

A COMPARISON OF BOTTLENOSE DOLPHIN WHISTLES IN THE ATLANTIC OCEAN: FACTORS PROMOTING WHISTLE VARIATION

LAURA J. MAY-COLLADO* AND DOUGLAS WARTZOK

George Mason University, Department of Environmental Science & Policy, MSN 5F2, 4400 University Drive, Fairfax, VA 22030, USA (LJM-C)

Florida International University, Department of Environmental Science, 11200 SW 8th Street, Miami, FL 33199, USA (DW)

Whistles are narrowband, frequency-modulated sounds produced by many cetaceans. Whistles are extensively studied in delphinids, where several factors have been proposed to explain between- and within-species variation. We examined factors associated with geographic variation in whistles of common bottlenose dolphins (*Tursiops truncatus*) by assessing the role of ambient noise, noise from boats, and sympatry with other dolphin species, and reviewing and comparing whistle structure across populations in the western and eastern Atlantic Ocean. Whistles of adjacent populations differed, particularly in frequency parameters. A combination of factors may contribute to microgeographic whistle variation, including differences in ambient noise levels (dolphins produced relatively higher frequency whistles in the noisiest habitat), and differences in number of boats present (when multiple boats were present, dolphins whistled with greater frequency modulation and whistles were higher in maximum frequency and longer than when a single boat was present). Whistles produced by adjacent populations were relatively similar in structure. However, for clearly separated populations, the distance between them did not relate directly to whistle structure. We propose that plasticity in bottlenose dolphin whistles facilitates adaptation to local and changing conditions of their habitat, thus promoting variation between populations at different geographic scales.

Key words: ambient noise, boat traffic, Costa Rica, Panama, *Sotalia*, sympatry, *Tursiops*

Most toothed whales emit frequency-modulated tonal sounds that are narrowband in frequency, with most of their energy below 20 kHz (Au 2000; Richardson et al. 1995). In true dolphins (Delphinidae), tonal sounds are typically referred to as whistles, and are emitted especially during social interactions that involve group cohesion, individual recognition, and recruitment during feeding activities (e.g., Acevedo-Gutiérrez and Stienessen 2004; Caldwell and Caldwell 1965; Caldwell et al. 1990; Janik 2000; Janik et al. 1994; Tyack 1997). Caldwell et al. (1990) classified whistles of common bottlenose dolphins (*Tursiops truncatus*) into “signature whistles” (or contact calls) and “variant whistles.” Signature whistles are stereotypic and individual-specific signals that are stable over time and are used for group cohesion. Conversely, variant whistles are not individual-specific, are much less stable, and are produced in a variety of social contexts.

In many animals, signal variation has provided insights into the dispersal capabilities of species (e.g., McGregor et al. 2000; Mundinger 1982), isolation and genetic divergence between groups or populations (e.g., Ford 2002; Lemon 1966; McGregor et al. 2000), and adaptation to ecological conditions (e.g., Boncoraglio and Saino 2007; Brumm 2006; Gillam and McCracken 2007; Marler 1960; Peters et al. 2007). Variations in dolphin whistle structure have been generally referred to as geographic variations, and not dialects. Dialects—signals shared by a group of organisms that are slightly different from those of neighboring groups—are well known in birds but rare in cetaceans. For example, where some species of birds within an area share the same song, variations of the song in neighboring areas are often referred to as dialects. The only 2 examples of sound variation interpreted as a dialect in cetaceans are the calls of killer whales (*Orcinus orca*) and the codas of sperm whales (*Physeter macrocephalus*—Ford 2002).

Dolphin species vary in whistle frequency parameters (e.g., Matthews et al. 1999; Rendell et al. 1999; Steiner 1981; Wang et al. 1995a). Several factors have been proposed to explain this variation, including phylogeny, sociality, zoogeography, and

* Correspondent: lmaycollado@gmail.com

morphological constraints. Recently, comparative phylogenetic studies by May-Collado et al. (2007a, 2007b) examined the evolution of some frequency components in cetacean tonal sounds. Their findings suggest that the evolution of minimum frequency in cetaceans appears to be influenced by body size and group size, whereas whistle complexity (measured in terms of mean number of inflection points) is influenced by social structure. Within species, whistles vary primarily in frequency modulation (mean number of inflection points) and duration (e.g., Azevedo et al. 2007; Morisaka et al. 2005a; Wang et al. 1995b). High intraspecific variability in these 2 parameters may indicate transmission of emotional information (e.g., presence of food, danger, or alertness) but also may reflect high inter-individual variation, aiding individual differentiation (Norris et al. 1985; Steiner 1981; Wang et al. 1995a, 1995b). Although there is little intraspecific variation (low coefficient of variation) in frequency parameters, populations do differ in frequency sufficiently to allow discrimination among them (e.g., Azevedo and Van Sluys 2005; Morisaka et al. 2005a; Rossi-Santos and Podos 2006) at both microgeographic (between neighboring populations [e.g., Ansmann et al. 2007; Azevedo and Van Sluys 2005; Baron et al. 2008; Barzúa-Durán and Au 2002, 2004; Morisaka et al. 2005a; Rossi-Santos and Podos 2006; Wang et al. 1995a]) and macrogeographic (between widely separated populations [e.g., Baron et al. 2008; Camargo et al. 2007; Wang et al. 1995a]) scales.

Although our understanding of whistle structure, production rate, and use in dolphin societies is growing, the causes or factors promoting whistle variation remain poorly understood. Some studies suggest a general geographical pattern relating to distance, that is, the further apart the populations the more different whistle structure is (e.g., Azevedo and Van Sluys 2005; Barzúa-Durán and Au 2002, 2004; Rossi-Santos and Podos 2006; Wang et al. 1995a). Some exceptions to this generalization have been found, including a recent study of spinner dolphins (*Stenella longirostris*) where some distantly separated populations from the Atlantic and Pacific oceans were more similar to each other than to neighboring populations (Camargo et al. 2007). In addition to distance or degree of isolation, 2 recent studies attributed geographic variation in whistles to acoustic characteristics of the environment, such as ambient noise (Ansmann et al. 2007; Morisaka et al. 2005b). Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) emit low-frequency whistles with little modulation in noisy environments, possibly as a strategy to avoid masking and attenuation by ambient noise from high-frequency sources such as dolphin-watching and fishing boats, or ferries, because high-frequency sounds attenuate more rapidly over long distances than do lower-frequency sounds, and high-frequency modulations are easily masked by noise (Morisaka et al. 2005b). Conversely, a comparison between whistles of short-beaked common dolphins (*Delphinus delphis*) from the English Channel (British Isles) and the Celtic Sea found that dolphins from the presumably noisiest site, the English Channel, emitted higher-frequency whistles (Ansmann et al. 2007) as a strategy to avoid masking by the low-frequency ambient noise produced by the

high vessel traffic in the area, although no measurements of actual ambient noise were taken in this study.

