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Differences in the whistles of two ecotypes of bottlenose dolphins from the Gulf of California

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Abstract: Intraspecific whistle variation in dolphins has been explained in the context of geographical isolation, soundscape, and social structure. Whistles of two ecotypes of bottlenose dolphins from La Paz Bay, Gulf of California, were analyzed. Both ecotypes showed similar whistle contours. However, they could be identified by contour maximum frequency which was predominantly above 15 kHz for oceanic dolphins and below 15 kHz for coastal dolphins. The different whistle frequencies of the two ecotypes could result from differences in group size and acoustic characteristics of their respective habitats, suggesting potential future passive acoustic monitoring applications. © 2023 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

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1. Introduction

The common bottlenose dolphin (*Tursiops truncatus*) is one of the most abundant and widely distributed cetacean in the world (Wells *et al.*, 2019). Throughout its distribution, a coastal and an oceanic ecotype have been described (Wells and Scott, 1999). The two ecotypes differ in morphology (Díaz-Gamboa, 2003), genetic structure (Segura *et al.*, 2006), group size, and habitat use (Bearzi *et al.*, 2009; Viloría-Gómora and Medrano-González, 2015), diet (Barros *et al.*, 2000), and whistle repertoire (Hoffmann *et al.*, 2012; Peters, 2018). Specifically in the Gulf of California, the coastal ecotype is larger with lighter pigmentation and a shorter rostrum compared to the oceanic counterpart (Díaz-Gamboa, 2003; Salinas Zacarías, 2005; Segura *et al.*, 2006). The ecotypes also differ in group size. The oceanic ecotype is generally found in groups of up to 300 dolphins, while the coastal one lives in groups with less than 20 dolphins (Salinas Zacarías, 2005).

The common bottlenose dolphins produce narrow-band frequency-modulated whistles for communication (King and Janik, 2013), with a frequency range of 1–35 kHz and variable duration (May-Collado and Wartzok, 2008; Richardson *et al.*, 2013). Intraspecific whistle variations in common bottlenose dolphin populations were found at both macro- and micro-geographic scales (Wang *et al.*, 1995; May-Collado and Wartzok, 2008; Papale *et al.*, 2014; Peters, 2018; Luís *et al.*, 2021).

Differences in vocalizations between neighboring populations of potentially interbreeding individuals are called dialects and can be transmitted through learning. On the contrary, differences over long distances and between populations that normally do not interbreed are referred to as geographical variation (Conner, 1982). Dialects have been found in killer whales (Filatova *et al.*, 2012), sperm whales (Rendell and Whitehead, 2003), and short-finned pilot whales (Van Cise *et al.*, 2018). However, whistle characteristics variations in dolphins have been generally considered geographical variations more than dialects (May-Collado and Wartzok, 2008). Neighboring dolphin populations have been previously distinguished based on differences in their whistle contour frequency and duration (May-Collado and Wartzok, 2008; Hoffmann *et al.*, 2012; Peters, 2018). In contrast, variation in whistle modulation (e.g., inflection points and number of loops) is thought to be related to the emotional state of dolphins such as danger, alertness, and stress (Esch *et al.*, 2009; Perez-Ortega *et al.*, 2021), and whistle contour type appears to be related to the behavior (Díaz López, 2011).

However, the causes of intraspecific whistle differences still need clarification. For species characterized by a fission-fusion social structure such as the common bottlenose dolphin (Connor *et al.*, 2000), acoustic variations have been associated with group size and composition (Wang *et al.*, 1995; Heiler *et al.*, 2016; La Manna *et al.*, 2020). Variables such as geographic distance and population genetic structure may also play an important role in whistle geographical variation

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(Papale *et al.*, 2014). Dolphin whistle frequency and temporal characteristics are useful in outlining the presence of distinct groups based on genetic and environmental features (Papale *et al.*, 2021). Some researchers suggest that the further apart the populations, the greater the difference in whistles (Bazúa-Durán and Au, 2004; Rossi-Santos and Podos, 2006). However, some exceptions have been found in the whistles of spinner dolphins of Brazil (Camargo *et al.*, 2006).

Moreover, according to the environmental adaptation hypothesis (Ey and Fischer, 2009) dolphins could modify their whistle frequency characteristics to specific environmental situations. Since sound transmission and ambient noise can vary locally, dolphin populations with different acoustic environments may show variation in whistle characteristics, contributing to the geographical acoustic divergence (May-Collado and Wartzok, 2008; Papale *et al.*, 2015; Fouda *et al.*, 2018; La Manna *et al.*, 2020). Whistle variation could also be related to morphological differences in body size between populations, with bigger animals producing lower frequency signals (Morton, 1977).

