

EFFECTS OF AMBIENT NOISE ON THE WHISTLES OF INDO-PACIFIC BOTTLENOSE DOLPHIN POPULATIONS

TADAMICHI MORISAKA,* MASANORI SHINOHARA, FUMIO NAKAHARA, AND TOMONARI AKAMATSU

Department of Zoology, Kyoto University, Kitashirakawa-oiwake, Sakyo, Kyoto 606-8502, Japan (TM, MS)

College of Community Development, Tokiwa University, 1-430-1 Miwa, Mito-shi, Ibaraki 310-8585, Japan (FN)

National Research Institute of Fisheries Engineering, Ebidai, Hasaki-cho, Kashima-gun, Ibaraki 314-0345, Japan (TA)

Communication among animals should use signals that are most efficient in their particular habitat. Here, we report data from 3 populations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Japan that produce whistles transmitted efficiently through environmental ambient noise. We compared the characteristics of the ambient noise in the dolphins' habitats and the whistles produced. In habitats with less ambient noise, dolphins produced whistles at varying frequencies with greater modulations; when ambient noise was greater, dolphins produced whistles of lower frequencies with fewer frequency modulations. Examination of our results suggests that communication signals are adaptive and are selected to avoid the masking of signals and the attenuation of higher-frequency signals. Thus, ambient noise may drive the variation in whistles of Indo-Pacific bottlenose dolphin populations.

Key words: ambient noise, geographical variation, Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, whistle

Many studies of acoustic communication have revealed that acoustic signals of animals, especially the frequency and temporal structure of signals, change in response to the acoustic environment, to ensure that acoustic information is reliably transmitted (Morton 1975; Wiley and Richards 1978). Characteristics of acoustic signals are affected by the acoustic environments among habitats (Sugiura et al. 1999), and geographical variation in animal acoustic signals can result from differences in acoustic environments (Morton 1975). Morton (1975) reported that the physical structures used by tropical birds to produce sound result from selection pressures imposed by the acoustic environments of forest, edge, and grassland habitats. In addition, Ryan and Brenowitz (1985) suggested that ambient noise affects bird songs. Differences among bird songs from different acoustic environments make the songs geographically distinct. Japanese macaques (*Macaca fuscata*) produce calls at efficient frequencies for their particular habitats in that ambient noise and transmission loss differences are related to geographical variation in their calls (Sugiura et al. 1999). Pygmy marmosets (*Cebuella pygmaea*) also use calls most suited to the characteristics of their acoustic environment (de la Torre and Snowdon 2002). Compared with what is known about how calls are adapted to environmental

constraints among terrestrial animals, little is known about how environmental factors influence animal communication channels for aquatic animals (Au 1990).

Physical characteristics of water and air differ considerably. Sound travels faster and for much greater distances in water than in air. Many aquatic animals, including crustaceans, fish, and marine mammals, use acoustic signals to communicate (Tyack 1998). However, ambient noise, especially in the shallow sea (<60 m deep) at latitudes less than 40°, is extremely high. Among the many sources of ambient noise, such as wind, wave, surf, human activity, and other organisms, a major source is biological noise from other animals, such as snapping shrimp (Au and Banks 1998; Knudsen et al. 1948). Noisy environments induce marine animals, including cetaceans, to produce sounds that transmit efficiently in their habitats. For instance, a beluga whale (*Delphinapterus leucas*) shifted its biosonar signals to higher frequencies and intensities after it was experimentally moved to a noisier environment (Au et al. 1985). Empirical studies have suggested that the bottlenose dolphin (*Tursiops truncatus*) and the false killer whale (*Pseudorca crassidens*) also adapt their biosonar signals to their environments (Au 1993; Au et al. 1974). If acoustic profiles differ among habitats, the restrictions of these profiles may cause geographical variation in the acoustic signals of animals.

