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7		Given Name	<b>E.</b>
8	Corresponding	Suffix	
9	Author	Organization	University of Torino
10		Division	Life Science and Systems Biology Department
11		Address	Via Accademia Albertina 13, Torino 10123, Italy
12		e-mail	elena.papale@unito.it
13		Family Name	<b>Azzolin</b>
14		Particle	
15		Given Name	<b>M.</b>
16		Suffix	
17	Author	Organization	University of Torino
18		Division	Life Science and Systems Biology Department
19		Address	Via Accademia Albertina 13, Torino 10123, Italy
20		e-mail	
21		Family Name	<b>Cascão</b>
22		Particle	
23		Given Name	<b>I.</b>
24		Suffix	
25	Author	Organization	Universidade dos Açores
26		Division	Departamento de Oceanografia e Pescas, IMAR and LARSyS Associated Laboratory
27		Address	Horta 9901-862, Portugal
28		e-mail	
29	Author	Family Name	<b>Gannier</b>

30		Particle	
31		Given Name	<b>A.</b>
32		Suffix	
33		Organization	Groupe de Recherche sur les Cétacés (GREC)
34		Division	
35		Address	Antibes, France
36		e-mail	
<hr/>			
37		Family Name	<b>Lammers</b>
38		Particle	
39		Given Name	<b>M. O.</b>
40		Suffix	
41		Organization	Ocean Wide Science Institute
42	Author	Division	
43		Address	PO Box 61692, Honolulu 96744, HI, USA
44		Organization	University of Hawaii
45		Division	Hawaii Institute of Marine Biology
46		Address	Kaneohe 96744, HI, USA
47		e-mail	
<hr/>			
48		Family Name	<b>Martin</b>
49		Particle	
50		Given Name	<b>V. M.</b>
51		Suffix	
52	Author	Organization	Society for the Study of Cetaceans in the Canary Archipelago (SECAC)
53		Division	
54		Address	Edif. Antiguo Varadero 1ª planta Local 8 B, Urb. Puerto Calero, Yaiza 35571, Isla de Lanzarote, Spain
55		e-mail	
<hr/>			
56		Family Name	<b>Oswald</b>
57		Particle	
58		Given Name	<b>J.</b>
59		Suffix	
60	Author	Organization	Bio-Waves, Inc.
61		Division	
62		Address	144 W. D Street, Suite #205, Encinitas 92024, CA, USA
63		e-mail	

64	Family Name	<b>Perez-Gil</b>
65	Particle	
66	Given Name	<b>M.</b>
67	Suffix	
68	Organization	Society for the Study of Cetaceans in the Canary Archipelago (SECAC)
69	Division	
70	Address	Edif. Antiguo Varadero 1ª planta Local 8 B, Urb. Puerto Calero, Yaiza 35571, Isla de Lanzarote, Spain
71	e-mail	
<hr/>		
72	Family Name	<b>Prieto</b>
73	Particle	
74	Given Name	<b>R.</b>
75	Suffix	
76	Organization	Universidade dos Açores
77	Division	Departamento de Oceanografia e Pescas, IMAR and LARSyS Associated Laboratory
78	Address	Horta 9901-862, Portugal
79	e-mail	
<hr/>		
80	Family Name	<b>Silva</b>
81	Particle	
82	Given Name	<b>M. A.</b>
83	Suffix	
84	Organization	Universidade dos Açores
85	Division	Departamento de Oceanografia e Pescas, IMAR and LARSyS Associated Laboratory
86	Address	Horta 9901-862, Portugal
87	Organization	Woods Hole Oceanographic Institution
88	Division	Biology Department
89	Address	MS#33, Woods Hole 02543, MA, USA
90	e-mail	
<hr/>		
91	Family Name	<b>Giacoma</b>
92	Particle	
93	Given Name	<b>C.</b>
94	Suffix	
95	Organization	University of Torino
96	Division	Life Science and Systems Biology Department
97	Address	Via Accademia Albertina 13, Torino 10123, Italy

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102	Abstract	<p>To improve our understanding of the complex genetic and ecological structure of bottlenose dolphin (<i>Tursiops truncatus</i>) populations, we examined the acoustic features of communication signals from two geographically contiguous areas: the Central–Eastern North Atlantic and the Mediterranean Sea. Variations in the whistles were evaluated for four locations. Ten signal parameters were measured and used to statistically differentiate between the areas. Over 79 % of sightings were correctly classified by discriminant function analysis, confirming an acoustic differentiation between the two basins. The results of cluster analysis using the mean values of the parameters for each sighting showed that the three easternmost sightings from the Mediterranean and one sighting from the Canary archipelago formed a separate cluster from the rest of the Atlantic. The two sightings from the Alboran Sea in the west Mediterranean were grouped with the Atlantic recordings. There was more variability in whistles from the Atlantic Ocean consistent with data from genetic and photo-identification studies that document resident and non-resident animals in the area. The results suggest that the Alboran area may be inhabited by animals differentiated from the rest of the Mediterranean basin as a result of habitat features.</p>
103	Keywords separated by ' - '	Bottlenose dolphin - Intra-specific differences - Mediterranean - Atlantic - Whistles
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# Acoustic divergence between bottlenose dolphin whistles from the Central–Eastern North Atlantic and Mediterranean Sea

E. Papale · M. Azzolin · I. Cascão · A. Gannier ·  
M. O. Lammers · V. M. Martin · J. Oswald ·  
M. Perez-Gil · R. Prieto · M. A. Silva · C. Giacoma

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**Abstract** To improve our understanding of the complex genetic and ecological structure of bottlenose dolphin (*Tursiops truncatus*) populations, we examined the acoustic features of communication signals from two geographically contiguous areas: the Central–Eastern North Atlantic and the Mediterranean Sea. Variations in the whistles were evaluated for four locations. Ten signal parameters were measured and

used to statistically differentiate between the areas. Over 79 % of sightings were correctly classified by discriminant function analysis, confirming an acoustic differentiation between the two basins. The results of cluster analysis using the mean values of the parameters for each sighting showed that the three easternmost sightings from the Mediterranean and one sighting from the Canary archipelago formed a separate cluster from the rest of the Atlantic. The two sightings from the Alboran Sea in the west Mediterranean were grouped with the Atlantic recordings. There was more variability in whistles from the Atlantic Ocean consistent with data from genetic and photo-identification studies that document resident and non-resident animals in the area. The results suggest that the Alboran area may be inhabited by animals differentiated from the rest of the Mediterranean basin as a result of habitat features.

