A characterization of Guyana dolphin (*Sotalia guianensis*) whistles from Costa Rica: The importance of broadband recording systems

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Knowledge of the whistle structure in Guyana dolphins comes mostly from Brazilian populations where recordings have been made using limited bandwidth systems (18 and 24 kHz). In Brazil, Guyana dolphin whistle frequency span is 1.34–23.89 kHz, but authors have suggested that limits of their recording system may underestimate frequency span. Whistles of Guyana dolphins from Costa Rica were studied using a broadband recording system. How bandwidth limitations affect the understanding of whistle structure and species classification between sympatric dolphin species was evaluated. In addition, whistles were compared to Brazilian populations. Guyana dolphin whistle frequency span was 1.38 up to 48.40 kHz, greater than previously reported. Bandwidth limitations explained 89% of the whistle variation between studies, and increase in bandwidth improved the whistle classification of Guyana dolphins. Whistle duration and minimum frequency were the most important variables in dolphin species classification. Finally, after accounting for differences in recording systems, Costa Rican Guyana dolphins whistled with significantly higher frequency than Brazilian populations, providing evidence for a postulated increase in frequency from south to north. The study concludes that equipment with an upper frequency limit of at least 50 kHz (150 kHz for harmonics) is required to capture the entire whistle repertoire of the Guyana dolphin.
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I. INTRODUCTION

The Guyana dolphin (*Sotalia guianensis*) previously considered a marine form of the freshwater Tucuxi dolphin (*Sotalia fluviatilis*) (da Silva and Best, 1996) is today recognized as a separate species based on morphological (Monteiro-Filho *et al.*, 2002) and molecular evidence (Cunha *et al.*, 2005; Caballero *et al.*, 2007). The species occurs in bays, estuaries, river mouths, and shallow coastal waters along the western Atlantic Ocean from Southern Brazil to Northern Nicaragua, and possibly Honduras (da Silva and Best, 1996; Carr and Bonde, 2000; Edwards and Schnell, 2001; Flores, 2002).

Despite the relatively broad distribution of the species most of what is known about its acoustic behavior and biology is from populations along the Brazilian coast from which echolocation clicks, pulsed sounds (e.g., calls and gargles), and whistles have been described (e.g., Wiersma, 1982; Terry, 1983; Monteiro-Filho and Monteiro, 2001; Azevedo and Simão, 2002; Erber and Simão, 2004; Azevedo and Van Sluys, 2005; Rossi-Santos and Podos, 2006). Whistles are

the most studied sound type, and several whistle acoustic variables have been recently described from Brazilian populations (Monteiro-Filho and Monteiro, 2001; Azevedo and Simão, 2002; Erber and Simão, 2004; Azevedo and Van Sluys, 2005; Pivari and Rosso, 2005; Rossi-Santos and Podos, 2006). Monteiro-Filho and Monteiro (2001) first described Guyana dolphin whistles as low in frequency (up to 6 kHz) but a more extensive study revealed a much wider whistle frequency range (1.34–23.89 kHz) (Azevedo and Van Sluys, 2005). However, as noted by Azevedo and Van Sluys (2005), some of the recorded whistles looked "cut off" by the upper frequency limit of their recording systems, suggesting Guyana dolphins can emit high frequency whistles exceeding the 24 kHz recording limit. Several toothed whale species have been shown to emit whistles with high fundamental maximum frequencies, up to 24 kHz in spinner dolphins and Atlantic spotted dolphins (e.g., Lammers *et al.*, 1997, 2003; Oswald *et al.*, 2004), 29 and 41 kHz in bottlenose dolphins (Boisseau, 2005; May-Collado and Wartzok, 2008), 35 kHz in white-beaked dolphins (Rasmussen and Miller, 2002; Rasmussen *et al.*, 2006), 24 kHz striped and common dolphins (Oswald *et al.*, 2004), and 48.10 kHz in botos (May-Collado and Wartzok, 2007).

The importance of selecting recording systems with bandwidth appropriate for the study species is fundamental

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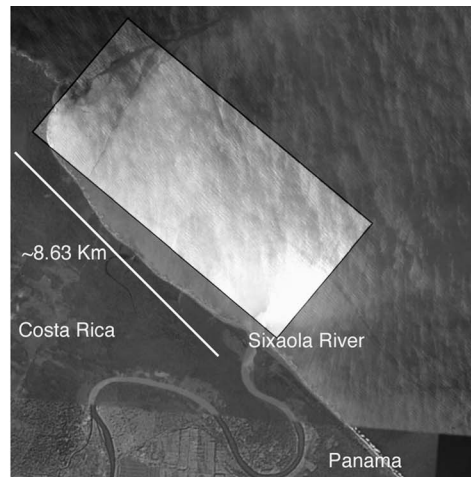b)Electronic mail: wartzok@fiu.edu

FIG. 1. Map showing the location of the Gandoca-Manzanillo Wildlife Refuge (9°59.972′ N, 82°60.530′ W) in Costa Rica and the surveyed area.

in understanding dolphin whistle structure and its geographical variation (Bazúa-Durán and Au, 2002; Au *et al.*, 1999), as well as for species classification (Oswald *et al.*, 2004). Acoustic methods have become an important tool for species identification in the field, but the success of such methods relies on the use of recording systems and analysis bandwidths proper for the species under study (Oswald *et al.*, 2004). Oswald *et al.* (2004) showed how an increase in recording system bandwidth improved the correct whistle classification for four sympatric dolphin species in the Eastern Tropical Pacific.

Although the understanding of Guyana dolphin whistle acoustic structure is growing, knowledge remains disproportionately concentrated on Brazilian populations and to a limited portion (below 24 kHz) of the frequency span of the species. Populations in other areas need to be studied to determine if there are latitudinal gradients in whistle parameters and recordings need to be made with equipment capable of recording over a greater bandwidth. The goal of this study is to (1) describe whistles of a small resident population of Guyana dolphins from Costa Rica (at its northern limit) using a broadband recording system, (2) evaluate the effect of the frequently used bandwidth recording systems (18 and 24 kHz) on whistle structure and whistle classification with respect to the sympatric bottlenose dolphin, and finally (3) compare whistle structure between Costa Rican and Brazilian populations to provide insights on whistle geographic variation after accounting for differences in recording systems' bandwidth.

