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Whistle Acoustic Parameters in Atlantic Spotted Dolphins (*Stenella frontalis*) and Bottlenose Dolphins (*Tursiops truncatus*) in Two Locations in The Bahamas and Comparisons with Other Populations

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Abstract

Population-level differences in acoustic parameters of delphinid whistles may play a key role in dolphin communication and social interactions by aiding in individual differentiation or identification and may convey other additional information. Concurrent acoustic and video recordings were collected from sympatric species of Atlantic spotted dolphins (*Stenella frontalis*) and Atlantic bottlenose dolphins (*Tursiops truncatus*) in two locations in The Bahamas, and the acoustic parameters of their whistles were described. The acoustic whistle parameters of these two sympatric species in Bimini, The Bahamas, were also compared. The mean acoustic parameters of spotted dolphin whistles in the Bimini community were higher in frequency than those of bottlenose dolphins, but bottlenose dolphins produced whistles that had larger delta and higher maximum frequencies than those of spotted dolphins. Spotted dolphins displayed greater use of whistles with broad-band, non-tonal properties. As with other odontocete species examined so far, the two whistle parameters with the highest intraspecific variability in these species were duration and number of inflection points, which may aid in individual differentiation or identification. Interspecific social, sociosexual, and aggressive encounters have been observed between spotted and bottlenose dolphins in The Bahamas, and differences in acoustic parameters between these two sympatric species may enable them to differentiate between conspecifics and non-conspecifics. Comparisons between whistle acoustic parameters in the Bimini dolphin communities and those reported for other spotted and bottlenose dolphin populations are also discussed.

Key Words: Atlantic spotted dolphin, *Stenella frontalis*, bottlenose dolphin, *Tursiops truncatus*, acoustic parameters, whistle

Introduction

Dolphins are highly complex social mammals that use a rich variety of whistles and other acoustic signals during social interactions. Descriptions of the whistle acoustic parameters produced by a population of dolphins provides valuable baseline data that can allow for comparisons of whistle characteristics among and across groups, populations, species, behavioral states, and changing acoustic and social environments.

Several studies have described the acoustic parameters of whistles used by free-ranging Atlantic spotted dolphins (*Stenella frontalis*) (Lammers et al., 2003; Baron et al., 2008; Azevedo et al., 2010; Papale et al., 2015), bottlenose dolphins (*Tursiops* spp.) (e.g., Boisseau, 2005; Azevedo et al., 2007; Hawkins, 2010), and several other delphinid species (e.g., Corkeron & Van Parijs, 2001; Bazúa-Durán & Au, 2004; Azevedo & Van Sluys, 2005; Andrade et al., 2015; Barrios-Garrido et al., 2016; Lima et al., 2016). Comparisons of acoustic characteristics across species revealed several patterns. One pattern was that similarities and differences in whistle acoustic parameters among species were due in part to phylogenetic relationships and body size (Steiner, 1981; Ding et al., 1995a; Rendell et al., 1999; May-Collado et al., 2007). Another pattern was that the bottlenose dolphin tended to have parameters that were distinct from other species (Steiner, 1981; Ding et al., 1995a; Rendell et al., 1999; Oswald et al., 2003, 2007). The bottlenose dolphin has a distribution that often overlaps with other species (Steiner, 1981), and it is not uncommon to find bottlenose dolphins in mixed-species schools (Oswald et al., 2008). If bottlenose dolphins use whistles for intraspecific communication, it would be beneficial to use characteristic whistles that are easily distinguished from non-conspecific whistles (Steiner, 1981). Lastly, studies reporting on the whistle parameters of 13 different Delphinidae species consistently found that the two whistle parameters with the highest intraspecific variability were duration and number of inflection points (Steiner, 1981; Ding et al., 1995a, 1995b; Rendell et al., 1999; Oswald et al., 2003; Bazuá-Durán & Au, 2004; Morisaka et al., 2005; May-Collado & Wartzok, 2008). These two parameters may play an important role in dolphin communication by aiding in individual differentiation or identification (Ding et al., 1995a; Rendell et al., 1999; May-Collado & Wartzok, 2008) as well as in the conveyance of other additional information (Ding et al., 1995a, 1995b) such as emotional state (Rendell et al., 1999; Morisaka et al., 2005; May-Collado & Wartzok, 2008).

Although the spotted and bottlenose dolphins residing off Bimini, The Bahamas, have been the subjects of long-term field studies (Melillo et al., 2009; Dudzinski et al., 2012; Melillo-Sweeting et al., 2015), no study has reported on or compared the acoustic parameters of whistles used by these two species. Three studies reported on a subset of whistle acoustic parameters in an allopatric White Sand Ridge (WSR), The Bahamas, spotted dolphin community: (1) Lammers et al. (2003) provided data on a subset of whistle acoustic parameters (minimum and maximum frequency), (2) Ding et al. (1995a) reported on whistles recorded with a hydrophone with a flat frequency response of ~15 kHz, and (3) Bebus & Herzing (2015) provided data on acoustic parameters of signature whistles.

The spotted and bottlenose dolphins in the Bahamas live in fission-fusion societies similar to those of other populations of bottlenose dolphins described by Wells et al. (1987) and Connor et al. (2000) in which individuals associate in groups that frequently change in size and composition. In addition, these two species residing in The Bahamas have complex social, sociosexual, and agonistic interspecies interactions (Herzing & Johnson, 1997; Herzing et al., 2003; Melillo et al., 2009). Long-term studies reported ~13% of Bimini encounters (Melillo et al., 2009) and ~15% of WSR encounters (Herzing & Johnson, 1997) were mixed-species encounters.

The current study has four objectives: (1) it describes and compares seven whistle parameters in two sympatric species, Atlantic spotted dolphins and Atlantic bottlenose dolphins (*Tursiops truncatus*), endemic to the waters around the Bimini islands of The Bahamas; (2) it describes the acoustic whistle parameters of a community of Atlantic spotted dolphins in WSR, The Bahamas—this analysis includes a larger set of whistles (not differentiating between signature and non-signature whistles) than previously reported, adding to the extant data on WSR spotted dolphin whistles; (3) it compares whistle acoustic parameters between the two allopatric communities of Atlantic spotted dolphins in Bimini and WSR; and (4) this study compares the whistle acoustic parameters of Atlantic spotted and bottlenose dolphin communities in The Bahamas to those published for the same species in other regions of the world.