E. Papale (✉) · M. Azzolin · C. Giacoma  
Life Science and Systems Biology Department, University of Torino,  
Via Accademia Albertina 13, Torino 10123, Italy  
e-mail: elena.papale@unito.it

I. Cascão · R. Prieto · M. A. Silva  
Departamento de Oceanografia e Pescas, IMAR and LARSyS  
Associated Laboratory, Universidade dos Açores, Horta 9901-862,  
Portugal

A. Gannier  
Groupe de Recherche sur les Cétacés (GREC), Antibes, France

M. O. Lammers  
Ocean Wide Science Institute, PO Box 61692, Honolulu, HI 96744,  
USA

M. O. Lammers  
Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe,  
HI 96744, USA

V. M. Martin · M. Perez-Gil  
Society for the Study of Cetaceans in the Canary Archipelago  
(SECAC), Edif. Antiguo Varadero 1ª planta Local 8 B, Urb. Puerto  
Calero, Yaiza 35571, Isla de Lanzarote, Spain

J. Oswald  
Bio-Waves, Inc., 144 W. D Street, Suite #205, Encinitas, CA 92024,  
USA

M. A. Silva  
Biology Department, Woods Hole Oceanographic Institution,  
MS#33, Woods Hole, MA 02543, USA

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## Introduction

The bottlenose dolphin is widely distributed in temperate and tropical waters worldwide. Morphologic differences have, in the past, led to the subdivision of the genus into different species (Hershkovitz 1966). Currently, three species, *Tursiops truncatus*, *Tursiops aduncus* and *Tursiops australis* (Charlton-Robb et al. 2006, 2011), are recognized with the occurrence of local subspecies (e.g. *T. truncatus-ponticus* in the Black Sea; Viaud-Martinez et al. 2008) and nearshore and offshore ecotypes for a number of geographic locations (Ross 1977, 1984; Walker 1981; Duffield et al. 1983; Ross and Cockcroft 1990; Van Waerebeek et al. 1990; Mead and Potter 1995). Pelagic forms of *T. truncatus* have been reported to range primarily between the 200 and 2,000-m isobaths

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(Wells et al. 1999). In the North-western Atlantic, this pelagic ecotype occurs mainly in waters beyond 34 km from shore and 34 m depth, while the coastal form occurs within 7.5 km from shore (Torres et al. 2003). In the Gulf of California, a distribution break was found around the 60-m isobath (Segura et al. 2006). In the Central–Eastern North Atlantic, no population structure was evident for either ecotype (Quérrouil et al. 2007). Resident populations of *T. truncatus* exist around the Canary Islands and the Azores archipelago (Silva et al. 2008). Nevertheless, in the latter, photo-identification data suggest that resident individuals mix and interact with non-resident individuals rarely observed in the area (Silva et al. 2008). In the Mediterranean Sea, bottlenose dolphins (*T. truncatus*) are thought to belong to the coastal ecotype (Notarbartolo di Sciara G and Demma 2004; Gannier 2005) despite being regularly observed in deep waters near the continental slope (Forcada et al. 2004) or beyond the continental shelf (Bearzi et al. 2004; Ben Naceur et al. 2004).

The bottlenose dolphin (*T. truncatus*) is a highly vocal species that shows great plasticity in its communication signals (May-Collado and Wartzok 2008). In this study, we refer to whistle as unpulsed, narrow-band signals, lasting between 0.1 and 4 s. The acoustic frequency of whistles is usually modulated, showing distinct contours of the fundamental frequencies (Caldwell et al. 1990). The whistles of bottlenose dolphins (*T. truncatus*) have been classified by Caldwell et al. (1990) into signature whistles, stereotypic and individual-specific signals that are stable over time and are used for group cohesion and variant whistles produced in a variety of social contexts. Furthermore, Caldwell and Caldwell (1972) and Reiss and McCowan (1993) reported that bottlenose dolphins are able to spontaneously copy sounds from the environment, and Tyack (1986) showed that they can also copy the whistles of conspecifics. Since acoustic transmission and ambient noise conditions can be locally different, animals may change the frequency and temporal structure of signals in response to the acoustic environment to ensure the transfer of information (May-Collado and Wartzok 2008). Local conditions of the acoustic environments experienced by a population can be reflected in differing traits of the acoustic structure of whistles and contribute to their geographic variation (May-Collado and Wartzok 2008). Furthermore, geographic variation can be related to morphological differences in the structure of the vocal apparatus and in overall body size. The call parameter most affected by body size is minimum frequency (May-Collado et al. 2007).

Intra-specific variations in the acoustic parameters of whistles have been successfully used to distinguish populations of many odontocete species, particularly bottlenose dolphins (Wang et al. 1995; Jones and Sayigh 2002; Morisaka et al. 2005; Azzolin 2008; Baron et al. 2008; May-Collado and Wartzok 2008; Hawkins 2010). Here, we evaluated differences in the acoustic characteristics of the signals produced

by bottlenose dolphins across the Central–Eastern North Atlantic and the Mediterranean Sea, and we tested population discriminability using whistles.

