Scanning sonar of rolling porpoises during prey capture dives

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SUMMARY

Dolphins and porpoises have excellent biosonar ability, which they use for navigation, ranging and foraging. However, the role of biosonar in free-ranging small cetaceans has not been fully investigated. The biosonar behaviour and body movements of 15 free-ranging finless porpoises (*Neophocaena phocaenoides*) were observed using electronic tags attached to the animals. The porpoises often rotated their bodies more than 60 deg., on average, around the body axis in a dive bout. This behaviour occupied 31% of the dive duration during 186 h of effective observation time. Rolling dives were associated with extensive searching effort, and 23% of the rolling dive time was phonated, almost twice the phonation ratio of upright dives. Porpoises used short inter-click interval sonar 4.3 times more frequently during rolling dives than during upright dives. Sudden speed drops, which indicated that an individual turned around, occurred 4.5 times more frequently during rolling dives than during upright dives. Together, these data suggest that the porpoises searched extensively for targets and rolled their bodies to enlarge the search area by changing the narrow beam axis of the biosonar. Once a possible target was detected, porpoises frequently produced short-range sonar sounds. Continuous searching for prey and frequent capture trials appeared to occur during rolling dives of finless porpoises. In contrast, head movements ranging ±2 cm, which can also change the beam axis, were regularly observed during both dives. Head movements might assist in instant assessment of the arbitrary direction by changing the beam axis rather than prey searching and pursuit.

Key words: biologging, echolocation, cetacean, dolphin, finless porpoise, sonar.

INTRODUCTION

Dolphins and porpoises use narrow ultrasonic beams for echolocation (Au, 1993). The beam width of bottlenose dolphin sonar is 10 deg. (Au, 1993), and that of the harbour porpoise is 16 deg. (Au et al., 1999). An acoustic lens and reflectors (Cranford et al., 1996; Aroyan et al., 1992) focus the ultrasonic beam on a target, such as a prey item. Dolphins and porpoises emit outgoing sonar signals from the melon on the forehead, with a slight upward beam axis of approximately 5 deg. elevation (Au et al., 1999). However, Philips and colleagues (Philips et al., 2003) showed that the beam of Risso's dolphin (*Grampus griseus*) is directed downward. A computer simulation of the transmission beam pattern of the common dolphin (*Delphinus delphis*) indicated that the skull and air sacs play a role in beam formation (Aroyan et al., 1992). This simulation showed low-intensity transmission signals in the ventral direction, assuming that the sound source is in the monkey lips/dorsal bursae (MLDB) complex. These studies have shown that the sonar signal beam pattern in odontocetes is directional, and suggest that the area outside the beam axis could be less sensitive to dolphin and porpoise echolocation.

The use of a narrow focused beam gives odontocetes excellent target discrimination. Once the animals focus on a target, the size and distance of the target and its shape (Harley et al., 2003) and structure (Au, 1993) can be discriminated. The sonar behaviour of large-toothed whales (Miller et al., 2004; Madsen et al., 2005; Zimmer et al., 2005; Johnson et al., 2006; Johnson et al., 2008; Tyack et al., 2006; Ward et al., 2008) and small porpoises (Akamatsu et al., 2005a) has been investigated using electronic tagging technology. These studies showed frequent use of sonar just before possible prey capture. The buzz sound of beaked whales and sperm whales, and the approach phase of finless porpoises have short inter-click intervals, which suggests a short sensing distance to a target, possibly prey, prior to capture trial. Once odontocetes find a target, they display clear range-locking behaviour at a specific distance, both in captivity (Verfus et al., 2005; Verfus et al., 2009) and in the wild (Jensen et al., 2009; Akamatsu et al., 2005a).

A different strategy is needed to find prey within a vast volume in which vision is limited. For example, Ghose and Moss (Ghose and Moss, 2003) and Surlykke and colleagues (Surlykke et al., 2009) demonstrated that the flying bat (*Eptesicus fuscus*) first scans the space around it with a sonar beam and then centres the beam axis on an insect. Scanning sonar is commonly used in ocean fishery surveys. The axis of a narrow multi-beam fan is electronically operated to achieve fine spatial resolution and a wide scanning area (Trenkel et al., 2008). Although the off-axis source level of sonar signals of porpoises is effective for fish detection at a short distance (Akamatsu et al., 2005b), a strong on-axis beam is most useful for long-range sensing. For echolocating animals, beam axis scanning by changing the orientation of the head and body represent possible methods for enlarging the search area.

