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Geographic variations in the whistles among three Indo-Pacific bottlenose dolphin *Tursiops aduncus* populations in Japan

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ABSTRACT: Whistles of Indo-Pacific bottlenose dolphins from three populations in Japan were collected and analyzed quantitatively. Geographic variations in the whistles among populations were found. Significant differences in the whistles among years within each population were also found, but those differences could not explain whole differences among populations because some parameters of the whistles had more differences among populations than among years within each population. As changes with time in the whistles within each population might cause the geographic variations among populations, researchers should take the yearly change within populations into consideration when they study the geographic variation in the whistle of dolphins.

KEY WORDS: **geographic variations, Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, vocal communication, whistle.**

INTRODUCTION

Indo-Pacific bottlenose dolphins *Tursiops aduncus* are small toothed whales which reside year-round in coastal waters. Since their habitats usually overlap areas of human activity such as fisheries, problems often occur between the dolphins and human, including the conflict with fishermen over prey fish. In contrast, the popularity of contact with dolphins has recently increased and other problems occur between the dolphins and humans such as the impact of dolphin-watching boats. We need a site-specific or population-based management program for each site or population, to reduce these problems effectively. It is, therefore, primarily important to identify populations (stocks) or to know the relationships between and among populations. Here, we conducted acoustic monitoring of the populations because the technique is much easier than genetic monitoring.

Bottlenose dolphins had been regarded as one species with two types, *aduncus* and *truncatus,* in the Indo-Pacific regions before some recent morphological and molecular studies revealed that these types are separate species, *T. aduncus* (Indo-Pacific bottlenose dolphin) and *T. truncatus* (bottlenose dolphin).[1–3]

Indo-Pacific bottlenose dolphins communicate with each other in various ways, especially using sounds. They produce two categories of sound; pulsed calls and whistles.[4] A whistle is a narrow-band and frequency-modulated sound and thought to function as a group cohesion call.[5]

Wang *et al.* reported whistle differences among populations of bottlenose dolphins.[6] There was a possibility, however, that the whistle differences could have been caused by species differences not by populational differences within a species because the subject species of their paper might have included both species, *T. aduncus* and *T. truncatus*. Recently, a few studies revealed the geographic variations in the whistles of single odontocete species such as bottlenose dolphins *T. truncatus*,[7,8] spinner dolphins *Stenella longirostris*,[7–9] and other species[10] but not Indo-Pacific bottlenose dolphins. One of our objectives is to verify the geographic variations in the whistles of Indo-Pacific bottlenose dolphins.

Geographic variations in animal sounds, which are usually divided between microgeographic and macrogeographic variations,[11] can result from

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various factors such as ecologic, genetic, social and historical factors.[12] It can be expected to find a change with time in the dolphin whistles within each population whether any factors cause geographic variations or not. There is also a possibility that the whistle differences can be caused by changes within each population, not by the geographic differences among the populations. Another objective of the present paper is to compare the whistle differences among years within each population and those among populations and to verify the geographic variations in the whistles of Indo-Pacific bottlenose dolphins.

MATERIALS AND METHODS

Subject animals and study areas

We collected sound data from three populations of Indo-Pacific bottlenose dolphins residing around the coastal area off Ogasawara Islands (OGA), Tokyo (142°11′E, 26°05′N), Mikura Island (MIK), Tokyo (139°36′E, 33°52′N) and Amakusa-Shimoshima Islands (AMA), Western Kyushu (130°07′E, 32°33′N) in Japan (Fig. 1). These dolphins were recognized as Indo-Pacific bottlenose dolphins by genetic analyses and appearances.[13–15]

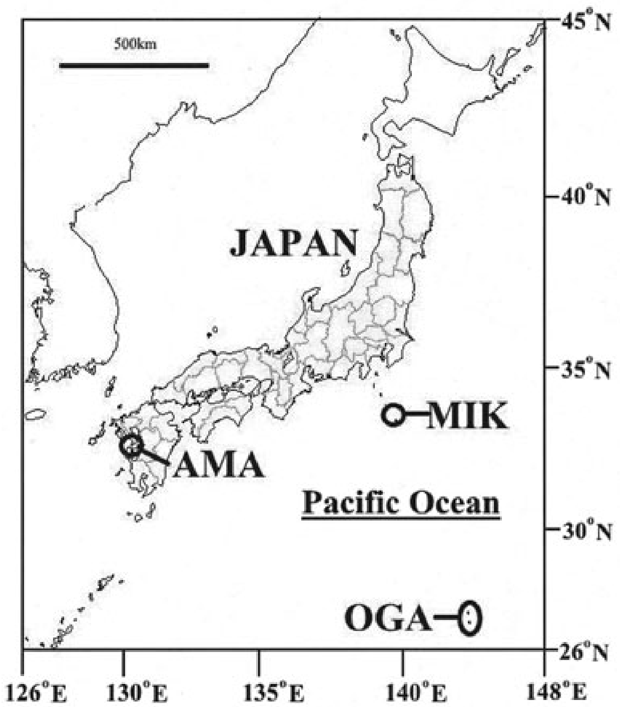

Fig. 1 Map of the Ogasawara Islands (OGA), Mikura Island (MIK) and Amakusa-Shimoshima Islands (AMA) in Japan.

