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Whistles of bottlenose dolphins: comparisons among populations

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Abstract

Bottlenose dolphin whistle structure was compared among populations, by spectral and statistical analysis. Differences in whistle structure were greater between far separated than closer areas. Animals from nearby areas may influence each others' whistles by mimicry, but may also have similar whistles due to periodic change of individuals across areas. Whistle differences among groups in adjacent areas were small. Dolphins in non-adjacent areas presumably developed unique acoustic characteristics due to geographic isolation. The characteristics of whistle structures could potentially be used to distinguish among populations. Frequencies of the major energy of dolphin whistles were higher than the major frequencies of background noise, and a specific acoustical niche relative to environment may be hypothesized.

Introduction

Dolphin acoustic researchers have long been interested in potential population differences of whistles within a species. Evans & Dreher (1962) noted that some identical or near identical whistle contours (frequency vs. time representation) were used by wild Pacific and captive Atlantic bottlenose dolphins (*Tursiops truncatus*). Taruski (1976, 1979) described regional differences, or 'dialects', in pilot whale (*Globicephala* spp.) whistle vocalizations. Graycar (1976) found no evidence for the existence of area-related whistle 'dialects' for bottlenose dolphins from the Atlantic coast of Florida and the Gulf of Mexico. However, there was evidence for sex, age, and sex-age class whistle differences between and within local regions. He considered that it was probably the isolation of ecologically well-adapted dolphin groups that resulted in whistle differences (Graycar, 1976). However, Graycar's data were in great part obtained from the dolphins kept in commercial aquaria, and only a 'representative' signature whistle from each dolphin was described by sonogram. All other data were obtained by using the 'audio-visual' method, which could only measure whistle duration and number of loops per whistle, with inaccuracy of duration as high as one tenth of one second (Graycar, 1976), too large for whistles shorter than 1 second.

Steiner (1980, 1981), compared whistles within each of five north Atlantic delphinid species by use of statistic discriminant analysis, and concluded that the analysis could not unambiguously discriminate individual whistles.

Cass (1987) attempted to determine if wild Pacific bottlenose dolphins could be separated into coastal and offshore populations by their whistle repertoires. Her discriminant analysis of 554 whistles revealed high variation within the coastal population and low variation between coastal and offshore dolphins. Cass concluded that relatively low classification scores, and a bimodal but overlapping canonical variable distribution, precluded the use of whistle variables to discriminate reliably between coastal and offshore populations. The populations may differ ecologically, but they are not clearly distinct in their whistles. Also, the discrimination among most groups within the coastal population and between the only two groups within the offshore population were weak. However, the inability to discriminate whistle differences in Cass's study may have been due to small sample sizes. Her recordings were made opportunistically in a small area, so that different recordings may not have represented samples from different regions or groups.

This paper investigates potential population differences of bottlenose dolphin whistles by using more recent spectral and statistic analysis techniques, and attempts to relate whistles to different habitat types and life habits among populations.

Materials and methods

Study areas

The major study areas are three non-adjacent regions along the Texas Coast of the Gulf of Mexico:

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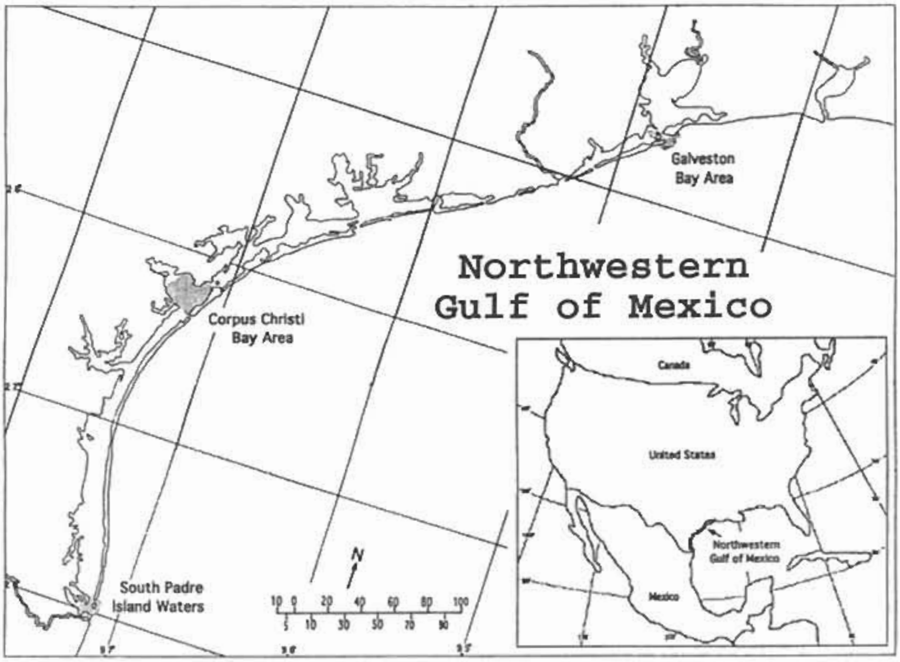

Figure 1. Map of the Northwestern Gulf of Mexico, Texas. Shaded areas represent regions in which the whistles of bottlenose dolphins, *Tursiops truncatus*, were recorded. Distance scale is in kilometers.

Galveston Bay, Corpus Christi Bay, and South Padre Island waters (Fig. 1). Each is known to have a resident group of bottlenose dolphins, with some individuals moving between them (Jones, 1991; Bernd Würsig, pers. observations). Other areas from which we analyzed recordings and which are more distant from each other, include Golfo San José, Argentina; the Gulf of California, Mexico; Taiji, Japan; and Shark Bay, West Australia.

