

Bottlenose dolphins that forage with artisanal fishermen whistle differently

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Abstract

Acoustic communication is a taxonomically widespread phenomenon, crucial for social animals. We evaluate social sounds from bottlenose dolphins (*Tursiops truncatus*) of Laguna, southern Brazil, whose social structure is organized around a cooperative foraging tactic with artisanal fishermen. This tactic involves stereotyped and coordinated behaviour by dolphins and fishermen and is performed by a subset of the dolphin population, splitting it into two distinct social communities. We compared the acoustic parameters and type of whistles emitted by dolphins of the “non-cooperative” and “cooperative” communities, both during their interactions with fishermen and in times where dolphins were engaged in other types of foraging. Our findings show how dolphins’ social sounds differ between foraging tactics and social communities. The frequencies of six whistle types (ascending, descending, concave, convex, multiple, flat) were significantly dependent on tactics and communities. Ascending whistles were more common than expected during foraging without fishermen, and among dolphins of the non-cooperative community. Whistle acoustic parameters (duration, number of inclination changes and inflection points, and initial, final, maximum, minimum frequencies) also varied between social communities. In general, whistles emitted by cooperative dolphins, mainly when not interacting with fishermen, tended to be shorter, had higher frequency and more inflections than those emitted by non-cooperative dolphins. These results suggest that different whistles may convey specific information among dolphins related to foraging, which we hypothesize promote social cohesion among members of the same social community. These differences in acoustic repertoires add a new dimension of complexity to this unique human–animal interaction.

KEYWORDS

acoustic signals, foraging, human–animal interaction, social behaviour, social structure, vocal communication

1 | INTRODUCTION

Acoustic communication is fundamental in the lives of many animal taxa, as it can facilitate reproductive, agonistic and feeding activities (Alves, Vasconcelos, Amorim, & Fonseca, 2011; Au, 1993; Brinkløv

& Surlykke, 2011; Gil-Guevara & Amézquita, 2011). Moreover, communication is an inherently social behaviour (McGregor, 2005). Many cetacean species, for instance, rely on frequency-modulated tonal sounds called whistles to communicate underwater (e.g., Herman & Tavolga, 1988; Popper, 1980; Purves & Pilleri, 1983). There is much

variation in the structure of these sounds, both among species and within a species' repertoire. The features of whistles allow for acoustic distinction between different dolphin species (Lima et al., 2016; Matthews, Rendell, Gordon, & Macdonald, 1999; Oswald, Barlow, & Norris, 2003; Rendell, Matthews, Gill, Gordon, & Macdonald, 1999; Steiner, 1981), and even between populations of the same species (Andrade et al., 2015; Deconto & Monteiro-Filho, 2013; May-Collado & Wartzok, 2008; Wang, Wursig, & Evans, 1995). Further, differences in whistle features within a population may reflect individual variation within these communication signals (e.g., signature whistles; Caldwell & Caldwell, 1965; Caldwell, Caldwell, & Tyack, 1990; Janik, Sayigh, & Wells, 2006; King & Janik, 2013) or reveal behavioural context specificity. For instance, the types of whistles emitted by a group of dolphins can be different when they are socializing, travelling, milling, resting or foraging (e.g., Díaz López, 2011; Hawkins & Gartside, 2010; Papale et al., 2016).

The sharing of social sounds such as these is essential for animals to function well within their social environments (McGregor, 2005). Killer and sperm whales rely on group-specific acoustic signals to navigate through the multiple tiers of their societies (e.g., Deecke, Barrett-Lennard, Spong, & Ford, 2010; Gero, Whitehead, & Rendell, 2016). In societies with fission–fusion dynamics, observed in many dolphin species, social sounds such as whistles can aid social behaviours (e.g., King & Janik, 2013) including individual recognition (Janik et al., 2006) and group cohesion (Janik & Salter, 1998; Quick & Janik, 2012), which in turn facilitate foraging (e.g., King & Janik, 2015; Ridgway, Dibble, Van Alstyne, & Price, 2015).

Dolphins forage using echolocation, a sonarlike ability to locate prey (Au, 1993; Au, Benoit-Bird, & Kastelein, 2007; Au, Branstetter, Benoit-Bird, & Kastelein, 2009; Yovel & Au, 2010), which they often do in groups (e.g., Benoit-Bird & Au, 2009). However, a complex task such as group foraging (e.g., Shane, 1990) may also require dolphins to use social sounds such as whistles to assist group coordination or to convey specific information about the target prey to group members (e.g., Acevedo-Gutiérrez & Stienessen, 2004; Ridgway et al., 2015). Thus, we could expect variations in whistle repertoire of dolphins during different foraging contexts, such as when dolphins forage alone, in groups or when they adopt a specialized foraging tactic. The bottlenose dolphin (*Tursiops* sp.) displays a remarkable behavioural flexibility when it comes to foraging strategies (see Whitehead & Rendell, 2014), making this species an ideal candidate for investigating differences in communicative sounds during foraging contexts.

