



Diel changes in the movement patterns of Ganges River dolphins monitored using stationed stereo acoustic data loggers

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ABSTRACT

We monitored the underwater movements of Ganges River dolphins using stationed stereo acoustic data loggers. We estimated these movements using changes in the relative angle of the sound source direction (trajectory). Of the total acoustic recordings (66 h), 26.2% contained trajectories of dolphins, and 78.6% of these trajectories involved single animals, suggesting that dolphins tended to swim alone and were localized near the monitoring station. The observed trajectories were categorized as follows: staying type characterized by small changes in the sound source direction, moving type A (moving in the same direction), and moving type B (moving up and down the stream during recording). The average interpulse intervals of sounds in moving types A and B were significantly shorter than that of the staying type, suggesting that dolphins produce the former types of trajectories to echolocate across shorter distances during movement. The frequency of occurrence of moving type A increased during the night, whereas that of type B increased in the late afternoon and that of the staying type increased during the daytime. These results indicate that dolphins moving at night tended to use short-range echolocation, whereas during the day, they remained in relatively small areas and used long-range sonar.

Key words: A-tag, diel activity pattern, echolocation, Ganges River dolphin, *Platanista gangetica gangetica*, passive acoustic monitoring.

Ganges River dolphins (*Platanista gangetica gangetica*) are a freshwater species inhabiting the Ganges, Brahmaputra-Meghna, and Sangu-Karnaphuli River

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systems of India, Bangladesh, and Nepal (Smith *et al.* 1994, Sinha *et al.* 2000, Smith *et al.* 2001). The population of Ganges River dolphins was recently estimated to number in the thousands (Smith and Reeves 2000), although the population is gradually decreasing due to multiple threats such as bycatch, collisions with boats, and pollution caused by human activities, including agricultural runoff and industrial wastewater (Sinha *et al.* 2000, Smith and Braulik 2008). Ganges River dolphins are listed by the IUCN as an “endangered” species (IUCN 2010). Conservation efforts that include protected areas and education programs for local communities have been established in India and Bangladesh (Smith *et al.* 2010, Choudhury *et al.* 2009). However, these measures are based solely on the population density and distribution of dolphins at a regional scale collected during visual census surveys (*e.g.*, Smith 1993; Smith *et al.* 1994, 2001; Bashir 2010). Thus, to prevent the extinction of this dolphin species, effective conservation measures based on ecological and behavioral information, such as diel activity patterns and habitat use, are required.

To better understand many of the threats facing the Ganges River dolphin, and reduce potential conflicts with humans (*e.g.*, fisheries), it is important to understand the dolphin’s spatial and temporal movements. In particular, the diel activity patterns of the dolphins would provide useful information for managing fishing and transportation, if time-sharing regulations between dolphins and humans are practical in the focal area (*e.g.*, Danil 2005).

Some marine species show diel activity patterns that are correlated with the diel vertical movements of plankton. For example, pantropical spotted dolphins (*Stenella attenuata*) start to dive deeper and faster immediately after sunset, suggesting that they forage on organisms that are associated with the deep-scattering layer, which rises up to the surface after dark (Baird *et al.* 2001). The abundance pattern of spinner dolphins (*Stenella longirostris*) was reported to match the pattern of their prey, both horizontally and vertically, suggesting that spinner dolphins follow the vertical and horizontal diel migrations of their prey (Benoit-Bird and Au 2003). Echolocation click rates of Risso’s dolphins (*Grampus griseus*) are higher at night than during the day, which suggests that they forage at night (Soldevilla *et al.* 2010). Similar diel patterns of echolocation clicks have been observed in Heaviside’s dolphins (*Cephalorhynchus heavisidii*) (Leeney *et al.* 2011). However, some species do not show diel patterns, but rather show other types of patterns. For example, in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, the acoustic pattern is related to the tides (Philpott *et al.* 2007).

In the Ganges River, plankton density increases in the morning, decreases at noon, and then increases again in the evening. This change in plankton density is affected by temperature and human activities such as bathing (Sinha *et al.* 1992). Thus, it is predicted that the diel activity patterns of river dolphins may be different from those of marine species due to differences in ecological conditions between the ocean and rivers. Several studies have examined the behavior of Ganges River dolphins in both the wild and in captivity (Herald *et al.* 1969; Pilleri 1970, 1979; Sinha *et al.* 2010). However, the muddy waters of the Ganges River have prevented underwater visual observations of this species. Thus, previous studies of daily activity patterns have been limited to analyses of the frequency and patterns of surfacing behavior in the daytime (Pilleri 1970, Sinha *et al.* 2010). To date, no information has been published on the diel activity patterns of Ganges River dolphins.