Scanning behaviour can also compensate for the directional acoustic beam, which is not coaxial with the body longitudinal axis. Watwood and colleagues (Watwood et al., 2006) suggested that scanning large parts of the water column during the descent may enable sperm whales to find profitable prey patches from a distance and reduce search time at the bottom of the dive. The Indus River dolphin (*Platanista gangetica minor*) is reported to swim on its side near the bottom of muddy rivers, while echolocating more or less continuously (Herald et al., 1969). The upside-down orientation of the narwhal allows it to position its tusk near the bottom to scare,

and subsequently guide, demersal prey towards its mouth like a shovel (Dietz et al., 2007). This orientation also improves sonar use and may protect the fragile lower jaw.

In this study, we observed porpoise body and head movements simultaneously with outgoing sonar sounds. A biologging technique was used for *in situ* observations of sensing behaviour.

MATERIALS AND METHODS
Biologging systems and *in situ* calibration

Acoustic data loggers (A-tag; Marine Micro Technology, Saitama, Japan) and behavioural data loggers (PD2GT; Little Leonardo, Tokyo, Japan) were attached to 25 finless porpoises *Neophocaena phocaenoides* G. Cuvier 1829 (Fig. 1), which were then released into an oxbow of the Yangtze River (29.47′–29.51′N, 112.32′–112.37′E). This oxbow lake, which is part of the Tian-e-Zhou Baiji National Natural Reserve of the Yangtze River, Hubei, China, is approximately 21 km long and 1.2 km wide. The reserve was established by the Chinese government in 1992 to protect baiji (*Lipotes vexillifer*) and finless porpoises. A net approximately 1 km long was used to divide the oxbow transversely, and a round, fine-mesh net was used to encircle the animals. Fishermen then waded into the shallow water and captured the animals individually. Animals were temporarily released into a net enclosure for 24 h to calm down. The enclosure was established close to shore and measured approximately 30 m×60 m with a maximum depth of 3.5 m. Body size and mass were measured and a blood sample was collected just before the animal was released. The animals were tagged and released within 2 days of capture. The capture procedure has been described in detail previously (Akamatsu et al., 2005a).

The miniature acoustic data logger consisted of two ultrasonic hydrophones (MHP-140ST; Marine Micro Technology, Saitama, Japan) with a band-pass filter (–3 dB with a 55–235 kHz range), a high-gain amplifier (+60 dB), a CPU (PIC18F6620; Microchip, Detroit, MI, USA), flash memory (128 MB), and an off-the-shelf lithium battery (CR2) housed in an aluminium case that was pressure resistant to a depth of 200 m. A pulse event recorder (A-tag) stored the received sound pressure and time-arrival difference between the two hydrophones every 0.5 ms, which is less than the minimum inter-

Fig. 1. A finless porpoise with the acoustic and the behaviour data loggers attached by a suction cup. The sound arrived from the front hydrophone first. It was proved that off-axis signal could be recorded at this location of the hydrophone (Akamatsu et al. 2005b). Note that the data logger is located behind the pivot point of the cervical vertebrae above the pectoral fin, which is the presumed centre of movement of the head.

click interval of finless porpoises (Li et al., 2007). To save memory, we recorded sound pressure only above a pre-set detection threshold level (134 dB peak-to-peak re 1 μPa). The time-arrival difference was measured separately from sound pressure. A pulse above the preset threshold level triggered the counter to measure delay time between the two hydrophones at 271 ns resolution. The baseline length of the two hydrophones was 105 mm, which corresponds to the maximum time difference of 70 μs 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.

A behavioural data logger (PD2GT, Little Leonardo, Tokyo, Japan) recorded depth, swimming speed relative to the water, and acceleration in the longitudinal and transverse axes. The data logger had depth, temperature, two-axis acceleration sensors, and a propeller sensor to measure swimming speed relative to the water. The sampling intervals for depth, speed and acceleration were 1, 0.125 and 0.0625 s, respectively.

Swimming speed was calibrated by changes in depth and vertical velocity vector (Fletcher et al., 1996). When the tagged porpoise descended or ascended vertically, the change in depth per second corresponded to the swimming speed relative to water. A custom-made software program written using IGOR PRO 5.03 (WaveMetrics, Lake Oswego, OR, USA) by T.A. picked up vertical swimming events and calculated the conversion constant from the rotation of the propeller sensor per second to vertical speed (m s^{-1}), calculated from the depth differential. This allowed a precise measurement of the change in depth that served as a reliable reference value for calibrating propeller rotation, which depended on water speed and the position of the sensor on the animal, due to the modified current around its body. Thus, the method of Fletcher and colleagues (Fletcher et al., 1996) that we employed was useful for *in situ* calibration, as opposed to calibration in a tank.