Methods

Study Communities and Field Sites

Four communities of wild dolphins were part of the study: two sympatric communities of Atlantic spotted dolphins and Atlantic bottlenose dolphins inhabiting the waters off the Bimini Islands, and two sympatric communities of Atlantic spotted dolphins and Atlantic bottlenose dolphins inhabiting the waters of WSR. All four dolphin communities were coastal ecotypes. WSR is a shallow sandbar ~64.5 km north of Grand Bahama Island and ~145 km from the Bimini Islands. The visibility and depth were recorded for each encounter; the water depth at WSR was 5 to 16 m; and at Bimini, it was was 3.5 to 12 m. Underwater visibility at both sites ranged from 6 to 30+ m, depending on the weather.

In Bimini, the Atlantic spotted dolphin community was estimated to be approximately 120 animals, and the Atlantic bottlenose dolphin community was estimated to be more than 70 individuals (K. Melillo-Sweeting, unpub. data, 2006-2011). In WSR, the Atlantic spotted dolphin community was estimated to be approximately 220 individuals, and the resident Atlantic bottlenose dolphin community was estimated to be at least 200 individuals (Herzing, 2015). Many of the animals at the two sites have become acclimated to boats and the presence of humans in the water through commercial swim-with-dolphin programs, ecotourism expeditions, and long-term behavioral and population field studies (Dudzinski, 1998; Kaplan & Connor, 2007; Melillo et al., 2009; Dudzinski et al., 2012; Herzing, 2015), so the four communities offered the opportunity to collect underwater recordings of whistles from close proximity to individuals and social groups during interactions.

Although both dolphin species have been studied for over 14 y in Bimini (Melillo et al., 2009) and over 30 y in WSR (Kaplan & Connor, 2007; Herzing, 2015), Atlantic bottlenose dolphins at both sites tend to spend less time in the vicinity of human swimmers and boats. In contrast, Atlantic spotted dolphins are encountered more frequently and for longer periods of time than Atlantic bottlenose dolphins; thus, more data have been collected on Atlantic spotted dolphins.

Data Collection

In Bimini, data were collected over 10 wks during the summers of 2009 through 2013. The field site off Bimini was accessed using either a 19.8-m live-aboard sailboat or a 12.8-m Hatteras motorboat. Boat searches along the Bimini banks were undertaken in the Hatteras 5 d/wk for 5 to 6 h/d, and 3 to 5 d/wk for 10 h/d from the sailboat. In WSR, data were collected over a total of 3 wks during the summers of 2009 through 2011. The WSR field site was accessed using either a 19.8-m live-aboard sailboat or a 25.9-m research yacht. These vessels were anchored or traveling on site for 1-wk periods. Eleven hours of observation effort were expended each day at the WSR site. At both sites, when dolphins were observed in the vicinity of the moving vessel, vessel speed was reduced and engines were put in neutral to allow one of the authors/researchers (JDK) and student research assistant(s) to enter the water to record behavior. When using an anchored vessel as a research platform, a researcher and student research assistant(s) entered the water when dolphins were observed approaching the vessel. If the dolphins remained in the vicinity, the researcher and assistant(s) began collecting data.

Concurrent video and acoustic recordings were captured with an HD/Mini-DV Canon HV30 video camera encased in a custom-designed and built underwater housing (The Sexton Company LLC, Salem, Oregon, USA) with SQ26 hydrophone input (Cetacean Research Technology, Seattle, Washington, USA) and either an M-Audio Micro Track II (M-Audio, Cumberland, Rhode Island, USA) or a TASCAM DR-05 (TEAC America, Inc. Montebello, California, USA) recording system. During some trips, additional acoustic recordings were collected with a second SQ26 hydrophone and M-Audio Micro Track II recording system by a second researcher (DR) onboard the research vessel. This second hydrophone was suspended over the vessel side to a depth of ~1.8 m. The SQ26 hydrophone had a recording bandwidth of 0.02 to 50 kHz, with a flat frequency response from 50 Hz to 32 kHz (± 3 dB) and a sensitivity of -169 dB re 1 V/µPa. Recordings were sampled at a rate of 96 kHz, providing a Nyquist frequency for all recordings of 48 kHz. Research assistants recorded supplemental video and took photographs of the dolphins that were used to identify and age individual dolphins to determine group composition.

Encounters were defined as (1) in-water observations lasting at least 1 min during which time at least one dolphin was within visual range of the researcher or (2) when data were collected from on-board the vessel if dolphins were visible from the surface and remained within 30 m of the boat for at least 1 min. If more than one encounter occurred on the same day, the encounters were considered distinct if at least 1 h lapsed between sightings of dolphin groups (including both surface and underwater sightings) or if all or most of the dolphins present in the new encounter were not present in the previous encounter. IDs of dolphins present in each encounter were later confirmed by review of video footage to determine whether a new encounter was comprised of different dolphins than the previous encounter. For each encounter, start and end time, species, group size, and group composition were recorded. Changes in group size and composition were also noted. Dolphins were considered to be in the same group if they were within 30 m of any animal in the group.

Data Analysis of Acoustic Parameters and Whistle Contours

Raven Pro 1.5™ acoustic analysis software (Cornell Laboratory of Ornithology, Cornell, New York, USA) was used to measure acoustic parameters of whistles and to create spectrograms that could be visually categorized with a fast Fourier transform (FFT) size of 1,024 points, an overlap of 50%, and using an 890 sample Hann window. Whistles were included in the analysis if they had a good signal-to-noise ratio in which the spectral contours were clearly visible and if the start, end, minimum, and maximum frequencies were clearly distinguishable and measurable in a spectrogram. If whistles overlapped, they were included in the analysis only if no more than two whistles overlapped and each of the two whistles was clearly distinct. Whistles from mixed-species groups were excluded from the analysis.

