REVIEW

Foraging and feeding ecology of *Platanista*: an integrative review

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ABSTRACT

1. Limited visual perception in aquatic environments has driven the evolution of diverse sensory modalities in aquatic mammals. Dolphins largely use echolocation for prey capture in the face of limited visual and olfactory cues. Multiple foraging modes exist, although an understanding of how sensory systems are adapted to environmental and prey characteristics is limited. This is especially true for animals with extreme sensory specialisation, such as South Asian river dolphins of the genus *Platanista*. This taxon is effectively blind and retains plesiomorphic traits from its once-diverse ancestors. Distributed in murky rivers of the Indus-Ganga-Brahmaputra basins, it is thought to use mainly echolocation for feeding on fish and shrimp.

2. We hypothesised that foraging modes used by *Platanista* differ according to prey position in the water column (at the river surface, mid-column, and bottom) and are mediated by ecomorphology, acoustics, prey characteristics, and habitat features.

3. To test this, we combined a detailed review of the literature (anatomy–physiology–morphology studies, observations in captivity) with preliminary field observations and acoustics studies to investigate foraging mode selection.

4. *Platanista* displays peculiar foraging and feeding behaviours, including side swimming, rotational feeding, and grasp-suction feeding. Feeding is restricted to small prey with low body depth. At the river surface and bottom, echolocation-based foraging may not be efficient due to acoustic reflection or reverberation effects.

5. *Platanista* uses echolocation clicks to scan and detect prey at distances of about 20 m across the river mid-column, possibly switching to passive listening at the surface, and electroreception at the bottom, to maximise prey capture rate and feeding success.

6. *Platanista* is remarkable for its ability to persist in some of the most intensively used and abused river basins of the world. Using echolocation, electroreception, and passive listening might reduce overall foraging costs and contribute to the adaptability of the taxon.

INTRODUCTION

Limited visual perception in freshwater and marine environments (Aksnes & Giske 1993) has driven the evolution of diverse compensatory sensory mechanisms or modalities for feeding and foraging in aquatic animals (e.g. Rice 1983, Atema et al. 1988, Bullock et al. 2006, Czech-Damal et al. 2012a). These modalities involve foraging by aquatic invertebrates and vertebrates with the use of acoustic, chemical, electrical, and magnetic perception to overcome visual constraints (Ladich 2000, Albert & Crampton 2005, Patullo & Macmillan 2010, Kremers et al. 2016, Torres 2017). Selection of foraging modes (Helfman 1988) is influenced by energetic and metabolic costs imposed by environmental factors (Evans & Awbrey 1988, Higginson & Ruxton 2015), ecomorphological constraints on feeding performance (Wood & Evans 1980, Kane 2009, Kremers et al. 2016), characteristics of prey eaten (Bowen et al. 2002, Benoit-Bird 2004), and competitive interactions with other taxa. In odontocetes (toothed whales, porpoises, dolphins; Mammalia: Cetacea), the use of echolocation for prey capture evolved as a dominant foraging mode (Wood & Evans 1980, Benoit-Bird et al. 2004, Nummela et al. 2007), alongside limited visual and olfactory senses (Atema et al. 1988, Freitag et al. 1998, Kremers et al. 2016). Diverse foraging modes exist in odontocetes (Barros & Myrberg 1987, Czech-Damal et al. 2012a, Kremers et al. 2016), yet an understanding of how their sensory systems function in relation to environmental and prey characteristics at different scales is limited (but see Torres 2017 for a comprehensive review).

In particular, the relationship between sensory systems and foraging needs to be explored in odontocetes with extreme sensory specialisation (Gutstein et al. 2014, Torres 2017). A good candidate taxon for such an investigation is the South Asian river dolphin genus *Platanista*, a group considered to be one of the most evolutionarily primitive of extant cetaceans (Reeves & Brownell 1989, Nowak 2003, Moreno 2004), diverging about 20–30 million years ago in the Miocene (Cassens et al. 2000, Hamilton et al. 2001). The genus is the only living representative of a once globally distributed lineage of long-snouted coastal dolphin forms that diversified during multiple marine transgression episodes (Cassens et al. 2000, Hamilton et al. 2001, Lambert & Muizon 2013). *Platanista* may have retained some traits of terrestrial ancestors (Pilleri 1974, Nummela et al. 2007, Gutstein et al. 2014). *Platanista* comprises two extant subspecies (Indus and Ganges dolphins) of obligate freshwater cetaceans distributed in the Indus–Ganges–Brahmaputra basins of South Asia. Evolution in these sediment-laden, murky rivers has led to extreme regression of the crystalline lens of the eye in *Platanista* (Herald et al. 1969, Pilleri 1974, Purves & Pilleri 1975), rendering them effectively blind. In captivity, Indus dolphins touch the tank floor while moving, like blind people feeling for obstacles (Pilleri & Gihr 1976). With their pinhole-eyes, *Platanista* may only be able to resolve light and dark horizons (Herald et al. 1969, Waller 1983) and are thought to rely mainly on echolocation for foraging and feeding (Purves & Pilleri 1975, Reeves & Brownell 1989, Nowak 2003, Moreno 2004, Lal Mohan & Kelkar 2015). Use of high-frequency clicks at low sound source levels and side swimming (with sideways tail movements) may both enable effective navigation in shallow water (Herald et al. 1969, Pilleri 1970a, Pilleri et al. 1971a,b, 1977, Purves & Pilleri 1975, Gihr et al. 1976, Jensen et al. 2013, Sasaki-Yamamoto et al. 2013). Side swimming may also be used for orientation with reference to the sunlit water surface and darker bottom (Herald et al. 1969, Pilleri 1974, Waller 1983).

