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The potential of passive acoustic monitoring for the study of ecological interactions among freshwater Amazonian dolphins and fishes

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Abstract

The acoustic behavior of Amazonian aquatic fauna and the importance of its soundscape are poorly understood. Sounds produced by wild river dolphins (Amazon River dolphin, *Inia geoffrensis*, and tucuxi, *Sotalia fluviatilis*) and those of unidentified fishes were recorded from a drifting boat on six different days (8.5 h duration) in July 2012, in the Pacaya-Samiria National Reserve of Peru. Unidentified sounds of fishes were dominated by four broad types: pulsed stridulation, long stridulation, long pulse, and short pulse. Dominant sounds produced by dolphins included echolocation click trains, burst-pulses, whistles, and bubble bursts. Soniferous activity was quantified as total sound duration per 10 s of recording and compared between dolphins and fishes for each sound type and all types combined. Soniferous activity was highly variable among days, with echolocation click trains (7.7 s min^{-1}) and pulsed stridulation (0.33 s min^{-1}) being the dominant components. Soniferous activity of the dolphins and fishes was correlated (Spearman r = 0.49, P < 0.001). However, whether the correlation resulted from predator-prey interactions or other spatial factors could not be determined. Although preliminary in nature, this study is the first examination of the soniferous activity of both river dolphins and fishes in the Amazon and suggests passive acoustic monitoring has the potential to provide unique insight into ecological interactions in the system.

Keywords:
bioacoustics, biophony, ecoacoustics, soundscape, unidentified sounds

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Introduction

A wide variety of aquatic organisms depend on the use of sounds for their survival. The sounds they produce comprise the biological component of a habitat's characteristic soundscape, which is the sum of all types of sounds at a location (*e.g.*, see Pijanowski et al., 2011). Passive Acoustic Monitoring (PAM) in aquatic habitats involves the use of various technologies to record underwater sounds and document the spatial and temporal distributions of specific sounds, and/or to document the overall soundscape (*e.g.*, Lindseth & Lobel, 2018). Thus, PAM has become an important tool in marine fisheries and ecological research (Rountree et al., 2006; Luczkovich et al., 2008; Lindseth & Lobel, 2018), but has only recently begun to be applied in freshwater ecosystems (Anderson et al., 2008; Deichmann et al., 2018; Linke et al., 2018; Mickle & Higgs, 2018; Rountree et al. 2019, 2020; Desjonquères et al., 2020; Greenhalgh et al., 2020). Deichmann et al. (2018) and Martínez -Medina et al. (2021) specifically call for PAM studies in tropical ecosystems.

Although research describing sound characteristics of Amazonian fishes is increasing (*e.g.*, Kaatz et al., 2010; Tellechea et al., 2011, 2013; Kaatz & Stewart, 2012; Godinho et al., 2017; Smith et al., 2018; Rountree & Juanes, 2020; Raick et al., 2021), the use of PAM methods for fishes in the Amazon has been limited (Borie et al., 2014, 2019; Muñoz-Duque et al., 2021). Recently, pioneering studies used PAM methods to describe spatiotemporal patterns in disturbance and chorusing sounds of silver croaker, *Plagioscion squamosissimus* (Sciaenidae), and five species of Characiform fishes (Borie et al., 2014, 2019), and spawning sounds of bocachico *Prochilodus magdalenae* (Prochilodontidae, Muñoz-Duque et al., 2021). Similarly, although there is a long history of research on the acoustic behavior of cetaceans in marine systems (Mellinger et al., 2007; Zimmer, 2011) there are relatively few PAM studies of riverine dolphins, despite the need for them (Trone et al., 2015; Yamamoto et al., 2015; Campbell et al., 2017; Martínez-Medina et al., 2021; Muirhead, 2021; Erbs et al., 2023).

The Pacaya-Samiria National Reserve (PSNR) in Peru is home to a wide diversity of fishes, with estimates of up to 240 species (Correa, 2005; Correa et al., 2008; Ortega & Hidalgo, 2008). Although soundscape data have not previously been reported from the PSNR, many of these species are known to be soniferous, including catfishes (Siluriformes), cichlids (Cichlidae), and piranha (Serrasalmidae) (see recent taxonomic reviews of sound production in fishes - Looby et al., 2020; Rice et al., 2022). As part of the broader survey of fishes, the sounds of piranha species were described based on auditioning handheld individuals captured in the PSNR (Rountree & Juanes, 2020). Work is ongoing to describe the sounds of 23 other fish species that were auditioned during the survey and examples of sounds made for each are available online (Rountree, 2023). However, there is little published information about the sounds produced by many of the other species reported in the region.

The Amazon River dolphin (*Inia geoffrensis*) and the tucuxi (*Sotalia fluviatilis*) inhabit freshwater systems in the Amazon, including the PSNR (*e.g.*, Layne 1958; Vidal et al., 1997; Martin et al., 2004; Campbell et al., 2017; Aliaga-Rossel & Duran, 2020). Although dolphin sounds have been characterized in other areas of the Amazon (May-Collado & Wartzok, 2007; Ladegaard et al., 2015; Trone et al., 2015; Amorim et al., 2016; Campbell et al., 2017; Olson, 2017; Melo-Santos et al., 2019; Melo et al., 2021a, b), they have only recently been studied in the PSNR (Muirhead, 2021). Like most delphinids, both species are known to produce narrowband tonal whistles and diverse pulse sounds for communication with conspecifics (May-Collado & Wartzok, 2007; Amorim et al., 2016; Olson, 2017), and echolocation clicks for sensing and perceiving the surrounding environment and during feeding for finding and capturing prey (*e.g.*, Ladegaard et al., 2015; Trone et al., 2015).

The association between sound production of dolphins and the acoustic behavior of their prey is unknown in the Amazon. All studied toothed whales, including Amazon River dolphins and the tucuxi, are known to produce a rapid series of echolocation clicks during feeding and navigation (Au, 2000; Au & Benoit-Bird, 2003; Au & Herzing, 2003). Additionally, bottlenose dolphins (*Tursiops truncatus*) produce numerous call types with low frequency energy concentrations during feeding thought to influence prey behavior (Nowacek, 2005). Experimental playbacks of dolphin "pops" elicit a stress response and rise in cortisol levels in Gulf toadfish (*Opsanus beta*) (Remage-Healey et al., 2006). Alternately, dolphin sounds were documented suppressing the calling rate of silver perch (*Bairdiella chrysoura*) (Luczkovich et al., 2000).

