

RESEARCH ARTICLE

Characterizing Chilean blue whale vocalizations with DTAGs: a test of using tag accelerometers for caller identification

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ABSTRACT

Vocal behavior of blue whales (*Balaenoptera musculus*) in the Gulf of Corcovado, Chile, was analysed using both audio and accelerometer data from digital acoustic recording tags (DTAGs). Over the course of three austral summers (2014, 2015 and 2016), seventeen tags were deployed, yielding 124 h of data. We report the occurrence of Southeast Pacific type 2 (SEP2) calls, which exhibit peak frequencies, durations and timing consistent with previous recordings made using towed and moored hydrophones. We also describe tonal downswept (D) calls, which have not been previously described for this population. As being able to accurately assign vocalizations to individual whales is fundamental for studying communication and for estimating population densities from call rates, we further examine the feasibility of using high-resolution DTAG accelerometers to identify low-frequency calls produced by tagged blue whales. We cross-correlated acoustic signals with simultaneous tri-axial accelerometer readings in order to analyse the phase match as well as the amplitude of accelerometer signals associated with low-frequency calls, which provides a quantitative method of determining if a call is associated with a detectable acceleration signal. Our results suggest that vocalizations from nearby individuals are also capable of registering accelerometer signals in the tagged whale's DTAG record. We cross-correlate acceleration vectors between calls to explore the possibility of using signature acceleration patterns associated with sounds produced within the tagged whale as a new method of identifying which accelerometer-detectable calls originate from the tagged animal.

KEY WORDS: *Balaenoptera musculus*, Acoustic behavior, DTAG, Downsweep call, D call, Cross-correlation

INTRODUCTION

The Gulf of Corcovado, Chile, is home to a relatively newly discovered population of approximately 303 blue whales, *Balaenoptera musculus* (Linnaeus 1758), a species hunted to near extinction off the coast of Chile and notoriously slow to recover (Hucke-Gaete et al., 2004; Branch et al., 2004; Williams et al.,

2011). We refer to this group of Southeast Pacific blue whales as 'Chilean blue whales', in accordance with other studies. A number of previous research efforts in this important feeding ground for Chilean blue whales have focused on their ecology (Branch et al., 2007a; Williams et al., 2011), genetics (LeDuc et al., 2007), acoustic behavior (Buchan et al., 2014, 2015), and potential for anthropogenic impacts (Colpaert et al., 2016). We used non-invasive digital acoustic recording tags (DTAGs; Johnson and Tyack, 2003) outfitted with hydrophones, accelerometers, magnetometers and depth sensors to study communication and diving behavior of individual whales (Bocconcelli et al., 2016).

Previous passive acoustic recordings in the Southeast Pacific have discovered two call types (Cummings and Thompson, 1971; Stafford et al., 1999; Buchan et al., 2014), but the vocal repertoire of this population remains poorly understood. Geographical distribution and genetic evidence suggest that Chilean blue whales are distinct from Antarctic blue whales (Branch et al., 2007b; LeDuc et al., 2007). Chilean blue whales have been described as intermediate in size to Antarctic (*Balaenoptera musculus intermedia*) and pygmy (*Balaenoptera musculus breviceauda*) blue whales (Branch et al., 2007a). Following from this anatomical description, the first goal of our study was to characterize the blue whale vocal repertoire in the Gulf of Corcovado area, especially to test if the acoustic parameters of Chilean blue whale vocalizations are intermediate to those of other Southern Hemisphere populations.

Our second goal was to test the feasibility of using high-resolution DTAG accelerometers to identify low-frequency calls produced by the tagged animal, a method described by Goldbogen et al. (2014) for fin whales. The ability to accurately assign vocalizations to individual whales would greatly enhance studies of behavior and communication, and could also enable measurement of individual call rates, which are necessary for estimating population densities from passive acoustic data (e.g. Marques et al., 2013). The study by Goldbogen et al. (2014) demonstrated that accelerometers on the surface of fin whales could detect vibrations synchronous with low-frequency calling and found that accelerometer signals were not consistent with particle acceleration of calls coming from other whales; however, it remains unclear if sound pressure waves from other individuals can excite detectable acceleration signals in the tagged animal. In this study we used cross-correlation of acoustic and acceleration signals to test the hypothesis that calls from nearby whales may also register acceleration signals that can be detected by the DTAG accelerometer.

MATERIALS AND METHODS

This work was conducted under Chilean research permit PINV 38-2014 Ballena Azul, Golfo Corcovado, from the Ministerio de Economía, Fomento y Turismo, Subsecretaría de Pesca y Acuicultura. Field efforts were carried out during February and March of 2014, 2015 and 2016 in the Gulf of Corcovado, Chile.

