Hunting, Fighting, or Playing with Bubbles: Possible Usage and Acoustic Characteristics of Bubble Burst Sounds Produced by the Amazon River Dolphin (*Inia geoffrensis*)

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Abstract

Acoustic characteristics of bubble production by an odontocete were documented for the first time. Bubble sounds produced by the Amazon river dolphin (*Inia geoffrensis*) were recorded incidentally as part of a survey of fish sounds in the Pacaya–Samiria National Reserve of Peru on six dates between 4 and 24 July 2012. Dolphins were observed to periodically produce large clouds of bubbles underneath or near the survey boat (averaging 7/survey or 8/h) as it drifted through areas of actively foraging dolphins. The bubble production was classified as bubble bursts due to their similarity to bubble bursts produced by other cetaceans. Bubble burst sounds had a mean peak frequency of 402 Hz and duration of 8.9 s (*n* = 51). Bubble bursts were temporally clustered with an average interval of 169 s (0.1 to 1,187 s) between bursts. Bubble bursts were disproportionately more likely to be present when fish sounds were also present, but it is not known if the association was due to predation or other factors. A review of the literature finds similar bubble production has been reported in at least 14 other species of cetaceans (4 mysticetes and 10 odontocetes). Most are commonly associated with play, surprise, agonistic, and foraging behaviors. We discuss each of these possibilities and conclude that Amazon river dolphin bubble burst behavior is most likely related to foraging or aggressive behavior because the behavior occurred in feeding areas and appeared to be directed at the drifting boat. We further propose a novel hypothesis that the bubble bursts are a hunting strategy used to disperse prey associated with floating vegetation mats and other forms of drifting materials used by fishes for shelter. Future research is needed to better understand the behavior associated with bubble production by the Amazon river dolphin.

Key Words: boto, *Inia geoffrensis*, soundscape, sound production, passive acoustic monitoring, river dolphin

Introduction

While conducting a survey of fish sounds in the Samiria River, Peru, a unique bubble production behavior by the Amazon river dolphin (*Inia geoffrensis*) was visually and aurally observed. Subsequently, a literature review revealed the phenomenon had not been previously described, except for an anecdotal observation (Layne, 1958). Therefore, the goals of this article are (1) to provide documentation of the acoustic properties of the bubble bursts, (2) to review possible functions of the behavior, and (3) to suggest potential applications of passive acoustic monitoring (PAM) of Amazon river dolphins.

The Amazon river dolphin is widely distributed in South American rivers where many populations are in decline and of conservation concern (Smith & Smith, 1998; McGuire & Aliaga-Rossel, 2007, 2010; Shostell & Ruiz-García, 2010; Trujillo et al., 2010; Gomez-Salazar et al., 2012; Hrbek et al., 2014; Williams et al., 2016; da Silva & Martin, 2018; Aliaga-Rossel & Duran, 2020). Amazon river dolphins tend to be less social than many other odontocetes (da Silva & Martin, 2018) and occur in small group sizes of two to eight individuals (McGuire & Winemiller, 1998; Martin et al., 2004; Aliaga-Rossel et al., 2006; May-Collado & Wartzok, 2007; Gomez-Salazar et al., 2012). Visual surveys have been used for decades to monitor populations and observe behavior (e.g., Layne, 1958; Vidal et al., 1997; Martin et al., 2004; Bodmer et al., 2017a, 2017b); however, there have been calls to incorporate PAM methods into the more traditional visual methods to obtain better population estimates and an improved understanding of dolphin behavior and ecology

(Yamamoto et al., 2015; Campbell et al., 2017). To be effective, PAM monitoring requires a detailed understanding of both purposeful and incidental sound production by the targeted animals. Wild river dolphins are known to produce a wide variety of purposeful vocalizations, including echolocation clicks, whistles, and low frequency sounds (e.g., Ding et al., 2001; Podos et al., 2002; May-Collado & Wartzok, 2007; Yamamoto et al., 2015; Olson, 2017; Melo-Santos et al., 2019; Melo et al., 2021a, 2021b). Researchers are already using this information to better understand habitat preferences and behaviors, and to distinguish among river dolphin species (Podos et al., 2002; Martin et al., 2004; Amorim et al., 2016; Olson, 2017; Melo et al., 2021a, 2021b). Unfortunately, the acoustic properties of bubble production in the Amazon river dolphin have not been reported, and sounds associated with bubble production as an indicator of the dolphin's presence and behavioral activities have not been considered.

Bubble production behavior by wild dolphins has not previously been described for the species except for a single anecdotal observation during a 1956 expedition to Colombia (Layne, 1958). However, captive individuals have previously been reported to create bubble rings with their mouths as part of play behavior (Gewalt, 1989). Bubble production by cetaceans is known to exhibit several different forms, ranging from small streams of bubbles produced during some types of vocalizations to bubbles produced for various functions which have been classified into three main types: (1) bubble trails, (2) bubble bursts, and (3) bubble rings (see reviews in Trudelle, 2010; Moreno & Macgregor, 2019). Our review focused on findings of large-volume bubble production to facilitate comparison with the bubble production reported herein and found at least 15 species of cetaceans (4 mysticetes and 11 odontocetes) have been reported to exhibit some type of purposeful, large-volume bubble (Table 1). Purposeful bubble production has been most frequently associated with foraging behavior (9 species), agonistic or threat responses (7 species), play (4 species), or surprise (4 species). More than one of these behavioral categories associated with bubble production have been reported for seven species (Table 1). Despite the fact that bubble production appears to be widespread among cetaceans (Table 1), the acoustic properties of the phenomenon have only been briefly described for two cetaceans: (1) the gray whale (*Eschrichtius robustus*; Cummings et al., 1968; Swartz & Cummings, 1978; Dahlheim, 1987; Crane & Lashkari, 1996; Charles, 2012; Frouin-Mouy et al., 2020) and (2) the humpback whale (*Megaptera novaeangliae*; Dunlop et al.,

2007, 2008; Wiley et al., 2011), and they have not yet been described in any odontocete species. The prevalence of bubble production behavior among cetaceans suggests the need for more directed attention to the phenomenon and its associated behavior as well as its potential for incorporation into PAM surveys of dolphin presence and behavior.

