A multimodal detection model of dolphins to estimate abundance validated by field experiments

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Abundance estimation of marine mammals requires matching of detection of an animal or a group of animal by two independent means. A multimodal detection model using visual and acoustic cues (surfacing and phonation) that enables abundance estimation of dolphins is proposed. The method does not require a specific time window to match the cues of both means for applying mark-recapture method. The proposed model was evaluated using data obtained in field observations of Ganges River dolphins and Irrawaddy dolphins, as examples of dispersed and condensed distributions of animals, respectively. The acoustic detection probability was approximately 80%, 20% higher than that of visual detection for both species, regardless of the distribution of the animals in present study sites. The abundance estimates of Ganges River dolphins and Irrawaddy dolphins fairly agreed with the numbers reported in previous monitoring studies. The single animal detection probability was smaller than that of larger cluster size, as predicted by the model and confirmed by field data. However, dense groups of Irrawaddy dolphins showed difference in cluster sizes observed by visual and acoustic methods. Lower detection probability of single clusters of this species seemed to be caused by the clumped distribution of this species. © *2013 Acoustical Society of America*. [http://dx.doi.org/10.1121/1.4816554]

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I. INTRODUCTION

Accurate estimation of abundance is important for conservation and risk management of wildlife. Line transects are widely used to quantitatively estimate the numbers of wild animals (Jewell *et al.*, 2012; Buckland *et al.*, 2001). However, detection misses for submerged marine mammals are unavoidable. In the case of minke whale observations, because of diving and the general difficulty in sighting, whales on the track line cannot be found completely (Schweder, 1999). For abundance calculations, an estimation of the missing ratio is as important as correct detection probability. To estimate the missing ratio, researchers often use a mark-recapture method, which requires double-independent detections of an animal or group based on matching of individual photo IDs (Calambokidis and Barlow, 2004; Durban *et al.*, 2005).

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Acoustic detection has been proposed as an observation method independent of visual and satellite observations (Kyhn *et al.*, 2012; Sveegaard *et al.*, 2011). Unlike photo ID comparison of body color pattern or scars of individual, acoustic recapture is not easy because the acoustic characteristics of phonated sound can be changed. Sounds produced by animals can be mimicked by other individuals (Tyack, 1986). In these years, combination of acoustic and visual census is getting common for the survey of cetaceans (Rankin *et al.*, 2007). Here, the problem is the matching of two independent, visual and acoustic, detections. Visual and acoustic cues based on timing, such as the time of phonation and surfacing, do not always match, and delays exist when a hydrophone array towed behind the survey boat carrying visual observers. An automatic algorithm has been proposed using an arbitrary time window as a convenient criterion to match the visual and acoustic detections of porpoises (Akamatsu *et al.*, 2008). When two independent cues happened within the same time window, the detection was defined as a matched event. The method is advantageous for the automatic matching of different methods, such as acoustic and visual observations, but risks false matchings and matching misses. The matching of detection events should be defined without using a time window of arbitrary length.

In this study, we propose a multimodal detection model using visual and acoustic cues. It provides abundance within a strip width without defining a time window to match the two cues. The proposed model was validated using data obtained from simultaneous visual and acoustic observations of two different species in different habitats.

II. MATERIALS AND METHODS

A. Visual and acoustic detection

A visual observer detects a dolphin—or a group of dolphins—when it surfaces. An acoustic receiver detects the sound when a dolphin produces sounds. Both observation methods could miss some animals, and thus detection probabilities of both acoustic (Pa) and visual (Pv) methods should be assumed.

Multimodal matching is defined as detection by both methods within a pre-fixed time window (Akamatsu *et al.*, 2008). The time window allows simple comparisons of matched detection events as follows. The observed duration is divided into periodic time windows. If any animals, no matter how many, are observed within the time window, the time window detection is designated as positive. If not, the time window is negative. A matched time window is defined as simultaneous positive detection by visual and acoustic observations. Cluster size is defined as the number of individuals detected within a time window, and differs from biological group size. We use "cluster size" to indicate the number of observed animals in a time window to differentiate it from group size.

B. Detection probabilities of dispersed dolphins

The numbers of positive time windows of acoustic (Na) and visual (Nv) detections as well as the number of matched time windows (M), can be observed. Assuming both methods cover the same detection distance from a cruise line, the total number of positive time windows (N) and the detection probability of acoustic (Pa) and visual (Pv) methods can be calculated using available parameters, as shown in Eqs. (1)–(3), based on the mark-recapture method.