Data collection

Vocalization recordings from the three primary Texas study areas were collected by the authors, using a C. Clark hydrophone and a Marantz PMD 430 Recorder, from 17-foot or 22-foot Boston Whalers. Environmental, behavioural, group size, and group structure information were recorded on data sheets, with voice comments on behaviours and other factors made onto the narrative channel of the tape recorder. Recordings were made while animals were in a variety of behavioural states such as feeding, milling, resting, socializing, travelling (see Shane, 1980, for definitions). Recordings from non-Texas areas were made with a variety of hydrophones and recorders. However, frequency response for all recordings was in the human hearing range, from about 100 Hz to about 15 Hz.

Analysis procedures

Signal spectral analysis: All recordings were analyzed with the IBM PC based 'Signal' analysis system (Engineering Design). The analysis frequency range was set between 0–20 kHz or 0–25 kHz. Sonograms were visually inspected using a Real Time Spectrogram (RTS) program while simultaneously listening to the original recording. All signals with suitable signal to noise ratios were selected for analysis. By use of the enhancing function of the 'Signal' system, signal frequencies as high as 25 kHz or higher could be read and measured, even though some of the original recording systems' flat response was below that frequency. The sonograms were produced with frequency resolution of 98 Hz when analysis bandwidth was 20 kHz, or 122 Hz when analysis bandwidth was 25 kHz. Parameters were measured directly on the computer screen using the cursor supplied by the 'Signal' program. For each whistle, ten variables were measured: 1) beginning frequency; 2) end frequency; 3) minimum frequency; 4) maximum frequency; 5) duration;. 6) number of inflection points (defined as a change in the slope of the sonogram contour from negative to positive or vice versa); 7) beginning sweep (up=1 or down=0); 8) end sweep (up=1 or down=0); 9) harmonics

Table 1. Descriptive statistics—smallest value, largest value, mean, standard deviation, and coefficient of variation for all variables of whistles of bottlenose dolphins in Galveston (G, n=811), Corpus Christi (CC, n=617), and South Padre Island (SPI, n=549). Frequency is in kHz, duration is in sec., C.V.=coefficient of variation.

Variable	Location	Smallest	Largest	Mean	Std. Dev.	C.V.
Beginning Frequency	G	2.50	20.66	7.95	2.88	36.06
	CC	2.89	6.75	7.43	2.44	32.81
	SPI	3.13	18.75	8.70	2.95	33.91
End Frequency	G	2.00	21.61	9.02	3.96	43.96
	CC	2.34	20.66	8.71	4.04	46.31
	SPI	2.59	14.92	6.40	2.44	38.11
Minimum Frequency	G	1.86	18.92	5.98	2.30	38.54
	CC	2.11	14.53	5.88	2.65	27.68
	SPI	2.58	9.45	5.37	1.12	20.78
Maximum Frequency	G	3.91	21.61	11.95	3.08	25.81
	CC	3.44	20.75	11.43	3.80	33.19
	SPI	4.53	19.14	10.33	2.80	27.08
Duration	G	0.05	3.20	0.75	0.46	61.87
	CC	0.05	2.63	0.69	0.41	60.50
	SPI	0.09	2.08	0.60	0.26	43.66
Number of Inflection	G	0	17	2.57	2.62	101.82
	CC	0	37	2.14	2.97	138.49
	SPI	0	15	1.37	1.65	119.84
Beginning Sweep	G	0	1	0.58	0.49	84.80
	CC	0	1	0.65	0.48	74.24
	SPI	0	1	0.45	0.50	110.76
End Sweep	G	0	1	0.58	0.49	84.80
	CC	0	1	0.53	0.50	94.25
	SPI	0	1	0.35	0.48	135.84
Harmonics	G	0	1	0.28	0.45	161.98
	CC	0	1	0.23	0.42	183.89
	SPI	0	1	0.22	0.42	187.24
Break of Contour	G	0	1	0.64	0.48	75.46
	CC	0	1	0.66	0.48	72.41
	SPI	0	1	0.59	0.49	84.15

(yes=1 or no=0); 10) break of contour (yes=1 or no=0).

Statistical analysis: PC-SAS (an IBM-PC computer software system for data analysis) and STATVIEW (a Macintosh computer program for data analysis) were used for statistical analysis (SAS Institute, Inc., 1985; BrainPower, Inc., 1986). To facilitate the comparison of this study with past results, statistical analysis methods were basically the same as the ones used by Cass (1987), Graycar (1976), and Steiner (1980), with some modifications. The Mahalanobis D^2 statistic, F statistic, Canonical variable, and percent correct classification scores were used to compare overall whistle structures among populations (for details of statistic analysis, see Steiner, 1980 & Wang, 1993). The ANOVA procedure of the STATVIEW program was used to calculate differences between each pair of variables among populations. The descriptive statistics for populations, including the smallest values, largest values, means, standard deviations, and coefficients of variation for all measured variables, were also calculated with STATVIEW (BrainPower Inc., 1986).

Results

Comparisons among three regions of the Texas gulf coast

1. Descriptive statistics

A total of 811 whistle samples were obtained from Galveston, 617 from Corpus Christi, and 549 from South Padre Island.

