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Original Investigation

Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: Influence of behaviour

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A R T I C L E   I N F O

A B S T R A C T

Bottlenose dolphins (*Tursiops truncatus*) are an extremely vocal mammalian species and vocal communication plays an important role in mediating social interactions. Very little is known about how wild bottlenose dolphins use whistles in different contexts and no data exist for context specificity of whistle characteristics. This study describes, for the first time in the Mediterranean Sea, the whistle characteristics of bottlenose dolphins in their natural repertoire. Over 35 h of behavioural observations and simultaneous recordings, 3032 tonal, frequency modulated whistles were detected. Our findings further support, for the first time in wild bottlenose dolphins, the suggestion that acoustic features may be good predictors of behavioural state and vice versa. These results advocate that these parameters may be used to communicate specific information on the behavioural context of the individuals involved. Additionally, visual inspection reveals that upsweeps and multi-looped whistles play an important role in the natural communication system of bottlenose dolphins. Likewise, this study demonstrates how dynamic bottlenose dolphin whistle characteristics are and how important it is to consider many factors in analysis. High intra-specific variability in whistle characteristics demonstrates its integral role in the complex social lives of wild bottlenose dolphins.

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Introduction

During acoustic communication, an animal transmits information to other individuals using sound signals and thus attempts to influence the behaviour of these individuals to its own advantage (Slater, 1983). Dolphins (family: Delphinidae) are an extremely vocal mammalian family and vocal communication plays an important role in mediating social interactions (Herzing, 2000; Janik, 2009). Most studies of delphinid vocalizations have concentrated on bottlenose dolphins, *Tursiops truncatus* and *T. aduncus* (e.g. Lilly and Miller, 1961; dos Santos et al., 1990; Smolker et al., 1993; Janik et al., 1994; Connor and Smolker, 1996; Janik and Slater, 1998; Sayigh et al., 1999; Boisseau, 2005; Acevedo et al., 2007; May-Collado and Wartzok, 2008; Díaz López and Shirai, 2009).

Bottlenose dolphins can produce two primary types of sounds thought to play a role in social interactions: (i) tonal, frequency modulated whistles, and (ii) rapid repetition rate "burst-pulse" click train (Herman and Tavolga, 1980; Popper, 1980; Herzing, 2000; Boisseau, 2005; Janik, 2009, Díaz López and Shirai, 2009). Tonal, frequency modulated whistles have been the most commonly studied social signals in bottlenose dolphins so far. Whistles

are generally used in dolphins acoustic studies because they can be recorded in high numbers with good signal-to-noise ratios and they possess numerous characteristics that can be easily measured from their frequency contours (Ralston and Herman, 1995; Boisseau, 2005).

Bottlenose dolphin whistles play an important role in maintaining contact between dispersed individuals (Smolker et al., 1993; McCowan and Reiss, 1995a, Janik and Slater, 1998; Janik, 2000; Acevedo-Gütiérrez and Stienessen, 2004; Watwood et al., 2004; dos Santos et al., 2005; Esch et al., 2009; Díaz López and Shirai, 2009). Bottlenose dolphins live in complex fission-fusion societies where acoustic communication provides a guide for members of a group to gain information about each other in order to interact more effectively (Smolker et al., 1992; Connor et al., 2000). The fine-scale acoustic features of the whistle are thought to play a significant role in the exchange of information between individuals (Janik and Slater, 1998; Sayigh et al., 1990, 1999). Bottlenose dolphins produce individually specific whistles called signature whistles (Caldwell and Caldwell, 1967; Caldwell et al., 1990; Sayigh et al., 2010) that appear to play an important role in social interactions and in maintaining group cohesion (Janik and Slater, 1998). Thus, the individually distinctive nature of signature whistles provides a mechanism for individual recognition among conspecifics (Sayigh et al., 1999). The rest of whistles are considered non-signature whistles, which do not have individually distinctive frequency

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modulation patterns (Watwood et al., 2004). Janik and Slater (1998) found that captive bottlenose dolphins primarily produced signature whistles when one individual was separated from the rest of the group members. However, when all of the animals were together, they primarily produced non-signature whistles.

Whistle acoustic features, such as frequency and duration components, have been used for characterization of whistles of bottlenose dolphins, allowing comparisons among groups and populations (Wang et al., 1995; Rendell et al. 1999; Bazúa-Duran and Au, 2004; dos Santos et al., 2005; Azevedo et al., 2007). However, whistle characteristics of Mediterranean bottlenose dolphins are poorly understood.

Variation in whistle characteristics of free-ranging bottlenose dolphins has been examined in various studies (Buckstaff, 2004; Cook et al., 2004; Jones and Sayigh, 2002). High intra-specific variability in whistle parameters may indicate transmission of emotional information (e.g., presence of food, danger, or alertness) but also may reflect high interindividual variation, aiding individual differentiation (Steiner, 1981; Wang et al., 1995a, 1995b; Morisaka et al., 2005; Azevedo et al., 2007).

This study represents the first attempt in the Mediterranean basin to outline the whistle characteristics of Mediterranean free-ranging bottlenose dolphins. These dolphins have been the focus of a long-term study along the north-eastern coast of Sardinia (Italy). The study area provides a unique opportunity to study vocal production of wild bottlenose dolphins because on a year round, daily basis, groups of dolphins tend to follow predictable spatial patterns foraging and socializing onshore. Additionally, human activities influence the distribution of food resources and dolphins behaviour (Díaz López, 2006a,b; Díaz López, 2009), which promote the evolution of social organizations (Díaz López and Shirai, 2008) and individual preferences for the area (Díaz López and Shirai, 2007).

The main goal of this study is to provide, for the first time, a description of whistle characteristics of Mediterranean common bottlenose dolphins. Another objective of the present study is to provide insights on whistle variation by evaluating whether behavioural activity is associated with whistle characteristics within this population.