Here, we assume that the dolphins are dispersed and can be detected one by one in different time windows. In this case, N is nearly equal to the total number of existing animals, and the cluster size is nearly equal to 1. In the same manner, Pa and Pv are nearly equal to the detection probabilities of an individual animal:

$$\mathrm{N} = \mathrm{Na} \times \mathrm{Nv}/\mathrm{M}, \tag{1}$$

$$\mathrm{Pa} = \mathrm{M}/\mathrm{Nv}, \tag{2}$$

$$\mathrm{Pv} = \mathrm{M}/\mathrm{Na}. \tag{3}$$

However, the detection probability is reduced when the length of the time window is short. Acoustic and visual cues may not be available simultaneously in a short period. When the length of the time window (tw) is smaller than the cue production interval, such as the surfacing or phonating intervals, the detection probability is reduced. The probability of the time window contains a cue decrease linearly when the duration of the time window is shorter than the minimum cue production interval. Assuming an average phonating interval (ta) and surfacing interval (tv), the acoustic and visual matching probability P(V^A) of a time window can be written as follows:

$$\mathrm{P(V\hat{\ }A)} = \mathrm{Pa} \times \mathrm{Pv} \quad \text{where } \mathrm{ta} < \mathrm{tv} < \mathrm{tw}, \tag{4}$$

$$\mathrm{P(V\hat{\ }A)} = \mathrm{Pa} \times \mathrm{Pv} \times (\mathrm{tw}/\mathrm{tv}) \quad \text{where } \mathrm{ta} < \mathrm{tw} < \mathrm{tv}, \tag{5}$$

$$\mathrm{P(V\hat{\ }A)} = \mathrm{Pa} \times (\mathrm{tw}/\mathrm{ta}) \times \mathrm{Pv} \times (\mathrm{tw}/\mathrm{tv}) \quad \text{where } \mathrm{tw} < \mathrm{ta} < \mathrm{tv}. \tag{6}$$

For example, for finless porpoises, ta is 5–6 s (Akamatsu *et al.*, 2008) and tv is 70.9 s (Akamatsu *et al.*, 2002). After more than "tv seconds," a porpoise is likely to surface and produce several click trains. In this case, the matched detection probability is the product of Pa and Pv [Eq. (4)]. At less than "tv seconds," no visual cue may be available. Assuming that surfacing occurs evenly at any time within a time window, we find that the visual detection probability reduces linearly according to the duration of the time window [Eq. (5)]. If the time window is less than ta, the acoustic detection probability also decreases linearly according to the length of the time window [Eq. (6)]. That is, if observers (including a passive acoustic device) wait long enough for at least one cue to be available from both modalities, the detection probability will be constant. Otherwise, the positive matching probability decreases linearly [Eq. (5)] or by a square-law [Eq. (6)] according to the length of the time window tw. Once the matched detection probability P(V^A) is available, the estimated abundance can be expressed as

$$\text{Estimated abundance} = \mathrm{M}/\mathrm{P(V\hat{\ }A)}. \tag{7}$$

The numbers of individuals detected acoustically Na and visually Nv are independent of the length of the time window as long as the animals are detected individually. Equations (4) and (7) show that the estimated abundance N is constant when $\mathrm{tw} > \mathrm{tv}$. However, it increases as tw^{-1} where $\mathrm{tv} \gg \mathrm{tw} > \mathrm{ta}$. N diverges as tw^{-2} when tw is close to 0, where $\mathrm{ta} > \mathrm{tw}$.

C. Detection probabilities of condensed dolphins

A large cluster group can be detected more easily because the probability of detecting at least one animal among many is larger than that of a single animal cluster. Detection probability of an arbitrary cluster size by visual and acoustic means can be calculated as follows, based on single cue detection probabilities.

Here, we assume that the detection probability of a single individual (pa and pv) is constant whether the animal is in a group or isolated. If two individuals exist, the probability of detecting at least one animal by both visual and acoustic means within a time window, $\mathrm{P(V{^\wedge}A)_2}$, can be calculated using Eq. (8). To arrive at this, the probabilities of missing both animals acoustically and visually (1-pa)^2 and (1-pv)^2, respectively, should be subtracted from 1. However, $\text{(1-pa)}^2 + \text{(1-pv)}^2$ includes missing probability by both modalities, $\text{(1-pa)}^2\text{(1-pv)}^2$, twice, which should be corrected:

$$\mathrm{P(V{^\wedge}A)_2} = 1 - [\text{(1-pa)}^2 + \text{(1-pv)}^2 - \text{(1-pa)}^2\text{(1-pv)}^2]. \tag{8}$$

The detection probability of cluster size n, $\mathrm{P(V{^\wedge}A)_n}$, is the probability of detecting at least one animal by two modalities. Even if cluster size n animals actually exist, the probabilities of no animal being detected, acoustically or visually, are (1-pa)^n and (1-pv)^n, respectively. Again, $\text{(1-pa)}^n + \text{(1-pv)}^n$ includes the probability of completely missing all animals by both modalities, $\text{(1-pa)}^n\text{(1-pv)}^n$, twice, which should be corrected [Eq. (9)]. As shown in Fig. 1, the calculated matching probability increases quickly with group size:

$$\mathrm{P(V{^\wedge}A)_n} = 1 - [\text{(1-pa)}^n + \text{(1-pv)}^n - \text{(1-pa)}^n\text{(1-pv)}^n]. \tag{9}$$

Ideally, the probability of the positive time window of acoustic observation is

$$\mathrm{Pa} = \mathrm{C}_1 \times \mathrm{pa} + \mathrm{C}_2 \times [1 - \text{(1-pa)}^2] + \mathrm{C}_3 \times [1 - \text{(1-pa)}^3] + \cdots + \mathrm{C}_n \times [1 - \text{(1-pa)}^n], \tag{10}$$

where $\mathrm{C_n}$ is the ratio of cluster size n. Pa is the probability that at least one animal is detected in a time window. Each component of C can be measured from the actual distribution pattern of the animals.

