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A functional data analysis approach for modelling frequency-modulated tonal sounds in animal communication

Maria Silvia Labriola[1,2,3,4] | Petra Oswine Pammer[5] | Giulia Pedrazzi[1,4] | Giancarlo Giacomini[1] | Giovanna Jona Lasinio[5] | Daniela Silvia Pace[1,6]

[1]Department of Environmental Biology, Sapienza University of Rome, Rome, Italy; [2]PhD Program in Evolutionary Biology and Ecology, University of Rome Tor Vergata, Rome, Italy; [3]Department of Biology, University of Rome Tor Vergata, Rome, Italy; [4]Echoes-Capitoline Centre for Marine Research–ETS, Rome, Italy; [5]Department of Statistical Sciences, Sapienza University of Rome, Rome, Italy and [6]CNR – Institute for the Study of Anthropogenic Impacts and Sustainability in the Marine Environment – Capo Granitola Unit, Torretta Granitola, Trapani, Italy

Correspondence
Maria Silvia Labriola
Email: maria.silvia.labriola@uniroma2.it

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Abstract

1. Frequency modulation (FM) is believed to play a major role in encoding information in tonal vocal communication. However, most studies aimed at investigating acoustic variability rely on the manual measurement of acoustic parameters, and the implementation of multivariate techniques, which represent only partially sound FM. Thus, innovative modelling approaches able to capture local FM dynamics are needed for tonal sounds modelling. These kinds of methodological developments in bioacoustics might be key for further understanding animal behaviour and ecology.
2. We propose the application of a functional data analysis (FDA) approach to model extracted FM patterns, which entails the transformation of acoustic signals into continuous functions. We describe a Raven-to-R FDA workflow for modelling tonal sounds and we highlight two of its potential applications for classification aims and FM analysis in relation to behavioural, social, and environmental factors. For illustrative purposes, the approach performance was tested on FM patterns (contours) of signature whistles emitted by bottlenose dolphins (*Tursiops truncatus*), to investigate their acoustic variability and potential information content.
3. Our results show that tonal sounds are inherently of functional nature and can be treated as such for FM analysis. We found that building the FDA sound curves using 25 B-spline basis functions was the most appropriate setting for the functionalisation of dolphin whistles. Our approach was able to accurately reconstruct the FM patterns of the modelled tonal sounds and even to capture their fine-scale modulations, with a precision of 80%. Functional clustering showed an accuracy up to 89% for short whistles. Estimated functional coefficients of the regression model suggested that different contextual factors have a significant effect on the FM patterns of SWs.

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4. The adoption of an FDA approach appears to be quite promising for the study of frequency-modulated tonal sounds, both for classification aims and in-depth FM analysis. The limitations and advantages of the approach were discussed. We developed and tested a new methodology able to fill knowledge gaps in animal communication, and we anticipate it will lead to advances in the ethological and ecological understanding of wild animal populations.

KEYWORDS
animal communication, bioacoustics, bottlenose dolphin, FDA, FM, signals, signature whistles, tonal sounds

1 | INTRODUCTION

Frequency modulation (FM) plays a key role in encoding and transmitting information in tonal vocal communication. Animals often adjust the frequency of their vocalisations to suit different purposes in different contexts, reflecting the modalities by which a species interacts with its surroundings and fulfills its ecological role and needs (Burnham & Duffus, 2023). Such adaptations are crucial for ensuring that signals are detected and interpreted correctly by conspecifics, thereby enhancing survival and reproductive success. For example, bottlenose dolphins (*Tursiops truncatus*) can increase whistle frequency during interactions with trawling fishery to support foraging strategies (Rako-Gospić et al., 2021). FM also serves specific social functions across species. Notably, banded wrens (*Thryophilus pleurostictus*) use FM trills during aggressive territorial displays and to attract mates (Trillo & Vehrencamp, 2005). Bottlenose dolphins, on the other hand, modify their signature whistles to aid vocal learning and strengthen social bonds (Sayigh et al., 2023). In elephants (*Loxodonta* spp., *Elephas maximus*), FM in rumbles and trumpets provides insight into the emotional state of the callers, revealing complex layers of social communication (Fuchs et al., 2021; Soltis et al., 2005). Additionally, FM can represent an adaptive response to anthropogenic stressors. For instance, right whales (*Eubalaena* spp.) have been shown to shift their call frequencies to compensate for acoustic masking caused by low-frequency human-generated noise (Parks et al., 2007).

Despite its relevance, FM is only partially represented by the traditional bioacoustics framework (Stowell & Plumbley, 2014), which relies on the manual measurement of several spectro-temporal features (commonly referred to as 'acoustic parameters') (Kershenbaum et al., 2018; May-Collado & Wartzok, 2008; Papale et al., 2017; Wood et al., 2005). These features are carefully chosen to describe the acoustic characteristics of each sound, but they often reduce continuous signals into discrete data, potentially losing valuable information. Whilst frequency-related features such as minimum and maximum frequencies or inflection points (i.e. slope changes in the frequency contour), can quantify aspects of FM, they often fall short of fully representing the local dynamics and nonstationarities of acoustic signals. This limitation points to a deep need for alternative modelling approaches that can comprehensively depict FM sounds.

In the present work, we propose an innovative statistical approach using functional data analysis (FDA) to model FM patterns and highlight some of its potential applications for classification aims and FM analysis. FDA is the branch of statistics exploring functional data, which provides information about curves, profiles, or anything else varying over a continuum (Ramsay & Dalzell, 1991; Ramsay & Silverman, 2002; Kokoszka & Reimherr, 2017). FDA has been long used in environmental and ecological sciences, especially when dealing with time series such as climate data, hydrographic profiles analysis, and river flow patterns (Ainsworth et al., 2011; Assunção et al., 2020; Ullah & Finch, 2013). Only recently applications in the bioacoustics field have found their way to these techniques (Ariza et al., 2023; MacGillivray et al., 2022).

The originality of our proposal lies in the adaptation of the FDA methodology to tonal sounds modelling, which entails the transformation of acoustic data into continuous functions. Using bottlenose dolphin signature whistles as a case study, we (1) describe a semi-automatic Raven-to-R workflow to easily extract FM patterns and model them accordingly to the FDA approach; (2) apply a model-based clustering method for functional data to automatically classify modelled sounds; (3) perform a linear regression with functional responses to investigate FM patterns in relation to behavioural, social, and environmental factors (i.e. contextual factors). Our goal is to provide new insights into animal behaviour and ecology by developing a modelling procedure able to capture the degree of tonal sounds variability and adaptability in relation to different drivers and conditions. In a more general view, we present a methodological approach with several possible applications not only in the bioacoustics field but in all conditions in which a fine characterisation of variations in continuous functions is required.

2 | MATERIALS AND METHODS

2.1 | Case study—Bottlenose dolphin signature whistles

We developed our method using recorded tonal sounds emitted by bottlenose dolphins as illustrative input data, with the aim of testing the approach performance on field recordings. We specifically

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chose to model signature whistles (i.e. individually distinctive vocalisations characterised by a unique and stereotyped FM pattern; hereafter SWs) guided by the major interest of the scientific community in the matter (Janik & Sayigh, 2013) and following new evidence of their acoustic variability (La Manna et al., 2022; Sayigh et al., 2023). Traditionally viewed as fixed and unchanging vocalisations (as their overall FM pattern remains stable over time to convey individual identity; Janik et al., 2006), SWs have been discovered to exhibit a certain degree of plasticity in response to specific activities and environmental conditions. Janik et al. (1994) first hypothesised that SWs also encode context-related information, as variations in their frequency parameters were observed depending on dolphins' behavioural state and performance in discrimination tasks. Notably, Sayigh et al. (2023) demonstrated that female bottlenose dolphins produce SWs with significantly higher maximum frequencies and wider frequency ranges in the presence of their dependent calves. Moreover, between-populations SWs' variability and the factors underlying their differentiation were only recently described (La Manna et al., 2022). Thus, it is reasonable to believe that dolphins may modulate SWs' frequency patterns in response to different environmental, social, and behavioural factors. On the other hand, as SWs are thought to be the result of social learning and adaptive processes (Fripp et al., 2005), acoustic similarities between SWs may provide crucial insights into current differentiation patterns of the species, possibly suitable for the designation of conservation units (Papale et al., 2021; Whitehead et al., 2023).