Indo-Pacific bottlenose dolphins are small-toothed whales that reside year-round in coastal waters, commonly forming large aggregations. They disperse across temperate oceans including those around South Africa, Australia, India, China,

* Correspondent: chaka@terra.zool.kyoto-u.ac.jp

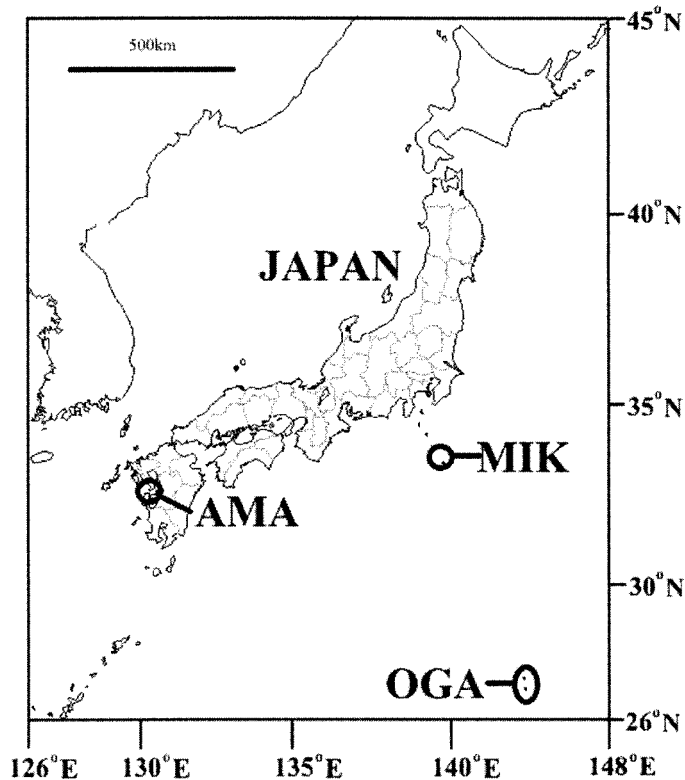


FIG. 1.—Map of the Ogasawara Islands (OGA), Mikura Island (MIK), and Amakusa-Shimoshima Islands (AMA), Japan, where *Tursiops aduncus* calls were recorded.

and Japan (Kasuya et al. 1997; Ross and Cockcroft 1990). Recent morphological and molecular studies have revealed that *T. aduncus* is distinct from *T. truncatus* (LeDuc et al. 1999; Ross and Cockcroft 1990; Wang et al. 1999, 2000a, 2000b).

Bottlenose dolphins produce 2 types of sound for communication: pulsed calls and tonal calls (Tyack and Clark 2000). A whistle is a tonal call with a narrow band and a frequency-modulated pure tone. Whistles are thought to function as group cohesion or contact calls (Janik and Slater 1998). Each individual produces various types of whistles. Wang et al. (1995a) reported geographical variation in whistles of bottlenose dolphins. However, in light of recent discoveries related to the taxonomy of this genus, the authors may have actually studied 2 species together, which would confound their results (Wang et al. 1995a). In a preliminary study before this one, we compared whistles of the 3 Indo-Pacific bottlenose dolphin populations described in this paper by measuring 10 variables (Wang et al. 1995a) including beginning frequency, end frequency, minimum frequency, maximum frequency, duration, number of inflections, beginning sweep, end sweep, harmonics, and break of contour (Morisaka et al., in press). Examination of our data suggested geographical variation among populations. We hypothesized that the geographical variation may result from variations in acoustic environments in their habitats. In the current study, we examined acoustic characteristics of 3 Indo-Pacific bottlenose dolphin (*T. aduncus*) populations in Japan and compared these characteristics with those of environmental am-

bient noises in their habitats in order to investigate effects of ambient sound on the whistle structure of bottlenose dolphins.

MATERIALS AND METHODS

All of our procedures were conducted according to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Data were collected in coastal areas off the Ogasawara Islands, Tokyo (142°11'E, 26°05'N); Mikura Island, Tokyo (139°36'E, 33°52'N); and the Amakusa-Shimoshima Islands, Western Kyushu (130°07'E, 32°33'N), Japan (Fig. 1). Around the Ogasawara Islands, about 200–300 dolphins may reside near the Chichi-jima and Haha-jima islands (Shinohara 1998). Around Mikura Island, 138 resident dolphins have been identified (Kogi et al. 2004), and around the Amakusa-Shimoshima Islands, 218 dolphins are permanent residents (Shirakihara et al. 2002). The dolphins were confirmed to be Indo-Pacific bottlenose dolphins (*T. aduncus*) by genetic analysis and observation of external appearance (Kakuda et al. 2002; Mori et al. 1996; Shinohara 1998; Shirakihara et al. 2003).

