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ΝΟΤΕ

Comparison of common bottlenose dolphin whistles in tropical waters

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Vocal signaling is the primary communication modality in delphinid populations (Janik, 2005), with high diversity in their calling behaviors and often abundant emission rates (Jones et al., 2020; Luís et al., 2021). Their vast acoustic repertoire includes echolocation click trains and burst-pulse sounds, as well as frequency-modulated narrow-band whistles (Janik & Slater, 1998; Jones et al., 2020). The latter, which are associated with interindiviual communication, are the most extensively studied sound type produced by dolphins (Au, 2004; Caldwell & Caldwell, 1965; Herzing & dos Santos, 2004; Rio et al., 2022).

The ecological flexibility of common bottlenose dolphins (*Tursiops truncatus*) is a striking characteristic of this species. It is evidenced by the species' wide global distribution, including estuarine habitats and coastal and oceanic waters, in both temperate and tropical regions (Costa et al., 2016, 2021; Oviedo Correa et al., 2019; Viaud-Martínez et al., 2008; Wickert et al., 2016). Their vocal repertoires are flexible and varied, and may reflect different contexts, behavioral states, or environmental conditions. These dolphins exhibit a relatively high level of intraspecific acoustic variation (e.g., Baron et al., 2008; La Manna et al., 2017, 2019, 2020; Lima et al., 2020; Luís et al., 2021; May-Collado & Wartzok, 2008; Morisaka et al., 2005; Papale et al., 2014; Wang et al., 1995) making acoustic monitoring challenging as it requires unraveling intra- and interpopulation variations.

Many factors influence differences in vocal repertoires between populations, and these factors can influence dolphin acoustic behavior individually or in association with each other. There is some evidence to suggest that longer geographical distances between dolphin populations are linked with greater acoustic differences (Azevedo & Van Sluys, 2005; Morisaka et al., 2005; Wang et al., 1995). Geographically distant groups, for example, can acoustically diverge from each other due to genetic drift or isolation, whereas genetically connected groups can still diverge from each other due to culture (Yurk et al., 2002). Cultural divergence in bottlenose dolphins is likely to happen due to social learning of acoustic signals, which is facilitated by the elasticity of this species' social organization (Bain, 1986; Ford, 1991; Janik & Slater, 2000; Rendell et al., 2019). Simple social and behavioral factors are enough to influence the acoustic and temporal parameters of a dolphin population (May-Collado & Wartzok, 2008; Quick & Janik, 2008). In addition, variation in habitat characteristics, such as local underwater noise levels, can also affect acoustic divergence between populations (Azevedo & Van Sluys, 2005; Baron et al., 2008; Lima et al., 2020; Morisaka et al., 2005; Papale et al., 2014; Rossi-Santos & Podos, 2006; Wang et al., 1995). For example, for each 1 dB increase in ambient noise in Tampa Bay (western Florida), T. truncatus groups increased minimum frequency by 121 Hz, maximum frequency by 108 Hz, and peak frequency by between 122 and 144 Hz (van Ginkel et al., 2018). This may be explained by the "Acoustic Adaptation Hypothesis" (AAH), which posits that dolphins sometimes change the characteristics of their whistles in the presence of underwater noise in favor of signal transmission (Ansmann et al., 2007; Bittencourt et al., 2017; Luís et al., 2021; May-Collado & Wartzok, 2008; Morisaka et al., 2005).

The present study focuses on an understudied region and investigates the variation in whistles emitted by common bottlenose dolphins from Revillagigedo Archipelago (RVG; Pacific Ocean, Mexico), Saint Peter and Saint Paul Archipelago (SPSP; mid-equatorial North Atlantic Ocean, Brazil), and from the western Coast of Aragua (WCA; South Caribbean, Venezuela). The first two locations are similar pelagic habitats, but they are geographically far from each other. The SPSP population is distributed in the middle of the Atlantic, far from the coast (~1,100 km), but is not genetically closed since there is haplotype flow with North Atlantic populations (Castilho et al., 2015). The current study is the first step towards providing an overview of geographic whistle variation among the herein assessed locations.