Several video and photo identification studies have revealed that a resident group of Indo-Pacific bottlenose dolphins lives throughout the year around each area. Approximately 200–300 dolphins may reside around the Chichi-jima and Haha-jima Islands of OGA,[16] 138 dolphins around MIK,[17] and 218 dolphins around AMA.[18]

Sound recordings and analysis

Whistle recordings were conducted at the various locations by various recording equipment. Sounds were recorded in June 1998 and August 1999 in OGA; from June through to July 1996, in June 1997, and from September through October 2000 in MIK; and September 1998, March 2001 and September 2002 in AMA. All recording systems were responsible up to about 20 kHz.

For the spectrum analysis, Avisoft-SASLab Pro Version 4.0 software (Raimund Specht, Berlin, Germany) was used. We set frequency resolution at 93 Hz and time resolution at 5.3 ms with Hamming Window. The 1 kHz high-pass filter was applied in advance.

We selected whistles with a good signal to noise ratio. Moreover, we discarded whistles which were successively recorded and had the same contour in order to minimize the possibility of collecting many whistles from the same individuals.

We extracted 10 parameters from each whistle following Wang *et al.*:[6] (i) Beginning Frequency; (ii) End Frequency; (iii) Minimum Frequency; (iv) Maximum Frequency; (v) Duration; (vi) Number of Inflection Points (defined as a change from positive to negative or negative to positive slope); (vii) Beginning Sweep (upsweep = 1, downsweep = 0); (viii) End Sweep (upsweep = 1, downsweep = 0); (ix) Harmonics (yes = 1, no = 0); and (x) Break of Contour (yes = 1, no = 0; Fig. 2).

Statistical analysis

We found inequality of variances of all whistle parameters except Beginning Frequency ($F = 2.05$, d.f. = 2, $P = 0.13$) among three populations by Bartlett's test for homogeneity of variances. We then transformed all whistle parameters to near-normality by a Box-Cox transformation with most fitted λ value. One-way ANOVA was used for comparisons of all whistle parameters after transformation among three populations. We then compared these parameters between all pairs of three populations using Tukey–Kramer honestly significant difference test by JMP software ver. 5.01 (SAS Institute Inc., Cary, NC, USA).

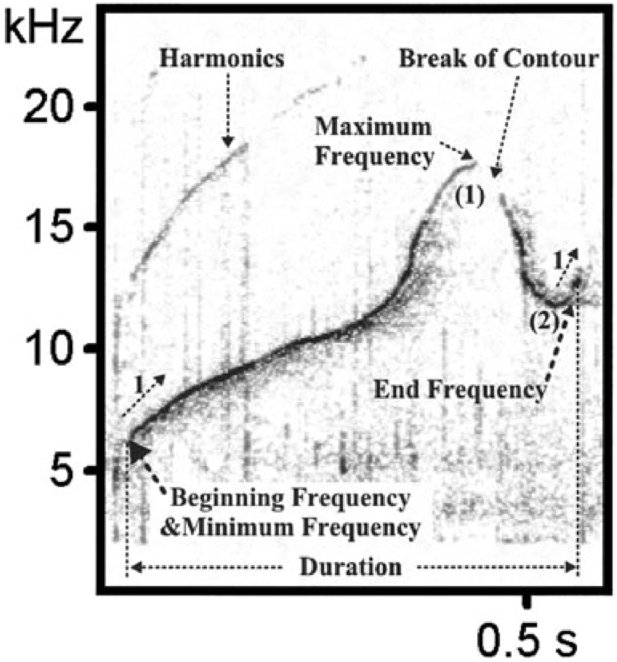

Fig. 2 The example of the whistle contour from Mikura Island populations and 10 parameters of each whistle. In this case, both Beginning Sweep and End Sweep are given the value 1 because the slopes of both sweeps are positive. (1) and (2) in the figure indicate the inflection points, and Number of Inflection points is, therefore, given the value 2. Harmonics is given the value 1 in this case because harmonics is present in the spectrogram.

