Received: 28 October 2019 | Accepted: 16 March 2020
DOI: 10.1111/mms.12690

NOTE

Marine Mammal Science

Geographic variation in the whistles of bottlenose dolphins (*Tursiops* spp.) in the southwestern Atlantic Ocean

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Description of whistle characteristics and acoustic behavior of *Tursiops* spp. are available throughout the world (Quick and Janik, 2008; Santos, Louro, Couchinho, & Brito, 2005; Schultz & Corkeron, 1994; Steiner, 1981; Wang, Würsig, & Evans, 1995), though most studies have been carried out in the Northern Hemisphere. In the southwestern Atlantic Ocean (SWAO), descriptions of whistles of bottlenose dolphins from the Patos Lagoon estuary (Azevedo, Oliveira, Dalla Rosa, & Lailson-Brito, 2007) and from the Atlantic Uruguayan coast (Tellechea, Bouvier, Cambon-Tait, & Norbis, 2014) have been done, as well as comparisons between whistles recorded in the Tramandaí and in the São Pedro e São Paulo archipelago, located 1,000 km away from the coast in the central equatorial Atlantic Ocean (Hoffmann et al., 2012). Also, whistles of bottlenose dolphins recorded in the SWAO were included in comparisons among several dolphin species (Amorim et al., 2019; Lima et al., 2016) and whistles of an unknown ecotype of bottlenose dolphins recorded in San José gulf, Argentina were included in a geographic variation study (Wang et al., 1995).

The SWAO provides an excellent opportunity to investigate whistle geographic variation of *Tursiops* spp. at local and regional scales, since recent studies indicate that there are two separate forms of the genus inhabiting these waters (Costa, Rosel, Daura-Jorge, & Simões-Lopes, 2016; Fruet et al., 2017; Wickert, Von Eye, Oliveira, & Moreno, 2016): *Tursiops truncatus gephyreus* (Lahille's bottlenose dolphin), distributed from southern Brazil to central Argentina, and *Tursiops truncatus truncatus* (common bottlenose dolphin), which is widely distributed along the SWAO, including southeastern Brazil (Oliveira et al., 2019). Lahille's bottlenose dolphins are found in relatively small populations coastally and associated with estuaries, river mouths, and lagoons (Fruet, Secchi, Di Tullio, & Kinas, 2011; Fruet et al., 2017; Genoves, Fruet, Di Tullio, Möller, & Secchi, 2018; Laporta, Martins, et al., 2016; Simões-Lopes & Fabian, 1999), whereas common bottlenose dolphins form relatively large, panmictic populations (Oliveira et al., 2019). We present a comparison between the whistles of Lahille's bottlenose dolphins recorded in southern Brazil and Uruguay and common bottlenose dolphins recorded in southeastern Brazil, and a comparison among the three adjacent populations of Lahille's bottlenose dolphins in southern Brazil and Uruguay.

Data collection occurred between 2004 and 2017 in four regions: Rio de Janeiro coast (southeastern Brazil) for common bottlenose dolphins, the Tramandaí channel, Patos Lagoon estuary and adjacencies (southern Brazil), and Uruguay (along the coast, between La Paloma and Cabo Polonio, Rocha department) for Lahille's bottlenose dolphins (Figure 1, Table 1). These four areas differ in environmental characteristics and anthropogenic use. In Rio de Janeiro, the study area was the only one in open waters, with larger water depth than the other locations (Table 1). This area presents heavy ship traffic due to port activity. Frequent ship traffic due to port activity is also found in Patos