D. Abundance estimation

The total number of individuals (nA) within the observable range of an acoustic detector can be expressed as

$$\mathrm{nA} = \mathrm{na}/\mathrm{pa}, \tag{11}$$

where na is the raw number of individuals detected acoustically and pa is the acoustic detection probability of an individual. The pa can be calculated from the number of time windows in which only one animal was detected visually and acoustically (m), and the number of positive time windows of visual observations that include only one animal (nv′):

$$\mathrm{pa} = \mathrm{m}/\mathrm{nv}'. \tag{12}$$

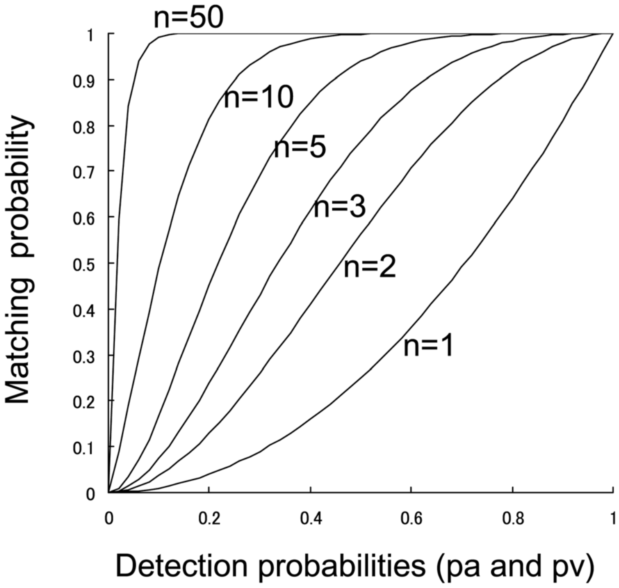

FIG. 1. Calculation of the matching probability of positive time window by two independent observations based on Eq. (9). Cluster size, the number of existing animals in a time window (N) was set at 1, 2, 3, 5, 10, or 50). We assumed pa = pv to simplify the calculation, and changed this from 0 to 1. The matching probability of a large cluster (50) is nearly equal to 1, whereas it is small for a cluster size of 2. This shows that a very large group can be detected by any means, but a small group can easily be missed.

When we combine Eqs. (11) and (12), the total number of individuals (nA) can be expressed as

$$\mathrm{nA} = \mathrm{na} \times \mathrm{nv}'/\mathrm{m}. \tag{13}$$

In summary, time windows that include only one individual are used to calculate the detection probability of an animal. Then, we calculated the total number of animals using that probability and the total number of animals detected.

In a similar manner, the total number of individuals (nV) within the truncated range of a visual observer can be expressed as

$$\mathrm{nV} = \mathrm{nv}/\mathrm{pv}, \tag{14}$$

where nv is the raw number of individuals detected visually and pv is the visual detection probability of an individual. The pv can be calculated from the number of time windows in which only one animal was detected visually and acoustically (m), and the number of positive time windows of acoustic observations that include only one animal (na′):

$$\mathrm{pv} = \mathrm{m}/\mathrm{na}'. \tag{15}$$

When we combine Eqs. (14) and (15), the total number of individuals (nV) can be expressed as

$$\mathrm{nV} = \mathrm{na}' \times \mathrm{nv}/\mathrm{m}. \tag{16}$$

Note that the numbers of animals estimated by the acoustic (nA) and visual (nV) methods differ [Eqs. (13) and (16)].

Using Eqs. (13) or (16), abundance within the observable range can be estimated. The constants na and nv are the numbers of individuals observed acoustically and visually, respectively. On the other hand, pa and pv, which are the detection probabilities of a single individual, are calculated using observable parameters. In practice, it is not possible to confirm that only one animal is present in a time window, because a single detection does not necessarily indicate the presence of just one animal. In this study, we selected events of single animal detection by acoustic and visual observation as representative of single animal detection to calculate the detection probability of both modalities. The effects of detected cluster size are discussed below.

E. Study sites

Two different species were observed in this study, Ganges River dolphins, *Platanista gangetica gangetica*, and Irrawaddy dolphins, *Orcaella brevirostris*, as examples of dispersed and condensed distributions to validate our model.

A small, isolated population of Ganges River dolphins in the middle reaches of the Ganges River surveyed by Behera (1995), located at Karnabas, Uttar Pradesh, India (N28°20.8′, E78° 16.4′ –N28°14.3′, E78°22.0′), was observed acoustically and visually. This habitat is divided from the lower reaches by a dam (N28°11′30, E78°24′00), which impounds water for agriculture. In the upper stream, very shallow areas prevent the dolphins from swimming upstream. The small population, estimated at 28 individuals, was essentially confined to the 28-km-long stretch around the research area (Bashir *et al.*, 2010). Our observations were conducted from 17 to 20 February 2008 in a stretch approximately 18 km long in this section of the river. The width of the river was less than 100 m and varied with location. A small, rigid-hulled boat (3 m long, WWF India) conducted a round-trip each day in this section at 10 km/h speed relative to the water, which was measured in stable water area with fixed engine rotation. The speed relative to the ground was 6–13 km/s, depending on the speed of the water current.