## Methods

### Study populations and data collection

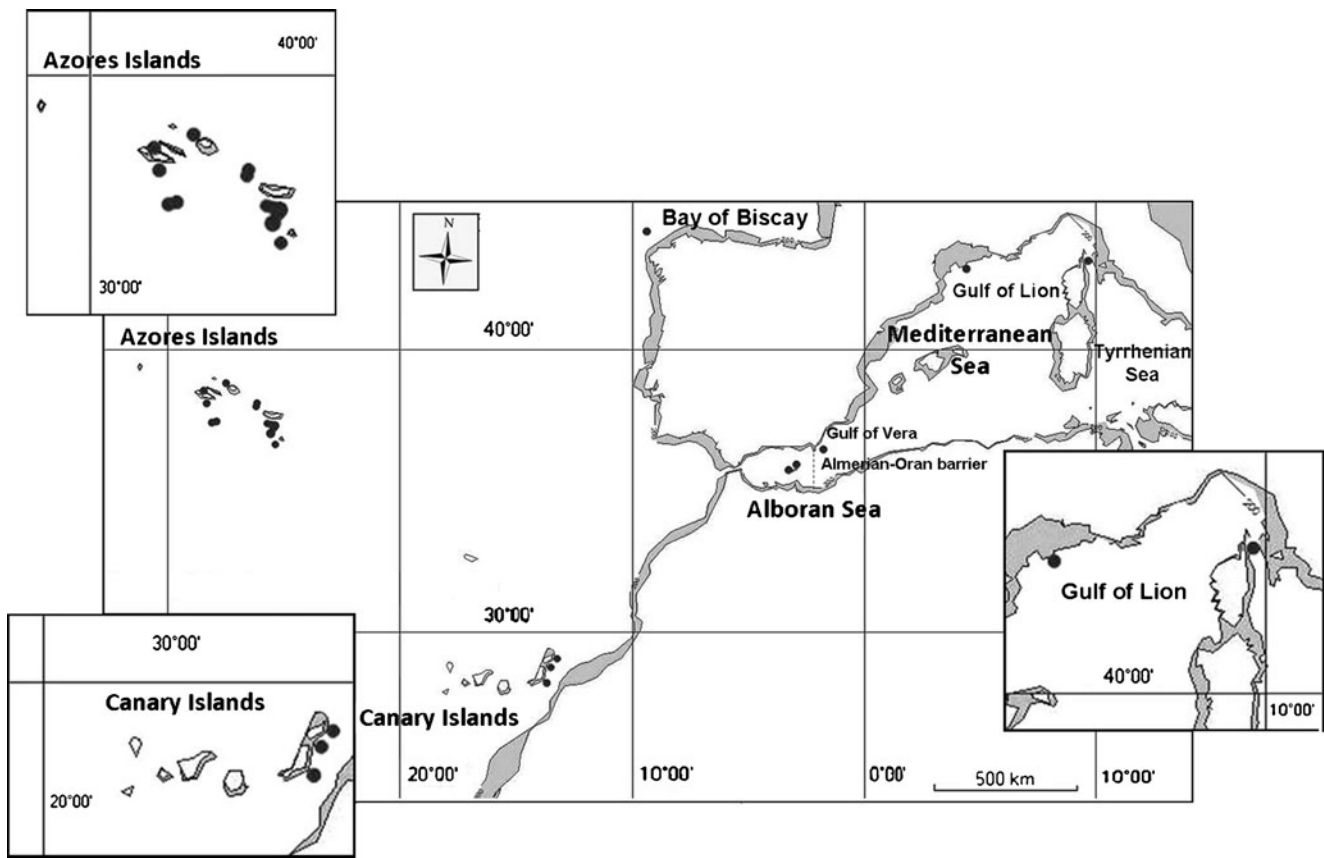
Recordings of bottlenose dolphin (*T. truncatus*) whistles were collected from four geographic locations: the Mediterranean Sea, the Azores archipelago, the Canary archipelago and the Bay of Biscay (Fig. 1 and Table 1).

The Mediterranean Sea is a semi-enclosed basin, located between 30° and 46° North and 6° West and 36° East, composed of two main sub-basins (eastern and western). The Mediterranean connects with the Atlantic Ocean through the Strait of Gibraltar. Data were only collected from the western sub-basin: in the Tyrrhenian, the Gulf of Lion (France), the Gulf of Vera (Spain; Eastern Almeria) and in the Alboran Sea (to the west of the Almerian-Oran barrier). Water depths can reach 3.8 km in the centre of the Tyrrhenian Sea. The Centre de Recherche sur les Cétacés (GREC) provided the data from this location using either a mono towed hydrophone with *Benthos* AQ4 (in 1999) or a stereo towed hydrophone with the same elements (in 1998), with a linear flat response between 1 and 15 kHz±1 dB and between 15 and 30 kHz±3 dB (sensitivity of -156 dB re 1 V/μPa), a 29-dB pre-amplifier and 200 Hz high-pass filter. An external high-pass filter unit (Magrec Ltd.) set to 1 kHz was used on the hydrophone output to improve the quality of recordings.

The Azores archipelago is located between 36° and 40° North and 24° and 32° West and is composed of nine islands divided into three subgroups (western, central and eastern), extending about 600 km along a northwest–southeast axis. The islands are situated about 1,500 km from the Portuguese coast. The seabed around the islands is deep (around 1.50 km at 3 km off shore) with numerous scattered seamounts (Morato et al. 2008). The Department of Oceanography and Fisheries, Centre of IMAR of the University of the Azores (IMAR-DOP/UAç) and the International Fund for Animal Welfare-United Kingdom (IFAW) provided the recordings from the area using either an omnidirectional hydrophone (HTI-94-SSQ) with a linear flat response between 2 and 30 kHz±1 dB (sensitivity of -198 dB re 1 V/μPa) or a towed array with two hydrophones (*Benthos* AQ4).

The Canary Islands archipelago is located between 27° and 30° North and 13° and 19° West about 1,200 km from the Azores archipelago and 115 km west from the African coast. It is composed of seven main islands and extends 500 km. Water depth around the archipelago can reach more than 1 km at 1.8 km from the coast. The Society for the Study of Cetaceans in the Canary Archipelago (SECAC) obtained the recordings





**Fig. 1** Location of recordings analyzed for the Atlantic Ocean and Mediterranean Sea. *Black dots* represent the approximate position of sightings. *Inserts* show details of locations where sightings were closer. Depth contour of 200 m is shown in grey

155 used in this study using a towed array with four elements: two  
 156 hydrophones (*Benthos* AQ4) and two spherical ceramic hy-  
 157 drophone elements with a frequency response of ~2–150 kHz  
 158 (Seiche UK Ltd.) with a sensitivity for the front element  
 159 of –161 dB re 1 V/μPa and the rear element of –158 dB re  
 160 1 V/μPa.

161 The Bay of Biscay is situated between 43° and 50° North  
 162 and 1° and 10° West and is characterized by variable sea  
 163 depths, ranging from the shallow continental shelf (less than  
 164 0.10 km) to the abyssal plain (greater than 4 km) with subma-  
 165 rine canyons, seamounts and a steep continental slope. The  
 166 width of the continental shelf varies from 110 to 185 km in the  
 167 northern part of the bay (up to 45° N) to 46 km in the southern  
 168 part and is as narrow as 5.5 km at the latitude of the Capbreton  
 169 trough. The IFAW provided data from this location with the  
 170 same instruments used in the Azores area. We only used  
 171 recordings for which the species was confirmed visually and  
 172 when it was visually certain that no other odontocetes were  
 173 present in the area.