Methods

The study was conducted within the Pacaya–Samiria National Reserve (PSNR) in Peru under the umbrella of Operation Wallacea (www.opwall. com) as part of a survey of fish sound production (Rountree, 2020; Rountree & Juanes, 2020). The PSNR is contained within the confluence of the Marañón and Ucayali Rivers where the main stem of the Amazon River originates. Operation Wallacea has conducted regular dolphin surveys of the region since 2009 as part of their long-term monitoring program (Bodmer et al., 2017a, 2017b). Operation Wallacea typically conducts daily dolphin surveys from either a 12-m wooden or aluminum boat that is allowed to drift (averaging 2 km/h) with the current while staff and students (typically 4 to 12 individuals) conduct a visual survey for the presence of dolphins. Two surveys are conducted each day covering a 5-km stretch of the Samiria River centered at a base station. An "upstream" survey begins approximately 2 to 3 km upstream and drifts toward the base station, while a "downstream" survey starts from the base station and drifts downstream.

While conducting a separate 3-wk survey of fish sounds in the region during the low water season (July 2012), RAR was able to accompany the dolphin survey on eight dates between 4 and 24 July to obtain additional fish sound data. All eight dolphin surveys were conducted between 1400 to 1700 h from a 12-m wooden boat within a 5-km stretch of the Samiria River (4° 54.119' S, 74° 22.077' W to 4° 52.457' S, 74° 21.452' W) that varied between 100 to 150 m in bank-to-bank width. During the first survey (4 July), an uncalibrated, variable (dial) gain Aquarian model (Aquarian Audio Products, Anacortes, WA, USA) hydrophone was used to continuously listen to the soundscape, but no recordings were made. During the third survey (7 July), only intermittent recordings were made with the Aquarian hydrophone, and data are not included herein. During each of the remaining six surveys (Table 2), an uncalibrated SQ26-08 hydrophone (sensitivity = -169.00 re 1V/μPa rms; Cetacean Research Technology, Seattle, WA, USA) was used to continuously monitor the soundscape. The hydrophone was suspended over the side of the boat at a depth of approximately 1 m below the water surface,

Table 1. Contexts in which large-volume bubble production (bubble bursts and other productions with similar features) have been documented across cetacean species. Contexts are determined based on the cited authors' descriptions and interpretations. They are each best summarized as follows: Foraging (Communicative) – bubbles are produced during prey search, capture, or ingestion and without a clear physical benefit and are, thus, presumed to be communicative; Foraging (Physical use) – bubbles produced alter the immediate physical environment in a manner which aids in prey search, capture, or ingestion; Disturbance/stress – bubbles are present in a context which is interpreted as putting physical or emotional strain on the animal; General social – bubble is produced during interactions that do not fall into one of the other categories; Play – bubble is produced during play behavior but it is not interacted with; Play object – bubble is manipulated following production in a manner presumed to be play; Sexual – bubble is produced during behavior involving genitals; Surprise, excitement, interest, curiosity, response to object – bubble is produced following a change in the environment or as a presumed response to novelty; Threat/agonistic – bubble is produced during conflict or conflict-related displays; and Unknown – behaviors surrounding bubble production are not reported or are unclear in use.

Species, Common name	Context	Citation
Mysticetes		
Balaenoptera brydei, Bryde's whale	Foraging (Physical use)	S. S. Sadove, pers. comm., cited in Sharpe & Dill, 1997; Neumann & Orams, 2010
Balaenoptera physalus, fin whale	Foraging (Physical use)	V. Deecke, pers. comm., cited in Sharpe & Dill, 1997
Eschrichtius robustus, gray whale	Disturbance/stress	Charles, 2012
	Threat/agonistic	Birtles et al., 2002
	Unknown	Cumming et al., 1968; Swartz & Cummings, 1978; Dahlheim, 1987; Crane & Lashkari, 1996; Charles, 2012; Burnham et al., 2018; Frouin-Mouy et al., 2020
Megaptera novaeangliae, humpback whale	Foraging (Physical use)	Jurasz & Jurasz, 1979; Hain et al., 1982; D'Vincent et al., 1985; Sharpe & Dill, 1997; Dunlop et al., 2008; Wiley et al., 2011; Qing et al., 2019; Bryngelson & Colonius, 2020
	General social	Baker & Herman, 1984; Reidenberg & Laitman, 2007
	Sexual	Baker & Herman, 1984
	Threat/agonistic	Baker & Herman, 1984; Helweg et al., 1992
Odontocetes		
Cephalorhynchus commersonii, Commerson's dolphin	Threat/agonistic	Bowles & Anderson, 2012
Cephalorhynchus hectori, Hector's dolphin	Play	Slooten, 1994
	Threat/agonistic	Slooten, 1994
Delphinapterus leucas, beluga whale	General social	Hill et al., 2011
	Play object	Delfour & Aulagnier, 1997
	Threat/agonistic	Hill et al., 2011
Delphinus delphis, short-beaked common dolphin	Foraging (Physical use)	Neumann & Orams, 2010
Inia geoffrensis, Amazon river dolphin	Play object	Gewalt, 1989
	Unknown	Layne, 1958, Layne & Caldwell, 1964
Lagenorhynchus obscurus, dusky dolphin	Foraging (Communicative)	Trudelle, 2010; Vaughn et al., 2010
Orcinus orca, killer whale	Foraging (Communicative)	Visser et al., 2008
	Foraging (Physical use)	Similä & Ugarte, 1993; Visser et al., 2008
	Surprise, excitement, interest, curiosity, response to object	Delfour & Marten, 2001; Hanna et al., 2017

Pseudorca crassidens, false killer whale	Foraging (Physical use)	Zaeschmar et al., 2013
	Surprise, excitement, interest, curiosity, response to object	Delfour & Marten, 2001
Stenella frontalis, spotted dolphin	Foraging (Physical use)	Fertl & Würsig, 1995
	Sexual	Herzing, 1996
	Threat/agonistic	Dudzinski, 1996, 1998; Herzing, 1996
Steno bredanensis, rough-toothed dolphin	Surprise, excitement, interest, curiosity, response to object	Lilley et al., 2018
Tursiops truncatus, bottlenose dolphin	Foraging (Physical use)	Fertl & Wilson, 1997; Zaeschmar et al., 2013
	Play object	McCowan et al., 2000
	Sexual	Moreno, 2017
	Surprise, excitement, interest, curiosity, response to object	Pryor, 1990; Marten et al., 1996; McCowan et al., 2000; Clark et al., 2013; Moreno, 2017; Lilley et al., 2018; Alexander et al., 2021
	Threat/agonistic	Overstrom, 1983; Shane, 1990; McCowan et al., 2000; Bowles & Anderson, 2012; Moreno, 2017
Unspecified	Surprise, excitement, interest, curiosity, response to object	Pryor, 1990

Table 2. Survey dates, times, and locations with counts and rate of observed bubble bursts (including double bursts counted as 2). Sample and bit rate at which the sounds were digitized are also indicated.