Despite the inherent social fluidity of dolphin societies (e.g., Lusseau et al., 2006), specialized foraging tactics often structure the social relationships of individuals into distinct social units. Two clear illustrations came from small bottlenose dolphin populations in the Southern Hemisphere. In Shark Bay, Australia, a subset of the population has specialized in the use of sponges to forage for fish at the sea bottom. After controlling for all confounding factors, it became clear that spongers spend more time together among themselves, forming social communities that are distinct from non-spongers (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012). Similarly, in Laguna, southern Brazil, a subset of the dolphin population has specialized in

foraging with the assistance of artisanal fishermen (Simões-Lopes, 1991), in an apparent cooperation where both parties reap similar benefits: a greater number of fish that are also larger in size (Simões-Lopes, Fábian, & Menegheti, 1998). During this foraging tactic—the so-called “cooperative fishery”—small groups of dolphins engage in circular movements chasing mullet shoals towards a line of fishermen that await in shallow waters until cued by specific behavioural displays from the dolphins to cast their nets (Simões-Lopes et al., 1998). This foraging tactic shapes this dolphin society by defining distinct social communities (i.e., sets of individuals that associate more often with each other than with the rest of the population): the cooperatives (dolphins that forage independently and routinely interact with fishermen) and non-cooperatives (dolphins that only forage independently, never with fishermen) (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012).

Here, we evaluate the possible influence of this specialized foraging tactic on the acoustic behaviour of the small and resident population of bottlenose dolphins of Laguna. Given that whistles function for communication (e.g., Herzing, 2000; Janik et al., 2006; King & Janik, 2015), our hypothesis is that such social sounds could assist dolphins in coordinating their activities during foraging, and promote social cohesion among individuals that routinely use the same foraging tactic. If so, we would expect variation in the types and acoustic features of whistles used in two different contexts: when dolphins forage independently vs. with the assistance of fishermen; and/or between members of the cooperative vs. non-cooperative social communities. Therefore, we ask: Are the repertoire of whistle types and the whistle acoustic parameters related to the foraging tactics, to the social community structure, or both? Such differences in acoustic behaviour would suggest dolphins use whistles to regulate their foraging performance and/or facilitate their social organization.

2 | MATERIAL AND METHODS

2.1 | Sampling design

We studied the bottlenose dolphin population that resides off Laguna, southern Brazil (28°28'54"S; 48°46'56"W; Figure 1), to describe their acoustic behaviour when they were foraging with artisanal fishermen and independently. We recorded acoustic data from a 5-m research vessel and from four known sites ashore where the dolphin–fisherman interaction routinely occurs (Figure 1) and photographed their dorsal fins for individual photo-identification (Daura-Jorge et al., 2012). During boat-based surveys, we actively searched for dolphins and recorded all encountered groups, with the hydrophone placed at 0.5–1 m deep and the engine off to avoid background noise. During the sampling from ashore, we recorded all groups of dolphins that visited the interaction sites, with the hydrophone placed at 0.3–0.5 m deep.

To control for behavioural context, we only recorded dolphins when they were foraging. For each sampled focal group, we first determined their current foraging tactic as follows. We defined the

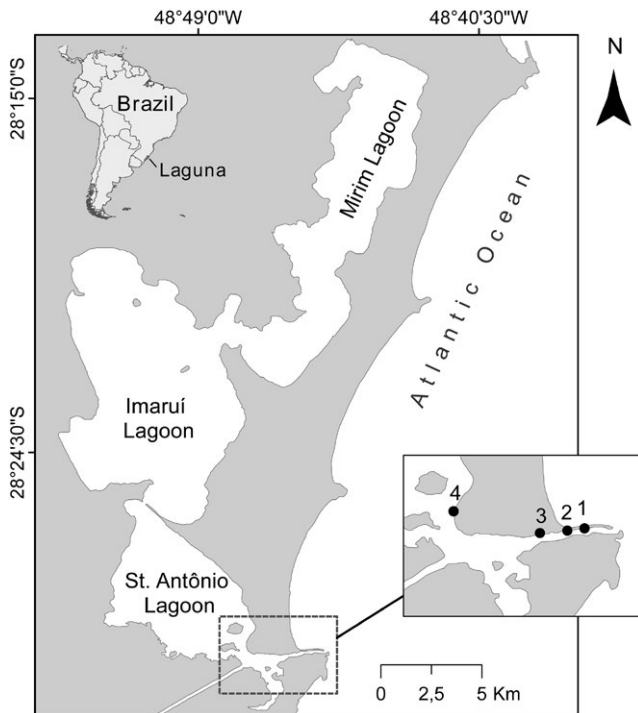


FIGURE 1 Map of the study area with inset highlighting the four sampling sites on shore

