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Vocalizations Produced by Bottlenose Dolphins (*Tursiops truncatus*) during Mouth Actions in Aggressive and Non-aggressive Contexts

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Dolphins exchange information with conspecifics using different types of vocalizations that are often associated with specific behaviors. The present study used simultaneous acoustic and video recordings of captive bottlenose dolphins (*Tursiops truncatus*) in Honduras to describe potential correlations between the type of mouth actions (open mouth, mouthing, bite) and associated vocalizations (whistle, whistle squawk, chirp, moan, burst-pulse A, burst-pulse B, clicks). Literature on sound-behavior relationships among odontocetes with the noted infrequent systematic analyses of mouth actions highlights the need for this investigation. The influence of aggression on vocalization use was also addressed. From this observational study a series of general expectations on the interaction of sound, mouth action, and aggressive context are presented. Mouth actions are associated with vocalizations more often than not, and results suggest an overall flexible association of vocalizations during mouth actions, with the production of various sounds altered during aggressive contexts. There is an apparent distinction of frequency-modulated sounds with mouthing, suggesting that frequency parameters are an important characteristic of information exchange during mouth actions, and further that mouth actions are individually distinct behaviors. A dichotomy of burst pulse sounds in association with aggressive and non-aggressive contexts also introduces the need to analyze pulsed sounds according to inter-pulse interval. This paper proposes that there may be an interactive function to the use of vocalizations during mouth actions that is not yet understood.

While many species use diverse sensory modalities to communicate with conspecifics, odontocete communication occurs primarily through physical and acoustic exchanges (Herman & Tavolga, 1980). Odontocete vocalizations from various species include both pulsed and tonal sounds (Au, 2000; Tyack & Clark, 2000). Frequency characteristics of dolphin vocalizations span 100 Hz through 100 kHz depending on the species (Tyack & Clark, 2000) and the recording equipment. Across odontocete species, bottlenose dolphin (*Tursiops truncatus*) vocalizations are among the most studied (Tyack & Clark, 2000) and include a variety of vocalizations with differing parameters (Janik, 2009). Whistles are frequency-modulated (FM), tonal vocalizations most often recorded below 20 kHz within the human hearing range (Lammers, Au, & Herzing, 2003). A sub-category of tonal vocalizations termed chirps has been reported in several dolphin species (documented in eastern Pacific common dolphins, *Delphinus delphis bairdi*, by Caldwell & Caldwell, 1968; in Atlantic bottlenose dolphins by Caldwell & Caldwell, 1970; in Hawaiian spinner dolphins, *Stenella longirostris*, by Driscoll as cited in Bazúa-Durán & Au, 2002; in bottlenose dolphins by Herzing, 1996). In bottlenose dolphins, these vocalizations have been reported as shorter, less than 100 ms, and high in frequency, between 6 and 16 kHz (Caldwell & Caldwell, 1970). In contrast, low frequency calls produced by bottlenose dolphins are characterized by fundamental frequencies ranging from 260 to 1280 Hz (Schultz, Cato, Corkeron, & Bryden, 1995) or 150 to 240 Hz (*moans*, van der Woude, 2009) with durations widely ranging from 0.2-8.7 s (van der Woude, 2009). Pulsed vocalizations are further differentiated into echolocation clicks and burst-pulse vocalizations (Tyack & Clark, 2000). Burst-pulse vocalizations are composed of a series of clicks (Janik, 2009), and are identified by their repetition rate (dos Santos, Caporin, Moreira, Ferreira, & Coelho, 1990) or inter-pulse interval (IPI) (in false killer whales, *Pseudorca crassidens*, by Murray, Mercado, & Roitblat, 1998). These vocalizations have highly variable amplitudes and emission rates (Popper, 1980). Given the diverse and

varied repertoire of dolphin vocalizations, it is likely that vocalizations have different uses, which makes their study in relation to behavior type and context important.

Dolphins use a combination of tactile and acoustic signals to communicate information to conspecifics (Dudzinski, 1998). Relationships between behavioral repertoire and acoustic signals have been described for several dolphin species (bottlenose dolphins, pantropical spotted dolphins, *Stenella attenuata*, Hawaiian spinner dolphins, Atlantic spotted dolphins, *Stenella frontalis*, killer whales, *Orcinus orca*, and Hector's dolphins, *Cephalorhynchus hectori*; see review in Herzing, 2000). Although dolphin vocalizations are rarely limited to one specific behavioral context, certain vocalizations may be produced more or less frequently within differing contexts. Burst-pulse vocalizations and whistle squawks are common during aggression (documented in bottlenose dolphins by Blomqvist & Amundin, 2004; in spotted dolphins by Herzing, 1996) as well as sexual play (Herzing, 1996). Click trains are emitted as individuals explore an area (in spotted dolphins by Dudzinski, 1998), but have also been documented during social interactions of Pacific humpback dolphins (*Sousa chinensis*, Van Parijs & Corkeron, 2001). Whistles are produced in group-settings during instances of aggression (Dudzinski, 1998), in association with play behaviors and conspecific rubbing (Dudzinski, 1998), during mother-calf reunions (Herzing, 1996; in bottlenose dolphins by Smolker, Mann, & Smuts, 1993), or for identification (Caldwell & Caldwell, 1965; see review in Janik & Sayigh, 2013). Furthermore, whistles have been documented frequently during socializing (dos Santos et al., 1990; Hernandez, Solangi, & Kuczaj, 2010; Quick & Janik, 2008), implying a communicative function. Chirps have specifically been noted during foraging (Herzing, 1996). It is evident from the literature that behavioral context plays a role in the type of vocalizations emitted by dolphins; however, few studies have examined the relationship between mouth action and vocalization production.