Date	Start (h)	Survey duration (m)	Sample rate	Bit rate	Start location	No. bursts	Bursts/h
5 July 2012	1440	110	48	16	4° 52.457' S, 74° 21.452' W	15	8
8 July 2012	1444	86	48	24	4° 52.506' S, 74° 21.489' W	0	0
11 July 2012	1443	86	48	24	4° 52.509' S, 74° 21.476' W	0	0
19 July 2012	1413	103	48	24	4° 52.576' S, 74° 21.412' W	0	0
21 July 2012	1507	36	96	24	4° 53.801' S, 74° 21.686' W	26	43
24 July 2012	1513	88	96	24	4° 54.119' S, 74° 22.077' W	18	12
Total		509				59	

and sounds were monitored continuously with headphones, except for short periods when sounds were played over a speaker to allow students to hear them. The first four surveys were downstream drifts, while the last two were upstream drifts. The upstream drifts passed through the confluence of the Samiria River and a small tributary draining Huisto Lake (at approximately 4° 53.891' S, 74° 20.929' W).

Sounds were recorded to a Zoom H1 digital recorder (Zoom North America, Hauppauge, NY, USA) at 24 bit, with a sample rate of either 48 or 96 kHz. Since the boat and hydrophone were drifting with the current, flow noise was kept to a minimum. Because the hydrophone was constantly monitored, any contact with drifting materials could

be immediately detected and addressed. No significant issues with drifting or submerged materials were encountered. During the first survey (4 July), it was noticed that considerable noise from student movements was being transmitted into the water through the hull of the ship. Therefore, on subsequent surveys, students were instructed to limit their movements as much as possible and avoid bumps and bangs on the deck or sides of the boat, although they were allowed to talk freely. Although not quantified, this greatly reduced noise generated from the drifting boat. On the last two surveys, an attempt was made to record dolphin behavior on video with a hand-held camera (Pentax Optio G-II; Ricoh Imaging Co., Ltd, Tokyo, Japan).

Acoustic measurements of all bubble production sounds were made in *Raven Pro*, Version 1.5, acoustic software (Bioacoustics Research Program [BRP], 2014). Duration variables were measured from the sound waveform, while frequency variables were measured from the spectrogram with a Hann window size of 1,024 samples (10.7 ms), a fast Fourier transform (FFT) size of 1,024 samples (93.8 Hz), and a 50% overlap (Hop size 512). Because the upper and lower frequency and time ranges of the bubble production sounds were ambiguous, the more robust measurements of frequency and time percentiles were reported (see Charif et al., 2010). All measured parameters are defined in Supplementary Table S1 (supplemental materials for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammals journal.org/index.php?option=com_content&view =article&id=10&Itemid=147).

In addition, as part of the broader fish sound survey, all fish sounds were annotated in the dolphin survey recordings, which allowed us to test for a possible correlation between the presence of fish sounds and the occurrence of bubble sounds. Fish sounds were identified based on similarity to known fish sounds but cannot yet be identified to species. Fish are known to produce a wide variety of drumming, stridulation, and air-movement sounds, with peak frequencies below 10 kHz, that are variously described as bumps, squeaks, barks, squeals, groans, moans, honks, and knocks, among others (see reviews of the diversity of fish sounds in Tavolga et al., 1981; Ladich & Fine, 2006; Kasumyan, 2008; Parmentier et al., 2017; Looby et al., 2022; Rice et al., 2022). Although, to our knowledge, fish sounds were not previously recorded from the PSNR region, a wide variety of fishes in the Amazon are known to be soniferous, including many catfish (Siluriformes), cichlid (Cichlidae), piranha (Serrasalmidae), and other species (e.g., Kaatz et al., 2010; Kaatz & Steward, 2012; Rountree & Juanes, 2020). Results from the broader fish sound survey, including verified sound production by 32 species of fish, will be published elsewhere, but example sounds of all species are publicly available online (Rountree, 2020). Sounds produced by piranha species obtained during the fish sound survey have previously been published (Rountree & Juanes, 2020). Work is ongoing to compare these known fish sounds to those recorded during the dolphin and fish sound surveys. However, since it is not yet possible to assign species to specific sounds, we lumped all fish sounds into a single category to compare with the occurrence of dolphin bubble sounds, with the goal of determining if dolphin bubble sounds were more frequent when higher soniferous fish activity also occurred. Other types of sounds produced by the river dolphin were noted (e.g., whistles, echolocation clicks) but have not yet been quantified pending review by experts.

Because counts of fish sounds are problematic until more is known about what constitutes single sounds, we examined the association between fish sounds and dolphin bubble production sounds in two different ways. First, a Fisher's exact test (Fleiss et al., 2013) was performed on data categorized by presence or absence of both bubble sounds and fish sounds within 10-s intervals throughout the recordings using Real Statistics Resource Pack software, *Release*, Version 7.6 (Zaiontz, 2021). A significant test would indicate that the presence of dolphin bubble production was not independent from the presence of fish sounds. An odds ratio (McHugh, 2009) could then be used to estimate the magnitude of the increase in bubble sound presence when fish sounds are also present (calculated as bubbles present/bubbles not present, given fish sounds divided by bubbles present/bubbles not present, given no fish sounds). Secondly, the non-parametric Spearman rank correlation coefficient was used to test for a temporal correlation between the sum duration of fish sound production activity and sum duration of dolphin bubble sounds in each 10-s interval using *SAS/STAT* software, Version 12.1 (SAS Institute Inc., 2012). To avoid pseudoreplication, the Spearman rank correlation was conducted on data averaged over a 5-min period which represented a time span many times longer than the maximum bubble sound duration but short enough to provide good temporal resolution (the same tests were performed on data averaged over 10-min periods with similar results). Note that since data are not georeferenced, we were testing for temporal correlation rather than spatial.

