

Variation in the production rate of biosonar signals in freshwater porpoises

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The biosonar (click train) production rate of ten Yangtze finless porpoises and their behavior were examined using animal-borne data loggers. The sound production rate varied from 0 to 290 click trains per 10-min time interval. Large individual differences were observed, regardless of body size. Taken together, however, sound production did not differ significantly between daytime and nighttime. Over the 172.5 h of analyzed recordings, an average of 99.0% of the click trains were produced within intervals of less than 60 s, indicating that during a 1-min interval, the number of click trains produced by each porpoise was typically greater than one. Most of the porpoises exhibited differences in average swimming speed and depth between day and night. Swimming speed reductions and usage of short-range sonar, which relates to prey-capture attempts, were observed more often during nighttime. However, biosonar appears to be affected not only by porpoise foraging, but also by their sensory environment, i.e., the turbid Yangtze River system. These features will be useful for passive acoustic detection of the porpoises. Calculations of porpoise density or abundance should be conducted carefully because large individual differences in the sound production rate will lead to large estimation error. © 2013 Acoustical Society of America. [<http://dx.doi.org/10.1121/1.4796129>]

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I. INTRODUCTION

Many animals produce species-specific sounds. Acoustic signaling, particularly underwater, plays an important role in cognition and the social interactions of animals inhabiting aquatic systems in which non-acoustic cues such as light are less available. Researchers have exploited this characteristic to monitor aquatic animals using passive acoustic monitoring (PAM). PAM has been used to observe the presence, species identity, movement, and distribution of cetaceans (reviewed by Mellinger *et al.*, 2007), pinnipeds (reviewed by Van Opzeeland *et al.*, 2008), sirenians (e.g., Phillips *et al.*, 2004; Ichikawa *et al.*, 2006), and fish (reviewed by Luczkovich *et al.*, 2008).

In PAM, detection performance strongly depends on the production rate of acoustic cues of the target animals

(Kimura *et al.*, 2010; Marques *et al.*, 2011; Kyhn *et al.*, 2012). The production rate of the target sound should be determined in advance of PAM to evaluate its effectiveness. A low sound production rate would reduce the detection ratio within a limited observation period. Lack of acoustic detection does not necessarily indicate the absence of animals but may result from silence of the target animals (Mackenzie *et al.*, 2006). Neither possibility can be rejected without information on the sound production rate of the target species and how this rate changes in relation to environmental and individual variability.

Tagging or biologging with acoustical monitoring devices such as D-tags (reviewed by Johnson *et al.*, 2009), A-tags (Akamatsu *et al.*, 2005a), or B-probes (e.g., Oleson *et al.*, 2007) has been verified as a useful method to estimate the underwater phonating behavior of target whales, dolphins, and porpoises. Previous studies on phonating cetaceans using acoustic tagging have shown that the sound production rate of large-toothed whales is condition-dependent. Cuvier's whales (*Ziphius cavirostris*; Tyack *et al.*, 2006), Blainville's beaked whales (*Mesoplodon densirostris*; Aguilar de Soto *et al.*, 2012), and sperm whales (*Physeter macrocephalus*; Watwood *et al.*, 2006) only begin

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their acoustic sensing below 100 m depth. Additionally, their diving behavior and accompanying vocalizations can differ between daytime and nighttime (Arranz *et al.*, 2011). However, knowledge of condition-dependent phonating rates in small odontocetes, such as dolphins and porpoises, is still limited.

The phonating behavior of small odontocetes is quite different from that found in large odontocete species. Click trains, sequences of ultrasonic pulses produced by dolphins or porpoises, are used for orientation underwater and for prey capture (Au, 1993). Especially for porpoises, click trains are easy to identify and detect against background noise given their high-frequency and narrowband sonar signals (Au, 1993), which are suitable for PAM. Akamatsu *et al.* (2005b), Akamatsu *et al.* (2007), and Kimura *et al.* (2010) demonstrated that harbor porpoises (*Phocoena phocoena*) and Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) produce click trains at intervals as short as a few seconds on average. However, the time dependence of and individual differences in click train production have not yet been documented. In this study, we examined the possible time-dependent click train production rate of ten Yangtze finless porpoises (*N. asiaeorientalis asiaeorientalis*) using animal-borne data loggers. Behavior changes may also result in changes of the click train production rate; thus, swimming and possible foraging behaviors, such as swimming speed reductions and use of short-range sonar, observed in a previous study (Akamatsu *et al.*, 2010), were also compared between daytime and nighttime. Cetaceans are known to swim continuously (reviewed by Lyamin *et al.*, 2008). Although the Yangtze finless porpoises also swim and dive most of the time (Sakai *et al.*, 2011), no study to date has compared the behavior of this species between the daytime and nighttime.