The analysed acoustic data were collected between 2019 and 2023 in the central Tyrrhenian Sea (Mediterranean Sea, Italy) during boat-based focal follows (for details on data collection procedures see Pace et al., 2019, 2021; Pace, Ferri, et al., 2022; Pace, Tumino, et al., 2022). Recordings were acquired using a towed array of two hydrophones Aquarian Audio H1c-2018 provided by Nauta srl (sensitivity −199 dB re 1 V/μPa, bandwidth <0.1 Hz to >100 kHz) and a digital sound interface Roland Quad Capture UA55 (24-bit and 192 kHz sampling format). Contextual information, including behavioural, social, and environmental factors, was recorded in real time or estimated later based on photographs and the position of the research vessel:

- Group size (number of individuals photo-identified during the sighting);
- Presence/absence of calves (defined as individuals of about 1/3 the length of an adult, with often/sometimes visible foetal folds, always swimming close to an adult just behind the dorsal fin) in the group;
- Predominant behaviour (i.e. behavioural state in which more than 50% of the animals are involved);
- Interaction with fishing gears (trawl nets or gillnets/pots);
- Seafloor depth (obtained from the GEBCO).

The applied behavioural catalogue is reported in Table 1 in Appendix A. No permission nor ethical approval was needed for our fieldwork because of its non-invasive nature.

SWs were identified in Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2023) following the SIGID method (Janik et al., 2013), based on their temporal patterning, and assigned a unique code specific to their individual FM pattern. Visual inspection of the spectrograms was performed with the following settings to optimise whistles' visualisation and selection: Hamming window, size 1024, DFT 1024, overlap 50%, hop size 512, frequency resolution 187.5 Hz.

As SWs are primarily emitted in bouts (Janik et al., 2013), their context-related variability in the dataset was preliminarily investigated by comparing intra-whistle variability within single bouts and between bouts. Variability was measured by computing acoustic dissimilarities between individual-specific whistles using dynamic time warping (DTW; Buck & Tyack, 1993).

2.2 | Proposed approach

The proposed Raven-to-R workflow for modelling tonal sounds through an FDA approach is reported in Figure 1. FM pattern extraction is conducted through the automatic peak frequency contour (PFC) measurement in Raven Pro (see Section 2.2.2 for details). Extracted contours are then imported in R using the *Raven* package (Araya-Salas, 2020), which enables direct data exchange between R and Raven.

We provide here comprehensive guidelines and methodologies for selecting and post-processing acoustic data (segmentation, quality grading, treatment of outliers, and zero-filling), as some specific requirements need to be met in order for FDA to work properly and produce reliable results. In the final stage (functionalisation), each sound is modelled by transforming its PFC into a continuous function, reproducing its FM pattern. This approach does not require the manual measurement of acoustic parameters and allows for the in-depth analysis of tonal sounds FM using continuous mathematics.

2.2.1 | Audio segmentation and quality grading

The initial audio segmentation is performed by visually inspecting the spectrograms in Raven Pro and manually selecting continuous ranges of times and frequencies containing the sounds of interest. Manual selection is preferred over any machine-learning tool to ensure the highest accuracy possible and avoid unnecessary noise that might hinder the contour extraction process. It should be noted that overlapping ambient noise, including anthropogenic noise or other biological sounds, might affect the reliability of the approach. To minimise noise-related issues, a quality score (Q) ranging from Q1 to Q4 is assigned to each sound (Figure 2), depending on its signal-to-noise ratio (SNR). Table 1 contains useful criteria for the quality grading of tonal sounds in field recordings. Users may also plot the PFC measurement on the spectrogram view in Raven Pro to visually inspect the extracted frequency values. Only good-to-high-quality signals (Q3 and Q4) can be deemed suitable for FDA.

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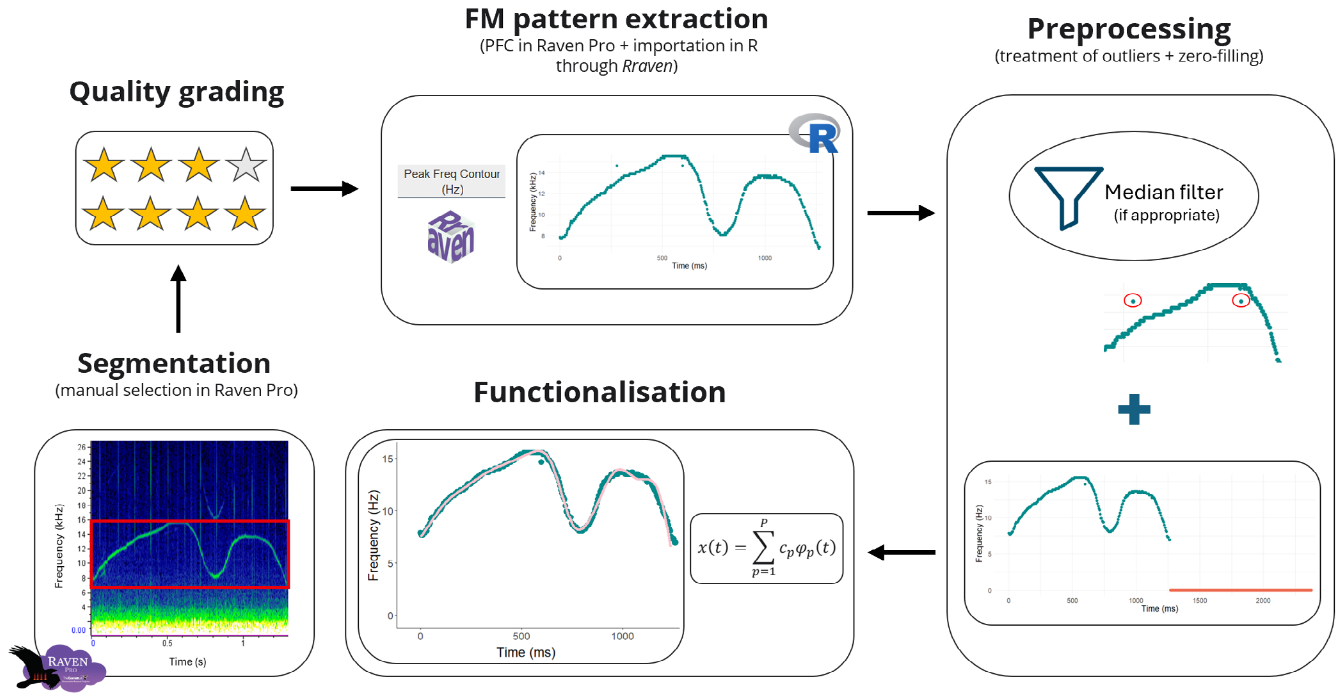

FIGURE 1 Graphical workflow for modelling tonal sounds through a functional data analysis approach. Each signal of interest is selected and assigned to a quality score. FM patterns of good-to-high quality signals are extracted and imported in R for preprocessing, including outliers removal and zero-filling. Finally, each tonal sound is modelled as a continuous function, allowing for in-depth FM analysis.

