Off-axis sonar beam pattern of free-ranging finless porpoises measured by a stereo pulse event data logger

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The off-axis sonar beam patterns of eight free-ranging finless porpoises were measured using attached data logger systems. The transmitted sound pressure level at each beam angle was calculated from the animal's body angle, the water surface echo level, and the swimming depth. The beam pattern of the off-axis signals between 45° and 115° (where 0° corresponds to the on-axis direction) was nearly constant. The sound pressure level of the off-axis signals reached 162 dB re 1 μPa peak-to-peak. The surface echo level received at the animal was over 140 dB, much higher than the auditory threshold level of small odontocetes. Finless porpoises are estimated to be able to receive the surface echoes of off-axis signals even at 50-m depth. Shallow water systems (less than 50-m depth) are the dominant habitat of both oceanic and freshwater populations of this species. Surface echoes may provide porpoises not only with diving depth information but also with information about surface direction and location of obstacles (including prey items) outside the on-axis sector of the sonar beam. © 2005 Acoustical Society of America.

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I. INTRODUCTION

The sonar beam of dolphins and porpoises is known to be highly directional (Norris and Evans, 1967; Au et al., 1978; Au, 1980; Au et al., 1986, 1987, 1995, 1999). A beamfocusing system of sonar signals has been proposed for the head region of dolphins and porpoises wherein the skull reflects sounds ahead while the melon organ focuses the sound beam (Au, 1993). This model is supported by numerical simulations of sound propagation (Aroyan et al., 1992). The focused beam of odontocete sonar is advantageous in that it allows animals to concentrate sound energy ahead for the long-range detection of prey. Directional beams have a better signal-to-noise ratio than do omni-directional beams. As top predators in the oceans and rivers, toothed whales use signals produced in a directional beam to assist in the early detection of remote prey items. The sonar range of odontocetes such as finless porpoises Neophocaena phocaenoides and baiji Lipotes vexillifer is estimated to reach several tens of meters in open water systems (Akamatsu et al., 1998).

It is also known that the off-axis beam of odontocete sonar is of sufficient intensity to be recorded (Au, 1980). However, the function of these off-axis signals has not been investigated. In bats, sonar signals are used not only for prey capture but also for acoustic scene analysis (Moss and Surlykke, 2001). Off-axis sonar signals in odontocetes might be used for environmental recognition. The scanning sector of an off-axis beam is wider than that of an on-axis beam. Obstacles outside the on-axis beam sector could be detected by receiving off-axis beam echoes. Whether odontocetes can receive echoes of off-axis beams from obstacles in the wild has not been investigated.

Moreover, the sound beam pattern of dolphins and porpoises has not been measured under free-ranging conditions except for white-beaked dolphin Lagenorhynchus albirostris (Rasmussen et al., 2004). The relative body angle and the distance between the sound source and the hydrophone must be measured to determine the beam pattern. These experimental constraints made measurements of the beam pattern possible only in controlled captive environments, otherwise several criteria are needed to determine the relative direction of an animal to the hydrophone (Rasmussen et al., 2004). The source level of the sonar signals is highly dependent on the echolocation tasks (Au, 1980; Au and Benoit-Bird, 2003). In the open water and under free-ranging conditions, the off-axis beam intensity is potentially different from that observed in captivity, as wild dolphins and porpoises have the complicated task of detecting remote prey.

Using a stereo acoustic data logger, we measured the ultrasonic pulse intensity of sonar signals and echoes from the water surface that are received at the body of the freeranging Yangtze finless porpoise (Neophocaena phocaenoides asiaeorientalis) in an open water system. The off-axis sonar beam pattern was calculated for eight free-ranging animals. We show that the water surface echoes of off-axis signals are sufficient intensity for reception by finless porpoises in their habitat.

II. MATERIALS AND METHODS

A. Study site and animals

The experimental site was an oxbow lake of the Yangtze River, Hubei, China (29.30-29.37'N,112.13-112.48'E).

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FIG. 1. Measurements of body angle and the off-axis beam intensity. The "surge" and "heave" directions of the animal are indicated in the upper left inset. The body angle can be calculated by the surging body acceleration (SA) and the gravity force (G). The water surface echo of the off-axis sound was received by the acoustic data logger attached to the side of the animal. Spherical propagation was assumed in calculating the transmission loss (TL) of the sound during the round trip to the water surface. The absorption coefficient α is also included in the transmission loss.