Multivariate discriminant function analysis was used for raw data of all whistle parameters to classify whistles among and between populations and years by JMP software (SAS Institute). To evaluate correct classification scores, we compared the number of whistles which classified to the correct population with random chance level which was expected (50% for two groups, 33% for three, and 12.5% for eight) using normal approximation to the binomial test manually. Bonferroni adjustments to the significance level were made in the multiple comparisons to maintain the experimental-wise error rate.

Nested ANOVA was used to estimate the magnitude of variance components attributable to variation between populations, between years within populations, and between whistles within years for each parameter using transformed data.[19]

RESULTS

A total of 1613 whistles from three populations were analyzed. Summarized data (means, standard deviations, coefficients of variation [CV], and sample sizes) are shown in Table 1 and in Fig. 3. The frequency parameters (Beginning Frequency, End Frequency, Minimum Frequency and Maximum Frequency) generally showed the least coef-

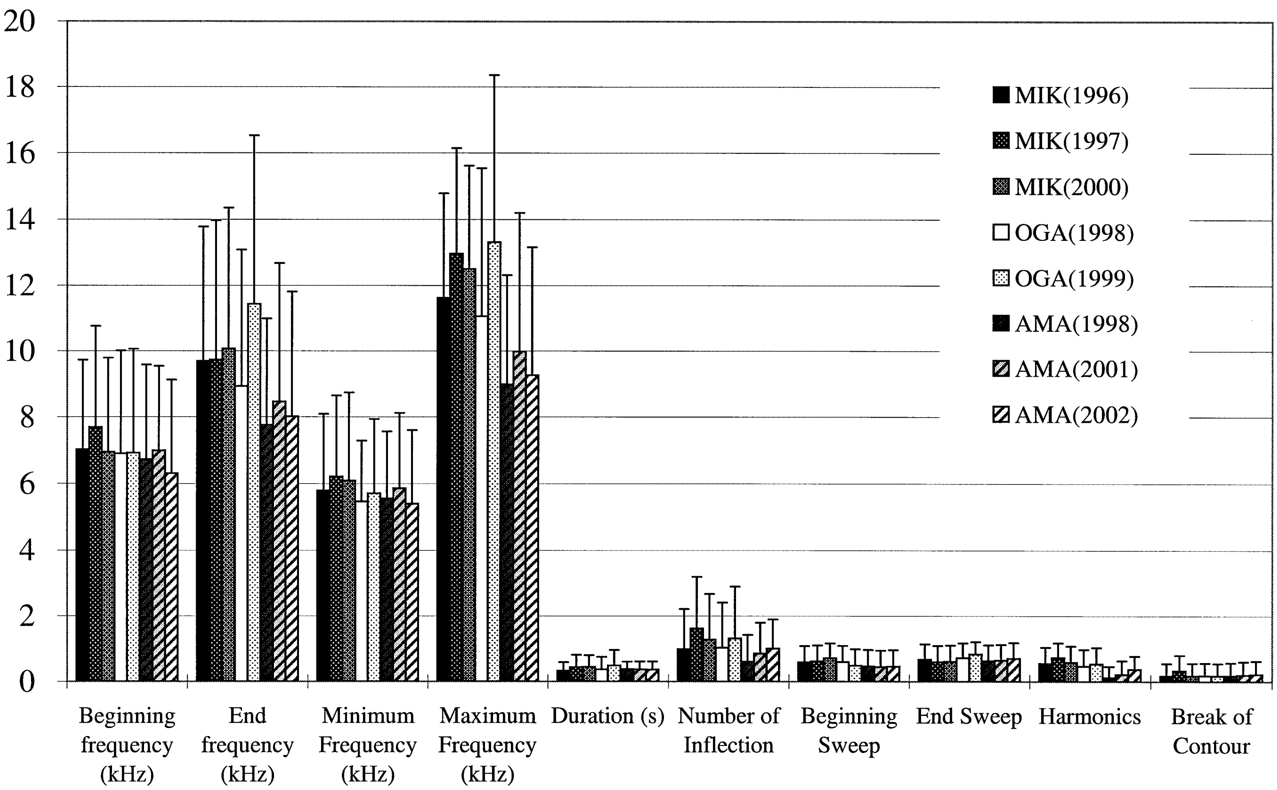

Fig. 3 Means for measured whistle parameters of all years and populations. Bar indicates standard deviation.