174 Sound analysis

175 We analyzed recordings by creating spectrograms in CoolEdit  
 176 2000 (Syntrillium Software, USA; Blackmann-Harris window;

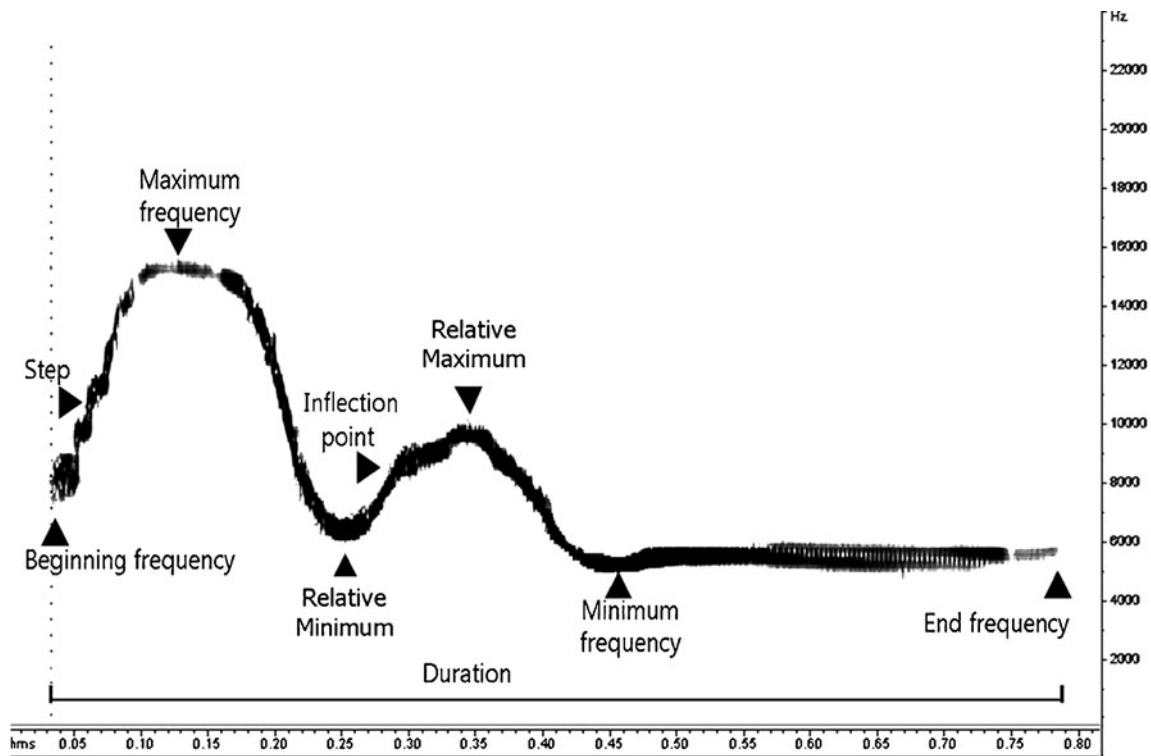
256–512 band resolution; 2048 FFT size). We sampled all data  
 at 48 kHz except for a few Mediterranean recordings collected  
 at 44.1 kHz for which none of the maximum frequencies was  
 over Nyquist nor frequency parameters or harmonics of the  
 signals presented overturned contours. Each extracted sound  
 was classified by assigning a signal quality index from zero  
 (weak or overlapped with other sounds) to three (good signal-  
 to-noise ratio and definition of the contour). When the gap  
 between consecutive whistles was larger than 200 ms, these  
 were analyzed as individual whistles (Bazua-Duran and Au  
 2002).

Only whistles classified as two or three (with the highest  
 intensity) were used in the analysis in order to avoid using  
 sounds of groups outside the visual range. From each whistle  
 contour, ten parameters were measured manually following  
 the method adopted by Oswald et al. (2003, 2007), Azzolin  
 (2008) and Papale et al. (2013). These included duration,  
 beginning frequency, end frequency, minimum frequency,  
 maximum frequency, number of inflection points (mathematic  
 definition in sine function of a change from positive to nega-  
 tive or negative to positive slope), steps (a rapid discontinuous  
 change in frequency), number of minima in the contour and  
 number of maxima in the contour (relative maximal and  
 minimal points in the whistle contour) (Fig. 2). We also

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**Table 1** Summary of data collected, locations, periods, instruments used, distance from the coast and depth where recordings have been collected

t.l.1	Area	Instruments	Research group	Sampling rate	Frequency response of the hydrophones	Sightings	Hours of recording	Total whistles	Selected whistles	Bathymetry range	Coast ranging
t.l.3	Azores archipelago	Omnidirectional hydrophone (HTI-94-SSQ) or towed array with two hydrophones Benthos AQ4	IMAR-DOP/UAç IFAW	48 kHz 48 kHz	1. ±1 dB 1 Hz–15 kHz and ±3 dB 15–30 kHz 2. ±1 dB 2Hz–30 kHz	20	5.32	866	352	Between 0.88 and 1.79 km	1.60–45 km
t.l.4											
t.l.5	Bay of Biscay	Omnidirectional hydrophone (HTI-94-SSQ) or towed array with 2 hydrophones Benthos AQ4	IFAW	48 kHz	1. ±1 dB 1Hz–15 kHz and ±3 dB 15–30 kHz 2. ±1 dB 2Hz–30 kHz	1	0.18	94	94	1 km	42 km
t.l.6	Canary archipelago	Towed array with four elements; two hydrophones Benthos AQ4 and two spherical ceramic hydrophone elements with a frequency response of ~2–150 kHz (Setche UK Ltd.)	SECAC	192 kHz	±1.5 dB 1Hz–15 kHz ~2–150 kHz	3	2.25	186	94	Between 0.50 and 1.20 km	5–17 km
t.l.7	Mediterranean Sea (from Tyrrhenian to Alboran Sea)	Stereo towed hydrophone with Benthos AQ4 in 1998 and mono towed with AQ4 in 1999	GREC	44.1 kHz 48 kHz	±2 dB 200Hz–30 kHz	5	3.06	577	207	Between 0.20 and 1.20 km	6–71 km



**Fig. 2** Sample spectrogram representing a bottlenose dolphin whistle. Parameters manually measured for each whistle are shown: signal duration, beginning frequency, end frequency, minimum frequency, maximum frequency, the number of inflection points, the number of steps

and the number of relative minima and relative maxima in the contour. Frequency range was calculated as maximum frequency minus minimum frequency