cooperative foraging tactic whenever dolphins herd fish schools towards the line of artisanal fishermen, who in turn casted their nets (as detailed in Simões-Lopes et al., 1998). To ensure we used only recordings of individuals in foraging activity, we considered a group of dolphins foraging with fishermen as all individuals within a radius of 200 m displaying the behavioural events and cues described in Simões-Lopes et al. (1998). We defined the non-cooperative foraging tactic when individuals were diving frequently and asynchronously and at various directions (as in Karczmarski, Cockcroft, & Mclachlan, 2000), and considered a group of dolphins foraging without fishermen as all individuals foraging within a radius of 100 m. Behaviour and visual estimates of distances between dolphins were recorded by trained researchers.

When an outsider dolphin approached any focal group, we aborted the sampling and discarded the data. Any recording with background noise (e.g., boating activities) that could interfere in the acoustic analysis was also discarded. Given the relationship between the amplitude of whistles and proximity of individuals to our hydrophone, faint whistles were assumed to correspond to individuals further away—outside of the focal group—and so were discarded. On the few occasions, the same group was recorded more than once during a sampling day, we analysed only one randomly chosen recording per group per day to ensure independence among samples.

2.2 | Acoustic sampling

We recorded dolphins' acoustic behaviour during two sampling periods to evaluate whether whistle type repertoires and whistle

acoustic parameters differ between the foraging tactics (cooperation, not cooperation), the social communities (cooperatives, non-cooperatives) and both (cooperatives interacting or not with fishermen, and non-cooperative dolphins). We carried out the first sampling period during 11 days between March 2010 and September 2011, using a hydrophone Aquarium AQ-9 of frequency response from 0.01 to 100 kHz (-180 dB re: $1 \mu\text{Pa/V}$) plugged into a Sony PCM-M1 digital audio tape (DAT) recorder with sampling rate of 48 kHz (maximum recordable frequency of 22 kHz). All DAT recordings were digitized in RAVEN software version Lite 1.0, then analysed using sampling frequency of 44.1 kHz and 24 bit. Because the software only digitizes 1-min recordings, we split the DAT recordings into 55-s segments. To homogenize effort across groups and to minimize temporal autocorrelation, we randomly selected up to 12 segments per group.

During the first sampling period, we did not assign recordings to individual photo-identification data. This first data set contained recordings of groups of dolphins foraging with fishermen and groups of dolphins foraging independently, regardless of the social community the individuals belonged to. One caveat of this period is that using recording frequency of 48 kHz and sampling frequency up to 22.05 kHz, we may have not captured the whole spectrum of social sounds (Hiley, Perry, Hartley, & King, 2017). However, we may have not missed a large proportion of whistles in the first period because the maximum whistle frequency was rarely above the 22 kHz limit, as shown by only 1% of the whistles being higher than 20 kHz during the 96 kHz recordings of the second period (below). Thus, although limited, our sampling was representative.

We carried out the second sampling during a period of 30 days between June 2013 and May 2014 using the same hydrophone from the first sampling period, but this time plugged to a Sony PCM-M10 digital recorder with sampling rate of 96 kHz (maximum recordable frequency of 48 kHz). All recordings of this period were analysed in RAVEN software version Pro 1.5, with sampling frequency of 96 kHz and 24 bit. These digital recordings were longer than the first period. To standardize sampling effort across groups, we split the recordings into 5-min segments and analysed the same number of segments per group. When the same whistle was repeatedly emitted during a recording, we attempted to minimize potential pseudo-replication by randomly selecting twice as many whistles as individuals in the group for the analysis (e.g., Herman & Tavolga, 1988; Matthews et al., 1999; Kershenbaum et al., 2014); when the group contained a single individual, we randomly selected only two whistles from the same recording.

For the second period, we assigned recordings to social communities via photo-identification data. All individuals identified in photographs during the recordings were classified as cooperative or non-cooperative, based on the social community previously defined by Daura-Jorge et al. (2012). Thus, this second data set contained recordings of foraging dolphins known to be members of the non-cooperative social community, and of dolphins known to be members of the cooperative community, both when they were foraging independently and with fishermen.

2.3 | Whistle type repertoires: Classification and analysis

We classified whistles into types through visual and aural inspection following previous studies (e.g., Bazúa-Durán, 2004; Azevedo & Van Sluys, 2005; Azevedo, Oliveira, Rosa, & Lailson-Brito, 2007; Díaz López, 2011). All whistles recorded during both sampling periods with good signal-to-noise ratio (SNR; i.e., time and frequency parameters distinguishable from background noise) were classified into six types of frequency modulation: ascending (initial frequency less than final frequency and without inflection points), descending (initial frequency greater than final frequency and without inflection points), convex (beginning ascending and ending descending, with an inflection point), concave (beginning descending and ending ascending, with an inflection point), multiple (more than one inflection point, descending to ascending, or vice versa) and flat (no frequency variation).