Alternatively, Steiner (1981) suggested that zoogeographical relationships also may play an important role in whistle variation. Steiner (1981) observed that differences in whistle structure were greater between sympatric species than between allopatric species. This observation is in a way congruent with the “species recognition hypothesis” (Sætre et al. 1997), which states that song structure among closely related species has evolved to reduce hybridization. Other alternative hypotheses for whistle variation in dolphins include intraspecific variation in group fluidity (Barzúa-Durán and Au 2002), learning, and genetic differentiation (Azevedo and Van Sluys 2005; Camargo et al. 2007; Rossi-Santos and Podos 2006).

The goal of this study is to provide a description of bottlenose dolphin whistles in 2 poorly known adjacent populations in the Caribbean of Costa Rica and Panama and provide insights on whistle variation by evaluating whether ambient noise, number of boats present, and zoogeographical relationships are associated with whistle variation between these 2 adjacent populations. We then summarize 8 published studies on bottlenose dolphin whistles from the western and eastern Atlantic to more broadly assess the role of distance on whistle variation.

MATERIALS AND METHODS

Study areas.—The Wildlife Refuge Gandoca-Manzanillo is located along the Caribbean coast of Costa Rica, about 35 km north of Bocas del Toro (Fig. 1). The surveyed area was limited to an area of 9.83 km² within the refuge. The bottom is muddy and the depth is relatively shallow, ranging from 10 to 40 m. Water transparency is generally less than 0.5 m because of high sediment input from the Sixaola River. Boat traffic is relatively low, but a few powered boats are used in the refuge for local fishing and tourism (sport fishing and dolphin-watching). There are 2 small resident populations of dolphins, 1 of the Guyanese dolphin (*Sotalia guianensis*) and 1 of the common bottlenose dolphin. The species are sympatric within the limits of the refuge, where they regularly form mixed-species groups (Azevedo-Gutiérrez et al. 2005; Forestell et al. 1999; Gamboa-Poveda and May-Collado 2006). Preliminary photo-identification suggests that only some of the identified bottlenose dolphins are resident to the refuge; most appear to have a wider range that includes offshore waters (L. J. May-Collado, in litt.).

In the Archipelago of Bocas del Toro, survey effort covered approximately 79.2 km² within the inner part of the Archipelago, which is characterized by shallow, clear waters < 20 m deep and variable bottom substrate (mud, coral, sea grass, and mangroves). The main means of transportation between the islands and mainland are powered boats and canoes. In this area, only bottlenose dolphins are present. The most popular dolphin-watching place is Bocas Torito (also called Dolphin Bay) where animals are predictably found and dolphin-watching activities concentrate.

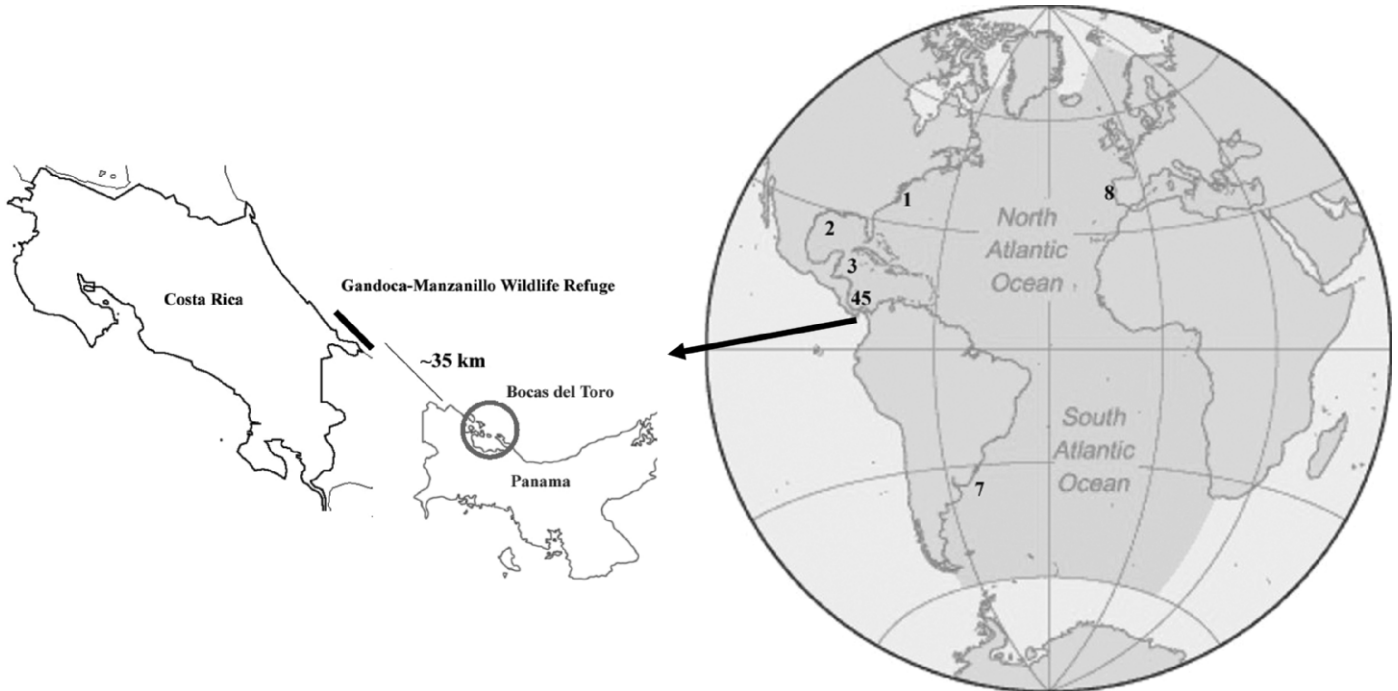


FIG. 1.—Map showing the location of all studies of whistle structure of bottlenose dolphins (*Tursiops truncatus*) in the Atlantic Ocean. 1 = Western Atlantic (Baron et al. 2008; Steiner 1981); 2 = Gulf of Mexico, United States (Baron et al. 2008; Wang et al. 1995a); 3 = Turneffe Atoll, Belize (Campbell 2004); 4 = Gandoca-Manzanillo, Costa Rica (this study); 5 = Bocas del Toro, Panama (this study); 6 = Patos Lagoon, Brazil (Azevedo et al. 2007); 7 = Golfo de San Jose, Argentina (Wang et al. 1995a); and 8 = Sado Estuary, Portugal (dos Santos et al. 2005).

For comparisons with other populations on the western and eastern Atlantic, we selected studies that provided information for at least 6 standard whistle parameters (see below). The studies were divided into 5 regions: western North Atlantic (Baron et al. 2008; Steiner 1981), Gulf of Mexico (Baron et al. 2008; Wang et al. 1995a), northern Caribbean in Central America (Belize—Campbell 2004), southern Caribbean in Central America (this study), South Atlantic (Azevedo et al. 2007; Wang et al. 1995a), and eastern Atlantic (dos Santos et al. 2005; Fig. 1).