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DTAGs were attached to the dorsal regions of blue whales using an 8 m carbon fiber pole and were held on with four suction cups (Johnson and Tyack, 2003; Bocconcelli et al., 2016). DTAGs were programmed to release after periods of up to 24 h. Tags were equipped with very high frequency (VHF) transmitters to track the whales during deployments and to retrieve the tag post-release. The tags contained two hydrophones programmed to sample at either 120 or 500 kHz, as well as depth sensors and 3-axis accelerometers and magnetometers, which sampled at either 200 or 500 Hz.

Acoustic data were serially downsampled to 1000 Hz with a low-pass anti-aliasing filter and recordings were audited manually by inspection of spectrograms [256-point fast Fourier transform (FFT), Hamming window, 90% overlap]. Call types were categorized visually, following categorizations made in the literature (e.g. Oleson et al., 2007; Buchan et al., 2014). Signal start and end times were selected by hand. Measured parameters for all calls included duration of the middle 97% of signal energy (Madsen et al., 2004), peak frequency and center frequency. Start and end frequencies of downswept (D) calls were calculated from signal contours that traced peak frequencies along a spectrogram.

In order to examine accelerometer signals associated with acoustic signals, aligned audio and accelerometer spectrograms were visually compared using custom MATLAB software (all scripts are available at: https://github.com/msaddler/MRS/tree/master/MS_DTAG_code). Accelerometer signals for downswept calls were high-pass filtered above 20 Hz (sixth order Butterworth filter) and for all other call types above 5 Hz (sixth order Butterworth filter) to reduce low-frequency noise. Downswept calls were filtered with a higher cut-off frequency because their acoustic signals contained no energy below 20 Hz. In order to quantitatively determine if accelerometer signals were associated with acoustic signals, audio data were further downsampled to the accelerometer's sampling rate. The downsampling process included a low-pass eighth order Chebyshev Type I IIR filter to avoid aliasing. Peak-to-peak and root mean square amplitudes were calculated from concurrent acoustic and acceleration signals (Goldbogen et al., 2014). Feeding lunges were detected in the DTAG record primarily as rapid decelerations in the speed calculated from flow noise, although body rolls were also taken into account (Goldbogen et al., 2006).

As accelerometer signals were very often dominated by low-frequency noise that overlapped with blue whale signals, we used cross-correlation to examine the phase match between concurrent acceleration and audio signals. Acoustic signals were cross-correlated with the concurrent acceleration signals from each of the three orthogonal accelerometer axes (x , y and z in the DTAG's frame) in order to determine if an acoustic signal was also detected on the accelerometer. Acceleration vectors for all possible pairs of calls in the same tag deployment were also cross-correlated to look for consistent acceleration patterns that might identify calls coming from the same source (e.g. the tagged whale). To eliminate effects of signal amplitudes, each acoustic and accelerometer signal was first normalized by subtracting the signal's mean and dividing by its standard deviation. Normalized signals were then cross-correlated using the MATLAB function *xcorr* (Signal Processing Toolbox). The peak value of the cross-correlation function was used to quantify the phase match between two signals. The normalized peak cross-correlation coefficient of two discrete time series f and g is calculated according to the equation:

$$\text{Coeff} = \max \left[\frac{1}{\sqrt{N_f N_g}} \text{xcorr} \left(\frac{f - \bar{f}}{\sigma_f}, \frac{g - \bar{g}}{\sigma_g} \right) \right], \quad (1)$$

where N_f and N_g are the lengths of the vectors f and g , respectively. Similar cross-correlation methods have been applied in acoustic signal localization contexts (Spiesberger and Fristrup, 1990; Omologo and Svaizer, 1994).

A cross-correlation peak coefficient threshold was used to decide if synchronous audio and acceleration signals were considered correlated or not. The threshold was determined by visually inspecting cross-correlation functions of aligned audio and accelerometer signals for the presence of a strong peak. The threshold was supported by an observed bimodal distribution of peak coefficients and by examining accelerometer spectrograms to confirm that correlated accelerometer signals were visible.