Methods

Data collection

The data analyzed for this study were collected from resident free-ranging bottlenose dolphins in the north-eastern waters of Sardinia (Italy) from 2006 to 2008. Data were collected as part of a long-term study, in which acoustic recording and behavioural observations (from surface and underwater) were made year round.

Surveys for dolphins were conducted from a 5-m research vessel, with a 40-hp outboard engine.

Observations were considered satisfactory when the visibility was not reduced by rain or fog, and sea conditions were <3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale). In each encounter, individuals were identified in situ based on natural marks, nicks, scars, or unique skin pigmentations on the dorsal fin and surrounding area (Würsig and Jefferson, 1990). Photographs and video recordings were also used to document and verify visible surface and underwater activities.

Sex was determined by direct observation of the genital region. Males were identified by a gap between the uro-genital slit and the anus, lack of mammary slits, or observation of an erection. Females were identified by observation of mammary slits. Calves were defined as dolphins two thirds or less the length of an adult, they consistently swam beside and slightly behind (Shane, 1990).

Adults were those estimated to be longer than 2.5 m (Díaz López, 2006a).

In each survey, the first recording sample was collected at least 20 min after the initial sighting to allow the dolphins time to habituate to our presence, and no other cetacean species or dolphin group were observed in the vicinity (Díaz López and Shirai, 2009). To record dolphin sounds and behaviour, we stationed the vessel within 2–50 m of the periphery of the group, with the engine off and lowered a hydrophone to a depth that varied between 7 and 9 m. We used an omni-directional hydrophone, with a frequency response of 0.02–100 kHz connected to a preamplifier. Dolphin signals were digitally sampled using a professional 2-channel mobile digital recorded (M-Audio) at a rate of 44.1 kHz and 16 bites, providing a maximum frequency for all recordings of 22.05 kHz. This maximum frequency is suitable for detecting and recording most bottlenose dolphin whistles (Herzing, 2000; Boisseau, 2005; Janik, 2009).

Acoustic recordings were collected continuously during focal group observations and monitored via headphones for quality assurance. Observations of surface behaviour of dolphins were narrated onto one channel while the hydrophone was recorded simultaneously onto the other channel. Behavioural data were collected using focal group continuous sampling (Altmann, 1974; Mann, 2000), whilst "ad libitum" sampling (Altmann, 1974) was used during underwater observations. Underwater observations of the focal group were carried out by one observer with snorkel gear. The more detailed descriptions of underwater behaviour, sex determination and events were later compared with the commentary on the acoustical recording.

During focal observation sessions selected focal groups were observed for extended periods, often the course of several hours. A potential problem with focal group sampling noted by Mann (2000) is that group composition may change. This needs to be guarded against by adopting an appropriate protocol for occasions when groups split (Mann, 2000). Thus, during this study, we distinguish the term group as either a solitary animal or any aggregation of dolphins in the visual area, usually involved in the same activity, following Díaz López (2006a). One observer monitored the focal group and two observers reported position and behaviour of other members of the group in order to control changes in group composition. The encounter continued until the focal group changed composition or was lost; a group was considered lost after 15 min without a sighting (Díaz López, 2006a). The group size was assessed visually in situ, and the data were later verified with photographs and videos taken during each sighting.

Two additional lines of evidence make us nearly certain that recorded whistles were produced by the observed focal group of bottlenose dolphins. First, the amplitude of these sounds corresponded closely to the proximity of individuals; in particular, the highest-amplitude sounds always occurred with bottlenose dolphins alongside our boat position. Secondly, throughout the entire study period, whistles were never recorded in presence of more than one group of bottlenose dolphins in the area. The inclusive definition of a dolphin focal group, to account for all individuals producing sound, was employed (Wang et al., 1995a, 1995b; Erber and Simao, 2004; Bazúa-Durán, 2004; Morisaka et al., 2005; dos Santos et al., 2005; Boisseau, 2005; Pivari and Rosso, 2005; Azevedo et al., 2007; Baron et al., 2007; Quick and Janik, 2008) because during this study was not possible to ascertain which dolphin produced a whistle.

The long-term nature of this study allowed me to confirm that the field data collection and observational studies did not induce significant behavioural changes or stress to the study animals. These bottlenose dolphins have been under study since 1991; they are well habituated to human observers and can be recognized individually based on natural marks, nicks, scars, or unique skin

pigmentations on the dorsal fin and surrounding area. To minimise the effect of the research vessel on dolphins behaviour data were collected when the engine was off, the boat drifted during the observations without an anchor, and whilst the boat was present in the area before the dolphins' arrival. Similarly, a standard criteria, used by our group since 1999 (Díaz López, 2006b; Díaz López, 2009), was adopted to make the effects of the underwater observer on the dolphins' behaviour standard across samples.

Observed behaviours were divided into "Predation", "Depredation", "Travelling", and "Socializing". As described by Díaz López and Shirai (2009), "Predation" refers to bottlenose dolphins preying on free-ranging prey, whereas "Depredation" refers to dolphins taking, or attempting to take, prey that are confined in fish farm cages or that have been caught in fishing nets. "Travelling" involved swimming on a consistent course, with all the members of the group generally spaced within a few body lengths of each other, with rhythmic surfacings followed by shallow dives. "Socializing" animals were involved in active surface and underwater behaviour that included interactions with other group members (body contact, erection, charge, slapping, intromission, petting, etc.) and aerial activity. The definition and duration of each behavioural category was attempted a posteriori following data analysis strictly based on objective, non-discrete parameters, including specifically observed behavioural events, area, dive duration, swimming direction and speed, contact among individual dolphins, presence of fishing gears, and other variables (Díaz López, 2006a).

Out of all the behavioural categories, "Predation" was most commonly observed (39% of recordings), followed by "Depredation" activities (30% of recordings), "Socializing" (17% of recordings), and "Travelling" (14% of recordings).