A consistent pattern exists in the coefficients of variation calculated for different regions (Table 1). In all cases, the frequency variables have the lowest coefficients of variation, and duration and number of inflection points have much higher coefficients of variation (the final four variables are arbitrary

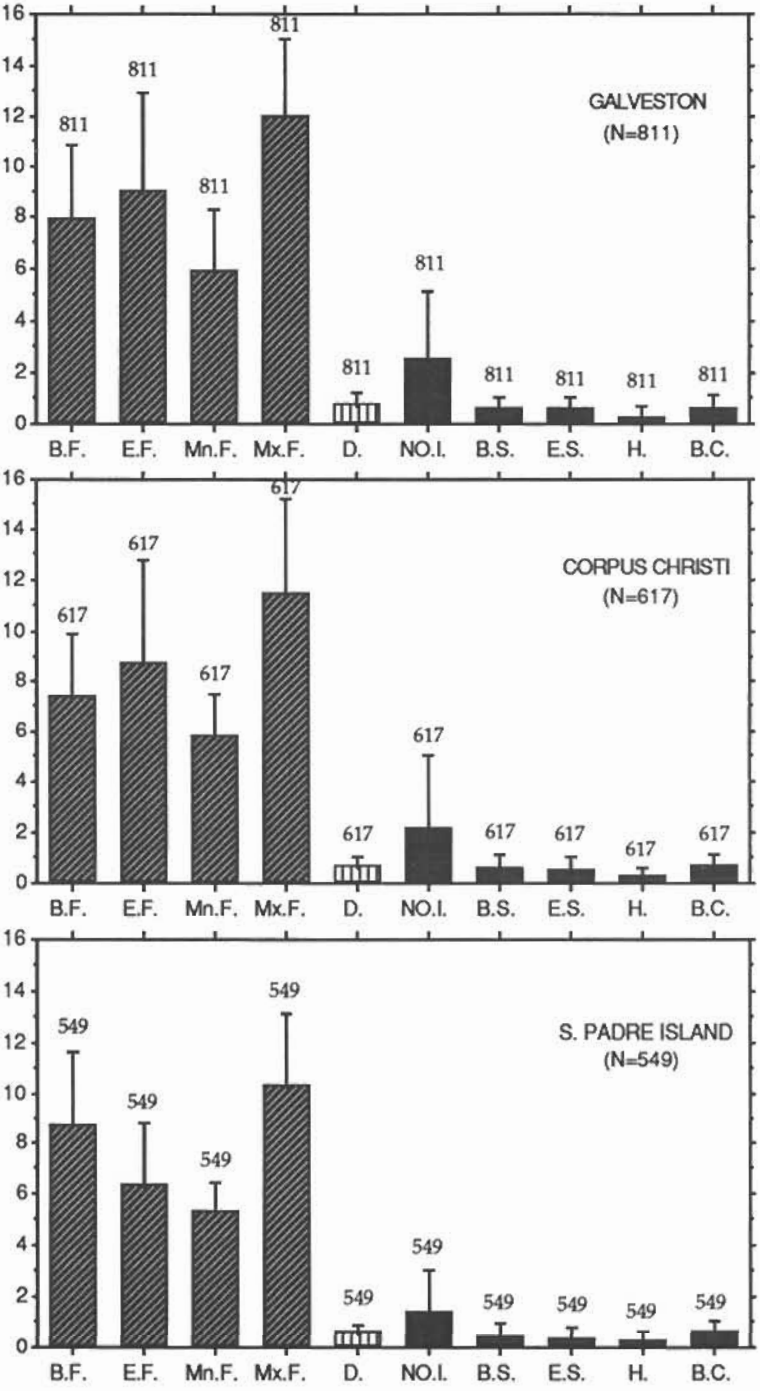

Figure 2. Mean values of all measured variables of whistles from three regions along the Texas coast. Standard deviation is shown by vertical line. B.F. = Beginning Frequency, E.F. = End Frequency, Mn.F. = Minimum Frequency, Mx.F. = Maximum Frequency, D. = Duration, NO.I. = Number of Inflection Points, B.S. = Beginning Sweep, E.S. = End Sweep, H. = Harmonics, B.C. = Break of Contour. Frequency is in kHz, duration is in sec.

Table 2. Results of discriminant analyses of pairwise and three way comparisons among three regions along the Texas coast.

Comparisons	n	D^2	F-Values[a]	% Corr. Class.[b]
Galveston vs. Corpus Christi	811/617	0.1	3.52	54.06
Galveston vs. S. Padre Island	811/594	1.34	45.76	72.10
Corpus Christi vs S. Padre Island	617/594	1.06	31.74	69.12
Three Way Comparison	811/617/594		23.51	46.88[c]