While conducting a survey of the sounds of fishes in the PSNR during July 2012 (Rountree & Juanes, 2020), we had the opportunity to record the underwater soundscape during several visual surveys of river dolphins conducted by Operation Wallacea (http://www.opwall.com). Operation Wallacea is an international program that brings scientists and students from European and North American universities together to conduct long-term environmental monitoring in expeditions at many places around the world. Expeditions have been conducted in the PSNR annually since 2009 (Bodmer et al., 2018). These recordings constitute the first known attempt to simultaneously consider sounds produced by both dolphins and fishes in the Amazon. In addition, while in the field we noticed that sounds of fishes seemed to be more prevalent in areas where the dolphins were actively feeding. Since some dolphins are thought to use passive listening to hunt soniferous fishes (see review in Pate & McFee, 2012), we hypothesized that river dolphins may exhibit similar behavior. Using PAM technology, the goals of this paper were to: 1) present preliminary data on the sounds of wild dolphins and fishes in the PSNR; 2) determine if there is a temporal correlation between sounds of dolphins and fishes; 3) discuss potential causes of any correlation; and, 4) discuss the potential of PAM to elucidate ecological interactions among disparate taxa in freshwater habitats.

Material and Methods

The study was conducted within the PSNR which is contained within the confluence of the Marañón and Ucayali rivers where the main stem of the Amazon River originates (Fig. 1). Operation Wallacea conducts annual visual surveys for dolphins in the PSNR, typically from small boats while drifting (averaging 2 km^h) (Bodmer et al., 2018).

Acoustic recordings

Underwater sounds were recorded on six different days from a 12 m wooden boat that was allowed to drift for approximately 1-2 hours between 1400 and 1700 h local time, within a 10 km stretch of the Samiria River (Fig. 1, Table 1). Downstream drifts began at a central location (centered at 4°52'44" S, 74°21'26" W),

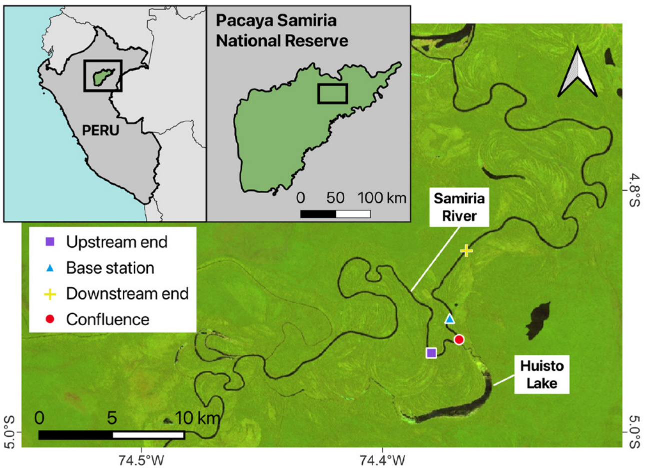


Figure 1. Study area in the Samiria River, part of the Pacaya-Samiria National Reserve (PSNR) in Peru. Dolphin surveys were conducted from a drifting wooden boat. Downstream drifts started at the base station and floated downstream, while upstream drifts started some distance upstream and floated down towards the base station. For clarity, only the maximum upstream start and downstream end locations are shown. The confluence of the Samiria River and a small tributary draining Huisto Lake is also indicated.

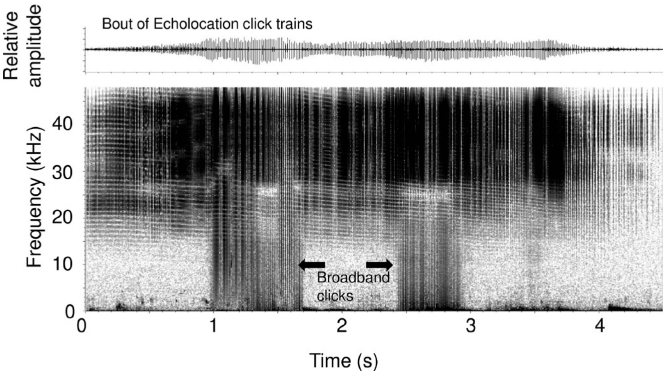


Figure 2. Example of an approximately 4 s bout of overlapping echolocation click trains produced by the river dolphins. Bouts were separated from other bouts by intervals of at least 0.5 s when no clicks were detectable at the sample rate. Clicks extending below 20 kHz appear in the spectrogram when they are close to and directed towards the hydrophone. Note, because of the insufficiently high sample rate preventing quantification of the full bandwidth, only duration was measured for bouts of echolocation clicks. Spectrogram parameters: unfiltered 1,024-point Hann windowed FFTs with 50% overlap.

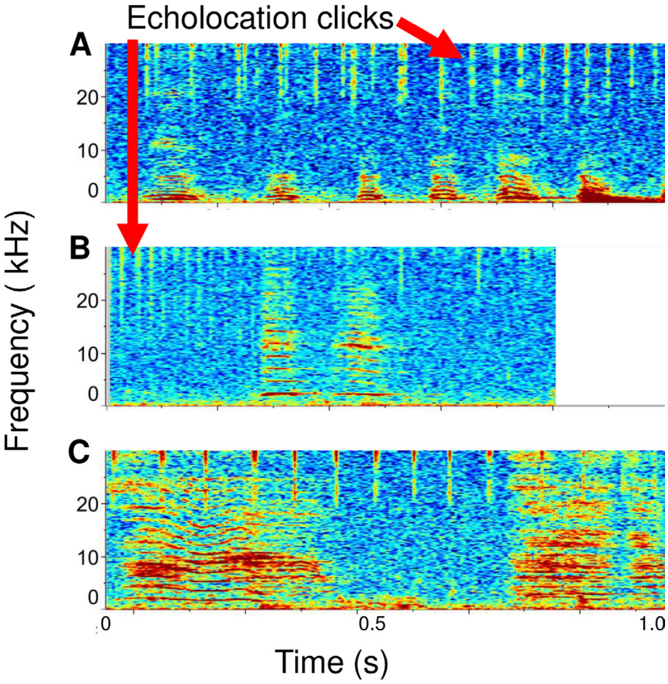


Figure 3. Examples of three types of burst pulse sounds recorded from dolphins (after Melo-Santos et al., 2019). A) six short two-component burst pulses; B) two short burst pulses with subharmonics; C) two examples of a miscellaneous burst pulse type. Echolocation clicks can also be seen in each graph. All spectrograms are shown on the same frequency (0 – 30 kHz) and time (1 s) scales. Spectrogram parameters: unfiltered, 1,024-point Hann windowed FFTs with 50% overlap.

while upstream drifts began approximately 5 km upstream. The upstream drifts passed through the confluence of the Samiria River and a small tributary draining Huisto Lake (approximately at 4°53′53″ S, 74°20′55″ W). On each day, the underwater soundscape was continuously recorded and monitored in real-time using an uncalibrated SQ26-H1 recorder system with a SQ26-08 Hydrophone (Sensitivity = -169.00 re. 1V µPa-1 rms, Cetacean Research Technology, Seattle, WA). Sounds were continuously recorded to a Zoom H1 digital recorder (Zoom North America, Hauppauge, NY) at 16 bit or 24 bit and a sample rate of either 48 or 96 kHz (Table 1). The hydrophone was suspended over the side of the boat at a depth of approximately 1 m below the water's surface.

