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Whistle Repertoire And Structure Reflect Ecotype Distinction Of Pantropical Spotted Dolphins In The Eastern Tropical Pacific

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WHISTLE REPERTOIRE AND STRUCTURE REFLECT ECOTYPE DISTINCTION OF PANTROPICAL SPOTTED DOLPHINS IN THE EASTERN TROPICAL PACIFIC

A thesis presented

by

Manali Rege-Colt

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ABSTRACT

The pantropical spotted dolphin in the Eastern Tropical Pacific (ETP) is found in two genetically and phenotypically distinct ecotypes, coastal and offshore. These habitats have distinct acoustic characteristics and sound fields, which can lead to the evolution of distinct acoustic communication. Whistles are tonal sounds widely used by dolphins as they mediate species and individual recognition and social interactions. Here we study the intraspecific variation of pantropical spotted dolphin ecotypes in their whistle acoustic structure and repertoire. To compare spotted dolphin whistle repertoires, we used recordings obtained from boat-surveys throughout the species distribution in the ETP. Random forest classification performed with an accuracy of 83.99% and identified duration and peak and minimum frequency as most informative in distinguishing between ecotypes. Overall, coastal spotted dolphins produced whistles that were shorter in duration and lower in frequency than offshore dolphins. Ecotypes produced whistle repertoires that were similar in diversity, but different in contour composition, with the coastal ecotype producing 'simpler' whistles than offshore dolphins. The results of this study suggest that acoustic adaptations to coastal and offshore environments are important contributors to intraspecific variation of dolphin whistle repertoires.

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1. Introduction

Dolphins produce narrowband and frequency modulated tonal sounds, called whistles, that vary in duration and have fundamental frequencies ranging between 1 and 75 kHz (Lammers et al., 2003; May-Collado and Wartzok 2008, Samarra et al., 2010). Whistles are important in dolphin communication, as they convey information about identity, behavioral state, environment, and stress levels (Janik et al., 1994, May-Collado and Wartzok, 2008, Perez-Ortega et al., 2021). They are also used for group cohesion, coordination of activities, and maintaining communication when separated (King et al., 2019, 2021, Jakkola et al. 2018). In Indo-pacific bottlenose dolphins (*Tursiops aduncus*)(Morisaka et al., 2005 Hawkins, 2010), striped dolphins (*Stenella coeruleoalba*) (Papale et al., 2013), Guiana dolphins (*Sotalia guianensis*) (Rossi-Santos and Podos, 2006), bottlenose dolphins (*Tursiops truncates*) (May-Collado and Wartzok, 2008) and short beaked common dolphins (*Delphinus delphis*) (Azzolin et al., 2019), within species variation in whistle frequency and duration has been explained in the context of geographical and behavioral constraints (Rossi-Santos and Podos, 2006, May-Collado and Wartzok 2008, Azzolin et al., 2013, Papale et al., 2013, La Manna et al., 2021, Luis et al., 2021), within and between species social interactions (May-Collado 2010), and ecological adaptations (Morisaka et al., 2005, Perez-Ortega et al., 2021). In contrast, factors contributing to the variation in dolphin whistle repertoires diversity and complexity are less understood but may be dependent on group size and strength of conspecific associations (May-Collado et al., 2007), and culture (Oswald et al., 2021).

The pantropical spotted dolphin (*Stenella attenuata*) occurs in tropical and subtropical regions between 30-40 degrees north and 20-40 degrees south (Perrin,2009; Kiszka and Braulik, 2018). Despite its abundant distribution there is little information about their whistle repertoire. Studies in Brazil and the ETP have describe their whistles as consisting primarily of convex contours with frequency ranging from 8.2 to 31.1 kHz. (Oswald et al., 2003 ; Oswald et al., 2004 ; Oswald et al., 2007 ; Silva, 2016 ; Gong et al., 2019 ; Poupard et al., 2019 ; Pires et al. 2021). In the Eastern Tropical Pacific (ETP), pantropical spotted dolphins are classified into coastal (*S. attenuata graffmani*) and offshore (*S. attenuata attenuata*) ecotypes, with the latter divided into northeastern and western-southern stocks (Perrin et al., 1994, Escorza-Treviño et al., 2005). This classification is supported by phenotypic differences in skull morphology, body size, and spotting patterns (Perrin et al., 1991, 1994), genomic data (Escorza-Treviño et al., 2005, Leslie et al., 2019, Leslie and Morin 2018) and behavioral data (i.e., group size) (Perrin et al., 1985). The larger coastal ecotype is heavily spotted (Perrin and Hohn 1994), and lives within 200 km of the coast of Central America in groups of up to 50 individuals (Perrin et al., 1985; Dizon et al., 1994). In contrast, the offshore ecotype is lightly spotted and lives in pelagic habitats in groups of hundreds of individuals (Perrin and Hohn 1994). Molecular evidence suggests that the coastal and offshore ecotypes are genetically distinct and diverged (Leslie et al., 2019) and that coastal populations throughout Central America are genetically structured (Escorza-

Treviño et al., 2004), overall supporting recognition of ecotypes as separate conservation and management units.

The ecotype distinction of pantropical spotted dolphins warrants investigation into whether differences in habitat translate into their acoustic repertoire. Dolphins living in coastal and offshore habitats experience different soundscapes and sound fields (Erbe et al., 2019). These differences can directly affect propagation of acoustic signals, and drive changes in signal structure to overcome such constraints (Morisaka et al., 2005, Rako Gospic and Picciulin, 2016; Morisaka et al., 2016, Erbe et al., 2019), as predicted by the "acoustic adaptation hypothesis" (AAH) (Morton 1975). The AAH states that in response to environmental constraints, animals adjust their signals to maximize signal propagation and experience less attenuation and degradation. Genetic differentiation between spotted dolphin ecotypes and subsequent habitat specialization can be further reinforced by acoustic repertoire differentiation (Servedio 2004, Oloffson et al., 2011, Mason et al., 2014).

In this study we compare the whistle acoustic structure and repertoire diversity of offshore and coastal pantropical spotted dolphins. Our objectives are three-fold. This study (1) assesses the ability to differentiate between coastal and offshore whistles based on fundamental frequency contour, (2) explores how ecotype whistles are distinct in their acoustic structure using standard parameter measurements, and (3) compares the composition and diversity of whistle repertoires between ecotypes. We hypothesize that given ecotype distinction, overall repertoire diversity will differ, and that contour composition, whistle frequency and temporal characteristics should reflect acoustic adaptations to their distinct soundscapes (Mortin 1975). This study provides insights on the potential role of habitat specialization on dolphin whistle repertoire, with applications to identification of spotted dolphin ecotypes in passive acoustic monitoring efforts in the ETP.

2. Results

A total of 1,312 whistles (coastal= 657, offshore=655) were extracted from 11.2 hours of total recording effort (Table S1) and descriptive statistics of whistle acoustic structure by ecotype is shown in Table S2. Due to differences in recording sampling rate, whistles were subsampled at a sampling rate of 44.1 kHz resulting in subsample of 958 whistles (coastal= 492 coastal, offshore=466 offshore).

2.1 Ecotype Classification

Non-Metric Multidimensional Scaling (NMMDS) shows that the repertoires of both ecotypes overlap in their fundamental frequency contour but with potential for classification (Fig.1a). The k-medoids cluster analysis classified with a 70.06% accuracy whistle frequency contours by ecotype, with a total of 69.91% of the variation between ecotypes was explained by two dimensions (Fig.1b).

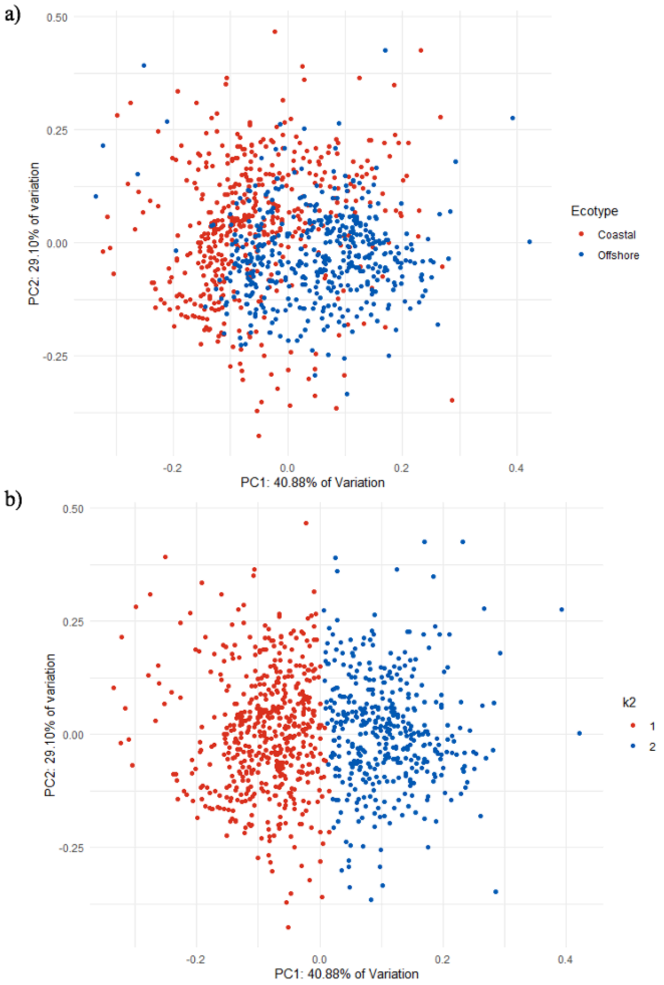


Figure. 1. Non-metric multidimensional scaling of coastal and offshore ecotype whistles based on (a) a dissimilarity matrix in which the relative distance between points is representative of their (dis)similarity and a (b) K-medoids cluster analysis in which the combined dataset of coastal and offshore whistles was blindly clustered into k=2 groups based on their dissimilarity.