There has been substantial and long-standing interest in the evolutionary biology of *Platanista* (e.g. Hamilton et al. 2001, Gutstein et al. 2014), its morphological and anatomical peculiarities (e.g. Anderson 1879, Kukenthal 1909, Herald 1969, Herald et al. 1969, Takahashi & Yamasaki 1972, Pilleri & Gihr 1976, Pilleri et al. 1976), and convergence of its form with other riverine vertebrates such as gavialine crocodiles (Taylor 1987, McCurry et al. 2017a,b). Captive studies in the 1970s in the United States, Switzerland, and Japan (e.g. Herald 1969, Pilleri et al. 1970, 1971a, Kasuya 1972, Gihr et al. 1976), and behavioural observations in the wild (e.g. Reeves & Brownell 1989, Smith & Reeves 2012, Lal Mohan & Kelkar 2015) together provide substantial information on the taxon's ecology. Yet, descriptions of foraging and feeding in *Platanista* are largely restricted to information from stomach contents (e.g. Butt 1977, Sinha et al. 1993, Choudhary et al. 2006) or anatomical specialisations (e.g. Thewissen & Nummela 2008, Gutstein et al. 2014). As a result, despite a large body of work, a coherent framework remains wanting for a comprehensive understanding of *Platanista* foraging and feeding ecology. The sensory ecology of *Platanista* offers an exciting opportunity to explore potential factors driving diversification of foraging modes (Kane 2009, Kremers et al. 2016) and adaptations to their dynamic environment (Jordan & Ryan 2015, Torres 2017).

In this review, we bring together multiple lines of evidence on the interactions of foraging and feeding by *Platanista* with its ecomorphology, anatomy, physiology, prey types, echolocation characteristics, movement behaviour, and river soundscape features. Specifically, we test the hypothesis that foraging modes used by *Platanista* differ according to prey position in the water column, that is, at the surface, mid-column, and river bottom. For this, we combine a detailed review of the literature (on *Platanista* anatomy, morphology, ecology, evolution,

acoustics, and prey characteristics) with some preliminary observations on feeding behaviour, acoustics, and stomach contents (in the Ganga river, India). We discuss potential foraging modes used by dolphins to feed in diverse riverine habitats, subject to sensory (internal) and environmental (external) constraints on prey capture, ingestion, and foraging mode selection. Our review helps generate novel hypotheses on the diversification of foraging modes in odontocetes with extreme sensory specialisations.

METHODS

Literature review

PLATANISTA BIOLOGY, ECOLOGY, AND EVOLUTION

We reviewed a total of 172 articles, covering all available published biological and ecological work related directly or indirectly to *Platanista* from 1879 to the present day. For this review, we selected 105 articles, of which 42 were mainly related to the foraging and feeding ecology of *Platanista*; 28 with the general biology of riverine, coastal, or estuarine dolphins; 18 provided theoretical insights on sensory ecology and foraging by aquatic animals; and 17 pertained to the biology of dolphin prey.

Articles were found by searching online resources and in institutional and university libraries; videos and photographs from the internet were also used (but were not included as articles). For searches on *Platanista*, we included the following relevant names: *Platanista gangetica, Platanista indi, Platanista gangetica gangetica, Platanista minor, Platanista gangetica minor,* Ganges river dolphin, Gangetic dolphin, South Asian river dolphin, Indus river dolphin, Indus dolphin, Susu, Bhulan. With a possible species split pending (see Braulik et al. 2015), we considered the Ganges and Indus subspecies (*Platanista gangetica gangetica* and *Platanista gangetica minor*) as putatively similar in terms of biology and ecology. We found literature spanning anatomical-ecomorphological-physiological studies, researche in captivity and in the wild, population surveys, behaviour, stomach contents, acoustics, convergent morphological traits, phylogenetic, and evolutionary studies. Monographs by Anderson (1879), Herald et al. (1969), Pilleri et al., and Kasuya et al., in the 1970s, were the main sources of information for anatomy, morphology, and behaviour, described from their captive and invasive studies.

LIFE-HISTORY TRAITS AND SENSORY ECOLOGY OF FISH AND SHRIMP PREY

Sources for prey characteristics included research articles, reviews, books, and monographs (details above) that described (1) fish/shrimp prey along with other stomach contents and (2) life-history and sensory traits of fish/shrimp prey. A database was compiled on fish and shrimp prey groups (with approximately 45 species) from these sources (for wild and captive *Platanista*). We added details of prey species from our own records of dolphin stomach contents to the database. The database compiled information on occurrence of prey groups in stomach contents, prey length, prey body depth (maximum distance between dorsal and ventral surfaces), sensory characteristics (sound production, hearing, swim-bladder form, swimming, electroreception), presence of specialised organs, schooling habits, and habitat preferences in prey species (for substrate type, water depth, underwater structure, etc.).

Field observations and preliminary acoustic studies

STUDY AREA

We conducted preliminary field observations and acoustic studies in a 100-km stretch of the Ganga River in the Bhagalpur district of Bihar, India (site details in Choudhary et al. 2006 and Kelkar et al. 2010). This stretch is characterised by large meanders, side-channels, and deep pools. Average dry-season depth was 2–40 m and flow velocity was 1.5–1.8 m s^{-1}. Acoustic studies were done at Barari (2–14 m depth) and Kahalgaon (6–30 m depth).

OBSERVATIONS ON DOLPHIN CARCASSES AND STOMACH CONTENTS

Our team has been involved in conservation awareness programmes with local fishers for over 16 years (2000–2017), due to which dolphin hunting has reduced, but fisher informants report accidental bycatch mortality. On eight occasions when mortality was reported (of two adult males, one adult female with foetus, one subadult female, four calves), we were able to sample stomach contents from dolphin carcasses and record the size, species, and morphological characteristics of prey items. Stomach contents were cleaned with water, and remains of fish manually separated from other items and dried for further investigation. Partially digested fish and crustacean prey items in the stomach were sufficiently intact to be identified to the genus or species levels. Highly degraded boluses were not used for prey identification.

We took photographs of the dolphins and recorded their: (1) body measurements, (2) rostrum characteristics, (3) digestive tract features, (4) status of teeth, (5) body condition, and cause of death.

BEHAVIOURAL OBSERVATIONS OF LIVE, WILD DOLPHINS

We compiled our visual observations on surface feeding events by wild Ganges dolphins in diverse habitats (deep pools with eddy countercurrents, confluences, shallow river banksides, side-channels). Observations were made opportunistically, and the location and timing of unambiguous feeding events were logged during river surveys, occasionally during continuous 24-hour monitoring. Only surface feeding events were observable and were defined based on: seeing fish in rostrum of surfacing dolphins, fish jumping out of the water after dolphins were seen splashing, side swimming (with flippers out of water), or tail-slapping with rapid circular movements in shallow water.