Dolphins may communicate using their mouths as either a visual or tactile signal, which has been documented in other species (e.g., dogs: Godbout & Frank, 2011; human infants: Rochat, 1989; and rats: Smotherman, Arnold, & Robinson, 1993). Three types of dolphin mouth actions have been observed: open mouth, mouthing, and bite (Seay, Levengood, Gross, Dudzinski, & Kuczaj, 2011). The aggressive context of these behaviors is varied across the literature. Biting often includes an aggressive or threatening intent (Dudzinski, 1998; Herman & Tavolga, 1980; Holobinko & Waring, 2010; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005; Shane, Wells, & Würsig, 1986) and the presence of rake marks on conspecifics has been linked to fighting (Lockyer & Morris, 1985) and calf play behavior (Scott et al., 2005). Open mouth events are observed in antagonistic social exchanges (Overstrom, 1983) and are often indicative of fighting or aggression (Holobinko & Waring, 2010; Samuels & Gifford, 1997). In contrast, mouthing has been observed in non-aggressive contexts involving rough-toothed dolphins (*Steno bredanensis*) (Kuczaj & Yeater, 2007). The differentiation in aggression levels during which these types of behaviors are observed is suggestive of the social significance of the behaviors, and thus warrants the exploration of possible meaningful acoustic exchanges.

That dolphins communicate in different ways and exchange different information depending on aggression levels allows for detailed examination of vocalization-behavior comparisons. The current study examines three types of mouth actions (open mouth, mouthing, and bite) to characterize vocalizations given aggressive and non-aggressive contexts. Two general expectations highlight findings from previous literature as applied to this novel study. First, a difference in the use of vocalization types will be evident through comparisons of the presence or absence of vocalizations with respect to mouth action type and the number of each vocalization heard during open mouth, mouthing, and bite behaviors. Second, there will be a difference in the vocalizations produced during all mouth actions dependent upon the aggressive context of the mouth

action. The goal of the study is to descriptively examine vocalizations that occur with three different mouth actions given aggressive context.

Method

Study Site and Population

Video and audio recordings collected from bottlenose dolphins at the Roatan Institute for Marine Science (RIMS), Anthony's Key Resort in Roatan, Bay Islands, Honduras, between March 2010 and June 2011 were analyzed. The dolphins were housed in a 300 m² enclosed natural lagoon with a maximum depth of eight meters. The lagoon sea floor is characterized by sand, coral, and sea grass beds. The dolphin population at RIMS during data collection included 24 dolphins: 13 males and 11 females. According to Dudzinski et al. (2012), the dolphins at RIMS maintain a group structure that is similar in age and sex organization to wild dolphin populations in Shark Bay, Australia (Connor, Mann, & Watson-Capps, 2006) and around Mikura Island, Japan (Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004).

Data Collection

Simultaneous video and audio recordings of underwater behaviors and concurrent vocalizations were collected opportunistically by the second author using a Canon 7D with Tokina 2.8 11-16mm lens (Canon, Inc., Toky, Japan) and a Nauticam underwater housing with hydrophone (Nauticam USA, Fort Lauderdale, Florida). Recordings were made on 16 days between March and July of 2010 and on 9 days between March and June of 2011. Each recording session occurred between 0600 and 0700 hours, and lasted for approximately one hour. During these sessions, all dolphins were together in the enclosure, free to move around and associate without human influence other than the second author. No other staff or visitors were present, eliminating possible limitations resulting from training or feeding regimes. Focal follows were used to record behavioral exchanges.

Behavioral Data

Mouth actions were coded as open mouth, mouthing, or bite directed towards a conspecific. Each coded instance, or behavioral event, of a mouth action was defined as beginning with the visible onset of the behavior from an individual dolphin and ending as soon as that behavior type was no longer occurring. The term *mouth actions* in this manuscript refers to all three types of behaviors examined in this study. Mouthing is physical contact identified when one dolphin's mouth is around a body part of another dolphin, without force from teeth. Open mouth behaviors are those directed at conspecifics but without contact between two individuals. Bites are characterized by one individual powerfully closing its mouth around a second individual or raking its teeth along another individual (definitions adapted from Dudzinski, 1996; Seay, et al., 2011). A behavior was considered "directed" at a conspecific when the *mouthing* dolphin was oriented directly towards a second dolphin within a single body length.

Contexts were initially examined as orient, herding, aggressive, social, socio-sexual, and swim by. For analyses, all contexts with the exception of aggression were collapsed to refer to all non-aggressive situations, for consistency with literature on mouth actions that documents the aggressive context of such behaviors. Aggressive contexts frequently involved sharp or fast changes in head direction or chasing behaviors (Seay et al., 2011). Behavior types were re-coded by the first author from data presented by Seay et al. (2011) for reliability measures.