Table 1. Results of confusion matrix from k-medoids clustering analysis with an accuracy of 70.06%.

	Reference	
Prediction	Coastal	Offshore
Coastal	374	167
Offshore	118	293

The random forest (RF) model classified whistle contours by ecotype with 83.99% accuracy (95% CI from 79.39%-87.91%). After a 67%-33% split of the data, 626 whistles (313 whistles per ecotype) were included in the training set and 306 whistles (153 whistles per ecotype) created the test set. The final RF model considered two random predictor variables (mtry=2) at each node split out of the seven possible predictors and grew 300 trees. The model had an OOB error rate of 16.61% and a kappa statistic of 0.68. Using the kappa statistic scale as per Landis and Koch (1997), the model is in "substantial" agreement with the true population.

Table 2. Results from the confusion matrix of random forest model performance on test data with an accuracy of 83.99%

	Reference	
Prediction	Coastal	Offshore
Coastal	131	27
Offshore	22	126

Mean Decrease in Accuracy (MDA) and Mean Decrease in Gini (MDG) values showed that duration, peak frequency (PF), and minimum frequency (MF) (in this order) were the predictor variables that allowed for the most accurate classification of whistles by ecotype. Statistically, the permutation of the previously listed parameters in the model resulted in the highest decrease in accuracy and node homogeneity. Partial Dependence Plots (PDP) provided insight into how the RF classified whistles using the top three most important predictors (Fig. 2). The duration PDP shows that whistles with a duration of at most ~0.6 seconds have a maximum likelihood of being accurately classified as the coastal ecotype, while whistles with a duration of at least 1 second are likely to be classified as the offshore ecotype. Meanwhile, the peak frequency PDP shows that whistles with peak frequency values less than or equal to 10 kHz are most likely to be classified as the coastal ecotype, while offshore whistles can be classified as having peak frequency greater than or equal to 10 kHz. The minimum frequency PDP shows that whistles with minimum frequency less than or equal to 6 kHz are most likely to be classified as the coastal ecotype while offshore whistles are accurately classified with minimum frequency above 10 kHz.

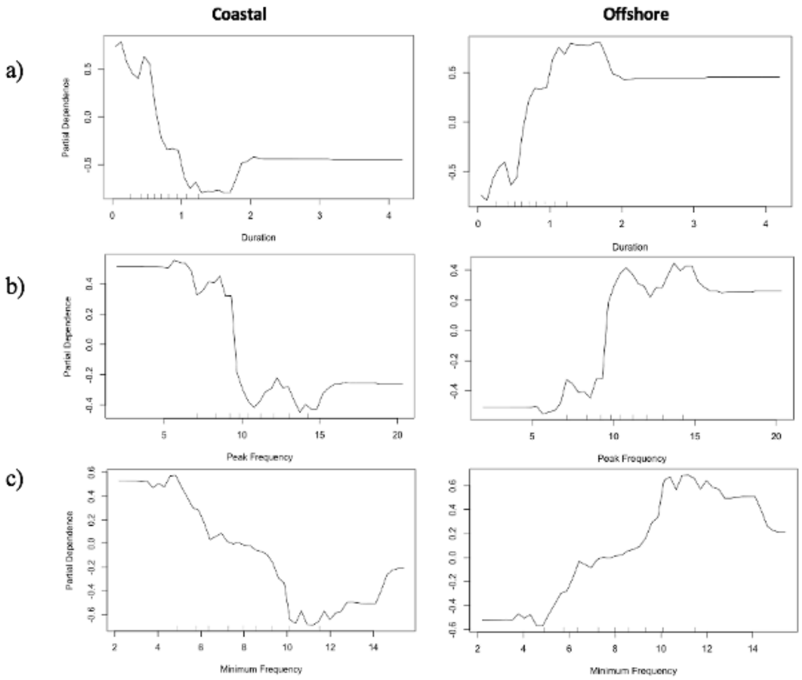


Figure. 2. Partial dependence plots of the acoustic parameters that best predicted ecotype in the random forest analysis based on MDA variable importance where a) shows the partial dependence on classifying the whistles by duration, b) on peak frequency and c) on minimum frequency. Partial dependence, or the impact of the variable of interest on classification accuracy is found on the y-axis with partial dependences above 0 having impact.

2.2 Repertoire Analysis

ARTwarp categorized 526 coastal whistles and 444 offshore whistles into 238 categories, of these 86 categories were unique to coastal dolphins, 80 to offshore dolphins, and 72 were shared between ecotypes. When ecotype datasets were categorized separately, ARTwarp categorized 700 coastal whistles into 159 categories and 444 offshore whistles into 130 categories (Fig. S3). These category counts are only used to compare general composition and not used to compare diversity due to the large difference in sample size. Overall, both spotted dolphin ecotypes produced whistles with sine, upsweeps, down sweeps, constant frequency, convex, and concave contours. However, in general upsweep (51%) and sine (24%) were most abundant in the coastal dolphin repertoire while upsweeps (34%), sine (21%), and convex (21%) were most common in the offshore dolphin repertoire (Fig. 4).

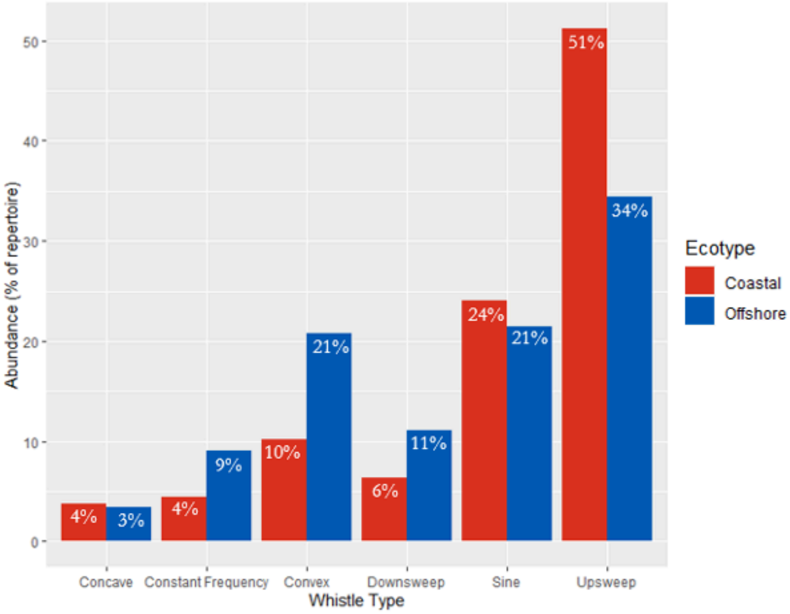


Figure. 4. Overall abundance of whistles per whistle type within ecotype repertoires based on ARTwarp categorization of individual datasets.

Repertoire diversity based on equal sample coverage of 90.25% resulted in species richness asymptotic estimates of 208.85 offshore whistle categories and 202.55 coastal categories, Shannon Diversity estimates at 123.61 offshore categories and 113.16 coastal categories, and Simpson Diversity estimates of 80.05 offshore categories and 75.55 coastal categories (Table 1, Fig.5). However, 84% confidence intervals of rarefaction and extrapolation curves overlap, deeming this difference in effective number of categories biologically insignificant (Gotelli and Colwell, 2010).

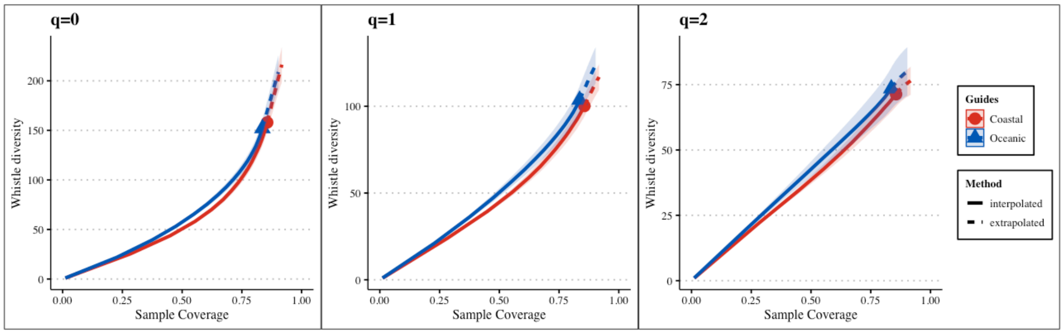


Figure. 5. R/E coverage-based curves for Hill numbers q=0,1,2 of the offshore and coastal whistle repertoires in which data was extrapolated within an 84% CI. Due to overlap of the 84% CI's, there is no biologically significant difference in repertoire diversity seen between ecotype repertoires.