ACOUSTIC STUDIES: ESTIMATING PREY DETECTION DISTANCE AND ECHOLOCATION CLICK DEPTH

To assess water column use by foraging dolphins, we made acoustic recordings of echolocation clicks, in order to: (1) calculate sound source levels and minimum target prey detection distances, and (2) estimate click depth (based on Rudstam et al. 2003, Au et al. 2007; see Appendices S1 and S2 for details of recording setup and calculations). Recordings were made over four days in November 2015. Before recordings, river depth and substrate characteristics were measured and local fish species composition was recorded. Two A-Tags (MMT Corp, Japan; with two hydrophones each) were used to log bearings of click trains, and one calibrated SH-200K hydrophone (System Intec, Japan) was used to record clicks. These were set up as a linear array: the A-Tags were tied to the ends of a 3-m-long metal pole with the hydrophone in the centre, which was suspended from a fishing or rowing boat to make recordings. Sound source distance was calculated from time-of-arrival differences in each A-Tag's hydrophone pair, using only 'on-axis clicks' ($n = 47$ trains) for analyses, based on Bahl et al. (2007) and Morisaka et al. (2011). For estimating sound source level, the array was suspended horizontally (parallel to the river bed). Due to left-right ambiguity of the A-Tags, the exact position of the dolphins could not be determined. Dolphins usually produce a pulse immediately after hearing the previous sound's echo, so Inter-Pulse Intervals (IPI) can be used as a proxy for how far dolphins actually perceive targets when they are emitting clicks (Sugimatsu et al. 2008, Morisaka et al. 2011, Jensen et al. 2013). The minimum target prey detection distance was calculated from sound source levels. For estimating echolocation click depth, the same A-Tag setup was suspended vertically (perpendicular to the river bed). Data were then checked for the highest frequency for all bearing angles (along the vertical plane) of click bouts

logged be each of the two A-Tags, to estimate click depths. Our recordings were made in random directions and not with specific individuals facing the array, and indicated only the general tendency of click emission at different depths by *Platanista*. We calculated depths at which echolocation clicks were emitted ($n = 29$), as: [estimated sound source depth (m)/river depth (m)]*100, to account for variable recording depths (range 5–20 m), with the surface at 0%. For all further analyses, we defined the 'surface' as the depth layer from 0% (surface) to 20% of depth, 'mid-column' from 20 to 80%, and 'bottom' from 80 to 100%.

RESULTS AND DISCUSSION

Ecomorphological, anatomical, and physiological peculiarities of *Platanista*

GRASP-AND-SUCTION FEEDING

Werth (2006) described feeding modes in odontocetes based on their position along a ram-suction feeding continuum. Typically, short-snouted species use more suction than long-snouted cetaceans, although mechanisms vary (Werth 2006, McCurry et al. 2017b). *Platanista* may use a grasp-and-suction feeding mechanism, in which suction is used for intraoral transport of prey into the gullet (McCurry et al. 2017b) after prey items are first grasped by 'lateral snapping' (Hocking et al. 2017) of the larger teeth at the long rostrum's anterior end (Fig. 1a). Captured prey is then passed into the throat, aided by the tongue and hyoid musculature (Reidenberg 2007). Arvy and Pilleri (1970) noted that the tongue of *Platanista* is remarkably large for a mammal known not to chew food. The tongue is extremely smooth, but has free edges with perforated mammillae (a characteristic unique to *Platanista* among mammals; Arvy & Pilleri 1970). The lower surface of the tongue is attached to the floor of the mouth, and the curved edges are probably used to form a channel for quick ingestion. Arvy and Pilleri (1970) also noted two longitudinal paramedian fissures behind the tongue and a V-shaped mark opening into the glossopharynx, which could act as accessory structures to channel prey inward. The suction thrust required for deglutition might be produced with curved buccal folds and throat muscles, and by lowering of the larynx while ingesting prey (Fig. 1b). Pilleri et al. (1970, 1971a) did mention these behaviours but did not explicitly consider suction. Suction power decreases with increase in snout length (Werth 2006, van Wassenbergh & Aerts 2009), but the tongue may aid suction for swallowing in both short-snouted juveniles and long-snouted adults. Captive observations on Indus dolphins indicate that fish are grasped in the teeth and
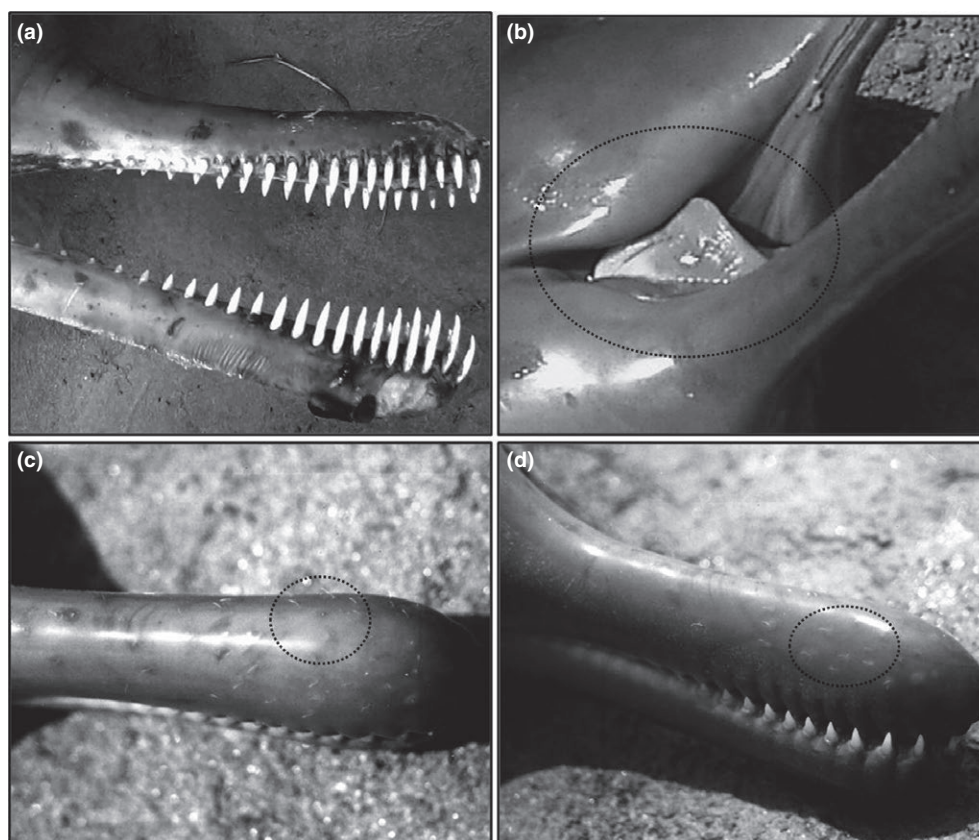
Fig. 1. Photographs (not to scale) showing some peculiar ecomorphological traits of *Platanista*: (a) Interlocking teeth with longer teeth at the rostrum tip, for grasping and snapping prey firmly, (b) fleshy hyolingual apparatus and tongue for suction-feeding, and (c) dorsal view and (d) side view of vibrissae in river dolphin calf. All photos by authors.

repositioned parallel to the snout and melon axis (Gihr et al. 1976). Fish are swallowed fast and then passed into the gullet with a backward head tilt, indicating the possible use of suction. If fish caught perpendicular to the rostrum escape during repositioning in the mouth, they die rapidly due to bite marks (Pilleri 1972, our field observations). We observed frequent surfacing (short dives) by Ganges dolphins during feeding events.