Seven acoustic whistle parameters were measured: minimum frequency, maximum frequency, start frequency, end frequency, duration, delta frequency (difference between minimum and maximum frequency in a whistle contour), and number of inflection points (Figure 1). These seven parameters were chosen to be consistent with previous studies of spotted dolphins (Ding et al., 1995a; Baron et al., 2008; Azevedo et al., 2010), bottlenose dolphins (e.g. Morisaka et al., 2005; May-Collado & Wartzok, 2008; Hawkins, 2010), and with studies comparing whistle parameters among several delphinid species or populations (e.g., Rendell et al., 1999; Oswald et al., 2003; Bazúa-Durán & Au, 2004; Baron et al., 2008; Papale et al.,

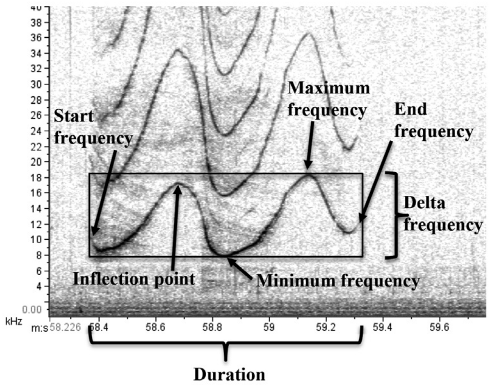

Figure 1. Acoustic parameter measurements used to examine and compare whistles produced by Atlantic spotted dolphins (*Stenella frontalis*) in Bimini and WSR and by Atlantic bottlenose dolphins (*Tursiops truncatus*) in Bimini

2015; Lima et al., 2016). An *inflection point* was defined as a point in the whistle contour where the contour changed from ascending to descending or vice versa (Azevedo et al., 2010; Hawkins, 2010). An inflection point was operationally defined in this study as a change in ascending or descending frequency > 1,000 Hz. It is possible, however, that inflection points with smaller changes in frequency may contain information relevant to dolphins. Measurements were made on the fundamental frequency of whistle contours. Multi-looped whistles, whether continuous or with breaks of 0.1 s or less, were considered one whistle for the purposes of measuring parameters.

Dolphins frequently produce repetitions of the same or similar whistles in bouts (Janik et al., 2013). In an attempt to control for overrepresentation of the same whistle type from the same individual in this current study, when a sequence of the same or similar whistles were repeated in rapid succession in which the inter-whistle interval was less than the duration of the individual whistles within the sequence, it was assumed that the whistles were likely produced by the same dolphin. In these cases, only one of the whistles in the sequence was included in the measurement of acoustic parameters. The whistle used for analysis from these sequences was chosen as follows: for the first sequence recorded in an encounter, the first whistle in that sequence was used; for the next sequence, the last whistle of that sequence was used; for the third sequence, one of the middle whistles in the sequence was used; and for the fourth sequence, a whistle in a different middle position was used. In the rare event that five or more sequences of the same whistle contour occurred in the same encounter, this order of selection was repeated.

Some whistles had broad-band, pulse-like components during parts of the whistle (Figure 2). This has been previously reported as a whistle that is less pure-tone and more "raspy" or coarse in quality (Lammers et al., 2003) with a "blurring" of the narrow-band contour on a spectrogram (Dudzinski, 1996; Papale et al., 2016). Whistles were categorized as either containing or not containing broad-band components from visual and aural review of whistle spectrograms by one of the authors (JDK). The proportion of whistles with broad-band components were described for each community of dolphins.

Statistical Analysis

ANOVAs were run to determine whether the seven measured acoustic parameters of whistles differed (1) between sympatric species of spotted dolphins and bottlenose dolphins (between-species comparison) and (2) between allopatric communities of spotted dolphins (within-species comparison). A multivariate discriminant function analysis was performed to ascertain how well these parameters could predict whether whistles were produced by spotted or bottlenose dolphins. Predictor variables were number of inflection points, duration, and start, end, minimum, maximum, and delta frequencies. Because the bottlenose dolphin data were moderately positively skewed, all whistle parameters were first square root transformed to normalize the data before performing the ANOVAs and discriminant function analysis when comparing species. Square root transformations also had the

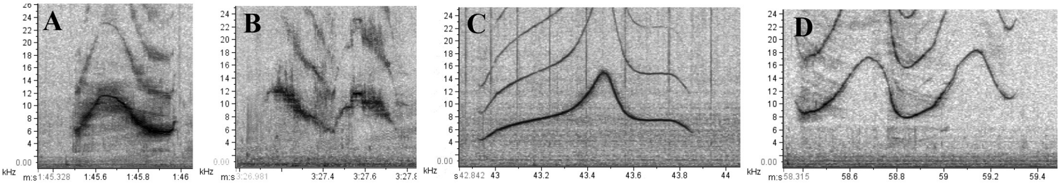

Figure 2. A & B are examples of "raspy" whistles; and C & D are examples of tonal, non-raspy whistles.

benefit of reducing the effect of outliers. When assumption of homogeneity of variance was violated, the Welch F-ratio was reported. Statistical analyses was performed using *SPSS*, Version 24.

Results

Survey Efforts and Acoustic Recordings

Bimini Spotted and Bottlenose Dolphins—A total of 1,269 whistles were analyzed from 693 min of recordings of Atlantic spotted dolphins. These recordings were collected over 24 d and across 40 different encounters during 2009 through 2012. Group sizes ranged from one to more than 30 dolphins (M = 6.70, SD = 5.70) and were comprised of a mixture of juveniles, adults, and calves. In 2013, more than 50 dolphins were reported to move from WSR to Bimini in what was described as a "major shift in distribution" (Herzing et al., 2015). Because it was not possible to individually identify all dolphins in all encounters, we were not always able to determine if a spotted dolphin encounter in 2013 in Bimini included both WSR and Bimini spotted dolphins. Therefore, all 2013 spotted dolphin recordings were excluded from the analysis to avoid confounds.

A total of 198 bottlenose dolphin whistles were analyzed from 175 min of recording. These recordings were collected over six encounters recorded on six separate days from 2010 through 2013. Group size ranged from three to 14 dolphins (M = 4.94, SD = 2.48).

White Sand Ridge Spotted and Bottlenose Dolphins—A total of 139 WSR spotted dolphin whistles were analyzed from 106 min of recordings. These recordings were collected over 7 d across 15 different encounters in 2010 and 2011. Group sizes ranged from one to nine dolphins (M = 4.31, SD = 2.42) and were comprised of a mixture of juveniles, adults, and calves. There were three encounters with WSR bottlenose dolphins across 2 d in 2011, but no whistles met the criteria for a good signal-to-noise ratio, therefore no WSR bottlenose dolphin whistles were included in the analysis. Search efforts in 2009 in WSR were unsuccessful; thus, there were no WSR data for 2009 for either species.