Table 1 Means, standard deviations (SD), coefficients of variation (CV) and sample sizes for measured whistle parameters

Location	Year		Beginning frequency (kHz)	End frequency (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Duration (s)	No. inflection points	Beginning sweep	End sweep	Harmonics	Break of contour	No. whistles analyzed
MIK													
	1996	Mean	7.03	9.70	5.79	11.63	0.32	0.98	0.59	0.67	0.55	0.17	394
		SD	2.70	4.08	2.30	3.16	0.26	1.22	0.49	0.47	0.50	0.38	
		CV	38.46	42.12	39.69	27.20	81.30	124.20	83.23	70.26	91.36	219.23	
	1997	Mean	7.70	9.74	6.21	12.97	0.44	1.62	0.62	0.59	0.73	0.33	207
		SD	3.07	4.23	2.43	3.18	0.37	1.57	0.49	0.49	0.45	0.47	
		CV	39.83	43.46	39.13	24.49	84.35	97.31	78.75	82.84	61.05	143.32	
	2000	Mean	6.95	10.07	6.10	12.51	0.44	1.28	0.71	0.61	0.58	0.18	250
		SD	2.84	4.29	2.64	3.12	0.36	1.40	0.45	0.49	0.49	0.38	
		CV	40.88	42.58	43.32	24.92	80.81	109.48	63.73	79.78	85.27	216.81	
	Total	Mean	7.17	9.82	5.98	12.21	0.39	1.22	0.63	0.63	0.60	0.21	851
		SD	2.85	4.18	2.44	3.20	0.33	1.39	0.48	0.48	0.49	0.41	
		CV	39.73	42.57	40.77	26.20	84.27	113.45	76.13	75.93	81.62	193.19	
OGA													
	1998	Mean	6.90	8.93	5.47	11.06	0.37	1.03	0.60	0.72	0.47	0.18	107
		SD	3.11	4.15	1.83	4.48	0.38	1.38	0.49	0.45	0.50	0.38	
		CV	45.11	46.50	33.39	40.52	103.41	133.92	82.35	62.71	107.27	216.22	
	1999	Mean	6.92	11.44	5.71	13.32	0.49	1.31	0.49	0.84	0.54	0.17	140
		SD	3.14	5.10	2.23	5.04	0.47	1.58	0.50	0.37	0.50	0.38	
		CV	45.35	44.56	39.03	37.86	95.92	120.07	103.27	44.50	93.43	220.64	
	Total	Mean	6.91	10.35	5.61	12.34	0.44	1.19	0.53	0.79	0.51	0.17	247
		SD	3.12	4.86	2.06	4.93	0.44	1.50	0.50	0.41	0.50	0.38	
		CV	45.15	46.98	36.82	39.93	99.88	125.86	93.53	52.37	98.99	218.25	
AMA													
	1998	Mean	6.73	7.76	5.56	8.98	0.38	0.61	0.46	0.63	0.13	0.18	229
		SD	2.85	3.23	2.00	3.33	0.22	0.81	0.50	0.48	0.33	0.39	
		CV	42.33	41.59	36.06	37.09	58.80	133.91	107.96	77.00	263.19	211.47	
	2001	Mean	6.99	8.47	5.87	9.98	0.37	0.85	0.45	0.65	0.22	0.20	179
		SD	2.55	4.21	2.25	4.21	0.24	0.94	0.50	0.48	0.41	0.40	
		CV	36.50	49.77	38.43	42.19	66.51	109.60	111.56	73.90	190.00	199.86	
	2002	Mean	6.31	8.01	5.40	9.26	0.36	1.01	0.46	0.70	0.36	0.22	107
		SD	3.12	4.16	2.50	4.37	0.31	0.87	0.50	0.46	0.48	0.42	
		CV	49.45	51.90	46.32	47.24	85.49	86.60	109.31	65.63	132.67	186.84	
	Total	Mean	6.74	8.06	5.63	9.39	0.37	0.78	0.46	0.65	0.21	0.20	515
		SD	2.82	3.80	2.21	3.90	0.25	0.88	0.50	0.48	0.41	0.40	
		CV	41.81	47.14	39.16	41.55	67.33	113.77	109.26	73.37	195.46	201.42	

AMA, Amakusa-Shimoshima Islands; MIK, Mikura Island; OGA, Ogasawara Islands.

Table 2 Results of pairwise comparisons for all whistle parameters between populations

	Beginning frequency	End frequency	Minimum frequency	Maximum frequency	Duration	Number of inflection points	Beginning sweep	End sweep	Harmonics	Break of contour
MIK versus OGA	ns	ns	ns	ns	ns	ns	*	**	*	ns
MIK versus AMA	**	**	*	**	ns	**	**	ns	**	ns
OGA versus AMA	ns	**	ns	**	ns	**	ns	**	**	ns

$*P < 0.05$; $**P < 0.01$; ns, $P > 0.05$.
AMA, Amakusa-Shimoshima Islands; MIK, Mikura Island; OGA, Ogasawara Islands.

ficients of variation, while the Duration and Number of Inflection Points showed the greater. Beginning Sweep, End Sweep, Harmonics and Break of Contour cannot be comparable with the other parameters because these four parameters are arbitral binary numbers and the other parameters are measured values.