We built two log-linear models to test the null hypothesis that the frequencies of emission of whistle types were independent of the foraging tactics (cooperation and not cooperation) and the social communities (cooperatives and non-cooperatives). We fitted the models to their corresponding contingency tables using the iterative proportional fitting algorithm, which finds the maximum deviation between observed and fitted margins of the tables, and we used the likelihood ratio test to determine whether the frequencies were different. To perform multiple comparisons among pairs of whistle types, we used a post hoc chi-square test, considering the significance level of $\alpha = .05$ with Bonferroni correction.

2.4 | Whistle acoustic variation: Parameters and analysis

To test whether whistles varied between foraging tactics, social communities or both, we compared seven acoustic parameters

(Figure 2). For all whistles with good SNR recorded during the second sampling period, we measured duration (s), initial, final, maximum, and minimum frequencies (Hz), number of inclination changes (points where frequency modulation changes its slope, without necessarily changing from ascending to descending, or vice versa) and number of inflections (points where there is a change in the slope of the whistle contour from ascending to descending or vice versa).

We built three discriminant function analysis (DFA) models to search for linear combinations of the quantitative acoustic parameters that best characterize the separation between the following three sets of whistle samples. (i) Foraging tactic: Cooperation and Not Cooperation, using whistles recorded in each foraging context regardless of the individual identity and the social community it belonged to; (ii) Social community: Cooperative and Non-Cooperative, using whistles recorded by known individual dolphins from the two social communities, regardless the foraging tactic they were engaged in during the recording; and (iii) Mixed: Cooperative dolphins when interacting with the fishermen, cooperative dolphins when not interacting with fishermen, and non-cooperative dolphins. In the three cases, we departed from the full DFA model with all acoustic parameters, and used backward stepwise leave-one-out cross-validation to search for models with fewer variables that may have higher prediction accuracy. To cross-validate the three sets of whistle samples used in the DFA models, we used a multivariate analysis of variance (MANOVA) and Hotelling T^2 test. In the latter, only five acoustic parameters were used: duration and initial, final, maximum and minimum frequencies. We previously assessed the normality of the acoustic parameters used in the DFA and MANOVA with a Shapiro-Wilk test and used a log transformation when necessary. All statistical analyses were performed in R version 3.1.1 (R Core Team, 2014), using MASS and vegan packages.

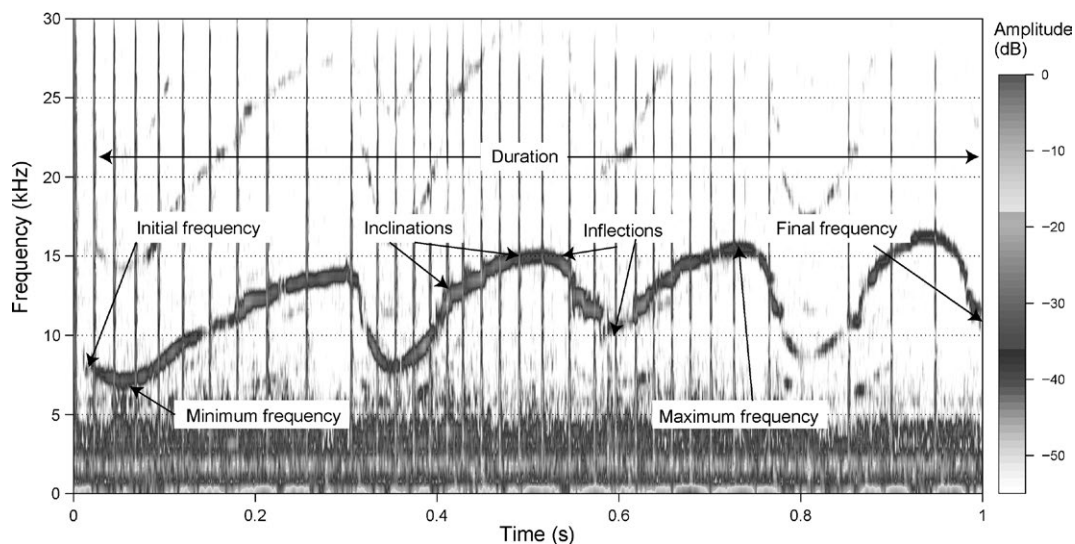


FIGURE 2 Representative recording with multiple whistles and the acoustic parameters measured (sonogram prepared using package SEEWAVE in R environment)

3 | RESULTS

During the first sampling period, we recorded a total of 3.5 hr of acoustic data from 32 focal groups of dolphins (16 interacting and 16 not interacting with fishermen) and sampled a total of 1,708 whistles. During the second sampling period, we recorded a total of 4.3 hr and analysed 364 whistles of 32 groups composed by a total of 39 photo-identified individual dolphins (22 from the non-cooperative and 17 from the cooperative social community).