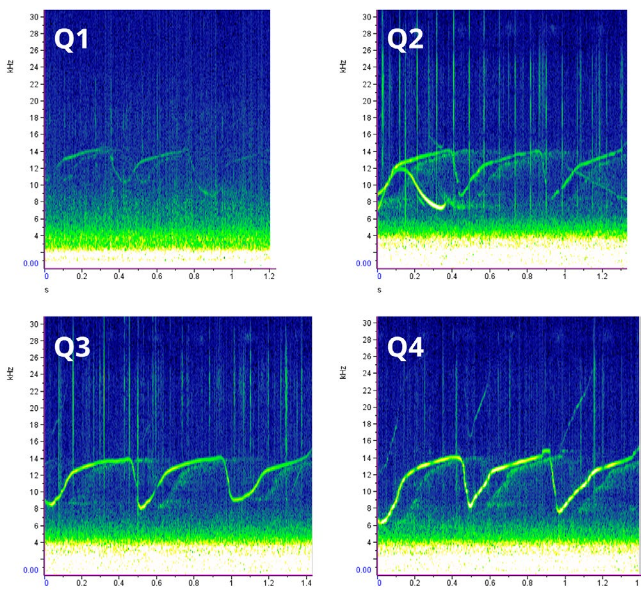

FIGURE 2 Spectrogram view of bottlenose dolphin signature whistles with the same contour assigned to different quality scores: Q1 (top left), Q2 (top right), Q3 (bottom left), Q4 (bottom right). Spectrogram settings: Hamming window, size 1024, DFT 1024, overlap 50%, hop size 512, frequency resolution 187.5 Hz.

2.2.2 | FM pattern extraction

As already mentioned, FM patterns of selected sounds are automatically extracted using the PFC measurement in RavenPro, which produces an estimate of the sound fundamental frequency through a pitch-tracking algorithm. Specifically, the algorithm extracts the frequency at which the maximum power occurs (Peak Frequency) for each spectrogram slice, returning a series of numbers representing the predominant sound. In the case study, given the set spectrogram parameters (sampling rate 192 kHz, hop size 512), frequency values were sampled at intervals of 2.6 ms. Thus, each tonal sound can be defined as a vector $w_i = (f_{i1}, \ldots, f_{i\,ni})$, where $i = 1, \ldots, N$, and n_i is the number of measured values, that is the number of 2.6-ms-long segments contained in the ith sound.

Following the above procedure, acoustic data are transformed into vectors of discrete observations, initially recorded in a continuous dimension (time) that is also discretised as requested as input in FDA software.

Although alternative tools for the extraction of tonal sounds FM patterns exist (Kershenbaum & Roch, 2013; Lin et al., 2013), the PFC measurement is preferred for its direct availability in Raven Pro, which is commonly used by many bioacousticians, and therefore for its subsequent ease of integration in the traditional acoustic analysis process (Fournet et al., 2018; Hamilton et al., 2024; La Manna et al., 2022; Pace, Tumino, et al., 2022). The extraction accuracy was evaluated by adapting the methods proposed by Roch et al. (2011). Ground truth information was collected on a randomly selected validation set (accounting for 10% of the entire dataset), in which different classes of sound duration were equally represented. A trained analyst (first author M.S.L.) placed points along a whistle contour in Raven Pro to manually measure accurate frequency values. The absolute frequency difference between the detection and ground truth value was computed for each overlapping point (within 2.6 ms) between an extracted PFC measurements and a specific ground

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TABLE 1 Quality grading criteria for tonal sounds in an FDA framework.

Quality score	Sound characteristics
Q1	Sound fairly audible and with an FM pattern not clearly visible on the spectrogram (acoustic parameters not measurable)
Q2	Sound audible and with an FM pattern clearly visible on the spectrogram from the beginning to the end (acoustic parameters measurable), but too weak, overlapped with other sounds of similar intensity, or masked by simultaneous noise (peak frequency contour not measurable)
Q3	Sound audible, with an FM pattern clearly visible on the spectrogram from the beginning to the end, and more intense than other overlapped sounds and background noise
Q4	Sound is clearly audible and predominant on the spectrogram

truth tonal. Only PFCs with a median difference lower than 400 Hz (a few frequency bins away) were marked as valid detections. Precision was defined as the percentage of valid detections, whilst deviation was a measure of the median frequency deviation between the path of ground truth and its corresponding detection (Roch et al., 2011).

All the extracted PFCs are then simultaneously imported in R for preprocessing and FDA modelling, thanks to a recently developed R interface that relies mainly on functions from the *Rraven* package (Araya-Salas, 2020). The imported discrete data can be represented as a $n \times N$ matrix $\boldsymbol{F}$ with as many columns as the number of analysed sounds (N), each one defined as a finite set of n_i measured frequency values representing its FM pattern, and as many rows as the n_i of the longest sound in the data (n):

$$\boldsymbol{F} = \left[f_{11}\, f_{21} \ldots f_{N1}\, f_{12}\, f_{22} \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots f_{N\,n-1}\, f_{1n}\, f_{2n} \ldots f_{N\,n} \right].$$

Since tonal sounds can have different durations, their PFCs (w_i) will be composed of a different number n_i of measured values, leading to the presence of numerous missing values (NAs) in matrix $\boldsymbol{F}$, apart from the column corresponding to the longest sound in the data. However, input data for the FDA are required to have the same number of observations, so signals need to be aligned (see Section 2.2.4).

2.2.3 | Post-processing—Treatment of outliers

As with all automatic tools, the PFC measurement is still not exempt from detection errors and requires a supplementary step dedicated to output verification and correction. Specifically, high-amplitude ambient noise can sometimes lead to the improper assignment of some PFC time points to frequency values belonging to other sounds with higher intensities than the sound of interest. In these cases, extracted PFCs are affected by the presence of outliers, which graphically stand out due to their significant deviation from the pattern (see Appendix B). Hence, we suggest applying filtering techniques to remove or replace outliers. We adopted a median-based filtering procedure implemented in R to detect outliers in the PFCs of tonal sounds with different durations and smooth them. Here, outliers are defined as those elements in a PFC vector w_i (any column in the matrix $\boldsymbol{F}$) whose deviation from the local median exceeds a user-defined adjustable threshold t. Thus, for each frequency value f_{ij}, where $j=0, \ldots, n_i$, a local median is computed as the median of the preceding m values: $\mu_{ij} = \text{median}(\{k = j - m, \ldots, j - 1\})$.

Hence, if $\delta_{ij} = \left| f_{ij} - \mu_{ij} \right| > t$, the specific frequency value is considered an outlier, and it is replaced by the mean of its adjacent elements: $f'_{ij} = \frac{1}{2}\left(f_{i\,j-1} + f_{i\,j-1}\right)$.

In the case study, the local median was calculated using $m=5$. At the same time, the threshold t was arbitrarily set as $t=2.8$ after several attempts to identify the one that best fitted the data (i.e. that led to the lowest deviation from the actual FM patterns of the sounds, as visualised in Raven Pro). In specific cases (see Appendix B), we adapted the threshold value to the sound's characteristics and defined it as the standard deviation of the input vector: $sd_i = \sqrt{\frac{\sum_{j=1}^{n_i}\left(f_{ij} - \bar{f}\right)^2}{n_i - 1}}$.

The two parameters can, and have to, be adapted depending on the data.

Appendix B presents detailed general guidelines for applying the proposed outliers filters to PFCs of frequency-modulated tonal sounds. The procedure is semi-automatic as it still requires visual examination to avoid unwanted data modifications. Precision and median deviation from the ground truth frequency of the PFC measurements (see Section 2.2.2) were computed before and after applying the median filters.