II. METHODS

A. Study site

The only resident population of Guyana dolphins in Costa Rica inhabits the protected waters of the Gandoca-Manzanillo Wildlife Refuge on the southern Caribbean coast of Costa Rica (Fig. 1) (May-Collado, 2008). An ongoing photoidentification study suggests the population is relatively small and shows high site fidelity (Gamboa-Poveda and May-Collado, 2006). In addition to the Guyana dolphins, bottlenose dolphins (*Tursiops truncatus*) are also common in

the Refuge, where the two commonly form mixed-species groups (Forestell *et al.*, 1999; Acevedo-Gutiérrez *et al.*, 2005; Gamboa-Poveda and May-Collado, 2006). Overall ambient noise levels (third octave) in the Refuge at the following frequencies 2, 6, 10, 14, and 18 kHz are 99.58, 98.18, 98.61, 104.02, and 92.10 dB, respectively (see May-Collado and Wartzok, 2008).

B. Whistle recordings and analysis

Surveys and recordings were carried out from a 10 m fiberglass boat with two engines (215 hp/4-stroke) and were restricted to an area of approximately 9.83 km^2 within the Refuge (Fig. 1). Because of the commonality of mixed-species groups in the area and the omnidirectional nature of our recording system it was important to ensure that only single-species groups of Guyana dolphins were present during the recording sessions. Therefore, only groups recorded under excellent weather conditions that allowed unambiguous confirmation and that no other dolphin species was present were used. Guyana and bottlenose dolphins contrast greatly in their fin morphology and surface behavior, allowing for confident distinction between single-species and mixed-species groups at relatively long distances. Twelve single-species groups of Guyana dolphins were recorded and 422 high quality whistles were selected for analysis. Whistles were recorded during a variety of behaviors, particularly foraging, traveling, and socializing, as well as in the presence and absence of other boats in addition to the research boat (see Table I).

Guyana dolphin signals were recorded using a broadband system consisting of a RESON hydrophone (−203 dB re 1 V/μPa, 1 Hz to 140 kHz) connected to AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400–500 kHz, 16 bits) that sent the signals to a laptop. All recording sessions were made with the research boat engine off. Recordings were made continuously in files of 2–3 min at sampling rates ranging from 384 to 500 kHz. Recordings were obtained over four periods of 1 week each (July 2004, September 2005, November 2005, and September 2006).

TABLE I. Total recorded and analyzed time for each study site. Note that the total number of whistles emitted is given only for the three most common behavioral categories during recording sessions.

Year	No. of individuals/ No. of whistles	No. of whistle per behavior			Total recorded time (min)/ analyzed (min)	Total recorded time (min) in the presence of just the research boat/ plus other boats
		Social	Foraging	Travel		
Total	155[a]/422	148	166	91	1465.89/529.10	308.5/220.6
2004	76/181	38	103	39	525.14/374	240.65/133.35
2005	15/110	⋯	44	52	622.35/74.76	31.87/42.89
2006	64/131	110	19	⋯	318.40/80.34	35.98/44.36

[a]The total number of individuals present in all recording sessions does not represent different animals. About 60% of the animals were the same based on photo-ID data.

Table I provides information on time recorded and analyzed in relation to documented behavioral activities and boat presence (in addition to the research boat).

Guyana dolphin whistles were analyzed manually using the program RAVEN 1.1 (Cornell Laboratory of Ornithology, New York) with a fast Fourier transform size of 1024 points, an overlap of 50%, and using a 512–522 sample Hann window. High quality whistles are those with a clear and dark contour from start to end (see Fig. 2). The maximum number of whistles to be analyzed per group was based on four times the number of individuals present in the group (for a similar method, see Azevedo and Van Sluys, 2005). Since the recordings were continuous but segmented into acoustic files of 2–3 min, dolphin whistles were selected from every other

file. For each selected file all high quality whistles were selected avoiding oversampling those whistles with the same contour. Based on simultaneous photoidentification taken during each recording session, it is known that at least 60% of the photoidentified dolphins were consistently present across recording sessions. Thus, whistle selection was done with the purpose of minimizing oversampling of individuals more than groups.

Seven standard whistle variables were measured on the fundamental frequency of each: starting frequency (SF), ending frequency (EF), minimum frequency (MinF), maximum frequency (MaxF), delta frequency (DF=MaxF−MinF), duration (s), and number of inflection points (see, e.g., Wang et al., 1995; Oswald et al., 2003, 2004; Erber and Simão
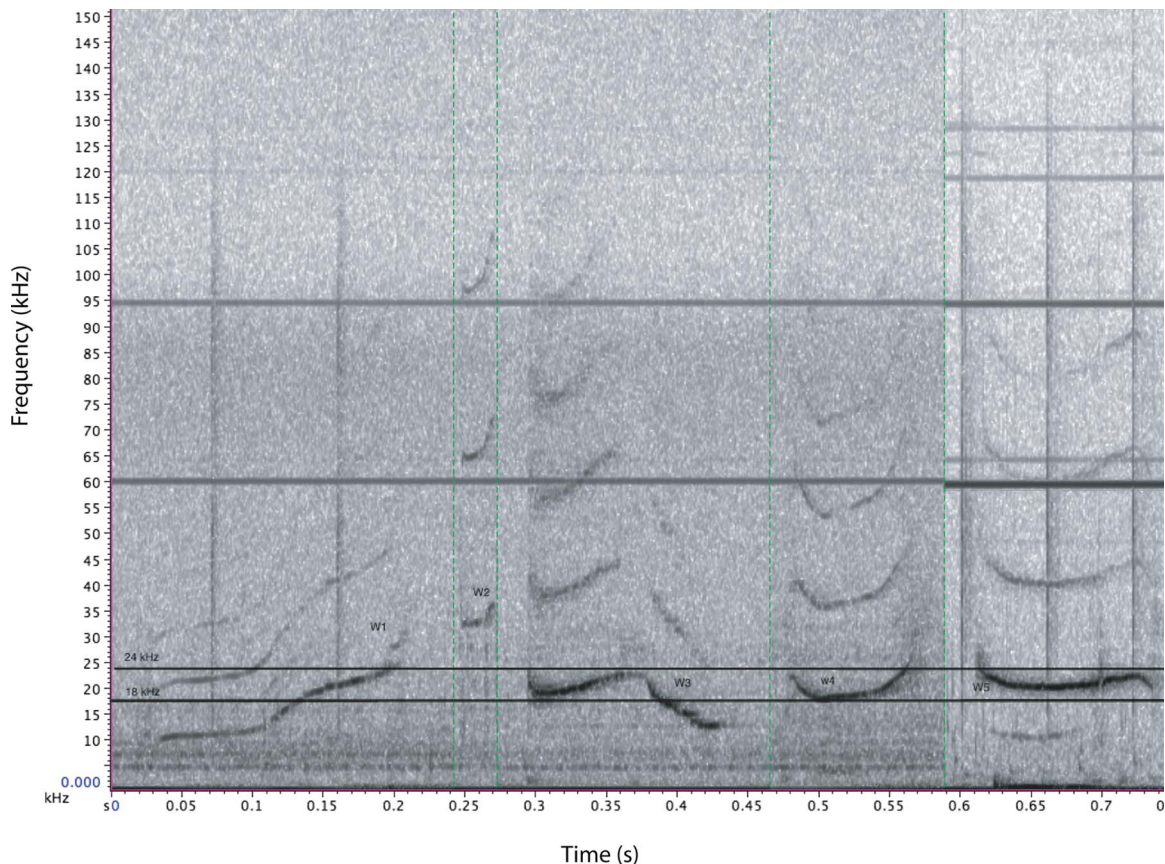