Acoustic analysis

To identify sounds produced by fishes and dolphins, post-processing of acoustic signals was conducted by listening to all recordings in their entirety while simultaneously viewing spectrograms (1,024 FFT, Hanning window, 50% overlap) and waveforms of sounds with Raven Pro 1.5 acoustic software (Bioacoustics Research Program, 2014). Dolphin sounds were classified following Melo-Santos et al. (2019) as: broadband echolocation click trains (Fig. 2); various broadband burst pulses; narrow-band frequency modulated whistles (Fig. 4A); and sounds associated with bubble bursts (Fig. 4B). We further subdivided the burst pulse sounds into the two most observed by Melo-Santos et al. (2019) whenever possible: short-two-component burst-pulses, and short-burst pulses with subharmonics (Fig. 3). All other burst pulse types were lumped into a miscellaneous burst-pulse category (Fig. 3). Echolocation clicks were not individually annotated, but annotated as bouts of one or more overlapping click trains separated from other bouts by intervals of at least 0.5 s when no clicks were detectable at the sample rate (Figs 2, 4A). Many of the echolocation click trains contained high repetition rate buzzes (*e.g.*, DeRuiter et al., 2009; Wisniewska et al., 2014; Ladegaard et al., 2017). Interestingly, although river dolphin echolocation clicks are usually described as high frequency with mean fundamentals ranging from 46 - 100 kHz and limited energy

Table 1. Details on the timing of boat surveys, locations, and parameters of acoustic recordings

Type	Date	Start	End	Duration (h:min)	Sample Rate (kHz)	Bit Rate	Start Location
downstream	7/5/2012	14:40	16:35	1:55	48	16	4°52′27″ S, 74°21′27″ W
downstream	7/8/2012	14:44	16:30	1:46	48	24	4°52′30″ S, 74°21′29″ W
downstream	7/11/2012	14:43	16:20	1:37	48	24	4°52′30″ S, 74°21′28″ W
downstream	7/19/2012	14:13	16:00	1:47	48	24	4°52′34″ S, 74°21′25″ W
upstream	7/21/2012	15:07	15:57	0:50	96	24	4°53′4″ S, 74°21′41″ W
upstream	7/24/2012	15:13	17:00	1:47	96	24	4°54′07″ S, 74°22′05″ W

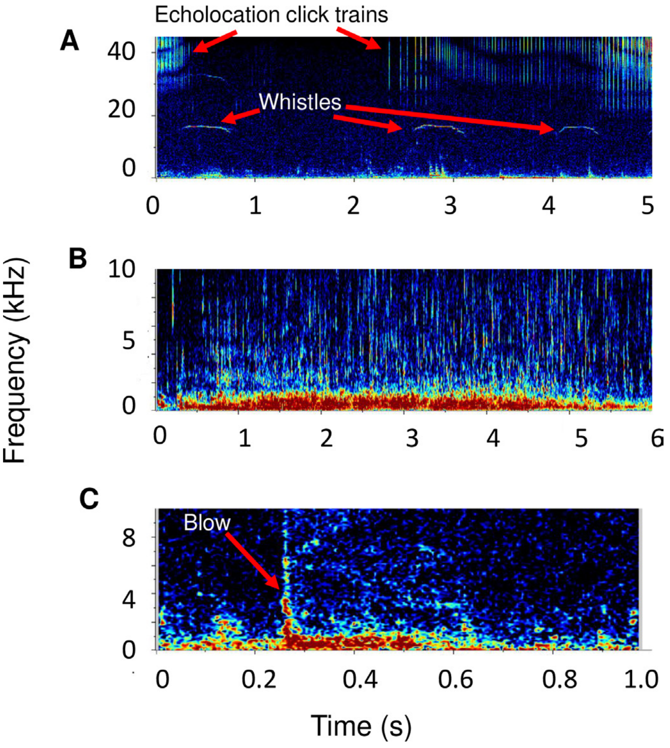


Figure 4. Examples of river dolphin sound type categories: A) three whistles, arrows point to the fundamental (the end of one echolocation click train bout and start of another are also indicated); B) an approximately six-second-long bubble burst (only produced by the Amazon River dolphin); and C) miscellaneous sounds represented here by the underwater sound of a dolphin blow produced as an Amazon River dolphin took a breath at the water surface. Numerous other miscellaneous sounds not shown. Spectrogram parameters: unfiltered, 1,024-point Hann windowed FFTs with 50% overlap. Note different vertical and horizontal scales.

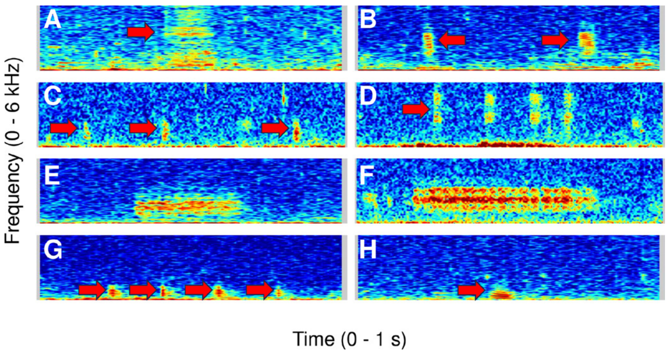


Figure 5. Examples of some of the most common sound types attributed to fishes: A-D) a wide diversity of pulsed stridulation sounds labeled "creaks" were the most commonly occurring sounds, here represented by a few examples; A) single long duration creak; B) two short broadband creaks; C) three short low frequency creaks; D) high frequency creak train; E-F) Long stridulation sounds arbitrarily labeled "screech" types were also common; E) low frequency short duration screech; F) high frequency long duration screech; G) trains of 1 to many low frequency short pulsed sounds labeled "knocks" were less frequently encountered; H) a diversity of low frequency and long pulsed sounds often with harmonics were labeled "bark" sounds. The bark example here (H) is similar to piranha sounds reported from the study area (Rountree & Juanes, 2020). All sounds are shown on the same frequency (0 – 6 kHz) and time (1 s) scales. Spectrogram parameters: unfiltered, 1,024-point Hann windowed FFTs with 50% overlap.