Odontocetes produce high-frequency pulse sounds for echolocation (Au 1993). In the 1960s and 1970s, studies of the acoustics and anatomy of captive Ganges River dolphins indicated that this species lacks a crystalline eye lens, suggesting that they can only sense light intensity and are unable to obtain a clear image of underwater obstacles. In lieu of acute vision, the dolphins constantly emit echolocation pulses to search their surroundings (Herald *et al.* 1969); these are short pulses of about 40 μ s with a dominant frequency of 65 kHz (Bahl *et al.* 2007). Indus River dolphins (*Platanista gangetica minor*) are also nearly blind and constantly produce echolocation pulses (Pilleri 1979). Together, these studies suggest that river dolphins primarily rely on acoustic sensing systems.

Recently, passive acoustic methods have been used to observe cetaceans. Recording sound pulses with multiple hydrophones makes it possible to detect the presence, movement, number, and behavior of echolocating odontocetes (*e.g.*, Carstensen *et al.* 2006, Kimura *et al.* 2009, Li *et al.* 2009, Akamatsu *et al.* 2010).

In this study, we applied a stationary passive acoustic monitoring method to observe the underwater movements of Ganges River dolphins, with a particular focus on their diel activity patterns. We recorded their clicks continuously for more than 24 h and examined the diel changes in the clicks and the trajectories of the sound sources. We discuss the possible factors that affect their diel activity patterns and the implications of the results for effective conservation measures.

MATERIAL AND METHODS

Study Site

The study site was the middle reach of the Ganges River, located in Karnabas, in the state of Uttar Pradesh, India (28°16'16"N, 78°9'43"E; Fig. 1). Observations were conducted at three separate times, during 6–8 February 2007, 17–21 February 2008, and 11–16 November 2008. At the study site, the river had a bottleneck that was approximately 200 m wide during the three study periods. The river section was divided by a dam in the lower reach (28°11'30"N, 78°24'00"E). In the upper stream, there were areas of very shallow water,

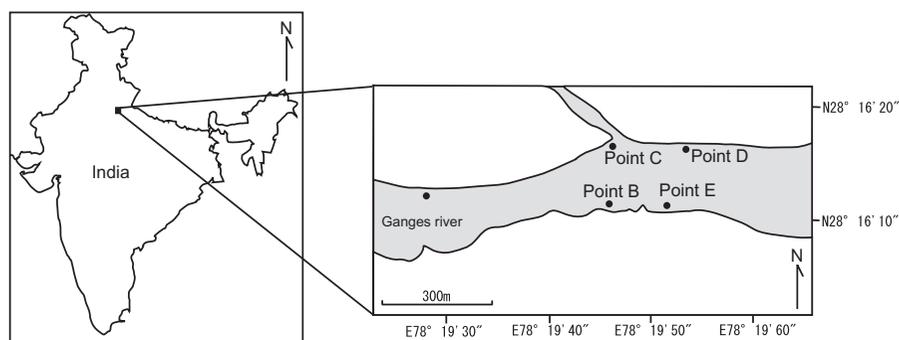


Figure 1. Study site and position of the A-tag during each survey period.

preventing dolphins from passing. Both the dam and the shallow area were about 10 km away from the study site. Thus, the small population of this species (28 individuals) was nearly confined within a short, 28 km stretch around the research area (Bashir *et al.* 2010).

Observation System and Methods

The ultrasonic pulse sounds of free-ranging Ganges River dolphins living in the research area were recorded using underwater stereo acoustic data loggers (A-tags; Marine Micro Technology, Saitama, Japan). A-tags are ultrasonic pulse event recorders that do not record raw waveforms. A-tags record the peak sound pressure of each pulse, the absolute time of the sound detection, and the sound source direction of pulses encoded in the time arrival difference between two hydrophones. A-tags consist of two hydrophones, a passive band-pass filter (55–235 kHz), CPU, flash memory (128 MB), and batteries (a CR2 lithium battery or an UM-1 alkaline battery for long lifetime). The intensity and time arrival difference of high-frequency pulse sounds were recorded when the received sound pressure level was higher than the preset threshold of 129 dB re 1 μ Pa p-p. The A-tags sample pulse events at 2 kHz or 500 Hz. When a click is detected by either hydrophone, an A-tag waits 0.5 ms or 2 ms (which corresponds to a 2 kHz or 500 Hz sampling rate) and stores the peak sound pressure of the click as well as the difference in the sound arrival time between the stereo hydrophones. The sampling frequency depended on the baseline length between the two hydrophones. When a sound triggered either the primary or secondary hydrophone, an independent high-speed counter began to measure the sound arrival time difference until the other hydrophone was triggered. The counting intervals of the time difference counter were 0.271 μ s for the 2 kHz sampling and 1.084 μ s for the 500 Hz sampling. The independent time difference counter ran very quickly within this recording interval. The relative angle of the sound source from the A-tag was calculated using the sound arrival time difference and the length of the baseline between the two hydrophones (Akamatsu *et al.* 2005a). Table 1 lists the recording parameters and recording sessions of the A-tag used in this study.