FIG. 2. (Color online) Examples of different whistles (fundamental and harmonics) emitted by Guyana dolphins from Gandoca-Manzanillo Wildlife Refuge, Costa Rica. The horizontal lines represent the mimicked bandwidth limits at 18 and 24 kHz.

TABLE II. Summary of descriptive statistics of whistle parameters for Guyana dolphins from Costa Rica and Brazil. The light-gray rows provide summary statistics for the pairwise comparisons between studies (n=whistle sample size, SD=standard deviation, CV=coefficient of variation, and *=significant results a the level of $p \leq 0.02$). Note that some of these studies in Brazil referred to the Guyana dolphin (*Sotalia guianensis*) as the marine ecotype of the tucuxi also referred as marine tucuxi or estuarine dolphin (*Sotalia fluviatilis*) but two separate species are recognized today. ψ=The whistle subsample 2 containing whistles with maximum frequency below 18 kHz were further subsampled to obtained only whistles emitted during foraging activities, n=48 whistles. See bottlenose dolphin whistle characteristics in May-Collado and Wartzok, 2008.

Study	Recording bandwidth (kHz)	Stats	MinF	MaxF	DeltaF	StartF	EndF	PeakF	$\frac{1}{4}$ Freq	$\frac{1}{2}$ Freq	$\frac{3}{4}$ Freq	Duration	IP	Harmonics
Monteiro-Filho and Monteiro (2001) Cananeia, Southern, Brazil (During various behaviors)	~8	Mean Range CV% n=214	0.3	6	⋯	⋯	⋯	⋯	⋯	⋯	⋯	0.07–0.21	⋯	⋯
Azevedo and Simão (2002) Guanabara Bay, Brazil (During various behaviors)	18	Mean±SD Range CV% n=5086	⋯	⋯	⋯	7.9±2.9	12.7±4.5	⋯	⋯	⋯	⋯	0.102.5±0.081	⋯	⋯
vs Whistle subsample 1		t-test df p-value	⋯	⋯	⋯	10.03 5192 <0.0001*	2.78 5192 0.0054*	⋯	⋯	⋯	⋯	NS	⋯	⋯
Erber and Simão (2004) Sepetiba Bay, Brazil (During various behaviors)	24	Mean±SD Range CV% n=3350	10.521 ±4.518 1.031–10.98 42.9%	13.312 ±4.85 1.171–17.49 27.7%	12.803±7.05 1–7.21 177.5%	10.704 ±4.97 1.03–11.06 46.5%	13.312 ±5.863 3.2–16.83 34.8%	⋯	11.11 ±4.72 2.74–12.07 39.1%	13.66 ±6.186 2.33–15.11 45.3%	15.368 ±6.441 2.053–21.7 41.9%	0.789 ±3.12 0.09–2.28 395.3%	1.3 ±1 0–9 110.5%	1.4±1 1–10 68.3%
vs Whistle subsample 2		t-test df p-value	4.51 3770 <0.0001*	23.41 3770 <0.0001*	15.17 3770 <0.0001*	8.96 3770 <0.0001*	14.02 3770 <0.0001*	⋯	17.82 3770 <0.0001*	5.02 3770 <0.0001*	6.82 3770 0.048	3.92 3770 <0.0001*	16.60 3770 <0.0001*	8.63 3770 <0.0001*
Azevedo and Van Sluys (2005) Southern and Northern Brazil (During various behaviors)	24	Mean±SD Range CV% n=696	9.22 ±3.44 1.34–20.3 37.3%	19.05 ±2.97 9.23–23.89 15.6%	9.83 ±4.03 0.21–22.20 41%	9.57±3.76 1.34–21.93 39.3%	18.82 ±3.10 9.23–23.75 16.5%	⋯	11.73 ±3.53 3.9–21.7 30.1%	13.85 ±3.58 5.7–23.4 25.8%	15.99 ±3.43 7.4–23.6 21.5%	0.308±0.137 0.038–1.064 44.6%	0.37 ±1.02 0–8 275.7%	⋯
vs Whistle subsample 1		t-test df p-value	9.10 1116 <0.0001*	8.19 1116 0.83	9.45 1116 0.0056*	13.29 1116 <0.0001*	2.43 1116 <0.0001*	⋯	11.54 1116 <0.0001*	6.16 1116 <0.0001*	0.048 1116 0.96	11.88 1116 <0.0001*	1.44 1116 0.15	⋯

TABLE II.   (*Continued.*)