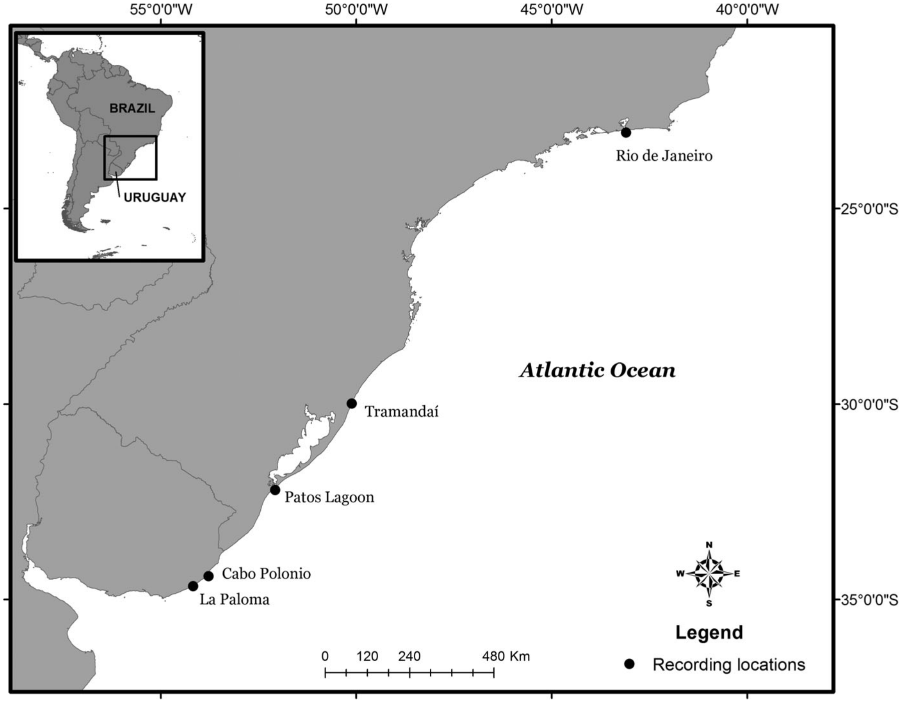

FIGURE 1 Map of the different regions where the recordings of whistles of *Tursiops* spp. were made for Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*), between La Paloma and Cabo Polonio in Uruguay, and Patos Lagoon estuary and the Tramandaí channel in southern Brazil, and for common bottlenose dolphins (*Tursiops truncatus truncatus*), in Rio de Janeiro, Brazil.

TABLE 1 Information about the groups of *Tursiops truncatus gephyreus* (Uruguay, Patos Lagoon estuary, and Tramandaí) and *Tursiops truncatus truncatus* (Rio de Janeiro) recorded in the southwestern Atlantic Ocean (SWAO) and sample size of whistles used in the comparisons for each region

Region	Month/year of recording	Number of groups recorded	Number of individuals per group	Water depth (m)	Number of selected whistles
Uruguay	Jan 2017 to May 2017	8	2–10	3.7–4.4	42
Patos Lagoon estuary	Jan 2017 to Jan 2018	64	1–30	2.0–21	100
Tramandaí	Jan 2004 and Apr 2013	4	2–8	3.0–6.4	100
Rio de Janeiro	Mar 2014	1	50	50	91

Lagoon estuary, however, along the open coast, smaller boats such as artisanal gillnet fishery boats are more common. In the Tramandaí channel, there is generally ship traffic associated with an oil terminal and artisanal fishery boats. The study area in Uruguay presents a small port of artisanal fishery and recreational boats in La Paloma.

Hydrophones with different specifications were used to record whistles among the locations. A calibrated C54XRS hydrophone (http://www.cetaceanresearch.com; −165 ± 3.0 dB re: 1 V/μPa, 9 Hz–100 kHz) was used in Rio de Janeiro and another hydrophone of the same model (http://www.cetaceanresearch.com; −185 dB ± 3 re:1 V/μPa, 16 Hz–44 kHz) was used in the Tramandaí channel. A HTI-96-MIN hydrophone (http://www.hightechincusa.com; −165 ± 1.0 dB re:1 V/μPa, 5 Hz–30 kHz) was used in Patos Lagoon estuary and in Uruguay. A Tascam DR-680 recorder (96 kHz sample rate) was used for recordings in Rio de Janeiro, Patos Lagoon, and Uruguay, and a Fostex FR-2 recorder (88.2 kHz sample rate) was used in the Tramandaí channel. The hydrophone was placed at a depth of 2–5 m for all recordings. Recordings were made aboard outboard-powered boats up to 7.5 m in length, with the engines turned off and under similar weather conditions (Beaufort sea states ≤2), except in the Tramandaí channel, where they were made from land, 3 m from the coast by the use of an extension, which was suspended above the water and had the hydrophone submerged from its distal end.

