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Quiet Signals of Burmeister's Porpoises (*Phocoena spinipinnis*) Recorded in Chile and Peru

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ABSTRACT

Burmeister's porpoises are cryptic and challenging to detect visually. More information on their acoustic signals could facilitate the use of passive acoustic monitoring (PAM) and help to better understand their ecology. Here, clicks were recorded from two different Burmeister's porpoise populations, one in Chile and the other in Peru, using a 4-channel hydrophone array and a single-channel hydrophone recorder. Burmeister's porpoises produced narrowband high-frequency (NBHF) echolocation clicks, typical of all species of porpoises and a few other odontocete species. Feeding buzzes and burst-pulse sounds, likely used for communication, were also recorded. Echolocation click frequency parameters resembled those of harbor porpoises, with a peak frequency of 137 ± 2 kHz and a rms bandwidth of 7 ± 3 kHz, but duration was longer (132 ± 39 μs) than clicks from other NBHF odontocetes. Echolocation click source levels (137 ± 13 dB re 1 μPa rms) and energy levels (100 ± 13 dB re 1 μPa^{2}s at 1 m) were considerably lower than clicks from other NBHF species. The quiet signals used by Burmeister's porpoises affect maximum detection range of prey as well as conspecific communication. Low source levels may prevent porpoises from being detected by predators and aid echolocation in cluttered environments. When designing PAM efforts for this species, low source levels should be considered as the longer durations only partly compensate for the detectability of these signals.

1 | Introduction

The Burmeister's porpoise (*Phocoena spinipinnis*) is a small cetacean found in coastal waters off South America (Peru, Chile, Argentina, and Uruguay; Brownell and Praderi 1984; Clay et al. 2018; Reyes 2018). This range encompasses temperate and sub-Antarctic waters with habitats varying from open coasts to fjords and channels. There is evidence of genetic differences between Peruvian and Chilean-Argentinian porpoises of this species (Rosa et al. 2005), even though most aspects of their population biology as well as behavioral ecology remain poorly understood.

Burmeister's porpoises are classified as "Near threatened" on the IUCN Red List of Species (Félix et al. 2018). Bycatch is the main source of anthropogenic mortality, as Burmeister's porpoises inhabit waters with intense fisheries (García-Cegarra et al. 2024; Lescrauwaet and Gibbons 1994; Mangel et al. 2010; Reeves et al. 2013). Efficient conservation and management actions require implementation of suitable monitoring methods to help understand the status of populations. However, Burmeister's porpoises are difficult to detect visually due to their small size, small dorsal fin, and elusive behavior. An attractive alternative to visually surveying could be passive acoustic monitoring (PAM) using stationary or movable acoustic recorders. For other

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cetaceans such as harbor porpoises (*P. phocoena*), PAM has become a popular technique to obtain data on distribution and abundance (e.g., Amundin et al. 2022).

Porpoises and a few other odontocetes produce narrowband high-frequency (NBHF) echolocation clicks with a peak frequency between 120 and 140 kHz (Møhl and Andersen 1973; Morisaka and Connor 2007; Silber 1991). There are few other natural sounds at these frequencies, making porpoise signals easy to detect and to classify. The NBHF clicks are also easy to discriminate from most other odontocetes, which produce broadband clicks that can contain frequencies from below 20 to above 100 kHz (Au 1993). Species producing NBHF clicks such as Burmeister's porpoises, appear highly suitable to apply PAM methodology to study occurrence and habitat use (Félix et al. 2018; Reyes Reyes et al. 2018).

To perform relevant and efficient PAM studies, it is important to know the full acoustic repertoire of the target species. Our understanding of the acoustic signals of Burmeister's porpoises is limited and stems from one study conducted at the southern limit of their distribution (Reyes Reyes et al. 2018). This study reported that Burmeister's porpoises only produce NBHF clicks. There is currently no information on source levels or signal parameters of buzz signals, which are highly repetitive clicks used by odontocetes during foraging (e.g., Miller et al. 1995; Wisniewska et al. 2014). Burst-pulse signals, which have intraspecific communicative functions in NBHF species, including harbor porpoises as well as delphinids (Herzing 1996; Lammers et al. 2004; Simard et al. 2008; Clausen et al. 2010; Sørensen et al. 2018; Martin et al. 2019), have not been described for this species. Data on different click signal types (i.e., echolocation click trains, buzzes, and burst-pulses) are important for designing efficient PAM methods for Burmeister's porpoises, particularly in areas where they overlap with other NBHF click-producing species.

The aim of this study was to describe the acoustic repertoire of Burmeister's porpoises from two populations in different habitats. Animals were recorded in Chile and Peru, and parameters from different signal types, including source levels, were derived and compared.