Acoustic Data

Audio recordings were extracted as .mov files from the videos, and vocalizations were digitized at a sampling rate of 48 kHz. Spectrograms were generated using the Raven Pro 1.4 Interactive Sound Analysis Software developed by the Cornell Lab of Ornithology. Spectrogram parameters were set to remain stable throughout analysis: fast fourier transform size of 2048, Hann, 50% overlap, window size 1200, hop size 12.5 ms. The camera with single hydrophone setup used for data collection made it impossible to determine the directionality of sound to localize a vocalization to an individual dolphin. All vocalizations recorded during each mouth action were analyzed, but some vocalizations may have been produced by dolphins not engaging in mouth actions. The quantity of each vocalization was recorded, along with mouth action type and aggressive context. Mouth actions that occurred with no detectable dolphin vocalizations within the human hearing range were also examined.

Vocalizations analyzed included whistles, whistle squawks, chirps, moans, burst-pulses, and click trains. Both tonal and burst-pulse vocalizations were chosen to represent the variability of dolphin vocalizations (Popper, 1980; Tyack & Clark, 2000). All vocalizations were coded visually from spectrograms. Inter-observer reliability using a Pearson correlation coefficient was obtained using 20% of the data. Both coders reached 80% reliability for each vocalization. Burst-pulse vocalizations and click trains were also coded to identify IPI and determine IPI ranges for each pulsed vocalization category (Au, 2000; dos Santos et al., 1990; Herzing, 2000; Tyack & Clark, 2000). This process was confirmed using a second blind researcher who coded the IPIs of the same subset of vocalizations.

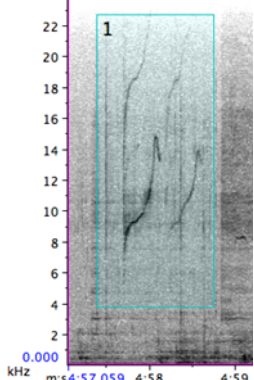
Data Analysis

Vocalizations were coded using a one-zero sampling method during each type of mouth action. The presence or absence of each type of vocalization was compared across open mouth, mouthing, and bite events using a Pearson’s chi-square test. The total number of each vocalization was then compared during all instances of each type of mouth action using one-way analyses of variance for each behavior (open mouth, mouthing, and bite). Due to violation of the homogeneity of variance assumption in Levene’s statistic, results given for each behavior type are reported as F values for the Brown-Forsythe robust test of equality of means.

For statistical analyses of vocalizations produced during aggressive or non-aggressive contexts, all three mouthing actions were combined because of small sample sizes. The total number of each vocalization was compared between aggressive and non-aggressive mouth actions using a one-way analysis of variance. Due to violation of the homogeneity of variance assumption in Levene’s statistic, results for comparison of vocalizations by aggressive context are reported as F values for the Brown-Forsythe robust test of equality of means. The presence or absence of each type of vocalization was also compared across mouth actions between aggressive and non-aggressive contexts using a Pearson’s chi-square test.

A 3-way analysis of vocalization type, behavior type, and aggressive context could not be performed due to violation of assumptions. Descriptive results for this analysis are presented. All statistics were run using IBM SPSS version 21.

Table 1
Operational Definitions and Spectrogram Examples of Each Vocalization Type

| Vocalization | Spectrogram |
|--|--|
| <p>Whistle: Narrowband, frequency modulated (Herzing, 1996) sounds having tone (Caldwell & Caldwell, 1968). Whistles counted individually if consecutive whistles separated by > 0.03 s (Gridley, Berggren, Cockcroft, & Janik, 2012) or not continuous from end of whistle A to start of whistle B.</p> |  |

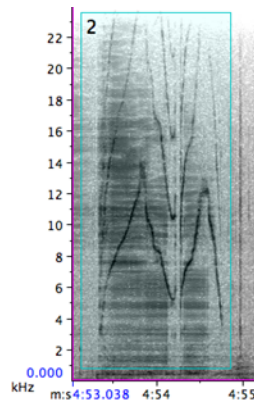
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Table 1 continued

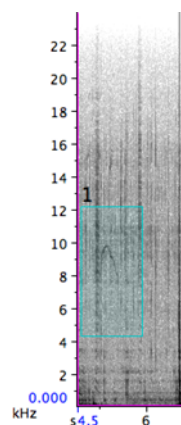
Vocalization

Spectrogram

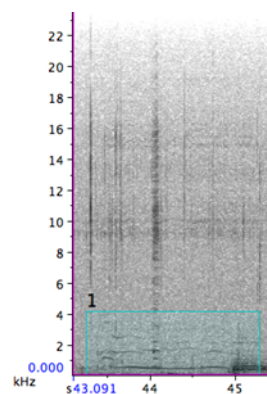
Whistle Squawk: Whistle with broadband burst pulse characteristics during some duration of the whistle (Herzing, 1996; Killebrew, Mercado, Herman, & Pack, 2001). Counted separately for each whistle/burst pulse involved.



Chirp: Brief and pure tone (Caldwell & Caldwell, 1968) whistle less than 0.30 s in duration (Driscoll, 1995 as cited in Bazúa-Durán & Au, 2002) that covers a range of frequencies, often upsweep (Caldwell & Caldwell, 1968).



Moan: Sounds with modulated fundamental frequencies less than 0.50 kHz (van der Woude, 2009) of differing duration.