In the recording sessions in all the regions, whenever a group of *Tursiops* spp. was encountered, the number of individuals was counted, and the area was checked to confirm if there were no other groups around. Recordings files generally ranged from two to five minutes in duration, were monitored by the use of headphones, and were interrupted whenever a change in the group activity was observed. In Rio de Janeiro, the recordings were opportunistic, however, there were more individuals in the one group recorded than in any group found in the other regions (Table 1). In Uruguay and southern Brazilian regions, the same individuals may have been present in more than one group and recording day, since the majority of these populations is composed of year-round residents that are resighted through many consecutive years (Laporta, Fruet, and Secchi, 2016a). However, encountering the exact same group on different days is rare, since the nonrandom association between individuals observed in Patos Lagoon and Uruguay consists mostly from short-term relations (Genoves et al., 2018; Menchaca, Laporta, and Tassino, 2019). Also, the recording days in the Tramandaí channel are approximately 9 years apart, which makes it unlikely to involve the same groups.

Good quality whistles with complete, clear spectral contours were manually selected for analysis of acoustic parameters, which was done in Raven 1.5 (Cornell Lab of Ornithology; FFT of 512 points, Hanning window, 50% overlap). Then, 100 whistles of each Patos Lagoon and the Tramandaí channel were randomly selected for analysis to have a more evenly sized sample for comparisons with the other regions (Table 1), since more good-quality whistles were obtained from these regions than the others. In Patos Lagoon, 1,926 good quality whistles were obtained from 18 hr and 54 min of recordings that were made from 64 dolphin groups with one to 30 individuals per group, in 22 days. In the Tramandaí channel, 137 good quality whistles were obtained from 2 hr and 23 min of recordings that were made in 2 days of four groups with two to eight individuals. In Uruguay and Rio de Janeiro, 42 and 91 good quality whistles were selected from 2 hr and 47 min and 1 hr and 25 min of recordings, respectively. Recordings in Uruguay were made from eight groups, ranging from two to ten individuals, in 3 days, while in Rio de Janeiro recordings were of one group with 50 individuals. Whistles from Patos Lagoon and the Tramandaí channel were selected from different groups from all the days of recordings in these regions, so that different social contexts could be represented. Also, if a whistle contour form was found repeated more than once in a sequence, only one was selected for analysis. These criteria were chosen in order to minimize oversampling of the same groups and/or individuals.

Seven variables were measured from each whistle: starting frequency (SF); ending frequency (EF); minimum frequency (MINF); maximum frequency (MAXF); duration (DUR); delta frequency (DF – difference between maximum and minimum frequency); and number of inflection points (INF, defined as a change in the whistle contour from ascending to descending or vice-versa). Mean frequency (MF) was calculated as the average of the frequency variables extracted from the contour. These parameters were chosen to be consistent with previous acoustical studies of delphinids (Andrade et al., 2015; Azevedo et al., 2010, 2007; Bazúa-Durán and Au, 2004; Lima et al., 2016; May-Collado & Wartzok, 2008; Santos et al., 2005).