2.2.4 | Post-processing—Zero-filling

To transform a set of discrete vectors into functional objects, FDA requires all samples to be aligned, meaning that they need to have the same number of observations. It should be mentioned that dolphin whistles are commonly aligned through the DTW algorithm, which specifies the optimal warping of an observed contour to fit a reference contour (Buck & Tyack, 1993). However, DTW is unsuitable for aligning a set of signals for FDA, given that a DTW alignment of different signals to a reference median contour returns sequences that can still have different

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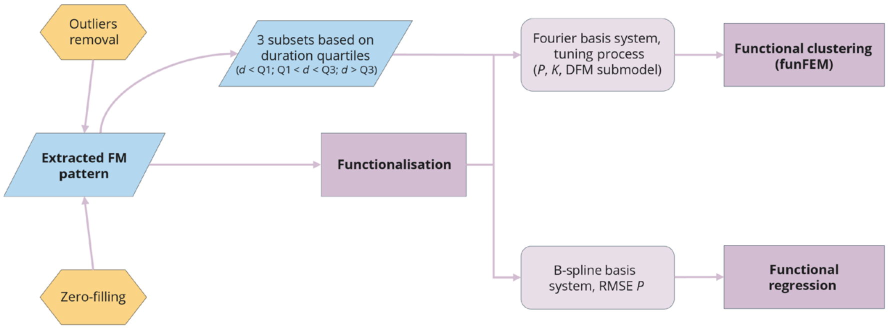

FIGURE 3 Graph illustrating the two different FDA settings adopted in the case study for the purposes of functional clustering and functional regression analysis.

lengths. We reported a complete exploration of DTW methods in Appendix C.

To manage the misalignment problem in a large dataset containing different SWs we propose taking the longest sound's duration as a reference point and filling with zeros every other shorter signal (0 kHz representing the absence of sound). As a result, all analysed sounds have the same length and can be modelled through an FDA approach. One reason in favour of this procedure is that it preserves the acoustic dynamics of the signals in terms of FM across time, and consequently, their information content. This is especially important for functional regression purposes, where the interpretation of the results depends on a two-dimensional space, and thus, preserving the meaningfulness of the relationship between variables of interest is critical.

2.2.5 | Functionalisation of tonal sounds

In an FDA framework, extracted FM patterns are regarded as discretisation of smooth functions of time. Consequently, a 'functionalisation' of the original discrete data is performed through the methods implemented in the R package *fda* (Ramsay et al., 2020). The columns of matrix **F** are transformed into N functions $x_i(t)$, whose values can be derived for any t, reproducing faithfully the FM of all analysed sounds. Following Ramsay and Silverman (2002), functions are built as linear combinations of a set of P functional building blocks (i.e. basis functions) φ_p, with $p=1, \ldots, P$ (Equation 1). These basis functions are linearly independent and defined over a common domain, the same as the functional data.

$$x_i(t) = \sum_{p=1}^{P} c_{ip}\varphi_p(t), i = 1, \ldots, N, \tag{1}$$

where the parameters c_{ip} are coefficients of the basis functions expansion, determining the data smoothing process (Ullah & Finch, 2013).

In matrix terms, the set of FM functions ($x(t)$) derives from the product between a $N \times P$ matrix **C** storing the coefficients c_{ip} of all whistles and a P-dimensional vector containing the basis functions:

$$x(t) = C \bullet \varphi(t). \tag{2}$$

Operationally, to model tonal sounds through the described approach, one must first select an appropriate basis system and choose the number of basis functions to combine. We found the spline basis system with a large number of basis functions (always smaller than the lowest n_i to avoid overfitting or undersmoothing of the data) to be the most appropriate setting for the functionalisation of highly modulated tonal sounds. In particular, cubic B-splines are preferred since they provide a good balance between flexibility and smoothness, allowing for the representation of more erratic FM patterns (Ramsay et al., 2009). We then compute the root mean square error (RMSE, i.e. mean difference between the observed frequencies and the smoothed function values) to compare and select the optimal number of basis functions. However, no single answer is best for all tonal sounds, so the two specifications should be given after carefully exploring all available options, considering the data's characteristics and the objectives of the analysis.

In our case study, we decided to work with two different settings for the two FDA tools presented in this article (Figure 3), following the procedure given above. We used a number P of spline basis functions chosen according to the RMSE to functionalise the FM patterns that were later analysed through functional regression (Section 2.3.2). Specifically, the heuristic elbow method (i.e. the 'knee of the curve' is used as a cutoff point) was applied to the RMSE plot to choose the optimal number P of B-spline basis functions to prevent overfitting the models whilst still preserving sounds FM. To implement functional cluster analysis (Section 2.3.1), we adopted a different basis set that was computationally more efficient and allowed to enhance recurring signal behaviours. The functional clustering was performed using the Fourier basis, and the number (P) of basis functions was chosen as illustrated in Section 2.3.

Once the basis system is selected, the coefficients matrix **C** can be estimated through the smoothing approach implemented in the *fda* function *smooth.basis* (Ramsay et al., 2020), whose fitting criterion is the weighted least squares.

The overall accuracy of the functionalisation was assessed by computing the median frequency deviation between the ground truth path and its corresponding functional model (Roch et al., 2011). Additionally, acoustic parameters, namely, the number of local minima and maxima, were found by differentiation for each functional

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object in the validation test (see Section 2.2.2). The difference between the number of minima and maxima found on each function and manually measured in Raven Pro on its corresponding whistle contour was computed. Only functional models with a difference of 0 or 1 were marked as valid. The precision of the functionalisation was defined as the percentage of valid models.

2.3 | Potential applications

An FDA framework offers the possibility of analysing and classifying the FM patterns of tonal sounds through a variety of tools. Here, we present two applications of the FDA that might actively contribute to ecological knowledge and bioacoustics research.

2.3.1 | Functional clustering

Smoothed functional curves representing animal tonal sounds can be classified through functional clustering techniques, to group similar FM patterns. In the case of bottlenose dolphin SWs, their distinctive FM patterns allow for detecting and monitoring specific individuals and are commonly classified by human observers.

We propose the application of the funFEM algorithm, based on the discriminative functional mixture (DFM) model (Bouveyron et al., 2015), as implemented in the R package *funFEM* (Bouveyron, 2021), to classify functionalised tonal sounds. The method is explained in detail in Appendix E. Model choice involves defining the number of clusters, the number of basis functions to describe the functional data, and the DFM submodel. Model evaluation can be performed through a 'tuning' procedure based on maximising the BIC and the ICL criteria (Baudry, 2015; Schwarz, 1978).

However, since preliminary results revealed that funFEM clustering outputs could be dramatically influenced by the zero-filling process, we strongly recommend dividing the analysed sounds into groups based on duration (which defines the number of added zeros) and performing a functional cluster analysis on each group separately. In our case study, SWs were divided into three groups using the first and third quartiles' values as duration thresholds, leading to groups of comparable sizes. In the tuning procedure, we considered all the different DFM submodels, a number of basis functions between 10 and 30, and a number of clusters between 3 and 6. The classification quality of the clustering was assessed by calculating the proportion of curves assigned to the correct cluster for each individual SW contour. The correct cluster of each SW was defined as the one containing the majority of its replicates. The resulting clusters were characterised by computing the median contour of each cluster.