Chilika Lagoon in India is one of two brackish-water lagoons in the world that are home to Irrawaddy dolphins (the other is Songkhla Lake, Thailand). This lagoon is 60 km long and 22 km wide with an average water-spread area of 1100 km^2. Irrawaddy dolphins occupy the connecting channel to the sea named "Outer channel" of Chilika Lagoon. This area, approximately 20 km long with an area of 30 km^2, were surveyed from 29 January to 2 February 2007 and from 24 to 29 February 2008. The width of the Outer channel varied from 300 to 1200 m. Tidal currents introduce seawater on a daily basis through the estuary area, enhancing the biological productivity of the lagoon (Mohanty *et al.*, 2007; Panda *et al.*, 2008; Khan *et al.*, 2011). A wooden boat, usually used for dolphin-watching cruises in this area, was hired for the survey. It was operated at approximately 10 km/h in the same manner as the Ganges River dolphin survey and used to cruise from the new mouth area (N19°40.1′, E85°30.6′) close to the Bay of Bengal, to a bottleneck of the main body of Chilika (N19°42.1′, E85°25.1′). According to the regular visual survey conducted by Chilika Development Authority, 53 to 58 of Irrawaddy dolphins inhabited in the surveyed area.

F. Observation protocol

In both study areas, we conducted visual observations as well as acoustic recording in transects. Two experienced visual observers recorded distance, direction, and the number of animals in a group by naked eyes, with one conducting observations 90° to the left and the other to the right of the boat. A second team of observers alternated every 30 min. This means at least four experienced persons, including the authors of this paper (TA, BS, KM) were in responsible for of visual observations. Eye height was 2 m from the water surface. A large protractor was placed in front of each visual observer, so that the relative direction to the animal could be recorded correctly. The reference direction was always the direction of the bow of the boat, which was the same system used for acoustic monitoring. The stereo hydrophone logger (A-tag) was parallel to the cruise line, with the acoustic system towed behind the boat. The observer checked the detection time and compared the acoustic detections in second order. Visual observers counted animals individually but were allowed to record minimum group size and detection time as well when multiple individuals surfaced simultaneously at close distance. Visual detection data were truncated to within 300 m perpendicular to the cruise line to adjust the detection range of the acoustic monitoring system (Akamatsu *et al.*, 2008). In the case of Ganges River dolphins, no truncation was performed because the width of the river was less than 300 m for the entire stretch of the surveyed area.

An A-tag passive stereo acoustic data logger (ML200AS2; Marine Micro Technology, Saitama, Japan) was used for passive acoustic monitoring of both dolphin species. The A-tag was fixed to the end of a 30 m rope, which prevented contamination from engine noise and cavitation. We towed the A-tag simultaneously while conducting visual observations. A pulse-event recorder measured the sound pressure level of ultrasonic pulses and the time arrival difference between the two hydrophones, which were separated 189 mm. It consisted of two ultrasonic hydrophones (MHP 140ST; Marine Micro Technology) with a passive band-pass filter circuit (−3 dB, with a range of 55–235 kHz), a high-gain amplifier (+60 dB), a CPU (PIC18F6620; Microchip, Detroit, MI, USA), flash memory (128 MB), and an off-the-shelf lithium CR2 battery housed in a waterproof aluminum case.

The inter-pulse interval of a typical click train of odontocetes is several tens of milliseconds, and exhibits a smooth change in sound pressure level (Au, 1993). Click trains were

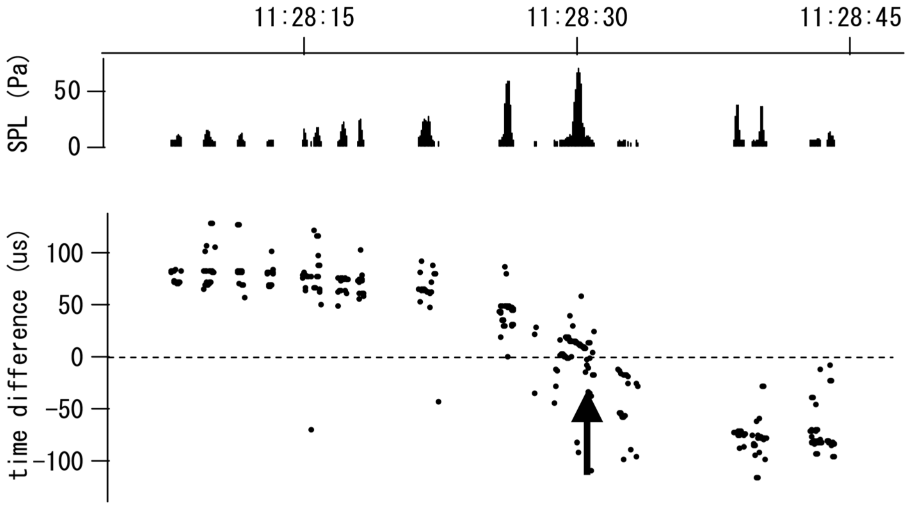

FIG. 2. Trace of the angle of a sound source, corresponding to one animal. A Ganges River dolphin produced click trains within 40 s and passed by the towed acoustic data logger. The zero crossing point at 11:28:30 is indicated by the arrow. At this time, the animal was located perpendicular to the stereo hydrophone, because the difference in the time arrival of the sound was 0.

visualized using Igor Pro software (WaveMetrics, MA, USA) application developed for this study. No offline filter was used, because the noise level in the focal areas was very low. Unlike the ocean, the focal waters were fresh or brackish and had few noise sources, such as waves, bubbles, and snapping shrimp.