[a] All F-values are significant at $P<0.0001$

[b] Random chance level = 50%

[c] Random chance level = 33.33%

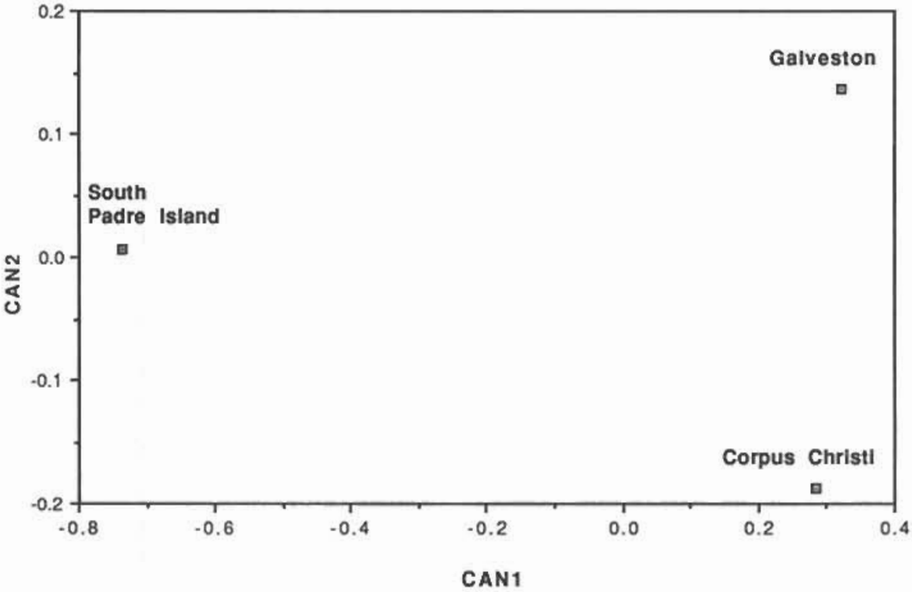

Figure 3. The 1st two canonical variates as computed for three regions along the Texas coast.

binary numbers representing the data; their means, standard deviations, and coefficients of variation are not comparable). Therefore, the frequency variables have relatively low intra-group variability, and duration and number of inflection points have relatively high intra-group variability. The whistles of South Padre Island animals have a relatively higher beginning frequency and lower end frequency, which is opposite to the patterns observed for whistles from Corpus Christi and Galveston Bay (Fig. 2).

2. Pairwise and three way comparisons among three regions

The results of discriminant analysis of pairwise and three way comparisons among three regions are shown in Table 2. All F-values for all pairwise comparisons are significant at the $P<0.0001$ level, indicating that the multivariate mean vectors of the whistles are statistically different among regions. However, the Mahalanobis D^2 values are small, and the percent correct classification scores (55–72) are low. For the three way comparison, the F-value is also significant at the $P<0.0001$ level, but the percent correct classification score is also low (48). These results indicate that even though there are significant differences among whistles from the different regions along the Texas coast, these differences are small enough that individual whistles are poorly discriminated.

On the other hand, the two sample size-independent statistic values, the D^2 values and

Table 3. The results of one factor ANOVA analysis (Scheffé F-test) between each pair of variables between each two regions.

Comparisons	B.F.	E.F.	Mn.F.	Mx.F.	D.	NO.I.	B.S.	E.S.	H.	B.C.
Corpus Christi vs.	12.93*	1.82	0.75	7.96*	8.81*	8.28*	5.87*	3.85*	4.19*	0.55
Galveston	(−0.51)	(0.29)	(−0.09)	(−0.51)	(−0.07)	(−0.43)	(0.06)	(−0.05)	(−0.05)	(0.02)
Corpus Christi vs.	66.54*	144.75*	41.35*	33.22*	17.80*	30.86*	48.55*	40.15*	0.07	6.42*
S. Padre Island	(−1.27)	(2.32)	(0.52)	(1.11)	(0.08)	(0.77)	(0.20)	(0.18)	(0.01)	(0.07)
S. Padre Island vs.	22.90*	200.18*	35.78*	102.48*	53.10*	96.32*	24.53*	76.57*	5.29*	3.87*
Galveston	(0.75)	(−2.60)	(−0.61)	(−1.62)	(−0.15)	(−1.20)	(−0.13)	(−0.23)	(−0.05)	(−0.05)

*Scheffé F-Test values are significant at 95%
Mean difference of the variables between the two regions are in ( )
BF. = Beginning Frequency; E.F. = End Frequency; Mn.F. = Minimum Frequency; Mx.F. = Maximum Frequency; D. = Duration; NO.I. = Number of Inflection Points; B.S. = Beginning Sweep; E.S. = End Sweep; H. = Harmonics; B.C. = Break of Contour.

percent correct classification scores, are higher for the comparison between Galveston and South Padre Island than the ones between Galveston and Corpus Christi, and the ones between Corpus Christi and South Padre Island. Fig 3 (which is a spatial plot of the first two canonical variables as determined by the discriminant analysis) indicates that South Padre Island is relatively separated from the other two regions, and the distance between South Padre Island and Galveston is greater than the one between Galveston and Corpus Christi, and the one between Corpus Christi and South Padre Island.

The pairwise variables between Galveston and South Padre Island are all significantly different (Table 3). Meanwhile, most of the mean differences of the variables for the comparison between Galveston and South Padre Island are greater than the ones for the comparison between Galveston and Corpus Christi, and the ones between Corpus Christi and South Padre Island.

Comparisons among five widely-spaced areas

1. Descriptive statistics

A total of 110 whistle samples were obtained from Argentina, 110 from the Gulf of California, 215 from Japan, 658 from Australia, and 2022 from Texas (all whistle samples from the three previously-analysed inlet regions along the Texas gulf coast). The descriptive statistics of these whistle samples from the five areas are given in Table 4.

A consistent pattern exists in the coefficients of variation calculated for different areas (Table 4). Overall, the frequency variables have the lowest coefficients of variation, and duration and number of inflection points have much higher coefficients of variation. Therefore, the frequency variables have relatively low intra-population variability, and duration and number of inflection points have relatively high intra-population variability. Meanwhile, the mean beginning frequency of Australia animals is lower than their mean end frequency, which is opposite to the patterns of the other population whistles. Overall, Australia animals also have a relatively lower range for all four frequency variables.