Whistles selection and categorization

The acoustic recordings were played back on a PC computer as spectrograms using SPECTOGRAM® 6.2.3 software. A 1024-point Hamming window was used to plot all spectrograms. We set the frequency resolution at 43.1 Hz, the display frame duration was 2 ms, and the dynamic range was −90 dB.

Whistles were identified based on visual and aural analysis. Whistles were separated into three different quality categories ("poor", "fair", and "good"), based on their spectrogram quality. Only "good" whistles, with relatively high amplitude, were selected and used for subsequent analyses, their root mean square amplitude was more than 10 dB above background noise (Boisseau, 2005). Selected whistles were transcribed by noting the date and time. Afterwards, a group size, a social group composition, and a behavioural category were assigned to each selected whistle as a result of the photo-identification and behavioural analysis respectively.

The contour of each whistle was determined by visual analyses of the frequency modulation by at least two experienced observers and was then categorized into the following types: "Rise" (whistles with no inflection points and ascendant frequencies), "Fall" (whistles with no inflection points and descendent frequencies), "Wave" (whistles with one inflection point and ascendant-descendent frequencies), "U-shape" (whistles with one inflection point and descendent-ascendant frequencies), "Sine" (whistles with two inflection points), "Flat" (whistles with no inflection points and constant frequency (Azevedo et al., 2007), and "Multi-looped" whistles (whistles with more than two inflection points).

Quantitative measurement of whistle acoustic features

Whistle characteristics were measured from spectrogram windows using Soundruler software on a PC computer. I set the display frame duration at 1 ms with a 1024-point Hamming window. Due to
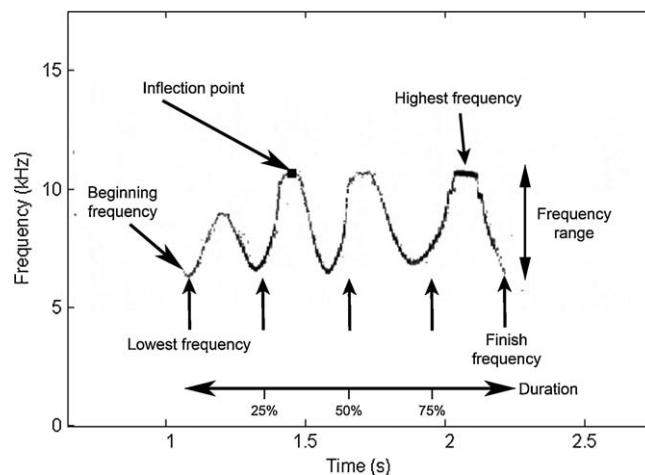

Fig. 1. Spectrogram of a bottlenose dolphin's whistle recorded in Sardinia (Italy) indicating seven of the ten acoustic variables analyzed. FFT = 1024, display frame duration = 2 ms.

upper-frequency limitations (22.05 kHz), harmonic bands were not considered, and only the fundamental frequency of each selected whistle contour was measured. Ten acoustic parameters measured from each selected whistle were dictated by its structure: duration (ms), start and end frequency (Hz), minimum and maximum frequency (Hz), frequency range (Hz), frequency at 1/4, 1/2 and 3/4 of duration (Hz), and number of inflection points. An inflection point is a change in the slope of the whistle contour from negative to positive, or vice versa (Pivari and Rosso, 2005). These whistle parameters were chosen both for consistency with previous acoustical studies (for example Erber and Simao, 2004; Bazúa-Durán, 2004; Morisaka et al., 2005; Pivari and Rosso, 2005; Azevedo et al., 2007; Baron et al., 2007), and because they could be easily measured manually from a spectrogram. Fig. 1 represents a spectrogram of a whistle indicating all the measured acoustic parameters.

Statistical analysis

A common problem of behavioural studies has been the pooling effect, where multiple measurements on the same individual or group are considered independent of each other (Hulbert, 1984). Whistles could not be considered independent samples for statistical analyses because it was not possible to determine if individual whistles came from the same or different animals. In order to limit the lack of independence arising from repeated sampling of the same individuals and to control the different percentages of time spent in any one behaviour, whistles were randomly selected from all four behaviours for all three years of data. The target sample size was arbitrarily set at 50 whistles per year for each proposed behaviour. Thus for subsequent statistical analysis, 600 randomly selected whistles would be available. All variables were tested for normality using Shapiro-Wilks test prior to statistical analysis. As some data were not normally distributed the variables were transformed to near-normality by a Log 10 transformation.

Whistle acoustic features may be highly correlated or "redundant" with one another. Therefore, Principal Component Analysis (PCA) was conducted to (i) isolate independent and uncorrelated acoustic variables from the original set of 10 whistle acoustic features and (ii) meet the assumption of independence for subsequent analysis. The principal components method of extraction begins by finding a linear combination of variables (component) that accounts for as much variation in the original variables as possible. The eigenvalues represent the variance extracted by each component, and are expressed as a percentage of the sum of all

Table 1
Descriptive statistics for acoustic whistles parameters of wild bottlenose dolphins relative to activity patterns. The duration was measured in milliseconds and frequency variables were measured in Hz.