Comparison of Acoustic Parameters Between Sympatric Species in Bimini

Bimini spotted and bottlenose dolphin whistle acoustic parameters are reported in Table 1. The mean frequencies of five whistle parameters (start, end, minimum, and maximum frequencies, and number of inflection points) of spotted dolphins, the smaller of the two species, were significantly higher than those of bottlenose dolphins (Table 2). In both species, the acoustic parameters that had the highest variability (measured as coefficient of variation) were duration and number of inflection points.

Although spotted dolphin whistles had higher mean maximum frequencies than did bottlenose dolphin whistles, some of the whistles produced by bottlenose dolphins reached much higher maximum frequencies than those produced by spotted dolphins. The highest maximum frequency recorded for bottlenose dolphins was 41.55 kHz as compared with the highest maximum frequency of 29.43 kHz recorded for spotted dolphins. Additionally, bottlenose dolphins produced a greater percentage of whistles with frequencies extending above 25 kHz than spotted dolphins produced. In fact, 14.1% (n = 28) of the whistles produced by bottlenose dolphins (N = 198) had frequencies that extended above 25 kHz, and 4.5% (n = 9) reached frequencies above 30 kHz. In contrast, only 2.4% (n = 31) of spotted dolphin whistles analyzed (N = 1,269) extended above 25 kHz, and none of the whistles recorded extended above 30 kHz (Figure 3).

Several whistles were excluded from analysis due to poor signal-to-noise ratio. Given increased attenuation of higher frequencies, this criterion may have excluded a disproportionate number of whistles with high-frequency components from the initial analysis. Because the maximum frequencies in bottlenose dolphin whistles in the first analysis were higher than those reported in other studies, a second analysis of bottlenose dolphin whistles was conducted with a larger second set of data that included whistles with a moderate signal-to-noise ratio in which at least the majority of the whistle contour was clearly visible. This second analysis revealed similar differences between species as found in the first analysis: 14.1% (n = 44) of all bottlenose dolphin whistles analyzed (N = 311), including both whistles with good signal-to-noise ratio and moderate signal-to-noise ratio had high frequencies of ≥ 25 kHz, and 5.1% (n = 16) extended to frequencies > 30 kHz. When combining all spotted dolphin whistles with a good signal-to-noise ratio and a subset of additional whistles with a moderate signal-to-noise ratio (N = 1,595), only 2.0% (n = 32) reached frequencies > 25 kHz, and no whistles were > 30 kHz.

A discriminant function analysis tested whether the acoustic parameters measured could predict which whistles were produced by spotted or bottlenose dolphins. The analysis had a Wilks Lambda equal to 0.854 ($p < 0.001$) and a canonical correlation of 0.382, and explained 15.05% of the variation between species. Closer analysis of the structure matrix revealed that minimum frequency (0.781) was the strongest predictor, followed by start frequency (0.540) and end frequency

Table 1. Whistle acoustic parameters examined for the Atlantic bottlenose dolphin (*Tursiops truncatus*) community in Bimini, and the Atlantic spotted dolphin (*Stenella frontalis*) communities in Bimini and WSR. Frequencies are in kHz and time in seconds (s). Sample size for frequency and duration measurements: Bimini bottlenose dolphins, $N = 198$; Bimini spotted dolphins, $N = 1{,}269$; and WSR spotted dolphins, $N = 139$. Sample size for inflections: Bimini bottlenose dolphins, $N = 193$, Bimini spotted dolphins, $N = 1{,}209$; and WSR spotted dolphins, $N = 126$.

Species, field site		Start frequency	End frequency	Min frequency	Max frequency	Delta frequency	Duration	Inflections
Bottlenose dolphins, Bimini	M ± SD	6.75 ± 3.72	8.47 ± 5.47	4.98 ± 1.97	14.92 ± 7.76	9.94 ± 7.25	0.68 ± 0.53	2.46 ± 3.82
	Range	2.19-25.67	1.10-41.55	0.80-20.85	2.86-41.55	0.63-37.66	0.06-4.03	0-25
	CV (%)	55.11	64.58	39.56	52.01	72.94	77.94	155.28
Spotted dolphins, Bimini	M ± SD	8.56 ± 2.90	9.89 ± 4.10	6.95 ± 2.19	15.86 ± 4.60	8.91 ± 4.44	0.74 ± 0.47	2.61 ± 2.40
	Range	1.42-19.05	0.86-25.61	0.86-16.06	1.88-29.43	0.41-22.71	0.02-2.23	0-19
	CV (%)	33.88	41.46	31.51	29.00	49.83	63.51	92.31
Spotted dolphins, WSR	M ± SD	9.10 ± 2.66	9.10 ± 3.52	6.88 ± 1.80	14.38 ± 3.47	7.50 ± 3.68	0.59 ± 0.49	1.95 ± 2.46
	Range	3.88-16.89	2.36-22.07	2.36-14.43	7.04-22.81	1.32-16.21	0.03-2.08	0-13
	CV (%)	29.23	38.68	26.16	24.13	49.07	83.05	126.15

Table 2. Comparison of acoustic parameters between Atlantic spotted and bottlenose dolphins in Bimini

Factor	ANOVA	p	η^2
Start frequency	$F(1, 1465) = 78.70$	< 0.001	0.051
End frequency*	$F(1, 236.52) = 21.35$	< 0.001	0.020
Minimum frequency	$F(1, 1465) = 156.93$	< 0.001	0.097
Maximum frequency*	$F(1, 222.09) = 7.53$	0.007	0.010
Delta frequency*	$F(1, 228.41) = 0.52$	0.47	0.001
Duration	$F(1, 1465) = 2.49$	0.12	0.002
Inflection points	$F(1, 1400) = 5.88$	0.02	0.004

*Because the assumption of homogeneity of variance was violated, the Welch F-ratio is reported here.

(0.360). Classification results showed that 85.9% of whistles were correctly classified as spotted or bottlenose dolphin whistles; however, spotted dolphin whistles were classified with much better accuracy (96.5%) than were bottlenose dolphin whistles (19.2%).