2. Pairwise and five way comparisons among five areas

The results of discriminant analyses of pairwise and five way comparisons among five areas are shown in Table 5. F-values for pairwise comparison are significant at the $P<0.0001$ level. Even though there are some differences among the D^2 values and percent correct classification scores between different comparisons, all the D^2 values are relatively large, and all the percent correct classification scores (77–97) are relatively higher than at random chance level (50). For a five way comparison, the F-value is also significant ($P<0.0001$) and the percent correct classification score (63) is higher than at random chance level (20). Almost all pairwise variables among different areas are significantly different (Table 6). Thus, there are statistical differences in whistle structures among different areas, and for some of them the differences are great enough that individual whistles can be discriminated very easily, with correct classification almost bordering on 100 percent.

Meanwhile, the Mahalanobis D^2 values are greater than the ones obtained by the comparisons among the three regions along the Texas coast, and all the percent correct classification scores are also higher. Therefore, whistle structure differences among these five non-adjacent areas are much greater than the ones among the three regions along the Texas coast.

Table 4. Descriptive statistics—smallest value, largest value, mean, standard deviation, and coefficient of variation for all variables of whistles of bottlenose dolphin in Argentina (Ar, n=110), Gulf of California (GC, n=110), Japan (J, n=215), Australia (Au, n=658), and Texas (T, n=2022). Frequency is in kHz, duration is in sec., C.V.=coefficient of variation.

Variable	Location	Smallest	Largest	Mean	Std. Dev.	C.V.
Beginning Frequency	Ar	1.17	16.09	9.24	2.74	29.65
	GC	5.78	17.27	12.10	2.89	23.91
	J	3.75	15.23	10.33	2.41	23.31
	Au	1.09	13.98	3.84	1.42	36.92
	T	2.50	20.66	8.01	2.81	35.09
End Frequency	Ar	3.05	15.94	6.63	2.29	34.60
	GC	3.44	17.42	9.19	3.44	37.45
	J	3.67	15.55	8.87	2.21	24.90
	Au	0.94	21.02	7.56	3.80	50.25
	T	2.00	21.61	8.16	3.78	46.38
Minimum Frequency	Ar	1.17	10.08	5.91	1.5	25.71
	GC	3.17	1.56	6.91	2.11	30.48
	J	3.20	10.70	7.37	1.54	20.89
	Au	0.94	8.28	3.57	0.97	27.19
	T	1.86	18.92	5.77	1.84	31.82
Maximum Frequency	Ar	9.38	17.11	13.65	1.54	11.28
	GC	7.34	17.42	13.68	1.72	12.55
	J	4.53	15.55	11.62	2.00	17.18
	Au	3.98	21.02	10.57	3.02	28.55
	T	3.44	1.61	11.32	3.31	29.24
Duration	Ar	0.18	0.27	1.14	0.49	42.74
	GC	0.19	1.59	0.66	0.35	53.10
	J	0.06	1.76	0.62	0.34	55.23
	Au	0.10	2.41	0.68	0.35	50.90
	T	0.05	3.20	0.68	0.40	58.85
Number of Inflection	Ar	0	8	1.58	1.24	78.66
	GC	0	8	1.15	1.32	115.16
	J	0	5	0.88	0.79	88.90
	Au	0	9	1.63	1.53	94.37
	T	0	37	2.09	2.54	121.80
Beginning Sweep	Ar	0	1	0.54	0.50	93.40
	GC	0	1	0.22	0.42	190.16
	J	0	1	0.34	0.48	139.80
	Au	0	1	0.92	0.27	28.70
	T	0	1	0.56	0.50	88.25
End Sweep	Ar	0	1	0.16	0.36	234.96
	GC	0	1	0.38	0.49	127.82
	J	0	1	0.56	0.50	88.35
	Au	0	1	0.47	0.50	106.68
	T	0	1	0.50	0.50	100.32
Harmonics	Ar	0	1	0.16	0.37	227.11
	GC	0	1	0.13	0.34	263.06
	J	0	1	0.04	0.19	509.86
	Au	0	1	0.76	0.43	56.72
	T	0	1	0.25	0.43	175.21
Break of Contour	Ar	0	1	0.92	0.28	29.99
	GC	0	1	0.95	0.23	24.13
	J	0	1	0.47	0.50	106.49
	Au	0	1	0.88	0.35	37.76
	T	0	1	0.63	0.48	76.97