II. MATERIALS AND METHODS

A. Study sites and biologging procedure

Tagging experiments were conducted to examine the echolocation behavior of Yangtze finless porpoises in an old course oxbow of the Yangtze River (29.47°–29.51° N, 112.32°–112.37° E) in Shishou, Hubei Province, China, in October 2004, April 2006, and April 2008. This oxbow was formerly a part of the Yangtze River but was naturally cut from the main stream in 1972. It was designated as a seminatural reserve for *ex situ* protection of the baiji (*Lipotes vexillifer*) and the Yangtze finless porpoises by the Chinese government in 1992 and became a part of the Tian-e-Zhou Baiji National Natural Reserve of the Yangtze River. Some porpoises have been introduced to the reserve from the main-stream of the Yangtze River since the 1990s, and others were born in the oxbow (Wang *et al.*, 2000; Wang *et al.*, 2006). The oxbow is about 21 km long and 1–2 km wide and has a maximum depth of about 35 m and less than 1 m visibility, which is approximately the same width, depth, and visibility as the wild habitat of the porpoise in the Yangtze River. The porpoises capture their own natural prey such as fish and shrimp. Daytime and nighttime occurred from

approximately 06:30 to 18:30 and 18:30 to 06:30, respectively, in October and April, at the study site.

Before the tagging operation, the animals were captured from the oxbow and temporarily released into a net enclosure for 24 h to calm down. The enclosure was established close to shore and measured approximately 30 × 60 m with a maximum depth of 3.5 m. The capture procedure has been described in detail previously (Akamatsu *et al.*, 2005a).

The animals were tagged and released within 2 days of capture. The porpoises were outfitted with two tags, an acoustic data logger (A-tag, 62 g, 21 mm in diameter, 115 mm in length without hydrophone, Marine Micro Technology, Saitama, Japan) and a behavioral data logger (W250-PD2GT, 122 mm in length, 22 mm in diameter, 73 g in air; Little Leonardo Ltd., Tokyo, Japan) using suction cups.

Each A-tag consisted of two ultrasonic hydrophones approximately 105 mm apart, a high-gain amplifier (+60 dB), a central processing unit (PIC18F6620, Microchip, Detroit, MI), flash memory (128 MB), and a lithium battery (CR2) housed in a waterproof aluminum case that was pressure-resistant to a depth of 200 m. The hydrophones (−201 dB re 1 V/ μ Pa sensitivity) have a resonant frequency of 120 kHz (100–160 kHz, 5-dB bandwidth) and a bandpass filter of 55–235 kHz (−3 dB). This filter received the frequency band of Yangtze finless porpoise biosonar signals, which exhibit peak frequencies between 87 and 145 kHz, with an average of 125 ± 6.92 kHz (Li *et al.*, 2005). The A-tag is a pulse event data logger that stores the time, received sound pressure, and time-arrival difference between the two hydrophones every 0.5 ms, which is less than the minimum inter-click interval of finless porpoises (Li *et al.*, 2007). The time difference can be converted to a relative angle to identify the sound-source direction. The waveform and frequency of received sound are not recorded. To save memory, we recorded sound pressure only above a preset detection threshold level (134 dB peak-to-peak re 1 μ Pa). The time-arrival difference was measured separately from sound pressure. A pulse above the preset threshold level triggered the counter to measure the delay time between the two hydrophones at 271-ns resolution. The baseline length of the two hydrophones was 105 mm, which corresponds to a maximum time difference of 70- μ s sound-arrival in water. Given the 271-ns resolution, the time-arrival difference was digitized within ± 258 counts (70/0.271). Upon detection of the first pulse above the trigger level within each 0.5-ms period, the high-speed counter at 271-ns resolution measured the time difference until the trigger level occurred at the other hydrophone. At the end of the 0.5-ms time bin, the sound intensity at the primary hydrophone and the separately measured time-arrival difference were stored.