3.1 | Variation in whistle type repertoire

From the first sampling period, we classified 1,691 whistles: 695 emitted by any dolphin engaged in the cooperative foraging tactic and 996 emitted by any dolphin foraging independently. From the second sampling period, we classified 404 whistles: 287 from members of the cooperative social community, and 117 from the non-cooperative community. Overall, descending and ascending whistles were more frequent, accounting for 69.2% and 50.5% of the total whistles analysed for the first and second periods, respectively.

However, the frequencies of whistle types were dependent of both the foraging tactic ($LR_{\chi^2_{0.05,5}} = 66.6, df = 5, p < .001$) and the social community ($LR_{\chi^2_{0.05,5}} = 42.5, df = 5, p < .001$). Notably, ascending whistles were prominently more common than expect during the foraging tactic not involving cooperation with fishermen (Figure 3a). Indeed, the post hoc pairwise comparison showed significant differences for

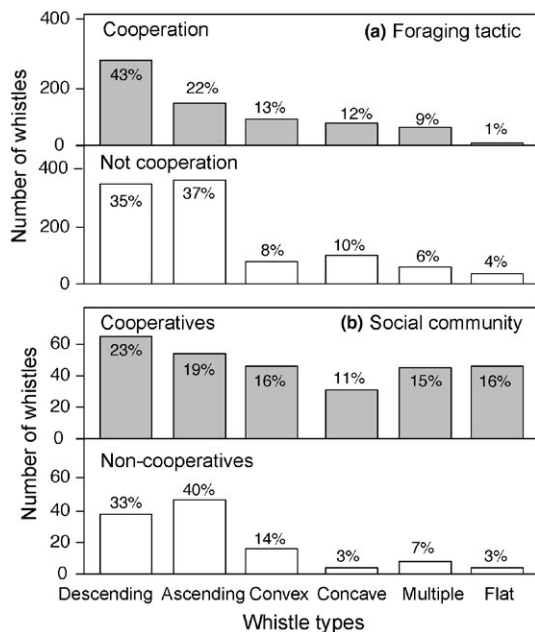


FIGURE 3 Whistle types emitted by bottlenose dolphins in different foraging contexts. (a) Foraging tactics: whistles types recorded during cooperation and not cooperation foraging contexts. (b) Social community: whistles types recorded from individual cooperative and non-cooperative dolphins. Bars indicate the absolute number and percentage of whistles of each category

the following partitions of the contingency table of foraging tactics: ascending type vs. descending ($p < .001$), vs. convex ($p < .001$), vs. concave ($p < .01$) and vs. multiple ($p < .001$) types. For whistle types compared between social communities, ascending whistles were more common among the non-cooperative dolphins (Figure 3b). The pairwise comparison among types supported these differences: ascending type vs. concave ($p < .01$), vs. multiple ($p < .01$) and vs. flat types ($p < .001$).

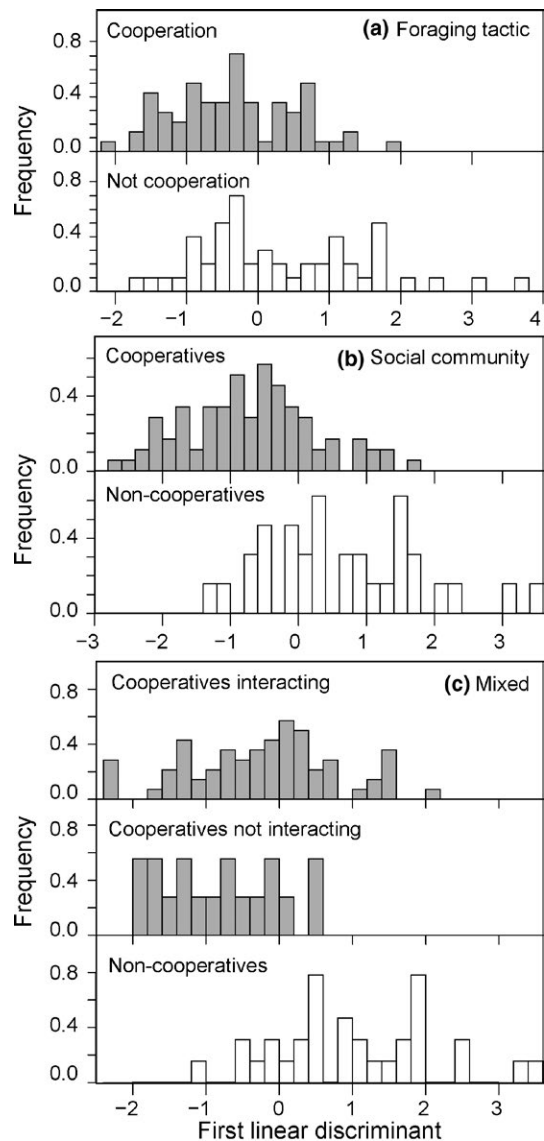


FIGURE 4 Distribution of whistle acoustic parameters along the first linear discriminant axes of the three discriminant function analysis (DFA) models that attempted to separate whistle samples by (a) foraging tactic, (b) social community and (c) mixing both. The DFA model in (a) included whistles recorded from not individually identified dolphins during cooperation and not cooperation contexts. The model in (b) included whistles recorded from individually identified dolphin members of the cooperative and non-cooperative social communities. The model in (c) included whistles from dolphin members of cooperative community when interacting or not with fishermen, and dolphin members of the non-cooperative community