We examined the change in direction of click trains (Fig. 2). As a phonating dolphin passed the moving survey boat, a dotted line changing direction from positive to negative corresponded to the dolphin (Kimura *et al.*, 2009). The detection time was defined at the zero crossing point, which indicated that the animal was on a perpendicular line to the cruise course and the hydrophones. Because the A-tag stereo hydrophone was towed parallel to the cruise line, no difference in time arrival to the hydrophones indicated that the sound source was located perpendicular to the course.

III. RESULTS

Figure 3 shows the survey lines and the positions of visual and acoustic detections in a day using identical scale. The same cruise line was used four times in the Ganges River and 11 times in Chilika Lagoon. In the accumulated data, we detected 54 Ganges River dolphins visually and 69 acoustically during the observation period. In Chilika Lagoon, we detected 190 Irrawaddy dolphins visually and 160 acoustically. Visual detection of Irrawaddy dolphins over 300 m distant from the boat did not match with acoustic

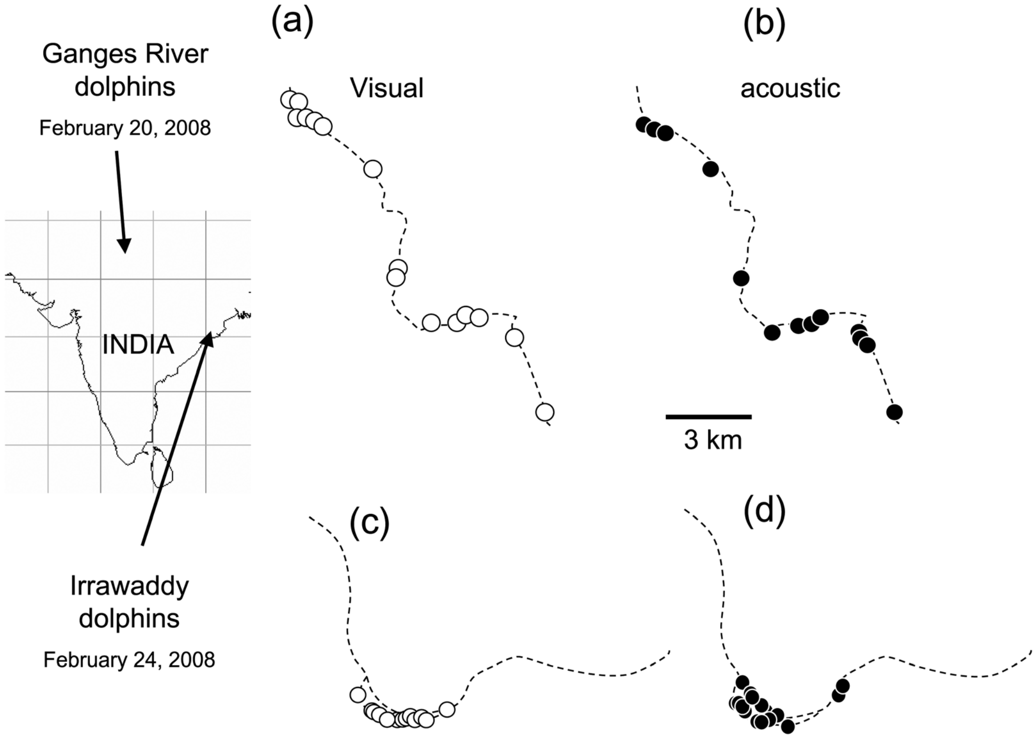

FIG. 3. Cruise line (dotted lines) and position of detections of Ganges River dolphins (a and b) and Irrawaddy dolphins (c and d) in a single day. Visual and acoustic detections of each species are shown as white and black circles, respectively. Note the dispersed distribution of Ganges River dolphins in contrast to the condensed distribution of Irrawaddy dolphins.

detection within a 1 min time window. This suggests the acoustic detection distance of 300 m was appropriate for Irrawaddy dolphins at that site. As can be seen in the Fig. 3, the distribution of Ganges River dolphins was scattered. In contrast, the highest density of Irrawaddy dolphins was localized in the middle of the cruise line. These are used as examples of dispersed and condensed distributions.

Changes in the average cluster size in relation to the time window depended on the spatial distribution of dolphins (Fig. 4). Ganges River dolphins were distributed sporadically and were detected individually. This resulted in a gradual increase in cluster size in relation to the length of the time window. On the other hand, Irrawaddy dolphins were concentrated in the middle part of the cruise line. The Outer channel is affected by tidal currents and is highly biologically productive water. In the northern area of the survey line, contained fixed pound trap-nets, and we did not observe any dolphin there during our survey [Figs. 3(c) and 3(d)]. The concentrated distribution caused a quick increase in cluster size in relation to the length of the time window or unit distance of the cruise line. Among 152 encounters of groups, 30 visual observation encounters contained multiple Irrawaddy dolphins. For Ganges River dolphins, 5 of 48 encounters contained multiple dolphins, indicating that Irrawaddy dolphins were concentrated in a smaller area than Ganges River dolphins.