The behavioral data logger recorded depth, swimming speed relative to the water using a propeller sensor, and surge and heave acceleration. The rotation of the propeller sensor per second was converted to vertical speed (m/s) in IGOR PRO 6.03 (WaveMetrics, Lake Oswego, OR) by Akamatsu. The sampling intervals for depth, swimming speed, and acceleration were 1, 0.125, and 0.0625 s, respectively.

The A-tag and the behavior tag were always attached to the right and left side of the animal body above the pectoral fin, respectively, about 30 cm from the head. The hydrophones of the A-tag were positioned about 30–40 cm behind the porpoise's blowhole. After body size and weight were measured and sex was checked, the animal was released. Upon spontaneous release of the suction cup, the tag was retrieved using a VHF radio transmitter (MM110; Advanced Telemetry Systems, Isanti, MN) fixed at the tail of a float on each tag.

B. Data analysis

Signal processing was conducted using a custom-made program developed in IGOR PRO 6.03 (WaveMetrics, Lake Oswego, OR). Abnormal behavior of the tagged animals, such as frequent short dives, was only observed in a few individuals, and all animals appeared to become habituated soon after release. The first part of the data (4–9 min) was excluded from the analysis by looking at data both to remove the effect of release and to fit 10 min time window. The last part of the data was also removed if the sound pressure level or acceleration and speed change became smaller, which was considered as tag-detaching.

The click train was defined based on Kimura *et al.* (2010) as a group of more than six pulses interspersed between 2 and 100 ms apart. The pulse within 2 ms after the direct path pulse was eliminated as a possible reflection. Because the mean minimum lag time to process returning echoes inside an animal brain is 2.5 ms (Au, 1993), porpoise sounds are likely not excluded in this processing. During signal processing, we extracted click trains from recordings for which the dive duration was longer than 0.1 s. To exclude splash noises during respiration, we did not use acoustic data recorded 2 s before and after respiration, which was defined as when the animal's depth was less than 0.3 m and its swimming speed was slower than 0.2 m/s. Because we attached the tags to the side of the body about 30 cm from the blowhole, a depth of less than 0.3 m was recorded by the behavioral data logger. At this moment, the propeller sensor is stopped in the air. Although clicking may occur at the surface, we cannot extract these click trains due to splash noise.

Click trains produced by a tagged animal were identified using the time difference of the same sound recorded in two hydrophones of the acoustic tag (Akamatsu *et al.*, 2010). Click trains from a tagged animal come from a specific angle range because the relative direction from the acoustic tag to the sound source below the blowhole was relatively constant. Only click trains coming from an angle of $\pm 34^\circ$ were considered to have been produced by the tagged animal; this angle range corresponded to a 12-cm shift in the position of the head relative to the body (Akamatsu *et al.*, 2010). If another porpoise phonated from a location ahead of the tagged animal and it exceeded the threshold and passed the other filters, we were not able to distinguish its signal from the signals of the tagged animal. We excluded sounds received in only one hydrophone, which did not trigger the second one. In this case, the time difference of the wave or bearing angle information of the sound source was not

available even if the tagged animal produced it. The click train production rate was defined as the number of click trains produced per 10 min time bin.

We compared the swimming speed and duration of dives, which were defined as diving deeper than 1 m, between day and night. The duration of speed reductions and short-range sonar use were also examined as an index of possible foraging behavior (Akamatsu *et al.*, 2010). A swimming speed reduction was defined as speeds less than 0.5 m/s when the porpoise was deeper than 2 m. A short-range sonar incident was defined as a click train having less than 10-ms intervals at most. To measure the duration of dives and swimming speed reduction, we used Ethographer ver. 1.42 under an Igor Pro platform made by Sakamoto (Sakamoto *et al.*, 2009).