201 calculated the frequency range (maximum frequency–mini- 224  
 202 mum frequency). Since we could not know the emitter, we 225  
 203 considered on the whole dataset a mean of four sounds per 226  
 204 animal per sighting. Furthermore, to avoid overestimation of 227  
 205 the most repeated whistle structure due to the occurrence of 228  
 206 possible signature whistles (Caldwell et al. 1990; Sayigh et al. 229  
 207 1990, 1998; Janik et al. 1994; Tyack 1997; Janik and Slater 230  
 208 1998; Janik 2000; Fripp et al. 2005) or mimicry between 231  
 209 individuals, the contribution to the entire data set from signals 232  
 210 with contour similar to another one was not allowed to exceed 233  
 211 14 %. To prevent any type of statistical bias due to this 234  
 212 percentage, we randomized ten times the new dataset and 235  
 213 compared 80 % of the data contained in each randomized 236  
 214 dataset. Since we obtained different results only for the fre- 237  
 215 quency range, parameter strictly related to the maximum and 238  
 216 minimum frequencies, we decided not to consider it in the 239  
 217 analysis. 240

218 **Data analysis**

219 For each parameter, within- and between-basin coefficients of 244  
 220 variation (CVs) were calculated as the ratio of the standard 245  
 221 deviation to the mean (using all whistles for within-basin 246  
 222 calculations and the mean value for each location for 247  
 223 between-basin calculations) and expressed as a percentage 248

(Lehner 1998). In order to evaluate which parameters are more 224  
 225 likely to contribute to differences between whistles from dif- 226  
 227 ferent locations (the Mediterranean, the Azores, the Canary 228  
 229 Islands and the Bay of Biscay), we compared inter-area CVs 230  
 231 and intra-area CVs. The statistical software package PASW 232  
 233 Statistics 18.0 (SPSS Institute Inc., Chicago, IL, USA) was 234  
 235 used to create descriptive statistics (mean and standard devi- 236  
 237 ation). Since the data were not normally distributed, we used 238  
 239 the Mann–Whitney non-parametric test to determine whether 240  
 241 and which whistle parameters varied between areas. We per- 242  
 243 formed a discriminant function analysis (DFA) using the mean 244  
 245 values for each sighting to determine whether whistles record- 246  
 247 ed could be correctly classified to the sampling areas. In this 247  
 248 case, all the assumptions of the DFA were met. The leave-one- 249  
 out procedure (Lachenbruch and Mickey 1968) was then used 250  
 for cross-validation. Unfortunately, the sample from the Bay 251  
 of Biscay was only represented by a single sighting, so, in 252  
 view of the possibility of bias due to the homogeneity of 253  
 signals in a short period and a single group, the recording 254  
 was not considered in univariate and discriminant function 255  
 analyses. Finally, we performed a hierarchical cluster analysis 256  
 (using the within groups average linkage method) with the 257  
 mean values for each sighting to classify them into the four 258  
 study locations: Azores, Bay of Biscay, Canaries and 259  
 Mediterranean Sea. For all of the multivariate statistics, we 260

249 did not consider frequency range as a predictor variable due to  
 250 its relationship with maximum and minimum frequency pa-  
 251 rameters (Fig. 3).

252 **Results**

253 Study effort

254 For the Mediterranean Sea, we analyzed 3.06 h of recordings  
 255 from which we extracted 577 whistles. For the statistical anal-  
 256 ysis, we considered 207 good quality sounds that originated  
 257 from five sightings. For the Canary archipelago, we analyzed  
 258 2.25 h and extracted 186 whistles. We considered 94 sounds  
 259 belonging to three sightings. For the Azores archipelago, 5.32 h  
 260 from 20 sightings were investigated. We extracted 866 whistles  
 261 and 352 of them were analyzed. In the Bay of Biscay, 0.18 h of  
 262 recordings from one sighting were collected from which 94  
 263 whistles were extracted and analyzed (Table 1).

264 Whistle variation between the Atlantic Ocean  
 265 and the Mediterranean Sea

266 Parameters related to signal frequency were significantly higher  
 267 in the Atlantic Ocean than in the Mediterranean, especially the  
 268 beginning (Mann–Whitney test  $N=747$ ,  $Z=-6.03$ ,  $P<0.001$ ),  
 269 minimum ( $Z=-4.07$ ,  $P<0.001$ ) and maximum ( $Z=-3.95$ ,  $P<$   
 270  $0.001$ ) frequencies. Mean values of signal modulation param-  
 271 eters, such as number of inflections and number of minima, were  
 272 significantly lower in the Atlantic Ocean ( $Z=5.20$ ,  $P<0.001$ ;  
 273  $Z=2.95$ ,  $P<0.001$ ). The number of steps, maxima, end

frequency and signal duration did not show significant differ- 274  
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 differences between the basins ( $Z=-0.68$ ,  $P=0.49$ ;  $Z=-0.63$ ,  $P=$   
 $0.53$ ;  $Z=-1.59$ ,  $P=0.11$ ;  $Z=-1.49$ ,  $P=0.13$ ; Table 2). The  
 sightings could be correctly classified using DFA for 79.3 % of  
 cross-validated cases (Table 3). The parameters that contributed  
 to the classification were end frequency (coefficient=0.89) and  
 number of inflection points (coefficient=0.68).

Whistle variation within and between areas 281

282 We performed a hierarchical cluster analysis using the mean 282  
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 values for the parameters for each sighting. The cluster anal-  
 ysis grouped three sightings from the Mediterranean Sea with  
 one from the Canary archipelago. Three sightings from the  
 Azores were also clustered separately from the other sightings  
 from the region. The rest of the Atlantic sightings (2 from the  
 Canaries, 17 from the Azores and 1 from the Bay of Biscay)  
 were grouped together with the two sightings from the  
 Alboran Sea (Fig. 4). The DFA performed using the mean  
 values of the parameters for each sighting confirmed the  
 results of the hierarchical cluster analysis. In this case, we  
 excluded the Bay of Biscay because it contributed only one  
 sighting. From the scatter plot of the analysis, it was possible  
 to graphically identify one group encompassing the Azores,  
 two sightings from the Alboran Sea (Mediterranean basin) and  
 two from the Canaries and another group with the rest of the  
 Mediterranean and Canarian sightings (Fig. 3).