Recordings.—Signals were recorded using a broadband system consisting of a RESON hydrophone 4033 (−203 dB re 1 V/μPa, 1 Hz to 140 kHz; RESON Inc., Goleta, California) connected to an AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400–500 kHz, 16 bit; Avisoft Bioacoustics, Berlin, Germany) that sent the signals to a laptop computer.

Ambient noise was recorded at 5 stations in Bocas del Toro (Drago, Bocas Torito, Cerro Brujo, Islas Pastores, and Almirante Bay) and at 3 in Gandoca-Manzanillo (Beginning, Middle, and Ending of the refuge) at 500- and 384-kHz sampling rates. One-minute ambient noise files were recorded every 5 min over a period of 15 min at each station at a known gain level. To estimate ambient noise level, we 1st used a calibrated ITC-1001 sound projector (International Transducer Corporation, Santa Barbara, California) to send 2-, 6-, 10-, 14-, 18-, and 22-kHz sine waves to the recording system. Projector and hydrophone were separated by 7.3 m. The root mean square voltage input to the ITC-1001 was measured at each frequency, and the received sound level at 7.3 m was

calculated based on spherical spreading. Then 1 s was randomly selected for each of the above frequencies (control) and another 1 s from each of the 3 ambient noise files (both had the same sampling rate at 500 kHz) recorded at each location. For ambient noise files with the 384-kHz sampling rate, we selected 1.3 s to compensate for differences in sampling rate with the control (500 kHz), so that both files had the same number of points rather than the same length of time. Each control 1-s file was joined separately with 1 s (or 1.3 s) of ambient noise using the software Media Join 1.0 (2004–2005; Mystic Media, Hampstead, North Carolina). The joined files

TABLE 1.—Amounts of time that whistles of bottlenose dolphins (*Tursiops truncatus*) were recorded and analyzed at 2 study sites in the Caribbean (see Fig. 1) for each year of this study. Boldface type indicates totals for each study site.

Study site and year	Total recorded time (min)	Total analyzed (min)	Time of dolphin interactions with single/multiple boats (min)
Gandoca-Manzanillo^a	1,496.53	176.58	176.58/3
2004	467.06	41.37	41.37/0
2005	697.57	44.31	44.31/0
2006	331.9	90.9	87.9/3
Bocas del Toro	1,742.32	1,122.9	634.6/488
2004	382.82	276.8	146.27/130.53
2007	1,359.5	1,022.4	632.58/389.68

^a Most recording time is with mixed-species groups of *Sotalia guianensis* and *Tursiops truncatus*.

were opened in RAVEN PRO 1.3 beta version build 20 (2003–2007; Cornell Lab of Ornithology, Ithaca, New York), and we measured the average relative power in decibels for the control and ambient noise segment at the center frequency and 3rd octave. Although RAVEN provides only relative, not absolute, power levels, we knew the actual recorded levels in the control segments and could then calculate the levels of ambient noise.

Dolphin whistles were recorded continuously (in 3-min files) with a sampling rate between 384 and 500 kHz. Table 1 provides information about the recording time needed to obtain high-quality whistles from each study site. The total number of high-quality whistles selected for analysis was based on group size, where the maximum number of whistles included per group was 3 times the number of individuals in the group. High-quality whistles were those whistles with the entire contour visible; this was important in order to measure adopted frequencies at 19 points along the contour (see below).

Selected whistles were analyzed in RAVEN 1.2 (2003–2007; Cornell Lab of Ornithology) with a fast Fourier transform size of 1,024 points, an overlap of 50%, and using a 512- to 522-sample Hann window. We measured 9 standard parameters: start frequency (Start), ending frequency (End), minimum frequency (Min), maximum frequency (Max), delta frequency (Delta; $\text{Max} - \text{Min}$), peak frequency (Peak; measured in the whistle contour where intensity was the highest), duration (s), number of inflection points, and number of harmonics (see Azevedo et al. 2007; dos Santo et al. 2005; Wang et al. 1995a, 1995b). In addition, we followed Morisaka et al. (2005b) by measuring adopted frequencies (McCowan 1995) in order to estimate the frequency distribution of a whistle. Nineteen equally sized intervals were set in every whistle by dividing its duration by 20 frequency points (McCowan 1995). These same adopted frequencies were used to calculate a coefficient of frequency modulation for each whistle (McCowan and Reiss 1995). The coefficient measures changes in complexity of whistle contour and represents the magnitude of frequency modulation in a whistle. High coefficients of frequency modulation indicate high frequency modulation (see Morisaka et al. 2005b).

Sample size for comparisons.—Comparisons of whistles from Gandoca-Manzanillo and Bocas del Toro were performed using only whistles from acoustically independent groups from each population. In each recording session, group members were photo-identified while being recorded, using natural marks on both sides of the dolphin dorsal fin for individual recognition (Würsig and Jefferson 1990). Group membership varied considerably, and an array of member combinations occurred during the period of this study. We only included groups for which photo-identification data were available and considered acoustically independent those groups with 0–10% membership similarity, based on total group size. This rather strict selection limited the number of high-quality whistles and groups available for analysis, but because our recording equipment was not optimal for individual discrimination, group independence was important for between-population comparisons. In addition, in Gandoca-Manzanillo sample sizes were further reduced because of the common occurrence of

mixed-species groups of bottlenose dolphins and Guyanese dolphins in the area. Only recordings from groups that were exclusively *T. truncatus* were used for the between-population analysis. For within-population analysis, groups of *T. truncatus* with membership similarity > 10% were included.

Boat traffic and dolphin–boat interactions.—In Bocas del Toro, boats are used for local transportation, fishing, and dolphin-watching activities and in Gandoca-Manzanillo, for local fishing and tourist activities such as sport fishing and dolphin watching. The majority of boats in Bocas del Toro are powered with engines of between 50 and 150 hp, whereas in Gandoca-Manzanillo engines are <50 hp (Taubitz 2007). Acoustic recordings were made from our research boats (10-m boat in Gandoca-Manzanillo and 6-m boat in Bocas del Toro) with the engine off at all times.

Although we tried to reduce disturbance to the group as we 1st approached it, we were unable to estimate if our boat had an effect on dolphin whistle structure. Because of this limitation, we restricted analysis to simply comparing whistle parameters between presence of a single boat (the research boat, engine off) and multiple boats (2–15 whale-watching boats, including our research boat). Basically, the number of boats present in each recording session was used as an indirect measure of engine noise levels.