Figure 5 compares the detection probabilities of the visual and acoustic methods using single cluster (pv, pa) *versus* all clusters (Pv, Pa). The detection probability increased quickly, as predicted by Eqs. (4)–(6), before leveling off over longer time windows. As shown in the lower insets in Figs. 5(c) and 5(d), detection probabilities of all cluster sizes were fairly similar among species for time window longer than 500 s. Acoustic detection probability (Pa) was 80%, approximately 20% higher than visual detection probability (Pv). These detection probabilities of a single cluster, acoustically (pa) and visually (pv) were reduced from Pa and Pv for both species. Note that pa and pv for Irrawaddy dolphins [Fig. 5(b)] were lower than those for Ganges River dolphins unlike the all cluster cases.

The estimated abundance of each species [calculated using Eqs. (13) and (16)] in one cruise of the study area is shown in Fig. 6. In practice, the survey cruise was conducted four times for Ganges River dolphins and 11 times for Irrawaddy dolphins, as mentioned previously. Both estimators, N, stabilized when the time window was longer than 500 s. The estimated abundances of Ganges River dolphins averaged between time windows from 500 to 1000 s were 26.9 and 24.8 individuals using visual and acoustic detection probabilities, respectively. The estimated abundances of Irrawaddy dolphins were 56.1 and 32.4 individuals using visual and acoustic detection probabilities, respectively.

IV. DISCUSSION

Passive acoustic monitoring of cetaceans is becoming widely used for observing the marine mammals (e.g., Barlow and Taylor, 2005; Mellinger, 2007). Odontocetes in particular are suitable species for passive acoustic detection due to their frequent biosonar signal production (Akamatsu *et al.*, 2007). However, counting existing animals acoustically is difficult. For example, density estimation requires various sound source characteristics including sound production rate (Kyhn *et al.*, 2012; Kimura *et al.*, 2010). For quantitative passive acoustic monitoring of cetaceans, the visual-acoustic mark-recapture method is effective, according to the model and data of the present study.

A. Appropriate time window

To detect animals, a cue must be available, whether visual or acoustic. An observer or a detector must wait for at least one likely cue to be produced. Otherwise, detection probability will be underestimated and abundance will be overestimated. As shown in Fig. 5 detection probability

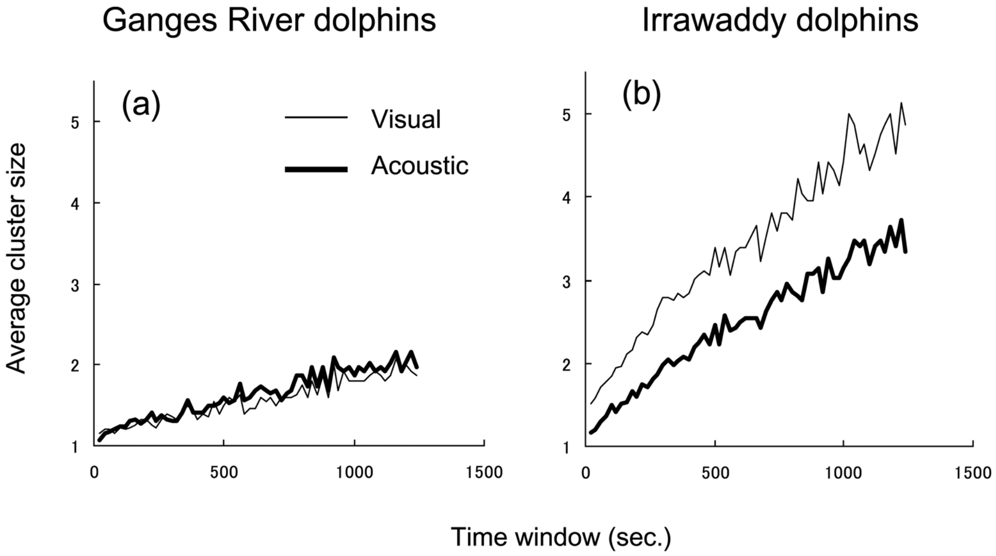

FIG. 4. Average cluster size depends on the length of the time window. The cluster size of Ganges River dolphins (a) increased moderately due to their sporadic distribution, which caused them to be detected individually. The average cluster size even a long (500 s) time window was less than two dolphins. In contrast, the cluster size of Irrawaddy dolphins (b) increased rapidly with the length of the time window.