Visual and aural review of spectrograms indicated that some whistles had broad-band, pulse-like properties during parts of the whistle (Figure 2). Of the spotted dolphin whistles analyzed ($N = 1{,}269$), 23.6% ($n = 300$) had broad-band qualities, while only 3.0% ($n = 6$) of bottlenose dolphin whistles ($N = 198$) showed this broad-band feature.

Comparison of Acoustic Parameters Between Allopatric Communities of Spotted Dolphins in WSR and Bimini

A comparison of whistles between the WSR and Bimini communities of spotted dolphins (Table 1) indicated a significant difference in the acoustic parameters of these whistles. Whistles produced by the Bimini spotted dolphins had significantly lower start frequencies, higher maximum and end frequencies, and bigger delta frequencies than those of WSR spotted dolphins (Table 3). Bimini spotted dolphin whistles also had significantly longer durations and significantly more inflection points than did WSR spotted dolphin whistles (Table 3). As in the Bimini spotted and bottlenose dolphins, the acoustic parameters that had

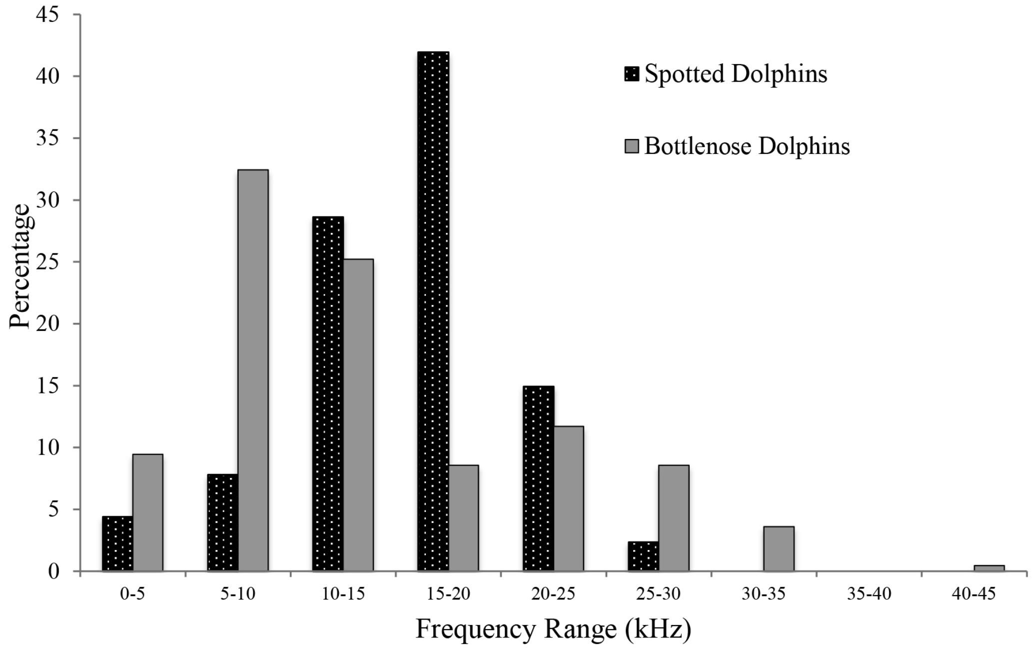

Figure 3. A comparison of whistle maximum frequencies produced by Bimini populations of Atlantic spotted and bottlenose dolphins. This shows the percentage of whistles that reach these maximum frequencies.

the highest variability (measured as coefficient of variation) for the WSR spotted dolphins were duration and number of inflection points (Table 1). Similarities were found when comparing the percentage of whistles that had broad-band qualities; 29.5% (*n* = 41) of the WSR spotted dolphin whistles (*N* = 139), and 23.6% (*n* = 300) of the Bimini spotted dolphin whistles (*N* = 1,269) had broad-band qualities.

Comparison of Bimini Bottlenose Dolphin Whistle Acoustics Parameters to Those Reported in Other Bottlenose Dolphin Populations

Acoustic parameters of Bimini bottlenose dolphin whistles were compared to those reported in eight studies for 17 other populations of bottlenose dolphins (Table 4). The mean start, end, and minimum frequencies of Bimini bottlenose dolphin whistles fell below the means for most other populations. Specifically, the mean start frequency of Bimini bottlenose dolphin whistles was lower than the mean start frequencies of whistles from bottlenose dolphins in 16 of 17 other reported populations, the mean end frequency was lower than that found in 14 of 17 other populations, and the mean minimum frequency was lower than those of all 17 other populations compared (Table 4). However, the mean maximum frequency in the Bimini dolphins was higher than that reported for 12 of 17 other populations. The whistles recorded from the Bimini bottlenose dolphins also contained higher frequencies than those reported in other populations. Only one study (May-Collado & Wartzok, 2008) reported whistles that extended to frequencies above 25 kHz; the highest reported frequencies recorded were 28.48 kHz in the Gandoca-Manzanillo, Costa Rica, population and 26.54 kHz in the Bocas del Toro, Panama, population. These frequencies were still lower than those found in the present study (up to 41.6 kHz).

Comparison of The Bahamas Spotted Dolphin Whistle Acoustics Parameters to Those Reported in Other Spotted Dolphin Populations

Comparisons between The Bahamas spotted dolphin communities and other spotted dolphin populations were less extensive as there were very few reports, excepting Azevedo et al. (2010) and Papale et al. (2015), on whistle acoustic parameters in populations of spotted dolphins in non-Bahamian waters (Table 5). Two other studies were included in this comparison, although these studies pooled samples from spotted dolphins all along the U.S. Atlantic coast rather than sampling from specific populations (Steiner, 1981; Baron et al., 2008). Comparisons revealed a

Table 3. Comparison of acoustic communities between allopatric populations of Atlantic spotted dolphins in The Bahamas

Factor	ANOVA	p	η^2
Start frequency	$F(1, 1{,}406) = 5.35$	0.02	0.004
End frequency*	$F(1, 182.22) = 4.76$	0.03	0.003
Minimum frequency*	$F(1, 189.84) = 0.001$	0.98	< 0.000
Maximum frequency*	$F(1, 198.77) = 15.47$	< 0.001	0.007
Delta frequency	$F(1, 1406) = 9.94$	0.002	0.007
Duration*	$F(1, 161.81) = 14.24$	< 0.001	0.012
Inflection points*	$F(1, 146.96) = 14.96$	< 0.001	0.013

*Because the assumption of homogeneity of variance was violated, the Welch F-ratio is reported here.

few differences in whistle acoustic parameters between populations and regions. The mean end frequencies of The Bahamas spotted dolphin whistles (both the Bimini and the WSR communities) were lower than those reported in other populations and the samples pooled off the Atlantic coast (Table 5). Minimum frequencies were lower than those reported in the Brazil and Canary archipelago populations and the samples pooled from the Western North Atlantic (Table 5).