This was an old course of the Yangtze River, 1–2 km in width and 21 km in length. The maximum depth was approximately 20 m, which occurred along the outer bank of the hoop-shaped lake; most of the lake was shallower than 10 m. The main stream of the river inundates the oxbow during the rainy season. The underwater visibility is less than 1 m owing to turbidity. Finless porpoises in this reserve reproduce annually without supplementary feeding by humans (Wei *et al.*, 2002). The environment of this oxbow is considered to be quite similar to that of the main stream of the Yangtze River (Zhang *et al.*, 1995).

All animals used in this experiment were safely captured in October 2003 and temporally housed in an enclosure ($\sim 30 \times 60$ m with a maximum depth of 3.5 m) established in an inlet adjacent to the oxbow. They were maintained in this enclosure for at least 24 h for the alleviation of stress levels prior to release.

B. Data logger systems and attachment

An acoustic data logger (W20-AS, Little Leonardo, Japan) was used to measure the sound pressure levels of sonar signals. The data logger could record the intensity of ultrasonic pulse events over 129 dB re 1 μ Pa peak to peak level up to 2000 times in a second, and its dynamic range was 31 dB. The data logger had directional sensitivity (see later discussion and Fig. 5) similar to the directional hearing of dolphins and porpoises; thus the detection threshold of the data logger at the on-axis direction (0°) was 129 dB compared with 140 dB when the sound came from a 90° off-axis direction. Because of the contamination of internal thermal noise of the data logger system, a relatively higher detection threshold of 129 dB was intentionally employed compared with the audible threshold level of dolphins and porpoises.

A behavior data logger (PD2GT, Little Leonardo, Japan) was simultaneously used to measure the body angle. In the behavior data logger, an accelerometer with two axes measured the surging and heaving body acceleration, including static gravity force. The surging and heaving acceleration could be converted to the pitch and roll angle of the animal's body (Fig. 1). For example, one gravity force of surging

acceleration corresponded to a vertical ascent in which the body angle was perpendicular to the water surface, while a horizontal body direction was indicated by zero surging acceleration. To eliminate the higher frequency components of accelerations caused by body vibrations, moving averages of acceleration over 100-ms time intervals were used. The dynamic range of the acceleration measurement was \pm five gravity force with 10-bit resolution. The behavioral data logger also recorded the swimming depth and speed and the experienced water temperature.

The acoustic and behavior data loggers were attached on both sides of eight animals by suction cups (Product No. 40-1525-0, Canadian Tire Co. Ltd., Canada). This attachment methodology was simple and less invasive. Each data logger was assembled with a suction cup, a float (expanded polyvinyl chloride Klegecell No. 55, pressure resistant to 8 atm, Kaneka Co. Ltd., Japan), and a transmitter (MM130, Advanced Telemetry Systems, USA). After the experiment, the drag force of the two data logger systems was measured in the experimental towing tank at the National Research Institute of Fisheries Engineering, Japan. The drag force was found to be less than 60 gram-force at the cruising speed of finless porpoises (0.89 m/s).

C. Data analysis

The acoustic data logger recorded direct-path signals from the sound source as well as water surface reflections. The direct-path signal traveled to the acoustic data logger directly from the sound source under the blow hole of the animal (Cranford et al., 1996). The water surface echo is the reflected off-axis signal which is transmitted upward from the animal. The water surface echo delay from the directpath signal should be identical to the two-way sound travel duration between the animal's depth and the surface. Only pulses delayed within ± 1 ms from the calculated delay time according to the animal's depth were used for the analysis. This means that we accepted an error of ± 75 cm in depth (~ half the body length of the animals). Echoes received within 1 m of the water surface were also excluded to avoid noise contamination during respiratory splashing. The water surface echo level was scaled by the directional sensitivity of the acoustic data logger, using the body angle simultaneously measured by the behavior data logger. Assuming spherical sound propagation and flat water surface, the transmission loss during the round trip between the animal and the water surface was $20 \log 2d$ (dB) $+ 2\alpha d$, where d is the swimming depth and α is the absorption coefficient, respectively (Fig. 1). The absorption coefficient at the sonar frequency of 140 kHz in finless porpoises (Akamatsu et al., 1998) is no more than 0.04 dB/m (Urick, 1983). We calculated the sound pressure level of the transmitted off-axis signal at 1 m from the animal by adding the water surface echo level and the transmission loss.