Roll and pitch angle could be calculated from the raw acceleration measured by the behavioural tag. However, the measured acceleration depended on the position of the tag on the animal. Thus, we needed an *in situ* calibration method for the body angle as well. When a porpoise exposes its blowhole above the surface, the roll angle is assumed to be zero, as the porpoise should be in an upright position. Hence, we averaged all of the dorsoventral accelerations of each individual during inter-bout respiration periods within 30 cm of the surface. This value was used as the reference value of 0 deg. roll angle (upright position). A porpoise's head is down when it descends and up when it ascends. The pitch angle of a porpoise averaged for a long time was assumed to be horizontal. Accelerations based on the longitudinal axis were averaged over the period of tag attachment to the animal. This value was referred to as 0 deg. pitch angle (horizontal position). The pitch angle, which was calculated from the animal's acceleration along the longitudinal axis of the body, was +90 deg. when the animal was positioned with its head pointing straight down to the bottom. The roll angle was calculated using acceleration along the dorsoventral axis of the animal's body with respect to the gravity vector. When the animal was positioned dorsal side up (roll angle +90 deg.), acceleration was measured at +9.8 m s^{-2}, which is the acceleration due to gravity. When the animal was ventral side up (–90 deg.), the acceleration was the negative of the acceleration due to gravity (–9.8 m s^{-2}). When the animal was positioned head up or down, the maximum dorsoventral acceleration

is expressed as a product of acceleration due to gravity and the cosine of the pitch angle, which was used for the calculation of roll angle. Calculated roll angles fall between 0 and 180 deg. only and no negative value exists.

The clocks in the acoustic and behaviour tags were synchronized in advance, allowing sensing behaviour to be matched with specific body movements and dive categories. The clocks in the acoustic and behaviour data loggers drift by up to 2 s per day. To synchronize the clocks between loggers on a single animal, splash noises associated with respiration were used as signals for data matching. During respiration, porpoises tend to produce a splash, which creates broadband noise. At this moment, the propeller sensor is stopped in the air. We compared the pattern of successive respirations recorded by both the acoustic and the behaviour data loggers and removed clock drift and any initial offset.

Tags were attached by a suction cup to the side of the body above the pectoral fin (Fig. 1). Acoustic tags were always attached on the right side and behaviour tags on the left side. The hydrophone on the acoustic tag was positioned approximately 30 cm behind the blowhole of the animal. After spontaneous release, the suction cups were retrieved using VHF radio signals (MM110; Advanced Telemetry Systems, Isanti, MN, USA). Data from tags remaining on animals more than 7 h after the porpoises were released were used for further analysis. This research was conducted under a permit issued by the Fisheries Management Department of Hubei Province, China.

Acoustic data processing

Phonation duration is the time between the beginning and the end of the click train. The beginning and end of a click train was defined as an inter-click interval that was longer than 200 ms, which is the same criterion used in a previous analysis (Akamatsu et al., 2005a). The distribution of inter-click intervals in free-ranging finless porpoises showed a local minimum around 200 ms and 90% of the inter-click intervals were shorter than 276 ms (Akamatsu et al., 1998). The animals tagged in the present study also showed an almost negligible number of inter-click intervals at 200 ms. The phonation duty cycle of a dive was defined as the accumulated phonation durations over the dive time of each individual. The beginning and end of a dive bout was defined as the period during which a porpoise exceeded a depth of 30 cm, which is six times the resolution of the depth sensor and rejects signal contamination from splash noises near the surface.

Biosonar signals were extracted by reducing noise components, according to the following procedure. Biosonar signals from nearby individuals were eliminated by removing sound source angles outside the direction of the self-vocal source ±34 deg., which corresponded to a 12 cm shift of the head relative to the body. This was three times greater than the mean shift of the sound source due to head movements of tagged animals, as shown in Results. Therefore, signals coming from outside this range were judged to be from another individual. Low-intensity clicks below 5 Pa peak-to-peak (134 dB peak to peak re 1 μPa) were eliminated from the data set to avoid noise contamination. This threshold is just above the internal electronic noise level of the acoustic data logger. Click trains containing fewer than six clicks were also discounted to eliminate noise contamination (Akamatsu et al., 2005a), as echolating porpoises usually produce a sequence of ultrasonic pulses (Au, 1993). Randomly changing inter-click intervals were considered to be noise, with randomness defined as a change in the inter-click interval that was not between one-third and three times that of the previous inter-click interval (Kimura et al., 2009).

The average, maximum, minimum and standard deviations of the sound pressure level, sound source direction, and inter-click interval were calculated for each dive bout.