299 Inter-area CVs of frequency parameters were generally 299  
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 lower, especially when compared with corresponding intra-  
 area values (Table 2). Maximum frequency and range of  
 frequency had the lowest inter-area CVs. The inter-area CVs  
 for number of inflection points and steps ( $CV=36.18$ ,  $42.25$ )  
 were nearly double those for other modulation parameters and  
 had only slightly higher intra-area CVs.

306 In order to evaluate the differences found between the 306  
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 Alboran Sea sightings and the rest of the Mediterranean  
 (Eastern Almeria), we compared the mean values of the param-  
 eters. Signal duration in the Alboran Sea was significantly  
 longer (Mann–Whitney test  $N=207$ ,  $Z=3.55$ ,  $P<0.001$ ), while  
 beginning, end and minimum and maximum frequencies were  
 lower than in the rest of the Mediterranean ( $Z=-3.64$ ,  $P<$   
 $0.001$ ;  $Z=-7.52$ ,  $P<0.001$ ;  $Z=-6.22$ ,  $P<0.001$ ;  $Z=-4.98$ ,  $P$   
 $<0.001$ , respectively). In particular, the mean value of the end  
 frequency parameter in the Alboran Sea was almost half the  
 other Mediterranean sounds. Thus, this explains the differences  
 among the parameter comparison for which there is no signif-  
 icant difference in end frequency and the DFA, where end  
 frequency is the most important parameter to discriminate  
 between Atlantic and Mediterranean. The number of inflection  
 points and number of maxima were double or higher ( $Z=2.52$ ,  
 $P=0.01$ ;  $Z=5.29$ ,  $P<0.001$ ; Table 4). The number of steps and  
 the number of minima ( $Z=-0.82$ ,  $P=0.41$ ;  $Z=1.73$ ,  $P=0.08$ )  
 did not show any variation.

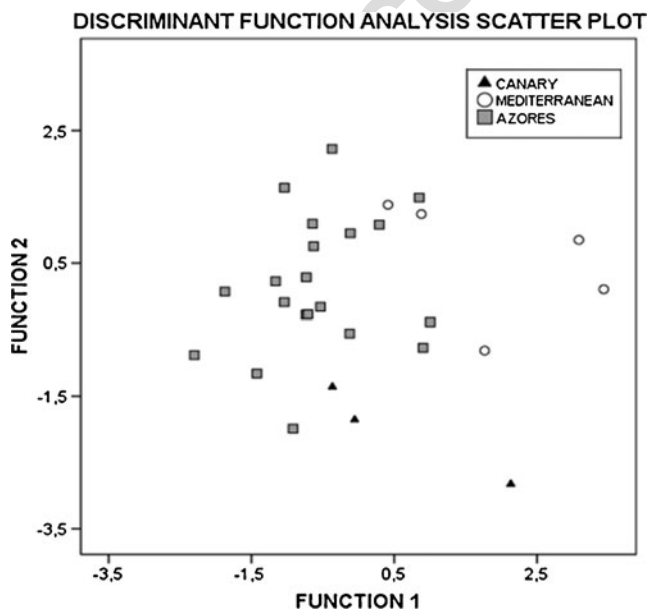


Fig. 3 Scatter plot of the discriminant function analysis performed using the mean values of each parameter for the sightings (Azores Islands, 20 sightings; Canary Islands, 3 sightings; Mediterranean Sea, 5 sightings)

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**Table 2** Means and intra- and inter-area CVs for each parameter in the areas. The CVs are expressed in percentage

Parameters	Mediterranean Sea			Canary archipelago			Azores archipelago			Bay of Biscay			Inter-area CV	Atlantic Ocean		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV		Mean	SD	CV
Duration (s)	1.03	0.58	55.73	0.77	0.52	66.97	0.97	0.49	50.18	1.10	0.43	39.07	14.61	0.96	0.49	51.34
Beginning frequency (Hz)	8315	3580	43.06	11125	4419	39.72	10094	4081	40.43	9406	3591	38.18	12.13	10153	4087	40.25
End frequency (Hz)	9342	4512	48.29	11908	4625	38.83	8658	4088	47.22	11309	4560	40.32	15.05	9685	4491	46.37
Minimum frequency (Hz)	6134	2080	33.91	7204	1827	25.35	6360	2001	31.47	7187	1614	22.45	8.27	6650	1947	29.28
Maximum frequency (Hz)	14186	3674	25.90	16270	5005	30.76	15257	3900	25.56	16962	2423	14.28	7.73	15729	3963	25.19
Range of frequency (Hz)	8052	3428	42.57	9066	5099	56.25	8897	3491	39.24	9775	2543	26.01	7.91	9079	3694	40.69
Inflection points	2.93	2.42	82.69	1.18	1.77	150.04	2.12	2.55	120.18	2.90	2.40	82.52	36.18	2.09	2.45	117.22
Steps	2.42	3.15	130.04	1.01	1.79	177.42	3.20	3.90	121.57	2.01	2.37	117.94	42.25	2.61	3.49	133.30
Number of minima	1.17	0.94	79.70	0.81	1.12	138.46	1.13	1.25	110.14	0.89	1.14	127.61	17.89	1.04	1.21	117.33
Number of maxima	1.16	0.99	84.72	0.90	1.04	114.75	1.20	1.13	93.51	1.22	1.09	89.02	13.19	1.16	1.11	95.97

Although the Atlantic sightings could be grouped together, as evidenced by the DFA, the heterogeneity highlighted in the cluster analysis within the Central–Eastern North Atlantic led us to evaluate the variation of the parameters in particular between the Canary archipelago and the Azores islands. Significant differences were found in parameters related to frequency (Mann–Whitney test:  $N=446$ , beginning frequency  $Z=-2.05$ ,  $P<0.04$ ; end frequency  $Z=-6.09$ ,  $P<0.001$ ; minimum frequency  $Z=-3.63$ ,  $P<0.001$ ) and signal duration ( $Z=4.23$ ,  $P<0.001$ ). Other parameters that also showed significant variation between the locations were number of inflection points ( $Z=3.64$ ,  $P<0.001$ ), steps ( $Z=6.37$ ,  $P<0.001$ ), minima ( $Z=2.83$ ,  $P<0.001$ ) and maxima ( $Z=2.64$ ,  $P<0.001$ ). Maximum frequency did not show any differences ( $Z=-1.34$ ,  $P=0.18$ ).