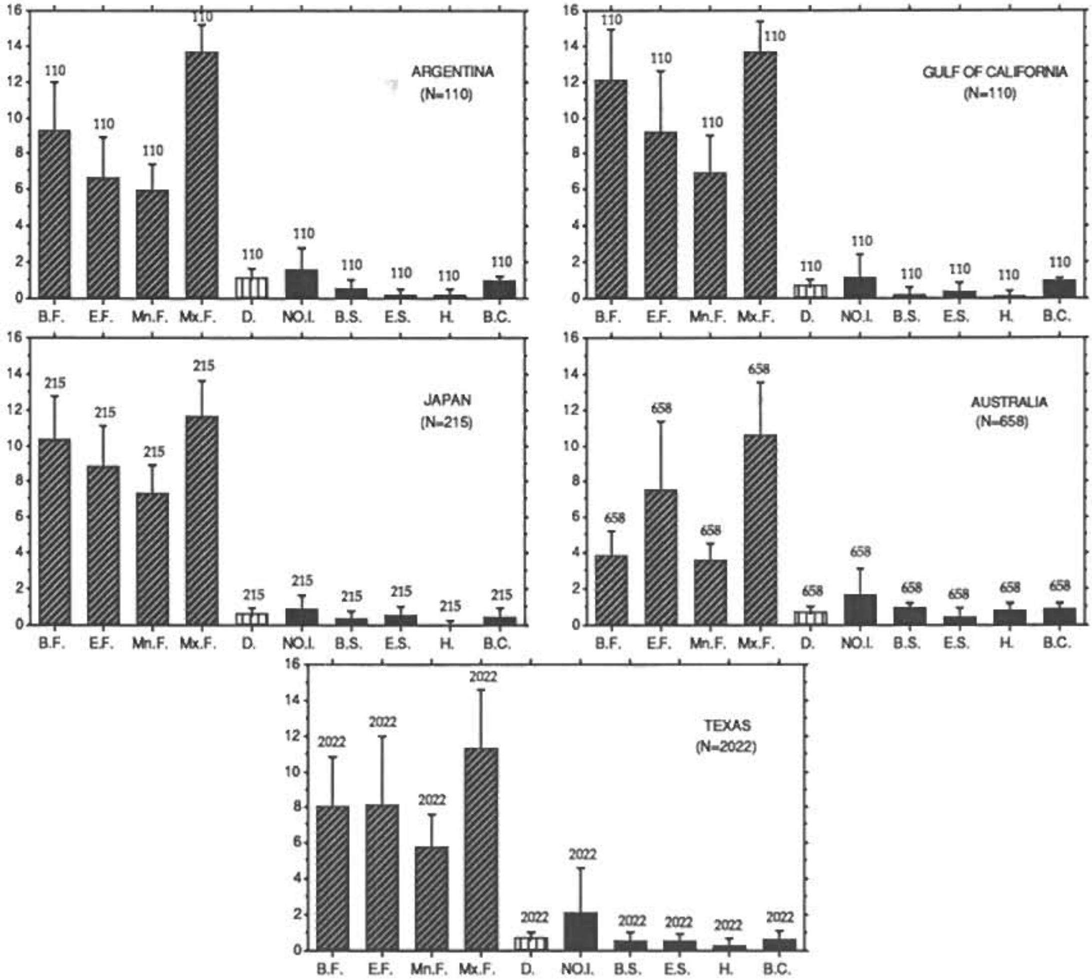

Figure 4. Mean values of all measured variables of whistles from five areas. Standard deviation is shown by vertical line. B.F. = Beginning Frequency, E.F. = End Frequency, Mn.F. = Minimum Frequency, Mx.F. = Maximum Frequency, D. = Duration, NO.I. = Number of Inflection Points, B.S. = Beginning Sweep, E.S. = End Sweep, H. = Harmonics, B.C. = Break of Contour. Frequency is in kHz, duration is in sec.

The spatial plot of the first two canonical variables as determined by discriminant analysis from the five way comparison among all five areas is shown in Fig. 5. Australia is relatively separated from the other areas. This is consistent with the results we obtained by comparing the D^2 values and percent correct classification scores among different comparisons given in Table 5. In fact, almost all the comparisons involving Australia have the highest correct classification scores (three out of four). Meanwhile, four comparisons involving Australia have relatively greater Scheffé F-values, irrespective of sample size (Table 6). The differences of the mean values of the variables, especially frequency variables, among Australia and the other four areas, are relatively larger than the differences among other areas. These results suggest that the whistles of Australia are relatively more different than the ones among the other areas.

Discussion

Intra-population variability of the variables

The present analysis shows that frequency variables have relatively low intra-population variability, and duration and number of inflection points have relatively high intra-population variability. Norris *et al.* (1985) hypothesized that whistles are 'parts of analogic series in which varying emotional levels

Table 5. Results of discriminant analyses of pairwise and five way comparisons among five areas.

Comparisons	n	D^2	F-Values[a]	% Corr. Class.[b]
Argentina vs. G. California	110/110	2.17	11.44	76.82
Argentina vs. Japan	110/251	5.57	39.41	87.69
Argentina vs. Australia	110/658	18.81	175.21	97.14
Argentina vs. Texas	110/2022	4.74	49.24	86.96
G. California vs. Japan	110/215	3.68	26.04	83.69
G. California vs. Australia	110/658	26.20	244.01	96.61
G. California vs. Texas	110/2022	3.01	31.31	81.94
Japan vs. Australia	215/658	18.88	302.86	97.02
Japan vs. Texas	215/2022	1.61	31.13	77.38
Australia vs. Texas	658/2022	4.29	212.41	85.11
Five Way Comparison			81.24	58.23[c]

[a] All F-values are significant at $\alpha = 0.0001$ level
[b] Random chance level = 50%
[c] Random chance level = 20%

relate to changes in the sounds. (They are) individual identifiers that may be modulated to carry additional analogic information about emotional state, level of alertness, the presence of food or danger, and similar information'. Steiner (1981) also suggested that duration and number of inflection points 'may have been important for individual differentiation'. It is likely that the relatively high intra-population variability of duration and number of inflection points of the whistles reflects the results of the animal's modulating these parts of the whistle structures for carrying additional analogic information, and may also be a reflection of their relatively high inter-individual variabilities which could be used for individual differentiation between dolphins. Frequency variables stay relatively stable, which may in part be due to evolutionary adaptation to the environment, and may also be related to a limitation of sound production capability of body size (see Wang, 1993).