Behaviour		Duration	Fi	$F_{1/4}$ (Hz)	$F_{1/2}$ (Hz)	$F_{3/4}$ (Hz)	Ff (Hz)	Fmin (Hz)	Fmax (Hz)	FM (Hz)	IP
Depredation (N=150)	Mean+SE	758±40	9201±294	10,058±349	10,913±329	11,909±386	12,763±476	7916±257	14,300±335	6504±271	1.8±0.2
	Min–max	131–1886	3381–16,913	4286–18,713	4501–15,263	4630–16,603	3984–18,842	3381–4630	4630–18,842	818–12 808	0–11
Predation (N=150)	Mean+SE	759±80	9596±363	9767±308	11,025±356	11,292±418	11,650±572	7843±283	14,154±397	6467±331	2.3±0.4
	Min–max	36–4239	5418–21,985	5101–19,663	4995–19,525	5101–19,113	3575–21,516	3575–17,738	5418–21,985	0–13 313	0–22
Social (N=150)	Mean+SE	413±30	8627±277	9347±296	9762±321	10,223±351	10,496±403	8021±285	1173±364	3692±304	0.8±0.2
	Min–max	40–1740	2988–13,026	3622–14,188	4150–15,879	4045–14,928	4150–16,090	2988–12,709	4150–16,090	0–10 672	0–6
Travel (N=150)	Mean+SE	467±60	8586±535	8935±545	9347±625	9606±617	9444±731	7361±432	11,019±719	3659±434	1.4±0.3
	Min–max	55–174	2882–17,875	2882–14,850	2988–18,563	3094–14,716	3094–16,820	2882–11,290	3094–19,663	106–9488	0–8
Total (N=600)	Mean+SE	621±31	9070±173	9603±175	10,411±191	10,946±215	11,356±271	7855±149	13,086±222	5312±183	1.6±0.1
	Min–max	36–4239	2882–21,985	2882–19,663	2988–19,525	3094–19,113	3094–21,516	2882–17,738	3094–21,985	0–13 313	0–22

N, number of samples; SE, standard error. Fi = beginning frequency at start of whistle; $F_{1/4}$ = frequency at 1/4 of whistle duration; $F_{1/2}$ = frequency at 1/2 of whistle duration; $F_{3/4}$ = frequency at 3/4 of whistle duration; Ff = finish frequency at end of whistle; Fmin = lowest frequency attained by whistle; Fmax = highest frequency attained by whistle; FM = frequency modulated range calculated as Fmax minus Fmin; IP = number of inflection points.

Table 2
Descriptive statistics for acoustic whistles parameters for bottlenose dolphin whistles types along the north-eastern coast of Sardinia (Italy). The duration was measured in milliseconds and frequency variables were measured in Hz.

Type		Duration	Fi	$F_{1/4}$ (Hz)	$F_{1/2}$ (Hz)	$F_{3/4}$ (Hz)	Ff (Hz)	Fmin (Hz)	Fmax (Hz)	FM (Hz)	IP
Rise (N=234)	Mean+SE	379+22	8623+236	9691+273	10,909+301	12,065+347	13,313+391	8623+236	13,313+391	4690+291	0
	Min–max	36–1003	2882–14,634	2882–14,634	2988+15,675	3094–17,188	3094–19,136	2882–14,248	3094–19,136	106–10,968	0–0
Multi–loop (N=126)	Mean+SE	1209+91	8809+377	9695+344	9668+389	9252+389	8421+484	6395+284	12,498+356	6312+258	2.3+0.4
	Min–max	151–424	4679–21,422	5775–15,813	4995–16,775	5319–16,603	3575–21,516	3575–14,898	9260–21,516	3575–12,788	3–22
U-Shape (N=84)	Mean+SE	641+57	9743+380	8938+462	9868+468	12,054+521	14,006+646	8094+283	14,760+567	6919+538	1+0
	Min–max	89–1628	5735–14,492	5312–18,713	4890–17,672	5207–17,766	5270–18,842	4890–12,899	5735–18,842	689–12,808	1–1
Sine (N=72)	Mean+SE	689+53	10,110+700	10,441+654	11,447+642	10,347+561	10,329+655	7679+447	13,820+599	6149+432	2+0
	Min–max	299–1433	3381–21,985	4286–19,663	4673–19,525	4630–19,113	4679–18,975	3381–17,738	4845–21,985	1464–13,313	2–2
Wave (N=42)	Mean+SE	495+71	8233+556	9831+480	11,244+389	11,620+668	9504+733	7561+329	12,603+515	5041+467	1+0
	Min–max	169–1252	3833–14,449	6697–14,611	7320–14,363	6580–15,125	4045–15,033	3833–11,124	7320–15,562	1585–8225	1–1
Fall (N=36)	Mean+SE	134+24	9423+699	8548+602	8117+629	7768+648	7611+670	7611+670	9423+699	1811+620	0
	Min–max	55–423	4150–14,766	4150–13,026	3939–13,026	3939–12,920	3833–12,709	3833–12,709	4150–14,766	105–8063	0–0
Flat (N=6)	Mean+SE	179+26	10,462+2856	10,145+3118	10,137+3053	10,462+2856	10,462+2856	10,462+2856	10,462+2856	0+0	0+0
	Min–max	128–217	4995–14,634	4150–14,634	4256–14,505	4995–14,634	4995–14,634	4995–14,634	4995–14,634	0–0	0–0

N, number of samples; SE, standard error. Fi = beginning frequency at start of whistle; $F_{1/4}$ = frequency at 1/4 of whistle duration; $F_{1/2}$ = frequency at 1/2 of whistle duration; $F_{3/4}$ = frequency at 3/4 of whistle duration; Ff = finish frequency at end of whistle; Fmin = lowest frequency attained by whistle; Fmax = highest frequency attained by whistle; FM = frequency modulated range calculated as Fmax minus Fmin; IP = number of inflection points.

eigenvalues (i.e. total variance). Regularly, a few components will account for most of the variation, and these components can be used in place of the original variables during subsequent statistical analysis (McCowan et al., 1998; Boisseau, 2005).

To test if whistle characteristics would vary with behaviour, I conducted multivariate discriminant function analyses on the component loadings from principal component analysis. Discriminant function analysis identifies a linear combination of quantitative predictor variables that best characterize the differences among groups. For the purposes of this study, discriminant analysis was used in a descriptive sense for revealing major acoustic differences between the groups. Variables are combined into one or more discriminant functions. Based on these discriminant functions, the classification procedure assigns each variable to its appropriate group (correct assignment) or to another group (incorrect assignment). The larger the standardized coefficients for each type of variable in each discriminant function, the greater the contribution of the respective variable to the discrimination between groups. For external validation we used the cross-validation classification technique, in which each case is classified by the functions derived from all cases other than that one.