2.3.2 | Functional regression

Under an FDA framework, the variability of the functional curves in a dataset can be analysed with different independent variables using a functional regression model (Morris, 2015). We present a promising application of FDA to concurrently explore the relationship between sounds FM and any contextual factor, including behavioural, social, and environmental drivers. The smoothed FM patterns of the tonal sounds of interest can be treated as the functional response of a functional linear model, with a set of scalar covariates describing the context of emission. The model takes the form:

$$x_i(t) = \beta_0(t) + \sum_{j=1}^{J} v_{im}\beta_m(t) + \varepsilon_i(t), \tag{3}$$

where $x_i(t)$ is the smoothed FM pattern playing the role of functional response, $\beta_0(t)$ is the intercept, v_{ij}, $m=1, \ldots, M$, are the values of the M scalar covariates, $\beta_j(t)$ are the functional coefficients, and $\varepsilon_i(t)$ is the error term of the model. The functional coefficients and the error term depend on t and thus are not scalar but vary in the continuum of the time window T defined by the longest tonal sound in the dataset. The functional regression model can be built using the *fRegress* function in the *fda* package (Ramsay et al., 2020). Functional coefficients $\beta_j(t)$ are estimated using a linear regression conducted at each time t_ℓ, $\ell=1, \ldots, n_i$, and can be smoothed throughout the time window T by minimising an adjusted version of the sum of squared errors (SSE), the penalised sum of squared errors (PENSSE). 95% confidence intervals should be computed for each regression coefficient.

Ultimately, the FM pattern of each modelled tonal sound can be seen as the result of the sum of the product of each regression coefficient with the value of the corresponding variable observed at time t_ℓ. The resulting functional coefficients allow us to identify the variables significantly associated with the observed FM patterns and illustrate how these relationships vary across the entire duration of the sounds. A variable's association is deemed significant when the estimated coefficient is non-zero, indicating a deviation of the FM pattern from the mean frequency at the time point t_ℓ, and confidence bands do not cross zero in the same time point. The coefficients' sign (positive or negative) shows whether a variable is associated with an increase or decrease in frequency, whilst their dynamics over time reveal how the strength and direction of this relationship change throughout the sound duration.

In our study, the functionalised dolphin SWs were treated as the functional response of a linear model with the following set of context-related independent variables (see Section 2.1 for details):

1. Natural feeding, without interaction with any human activities (coded as *Feednat*);
2. Interacting with/feeding on trawl nets (*Feedtrawl*);
3. Interacting with/feeding on gillnets/pots (*Feedgil*);
4. Socialising (*Soc*);
5. Presence of calves (*Calf*);
6. Group size (*Groupsize*);
7. Depth (*Depth*).

Among these, behavioural variables (*Feednat*, *Feedtrw*, *Feedgil*, *Soc*) and *Calf* were expressed as binary variables, with 1 denoting when the

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SW	$N_{replicates}$	Mean total dissimilarity	Mean intra-bout dissimilarity	Mean inter-bouts dissimilarity
SW_045	70	21,5	8,2	20,4
SW_024	49	12,6	8,8	13,2
SW_060	39	53,9	21,5	53,2

TABLE 2 Mean intra-whistle variability within single bouts and between bouts, computed as pairwise acoustic dissimilarity using DTW, of three individual signature whistles.

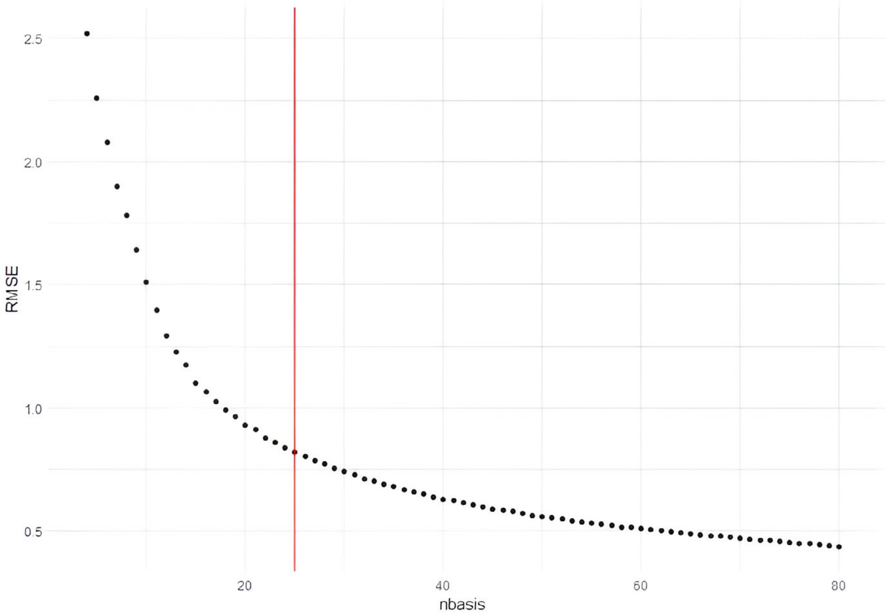

FIGURE 4 RMSE of the FDA dolphin SW models for different numbers of B-spline basis functions. The vertical red line intersects the elbow of the curve, corresponding to the optimal number of B-spline basis functions ($P=25$).

action/presence was observed and 0 otherwise. SWs' duration (coded as *DeltaTime*) was also included as a covariate in the model to account for the effect of zero-filling on the modelled curves. Moreover, as the analysed dataset happened to have a significantly higher number of replicates (10 or more) for some SWs (see Figure 1 in Appendix A), 19 additional dummy variables, aimed at modelling the influence of these specific FM patterns, were included in the model.

The overall statistical significance of the model was studied by running a permutation *F*-test using the *fda* function *Fperm.fd* (Ramsay et al., 2020), testing for no-effect of contextual factors on the FM patterns after a random permutation of response curves.

3 | RESULTS

We tested our approach performance on 1932 wav files (9329 min of recording, about 311 h) of bottlenose dolphin vocalisations collected in the field. Out of 2031 identified SWs, 721 were graded as good-to-high quality (Q3 or Q4) and therefore deemed suitable for functional analysis purposes. Expert human observers previously classified the 721 SWs into 91 individually distinctive FM patterns. A breakdown of the number of SW replicates and bouts per context category is reported in Appendix A. Only SWs with at least 35 replicates were used to measure DTW dissimilarity (used as proxy for intra-SW variability) between individual-specific whistles. Mean intra-whistle variability within single bouts was higher than between bouts in all cases (Table 2).

A number of 550 SWs (76% of the total), belonging to 58 individual contours, were used in the functional clustering. We reduced the original dataset in size by removing sounds with strong background noise and duration 'outliers' (lasting more than 2 s), and by selecting only individual SW contours with at least three replicates in the dataset. Three SWs groups of comparable sizes were obtained, respectively containing short whistles ($N=165$, lasting less than 0.5 s, belonging to 15 individual contours), medium whistles ($N=207$, lasting between 0.5 s and 1 s, belonging to 27 individual contours), and long whistles ($N=178$, lasting between 1 and 2 s, belonging to 25 individual contours).

3.1 | FM pattern extraction

The peak frequency contour measurement of Raven Pro extracted FM patterns of SWs with a precision of 87%. Precision increased after applying the median filters, up to 93%. The median deviation from the ground truth frequency was reasonably low (186 Hz, MAD = 213), and decreased after applying the median filters (178 Hz, MAD = 195).

3.2 | Functionalisation

We modelled the extracted FM patterns of dolphin SWs through an FDA approach and thus transformed them into smooth functions of time. The elbow method applied to the RMSE plot pointed to 25 as

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the optimal number P of B-spline basis functions (Figure 4). When using more than 25 basis functions, no significant improvements could be found in terms of RMSE.

Figure 5 shows six selected SWs in discrete form and their functionalised form built using 25 spline basis functions, allowing for a visual comparison of the modelled signals against their original spectrogram-based representations. All functional models can be inspected in Appendix D. The median frequency deviation of the models from the ground truth was 429 Hz (MAD = 509). Our FDA approach was able to model SWs with a functionalisation precision of 80% based on the number of local minima and of 81% based on the number of local maxima.