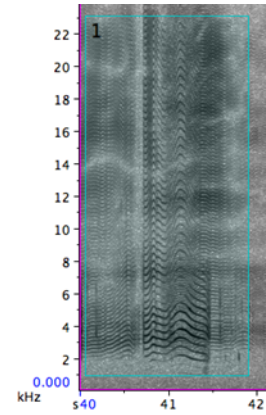
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Table 1 continued

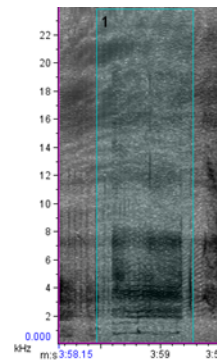
Vocalization

Spectrogram

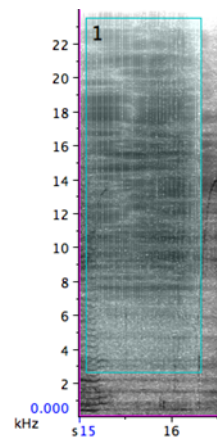
Burst-Pulse A: A broadband, wideband vocalization (Killebrew et al., 2001) with clear horizontal bars, visibly separated by white space on the spectrogram. IPI below 0.009 s.



Burst-Pulse B: A broadband, wideband vocalization (Killebrew et al., 2001) that appears patterned or blurred on a spectrogram. IPI between 0.010 s and 0.019 s.



Click Train: Definitive, short, broadband (Killebrew et al., 2001) sounds (vertical lines on spectrogram) that are repeated rapidly. IPI above 0.020 s.



Note. All images from current study

Results

A total of 1,513 min and 50 s of video and audio were collected. All mouth actions were documented from these data, resulting in 20 min and 22 s of mouth actions ($N = 677$ events). Open mouth behaviors ($n = 629$) accounted for 93% of all mouth actions. Mouthing ($n = 24$) and bite ($n = 24$) each comprised 7% of documented mouth actions.

Ranges of IPIs for burst-pulse type A, burst-pulse type B, and click trains are included with visual definitions for each vocalization category (Table 1). These ranges were defined by first determining the minimum and maximum IPI, and dividing this total range in half; the lower IPIs were labeled as A and the higher IPIs were labeled as B. This was done to provide an unbiased distinction between burst-pulse vocalizations types based on their IPI, rather than their spectrogram appearance. Click trains were then defined as vocalizations with the highest IPIs, beyond the range of burst-pulse vocalizations. Burst-pulse type A vocalizations had longer IPIs than burst-pulse type B, which were closer in rate to those of click trains. Additionally, burst-pulse type A had visible frequency modulation on the spectrogram, likely an artifact of the higher repetition rate, or shorter IPI (Watkins, 1967).

Mouth Actions without Documented Vocalizations

Only 10% of all mouth actions ($n = 68$) were recorded without vocalizations, and 94% of these instances were open mouth events ($n = 64$). A total of 97% of mouth actions without audible vocalizations also occurred in association with non-aggressive contexts ($n = 66$). Sample size prohibited analysis with either parametric or non-parametric tests due to assumption violations.

Vocalizations and Mouth Actions

There was a significant association between behavior type and whistle production, $\chi^2(2) = 12.58$, $p < 0.050$. Whistles were the only sound type for which the production of vocalizations was significantly related to the type of mouth action. Approximately 30% of all mouth actions were in association with whistles, and a majority of those behavioral events were mouthing (Table 2). Assumptions were violated for chi-square tests for chirps and moans, and no other vocalization types showed a significant association between behavior type and sound production.

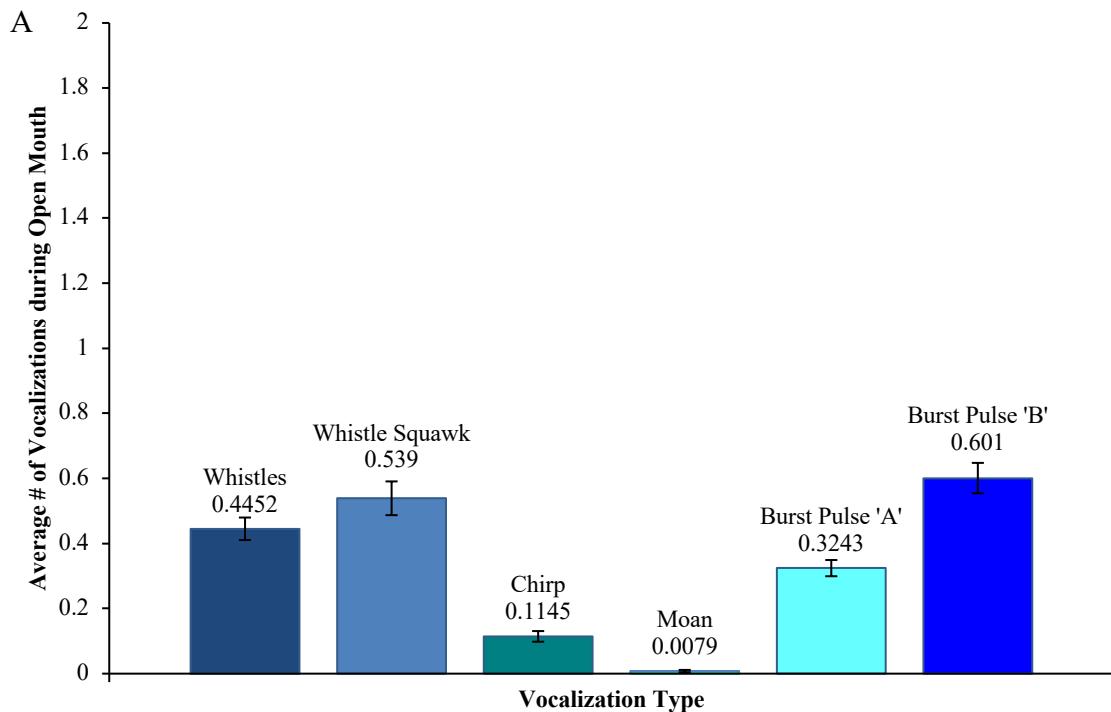
Table 2
Whistles According to Behavior Type