Discussion

This study found differences in acoustic parameters of whistles recorded from sympatric communities of spotted and bottlenose dolphins. The mean acoustic parameters of spotted dolphins were higher in frequency than those of bottlenose dolphins, but bottlenose dolphins produced whistles that extended to higher frequencies than those of spotted dolphins. Spotted dolphins displayed far greater use of amplitude-modulated whistles as compared to bottlenose dolphins. The parameters of the whistles produced by the dolphin communities in Bimini, The Bahamas, differed from those of whistles produced by populations of the same species in other regions of the world.

Comparison of Acoustic Parameters Between Sympatric Species of Bottlenose Dolphins and Spotted Dolphins in Bimini

Finding differences in acoustic parameters between bottlenose dolphins and a sympatric dolphin species is not surprising. *Tursiops* spp. in particular are found in mixed-species groups in many populations throughout the world (Connor et al., 2000; Oswald et al., 2008) and often have whistle acoustic parameters that are distinct from species with which they overlap. Steiner (1981) and Ding et al. (1995a) suggested it may be important for sympatric species to have whistles that are easily distinguished from whistles of non-conspecifics. Schultz & Corkeron (1994) compared sympatric species of bottlenose and Pacific humpback dolphins (*Sousa chinensis*) and found that whistles of bottlenose dolphins had significantly longer durations and significantly lower start, end, minimum, and maximum frequencies. May-Collado (2010) reported that bottlenose dolphins had significantly lower minimum, maximum, start, and end frequencies, larger delta frequencies, longer durations, and more inflection points than the smaller sympatric species of Guiana dolphins (*Sotalia guianensis*). Frankel et al. (2014) compared bottlenose and Atlantic spotted dolphins inhabiting the Gulf of Mexico coast waters off Florida and found that median, minimum, and maximum frequencies of bottlenose dolphin whistles were significantly lower, and median durations of the bottlenose dolphins' whistles were significantly shorter. Bimini bottlenose dolphins showed a similar pattern; the whistles recorded from the Bimini bottlenose dolphins had lower mean frequency parameters than the Bimini spotted dolphins with which they intermingled in mixed-species groups. Differences in acoustic parameters and other whistle features between these two sympatric species may enable dolphins to acoustically differentiate between conspecifics and non-conspecifics.

It is worth noting, however, that other studies have found that the whistle acoustic parameters of bottlenose dolphins were distinctive from whistle parameters not just of sympatric species but from many other species as well. Oswald et al. (2003, 2007) compared the whistle characteristics of nine delphinid species and found that bottlenose dolphins were one of the species with the most distinctive whistles with longer durations, more inflection points, lower minimum frequencies, and higher maximum frequencies. Ding et al. (1995a) compared the whistles of six Delphinidae species and found that the whistles of *T. truncatus* were the most

Table 4. Reported acoustic parameters for bottlenose dolphin populations. Frequencies (Frq) are in kHz. "Rec frq" refers to the upper frequency limit for the recording system used for the study.

Location	*N*	Start frq (M ± SD)	Start frq range	End frq (M ± SD)	End frq range	Min frq (M ± SD)	Min frq range	Max frq (M ± SD)	Max frq range	Rec frq
Bimini, Bahamas[1]	198	6.75 ± 3.72	2.19-25.67	8.47 ± 5.47	1.10-41.55	4.98 ± 1.97	0.80-20.85	14.92 ± 7.76	2.86-41.55	48
Azores archipelago[2]	352	10.09 ± 4.08	--	8.66 ± 4.09	--	6.36 ± 2.00	--	15.26 ± 3.90	--	24
Golfo San José, Argentina[3]	110	9.24 ± 2.74	1.17-16.09	6.63 ± 2.29	3.05-15.94	5.91 ± 1.50	1.17-10.08	13.65 ± 1.54	9.38-17.11	15
Bay of Biscay[2]	94	9.41 ± 3.59	--	11.31 ± 4.56	--	7.19 ± 1.61	-	16.96 ± 2.42	---	24
Patos Lagn Estuary, S. Brazil[4]	788	8.28 ± 3.11	3.1–20.8	8.37 ± 3.70	2.8–22.3	5.96 ± 2.15	1.2–17.2	12.21 ± 3.20	3.6–22.3	24
Canary archipelago[2]	94	11.13 ± 4.42	--	11.91 ± 4.63	--	7.20 ± 1.83	--	16.27 ± 5.01	--	96
Gand.-Manzanillo, Costa Rica[5]	77	8.43 ± 3.66	1.61-17.21	13.15 ± 5.57	4.13-27.14	5.68 ± 2.24	1.61-10.85	17.61 ± 4.93	8.77-28.48	140
Isla del Coco, Costa Rica[6]	88	12.82 ± 2.82	--	9.39 ± 2.55	--	8.51 ± 1.81	--	13.98 ± 2.63	--	14
Isla del Coco, Costa Rica[6]	26	10.18 ± 4.82	--	8.91 ± 3.72	--	7.51 ± 3.02	--	12.41 ± 4.07	--	14
Taiji, Japan[3]	215	10.33 ± 2.41	3.75-15.23	8.87 ± 2.21	3.67-15.55	7.37 ± 1.54	3.20-10.70	11.62 ± 2.00	4.53-15.55	15
Mediterranean Sea[2]	207	8.32 ± 3.58	--	9.34 ± 4.51	--	6.13 ± 2.08	--	14.19 ± 3.67	--	30
Gulf of California, Mexico[3]	110	12.10 ± 2.89	5.78-17.27	9.19 ± 3.44	3.44-17.42	6.91 ± 2.11	3.17-1.56	13.68 ± 1.72	7.34-17.42	15
Mississippi Sound, Gulf of Mexico[7]	430	7.48 ± 2.52	1.45-15.78	9.83 ± 3.48	2.80-20.91	5.94 ± 1.63	1.02-12.42	12.00 ± 3.28	3.15-22.91	24
Walvis Bay, Namibia[8]	693	8.64 ± 3.56	1.76–21.52	7.21 ± 3.10	1.58–21.09	5.72 ± 1.99	1.58–16.30	12.88 ± 2.87	6.05–23.24	30
Bocas del Toro, Panama[5]	74	9.80 ± 3.7	3.38-23.0	9.06 ± 4.2	1.64-22.2	5.61 ± 1.80	1.6-12.68	15.8 ± 3.6	1.7-26.54	140
Sado Estuary, Portugal[9]	735	5.8 ± 1.8	2.0-15.3	12.1 ± 4.4	2.2-21.0	5.4 ± 1.2	2.0-9.0	15.0 ± 2.7	7.9-21.0	20-22
Galveston, Texas[3]	811	7.95 ± 2.88	2.50-20.66	9.02 ± 3.96	2.00-21.61	5.98 ± 2.30	1.86-18.92	11.95 ± 3.08	3.91-21.61	20-25
Corpus Christi, Texas[3]	617	7.43 ± 2.44	2.89-6.75	8.71 ± 4.04	2.34-20.66	5.88 ± 2.65	2.11-14.53	11.43 ± 3.80	3.44-20.75	20-25
South Padre Island, Texas[3]	549	8.70 ± 2.95	3.13-18.75	6.40 ± 2.44	2.59-14.92	5.37 ± 1.12	2.58-9.45	10.33 ± 2.80	4.53-19.14	20-25