Revillagigedo Archipelago (18°50'0"N, 112°50'0"W) is located in the eastern Pacific Ocean, approximately 390 km southwest of the southern tip of Baja California Peninsula and 720 km west to Mexico's mainland (World Heritage Committee, 2016). All data were collected from a liveaboard vessel (33.5 m in length, 7.5 m in width); engines off, anchored on permitted areas (permission N. SGPA/DGVS/00823/20). Underwater recordings were conducted with the aid of Hydrophone System BuninTech H0220 (final sensitivity at gain of 52 dB by GainBox: -152 dB re 1 V/uPa ±3 dB; flat frequency response: 5 Hz-80 kHz) placed 5 m below the surface, connected to a Tascam DR-100MKIII digital recorder. All recordings were made at a sample rate of 96 kHz and 24-bit resolution (Table 1). Acoustic data were collected from December 28, 2020, to January 3, 2021, around three of the four islands (San Benedicto, Socorro Island, and Roca Partida Island; Figure 1, Table 1). Daytime visual confirmation of dolphins was obtained at daylight. Recordings were collected from up to 11 individuals who were sighted four times. In total, 63 hr 32 min 59 s of acoustic recordings were used for the analysis (Rio et al., 2022). Although the RVG acoustic data were sampled during the Covid-19 period, the level of vessel activity should have been similar to current levels for the location, since the reduction in vessel activity around the Archipelago occurred prior to 2020 (information from the Parque Nacional Archipiélago de Revillagigedo). Access to the RVG is generally restricted (DOF, 2017) and the number of permissions provided did not change from 2020 to 2023 (information from the Parque Nacional Archipiélago de Revillagigedo).

Saint Peter and Saint Paul Archipelago is a small group of islands in the Mid-Atlantic Ridge ($0^{\circ}55'06''N$, 29°20'48''W); located 1,100 km from the northern Brazilian coast and 1,800 km from Guinea Bissau, Africa (Figure 1). Recordings were collected during 13-day field trips from **2007 to 2009** (Table 1). Group sizes ranged from 7 to 25 individuals in all recordings. In total, 8 hr 29 min 38 s of acoustic recordings were used for the analysis. Data collection in SPSP was carried out with a calibrated C54XRS hydrophone (http://www.cetaceanresearch.com; -185 dB ± 3.0 dB re:1 V/µPa, 16 Hz-44 kHz) connected to a Fostex FR-2 recorder (at 48 kHz sample rate and

TABLE 1 Information about the populations of *Tursiops truncatus* recorded in the three study areas: Archipelago of Revillagigedo (RVG) in the Mexican Pacific, Archipelago of Saint Peter and Saint Paul (SPSP) in the Brazilian Atlantic, and the Western Coast of Aragua (WCA), Venezuela.

Region	Year of recording	Recording time	Deployment depth	Sampling rate/bit	Number of individuals	Number of selected whistles	Behavioral states
RVG ^a	2020-2021	63 hr 32 min 59 s	5 m	96 kHz/24 bit	11	434	feeding, socialization, traveling
SPSP ^b	2007-2009	8 hr 29 min 38 s	10 m	48 kHz/24 bit	7 to 25	720	feeding, socialization, traveling
WCA ^c	2008	1 hr 4 min 6 s	10 m	48 kHz/24 bit	10 ± 8	518	feeding, socialization, traveling and resting

These data were compiled based on Rio et al. (2022)^a, Hoffmann & Freitas (2018)^b, and Romero-Mujalli et al. (2014)^c.



FIGURE 1 The locations of the three study sites: Revillagigedo Archipelago (RVG), including Isla San Benedicto, Isla Socorro, Isla Roca Partida, and Isla Clarión in the Pacific Ocean, Mexico (left), western Coast of Aragua (WCA) off Venezuela in the South Caribbean (top middle), and Saint Peter and Saint Paul Archipelago (SPSP) in the mid-equatorial North Atlantic Ocean, Brazil (right).