SIDE SWIMMING

Side swimming, a unique behaviour observed first in captive *Platanista*, is generally associated with the exploration of their surroundings and prey capture in the water column (Herald et al. 1969, Pilleri et al. 1970, Pilleri 1974, Waller 1983). Some authors have suggested that side swimming might be due to the restricted, homogenous, and enclosed aquarium tanks where the Indus dolphins were kept (Haque et al. 1977), and is perhaps rare and not associated with foraging in the wild. But we have observed side swimming accompanying feeding activity by Ganges dolphins in a

shallow (<1 m depth) confluence zone in the Ganga and Gandak Rivers, on some occasions, where the flippers of the dolphin were visible above the water. Circular side swimming appears to be a common behaviour in shallow river channels. Video evidence of this behaviour in wild Ganges dolphins comes from the Giruwa/Ghaghra River in India (Jackson 2010). *Platanista* have the longest inner ear canals of any extant cetacean (Thewissen & Nummela 2008, Gutstein et al. 2014). The vestibular system and canals (organs of balance in cetaceans; Thewissen & Nummela 2008) might have enabled the excellent manoeuvring abilities of *Platanista* (e.g. for side swimming in shallow waters), given their high neck motility (Kasuya & Haque 1972, Pilleri 1972, Spoor et al. 2002). Pilleri and Gihr (1976) suggest that the structurally complex diverticula of the Eustachian air sac system might also enhance sound production and hearing in *Platanista*. *Platanista* have acute and directional hearing, its focus fine-tuned by upward and downward bending movements of the flexible neck and head, during both normal and side swimming (Thewissen & Nummela 2008, Jensen et al. 2013).

PECULIAR DIGESTIVE ANATOMY

The presence of an intestinal caecum, few goblet cells in the intestines but many in the rectum, shorter intestines than expected by allometry, and narrow oesophagus are peculiar features of the *Platanista* digestive system (Yamasaki & Takahashi 1971, Takahashi & Yamasaki 1972) compared with that of other odontocetes. Langer (2017) reviews caecal evolution in mysticetes and older cetartiodactyls and suggests that the *Platanista* caecum may play a role in the degradation of prawn chitin, noting that prawns are common prey items. Langer also emphasises the need to study gut microbial activity in *Platanista* in relation to the caecum. Curiously, Gihr et al. (1976) reported sustained observations of coprophagy (the dolphins fed on their own faeces) in three captive subadult and adult Indus dolphins. Two types of stools (diameter 1–2.5 cm) were noted. The first, greenish softer type was eaten, and the second, black, cylindrical, and harder type was not eaten. Coprophagy could have been induced by captive stress in these animals, as Gihr et al. (1976) suggested. Coprophagy is known (and related to the caecum) in both wild and captive leporids, perissodactyls, most suids, and some rodents (Hirakawa 2001, Langer 2017). Thus, it remains to be seen whether the *Platanista* caecum and the observed coprophagy are connected.

ACOUSTIC CLICKS AND HEARING IN *PLATANISTA*

The acoustic repertoire of *Platanista* includes clicks and burst-pulses (rapidly emitted click trains). Audible jaw-snapping sounds made by *Platanista* were thought to be unrelated to feeding (Andersen & Pilleri 1970). Hypertrophied maxillary crests in *Platanista* offer precise directionality to emitted clicks (Jensen et al. 2013), and only fish passing in a 10º cone before the snout were caught by captive Indus dolphins (Pilleri et al. 1977). Captive *Platanista* approached within 10–15 cm of fish and opened their jaws up to 10 cm wide to snap fish up rapidly (Gihr et al. 1976). Zbinden et al. (1978) provide the only available information on the hearing range of *Platanista*. In response to pure tones played to Indus dolphins at various frequencies and intensities, Zbinden et al. (1978) detected two hearing sensitivity peaks at c. 10 kHz and c. 70 kHz. Southall et al. (2007) suggest that *Platanista,* like other river dolphins, can hear a wide frequency range from 1 to 105 kHz, with which Zbinden et al.'s audiogram results are roughly consistent. The 70-kHz hearing sensitivity peak is important for echolocation and communication, as it matches the frequencies of clicks emitted by Indus dolphins (Gihr et al. 1976, Zbinden et al. 1978). Zbinden et al. indicated that the 10-kHz sensitivity peak could be a sampling artefact, but it is possible that this peak is real and helps dolphins detect prey sounds and respond to foraging stimuli. Some catfish can produce broadband burst-pulses up to 10 kHz, as do twitching freshwater shrimps of the families Palaemonidae and Penaeidae (Schmitz 2002), both of which are common prey items. However, these possibilities need confirmation with future studies.

Our preliminary acoustic studies showed that Ganges dolphins at Bhagalpur had sound source level (peak-to-peak) = mean 171.8 ± SD 3.6 dB re 1 μPa at 1 m, and Inter-Pulse Interval (IPI) = mean 27.5 ± SD 4.0 ms, in both shallow and deep locations. Based on these variables, we calculated a distance of c. 20 m for dolphins to detect a fish of size 6–7 cm in the river mid-column. These are preliminary results, but provide the first calculation of target prey detection distance in *Platanista*. The number of acoustic clicks emitted in the river mid-column was four times greater than that at the river surface or bottom (Fig. 2, Table 1).