Sound recordings of ambient noise.—Adrift aboard recording vessels, we recorded ambient noise when other vessels were not within 1 km. The recordings were conducted at 15- to 30-m water depth during calm seas (Beaufort wind force <4) with no rain. We recorded ambient noise in the dolphins' ranges with a calibrated hydrophone (Oki ST1001 or ST1020, Tokyo, Japan) connected to a preamplifier (Oki SW1007 or SW1020, respectively) and a digital audiotape recorder (Sony TCD-D8, Tokyo, Japan). The frequency response was set between 1 and 24 kHz. At each area, 19–26 recording sessions of ambient noise with sampling every 3 min were conducted with a hydrophone located 10 m below the surface. In the Ogasawara Islands, there were 26 recording sessions at 26 locations, made on 28 and 30 August 1999. Around Mikura Island, there were 19 recording sessions at 19 recording sessions at 13 locations, made on 10–11 September 2000 and on 8 and 10 July 2003. In the Amakusa-Shimoshima Islands, there were 23 recording sessions at 16 locations, made on 2 and 7 September 2002 and on 20–21 October 2003. Water temperatures were recorded simultaneously with acoustic signals.

Whistles.—Frequency responses varied as whistles were recorded opportunistically from dolphins throughout the study area, but all recordings extended beyond 20 kHz. In Ogasawara Islands, recordings were made on June 1998 with Hi-8 Video (Kyocera KX-H3, Kyoto, Japan). Around Mikura Island, recordings were made in June–July 1996 and in June 1997 with Hi-8 Video (Sony CCD-TR2000, Tokyo, Japan). At Ogasawara Islands in August 1999 and Mikura Island in September–October 2000, we recorded sounds and behaviors by using an underwater video system modified from Dudzinski (1999; Sony DCR-TRV900, Tokyo, Japan). In Amakusa-Shimoshima Islands, recordings were made in September 1998 with a calibrated hydrophone (Oki ST1020, Tokyo, Japan) connected to a preamplifier (Oki SW1020) and a digital audiotape recorder (Sony TCD-D8, Tokyo, Japan) and in September 2002 with a calibrated hydrophone (Oki ST1001) connected to a preamplifier (Oki SW1007) and a digital audiotape recorder (Sony TCD-D8).

Sound analysis.—For all sound analyses, Avisoft-SASLab Pro version 4.0 software (Specht 2001) was used. Traditionally, characteristics of dolphin whistles have been analyzed by measuring variables from each whistle (beginning frequency, end frequency, minimum frequency, maximum frequency, duration, and number of inflections—Rendell et al. 1999; Steiner 1981; Wang et al. 1995a), but we calculated the adopted frequency and coefficient of frequency modulation for each whistle in this study instead of those traditional variables.

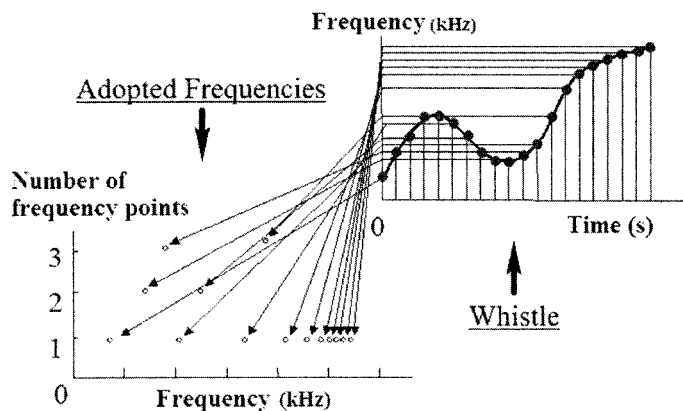


FIG. 2.—A schematic diagram of adopted frequencies of vocalizations. A whistle (upper right) is divided into 19 equal time intervals and 20 calculated frequency points, which are the representative frequencies of the whistle. We count number of frequency points at each frequency and plot on a figure (lower left). We put these data from each population together and regard them as the distribution of adopted frequencies of each population, which represented actual frequency range of whistles from each population.

Ambient noise.—We set the frequency resolution at 375 Hz and the time resolution at 2.67 ms, with a humming window and a 1- to 22-kHz band-pass filter. From the 3-min samplings taken at each location, we randomly selected three 4-s samples of ambient noise at intervals longer than 25 s. We averaged 3 amplitude spectra from each location and used the average in analyses.

Whistles.—We set the frequency resolution at 93 Hz and the time resolution at 5.3 ms, with a humming window and a 1-kHz high-pass filter in the Avisoft-SASLab Pro software. We selected whistles with good signal-to-noise ratios. For each whistle, the adopted frequency and coefficient of frequency modulation were calculated in order to clarify the effects of frequency range usage and frequency modulations on the whistles.