Descriptive statistics were calculated to provide mean, standard deviation, median, and range for each whistle parameter measured (Table 2). Because initial graphic exploration of the data indicated that acoustic parameters were not normally distributed and that, in general, homoscedasticity could be assumed (Quinn and Keough, 2002), nonparametric Kruskal-Wallis analysis was done ($p < .05$) to investigate possible differences among whistles of the four regions for each acoustic parameter. This test was followed by a post-hoc multiple comparison of mean ranks test to examine the pairwise comparisons between regions. To control for type I error, the Bonferroni procedure was applied to each pairwise comparison (Quinn and Keough, 2002), so the significance level was adjusted to $\alpha = 0.008$. Principal Component Analysis (PCA) was used to determine which factors best explained the variations in the data set and which acoustic parameters presented strong correlations (above 0.7) with these factors (Quinn and

TABLE 2 Mean ± standard deviation, median, and minimum-maximum values of acoustic parameters of whistles of *Tursiops truncatus gephyreus* (Uruguay, Patos Lagoon estuary and the Tramandaí channel) and of *Tursiops truncatus truncatus* (Rio de Janeiro). Frequency measurements include starting (SF); ending (EF); minimum (MINF); maximum (MAXF); delta (DF- difference between maximum and minimum frequency); and mean (MF). These are reported in kHz. Other acoustic parameters include duration (DUR) reported in seconds and number of inflection points (INF)

Parameters	Uruguay (*n* = 42)	Patos Lagoon estuary (*n* = 100)	Tramandaí (*n* = 100)	Rio de Janeiro (*n* = 91)
SF	7.0 ± 3.1 5.6 (2.6–14.0)	7.2 ± 3.4 6.4 (2.1–17.3)	6.5 ± 2.5 5.8 (2.7–14.2)	12.3 ± 3.7 11.6 (6.8–27.2)
EF	6.7 ± 2.3 6.5 (3.5–13.2)	7.8 ± 4.0 6.3 (1.9–19.1)	8.9 ± 3.3 8.5 (3.1–17.3)	13.3 ± 4.4 13.3(3.7–27.4)
MINF	4.9 ± 1.6 4.3 (2.6–9.6)	4.5 ± 1.4 4.2 (1.8–7.6)	5.3 ± 1.6 5.2 (2.2–12.5)	10.0 ± 2.9 9.9 (3.7–18.4)
MAXF	10.6 ± 3.5 11.3 (4.6–17.2)	12.4 ± 3.5 12.7 (4.0–21.1)	11.4 ± 2.3 11.2 (7.0–21.2)	17.2 ± 4.3 17.2 (8.8–33.1)
DF	5.7 ± 3.8 4.8 (0.5–13.9)	7.9 ± 3.6 8.0 (0.6–17.6)	6.1 ± 2.6 6.1 (0.7–15.5)	7.2 ± 3.9 6.4 (1.3–21.8)
MF	7.0 ± 1.9 7.1 (3.5–10.6)	8.0 ± 2.1 8.2 (3.0–13.5)	7.6 ± 1.5 7.5 (5.3–13.6)	12.0 ± 2.7 12.2(5.9–19.2)
DUR	0.7 ± 0.5 0.8 (0.06–2.0)	0.7 ± 0.4 0.5 (0.08–1.8)	0.6 ± 0.5 0.3 (0.05–2.9)	0.8 ± 0.6 0.6 (0.1–2.6)
INF	1.8 ± 2.0 1.0 (0–8)	1.5 ± 1.8 1.0 (0–10)	1.4 ± 1.9 1.0 (0–9)	1.4 ± 1.6 1.0(0–8)

Keough, 2002). The coordinates of the two main factors of the PCA were then used in a cluster analysis (joining tree method, single linkage and Euclidean distance) to determine potential similarities in the acoustic parameters of whistles by region (Quinn and Keough, 2002). Statistical analysis was done in Statistica 7.0 (Stasoft, Inc., Tulsa, OK).