The effect of boat number was not estimated for Gandoca-Manzanillo because almost all recording sessions occurred with the presence of only the research boat. Analyses for Bocas del Toro were performed using data only from Bocas Torito, because it is here where dolphin watching is concentrated and predictable. The bay is small enough to allow observation from one end to the other, so we were confident that what we referred to a single-boat presence was solely our research boat with the engine off (low levels of engine noise). Multiple boats were from 2 to 15 dolphin-watching boats (high levels of engine noise) present in the bay that followed and observed the animals with engines on, while we recorded with our engine off. In addition, we made sure to arrive at Bocas Torito a couple hours before any dolphin-watching boat entered the bay. Because we were interested in determining potential responses in whistle structure to from 1 to multiple boats, we selected high-quality whistles from groups with all levels of membership similarity. Therefore, sample size of whistles for this analysis was larger than for between-population comparisons.

Statistical analysis.—All statistical analyses were performed in JMP 7.0 (2007; SAS Institute Inc., Cary, North Carolina). For within-population whistle variation, we used the Kruskal–Wallis test to determine if groups within study areas varied in standard whistle parameters (Min, Max, Delta, Start, End, Peak, duration, number of inflection points, and number of harmonics), the coefficient of modulation, and adopted frequencies. Comparisons between adjacent populations were done using the nonparametric Mann–Whitney *U*-test. Alpha critical values for multiple comparisons were adjusted using sequential Bonferroni. With the exception of the variables number of inflection points and number of harmonics, all whistle parameters were Box–Cox transformed to adjust their

distribution to nearly normal (Sokal and Rohlf 1995). Then we used a multivariate discriminant function analysis (with a discriminant linear method) to classify whistles within and between populations, and we compared the coefficient of frequency modulation considering the effect of population, single versus multiple boats, whistle duration, and their interactions (see Morisaka et al. 2005a) with an analysis of covariance (ANCOVA).

Comparisons between populations in the Atlantic Ocean were performed by pairwise comparisons of their mean values for frequency and time parameters. First, we tested the assumption of equal variance with Levene's *F*-test and then used a *t*-test when variances were equal or a Welch *t*-test when variances were unequal. To visualize which populations were more similar to others we used a hierarchical cluster analysis, with cluster groups based on similarity of their mean values.

Ambient noise was compared between and within study sites with the median test, which is a nonparametric test that ranks values either 1 or 0 depending on whether a point is below or above the median. To determine if whistle structure varied between the presence of a single boat (the research boat) and multiple boats (whale-watching boats), we compared whistle parameters using a Mann-Whitney *U*-test. Finally, we tested if sympatry between bottlenose dolphins and Guyanese dolphins in Gandoca-Manzanillo influenced whistle structure of bottlenose dolphins. Specifically, we evaluated whether the magnitude of the differences in whistle parameters was significantly greater for bottlenose dolphins when mixed with Guyanese dolphins, in Gandoca-Manzanillo, compared to bottlenose dolphins alone, in Bocas del Toro. We compared the differences between mean values for each whistle parameter with a chi-square test.

RESULTS

Within-population variation.—We obtained a total of 77 high-quality whistles from 4 groups at Gandoca-Manzanillo and 214 whistles from 23 groups at Bocas del Toro. Groups from Gandoca-Manzanillo did not vary in their whistle structure ($P > 0.05$). In contrast, significant differences were found between bottlenose dolphin groups at Bocas del Toro, particularly in minimum frequency ($\chi^2 = 64.64$, *d.f.* = 22, $P < 0.0001$), maximum frequency ($\chi^2 = 50.54$, *d.f.* = 22, $P = 0.0005$), delta frequency ($\chi^2 = 34.43$, *d.f.* = 22, $P = 0.044$), start frequency ($\chi^2 = 44.78$, *d.f.* = 22, $P = 0.003$), ending frequency ($\chi^2 = 38.34$, *d.f.* = 22, $P = 0.017$), and mean number of harmonics ($\chi^2 = 44.33$, *d.f.* = 22, $P = 0.003$).

Between-population variation.—We compared 77 whistles from Gandoca-Manzanillo with 74 whistles from Bocas del Toro. A discriminant analysis classified correctly 81.1% (Bocas del Toro) and 63.6% (Gandoca-Manzanillo) to their respective populations. Populations were distinct in whistle frequency, particularly in maximum frequency ($\chi^2 = 12.18$, *d.f.* = 1, $P = 0.0005$), ending frequency ($\chi^2 = 17.13$, *d.f.* = 1, $P < 0.0001$), delta frequency ($\chi^2 = 4.8$, *d.f.* = 1, $P = 0.03$), and also in number of harmonics ($\chi^2 = 4.13$, *d.f.* = 1, $P = 0.04$). In general, dolphins at Bocas del Toro whistled with lower delta

and maximum and ending frequencies and produced whistles with lower mean number of harmonics compared to bottlenose dolphins from Gandoca-Manzanillo (Table 2). The coefficient of frequency modulation correlated with duration ($R^2 = 0.39$, $P < 0.001$) but not with population or their interaction. Population had an effect on adopted frequencies (ANCOVA, $F = 4.93$, *d.f.* = 1, $P = 0.026$).

We analyzed the potential effect of ambient noise, presence of single versus multiple boats, and mixed- versus single-species groups on whistle variation between the 2 populations. Overall, ambient noise levels at Gandoca-Manzanillo were higher than at Bocas del Toro ($\chi^2 = 8.42$, *d.f.* = 1, $P = 0.0037$; Fig. 2a). There were no significant differences in ambient noise levels within Gandoca-Manzanillo ($P > 0.05$; Fig. 2b). In Bocas del Toro, noise levels were significantly higher in Drago, Cerro Brujo, and Bocas Torito ($\chi^2 = 16.31$, *d.f.* = 4, $P = 0.0026$; Fig. 2b).

In Bocas Torito, groups recorded in the presence of a single boat (groups = 14, whistles = 84) varied in minimum frequency ($\chi^2 = 0.015$, *d.f.* = 13, $P = 0.005$) and ending frequency ($\chi^2 = 23.34$, *d.f.* = 13, $P = 0.038$). Groups recorded in the presence of multiple boats (groups = 9, whistles = 105) varied in minimum frequency ($\chi^2 = 24.23$, *d.f.* = 8, $P = 0.002$), delta frequency ($\chi^2 = 24.13$, *d.f.* = 8, $P = 0.002$), start frequency ($\chi^2 = 30.47$, *d.f.* = 8, $P = 0.0002$), ending frequency ($\chi^2 = 26.91$, *d.f.* = 8, $P = 0.0007$), and duration ($\chi^2 = 16.33$, *d.f.* = 8, $P = 0.038$). Whistle structure varied between the presence of a single boat versus multiple boats. In general, dolphins in the presence of multiple boats produced longer ($\chi^2 = 6.27$, *d.f.* = 1, $P = 0.012$) whistles showing higher maximum frequency ($\chi^2 = 13.67$, *d.f.* = 1, $P = 0.0002$), mean number of inflection points ($\chi^2 = 5.36$, *d.f.* = 1, $P = 0.021$), and coefficient of frequency modulation ($\chi^2 = 3.92$, *d.f.* = 1, $P = 0.048$; Fig. 3).