Study	Recording bandwidth (kHz)	Stats	MinF	MaxF	DeltaF	StartF	EndF	PeakF	$\frac{1}{4}$ Freq	$\frac{1}{2}$ Freq	$\frac{3}{4}$ Freq	Duration	IP	Harmonics
Pivari and Rosso (2005) Southeastern Brazil (During foraging) vs Whistle sub-sample 3$^{\psi}$ (during foraging,)	18	Mean ± SD	7.97 ± 2.89	14.46 ± 2.88	6.48 ± 3.13	8.15 ± 3.0	14.35 ± 3.0	...	...	...	...	0.229 ± 0.110	0.17 ± 0.51	...
		Range	1.0–15.80	2.2–17.90	0–16.30	1.0–16.0	2.0–17.9					0.038–0.627	0–4	
		CV%	36.20%	19.91%	48.29%	36.77%	21.20%					47.87%	294.7%	
		n=3235												
		t-test	3.38	NS	2.91	5.56	NS	...	...	...	...	NS	NS	...
		df	3281		3281	3281								
		p-value	0.0007*		0.0037*	<0.0001*								
This study Gandoca-Manzanzillo, Costa Rica (During various behaviors)	200–250	Mean±SD	12.31 ± 5.16	21.21 ± 5.82	9.02 ± 5.71	13.83 ± 6.16	19.51 ± 6.36	16.11 ± 5.59	15.37 ± 5.35	16.60 ± 5.33	17.60 ± 5.36	0.200 ± 0.187	0.440 ± 1.03	0.932 ± 1.38
		Range	1.38–35.75	3.0–48.40	0.95–29.30	1.13–47.36	1.52–47.36	1.76–39.06	1.10–39.06	1.13–37.60	5.37–39.06	0.007–1.027	0–8	0–13
		CV%	41.90%	27.45%	59.14%	44.59%	32.62%	34.68%	34.88%	32.18%	30.45%	93.52%	234.57%	148.53%
		n=422												
Whistle subsample 1	24	Mean ± SD	11.57 ± 3.94	19.01 ± 3.44	7.63 ± 4.74	12.99 ± 4.77	17.43 ± 4.10	15.33 ± 3.71	14.30 ± 3.81	15.19 ± 3.51	16.00 ± 3.24.	0.031 ± 0.573	0.459 ± 0.97	0.856 ± 1.35
		Range	1.38–19.13	3.0–23.98	0.95–17.80	1.13–23.38	1.52–23.98	1.76–23.24	1.10–21.68	1.13–22.56	5.37–21.97	0.02–1.05	0–7	0–10
		CV%	34.04%	18.07%	53.22%	36.74%	23.56%	25.09%	26.62%	23.06%	20.24%	96.24%	212%	143.80%
		n=335												
Whistle subsample 2	18	Mean ± SD	9.57 ± 3.16	14.93 ± 2.72	5.60 ± 2.78	10.75 ± 3.77	13.91 ± 2.97	12.27 ± 2.59	11.77 ± 2.70	12.27 ± 2.58	12.84 ± 2.46	0.097 ± 0.10	0.35 ± 0.71	0.86 ± 1.58
		Range	1.46–17.69	3.0–17.99	1.06–14.26	1.13–17.67	3.0–17.99	1.76–16.87	1.10–17.25	1.13–17.25	5.37–16.99	0.02–0.105	0–4	0–10
		CV%	33.1%	18.19%	49.74%	35.06%	21.36%	21.10%	22.95%	21.06%	19.17%	103.2	203.1%	184.10%
		n-108												

2004; Bazúa-Durán and Au, 2002, 2004; Azevedo and Van Sluys, 2005; Baron et al., 2008). In addition, the contour was divided into four parts equally distributed in time to measure the frequency at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the contour. These three frequency measurements are standard in Guyana dolphin whistle studies (see Azevedo and Van Sluys, 2005; Erber and Simão, 2004; Rossi-Santos and Podos, 2006). Peak frequency (PF) was also measured and is defined as the frequency at which maximum power occurs (Bazúa-Durán and Au, 2002, 2004; May-Collado and Wartzok, 2007) and number of harmonics (e.g., Wang et al., 1995; Erber and Simão, 2004). Whistle contours were categorized as ascending, descending, ascending-descending, descending-ascending, and constant in frequency, sine, and others (see Azevedo and Van Sluys, 2005; Erber and Simão, 2004).

C. Effect of recording systems' bandwidth

To evaluate the effect of bandwidth limit on understanding Guyana dolphin whistle structure the 422 analyzed dolphin whistles (full data set) were subsampled into a data set containing all whistles with maximum frequency below 18 kHz ($n = 108$ whistles, subsample 1) to "mimic" the recording system used by Azevedo and Simão (2002) and Pivari and Rosso (2005) with a bandwidth up to 18 kHz, and a data set containing whistles with maximum frequency below 24 kHz ($n = 335$ whistles, subsample 2) to mimic the recording system of Erber and Simão (2004) and Azevedo and Van Sluys (2005) with a bandwidth up to 24 kHz. Whistle frequency variables were then compared for the three data sets using multivariate statistics; see Sec. II E.

Because bandwidth limit has been shown to have an important effect on dolphin whistle correct classification among dolphin species (see Oswald et al., 2004), the effect of bandwidth limits was also evaluated on whistle classification of the sympatric Guyana dolphins and bottlenose dolphins. A total of 77 bottlenose dolphin whistles were obtained from a previous study in the same study area and following the same recording protocol used in this study (see May-Collado and Wartzok, 2008). Because these whistles were recorded at an upper frequency of 192–250 kHz, bottlenose dolphin whistles were also subsampled to mimic the limited bandwidth, 18 and 24 kHz, for comparison purposes.

D. Whistle comparison with other studies (populations)

Comparisons between populations were made using published data on mean values for SF, EF, MinF, MaxF, DF, $\frac{1}{4}F$, $\frac{1}{2}F$, $\frac{3}{4}F$, and duration, and when possible the mean number of inflection points and harmonics were also included (see Table II). To account for differences in bandwidth between studies, the whistle variables reported by Azevedo and Simão (2002) and Pivari and Rosso (2005) were compared to the whistle subsample 1 (whistles with maximum frequency below 18 kHz), and whistle variables reported by Erber and Simão (2004) and Azevedo and Van Sluys (2005) were compared to subsample 2 (whistles with maximum frequency below 24 kHz).

Finally, it is important to emphasize that the Guyana dolphin (S. guianensis), an exclusively marine species, was recently recognized as a separate species from the freshwater Tucuxi dolphin (S. fluviatilis) (see Monteiro-Filho et al., 2002; Cunha et al., 2005; and Caballero et al., 2007). Because of this recent taxonomic change, the studies above identified the dolphins as S. fluviatilis. However, all studies considered in Table II for comparison correspond to the Guyana dolphin (S. guianensis) as all of them took place in marine environments.