2 | Materials and Methods

2.1 | Field Site and Data Collection

Recordings of Burmeister's porpoises were collected during 12 days in January and February 2023 along the Queilén Channel (13 km long and 3–5 km wide, adjacent to Isla Grande

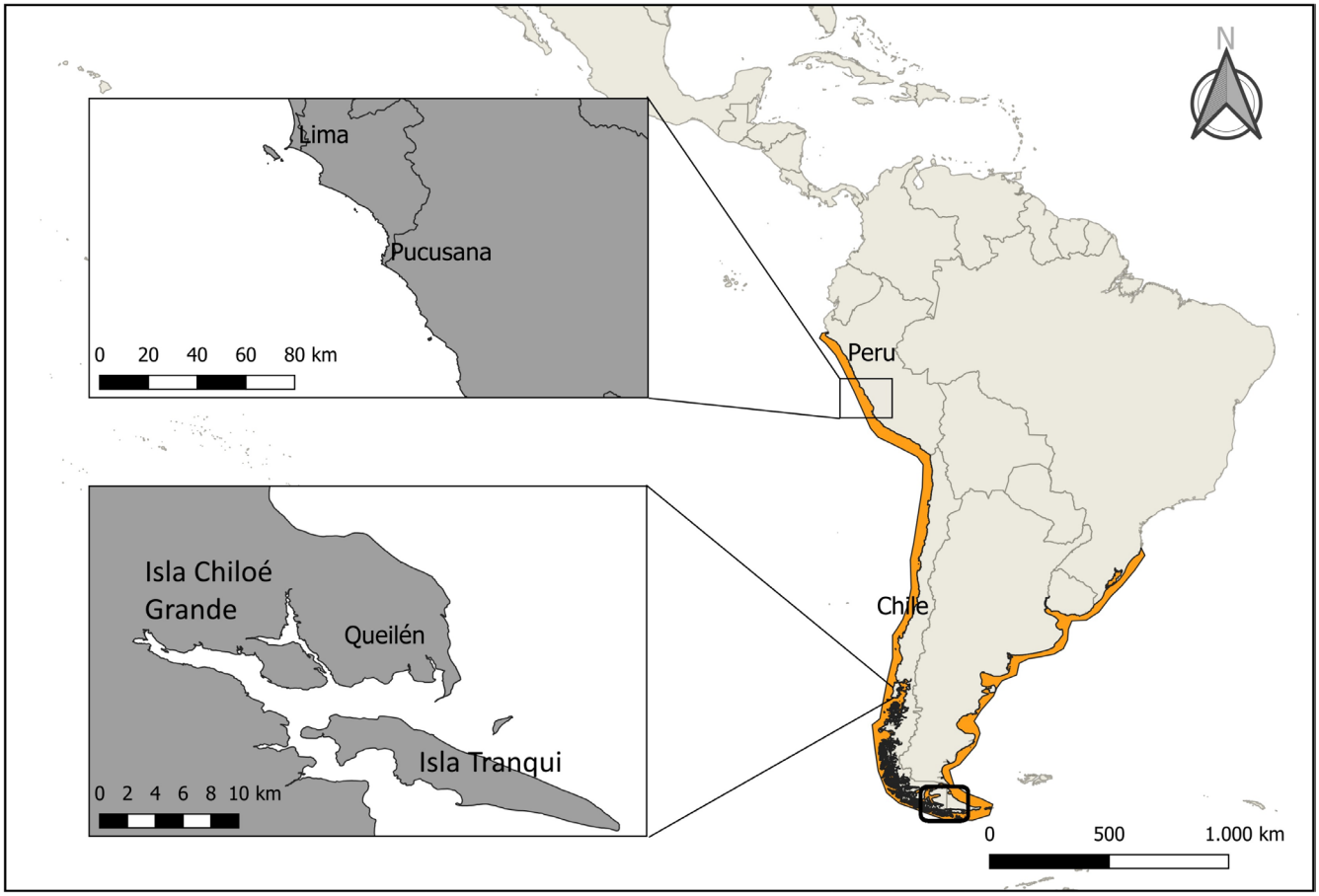

FIGURE 1 | Distribution range of the Burmeister's porpoise in South America shown in orange (from IUCN 2008). Insert maps show the two study areas in Pucusana, Peru (top) and in the Channel of Queilén between Isla Chiloé Grande and Isla Tranqui, Chile (bottom). The recording location of a previous study by Reyes Reyes et al. (2018) is framed with a rectangle.

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de Chiloé, Chile) and 15 days in February 2024 within 50 km from Pucusana, Peru (Figure 1).

For the first four survey days in Chile, recordings were made from a 13 m whale-watching vessel, and for the remaining 8 days from a 5 m wooden skiff. On the whale-watching vessel, searches for cetaceans were conducted during 2-h tours with tourists onboard. In the event of a porpoise sighting, the vessel stopped, the engine was switched off, and the hydrophones were deployed. Visual and/or acoustic searches were made from the skiff by the three-person research team and lasted up to 5 h (hydrophones were deployed while the engine was switched off). In addition to Burmeister's porpoises, the Queilén Channel is often visited by Chilean (*Cephalorhynchus eutropia*) and Peale's (*Cephalorhynchus australis*) dolphins, both of which produce NBHF clicks (Götz et al. 2010; Kyhn et al. 2010; Martin et al. 2024). During Burmeister's porpoise encounters, the area was visually scanned for other cetaceans to assess the risk of confounding the recordings with clicks from other species. Only recordings where porpoises were the only visually sighted cetacean species were used for analysis.