For our recordings, the A-tag was affixed to a bamboo rod and positioned at 50 cm depth. The A-tag was installed horizontally parallel to the river flow line (Fig. 1). The primary hydrophone was always oriented directly upstream to identify the swimming direction of each phonating animal. The A-tag was deployed for several hours to several days. To compare results between acoustic and visual observations, stationed visual observations were conducted from the river bank immediately behind the A-tag between 0830 and 1100 on 8 February 2008. The distance between the A-tag and the visual observer was less than 5 m. During the visual observations, the number of animals, time of day, and swimming direction were recorded.

Data Analysis

We analyzed acoustic event data using custom software written by TA, the second author, for Igor Pro ver. 5.0 (WaveMetrics, Lake Oswego, OR). The hardware detection threshold was slightly different between the systems (Table 1). In the analysis, we used received sounds of 132 dB re 1 μ Pa or higher

Table 1. Recording parameters and recording sessions of the A-tag acoustic recording system.

Event sampling rate	A/D conversion	Detection threshold	Installed point	Start time of recording	Recording duration				
2 kHz	0.271 μ s	128 dB re 1 μ Pa	Point A	2/6 1505	2 h 43 min				
				2/7 0941	8 h 43 min				
				2/8 0814	2 h 45 min				
				2/6 1515	2 h 25 min				
				2/7 0959	24 h 57 min				
				2/7 0940	4 h 1 min				
				2/6 1516	2 h 43 min				
				2/7 0934	9 h 12 min				
				2/8 0833	2 h 10 min				
				2/6 1402	3 h 58 min				
				2/7 1021	6 h 45 min				
				2/8 0835	2 h 13 min				
				0.5 kHz	1.084 μ s	126 dB re 1 μ Pa	Point B	2/17 1003	22 h 53 min
								2/18 0952	70 h 34 min
Point C	11/11 1719	22 h 29 min							
Point D	11/13 1650	48 h 15 min							
Point E	11/15 1625	17 h 05 min							

to standardize the data set. A pulse sound delayed within 1 ms of the previous pulse was considered to be water surface reflection and was excluded from data analysis. Pulses that triggered both hydrophones of the A-tag were used for analysis. A single triggered signal did not permit calculations of the time difference between the two hydrophones; thus, in these cases, no trajectory of the sound source direction could be determined.

The sonar signals of dolphins and porpoises exhibit a pulse train structure (Au 1993). In this study, 97% of the interpulse intervals were under 100 ms. A pulse train was defined as a series of pulses in which the intervals were 100 ms or shorter. Thus, interpulse intervals greater than 100 ms were not used for the statistical analysis of the difference among trajectory types.

In previous studies of finless porpoises (*Neophocaena phocaenoides*) in the Yangtze River (Akamatsu *et al.* 2005b, 2010), the minimum number of pulses in a pulse train was set at five or six to exclude noise contamination that was mostly due to biological and anthropogenic sources. In this study area, biological noise sources were uncommon but noise from boats or bubbles at the water surface were accidentally recorded as click trains. Therefore, the threshold was set conservatively to distinguish clicks from such noises; the minimum number of pulses in a train was set at five. Then these pulse trains were visually analyzed to identify each animal.

Figure 2 presents sample data of a single animal passing by the passive acoustic monitoring system. The top view shows the sound pressure of each pulse. In the bottom inset, black dots represent the relative angle of the sound source from the A-tag. A single trajectory of the sound source angle corresponds to one animal moving from the upper stream side to the lower stream side, and 180° corresponds to the upstream direction and 0° corresponds to the downstream direction.

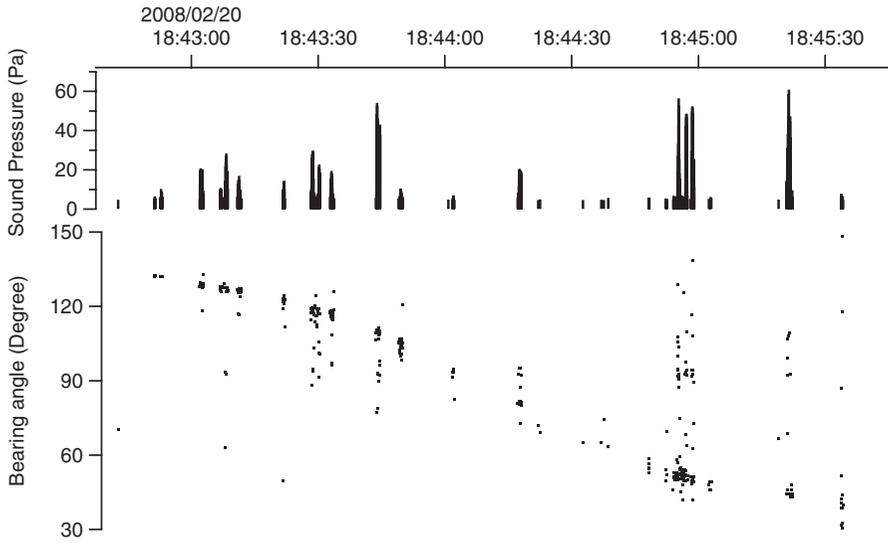


Figure 2. Recorded data of the passive acoustic monitoring system, indicating sound pressure (upper inset) and the sound arrival time difference (lower inset). Black dots represent the relative angle of the sound source from the A-tag.