Population characteristics of whistles

Before one can determine differences in whistle structures among populations, one must first determine variability in whistle structures within populations. The results of this study suggest that while there may be differences between whistles from different or the same individuals within the same population, there are still some characteristics which are unique for each population. For example, for the comparisons among five different populations from five non-adjacent areas (Argentina, the Gulf of California, Japan, Australia, and Texas), overall, the whistles from Argentina and the Gulf of California have relatively higher maximum frequency, but the durations of the whistles from Argentina are relatively longer than the ones from the Gulf of California; the whistles from Japan have relatively smaller numbers of inflection points and shorter durations; the whistles from Texas have about the same length of duration but relatively larger numbers of inflection points; and the whistles from Australia have much lower beginning frequency and minimum frequency, although the duration is about in the same range with the whistles from Gulf of California, Japan, and Texas (see Table 4). Meanwhile, the differences of the whistles among these five non-adjacent areas are much greater than the differences among the more adjacent areas along the Texas gulf coast (Galveston Bay, Corpus Christi Bay, and South Padre Island waters). Each population of dolphins in each non-adjacent area may have been isolated geographically from the others, and developed their own

Table 6. The results of one factor ANOVA analysis (Scheffé F-test) between each pair of variables between each two areas.

Comparisons	B.F.	E.F.	Mn.F.	Mx.F.	D.	NO.I.	B.S.	E.S.	H.	B.C.
Argentina vs.	56.59*	42.00*	16.32*	0.02	69.94*	6.37*	26.32*	15.35*	0.58	0.64
G. California	(−2.86)	(−2.56)	(−1.00)	(−0.03)	(0.48)	(0.44)	(0.32)	(−0.23)	(0.04)	(−0.3)
Argentina vs.	13.68*	72.53*	65.97*	87.01*	127.99*	38.07*	12.05*	58.23*	16.51*	76.45*
Japan	(−1.10)	(−2.23)	(−1.46)	(2.03)	(0.53)	(0.70)	(0.20)	(−41)	(0.13)	(0.45)
Argentina vs.	980.71*	6.17*	454.38*	109.29*	146.60*	0.08	147.49*	39.83*	186.59*	1.65
Australia	(5.39)	(−0.93)	(2.34)	(3.07)	(0.46)	(−0.04)	(−0.39)	(−0.31)	(−0.59)	(−0.04)
Argentina vs.	19.84*	17.50*	0.61	53.89*	134.75*	4.31*	0.29	50.57*	3.85*	38.91*
Texas	(1.23)	(−1.52)	(0.14)	(2.33)	(0.46)	(−0.51)	(−0.03)	(−0.34)	(−0.08)	(0.29)
G. California vs.	34.01*	1.04	5.00*	85.04*	1.03	5.00*	5.17*	9.76*	9.57*	89.80*
Japan	(1.77)	(0.32)	(−0.46)	(2.06)	(0.05)	(0.26)	(−0.12)	(−0.18)	(0.09)	(0.48)
G. California vs.	2200.06*	17.78*	731.08*	110.54*	0.26	9.56*	553.62*	2.83	214.63*	4.58*
Australia	(8.25)	(1.63)	(3.34)	(3.11)	(−0.02)	(−0.48)	(−0.71)	(−0.09)	(−0.63)	(0.07)
G. California vs.	219.49*	7.82*	39.55*	55.27*	0.23	14.91*	50.96*	5.69*	8.07*	46.82*
Texas	(4.08)	(1.03)	(1.14)	(2.36)	(−0.02)	(−0.94)	(−0.34)	(−0.12)	(−0.12)	(0.32)
Japan vs.	2316.68*	22.91*	1810.14*	22.62*	5.64*	46.22*	510.70*	5.84*	567.52*	185.28*
Australia	(6.49)	(1.31)	(3.80)	(1.05)	(−0.06)	(−0.74)	(−0.58)	(0.10)	(−0.71)	(−0.41)
Japan vs.	135.71*	7.30*	151.68*	1.73	5.20*	47.74*	39.49*	3.21	49.40*	20.70*
Texas	(2.32)	(0.71)	(1.60)	(0.30)	(−0.07)	(−1.21)	(−0.22)	(0.06)	(−0.21)	(−0.16)
Australia vs.	1335.72*	12.35*	866.69*	26.19*	0.00	19.60*	319.81*	1.84	700.12*	149.42*
Texas	(−4.17)	(−0.60)	(−2.20)	(−0.74)	(0.00)	(−0.46)	(0.36)	(−0.03)	(0.51)	(0.25)

*Scheffé F-test values are significant at 95%

Mean difference of the variables between the two areas are in ( )

B.F. = Beginning Frequency; E.F. = End Frequency; Mn.F. = Minimum Frequency; Mx.F. = Maximum Frequency; D. = Duration; NO.I. = Number of Inflection Points; B.S. = Beginning Sweep; E.S. = End Sweep; H. = Harmonics; B.C. = Break of contour.

acoustic characteristics. Nottebohm (1969) noted for birds that 'it was not surprising that populations of the same species, separated by large distances, would exhibit differences in at least some characteristics due to genetic isolation. Each population would be affected by different evolutionary and environmental influences' (see also Conner, 1982). This characteristic of different whistle structures could potentially be used to distinguish among different populations. As a matter of fact, some of the percent correct classification scores for comparisons among non-adjacent areas in this study are almost 100.