In Peru, daily surveys were made from a 9 m repurposed gillnet fishing vessel. Other odontocetes frequently sighted in this area include dusky dolphins (*Aethalodelphis obscurus*) and common dolphins (*Delphinus delphis*), which both produce broadband clicks instead of NBHF clicks (Au and Würsig 2004; Cosentino et al. 2022). As broadband clicks are easy to distinguish from NBHF clicks, there was no risk of confounding the recordings of Burmeister's porpoises with other species in this area. A team of visual observers was positioned on the bow of the vessel and scanned a 180° area around the track line. Five visual observers rotated positions every half hour, moving from the right observer position to the left observer, followed by two rounds as data recorders, and then a rest period. All cetacean sightings were recorded, including distance and sighting angle from the bow.

2.2 | Acoustic Equipment

In Chile, two different recording systems were used. A 4-channel hydrophone array (SoundTrap 4300HF from Ocean Instruments, New Zealand) equipped with four HTI-96-Min hydrophones (High Tech Inc.) recorded with a 288 kHz sampling rate per channel and 16-bit resolution, and with a 1-pole built-in antialiasing filter. Hydrophones were mounted 50 cm apart on a 1.5 m long hollow PVC rod and deployed horizontally at 2 m depth and 3 m from the vessel using ropes and buoys. During deployments, seafloor depths ranged between 50 and 80 m. Additional recordings were made with a single channel acoustic recorder (SoundTrap 300HF from Ocean Instruments, New Zealand), recording with a 576 kHz sampling rate and with a 1-pole built-in antialiasing filter at 150 kHz. Recordings were digitized with a 16-bit resolution, and settings were configured to include high gain (+12 dB) and a high pass filter to reduce noise below 400 Hz. It was also deployed at 2 m depth and 3 m lateral distance from the boat using ropes, weights, and buoys. Both SoundTrap recorders were deployed immediately after a visual detection of Burmeister's porpoises or during focal scans while searching for individuals.

In Peru, only the SoundTrap 300HF was used. The hydrophone was mounted in a tow-body (TB-48; Barlow Acoustic Gadgets, Analysis and Design, https://barlowagad.com), allowing the device to be towed with a rope extending approximately 180 m behind the boat. The maximum survey speed was limited to 5.5 knots (10 km/h) to keep the hydrophone at depths between 5 and 8 m below the surface. Since only the single-channel SoundTrap 300 HF was used, it was not possible to estimate click source levels.

The frequency-dependent sensitivity of the single-channel and four-channel SoundTraps (with all four HTI hydrophones connected) was determined by relative calibration against a Reson 4014 hydrophone, whose sensitivity was determined using reciprocity calibration (Au and Hastings 2008). The sensitivity within the frequency range 120–144 kHz was tested before and after fieldwork. The clipping level was 176 dB re 1 μPa peak within the frequency range 100–160 kHz for the single-channel SoundTrap, and 183 dB re 1 μPa peak (range 182–183 dB) within 100–140 kHz for the four-channel SoundTrap.

2.3 | Click Extraction and Analysis

All recordings collected in Chile were visually screened through inspection of the spectrogram display in Adobe Audition (Adobe Systems Inc., San Jose, CA) to manually identify porpoise signals. A Blackman-Harris window function was used with a 512-point spectral resolution and a dynamic range of 130 dB. The duration of record viewed varied between 0.5 and 0.8 s.

The recordings made in Peru were processed using a custom NBHF click detector and classifier in PAMGuard (PAMGuard Version 2.02.07, 2023) to identify periods containing NBHF clicks in the recordings. PAMGuard was used exclusively to detect porpoise clicks in the recordings. The digital pre-filter was a four-pole Butterworth band-pass filter at 70–200 kHz, and the digital trigger filter was an eight-pole Butterworth bandpass filter at 100–170 kHz. The signal-to-noise ratio (SNR) threshold for click detection was 10 dB and the maximum click length was 1024 samples, including a pre- and post-period of 40 samples each, and a minimum click separation of 100 samples. The click detector in PAMGuard works by comparing a certain given frequency range (test band) against a control band so that when the amplitude of the signal in the test band surpasses the control band at a given threshold, it will mark a detection. All classification parameters are listed in Table 1. Whenever the signal was louder in frequencies lower than 120 kHz, it was marked as "noise" and discarded. Signals with a high average and/or peak frequency, and in which frequencies above 112 kHz were more intense than frequencies below 100 kHz, were marked as "porpoise" or "possible porpoise" and saved for later inspection. Clicks marked as "porpoise" were more restrictive, while the classification criteria for "possible porpoise" were more relaxed (Table 1).

On multiple occasions, acoustic detections of NBHF signals were identified in PAMGuard when there was no confirmed simultaneous visual sighting. All acoustic detections made in

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TABLE 1 | Parameters used in PAMGuard to classify click detections.

Classification	Energy band			Peak frequency (kHz)	Mean frequency (kHz)
	Test band (kHz)	Control band (kHz)	Threshold (dB)		
Noise 1	70–100	120–150	2	—	—
Noise 2	100–120	120–150	2	—	—
Porpoise	120–160	50–100	10	125–140	120–145
		100–120	6		
Possible porpoise	112–144	60–90	8	118–140	—
		90–110	6		

PAMGuard were carefully reviewed and confirmed through visual inspections of spectrograms in Adobe Audition, using the same methods as with the recordings from Chile, and only good-quality, non-overlapping clicks were selected for further analysis.