A total of 333 whistles were analyzed from the four regions (Table 1). We only found significant differences in frequency parameters (Kruskal-Wallis test, $H[3,\ n = 333]$, $p < .001$) among the whistles of bottlenose dolphins recorded in the different regions. Whistles from Rio de Janeiro averaged from 4 kHz to 7 kHz higher for five frequency parameters (SF, EF, MINF, MAXF, and MF) than the whistles of the dolphins recorded southward (multiple comparison test, $p < .001$) and no differences were observed in DF values (multiple comparison test, $p > .008$). Among southward dolphins, whistles recorded in the Tramandaí channel presented lower DF values (multiple comparison test, $p = .0008$) than the ones recorded in the Patos Lagoon estuary. Whistles recorded in the Patos Lagoon estuary presented higher DF values (multiple comparison test, $p = .003$) than the ones recorded in Uruguay. We found no significant differences between whistles recorded in the Tramandaí channel and in Uruguay (multiple comparison test, $p > .008$). All tables with the results for Kruskal-Wallis and post-hoc pairwise comparisons among regions for each acoustic parameter are given in the supplementary materials (Tables S1—S8). The PCA results showed that factors 1 and 2 explained 74.1% of the variation in the data set, with eigenvalues of 47.9% and 26.2%, respectively. Except for DF, all frequency parameters showed strong correlations with factor 1, while DUR and INF showed strong correlations with factor 2 (Table 3). Cluster analysis showed that greater differences were found between whistles recorded in Rio de Janeiro and the other regions, while fewer differences appeared to be in the finer geographic scale between whistles recorded in the southern Brazilian localities and the ones recorded in Uruguay (Figure 2).

Whistles emitted by bottlenose dolphins showed considerable variability in acoustic parameters. The largest differences were found in frequency parameters among whistles recorded in regions separated by longer distances, a result previously reported in other delphinid studies (Azevedo & Van Sluys, 2005; Baron, Martinez, Garrison, & Keith, 2008; Rossi-Santos & Podos, 2006; Wang et al., 1995). The apparent lack of differences in duration and

Parameters	Factor 1	Factor 2
SF	**0.76**	−0.12
EF	**0.73**	−0.35
MINF	**0.75**	−0.48
MAXF	**0.94**	0.18
DF	0.49	0.63
MF	**0.99**	−0.04
DUR	0.20	**0.82**
INF	0.13	**0.80**

TABLE 3 Factor–variable correlations (factor loadings) of acoustic parameters of whistles of *Tursiops truncatus gephyreus* (Uruguay, Patos Lagoon estuary and the Tramandaí channel) and of *Tursiops truncatus truncatus* (Rio de Janeiro) with factors 1 and 2 from principal component analysis. These factors explain 74.1% of the variance (47.9% and 26.2%, factor 1 and factor 2, respectively). Bold numbers represent strong correlations of acoustic parameters to each factor

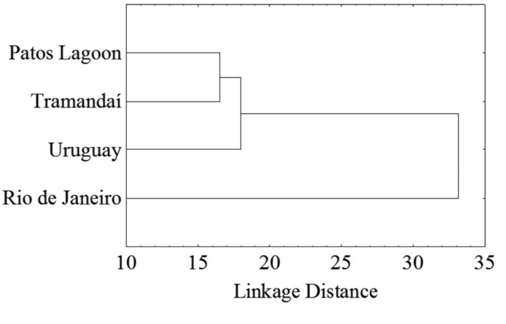

FIGURE 2 Cluster results (joining tree method, single linkage and Euclidean distance) based on coordinates of factors 1 and 2 of the PCA done with acoustic parameters from whistles of Lahille's dolphins (Uruguay, Patos Lagoon estuary and the Tramandaí channel, in southern Brazil) and common bottlenose dolphins (Rio de Janeiro, Brazil). These factors explained 74.1% of the variation among whistles. Shorter linkage distances in the cluster represent higher similarities than longer ones.

number of inflection points in the present study may be influenced by the high intrapopulation variability normally found for these parameters (Steiner, 1981; Wang et al., 1995). Variation in these parameters may be the result of individuals modulating these parts of the signal in order to transmit additional information and could be a function of interindividual variations (Wang et al., 1995), while frequency variables tend to stay more stable at individual level (Bazúa-Durán and Au, 2004; Wang et al., 1995).