below 10 kHz (*e.g.*, Ladegaard et al., 2015; Melo at al., 2021b), they have been documented to produce lower frequency click trains with high energy below 20 kHz when fishing (see review in Trone et al., 2015). The unusual bubble burst sounds (Fig. 4B) are described in detail in a separate paper (Rountree et al., 2022) and are not discussed further here. A wide variety of rare sounds attributed to dolphins was included in a miscellaneous category for the purposes of this paper. One miscellaneous sound of interest was produced underwater by dolphins taking a breath at the surface and labeled dolphin blow (Fig. 4C). However, dolphin blows were only annotated and measured when they could be validated by examining short video clips (total 13 min 39 s of recordings) taken with a hand-held camera (Pentax Optio G-II, Pentax Ricoh Imaging Co., Ltd) that had been synchronized with the underwater sound recordings. Dolphin blows were audible both above and below water in the videos.

Sounds were attributed to fishes due to their overall similarity to other known sounds produced by fishes, and sounds recorded from hand-held fishes as part of the separate survey (Rountree & Juanes, 2020; Rountree, 2023). All sounds of fishes were measured but could not be assigned to species due to limited data on sound production by fishes in the region, and the observed high variation in measured characteristics. However, the sounds of fishes were grouped into four major types that variously occurred singly or in series: short pulsed stridulations, labeled as "creaks"; long stridulations, labeled as "screech"; short duration pulses often with harmonics, labeled as "barks"; and short pulses, labeled as "knocks" (Fig. 5). Infrequent sounds not fitting these categories were grouped into an "other" category, and excluded from the analyses.

Acoustic measurements of selected parameters of all sounds were made in Raven following Charif et al. (2010). Frequency measures (Hz) included the peak frequency (frequency with highest energy), the 5th and 95th percentiles (the frequency that divides the sound selection into two frequency intervals containing 5% and 95% of the energy in the selection), and the full bandwidth. In addition, the interquartile range of the bandwidth (IQR-BW) was also measured. Sound duration and the 90th percentile duration are also reported. The full frequency bandwidth for the echolocation click train bouts could not be measured due to the low sample rate recorded, however since the river dolphin echolocation clicks extend below 20 kHz, we were able to identify and measure the duration of click bouts in the spectrogram as the time between the first and last detectable clicks in the bout (Figs 2, 4a). Similarly, we do not report frequency measurements for Amazon River dolphin whistles since they can extend up to 48 kHz (May-Collado & Wartzok, 2007). However, whistle duration was measured from the start to end of the fundamental (Fig. 4a). The durations of all individual annotations for each sound type were summed within 10 s time bins and then averaged over five-minute periods to examine the correlation between sounds of fishes and dolphins using SAS/STAT software, Version 12.1 (SAS Institute Inc., 2012). However, because temporal patterns in sounds of dolphins and fishes are not comparable among days, the nonparametric Spearman rank partial correlation coefficient was used to control for day effects. Only the most common sound types of dolphins and fishes were tested for correlations. Two types of short burst dolphin sounds (short two-component

Table 2. Mean (± SE) for selected sound characteristics for the Amazon River dolphin and major unidentified sound categories of fishes. For frequency variables, the 5th percentile, peak and 95th percentiles are given as well as the interquartile bandwidth (IQR BW) and full bandwidth (Total BW). The 90th percentile and full duration are also given.

		Frequency variable (Hz)					Durations (ms)	
Sound type	**N**	**5%**	**Peak**	**95%**	**IQR BW**	**Total BW**	**90%**	**Total**
Dolphin sounds								
Burst pulse: short two-component[a]	317	1592 ± 60	3333 ± 159	10955 ± 335	3277 ± 184	16913 ± 371	69 ± 2	106 ± 2
Burst-pulse: short with subharmonics[a]	37	2337 ± 196	4708 ± 453	12658 ± 708	3589 ± 360	16083 ± 979	128 ± 11	179 ± 13
Total short burst pulse	354	1589 ± 59	3477 ± 152	11133 ± 310	3309 ± 169	16827 ± 347	75 ± 2	113 ± 3
Other burst pulse[a]	20	1031 ± 229	2423 ±458	8923 ± 1486	2576 ± 571	12534 ± 1628	213 ± 52	283 ± 66
Echolocation click trains[b]	1741						1765 ± 54	2257 ± 68
Whistles[b]	86						456 ± 61	587 ± 69
Bubble burst	55	91 ± 6	403 ± 29	2287 ± 213	380 ± 17	12737 ± 530	6962 ± 520	10153 ± 726
Dolphin blow[a]	19	141 ± 27	476 ± 97	5948 ± 821	1226 ± 278	10438 ± 1005	551 ± 94	740 ± 127
Total other	49	887 ± 160	1292 ± 190	5383 ± 635	1456 ± 331	7918 ± 955	1167 ± 225	1504 ± 289
Fish sounds								
Creak: pulsed stridulation	3072	1626 ± 9	2220 ± 14	3030 ± 14	653 ± 8	1819 ± 15	37 ± 1	54 ± 1
Screech: long stridulation	516	1179 ± 20	1655 ± 25	2486 ± 27	599 ± 12	1688 ± 27	293 ± 10	373 ± 11
Bark: long pulse	153	262 ± 11	522 ± 23	937 ± 33	271 ± 17	943 ± 40	82 ± 6	115 ± 7
Knock: short pulse	158	393 ± 20	690 ± 30	1132 ± 44	312 ± 17	1063 ± 48	18 ± 1	30 ± 1
Other[a]	90	748 ± 70	1215 ± 87	2110 ± 105	643 ± 47	1904 ± 112	193 ± 42	247 ± 48

a = not used in analyses, b = sample size not sufficient for measurements other than duration

and short with subharmonics) were combined into one pooled "short burst" category for analysis of temporal trends due to their overall similarity.