E. Statistical analyses

The statistical softwares SPSS 16.0, 2007 (SPSS Inc.) and JMP 2007® (SAS Institute Inc.) were used for statistical analyses. Descriptive statistics were performed to provide mean, standard deviation, frequency range, and coefficient of variation values for each whistle. All whistle variables were Box-Cox transformed (except for the number of inflection points and harmonics) to normalize their distribution (Sokal and Rohlf, 1995). Multivariate analyses of variance (MANOVAs) were performed to determine whether whistle variables SF, EF, MinF, MaxF, DF, PF, $\frac{1}{4}F$, $\frac{1}{2}F$, $\frac{3}{4}F$, and duration vary with bandwidth limits, sympatric species, and their interaction. The Box's M-test was used to evaluate homogeneity among covariance matrices. Because MANOVA performs multiple univariate ANOVA analyses, type I error was controlled using a Bonferroni procedure to adjust the level of significance. The same procedure was used for multiple pairwise comparisons of whistle variables among group factors. A scatter plot between starting and ending frequencies was made to visualize the differences in frequency span between bandwidths.

To examine the effect of bandwidth on whistle classification between the two sympatric dolphin species, a discriminant analysis was performed for each whistle data set separately using whistle SF, EF, MinF, MaxF, DF, PF, and duration as predictors. Since the covariance matrices for the species were significantly different (Box's $M = 1208.02$, df1 $= 140$, $p < 0.0001$) we adjusted the prior probabilities by computing classification scores from group size. The canonical correlation (equivalent to Pearson's correlation and proper for two groups) was used to determine the efficacy of the discriminant function. The chi-square statistics test was used to assess how well the discriminant function does versus chance alone at the statistical significance level of 0.05 (Green and Salkind, 2003). The cross-validation method was used to calculate correct classification scores for the discriminant functions and the Kappa index as well as a chi-square test were performed to evaluate the accuracy of the classification at the p-value level of $p = 0.05$ (Green and Salkind, 2003). Box plots were generated to compare whistle structure between species.

For comparisons between populations published whistle data on mean (and standard deviation) SF, EF, MinF, MaxF, DF, PF, $\frac{1}{4}F$, $\frac{1}{2}F$, $\frac{3}{4}F$, and duration were used to compare with either subsample 1 (18 kHz) or subsample 2 (24 kHz) depending on the recording system used in the published study. Before performing each pairwise comparison the assumption of equal variance was tested using Levene's F-test. When
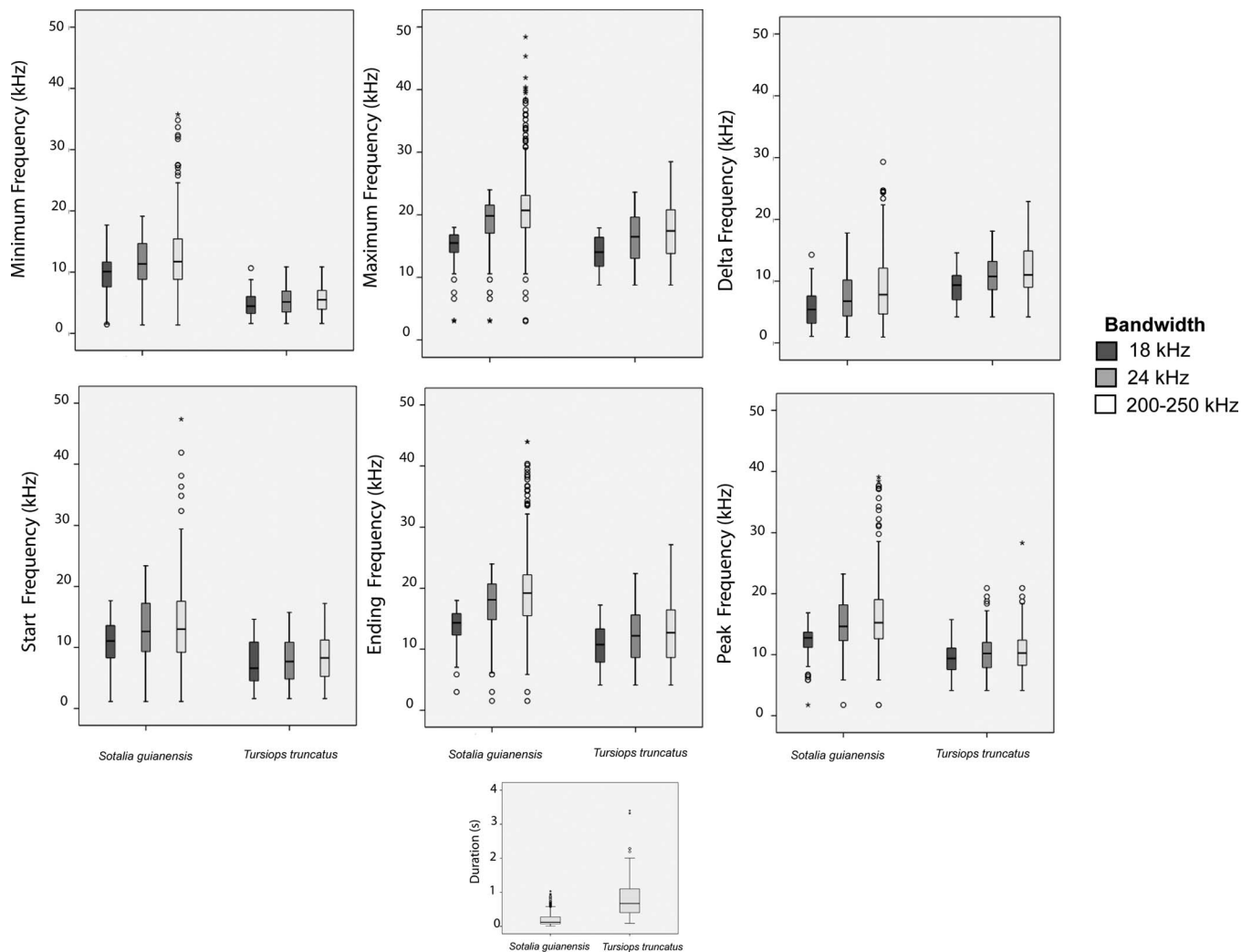
FIG. 4. Whistle variation in frequency and time parameters of both sympatric dolphin species whistles recorded using the broadband recording system (200 Hz–250 kHz).

variances were equal the *t*-test was used and the Welch *t*-test for unequal variances. The Bonferroni procedure was also used here to adjust the level of significance for the multiple comparisons.