To test for differences in the whistle characteristics between selected groups, I conducted a multivariate analysis of variance MANOVA. The one-way or nested ANOVA (including Levene's statistic for homogeneity of variances and Welch F test in the case of unequal variances) was conducted to test the equality of means of several univariate samples. If the test shows significant inequality of the means, a Tukey's post hoc contrast was performed. A contingence table analysis (based on Chi-square test) was used to investigate the relative frequency of occurrence of the various whistle types in relation to the different behaviours.

All the statistical tests and mathematical analysis were performed with PAST (Hammer et al., 2001) and MINITAB® Release 14.1 software packages. The data are presented as means ± SE. Statistical significance was tested at the $P < 0.05$ level.

Results

Over the 35 h of observations and simultaneous recordings, 3032 tonal, frequency modulated whistles were detected. A total of 1050 "good" whistles, with relatively high amplitude, were analyzed. In order to limit the lack of independence arising from repeated sampling of the same individuals and to control behavioural variation, 600 whistles (57% of the analyzed whistles) were randomly selected from all four behaviours for all three years of data. Summarized data (mean, standard error, minimum and maximum) of whistles produced by groups of free ranging undisturbed bottlenose dolphins are shown in Table 1.

Of the 600 randomly selected whistles, a total of 14 different bottlenose dolphin social groups were recorded, corresponding with 27 identified bottlenose dolphins (6 males, 9 females, 5 unsexed, and 7 calves). Group size varied from 2 to 13 individuals (mean = 5.1 ± 1). Groups were composed of either only adults (9 groups) or adults and mother–calf pairs within the group (5 groups). In total, the 27 dolphins were sighted a mean of 3 ± 0.5 times during the study. On average each individual associated with 8 ± 0.7 partners.

Summarized data (mean, standard error, minimum and maximum) for acoustic parameters of bottlenose dolphin's whistles for each whistle category are shown in Table 2. Visual inspection revealed that a rise whistle type, also named upsweep or type 2 whistle (McCowan and Reiss, 1995), was the most observed whistle contour (comprised 39% of the whistle repertoire) followed by multi-loop whistles (21%), U-shape (14%), Sine (12%), Wave (7%), Fall (6%), and Flat (1%) (Fig. 2). As the type 2 whistle exemplars in

Table 3
Principal component loadings of acoustic features, their eigenvalues, and their percent variance explained for whistles produced by groups of wild bottlenose dolphins.

Acoustic feature	Principal component		
	1	2	3
Duration *(ms)*	0.26	−0.85	0.06
Fi (Hz)	0.84	−0.00	−0.35
$F_{1/4}$ (Hz)	0.89	0.00	−0.12
$F_{1/2}$ (Hz)	0.89	0.07	0.14
$F_{3/4}$ (Hz)	0.79	0.11	−0.33
Ff (Hz)	0.83	0.19	0.25
Fmin (Hz)	0.84	0.41	−0.19
Fmax (Hz)	0.94	−0.22	0.13
FM (Hz)	0.54	−0.65	0.40
Inflection points	−0.20	−0.61	−0.67
% variance explained	56.3	18	10

Fi = beginning frequency at start of whistle; $F_{1/4}$ = frequency at 1/4 of whistle duration; $F_{1/2}$ = frequency at 1/2 of whistle duration; $F_{3/4}$ = frequency at 3/4 of whistle duration; Ff = finish frequency at end of whistle; Fmin = lowest frequency attained by whistle; Fmax = highest frequency attained by whistle; FM = frequency modulated range calculated as Fmax minus Fmin; Inflection points = number of inflection points.

McCowan and Reiss (1995) were not presented on standardized time axes, multiple exemplars of this whistle type on standardized time axes are presented in Fig. 3.

Whistles types were highly associated with behaviours (Contingency table $\chi^2 = 1\,266$, d$f = 18$, $p < 0.001$). Particularly, rise whistles appear to be associated with social behaviours and multi-loop whistles were more closely associated with predation activities (Fig. 4).

Independent components of whistle contour variability

Principal component analysis generated 10 statistically independent components. The first three components accounted for 84.3% of data variance, suggesting the complexity of the data set can be reduced to three components with a 15.7% loss of information (Table 3). Two features combined suggest the first three components may be used to summarise the dataset effectively: (i) the eigenvalues for these components were greater than one and (ii) the screen plot of all ten eigenvalues shows a change in gradient after the third component, suggesting these additional components are redundant to an extent.

Component 1 accounts for 56.3% of the variance of the data set and is most closely correlated with a measure of the highest frequency attained by whistle. This maximum frequency loaded highly with Component 1. Moreover, it was observed that frequency parameters were strongly correlated.

Component 2 accounts for 18% of data variance and is strongly correlated with whistle duration. In addition, component 3 is correlated with number of inflection points and accounts for 10% of variance. This is important to consider given that multi-loop whistles comprised 21% of the acoustic sample and the number of inflection points was related to the number of loops in a particular multiple loop whistle.