FEEDING HABITATS AND TIME-ACTIVITY PATTERNS

Shallow river channels and bank-side areas adjoining deeper pools were intensively used for foraging by *Platanista*, as shown by our opportunistic visual observations. Four feeding peaks per day were estimated from timings of feeding events, corresponding to early morning (~0600 h), late morning (~1100 h), evening (~1700 h), and midnight (~0100 h). Our observations are similar to Anderson's (1879) description that *Platanista* feed both day and night, and mostly match activity peaks reported by other authors (Sinha & Kannan 2014). But captive and field observation studies in the 1970s and more recent acoustic studies (e.g. Sasaki-Yamamoto et al. 2013) in the Ganga River suggested exclusively crepuscular and nocturnal feeding. In captive Indus dolphins, sporadic snapping of jaws at fish was seen in daytime, but most active foraging took place during the quieter evening or at night. Feeding rates and timings also varied with habitat differences or season (Gihr et al. 1972).

Characteristics of fish and shrimp prey eaten by dolphins

FEEDING IS LIMITED MAINLY BY PREY SIZE

Anderson (1879) reported that *Platanista* fed on fishes and shrimps, an accurate report confirmed unequivocally by all subsequent observations. *Platanista* feed on a diverse assemblage of fish and shrimp or prawn species (at least 45 species, Table 2; Butt 1977, Sinha et al. 1993, Choudhary et al. 2006). Small prey items (<20–30 cm) with low body depths dominating the prey-size distribution suggest that
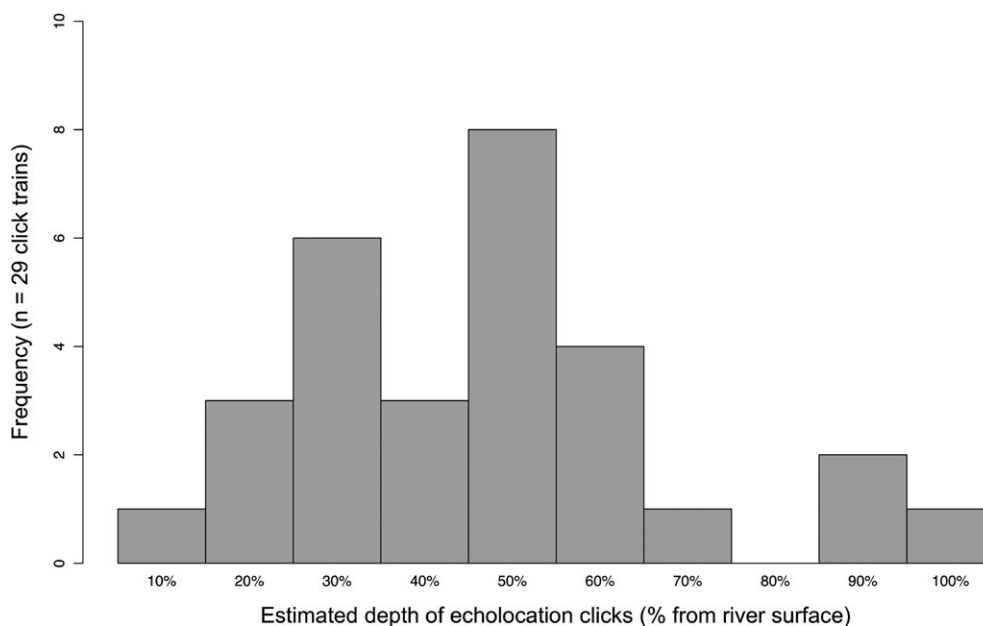
Fig. 2. Histogram of echolocation clicks emitted by *Platanista* at different water depths (this study, *n* = 29) with river surface assumed at 0%. The greatest use of echolocation was recorded in the river mid-column, not at the surface or bottom.

Table 1. Summary of reviewed evidence with data sources, on probable foraging modes used by *Platanista* at the river surface, mid-column, and bottom. Foraging modes for which strong evidence is available are in bold

Depth layer	Evidence	Main data sources	Probable foraging mode
River surface	Rotational feeding, side swimming, and tail slapping at surface to capture small fishes in schools	Authors: field observations, Pilleri et al. (1970), Jackson (2010)	**Passive listening before prey capture**
	Clupeid prey hear ultrasound, fish swim-sound frequency overlaps with *Platanista* hearing range	Popper et al. (2004), Zbinden et al. (1978), Moulton (1960)	
	Fewer echolocation clicks at river surface	Authors: preliminary acoustic studies	
Mid-column	Highest use of high-frequency echolocation clicks in mid-column	Authors: acoustic studies	**Active acoustic usage in mid-column**
	Females and calves observed feeding near fixed nets, in clutter	Jensen et al. (2013): acoustics Authors: field observations	Gleaning of prey in complex habitats
	Bits of vegetation and fragments of gillnet in dolphin stomach contents	Sinha et al. (1993), Authors: field observations	
Bottom	Many benthic prey species are active producers of low frequency sounds (*Mystus, Rita, Heteropneustes, Ompok, Glossogobius*, prawns)	Heyd and Pfeiffer (2000), Schmitz (2002), Kaatz et al. (2010)	Dolphins might not be able to hear most sounds made by fish, no support for listening
	Presence of vibrissae and innervated vibrissal crypts in calves, but rarely seen in adults.	Japha (1912), Pilleri and Gihr (1977), Czech-Damal (2007), Authors: field observations	**Electroreception** (in calves and young animals)
	Dolphin foraging common in shallow areas, less use of acoustics at river bottom	Pilleri (1972), Moreno (2004), Choudhary et al. (2012), Sinha and Kannan (2014), Lal Mohan and Kelkar (2015), Authors: field observations & acoustic studies	
	Mud-probing and rooting behaviour at river bottom	Pilleri et al. (1971a), Pilleri et al. (1971b), Reeves and Brownell (1989)	
	Fish and shrimp prey of dolphins emit weak electric pulses, and have well-developed ampullary organs (electroreceptors) in integument	Srivastava and Seal (1980), Morshnev and Ol'Shanskii (1997), Patullo and Macmillan (2010)	

size is one of the main criteria for feeding selectivity, rather than prey species. *Platanista* have narrow oesophagi (Takahashi & Yamasaki 1972) and weak jaw muscles owing to their gracile pincer jaws (Taylor 1987), constraining feeding on large prey (Kelkar et al. 2010). Fish sizes in dolphin stomach contents range from 3.5 to 20 cm; 40–50 cm long fish are rare, and if present have low body depth. We recorded a 36.5 cm long spiny eel *Mastacembelus armatus* in the stomach of an adult female Ganges dolphin. According to Pilleri (1970b), fishes of 7–8 cm long were mainly eaten, although fish skull sizes ranged from 5 to 9 cm in larger Indus dolphin specimens, indicating that 30–35 cm long catfish might be taken. The largest fish recorded so far in the diet of *Platanista* is a 50-cm long *Sperata aor* catfish with skull 20 cm long and 8 cm in diameter, found in the stomach of a large female Indus dolphin by Pilleri (1970b).