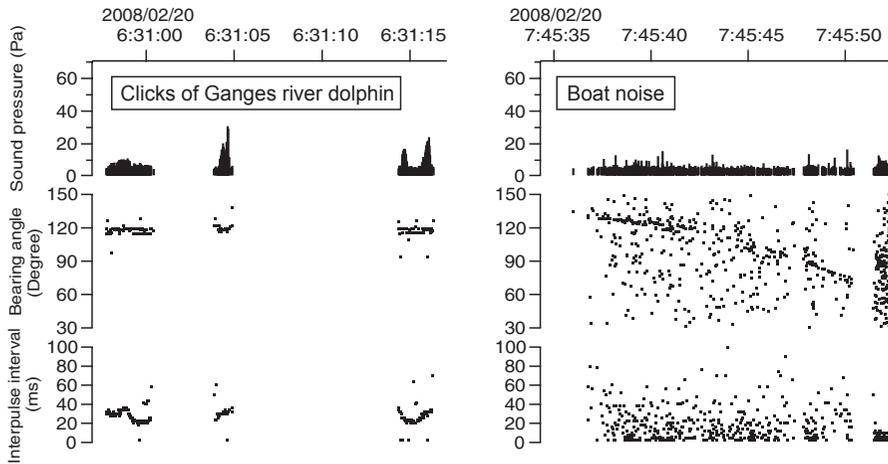


Figure 3. Discrimination between the trajectories of the dolphins and boats. The inter-pulse interval of dolphins converged and changed smoothly, whereas those of boat noise diffused and changed randomly.

The inter-pulse intervals of the biosonar signals changed smoothly (Akamatsu *et al.* 2005b), whereas those of boat noise changed randomly (Fig. 3). Hence, we distinguished between the trajectories of the dolphins and boats using the inter-pulse interval (Kimura *et al.* 2009) and eliminated the latter from the data set.

Acoustic Observations of Individual Animals

To define the acoustic trajectories of dolphins, two acoustic detections from different sound sources (dolphins) must be separated. A single trajectory was defined as an independent trajectory (a series of pulse trains) that was separated by more than 5 min from previous or subsequent pulse trains. We conservatively defined trajectories appearing within 5 min as coming from a single individual. If the interval of trajectories was more than 5 min, the two trajectories were considered to have originated from two different animals. Although no swimming speed data of the Ganges River dolphins are available, dolphins could travel 300 m distance during 5 min assuming 1 m/s, which is a slower speed than typical small odontocetes. The effective acoustical recording area of an A-tag is approximately 300 m for the case of Yangtze finless porpoises (Kimura *et al.* 2009). Ganges River dolphins were thus considered to be out of acoustical range if they swam on a direct course for 5 min. Otherwise, dolphins could be detected nearly continuously when they stay within the detection range as shown later. Note that any fixed point observation either visual or acoustical methods cannot avoid double counting. Thus, it is possible that two trajectories separated by more than 5 min were from the same individual.

When only one trajectory was recorded, the start time of detection was defined as the time of the first pulse train in the trajectory. The end time of detection was defined as the time of the last pulse train. Short trajectories of less than 20 s were not used for analysis, as these were difficult to categorize into movement types, which are described in the Results section. We also excluded unclear trajectories with noise contamination and mixed trajectories for which we could not analyze each trajectory separately.

When the relative angle of the sound source direction from the A-tag is close to 0° or 180°, horizontal variation in the relative angle with movement of the sound source recorded by the A-tag becomes small. Thus, estimating the movement of the sound source when its relative angle was close to 0° or 180° was difficult. Therefore, trajectories that appeared in the angle ranges of 0°–50° and 130°–180° were also eliminated.

In the analysis of multiple-animal trajectories, we analyzed all situations in which more than two trajectories were recorded simultaneously and were separated from each other by more than 10°. However, when two trajectories were recorded simultaneously, we assumed that there were at least two animals in the recording area.

RESULTS

The total duration of acoustic observation was 252 h, of which recordings of sound source trajectories constituted 56 h. Of these trajectories, 78.6% of the total phonation-detection time was estimated to contain trajectories of a single animal, whereas 21.4% were those of multiple animals (Fig. 4).