| | Total Number | Percentage |
|-------------------------------------|--------------|------------|
| Total Behavior Events with Whistles | 209 | 31% |
| Open Mouth Events with Whistles | 189 | 30% |
| Mouthing Events with Whistles | 15 | 63% |
| Bite Events with Whistles | 5 | 21% |

Open mouth. When production of each vocalization was examined during open mouth actions, there was a significant difference between vocalization categories, $F(5, 21978) = 48.16, p < 0.001$. Games-Howell post-hoc analysis revealed that whistles, whistle squawks, and burst-pulse A and B were all emitted more frequently than either chirps or moans, all at $p < 0.001$. Whistle squawks ($p < 0.010$) and burst-pulse B ($p < 0.001$) were more common than burst-pulse A. Chirps were emitted more often than moans, $p < 0.001$ (Figure 1A).

Mouthing. Vocalizations also differed significantly when produced during mouthing, $F(5, 67) = 4.37, p < 0.010$. Specifically, Games-Howell post-hoc analysis revealed that whistles were emitted more frequently than moans, $p = 0.006$ (Figure 1B). No other vocalizations differed in production when associated with mouthing.

Biting. A total of 34 vocalizations were associated with bite actions across the data set, of which 9 were frequency-modulated sounds, 10 were burst-pulse sounds, and 15 were whistle squawks. No moans were documented. Due to these small sample sizes, an analysis of type of vocalization associated with bite actions using the Brown-Forsythe robust test of equality of means could not be performed.



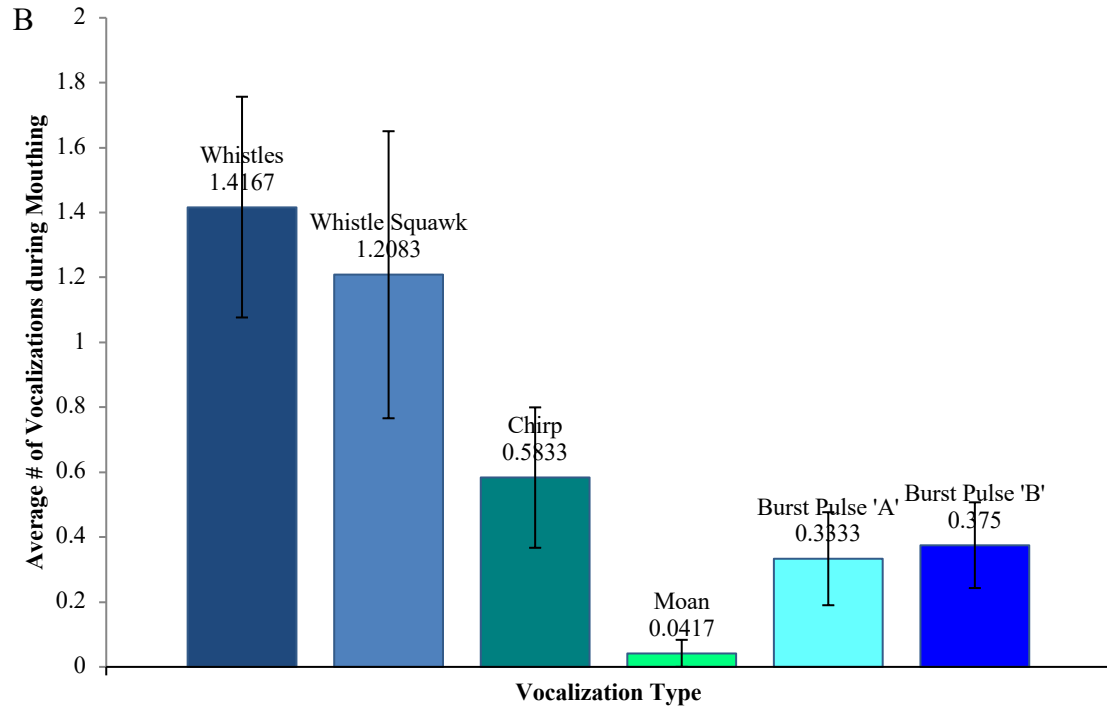


Figure 1. The average number of vocalizations produced during (A) open mouth and (B) mouthing events.

Vocalizations and Aggression

All vocalizations, with the exception of moans, differed in production according to aggressive or non-aggressive context. Specifically, more whistles, $F(1, 339.76) = 18.16, p < 0.001$, chirps, $F(1, 311.05) = 8.08, p < 0.010$, and burst-pulse A, $F(1, 251.49) = 10.52, p < 0.010$ were produced during non-aggressive contexts than during aggressive contexts (Figure 2). Conversely, whistle squawks, $F(1, 148.77) = 25.07, p < 0.001$ and burst-pulse B, $F(1, 141.58) = 21.94, p < 0.001$ vocalizations were produced more frequently in aggressive contexts (Figure 2).