Despite mainly size-based prey selection, some fish species were also avoided in captivity. Captive Indus dolphins took mostly *Leuciscus leuciscus* (a carplet) and *Idus* sp. (Pilleri et al. 1970). Fishes such as powan *Coregonus larvatus*, common carp *Cyprinus carpio*, tench *Tinca* sp., and perch *Perca fluviatilis* that were fed to the dolphins were swallowed but immediately egested, and scales, skeletons, and swim bladders were vomited out in a dense mass. Trout (*Salmo trutta*) were totally ignored. Even fish that were filleted to resemble the shape and size of preferred prey (*Leuciscus*) were refused for unknown reasons (Pilleri et al. 1970). Smaller dolphins ate 0.6–1.8 kg fish per day, and larger ones ate 1.3–3 kg fish per day, with higher amounts ingested in the rainy season and the lowest intake during winter (in Switzerland; Gihr et al. 1972, 1976). Weak or injured fish were left untouched, and only fishes with good body condition were eaten.

Analyses of stomach contents from both Indus and Ganges dolphins (Pilleri 1970b, Sinha et al. 1993) have revealed many items other than fish and shrimp. These items included aquatic hemiptera and coleoptera, pieces of vegetation, fruit seeds, date stones, small fruits, water snail opercula, and shell fragments, which came mostly from the stomachs of the fish digested by the dolphins (Pilleri 1970b, Sinha et al. 1993, Sinha & Kannan 2014). Nematodes forming a crumbly mass with the chitin of aquatic insects (one species identified as *Contracaecum lobatum*) were abundant in stomachs of Indus dolphins (Pilleri et al. 1970).

PREY DISTRIBUTION IN THE WATER COLUMN

Fish and shrimp prey in *Platanista* stomach contents examined in earlier studies included species found throughout the water column, but benthic prey dominated the diet (Butt 1977, Sinha et al. 1993, Choudhary et al. 2006). Overall, about 31% of the prey items were surface-dwelling

species, 23% were mid-column-dwelling, and 46% were bottom-dwelling. Surface prey mainly included Clupeid (shads) and Cyprinid fishes (small carps, barbs). Mid-column prey groups (barbs, catfishes, perchlets) were mostly associated with cluttered underwater habitats and riverine vegetation, whereas benthic groups were mud-dwelling catfishes, gobies, shrimps, and spiny eels (Table 2).

Variation in foraging and feeding modes in the water column

BEHAVIOURAL OBSERVATIONS NEAR THE SURFACE

We recorded rotational feeding and tail slapping by Ganges dolphins at the surface (Table 1). Rotational feeding behaviours are typical of gape-limited predators (Helfman & Clark 1986) and need to be explored in *Platanista*. During feeding events, Ganges dolphins showed intense activity and chased fish by churning the water with rapid and vigorous circular swimming near the surface; small fish were often tossed in the air. When feeding at the surface in the Chambal River, dolphins spent a substantial amount of time in an upright position almost perpendicular to the river surface, while catching and swallowing small (5–10 cm) fishes that were jumping in the air (T. Nair, personal communication). During surface feeding events, birds such as river terns *Sterna aurantia*, little terns *Sternula albifrons*, black-bellied terns *Sterna acuticauda*, gulls *Larus* sp., and white-throated kingfishers *Halcyon smyrnensis* were recorded in association with dolphins (Lal Mohan & Kelkar 2015, T. Nair, personal communication, authors: field observations).

PASSIVE LISTENING FOR PREY CAPTURE NEAR THE SURFACE

We found that echolocation clicks were used less at and near the river surface, than in the water column (Fig. 2). It is possible that transmission loss due to acoustic reflection, or scattering due to river waves, wind, and changes in the medium, occurs at the surface (Trevorrow 1998). Lower click rates might also be related to hearing sensitivities of dolphins and prey. Several species of surface-living marine and riverine clupeid fishes can detect ultrasounds produced by dolphins (Mann et al. 1998, Popper et al. 2004). Ganges dolphins commonly feed on river clupeids (Sinha et al. 1993, Choudhary et al. 2006). It is therefore likely that, while feeding near the surface, echolocating dolphins use passive listening (Table 1). Sounds produced by swimming, schooling clupeids have frequencies of 1–2 kHz (e.g. Moulton 1960), and are within the range audible to *Platanista* (Zbinden et al. 1978). Passive listening for schooling and ultrasound-detecting fish, rather than non-schooling prey, near the surface may

improve prey capture efficiency, as has been shown for bottlenose dolphins (Wood & Evans 1980, Barros & Myrberg 1987, Gannon et al. 2005).

IN THE RIVER MID-COLUMN

According to our preliminary results, the dolphins' use of echolocation clicks for detection, capture of prey, etc. was highest in the river mid-column (Fig. 2, Table 1). The echolocation depth ratio was 42.7% (SE 20.4%), taking the surface to be at 0%, in both shallow and deep locations (n = 29 click trains; Appendix S3). However, these analyses do not tell us how far dolphins could be scanning both surface and bottom habitats by echolocating in the mid-column. Dolphins may mostly use the mid-column to scan the river depth layer, and on detecting fish, switch between foraging modes for prey capture. Jensen et al. (2013) found that Ganges dolphins used low-source level sounds to reduce sound scattering in shallow rivers, but did not calculate prey detection distance. Pilleri et al. (1970, 1971b, 1977) reported that Indus dolphins foraged in the mid-column by using echolocation clicks and detected fish acoustically from several metres away. The dolphins opened their mouths wide when they were 50–70 cm from the fish, and the clicks stopped when the prey was swallowed. High-frequency clicks of *Platanista* are able to resolve fine-scale differences in cluttered environments, in a way that is functionally similar to echolocation used by vegetation-gleaning, frequency-modulating insectivorous bats (Jensen et al. 2013). *Platanista* often feed near riverbanks with vegetation or around stake-nets fixed by fishers on bamboo poles, where fish concentrate. Feeding by gleaning from these structures is evidenced by the occurrence of net fragments and vegetation pieces in dolphin stomach contents (Table 1).