3.2 | Variation in whistle acoustic parameters

We used 120 whistles from the second period in the DFA models: 32 whistles from groups formed by a total of 15 non-cooperative individuals; 70 whistles from groups formed by 16 cooperative individuals when interacting with fishermen; and 18 whistles from groups formed by five cooperative individuals when not interacting with fishermen. Four cooperative individuals were recorded in both foraging contexts. Overall, the DFAs revealed that whistle samples could be separated by social communities and the combination of foraging tactic and social community, but not by foraging tactic alone (Figure 4).

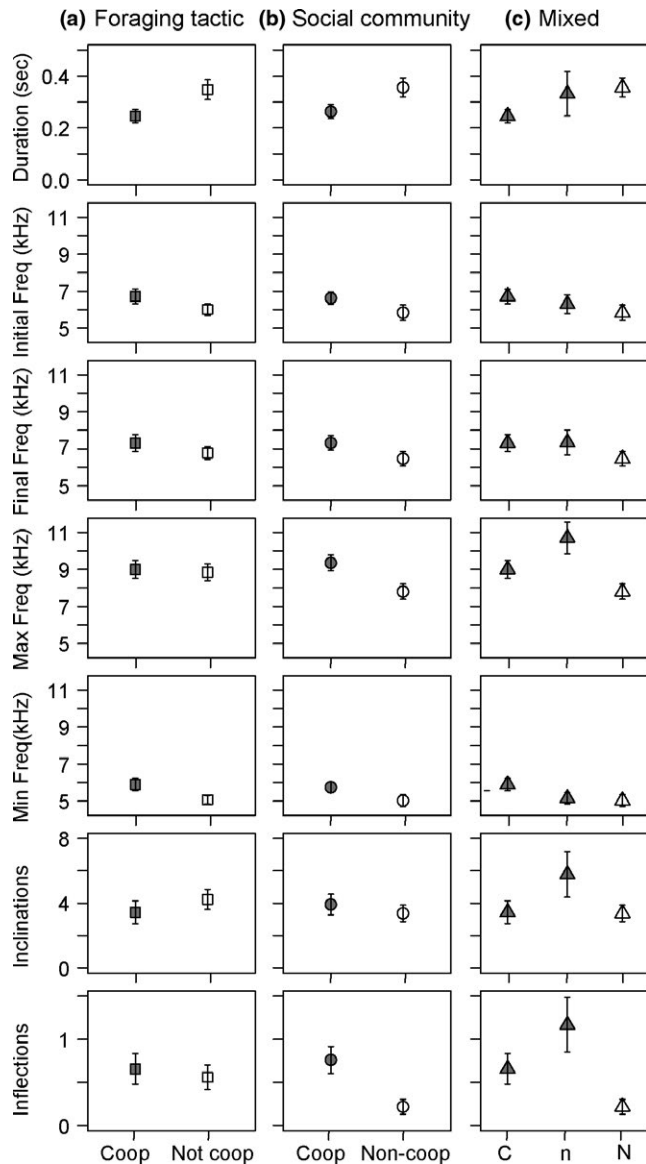


FIGURE 5 Mean acoustic parameters of the sets of whistles samples used in the three discriminant function analyses models: (a) foraging tactic: cooperation (Coop) and not cooperation (Not Coop); (b) social community: cooperative dolphins (Coop) and non-cooperative dolphins (Non-coop); (c) mixed: cooperative dolphins interacting with fishermen (C), cooperative dolphins not interacting with fishermen (n) and non-cooperative dolphins (N). Whiskers indicate standard error of the mean

The most accurate DFA model attempting to distinguish whistle samples only by foraging tactics contained all acoustic parameters (Foraging tactic ~ 5.16 duration + 0.48 initial frequency + 1.61 final frequency - 0.98 maximum frequency - 1.71 minimum frequency + 0.82 inclination changes - 1.92 inflections). This full model had low ability to separate (0.339), and indeed, the attempted separation was not significant (MANOVA Hotelling $T^2 = 0.077$, $df = 1$, $F = 1.761$, $p = .126$). The consequent overlap of the samples along the first linear discriminant axis (Figure 4a) suggested that acoustic parameters of the whistles emitted by any dolphin during the cooperative foraging tactic were not significantly different than those emitted by any dolphin foraging without fishermen. Although the frequency of use of whistle types tended to be different between the two foraging contexts (Figure 3a), on average the acoustic features of these whistles did not vary markedly (Figure 5a).