Acceleration vectors of all possible pairs of D calls in a single deployment were cross-correlated across all three accelerometer axes and the resulting peak coefficients were calculated. The same threshold value from the audio-acceleration cross-correlations was used to determine which calls in the deployment were designated as having highly correlated acceleration signals. The single group of calls in one deployment with highly correlated acceleration signals across all three axes are referred to as 'intra-correlated' calls. Peak cross-correlation coefficients from each distinct pair of D calls were first averaged across the three accelerometer axes and then sorted into three categories: those between two members of the intra-correlated group, those between two non-members of the intra-correlated group, and those between a member and a non-member of the intra-correlated group. A Kruskal–Wallis test was used to determine if the peak coefficients from cross-correlating acceleration vectors between all pairs of D calls came from the same distribution. *Post hoc* analysis was performed using a multiple comparison test with the Dunn–Šidák correction in order to test for significant differences between the means of coefficient categories.

In order to assess if the high correlation of accelerometer signals in the intra-correlated group was due to acceleration signals associated with vocalizations rather than with non-acoustic behaviors, the cross-correlation analysis was repeated with accelerometer noise signals. Sample noise signals with durations equal to the D calls were taken immediately preceding and following each D call. All possible pairs of pre- and post-call noise signals were cross-correlated with one another. Acoustic signals from all D calls in a single deployment were also pairwise cross-correlated as a positive control. Cross-correlating acoustic signals assessed whether the D calls were sufficiently stereotyped to reasonably expect that their associated accelerometer signals might also be correlated.

RESULTS

A total of 17 tags were deployed during February and March of 2014, 2015 and 2016 in the Gulf of Corcovado (Fig. 1). From the 124 h combined tag record, we found that the primary call types of this population are Southeast Pacific type 2 calls (SEP2 calls, described by Stafford et al., 1999 and Buchan et al., 2014) and tonal downswept calls (D calls, described by Thompson et al., 1996, McDonald et al., 2001 and Oleson et al., 2007), although we also recorded numerous highly variable vocalizations (Fig. 1). The variable sounds most often had relative broadband frequency emphasis (between 40 and 300 Hz), were not stereotyped, sounded grunt-like, and are not analysed further here. We found a great deal of variation in the number and types of calls recorded between individual tag deployments. Three tag deployments that lasted at least one hour recorded no discernable vocalizations (Fig. 1). For 10 of the 17 deployments, the tagged whale was at least loosely associated with one or more other blue whales. Three tags (bm14_082a, bm15_048a and bm15_054a) were deployed on