Apart from the geographic distance, two nonexclusive scenarios may explain the differences between the whistles of bottlenose dolphins recorded in Rio de Janeiro and the ones in southern Brazil and Uruguay. In the first one, whistle divergences may be consistent with the findings of genetic and morphological studies. This suggests that the bottlenose dolphins from coastal waters in southern Brazil and Uruguay classify as a different taxonomic unit (species or subspecies) from those found in the southeastern Brazil, including Rio de Janeiro (Fruet et al., 2014; Oliveira et al., 2019; Wickert et al., 2016). In the second, whistle variability may be related to differences in environmental acoustic conditions (May-Collado & Wartzok, 2008; Morisaka, Shinohara, Nakahara, & Akamatsu, 2005) and ecological characteristics (Bazúa-Durán, 2004; Bazúa-Durán and Au, 2004).

Differences in frequency parameters were previously reported as showing high interspecific variation relative to variation between locations (Rendell, Matthews, Gill, Gordon, & Macdonald, 1999). This may reflect either genotypic influences on whistle parameters due to isolation between populations or influences of large geographic distances on acoustic characteristics and genotype independently (Papale et al., 2014b). Large geographic distances with low or nonexistent intermixing of individuals have lowered the vocal influence among groups and have contributed to the differences in whistle parameters of populations of *Tursiops* spp. in other regions (Baron et al., 2008; Papale et al., 2014a).

Residency and strict coastal habits of the Lahille's bottlenose dolphins in southern Brazil (Fruet, Daura-Jorge, Möller, Genoves, & Secchi, 2015; Fruet et al., 2011; Giacomo & Ott, 2016; Simões-Lopes & Fabian, 1999) and Uruguay (Laporta, Martins, et al., 2016) may have led to some of the differences observed in frequency parameters. These populations may have acoustic adaptations to the specific coastal environment they use, while the bottlenose dolphins found in Rio de Janeiro have not been identified as year-round residents and tend to be further from the coast. Differences in bottlenose dolphin whistles among areas in the Central-Eastern North Atlantic have been associated with adaptation to specific acoustic and social environments (Papale et al., 2014a). Habitat preferences between bottlenose dolphins recorded in the Gulf of Mexico and North Atlantic have also been suggested to influence differences in whistle characteristics between these areas, due to differences in noise levels or acoustic transmission properties (Baron et al., 2008).

The lower divergences found among whistles recorded in southern Brazil and Uruguay may be the result of the social connections among these populations and are in agreement with a genetic study that suggested the inclusion of these in an evolutionary significant unit (ESU) formed by local management units functioning as a metapopulation (Fruet et al., 2014). Resighting of an individual from Tramandaí moving to the adjacent Patos Lagoon (Laporta, Martins, et al., 2016), as well as individuals considered residents of the Uruguayan coast moving to adjacent coastal waters of Patos Lagoon estuary (Laporta, Martins, et al., 2016), confirmed the intermixing among local populations (Fruet et al., 2014). A recent study showed that some of those individuals sighted in Uruguay are socially connected to the social units composed of resident dolphins that are found at the mouth of Patos Lagoon estuary and in adjacent coastal waters (Genoves et al., 2018). Whistle similarities in macro- and micro-geographic comparisons among populations of other species, such as short-beaked common dolphins (*Delphinus delphis*) in the Mediterranean Sea and the Atlantic Ocean, have previously been suggested to be associated with gene flow among regions (Papale et al., 2014b). The lower divergences in whistle structure among these regions may also reflect similarities in ecological factors such as degree of fluidity of groups and other population structure characteristics (Bazúa-Durán, 2004). Efforts to obtain a larger sample in Uruguay, as well as to associate acoustics with the information on the population structures of the *Tursiops truncatus gephyreus* may aid in our understanding of the factors of these similarities.

The influence of distinct underwater noise levels among areas due to differences in ship traffic or sound transmission characteristics should be considered in future comparisons between the two subspecies and different areas. This is important because several studies have shown association between variations in acoustic parameters of whistles and environmental noise characteristics (Bittencourt et al., 2016; Lesage, Barrette, Kingsley, & Sjare, 1999; May-Collado & Wartzok, 2008; Morisaka et al., 2005). Also, the influence of behavioral state on whistle variation is another aspect that should be included in future comparisons, since several studies of different delphinid species have associated differences in whistle characteristics with variation in behavior (Azevedo et al., 2010; Bazúa-Durán & Au, 2004; Díaz López, 2011; May-Collado, 2013). However, investigating the effect of these factors was beyond the scope of this study.