Results

Dolphins were observed in all six surveys recorded between 5 and 24 July 2012. Typically, dolphins occurred in small groups of two to six Amazon river dolphins and one to three gray dolphins (*Sotalia fluviatilis*). A maximum of nine dolphins (6 Amazon river and 3 gray) were observed at a location. In three of the surveys (1 downstream and 2 upstream drifts), a unique bubble production behavior by the Amazon river dolphin was visually and aurally observed. Bubble production took the form of a sudden, intense cloud of large bubbles arising from under or near the drifting boat (Figure 1; Supplementary Video S1), which were categorized as bubble bursts (*sensu* Moreno & Macgregor, 2019). Although bubbles could be seen moving downstream with the current, the bubble bursts should not be confused

with the bubble trail type production which are typically continuous, long-duration, thin bubble productions with very little air released at a time. Bubble production behavior tended to occur in areas where small groups of Amazon river dolphins (approximately 2 to 6) appeared to be actively feeding based on their surface roll and diving behavior (following Layne, 1958; Podos et al., 2002) as related to the senior author by the dolphin survey team (examples can be observed in Supplementary Video S1). Although not quantified, all bubble bursts were estimated to occur from 2 to 8 m from the hydrophone. Although the water was too opaque to allow direct observation of bubble production details, on at least two occasions, an Amazon river dolphin was observed by one or more passengers apparently producing the bubble burst. In several other cases, dolphins, or their wakes, were observed moving away from the bubble burst area. Unfortunately, video confirmation was not obtained, but some bubble burst events were captured on video well after they had started (Supplementary Video S1). Gray river dolphins were never observed to approach the boat and are not believed to have produced bubble bursts. When asked about the bubble burst behavior, the boat pilot said they were often observed during the surveys and that it was assumed that the dolphins were "playing" with the boats.

Sounds produced in association with 55 bubble bursts by Amazon river dolphins were recorded (Figures 2 & 3; Table 3; Supplementary Audio S1 & S2)—47 as single bursts and four as double bursts. Single bursts ranged in duration from a brief burst (3.4 s) to a prolonged burst (19.3 s; mean = 8.9 s). Double bursts occurred when a second burst occurred toward the end of an initial burst, and the two partially overlapping bursts could not be measured separately. Double bursts ranged from 18.7 to 31.5 s in duration. Bubble bursts were temporally clustered, averaging 7/survey or 8/h, with average burst interval (time between the end of one to beginning of the next for all bursts) of 169 s (0.1 to 1,187 s). In addition to the four double burst events, two to three bursts occurred within a 60-s time span on five occasions. An example of three bubble bursts occurring in rapid succession is provided in Figure 3 (corresponding to Supplementary Audio S2).