3.3 | Functional clustering

Model evaluation through the maximisation of the BIC and the ICL criteria is reported in Appendix E. Among the 12 available models, DFM[Σ_k β_k] was chosen for short and long whistles and DFM[Σ_k β] for medium whistles. The two criteria were optimised in the presence of 4 clusters and 5 Fourier basis functions for all three groups. The composition of the clusters for the three groups is reported in Table 5 in Appendix F.

Clustering results for short whistles are reported below, whilst results for medium and long whistles can be found in Appendix F. Figure 6 shows the partitioning of short whistles within the first two dimensions of the discriminative functional subspace. The composition of the clusters was mostly homogeneous, with blocks of the same colour units separated from each other. A general characterisation of each cluster was derived by computing its median contour (Figure 7). Some clusters were clearly more homogeneous than others, as suggested by their smaller deviance from the median curve. Context-related variability within each cluster was also investigated (Figure 8).

The proportions of curves assigned to the correct cluster for each individual SW contour in the three duration groups are reported in Appendix F. We calculated the accuracy of each classification model as the mean proportion of individual-specific curves classified correctly. The clustering performances were 89%, 79%, and 71% for short, medium, and long whistles, respectively.

3.4 | Functional regression

The functional regression model was estimated using the smoothed FM patterns of the 721 SWs, built with 25 spline basis functions, as the functional response $x_i(t)$ and the scalar covariates v_{im}, $m = 1, \ldots, 27$. The coefficients' estimates function $\beta_0(t)$ and $\beta_m(t)$, $m = 1, \ldots, 8$, for the contextual factors are shown in Figure 9, together with the corresponding 95% confidence bands, whilst the coefficients representing the influence of the SWs with a high number of replicates in the dataset $\beta_m(t)$, $m = 9, \ldots, 27$, are reported in Appendix G. Overall, our method showed that different contextual factors have a significant effect on the FM patterns of SWs. Activities like natural feeding (*Feednat*) and socialising (*Soc*) played a role in lowering the frequencies, whilst the presence of calves (*Calf*) and interacting with/feeding on gillnets/pots (*Feedgil*) in increasing the frequencies. *Feedgil* was found to have the greatest influence. Most coefficients

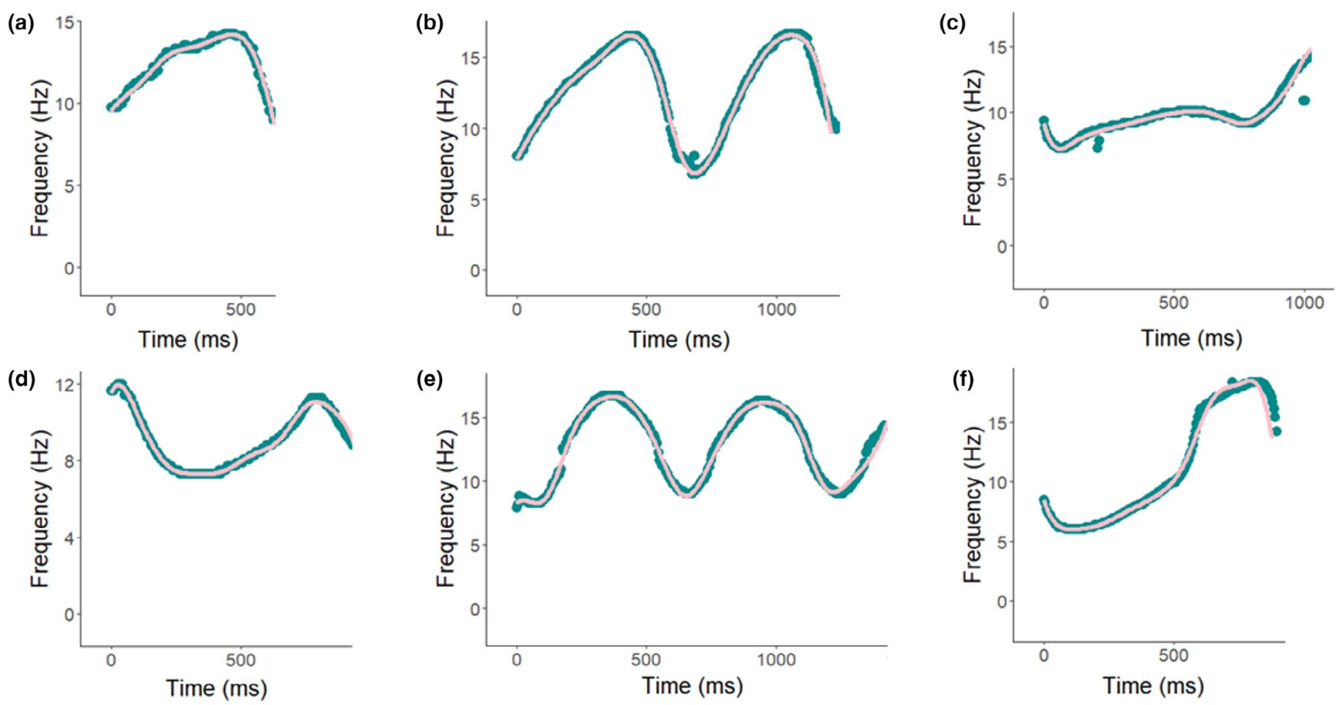

FIGURE 5 Six examples (a–f) of functionalised SWs built through 25 spline basis functions (in pink). The observed frequencies sampled through the PFC measurement are indicated in cyan. The added zeros are not shown.

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gradually flattened to zero towards the end, reflecting the decreasing information in each temporal subperiod. With fewer non-zero frequency observations, the variables had a more neutral effect in the final milliseconds.

Figure 10 reports the results of the permutation F-test for the functional regression model. The null hypothesis was strongly rejected, with the p-value being approximately zero throughout most of the time period. Additional model diagnostics were used to assess the model performance and the quality of the predictions (see Appendix H).

4 | DISCUSSION

Frequency modulation (FM) represents one of the primary mechanisms for acoustic communication, playing a crucial role in the behaviour and ecology of many animal species (Fuchs et al., 2021; Parks et al., 2007; Trillo & Vehrencamp, 2005). By varying sound frequencies, animals can adjust vocal signals to various contexts, such as foraging, territorial defence, mate attraction, and social bonding. These behavioural adaptations are key to survival, as they ensure that signals are effectively transmitted and well-received even in complex and very dynamic conditions, such as in noisy environments or during foraging activities that require social coordination (Burnham & Duffus, 2023). However, FM variation is analysed to a limited extent in traditional bioacoustics frameworks (Stowell & Plumbley, 2014), as they mostly rely on manually measured, discrete features (Kershenbaum et al., 2018; May-Collado & Wartzok, 2008; Papale et al., 2017; Wood et al., 2005), which can oversimplify FM and fail to capture its local dynamics. To address this, we proposed and tested the application of a functional data analysis approach to model FM patterns, describing in detail a promising workflow for the study of acoustic signals with a functional nature. The methodology was fully able to capture SWs' FM dynamics, which may encode individual/group identity and context-related information (Janik et al., 1994). The Raven Pro PFC algorithm here used to extract sound FM patterns performed similarly to other contour extraction algorithms (e.g. Roch et al., 2011), being able to retrieve ground truth tonals with a precision of 87%. However, differences in datasets and accuracy measures limit