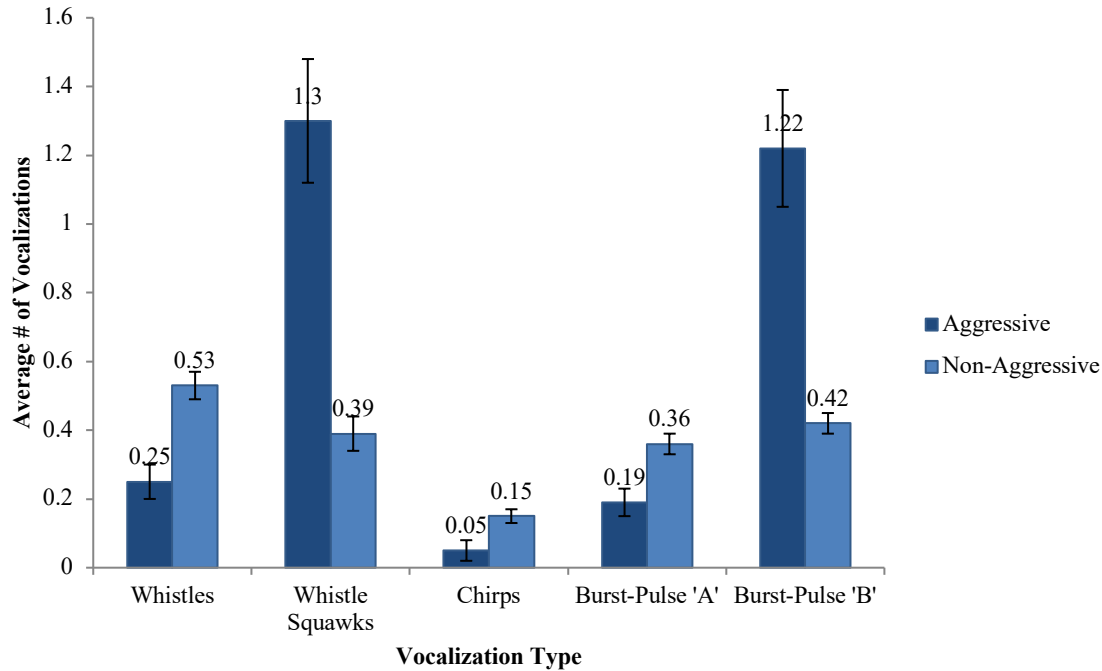


Figure 2. The average number of vocalizations produced during aggressive and non-aggressive contexts. All mouth actions were combined per context.

When presence or absence of vocalizations was examined, behavioral events within non-aggressive contexts were more commonly associated with vocalizations than behavioral events in aggressive contexts. More mouth actions in a non-aggressive context were associated with whistles, $\chi^2(1) = 9.59, p < 0.010$, whistle squawks, $\chi^2(1) = 50.61, p < 0.001$, chirps, $\chi^2(1) = 6.15, p < 0.050$, burst-pulse A, $\chi^2(1) = 10.03, p < 0.010$, burst-pulse B, $\chi^2(1) = 14.49, p < 0.001$, and clicks, $\chi^2(1) = 13.00, p < 0.001$, than behavioral events in aggressive contexts. Moans violated chi-square assumptions and could not be analyzed.

Vocalizations, Mouth Actions, and Aggression

Open mouth events were more common than instances of either mouthing or biting (Table 3). More mouth actions, regardless of behavior type, were documented concurrently with whistles in a non-aggressive context compared to an aggressive context (Table 3). The same was true for chirps and clicks. The proportion of mouth actions during which whistle squawks, burst-pulse A, and burst-pulse B were produced changed with respect to the aggressive context. Open mouth events in an aggressive context had a higher proportion of events with whistle squawks and burst-pulse B vocalizations and a lower proportion of events with whistles, chirps, and burst-pulse A in comparison to open mouth events in a non-aggressive context. Mouthing events in an aggressive context had a higher proportion of events associated with whistle squawks only, and a lower proportion of events during which other vocalizations were heard. Biting events were more often associated with whistle squawks and burst-pulse A in an aggressive context and less often associated with whistles. There was no difference in the proportion of bite events associated with chirps, moans, or burst-pulse B depending on the aggressive context. Almost no biting events were associated with chirps, regardless of the aggressive

context. Most mouth actions were not associated with moans, regardless of behavior type or aggressive context (Table 3).