Sounds associated with single bursts were broadband (mean 90% bandwidth = 2,219 Hz) with a mean, peak frequency of 402 Hz (SE = 30 Hz) (Figures 2 & 3; Table 3). Fish sounds tended to be short duration, averaging 0.33 s (0.01 s), and higher frequency, averaging 1,194 Hz (18 Hz) (*n* = 2,254) peak frequency. Examples of typical fish sounds that happened to overlap with a dolphin bubble burst sound can be seen in Figures 2 and 3. The presence of bubble bursts and fish sounds were not independent (Fisher's exact *p* < 0.001), with bubble bursts 4.81 times as likely to occur in a 10-s sampling window which also contained
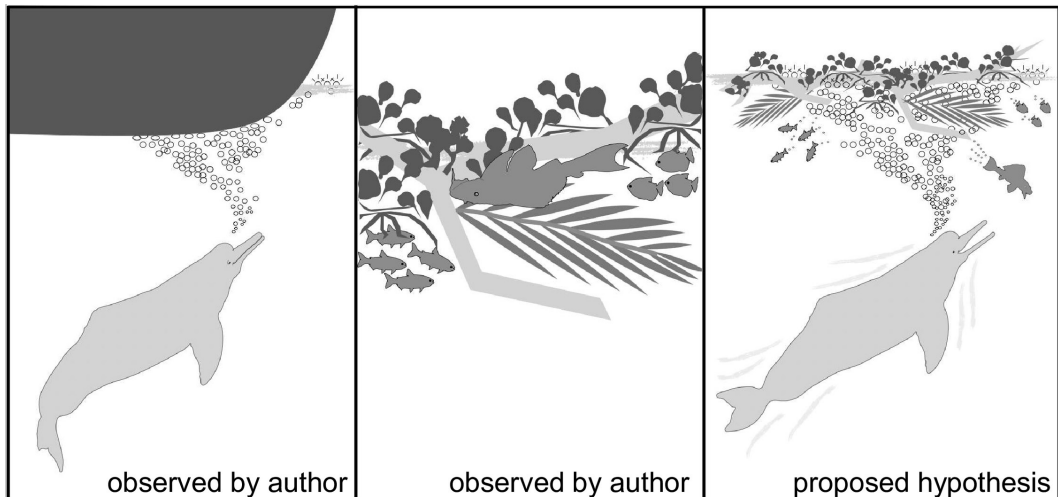
Figure 1. Artist's conception of (left) observed bubble burst production by Amazon river dolphin (*Inia geoffrensis*) beneath the drifting survey boat; (middle) example of known behavior of fishes that frequently cling to (e.g., loracarid catfishes) or shelter near and within (e.g., *Leporinus* and *Mylossoma* spp.) drifting or submerged plants, branches, and other materials (observed by author; P. Petry, pers. comm., 2 March 2022; Henderson & Hamilton, 1995; Petry et al., 2003; Schiesari et al., 2003; Correa et al., 2008; Carvalho et al., 2009); and (right) hypothetical use of bubble burst by dolphin to dislodge prey fishes sheltering within floating or drifting vegetation or other debris (illustration by S. K. McBride).
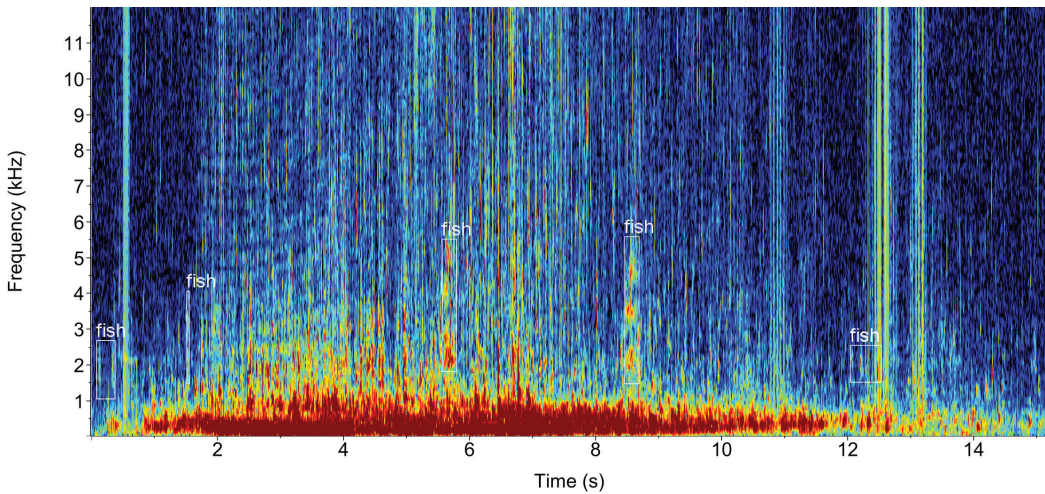
Figure 2. Example of a bubble burst produced by the Amazon river dolphin (corresponding to Supplementary Audio S1). Sounds produced by fishes that overlap with the bubble burst are labeled and enclosed in rectangles. Spectrogram parameters: unfiltered, 1,024-point Hann windowed FFTs with 50% overlap.
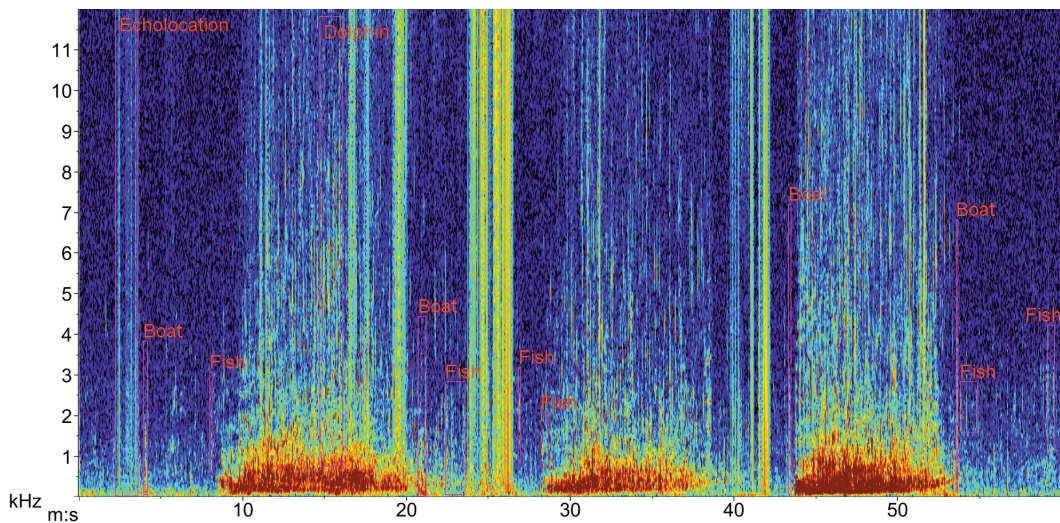
Figure 3. Example of three bubble bursts occurring in rapid succession (corresponding to Supplementary Audio S2). Other sounds that also occur in the same time period are shown in red, including echolocation clicks and other dolphin sounds, fish sounds, and boat noise (bumps and creaks). For clarity, only a few examples of each are shown. Spectrogram parameters: unfiltered, 1,024-point Hann windowed FFTs with 50% overlap.

fish (odds ratio 4.81 with a 95% CI of 3.14 to 7.36; Figure 4). The mean total duration of fish sounds per 5-min period was positively correlated with that of dolphin bubble burst sounds (Spearman r = 0.40, $p < 0.001$, n = 106), indicating that magnitude of fish sounds as measured by the total duration of all fish sounds per unit of time varied together with that of dolphin bubble burst sounds. Bangs, creaks, thumps, and other noises produced by the drifting

boat occurred throughout all drifts. Although the occurrence of such sounds was not quantified for the duration of each survey, 78% of the bubble bursts occurred within 5 s of a boat noise, and 54% within 2 s. Examples of typical boat-generated sounds are marked in Figure 3 and can be heard in Supplementary audio S2.

Since the survey was conducted during the low water season, extensive migrations of fishes

Table 3. Acoustic characteristic of Amazon river dolphin bubble sounds. Q1 = first quartile, Q3 = third quartile, and IQR = interquartile (parameter definitions in Supplementary Table S1).

Variable	Single bursts (*n* = 51)				Double bursts (*n* = 4)				All bursts (*n* = 55)			
	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Frequency (Hz)												
5th percentile	91	6	0	188	94	38	0	188	91	6	0	188
Q1 percentile	231	10	94	375	211	23	188	281	229	10	94	375
Peak	402	30	94	938	422	81	188	563	403	29	94	938
Q3 percentile	613	20	281	1,031	563	0	563	563	609	19	281	1,031
95th percentile	2,310	229	609	7,313	1,992	249	1,594	2,719	2,287	213	609	7,313
Bandwidth (Hz)												
IQR	382	18	141	750	352	23	281	375	380	17	141	750
90th percentile	2,219	229	469	7,219	1,898	277	1,500	2,719	2,195	214	469	7,219
Duration (s)												
90th percentile	6.16	0.34	2.94	15.34	17.17	2.27	13.47	23.72	6.96	0.52	2.94	23.72
Total	8.92	0.47	3.45	19.26	24.51	2.71	18.68	31.75	10.05	0.73	3.45	31.75
Burst interval*	173.51	37.87	0.07	1,187.24	114.94	46.25	17.44	211.95	168.92	35.09	0.07	1,187.24
Other												
Energy (dB)	138	2	95	167	154	0	153	155	139	2	95	167
Aggregate entropy	4.11	0.07	2.40	5.11	3.69	0.12	3.54	4.05	4.08	0.07	2.40	5.11
Average entropy	3.74	0.06	2.95	5.62	3.36	0.06	3.19	3.47	3.71	0.06	2.95	5.62

*Sample sizes 47, 4, and 51 for single, double, and all bursts, respectively

were observed moving down the Samaria River every day. Abundances appeared to be particularly high at the confluence of the Samaria River and the unnamed tributary draining Huisto Lake, where small numbers of Amazon river dolphins appeared to congregate daily for feeding. Although not observed during the dolphin surveys as no attempt to observe such behavior was made during the fish sound survey, various species of fishes (e.g., the catfishes *Ancistrus* sp., *Hypoptopoma gulare*, *Loricarichthys maculatus*, *Opsodoras stuebelii*, and *Ossancora punctata*) were anecdotally observed clinging to drifting branches, the underside of a dock, and moored canoes, or congregating among submerged vegetation along the river bank (e.g., *Leporinus* sp., *Mylossoma* sp., *Schizodon* sp., and various doradids) as depicted in Figure 1.