Behaviour data processing

Behaviour and acoustic data during short-duration (<30 s) dives deeper than 30 cm were not analyzed. These short dives often occur during successive inter-respiration intervals (Akamatsu et al., 2002). The remaining dives were categorized into two groups: dorsal side up (upright) dives and rolling dives. The average roll angle during a dive bout was calculated, to yield the mean body rotation around the longitudinal axis. Rolling swimming was defined as a mean roll angle in a dive bout greater than 60 deg. on average, and corresponded to one-half the acceleration due to gravity in a dive bout. If the mean roll angle in a bout was less than 60 deg., the dive bout was categorized as dorsal side up. The 60 deg. was chosen by visual assessment of the roll angle records in the preliminary analysis. As shown later in Fig. 2, when a porpoise kept a stable position, the roll angle was below 60 deg. When it started to roll, the roll angle rose over 60 deg.

The shift of the sonar sound source was calculated using the time-arrival difference of the sound to the stereo hydrophone. The sound source in porpoises is located beneath the blowhole (Cranford et al., 1996), and the data logger was placed behind the pivot point of the cervical vertebrae above the pectoral fin, approximately 30 cm behind the blowhole (Fig. 1). The shift of the sound source relative to the body of the animal was calculated using this distance and the recorded bearing angle of the sound source in the acoustic tag. Because of the short distance to the sound source compared with the baseline of the two hydrophones and the position of attachment of the acoustic data logger, an *in situ* calibration of the centre position of the head was used. We initially calculated the distribution of the time difference and then identified the most frequent time difference. We then only selected sounds that came from within the angle defined above. This data screening procedure removes offsets in the time difference, which depends on the geometry between the sound source and the hydrophone. Note that the direction of the baseline of the hydrophone was not completely aligned with the location of the sound source below the blowhole as depicted in Fig. 1. The calculated movement value was the component on the plane perpendicular to the baseline axis.

RESULTS
Acoustic sensing effort

We observed the sonar behaviour and body movement of finless porpoises simultaneously using time-synchronized data loggers (Fig. 2). Of the 25 porpoises, 15 were tagged for more than 7 h in a free-ranging condition, and the data from these animals were used for further analysis. The total recording time for the 15 animals was 271 h, including surface respiration dives. Excluding short dives that occurred during inter-respiration intervals, we obtained 186 h of effective dive recordings (2907 rolling dives and 6910 upright dives) with body movement and phonation behaviour. Rolling dives occupied 31% of the effective dive duration of the finless porpoises (Fig. 3A). The mean inter-click interval of the 15 animals during rolling dives (29.5 ms, s.d.=10.3) was significantly shorter than that during upright dives (42.5 ms, s.d.=9.7, Wilcoxon signed-rank test *P*<0.001, Fig. 3B), suggesting that the rolling porpoises searched shorter distances than did the upright porpoises.