Comparisons among populations

Results of tests for all whistle parameters between populations are given in Table 2. Duration and Break of Contour did not differ significantly between all population pairs (Duration: $F = 0.47$, d.f. = 2, $P = 0.62$; Break of Contour: $F = 0.86$, d.f. = 2, $P = 0.42$). There were much less differences in whistle parameters between MIK and OGA than those between MIK and AMA and between OGA and AMA. Whistles of AMA have relatively low End Frequency and Maximum Frequency.

The results of the discriminant function analysis of pairwise and three-way comparisons among the three populations are shown in Table 3. The whistles were statistically different between and among populations (F-values for all comparisons, $P < 0.0001$). The percentage of whistles classified to the correct populations among the three populations was 56.9% overall, and significantly greater than those expected by chance ($z = 20.1$; $P < 0.003$). Correct classification scores between populations were also greater than those expected by chance (all z-value; $P < 0.01$).

Figure 4 shows the plot of group centroids for the first two canonical discriminant functions of the three populations, and indicates that AMA is relatively separate from the other two populations.

Comparisons among years

The results of the discriminant analysis among years within each population and of eight-way comparisons among years are shown in Table 3. The whistles were statistically different among years within each population and among all year-populations because all F-values for all comparisons are significant at the $P < 0.001$ level. The percentage of whistles classified to the correct populations among the eight year-populations was 26.2% overall, and significantly greater than expected by chance ($z = 16.6$; $P < 0.001$). Correct classification scores among years within each population were also greater than expected by chance (all z-value; $P < 0.003$).

Table 3 Results of discriminant analyses of multiple comparisons among the three populations, among year within each population, and among eight year-populations

	Number of Whistles	Wilks χ	F value	% correct classification	chance level (%)	z-value
MIK versus OGA	851/247	0.94	6.92	62.84	50	8.48
MIK versus AMA	851/515	0.70	56.97	75.33	50	18.70
OGA versus AMA	247/515	0.80	18.57	71.78	50	11.99
Three-way comparison	851/247/515	0.72	28.26	56.91	33.3	20.07
Within MIK	394/207/250	0.86	6.70	46.77	33.3	8.28
Within OGA	107/140	0.88	3.32	66.40	50	5.09
Within AMA	229/179/107	0.88	3.29	46.80	33.3	6.44
Eight-way comparison	Total 1614	0.63	10.96	26.16	12.5	16.55

AMA, Amakusa-Shimoshima Islands; MIK, Mikura Island; OGA, Ogasawara Islands.

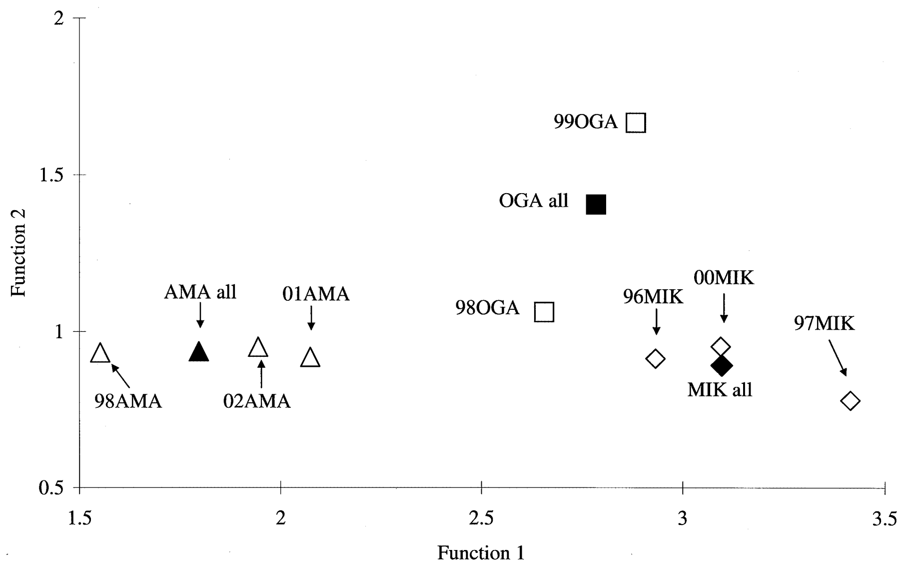

Fig. 4 Plot of group centroids (three populations and eight year-populations) for the first two canonical discriminant functions compared among the three populations. OGA all, OGA at all years; 98OGA, OGA at 1998; 99OGA, OGA at 1999; MIK all, MIK at all years; 96MIK, MIK at 1996; 97MIK, MIK at 1997; 00MIK, MIK at 2000; AMA all, AMA at all years; 98AMA, AMA at 1998; 01AMA, AMA at 2001; 02AMA, AMA at 2002. AMA, Amakusa-Shimoshima Islands; MIK, Mikura Island; OGA, Ogasawara Islands.