III. RESULTS

In total, 38 porpoises were tagged; of these, 10 porpoises (9 males and 1 female) retained both acoustic and behavior tags over 7 h and thus generated appropriate data for further analysis. The body length and mass of the ten animals were 143 ± 13 cm and 50 ± 12 kg [mean \pm standard deviation (S.D.)], respectively. Although body length was correlated with body weight, the click train production rate, swimming speed, and depth had no relationship with body size (Fig. 1).

The click train production rate of the ten porpoises varied from 0 to 290 click trains per 10-min time bin (Fig. 2). On average, they produced 95.9 ± 64.7 click trains (mean \pm S.D.) per 10 min, indicating that the inter-click-train interval was approximately 6.3 s on average. Over 99.0% of the inter-click-train intervals were shorter than 60 s. The click train production rate was not related to the mean swimming speed, diving duration, or depth over 10-min intervals ($R^2 < 0.1$).

One porpoise, ID 28, had only daytime data from 10:30 to 17:30 (Fig. 2). Thus, we used the data for the other nine porpoises for comparisons of day and night. No significant difference was observed in the click train production rate between day and night in six individuals (Table II). IDs 35 and 38 produced click trains more often at night, and ID 50 produced them more often during the day (Table II; Wilcoxon's signed-rank test, $p < 0.05$, 0.01, and 0.05, respectively). Taken together, however, click train production rate did not significantly differ between day and night (Wilcoxon's signed-rank test, $p = 0.58$).

The mean swimming depth and speed varied from 2.1 to 10.9 m and 0.6 to 2.2 m/s, respectively, and exhibited differences between day and night (Table II). Average swimming speed was faster during the day than at night in eight individuals (Table II); only ID 38 swam faster at night. Large individual differences were observed in dive duration (Table II). Three animals (IDs 30, 35, and 51) tended to dive longer during the day, but three others (IDs 38, 42, and 52) showed the opposite behavior. IDs 31 and 50 exhibited no differences between day and night. Swimming depth tended to be deeper during the day, although three animals (IDs 38, 50, and 52) showed the opposite behavior (Table II). Possible

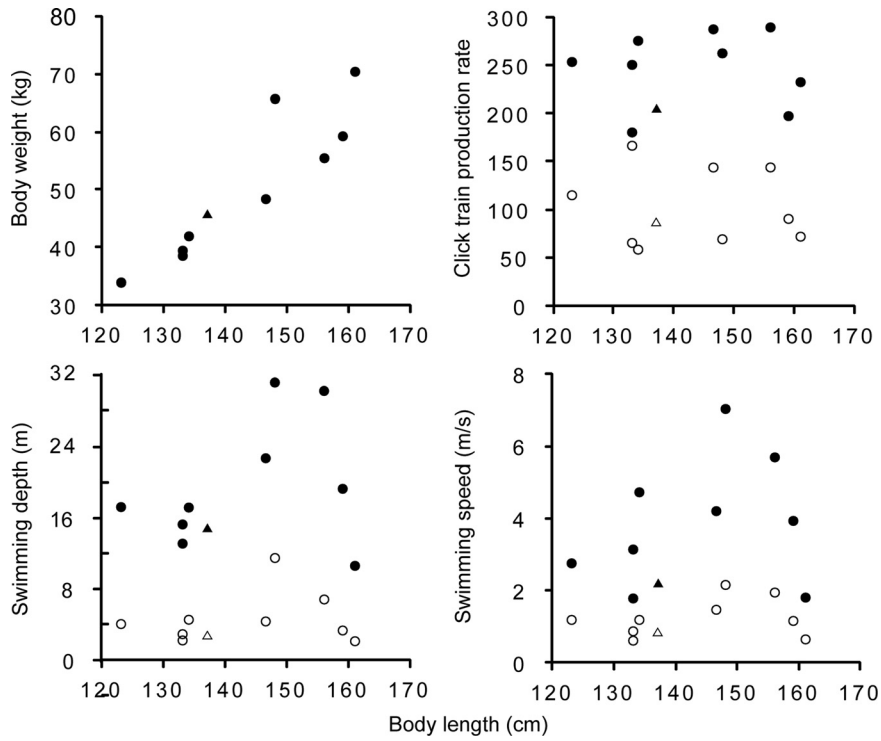


FIG. 1. Relationships of body length with body weight (top left), average (white) and maximum (black) click train production rate (i.e., the number of click trains produced in 10 min, top right), swimming depth (bottom left), and swimming speed (bottom right). The triangle indicates the female, ID 51.