Comparison of Visual and Acoustic Observations

For the simultaneous visual and acoustic observations conducted on 8 February 2008, 42 sightings were recorded by visual observation and three trajectories

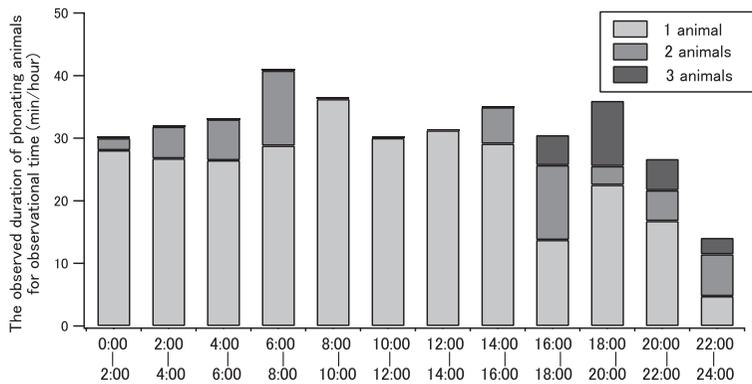


Figure 4. Observed duration of echolocating bouts of phonating animals.

were recorded by acoustic observation during 2.5 h. The 42 sightings were not necessarily 42 independent individuals. Observations were made from a fixed point. There are only 28 animals in the range of the study area (see Introduction) and it is hard to identify individual Ganges River dolphins using natural marks. Thus, double counting of the same animal could have occurred over the short 2.5 h period of visual observation. The aim of this part of the study was to compare the detection performance of acoustic and visual monitoring. The recording lengths of the three trajectories were 266, 141, and 50 s. The relative angles of the acoustic trajectories used for this analysis included all angles (0° – 180°). The mean distance between the sighted dolphins and the observer adjacent to the A-tag was 123.7 m (minimum: 50 m, maximum: 350 m). A total of 42 sightings occurred during the recording of the acoustic trajectories. The mean distance between the dolphin and the visual observer during these 13 sightings was 73.1 m (minimum: 50 m, maximum: 100 m). The mean distance for the other 29 sightings that did not correspond with the timing of the acoustic trajectories was 146.4 m (minimum: 60 m, maximum: 350 m). In total, 66% (10 of 15) of sightings within 80 m from the data logger corresponded to the acoustic recordings, whereas 27% (3 of 11) of sightings within 80–100 m were associated with the acoustic recordings. No sightings at distances of more than 100 m corresponded to the acoustic trajectories. Six sightings were recorded at 50 – 130 degrees, for which the mean distance between the dolphin and observer was 55 m (minimum: 50 m, maximum: 80 m). These six sightings corresponded with the acoustic recordings.

Types of Movements

The trajectory of the relative angle of the sound source could be categorized into the following three types: staying type, moving type A, and moving type B (Fig. 5). The staying type was defined as a trajectory in which the relative angle of the sound source only changed within a narrow range (10° – 20°). The moving type was defined as a straight or winding trajectory in which the relative angle of the sound source changed over 20° toward either the positive or negative direction. Moving type A was defined as straight trajectories in which the relative angle of the sound source changed constantly to the negative or positive

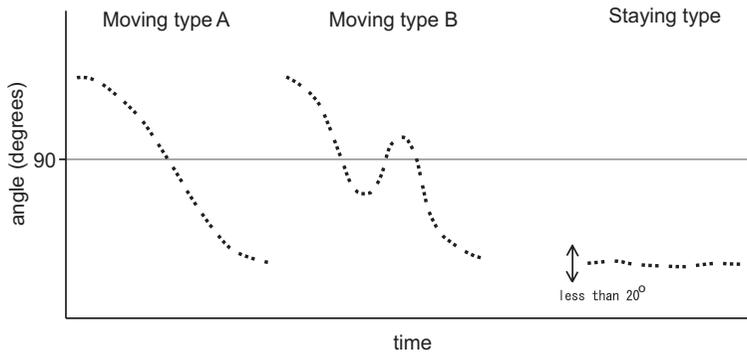


Figure 5. Schematic drawing of the three types of trajectories of the bearing angle of the sound source.

direction over time. Moving type B was defined as winding trajectories with at least one flexion point.

Characteristics of Each Trajectory Type

Within all data sets, 98 trajectories were identified (56.8 h, 68,556 clicks). Of these, 63 trajectories (6.8 h, 27,637 clicks) were moving type A. The mean trajectory length for moving type A was 6.5 min (maximum: 39.5 min, minimum: 0.4 min, SD: 8.2 min). Twenty trajectories (6.0 h, 15,247 clicks) of moving type B were recorded. The mean trajectory length for moving type B was 17.9 min (maximum: 81.1 min, minimum: 2.2 min, SD: 22.1 min). The remaining 15 trajectories (44.0 h, 25,672 clicks) were the staying type, for which the mean trajectory length was 176.0 min (maximum: 690.1 min, minimum: 5.2 min, SD: 204.1 min). The mean trajectory length for the staying type was significantly longer than the other two trajectory types (Scheffe's *F*-test, $P < 0.001$).