Results

Amazon River dolphins were observed in all six surveys recorded 5 - 24 July 2012 (Table 1), typically occurring in small groups of 2 - 6 individuals. Small groups of 1 - 3 tucuxi were occasionally observed on 5, 21 and 24 July. Because there was some overlap between sightings of the Amazon River dolphin and tucuxi, and we cannot reliably distinguish sounds between the two species, the dolphin sounds reported herein are not attributable to species except for bubble burst and dolphin blow sounds. Bubble bursts were produced by the Amazon River dolphin while underneath or within a few meters of the drifting boat (Rountree et al., 2022). The few tucuxi that were observed never approached the boat. Dolphin blows were only identified in the short portions of recordings that had accompanying video allowing identification.

Description of sounds

Echolocation click train bouts were the most frequently detected dolphin sound (n = 1741), averaging 2.26 s in duration (Fig. 2, Table 2). Many (17%, n = 290) of the bouts contained click trains with energy extending into low frequencies (Figs 2, 6, 7), including a secondary peak at approximately 2 kHz (Fig. 7). Dolphin bubble burst sounds exhibited the longest duration of up to 10 s (mean = 6.9 s, Table 2) and the lowest peak frequency (mean = 403 Hz). Other dolphin sounds were much shorter and were measured individually, including burst pulses, whistles, and miscellaneous sounds. Burst pulse sounds included short two-component, short burst pulse with subharmonics, and other burst pulse categories. Short two-component burst pulses (Fig. 3A) were the most frequent burst pulse sound type (n = 317), averaged 106 ms in duration with a peak frequency of 3,333 Hz (Table 2), while the less frequently occurring short burst pulse with subharmonics (n = 37, Fig. 3B) were slightly longer duration (179 ms) and higher frequency (mean peak frequency 4,708 Hz). A small number of burst pulses could not be placed in either of these categories (n = 20) and tended to be longer in duration (283 ms) and lower in frequency (2,423 Hz; Fig. 3C, Table 2). Whistles (n = 86, Table 2) were less common than the two-component burst pulses and averaged 587 ms in duration. The miscellaneous dolphin blow sounds were short (740 ms) low frequency sounds (peak 476 Hz; Fig. 4C, Table 2).

By far the most common sounds attributed to fishes were a wide range of creaks (n = 3,072), often in repeating trains (Fig. 5), averaging 54 ms duration and 2,220 Hz peak frequency (Table 2). Screeches were also common (n = 516), but much longer in

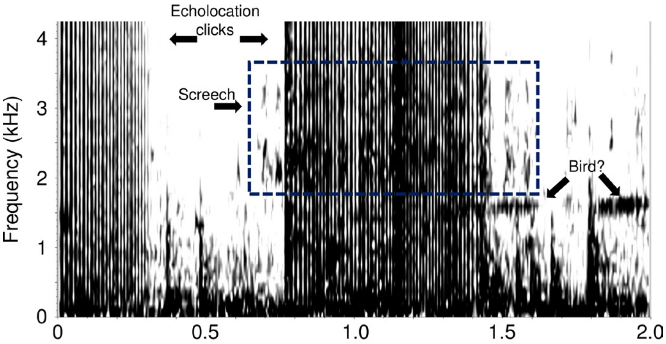


Figure 6. Example frequency overlap between a dolphin echolocation click train and fish screech sound (shown in dashed box). An unidentified sound, likely a bird, can also be heard. Spectrogram parameters: 5 kHz high-pass filter, 1,024-point Hann windowed FFTs with 50% overlap.

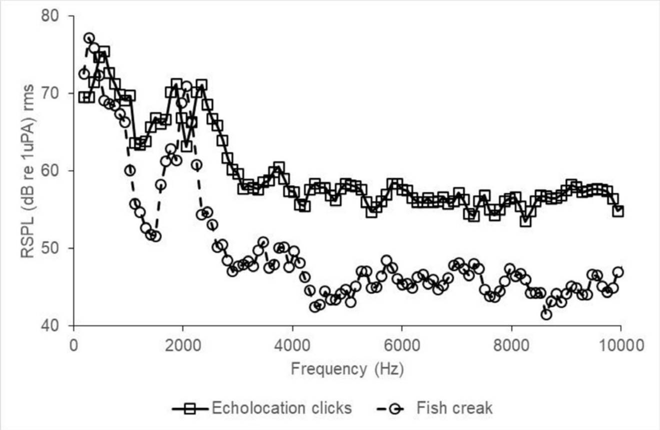


Figure 7. Example comparison of the power spectra of a typical fish creak sound with a typical dolphin echolocation click bout that occurred adjacent to each other, but did not overlap in time. Although the dolphin click train has most of its energy above 10 kHz (not shown), a secondary peak occurs at about 2 kHz which overlaps the peaks of many common unidentified sounds of fishes, such as creaks.

duration (375 ms) and lower in frequency (peak 1,655 Hz; Fig. 5; Table 2). Barks (n = 153) and knocks (n = 158) were also common, but lower in frequency (Table 2, Fig. 5).

Bandwidths of dolphin sounds except for echolocation click trains and whistles were found to overlap broadly with the sounds produced by fishes (Table 2). A comparison of the spectrogram of a dolphin echolocation click bout and fish screech sound that occurred at the same time (Fig. 6), and the relative power spectra of a fish screech that occurred just prior to, but separately from a click bout (Fig. 7), illustrates the overlapping frequency structures. Interestingly, although echolocation clicks had most of their energy above 20 kHz (*e.g.*, Figs 2, 4A), they also contained a secondary low frequency peak at approximately 2 kHz and peak relative amplitudes similar to creak and screech sounds (Figs 6, 7).

Temporal patterns

A total of 8.5 h of recordings were made during over 9 h of boat drifts across six days in July 2012 (Table 1). Echolocation click train bouts were the dominant dolphin sound type averaging 7.69 s min^{-1} total duration (*i.e.*, on average there were 7.69 s of click bouts for each minute of recording) for all drifts combined, and whistles the least averaging 0.10 s min^{-1} (Table 3). Total sounds produced by fishes averaged 0.79 s min^{-1} overall. Prevalence of sound types were highly variable among days and were greatest for all sound types on 21 July (Table 3, Fig. 8, Figs S1-3). Total sound durations of both dolphins and total fishes were an order of magnitude greater during upstream drifts than downstream drifts (Table 3).

All dolphin sound types were significantly correlated with each other (*i.e.*, the time occupied by sound types were correlated), though whistles were only weakly correlated with other dolphin sounds (r values < 0.4, Table 4, Fig. S1). Similarly, all sound types of fishes were significantly correlated with each other, with knock sounds least correlated with creak and bark sounds (Table 4, Fig. S2). All sound types of fishes were significantly correlated with all dolphin sound types except whistles, which were only weakly correlated with screech sounds (r = 0.23, Table 4). Total duration of recorded dolphin sounds was significantly correlated with the total duration of sounds of fishes (Table 4, Fig. 8). Creak and screech sounds had the highest correlations with echolocation click trains and bubble burst sounds (Table 4, Fig. S3).