Acoustic signals were classified based on their inter-click intervals (ICIs) which were calculated as the time between subsequent clicks following Martin et al. (2018). Three functional groups of NBHF signals were identified based on their ICIs: click trains, buzzes, and burst-pulses (Figure 2). NBHF echolocation click trains had ICIs longer than or equal to 13 ms (Figure 2A). Buzzes were click series with ICIs decreasing from 12 to less than 5 ms and were preceded by longer ICIs (e.g., DeRuiter et al. 2009) as illustrated in (Figure 2B). Burst-pulses were defined as an isolated series of clicks all having ICIs of less than 10 ms (sensu Lammers et al. 2004; Figure 2C).

All series of clicks found in the recordings were saved in separate files and classified according to the quality of the signals. For echolocation click trains, the selection criterion for further analysis was a SNR of at least 20 dB. High quality recordings were scarce for burst-pulse and buzz signals; thus, the selection criteria were reduced to a SNR of at least 10 dB. For the Peruvian recordings, click trains identified in PAMGuard with a SNR ratio above 20 dB were included in the analysis, even those lacking visual confirmation since there were no other NBHF clicking species in the area.

Spectral and temporal click parameters were measured using custom-written routines in MATLAB R2022 (The MathWorks Inc., USA). To measure ICIs, click trains were run through a click detection algorithm which detected and extracted any peaks of the signal envelope separated by more than 0.5 ms. Click detection was supervised for each click train, manually marking any missed detections and removing any spurious detections. The 5th (ICI_{5th}), 50th (ICI_{50th}), and 95th (ICI_{95th}) percentile ICIs were calculated across each click series. Individual click signals were filtered with a four-pole Butterworth bandpass filter between 70 and 250 kHz, and the power spectra were calculated with a 512-point 50% Tukey window centered on the peak envelope of each click. Signal duration (Dur_{10dB}, μs) was determined with a −10 dB amplitude criterion (see Madsen and Wahlberg 2007 for details). The received level (RL, in dB re 1 μPa) was determined as the root-mean-square of the signal within the −10 dB duration. Spectral characteristics, such as peak frequency (F_p, kHz), centroid frequency (F_c, kHz), −3 dB bandwidth (BW_{3dB}, kHz), −10 dB bandwidth (BW_{10dB}, kHz), and root mean square bandwidth (BW_{RMS}, kHz) were quantified from the click with the highest amplitude of each click series, assuming this click was the best representative of an on-axis click (sensu Madsen and Wahlberg 2007; Jensen et al. 2013). Q rms ratio (Q_{RMS}) was calculated as the centroid frequency divided by the RMS bandwidth (see Madsen and Wahlberg 2007 for details).

2.4 | Sound Source Localization and Estimation of Source Parameters

The source level (SL) is defined as the sound pressure level at 1 m range on the acoustic axis (Urick 1983), while the sound pressure level recorded by a hydrophone is termed the received level (RL). The source level is the sum of the transmission loss (TL) and the received level (Urick 1983):

$$SL = RL + TL$$

Villadsgaard et al. (2007) and DeRuiter et al. (2010) found that the transmission loss of 130 kHz harbor porpoise clicks in a shallow-water habitat was well approximated by spherical spreading plus frequency-dependent absorption. Geometric spreading loss may be different in different habitats with different sound velocity profiles, but for porpoise signals we have never observed it significantly deviate from spherical spreading. Assuming spherical spreading, the transmission loss is calculated as:

$$TL = 20\log_{10}(R) + \alpha R,$$

where R is the distance to the source and α is the frequency-dependent absorption constant, which at 135 kHz is 0.04 dB/m (Fisher and Simmons 1977).

The source level of the signal can be estimated if the range between the source and receiver is known. To obtain the range to the calling animal, recordings obtained with the linear array of four hydrophones were used to locate the sound following the methods by Wahlberg et al. (2001) and Madsen and Wahlberg (2007). A signal emitted by the source will arrive at the various receivers with different time delays due to different propagation path lengths from the source to

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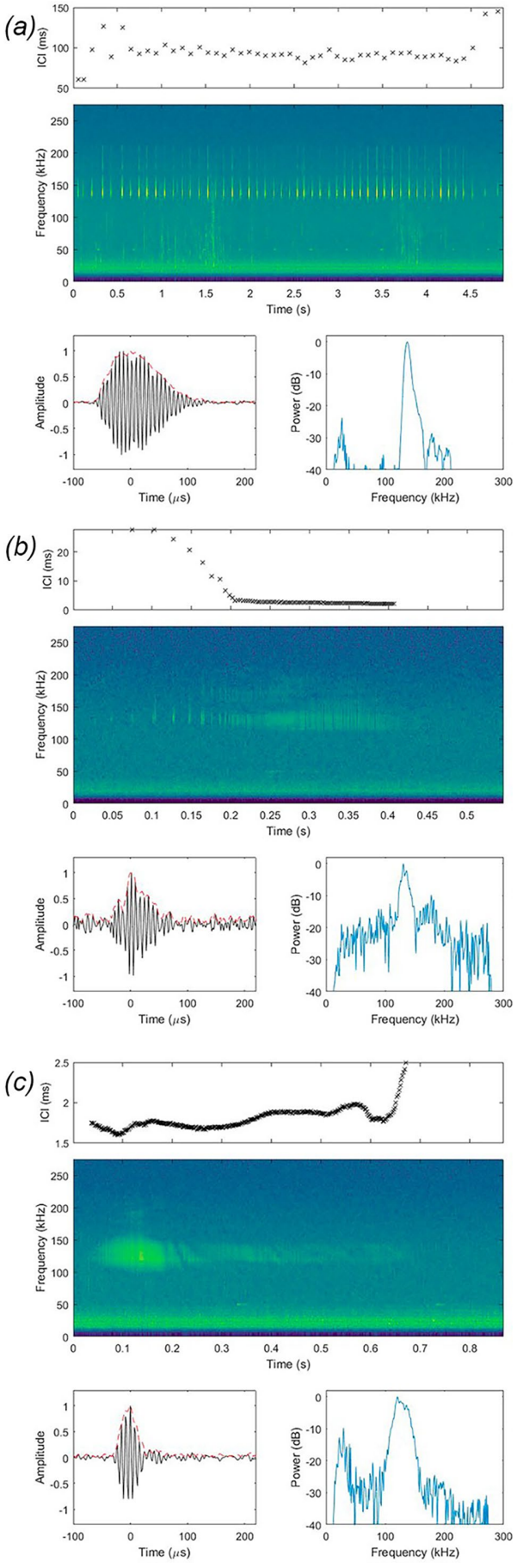