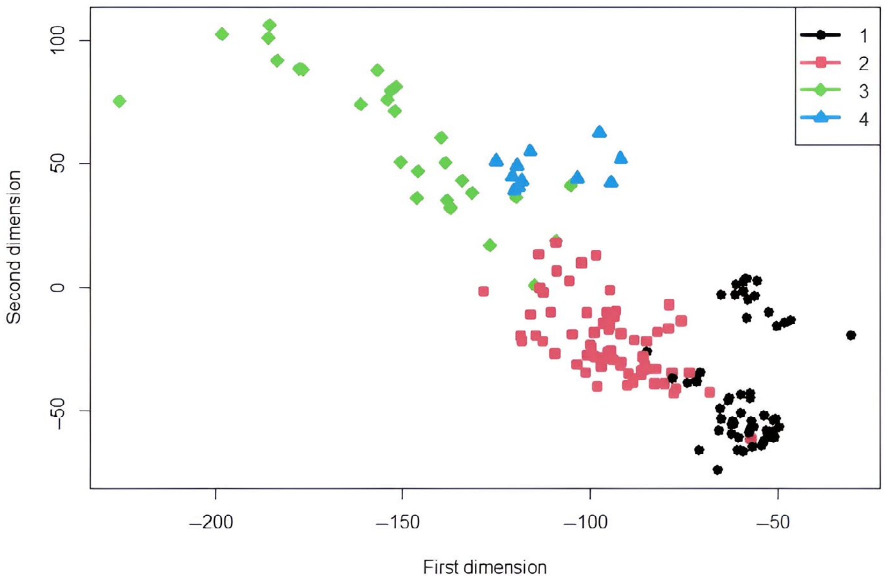

FIGURE 6 Short SWs plotted in the first two axes of the discriminative functional space, where colours and shapes correspond to the assigned cluster.

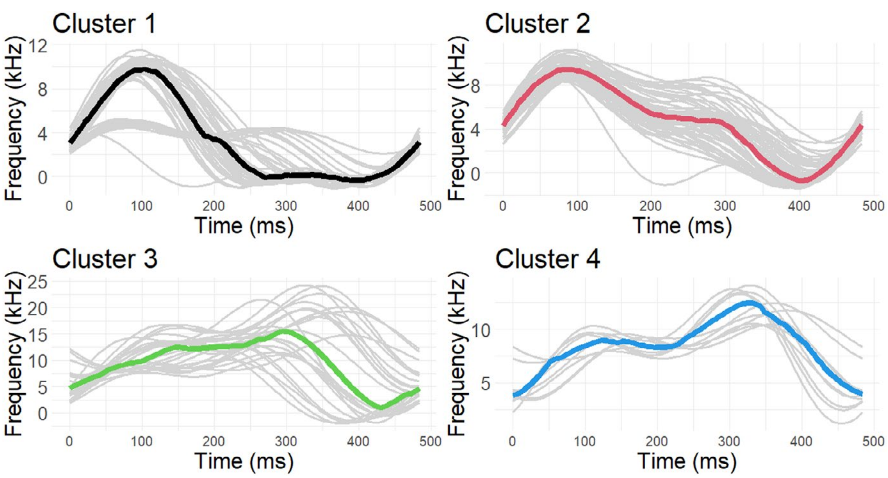

FIGURE 7 Smoothed curves built with five Fourier basis functions (grey) and median contour (coloured) of the four clusters of short whistles.

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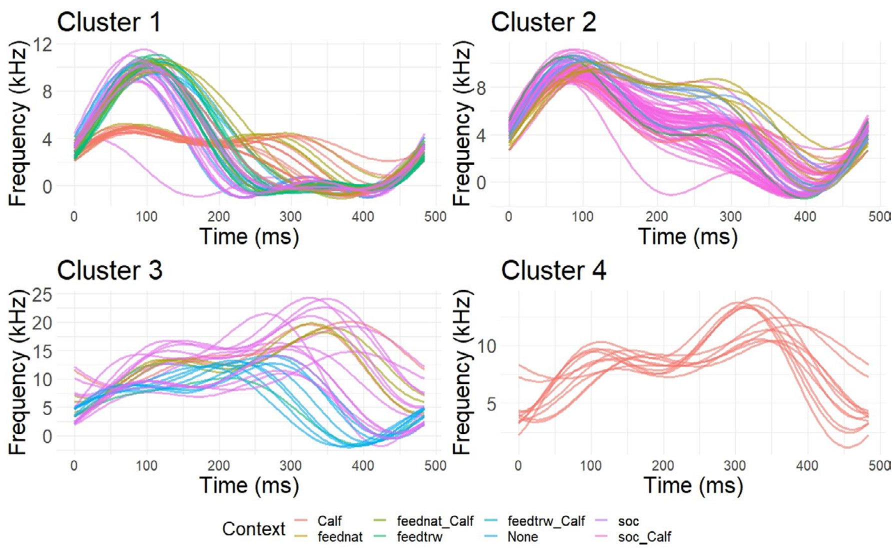
FIGURE 8 Smoothed curves built with five Fourier basis functions of the four clusters of short whistles, coloured by context (i.e. unique combinations of contextual factors).



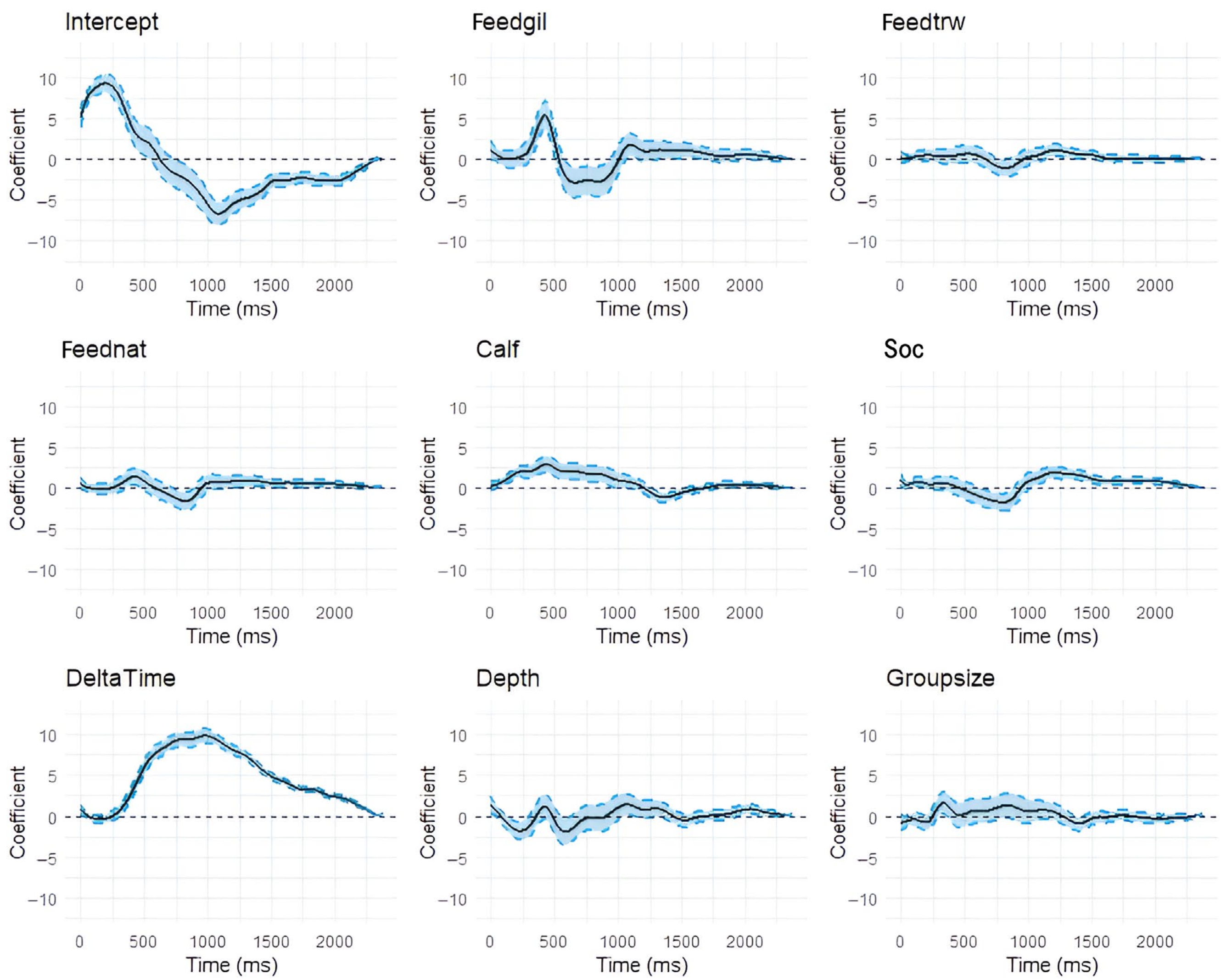


FIGURE 9 Estimated functional coefficients for the intercept and contextual factors in the functional regression model. The black solid line is the coefficient function versus time, and the blue shaded area represents its corresponding 95% confidence interval. Coefficients on the *y*-axis are to be interpreted like in linear regression analysis, for each time point.