Adopted frequencies are used to measure the frequency range actually used during a whistle. Range between minimum frequency and maximum frequency of a whistle also can indicate frequency range of the whistle, but it cannot evaluate an actual frequency distribution of a whistle within the range. In order to evaluate the frequency distribution of a whistle, we divided the duration of each whistle into 19 equal time intervals and calculated 20 frequency points, or adopted frequencies, of the whistle, after McCowan (1995). Adopted frequencies were regarded as the representative of frequencies of a whistle. We also calculated frequency distribution of these points for each population (Fig. 2), which represented actual frequency range of whistles from each population.

McCowan and Reiss (1995) used the coefficient of frequency modulation (COFM) to measure change in the complexity of whistle contour during development of infant bottlenose dolphins. To measure the frequency modulation of each whistle, we used the 20 frequency points described above in the following equation:

$$\text{COFM} = \sum_{(n=1,19)} |Y_{n+1} - Y_n| / 10,000, \quad (1)$$

where Y_n is the frequency at the n th frequency point (McCowan and Reiss 1995). Coefficient of frequency modulation represents the amount and magnitude of frequency modulation or change across each whistle. If a whistle has greater frequency modulation, the value of the coefficient of frequency modulation increases, and vice versa.

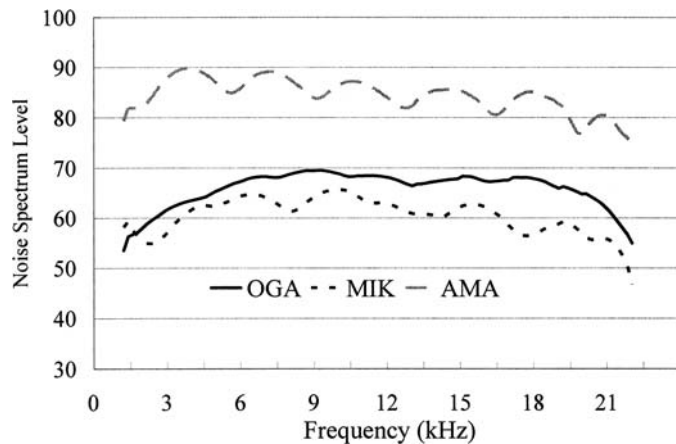


FIG. 3.—Ambient noise level at the Ogasawara Islands (OGA), Mikura Island (MIK), and Amakusa–Shimoshima Islands (AMA), Japan, from 1 to 22 kHz (with noise spectrum level decibels re $1 \mu\text{Pa}^2/\text{Hz}$).

Statistical analyses.—The Kruskal–Wallis nonparametric test, run in StatView software (SAS Institute Inc. 1998), was used to compare adopted frequencies among the 3 populations. Coefficient of frequency modulation data were adjusted to a nearly normal distribution by the Box–Cox transformation (Sokal and Rohlf 1995) and were then compared among the 3 populations by analysis of variance (ANOVA). We then compared adopted frequencies and coefficients of frequency modulation between all pairs of the 3 populations by using the Tukey–Kramer honestly significant difference test run in JMP software (SAS Institute Inc. 2002). The differences in whistle duration among populations were tested by using ANOVA after Box–Cox transformation. We compared coefficient of frequency modulation with whistle duration and population as factors by analysis of covariance (ANCOVA) to evaluate the explanatory power of duration, population, and their interaction (duration versus population).

RESULTS

Ambient noise.—Ambient noise was greatest at the Amakusa–Shimoshima Islands and lowest at Mikura Island (Fig. 3). Noise levels at Mikura Island and the Ogasawara Islands were similar except that Mikura Island seemed to experience lower frequencies. Ambient noise levels at each location were relatively flat and about 5–18 kHz. Noise levels at the Ogasawara Islands and Mikura Island at times dropped slightly below 5 kHz, but levels at the Amakusa–Shimoshima Islands remained high.

Whistles.—We analyzed 239 whistles from the Ogasawara Islands (1998, $n = 99$; 1999, $n = 140$), 255 whistles from Mikura Island (1996, $n = 54$; 1997, $n = 100$; 2000, $n = 101$), and 208 whistles from the Amakusa–Shimoshima Islands (1998, $n = 101$; 2002, $n = 107$).

Adopted frequencies.—Adopted frequencies differed significantly among the 3 populations (Kruskal–Wallis, $H = 941.6$, $P < 0.0001$) and between all population pairs (Tukey–Kramer honestly significant difference, $\alpha = 0.05$; Fig. 4).