Comparisons among behaviours

I employed discriminant function analysis to further investigate the relationship between behavioural state and whistle acoustic structure. The percentage of factor scores classified to the correct groups among the four behaviours was 50% overall, and the cross-validation yielded an average correct assignment of 45%. MANOVA supported the results of discriminant analysis showing that the selected whistle acoustic features were statistically different between behaviours (MANOVA, $F_{9,108} = 5.45$, *P < 0.001*).
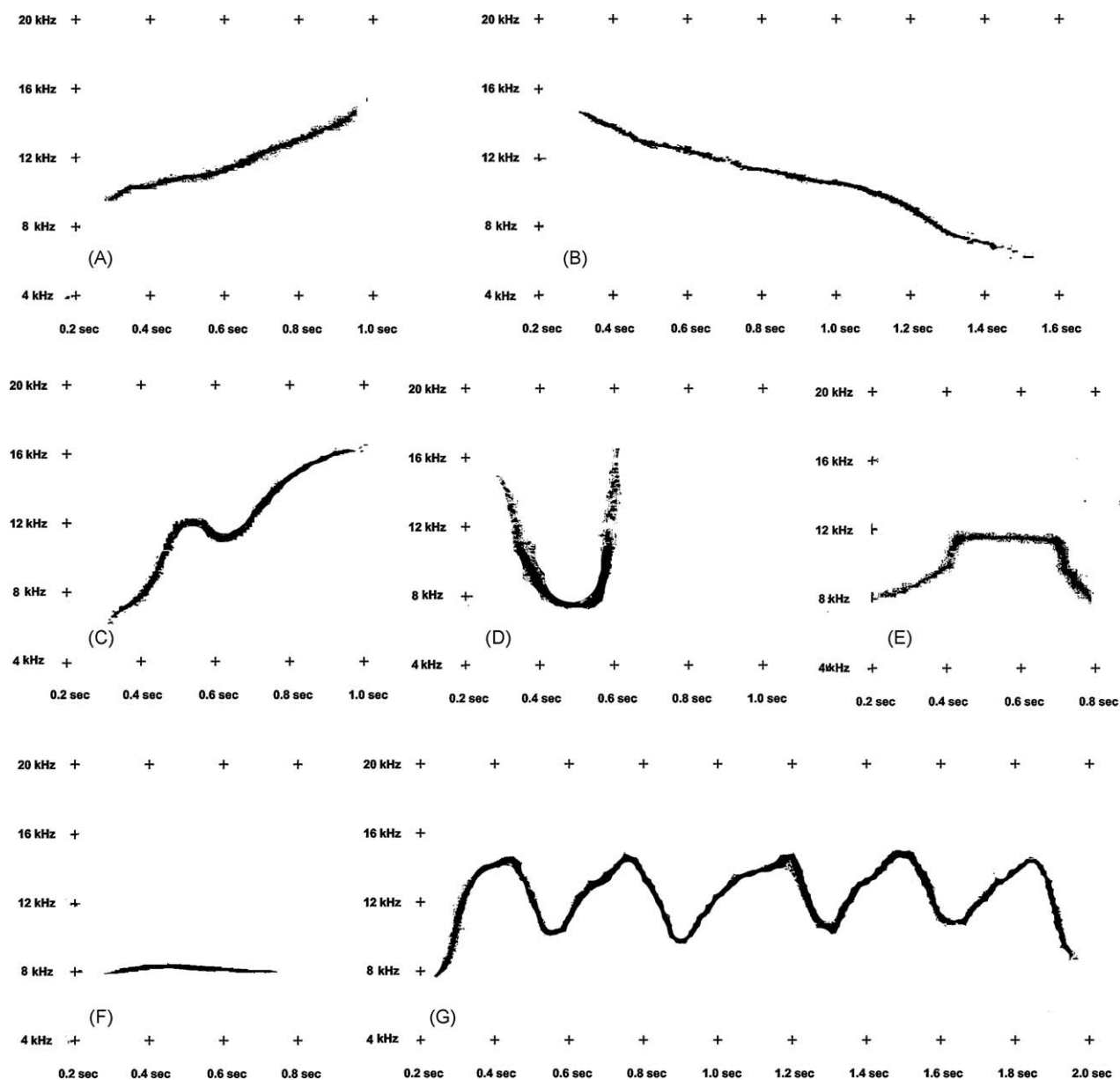
Fig. 2. Example spectrogram for all observed whistle types on standardized time axes. (A) Rise, (B) Fall, (C) Sine, D) U-shape, (E) Wave, (F) Flat, and (G) Multi-looped. FFT = 1024, display frame duration = 2 ms.

Moreover, ANOVA test attributed significative differences to the first component of whistle variability, and a post hoc Tukey's test reveals that differences were observed in groups of dolphins engaging in travelling (ANOVA, $F_{3,36}$ = 30.8, p < 0.001).

Both discriminant and MANOVA analyses could not discriminate effectively between behaviours when social group composition was not taken into account. Thus, a relation could be expected between social group composition and behavioural activity. I therefore conducted separate discriminant function analysis by behaviour within each observed social group to evaluate where differences might be found. Separate discriminant analysis by behaviours within the same social group yielded similar results (Table 4). MANOVA indicated that the activities were indeed significantly different from one another within social group (MANOVA, F-values for all comparisons p < 0.05). ANOVA test attributed significative differences to the first two components of whistle variability: maximum frequency and duration (ANOVA, F-values for all comparisons p < 0.05).

Discussion

Whistle acoustic features of wild unrestrained bottlenose dolphins in the Mediterranean Sea