On average, the animals continuously phonated 22.7% (s.d.=0.13) of the time during rolling dives (Fig. 3C), which was significantly
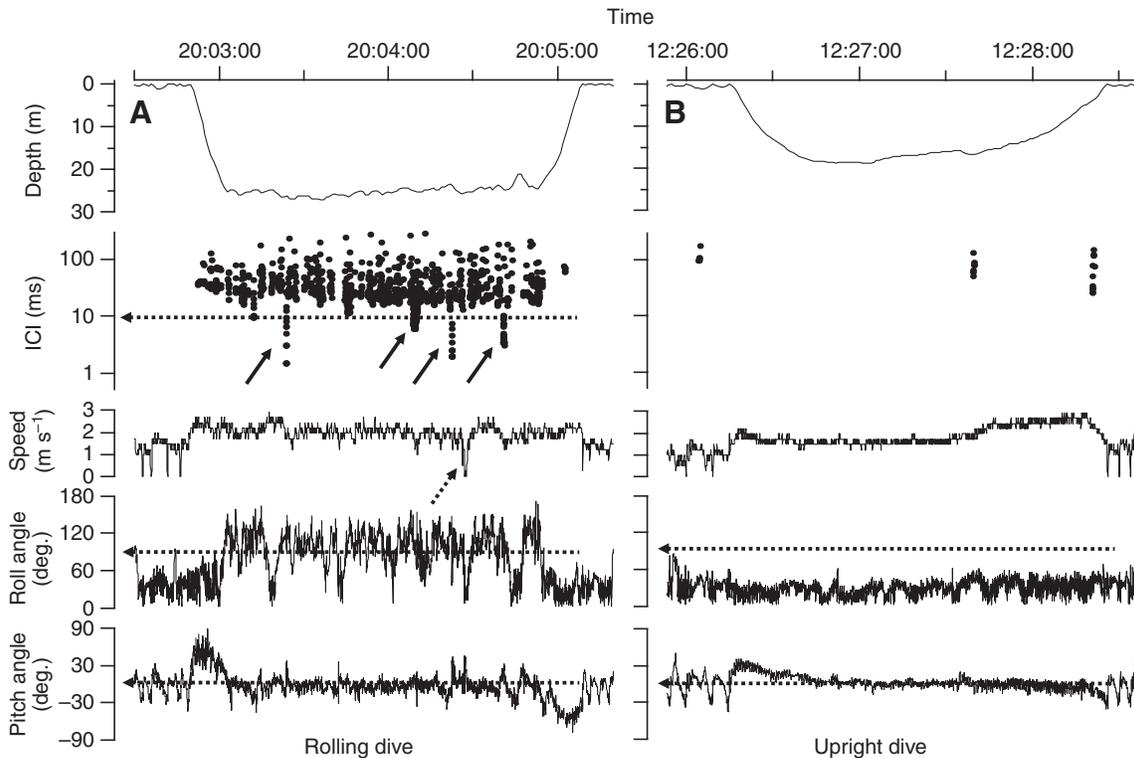
Fig. 2. Rolling dive (A) and upright dive (B). The depth profile, inter-click interval (ICI) of sonar signals, swimming speed, and roll and pitch angles were recorded. Arrows indicate short-range sonar sounds with a minimum inter-click interval less than 10 ms. Short-range sonar sounds were not observed in this upright dive. During rolling dives, the roll angle fluctuated around 90 deg. (dotted line) near the bottom, whereas upright porpoises swam dorsal side up, as indicated by a roll angle close to 0 deg. In contrast, the pitch angle was stable around zero in both dive types, except in descending (positively biased) and ascending (negatively biased) dives. Note that this animal swam at 2 m s^{-1} during almost all of its time on the bottom. However, its speed dropped occasionally (dashed arrow) just after short-range sonar sounds (third solid arrow from left).

greater than the phonation duty cycle of upright dives (12.7%, s.d.=0.09, Wilcoxon signed-rank test $P<0.001$). Rolling porpoises produced more clicks in 1 s (6.61, s.d.=4.8) than did upright porpoises (2.66, s.d.=2.1, Wilcoxon signed-rank test $P<0.001$, Fig. 3D). Thus, the sensing effort during rolling dives was far greater than that during upright dives. Rolling porpoises needed more frequent sonar updates.

The inter-click intervals in the pooled sonar signals of 15 animals showed a bimodal distribution (Fig. 4). Short inter-click intervals (below 10 ms) were frequently observed. The number of inter-click intervals had a local maximum at 25 ms and decreased nearly to zero at 200 ms.

The inter-click interval occasionally dropped below 10 ms (Fig. 2A, arrows). Hereafter, a click train with a minimum inter-
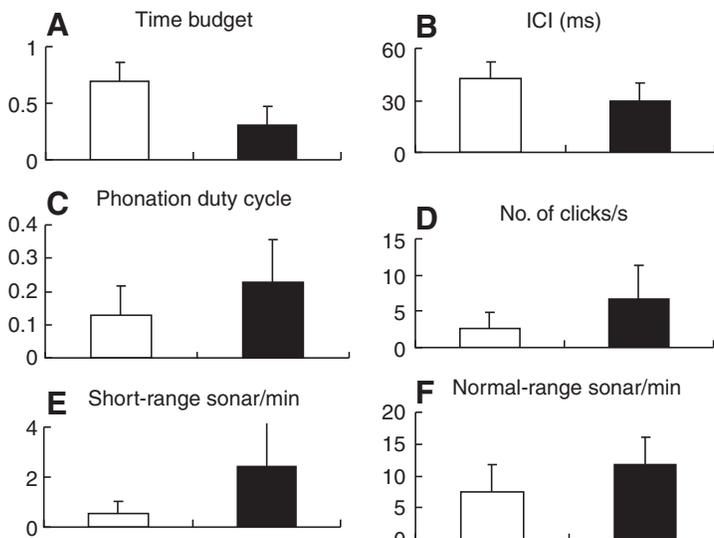
Fig. 3. Comparison of the sonar behaviour of 15 free-ranging porpoises between rolling dives (filled bars) and upright dives (open bars). Rolling dives and upright dives occupied 30% and 70%, respectively, of dive time (A). Inter-click interval (ICI) of sonar sounds was shorter during rolling dives (B). Both the phonation duty cycle (C) and the number of clicks per second (D) were higher in rolling dives than in upright dives. Sensing effort of short-range sonar (E) and normal-range sonar (F) was high during rolling dives. Note that normal-range sonar was observed more often than short-range sonar (comparison of ordinate between E and F). All of these differences were significant (Wilcoxon signed-rank test $P<0.001$).
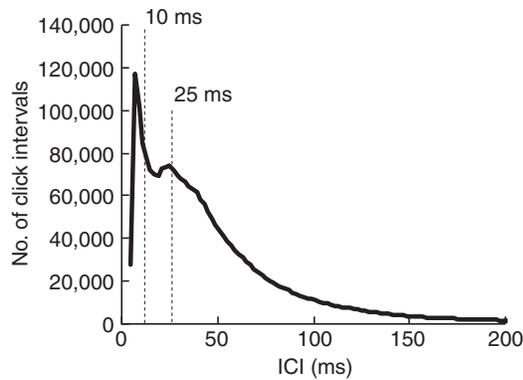
Fig. 4. Pooled distribution of inter-click intervals (ICI) produced by 15 free-ranging porpoises. A bimodal distribution is seen. Short inter-click intervals of less than 10 ms were frequently observed, but relatively long inter-click intervals of about 25 ms were also detected.