Ninety percent of the interpulse intervals ranged between 10 and 70 ms (Fig. 6). This range is wider than that reported by a previous study (20–50 ms, Herald *et al.* 1969), probably because the previous study was conducted on dolphins in captivity. Akamatsu *et al.* (1998) reported that the interpulse interval became shorter under captive conditions because dolphins in captivity adapted their echolocation to short-range detection. The mean interpulse interval of each moving type (A: 30.5 ± 14.8 ms, $n = 25,567$ and B: 32.9 ± 14.3 ms, $n = 14,600$) was significantly shorter than that of the staying type (41.9 ± 17.7 ms, $n = 25,361$; Scheffe's *F*-test, $P < 0.01$). The distribution of the interpulse interval for moving type trajectories peaked at 20–30 ms, and 80% of them ranged between 16 and 48 ms. In contrast, the distribution of the interpulse interval for staying type trajectories peaked at 40–50 ms, and 80% of them fell between 18 and 64 ms, exhibiting higher variation than the moving types (Fig. 6).

We did not observe the approach phase, which is characterized by a reduction in the interpulse interval or a buzz sound with a very short interpulse interval that is typically emitted just before foraging in some odontocetes (Miller *et al.* 2004; Madsen *et al.* 2005; Johnson *et al.* 2006, 2008; Akamatsu *et al.* 2010).

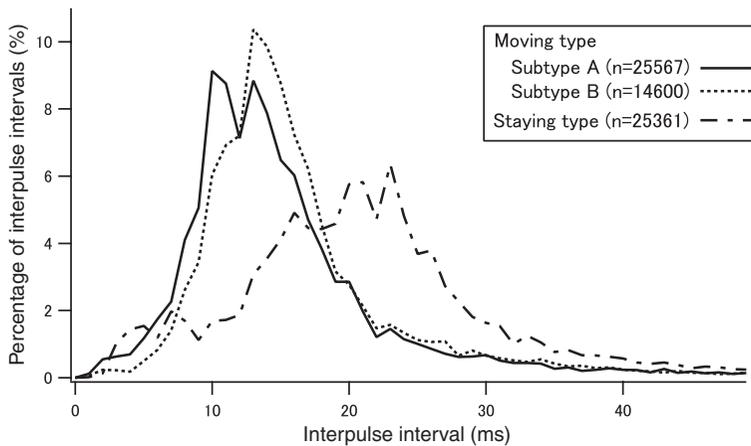


Figure 6. The relative frequency of the interpulse interval for moving type and staying type trajectories.

Among the moving type A trajectories, the mean time spent swimming upstream against the water flow (654.9 ± 642.7 s, $n = 37$) was significantly longer than the time spent swimming downstream (200.8 ± 205.3 s, $n = 26$; Mann Whitney U -test, $P < 0.001$).

Diel Activity Patterns

The relative frequency of the occurrence of moving type A was higher at night (60.7%, 1800–0600) than during the day (27.8%, 0600–1800). The relative frequency of moving type B increased to 54.7% in the late afternoon (1600–1800) but was less than 25% during other periods (Fig. 7). In contrast, the relative frequency of the staying type was higher during the day (48.6%) than at night (25.3%). Moving type A and moving type B increased at night and in the late afternoon, respectively, while the staying type increased during the daytime (Fig. 7), indicating that the dolphins tended to migrate at night and stay in relatively small areas during the day.

Analysis of Multiple-animal Trajectories

Of the total recording time, 21.4% constituted sounds from multiple animals at the same time. We defined the time during which the multiple trajectories were recorded simultaneously as one case for this analysis. Using this definition, 29 cases of multiple-animal trajectories were recorded. Among these, 24 cases involved two animals (15.5% of the total recording time), and 5 cases involved three individuals (5.9%).

In our analysis, we were able to determine various combinations of multiple trajectories occurring at the same time. Homogeneous combinations of moving-type trajectories of two trajectories occurred for 12 out of the 24 cases. Heterogeneous combinations of staying and moving types occurred in 11 cases. One case involved an unclear combination of trajectories. Homogeneous combinations of