Table 3
Total Number and Percentage of Behavioral Events Associated with Vocalizations

| | | Whistle | Whistle Squawk | Chirp | Moan | Burst Pulse 'A' | Burst Pulse 'B' | Clicks |
|----------------|------------|---------|----------------|--------|-------|-----------------|-----------------|---------|
| Aggressive | Open Mouth | 24/110 | 58/110 | 4/110 | 1/110 | 15/110 | 60/110 | 33/110 |
| | | 22% | 53% | 4% | 0.01% | 14% | 55% | 29% |
| | Mouthing | 1/6 | 5/6 | 0/6 | 0/6 | 0/6 | 1/6 | 3/6 |
| | | 17% | 83% | 0% | 0% | 0% | 17% | 33% |
| | Bite | 1/16 | 5/16 | 1/16 | 0/16 | 5/16 | 2/16 | 6/16 |
| | | 0.06% | 31% | 0.06% | 0% | 31% | 13% | 38% |
| Non-Aggressive | Open Mouth | 165/519 | 108/519 | 53/519 | 4/519 | 150/519 | 158/519 | 247/519 |
| | | 32% | 21% | 10% | 0.01% | 29% | 30% | 48% |
| | Mouthing | 14/18 | 4/18 | 6/18 | 1/18 | 5/18 | 6/18 | 13/18 |
| | | 78% | 22% | 33% | 0.06% | 28% | 33% | 72% |
| | Bite | 4/8 | 2/8 | 0/8 | 0/8 | 1/8 | 1/8 | 4/8 |
| | | 50% | 25% | 0% | 0% | 13% | 13% | 50% |

Discussion

Previous studies in a variety of odontocete species suggest that flexibility exists in the use of vocalizations during differing behavioral states and contexts. The combination of vocalizations and behavior may mean something different than the behavior or vocalization does individually (Dudzinski, 1998). The current study documents a relationship between vocalizations and mouth actions among a population of bottlenose dolphins. Mouth actions primarily occur in the presence of sound, suggesting that vocalizations play an important role within the framework of mouth actions. Results highlight that the use of sound is related to behavior type, with this relationship inconsistent across all vocalization types examined. While the aggressive context of a mouth action did not affect the consistent high production of vocalizations during open mouth behaviors, an examination of each mouth action individually revealed differences in sound type production according to the aggressive context. Flexibility in communicative sounds is critical for the developed communication systems and social societies of dolphins, supported in a multitude of research studies across cetacean literature (for review see Marino et al., 2007).

Variations in Vocalization Production

Overstrom (1983) concluded that vocalizations with burst-pulse elements were the only sounds documented during open mouth behaviors, suggesting that a specific behavior type or context may have a one-to-one relationship with a particular vocalization. Results from the analysis of variance tests refute this conclusion, documenting six different vocalizations in association with all three types of mouth actions, and seven vocalizations during open mouth displays. Dudzinski (1998) suggested that dolphins use the same

vocalizations across different behavioral contexts with those vocalizations modified to shift functionality. The current study suggests that the dolphins' use of communicative acoustic signals during mouth actions is flexible, evidenced by the inconsistent frequency of vocalization use during open mouth compared to mouthing events.

Open mouth events were marked by differences in the production of all vocalizations. During mouthing events, only whistles and moans significantly differed in number. If the use of vocalizations was fixed or predictable, all vocalization types should either be equivalently produced across all three types of mouth actions or all vary in number. Rather, results show that only whistles were produced more or less frequently during different mouth actions. The distinct lack of difference in sound use during mouthing, compared to open mouth, is likely important. There may be a different behavioral significance of open mouth and mouthing events that is conveyed through differences in vocalizations or by increased variation in sound repertoire during open mouth events. If the characteristics of sound are more critical during open mouth events, it could be interpreted that these behaviors are more diverse in meaning within the behavioral repertoire.

It is unknown why whistles and moans, both frequency-modulated, were the only vocalizations to differ in number during mouthing. Dolphins are skilled at differentiating between frequency changes in vocalizations, and do so best at around 10 kHz (Tyack & Clark, 2000). They also have the ability to detect as low as a 0.2% change in frequency levels of sound (Thompson & Herman, 1975). Dolphins likely transmit specific information in the frequency contours of vocalizations they produce as a means of communicating (Tyack & Clark, 2000). It is possible that these distinctions in frequency, more than IPI, are especially important to the dolphins during mouthing. Further work should address the acoustic parameters of these vocalizations, since research has shown that they differ relative to the context (Janik, Dehnhardt & Todt, 1994). Whistles were also the only vocalization shown to correlate with behavior type, and the majority of mouth actions documented in association with whistles were mouthing events. The significance of whistles and mouthing may be related to literature that connects mouthing events and non-aggressive contexts (see Kuczaj & Yeater, 2007). This further suggests a significance of frequency parameters during mouth actions, and introduces the question of what the function is of whistles during mouth actions. Describing the aggressive context of mouth actions provides a more detailed framework to examine vocalizations.

The Role of Aggression

There is little published research describing the association of mouth actions with or without aggressive indicators in bottlenose dolphins, but both biting and open mouth events have been described as occurring during aggressive interactions (Dudzinski, 1998; Herman & Tavolga, 1980; Holobinko & Waring, 2010; Overstrom, 1983; Saayman, Tayler, & Bower, 1973; Samuels & Gifford, 1997; Scott et al., 2005; Shane et al., 1986). The results of this study suggest that aggressive context is a key component to understanding vocalization use during mouth actions. Vocalizations are often used to assess the social context of interactions among bottlenose dolphins and other wild dolphin species (Herzing, 2000), but this study represents the first systematic attempt at understanding how vocalizations may be related to the aggressive context of mouth actions.

There was a difference in results related to aggression dependent upon whether vocalization count or presence/absence of a vocalization type was considered. Both analyses were included to highlight the variable nature of vocalization and behavior comparisons. Describing and comparing total counts of vocalizations across categories can be difficult if behavioral event totals or durations are not consistent. However, this type

of description can provide a basis for more fine-scale analysis of potential patterns to sound use (see review of acoustic sequences in Kershenbaum et al., 2016). Alternatively, using a one-zero analysis technique standardizes the dataset and provides a succinct interpretation of when vocalizations are present. This paper will not make in-depth conclusions based on the vocalization count analysis, but suggests that for a longitudinal dataset with sound source localization possible, this type of description would be informative.