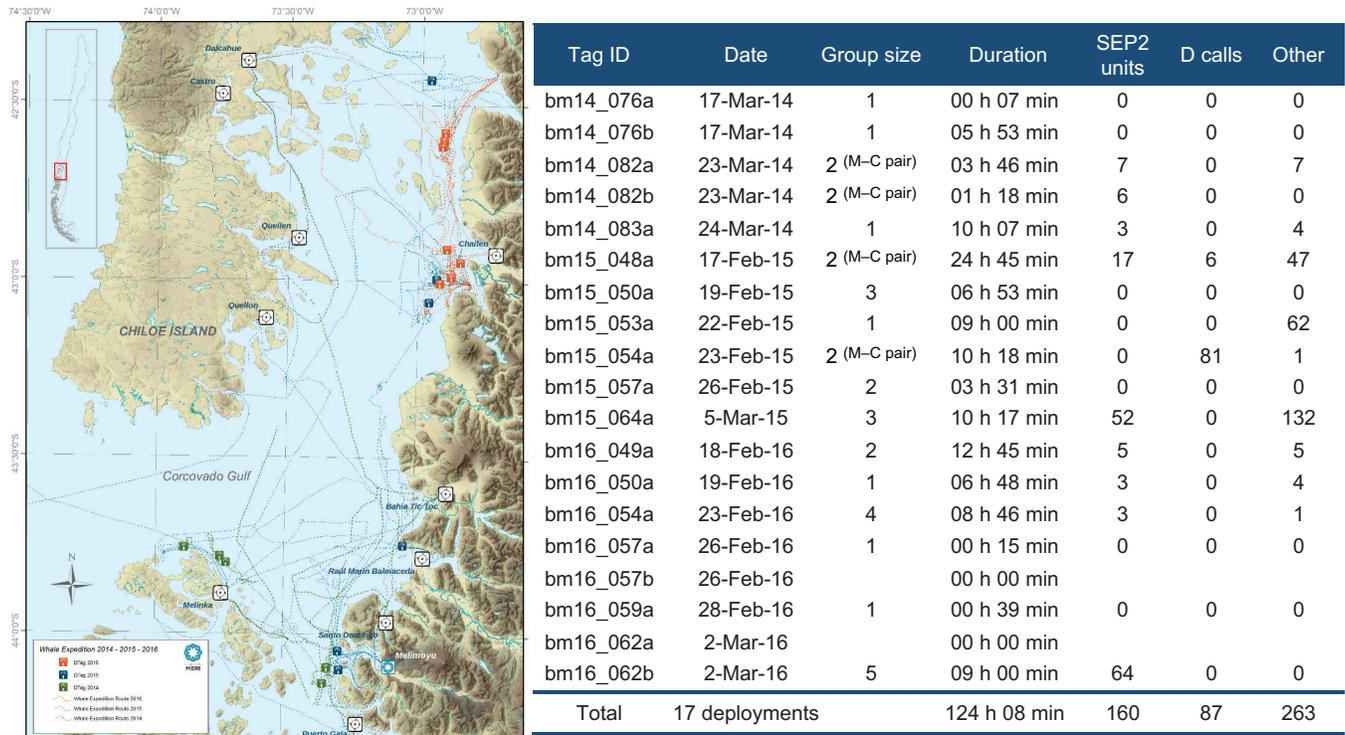


Fig. 1. Map of study region and summary of DTAG deployments. Orange, blue and green markers indicate where recording tags were deployed on blue whales (*Balaenoptera musculus*) in the austral summers of 2014, 2015 and 2016. White markers show locations of night anchorages. In the summary table, the 'Other' column represents highly variable, short duration sounds. The 'M-C pair' superscripts in the 'Group size' column indicate mother–calf pairs. Figure from Bocconcelli et al. (2016).

mothers closely associated with a calf, and one tag (bm14_082b) was placed on the calf in a mother–calf pair. Tags bm14_082a and bm14_082b were the only simultaneously deployed tags. Their deployments overlapped for about one hour, during which time only one SEP2 call was faintly recorded by the hydrophones on the calf's DTAG at a depth of 19.6 m. The same call was not picked up by the mother's DTAG, which was above or breaking the surface of the water at the time. Thus, our data include no calls simultaneously recorded by multiple DTAGs. Photographic identification images taken at the time of tagging indicate that 16 distinct whales were tagged in the 17 deployments (the same individual was tagged in deployments bm14_076a and bm14_076b).

The combined tag record contained a total of five complete SEP2 calls, which consist of two high-frequency precursors and four pulsed components (A2, B2, C2 and D2; see Fig. 2A). These five complete SEP2 calls were recorded during five different deployments. The majority of SEP2 recordings consisted of only a subset of the six call components. Measurements of frequencies and durations were made for all clearly identifiable SEP2 components (Tables 1 and 2), although total call durations were calculated using only recordings containing all six components. SEP2 calls recorded on DTAGs exhibited highly stereotyped timing and peak frequencies consistent with passive acoustic recordings of the same population (Stafford et al., 1999; Buchan et al., 2014; Table 1). A typical SEP2 call lasted for about one minute, and the four distinct low-frequency pulsed components had the following peak frequencies: A2 (56 Hz), B2 (94 Hz), C2 (24 Hz) and D2 (23 Hz). The first high-frequency precursor note at the beginning of the call (Pre-A2) had a peak frequency of 405 Hz, and the second precursor (Pre-D2), which separates the C2 and D2 components, had a slightly lower peak frequency of 375 Hz. These precursors

typically consisted of three short tones in close succession. Although the durations of and gaps between SEP2 call components are somewhat variable, the total duration of a SEP2 call remains quite consistent (64.0 ± 2.1 s; Table 2).

Of the 160 total SEP2 components recorded, 57 occurred when the tag was less than 5 m below the surface of the water. All of the calls containing these 57 components were interrupted by noise from the tag breaking the surface of the water. The mean depth \pm s.d. at which the other 103 SEP2 components were recorded was 54.4 ± 32.8 m. The mean depth \pm s.d. at which the 30 SEP2 components from the five complete calls were recorded was 29.8 ± 28.8 m. For all but one of the surfacing-interrupted calls, the hydrophone failed to pick up all six SEP2 components. Despite many of these calls being interrupted by surfacing noise and being incomplete on the acoustic record, several of the low-frequency A2, C2 and D2 components still registered concurrent signals on the tag accelerometer (Fig. 2B). In other instances, faint, incomplete SEP2 calls that were not interrupted by surfacing also registered on the accelerometers. Furthermore, we occasionally saw short but highly variable calls occurring at the same time as SEP2 calls. Series of these highly variable sounds were recorded in nine of the 17 tag deployments and we believe they were produced by blue whales. Stafford et al. (1999) describe similar but much less variable calls recorded on moored hydrophones. These calls can be seen overlaying components of a SEP2 call on both audio and accelerometer signal spectrograms in Fig. 2C. For all deployments in which more than three SEP2 call components were detected, the tagged animal was at least loosely associated with one or more other blue whales. All SEP2 components detected in deployments where the tagged whale was not visibly associated with other individuals were very faint on the acoustic spectrogram and undetectable on the accelerometer spectrograms.