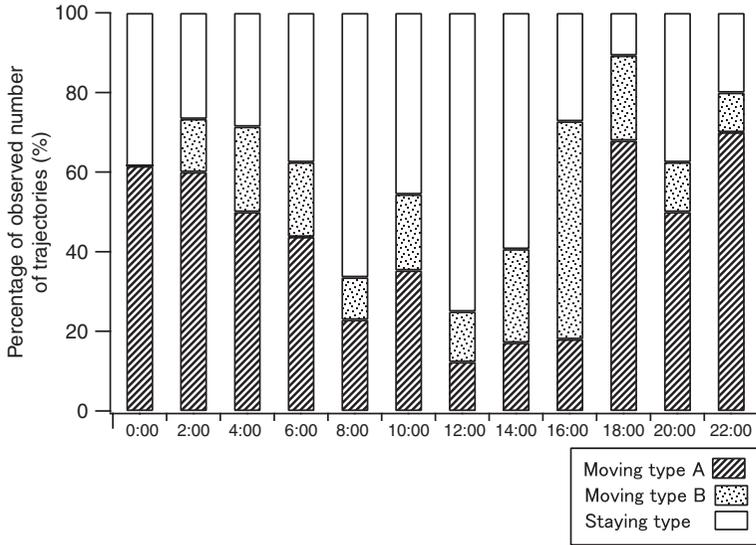


Figure 7. Changes in the relative frequency of the observed number of trajectories for each time bin. Note that the data were accumulated in 2 h time bins during one day.

staying types were not observed. For the five cases involving three trajectories, we observed the following four combinations of trajectories: three unclear trajectories ($n = 1$); two moving type A and one staying type ($n = 2$); one each of moving type A and B and one unclear trajectory ($n = 1$); and one moving type A and two staying types ($n = 1$).

The frequency of occurrence of multiple trajectories increased in the afternoon and at night (1500–0700), and no multiple trajectories were recorded from 0800 to 1400 (Fig. 4). Dolphin group size calculated from the recording time was 1.27 throughout the entire day, 1.2 during the daytime, and 1.37 at night.

DISCUSSION

Detection Range of A-tags

Our simultaneous acoustic and visual observations of Ganges River dolphins suggest that the effective distance for recording acoustic trajectories with our recording system (A-tag) is less than about 80 m, much shorter than that observed applying the same system to finless porpoises in the Yangtze River (maximum 478 m; Li *et al.* 2009). The shorter recording distance in our study suggests that the sound pressure produced by Ganges River dolphin clicks is weaker than those produced by the finless porpoise. The apparent source level of Ganges River dolphins has been estimated at 150–180 dB (Ura *et al.* 2007). In contrast, based on the effective recording distance, the average source level of the finless porpoise was estimated at 197 db (Li *et al.* 2009). However, this effective range for the finless porpoise is for detecting clicks, not acoustic trajectories. Thus, the effective range for detecting the clicks of Ganges River dolphins could be greater than 80 m.

Our results also indicate that our system was not always able to record clicks even at distances <80 m. The detection of clicks of Ganges River dolphins may have been particularly difficult because the directionality of sonar beams is relatively sharp in this species compared to other odontocetes (Herald *et al.* 1969). The unique skull of Ganges River dolphins is characterized by a broad maxillary crest that extends upward into the forehead melon, suggesting great directionality of their sonar beam (Herald *et al.* 1969). Some environmental factors could have also caused the shorter detection range of the A-tag. For example, when Ganges River dolphins were more than 100 m from the A-tag, a shallow area of water may have existed between the dolphin and the A-tag, perhaps causing an acoustic shadow area. Unfortunately, however, we cannot examine this possibility because we do not have data on differences in environmental conditions between our study area and that of Li *et al.* (2009). Visual sightings recorded at 50°–130° completely coincided with the acoustic observations. This suggests that the A-tag can record acoustic trajectories of Ganges River dolphins that swim within the range of 50°–130° at <80 m from the system.

Relationship Between Trajectory Types and Behavior

Three types of acoustic trajectory were observed in this study. Significant differences in the mean interpulse interval and trajectory length between the staying type and moving type B also suggest that these two trajectory types represent different behavioral and sensing categories.

The moving type A trajectory should be recorded when the sound source (dolphin) continually moves upstream or downstream. The moving type B trajectory represented dolphins changing their traveling direction at least once while swimming within the acoustically observable area. This trajectory type corresponds to behaviors in which dolphins swim in a winding trajectory. The staying type should be recorded when the dolphins remain in a relatively small area for a long period of time. The mean trajectory length of the staying type was the longest of the three types.

Interpulse intervals for moving type trajectories were shorter than those of the staying type, in both peak and range (Fig. 6). This suggests that the dolphins used echolocation over relatively short ranges while moving. In contrast, the dolphins appeared to echolocate over wider ranges during the staying trajectory than when moving. These results suggest that the moving and staying type involved different behaviors.

We were unable to estimate when and how dolphins foraged, because we did not observe the approach phase within our acoustic data set. We only observed movement of the sound sources. Therefore, our trajectory types do not represent behavioral categories indicated by body movements such as resting or foraging, as these are not acoustically observable in turbid water. However, the interpulse intervals of the moving type were significantly shorter than those of the staying type, suggesting that the former included foraging behavior and the latter included resting behavior.

Diel Changes in Movement Patterns

The frequencies of occurrence for moving types A and B increased at night and in the late afternoon, respectively, whereas that of the staying type increased

during the daytime (Fig. 7). These results indicate that the dolphins tended to migrate at night and remain in relatively small areas during the daytime. All previous studies of Ganges River dolphin behavior have been based only on observations of surfacing behavior in the daytime. Underwater behavior and behavior at night have not been previously documented.