It is worth examining the higher number of most vocalizations with burst-pulse elements in association with aggressive contexts and vocalizations with FM elements with non-aggressive behaviors. While these numbers may be biased, the simple difference in sound parameters according to aggression suggests again that vocalizations are not static, and that sound is related to aggressive context. In a study on both spotted and bottlenose dolphin vocalizations, there was a tendency for pulsed or click vocalizations, in comparison to FM vocalization types, to occur during aggressive behaviors (Herzing, 1996). During male-female consortships, male bottlenose dolphins in Shark Bay frequently produced pops, a pulsed vocalization, in association with aggression (Connor & Smolker, 1996). Aggressive interactions among female bottlenose dolphins have also been associated with pulsed vocalizations (Blomqvist & Amundin, 2004). The dichotomy of association of burst-pulse sounds with aggressive context also demonstrates the importance of analyzing individual pulsed vocalizations according to IPI, which has been done for other species (see Kershenbaum et al., 2016). Pulsed vocalizations with different click rates may be distinct enough vocalizations to have diverse uses during information exchange. Parameter categories including duration (Overstrom, 1983), frequency (Killebrew et al., 2001), amplitude, and energy distribution should be considered in subsequent studies to understand how burst-pulse sounds may function in mouth actions.

Taking into account the use of sound according to behavior type or aggressive context, a three-way analysis of vocalizations, mouth actions, and aggression is necessary. Current results suggest that FM vocalizations may be correlated with mouthing in a different way than with either open mouth or biting events. A comprehensive explanation of this result must consider the aggressive context of mouthing events. Across the wide range of studies examining bottlenose dolphin whistles, these vocalizations have been associated with social behavior (Quick & Janik, 2008) and specifically aggression (Dudzinski, 1998).

The Interaction of Behavior Type and Aggressive Context

Initial analyses confirm that aggressive context is related to the type of vocalizations used during mouth actions. The combined effect of behavior type and aggressive context is important to later elucidate the function of mouth actions by examining concurrent vocalizations. The proportion of behavioral events associated with burst-pulse A and burst-pulse B sounds differed depending on the aggressive context and type of mouth action. Behavior type did not influence the proportion of events with whistle squawks, whistles, or chirps. Whistles and chirps were always more often associated with non-aggressive contexts. Notable here is that both vocalizations are frequency-modulated, without pulsed elements. The distinction between frequency-modulated and pulsed sounds with aggressive context is further support for the importance of frequency-modulation in information exchange or interactions during mouth actions. Clicks followed the same pattern as whistles and chirps. The analysis of click presence may be an artifact of non-localized sound sources and the possibility that not all clicks were produced by dolphins engaging in mouth actions. Click production may not be significantly related to mouth actions, and echolocation signals are traditionally segregated from communication signals (dos Santos et al., 1990; Tyack, 2000; Zimmer, 2011). It is possible that not all clicks were detected due to the sampling rate of equipment, which should be examined during replication studies.

Regardless of behavior type, the significantly low production of both chirps and moans in comparison to all other vocalizations types is notable. Caldwell and Caldwell (1970) refer to chirps as a shortened whistle. Bazúa-Durán and Au (2002) commented that they found no real distinction for chirps as a unique vocalization category but included them for assessment purposes, as was done for this paper. Moans have previously been recorded during social interactions among bottlenose dolphins (Schultz et al., 1995), so their rare occurrence in association with mouth actions, which are also social in nature, requires further investigation. Conversely, it is possible that these extremely low-frequency vocalizations are not required for information exchange during mouth actions. In the literature, moans are infrequently noted (dos Santos et al., 1990), and they have been found in advance of interactions with humans or trainers (van der Woude, 2009). Accordingly, the moans documented during mouth actions could have been a result of the presence of the videographer in the water or emitted from dolphins engaging in other behaviors.

Concluding Remarks

Vocalizations during mouth actions were examined to accompany preliminary descriptions of mouth actions. Behaviors were characterized by a variety of vocalizations that differed in production across behavior type and aggressive context. For certain vocalizations, sound production only differed across specific behaviors or contexts. Bottlenose dolphins have a repertoire of numerous vocalizations (Tyack & Clark, 2000), but vocalizations were more or less prevalent during distinct mouth actions, suggesting a significance of sound during mouth actions. The combined use of both burst-pulse and tonal vocalizations across mouth actions may suggest that these sound classes have a concurrent function.

The results of this study provide new insight into information exchange during mouth actions. Replication should allow for sound localization to ensure that all vocalizations analyzed are produced from dolphins engaged in mouth actions to confirm these results. It may then be possible to determine the potential role of sex, age, or social ranking during mouth actions. Replications studies using more advanced hydrophone systems will also confirm or refute characteristics of mouth actions in silence, which are limited by the sample rate of the camera. Similar analyses using a longitudinal dataset will eliminate assumption violations during statistical analyses and provide for a robust evaluation across social context, life stage, and seasonality. To expand upon total vocalization count analyses and the influence of social context to identify possible signal-response exchanges, future work should analyze sounds directly preceding and following each mouth action.

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