Discussion

The relationship between dolphin activity and the behavior of their prey fishes in the Amazon is complex and understudied. A positive correlation between the sounds of dolphins and fishes was documented for the first time in the Amazon. Total sounds of fishes were positively correlated with all types of dolphin sounds except for whistles. The strongest correlation was between screech sounds of fishes and click train bouts of dolphins (Table 4). The sounds of fishes and dolphins may be linked for several reasons: 1) "listening dolphin hypothesis" where feeding dolphins home-in on sounds produced by fishes; 2) "predator-related sounds hypothesis" (*sensu* Ladich, 2022) where fishes produce sounds in reaction to a predation attempt; and 3) "ecological niche overlap hypothesis" where the distribution of fishes and dolphins overlap due to similar environmental abiotic and biotic conditions. These hypotheses are not mutually exclusive and may all contribute to the association between the soniferous activities of fishes and dolphins. A lack of correlation between the soniferous activity of dolphins and fishes would suggest that they do not produce sounds in the same general location and time further suggesting a limited role of sound in predator-prey behavior, and/or overlap in the habitat requirements for their sound production behaviors.

Listening dolphin hypothesis

Although little is known of the food habits of dolphins in the Amazon, they are known to prey on a wide variety of fishes in the families: Heptapteridae, Auchenipteridae, Characidae, Serrasalmidae, Pimelodidae, and Prochilodontidae (Aliaga-Rossel et al., 2010). All these groups of fishes are highly soniferous (see on-line data library Looby et al., 2020, 2023), and sounds from hand-held individuals from each group, except Hepatapteridae and Prochilodontidae, were recorded from the study area (example sounds are provided online - Rountree, 2023). Like the common bottlenose dolphin, the selection of soniferous species might

Table 3. Mean and SE total duration per minute of each major sound types of dolphins and fishes by date. For clarity 10 s means were scaled up to 1 min by multiplying by 6. Means of recordings pooled over drift type (upstream and downstream), and grand means are also shown. Burst pulse includes sounds pooled over both short two-component and short with harmonic burst pulses, but excludes other burst pulses. Sample size = total number of 10 s bins for each date and data grouping.

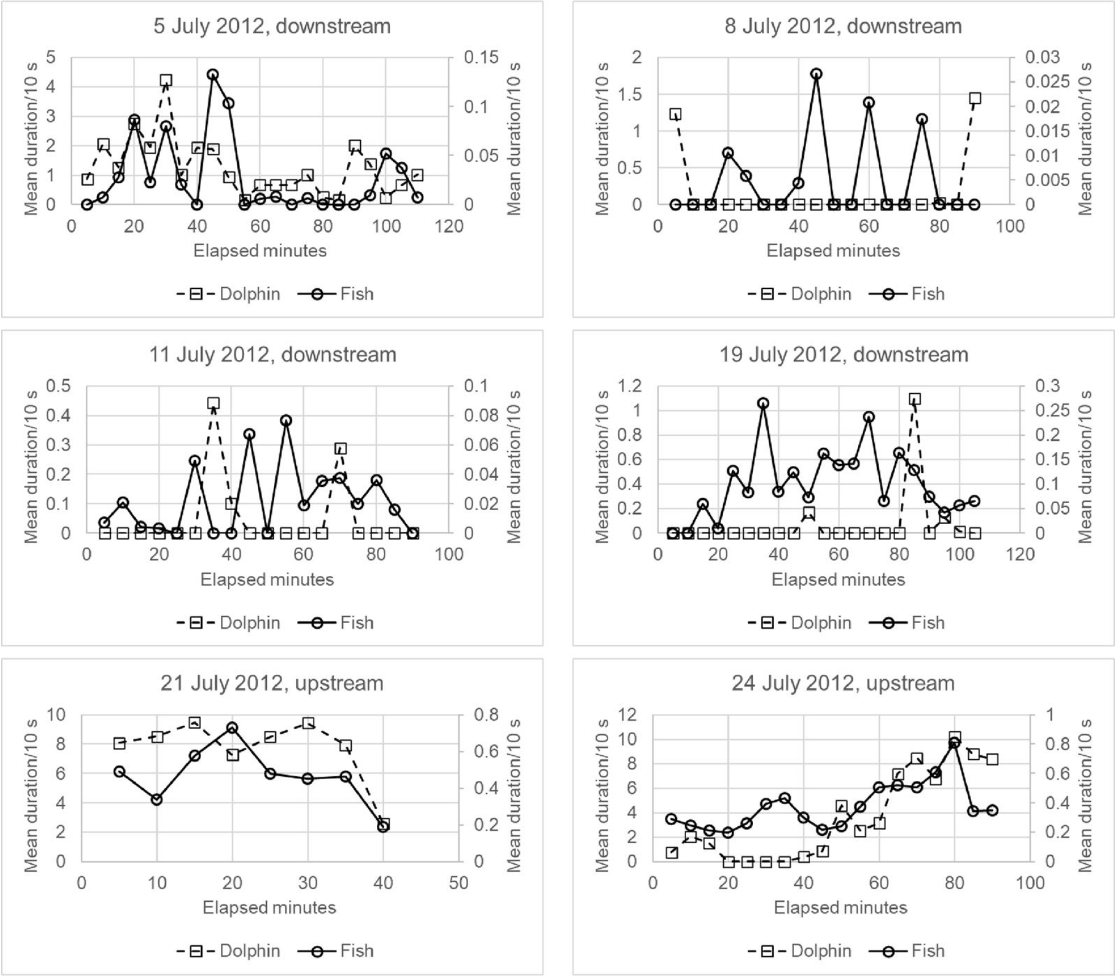
	5 July		**8 July**		**11 July**		**19 July**		**21 July**		**24 July**		**Downstream**		**Upstream**		**Total**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Dolphin sounds																		
echolocation click train	5.90	0.41	0.54	0.20	0.19	0.07	0.41	0.12	41.60	0.98	18.74	0.91	1.96	0.14	25.38	0.80	7.69	0.29
burst pulse	0.16	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.56	0.14	0.02	0.01	0.05	0.01	0.18	0.04	0.08	0.01
bubble burst	1.28	0.28	0.00	0.00	0.00	0.00	0.00	0.00	6.21	1.01	2.10	0.41	0.37	0.08	3.29	0.42	1.08	0.12
whistle	0.04	0.03	0.03	0.02	0.10	0.07	0.00	0.00	0.91	0.19	0.02	0.01	0.04	0.02	0.28	0.06	0.10	0.02
all dolphin sounds	7.57	0.57	0.57	0.21	0.29	0.10	0.41	0.12	49.59	1.45	21.40	1.16	2.47	0.19	29.59	1.03	9.11	0.36
Fish sounds																		
creak - pulsed stridulation	0.04	0.03	0.02	0.01	0.10	0.02	0.23	0.02	1.08	0.08	0.99	0.05	0.10	0.01	1.02	0.04	0.33	0.01
screech - long stridulation	0.06	0.03	0.00	0.00	0.03	0.01	0.33	0.05	1.48	0.14	1.07	0.08	0.11	0.02	1.19	0.07	0.38	0.02
bark - long pulse	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.01	0.09	0.03	0.12	0.02	0.01	0.00	0.11	0.01	0.03	0.00
knock - short pulse	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.01	0.00	0.01	0.00	0.01	0.01	0.01	0.00
all fish sounds	0.17	0.04	0.03	0.01	0.14	0.03	0.61	0.06	2.97	0.23	2.27	0.11	0.25	0.02	2.47	0.10	0.79	0.03
Sample size	662		518		517		617		218		532		2,314		750		3,064	