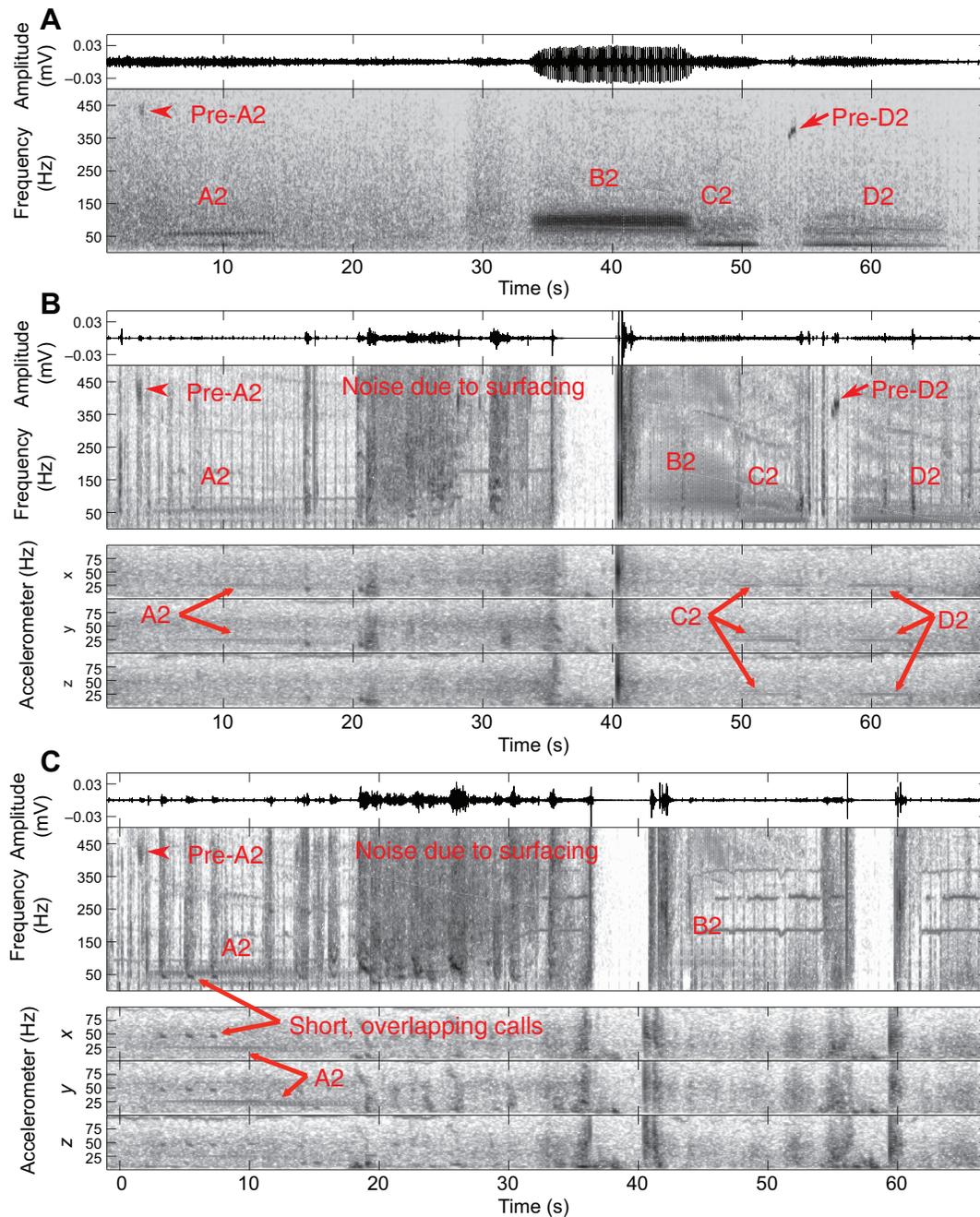


Fig. 2. Audio and accelerometer spectrograms of SEP2 calls. (A) Acoustic waveform and spectrogram of a complete SEP2 call recorded during deployment bm14_082b consisting of pulsed components A2, B2, C2 and D2 as well as both high-frequency precursors ('Pre-A2' and 'Pre-D2'; Buchan et al., 2014). The next two sections of the figure contain the acoustic waveform and spectrogram in the upper two panels, and spectrograms of the accelerometer's three orthogonal axes in the lower three panels. (B) SEP2 call from deployment bm15_064a interrupted by the tag breaking the water surface; A2, C2 and D2 components register clearly on the accelerometer spectrograms. (C) Faint and incomplete SEP2 call from deployment bm15_064a overlapped by short calls and surfacing noise. The A2 component registers a concurrent acceleration signal that is overlapped by the acceleration signals associated with the series of short calls. In all spectrograms, the wide vertical bands indicate when the DTAG is above the surface of the water. Narrower vertical bands are signals from the VHF antenna on the tag. Spectrogram parameters for all panels are: 256-point FFT, Hamming window, 99% overlap.