Table. 1. Asymptotic estimates of whistle category richness (q=0), Shannon Diversity (q=1) and Simpson Diversity (q=2) of coastal and offshore whistle repertoires based on equal sample coverage of 90.25%.

Hill Number	Ecotype	Estimate	LCL	UCL
q=0	Offshore	208.85	184.01	224.53
	Coastal	202.55	181.58	233.61
q=1	Offshore	123.61	109.96	137.26
	Coastal	113.16	101.38	124.94
q=2	Offshore	80.05	69.34	90.75
	Coastal	75.55	66.91	84.177

The permutation test of ARTwarp categories resulted in a true proportion of distinct categories at 69.75%, with a mean permuted proportion of 50.94%. The true proportion was significantly greater (p<0.001; two-tailed t-test) than expected from random sampling. In measuring compositional similarity, the Horn Index, which is sensitive dominant categories, in this case upsweep contours, calculated a high compositional similarity of 72.84% (± 0.08, Fig.4). In contrast, the Morisita-Horn Index is more sensitive to rare categories and estimated a low compositional similarity of 37.14% (± 0.04). The Morisita-Horn estimate of low compositional similarity refers to the difference in the distribution of whistle types within each repertoire (Fig. 4) and the differences between these indices illustrates the complexity of comparing dolphin whistle repertoires.

3. Discussion

Our results show that coastal and offshore ecotypes of pantropical spotted dolphins in the Eastern Tropical Pacific have diverse whistle repertoires that vary in acoustic structure and composition. This indicates that genetic distinctions (Escorza-Treviño, 2004; Leslie et al., 2019, Leslie and Morin 2018) and phenotypic specializations to their habitat (Perrin and Hohn, 1994) extend to their acoustic repertoire.

Overall, coastal pantropical spotted dolphins produced whistles that were characterized as being shorter in duration and lower in frequency than the offshore ecotype. Similar patterns have been found in other dolphin species with coastal and offshore ecotypes. For example, in New Zealand and Baja California coastal and offshore bottlenose dolphins share similar whistle repertoires, but varied in their frequency, with coastal dolphins also producing lower frequency whistles than their offshore counterparts (Peters 2018, Antichi et al., in review). Differences in whistle duration could be related to context and group size, which were not measured in this study. In spinner dolphins, Guiana dolphins, and bottlenose dolphins, whistle duration has been shown to be influenced by primarily by surface behaviors (Barzua-Duran and Au 2002, Hernandez et al., 2010; May-Collado and Quiñones-Lebrón 2014).

Several factors can influence signal frequency, including body size, group size, and adaptations to the acoustic environment. Coastal spotted dolphins are larger than offshore dolphins, which could explain some of the variation observed in minimum frequency. However, toothed whales body size only explains a small portion (28%) of the variation in minimum frequency, suggesting that acoustic environment and social structure may be more important in driving the evolution of low frequency signals in this lineage (May-Collado et al., 2007). Coastal spotted dolphins form smaller groups than offshore dolphins and live in habitats with higher acoustic activity due to a high marine biodiversity and habitat complexity (i.e., coral reefs, mangroves, estuaries) (Odea et al., 2012; Lefcheck et al., 2019; Eisele et al., 2020) and human presence (Chao et al., 2015; Erbe et al., 2019). In addition, coastal habitats are shallow, where signal propagation is hindered due to transmission losses to the water surface and seafloor (Erbe et al., 2019). These properties of the coastal environment can negatively impact the communication range of spotted dolphins, and result in selection for low frequency and relatively simple signals that propagate more successfully in noisier and 'cluttered' environments. For example, Quintana-Rizzo et al. (2006) found that in shallow waters, coastal, bottlenose dolphins increased their communication range by producing low-frequency whistles. In contrast, in offshore habitats where the loss of acoustic energy is reduced, pantropical spotted dolphins produced primarily higher frequency whistles. Similar patterns have been described for bottlenose dolphins in Croatia (Rako Gospic and Picciulin 2016) and Indo-Pacific bottlenose dolphins off the coast of the Amakusa- Shimoshima Islands in Japan (Morisaka et al. 2016). Overall, dolphins show a great degree of plasticity in their whistle frequency range, which allows them to quickly respond to changes in their acoustic environments (May-Collado and Wartzok 2008, Perez-Ortega et al., 2021). Therefore, given the importance that whistles play in dolphin societies (e.g., species recognition, social interactions), differentiation in whistle frequency niches and repertoire composition may have contributed to the divergence of these ecotypes, or once divergence occurred, adaptations to the respective environments reinforced the genetic separation of these ecotypes.

Regarding repertoire diversity, we find that overall, coastal and offshore ecotypes have similarly diverse whistle repertoires. We expected offshore dolphins to have a more diverse whistle repertoire than coastal dolphins, because they live in larger groups. However, coastal pantropical spotted dolphins have very fluid and interchanging group composition and are a highly abundant dolphin species in Central America (Dizon et al., 1994, Luis et al., 2021. As a result, our recording effort likely captured several distinct combinations of dolphin groups capturing high levels of whistle diversity.

The main difference between coastal and offshore ecotypes was in repertoire composition. Considering the relative abundance of whistle types making up the repertoires, upsweeps were the most common whistle type for both ecotypes, however the offshore repertoire showed a significantly more even distribution of whistle types. In the offshore repertoire, the combined relative abundance of sine, concave and convex whistles surpasses the relative abundance of upsweep whistles (45%; 34%), indicating greater use of frequency modulated contours by the offshore ecotype. Frequency modulation patterns in dolphins, can serve for species identification (Gruden et al., 2015, Oswald et al., 2021), carry information about the individual (Janik and Sayigh 2013), express emotional state during social interactions (Esch et al., 2009, Perez-Ortega et al., 2021, Gagne et al., in review) and adjust to noisy environments, where simpler whistles can propagate more successfully modulated whistles (Morisaka et al., 2005). These findings suggest that the proportion of modulated whistles in the repertoire of coastal and offshore dolphins may indicate species-specific differences in group size, social dynamics, and habitat specialization.

In conclusion, this study finds evidence of ecotype acoustic distinction that may contribute to or reinforce the divergence of these lineages via habitat specialization and consequently, in the mediation of group and social dynamics. While repertoire diversity is conserved across ecotypes, repertoire composition and frequency structure remain plastic and reflect local adaptations to coastal and offshore soundscapes. With anthropogenic-induced climate change rapidly increasing ocean temperatures and therefore increasing the speed of sound in marine habitats, this acoustic plasticity may prove to be crucial in adapting to increasingly noisy coastal and offshore habitats (Affatati et al., 2022). Finally, through the combined analysis of whistle acoustic structure and repertoire, we present whistle contours that are unique to each ecotype for consideration in the development of species and population classifiers for the analysis of passive acoustic monitoring data.

4. Methods

4.1 Study Area

This study took place in coastal and offshore waters of the ETP (Fig. S1). Recordings of the coastal ecotype were made during research boat surveys for humpback whales in Padre Ramos, Northern Nicaragua and San Juan del Sur, Southern Nicaragua. In El Salvador, the study area was from El Metalío to the northern part of Punta

Remedios within the National Park of Los Cóbanos. Here, boat surveys were completed across a total of 10 perpendicular transects. In both countries boat surveys were done using a small boat 7-10 m in length and a 60 HP engine. Boat surveys were from 7 a.m. to 4 p.m. and when dolphins were detected, information about groups size, behavior, and acoustic data was collected when possible. In both sites recordings were made using a Zoom Recorder with a sampling rate of up to 44.1 kHz using an Aquarian Scientific hydrophone model AS-1 (linear range: 1 Hz-100 Hz ±2dB; sensitivity -208dBV re ±2dB).

Recordings of offshore ecotype were collected as part of United States National Oceanic and Atmospheric Association (NOAA) cetacean abundance research cruises. The Stenella Abundance Research (STAR) surveys of 2000 and 2006 covered the area from the United States-Mexico border, south to the territorial waters of Peru and west to Hawaii. The Hawaiian Island and Ecosystem Assessment Survey (HICEAS) of 2002 took place in the United States Exclusive Economic (EEZ) of Hawaii from the island of Hawaii to the Kure Atoll in the northwest. The 2005 Pacific Islands Cetacean Ecosystem Assessment Survey (PICEAS) recorded vocalizations in the United States EEZ of the Palmyra Atoll, Kingman Reef, and Johnson Atoll in addition to the waters between these EEZ's and the Hawaiian Islands. Surveys were completed during daylight hours on predetermined line-transects in which researchers estimated school size and identified species using 25 x 150 high power binoculars on the ship's flying bridges (Kinzey et al., 2001). Cetacean vocalizations were detected with hydrophone arrays that were towed at a depth of 6-11 meters and between 200-300 meters behind the research vessel. The STAR2000 cruise used an array of 5 hydrophone elements with a frequency response of

15Hz-40 kHz ± 4dB at -132dBre 1 V/mPa. The HICEAS2002 cruise used an array of three hydrophone elements with a frequency response of 500 Hz-25 kHz ± 10 dB at -155 dB re 1 V/mPA. The PICEAS2005 cruise used an array of 3 hydrophone elements with a frequency response of 1-40 kHz ± 5 dB at -150 dB re 1 V/mPa. The STAR2006 cruise used an array of 2 hydrophone elements with a frequency response of 1-40 kHz ± 5 dB at -150 dB re 1 V/mPa. Vocalizations were recorded on Tascam DA-38 (STAR2000, HICEAS 2002, STAR2006) and Tascam DA-78 (PICEAS2005) multi-channel recorders with a sampling rate of at least 96 kHz.