click interval of less than 10 ms is defined as a short-range sonar sound, whereas the remaining click trains are defined as normal-range sonar sounds. Short-range sonar sound was observed 2.41 times min^{-1} (s.d.=2.17) during rolling dives (Fig. 3E), which is greater than that during upright dives (0.56 times min^{-1}, s.d.=0.46, Wilcoxon signed-rank test $P<0.001$). Short-range sonar sounds occurred 4.3 times more frequently in rolling dives than in upright dives. In comparison, normal-range sonar was observed 1.6 times more often in rolling dives than in upright dives (Wilcoxon signed-rank test $P<0.001$). This shows that the sonar effort was high during rolling dives; in particular, short-range sonar was used frequently in rolling dives. Within ±2 s from the middle of a click train of the short-range sonar, porpoise swimming speed dropped to zero in 24% of the short-range sonar sounds, whereas it rarely dropped in normal-range sonar sounds (Fig. 5).

Body and head movements

The roll angles of the 15 porpoises ranged from 0 deg. to 180 deg., which correspond to dorsal side up and upside-down positions,
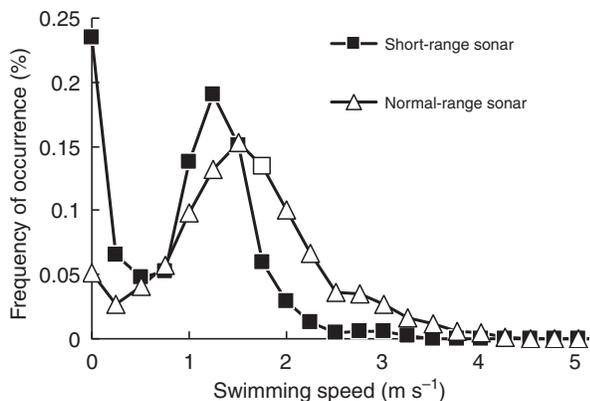
Fig. 5. Minimum porpoise swimming speed ±2 s from the time of short-range sonar sound production. In all, 24% of short-range sonar sounds were associated with a decrease in speed to 0 m s^{-1}. The minimum swimming speed associated with short-range sonar sounds was most often 1.25 m s^{-1} and rarely more than 2 m s^{-1}, whereas for normal-range sonar sounds it was most often 1.5 m s^{-1} and rarely greater than 3 m s^{-1}.

respectively (Fig. 6A). In upright dives, the porpoises remained dorsal side up (0–60 deg.) 93% of the time. However, the porpoises maintained a pitch angle close to zero in both dive types (Fig. 2 bottom, and Fig. 6B). This means the porpoises swam nearly horizontally most of the time whether they rolled or not, based on their longitudinal body axis, except during ascending and descending phases.