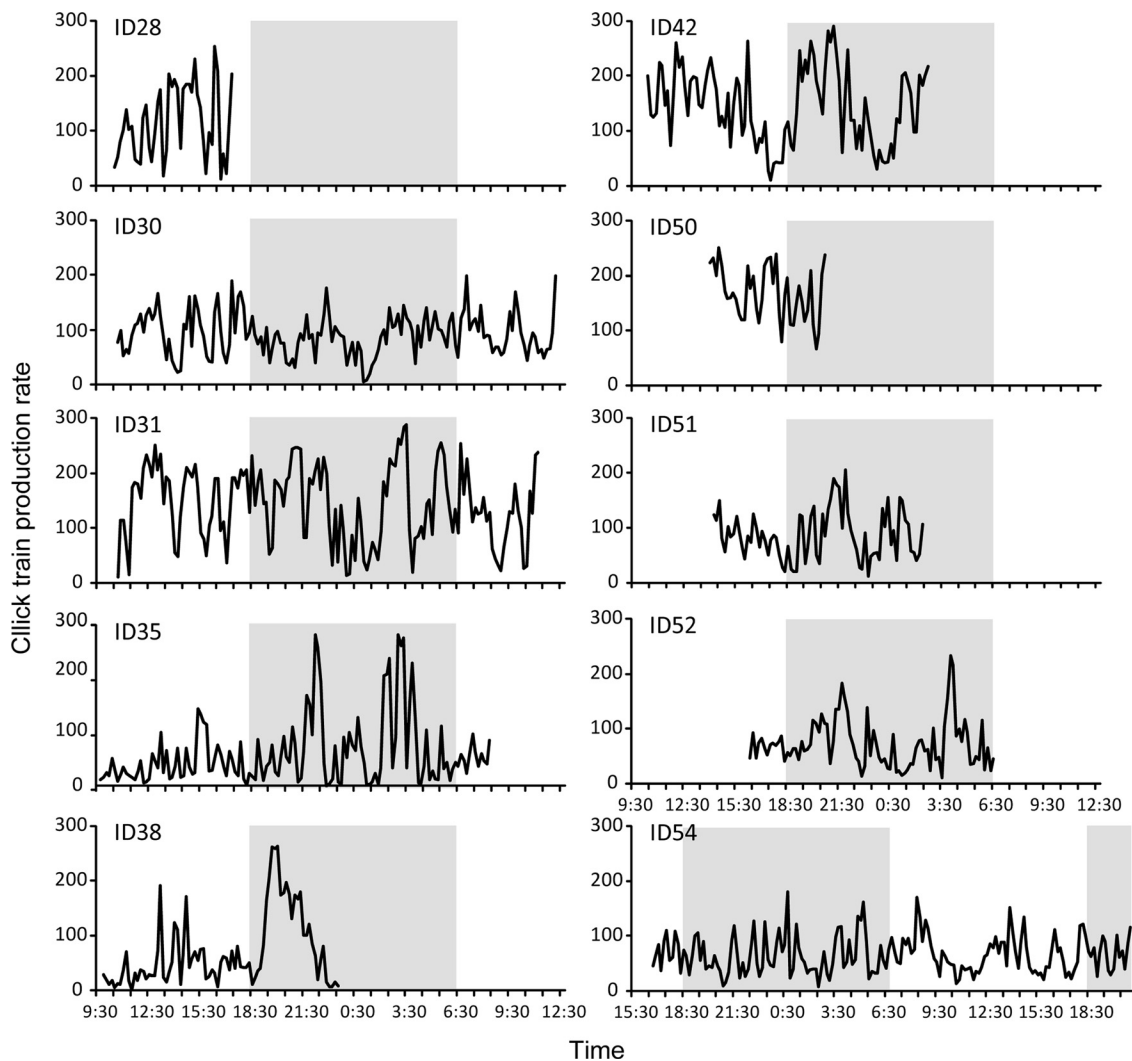


FIG. 2. The click train production rate of the tagged animals (i.e., the number of click trains produced in 10 min interval) while tagged. Gray areas indicate nighttime.