Finally, we tested the hypothesis that bottlenose dolphins living in sympatry with Guyanese dolphins may show significantly greater differences in whistle structure when with Guyanese dolphins than bottlenose dolphins occurring alone. There were no significant differences in the magnitude of the mean values across whistle structure (all $P > 0.05$).

Comparisons between widely separated populations.—Pairwise comparisons of 6 standard whistle parameters were performed between 6 regions in the western Atlantic and 1 in the eastern Atlantic Ocean (Table 2; Figs. 1 and 4). Whistle frequency and duration parameters varied significantly at both micro- and macrogeographical scales (Fig. 4). A hierarchical clustering method helped to visualize the similarity of populations across regions and study sites within the western Atlantic, based on mean values for whistle frequency, duration, and number of inflection points (Figs. 5a and 5b). Overall, the southern Central American populations were more similar to the western North Atlantic, whereas the northern Central American dolphins were more similar to the South Atlantic dolphins. As expected, adjacent populations were most similar to each other in whistle structure (Fig. 5b). However, apart from directly adjacent populations, distance was a poor predictor of similarity in whistles between populations.

TABLE 2.—Statistical description of whistle parameters for bottlenose dolphin populations in the western and eastern Atlantic Ocean (for Gandoca-Manzanillo and Bocas del Toro, information is based on acoustically independent groups and information in parentheses is for all groups regardless of group membership similarity). Parameters are defined in the “Materials and Methods.”^{a,b}

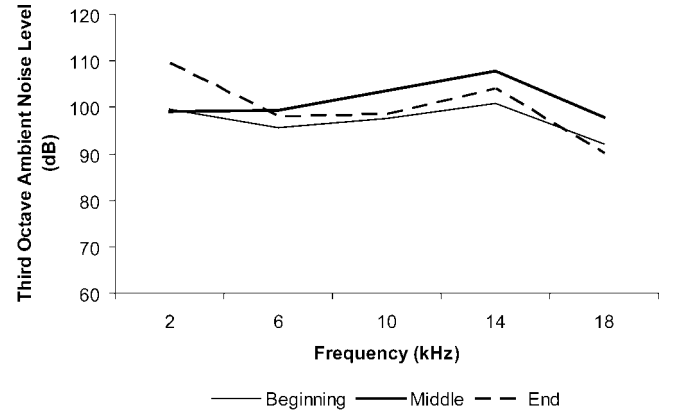
Location	Statistics	<i>n</i>	No. individuals	Min (kHz)	Max (kHz)	Delta (kHz)	Start (kHz)	End (kHz)	Peak (kHz)	Duration (s)	No. inflection points	No. harmonics	COFM
Western North Atlantic (Steiner 1981) ^b	Mean ± SD			7.33 ± 1.66	16.24 ± 2.69		11.26 ± 3.98	10.23 ± 3.64		1.30 ± 0.63	2.86 ± 2.45		
WNA1	Range	857	?										
	CV (%)												
Western North Atlantic (Baron et al. 2008) ^c	Mean ± SE	894	?	8.24 ± 0.24	15.03 ± 0.61		10.64 ± 0.55	12.40 ± 0.61		0.62 ± 0.06	1.43 ± 0.21	86	
WNA2	Range												
	CV (%)												
Gulf of Mexico (Baron et al. 2008) ^c	Mean ± SE	1,821	?	7.87 ± 0.20	16.19 ± 0.40		10.82 ± 0.35	11.17 ± 0.53		0.88 ± 0.05	3.02 ± 0.27		
GMX1	Range												
	CV (%)												
Gulf of Mexico (Wang et al. 1995b)	Mean ± SD	2,022	?	5.77 ± 1.84	11.32 ± 3.31		8.01 ± 2.81	8.16 ± 3.78		0.68 ± 0.4	2.09 ± 2.54	0.25 ± 0.43	
GMX2	Range												
	CV (%)												
Galveston, Texas (Wang et al. 1995b)	Range	811	?	1.86–18.92	3.91–21.61		2.50–20.66	2–21.61		0.05–3.20	0–37	0–1	
	CV (%)												
Gal	Mean ± SD			31.82	29.24		35.09	46.38		58.85	121.80	175.21	
				5.98 ± 2.30	11.95 ± 3.08		7.95 ± 2.88	9.02 ± 3.96		0.75 ± 0.46	2.57 ± 2.62	0.28 ± 0.45	
Corpus Christi, Texas (Wang et al. 1995b)	Range	617	?	1.86–18.92	3.91–21.61		2.50–20.66	2.0–21.61		0.05–3.20	0–17	0–1	
	CV (%)												
CC	Mean ± SD			38.54	25.81		36.06	43.96		61.87	101.82	161.98	
				5.88 ± 2.65	11.43 ± 3.80		7.43 ± 2.44	8.71 ± 4.04		0.69 ± 0.41	2.14 ± 2.97	0.23 ± 0.42	
South Padre Island, Texas (Wang et al. 1995b)	Range	549	?	2.11–14.53	3.44–20.75		2.89–6.75	2.34–20.66		0.005–2.63	0–37	0–1	
	CV (%)												
SPI	Mean ± SD			20.78	27.08		32.81	46.31		60.50	138.49	183.89	
				5.32 ± 1.56	12.85 ± 4.55		8.7 ± 2.95	6.40 ± 2.44		0.60 ± 0.26	1.37 ± 1.65	0.22 ± 0.42	
Northern Central America, Caribbean: Turneffe Atoll, Belize (Campbell 2004)	Range	216	140 ^d	2.58–9.45	4.53–19.14		3.13–18.75	2.59–14.92		0.09–2.08	0–15	0–1	
	CV (%)												
TUA	Mean ± SD			29	35		33.91	38.11		43.66	119.84	187.24	
				1.96–10.50	3.84–19.87		5.80 ± 2.04	11.85 ± 4.61		0.53 ± 0.38	0.89 ± 1.54		
Southern Central America, Caribbean: GM + BT	Range	151	116	5.52 ± 2.08	16.5 ± 4.83		8.76 ± 3.67	11.21 ± 5.34		1.00 ± 0.72	3.20 ± 3.81	1.60 ± 1.91	4.97 ± 5.50
	CV (%)												
SCC	Mean ± SD			1.60–11.91	1.70–28.48		1.61–21.97	4.1–27.14		0.06–3.81	0–20	0–13	0.32–48.74
				37.70	27.18		42.07	47.68		72.45	118.96	119.50	110.78
Gandoca-Manzanillo, Costa Rica	Range	77	18	5.68 ± 2.24	17.61 ± 4.93		8.43 ± 3.66	13.15 ± 5.57		0.89 ± 0.69	2.64 ± 3.41	2.34 ± 1.16	4.80 ± 6.53
	CV (%)												
GM	Mean ± SD			1.61–10.85	8.77–28.48		1.61–17.21	4.13–27.14		0.087–3.40	0–19	0–13	0.44–48.73
				39.30	28.00		43.50	42.4		77.1	129.5	115.7	136.0
Bocas del Toro, Panama (this study)	Range	74	98	5.34 ± 1.90	15.34 ± 3.65		9.10 ± 3.70	9.19 ± 4.27		1.10 ± 0.74	3.78 ± 4.11	1.16 ± 1.19	5.15 ± 4.23
	CV (%)												
BT—just independent groups	Range			(5.61 ± 1.8)	(15.8 ± 3.6)		(9.80 ± 3.7)	(9.06 ± 4.2)		(1.13 ± 0.66)	(3.69 ± 3.8)	(1.35 ± 1.8)	(5.00 ± 4.44)
	CV (%)			1.6–11.90	1.7–23.63		3.42–21.97	4.21–22.22		0.061–3.81	0–20	0–5	0.32–20.31
BT—all groups	Mean ± SD	(214)	(~142)	(1.6–12.68)	(1.7–26.54)		(3.38–23.0)	(1.64–22.2)		(0.061–3.81)	(0–20)	(0–15)	(0.05–32.14)
	Range			35.63	23.81		40.66	46.47		67.47	108.8	102.73	82.15
	CV (%)			(32.29)	(22.82)		(37.56)	(46.22)		(58.16)	(102.8)	(134.5)	(89.0)