Here, we study the whistle repertoire and acoustic structure of the coastal and oceanic ecotypes of common bottlenose dolphins in La Paz Bay, Gulf of California. Given the differences on genetics, habitat use, group size, and morphology, we hypothesize that whistle repertoire may vary between ecotypes.

2. Materials and methods

2.1 Data collection

This study took place in La Paz Bay (Fig. 1), Mexico, between October 2020 and September 2021. The recording effort was 15 h and 58 min from a total of 27 groups of dolphins recorded (coastal = 21, oceanic = 6; Fig. 1, supplementary material¹).

Boat surveys were conducted with a 7.3 m motorized research vessel under favorable weather conditions (Beaufort scale ≤ 2). Acoustic recordings were made with the engine off using a Reson TC4013.1 hydrophone (sensitivity $-211 \text{ dB}_{\text{Rms}} \pm 3 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$, frequency response 1 Hz to 170 kHz, omnidirectional) connected through a Reson VP2000 Voltage Preamplifier EC6081 (Reson, Coleta, CA) (50 dB gain, 500 Hz high-pass filter, 50 kHz low-pass filter) to a Marantz PMD661 (Marantz, Cumberland, RI) recorder (sampling rate 96 kHz, 24 bits resolution). For each recording session, the ecotype and group size were recorded. Coastal and oceanic ecotypes were distinguished visually based on their morphological differences (Díaz-Gamboa, 2003; Salinas Zacarías, 2005; Segura *et al.*, 2006). No mixed groups were encountered.

2.2 Acoustic analyses

Acoustic recordings were first inspected in the spectrogram view of Raven Pro (version 1.5 Cornell University, Laboratory of Ornithology, New York) in the time-frequency domain [512-point fast Fourier transform (FFT), 512 points Hann window, 50% overlap]. Non-overlapping whistles with complete and clearly visible contours were selected for further analysis in Luscinia (version 2.16.10.29.01) (Lachlan, 2007). In Luscinia, the spectrogram was set at 10 ms frame length, 5 ms time step, 48 kHz maximum frequency, 1024 spectrograph point, Hann window, and a 50% overlap. The fundamental frequency contour of each whistle was manually traced with the cursor and standard acoustic characteristics were automatically extracted in Luscinia (Fig. 2). To avoid pseudo-replication of stereotyped whistles, signals with identical time-frequency contours visually matched in Luscinia by a trained observer were considered only once.

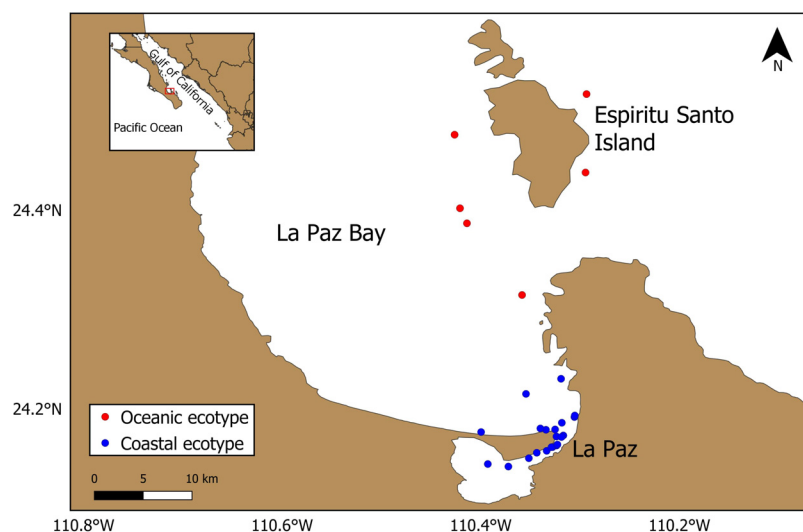


Fig. 1. Locations of the common bottlenose dolphin ecotypes considered in the analysis (generated with QGIS, version 3.6.3). Shapefile of Mexico was provided by Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO).