4.2 Whistle Data Collection

We used RAVEN PRO 1.5 build 37 (K. Lisa Yang Center for Conservation Bioacoustics, 2014) to create spectrograms of each recording with a fast Fourier transform (FFT) size of 1,024 points, an overlap of 50%, and using a 512-sample Hann window. Whistle detection was done manually, and selection was based on the following rules (1) only whistles with a clear and dark contour from start to end and (2) with unique contours were selected for acoustic data extraction; and (3) overlapping whistles were selected only if distinguishable from one another and were considered different whistles if separated by at least 200 ms (Bazua-Duran and Au, 2002). Whistles were selected to maximize the contour diversity of the data set. Selections were made with a border of 0.5 seconds to ensure that no contour was cut off during extraction.

Whistle selections were uploaded into Luscinia (Lachlan, 2007) for manual contour tracing and Beluga (Buck and Tyack, 1993) for automated contour extraction. Luscinia is a semi-automatic contour analysis software in which spectrograms are uploaded and contours can be manually traced to extract acoustic parameters for analysis

(Lachlan, 2016). The following standard settings were used during contour tracing: frame length (ms)= 5, tie step (ms)=1, spectrographic points=221, spectrographic overlap%=80, dynamic range (dB)=82, dereverb range (ms)=50, windowing function=Gaussian, frequency zoom=100, NR range1 (ms)=50, NR range2 (ms)=50. Dynamic range (dB) was used as a second assessment that all selections had adequate signal to noise ratio. Dynamic range adjusts the gray scale within the spectrogram and specifies the threshold after which point pixels are rendered as white and unable to be traced in Luscinia. In Luscinia, the following standard acoustic variables (e.g., Morisaka et al., 2005; May-Collado and Wartzok, 2008; Marley et al., 2017) were extracted from each whistle: minimum frequency (MF) (measures the frequency in the lowest point in the contour), maximum frequency (MXF) (measures the frequency at the highest point in the contour), start frequency (SF), end frequency, duration (D), delta frequency (DF) (this is the difference between MF and MXF) and peak frequency (PF) (frequency where the maximum amplitude occurred) (Fig. S2).

4.3 Statistical Analysis

Acoustic parameter measurements from Luscinia were exported into R (R Core Team, 2021) in order to compile descriptive statistics including mean, standard deviation, coefficient of variation, maximum and minimum values. Only offshore ecotype whistles with a maximum frequency of less than or equal to 22.05 kHz (466/653 whistles) were used for analysis from this point forward to be consistent with the lower sampling rate used in coastal surveys.

4.3.1 Objective 1: NMMDS and K-medoids clustering

In order to have a comparable sample size, a random subsample of the coastal dataset was created by omitting every 4th whistle within the dataset. Luscinia's built in dynamic time-warping (DTW) function was used to analyze the distribution of fundamental frequency contours based on measurements of time, fundamental frequency, fundamental frequency change and vibrato amplitude. These features were established as most important for the analysis of contour similarity within a dataset first in birds, then in dolphins (Lachlan et al. 2010, 2016; Lammers et al., 2003; Peters 2018). Fundamental frequency and fundamental frequency change have been deemed crucial to include based on the fact that delphinids are known to perceive both relative and absolute frequency changes (Thompson and Herman 1975). Vibrato amplitude is included as a measure of periodic oscillations within a contour. These contour features were normalized relative to each other by calculating the standard deviations of each parameter. Weightings used in the DTW were: Time-10.0 ms; Fundamental frequency-3.513; Fundamental Frequency Change- 2.413; Vibrato Amplitude- 1.973. DTW compresses or expands the time domain of spectrograms in order to maximize the frequency overlap of whistles being compared. Animals are known to be relatively insensitive to variation in signal duration and more sensitive to changes in frequency and therefore DTW prevents variations in length of whistle components from being the deciding categorization factor (Deecke and Janik, 2006).

After DTW, we performed a two-dimensional NMMDS analysis in Luscinia based on a dissimilarity matrix. NMMDS presents a scatter plot of the relative distance (based on (dis)similarity) between the sample whistles as calculated for the distance matrix. NMMDS visualizes the distribution of each dataset, as well as how their distributions cluster relative to each other. Luscinia's k-medoids cluster analysis assessed natural clustering of the species-wide dataset based on fundamental frequency contour alone.

4.3.2 Objective 2: Random Forest

Random forest (RF) classification determined the viability of and variable importance for distinguishing between coastal and offshore ecotypes using the randomForest package in R (R Core Team, 2021; Liaw and Wiener, 2002). RF classification is a non-parametric analysis that uses an ensemble of decision trees to categorize data based on predictor variables (Cutler et al., 2007). Each decision tree takes a bootstrapped sample of the dataset, classifies 2/3 and saves 1/3 as an out-of-bag (OOB) sample to assess the model's classification accuracy. A random selection of predictor variables is considered at each node within the tree to partition the data in a way that maximizes the homogeneity of the following nodes. The final classification of each whistle is based on the majority vote of all trees in the model. A random subsample was taken from the coastal ecotype dataset in order to match the 466 offshore ecotype sample size to ensure that the classification was not skewed. The ecotype datasets were combined into a species-wide dataset and split into training (67%) and testing (33%) with an equal distribution of each ecotype in each dataset. Pearson's correlation coefficients were calculated for each variable to ensure that overfitting did not occur due to correlation between variables (Gregorutti et al., 2017). The acoustic variables measured in Luscinia were used as the random forest's predictor variables. All Pearson correlation coefficients fell between ±0.8 and were therefore uncorrelated enough to be included in the model (Barkley et al., 2019).

The optimal random number of predictor variables (mtry) considered at each node was tuned using repeated k-fold cross-validation and the optimal mtry was determined by the model with the largest area under the receiver operating characteristic (ROC) curve. MDA gives the mean normalized measure of the loss in prediction performance if a variable is permuted (Cutler et al., 2007). The MDG gives a measure of how much each variable plays a role in the homogeneity of the nodes. For both measures, a higher value indicates higher importance.

A confusion matrix of the RF classification results, and Cohen's Kappa statistic were used to evaluate the model's performance. The confusion matrix displayed the number of correctly and incorrectly classified whistles for each ecotype. Cohen's Kappa statistic is a measure of the observed accuracy (the RF classification results) compared to the expected accuracy (random chance) and is an accepted method evaluating machine learning classifiers (Cohen, 1960; Cutler et al., 2007).

4.3.3 Objective 3: Repertoire Complexity and Diversity

We assessed contour repertoire diversity using ARTwarp to categorize contours extracted in Beluga. ARTwarp is a MATLAB program designed specifically with dolphin and whale acoustics in mind that uses DTW to compare whistle contours and automatically categorize contours based on contour similarity. ARTwarp categorizes the whistle frequency contours using an unsupervised adaptive resonance theory neural network. ARTwarp uses an unsupervised categorization algorithm based on an ART2 neural network (Deecke and Janik, 2006). The ART2 algorithm, compares input whistle contours to a set of reference whistle contours, and either determines the inputs to be similar enough to a reference whistle contour to be grouped with it, or dissimilar enough to warrant a new reference category. This decision point is based on a vigilance parameter that was set to 96% (as per Deecke and Janik, 2006). In this way, the reference categories continuously update based on the dataset. Additionally, DTW is applied. ARTwarp categorized each ecotype dataset individually and combined in order to compare ecotype repertoire diversity. For the separate ecotype repertoires, in addition to the vigilance parameter, each categorization had a maximum limit of 200 categories and 100 iterations. The species-wide categorization had a maximum of 400 categories and 100 iterations. These values were chosen through trial and error to allow the dataset to create as many categories as needed and use as many iterations as needed to correctly categorize each whistle based on a vigilance of 93%-96%. The categorization with a 96% vigilance was used for the following analysis to be consistent with previous literature. A 96% vigilance was determined appropriate specifically to capture signature whistles within a repertoire. Though it is unknown whether pantropical spotted dolphins have signature whistles, 96% vigilance was used to not discount their possible existence.

Ecotype repertoires were visually categorized further into general contour categories following Bazua and Au (2002) contour classification through visual inspection. Whistle categories were classified as ascending if increasing in frequency without inflection points, descending if decreasing in frequency without inflection points, convex if increasing in frequency and then decreasing in frequency with an inflection point, concave if decreasing in frequency then increasing in frequency with an inflection point, sine if multiple inflection points and constant if there is a change in frequency less than or equal to 1 kHz (Fig S4).