FIGURE 2 | Examples of Burmeister's porpoise click trains and signal types: (a) narrowband high-frequency (NBHF) click train, (b) NBHF buzz, and (c) NBHF burst-pulse. For each signal, the top panel shows inter-click intervals (ICIs) as a function of time, the middle panel is a spectrogram of the click series (FFT size 512, Hamming window, 50% overlap), the bottom left panel is the normalized waveform (solid line) and envelope (dashed line) of a single click extracted from the click series (512 samples, rectangular window), and the bottom right panel is the normalized power spectrum of the extracted click (FFT size 512, rectangular window). Sample rate 576 kHz.

the receivers (Spiesberger 1990, 2001). This time-of-arrival-difference (TOAD) can be used to calculate the distance and angle to the sound source. Recordings made with the hydrophone array were carefully examined. Only signals with maximal relative amplitude on at least one of the two central hydrophones were selected, as these are expected to be close to or on the acoustic axis of the clicking animal (Madsen and Wahlberg 2007). Localizations were calculated using routines written in MATLAB R2022 from the TOADs of the same signal across the different hydrophones using equations in Wahlberg et al. (2001).

As the array had a 144 kHz recording bandwidth limit, it captured the majority of the energy from the porpoise clicks, although it cut off a small portion of the upper frequency content. The single channel recorder had a recording bandwidth of 288 kHz and therefore recorded the entire click bandwidth. When comparing the array and single channel recordings, the array clicks lost 8%–19% of the total click energy, which corresponds to a decrease in estimated source levels of 1–2 dB. The single channel recordings were used to measure spectral and temporal parameters, for which range information was not necessary.

The energy density, which incorporates both signal duration and source level, provides a better understanding of how an animal perceives signals. The energy density was calculated using signals with source level estimates recorded on the linear hydrophone array. The calculation is described in Madsen and Wahlberg (2007) as:

$$E = SL_{RMS} + 10\ \log(T)$$

where E is the energy density; SL_{RMS} is the root mean square of the source level; and T is the duration of the signal.

3 | Results

In Chile, porpoise sightings occurred on five occasions across five survey days during a 12-day survey period. Group size varied from 1–5 individuals, and no dolphins were spotted during Burmeister's porpoise encounters. During visually confirmed encounters with Burmeister's porpoises, the hydrophones were typically deployed when the porpoises were within 50 m of the vessel, as individuals were difficult to find at longer distances. A total of 86 echolocation click trains, 13 buzzes, and 8 burst-pulses from Burmeister's porpoises were found in the recordings. Visual inspection of spectrograms of the single channel

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recordings resulted in 47 echolocation click trains, 10 buzzes, and 7 burst-pulses suitable for signal parameter analysis. For source level estimation, 68 click trains were selected from the 4-channel linear array recordings. Clicks extracted from both the ST300 HF and hydrophone array recordings were all recorded during periods with visual observations of porpoises.

In Peru, porpoises were sighted on 24 occasions during 15 survey days. Group sizes ranged from 1–3 individuals. In PAMGuard, 176 porpoise click trains were identified, of which 74 click trains met the SNR criteria and were included in the analysis. Two burst-pulses were identified in the recordings, but both had a low SNR and were therefore not included in the analysis. Furthermore, buzzes were not identified in the recordings from Peru.

3.1 | Spectral and Temporal Features

All measured clicks had a clear NBHF structure. Burmeister's porpoise echolocation clicks from Chile had an average (±SD) peak and centroid frequency of 137 (±2) kHz and 139 (±2) kHz, respectively, and were very similar to the Peruvian clicks ($F_p = 135 \pm 3$ kHz; $F_c = 137 \pm 3$ kHz) (Table 2). Buzz clicks had similar peak and centroid frequencies ($F_p = 136 \pm 2$ kHz; $F_c = 137 \pm 1$ kHz) and burst-pulse clicks a slightly lower average frequency emphasis ($F_p = 131 \pm 8$ kHz; $F_c = 134 \pm 3$ kHz) (Table 2). For echolocation clicks, the average RMS bandwidth was 7 (±3) kHz from Chile and 10 (±4) kHz from Peru (Table 2). The RMS bandwidth was 13 (±3) kHz for buzzes and 16 (±6) kHz for burst-pulses recorded in Chile. Echolocation click average duration was 132 (±39) μs from Chile and 109 (±36) μs from Peru. Click duration was shorter for buzzes (69 ± 10 μs) and burst-pulses (59 ± 12 μs) recorded in Chile (Table 2).