TABLE I. Detailed information of ten tagged finless porpoises with data from at least 7 h of both acoustic and behavior tags. ID 51 was the only female; all others were male.

ID	Released date	Duration for analysis	Body weight (kg)	Body length (cm)	Mean depth (m)	Mean speed (m/s)	10-min mean of the click train
28	13 Oct. 2004	7:00	34.0	123	4.0	1.2	115.6
30	13 Oct. 2004	25:40	59.4	159	3.4	1.2	91.0
31	13 Oct. 2004	24:40	48.5	147	4.0	1.5	144.5
35	21 Apr. 2006	22:50	42.0	134	4.5	1.2	59.0
38	21 Apr. 2006	13:50	65.8	148	10.9	2.2	69.8
42	21 Apr. 2006	16:40	55.6	156	6.8	2.0	144.6
50	3 Apr. 2008	6:50	38.6	133	2.1	0.6	167.2
51	3 Apr. 2008	12:20	45.8	137	3.4	0.9	87.3
52	3 Apr. 2008	14:20	70.5	161	2.4	0.7	72.5
54	3 Apr. 2008	28:30	39.5	133	3.0	0.9	66.0

feeding attempts, duration of swimming speed reductions, and usage of short-range sonar were observed more frequently at night in eight of nine individuals (Table III).

IV. DISCUSSION

Our results indicate that the click train production rate of the porpoises showed considerable individual variability. This variation was not related to body size (Fig. 1), although larger animals were anticipated to produce more sound to capture more prey to maintain their body weight. Some porpoises produced biosonar more often during the day or at night. However, the bias of sensing effort became smaller with increased sample size, and overall, no differences were observed between day and night (Fig. 2 and Table II). The Yangtze River is so turbid that visibility is quite limited and is generally less than 1 m even during the day. This low visibility could force these porpoises to use echolocation even when they are not foraging. Strong demand for acoustic sensing in turbid water could explain why the porpoises showed no difference in echolocation signals produced during the day and night. Note that these data were not sufficient to discuss diurnal or circadian rhythms, as the data set would need to include at least more than two 24-h cycles.

Large individual differences were observed in the click train production rate. For example, the average click train production rate varied from 59 (ID 59) to 167 (ID 50; Table I), which corresponds to 10- and 3.6-s inter-click-train intervals, respectively. Additionally, the click train production rate of the same individual also changed greatly over time (Fig. 2). Thus, during the PAM of porpoises, the calculation of density or abundance must be done carefully because the wide range of sound production rates would lead to a large estimation error of density estimated by the PAM (Kimura *et al.*, 2010). The large individual variation in acoustic and swimming behavior may reflect the small group size of this species. Gotz *et al.* (2006) reported that when rough-toothed dolphins (*Steno bredanensis*) swim in tight formation, they eavesdrop on the echoes of sonar signals of conspecifics and reduce their own sonar production, suggesting that the sound production rate may change with group size for gregarious species. However, our study species swims mostly alone or in small groups (Akamatsu *et al.*, 2008; Kimura *et al.*, 2009). Moreover, the click train production rate does not vary much with the number of surrounding animals in this species (Kimura *et al.*, 2010).

Four limitations must be acknowledged in our analysis, making our estimates of the sound production rate

TABLE II. Day-night differences in the number of click trains averaged in 10 min, i.e., click train production rate and swimming behavior. One and two asterisks indicate significant differences by Wilcoxon's signed-rank test, $p < 0.05$ and $p < 0.01$, respectively. As a whole, the click train production rate and dive duration did not differ between day and night. The porpoises swam faster during the day, with the exception of ID 38. The porpoises tended to dive longer and deeper during the day, with the exceptions of IDs 38, 42, and 52 and IDs 38, 50, and 52, respectively.