suggest a hunting strategy of passive listening for active sound producers (Barros & Wells, 1998; Gannon & Waples, 2004; Gannon et al., 2005; Berens McCabe et al., 2010; Pate & McFee, 2012; Ronje et al., 2017). For example, Gannon et al. (2005) suggested that bottlenose dolphins passively and silently listen for sounds of soniferous prey and then use their echolocation to actively track prey during pursuit. Such a strategy might be particularly effective for river dolphins, which occupy habitats of very low visibility.

Predator-related sounds hypothesis

Predator-related sound production has been reported in numerous fishes, although the purpose of the sounds is often uncertain (see review in Ladich, 2022). At least three types of stimuli might cause such behavior: 1) detection of dolphin sounds by the fish; 2) response to a direct attack from a dolphin; and 3) detection of the dolphin by the fish by other means (*e.g.*, visual, or olfactory senses). Previous studies have suggested that some soniferous fishes appear to have developed the ability to detect low frequency bottlenose dolphin sounds and respond with antipredator strategies such as reducing or eliminating sound production (Luczkovich et al., 2000; Remage-Healey et al., 2006; Luczkovich & Keusenkothen, 2008). In contrast, we observed the opposite trend of increased sound production by fishes with increased dolphin sound production.

Many of the soniferous fishes found in the study area are capable of hearing higher frequency sounds of up to 5,000 Hz or more (*i.e.*, those formally known as "hearing specialists" - see reviews: Popper & Fay, 1973; Ladich, 2000; Amoser & Ladich, 2005; Kasumyan, 2005; Popper & Fay, 2011; Ladich & Schulz-Mirbach, 2016; Putland et al., 2019). This suggests that potential fish prey of the river dolphins can detect the burst pulse, bubble burst, and blow sounds which have peak energies at frequencies well within their hearing range. Even fishes formally considered hearing generalists (see reviews above), would likely be able to hear bubble burst and blow sounds (Table 2). In addition, although most energy in echolocation click trains are far above the hearing of most fishes, many click trains do contain energy in the low frequencies well within the hearing range of many of its potential prey species (Figs 6, 7). Although high-frequency hearing is thought to have evolved in many freshwater fish taxa as a response to environmental filtering (*e.g.*, Ladich, 2000; Amoser & Ladich, 2005), it is possible that an evolutionary response to predation by freshwater cetaceans may also have played a role. A precedent for this suggestion is seen in the marine clupeid fishes which have been hypothesized to have evolved their ability to hear high frequency sounds in response to echolocating odontocete predators (Mann et al., 1998). The strong overlap in some fish sounds (Table 2) and the secondary frequency peak of the echolocation click trains (Figs 6, 7) suggest another intriguing possibility that the fish sound is a disturbance response to the detection of the dolphin sound, or perhaps, as with the fast repetitive tick (FRT) sounds of clupeids (Nøttestad, 1998; Hahn & Thomas, 2009), may function to confuse the dolphin's echolocation. Dolphins are known to increase the rate of echolocation clicks, often called "buzzes," when targeting and tracking specific prey individuals (*e.g.*, DeRuiter et al., 2009; Ladegaard et al., 2017). We hypothesize that fish that can hear the dolphin buzzes would have a warning advantage, allowing them a greater chance to evade the predator. Our observation of low frequency content of click train bouts within the prey's hearing range supports that hypothesis.


5 July 2012, downstream

8 July 2012, downstream

11 July 2012, downstream

19 July 2012, downstream

21 July 2012, upstream

24 July 2012, upstream

Figure 8. Comparison of temporal trends of mean total dolphin sound duration per 10 s interval averaged over 5 min (left axis), with that of total fish sounds (right axis). Trends for major sound type categories are presented in the Supplementary Material 1 Figs S1-3. Note different vertical and horizontal scales.

However, a simpler explanation may be that the correlation results from sound production by soniferous fishes being actively pursued or captured by the dolphin, without the necessity of a passive listening strategy by the dolphin, or the ability of the fish to detect dolphin sounds. The sounds of fishes observed during this study were similar to disturbance sounds produced by hand-held fishes during sound auditioning in the study area (Rountree & Juanes, 2020; Rountree, 2023), suggesting that the correlation may be due to the reaction of fish to attempted predation events. Indeed, 31 of 64 species captured in the study area were observed to produce sounds when held in the hand (Rountree, 2023). Under this scenario fishes would most likely be using sounds in an attempt to provoke a startle response in the predator when captured (see review by Ladich, 2022), and thus does not require that the fishes can detect the dolphin sounds, or conversely, that dolphins hunt by listening. If further study confirms a correlation between dolphin feeding activity and predator-related sound production by Amazon fishes, it might be possible to quantify prey capture attempts with PAM methods. Previous studies of marine dolphins have used data on dolphin echolocation buzzes as evidence of predation events (*e.g.*, Castellote et al., 2021, Todd et al., 2022), however we are not aware of studies reporting dolphin predation attempts based on fish sounds themselves. Further, recent studies have also documented a correlation between dolphin activity and fish choruses (Pine et al., 2017, 2018; Cheng et al., 2023), however we did not observe fish chorus activity during our study.