To calculate the beam pattern, a source level of the onaxis signal was needed as a reference. The acoustic data logger was fixed on the animal's body, and the sound travel distance of the direct-path signal was therefore constant. The received sound pressure level of the direct-path signal was considered to be in proportion to the source level of the sonar

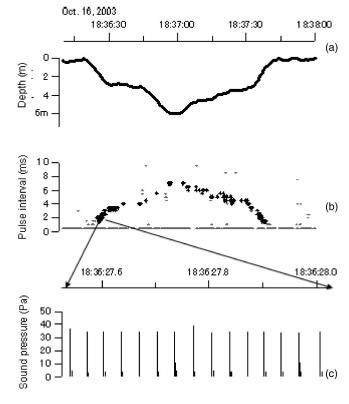


FIG. 2. The depth profile (a), the echo delay (b), and recorded samples of pulse events (c). The echo delay (b) is in proportion with the swimming depth (a) since the round trip time to the surface by underwater sound corresponds to the sound source depth. Especially in shallow water swimming depth, many echoes associated with the sonar signals as shown in double pulse structure in (c).

signals. Using the intensity of the direct-path signal as a reference, we calculated the relative intensity of the off-axis sound pressure level at 1 m from the animal (hereafter termed the "relative beam intensity"). Finally, we obtained the off-axis sonar beam pattern indicated by the relative beam intensity for each body angle of the eight finless porpoises.

III. RESULTS

All the acoustic and behavior data logger systems were retrieved within 3 days of release. They remained attached to the animals for 13.1 h on average and for a maximum of 36.8 h. The period of simultaneous attachment of both the acoustic and behavior data loggers for each individual was 8.75 h on average. During the experiment, the water surface of the lake was almost flat, with no waves. Such a calm condition happens often in the dry season. Assuming negligible reflection loss at the surface, the transmission loss during the round trip between the animal and the water surface was estimated as the spherical propagation, as previously indicated.

An example dive profile and the received echo delay of an animal (serial no. 8) are given in Fig. 2. In this case, the animal dove for 80 s and reached 6 m in depth [Fig. 2(a)]. Most of the interpulse intervals were interpreted as surface echoes (bold dots) during the entire dive bout [Fig. 2(b)].

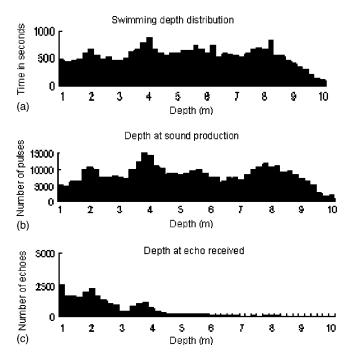


FIG. 3. The time that animals spent at each depth (a), the number of recorded direct-path signals at each depth (b), and the number of recorded echoes at each depth (c). The number of echoes decreased quickly as depth increased.

Many double pulses were observed [Fig. 2(c)], and the intrapulse interval within the double pulses corresponded to the calculated delay time.

The examination of all recorded dive statistics for porpoise 8 shows that this individual dived to depths of up to 10 m [Fig. 3(a)]. The simultaneous recording of dive behavior and sonar signals revealed that the porpoise produced sonar signals at all depths [Fig. 3(b)]. This animal spent relatively longer time periods at 2-, 4-, and 8-m depth and produced many pulses at these depths. The number of pulses per second at each depth was fairly consistent (mean 14.3 pulses/second, standard deviation 2.3). This finless porpoise used sonar almost continuously with relatively constant sensing effort at each swimming depth. However, surface echoes were frequently received by the acoustic data logger at depths of less than 6 m and were rarely received deeper than 6 m [Fig. 3(c)].

The animal swam horizontally most of the time but occasionally rolled (Fig. 4). The surging acceleration clearly peaked at \sim 0 [Fig. 4(a), black line], indicating that the animal mostly swam horizontally. The heaving acceleration ranged from -10 to +15 m/s² [Fig. 4(a), gray line]. The negative gravity force (-9.8 m/s²) of the heaving acceleration corresponded to the animal swimming in a supine posture. The heaving acceleration of this individual shows that the animal sometimes rolled.