Table 4 shows the correct classification and misclassification scores for all year-populations. Whistles of five year-populations classified to those of own year-populations compared to the expected chance level (MIK at 1997: $z = 13.0$; MIK at 2000: $z = 5.78$; OGA at 1998: $z = 3.25$; OGA at 1999: $z = 8.43$; AMA at 1998: $z = 18.4$; all $P < 0.001$). The other three of the eight year-populations had correct classification scores that were not significantly greater than those expected by chance (MIK at 1996: $z = -2.70$, $P = 0.007$; AMA at 2001: $z = -0.65$, $P = 0.52$; AMA at 2002: $z = 2.96$, $P = 0.003$). Although OGA at 1998, AMA at 2001 and AMA 2002 did not show any high classification scores which were significantly greater than those expected by chance, the correct classification score was the largest. Whistles of the four year-populations were significantly misclassified more than those expected by chance (MIK at 1996 as MIK at 2000: $z = 4.61$; MIK at 2000 as MIK at 1997: $z = 5.02$; AMA at 2001 as AMA at 1998: $z = 9.75$; AMA at 2002 as AMA at 1998: $z = 5.59$; all $P < 0.001$). Misclassified whistles, however, were classified to those at the other year within own population.

Figure 4 shows the plot of group centroids for the first two canonical discriminant functions of the eight year-populations when the discriminant analysis for three populations (not for the eight year-populations) were conducted. It showed that the differences among populations, especially AMA and the others, were obviously found in spite of the differences among year-populations within each population.

ANOVA

Table 3 indicated that the correct classification scores between populations were higher than those among year-populations within populations. Magnitudes of variance components and the

Table 4 Results of the discriminant analysis among year-populations

Actual		Classified as							
		MIK			OGA		AMA		
Location	Year	1996	1997	2000	1998	1999	1998	2001	2002
MIK	1996	**7.87**	17.26	20.05	13.71	17.01	9.14	9.39	5.58
	1997	6.76	**42.51**	17.87	5.80	15.46	2.90	5.31	3.38
	2000	6.00	23.20	**24.80**	10.40	18.00	8.80	4.00	4.80
OGA	1998	5.61	12.15	7.48	**23.36**	16.82	14.02	10.28	10.28
	1999	5.71	16.43	10.00	4.29	**36.43**	8.57	6.43	12.14
AMA	1998	0.87	2.18	7.86	6.99	5.24	**52.84**	9.61	14.41
	2001	1.68	6.15	8.38	7.82	12.85	36.87	**11.17**	15.08
	2002	1.87	15.89	5.61	3.74	14.95	30.84	4.67	**22.43**

Bold-face numbers are percent correct classification scores; others are percentages of misclassified whistles. The same population is outlined. Shaded areas indicate the classification score is greater than expected by chance ($a = 0.05$ level).
AMA, Amakusa-Shimoshima Islands; MIK, Mikura Island; OGA, Ogasawara Islands.

Table 5 Percentage variance components and results of nested ANOVA

	Beginning frequency	End frequency	Minimum frequency	Maximum frequency	Duration
Population	0.90**	5.31**	0.76**	16.10**	0
Year	1.17**	1.51**	0.58	3.54**	4.15**
Within-year	97.93	93.18	96.80	80.36	99.76

**$P < 0.01$

results of significance tests from the nested ANOVA for five parameters are shown in Table 5. There were no variance components among populations in Duration ($F = 0.09$, d.f. = 2, $P = 0.91$) and among years in Minimum Frequency ($F = 2.17$, d.f. = 2, $P = 0.06$), whereas there were higher significant variance components among populations in End Frequency and Maximum Frequency (End Frequency: $F = 31.5$, d.f. = 2, $P < 0.0001$; Maximum Frequency: $F = 105.7$, d.f. = 2, $P < 0.0001$) than those among years (End Frequency: $F = 4.23$, d.f. = 5, $P = 0.0008$; Maximum Frequency: $F = 9.78$, d.f. = 5, $P < 0.0001$). Variance components within year were constantly higher in all five parameters.