[1]Kaplan & Reiss, this study; [2]Papale et al., 2014; [3]Ding et al., 1995b (recordings were 15 kHz or higher); [4]Azevedo et al., 2007; [5]May-Collado & Wartzok, 2008; [6]Acevedo-Guitierrez & Stienessen, 2004 (recorded from two behavioral states: (1) feeding and (2) non-feeding); [7]Hernandez et al., 2010; [8]Gridley et al., 2015; [9]dos Santos et al., 2005

dissimilar. Steiner (1981) compared whistles from five different dolphin species, and like Ding et al. (1995a), found that *T. truncatus* had whistles that were very distinct from the other species compared.

Another distinguishing feature between species was the proportion of whistles with burst-pulse properties. This characteristic seemed to be more common in spotted dolphins than bottlenose dolphins; burst-pulse components were present in 23.6% of whistles analyzed from Bimini spotted dolphins and in only 3.0% of whistles analyzed from bottlenose dolphins. The pulse-like property that characterizes a portion of spotted dolphin whistles has been noted in other studies as well

Table 5. Reported acoustic parameters for spotted dolphin populations. Frequencies (Frq) are in kHz. "Rec frq" refers to the upper frequency limit for the recording system used for the study.

Location	*N*	Start frq (M ± SD)	Start frq range	End frq (M ± SD)	End frq range	Min frq (M ± SD)	Min frq range	Max frq (M ± SD)	Max frq range	Rec frq
Bimini, Bahamas[1]	1,269	8.56 ± 2.90	1.42-19.05	9.89 ± 4.10	0.86-25.61	6.95 ± 2.19	0.86-16.06	15.86 ± 4.60	1.88-29.43	48
WSR, Bahamas[1]	139	9.10 ± 2.66	3.88-16.89	9.10 ± 3.52	2.36-22.07	6.88 ± 1.80	2.36-14.43	14.38 ± 3.47	7.04-22.81	48
Ilha Grande Bay, SE Brazil[2]	1,092	8.85 ± 3.21	1.15-21.88	12.76 ± 3.80	1.56-22.35	8.04 ± 2.51	1.15-20.09	13.58 ± 3.64	3.00-23.44	24
Canary archipelago[3]	84	9.44 ± 2.03	6.17-19.88	14.62 ± 2.46	7.87-22.76	7.40 ± 1.04	5.24-12.55	17.93 ± 1.85	10.62-23.13	96
North Atlantic/ East Coast[4]	567	8.78 ± 3.39	--	11.86 ± 3.91	--	6.53 ± 2.16	--	13.30 ± 3.44	--	32
W. N. Atlantic: Cont. Shelf populations[5]	328	9.28 ± 0.36	--	12.26 ± 0.37	--	7.50 ± 0.21	--	14.17 ± 0.34	--	24
W. N. Atlantic: Off-shore populations[5]	1,377	9.08 ± 0.25	--	13.13 ± 0.35	--	7.51 ± 0.17	--	15.84 ± 0.32	--	24

[1]Kaplan & Reiss, this study; [2]Azevedo et al., 2010; [3]Papale et al., 2015; [4]Steiner, 1981 (Steiner reports these as *S. plagiodon*; coordinates suggest Florida and North Carolina); [5]Baron et al., 2008 (Baron reports SE, not SD)

(Lammers et al., 2003; Papale et al., 2016). Out of the 220 WSR spotted dolphin whistles analyzed by Lammers et al. (2003), approximately 41% had burst-pulse properties for at least part of the whistle, which the authors named "amplitude modulation" (p. 1631). This amplitude modulation in a signal degrades with distance, and Lammers et al. suggested that graded whistles may convey information about a behavioral, emotive, or referential condition to nearby individuals.

In accordance with previous findings that have related the frequency parameters of whistles to body size, the whistles of the larger of the two species in this study, the bottlenose dolphins, had lower mean start, end, minimum, and maximum frequencies than those of the smaller spotted dolphins. Studies have found that longer body lengths correlate with lower whistle frequencies (Ding et al., 1995a; Matthews et al., 1999; May-Collado et al., 2007). It should be noted that similarities and differences in whistle acoustic parameters among different species may also be due in part to phylogenetic relationships (Steiner, 1981; Ding et al., 1995a; Rendell et al., 1999); and when phylogenetic relationships are taken into account, this correlation between body size and frequency is not as strong as it would be if phylogenetic background was not considered (May-Collado et al., 2007). Specifically, May-Collado et al. (2007) found that when taking phylogenetic relationships into account, maximum frequency was not correlated with body length. Minimum frequency was still found to be correlated with body length, however, suggesting that this parameter may be constrained by body size.

In these sympatric species, minimum frequency was the strongest predictor differentiating spotted dolphin whistles from bottlenose dolphin whistles. This was the one parameter that was not significantly different between the Bimini and WSR spotted dolphin communities. Taken together, these findings suggest that minimum frequency parameters may be good predictors of species identity, which could help these sympatric dolphin species to differentiate between conspecifics and non-conspecifics when out of visual range.