**Discussion**

Given the complexity of the genetic and ecological characteristics of bottlenose dolphins (Hoelzel et al. 1998), two

scenarios can be put forward to interpret the variability observed in the communication sounds of the species in the Central–Eastern North Atlantic and the Mediterranean Sea:

- 1 No variation exists within the Central–Eastern North Atlantic, but a difference exists between the Atlantic Ocean and the Western Mediterranean Sea consistent with the partial isolation proposed by genetic studies, which have identified a single large population for each basin (Natoli et al. 2005), although with some gene flow between the Atlantic Ocean and the Western Mediterranean.
- 2 Significant differences exist between the characteristics of the signals of the locations of the same basin due to local conditions of the acoustic and social environments of resident individuals.

Unfortunately, data about the social (number of specimen per group, site fidelity, associated behaviour to whistles), ecological and physical environment (natural and anthropogenic noise, bathymetry, etc.) were not available for every site, and we could not assess the effect of these factors, but based on our acoustic results, we suggest that both scenarios coexist in the study area.

**Table 3** Assignment of the discriminant function analysis performed between the Atlantic Ocean and the Mediterranean Sea

Area	Predicted group membership (%)		Total (%)	Overall classification
	Atlantic Ocean	Mediterranean Sea		
Original	Atlantic Ocean 83.33	Mediterranean Sea 16.67	100	79.3 %
Cross-validated	Atlantic Ocean 83.33	Mediterranean Sea 16.67	100	

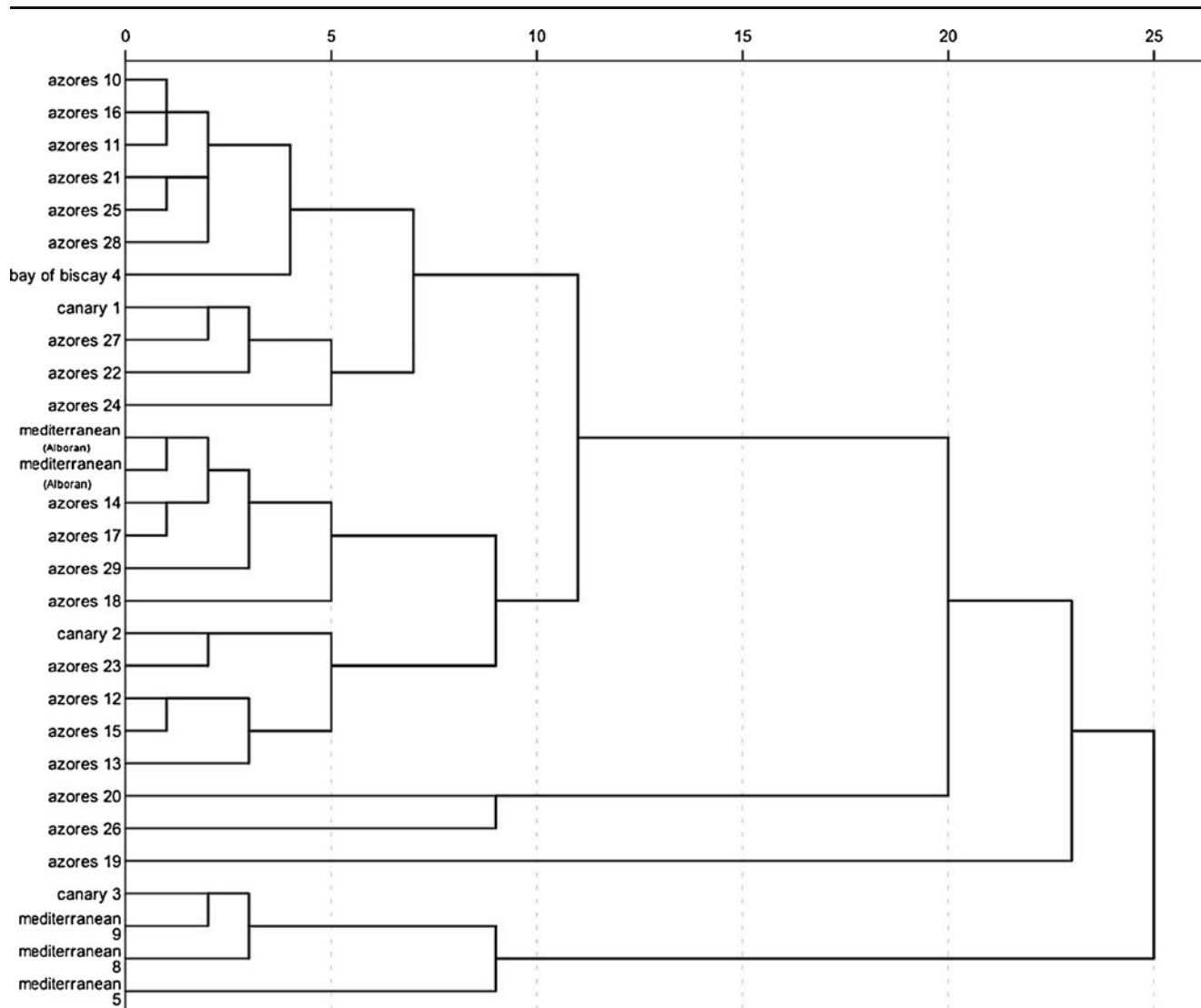


Fig. 4 Dendrogram of the hierarchic cluster analysis performed using mean values of each parameter for the sightings

**Table 4** Means and intra-area CVs for each parameter in the areas

Parameters	Alboran Sea			Eastern Almeria		
	N=177			N=30		
	Mean	SD	CV	Mean	SD	CV
Duration (s)	1.08	0.6	55.16	0.76	0.33	44.06
Beginning frequency (Hz)	7,953	3458	43.49	10,451	3,598	34.43
End frequency (Hz)	8,169	3,525	43.15	16,265	3,344	20.56
Minimum frequency (Hz)	5,720	1,823	31.88	8,577	1,826	21.29
Maximum frequency (Hz)	13,700	3,690	26.94	17,052	1,813	10.63
Range of frequency (Hz)	7,981	3,604	45.16	8,475	2,101	24.79
Inflection points	3.10	2.48	79.87	1.93	1.82	94.04
Steps	2.45	3.29	134.65	2.27	2.12	93.36
Number of minima	1.22	0.96	78.36	0.90	0.76	84.32
Number of maxima	1.31	0.98	74.76	0.33	0.55	164.00