To compare the composition of repertoires, a permutation test was performed based on the ARTwarp output of the combined ecotype dataset. This test was used to determine whether the proportion of ecotype specific categories was significantly greater than the expected proportion given a repertoire with no ecotype distinction. A total of 1000 permutations were performed by randomly resampling categories and determining the proportion of categories within samples that were ecotype specific. A two tailed test was used to calculate whether there was a significantly (<0.001) greater proportion of ecotype specific categories in the dataset than expected. Repertoire (dis)similarity was further explored using the SpadeR package in Rstudio (v0.1.1; Chao et al., 2016) to calculate pairwise similarity statistics. Abundance-based Horn and Morisita-Horn index measures were calculated in order to account for the relative abundance of whistles in each category and difference in sample size (Chao et al., 2005).

In order to analyze the diversity of repertoires as categorized by ARTwarp, an asymptotic estimate of species richness (in this case, whistle richness), Shannon diversity and Simpson diversity with Hill numbers was used (Chao et al., 2014). Hill numbers provided the effective number of whistle categories based on varying sensitivity to rare categories (q=0,1,2). Effective number of categories refers to the number of categories with equal abundance needed to get the same diversity measure (Chao et al., 2014). R/E curves were plotted based on sample completeness. Sample completeness is often measured by sample coverage which is the proportion of individuals (whistles) in the assemblage that belong to a category represented by the dataset. In other words, it is the proportion of whistles that belongs to a category represented by the dataset as opposed to a category that the dataset did not account for (Roswell et al., 2021). This method accounts for the inevitable failed detection of all categories that exist. In comparing the repertoire diversity of coastal versus offshore ecotypes, the coverage-based R/E sampling curves were analyzed at up to double the sample size of the smaller dataset (the offshore dataset) (as per Chao et al., 2014). Estimates of species richness, Shannon Diversity and Simpson Diversity were compared at a sample coverage of 90.25%.

Supplemental Material

Table S1. Sampling effort of recordings analyzed location and dates of field work as well as the and the total whistle sample size used.

Dataset	Location/Cruise	Field Period	Sampling Rate (kHz)	Sampling Effort (hours)	Sample Size
Coastal Ecotype	Los Cóbanos Ntl. Park, El Salvador	12/11/20-03/18/2021	44.1 kHz	1:58:07	322
	Padre Ramos, Nicaragua	04/07/17-04/15/2018	44.1 kHz	0:27:51	68
	San Juan del Sur, Nicaragua	09/12/2017-2/25/2020	44.1 kHz	1:58:15	267
Offshore Ecotype	STAR2000	07/28/2000-12/09/2000	150	0:39:06	148
	HICEAS2002	07/27/2002-12/09/2002	150	0:37:54	206
	PICEAS2005	07/28/2005-11/29/2005	96	3:33:30	298
	STAR2006	07/28/2006-12/07/2006	192	0:10:00	3

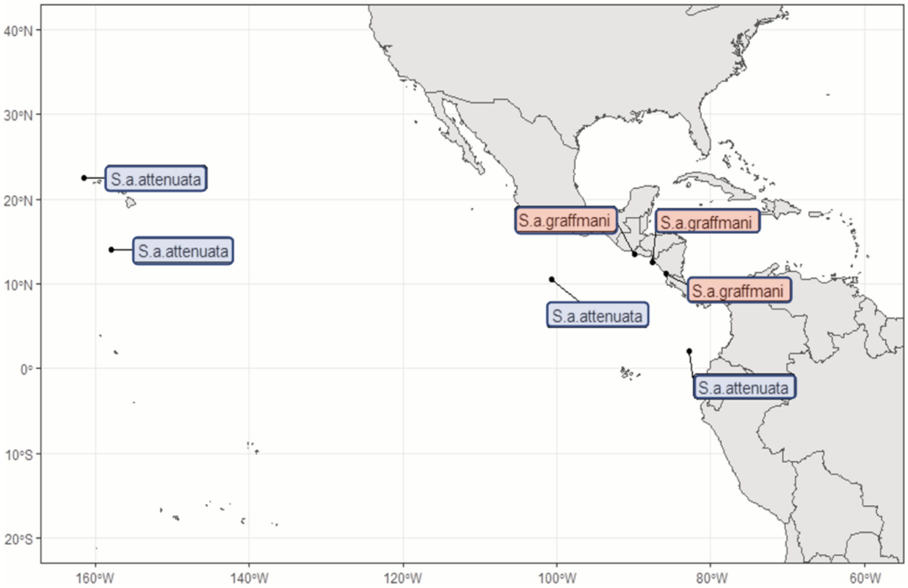
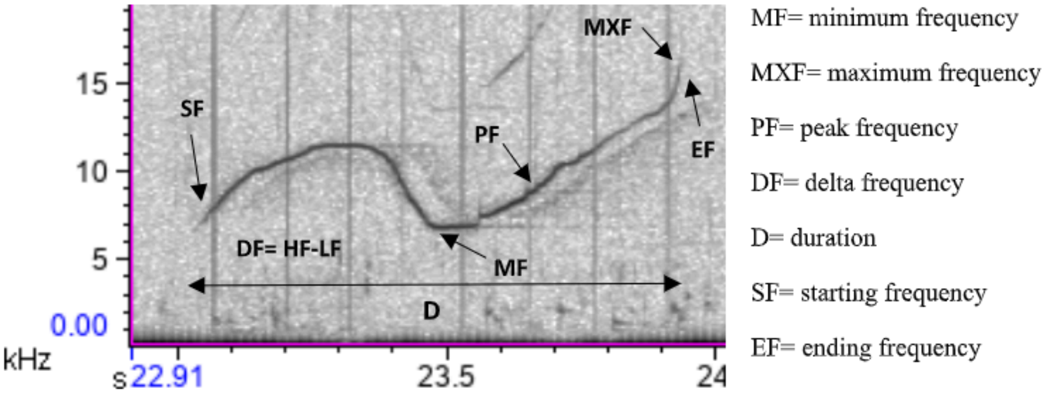


Figure S1. Map of locations where recordings were taken. Recordings of the coastal ecotype (*S.a. graffmani*) were collected from El Salvador and two locations in Nicaragua from over-the-boat hydrophones. Offshore ecotype (*S.a.* attenuata) recordings were collected from four areas in the Eastern Tropical Pacific using towed hydrophone arrays.



MF= minimum frequency
MXF= maximum frequency
PF= peak frequency
DF= delta frequency
D= duration
SF= starting frequency
EF= ending frequency

Figure S2. Example of a spectrogram showing a whistle's frequency and relative amplitude over time. Standard acoustic parameter measurements are highlighted and were extracted from each whistle in Luscinia.

Table S2. Descriptive statistics of pantropical spotted dolphin's contour frequency and temporal variables by ecotype.

Ecotype (sampling rate)		Max Freq (kHz)	Min Freq (kHz)	Start Freq (kHz)	End Freq (kHz)	Delta Freq (kHz)	Peak Freq (kHz)	Duration (s)
Coastal Ecotype (44.1 kHz)	Mean (±sd)	16.00 (±3.44)	7.16 (±2.42)	8.49 (±3.54)	14.85 (±4.22)	8.83 (±4.20)	9.51 (±2.70)	0.61 (±0.36)
	CoV	21.49%	33.83%	41.69%	28.39%	47.57%	28.36%	58.72%
	Max	21.96	18.69	21.56	21.96	19.26	19.29	2.70
	Min	6.53	1.65	1.66	3.87	0.09	1.97	0.02
Offshore Ecotype (44.1 kHz)	Mean (±sd)	17.62 (±2.98)	8.85 (±2.26)	10.75 (±3.80)	13.80 (±4.60)	8.77 (±3.50)	11.53 (±2.37)	0.91 (±0.41)
	CoV	16.90%	25.52%	35.34%	33.29%	39.93%	20.57%	44.70%
	Max	21.96	14.50	21.96	21.96	17.67	20.32	4.19
	Min	5.68	3.12	3.12	3.28	0.31	5.27	0.06
Offshore Ecotype (96 kHz)	Mean (±sd)	19.87 (±4.63)	8.90 (±2.31)	10.80 (±4.10)	15.96 (±6.35)	10.97 (±5.03)	12.10 (±3.19)	0.95 (±0.42)
	CoV	23.31%	25.99%	37.95%	39.82%	45.86%	26.35%	43.85%
	Max	36.12	17.24	27.72	36.12	27.08	32.19	4.19
	Min	5.68	1.85	1.85	3.28	0.31	5.27	0.06

Table S6. MDA and MDG of the predictor variables from the RF model in which duration, peak frequency and minimum frequency hold the most importance when classifying whistles by ecotype.