24-bit resolution; Table 1). For all recordings, the hydrophone was placed 10 m below the surface from an outboard-powered boat (7.5 m in length, with engines off).

The coast of Aragua State, Venezuela, South Caribbean, covers ~60 km. Its western portion is located between Turiamo Bay ($10^{\circ}28'N$, $67^{\circ}50'W$, western terminus) and Puerto Colombia ($10^{\circ}30'N$, $67^{\circ}36'W$, eastern terminus; Figure 1). All data were collected during 2004–2008 from a liveaboard ship (9 m in length, 2 m in width) with engines off. Group size of 11.95 (SD = 1.12) individuals was determined based on the ecological characterization of coastal *Tursiops truncatus* (Table 1). The total of 1 h 4 min 6 s of acoustic recordings was used for the analysis.

The recordings were collected with an omnidirectional SQ26-08 hydrophone (effective sensitivity = -169 dB (re 1 V/µPa), gain = 25 dB) placed 10 m below the surface, connected by a 10-m cable to a M-Audio Micro Track II solid state digital recorder (sampling rate 48 kHz, 24-bit resolution; Table 1).

The term "whistle" was herein used to describe a tonal sound with a narrow-band fundamental frequency longer than 0.1 s (Evans & Prescott, 1962; Lilly & Miller, 1961), and at least part of the fundamental frequency had to be higher than 3 kHz (Simard et al., 2011; van der Woude, 2009). All whistles with a good signal-to-noise (SNR) ratio (SNR \geq 10 dB; Wang et al., 2016), and complete, clear spectral contours were manually selected for the analysis. Spectrograms were plotted in Raven Pro 1.6.1 (Cornell Laboratory of Ornithology, Ithaca, NY), at 512 or 1,024 Fast Fourier Transform size (FFT), Hanning window and 50% overlap.

Whistles were classified into six categories, according to the contour (Azevedo et al., 2007). The adopted categories were (1) Upsweeps, (2) Downsweeps, (3) Inverted U-shapes (or ascending-descending), (4) U-shapes (or descending-ascending), (5) Wavering sinusoidal whistles, and (6) Flat (Dudzinski et al., 2002; Richardson et al., 1995).

The following spectral and temporal parameters were extracted from each whistle: start frequency (StaF; Hz), end frequency (EndF; Hz), minimum frequency (MinF; Hz) and maximum frequency (MaxF; Hz), bandwidth (BanF; Hz), duration (Dur; s), slope of the beginning sweep (i.e., ascending and descending trend as "positive" and "negative," respectively; BegS), slope of the ending sweep (positive or negative; EndS), and number of inflection points (i.e., change from a positive to negative aspect or vice versa; InfP).

Descriptive statistical analysis and Shapiro-Wilk's test were applied to all analyzed independent variables. According to the normality test, none of the acoustical or temporal data showed a normal distribution. Hence, comparisons between locations were performed through Kruskal-Wallis' tests, followed by Dunn's multiple comparisons tests. Parameters with arbitral binary numbers, such as BegS and EndS, were analyzed through Fisher's exact tests. All statistical analyses were performed in GraphPad 8 (GraphPad Software Inc., San Diego, CA) and R (R Core Team, 2019) software, at 95% significance level.

Acoustic recording time and whistle sample size are displayed in Table 1. The recording effort was higher in Mexico (RVG) compared to the others (SPSP and WCA). A total of 1,672 high-quality whistles were analyzed: 25.96% (n = 434) of them were extracted from RVG, 43.06% from SPSP (n = 720), and 30.98% from WCA (n = 518). Whistles were not evenly distributed among likely modulation types in each location (Figure 2); types 4 (U-shapes) and 6 (Flat) were the least common ones between WCA and RVG, and were not observed in SPSP. The other types varied in abundance at each of the assessed sites: type 1 (Upsweeps) prevailed in WCA (32.24% of whistles analyzed), type 3 (Inverted U-shapes) in SPSP (35.28%), and type 5 (Wavering) in RVG (31.87%; Figure 2). Type 2 (Downsweeps) was similarly observed among the three sites (19.69%, 25.97%, and 16.40%, in WCA, SPSP, and RVG, respectively; Figure 2).