Discussion

Bubble production behavior of the wild Amazon river dolphin is described for the first time other than in an anecdotal account of a single observation by Layne (1958). Significantly, we present the first description of the acoustic properties of bubble production in the Amazon river dolphin—the only description for any odontocete, and just the third species of cetacean. Currently, there is not enough information to determine the function of this behavior in Amazon river dolphins, although comparison with other cetaceans (Table 1) suggests several strong possibilities, including play, surprise, agonism, and foraging.

The use of bubbles in play behavior has been reported for captive Amazon river dolphins (Gewalt, 1989), as well as in at least three other cetaceans (Table 1); however, interpretation of object manipulation as play can sometimes be confused with other behavior such as social-sexual displays (Martin et al., 2008). Although we cannot rule out that the bubble bursts we observed were part of play behavior as assumed by the
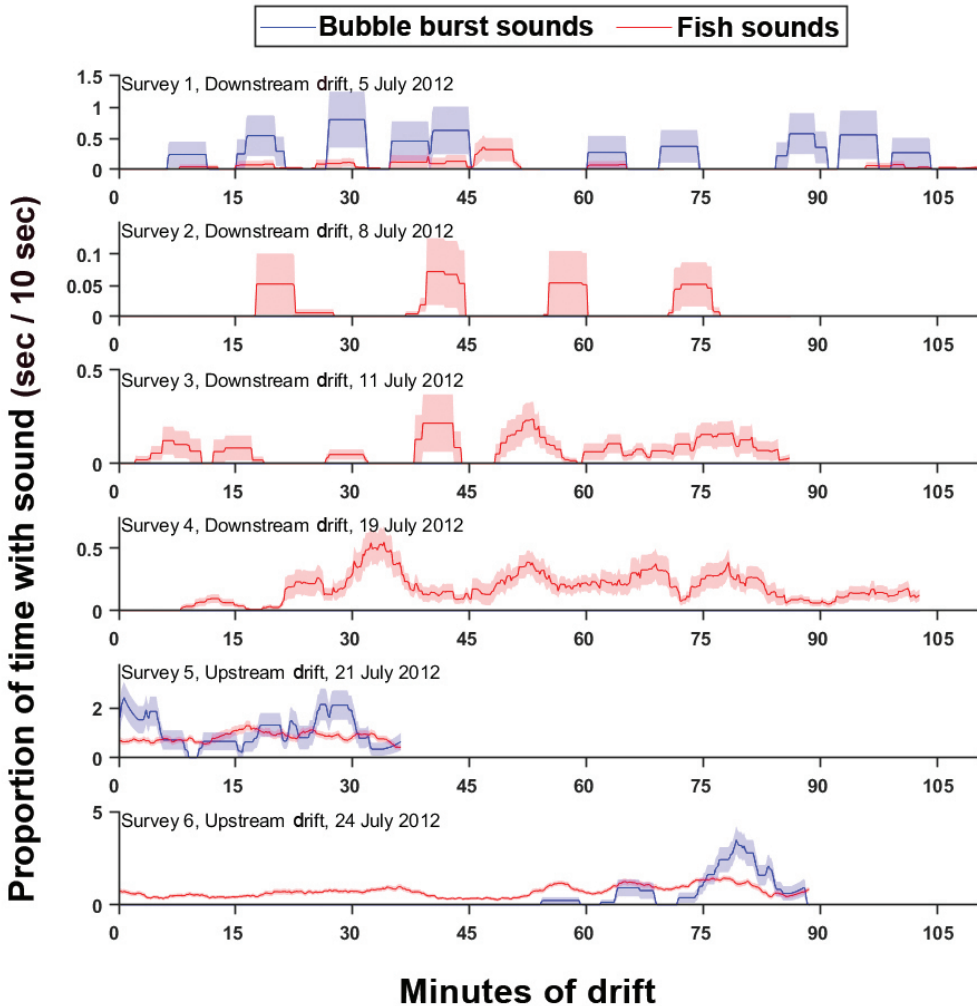
Figure 4. Bubble and fish sound presence over time for six drift surveys. Values were calculated using a moving average across 5 min; shading around each line indicates standard error as a moving average over a 5-min window. Bubble sounds are displayed in blue and fish sounds in red. **Note:** Vertical axes are on different scales.

local people, alternative explanations are probably more likely. In play behavior, the bubbles are typically treated as objects for manipulation (e.g., bubble rings; Gewalt, 1989). In that case, we would have expected dolphins to spend some time with the bubble bursts they created rather than leaving the vicinity as observed.

Bubble bursts and similar behaviors have been observed in response to surprise in four species of odontocetes (Table 1). The high percentage of bubble bursts that occurred within a few seconds of a noise from the boat (78%) supports a surprise reaction hypothesis; however, it may just be a coincidence since the boat continually produced

noises such as bangs, creaks, and thumps. The Amazon river dolphins were likely aware of the approach of the drifting boat from some distance away due to the noise it produced, but since we do not know how far the boat noises propagate in the system, or how far away the dolphins might be able to hear the sounds, we cannot rule out that bubble bursts may have been produced when individuals very close to the boat were surprised by a sudden bang or thump. On the other hand, no bubble bursts were observed during three of the surveys, and 22% of the bubble bursts did not have immediately preceding boat noises. In addition, since Operation Wallacea conducted daily surveys

along the same stretch of the Samiria River for the entire study period, one might expect the dolphins to become habituated to the drift boat's presence. Therefore, although the bubble burst behavior could be a response to a surprise, most likely from an unexpected noise from the drifting boat, it is less likely than other hypotheses for the behavior.