The examination of the body acceleration data measured only when surface echoes were received by the acoustic data logger reveals the absence of negative heaving acceleration [Fig. 4(b), gray line]. This means that the animal was swimming with its dorsal side uppermost when the surface echoes were detected. The surface echoes were not received during

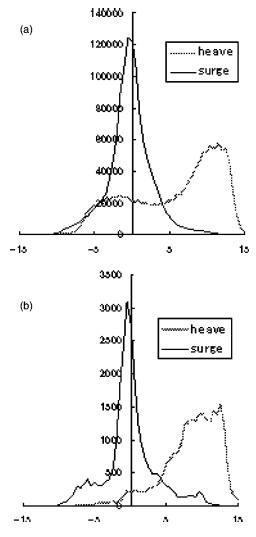


FIG. 4. The number of surging and heaving body accelerations during the entire observation period of animal 8 (a). The number of body accelerations only when surface echoes received is indicated in (b). The distribution of heaving acceleration when surface echo received (b) is positively biased relative to the distribution of (a), indicating that echoes were mostly received during swimming dorsal side uppermost.

swimming in a supine posture. These trends were also observed in the other seven experimental animals.

The off-axis beam pattern could be calculated for a limited range of angles because of the small sample size of near-vertical ascents and the directional sensitivity of the acoustic data logger. As shown in Fig. 4, we observed a very small number of events in which positive and negative gravity force occurred at $\pm 9.8 \text{ m/s}^2$ during surging acceleration. This means that the porpoises rarely ascended or descended in near-vertical postures, and this limited the availability of surface echo data from on-axis signals. When surface echoes were received, porpoise body angles were almost always within 45°-135° degrees (Fig. 5, black circles; 90° is horizontal). Additionally, the directional sensitivity of the acoustic data logger (Fig. 5, white circles) did not allow the reception of off-axis signals at greater than 120°. Over 120°, the detection threshold of the acoustic data logger was close to the thermal noise level of the electric circuit in the logger (dotted line). Therefore, the off-axis beam pattern was calcu-

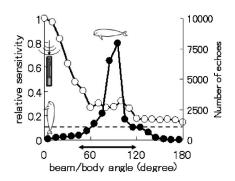


FIG. 5. Directional sensitivity of the acoustic data logger (white circles, left) and the number of received echoes at each body angle (black circles, right). The dotted line indicates the internal electric noise level of the acoustic data logger. As illustrated in the left side of the figure, the data logger is most sensitive when receiving sound coming from 0° (from the front). However, many echoes were received during horizontal swimming (body angle of 90°), and quite a few echoes were received during nearly vertical ascents (0°) and descents (180°) .

lated between 45° and 120° (this angle range is shown as an arrow in Fig. 5).

The averaged off-axis beam pattern of eight finless porpoises for every 10° bin of the body axis is indicated in Fig. 6. The off-axis beam pattern was almost constant across the entire range of this angle.

IV. DISCUSSION

The off-axis sonar beam pattern of free-ranging finless porpoises was obtained by using pulse event recorders attached to the animals. We see three major methodological advantages to our approach. First, there is no need to train animals to be stationed at a fixed point. The body angle was changed by the animal itself, and the intensity of the off-axis beams could be obtained from the water surface echo. Second, the sound pressure level of free-ranging animals can be obtained from the body angle information. The animals could swim freely, thereby enabling the measurement of sonar beam patterns of finless porpoises in the open water system. Third, this method does not require a relatively expensive multi-channel hydrophone system to measure beam patterns.

Many water surface reflections of off-axis signals were beyond the detection threshold level of the acoustic data logger (140 dB re 1 μ Pa, peak-to-peak at 90° of beam angle) during horizontal swimming. The surface echo could be received by the acoustic data logger as deep as 6 m [Fig. 3(c)]. The propagation loss during the round trip from 6 m in depth

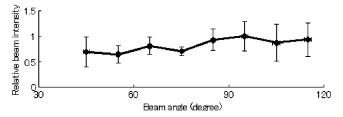


FIG. 6. Off-axis beam pattern of eight finless porpoises. The ordinate shows the relative beam intensity, and the value at 95° is set at 1 as the reference point.

to the surface was 22 dB. During the round trip to the surface, the absorption is estimated to be 0.48 dB which is negligible comparing with 22 dB. Therefore, the source level of the off-axis signal upward (90°) from the horizontally swimming animal was a maximum of 162 dB which is the summation of 140 dB echo level and 22 dB propagation attenuation. Comparing between Fig. 3(b) and (c), approximately half of the transmitted sound associated with surface echo at 1-m depth. This suggests that half of the off-axis sounds have over 146 dB source levels which is the summation of 140 and 6 dB propagation attenuation to the surface from 1-m depth. The lower echoes are out of the dynamic range of the data logger. Therefore, average source level of off-axis signals could not be estimated. Instead, 146 dB seems to be a fair indicator of the ordinary source level of the off-axis beam of finless porpoises.

