Receiver

The dolphin in the role of initiator was more likely to vocalize than the receiving dolphin, and when the rubber was the initiator, the dolphin was more likely to vocalize than the rubbee, especially for whistles. Dudzinski et al. (2010) found that the rubber was also more frequently the initiator; thus, the rubber and initiator may be using tactile and vocal communication jointly to convey a particular message to the rubbee/receiver or to other peers in the vicinity of the activity. With a vocal action, it is difficult to know absolutely who the intended recipient will be, and thus tactile behavior used in conjunction with vocalizations might help to make the receiver of the message clear. The use of the two signals, vocal and tactile, could be a way to emphasize the message the initiating rubber is trying to convey.

Because pectoral fin contact is generally viewed as an affiliative behavior, it may be used to strengthen bonds between two individual dolphins. In many other species, affiliative contact behavior, such as grooming or socio-sexual behavioral, plays an important role in the expression and negotiation of social bonds. A common example is found in bonobos (*Pan paniscus*), in which females engage in genital-genital rubbing, which is thought to strengthen bonds and influence conflict mediation (Kuroda 1980; de Waal 1987; Hohmann & Fruth 2000). It may be the case that pectoral fin contact possesses a function similar to that of genital-genital rubbing in bonobos and social grooming in other primates (Dudzinski et al. 2010); if so, then the purpose of a vocalization associated with a pectoral fin contact might be to greet the reciprocal dolphin, or to communicate the desire for tactile contact and potential bonding.

Interestingly, the receiver role, commonly filled by the rubbee, presented more click trains and overlap vocalizations, although there were only a few pectoral fin contacts associated with these vocalizations. Thus, click trains and overlap vocals by a rubbee/receiver might serve a different role than whistling in tactile contact exchanges. Frequently, click trains have been documented during courtship, discipline, play, and aggression (Herzing 2004).

High-repetition click trains (or burst pulse sounds) have been frequently recorded during aggressive displays (Overstrom 1983; McGowan & Reiss 1995). The higher frequency of click trains emitted by rubbees/receivers could indicate that the receiving dolphin is using click trains to display aggression towards the pectoral fin contact initiator. Alternatively, click trains could be used during male-female interactions as a courtship behavior, or even in male-male interactions as practice for sexual interactions (Connor et al. 1992; Connor et al. 2006). Examining more examples of pectoral fin contact associated with click trains could lead to a better understanding of how this vocal behavior might be used as a communication signal, as opposed to a navigation tool, within the framework of different dolphin interactions.

Gender Pairs

The distribution of gender within the individual dolphin pairs (male-male, male-female, female-female) engaged in pectoral fin contact did not affect associated vocalization (WHS, ECC, overlap); however, the majority of pectoral fin contacts were between male pairs for this dataset from RIMS. Larger sample sizes of male-female and female-female pairs or additional years of data from which to examine potential links between vocal and pectoral fin contact behaviors might provide a better understanding of how vocalizations might change or be used differently with different tactile activity. Pectoral fin contact between two males may have a different purpose than pectoral fin contact between two females, or between a mother and calf. Pectoral fin contact between two males may be used to strengthen bonds, since males form complex hierarchical alliances in competition for females (Connor et al. 1992, 1999, 2001). Females often form subgroups or chains of associates for protection from groups of sexually-charged males, often with other females in the same cycle of pregnancy (Smolker et al. 1992). Calves may spend several years in close proximity to their mother, and may often use tactile and vocal contact as a way to remain in communication (Mann & Smuts 1998).

The vocalizations associated with these different gender pair comparisons could provide further insight into how the meaning behind these tactile interactions varies. Dudzinski et al. (2010) found that the RIMS dolphins, especially males, engaged more frequently in pectoral fin contact behaviors than expected. Pectoral fin contacts produced in association with whistles could function as an affiliative complement rather than an aggressive intention. Because the dolphins at RIMS are never out of acoustic contact, they may not need to use whistles as an acoustic cue to identify themselves. Therefore the whistles accompanying this particular tactile behavior might act as a positive message in which the initiating dolphin vocalizes its intention for a non-aggressive interaction.

Alternatively, because these dolphins have a preference for same-sex rubbing partners (Dudzinski et al. 2010), it is possible that pectoral fin contact may be used for strengthening social bonds and partnerships. Vocalizations associated with these pectoral fin contact behaviors may further communicate affection and preference for a particular rubbing partner, and thus strengthen the relationship between two individuals.

Individual Vocalizer Identities

A few individual RIMS dolphins vocalized more frequently than others during pectoral fin contact. Ken, Maury, and Fiona frequently whistled during pectoral fin contact interactions. Ken was a calf in 2006, and a juvenile from 2007-2009. Fiona was a juvenile from 2006-2009, and Maury was an adult female. Interestingly, Gracie (an adult female) was the only female dolphin in the RIMS population to vocalize using whistles and click trains, as well as overlap during pectoral fin contacts. All other females who vocalized only produced whistles. Two of the older adult females, Cedena and Carmella, did not produce any vocalizations associated with pectoral contact, even though they both participated in pectoral fin contact. Cedena engaged in 11 pectoral fin contacts, only with Mrs. B, another adult female, and Bailey, who is Cedena's calf. Carmella engaged in 2 pectoral fin contacts, both with her un-named calf. Perhaps these older females do not need to use vocalizations when engaging in pectoral fin contact with their calves or with other pregnant females. Although click-trains have been observed in mother-calf interactions (McGowan & Reiss 1995), these particular pectoral fin contact events may not have been aggressive in nature, and thus didn't warrant any associated clicks.

Many males in the population were vocal, using all types of vocalizations, except for Paya, the oldest male. Paya was not documented to vocalize at all during this study, even though he also engaged in nine pectoral fin contacts. Jack (a calf-juvenile) was the most common vocalizer for ECC and overlap vocalizations. Jack was frequently in contact with Gracie, his mother. Jack may have been using these different vocalizations to practice different functions of acoustic and tactile behavior with his mother. Younger animals in the group may use vocalizations during pectoral fin contact more commonly than some of the older individuals precisely because they are younger and thus may need to learn proper etiquette and use of these communicative signals. Combining tactile and acoustic communication may help younger individuals communicate their desire for tactile contact appropriately. For example, two juveniles participating in pectoral fin contact may have a different function than that of a juvenile male and an adult male. The vocalization associated with the pectoral fin contact may make that distinction.

Conclusions

Overall, rubbers and initiators vocalized more often when involved in pectoral fin contact than did rubbees and receivers; however, rubbees/receivers used click trains and overlap vocalizations more frequently than rubbers/initiators, which suggests that different vocalizations might modify the intended message of a particular tactile behavior, in this case, pectoral fin contact. A whistle might indicate an affiliative tactile behavior, whereas click trains could indicate an aggressive or sexual tactile behavior. Alternatively, a WHS may be a request by the initiating dolphin for continued contact, while a click train in response by the receiver could suggest a desire not to participate. Alternatively, a click train produced by the receiver could also provide the initiator with a location on the body for the pectoral fin contact, as click trains are more directional than whistles.

Examining more pectoral fin contact events during which dolphins are using whistles, click trains, and overlap vocalization would be useful to elucidating the subtle complexities regarding how dolphins use multiple signals to share information with conspecifics. It would also be interesting to compare the results documented during this study to observations of joint vocal and tactile behavior by individuals from a wild population to see if vocal behavior might have a different context for wild dolphins when engaged in pectoral fin contacts.

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