The porpoises moved their heads side-to-side or up-and-down on a regular basis, but most frequently maintained the head in a straight forward-facing position (0 cm shift in Fig. 6C). Head shifts ranged from –2.0 cm to the left side to +1.9 cm to the right side. The range of shift was defined as half of the maximum occurrence shown in Fig. 6C. Head shifts reached –4 cm and +7 cm to the left and right or up and down. The asymmetric distribution was caused by the limited resolution of the time-arrival difference recorded by the acoustic tag. The positive end of Fig. 6C corresponds to the end-fire direction, and a small time difference change caused a large shift change. Limited bits of digital recording of the time difference (10 bit) caused relatively large variation in the end-fire direction. The distribution of head shifts for rolling and upright porpoises was similar in the two dive types.
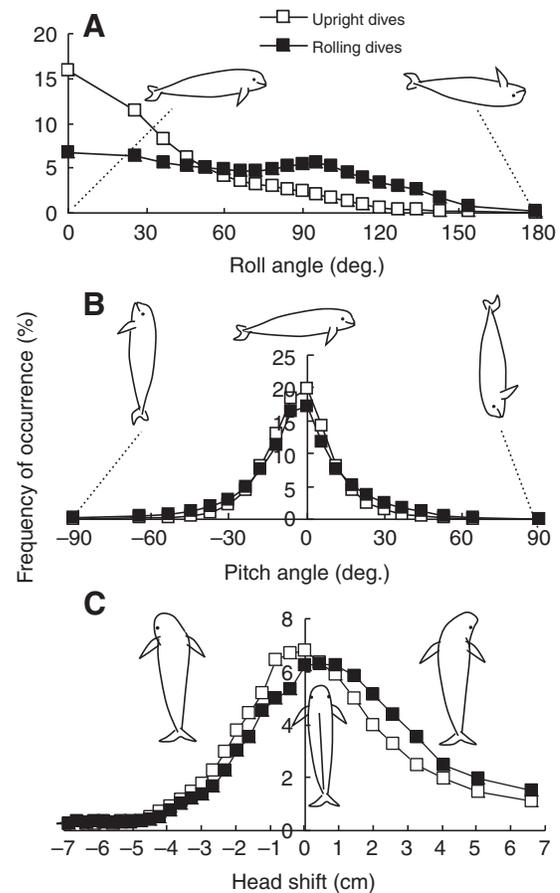
Fig. 6. Average accumulated roll (A) and pitch (B) angles of all porpoises in rolling and upright dives. During rolling dives, the roll angle changed from positive to negative, but the porpoise maintained a horizontal position with respect to its longitudinal body axis. (C) Porpoise head movements. Side-to-side head movements occurred regularly, ranging from –2.0 cm to the left to +1.9 cm to the right. Head movements did not differ between dive types.

DISCUSSION

The odontocete sonar beam has a narrow conical shape, similar to that of a flashlight, and consists of a lens and reflector. The melon organ of odontocetes functions as the acoustic lens of the sonar beam (Au et al., 2006), with the cranial bone and air sacs reflecting the ultrasonic sound (Aroyan et al., 1992). The harbour porpoise, which belongs to the same family as the finless porpoise, produces a beam that is 16 deg. wide (Au et al., 1999). Thus, the sonar beam of the porpoise covers 0.062 steradian (sr), which corresponds to 1% of the solid-angle projection to the hemisphere. Sound pressure levels outside the beam are 3 dB or less, compared with that of the on-axis beam, which means that the detection range is 70% or less. Finless porpoises produce click trains every 5.1 s (Akamatsu et al., 2005a) and swim at $1.2\,\mathrm{m\,s^{-1}}$, on average (Akamatsu et al., 2002). Thus, they can proceed 6 m, on average, without using sonar. If the head of a finless porpoise is in line with its body axis, the porpoise can pass through a large volume of water without acoustically scanning. As our acoustic tags had a 134 dB detection threshold and, thus, could miss a low-intensity sound record (Akamatsu et al., 2007), our measurements may not have captured low-intensity sonar signals. Hence, the sensing effort of the porpoises could be underestimated. However, low-intensity signals are not effective at long-range detection. Off-axis signals contribute little to the enlargement of the search volume because of their short sensing distance, compared with on-axis large source-level signals. In addition, the frontal abdominal area of finless porpoises may represent the low-intensity area of biosonar, as acoustic tags on the animals receive fewer echoes from the water surface when they swim upside down (Akamatsu et al., 2005b). This limits the search area, especially near the bottom, during upright swimming. When a narrow beam is used, beam-axis scanning can enhance scans of wide areas, which is how commercial scanning echo sounders function.

Body rolling by finless porpoises was combined with extensive search efforts. Independently observed acoustic sensing characteristics and behavioural dive types were strongly related in the present study. Rolling dives comprised 31% of the total dive time of the 15 animals, and the animals used sonar extensively during rolling dives, compared with upright dives. The phonation duty cycle of rolling dives was nearly double that of upright dives. Rolling behaviour might enlarge the search area of the porpoise by changing the beam axis of its sonar.