Whistle differences and animal movements

Although each region along the Texas gulf coast has a somewhat resident population of bottlenose dolphins, there is some degree of movement between these adjacent areas (Jones, 1991; Bernd Würsig, pers. observations). These movements make it possible that one group of dolphins is exposed to the whistles from other groups. Several studies have suggested that learning may play an important role in the development of dolphin whistles (Caldwell & Caldwell, 1979; Sayigh, 1992; Sayigh *et al.*, 1990, 1991) and dolphins have a good capability of mimicry (Richards *et al.*, 1984; Tyack, 1986). The data here indicate that even though there are significant differences between the whistles from different populations of dolphins from different regions along the Texas gulf coast, the differences are not great and individual whistles are poorly discriminated. In other words, there is some degree of similarity among different regions. We suggest that the movements of animals between different regions may be one of the reasons for the similarities among the whistles of different regions.

The differences between Corpus Christi and Galveston, and Corpus Christi and South Padre Island are smaller than the differences between South Padre Island and Galveston. This may be because the distance between South Padre Island and Galveston is much greater than the one between Corpus Christi–South Padre Island, and the one between Corpus Christi–Galveston (see Fig. 1). There is likely to be less movement between South Padre Island and Galveston than the closer more adjacent areas, and therefore less possibility for vocal exchange between the disparate areas. The similarity of whistle structures among these adjacent areas may also be due to periodic change of individuals across areas.

Whistle differences and ambient noise backgrounds

Several studies have examined the effects of non-biological noise, specifically the noise generated by

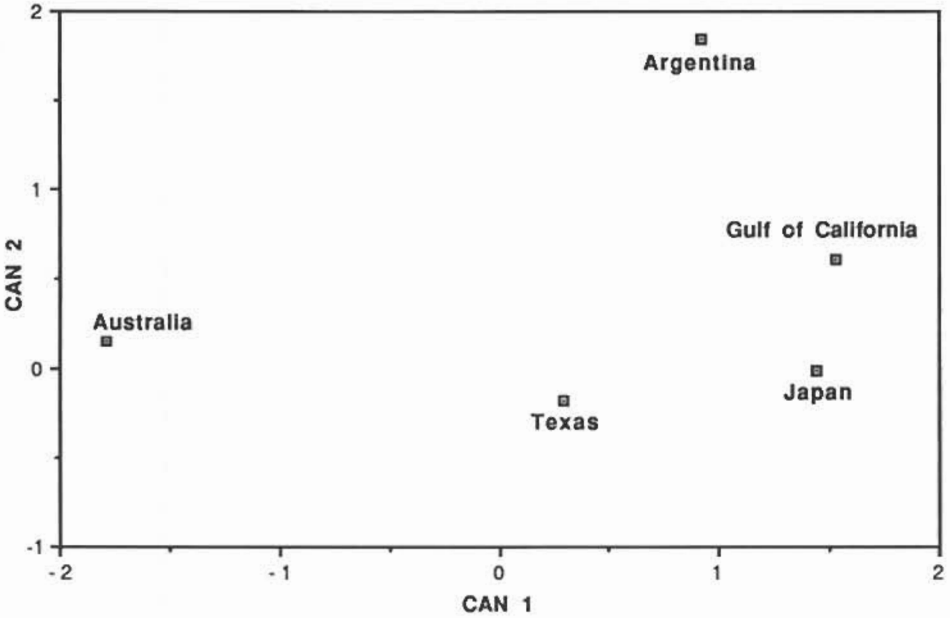

Figure 5. The 1st two canonical variates as computed for five areas.

offshore petroleum exploration, on the behaviour of marine mammals (for reviews, see Geraci & St Aubin, 1980; Myrberg, 1978, 1990; and Richardson *et al.*, 1983, 1991). Most of these studies examined the short-term behavioral reactions of the animals to noise, including their habituation or sensitization to the noise (e.g., Richardson *et al.*, 1985, 1986, 1987, 1990). Evans (1982) preliminarily evaluated the perception of detection of man-made noise (from icebreaker operation) by selected marine animals. While there was some masking of marine mammal signals it was not clear whether the resulting reduced sensitivity in any way provided a significant biological detriment to the animals. Dahlheim *et al.* (1984) measured levels of ambient noise and recorded underwater sounds produced by the California gray whale (*Eschrichtius robustus*) and bottlenose dolphins in a Baja California lagoon system. Their data showed that sounds produced by gray whales and bottlenose dolphins usually occurred at frequencies below and above, respectively, the main concentration of energy of the biological noise. They proposed that the cetaceans may have different acoustical niches possibly dictated by the constant high levels of ambient biological noise in the lagoon. Limited research has also suggested that bottlenose dolphins can shift the peak frequency of their echolocation sounds (clicks) to shun the interference of the background noises (Au, 1990; William Evans, pers. observations). Based upon the analysis of our recordings, we found that in Galveston, Corpus Christi, and South Padre Island, most energy of the background noises (including biological and non-biological) is below approximately 7 kHz, and almost all mean frequencies of the whistles of bottlenose dolphins in these three regions (except mean minimum frequency) are above 7 kHz. Furthermore, Galveston Bay is much noisier with much stronger industry noise background compared to Corpus Christi Bay, and South Padre Island waters are even more quiet with very little industry background noise. In general, the frequencies of the whistles of Galveston are significantly higher than the ones of Corpus Christi, and the ones of Corpus Christi are significantly higher than the ones of South Padre Island. It thus appears that there is a relationship of higher-frequency whistling with higher levels of human industrial noise. However, it is not certain that the correlation is a causative one, and we have not proved that dolphins shift their whistle frequencies relative to background noise. This possibility awaits investigation of background noise levels, their frequencies, and a more detailed analysis of dolphin whistles relative to noise.

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