SOUND PRODUCTION BY BENTHIC PREY: DO DOLPHINS LISTEN?

Of the benthic prey groups, 61% are known to produce sounds by stridulation or by active vocalisation (Table 2; Agrawal & Sharma 1965, Heyd & Pfeiffer 2000, Kaatz et al. 2010). Benthic catfishes and gobies use sounds mainly for communication (Ladich 2000, Lugli & Fine 2012), possibly at specific times of the year. The low frequencies of their sounds (0.5–1 kHz) are likely to be below dolphin hearing range (Zbinden et al. 1978). Hence, dolphins may not use listening at the river bottom for fish detection (Table 1). The greatest hearing sensitivity of dolphins, at around 10 kHz, may be best suited for hearing sounds made by shrimp. In general, dolphins can acoustically detect schooling fish (surface and mid-column fish with swim bladders) more effectively than

non-schooling fish. Benthic prey items are typically non-schooling fish, with swim bladders that are reduced, deflated (catfish), or absent (shrimp). Acoustic detection of sparse, non-reflecting, and buried benthic prey is also likely to be difficult because of muddy substrates and sound reverberation effects (Au 1992, Jensen et al. 2013). As a result, other sensory modalities might be at work in river bottom feeding.

ELECTRORECEPTION OF BENTHIC PREY IN *PLATANISTA*?

Of prey recorded in *Platanista* stomach contents, 41% of the species are known to emit weak electric pulses, of which 80% are dominant benthic prey species, mainly catfish, shrimps, prawns, and gobies (Table 2). There are limitations to the use of echolocation clicks at the river bottom (due to reverberation, absorption, etc.), and the possibility that electroreception is used instead by *Platanista* to capture these prey is supported by behavioural and anatomical evidence. Czech-Damal et al. (2012b) experimentally proved electroreception in the Guiana dolphin *Sotalia guianensis*, and also observed that mud-probing behaviours were linked to electroreception. Reeves and Brownell (1989) and Nowak (2003) reported mud-probing behaviour by *Platanista* at river bottoms. Pilleri et al. (1970) and Kasuya and Haque (1972) also documented rooting behaviours in captive Indus dolphins when they tried to pick up fine food particles from the tank floor, with their heads down and tails flicking upwards or held at an angle. Czech-Damal (2007) suggested electroreception as a likely strategy in dolphins, including *Platanista*, based on a review of vibrissal crypts in dolphins. Japha (1912) documented that *Platanista* had more profuse hairs than any other extant cetacean taxon, numbering 60–80 on the upper and lower jaws and 10–15 on the melon, and 16–18 tooth anlagen (Pilleri & Gihr 1977). Vibrissal hairs are highly innervated and their tactile function is well known (Kukenthal 1909). Our observations of dead animals show that adults have far fewer vibrissae than calves or no vibrissae in some cases. We also recorded the presence of vibrissae and vibrissal crypts, especially in calves and subadults of 1–1.2 m in length (Fig. 1c,d). Pilleri and Gihr (1977) reported the late ontogenetic development of the large maxillary crests in Indus and Ganges dolphin calves. Frainer et al. (2015) report similar late development in the franciscana *Pontoporia blainvillei*. *Platanista* calves start feeding on their own by 1–2 months of age (Kasuya 1972), and at that time, they may not have the precise acoustic detection abilities seen in adults. Sinha and Kannan (2014) found milk, shrimps, and insects in a 1.05-m-long Ganges dolphin's stomach, suggesting this as the approximate weaning size. Regular occurrence of shrimp in young dolphins' diets and observations of

Table 2. Database of prey groups (with genera and families of fish and shrimp prey) known from *Platanista* stomach contents. The database summarises age-classes and approximate lengths of prey eaten, prey occurrence in stomach contents, habitat/substrate preferences of prey, and whether prey are known to emit sounds or weak electric pulses. Other items (last row) are mostly secondarily ingested, that is, come from the stomachs of digested fish

Prey group	Genera (Family)	Age-class & total length (cm, range)	Occurrence in stomach contents	River column	Substrate preference	Sound production	Electrical pulses
Fishes							
Shads	*Clupea, Gudusia, Tenualosa, Gonialosa* (Clupeidae)	A, J; 5–15	Uncommon	S	SN	SW	N
Catfish	*Mystus, Sperata, Nangra, Rita* spp. (Bagridae)	A, J; 10–30 (to 50)	Common	BM	MD, VG	STR	Y
Catfish	*Wallago, Ompok* (Siluridae)	J; <20	Uncommon	S	SN, MD	N	Y
Stinging Catfish	*Heteropneustes fossilis* (Heteropneustidae)	A; <10	Uncommon	B	MD, VG	STR	Y
Catfish	*Bagarius* (Sisoridae)	J; <20	Uncommon	B	MD, RO	DOR	N
Catfish	*Pseudeutropius* (Schilbeidae)	A, J: <10	Uncommon	B	SD, MD	STR	Y?
Carps and carplets	*Catla, Labeo, Chela, Osteobrama, Cabdio, Tor, Salmophasia, Crossocheilus, Leuciscus*, Idus** (Cyprinidae)	J, A; 10–12	Uncommon	S	SN, VG	SW?	Y?
Barbs	*Puntius, Rasbora* (Cyprinidae)	A; <10	Common	M	VG	N	N
Glass perches	*Chanda, Parambassis* (Ambassidae)	A; <10	Common	SM	SN	N	N
Spiny eels	*Mastacembelus, Macrognathus* (Mastacembelidae)	A, J; 10–40	Common	B	MD	N	Y?
Goby	*Glossogobius* (Gobiidae)	A, J: 10–15	Common	B	MD	VOC	Y?
Featherbacks	*Notopterus, Chitala* (Notopteridae)	J; <20	Uncommon	SM	RO	N	Y
Loaches	*Botia* (Balitoridae)	A; <10	Uncommon	B	SN, RO	N	N
Snakeheads	*Channa* (Ophiocephalidae)	J; <20	Uncommon	BM	VG, MD	N	N
Gourami	*Colisa* (Osphronemidae)	A; <10	Uncommon	BM	MD	N	N
Mullet	*Rhinomugil* (Mugilidae)	J, A; 10–15	Uncommon	S	SN, VG	N	N
Invertebrates							
Prawns	*Penaeus* (Penaeidae), *Palaemon, Macrobrachium* (Palaemonidae)	A; 15–20	Common	B	MD	TL, STR	Y
Molluscs	*Indonia* (Bivalvia: Unionidae); other gastropod opercula	A; 5	Uncommon	B	MD	N	N
Insects	*Gomphus* sp. dragonfly nymph (Odonata: Zygoptera)	Nymph; <5–7	Uncommon	B	MD, SN	N	N
Other items	Aquatic hemiptera and coleoptera, chitin, seeds, vegetation pieces, net fragments		Uncommon	–	–	–	–