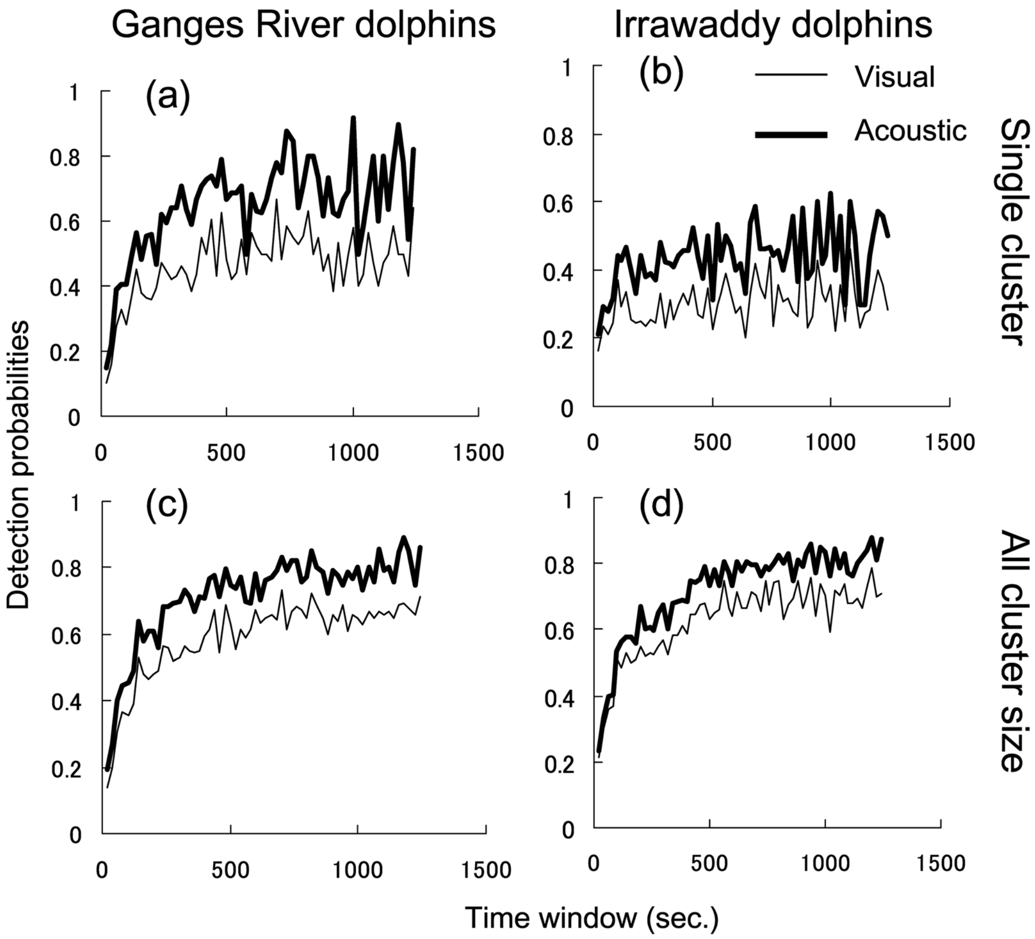

FIG. 5. Detection probabilities, calculated using single clusters [(a) and (b)], and all clusters [(c) and (d)]. The detection probabilities of Ganges River dolphins showed an approximately 10% difference between single-cluster data and all-cluster data, whereas the difference for Irrawaddy dolphins was 30%–40%.

quickly increased when the time window was short that was also supported by Eqs. (4)–(6). The present model seemed to fit with the actual detections and cue matching of wild dolphins.

Acoustic and visual methods were estimated to detect 60%–80% of all cluster sizes with a longer time window (Fig. 5). The proposed model suggested the detection probability would become constant when the time window is longer than surfacing interval of an animal (tv). As shown in Fig. 5, detection probability increased gradually, up to a 300–500 s time window, longer than the 120 s surfacing interval. The longer time window results in the detection of multiple cues, even if there is only a single animal present. A dolphin that surfaced or phonated twice in the time

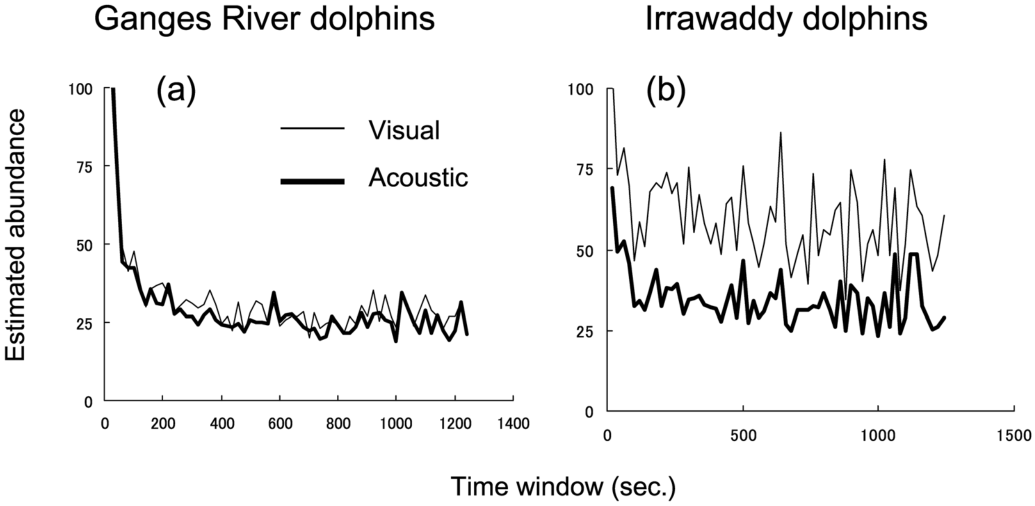

FIG. 6. Estimated abundances of Ganges River dolphins (a) and Irrawaddy dolphins (b) at the study sites using the multimodal detection method.

window is simply more likely to be detected. The transition zone of detection probability from 300–500 s seemed to be affected by the multiple cue effect of an individual. With a longer time window, of more than 500 s, detections are considered to be independent, and the calculated abundance is stable and largely independent of the length of the time window (Fig. 6). This means that use of a specific length of time window is not necessary for abundance estimation.