FIGURE 2 The percentage of whistle contour types emitted by common bottlenose dolphins from Revillagigedo Archipelago (RVG), Mexico; Saint Peter and Saint Paul Archipelago (SPSP), Brazil; and Western Coast of Aragua (WCA), Venezuela.

Mean parameter values were similar across locations (Table 2); EndF (11.44 \pm 4.60 kHz) and MaxF (15.87 \pm 3.12 kHz) were qualitatively higher at WCA, which also had the lowest Dur (0.73 \pm 0.50) and InfP (0.88 \pm 1.36) values. BanF and Dur reached maximum values at SPSP (8.63 \pm 3.01 kHz and 0.80 \pm 0.40, respectively) but the lowest MinF values (6.40 \pm 2.08) were recorded there. The highest mean value for InfP was documented at RVG (1.78 \pm 2.23), as well as the lowest BanF values (7.21 \pm 4.23 kHz).

The WCA population emitted whistles with mean MaxF values significantly higher (Kruskal-Wallis test; p < .05) than those recorded in oceanic sites, where no significant differences were found (Kruskal-Wallis test; p > .05) (Figure 3, Table 2). SPSP whistles had significantly lower StaF and MinF than RVG and WCA (Kruskal-Wallis test; p < .05), but these locations did not differ significantly in these two parameters (Kruskal-Wallis test; P > 0.05). On the other hand, SPSP whistles were significantly longer (Kruskal-Wallis test; p < .05) than those emitted in other locations, which, in turn, did not differ significantly from each other (Kruskal-Wallis test; p > .05; Figure 3). Dolphins at the Pacific Ocean population of RVG produced whistles within a significantly narrow BanF (Kruskal-Wallis test; p < .05), which was characterized by bimodal distribution (Figure 3). Bandwidth was not significantly different between SPSP and WCA (Kruskal-Wallis test; p > .05).

Finally, EndF and InfP were significantly different (Kruskal-Wallis test; p < .05) among all assessed dolphin populations; WCA had the highest mean frequency values recorded and the lowest values recorded for the signalmodulation variable (Figure 3, Table 2). With respect to other contour parameters, EndS was also significantly different (Fisher's exact test; p < .05) in all locations, whereas no significant difference in this parameter was found for BegS (Fisher's exact test; p .05).

The present study about geographic variation in tropical common bottlenose dolphin whistles showed variation between oceanic and coastal populations. Approximately one-third (32.24%) of whistles emitted by inshore dolphins (WCA) were of the ascending contour type (type 1; Figure 2). This total represents almost double the proportion presented by oceanic populations (RVG 16.17%; SPSP 15.42%). These findings are similar to previous results recorded for Cardigan Bay, western Wales, where a coastal bottlenose dolphin population produced a similar proportion of ascending contour type (35%; Massey, 2014). Moreover, Massey (2014) observed that whistles recorded at shallower depths (<20 m) mostly consisted of ascending whistle types. Upsweep whistles are usually shorter in duration and have no inflection points (no complex modulations), which is consistent with the Acoustic Adaptation Hypothesis (AAH). The AAH (Morton, 1975) predicts that the acoustic properties of a given species' vocalizations will have been selected for optimal transmission to overcome the constraints imposed by the features of their environment. As acoustic signals propagate through the water, they tend to degrade and attenuate (Dusenbery, 1992),