Key: *Observed in captivity; Age-class: A = Adult, J = Juvenile; River column use: S = Surface, M = Mid-column, B = Bottom; Substrate preference: SN = Sand, MD = Mud, RO = Rock, VG = Aquatic Vegetation; Sound production: SW = Swimming sounds (passive emission), STR = Stridulation, DOR = Dorsal Fin, VOC = Vocalisation, TL = Tail Strike (active emission), N = None reported; Electrical pulses: Y = Yes, N = Not known, Y? = Known for related genera. Fishes mostly possess swim bladders, although benthic species might have reduced and often deflated bladders. Prawns/shrimp do not have swim bladders.

Data sources: Prey characteristics (Moulton 1960, Agrawal & Sharma 1965, Mahajan 1966, Srivastava & Seal 1980, Mittal et al. 1995, Bruton 1996, Morshnev & Ol'Shanskii 1997, Heyd & Pfeiffer 2000, Ladich 2000, Schmitz 2002, Popper et al. 2004, Albert & Crampton 2005, Bullock et al. 2006, Kaatz et al. 2010, Patullo & Macmillan 2010, Lugli & Fine 2012); Stomach contents and direct feeding observations in captivity* (Pilleri 1970b, *Pilleri et al. 1970, Pilleri et al. 1971a, *Gihr et al. 1972, Pilleri 1972, Butt 1977, Haque et al. 1977, Reeves & Brownell 1989, Shreshtha 1989, Sinha et al. 1993, Choudhary et al. 2006, Kelkar et al. 2010, Smith & Reeves 2012, Lal Mohan & Kelkar 2015; authors: field observations).

mother-calf pairs feeding in shallow waters (Choudhary et al. 2012) both suggest that electroreception may be the main foraging mode in calves and juvenile dolphins (Table 1). Electroreception for prey detection might be slowly replaced by echolocation in adults foraging in the river mid-column.
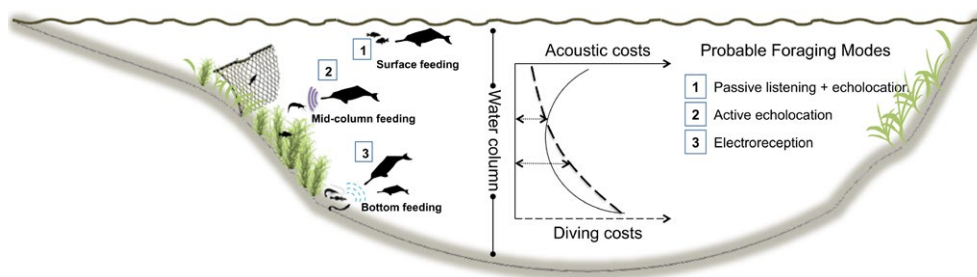
Fig. 3. Schematic diagram illustrating different foraging modes in *Platanista* in a hypothetical cross-section of the river column. Acoustic costs are the lowest in the mid-column, but diving costs increase nonlinearly with river depth. Total costs are, thus, the lowest in the mid-column. Echolocation can help in effective scanning of prey through the water column. At the river bottom, use of electroreception might help offset diving costs. Field observations show that dolphins, especially mother-calf pairs, tend to feed at the river bottom in shallow areas. [Colour figure can be viewed at wileyonlinelibrary.com]

CONCLUSION

Our review identifies some possibilities and provides suggestive evidence that foraging modes in *Platanista* may differ in river surface, mid-column, and bottom habitats, linked to their adaptive use of echolocation clicks, passive listening, and electroreception (Fig. 3). Our study contributes to knowledge on the sensory ecology and foraging behaviour of South Asian river dolphins, bringing together multiple sources of evidence into a coherent framework. Indus and Ganges dolphins have been geographically isolated from one another for 0.5 million years (Braulik et al. 2015), and may differ in some aspects of their foraging ecology. Despite technical difficulties in studying *Platanista* in captivity today or in observing them underwater, we believe that our review generates useful hypotheses for future experimental confirmation. Insights from the sensory ecology of the relict genus *Platanista* are also important for understanding mechanisms supporting its remarkable ability to persist in the most intensively used and abused river basins in the world. Echolocation-based feeding modes, supplemented by electroreception and passive listening, might serve to reduce foraging costs and, as a result, may contribute to the adaptability of the taxon (Czech-Damal et al. 2012a, Kremers et al. 2016). The energetic costs of echolocation, diving, and swimming in flowing water might also be regulated by these supplementary modes (Fig. 3). Future studies on ecomorphological traits and foraging performance could use these insights.

We postulate that highly specialised adaptations to foraging in murky riverine habitats, and traits retained from once-successful Miocene dolphin relatives (coastal-marine Platanistoidea, Gutstein et al. 2014) and older terrestrial ancestors (Pilleri & Gihr 1976, Pilleri et al. 1976, Nummela et al. 2007, Thewissen & Nummela 2008) might together confer high adaptability on *Platanista*. The functional correlation of electroreception with visually limited habitats (Torres 2017), though widespread in fishes, has, in mammals, only been confirmed in the duck-billed platypus *Ornithorhynchus anatinus* and the Guiana dolphin (Czech-Damal et al. 2012a,b).

Our review integrates different lines of research to describe sensory modes possibly used by *Platanista* for feeding on diverse prey in the river water column. It can, thus, contribute to studies on responses of endangered *Platanista* to effects of anthropogenic noise, vessel traffic, dredging disturbances, fishery interactions, dams, barrages, and embankments in riverine habitats. An understanding of foraging modes could provide insights into how exactly *Platanista* may or may not cope with various human-induced threats (Smith & Reeves 2012). This could be of great significance for the effective conservation of this evolutionarily fascinating taxon.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Sound recording methods and equipment.
Appendix S2. Recording system for click depth estimation in *Platanista*.
Appendix S3. Frequency distribution of *Platanista* acoustic activity in relation to depth.