III. RESULTS

A. Whistle characterization

Guyana dolphins from Costa Rica emitted whistles with a greater frequency span (1.38 up to 48.40 kHz) than previously reported in Brazilian studies using bandwidth-limited recorded systems (see Table II). The broadband recording system also allowed detection of high order harmonics for 37% of the total analyzed whistles (Table III and Fig. 2). Most of these whistles contained one and two harmonics, and up to 13 harmonics reaching frequencies up to 136 kHz. Guyana dolphin emitted whistles that were mainly ascending in frequency (57.6%) followed by constant (13%), descending (10.2%), ascending-descending (6.6%), descending-ascending (6%), and sine (6.6%).

B. Effect of bandwidth limits on whistle structure understanding

The means for Guyana dolphin whistle SF, EF, MinF, MaxF, DF, PF, and duration were significantly different among bandwidth limits [Wilk's $\Lambda = 0.01$, $F(14,2078) = 1.24 \times 10^3$, $p < 0.0001$], dolphin species [Wilk's $\Lambda = 0.60$, $F(7,1039) = 101.26$, $p < 0.0001$], and their interaction [Wilk's $\Lambda = 0.95$, $F(14,2078) = 4.02$, $p < 0.0001$]. About 89% of the multivariate variance found in whistle variables was associated with bandwidth limits, 41% to dolphin species, and only 2.6% to their interaction.

Dolphin whistles SF, EF, MinF, MaxF, DF, PF, $\frac{1}{4}F$, $\frac{1}{2}F$, $\frac{3}{4}F$, and duration varied significantly among bandwidths [Wilk's $\Lambda = 0.83$, $F(20,1680) = 8.1$, $p < 0.0001$, Table II]. Whistle maximum (16%), $\frac{3}{4}F$ (11%), and ending (10%) frequencies explained most of the whistle variation between bandwidths. Figure 3 shows how Guyana dolphin whistle frequency span (start-ending frequencies) changes considerably among bandwidths, with bandwidth at 200–250 kHz showing the entire frequency span of Guyana dolphins.

TABLE III. Maximum frequency descriptive statistics for harmonic components of 155 whistle harmonics emitted by Guyana dolphins.

| No. of harmonics	No. of whistles	Stats	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12	H13
H1	55	Mean ± SD	35.1 ± 10.1	...	...	...	...	...	...	...	...	...	...	...	...
		Range	19.9–78.6	...	...	...	...	...	...	...	...	...	...	...	...
H2	57	Mean ± SD	39.2 ± 14.17	53.5 ± 21.1	...	...	...	...	...	...	...	...	...	...	...
		Range	14.1–103.7	13.6–121.2	...	...	...	...	...	...	...	...	...	...	...
H3	18	Mean ± SD	35.6 ± 9.6	52.2 ± 16.5	65.6 ± 21.2	...	...	...	...	...	...	...	...	...	...
		Range	21.8–61.0	35.2–94.8	45.8–121.0	...	...	...	...	...	...	...	...	...	...
H4	12	Mean ± SD	37.1 ± 9.6	52.8 ± 13.8	65.3 ± 17.8	77.9 ± 21.1	...	...	...	...	...	...	...	...	...
		Range	21.8–53.4	40.4–78.8	48.5–85.4	62.5–77.9	...	...	...	...	...	...	...	...	...
H5	6	Mean ± SD	35.8 ± 9.0	55.2 ± 12.7	66.3 ± 15.5	82.2 ± 15.8	96.1 ± 15.8	...	...	...	...	...	...	...	...
		Range	20.2–43.7	34.9–65.0	40.2–66.3	59.4–78.6	78.5–91.2	...	...	...	...	...	...	...	...
H6	1	Value	42.2	57.8	77.3	87.1	92.9	105.8	...	...	...	...	...	...	...
H9	2	Range	23.7–25.2	29.6–36.9	43.2–49.8	59.3–61.5	71.1–79.5	85.4–87.2	91.9–97.3	101.8–114.0	112.5–120.7	...	...	...	...
H10	1	Value	22.1	43.5	50.1	64.1	70.2	80.5	90.5	102.2	110.3	121.3	...	...	...
H11	2	Range	22.6–22.7	29.1–29.7	39.4–39.7	50.5–61.7	60.3–69.7	69.3–78.1	79.1–86.1	89.1–93.1	98.6–101.7	105.9–107.6	115.9–131.6	...	...
H13	1	Value	24.8	29.8	41.0	48.9	62.1	68.6	82.6	90.6	102.6	107.2	117.3	124.3	135.9
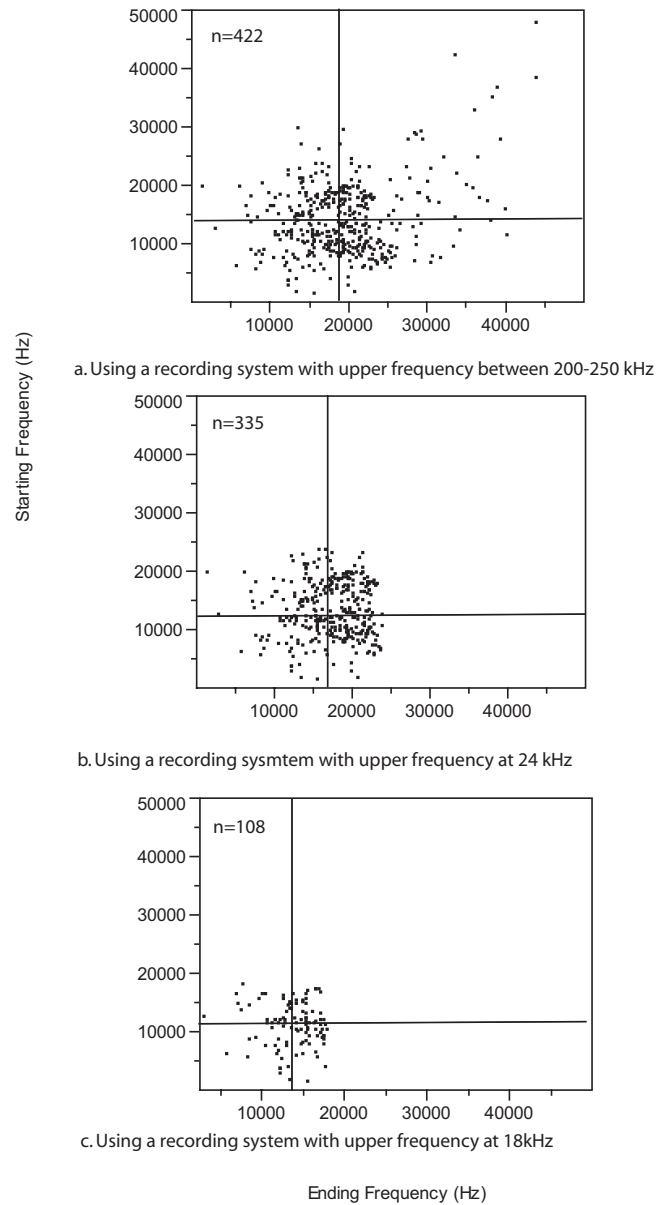
FIG. 3. Plot of whistle starting vs ending frequency for the full data set (422 whistles) using the broadband recording system (200 Hz–250 kHz) and subsampled whistle data sets with maximum frequencies below 18 and 24 kHz. The lines represent the mean value for starting and ending frequencies.