Other potential explanations for rolling are related to prey behaviour as well as the preferred capture orientation of the predator for certain prey types. In Hong Kong waters, finless porpoises appear to feed on bottom-dwelling and mid-water prey, suggesting that they feed at different levels of the water column (Barros et al., 2002). Chen and colleagues showed that freshwater shrimp and shellfish, as well as carp and catfish, were prey species of Yangtze finless porpoises (Chen et al., 1997). Rotating the body 90 deg. would seem beneficial for catching benthic prey. During side-swimming, when the rotation angle of the body is around 90 deg., the porpoise's mouth is open parallel to the bottom, and benthic prey such as freshwater shrimp and shellfish might be easier to capture and eat. However, our data did not support this hypothesis. The porpoises we tagged often rolled from an upside-down to an upright position (Fig. 6A) while maintaining an almost horizontal pitch angle (Fig. 6B). A relatively stable pitch angle did not affect the roll angle component, and the two were considered nearly independent. This demonstrates that porpoises roll while maintaining a horizontal position during swimming. Thus, porpoises are unlikely to continue side-swimming to capture nearby prey.

Rolling behaviour could comprise a technique for making small radius turns in the horizontal plane to pursue prey or to return to a prey patch. As shown in Fig. 2 (left), occasional drops in swimming speed match the short-range sonar events, but this happened in short duration. The porpoise continued rolling throughout the remainder of the observation period without speed reductions or quick changes in pitch angle. In addition, rolling was periodic in this example, with the period ranging from several seconds to more than 10 s, which indicates that rolling angular speeds were very slow.

The sensing distance is believed to be shorter during rolling dives than during upright dives. A simple correlation between inter-click interval and sensing distance may result from the particular tasks these animals were trained to perform (Thomas and Turl, 1990; Au, 1993). There is not a great amount of data either supporting or refuting a similar general correlation in wild free-swimming animals. Odontocetes require a lag time to process echoes (Au, 1993). In the search phase, trained harbour porpoises displayed a clear range-locking behaviour on landmarks, as indicated by a distance-dependent decrease in click intervals (Verfuss et al., 2009). Verfuss and colleagues reported that porpoises used a fairly constant click interval of about 50 ms in the initial part of the approach phase (Verfuss et al., 2009). The two-way sound travel distance calculated using the inter-click interval, however, does not always correspond to the target distance. The inter-click interval can be considered an index of sensing distance, simply identifying short or long ranges rather than representing sensing distance values in metres. A comparison of inter-click intervals among three species of dolphins and porpoises showed clear differences between individuals in the wild and in captivity, depending on the size of the environment (Akamatsu et al., 1998).

Rolling dives were also characterized by short-range sonar sounds having minimum inter-click intervals of less than 10 ms. The mean inter-click interval was also shorter in rolling dives. Short-range sonar sounds were often associated with speed drops (Fig. 5). This quick reduction in swimming speed to nearly zero indicates that the turning-around behaviour of porpoises (Akamatsu et al., 2002) is observed only during rolling dives. In sperm whales, the biologging system of Miller and colleagues recorded similar echolocating behaviour, with many rapid-click buzzes produced within 10 s of a depth inflection (Miller et al., 2004). Together, these data suggest that the porpoises engaged in extensive sensing efforts for targets with active rolling of their bodies. Once they found a target, they produced short-range sonar sounds frequently. Continuous searching of prey and occasional capture trials appeared to take place during the rolling dives of the finless porpoises.

In finless porpoises, the joints of the cervical vertebrae are flexible, allowing the animals to turn their necks at an angle to their longitudinal body axis. This allows another form of beam scanning, as indicated in Fig. 6C, which shows that head scanning occurred not only during rolling dives but also during upright dives. The distribution of head movements during the two types of dives was similar. Sound source shifts ranged from –2.0 cm to +1.9 cm from left to right, which corresponds to a change in head direction from –3.8 deg. to +3.6 deg. Head movements are quicker than body movements when changing the beam axis, as body rolling takes several seconds, even though an occasional quick twist of the body occurred (Fig. 2). Head movements might also be more energetically efficient than body movements and allow some flexibility in the approach trajectory towards prey. Thus, head movements might assist in instant assessment of the arbitrary direction. Head scanning sonar may target prey, predators, the water surface, or nearby obstacles. This could occur during both rolling and upright dives

and is consistent with our observations of the same pattern of head movement among different dive types.

As shown by the standard deviation in Fig. 3, sonar signal characteristics show individual variation, which means that data obtained from a small number of animals could lead to biased interpretations. For example, the number of short-range sonar events during rolling dives (Fig. 3E) shows a large standard deviation, which means that some individuals did not use short range sonar as frequently, even during rolling dives. Clearly, larger numbers of animals need to be tested for biosonar behaviour using the biologging technique.

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