The survey boat proceeded 1400 m at a speed of 10 km/h during a 500 s time window. Assuming that the dolphins stayed near the area in which they were originally detected and did not swim with the boat with same speed, two detections separated by 1400 m would likely be different animals. In this case, the two detections are independent, and the detection probability of each animal does not change.

B. Cluster size effect

The detection of an individual in a single time window does not mean that only one animal is present. The detection event consists of the detection of a single animal (single cluster) or of one of multiple animals (multiple cluster). If the contribution of a single animal detection is dominant, the detection probability and estimated abundance do not differ much between single-cluster and multiple-cluster calculations, as seen in Ganges River dolphin case, because the components of the multiple cluster C_2, C_3,… in Eq. (10) are negligible and C_1 is dominant. In this case, detection probability of all cluster sizes (Pa) is slightly larger than that of a single individual (pa), as seen in Figs. 5(a) and 5(c). Ganges River dolphins in our study showed sporadic spatial distribution (Fig. 3), and even during a long time window, cluster size did not increase markedly (Fig. 4). The calculated detection probabilities of a single cluster and multiple clusters did not differ notably.

On the other hand, the distribution of Irrawaddy dolphins was concentrated in the middle of the channel, resulting in simultaneous detection of multiple individuals. Relatively large number of multiple animal detections in a time window (30 among 152) was observed in Irrawaddy dolphins. In contrast, 5 of 48 encounters contained multiple dolphins. Acoustic detection also showed larger cluster size in a time window for Irrawaddy dolphins (Fig. 2). Although the detection probability for single clusters was small, the detection probabilities for all cluster sizes were similar in Irrawaddy dolphins and Ganges River dolphin [Figs. 5(c) and 5(d)], indicating a clumped distribution. Acoustic detection performed slightly better than the visual method for both species.

C. Abundance estimation and limitations

The visual and acoustic estimates of the total number of Ganges River dolphins were in good agreement. According to Eqs. (13) and (16), the estimators of the total number of animals can be calculated using the raw number of detected animals divided by the detection probability. Despite the different detection performances of the visual and acoustic methods, the total number of estimations was similar between the methods. Additionally, the numbers of Ganges River dolphins calculated by two estimators were 25 and 27 individuals (Fig. 6), which agreed with 28 individuals counted by Bashir *et al.* (2010) in the 28-km-long stretch of the present research area.

The heterogeneity of multimodal observation (visual and acoustic) is also an issue (Buckland *et al.*, 2004; Borchers *et al.*, 2006). Heterogeneity biases the quantitative measurement of abundance. Dolphins and porpoises produce multiple click trains during single dive between surfacing. Additionally, not only the distance to the animal, but also the directionality of the sound beam, noise level, and phonating behavior affect the detection performance of passive acoustic monitoring (Kimura *et al.*, 2010). According to Khan *et al.* (2011) and his personal communication, approximately 53–58 individuals of Irrawaddy dolphins exist in the surveyed area. Estimates of Irrawaddy dolphins were 32 and 56 by two estimators [Eqs. (13) and (16)], which showed heterogeneity [Fig. 6(b)]. Although the acoustic and visual detection probabilities of both species were similar (Fig. 5), the cluster size of Irrawaddy dolphins detected visually was larger than that detected acoustically (Fig. 4). This indicates that number of positive time windows, nv, for Irrawaddy dolphins was larger than na whereas the acoustic (pa) and visual (pv) detection probabilities did not differ [Eqs. (11) and (14)]. For such a dense grouping of animals, the visual method may exhibit superior cluster estimation, due to its generally larger counts of cluster size (Fig. 4). Another interpretation is that the sound production rate of a group was smaller than that of isolated individuals.

Underestimation of group size by the acoustic method may also explain the heterogeneity (Kimura *et al.*, 2009). The distance between the two hydrophones for the sound source bearing was short in the present study, which may have led to limited angle resolution of the sound sources. This made the discrimination of each individual acoustically difficult. The difference in detection range could also be a limitation. The maximum visual detection range was 500 m, greater than that of the acoustic method. Although visual detection data were truncated to within 300 m perpendicular to the cruise line to adjust the detection range of the acoustic monitoring system, a large group sighted further away from the boat was included occasionally. The condensed distribution of Irrawaddy dolphins seemed to affect the cluster size and visibility of large groups.

In summary, the predictions of the present model, such as detection probability and abundance estimation, were supported by the data obtained from wild dolphin populations. Dolphins are much smaller than baleen whales and more difficult to enumerate precisely. The present model could aid abundance estimation of small odontocetes, which produce biosonar sound frequently. Abundance estimation of dolphins using a multimodal cue detection method was sensitive in terms of the cluster size, which depends on the density and width of the habitat. Further validation and improvement of the model are necessary.

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