ID	Sample size	Number of click trains		Swimming speed (m/s)		Duration of diving (s)		Swimming depth (m)	
	Day / Night	Day / Night	p	Day / Night	p	Day / Night	p	Day / Night	p
30	82 / 72	96.8 ± 41.8 / 84.7 ± 34.5	0.11	1.2 ± 0.3 / 1.1 ± 0.4	**	423 ± 35 / 383 ± 52	**	4.0 ± 1.5 / 2.9 ± 1.4	**
31	76 / 72	140.9 ± 64.1 / 146.5 ± 75.1	0.45	1.6 ± 0.4 / 1.3 ± 0.3	**	465 ± 30 / 457 ± 23	0.15	4.5 ± 1.7 / 3.5 ± 1.3	**
35	65 / 72	41.8 ± 31.3 / 74.6 ± 77.6	*	1.4 ± 0.4 / 1.1 ± 0.3	**	461 ± 32 / 435 ± 41	**	5.5 ± 1.5 / 3.8 ± 1.4	**
38	52 / 31	46.2 ± 37.5 / 109.4 ± 82.8	**	2.1 ± 0.7 / 2.3 ± 0.5	*	500 ± 24 / 517 ± 24	**	10.5 ± 3.4 / 11.6 ± 4.5	*
42	49 / 50	141.5 ± 64.6 / 149.0 ± 73.3	0.75	2.1 ± 0.6 / 1.8 ± 0.5	**	472 ± 24 / 488 ± 34	**	7.0 ± 1.9 / 6.6 ± 2.1	0.09
50	27 / 14	177.3 ± 45.6 / 147.6 ± 50.5	*	0.7 ± 0.1 / 0.5 ± 0.1	**	395 ± 56 / 360 ± 78	0.83	2.1 ± 0.8 / 2.2 ± 0.7	0.14
51	26 / 48	82.0 ± 30.7 / 89.7 ± 50.9	0.75	1.0 ± 0.2 / 0.8 ± 0.2	**	429 ± 26 / 421 ± 29	*	3.9 ± 1.0 / 3.1 ± 0.9	0.09
52	14 / 72	65.6 ± 17.1 / 73.8 ± 46.9	0.19	0.9 ± 0.1 / 0.6 ± 0.1	**	379 ± 48 / 444 ± 28	*	2.2 ± 0.6 / 2.4 ± 0.6	0.43
54	83 / 88	67.2 ± 33.2 / 64.8 ± 35.5	0.38	0.9 ± 0.1 / 0.8 ± 0.1	**	373 ± 66 / 336 ± 67	0.38	3.5 ± 0.9 / 2.5 ± 0.8	**

TABLE III. Day-night differences in possible feeding behavior. Two and one asterisks indicate significant differences by Wilcoxon's signed-rank test, $p < 0.01$ and $p < 0.05$, respectively. The duration of swimming speed reduction (< 0.5 m/s at deeper than 2 m depth) was longer during the night, with the exception of ID 38. Short-range sonar (< 10 ms inter-click intervals) was observed more at night, with the exception of ID 30.

ID	Sample size	Duration of speed reduction (s)		Number of short-range click trains	
	Day / Night	Day / Night	p	Day / Night	p
30	82 / 72	8.6 ± 12.5 / 13.7 ± 22.7	0.28	4.2 ± 6.5 / 3.6 ± 6.3	0.4
31	76 / 72	7.1 ± 12.5 / 8.9 ± 11.6	*	4.6 ± 5.7 / 6.8 ± 7.8	*
35	65 / 72	20.7 ± 24.7 / 46.5 ± 62.8	*	4.0 ± 5.3 / 13.8 ± 31.4	*
38	52 / 31	12.1 ± 18.9 / 7.0 ± 7.9	0.24	2.2 ± 2.8 / 20.3 ± 22.4	**
42	49 / 50	6.0 ± 9.5 / 11.1 ± 17.0	0.27	8.8 ± 10.6 / 26.0 ± 30.9	**
50	27 / 14	20.3 ± 27.2 / 58.7 ± 36.7	*	6.7 ± 7.2 / 23.4 ± 13.5	**
51	26 / 48	5.0 ± 6.4 / 29.7 ± 42.8	**	1.4 ± 2.8 / 2.9 ± 3.7	*
52	14 / 72	8.3 ± 20.0 / 95.5 ± 119.7	0.08	0.4 ± 1.1 / 2.9 ± 5.2	0.12
54	83 / 88	1.9 ± 3.1 / 5.7 ± 8.9	**	0.5 ± 1.3 / 0.6 ± 1.7	0.95