The results from this study describe, for the first time in the Mediterranean Sea, the whistle characteristics of free-ranging bottlenose dolphins in their natural repertoire. Analysis of acoustic whistle variables showed a mean peak of frequency of about 13 kHz similar to those reported for other populations of wild bottlenose dolphins studied in this respect (Wang et al., 1995; Acevedo-Gütiérrez and Stienessen, 2004; Azevedo et al., 2007), but different to the peak of frequency reported for captive bottlenose dolphins of about 15 kHz (Caldwell et al., 1990). Additionally, the duration of whistles was similar to that reported for wild bottlenose dolphins in Texas (Wang et al., 1995), Isla del Coco in Costa Rica (Acevedo-Gütiérrez and Stienessen, 2004), Shark Bay in Australia (Wang et al., 1995), southern Brazil (Azevedo et al., 2007), and Taiji in Japan
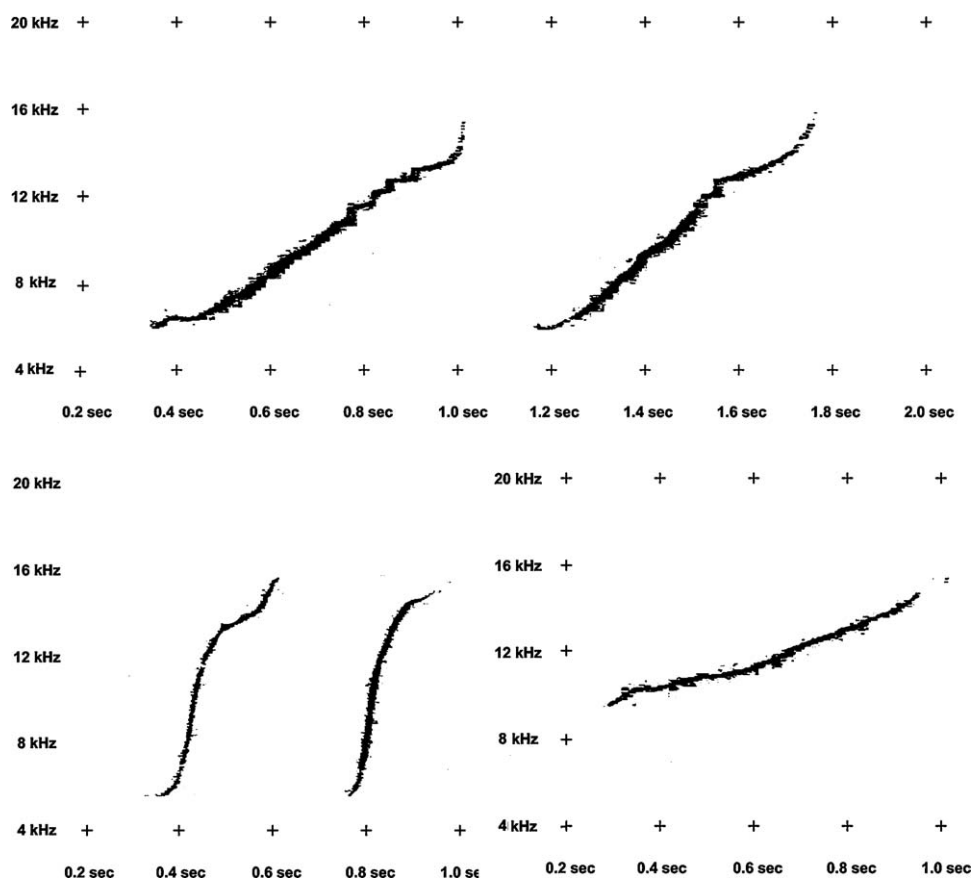
Fig. 3. Representative spectrogram of upsweep whistles on standardized time axes. FFT = 1024, display frame duration = 2 ms.

(Wang et al., 1995), with mean duration whistles about 600 ms. In a study from captive bottlenose dolphins Caldwell et al. (1990) described values of mean duration comparative higher, 960 ms. Similarly, for wild bottlenose dolphins Wang et al. (1995) found highest duration mean values in Golfo San José – Argentina with mean duration whistles 1114 ms.

Differences in the methods used for recording and analysing whistles can result in significant differences in the described whistle acoustic features across different dolphin populations. Although the measurement of these quantitative parameters could be useful for describing bottlenose dolphin whistles, one has to be mostly careful in comparing results across different dolphin populations. Each population is likely affected by different environmental influences (Conner, 1982) and whistle characteristics may be influenced by differences in habitat, ecology, social group and contextual behaviour of the different populations. Similarly, data from captive individuals can give us some information on whistle characteristics, but the function and production of whistles may be very different in the wild. For example, vocal production in birds is severely disrupted by captivity (Baptista and Morton, 1988).

Selected whistle acoustic features accounted for 84% of whistles variance, mainly the peak of frequency, duration, and number of inflection points, parameters that loaded highly with PCA components 1, 2, or 3 respectively. Bottlenose dolphins may modulate these acoustic parameters for carrying additional information such as behavioural activity, individual identity, stress levels, and so on (Steiner 1981; Wang et al., 1995a, 1995b, Morisaka et al., 2005, Azevedo et al., 2007, Esch et al., 2009). The strong correlation observed between frequency parameters, could indicate that these parameters are restricted or selected by some factors such as the

Table 4
Discriminant function analysis of whistles by behaviour within each observed social group.

| Observed behaviours D (depredation), P (predation), S (social), T (travel)	Social group	n	Classification score (cross-validation)	MANOVA (P value)
D, P, S, T	1	40	55% (49%)	$P < 0.01$
D, T, S	2	30	70% (60%)	$P < 0.01$
D, P, S	3	30	67% (54%)	$P < 0.01$
D, P, S	4	40	57% (50%)	$P < 0.05$
D, P	5	30	73% (66%)	$P < 0.05$
D, P, S	6	30	60% (52%)	$P < 0.05$
S, T	7	20	100% (100%)	$P < 0.01$
D, P, S	8	30	58% (52%)	$P < 0.01$
D, S, T	9	30	75% (70%)	$P < 0.01$
P, S, T	10	30	67% (56%)	$P < 0.01$
D, P, S, T	11	40	63% (50%)	$P < 0.01$
P, T	12	20	85% (70%)	$P < 0.01$
D, P, T	13	30	79% (70%)	$P < 0.05$
D, P, S	14	30	53% (48%)	$P < 0.01$
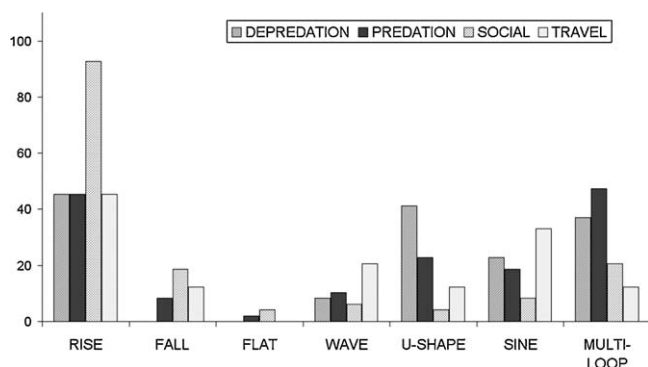
Fig. 4. Occurrence of the various whistle types in relation to the different observed behaviours.

size of sound production organs and muscles and/or the environmental background noise levels (Morisaka et al., 2005).