3.2 | Source Level Estimation

Source levels were estimated from 68 click trains recorded using the linear array. Of these, only 30 click trains contained clicks that met the on-axis criteria for inclusion in source level estimation. Click trains were estimated at distances ranging from 2 to 42 m from the array. The average SL was 140 (±13) dB re 1 μPa rms (range 115–158 dB) (Table 3). Assuming that measured source level clicks were recorded from porpoises inspecting the recording unit, we estimated how the porpoises adjusted SL with range. There was a 25 log (R) relationship between the estimated range and SL of the clicks measured from the hydrophone array (Figure 3).

For the 30 presumed on-axis clicks measured from the array, the average energy density was 100 (±13) dB re 1 μPa^{2}s at 1 m (range 77–119 dB).

4 | Discussion

Our study contributes to a more thorough description of Burmeister's porpoise clicks throughout the species' distribution range. Complementing Reyes Reyes et al. (2018) who recorded Burmeister's porpoises from their southern-most habitats in the Beagle Channel (Argentina) (54.8° S), we contribute recordings from the Chiloé archipelago (Chile) (42.8° S) and Pucusana (Peru) (12.5° S) more than 5000 km further north. Across these geographically and environmentally diverse locations, echolocation click frequency parameters (F_c and F_p) and bandwidth parameters (BW_{RMS}, BW_{3dB} and BW_{10RMS}) were highly similar, even though there was a tendency for higher maximum peak and centroid frequency values in the most southern recording location. Burmeister's porpoise peak and centroid frequency parameters were similar, but bandwidth

TABLE 2 | Signal parameters of NBHF signals produced by Burmeister's porpoises.

	NBHF click train	NBHF click train	NBHF buzz	NBHF burst-pulse
	Peru $n = 74$	Chile $n = 47$	Chile $n = 10$	Chile $n = 7$
Source parameters	**Mean ± SD [range]**	**Mean ± SD [range]**	**Mean ± SD [range]**	**Mean ± SD [range]**
ICI_{5th} (ms)[a]	75 ± 38 [19–171]	88 ± 33 [16–146]	8 ± 2 [2–11]	5 ± 2 [2–8]
ICI_{50th} (ms)[a]	93 ± 40 [28–180]	108 ± 34 [22–161]	9 ± 2 [2–11]	6 ± 3 [2–8]
ICI_{95th} (ms)[a]	126 ± 45 [46–248]	141 ± 31 [30–214]	11 ± 2 [4–12]	7 ± 3 [2–10]
F_P (kHz)[b]	135 ± 3 [126–141]	137 ± 2 [132–142]	136 ± 2 [130–138]	131 ± 8 [119–140]
F_C (kHz)[b]	137 ± 3 [129–153]	139 ± 2 [136–145]	137 ± 1 [134–139]	134 ± 3 [127–136]
BW_{rms} (kHz)[b]	10 ± 4 [4–26]	7 ± 3 [4–17]	13 ± 3 [10–20]	16 ± 6 [8–26]
BW_{3dB} (kHz)[b]	7 ± 3 [2–18]	6 ± 2 [2–11]	8 ± 5 [3–19]	12 ± 7 [2–21]
BW_{10dB}(kHz)[b]	18 ± 13 [8–75]	13 ± 6 [3–37]	26 ± 12 [14–55]	30 ± 5 [24–37]
Q_{RMS}[b]	15 ± 6 [6–31]	21 ± 6 [8–38]	11 ± 3 [7–14]	10 ± 4 [5–17]
Dur_{10dB} (μs)[b]	109 ± 36 [39–202]	132 ± 39 [64–235]	69 ± 10 [50–88]	59 ± 12 [40–73]

Note: The mean ± standard deviation and the range (in brackets) are reported for each parameter. ICI5th, ICI50th, and ICI95th represent the 5th, median (50th), and 95th percentile inter-click intervals, respectively. F_P corresponds to peak frequency; F_C is centroid frequency; BW_{3dB} is 3 dB bandwidth; BW_{10dB} is 10 dB bandwidth; BW_{RMS} is root mean square bandwidth; Q_{RMS} is the Q-ratio, calculated as F_C/BW_{RMS}; and Dur_{10dB} is 10 dB click duration.
[a]Indicates parameters measured across a click series.
[b]Indicates parameters measured for an individual click.

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TABLE 3 | Biosonar parameters of echolocation clicks of the Burmeister's porpoise (*Phocoena. spinipinnis*), the harbor porpoise (*P. phocoena*), and the vaquita (*P. sinus*).