Coefficient of frequency modulation.—Coefficients of frequency modulation were significantly lower at the Amakusa–Shimoshima Islands than at the other islands (ANOVA after Box–Cox transformation, $F = 51.54$, $P < 0.0001$; Tukey–

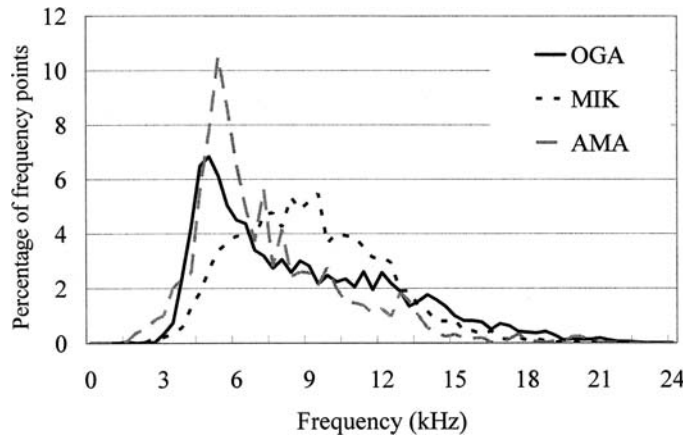


FIG. 4.—Adopted frequency distributions of whistles produced by 3 populations of bottlenose dolphins from the Ogasawara Islands (OGA), Mikura Island (MIK), and Amakusa–Shimoshima Islands (AMA), Japan. The y-axis represents percentage of frequency points from each population at the same frequency, or the number of frequency points divided by the sum of frequency points of each population and multiplied by 100.

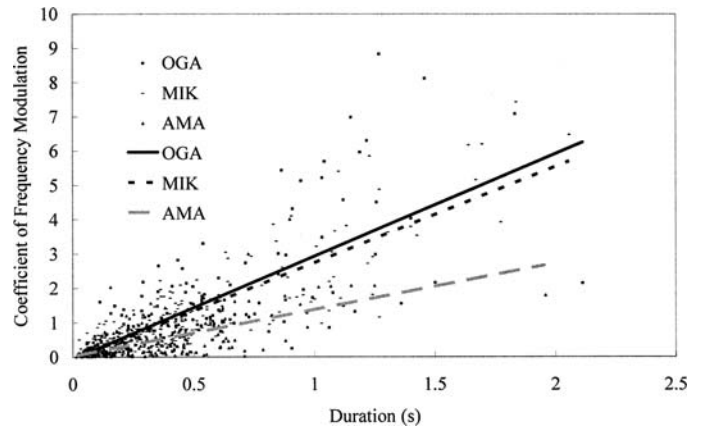


FIG. 5.—Relation between duration and coefficient of frequency modulation (COFM) of whistles recorded from 3 populations of bottlenose dolphins from the Ogasawara Islands (OGA), Mikura Island (MIK), and Amakusa–Shimoshima Islands (AMA). Regression lines are shown. Regression equations and R^2 values are as follows. OGA: $COFM_{OGA} = -0.06 + 2.99 \times \text{duration}$, $R^2 = 0.54$; MIK: $COFM_{MIK} = -0.06 + 2.80 \times \text{duration}$, $R^2 = 0.75$; AMA: $COFM_{AMA} = 0.03 + 1.35 \times \text{duration}$, $R^2 = 0.38$.

Kramer honestly significant difference, $\alpha = 0.05$; Table 1; Fig. 5). Whistle durations did not differ significantly among populations (ANOVA after Box–Cox transformation, $F = 2.82$, $P = 0.06$). Coefficients of frequency modulation correlated with duration, population, and their interaction term (ANCOVA; $F = 717.12$, $F = 38.81$, and $F = 26.43$, respectively; all $P < 0.0001$). Coefficients of frequency modulation did not differ between the Ogasawara Islands and Mikura Island.

DISCUSSION

We found between-site differences in ambient noise levels among habitats. The Amakusa–Shimoshima Islands had higher ambient noise levels than did the other 2 areas. These islands

TABLE 1.—Medians, 1st and 3rd quartiles, and averages of adopted frequencies, duration averages, and coefficients of frequency modulation averages of whistles from 3 populations of bottlenose dolphins from Japanese islands. Regression equations and R^2 values from Fig. 5 also are shown. CV, coefficient of variation.