D calls were found in only two deployments, with 81 of a total of 87 recorded in just one deployment. D calls were about one second in duration, sweeping downward on a spectrogram from about 100 to 50 Hz (Fig. 3). The start and end frequencies of these calls were quite variable, although most calls had peak energies near 65 Hz (Table 3).

Given the poor signal-to-noise ratios of most SEP2 calls, DTAG accelerometer detections were quantified only for D calls. A D call

was deemed to be detectable on the accelerometer if the peak cross-correlation coefficient of its audio and acceleration vectors was greater than 0.25 for at least one of the accelerometer's axes. Coefficients of greater than 0.25 were found to correspond visually with calls that were visible on a spectrogram of the accelerometer signal (256-point FFT, Hamming window, 99% overlap). The bimodal distribution of these maximum coefficients suggests that a peak cross-correlation coefficient threshold of 0.25 divides calls

Table 1. Peak frequencies of SEP2 call components

Peak frequency (Hz)	Pre-A	Unit A	Unit B	Unit C	Pre-D	Unit D
SEP2: this study	404.9±6.9 (N=16)	56.3±3.1 (N=15)	93.8±7.1 (N=23)	23.7±1.3 (N=19)	374.9±9.7 (N=15)	23.4±0.0 (N=16)
SEP2: Buchan et al. (2014)	414±15.5 (N=48)	55±12.1 (N=57)	84±7.6 (N=62)	35±16.6 (N=61)	356±9.7 (N=53)	37±17.3 (N=60)

Peak frequencies of DTAG-recorded SEP2 call components are compared with measurements from a previous passive acoustic study of this population. All values are reported as means±s.d.

into those that are and are not detectable by the tag accelerometer (Fig. 4). Of the 87 D calls recorded across two deployments, 38 were correlated with accelerometer signals along at least one of the tag's axes.

In the routine pre-processing of accelerometer data from the DTAGs, the timing of tag slips in all deployments was determined. Tag bm15_054a, which recorded the majority of D calls used for analysis of accelerometer data, was deployed on the blue whale's dorsal region anterior to the dorsal fin with a pitch (p)–roll (r)–heading (h) orientation of p: –11.0 deg (pitched down), r: –34.8 deg (rolled right) and h: 17.4 deg (angled right). Tag bm15_054a slipped only once shortly after being placed on the animal. All calls recorded in that deployment occurred after the tag slip. The tag's constant orientation (4.87 m forward of dorsal fin trailing edge and 0.17 m laterally from dorsal ridge to center of tag) was also confirmed by photographic identification and photogrammetry images taken throughout the deployment.

Among D calls that were detectable on the accelerometer, we examined the tri-axial acceleration vectors for consistent vibrations that could be indicative of calls produced from within the tagged whale. Two calls were considered to have highly correlated acceleration signals if the peak cross-correlation coefficients for their accelerometer signals were greater than 0.25 along all three of the accelerometer's orthogonal axes. A peak coefficient of greater than 0.25 was found to correspond with a strong peak visible in the cross-correlation function between two accelerometer signals (Fig. 5). Cross-correlation of the acceleration vectors between all of the D calls in deployment bm15_054a revealed that 10 calls had highly correlated accelerometer signals across all three axes. Within this group of 10 calls, each pair of acceleration signals was not necessarily correlated; however, each call in the group was connected to every other call in the group through a chain of highly correlated signals. These 10 calls with highly correlated acceleration signals were designated as 'intra-correlated' calls.