TABLE 2.—Continued.

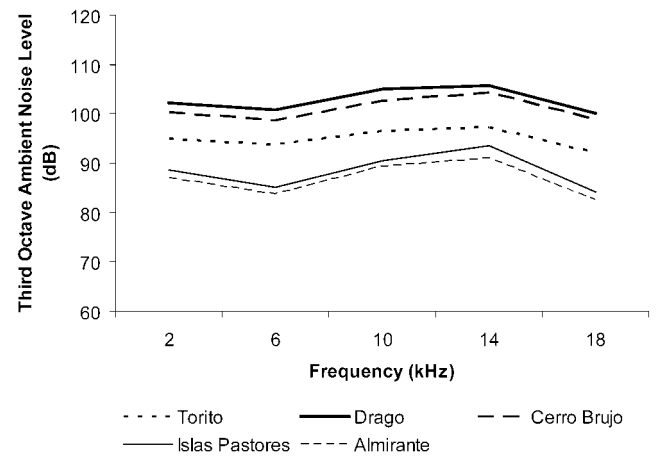
Location	Statistics	n	No. individuals	Min (kHz)	Max (kHz)	Delta (kHz)	Start (kHz)	End (kHz)	Peak (kHz)	Duration (s)	No. inflection points	No. harmonics	COFM
Patos Lagoon, Brazil (Azevedo et al. 2007)	Mean ± SD			5.96 ± 2.15	12.21 ± 3.20	6.25 ± 3.34	8.28 ± 3.11	8.37 ± 3.7		0.553 ± 0.394	1.42 ± 1.85		
	Range CV (%)	788	~40 ^e	1.2–17.2 36.1	3.6–22.3 26.2	0.1–16.6 53.4	3.1–20.8 37.6	2.8–22.3 44.2		0.553 ± 0.393 71.2	0–14 92.5		
Golfo de San Jose, Argentina (Wang et al. 1995b)	Mean ± SD			5.91 ± 1.5	13.65 ± 1.54		9.24 ± 2.74	6.63 ± 2.29		1.14 ± 0.49	1.58 ± 1.24	0.16 ± 0.37	
	Range CV (%)	110	?	1.17–10.08 25.71	9.38–17.11 11.28		1.17–16.09 29.65	3.05–15.94 34.60		0.18–0.27 42.74	0–8 78.66	0–1 227.11	
GSI Sado Estuary, Portugal (dos Santos et al. 2005)	Mean ± SD			5.4 ± 1.2	15.0 ± 2.7		5.8 ± 1.8	12.1 ± 4.4	9.2 ± 2.6	0.859 ± 0.396			
	Range CV (%)	735	?	2.0–9.0	7.9–21		2.0–15.3	2.2–21.0	3.5–20.4	0.257–4.130			

^a COFM = coefficient of frequency modulation; CV = coefficient of variation; WNA = western North Atlantic; GMX = Gulf of Mexico; Gal = Galveston; CC = Corpus Christi; SPI = South Padre Island; TUA = Turneffe Atoll; SCC = Southern Central America; GM = Gandoca-Manzanillo; BT = Bocas del Toro; PL = Patos Lagoon; GSI = Golfo de San Jose; SE = Sado Estuary.

^b Also contains groups recorded in the Caribbean.
^c Provides standard error information not standard deviation.
^d Nothing said about group membership similarity.
^e Possibly some animals were repeatedly recorded.



a. Gandoca-Manzanillo Wildlife Refuge, Costa Rica



b. Bocas del Toro, Panama

FIG. 2.—Third-octave ambient noise levels (median values) in decibels between and within study areas at 5 frequencies. a) Noise levels at 3 sites at Gandoca-Manzanillo; b) noise levels at 5 sites at Bocas del Toro.

DISCUSSION

In general, animals are believed to produce signals that are adapted to their particular environment (Peters et al. 2007). Several studies have shown that cetaceans respond acoustically to environmental noise in a variety of ways, including whistle production rate (e.g., Buckstaff 2004; Van Parijs and Corkeron 2001), shifts in signal frequency (Lesage et al. 1999), and an increase (e.g., Foote et al. 2004) or decrease (e.g., Buckstaff 2004) in signal duration. The observed differences in whistle structure between Gandoca-Manzanillo and Bocas del Toro may reflect a strategy of avoiding masking due to local ambient noise. Bottlenose dolphins from Gandoca-Manzanillo, which was particularly noisy at low frequencies, whistled with higher maximum, ending, and delta frequency than did dolphins living in Bocas del Toro.

Engine noise levels are presumably higher in Bocas del Toro because of intense boat traffic. In some areas, such as Bocas Torito, sources of engine noise are mainly dolphin-watching boats. Erbe (2002) estimated engine sound levels from whale-