DISCUSSIONS

The results indicate that the whistles of Indo-Pacific bottlenose dolphins from three populations significantly differ, especially between AMA and the other populations. Although whistles of OGA and MIK showed no significant difference in measures of single parameters except Beginning Sweep, End Sweep and Harmonics, the discriminant analysis explained a significant amount of variation between OGA and MIK.

The results also indicate that the whistles among year within populations differ significantly. The variances within year (or among individuals) had greater value than those among year, but the more differences among populations also found in End Frequency and Maximum Frequency than those among years within populations (Table 5). Also, the more differences among populations found than those among years within each population because the correct classification scores compared to random chance level between and among populations seem higher than those among years within each population (Table 3). Furthermore, the whistles of year-populations were misclassified to those of the own population not to those of the others (Table 4). These results indicated that the difference among populations were not yearly difference within populations but geographic variations in the whistles among populations.

Intra-population variability

The coefficients of variation of all populations, or the intrapopulation variability, showed a consistent pattern which was the same as Wang *et al.*[6] and Oswald *et al.*[8] The frequency parameters (Beginning Frequency, End Frequency, Minimum Frequency and Maximum Frequency) have relatively low intrapopulation variability, whereas the Duration and Number of Inflection Points have relatively high intrapopulation variability. As Wang *et al.* noted, the dolphins may modulate the Duration and the Number of Inflection Points for carrying additional 'analogic' information such as individual identities, emotional levels, and so on.[6] In contrast, the four frequency parameters were relatively stable, which indicated that these parameters were restricted or selected by some factors such as the size of sound production organs and muscles and/or the environmental background noise levels. Since those tendencies were not only within the genus *Tursiops* but also within the other species like genus *Stenella*, *Delphinus*, *Steno*, *Globicephala* and *Pseudorca*,[8] these parameters may have the same meaning in all delphinids species.

Differences among populations

Whistles of AMA had the most distinctive characteristics of all whistles in the three populations, whereas whistles of MIK and OGA could not be clearly separated from each other. Whistles of AMA have lower End Frequency, lower Maximum Frequency, fewer Number of Inflection Points and fewer Harmonics than those of the other populations. Maximum Frequency and End Frequency are the most useful of the 10 parameters to discriminate among these populations. In contrast, Duration and Break of Contour did not differ significantly among the populations. It can be because the animals modulate Duration and Break of Contour for carrying additional 'analogic' information as mentioned before.

Figure 2 and Table 3 indicate that the statistical distances of whistle characteristics between populations do not simply correlate with simple geographic distances between locations such as those in beelines. The differences between AMA and MIK are the greatest of all three population pairs, whereas the differences between MIK and OGA are small. The distance between AMA and MIK is about 900 km, between MIK and OGA is about 800 km, and between AMA and OGA is about 1300 km in a beeline (Fig. 1).

Geographic variations result from various factors. Wang *et al.* proposed some factors, such as individual movement to the other populations and ambient noise backgrounds, that might influence the whistles and make geographic variations.[6] Bazúa-Durán, however, suggested that the individual mixing between populations is not the only factor to be considered when we look at geographic variations in the whistles of dolphins.[7] Each population would be affected by different evolutionary and environmental influences.[20] We currently have no data on individual movements, gene flow, genetic relationships, historical processes or ecologic differences including ambient noise differences among MIK, OGA and AMA, and, therefore, further research is needed about the relationships among these populations.

From the results, there is a possibility that these populations are separate or independent populations. Further research, especially genetic analysis among the three populations, is still needed to confirm this possibility. We should adjust the treatment to each population for the problems between dolphins and humans if the populations are separate from each other.

Differences among years

Geographic variations in bird songs often arise simply as a consequence of vocal learning.[12] Vocal learning processes might make sounds within each group change but in the same direction because of copying errors,[12] adaptations for environments and/or other factors. Vocal learning might make neighboring social groups share sounds that differ from more distant groups.[21] Geographic variation, therefore, can result from the accumulation of change with time within each group.

Bottlenose dolphins show the ability of vocal learning and vocal imitation.[21–23] As sex difference in vocal learning was also reported,[24] the vocal learning process may make whistles change with time, or yearly, within each population. These yearly change must result in the geographic variation in the whistles.

The results indicated that whistles among year within each population also differ (Fig. 2). We, therefore, expect that some processes of vocal learning should be working at each population and the geographic variation might result from the accumulation of the changes with time in the whistles.