Whistle types of wild unrestrained bottlenose dolphins in the Mediterranenan Sea

The results of this study verify that upsweeps and multi-looped whistles play an important role in the natural communication system of wild unrestrained bottlenose dolphins. Thus, the present study supports the idea that upsweeps (whistles with no inflection points and ascendant frequencies) play an important role in the bottlenose dolphin whistle repertoire (Tyack, 1986; Janik et al., 1994; McCowan and Reiss, 2001). The spectral shape of these whistles closely resembled the predominant whistle type, named Type 2, used by captive bottlenose dolphins reported in McCowan and Reiss (1995a,b). However, Azevedo et al. (2007) found that whistles with more than one inflection point were the most frequent in southern Brazil.

Results from visual classification showed that could exist an association between types of whistles and behaviour. Similarly, it has been suggested that bottlenose dolphin whistle types may vary with particular surface activities. For example, whistles with few frequency modulations have been linked to periods of stress in captivity (Lilly and Miller, 1961; Caldwell et al., 1970), and in temporarily restrained dolphins (Esch et al., 2009). Janik et al. (1994) also suggested that context-related information was available in the whistles of captive bottlenose dolphins. In a group of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) along the coast of northern New SouthWales, Australia, flat and rise whistle types were associated with social behaviours, and sine whistles appeared to be used as group contact calls during travelling (Hawkins and Gartside, 2010).

However, the relation between whistle types and behaviours is difficult to measure when the contour of each whistle is determined by visual analyses of the frequency modulation. This classification method can result in misleading conclusions, as involves decisions by humans on the criteria used to define whistle contour categories. Further validation is needed to find out if this method represents a good approximation to how dolphins themselves classify whistles.

Does the same group of bottlenose dolphins produce different whistles in different behavioural contexts?

Very little is known about how wild unrestrained bottlenose dolphins use whistles in different contexts and no data exist for context specificity of whistle characteristics (Janik, 2009). Therefore, it is of great interest to understand how behaviour affects the properties of the whistles and how variations could be related to motivational states. During this study group composition was

taken into account. Our findings further support, for the first time in wild unrestrained bottlenose dolphins, the suggestion that peak of frequency and duration may be good predictors of behavioural state and vice versa. For example, whistles characterized by high peak of frequency (mean about 13 kHz) and long duration (mean about 760ms) could be linked to foraging activities (i.e. depredation and/or predation). Behaviour-related information was available in the whistles of bottlenose dolphins from the north-eastern coast of Sardinia. Results of a parallel study (Díaz López and Shirai, 2009), showing that whistle emission rates increased, especially in those activities involving excited depredation or socializing, confirmed that activity and whistle production were related. These findings are consistent with the hypothesis that whistles encode relatively specific information about the behaviour, and that they could have the property of functionally referential signals. These signals provide receivers with sufficient information to determine the context underlying signal production which, in turn, allows them to predict environmental events (Hauser, 1996).

Thus although whistle acoustic features may be associated with behavioural states, it is perhaps unreasonable to assume one is produced in direct response to the other. This evidence could suggest the differences between whistles are not solely attributable to disparities in behavioural state. It is hoped that the random selection of whistles from different behaviours among the three years of study would minimise effects such as individual variability (and potential signature whistle use). The whistle differences observed in some contexts could reflect the different effects on vocal production introduced by other variables such as motivation, physical demands, or vocal effort associated with whistling in those contexts. The large data set analyzed should help even out variability due to individual motivation. While individual motivation could change over time, the behavioural situations of travelling or foraging may be more consistent and so will have the dominate effect in the pooled data set.

Conclusions

Communication may be described as any action that affects another individual by either altering or maintaining the behaviour of the other individual (Slater, 1983). These findings demonstrate how dynamic bottlenose dolphin whistle characteristics are and how important it is to consider many factors in analysis. Findings suggested that whistle acoustic features may be used to communicate specific information on the behavioural context of the individuals involved. The variation of these whistle acoustic features demonstrates its integral role in the complex social lives of wild bottlenose dolphins, and suggests that the acoustic parameters of the whistles might be particularly sensitive to behavioural changes. Further observational and experimental research is needed to determine precisely how pervasive the effect of specific behaviours is upon whistle characteristics.

Focal group sampling with a random selection of whistles is not a panacea to studies of communication of wild bottlenose dolphins. Thus, where it is extremely difficult to determine whether individual whistles came from the same or different dolphins, and to collect detailed long-term data on their relationships and behaviour, utilising this method can provide effective information about dolphins communication and functional use. As with other monitoring techniques, the inclusive definition of focal group to account for all dolphins producing whistles contains biases that have to be accounted for when it is used. Even if these results could be biased by the focal group sampling, they are nonetheless of great interest because they present the first detailed study of whistle characteristics of wild unrestrained Mediterranean bottlenose dolphins. As a start, the analysis of whistle acoustic features, would

lead to more meaningful comparative discussions between authors. In the future, it may be less important to ask simply whether whistle modification can be detected in bottlenose dolphins as to determine the boundaries of such modification and its possible adaptive significance under natural circumstances.

Acknowledgements

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