	Locations				
Parameters	RVG (n = 434)	SPSP (n=720)	WCA (n = 518)	р	Total (n = 1,672)
Start (StaF)	11.28 [6.46-16.26] a	9.82 [5.61-12.69] b	11.01 [7.50–13.93] a	<.0001	10.57 ± 4.92
End (EndF)	9.74 [6.99-11.50] a	8.45 [5.29-10.67] b	11.44 [7.43–14.94] c	<.0001	9.71 ± 4.35
Minimum (MinF)	7.72 [5.53-8.99] a	6.40 [5.08-7.15] b	7.52 [5.87-8.71] a	<.0001	7.09 ± 2.47
Maximum (MaxF)	14.93 [10.22-19.61] a	15.03 [12.65-16.74] a	15.87 [13.99-17.85] b	<.0001	15.27 ± 3.90
Bandwidth (BanF)	7.21 [3.70-10.55] a	8.63 [6.99-10.11] b	8.35 [6.04-10.71] b	<.0001	8.17 ± 3.58
Duration (Dur)	0.77 [0.35-0.87] a	0.80 [0.51-0.99] b	0.73 [0.34-1.00] a	<.0001	0.77 ± 0.51
Inflection (InfP)	1.78 [0.00-3.00] a	1.17 [0.00-1.00] b	0.88 [0.00-1.00] c	<.0001	1.24 ± 1.76

 TABLE 2
 Mean (and interquartile range [IQR], 25th–75th percentile) of temporal (s) and spectral (kHz)

 parameters of whistles emitted by common bottlenose dolphins from Revillagigedo Archipelago (RVG), Mexico; Saint

 Peter and Saint Paul Archipelago (SPSP), Brazil; and Western Coast of Aragua (WCA), Venezuela.

Means in the same row followed by different lowercase letters were significantly different (p < .05) in the Kruskal-Wallis' test, followed by Dunn's multiple comparisons test, whereas mean values in the same row followed by the same letter were not statistically different (p > .05).



FIGURE 3 Violin plots showing the temporal and spectral parameters of whistles emitted by common bottlenose dolphin populations from Revillagigedo Archipelago (RVG), Mexico, Saint Peter and Saint Paul Archipelago (SPSP), Brazil; and western Coast of Aragua (WCA), Venezuela, including (1) minimum frequency (MinF), (2) maximum frequency (MaxF), (3) bandwidth (BanF), (4) start frequency (StaF), (5) end frequency (EndF), and (6) duration (Dur). Significant differences among locations are represented by an asterisk (Kruskal-Wallis test; p < .05), and no significant differences are represented by ns (Kruskal-Wallis test; p > .05).

but the signals in a shallow water region additionally suffer from reflection, scattering, and absorption due to the proximity of the boundaries formed by the sea surface and seabed (Bradbury & Vehrencamp, 2011; Rogers & Cox, 1988). Coastal environments can also receive organic matter input, that alter water proprieties, and the signals can degrade more easily or suffer sound distortion. Thus, it is possible that upsweep whistles found here propagate more effectively in coastal environments because they can overcome the challenges of sound degradation and attenuation. In the same way alarm calls in other animals are usually shorter than other complex social signals, so they stand out from the background noise in the environment (Seiler et al., 2013), simpler and more straightforward signals like ascending whistles may be better suited to shallow conditions, taking advantage of the same properties and enhancing their effectiveness in communication.

Overall, acoustic divergence in the bottlenose dolphin repertoire can be influenced by environmental acoustic adaptations (Baron et al., 2008; Jones & Sayigh, 2002; La Manna et al., 2013, 2017, 2019; Luis et al., 2016, 2021; Morisaka et al., 2005; Papale et al., 2014, 2015; Rako-Gospić & Picciulin, 2016; Wang et al., 1995), social and/or behavioral factors (May-Collado & Wartzok, 2008; Quick & Janik, 2008), and geographic isolation and/or genetic divergence (Janik & Slater, 2000; La Manna et al., 2013, 2017; Wang et al., 1995; Wilkins et al., 2012), and any or all of these factors may be influencing the acoustic and temporal parameters of whistle registered here.