In contrast, the DFA model attempting to distinguish whistles samples by dolphins of the two social communities (Figure 4b) yielded a clearer separation (DFA ability to separate = 0.640; MANOVA Hotelling $T^2 = 0.148$, $df = 1$, $F = 3.365$, $p = .007$). The most accurate model disregarded initial and minimum frequencies (Social community ~ 6.33 Duration + 1.38 final frequency - 2.25 maximum frequency + 0.77 inclination changes - 2.59 inflections) and indicated an overall differentiation between whistles of cooperative and non-cooperative dolphins. The whistle samples of the cooperatives were more concentrated towards negative values along the first linear discriminant axis (i.e., to the left), while the non-cooperatives' more concentrated around positive values (to the right) of this axis (Figure 4b). As emphasized by their extreme estimates of the DFA model coefficients, the variables that best explained the separation of the whistle samples by social community were duration, maximum frequency and number of inflections. On average, whistles emitted by cooperative dolphins were shorter but with higher frequency and more inflections than the whistles emitted by non-cooperative dolphins (Figure 5b).

Moreover, the whistles of non-cooperative dolphins tended to be different than those emitted by cooperative dolphins, especially when cooperatives were not interacting with fishermen (Figures 4c and 5). The most accurate DFA model mixing foraging tactic and social community discarded initial frequency (Mix ~ 6.21 duration + 1.25 final frequency - 2.56 maximum frequency + 0.43 minimum frequency + 0.72 inclination changes - 2.60 inflections) and had sufficient separation power to distinguish the three sets (Figure 4c; DFA ability to separate = 0.500; MANOVA Hotelling $T^2 = 0.226$, $df = 2$, $F = 2.527$, $p = .007$). The set of whistles emitted by cooperative dolphins when interacting with fishermen tended to be distributed around negative and positive scores of the linear discriminant axis (Figure 4c). However, the set of whistles emitted by cooperative dolphins when not interacting with fishermen tended to be more concentrated around negative scores (to the left), whereas the set of whistles emitted by non-cooperative dolphins were shifted towards positive scores, to the right of the linear discriminant axis (Figure 4c). The coefficient estimates for the first linear discriminant

of this model indicated that whistle duration, maximum frequency and number of inflections explain most of the separation. Combined, whistles recorded when dolphins were not interacting with fishermen—emitted either by cooperatives or non-cooperatives—were longer (Figure 5c). On average, whistles emitted by cooperative dolphins—either when interacting or not with fishermen—also had higher frequency and more inflection points than the whistles of the non-cooperatives (Figure 5c).

4 | DISCUSSION

Our findings show that bottlenose dolphins that routinely forage in cooperation with artisanal fishermen whistle differently than those that forage independently. The frequencies of use of the whistle types are dependent of the foraging tactic and social communities; notably, ascending whistles were more frequent than expected in the non-cooperative context, while concave, multiple and flat whistles were more frequent than expected for the cooperative dolphins. Moreover, dolphin members of different social communities emit whistles that differ in some acoustic features. The social community that routinely engage in the cooperative foraging typically emit shorter whistles with a higher frequency and more inflection points than the community of dolphins that only forage independently. These findings illustrate how social sounds can differ between subsets of individuals within the same population and suggest that dolphins may use slightly different whistles according to the behavioural context. In what follows, we discuss whether whistle variation could play a role in the execution of this distinctive foraging or reflect the social organization of this population around the two foraging tactics.

Population variation in acoustic repertoire is not uncommon, and whistle repertoires vary in a number of dolphin species (Rendell et al., 1999; Bazúa-Durán, 2004; Bazúa-Durán & Au, 2004; Azevedo & Van Sluys, 2005; Rossi-Santos & Podos, 2006; May-Collado & Wartzok, 2008; Papale et al., 2013). Interpopulation variation is commonly related to geographical segregation (Marler & Tamura, 1962; Winn et al., 1981), which may reflect acoustic adaptation to specific environment characteristics (e.g., Deconto & Monteiro-Filho, 2013; Leão, Monteiro-Filho, & Silva, 2015; May-Collado & Wartzok, 2008; Morisaka, Shinohara, Nakahara, & Akamatsu, 2005; Rendell et al., 1999) and/or innovation, selection and learning of sounds among individuals (e.g., Filatova et al., 2012; Wang et al., 1995; Yurk, Barrett-Lennard, Ford, & Matkin, 2002), which can also lead to social segregation within the same population (e.g., Cantor, Shoemaker, Cabral, Flores, & Whitehead, 2015; Deecke, Ford, & Spong, 2000; Filatova & Miller, 2015). As we studied a resident, nearly closed population in which all individuals use the same habitat (Daura-Jorge, Ingram, & Simões-Lopes, 2013), the possibility of geographical and environmental factors driving the divergence of whistle repertoires is unlikely. Instead, our study points to the importance of context specificity and social relationships in driving variation in acoustic communication signals. We suggest two hypotheses for the differences herein reported on the acoustic differences between dolphins foraging or not with fishermen.