A response to a threat or in agonistic interactions is the second most commonly reported bubble production behavior reported for cetaceans (2 mysticetes and 5 odontocetes; Table 1). Therefore, it is possible that the bubble burst behavior we observed may have been a response to a perceived threat from the drifting boat. Indeed, the idea that the Amazon river dolphins were reacting to the boat invading their feeding area was the first to occur to us. The strongest argument for the aggressive or threat response argument is that the bubble burst behavior appeared to be directed at the boat itself. However, on further consideration, it is not clear why the dolphins might have perceived the drifting boat as a threat. First, since Operation Wallacea conducted surveys daily in the same section of the river over an extended period (in our case 3 wks), one might expect increasing habituation to the boat's presence over time, with declining reaction during later surveys. Instead, bubble production behavior was most frequent during the last two surveys. Second, if the behavior were an aggressive response to the boat, one might expect it to be commonly encountered when a running boat passes near a group of dolphins. We did not observe such behavior, but further observations are needed to discount the possibility.

Bubble bursts or similar bubble production behavior have been reported as part of foraging behavior in nine cetacean species (3 mysticetes and 6 odontocetes; Table 1). Our observations that bubble bursts appeared to occur in areas of active dolphin feeding and the temporal correlation between bubble bursts and fish sounds suggest that the behavior is associated with foraging behavior. Dolphins might increase their feeding activity in response to an increase in fish sound activity if they hunt by listening (e.g., Gannon et al., 2005). Although some fish sounds overlapped bubble burst sounds, suggesting the possibility that fishes are producing disturbance sounds in response to a predation attempt, it is more likely to be a coincidence due to the high number of fish sounds. It is possible that the correlation between fish sounds and bubble bursts was simply due to location effects where both types of activity were common. The higher incidence of both fish sounds and bubble bursts during the last two surveys may have been due to the increasing concentration of fishes migrating downstream as the waters receded in the low water season. Further research is needed to determine if either fish sounds increase in response to dolphin predation or dolphin predation increases in response to fish sounds.

On the other hand, the bubble burst behavior did appear to occur in areas where Amazon river dolphins were actively feeding, such as the confluence of the Samiria River and the unnamed tributary, and it is known that other cetaceans use bubble production as part of their foraging behavior (e.g., Heithaus et al., 2017). Humpback whale use of bubbles to corral prey is well known (Jurasz & Jurasz, 1979; Hain et al., 1982; D'Vincent et al., 1985; Sharpe & Dill, 1997; Dunlop et al., 2008; Wiley et al., 2011; Qing et al., 2019; Bryngelson & Colonius, 2020); other mysticete species, such as the fin whale (*Balaenoptera physalus*; S. S. Sadove, pers. comm., cited in Sharpe & Dill, 1997) and Bryde's whale (*Balaenoptera brydei*; V. Deecke, pers. comm., cited in Sharpe & Dill, 1997), may use bubbles as part of foraging as well. At least five odontocete species have been reported to use bubble production during foraging to displace or trap prey, including bottlenose dolphins (*Tursiops truncatus*; Fertl & Wilson, 1997; Zaeschmar et al., 2013), Atlantic spotted dolphins (*Stenella frontalis*; Fertl & Würsig, 1995), short-beaked common dolphin (*Delphinus delphis*; Neumann & Orams, 2010), false killer whales (*Pseudorca crassidens*; Zaeschmar et al., 2013), and killer whales (*Orcinus orca*; Similä & Ugarte, 1993).

Use of bubble bursts as a visual cue for synchronization or other communicative function, such as when hunting, has been suggested for the dusky dolphin (Trudelle, 2010; Vaughn et al., 2010) and the killer whale (Visser et al., 2008). It is suggested that the bubble burst could provide either a visual cue itself or might be associated with a vocalization, such as whistles, that would serve the communication function (see review in Trudelle, 2010). Neither of these options appear likely for the Amazon river dolphin. We saw no indication of consistently coincident occurrence of the bubble burst and dolphin vocalization that might suggest the bubble bursts were a byproduct of sound production. A visual function is unlikely for the Amazon river dolphin both because of the low visibility in its habitats (much less than 1 m) and low visual acuity of the species (Mass & Supin, 1989). We suggest two other mechanisms for a communicative function of bubble bursts that, to our knowledge, have not been addressed previously. First, since dolphin sonar could readily detect bubble bursts (Leighton et al., 2008), it is possible that bubble emissions could be a proxy for a visual cue in a murky environment. In other words, the dolphin could easily detect the bubble

bursts with their sonar which could then serve as both a marker for time and location. Secondly, the sounds produced by the bubble burst could serve a similar purpose depending on the propagation distance of the sound and hearing acuity of the dolphin. More data on the acoustic properties of the bubble bursts, river dolphin hearing ability, and sound propagation together with concurrent animal behavior are needed to test this idea.

The apparent tendency for bubble production to occur in areas where dolphins were actively feeding, and the correlation between fish sounds and bubble burst sounds, supports the hypothesis that bubble burst behavior is part of the dolphin's foraging strategy. The strong clustering of bubble burst sounds, and frequent occurrence of two or more bursts in rapid succession, might suggest use of bubble bursts in cooperative hunting. However, the Amazon river dolphin is not known to cooperatively hunt (Dos Santos et al., 2012; Amorim et al., 2016). It is also puzzling that the bubble bursts appeared to be targeting the boat rather than occurring throughout the feeding area. The lack of observations of bubble burst behavior occurring more widely during feeding again points to a reaction to the boat's presence, which could be interpreted as aggressive behavior.