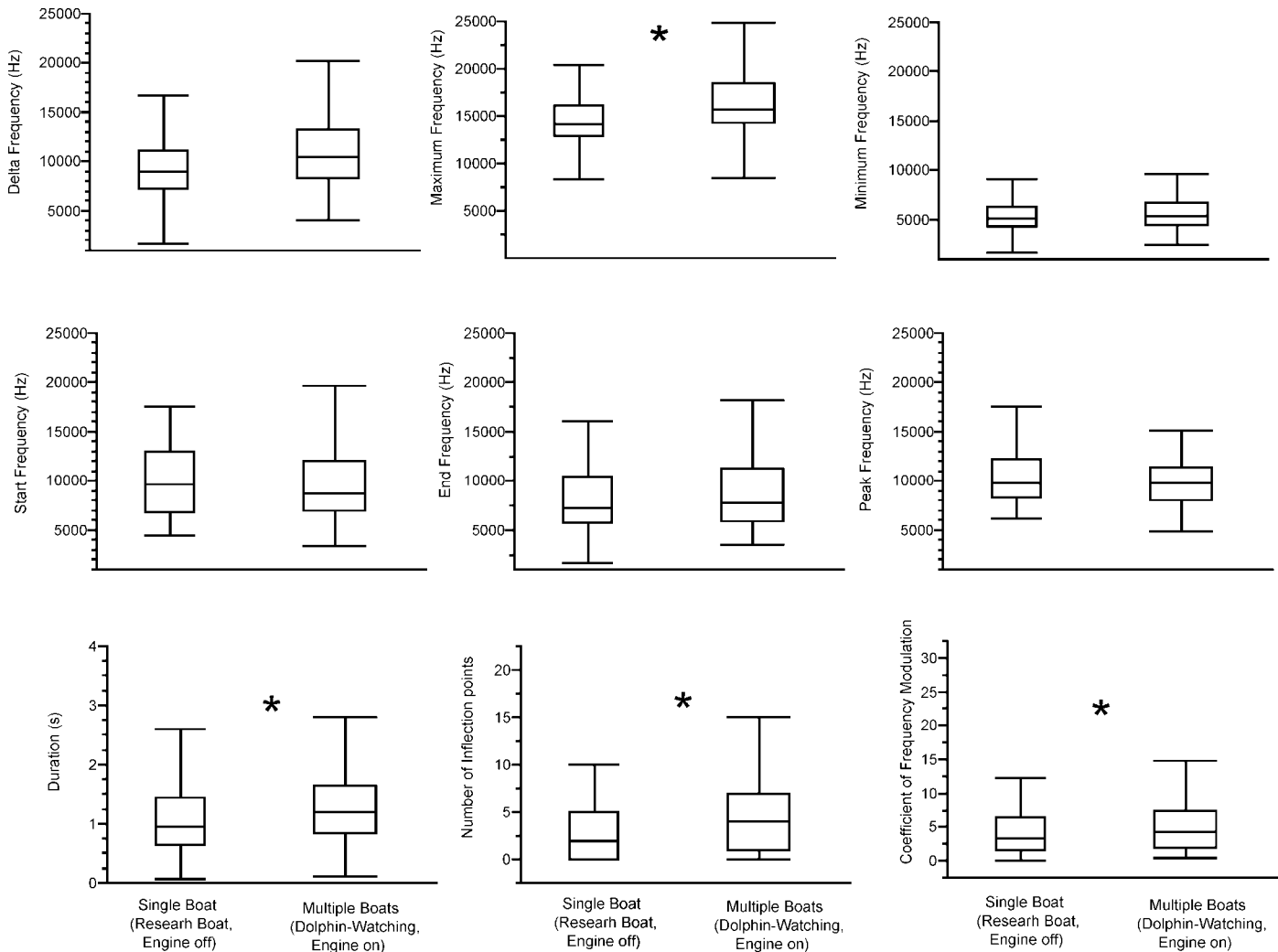


FIG. 3.—Whistle variation in frequency and time parameters of bottlenose dolphins (*Tursiops truncatus*) from Bocas Torito during recording sessions in the presence of a single (research boat) and multiple (dolphin-watching and research) boats (an asterisk [*] indicates significant differences).

watching boats to be 145–169 dB re 1 μ Pa at 1 m, more than sufficient to mask important signals such as the communicative whistles of dolphins (1–35 kHz—Richardson et al. 1995). Thus, engine noise produced by dolphin-watching boats can potentially be a factor promoting whistle variation within Bocas del Toro. In our study, more parameters of whistles varied significantly for groups of dolphins in the presence of multiple boats than in the presence of the research boat only. Dolphins also increased whistle maximum frequency, duration, and modulation in the presence of multiple boats compared to in the presence of a single boat. We could not directly account for potential effects of our own research boat on whistle structure. However, our results show that the effect of our research boat, if any, is less than that of multiple boats. Furthermore, the vast majority of groups recorded in Bocas Torito, during single and multiple boat interactions, were a subset of the same limited pool of individuals but in different group combinations. This suggests that we frequently recorded the same animals under both conditions. Therefore, the observed differences in whistle structure in the presence and

absence of boats likely reflected temporary shifts in whistle production from low (single) to high (multiple) whistle frequency and short (single) to long (multiple) whistle duration. The most likely explanation for this switch is avoidance of masking by high levels of engine noise. Engine noise is due to air bubbles that collapse near the blades of the propellers, which is the most significant source of noise above 2 kHz (Evans et al. 1992). Increasing propeller rotation rate also shifts engine noise to higher frequencies (Richardson et al. 1995), which would have greater potential for masking cetacean signals (Bain and Dahlheim 1994) and may explain the general response of these dolphins of increasing their maximum frequencies in the presence of boats in Bocas Torito.

Our results contrast with those of Buckstaff (2004), who found that bottlenose dolphin whistles did not change significantly in frequency range or duration in the presence of boats, and with the finding that other dolphin species such as the Indo-Pacific bottlenose dolphin use alternative strategies, such as lowering whistle frequency and modulation (Morisaka et al. 2005b). Increased occurrence of long whistles to overcome

	WNA1	GMX2	TUA (NC)	SCC	PL	GSJ	SE
	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP
WNA1	-----	***	***	! **	***	***	***
GMX1		-----	***	! **	***	! **	***
TUA (NC)			-----	! **	***	***	! *!
SCC				-----	! *!	! *!	! **
PL					-----	! **	***
GSJ						-----	***
SE							-----

N DISTANCE INCREASES FROM WNA TO GSJ S

Western North Atlantic Gulf of Mexico Central America, Caribbean South Atlantic Eastern North Atlantic

	GAL	CC	SPI		GM	BT
	MIN MAX START END DUR IP	MIN MAX START END DUR IP	MIN MAX START END DUR IP		MIN MAX START END DUR IP	MIN MAX START END DUR IP
GAL	-----	! **	***	GM	-----	! *!
CC	-----	-----	***	BT	-----	! **

Adjacent populations

Gulf of Mexico (along the coast of Texas)

South Central America, Caribbean

! Indicates similar whistle parameters

* Indicates significant differences at the p-value 0.05 level in whistle parameters

FIG. 4.—Pairwise comparison between populations across individual populations and regions from the western and eastern Atlantic Ocean.

signal interference also has been reported in the calls of 3 populations of killer whales where whale-watching activities have become intense (Foote et al. 2004). That dolphin species overcome masking by ambient and engine noise in different manners is evidence of how plastic these signals are. Finally, habitat use also may be an important factor promoting variation in dolphin whistle structure. Although recording sessions in both study areas occurred during the same behavioral activities (foraging, milling, social, and travel activities), strict selection of high-quality whistles reduced considerably the sample size for some of these behavioral categories, limiting the extent to which we could account for the role of behavior in whistle structure. Ensuring similar recording effort and sample sizes of high-quality whistles across behavioral categories could bring insights about the role of behavior on dolphin whistle structure at several geographical scales.