Studies of whistle acoustic parameters have consistently found that duration and number of inflection points were the two whistle parameters that had the highest intraspecific variability (measured as coefficient of variation) across Delphinidae species (Steiner, 1981; Ding et al., 1995a, 1995b; Rendell et al., 1999; Oswald et al., 2003; Bazúa-Durán & Au, 2004; Morisaka et al., 2005; May-Collado & Wartzok, 2008), which may mean these parameters play an important role in dolphin communication and may aid in individual differentiation or identification (Steiner, 1981; Ding et al., 1995a, 1995b; Rendell et al., 1999; Bazúa-Durán & Au, 2004; Morisaka et al., 2005; May-Collado & Wartzok, 2008; Díaz López, 2011) and the conveyance of other additional information (Ding et al., 1995a, 1995b). Consistent with these studies, the parameters with the greatest coefficients of variation in both spotted and bottlenose dolphins in Bimini were number of inflection points and duration.

Comparison of Acoustic Parameters Between Allopatric Communities of Spotted Dolphins in Bimini and WSR

There were significant differences in acoustic parameters of whistles between the two allopatric communities of spotted dolphins. The whistles from the Bimini community had lower start frequencies, higher maximum and end frequencies, larger delta frequencies, longer durations, and more inflection points than the WSR dolphin whistles. The difference in whistles may have been due in part to local ecological conditions, with factors such as habitat substrate, water depth, and boat traffic contributing to different acoustic landscapes. The Bimini community is found close to shore in an area with more boat traffic, while the WSR community study site is 64.3 km from land in an area with far less boat traffic (J. Daisy Kaplan, pers. obs.). Other studies have found that common dolphins (*Delphinus delphis*) (Ansmann et al., 2007), pilot whales (*Globicephala macrorhynchus* and *G. melas*) (Rendell et al., 1999), and bottlenose dolphins (Ding et al., 1995b; May-Collado & Wartzok, 2008) shifted acoustic parameters in relation to ambient noise. Studies have also found that some dolphins shifted frequencies with increased boat traffic—for example, bottlenose dolphins (La Manna et al., 2013; May-Collado & Quiñones-Lebrón, 2014*;* Heiler et al., 2016) and common dolphins (Papale et al., 2015). Atlantic spotted dolphins specifically were found to increase maximum and end frequencies with increased boat traffic (Papale et al., 2015).

Comparison of Bimini Bottlenose Dolphin Whistle Acoustic Parameters to Those Reported in Other Bottlenose Dolphin Populations

The start, end, and minimum frequency parameters of whistles reported herein for the Bimini bottlenose dolphin community fell below those reported for other *Tursiops* populations. However, the mean maximum frequency in the Bimini population was higher than that reported for 12 of 17 other populations. Additionally, the highest maximum frequencies recorded in the Bimini bottlenose dolphin community were higher than those reported in any other population: 5.1% of bottlenose dolphin whistles analyzed in this current study extended above 30 kHz, while the highest frequencies reported in other populations fell below 29 kHz. Notably, many studies used recording equipment and sampling rates that did not record frequencies above 30 kHz (Ding et al., 1995b; Acevedo-Gutiérrez & Stienessen, 2004; dos Santos et al., 2005; Azevedo et al., 2007; Hernandez et al., 2010; Papale et al., 2014; Gridley et al., 2015). Therefore, lower sampling rates and/or lower frequency responses of hydrophones in other studies may account for these population differences in reported maximum frequencies. Hiley et al. (2016) used a sampling rate of 96 kHz, as was used in the current study, when recording the whistles produced by bottlenose dolphins off the coast of Wales, and they reported signature whistles and non-signature whistles with fundamental frequency components above 30 kHz in the study population. Thus, the use of higher sampling rates in this current study may provide more accurate maximum frequency parameter measurements than many previous studies have provided. It is possible that even using a sample rate of 96 kHz (Nyquist of 48 kHz), some whistles at higher frequencies may not have been recorded. However, no whistles in this study were cut off at 48 kHz. It remains unclear whether the disparities found in maximum frequency across bottlenose dolphin populations reported are due to limits in sampling rate or are a true reflection of the maximum frequencies used by this species. The use of higher sampling rates in future studies may reveal that more populations are using higher frequency whistles. Although recording limitations may impact reported mean maximum frequencies, differences in this acoustic parameter between Bimini bottlenose dolphins and bottlenose dolphins in other populations may also be due to different acoustic landscapes, environmental conditions, social relationships, and/or behavior.

Comparison of The Bahamas Spotted Dolphin Whistle Acoustics Parameters to Those Reported in Other Spotted Dolphin Populations

Comparisons between The Bahamas spotted dolphin communities and other spotted dolphin populations were limited as there were very few reports on whistle acoustic parameters in populations of spotted dolphins in non-Bahamian waters. However, these limited comparisons showed that mean end and minimum frequencies of The Bahamas spotted dolphin whistles were lower than those reported in other spotted dolphin populations. Interestingly, the mean end and minimum frequencies of The Bahamas bottlenose dolphin whistles were also lower than those reported in other bottlenose dolphin populations.

Conclusions

This study described and quantified the acoustic parameters of whistles used by three communities of dolphins in The Bahamas: two Atlantic spotted dolphin communities in WSR and Bimini and one bottlenose dolphin community in Bimini. Consistent with previous comparative studies, the bottlenose dolphins, which are the larger of the two species, had lower mean frequency whistles than the smaller spotted dolphins. Also consistent with past findings, it was found that the acoustic parameters of bottlenose dolphin whistles, as compared with other sympatric delphinid species, tended to be distinct. The whistles of The Bahamas bottlenose dolphins had mean frequency parameters distinct from the sympatric community of spotted dolphins with which they interacted. In addition, spotted dolphins produced a higher proportion of whistles with burst-pulse qualities than did the bottlenose dolphins. The differences in whistle acoustic parameters from these sympatric communities of The Bahamas dolphins suggest that differences in acoustic parameters and other features of their whistles, such as the presence of burst-pulsed components concurrent with whistle production, may function to help individuals identify and distinguish members of their own group, a wider population of conspecifics, and other species.

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