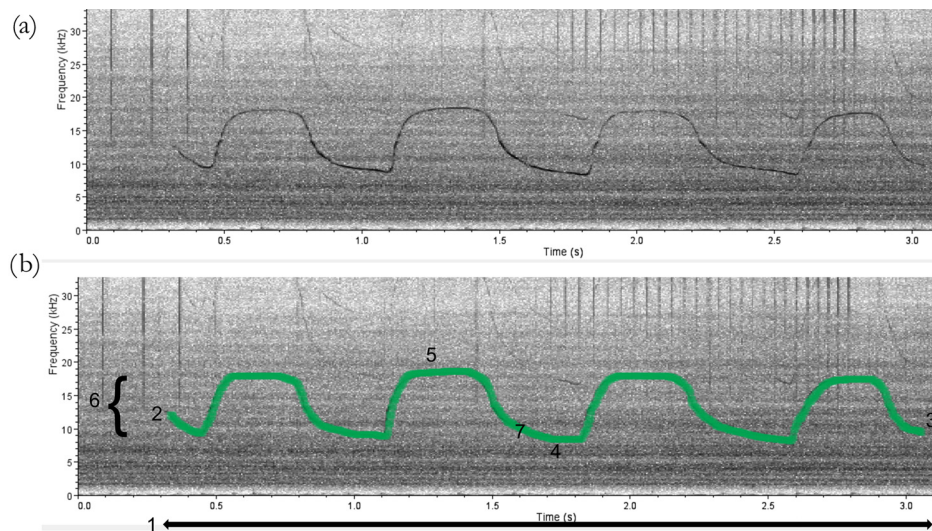


Fig. 2. Whistle analysis process in Luscinia software before (a) and after (b) the contour selection. Spectrogram: 1024 points FFT, Hann window, 50% overlap. (1) duration, (2) starting frequency, (3) ending frequency, (4) minimum frequency, (5) maximum frequency, (6) frequency range, (7) peak frequency.

A total of 920 whistles (coastal, $n = 505$; oceanic, $n = 415$) were obtained from the selection process and used for the following analyses.

2.3 Statistical analyses

The normality and homoscedasticity of the data were tested by Shapiro-Wilk and Levene's tests, respectively. As not all the data showed normal distribution, non-parametric Mann-Whitney U-tests were conducted to compare the whistle characteristics between the two ecotypes. Statistical significance was evaluated using a Bonferroni-adjusted alpha value calculated as the standard alpha value divided by the number of tests ($0.05/7$, α corrected = 0.007). All statistical analyses were performed in R software (version 4.2.1) with the RStudio interface (version 2022.07.2).

Random Forest analysis (Breiman, 2001; Liaw and Wiener, 2002) was used to classify whistles into ecotypes using the *randomForest* package (Liaw and Wiener, 2002). For the Random Forest analysis only, to prevent the difference in the number of whistles from each ecotype from affecting the classification results, the sample size was matched between ecotypes using random subsets of equal size (size = 415 whistles for both ecotypes). A random subset of approximately 2/3 of the samples (67%) was used as a training data set to generate the Random Forest, with approximately 1/3 of the data (33%) omitted as the out-of-bag sample for cross-validating the classification accuracy of the model (Efron and Tibshirani, 1997). The number of trees was set at 15 000 which produced stable out-of-bag error estimates. The number of candidate predictor variables at each node was 1, which was found to have the lowest out-of-bag error. A total of 100 Random Forest models were run using different subsets of the whistles to train and test the model configurations and to obtain average classification rates. The Gini Variable Importance index for each whistle characteristic was considered to assess the degree to which each variable contributes to the model predictions (Breiman, 2001; Oswald et al., 2021). Partial dependence plots (Hastie et al., 2001) of the variable with the highest contribution were made for both ecotypes to graphically characterize relationships between individual explanatory variables and predicted probabilities obtained from the Random Forest analysis.

The comparison of the whistle contour repertoire between the two ecotypes was made using Luscinia's dynamic time warping algorithm (DTW) (Lachlan et al., 2010; Lachlan et al., 2013). The algorithm aims to find the optimal alignment of acoustic features between whistles and then facilitates the comparison of pairs of whistles through the measurement of Euclidean distances along this alignment. The DTW considers the frequency modulation within whistles, resulting in a more holistic comparison of whistle contour structure than comparisons of a few specific acoustic variables. The acoustic features used for the analysis and the relative weightings selected were: time = 10; fundamental frequency = 1; fundamental frequency change = 1; vibrato amplitude = 0.25 (Lachlan et al., 2013; Lachlan et al., 2018; Peters, 2018).

The DTW algorithm generated a pairwise dissimilarity matrix between whistles and it was subsequently used to make a Nonmetric Multidimensional Scaling (NMDS) plot (Lachlan et al., 2013) to visually quantify the divergence between the two ecotypes. NMDS was based on a two-dimensional solution with a stress value of 0.05.