Predictor Variables	Mean Decrease Accuracy	Mean Decrease Gini
Duration (s)	45.32	70.53
Peak Frequency (kHz)	36.66	57.09
Minimum Frequency (kHz)	31.84	47.13
Delta Frequency (kHz)	24.25	31.48
Maximum Frequency (kHz)	22.94	32.28
Fundamental frequency end (kHz)	22.64	35.43
Fundamental frequency start (kHz)	20.08	38.55

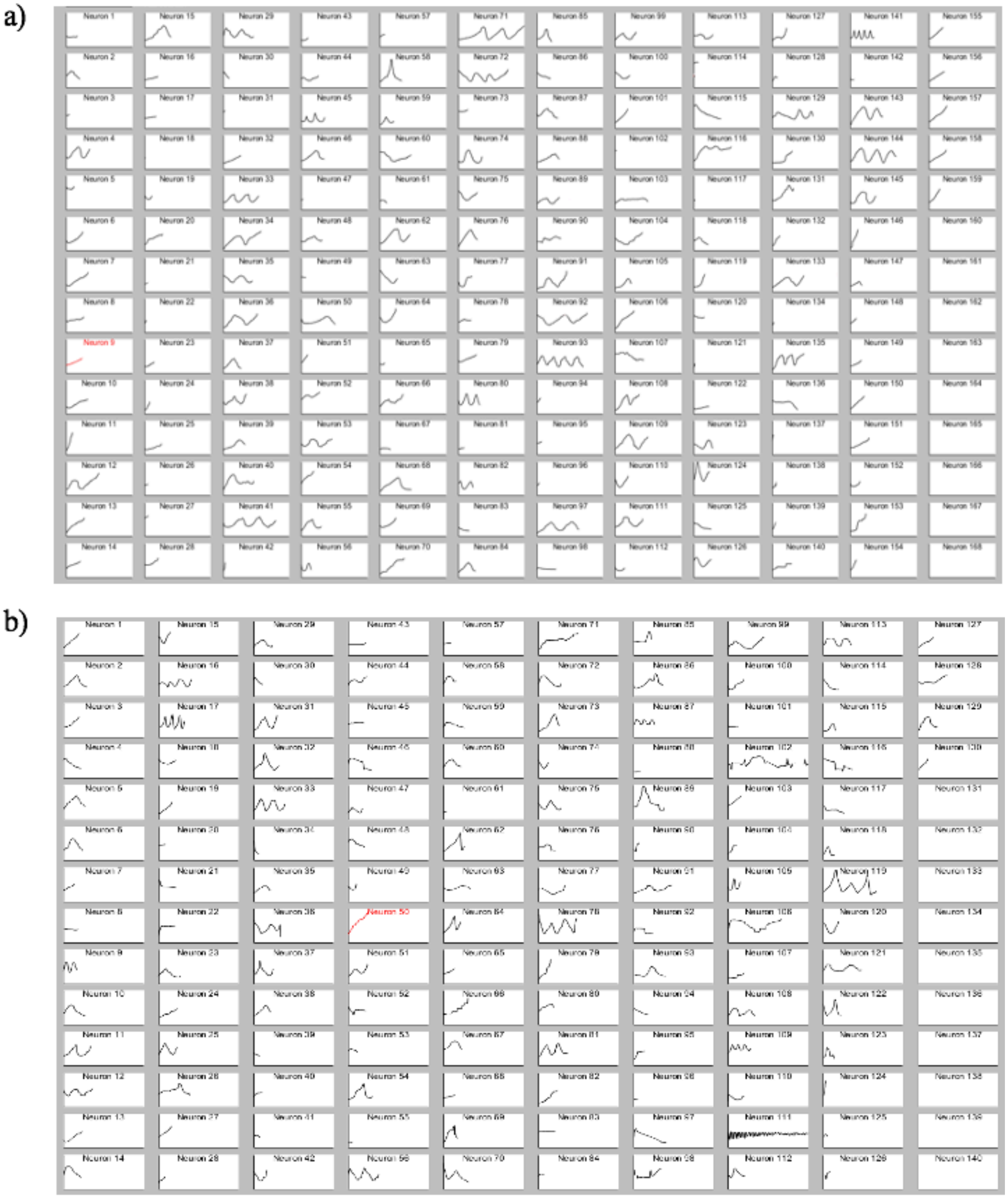


Figure S3. ARTwarp categorization of a) a subsample of the coastal dataset to better match the offshore dataset and b) the ARTwarp categorization of the offshore ecotype whistles where each box represents a biologically significant category of whistles. Both categorizations were given a 96% vigilance.

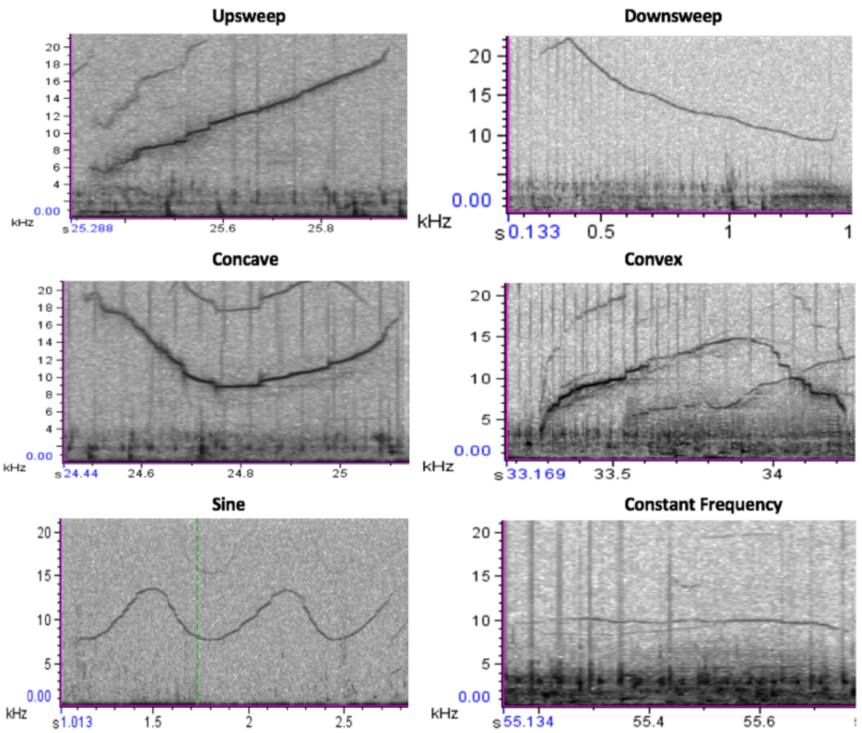


Figure S4. Example of whistle types used to further categorize ARTwarp's output categories for each ecotype's repertoire.

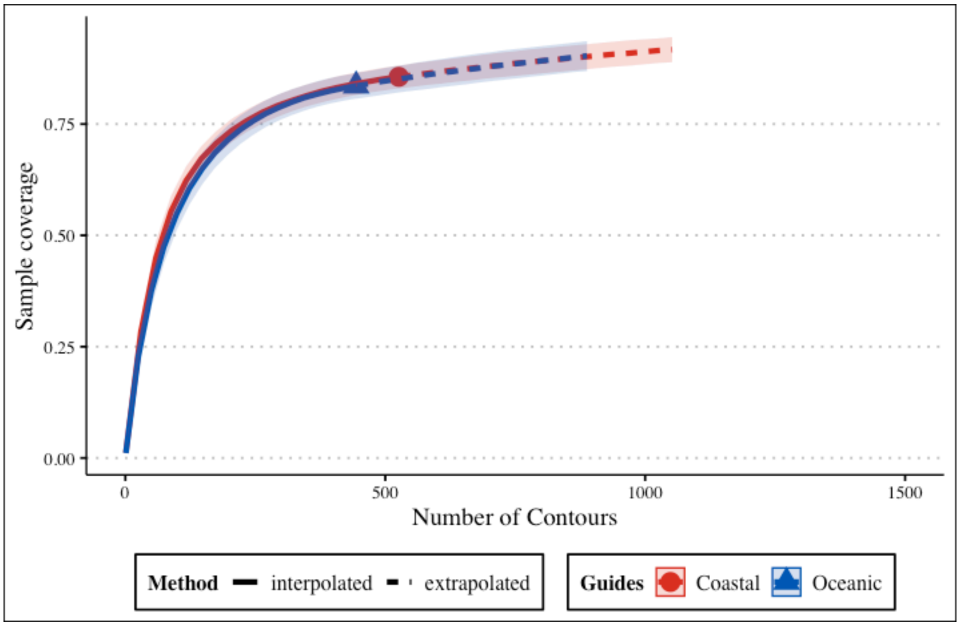


Figure S5. R/E sample completeness curve of the coastal and offshore ecotype datasets based on original sample sizes.

Bibliography

Affatati, Alice, Chiara Scaini, and Stefano Salon. 2022. "Ocean Sound Propagation in a Changing Climate: Global Sound Speed Changes and Identification of Acoustic Hotspots." *Earth's Future* 10(3):e2021EF002099. doi: 10.1029/2021EF002099.

Antichi, Simone, Maia Austin, Laura J. May-Collado, Jorge Urbán, Sergio Martínez-Aguilar, and Lorena Viloria-Gómora. in review. "Differences in the Whistles of Two Ecotypes of Bottlenose Dolphins in the Gulf of California." *JASA Express Letters*.

Barkley, Yvonne, Erin M. Oleson, Julie N. Oswald, and Erik C. Franklin. 2019. "Whistle Classification of Sympatric False Killer Whale Populations in Hawaiian Waters Yields Low Accuracy Rates." *Frontiers in Marine Science* 6.

Bazúa-Durán, Carmen, and Whitlow W. L. Au. 2002. "The Whistles of Hawaiian Spinner Dolphins." *The Journal of the Acoustical Society of America* 112(6):3064–72. doi: 10.1121/1.1508785.

Buck, John R., and Peter L. Tyack. 1993. "A Quantitative Measure of Similarity for *Tursiops Truncatus* Signature Whistles." *The Journal of the Acoustical Society of America* 94(5):2497–2506. doi: 10.1121/1.407385.