conservative. First, because we used a threshold level of 134.0 dB peak-to-peak re $1 \mu\text{Pa}$, low-level click trains could have been missed; thus, some click trains might have been eliminated from the analysis. However, we assumed that most of the sounds produced by the tagged porpoises were recorded because the source level of this animal has been estimated to be 180–209 dB re $1 \mu\text{Pa}$ pp at 1 m (Li *et al.*, 2009), and off-axis signals of harbor porpoises recorded close to the pectoral fin exhibit an attenuation of only 44 dB relative to the source level (Hansen *et al.*, 2008). To date, no studies have examined the off-axis attenuation of finless porpoises, but harbor porpoises and finless porpoises are considered to have similar acoustic characteristics. Second, the signals from the tagged animals were excluded if the sound was received by only one hydrophone, and we could not calculate the time difference between two hydrophones because we decoded the sound production of the tagged animal as clicks coming from an angle of $\pm 34^\circ$. Thus, the click train production rate might have been underestimated. The third limitation is the definition of click trains, i.e., a group of clicks interspersed with intervals between 2 and 100 ms. Therefore, if porpoises emitted one or more clicks at intervals of less than 2 ms or more than 100 ms, they would not have been identified as belonging to the same click train. Fourth, when an animal's depth was less than 0.3 m or its swimming speed was slower than 0.2 m/s within 2 s after respiration, we omitted the acoustic data to exclude splash noises.

The Yangtze finless porpoises dove almost continuously during both day and night (Table II), as would be expected because cetaceans swim continuously due to unihemispheric slow-wave sleep (reviewed by Lyamin *et al.*, 2008). Most of the porpoises exhibited differences in swimming behavior between daytime and nighttime (Tables II and III). Porpoises tended to feed more often during the night, as swimming speed reductions and usage of short-range sonar, which are related to prey capture attempts (Akamatsu *et al.*, 2010), were observed more often at night. This behavior is often related to an adaptation to the circadian rhythms of prey species (e.g., Baird *et al.*, 2001; Benoit-Bird and Au, 2003; Scott and Chivers, 2009). Finless porpoises living in seawater are considered to be opportunistic feeders preying on various fish species and crustaceans (Barros *et al.*, 2002; Park *et al.*, 2005;

Shirakihara *et al.*, 2008). The Yangtze finless porpoise may prefer to forage on nocturnal fish or shrimp.

Previous studies on echolocating cetaceans using tagging methods have mainly targeted large odontocetes such as *Mesoplodon*, *Ziphius*, or *Physeter* (reviewed by Johnson *et al.*, 2009). Diving behavior differs greatly between these whales and small odontocetes, i.e., dolphins and porpoises. Toothed whales employ a strategy of diving deeply and only echolocating in deep water. Whales such as *M. densirostris* (Aguilar de Soto *et al.*, 2012), *Z. cavirostris* (Tyack *et al.*, 2006), and *P. macrocephalus* (Watwood *et al.*, 2006) begin acoustic sensing at depths deeper than 100 or 200 m. In contrast, small odontocetes, especially porpoises, live in shallow waters and their echolocation behavior is considered to vary less with depth (Au, 1993). Our results indicate that the Yangtze finless porpoises exhibited large individual differences in biosonar production and swimming behavior. From a practical point of view, their frequent click train production, regardless of the time of day, offers an advantage for applying PAM in this species. However, the density may fluctuate widely if the click train production rate changes greatly within an individual, even per 10-min interval. The causes and effects of changes in the biosonar production rate, swimming behavior, and their relationship should be examined in future studies.

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