3. Results

Bottlenose dolphin whistles varied significantly between ecotypes. Dolphins of the oceanic ecotype produced whistles at a higher maximum frequency ($W = 61\,784$, $p < 0.005$), peak frequency ($W = 68\,436$, $p < 0.005$) and wider frequency range

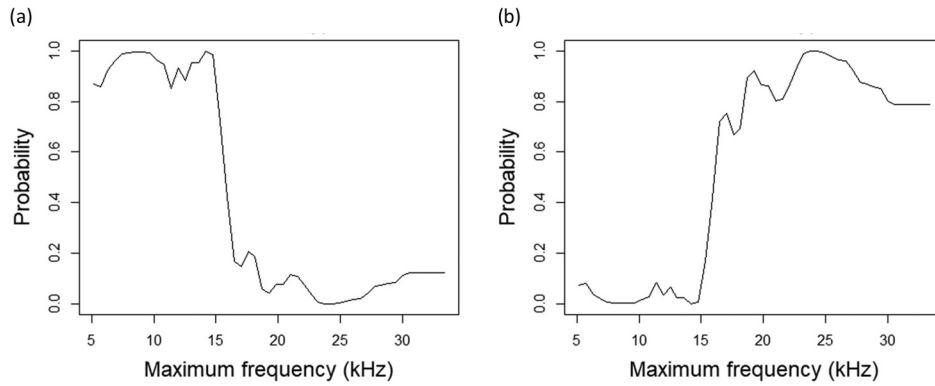


Fig. 3. Maximum whistle frequency partial dependence plot for coastal (a) and oceanic (b) ecotypes.

($W = 64\,708$, $p < 0.005$) compared to the whistles of the coastal ecotype. No significant differences were found in minimum frequency ($W = 96\,095$, $p > 0.005$), starting frequency ($W = 99\,671$, $p > 0.005$), ending frequency ($W = 102\,576$, $p > 0.005$), and duration ($W = 112\,827$, $p > 0.005$). Descriptive statistics and boxplots of the whistle characteristics are shown in the supplementary material.¹

The Random Forest model showed a mean accuracy of 71.19%. The Gini Variable Importance index identified maximum frequency, frequency range, and peak frequency the most important predictors of dolphin ecotype (see supplementary material¹).

Partial dependence plots showed that if the maximum frequency of the whistle was higher than 15 kHz, the chances of classifying that whistle contour as belonging to the oceanic ecotype increased. In turn, if the maximum frequency was lower than 15 kHz, there was a higher probability of classifying it into coastal ecotype (Fig. 3).

The NMDS showed a great overlap between the whistle contours of the two ecotypes, indicating similar whistle contour repertoires (Fig. 4). The percentage explained by the first two dimensions was 82.40%.

4. Discussion

This study finds that albeit whistle contour repertoires are similar between coastal and oceanic bottlenose dolphins, ecotypes can be distinguished based on whistle frequency. Correlations between genetic and acoustic structure have been already identified in common bottlenose dolphins. Papale *et al.* (2021) found that the variability of the whistles was consistent with their genetic differences suggesting acoustic analysis as a tool to discriminate different genetic groups even geographically close. In the present study, the best whistle predictors to distinguish between ecotypes are maximum frequency, frequency range, and peak frequency. Dolphins of the oceanic ecotype tended to produce whistles at higher frequencies than the coastal ecotype. This result agrees with previous studies conducted in New Zealand (Peters, 2018) and Brazil (Hoffmann *et al.*, 2012).

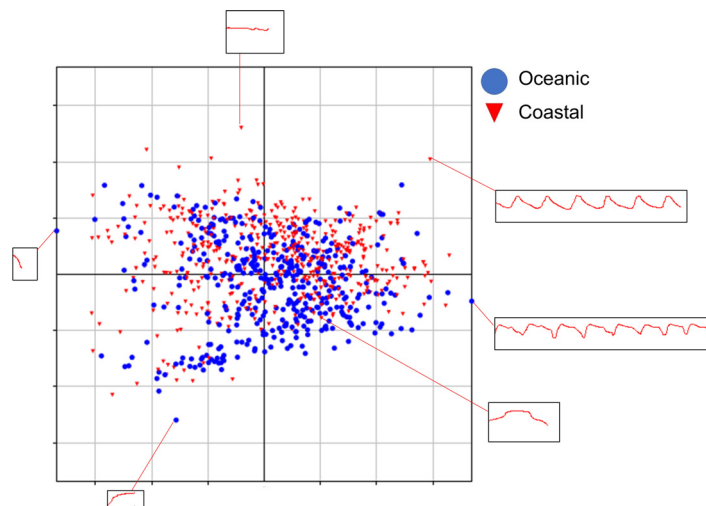


Fig. 4. NMDS of whistle comparisons. Each point represents a whistle contour (coastal, $n = 505$; oceanic, $n = 415$), and points that are close to each other have similar acoustic structure contours. Scales are not meaningful for NMDS ordinations and are omitted.