Chao, Anne, Robin L. Chazdon, Robert K. Colwell, and Tsung-Jen Shen. 2005. "A New Statistical Approach for Assessing Similarity of Species Composition with Incidence and Abundance Data." *Ecology Letters* 8(2):148–59. doi: 10.1111/j.1461-0248.2004.00707.x.

Chao, Anne, Nicholas J. Gotelli, T. C. Hsieh, Elizabeth L. Sander, K. H. Ma, Robert K. Colwell, and Aaron M. Ellison. 2014. "Rarefaction and Extrapolation with Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." *Ecological Monographs* 84(1):45–67. doi: 10.1890/13-0133.1.

Chao, Anne, Nicholas J. Gotelli, T. C. Hsieh, Elizabeth L. Sander, K. H. Ma, Robert K. Colwell, and Aaron M. Ellison. 2014. "Rarefaction and Extrapolation with Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." *Ecological Monographs* 84(1):45–67. doi: 10.1890/13-0133.1.

Chao, Anne, Yasuhiro Kubota, David Zelený, Chun-Huo Chiu, Ching-Feng Li, Buntarou Kusumoto, Moriaki Yasuhara, Simon Thorn, Chih-Lin Wei, Mark J. Costello, and Robert K. Colwell. 2020. "Quantifying Sample Completeness and Comparing Diversities among Assemblages." *Ecological Research* 35(2):292–314. doi: 10.1111/1440-1703.12102.

Cutler, D. Richard, Thomas C. Edwards, Karen H. Beard, Adele Cutler, Kyle T. Hess, Jacob Gibson, and Joshua J. Lawler. 2007. "Random Forests for Classification in Ecology." *Ecology* 88(11):2783–92.

Deecke, Volker B., and Vincent M. Janik. 2006. "Automated Categorization of Bioacoustic Signals: Avoiding Perceptual Pitfalls." *The Journal of the Acoustical Society of America* 119(1):645–53. doi: 10.1121/1.2139067.

Dizon, Andrew E., William F. Perrin, and Priscilla A. Akin. 1994. *Stocks of Dolphins (Stenella Spp. and Delphinus Delphis) in the Eastern Tropical Pacific: A Phylogeographic Classification*. Vol. 119. Seattle, Wash.: U.S. Dept. of Commerce, [National Marine Fisheries Service, Scientific Publications Office].

Eisele, Marius H., Sergio Madrigal-Mora, and Mario Espinoza. 2021. "Drivers of Reef Fish Assemblages in an Upwelling Region from the Eastern Tropical Pacific Ocean." *Journal of Fish Biology* 98(4):1074–90. doi: 10.1111/jfb.14639.

Erbe, Christine, Sarah A. Marley, Renée P. Schoeman, Joshua N. Smith, Leah E. Trigg, and Clare Beth Embling. 2019. "The Effects of Ship Noise on Marine Mammals—A Review." *Frontiers in Marine Science* 6.

Esch, H. Carter, Laela S. Sayigh, James E. Blum, and Randall S. Wells. 2009. "Whistles as Potential Indicators of Stress in Bottlenose Dolphins (Tursiops Truncatus)." *Journal of Mammalogy* 90(3):638–50. doi: 10.1644/08-MAMM-A-069R.1.

Escorza-Treviño, Sergio, Frederick I. Archer, Maria Rosales, Aimee Lang, and Andrew E. Dizon. 2005. "Genetic Differentiation and Intraspecific Structure of Eastern Tropical Pacific Spotted Dolphins, Stenella Attenuata, Revealed by DNA Analyses." *Conservation Genetics* 6(4):587–600. doi: 10.1007/s10592-005-9013-9.

Gong, Zining, Lijun Dong, Francesco Caruso, Mingli Lin, Mingming Liu, Jianchen Dong, and Songhai Li. 2019. "Echolocation Signals of Free-Ranging Pantropical Spotted Dolphins (*Stenella Attenuata*) in the South China Sea." *The Journal of the Acoustical Society of America* 145(6):3480–87. doi: 10.1121/1.5111742.

Gregorutti, Baptiste, Bertrand Michel, and Philippe Saint-Pierre. 2017. "Correlation and Variable Importance in Random Forests." *Statistics and Computing* 27(3):659–78. doi: 10.1007/s11222-016-9646-1.

Gruden, Pina, Paul White, Julie Oswald, Yvonne Barkley, Salvatore Cerchio, Marc Lammers, and Simone Baumann-Pickering. 2015. "Differences in Oscillatory Whistles Produced by Spinner (Stenella Longirostris) and Pantropical Spotted (Stenella Attenuata) Dolphins." *Marine Mammal Science* 1–15. doi: 10.1111/mms.12280.

Hawkins, E. R. 2010. "Geographic Variations in the Whistles of Bottlenose Dolphins (Tursiops Aduncus) along the East and West Coasts of Australia." *The Journal of the Acoustical Society of America* 128(2):924–35. doi: 10.1121/1.3459837.

Hernandez, Erica N., Moby Solangi, and Stan A. Kuczaj. 2010. "Time and Frequency Parameters of Bottlenose Dolphin Whistles as Predictors of Surface Behavior in the Mississippi Sound." *The Journal of the Acoustical Society of America* 127(5):3232–38. doi: 10.1121/1.3365254.

Janik, V. M., L. S. Sayigh, and R. S. Wells. 2006. "Signature Whistle Shape Conveys Identity Information to Bottlenose Dolphins." *Proceedings of the National Academy of Sciences* 103(21):8293–97. doi: 10.1073/pnas.0509918103.

Janik, Vincent M., and Laela S. Sayigh. 2013. "Communication in Bottlenose Dolphins: 50 Years of Signature Whistle Research." *Journal of Comparative Physiology A* 199(6):479–89. doi: 10.1007/s00359-013-0817-7.

K. Lisa Yang Center for Conservation Bioacoustics. (2014). Raven Pro: Interactive Sound Analysis Software (Version 1.5) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology.

King, Stephanie L., Simon J. Allen, Michael Krützen, and Richard C. Connor. 2019. "Vocal Behaviour of Allied Male Dolphins during Cooperative Mate Guarding." *Animal Cognition* 22(6):991–1000. doi: 10.1007/s10071-019-01290-1.

Kiszka, Jeremy, and Gill Braulik. 2018. *Stenella Attenuata - THE IUCN RED LIST OF THREATENED SPECIES*^{TM}.

La Manna, Gabriella, Nikolina Rako-Gospić, Gianluca Sarà, Federica Gatti, Silvia Bonizzoni, and Giulia Ceccherelli. 2020. "Whistle Variation in Mediterranean Common Bottlenose

Dolphin: The Role of Geographical, Anthropogenic, Social, and Behavioral Factors." *Ecology and Evolution* 10(4):1971–87. doi: 10.1002/ece3.6029.

Lachlan, R.F. (2016) Luscinia: a bioacoustics analysis computer program. Version 2.0 [Computer program].

Lachlan, R. F., L. Verhagen, S. Peters, and C. Ten Cate. 2010. "Are There Species-Universal Categories in Bird Song Phonology and Syntax? A Comparative Study of Chaffinches (Fringilla Coelebs), Zebra Finches (Taenopygia Guttata), and Swamp Sparrows (Melospiza Georgiana)." *Journal of Comparative Psychology (Washington, D.C.: 1983)* 124(1):92–108. doi: 10.1037/a0016996.

Lachlan, Robert F., Caroline A. A. van Heijningen, Sita M. ter Haar, and Carel ten Cate. 2016. "Zebra Finch Song Phonology and Syntactical Structure across Populations and Continents—A Computational Comparison." *Frontiers in Psychology* 7:980. doi: 10.3389/fpsyg.2016.00980.

Lammers, Marc, Whitlow Au, and Denise Herzing. 2003. "The Broadband Social Acoustic Signaling Behavior of Spinner and Spotted Dolphins." *The Journal of the Acoustical Society of America* 114:1629–39. doi: 10.1121/1.1596173.

Landis, J. Richard, and Gary G. Koch. 1977. "The Measurement of Observer Agreement for Categorical Data." *Biometrics* 33(1):159–74. doi: 10.2307/2529310.

Lefcheck, Jonathan S., Brent B. Hughes, Andrew J. Johnson, Bruce W. Pfirrmann, Douglas B. Rasher, Ashley R. Smyth, Bethany L. Williams, Michael W. Beck, and Robert J. Orth. 2019. "Are Coastal Habitats Important Nurseries? A Meta-Analysis." *Conservation Letters* 12(4):e12645. doi: 10.1111/conl.12645.

Leslie, Matthew S., Frederick I. Archer, and Phillip A. Morin. 2019. "Mitogenomic Differentiation in Spinner (Stenella Longirostris) and Pantropical Spotted Dolphins (S. Attenuata) from the Eastern Tropical Pacific Ocean." *Marine Mammal Science* 35(2):522–51. doi: 10.1111/mms.12545.

Leslie, Matthew S., and Phillip A. Morin. 2018. "Structure and Phylogeography of Two Tropical Predators, Spinner (Stenella Longirostris) and Pantropical Spotted (S. Attenuata) Dolphins, from SNP Data." *Royal Society Open Science* 5(4):171615. doi: 10.1098/rsos.171615.