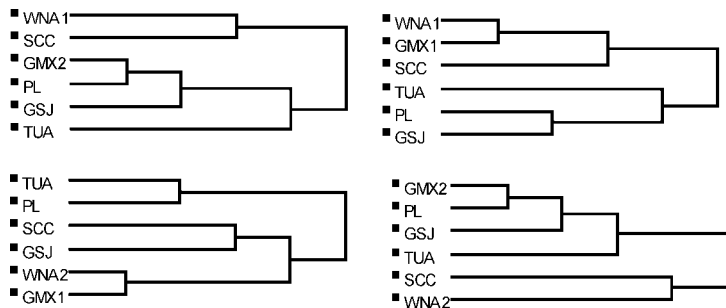
Although these 2 populations are distinct in several whistle parameters, they are more similar to each than to any other distant population. The same pattern was observed between another pair of adjacent populations, at Galveston and Corpus Christi (Wang et al. 1995b; Figs. 4 and 5). Similarity between adjacent populations may reflect connectivity in terms of individuals moving from 1 area to another. The distance between Gandoca-Manzanillo and Bocas del Toro is only 35 km. Although no dolphins have been identified yet that used both sites, it does not mean they are completely isolated. In contrast, when comparing neighboring, nonadjacent populations versus distant populations, absolute distance did not predict whistle similarity. For example, in contrast to what would be predicted by distance alone, the population in the southern Caribbean, Central America region (Gandoca-Manzanillo and Bocas del Toro) was more similar in whistle structure to both populations in the western North Atlantic and

the Gulf of Mexico (Baron et al. 2008), than to the population in Belize (Campbell 2004), which in turn was more similar to distant populations in the South Atlantic (Brazil [Azevedo et al. 2007] and Argentina [Wang et al. 1995a]). This suggests that apart from adjacent populations, populations within the same region are for the most part isolated, and similarities to distant populations could reflect similar acoustic conditions that prompt animals to respond in a similar manner.

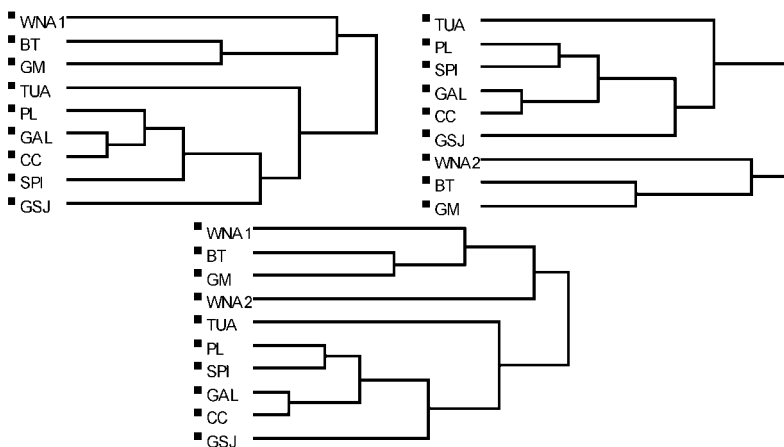
Dolphin whistles are important communicative signals used in a variety of contexts (e.g., Caldwell and Caldwell 1965; Caldwell et al. 1990; Fripp et al. 2005; Herzing 2000; Janik 2000; Tyack 2000; Watwood et al. 2004). Because of their important role in dolphin societies, some of the variation in whistles may reasonably be assumed to facilitate transmission efficiency and avoid signal masking. The factors that contribute to whistle variation may differ reflecting local conditions. Individual plasticity in bottlenose dolphins whistle structure may be adaptive when living in a continuously changing environment (e.g., changes in habitat acoustic structure). Our study provides insights on how ambient noise, number of boats (as a measure of engine noise), and zoogeographical relationships influence whistle structure. Local adaptation, in addition to distance and other factors may translate into population differentiation at different geographical levels.

RESUMEN

Los silbidos son sonidos de frecuencia modulada producidos por muchos cetáceos. Estos han sido extensamente estudiados particularmente en delfínidos, donde varios factores se han propuesto para explicar la variación entre y dentro especies. En este estudio examinamos varios factores asociados a la variación geográfica del delfín naríz de botella (*Tursiops*



a. Regions (WNA1 (Western North At.) Steiner 1981, WNA2=Baron et al. 2008, GMX1(Gulf of Mexico)=Baron et al. 2008, GMX2=Wang et. al 1995a, TUA (Belize, North Central America, Caribbean= Campbell 2004, SCC (South Central America, Caribbean)=This study, PL (Patos Lagoon, Brazil)=Azevedo et al. 2007, GSJ (Gulf of San Jose)=Wang et al. 1995a.



b. Sites (WNA1 (Western North At.) Steiner 1981, WNA2=Baron et al. 2008, Corpus Christi (CC), Galvestong (GAL) South Padre Is. (SPI)=Wang et. al 1995a, TUA (Belize, North Central America, Caribbean= Campbell 2004, Gandoca-Manzanillo (GM), Bocas del Toro (BT)(South Central America, Caribbean)=This study, PL (Patos Lagoon, Brazil)=Azevedo et al. 2007, GSJ (Gulf of San Jose)=Wang et al. 1995a.

FIG. 5.—A hierarchical cluster visualization of population similarity based on mean values for 6 standard whistle parameters (minimum, maximum, start and ending frequencies, duration, and number of inflection points). a) Similarity across regions and b) similarity between specific study sites within the western Atlantic Ocean. Black and gray stars highlight the relationships of Gandoca-Manzanillo and Bocas del Toro to other regions and study sites within the western Atlantic Ocean.

truncatus) que incluyen una evaluación del ruido ambiental y de botes, simpatría con otras especies de delfines; y una revisión y comparación de la estructura de los silbidos de varias poblaciones en el Océano Atlántico Oeste y Este. Los silbidos de poblaciones adyacentes difirieron en los parámetros de frecuencia. Una combinación de factores puede contribuir a esta variación microgeográfica de silbidos: diferencias en los niveles de ruido ambiental (los delfines produjeron silbidos con frecuencias relativamente mas altas en el ambiente mas ruidoso), y número de botes presentes (cuando múltiple botes estaban presentes, los delfines silbaron con mayor modulación, y los silbidos fueron mas altos en frecuencia máxima y mas largos que cuando solo un bote estaba presente). Los silbidos producidos por poblaciones adyacentes fueron relativamente similares en estructura. Sin embargo, en poblaciones claramente separadas, la distancia entre ellas no se relacionó directamente con la estructura del silbido. Proponemos que la plasticidad en los silbidos de delfines nariz de botella facilita

adaptación a condiciones locales y cambiantes de su hábitat, así promoviendo variación entre poblaciones a diferentes escalas geográficas.

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