	Ogasawara Islands	Mikura Island	Amakusa–Shimoshima Islands
Adopted frequencies (kHz)			
1st quartile	5.34	6.70	4.97
Median	7.69	8.72	6.09
3rd quartile	11.4	10.8	8.63
Mean	8.68	8.89	7.08
CV	45.5	32.8	43.6
Duration (s)			
Mean	0.43	0.44	0.35
SD	0.34	0.38	0.27
Coefficient of frequency modulation			
Mean	1.36	1.16	0.51
SD	1.64	1.22	0.58

are near a larger island, Kyushu, which has a sizeable estuary favored by cetaceans. Mikura Island and the Ogasawara Islands are isolated oceanic islands. Furthermore, boat noise was greater around the Amakusa–Shimoshima Islands, where dolphin-watching boats, fishing boats, and commuter ferries operate continuously.

The distributions of adopted frequencies also differed among the 3 populations, which indicated that frequency ranges or distributions of whistles differed among 3 populations. Dolphins in the Amakusa–Shimoshima Islands group produced whistles of lower frequencies, and dolphins in the Mikura Island group produced whistles of higher frequencies, relative to dolphins at the other sites. The distributions of adopted frequencies also differed among the 3 populations. Whistles among dolphins from the Ogasawara Islands had a broader frequency range (coefficient of variation [CV] = 45.5) and lower frequency peak than did those among Mikura Island dolphins, although the 2 dolphin groups had equal average adopted frequencies. Whistles at Mikura Island had the narrowest frequency range of all (CV = 32.8). The acoustic niche hypothesis, which states that cetaceans shift their communication sounds to be below or above ambient noise, was developed from studies of the gray whale (*Eschrichtius robustus*) and the bottlenose dolphin (Dahlheim et al. 1984; Wang et al. 1995a). Other animals have been suggested to use acoustic signals designed to bypass ambient noise, including tropical birds (Ryan and Brenowitz 1985) and the pygmy marmoset (de la Torre and Snowdon 2002).

The data from the present study do not support the acoustic niche hypothesis because they showed no relation between whistles and ambient noise. We suggest that dolphins may not be sensitive to spectra of ambient noise but rather to the entire suite of ambient noise in their habitats. The ambient noises in our study areas have relatively flat ranges, from 5 to 18 kHz, which is the range covered by whistles.

Adopted frequencies are thus a more appropriate measurement of the frequency effect of whistles than are traditional measurements of start frequency, end frequency, minimum frequency, and maximum frequency.

Consistent with other studies (Steiner 1981; Wang et al. 1995a), whistle durations did not differ among the 3 populations. Wang et al. (1995a) suggested that whistle durations have greater intrapopulation than interpopulation differences and that this trait might carry additional analogical information or might be used to distinguish individual dolphins.

The coefficients of frequency modulation were lowest at the Amakusa–Shimoshima Islands. The coefficients at Mikura Island and the Ogasawara Islands did not differ. The coefficient of frequency modulation measure has been used only by McCowan and Reiss (1995) in a study of whistle development in bottlenose dolphin infants. We found it to be a useful value for measuring frequency modulations of captive and wild dolphin whistles.

The greatest ambient noise was found at the Amakusa–Shimoshima Islands, where dolphins produced whistles of the lowest frequency and with the lowest coefficient of frequency modulation. Mikura Island and the Ogasawara Islands had low ambient noise levels, and dolphins there produced whistles of high frequency and greater frequency modulation. These results suggest that, at the Amakusa–Shimoshima Islands, communication signals are selected to avoid noise that might mask them; higher-frequency sounds cannot transmit over long distances, and frequency modulations are easily masked by other noise. Thus geographical variation in the whistles of Indo-Pacific bottlenose dolphin populations may originate from geographical differences in the ambient noises of their habitats.

We recorded ambient noise only during the day. However, Albers (1965) reported that snapping shrimp noise varies only slightly during the day, and is 2–5 dB higher at night. The ambient noise level between Amakusa–Shimoshima Islands and the other sites had clear difference even if snapping shrimp noise became 5 dB higher at night at only Amakusa–Shimoshima Islands. However, we cannot dismiss the possibility that whistles also may be affected by factors other than ambient noise (such as individual movement among habitats). Future studies should address genetic divergence at a scale that will fully describe the geographical variation of whistles.

This study also indicates that Indo-Pacific bottlenose dolphins produce whistles that easily transmit to the receiver in the presence of various environmental and ambient noises. Future study of dolphin whistles should consider that such noise probably exerts some selective force, at least with regard to behavior (e.g., Janik 2000), social patterns (e.g., McCowan et al. 1998), physiological responses (e.g., Wang et al. 1995b), and development (McCowan and Reiss 1995).