To address whether the high correlation of the accelerometer signals of these 10 calls was caused by shared patterns from the acoustic signal rather than from non-acoustic sources of acceleration (such as the whale's motion or behavioral state), two control analyses were performed. As a negative control, noise signals taken from the accelerometer record immediately preceding all of the 81 D calls in the deployment were pairwise cross-correlated across all

three axes [(81×80)/2=3240 distinct cross-correlations per axis, excluding autocorrelations]. The mean peak coefficient±s.d. of the pre-signal noise cross-correlations was 0.19±0.04 (N=9720). This was repeated using accelerometer noise samples taken immediately following all of the 81 D calls, yielding an identical result. No pair of noise signals yielded peak coefficients greater than 0.25 across all three axes both before and after the signal. Of the 6480 pairwise noise cross-correlations performed, only nine yielded slightly above-threshold peak coefficients on all three axes, but none of these corresponded to any of the 10 calls identified earlier as intra-correlated calls. As a positive control, all possible pairs of acoustic signals from the 81 D calls were cross-correlated (mean coefficient±s.d. 0.38±0.18, N=3240). Of the 3240 cross-correlations performed, 2390 yielded above-threshold peak coefficients, which included all 81 D calls. The same scheme used to identify the 10 D calls with intra-correlated accelerometer signals identified all 81 D calls as having highly correlated acoustic signals with one another. The peak coefficients for cross-correlations between acoustic signals within the 10 intra-correlated D calls (0.49±0.18, N=45) were higher (P<0.01, two-tailed unequal variance *t*-test) than those for cross-correlations between the 26 D calls from the same deployment that were detected on the accelerometers but were not assigned to the intra-correlated group (0.41±0.17, N=325).

The cross-correlation coefficients between the acceleration vectors of all possible pairs of D calls in deployment bm15_054a were first sorted into three groups for statistical analyses: those between two members of the intra-correlated calls (mean coefficient±s.d. 0.30±0.10, N=45), those between two non-members of the intra-correlated calls (0.20±0.02, N=2485), and those between a member and a non-member of the intra-correlated calls (0.20±0.03, N=710). Sample sizes reflect the number of unique cross-correlation pairs possible within each group with autocorrelations removed. A Kruskal–Wallis test followed by a *post hoc* multiple comparison test with the Dunn–Šidák correction indicated that the mean cross-correlation coefficient from member pairs was significantly higher than the means from both non-member and mixed pairs (P<0.0001). No significant difference was found between non-member and mixed coefficients. Repeating these tests using random samples of 45 coefficients from both the non-member and mixed groups yielded the same results, indicating that the statistically significant result is not merely caused by variation in sample sizes.

Table 2. Durations and timing of SEP2 call components

Durations (s)	Pre-A	Unit A	Gap A–B	Unit B	Gap B–C	Unit C	Gap C–D	Pre-D	Unit D	Call total
SEP2: this study	1.1±0.4 (N=16)	9.5±4.1 (N=15)	17.5±6.6 (N=16)	10.4±3.1 (N=23)	0.4±1.1 (N=23)	5.5±0.8 (N=19)	2.9±0.4 (N=20)	1.1±0.5 (N=15)	7.7±2.1 (N=16)	64.0±2.1 (N=5)
SEP2: Buchan et al. (2014)	0.7±0.1 (N=48)	9.5±6.9 (N=57)	19.5±1.7 (N=50)	12.6±0.4 (N=62)	0.3±0.3 (N=53)	4.5±0.8 (N=61)	2.2±0.7 (N=52)	1.0±0.2 (N=53)	8.0±2.7 (N=60)	59.6±6.7 (N=62)
SEP2: Stafford et al. (1999)		17.7±3.8 (N=23)	18.3 (N=1)	10.8±0.6 (N=9)	1.8 (N=1)	4.0±0.5 (N=23)			10.8±1.5 (N=23)	53.5 (N=1)

Timing characteristics of DTAG-recorded SEP2 calls are compared with measurements from previous passive acoustic studies of this population. All values are reported as means±s.d.