	P. spinipinnis **(This study[a], Reyes Reyes et al. 2018[b])**			***P. phocoena*** **(Kyhn et al. 2013)**		***P. sinus*** **(Silber 1991)**
Source parameters	**Chile[a] *n* = 47**	**Peru[a] *n* = 74**	**Argentina[b] *n* = 481[c]**	**Denmark *n* = 246**	**British Columbia *n* = 77**	**Mexico *n* = 43[c]**
ICI_{50th} (ms)	108 ± 35 [22–161]	93 ± 40 [28–180]	51 ± 26[d] [34–114]	—	—	103 ± 23[d] [19–144]
F_P (kHz)	137 ± 2 [132–142]	135 ± 3 [126–141]	135 ± 2 [133–164]	137 ± 6 [112–145]	140 ± 1 [137–143]	133 ± 4 [128–139]
F_C (kHz)	139 ± 2 [136–145]	137 ± 3 [129–153]	144 ± 5 [138–157]	136 ± 3 [126–144]	141 ± 2 [138–148]	—
BW_{rms} (kHz)	7 ± 3 [4–17]	10 ± 4 [4–26]	—	10 ± 2 [6–17]	8 ± 2 [5–14]	—
BW_{3dB} (kHz)	6 ± 2 [2–11]	7 ± 3 [2–18]	8 ± 0 [6–10]	17 ± 5 [5–36]	8 ± 3 [3–19]	17 ± 5 [11–28]
BW_{10dB} (kHz)	14 ± 6 [7–37]	18 ± 13 [8–75]	14 ± 4 [10–21]	—	—	—
Dur_{10dB} (μs)	132 ± 39 [64–235]	109 ± 36 [39–202]	133 ± 2 [131–162]	54 ± 8 [35–98]	88 ± 29 [48–189]	136 ± 41[f] [79–193]
SL_{10dB} (dB re 1 μPa rms)	140 ± 13[e] [115–158]	—	—	189 ± 5 [169–199]	178 ± 4 [170–189]	—
E_{10dB} (dB re 1 μPa^2s)	100 ± 13[e] [77–119]	—	—	135 ± 5 [114–144]	125 ± 4 [116–137]	—

Note: The mean ± SD is reported, and the range is provided in brackets below. ICI50th represents the median (50th) percentile interclick intervals. The remaining parameters were extracted from the highest amplitude click within a click train. F_P corresponds to peak frequency; F_C, centroid frequency; BW_{RMS}, root mean square bandwidth; BW_{3dB}, 3dB bandwidth; BW_{10dB}, 10dB bandwidth; Q_{RMS} is the Q-ratio, calculated as F_C/BW_{RMS}; and Dur_{10dB}, 10dB click duration.

[a]Refers to this study.

[b]Refers to the results by Reyes Reyes et al. 2018.

[c]*n* refers to all individual clicks with sufficient SNR ratio.

[d]Data represent measurements over all ICIs.

[e]Parameters extracted from *n* = 30 clicks.

[f]Duration of clicks measured with 20dB criterion.

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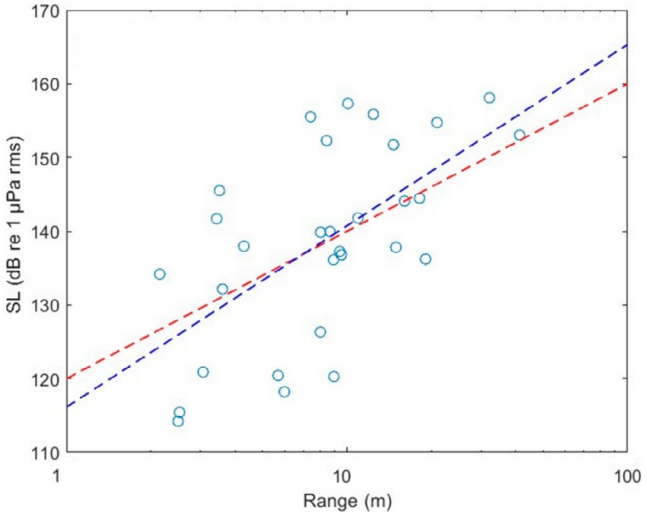

FIGURE 3 | Range between Burmeister's porpoise clicks and the array as a function of the source level (SL). The red stippled line is the spherical spreading model SL = 120 + 20 log (Range), and the blue stippled line is the linear regression equation of the data SL = 116 + 25 log (Range), with $R^2 = 0.37$.

was lower compared to harbor porpoises (Kyhn et al. 2013) and their closest relative, the vaquita (*Phocoena sinus*; Silber 1991; Table 3). It is not clear if the differences between populations and species are true differences or artifacts caused by different recording and analysis methods across studies.

The source level of Burmeister's porpoises was 38–49 dB lower than that reported for harbor porpoises (Table 3, Villadsgaard et al. 2007; Kyhn et al. 2013). The duration of Burmeister's porpoise clicks was similar across the three recording locations, as well as for vaquita clicks (though the latter were measured using a 20 dB duration metric). The duration of Burmeister's porpoise clicks was significantly longer than the duration of harbor porpoise clicks (Kyhn et al. 2013). It is possible that Burmeister's porpoises produce longer clicks partly to compensate for the low source level, in order to elevate the energy content of clicks and returning echoes. Burst-pulse and buzz clicks were much shorter, even though it is important to note that these measurements may have been biased as clicks were selected with a lower SNR ratio. However, shorter duration in burst-pulse and buzz clicks could also be explained by such signals being used at close range, where the reduced energy content may be of less concern.