Differences between ecotypes in body size, habitat, and group size could be contributing to this result. A fundamental rule in animal communication is that, to a large extent, an animal's body size is inversely correlated with its signal frequency (Morton, 1977). Our results seem to fit this hypothesis as Díaz-Gamboa (2003) based on morphometric data, described the coastal ecotype of the Gulf of California as larger than the oceanic counterpart. Although previous research has found that in cetaceans the relationship between body size and signal maximum frequency disappears after accounting for phylogenetic relationships (May-Collado *et al.*, 2007), it is possible that within a species, differences in body size can be important; however, this relationship has been poorly studied. Nevertheless, in the present study, no measures of the body size were performed, thus it is not possible to establish whether the coastal individuals recorded were larger than the oceanic ones.

Group size, independent of genetic or ecological differences, could also cause whistle variation (Heiler *et al.*, 2016; La Manna *et al.*, 2020). It could be possible that in the large groups of the oceanic ecotype, the dolphins more distant from each other are not able to communicate due to the acoustic masking by the conspecific sounds (Quick and Janik, 2008), so they tend to use higher frequencies whistles to communicate with the closer individuals. Peters (2018) for example, recorded higher frequency whistles in “noisier” larger groups of oceanic bottlenose dolphins.

Another factor that can contribute to differences in whistle frequency between dolphin ecotypes is the habitat, both environmental and anthropogenic features (Papale *et al.*, 2015; Fouda *et al.*, 2018; La Manna *et al.*, 2020). Differences in whistle frequencies between the two ecotypes could represent adaptations to the local acoustic environment.

In this study, the coastal ecotype was found close to La Paz city, where the predominant substrate consists of sand and mud, with a depth range between two and seven meters (Gómez-Valdés *et al.*, 2003). The oceanic dolphins were found around Espiritu Santo Island, surrounded by deep waters up to 800 meters (CONANP, 2014). Quintana-Rizzo *et al.* (2006) found that in shallow waters, where sound is reflected, scattered and absorbed by the surface and the seafloor, the active space of low-frequency whistles was larger than the one of high-frequency whistles. Coastal ecotype could emit low-frequency whistles to increase the active space of its signals.

In addition, anthropogenic noise could influence dolphin whistle acoustic structure (May-Collado and Wartzok, 2008; Heiler *et al.*, 2016; Fouda *et al.*, 2018; Perez-Ortega *et al.*, 2021; Antichi *et al.*, 2022a). In La Paz Bay the oceanic ecotype has been shown to decrease whistle frequencies in the presence of vessels while the coastal one increases them (Antichi *et al.*, 2022a). This result seems to exclude vessel noise as the explanation to the higher whistle frequencies of the oceanic ecotype compared to the coastal one. Moreover, the physical presence of the research vessel could also contribute to differences in whistle frequency between the two ecotypes (Antichi *et al.*, 2022b).

Finally, although whistles of oceanic and coastal dolphins varied in frequencies, their contour repertoires were very similar. Bottlenose dolphins have a relatively large whistle repertoire (Bazúa Durán *et al.*, 2013) that could vary according to different circumstances (Perez-Ortega *et al.*, 2021; Gagne *et al.*, 2022). It could be possible that, due to the large variability of the whistle contours, no particular distinction occurs when all the whistles are considered. In the present study, signature and non-signature whistles were both included. The two ecotypes belong to the same species and they could have had not enough divergence time to evolve with distinct whistle contours. In addition, the possible existing connectivity between them may provide opportunities for learning and sharing whistles (Jones *et al.*, 2020).

5. Conclusion

This study shows that oceanic and coastal bottlenose dolphin ecotypes in La Paz Bay share a similar whistle contour repertoire. However, the two ecotypes can be distinguished based on whistle maximum frequency, frequency range, and peak frequency. Differences in ecotype whistle frequency could aid in future passive acoustic monitoring in La Paz Bay.

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¹See supplementary material at <https://doi.org/10.1121/10.0019502> for further details.

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