Another possible function of bubble bursts is that they may be used as a novel hunting strategy to physically dislodge fish clinging to or otherwise sheltering within floating and submerged drifting materials. We hypothesize that the dolphins react to the drifting boat the same way they would react to floating vegetation mats and other drifting debris by producing bubble bursts in an attempt to disturb sheltering fish and drive them from shelter as depicted in Figure 1. This would account for their apparent targeting of the boat rather than using bubble bursts to herd or corral fish in the open water. Although we did not collect data on fish attraction to the drifting boat, it is likely that some fish quickly began to associate and shelter beneath the boat shortly after the drifts began. Fish sheltering within and associating with floating and drifting vegetation mats, sometimes referred to as floating meadows, is a well-known phenomenon in the Amazon region (Henderson & Hamilton, 1995; Petry et al., 2003; Schiesari et al., 2003; Correa et al., 2008; Carvalho et al., 2009), and river dolphins are known to take advantage of this as floating meadows are a preferred foraging habitat (e.g., McGuire & Winemiller, 1998; Martin et al., 2004; Yamamoto et al., 2015). As fish migrate downstream with the receding water levels, they likely also associate with other types of floating or submerged drifting materials such as branches, brush, and logs. Such behavior is well known in marine systems (e.g., Gooding, 1967;

Rountree, 1989; Gomes et al., 1998; Dempster & Kingsford, 2004; Wohl & Iskin, 2021) but has not received much attention in rivers of the Amazon region. Our anecdotal observations of various fishes, especially catfishes, clinging to the sides of moored canoes, rafts, and submerged branches suggests this type of behavior is likely to be important in the Amazon. Other scientists have observed similar behavior and attest to the importance of drifting material, especially woody material, as habitat for fishes (e.g., P. Petry, pers. comm., 2 March 2022). Many species of fishes, like those observed herein, are known to use woody material for shelter and are capable of clinging tightly to surfaces or wedging into crevices using strong erectile spines, sucker mouths, or other anatomical structures (e.g., Carvalho et al., 2009). Some of these fishes can hold their position on surfaces even in strong currents (Geerinckx et al., 2007; Gerstner, 2007). As water recedes from the flooded forest during the low water season, mats of floating vegetation as well as uprooted brush, tree branches, logs, and other types of woody material, drift down the rivers, creating important fish habitat and foraging opportunities for the dolphins. In fact, one important group of prey fishes for the river dolphin are the driftwood catfishes (Auchenipteridae; Aliaga-Rossel et al., 2010).

Given these facts, it would not be surprising for Amazon river dolphins to associate floating and drifting objects as potential food resources. In the low visibility habitats of the Amazon region, visual detection of fishes associated with drifting materials would often not be possible until approaching closely (< 1 m). In addition, the Amazon river dolphin is known to have low acuity vision, capable of resolving large moving objects (Mass & Supin, 1989). It would be difficult under these conditions to visually detect fishes hiding among the roots of floating vegetation mats or among the branches of drifting brush, let alone fishes clinging tightly to surfaces such as the bottom of a boat. Even if the dolphins are able to detect the presence of fishes associated with the drifting material using their echolocation, the problem of extracting the prey is still substantial. We hypothesize that Amazon river dolphins use bubble bursts to startle fishes in an attempt to chase them away from shelter where they can be more easily captured as depicted in Figure 1c. Noise and turbulence produced by the bubble burst could contribute to a startle effect. The use of bubble bursts in this manner is not without precedent in the literature. For example, false killer whales have been reported to use bubble bursts to dislodge mahi mahi (*Coryphaena hippurus*) from shelter underneath drifting boats (R. W. Baird, pers. comm., June 2011, cited in Zaeschmar et al., 2013). Similarly, Weddell seals (*Leptonychotes*

weddellii), an Antarctic pinniped, use a similar behavior of blowing bubbles to flush Antarctic fish from beneath platelet ice (Davis et al., 1999). These observations provide a precedent for our hypothesis that river dolphins use bubble bursts to flush prey associated with floating or drifting objects (Figure 1c). Although it is possible that fishes were associating with the drifting vessel during the surveys, attracting the dolphins, it is more likely that the dolphins are treating the drifting boat as if it were a floating vegetation mat and produce the bubble bursts under the boat in a search for unseen prey.

Future studies are needed to clarify the behavior associated with bubble burst production in the Amazon river dolphin. However, the fact that multiple behaviors associated with bubble burst behavior have been reported for seven species (Table 1) suggests that it is possible that the Amazon river dolphin might utilize bubble bursts in multiple behaviors. For example, the large bubbles, turbulence, and sound associated with bubble bursts might produce startle responses in conspecifics as well as prey and, thus, function in agonistic interactions. Use of PAM together with visual observations can help elucidate the behavior. The use of drones or other methods of aerial visual tools not only provide improved census of river dolphin populations (e.g., Fürstenau Oliveira et al., 2017) but also better data on behaviors. Coupling visual surveys with PAM promises to provide information on interactions of the dolphin with conspecifics and prey during bubble production events. Once behavior is verified, acoustic detection of bubble bursts can be added to the catalog of sounds used to document dolphin behavior, especially under conditions where visual methods are difficult such as during the night, in the flooded forest, or beneath floating meadows. For example, bubble bursts could be useful as a non-visual indicator of aggressive interactions or foraging attempts if the association of the bubble burst production with these behaviors is confirmed.

Although bubble production has been reported for just 15 cetacean species to date, the behavior will likely be found more widespread as observational data become available for other species. A lack of recognition of the potential importance of bubble production likely contributes to infrequent reports of such behavior. The wide range of behaviors associated with bubble production in cetaceans (Table 1) suggests that PAM, together with visual and other observation methods, might be a valuable tool to help understand these behaviors in other species. Two examples of how bubble burst sounds have already been used in gray whale PAM surveys include (1) as a marker

to aid in attribution of other sounds to gray whales (Burnham et al., 2018) and (2) to determine diel feeding patterns during the night when visual observations were not possible (Jurasz & Jurasz, 1979).

In conclusion, this study provides the first quantitative description of the acoustic structure associated with bubble burst sounds produced by Amazon river dolphins. Possible behaviors associated with bubble burst production are discussed, and it is concluded that foraging or aggressive behaviors are the most likely. Although research on the sound repertoire of the Amazon river dolphin has accelerated in the last two decades, only two studies have attempted to incorporate PAM methodologies into river dolphin surveys (Yamamoto et al., 2015; Campbell et al., 2017). These studies, together with our study, demonstrate that PAM of river dolphins can be done successfully in the Amazon region. Future studies that incorporate PAM into traditional river dolphin surveys, including identification of bubble burst sounds, promise to improve our understanding of the ecology and behavior of the species. Although the potential of PAM applications focused on bubble production in other cetaceans has been largely overlooked, it holds great promise as an additional tool in the study of cetacean behavior and ecology. However, before PAM of bubble production behaviors can be applied, detailed quantification of the acoustic characteristics of different types of bubble production by each species is required.

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