Finless porpoises are distributed in shallow waters within the Asian continental shelf. An aerial survey of finless porpoises in Japanese waters revealed that they were found in waters shallower than 50-m depth (Shirakihara *et al.*, 1994). They are suggested to have a bottom preference (Akamatsu *et al.*, 2002), possibly for prey capture purposes. They produce sonar signals frequently (Akamatsu *et al.*, 2000), and the echolocation performance of a finless porpoise in target discrimination is reported to be similar to that of a bottlenose dolphin, *Tursiops truncatus* (Nakahara *et al.*, 1997). The finless porpoise belongs to the same family as the harbor porpoise (*Phocoena phocoena*), in which the auditory threshold level is less than 70 dB (Andersen, 1970).

A finless porpoise with an auditory threshold level of 70 dB that is swimming at 50-m depth therefore receives off-axis signal surface echoes at a calculated level of 118 dB (40 dB propagation loss and 4 dB absoption), which is 48 dB higher than the potential auditory threshold level of finless porpoises. This means that finless porpoises are considered to receive surface echoes of off-axis signals with a sufficient signal-to-noise ratio at depths of up to 50 m.

Finless porpoises in our study almost always produced sonar signals, at any depth [Fig. 3(b)]. The maximum depth of the present study area was 20 m, and the maximum transmission loss during the round trip from the lake bed to the surface is 34 dB including 2 dB aborsption loss. Under these circumstances, the echo level received at the animal would be 128 dB. This means that finless porpoises in shallow water environments such as those of the present study can probably receive water surface echoes at all times.

Finless porpoises swam horizontally and dorsal side up when receiving the echoes [Fig. 4(b)]. Therefore, the beam pattern obtained in the present study is on the vertical plane of the dorsal side. Surface echoes could not be received when the animal was swimming in a supine posture. This suggests that the sonar beam of finless porpoises does not propagate ventrally. The upper jaw is a candidate insulator of sound propagated downward from the source. This also suggests that an off-axis sonar beam shadow area might exist on the ventral side of the animal.

The off-axis beam pattern is relatively constant at any measured direction (Fig. 6). Finless porpoises possibly recognize not only a target ahead but also other obstacles within

the off-axis beam sector. The sonar of porpoises might have wider coverage than formerly expected. For example, a 10-cm body length clupeoid fish is estimated to have a target strength of $-51.9 \, dB$ at 38 kHz, according to the formula presented by Foote (1987). The target strength of fish has a slightly negative relationship with the sound frequency. The change of the averaged target strength varies within a few dB in the wide frequency range (Sawada, 2002). Additionally, we should note that the off-axis sonar beam transmitted upward from the porpoise is projected to the ventral side of a fish, but usually the target strength of the fish is measured from the dorsal side. Besides these differences of conditions, we will use the estimated target strength by Foote's formula as an approximate value hereafter. If the fish is 3 m above a finless porpoise, the transmission loss during round trip is 19 dB, making the estimated echo level received by the animal 91 dB, which is still 21 dB above the potential auditory threshold level of a finless porpoise. From a physical point of view, the off-axis beam could be used by finless porpoises for prey and environmental cognition.

An advantage of interpreting the acoustical cues of surface echoes is that not only the depth but also the surface direction can be recognized. As shown in Fig. 4(a), finless porpoises sometimes roll during swimming in a turbid water system. During such a complicated body angle orientation, the directional cue of the surface may aid self-positioning in an environment in which visual cues are less effective. The 162-dB source level of off-axis signals is high enough to allow the bimodal use of sonar. The porpoise detects long-range targets using the on-axis beam and may recognize the environment and other targets out of the on-axis beam sector through off-axis signals. An "acoustical sidelong glance" is therefore considered to be physically possible with the use of sonar by finless porpoises.