Ecological niche overlap hypothesis

Spatial factors undoubtedly had an effect, as sounds of both dolphins and fishes were more frequent on the last two drifts which were from an upstream location (Tables 1, 2) and passed through a confluence of the Samiria River and a small tributary draining Huisto Lake (Fig. 1) where large concentrations of fishes were migrating with the receding waters. Dolphins in the Amazon are known to congregate at the confluence of rivers to feed (Martin et al., 2004; Gomez-Salazar et al., 2012). The high concentrations of migrating fishes at the confluence would likely also attract concentrations of predatory fishes such as large catfish and piranha. Thus, other potential reasons for habitat-related increases in fish soniferous activity might include increased interactions between prey fishes and predator fishes; differences in fish species composition; increased competition among soniferous species; and location of spawning habitats. Unfortunately, the factors influencing soniferous activity cannot be determined with the preliminary data presented herein. A better understanding of the species and behavioral context that produce specific sounds is needed.

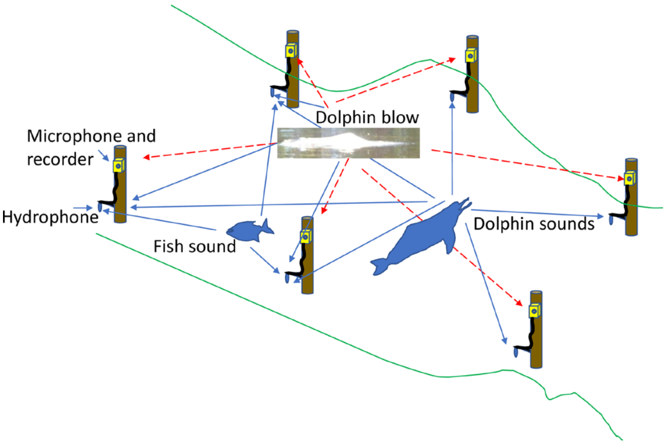


Figure 9. Hypothetical array for holo-soundscape research in the Amazon River. Above water sounds are localized and tracked by an aerial array, while underwater sounds are simultaneously tracked by a linked hydrophone array. Activities creating both aerial and underwater sounds (*e.g.*, dolphin blow and surface behavior) can be tracked by both systems providing information on linkages between the two systems, as well as validation of the source of some unknown sounds.

Future directions

This study illustrates the potential of passive acoustic monitoring (PAM) as a tool to conduct more comprehensive ecological studies in the Amazon that can help elucidate interactions among species and higher taxa. It is important to point out that incidental sounds produced by physiological processes of dolphins and fishes such as breathing, swimming, jumping, internal air movement, etc., can be informative for identifying dolphin occurrence and behavior similar to sounds produced for communication (Rountree et al., 2019, 2020). We agree with Greenhalgh et al. (2020) and Martínez-Medina et al. (2021) in their call for multidisciplinary PAM monitoring in tropical freshwater habitats. We further recommend that investigators conduct PAM surveys of the holo-soundscape (Rountree et al., 2019, 2020; Murchy et al., 2024) in which aerial, terrestrial and underwater sounds are recorded simultaneously. We suggest that georeferenced PAM surveys that incorporate holo-soundscape recordings could examine links between surfacing/breathing behaviors, dolphin sound production, and sounds of fishes and other aquatic organisms (Fig. 9). Hydrophone arrays have long been used to examine spatial-temporal distribution patterns of cetaceans, and are increasingly being used in studies of fishes (*e.g.*, Mouy et al., 2017). Passive acoustic arrays incorporating both microphones and hydrophones for simultaneous spatial location of aerial and underwater sounds hold great promise for freshwater dolphin studies, as well as broader studies in tropical community ecology, and the linkages between terrestrial and aquatic communities.

Documentation of the natural holo-soundscape in relatively remote Amazonian locations such as the PSNR is critically needed before the habitats are irrevocably impacted by anthropogenic noise. Additionally, a critical impediment in the use of PAM to monitor ecological interactions within aquatic communities is that currently most sounds cannot be identified. Although comprehensive digital libraries of known underwater sounds are in various stages of development (*e.g.*, Looby et al., 2020, 2023; Parsons et al., 2023), data for the Amazon (and other tropical freshwater systems) is limited (Looby et al., 2022). Until comprehensive libraries of sound source identities of fishes and other organisms in tropical freshwater systems are available, PAM studies are needed to document the spatial-temporal distribution of specific unidentified sounds, which can then be used to conduct studies to identify those sounds and their associated behavior. Unfortunately, the determination of specific

Table 4. Partial Spearman correlation matrix among major sound types based on total sound duration per 10 s averaged over 5 min periods (N = 105). Values represent the r statistic with an asterisk indicating the significance level (*** = p < 0.001, ** = p < 0.01, * = p < 0.05, ns = not significant).

	Dolphin Sounds					Fish sounds				
	Echolocation Click train	Burst pulse	Bubble bursts	Whistles	Total dolphin	Creak	Screech	Bark	Knock	Total Fish
Dolphin sounds										
Click train	1									
Burst pulse	0.62***	1								
Bubble bursts	0.70***	0.73***	1							
Whistles	0.34***	0.22*	0.30**	1						
Total dolphin	0.99***	0.65***	0.72***	0.38***	1					
Fish sounds										
Creak	0.34***	0.39***	0.49***	0.19ns	0.36***	1				
Screech	0.54***	0.39***	0.47***	0.23*	0.55***	0.52***	1			
Bark	0.36***	0.33***	0.38***	0.04ns	0.35***	0.37***	0.52***	1		
Knock	0.40***	0.27**	0.37***	0.04ns	0.39***	0.24*	0.44***	0.26**	1	
Total fish	0.48***	0.39***	0.50***	0.16ns	0.49***	0.83***	0.83***	0.52***	0.43***	1

sounds is a significant obstacle, until more robust methodologies are available to objectively classify individual sound types with high variability in acoustic characteristics and which occur in differing acoustic environments, resulting in further variation in acoustic characteristics.

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Disclosure statement

The authors report there are no competing interests to declare.

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Supplementary material

Supplementary Material 1

Figure S1. Comparison of temporal trends among dolphin sound types: mean total clicks (left axis), bubble burst (left axis), burst pulses (right axis), and whistles (right axis) per 10 s interval averaged over 5 min.

Figure S2. Comparison of temporal trends among fish sound types: mean total creaks (left axis), screeches (left axis), knocks (left axis), and barks (right axis) per 10 s interval averaged over 5 min.

Figure S3. Comparison of temporal trends among mean total dolphin clicks (left axis), fish creaks (right axis), and fish screeches (right axis) per 10 s interval averaged over 5 min.