364 Our results confirm the existence of a significant divergence  
365 between the Central–Eastern North Atlantic and the  
366 Mediterranean Sea. About 79 % of the sightings were correctly  
367 assigned to one of the two basins based on frequency and  
368 modulation parameters of the whistles. Furthermore, within  
369 the Atlantic Ocean, the sightings can be grouped together (both  
370 with DFA and cluster analysis) with the exception of one  
371 sighting from the Canary Islands that clusters with the  
372 Alboran Sea recordings. Our acoustic results suggest that  
373 bottlenose dolphins occurring in North Atlantic pelagic waters  
374 belong to a large oceanic population consistent with the results  
375 reported by genetic studies. Qu erouil et al. (2007) showed that  
376 bottlenose dolphins inhabiting the waters around the Azores  
377 and the island of Madeira have high gene flow, lack population  
378 structure within and between areas and are more similar to the  
379 pelagic populations of the Western North Atlantic than to  
380 dolphins from the Eastern Atlantic or the Mediterranean.  
381 Unlike coastal populations, oceanic bottlenose dolphins main-  
382 tain high levels of gene flow and genetic diversity (Natoli et al.  
383 2004, Qu erouil et al. 2007). Furthermore, in the Azores archi-  
384 pelago, Silva et al. (2008) reported the absence of habitat  
385 partitioning between resident and non-resident dolphins. In  
386 the Canary Islands, bottlenose dolphins do not seem to be island  
387 associated, but moved between several islands of the archipel-  
388 ago (Castrill n et al. 2011; Tobe na et al. 2013). This suggests a  
389 situation similar to the Azores Islands. Nevertheless, although  
390 sightings could be grouped together, large heterogeneity was  
391 found in the Central–Eastern North Atlantic, where differences  
392 in acoustic parameters may represent local adaptations to the  
393 acoustic and social environments.

394 Furthermore, the coefficients of variation showed a high  
395 variability within each location, especially for the Canary  
396 Islands and the Mediterranean Sea. In these locations, the  
397 acoustic sample came from just a few sightings; neverthe-  
398 less, results from the DFA and the hierarchical cluster  
399 analysis confirmed the variability highlighted, suggesting  
400 differences in the samples of both locations and the need  
401 for a more detailed study investigating micro-geographic  
402 variation.

403 Within the Mediterranean, sounds recorded from the  
404 Alboran Sea were significantly different from the recordings  
405 made in the Gulf of Vera, the Provencal and the Tyrrhenian  
406 Sea. The Alboran Sea whistles exhibited significantly lower  
407 frequency parameters and higher signal duration and modula-  
408 tion. Our acoustic results therefore suggest the presence of two  
409 different groups in the Mediterranean basin. Furthermore,  
410 although the mean values of the parameters from this area  
411 varied from those of Atlantic Ocean, the frequency parameters  
412 from the Alboran Sea were more similar to those from the  
413 Azores Archipelago. These results suggest that the Alboran  
414 Sea may be an area that is ecologically distinct from the rest of  
415 the Mediterranean and is perhaps a zone of transition between  
416 the Mediterranean and the Atlantic Ocean. Castellote et al.

(2012) reported that fin whale (*Balaenoptera physalus*) calls  
417 detected in the Alboran basin and the Strait of Gibraltar were  
418 more similar to calls recorded in the Azores than to calls  
419 recorded elsewhere in the Western Mediterranean. These au-  
420 thors suggest that North Atlantic fin whales cross the Strait of  
421 Gibraltar and enter the Mediterranean Sea, but do not venture  
422 further than the Alboran Sea. Similarly, our recordings from  
423 the Alboran area are different to the rest of the Mediterranean,  
424 allowing us to assume that within their distribution range  
425 Mediterranean bottlenose dolphins have more than one evo-  
426 lutionary unit (considered as a distinct local population within  
427 a species that has different behavioural and phenological traits  
428 and thus harbours enough genetic uniqueness to warrant its  
429 own management and conservation). Furthermore, since the  
430 closest recording was collected in the Gulf of Vera (40 km east  
431 of the Alboran Sea), the possible limits to the distribution of  
432 Alboran animals may be at the Eastern end of the Alboran Sea,  
433 where an interchange zone could be present but not picked up  
434 by our sampling. The oceanographic features of the area,  
435 represented by the Almeria-Oran front, have already been  
436 suggested as a barrier to the movement of some species that  
437 leads to the creation of local populations of prey and their  
438 predators (Natoli et al. 2005). Bottlenose dolphins show ge-  
439 netic differentiation on either side of this front (Natoli et al.  
440 2005), which is consistent with the acoustic results from our  
441 study.

442 In the Gibraltar area, the bottlenose dolphin population is  
443 considered strictly resident (Chico et al. 2011): in 2008, after  
444 9 years of study, the re-sighting rate was found to be 90 %. A  
445 recent genetic study identifies individuals from the area as a  
446 pelagic population (Louis et al. 2013). Therefore, the Alboran  
447 basin may be inhabited by animals differentiated from the rest  
448 of the Mediterranean as a result of distinct habitat features, for  
449 example the presence of seamounts scattered through the  
450 whole area and currents coming from the Atlantic Ocean.  
451 The similarity between the oceanographic features of the  
452 Atlantic and the Almerian barrier suggests that an offshore  
453 population in the area could explain the acoustic relationship  
454 with the population inhabiting the Central–Eastern North  
455 Atlantic. This interpretation has important conservation impli-  
456 cations since it suggests the presence of at least two different  
457 evolutionary units in the Mediterranean basin. Nevertheless,  
458 more data are needed to get new insights into the variability  
459 within the Mediterranean Sea especially where our relatively  
460 small sample size identified the possibility of a considerable  
461 acoustic difference.

462 The results reported here have value for the management of  
463 the species in the areas considered. Together with data from  
464 genetic studies, they provide a basis for defining bottlenose  
465 dolphin population ranges and give guidance to efforts aimed  
466 at defining conservation stocks. Despite common bottlenose  
467 dolphins' vocalizations being characterized by features under  
468 different selective forces and influenced by vocal production  
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470 learning, their variation can be considered a proxy for the  
 471 differentiation of evolutionary units that show genetic  
 472 variation.

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493  
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496  
 497 **Ethical standards** The work has been carried out without putting at  
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