Pilleri (1970) reported that Ganges River dolphins were active and foraged for fish at night in an enclosure in a clear river, although he provided no precise data on their diel activity patterns. Sinha *et al.* (2010) documented the activity rhythms of Ganges River dolphins based on periodic sampling of their surfacing behavior during the day. They reported that dolphins exhibited surfacing behavior more vigorously and frequently during morning and late afternoon but were less active from 1100 to 1500 (Sinha *et al.* 2010). Similarly, we demonstrated that staying type trajectories increased around noon and moving type trajectories increased in the afternoon (see Fig. 7). The staying type was the most frequent trajectory observed during the day, suggesting that much of the behavior observed in previous studies corresponded to the staying type trajectory.

The diel behavioral patterns of some marine cetaceans are correlated with the diel movements of their prey (*e.g.*, Baird *et al.* 2001, Benoit-Bird and Au 2003, Soldevilla *et al.* 2010, Leeney *et al.* 2011). For example, the echolocation clicks of harbor porpoises increase at night near floating piers where their prey gather (Carlström 2005, Todd *et al.* 2009). In the present study, moving type trajectories, which may reflect foraging behavior, increased at night. This suggests that the diel activity patterns of Ganges River dolphins could be affected by the diel patterns of their prey. The main prey types of the Ganges River dolphin are small fish and gastropods (Sinha *et al.* 1993). Plankton near the surface of the Ganges River increase at night and decrease during the day, and this diel migration might be affected by water temperature, light conditions, rainfall, and mass bathing of local people (Sinha *et al.* 1992). Therefore, the activity of plankton, potential prey for small fish, may affect diel changes in the activity of dolphins.

Another factor that could affect the diel behavior patterns of dolphins is human activity. Because the river in the study area is important to local people for bathing, washing, and fishing, it is possible that the Ganges River dolphins tended to migrate at night to avoid human activities during the daytime.

The diel behavior patterns observed in this study may also be specific to the study site and study period and may potentially differ across locations and seasons. Additional long-term research at various sites is necessary to clarify the nature and causes of, and the factors affecting, the diel activity patterns of the Ganges River dolphin. Such knowledge could improve our understanding of other riverine odontocetes, whose activity patterns remain generally unknown.

Habitat Preference

Kasuya and Aminul Haque (1972) reported that because of food distribution, Ganges River dolphins tend to aggregate in narrow places during the daytime, often at river confluences, downstream of shallow areas. Smith (1993) also noted that Ganges River dolphins were often observed at the upstream end of counter-current boundaries where eddies become aligned with the main flow. Sinha *et al.* (2010) observed that surfacing behavior of Ganges River dolphins within confluences occurred more frequently than when dolphins were in the main stream, although they did not present precise data. They also suggested that surfacing at

such locations may allow dolphins to minimize energy output while monitoring foraging opportunities in the flowing water. Amazon River dolphins have also often been observed at confluences, at bends of rivers, and in canals for foraging, resting, and social purposes (Martin *et al.* 2004, da Silva 2009).

Because our study area was located at a river confluence and downstream of a shallow area (Fig. 1), it was likely to be a habitat intensively used by dolphins of this area. Our results also indicated that many Ganges River dolphins used the study area throughout the entire day, including nighttime, although the number of recorded trajectories decreased around midnight (2200–2400, Fig. 4). These results suggest that Ganges River dolphins use the confluence area as habitat at all times of the day.

Group Size of Ganges River Dolphins

Our results suggest that the focal Ganges River dolphins were typically solitary. They tended to swim alone almost all day; 78.6% of the total recording time constituted sounds from a single animal. These solitary sounds were particularly frequent during the daytime; no multiple trajectories were recorded from 0800 to 1400 (Fig. 4). The frequency of occurrence of sounds from multiple animals increased at night (1600–2400), probably because dolphins tended to migrate at night while remaining alone within a narrow area during the day. The remainder of the total recording time constituted sounds from multiple animals.

Although we have limited data concerning the group size of Ganges River dolphins, Kasuya and Aminul Haque (1972) also reported that 80.4% of sightings during the day involved single animals, whereas 15% and 4.6% of sightings involved two or three animals, respectively. Their results correspond well with our acoustic and visual observations.

Conclusions

We successfully recorded the echolocation pulses of free-ranging Ganges River dolphins over 24 h using passive acoustic methods. Our method was effective for monitoring the underwater movements of these riverine dolphins. Our results indicate that the dolphins in the study area tended to migrate at night and to stay in narrow areas during most of the day. Our results also suggest that the study area was intensively used by Ganges River dolphins throughout the entire day. To facilitate the conservation of this species, it is important to evaluate the significance of such habitats for this species and to clarify their diel activity patterns more precisely through additional long-term studies using this method at various sites in the area.

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