ACKNOWLEDGMENTS

For the collection of whistle data from Ogasawara, we thank K. Mori, E. Kawa, M. Okiyama, and the local people of the Ogasawara Islands. The collection of data from Mikura was possible only because of Y. Hirose, everyone in Shigewo-Koubou, and K. Kogi. We also thank M. Kurimoto, K. Kato, N. Hirose, T. Hishii, Mikura-Jima

Bandou-Iruka Kenkyukai, Mikura-Jima Iruka Kyokai, T. Kishida, M. Sakai, and the local people of Mikura Island. We are indebted to M. Shirakihara and K. Shirakihara for collecting whistle data in the Amakusa–Shimoshima Islands. We thank S. Suzaki and the people working at Itsuwa-machi Fisherman's Association for the use of vessels. We also thank the members of the Animal Ecology Laboratory, Kyoto University (especially M. Sasabe), and many others who kindly helped us. We are grateful to M. Hori and T. Sota for their supervision. Finally, the thoughtful reviews of 2 anonymous reviewers are greatly appreciated.

LITERATURE CITED

- ALBERS, V. M. 1965. Underwater acoustics handbook—II. The Pennsylvania State University Press, University Park.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- AU, W. W. L. 1990. Target detection in noise by echolocating dolphins. Pp. 203–216 in *Sensory abilities of cetaceans, laboratory and field evidence* (J. A. Thomas and R. A. Kastelein, eds.). Plenum Press, New York.
- AU, W. W. L. 1993. *The sonar of dolphins*. Springer-Verlag, New York.
- AU, W. W. L., AND K. BANKS. 1998. The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay. *Journal of the Acoustical Society of America* 103:41–47.
- AU, W. W. L., D. A. CARDER, R. H. PENNER, AND B. L. SCRONCE. 1985. Demonstration of adaptation in beluga whale echolocation signals. *Journal of the Acoustical Society of America* 77:726–730.
- AU, W. W. L., R. W. FLOYD, R. H. PENNER, AND A. E. MURCHISON. 1974. Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *Journal of the Acoustical Society of America* 56:1280–1290.
- DAHLHEIM, M. E., H. D. FISHER, AND J. D. SCHEMP. 1984. Sound production by the gray whale and ambient noise levels in Laguna San Ignacio, Baja California Sur, Mexico. Pp. 511–541 in *The gray whale *Eschrichtius robustus** (M. L. Johns, S. L. Swartz, and S. Leatherwood, eds.). Academic Press, Orlando, Florida.
- DE LA TORRE, S., AND C. T. SNOWDON. 2002. Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea*. *Animal Behaviour* 63:847–856.
- DUDZINSKI, K. 1999. Intraspecific contact behavior and signal exchange among free-ranging dolphins—the view from underwater. *IBI Reports* (International Marine Biological Research Institute) 9:93–107.
- JANIK, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* 289:1355–1357.
- JANIK, V. M., AND P. J. B. SLATER. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour* 56:829–838.
- KAKUDA, T., Y. TAJIMA, TAJIMA, K. TAJIMA, K. KOGI, T. HISHII, AND T. K. YAMADA. 2002. On the resident “bottlenose dolphins” from Mikura water. *Memoirs of the National Science Museum (Tokyo)* 38:255–272.
- KASUYA, T., Y. IZUMISAWA, Y. KOMYO, Y. ISHINO, AND Y. MAEJIMA. 1997. Life history parameters of bottlenose dolphins off Japan. *IBI Reports* 7:71–107.
- KNUDSEN, V. O., R. S. ALFORD, AND J. W. EMLING. 1948. Underwater ambient noise. *Journal of Marine Research* 7:410–429.
- KOGI, K., T. HISHII, A. IMAMURA, T. IWATANI, AND M. K. DUDZINSKI. 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science* 20:510–526.