We assumed a spherical spreading sound transmission to be the best approximation to calculate SL of the recorded porpoises as demonstrated by Villadsgaard et al. (2007) and DeRuiter et al. (2010). Transmission loss can vary significantly in different habitats. At long ranges, transmission loss may be less due to interference between surface and bottom reflected sound paths, even though such effects have not been observed for porpoise signals in typical porpoise habitats. If transmission loss is smaller at long ranges than spherical, the estimated source levels would be lower than the ones reported here.

One possible reason Burmeister's porpoise clicks are low intensity may be to avoid unwanted returning echoes (i.e.,"clutter") when echolocating in shallow waters, or waters with many obstacles. A similar explanation has been suggested for other species where large differences in source levels have been observed. Ganges river dolphins (*Platanista gangetica*) produce lower source levels than marine dolphins of similar size (Jensen et al. 2013), and harbor porpoises echolocate at lower source levels in the Wadden Sea compared to Inner Danish waters and British Columbia (Dähne et al. 2020). In addition, trained harbor porpoises drastically reduced their source levels when moved to a more reverberant pool (Ladegaard and Madsen 2019). This adjustment of signal intensity to different habitats has been studied in echolocating bats, which decrease their signal amplitude in increasingly cluttered environments (Brinkløv et al. 2010; Jakobsen et al. 2013; Wahlberg and Surlykke 2014). More studies are needed on the acoustic environments of these species, including those of Burmeister's porpoises, to fully understand to what extent clutter and reverberation may affect the animal's choice of source levels.

Another reason for reducing source level could be that if porpoises target fish species that can hear ultrasound, it may be advantageous to lower the source level of outgoing clicks during predation attempts. However, only a handful of fish species, all of the family Alosidae, have so far been shown to be able to hear ultrasound (Mann et al. 2001), and it is unknown if any of these species would have a geographic overlap and be consumed by Burmeister's porpoises.

It has been proposed that the use of NBHF signals evolved as an adaptation to avoid detection by predators such as orcas (*Orcinus orca*; Morisaka and Connor 2007), which cannot hear well above 110 kHz (Branstetter et al. 2017; Szymanski et al. 1999). This idea has been challenged by recent studies suggesting that NBHF signals in porpoises evolved before orcas, and now extinct odontocetes may have provided similar pressures (Galatius et al. 2019). Burmeister's porpoises may be preyed upon by orcas and harassed by other delphinids (as known to occur between bottlenose dolphins and harbor porpoises; Ross and Wilson 1996). Using low click intensity levels could reduce the risk of being detected by delphinids. However, this strategy comes at a cost of reduced detection ranges, making it more difficult for porpoises to detect objects and navigate their environment effectively, as well as communicate with conspecifics. Even though Burmeister's acoustic signal echoes are longer than those from harbor porpoises, the energy content is ~30 dB less (Kyhn et al. 2013) and therefore detection distances to gill nets, for example, will be shorter than for harbor porpoises. Burmeister's porpoises may therefore be extremely vulnerable to bycatch in gill nets (García-Cegarra et al. 2024; Ortiz-Alvarez et al. 2025).

The 25 log (R) relationship observed between range and source level in Burmeister's porpoise clicks is close to the 20 log (R) relationship found in other odontocetes (e.g., Au and Benoit-Bird 2003; Villadsgaard et al. 2007; Kyhn et al. 2013). This suggests that Burmeister's porpoises were likely actively investigating the recording gear during data collection. With the strict on-axis criteria used in this study, we are confident that acoustic parameters are representative of recordings made close to the animal's acoustic axis. In our case, after locating the sound source of the clicks detected with the hydrophone array,

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the maximum estimated distance at which clicks were detected was 42 m, possibly indicating small detectable ranges to these animals from passive acoustic monitoring (PAM) equipment.

A comprehensive characterization of Burmeister's porpoise clicks is essential for developing PAM methodologies for this species. However, their exceptionally low source levels present a challenge, as their signals will be more difficult to detect using acoustic monitoring techniques. Addressing this limitation will be critical for improving population assessments and conservation efforts for Burmeister's porpoises. When using PAM techniques for this species, surveys need to be made with finer coverage than for species with higher source levels, and stationary data loggers should be placed closer together to obtain the same spatial coverage.

5 | Conclusions

Burmeister's porpoises produce NBHF signals similar in frequency content to other porpoise species. However, Burmeister's porpoise clicks have a longer duration and lower intensity than other NBHF species. These could be mechanisms to avoid detection by predators and to improve echolocation performance in cluttered environments. Low source levels recorded in this study question the distance at which this species can echolocate, though additional acoustic data are needed from individuals recorded in open water areas to better understand this relationship. The data presented here may be used to develop passive acoustic monitoring methods for this species.

Author Contributions

Ruth Ortés-Villauriz: investigation, writing – original draft, conceptualization, funding acquisition, methodology, formal analysis, data curation, visualization, software. **Magnus Wahlberg:** supervision, writing – review and editing, conceptualization, validation, funding acquisition, resources, project administration, methodology. **Daniel A. Gómez-Lobo:** methodology. **Joanna Alfaro-Shigueto:** resources, writing – review and editing. **Sonja Heinrich:** writing – review and editing, resources. **Jeffrey C. Mangel:** writing – review and editing, resources. **Clara Ortiz-Alvarez:** resources, writing – review and editing. **Morgan J. Martin:** conceptualization, methodology, validation, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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