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- Akamatsu, T., Wang, D., Nakamura, K., and Wang, K. (1998). "Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*), and bottlenose dolphin (*Tursiops truncatus*)," J. Acoust. Soc. Am. 104, 2511–2516.
- Akamatsu, T., Wang, D., Wang, K., and Naito, Y. (2000). "A method for individual identification of echolocation signals in free-ranging finless porpoises carrying data loggers," J. Acoust. Soc. Am. 108, 1353–1356.
- Akamatsu, T., Wang, D., Wang, K., Wei, Z., Zhao, Q., and Naito, Y. (2002). "Diving behavior of freshwater finless porpoises (*Neophocaena phocaenoides*) in an oxbow of the Yangtze River, China," ICES J. Mar. Sci. 59, 438–443.
- Andersen, S. (1970). "Auditory sensitivity of the harbour porpoise *Phocoena phocoena*," in *Investigations on Cetacea*, edited by G. Pilleri, Vol. II (Hirnanatomisches Institut, Berlin), pp. 255–259.
- Aroyan, J. L., Cranford, T. W., Kent, J., and Norris, K. S. (1992). "Computer modeling of acoustic beam formation in *Delphinus delphis*," J. Acoust. Soc. Am. 92, 2539–2545.
- Au, W. W. L. (1980). "Echolocation signals of the Atlantic bottlenose dolphin *Tursiops truncatus* in open waters," in *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish (Plenum, New York), pp. 251–282.
- Au, W. W. L. (1993). The Sonar of Dolphins (Springer, New York), pp. 1–277.
- Au, W. W. L., and Benoit-Bird, K. J. (2003). "Automatic gain control in the echolocation system of dolphins," Nature (London) 423, 861–863.
- Au, W. W. L., Floyd, R. W., and Haun, J. E. (1978). "Propagation of Atlantic bottlenose dolphin echolocation signals," J. Acoust. Soc. Am. 64, 411–422.
- Au, W. W. L., Moore, P. W. B., and Pawloski, D. (1986). "Echolocation transmitting beam of the Atlantic bottlenose dolphin," J. Acoust. Soc. Am. 80, 688–691.
- Au, W. W. L., Penner, R. H., and Turl, C. W. (1987). "Propagation of beluga echolocation signals," J. Acoust. Soc. Am. 82, 807–813.
- Au, W. W. L., Kastelein, R. A., Rippe, T., and Schooneman, N. M. (1999). "Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*)," J. Acoust. Soc. Am. 106, 3699–3705.

- Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M., and Gisiner, R. C. (1995). "Echolocation signals and transmission beam pattern of a false killer whale *Pseudorca crassidens*," J. Acoust. Soc. Am. 98, 51–59.
- Cranford, T. W., Amundin, M., and Norris, K. S. (1996). "Functional morphology and homology in the odontocete nasal complex: implications for sound generation," J. Morphol. 228, 223–285.
- Foote, K. G. (1987). "Fish target strengths for use in echo integrator surveys," J. Acoust. Soc. Am. 82, 981–987.
- Moss, C. F., and Surlykke, A. (2001), "Auditory scene analysis by echolocation in bats," J. Acoust. Soc. Am. 110, 2207–2226.
- Nakahara, F., Akira, T., Koido, T., and Hirud, H. (1997). "Target discrimination by an echolocating finless porpoise, *Neophocaena phocaenoides*," Marine Mammal Sci. 13, 639–649.
- Norris, K. S., and Evans, W. E. (1967). "Directionality of echolocation clicks in the rough-tooth porpoise, *Steno bredanensis* (Lesson)," *Marine Bio Acoustics*, edited by W. N. Tavolga (Pergamon, Oxford), pp. 305–316.
- Rasmussen, M. H., Wahlberg, M., and Miller, L. A. (2004). "Estimated transmission beam pattern of clicks recorded from free-ranging whitebeaked dolphins (*Lagenorhynchus albirostris*)," J. Acoust. Soc. Am. 116, 1826–1831.
- Sawada, K. (2002). "Study on the precise estimation of the target strength of fish," Bulle. of Fishe. Rese. Agency 2, 47–122 (in Japanese).
- Shirakihara, M., Shirakihara, K., and Takemura, A. (1994). "Distribution and seasonal density of the finless porpoise *Neophocaena phocaenoides* in the coastal waters of western Kyushu, Japan," Fishe. Scie. 60, 41–46.
- Urick, R. J. (1983). Principles of Underwater Sound, 3rd ed. (McGraw-Hill, New York), p. 423.
- Wei, Z., Wang, D., Kuang, X., Wang, K., Wang, X., Xiao, J., Zhao, Q., and Zhang, X. (2002). "Observations on behavior and ecology of the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*) group at Tian-e-Zhou Oxbow of the Yangtze River," Raffles Bull. of Zool., Suppl. 10, 97–103.
- Zhang, X., Wei, Z., Wang, X., Yang, J., and Chen, P. (1995). "Studies on the feasibility of establishment of a semi-natural reserve at Tian-e-zhou (swan) oxbow for baiji, *Lipotes vexillifer*," Acta Hydrobiol. Sinica 19, 110–123