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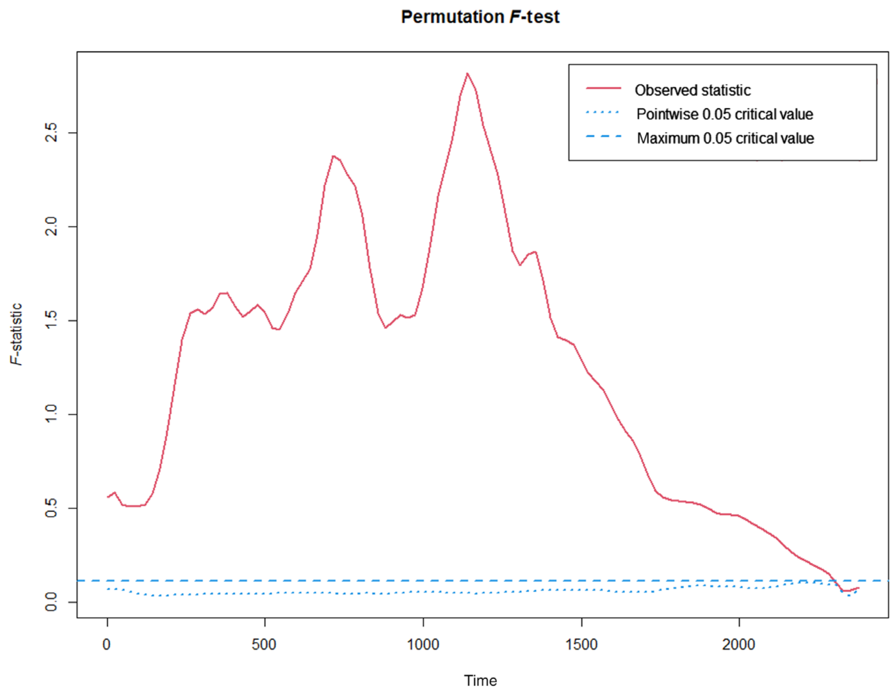

FIGURE 10 Permutation *F*-test for the functional regression model. *F*-statistics (ratio of residual variance to predicted variance) are represented in red, and their corresponding permutation critical values are shown in blue.

the possibility of comparisons with other algorithms. FM pattern extractions through PFC measurement were affected by noise-related outliers, suggesting this algorithm should be applied only when high SNR signals are available. This limitation was partially addressed by the development of ad hoc median-based filters, which increased the precision to 93%. However, the filters are tailored to the data and may require further fine-tuning to optimise performance under varying conditions.

Another challenge was managing non-aligned time sequences in the FDA. To address this, we used a zero-filling technique, which, whilst reducing overall FDA accuracy, was chosen over more common alignment methods like dynamic time warping (DTW; Buck & Tyack, 1993). Zero-filling was applied to our dataset as it preserved the original temporal dynamics of the signal without distorting or stretching it, maintaining the integrity of the data.

In total, we successfully modelled 721 FM patterns through our FDA approach, with a functionalisation precision of about 80%. In most cases, the functional models accurately reconstructed the FM patterns of the signature whistles, whilst accounting for minimal interference from the added zeros or remaining outliers. Moreover, we showed our approach can provide valuable insights in behavioural and ecological studies by employing functional clustering and regression to group similar FM patterns and uncover the multiplicity of factors influencing FM in tonal sounds.

In our case study, the functional clustering of bottlenose dolphin SWs correctly classified 89% of short whistles, 79% of medium-duration whistles, and 71% of long whistles, showing the algorithm's ability to recognise common shape-curves. As a comparison, k-means clustering on a SW distance matrix based on DTW dissimilarity (i.e. a widespread method to group individual SWs; Kershenbaum & Roch, 2013) achieved a classification accuracy of about 40% on our dataset (Appendix C). Functional clustering may be particularly appropriate to find acoustic similarities between FM sounds, possibly reflecting differentiation patterns of animal population. In the case of SWs, whose FM patterns tend to share similarities within social groups (Fripp et al., 2005), clustering techniques could be used to identify conservation units that are relevant to the proper implementation of management actions (Papale et al., 2021).

On the other hand, researchers have suggested that SWs vary depending on the context of their emission (Janik et al., 1994; La Manna et al., 2022; Sayigh et al., 2023). Our FDA approach quantified the influence of various behavioural, social, and environmental factors on SWs' frequency modulation. Interaction with gillnets or pots had the greatest effect, significantly increasing SW frequency, which aligns with the high arousal and cooperative behaviours observed in these settings (Gazda et al., 2005; Wells, 2019). Contrarily to other findings (Rako-Gospić et al., 2021), interaction with trawl nets showed no significant influence on SW structure, suggesting dolphins in the study area may not engage in extensive cooperation when feeding near trawlers. Additionally, SWs emitted in the presence of calves had higher frequencies, supporting the idea that adult dolphins adjust their whistles, possibly using 'motherese,' to aid bonding and vocal learning (Sayigh et al., 2023). Overall, these context-specific variations suggest that SWs serve multiple functions beyond identity signalling, enhancing communication efficiency and social bonding, further supporting dolphins' flexibility, adaptability, and acoustic plasticity (Burnham & Duffus, 2023; May-Collado & Wartzok, 2008).

In conclusion, this work served the aim of developing and testing a new methodology able to fill some knowledge gaps in animal communication encoded in the FM variability, advancing ethological and ecological understanding of wild animal populations.

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AUTHOR CONTRIBUTIONS

Maria Silvia Labriola, Daniela Silvia Pace, Petra Oswine Pammer, and Giovanna Jona Lasinio conceived the ideas and designed the methodology; Daniela Silvia Pace, Giulia Pedrazzi, Giancarlo Giacomini, and Maria Silvia Labriola collected the data; Maria Silvia Labriola, Petra Oswine Pammer and Giulia Pedrazzi analysed the data; Maria Silvia Labriola led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14446.

DATA AVAILABILITY STATEMENT

R codes and data used for the case study are available in: https://doi.org/10.5281/zenodo.13946115 (Labriola et al., 2024).

ORCID

Maria Silvia Labriola https://orcid.org/0009-0007-2666-8673
Giulia Pedrazzi https://orcid.org/0000-0002-2607-2606
Giovanna Jona Lasinio https://orcid.org/0000-0001-8912-5018
Daniela Silvia Pace https://orcid.org/0000-0001-5121-7080

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Appendix A. Case study dataset summary.
Appendix B. Median-based filters.
Appendix C. Dynamic Time Warping methods.
Appendix D. Functional models of signature whistles.
Appendix E. Functional clustering.
Appendix F. Additional clustering results.
Appendix G. Functional coefficients for additional variables.
Appendix H. Functional regression model diagnostics.

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