Liaw, Andy, and Matthew Wiener. 2002. "Classification and Regression by RandomForest." 2:5.

Luís, A. R., L. J. May-Collado, N. Rako-Gospić, T. Gridley, E. Papale, A. Azevedo, M. A. Silva, G. Buscaino, D. Herzing, and M. E. dos Santos. 2021. "Vocal Universals and Geographic Variations in the Acoustic Repertoire of the Common Bottlenose Dolphin." *Scientific Reports* 11:11847. doi: 10.1038/s41598-021-90710-9.

Mason, Nicholas A., Allison J. Shultz, and Kevin J. Burns. 2014. "Elaborate Visual and Acoustic Signals Evolve Independently in a Large, Phenotypically Diverse Radiation of Songbirds." *Proceedings of the Royal Society B: Biological Sciences* 281(1788):20140967. doi: 10.1098/rspb.2014.0967.

MATLAB 2015b, The MathWorks, Inc., Natick, Massachusetts, United States.

May-Collado, Laura J., Ingi Agnarsson, and Douglas Wartzok. 2007. "Phylogenetic Review of Tonal Sound Production in Whales in Relation to Sociality." *BMC Evolutionary Biology* 7(1):136. doi: 10.1186/1471-2148-7-136.

May-Collado, Laura J., Ingi Agnarsson, and Douglas Wartzok. 2007. “Reexamining the Relationship Between Body Size and Tonal Signals Frequency in Whales: A Comparative Approach Using a Novel Phylogeny.” *Marine Mammal Science* 23(3):524–52. doi: 10.1111/j.1748-7692.2007.02250.x.

May-Collado, Laura J., and Jaume Forcada. 2012. “Small-Scale Estimation of Relative Abundance for the Coastal Spotted Dolphins (Stenella Attenuata) in Costa Rica: The Effect of Habitat and Seasonality.” *Revista de Biología Tropical* 60:133–42.

May-Collado, Laura J., and Shakira G. Quiñones-Lebrón. 2014. “Dolphin Changes in Whistle Structure with Watercraft Activity Depends on Their Behavioral State.” *The Journal of the Acoustical Society of America* 135(4):EL193–98. doi: 10.1121/1.4869255.

May-Collado, Laura J., and Douglas Wartzok. 2008. “A Comparison of Bottlenose Dolphin Whistles in the Atlantic Ocean: Factors Promoting Whistle Variation.” *Journal of Mammalogy* 89(5):1229–40. doi: 10.1644/07-MAMM-A-310.1.

Morisaka, Tadamichi, Masanori Shinohara, Fumio Nakahara, and Tomonari Akamatsu. 2005. “Effects of Ambient Noise on the Whistles of Indo-Pacific Bottlenose Dolphin Populations.” *Journal of Mammalogy* 86(3):541–46. doi: 10.1644/1545-1542(2005)86[541:EOANOT]2.0.CO;2.

Morton, E. 1975. “Ecological Sources of Selection on Avian Sounds.” *The American Naturalist*. doi: 10.1086/282971.

O’Dea, Aaron, Natalia Hoyos, Félix Rodríguez, Brigida Degracia, and Carlos De Gracia. 2012. “History of Upwelling in the Tropical Eastern Pacific and the Paleogeography of the Isthmus of Panama.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 348–349:59–66. doi: 10.1016/j.palaeo.2012.06.007.

Olofsson, Helen, Alicia M. Frame, and Maria R. Servedio. 2011. “Can Reinforcement Occur with a Learned Trait?” *Evolution* 65(7):1992–2003. doi: 10.1111/j.1558-5646.2011.01286.x.

Oswald, Julie, Jay Barlow, and Thomas Norris. 2003. “ACOUSTIC IDENTIFICATION OF NINE DELPHINID SPECIES IN THE EASTERN TROPICAL PACIFIC OCEAN.” *Publications, Agencies and Staff of the U.S. Department of Commerce*.

Oswald, Julie N., Shannon Rankin, and Jay Barlow. 2004. “The Effect of Recording and Analysis Bandwidth on Acoustic Identification of Delphinid Species.” *The Journal of the Acoustical Society of America* 116(5):3178–85. doi: 10.1121/1.1804635.

Oswald, Julie N., Shannon Rankin, Jay Barlow, and Marc O. Lammers. 2007. “A Tool for Real-Time Acoustic Species Identification of Delphinid Whistles.” *The Journal of the Acoustical Society of America* 122(1):587–95. doi: 10.1121/1.2743157.

Oswald, Julie N., Sam F. Walmsley, Caroline Casey, Selene Fregosi, Brandon Southall, and Vincent M. Janik. 2021. “Species Information in Whistle Frequency Modulation Patterns of Common Dolphins.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 376(1836):20210046. doi: 10.1098/rstb.2021.0046.

Papale, Elena, Marta Azzolin, Irma Cascão, Alexandre Gannier, Marc Lammers, Vidal Martín, Julie Oswald, Mónica Pérez-Gil, Rui Prieto, Mónica Silva, and Cristina Giacoma. 2013. “Geographic Variability in the Acoustic Parameters of Striped Dolphin’s (Stenella Coeruleoalba) Whistles.” *The Journal of the Acoustical Society of America* 133:1126–34. doi: 10.1121/1.4774274.

Perez-Ortega, Betzi, Rebecca Daw, Brennan Paradee, Emma Gimbrere, and Laura J. May-Collado. 2021. "Dolphin-Watching Boats Affect Whistle Frequency Modulation in Bottlenose Dolphins." *Frontiers in Marine Science* 8:102. doi: 10.3389/fmars.2021.618420.

Perrin, William F. 2009. "Pantropical Spotted Dolphin: Stenella Attenuata." Pp. 819–21 in *Encyclopedia of Marine Mammals (Second Edition)*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen. London: Academic Press.

Perrin, William F., and Aleta Hohn. 1994. "Pantropical Spotted Dolphin Stenella Attenuata." Pp. 71–98 in.

Perrin, William F., Michael D. Scott, G. Jay. Walker, and Virginia L. Cass-Dudley. 1985. "Review of Geographical Stocks of Tropical Dolphins (Stenella Spp. and Delphinus Delphis) in the Eastern Pacific" edited by N. M. F. S. United States.

Peters, Catherine H. 2018. "Context-Specific Signal Plasticity of Two Common Bottlenose Dolphin Ecotypes (Tursiops Truncatus) in Far North Waters, New Zealand : A Thesis Submitted in Partial Fulfilment of the Requirements for the Degree of Doctor of Philosophy in Conservation Biology at Massey University, Albany, New Zealand." Thesis, Massey University.

Pires, Clara R., Marcos R. Rossi-Santos, Alexandre D. Paro, and Leonardo L. Wedekin. 2021. "Whistles of the Pantropical Spotted Dolphin (Stenella Attenuata) in Santos Basin, Western South Atlantic Ocean." *The Journal of the Acoustical Society of America* 149(5):3241–49. doi: 10.1121/10.0004950.

Poupard, Marion, Benjamin de Montgolfier, and Hervé Glotin. 2019. "Ethoacoustic by Bayesian Non Parametric and Stochastic Neighbor Embedding to Forecast Anthropic Pressure on Dolphins." Pp. 1–5 in *OCEANS 2019 - Marseille*.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rako Gospić, Nikolina, and Marta Picciulin. 2016. "Changes in Whistle Structure of Resident Bottlenose Dolphins in Relation to Underwater Noise and Boat Traffic." *Marine Pollution Bulletin* 105(1):193–98. doi: 10.1016/j.marpolbul.2016.02.030.

Roswell, Michael, Jonathan Dushoff, and Rachael Winfree. 2021. "A Conceptual Guide to Measuring Species Diversity." *Oikos* 130(3):321–38. doi: 10.1111/oik.07202.

Samarra, Filipa I. P., Volker B. Deecke, Katja Vinding, Marianne H. Rasmussen, René J. Swift, and Patrick J. O. Miller. 2010. "Killer Whales (Orcinus Orca) Produce Ultrasonic Whistles." *The Journal of the Acoustical Society of America* 128(5):EL205–10. doi: 10.1121/1.3462235.

Servedio, Maria R. 2004. "The Evolution of Premating Isolation: Local Adaptation and Natural and Sexual Selection against Hybrids." *Evolution; International Journal of Organic Evolution* 58(5):913–24. doi: 10.1111/j.0014-3820.2004.tb00425.x.

Silva, Tammy L., T. Aran Mooney, Laela S. Sayigh, Peter L. Tyack, Robin W. Baird, and Julie N. Oswald. 2016. "Whistle Characteristics and Daytime Dive Behavior in Pantropical Spotted Dolphins (Stenella Attenuata) in Hawai'i Measured Using Digital Acoustic Recording Tags (DTAGs)." *The Journal of the Acoustical Society of America* 140(1):421–29. doi: 10.1121/1.4955081.

Thompson, Roger K. R., and Louis M. Herman. 1975. "Underwater Frequency Discrimination in the Bottlenosed Dolphin (1–140 KHz) and the Human (1–8 KHz)." *The Journal of the Acoustical Society of America* 57(4):943–48. doi: 10.1121/1.380513.