Unfortunately, our data cannot thoroughly exclude the bias toward some individuals or some other possible factors which make whistles change yearly, but we have minimized the bias by discarding whistles which were successively recorded and had the same contour. We need further research on the whistle differences among and within individuals.

From the result in this study, researchers should take the yearly change, or change with time, within each population into consideration when we study the geographic variations in the whistle of dolphins.

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REFERENCES

1. Ross GJB, Cockcroft VG. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). In: Leatherwood S, Reeves, RR (eds). *The Bottlenose Dolphin*. Academic Press, New York. 1990; 101–128.
2. LeDuc RG, Perrin WF, Dizon AE. Phylogenetic relationships among the delphinids cetaceans based on full cytochrome *b* sequences. *Mar. Mamm. Sci.* 1999; **15**: 619–648.
3. Wang JY, Chou L-S, White BN. Osteological differences between two sympatric forms of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *J. Zool., Lond.* 2000; **252**: 147–162.
4. Tyack PL, Clark CW. Communication and acoustic behavior of dolphins and whales. In: Au WWL, Popper AN, Fay RR (eds). *Hearing by Whales and Dolphins*. Springer-Verlag, New York. 2000; 156–224.
5. Janik VM, Slater PJB. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* 1998; **56**: 829–838.
6. Wang DW, Würsig B, Evans WE. Whistles of bottlenose dolphins: comparisons among populations. *Aquat. Mamm* 1995; **21**: 65–77.
7. Bazúa-Durán C. Differences in the whistle characteristics and repertoire of bottlenose and spinner dolphins. *An. Acad. Bras. Cienc.* 2004; **76**: 386–392.
8. Oswald JN, Barlow J, Norris TF. Acoustic identification of nine delphinids species in the eastern tropical Pacific ocean. *Mar. Mamm. Sci.* 2003; **19**: 20–37.
9. Bazúa-Durán C. The whistles of Hawaiian Spinner Dolphins (*Stenella longirostoris*): description and geographic variations. PhD Thesis. University of Hawaii at Manoa, Honolulu. 2001.
10. Rendell LE, Matthews JN, Gill A, Gordon JCD, Macdonald DW. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *J. Zool., Lond.* 1999; **249**: 403–410.
11. Mundinger PC. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: Kroodsma DE, Miller EH (eds). *Acoustic Communication in Birds*. Academic Press, New York. 1982; 147–208.
12. Catchpole CK, Slater PJB. *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge. 1995.
13. Mori K, Amano M, Shinohara M. A taxonomical study of bottlenose dolphins occurring in Ogasawara water. In: Mori K (ed). *Annual Reports on the Regional Promotion (Tourism)*. Foundation of the Tokyo Island Promotion Public Corporation, Tokyo, Japan. 1996; 4–7 (in Japanese).
14. Kakuda T, Tajima Y, Arai K, Kogi K, Hishii T, Yamada TK. On the resident 'Bottlenose dolphins' from Mikura water. *Mem. Natn. Sci. Mus., Tokyo* 2002; **38**: 255–272.
15. Shirakihara M, Yoshida H, Shirakihara K. Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Amakusa, Western Kyushu, Japan. *Fish. Sci.* 2003; **69**: 654–656.
16. Shinohara M. Behavior and social structure of the bottlenose dolphin *Tursiops truncatus* revealed by underwater observation and DNA analysis. PhD Thesis. Kyoto University, Kyoto, Japan. 1998.
17. Kogi K, Hishii T, Imamura A, Iwatani T, Dudzinski MK. Preliminary demographic parameters and reproductive rates of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Mar. Mamm. Sci.* 2004; **20**: 510–526.
18. Shirakihara M, Shirakihara K, Tomonaga J, Takatsuki M. A resident population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Amakusa, western Kyushu, Japan. *Mar. Mamm. Sci.* 2002; **18**: 30–41.
19. Sokal RR, Rohlf FJ. *Biometry*, 3rd edn. W.H. Freeman and Company, New York. 1995.
20. Connor DA. Dialects versus geographic variation in mammalian vocalizations. *Anim. Behav.* 1982; **30**: 297–298.
21. Janik VM, Slater PJB. Vocal learning in Mammals. *Adv. Study Behav.* 1997; **26**: 59–99.
22. Watwood SL, Tyack PL, Wells RS. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behav. Ecol. Sociobiol.* 2004; **55**: 531–543.
23. Fripp D, Owen C, Quintana-Rizzo E, Shapiro A, Buckstaff K, Jankowski K, Wells R, Tyack P. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Anim. Cogn.* 2005; **8**: 17–26.
24. Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behav. Ecol. Sociobiol.* 1995; **36**: 171–177.