C. Effect of bandwidth limits on whistle classification

Whistle variables were significantly different between species (see Fig. 4 for comparison and statistics). The discriminant analyses correctly classified whistles with high success to the respective dolphin species regardless of bandwidth limits (Table IV). However, an increase in bandwidth slightly improved the classification success for Guyana dolphins. The "best" whistle variables to discriminate between dolphin species were whistle minimum frequency and duration for bandwidth limit at 200–250 kHz [MinF: Wilk's Λ = 0.73, $F(1,497) = 171.8$, $p < 0.0001$; duration: Wilk's Λ = 0.74, $F(1,497) = 170.8$, $p < 0.0001$] and at 24 kHz [MinF: Wilk's $\Lambda = 0.71$, $F(1,399) = 155.1$, $p < 0.0001$; duration: Wilk's $\Lambda = 0.72$, $F(1,399) = 154$, $p < 0.0001$]. Whistle duration was the most important variable for species discrimina-

TABLE IV. Classification results of the discriminant analyses for the three bandwidth-limited whistle data sets. The percentage for whistles correctly classified for each species is given in bold, all of which were significantly different (χ^2 test $p < 0.0001$) than expected by chance alone at the significance level of $p < 0.05$. Overall correct classification percentages are given at the bottom with their respective kappa index and χ^2 test statistics.

	Bandwidth 18 kHz Predicted species			Bandwidth 24 kHz Predicted species			Bandwidth 200–250 kHz Predicted species		
Actual species	Bottlenose dolphins	Guyana dolphins	n	Bottlenose dolphins	Guyana dolphins	n	Bottlenose dolphins	Guyana dolphins	n
Bottlenose dolphins	**76.7%**	23.3%	43	**66.7%**	33.3%	66	**63.6%**	36.4%	77
Guyana dolphins	11.1%	**88.9%**	108	3.9%	**96.1%**	335	3.8%	**96.2%**	422
Overall correct classification %	Overall 85.4%, kappa=0.75, $p < 0.0001$ χ^2 test $p < 0.0001$			Overall 91.3%, kappa=0.72, $p < 0.0001$ χ^2 test $p < 0.0001$			Overall 91.2%, kappa=0.66, $p < 0.0001$ χ^2 test $p < 0.0001$		

tion when using the 18 kHz bandwidth [Wilk's $\Lambda = 0.58$, $F(1,149) = 106.2$, $p < 0.0001$]. Overall, Guyana dolphin whistles have a higher minimum frequency and are much shorter in duration than bottlenose dolphins (Fig. 4).

D. Whistle comparison between populations

After accounting for differences in bandwidth, pairwise comparisons between this study and the studies of Erber and Simao (2004), Pivari and Rosso (2005), and Azevedo and Van Sluys (2005) suggest that Brazilian and Costa Rican dolphins vary significantly in whistle structure (Table II for statistics). In general Guyana dolphins from Costa Rica emitted whistles that were higher in almost every frequency parameter, while Brazilian dolphins emitted significantly longer whistles.

IV. DISCUSSION

Guyana dolphin whistles have been described using a variety of bandwidth-limited recording systems (generally 18 kHz and 24 kHz). The most recent study reported a whistle frequency span from 1.34 to 23.89 kHz (Azevedo and Van Sluys, 2005; bandwidth 24 kHz), but as the authors reported some of the observed whistles appeared to extend beyond the limits of the upper frequency of the recording system. Using a broadband recording system (up to 250 kHz) this study provides evidence that Guyana dolphins from Costa Rica can emit whistles beyond 24 kHz, joining a short list of cetacean species known to emit such whistles: the botos (May-Collado and Wartzok, 2007), bottlenose dolphins (Boisseau, 2005; May-Collado and Wartzok, 2008), white-beaked dolphins (Rasmussen and Miller, 2002), spinner dolphins (e.g., Lammers et al., 1997; Lammers et al., 2003; Oswald et al., 2004), spotted, striped, and common dolphins (Oswald et al., 2004). The Guyana dolphin has the widest whistle frequency span ever reported in delphinids (1.38 up to 48.40 kHz). Also of the analyzed whistles 37% contained harmonics, some of which reached frequencies up to 136 kHz. This is the first time high order harmonics have been reported for whistles emitted by Guyana dolphins. High order harmonics in dolphin whistle sounds have been described for only a handful of dolphin species (white-beaked dolphins, Rasmussen et al., 2006; spinner dolphins, Lammers and Au, 2002; killer whales, Miller, 2002). Lammers and Au (2002) showed that in spinner dolphins whistle di-

rectionality increased with frequency especially with regard to harmonics. The authors suggested that whistle harmonic structure can potentially carry information on the direction of movement of signaling animal (s) and therefore facilitate group coordination. This would be an interesting hypothesis to test in the future for Guyana dolphins.