Even though only one group of common bottlenose dolphins was recorded in this study, our results show large differences between their whistles and the ones of Lahille's bottlenose dolphins, in different frequency parameters. Simultaneously, the results point to fewer differences among the whistles of the populations of Lahille's dolphins, at a finer geographic scale, which belonged to more than one group and days of recording. Therefore, the results are in agreement with genetic and morphological studies that proposed two subspecies of *Tursiops* in the SWAO, but may also indicate adaptations to ecological and environmental characteristics in the different regions. Studying acoustic behavior is an important tool for our comprehension of macro- and microgeographic scale variation of bottlenose dolphins found in the SWAO.

ACKNOWLEDGMENTS

This work was supported by Rio de Janeiro State Government Research Agency (FAPERJ), Brazilian Council for Scientific and Technological Development (CNPq), Cetacean Society International, by the Organization for the Conservation of South American Aquatic Mammals – YAQU PACHA, Projeto GEF-MAR, the Brazilian Long-Term Ecological Research Program (PELD) from CNPq (Proc. 441492/2016-9), and the Fundação de Amparo a Pesquisa do Estado do Rio Grande do Sul (Proc. 16/2551-0000102-2). The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided access to the Portal de Periódicos and additional student support. For logistical support we thank the Faculdade de Oceanografia (UERJ), the Programa de Desarrollo de las Ciencias Básicas (PEDECIBA), the Iate Clube Jardim Guanabara, the Centro Nacional de Pesquisa e Conservação de Mamíferos Aquáticos - ICMBio/MMA, Ricardo Laporta and the National Direction of Aquatic Resources (DINARA-MGAP). Additionally, the work was possible due to the efforts of the staffs of the Museu Oceanográfico 'Prof. Eliézer C. Rios' FURG, the Laboratory of Ecology and Conservation of Marine Megafauna (ECOMEGA-FURG), and the Laboratory of Aquatic Mammals and Bioindicators (MAQUA). We also thank engineer Orlando Afonso, from the Brazilian Navy Research Institute (IPqM) for technical support and Pedro González and Cecilia Laporta for field assistance. I.M.S.L. was provided a FAPERJ Nota 10 scholarship, L.S.H. and S.M.B. a CNPQ scholarship, L.B. received a post-doctoral scholarship from FAPERJ (PDR-10), L.D.R., A.F.A., and J.L.B. have research grants from CNPQ (PQ2, PQ2, PQ1D, respectively). A.F.A. and J.L.B. also have research grant from UERJ (Prociência) and P.F.F. was provided a research fellowship GEF-MAR and CAPES-PNPD Institutional. There are no conflicts of interest to declare, with regards to anything that could influence the objectivity of the authors in collecting, interpreting, and reporting the findings presented in this study.

AUTHOR CONTRIBUTIONS

Isabela Lima: Conceptualization; data curation; formal analysis; investigation; methodology; resources; supervision; validation; visualization; writing-original draft; writing-review and editing. **Rihel Venuto:** Data curation; formal analysis; methodology; resources; visualization; writing-review and editing. **Carolina Menchaca:** Data curation; formal analysis; funding acquisition; methodology; resources; visualization; writing-review and editing. **Lillian Hoffmann:** Data curation; formal analysis; methodology; resources; visualization; writing-review and editing. **Luciano Dalla Rosa:** Data curation; funding acquisition; resources; writing-review and editing. **Rodrigo Genoves:** Visualization;

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Lima IMS, Venuto R, Menchaca C, et al. Geographic variation in the whistles of bottlenose dolphins (*Tursiops* spp.) in the southwestern Atlantic Ocean. *Mar Mam Sci*. 2020;36:1058–1067. https://doi.org/10.1111/mms.12690