First, we hypothesize that specific foraging tactics involving interactions with another species may require specific social sounds to function properly. This relies on the fact that foraging bottlenose dolphins increase whistle emission rate when foraging, suggesting that such sounds could assist behavioural coordination and group cohesion (e.g., Acevedo-Gutiérrez & Stienessen, 2004; King & Janik, 2015), and may use food-related acoustic signalling to share information on food source, such as the presence or location of prey, with their social affiliates (King & Janik, 2015; Ridgway et al., 2015). Bottlenose dolphins can also use certain whistle types in different behavioural contexts. For instance, off Sardinia, Italy, they emit more ascending whistles when socializing and more multiple whistles when foraging (Díaz López, 2011). In New South Wales, Australia, ascending and flat whistles are predominant when socializing, convex whistles when travelling and concave whistles when resting (Hawkins & Gartside, 2010). From the best of our knowledge, whistle variation in different contexts of the same behavioural state (i.e., during different foraging tactics) has not been investigated before. Our findings revealed that the frequencies of the whistle types are dependent on the foraging context. However, there was not a certain whistle type used remarkably often between the foraging contexts to suggest such sounds would convey specific information related the cooperative foraging, for instance as a call to initiate foraging, or to coordinate or inform the group about prey. On the other hand, whistle acoustic parameters—namely number of inflections, maximum frequency and duration—are more distinct between members of the two social communities than between any dolphin interacting or not with fishermen. Thus, social distinction among community members may play a bigger part in the acoustic differentiation found between the foraging tactics.

This leads us to the second hypothesis: that whistles may either help individuals to associate with or recognize those who execute the same foraging tactics. The cooperative fishery appears to have influenced the structuring of this bottlenose dolphin population into social communities (Daura-Jorge et al., 2012). We show that whistle repertoires may be mapped onto this social structure, as dolphins from different social communities tend to whistle differently. This finding reinforces that social relationships may contribute to divergence of acoustic repertoires, as in other toothed whales (e.g., Cantor et al., 2015; Deecke et al., 2000; Filatova & Miller, 2015). The potential influence of social structure in whistle repertoires aligns with the known importance of acoustic sounds for social relationships. For instance, in matrilineal cetacean societies, such as those of killer and sperm whales, distinct social sounds assist in the recognition of multiple social levels (e.g., Deecke et al., 2000; Gero et al., 2016). Male free-ranging bottlenose dolphins that form alliances to access females often share a common whistle type (Smolker & Pepper, 1999; Watwood, Tyack, & Wells, 2004), while dolphins in the same captivity facility tend to whistle more similarly over time (McCowan, Reiss, & Gubbins, 1998).

Along these lines, whistles may be used in the recognition of individuals from same social community. This is suggested not only by the

acoustic differences between community members, but in particular by the differences between whistles of cooperative dolphins when not interacting with fishermen and the whistles of non-cooperative dolphins. It is clear now that bottlenose dolphins use signature whistles to address each other and maintain social cohesion (Janik et al., 2006; Janik & Sayigh, 2013). As such, individually distinctive signature whistles likely contributed to the divergence we found in the acoustic parameters between the two social communities. Thus, we posit that within-community whistles may facilitate individual recognition (Janik & Sayigh, 2013) reinforcing the social ties among members from the same social community (see also Cantor & Whitehead, 2013). The cooperative foraging tactic itself distinguishes cooperative and non-cooperative dolphins; our findings on whistle differences strengthen this distinction.

In conclusion, our data show that there is an overall difference in the types and acoustic features of whistles produced by dolphins that routinely participate in a distinctive foraging tactic that involves the cooperation of artisanal fishermen. This association between acoustic communication, foraging tactic and social structure adds a new dimension of complexity to this local animal tradition. We acknowledge that our attempts to infer causes of the acoustic distinction and function of these social sounds remain speculative at the moment. The natural next step is to design field experiments to quantify the contribution of whistle type and acoustic parameters for the transmission of prey-related information (e.g., King & Janik, 2015; Ridgway et al., 2015) and for the maintenance of social relationships among dolphins (e.g., Janik et al., 2006; King & Janik, 2013). Although it imposes significant logistical challenges, this effort will illuminate the underlying behavioural processes of this foraging specialization. Understanding these processes is key for interpreting how this unique human-animal interaction emerged and spread in the Laguna but not in the neighbouring bottlenose dolphin populations.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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