A. Bandwidth limit and whistle structure

As shown by Oswald et al. (2004) in spinner, spotted, striped, and common dolphins the recording system bandwidth capabilities are a very important consideration when studying dolphin whistle acoustic characteristics. This study shows that limited bandwidth distorts the understanding of Guyana dolphin whistle frequency variables, particularly in whistle maximum, ending, and $\frac{3}{4}$ frequencies. Whistles selected to mimic narrowband recordings systems with bandwidths of 18 and 24 kHz limited the characterization of the whistle frequency span of Guyana dolphins to a portion of the actual frequency range (see Fig. 3). For instance, about 73 whistles (out of 422) had maximum frequencies that extended beyond the 24 kHz limit, and additional 14 whistles had minimum (and starting) frequencies above 24 kHz, and would have been completely missed by narrowband recording systems. In addition, most of the harmonics would have been missed with narrowband recording systems. In order to properly document whistle repertoire of Guyana dolphins (including harmonic components) a recording system with a bandwidth of at least 150 kHz is necessary.

B. Bandwidth limit and dolphin species whistle classification

Although narrowband recording systems obscure Guyana dolphin whistle frequency range the consequences of this for dolphin species whistle classification were minor, presumably because Guyana and bottlenose dolphin whistles are different enough to be discriminated with sparse data. Increase in bandwidth improved slightly correct classification percentages of whistles between species, which were in general high (85%–91%) compared to previous studies (e.g., Oswald et al., 2004; Rendell et al., 1999; Steiner, 1981). Both dolphin species were very distinct in their whistle structure, particularly in whistle minimum frequency and dura-

tion. Bottlenose dolphin whistles were much lower in minimum frequency and longer in duration than whistles emitted by the Guyana dolphins (see Fig. 4).

The clear distinction between Guyana dolphins and bottlenose dolphin whistles may be the result of a combination of factors as follows: (1) Phylogenetic distance, the two species belong to different subfamilies (e.g., LeDuc *et al.*, 1999; May-Collado and Agnarsson, 2006; Agnarsson and May-Collado, 2008); (2) body size, bottlenose dolphins are large (up to 3.0 m) and robust animals, while Guyana dolphins are small (up to 1.79 m) and slender (Rosas and Monteiro-Filho, 2002). Because body size and minimum frequency are negatively correlated in cetaceans (e.g., Matthews *et al.*, 1999; May-Collado *et al.*, 2007a), this intrinsic relationship may largely account for the clear distinction in whistle structure between the two dolphin species; and (3) differences in social structure. Bottlenose dolphins live in complex societies where some individuals sustaining long-term relationships (e.g., Mann *et al.*, 2000) while Guyana dolphins live in relatively simple and fluid societies with no apparent long-term relationships as in bottlenose dolphins (De Oliveira and Rosso, 2008). Interestingly, May-Collado *et al.* (2007b) found a relationship between social elements such as group size, and whistle minimum frequency and duration, where in general social species living in simple societies tended to emit whistles that were higher in frequency and shorter in duration. Previous dolphin species whistle classification studies have not taken into consideration these factors, but these seem to be key particularly when algorithms are being designed to improve classification scores for species identification. For instance, Oswald *et al.* (2004) obtained relatively low correct classification percentages between spinner, spotted, striped, and common dolphins (30%–37%); these species are closely related with relatively similar body size and social structures [but see study by Rendell *et al.* (1999)]. In contrast, Steiner (1981) obtained relatively high correct classification percentages between bottlenose, spotted, Atlantic-white sided dolphins, and pilot whales (57%–80%). These species are not closely related, and all four vary considerably in size and social structures. We proposed that future classification algorithms should take in consideration phylogenetic relationships, body size, and social structure as tools that can guide the algorithm to classify species.

C. Comparison between populations

After accounting for difference in recording equipment bandwidth, comparisons between whistles from the Costa Rican and the Brazilian populations showed significant differences in whistle structure. Brazilian dolphins emit longer whistles than the Costa Rican dolphins (Erber and Simão, 2004; Azevedo and Van Sluys, 2005). However, whistles from the Costa Rican dolphins were consistently higher in almost all whistle frequency variables described for the Brazilian populations (see Table II). These results provide corroborative evidence for the hypothesis proposed by Azevedo and Van Sluys (2005) and Rossi-Santos and Podos (2006) that Guyana dolphins' whistle frequency increases (particularly in minimum and starting frequencies) from south to north. A stronger test of this hypothesis must await a broadband recording study of the Brazilian populations, and other populations in between.

Several factors have been proposed to explain dolphin whistle geographical variations including dispersal capabilities of a species (McGregor *et al.*, 2000; Mundinger, 1982), isolation and genetic divergence between groups or populations (e.g., Ford, 2002; McGregor *et al.*, 2000), and adaptation to ecological conditions (e.g., Brumm, 2006; Gillam and McCracken, 2007; Morisaka *et al.*, 2005; Peters *et al.*, 2007). Rossi-Santos and Podos (2006) noticed in Guyana dolphin whistles a discontinuity particularly in whistle minimum and starting frequencies and suggested that this pattern could reflect dispersal limitations between populations. There appears to be a discontinuity in Guyana dolphin distribution in Central America and Panama, where pockets of Guyana dolphin populations occur along the Caribbean coast, one in the southern part of Panama (May-Collado, 2008), in the northern part of Nicaragua (Cayos Miskito Reserve) (e.g., Carr and Bonde, 2000; Edwards and Schnell, 2001), and the Costa Rican population, which appears to be restricted to the studied area [77.2% of the photoidentified animals are regularly observed in the Refuge year around (Gamboa-Poveda and May-Collado, 2006)].

V. CONCLUSIONS

This study confirms that the whistle repertoire (fundamental and harmonics) of the Guyana dolphin, *Sotalia guianensis*, extends beyond 24 kHz, with a frequency span among the greatest ever reported in delphinid species. The importance of a broadband recording system to study the entire whistle repertoire is demonstrated as prior studies using a narrowband recording system gave only an incomplete understanding of Guyana dolphin whistles. Although the dolphin species studied here are very distinct in their whistle structure, an increase in broadband recording systems slightly improved the whistle classification of Guyana dolphin species. Until broadband recording systems are used for more populations, the potential patterns in whistle geographical variation and factors promoting such variation remain poorly understood. However, this study provides evidence supporting the hypothesis that whistle frequency variables increase with latitude. Future studies on Guyana dolphin whistles should employ recording systems with bandwidth up to 50 kHz (for whistle fundamental) and up to 150 kHz (when considering high order harmonics) to ensure the inclusion of the entire whistle repertoire.

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