The difference in acoustic behavior between the coastal dolphin population of WCA and the pelagic group (RVG and SPSP) could be the result of the most notable difference between the sites (their acoustic habitat conditions), which would be supported by the AAH (Morton, 1975). On the other hand, several factors influencing sound

propagation in water, such as surface conditions, bottom boundary variability, water column sound velocity properties, bathymetry, vegetation, and bottom type (Forrest, 1994; Forrest et al., 1993; Jensen et al., 2009). While these were not a priority in our preliminary study, which focused on highlighting similarities and differences between the evaluated populations, they warrant further investigation.

Another possible explanation is the difference in vessel traffic among locations. The coastal location "WCA" could be the noisiest location, because it is an important fishing area and had a mean vessel density of 0.27 artisanal boats/km² (Cobarrubia-Russo et al., 2021). While this area is not a marine protected area, it is worth noting that fishing in Venezuela is strictly artisanal (Cobarrubia-Russo et al., 2021). In contrast, the oceanic study sites were within marine protected areas with visitation restrictions. For example, only four ships per island were allowed at the same time in RVG, anchored with engines off, and SPSP is a conservation unit under governmental protection in Brazil (Brazil, 2018). Hence, WCA could be noisier because of its more intense vessel traffic, which would lead to the significantly higher MaxF values registered, possibly in favor of signal transmission (AAH), above the frequency bands where vessel traffic is being produced. Some studies of *T. truncatus* and *Delphinus delphis* found that, during exposure to anthropogenic and natural noises, frequency parameters of whistles tend to increase and compensate for the masking effects of ambient noise on acoustic communication (Papale et al., 2015), which in line with the AAH suggests that animals adapt their vocalizations to optimize signal transmission in their specific environment.

Finally, in addition to the possible causes associated with the geographic differences discussed here, there are many social drivers for whistle features in bottlenose dolphins, including individual variation, social learning (e.g., mimicry), group size, group composition, and behavior (such as foraging, milling, social, and travel activities; Quick & Janik, 2008; May-Collado & Wartzok, 2008). For example, personalized acoustic signals, called signature whistles (SWs; Rio, 2023; Rio et al., 2022) express identity information. When they are not taken into consideration (to avoid overestimation of the most repeated whistle structure), they can influence geographic comparisons since they are emitted as repetitive patterns and represent nearly 50% of coastal and ocean bottlenose dolphin whistles produced by free-ranging animals in the wild (Rio et al., 2022).

In the future, continuous acoustic monitoring of the different assessed geographical regions could better clarify and parse out whether some or all of the recorded differences between whistles reflect environmental, social, behavior, genetic and/or methodological differences (for example, the large gap between recording years at compared locations and the different recording protocols at these sites are a limitation) that may have indirectly resulted from the geographic distance between sites. Therefore, before saying what variability component in the acoustic communication of geographically distinct delphinid populations reflects physical distance, or isolation, between these populations, one must first rule out, or take into consideration, the likely influence of genetic, cultural, social, and environmental aspects or the multicausal combination of factors. In addition, apparent acoustic geographic variation may simply correspond to transient variation among individuals within a given population. Future studies in these locations should focus on a fine-grained comparison of variations between whistle types, measure ambient noise levels in each location, and incorporate acoustic propagation modeling.

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AUTHOR CONTRIBUTIONS

Raul Rio: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. Daniel Romero-Mujalli: Data curation; formal analysis; writing – review and editing. Sergio Cobarrubia-Russo: Data curation; formal analysis; writing – review and editing. Hiram Rosales Nanduca: Writing – review and editing. Flávio Medeiros Vieites: Writing – review and editing. Thales Renato Ochotorena de Freitas: Project administration; writing – review and editing. Lilian Sander Hoffmann: Data curation; formal analysis; investigation; writing – review and editing.

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