- LEDUC, R. G., W. F. PERRIN, AND A. E. DIZON. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome *b* sequences. *Marine Mammal Science* 15:619–648.
- MCCOWAN, B. 1995. A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (*Delphinidae*, *Tursiops truncatus*). *Ethology* 100:177–193.
- MCCOWAN, B., AND D. REISS. 1995. Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): role of learning. *Journal of Comparative Psychology* 109:242–260.
- MCCOWAN, B., D. REISS, AND C. GUBBINS. 1998. Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 24:27–40.
- MORI, K., M. AMANO, AND M. SHINOHARA. 1996. A taxonomical study of bottlenose dolphins occurring in Ogasawara water. Pp. 4–7 in *Studies on the ecology of bottlenose dolphins in Ogasawara water, 1995 annual reports on the regional promotion (tourism)* (K. Mori, ed.). Foundation of the Tokyo Island Promotion Public Corporation, Tokyo, Japan (in Japanese).
- MORISAKA, T., M. SHINOHARA, F. NAKAHARA, AND T. AKAMATSU. In press. Geographic variations in the whistles among three Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations in Japan. *Fisheries Science*.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. *American Naturalist* 109:17–34.
- RENDELL, L. E., J. N. MATTHEWS, A. GILL, J. C. D. GORDON, AND D. W. MACDONALD. 1999. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *Journal of Zoology (London)* 249:403–410.
- ROSS, G. J. B., AND V. G. COCKCROFT. 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). Pp. 101–128 in *The bottlenose dolphin* (S. Leatherwood and R. R. Reeves, eds.). Academic Press, New York.
- RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist* 126:87–100.
- SAS INSTITUTE INC. 1998. StatView software for Windows. Version 5. SAS Institute Inc., Cary, North Carolina.
- SAS INSTITUTE INC. 2002. JMP statistical discovery software. Version 5. SAS Institute Inc., Cary, North Carolina.
- SHINOHARA, M. 1998. Behavior and social structure of the bottlenose dolphin *Tursiops truncatus* revealed by underwater observation and DNA analysis. Ph.D. dissertation, Kyoto University, Kyoto, Japan.
- SHIRAKIHARA, M., K. SHIRAKIHARA, J. TOMONAGA, AND M. TAKATSUKI. 2002. A resident population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Amakusa, western Kyushu, Japan. *Marine Mammal Science* 18:30–41.
- SHIRAKIHARA, M., H. YOSHIDA, AND K. SHIRAKIHARA. 2003. Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Amakusa, western Kyushu, Japan. *Fisheries Science* 69:654–656.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. 3rd ed. W. H. Freeman and Company, New York.
- SPECHT, R. 2001. Avisoft-SASLab pro (Sound Analysis and Synthesis Laboratory). Version 4.0. Raimund Specht, Berlin, Germany.
- STEINER, W. W. 1981. Species-specific differences in pure tonal whistle vocalizations of five western North Atlantic dolphin species. *Behavioral Ecology and Sociobiology* 9:241–246.
- SUGIURA, H., T. TANAKA, AND N. MASATAKA. 1999. Sound transmission in the habitats of Japanese macaques and its effect on populational differences in coo calls. *Journal of the Acoustical Society of Japan* 55:679–687 (in Japanese).
- TYACK, P. L. 1998. Acoustic communication under the sea. Pp. 163–220 in *Animal acoustic communication* (S. L. Hopp, M. J. Owren, and C. S. Evans, eds.). Springer-Verlag, Berlin, Germany.
- TYACK, P. L., AND C. W. CLARK. 2000. Communication and acoustic behavior of dolphins and whales. Pp. 156–224 in *Hearing by whales and dolphins* (W. W. L. Au, A. N. Popper, and R. R. Fay, eds.). Springer-Verlag, New York.
- WANG, D., B. WÜRSIG, AND W. E. EVANS. 1995a. Whistles of bottlenose dolphins: comparisons among populations. *Aquatic Mammals* 21:65–77.
- WANG, D., B. WÜRSIG, AND W. E. EVANS. 1995b. Comparisons of whistles among seven odontocete species. Pp. 299–323 in *Sensory systems of aquatic mammals* (R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall, eds.). De Spil Publishers, Woerden, Netherlands.
- WANG, J. Y., L.-S. CHOU, AND B. N. WHITE. 1999. Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *Molecular Ecology* 8: 1603–1612.
- WANG, J. Y., L.-S. CHOU, AND B. N. WHITE. 2000a. Osteological differences between two sympatric forms of bottlenose dolphins (genus *Tursiops*) in Chinese waters. *Journal of Zoology (London)* 252:147–162.
- WANG, J. Y., L.-S. CHOU, AND B. N. WHITE. 2000b. Differences in the external morphology of two sympatric species of bottlenose dolphins (genus *Tursiops*) in the waters of China. *Journal of Mammalogy* 81:1157–1165.
- WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69–94.

Submitted 17 April 2004. Accepted 9 September 2004.

Associate Editor was William L. Gannon.