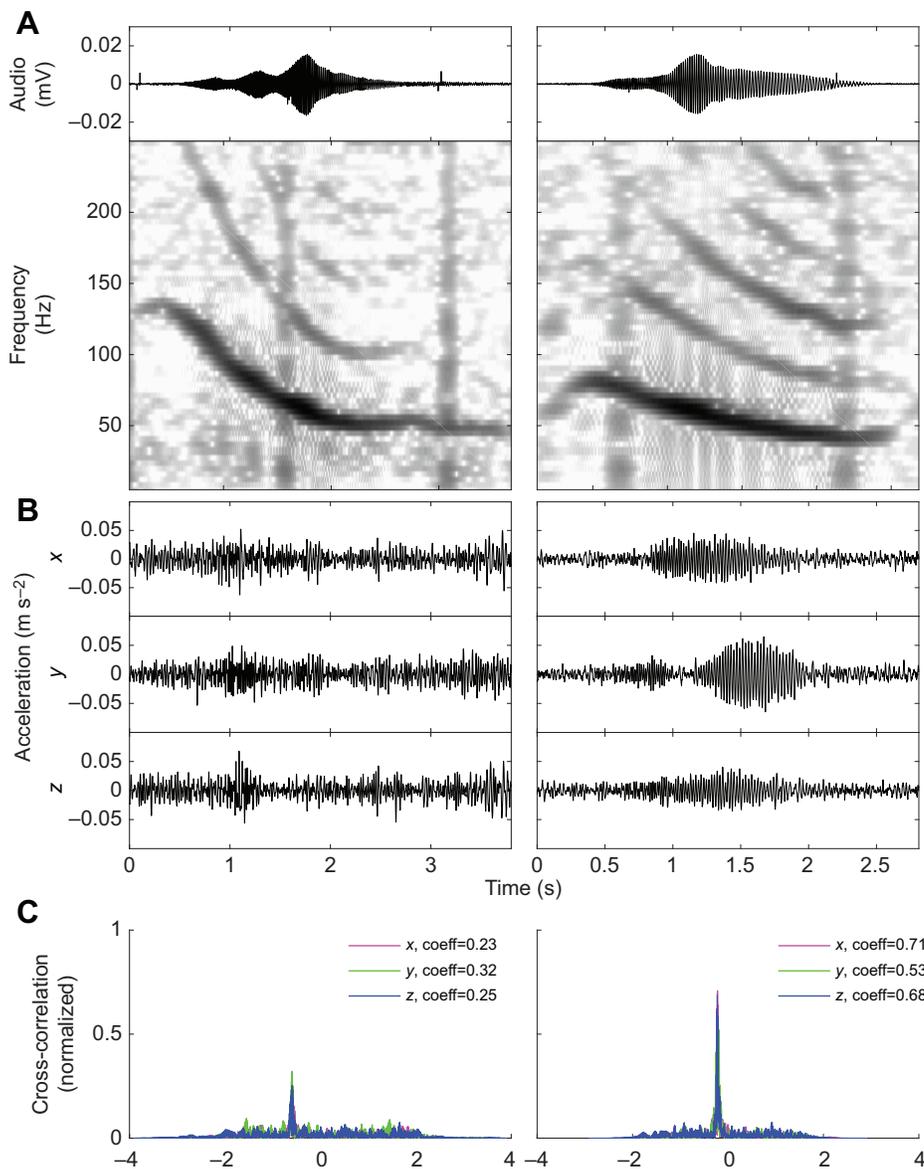


Fig. 3. D calls recorded on the tag hydrophone and tri-axial accelerometer. (A) Acoustic waveforms and spectrograms of two tonal downswEEP calls (256-point FFT, Hamming window, 99% overlap). (B) Concurrent accelerometer readings from the tag's three orthogonal axes. (C) Cross-correlation functions between the acoustic signal and each of the three accelerometer signals. Peak coefficient (coeff) values for each cross-correlation are listed in the keys, indicating that the call on the left was deemed detectable on the y- and z-axes, while the call on the right was clearly detectable on all three accelerometer axes. These two downswEeps illustrate the variability in frequency range of D calls. Although the two acoustic signals are very similar in amplitude, the call on the right is associated with a stronger acceleration signal. For the call on the right, the aligned accelerometer signals from the x- and y-axes are offset by about 0.25 s, a pattern seen in many of the strongest D calls presumed to be produced by the tagged whale in deployment bm15_054a.

The 10 intra-correlated D calls were all found to be relatively strong calls, although their audio and acceleration peak-to-peak amplitudes showed considerable variation (Fig. 5). We also observed that the accelerometer signals from at least six of the 10 intra-correlated D calls displayed a characteristic offset, where the acceleration signal was detected along the tag's x-axis slightly before it was detected along the y-axis. The call on the right of Fig. 3 exhibits this characteristic offset. The intra-correlated D calls also tended to have slightly lower characteristic frequencies and smaller

standard deviations in measured parameters than the rest of the D calls (Table 3). Two-tailed unequal variance *t*-tests indicated that the center and end frequencies of the 10 intra-correlated D calls were significantly lower than those of the other 71 D calls in deployment bm15_054a ($P < 0.01$).

D call production was mapped onto the tag's dive profile (Fig. 6). D calls were detected at an average depth of about 16 m, with the 10 intra-correlated D calls occurring at depths between 2 and 14 m. D calls registering concurrent accelerometer signals were detected at

Table 3. Signal parameters of downswEEP D calls

	Peak frequency (Hz)	Center frequency (Hz)	Start frequency (Hz)	End frequency (Hz)	Duration (s)	Depth (m)
All D calls	65.3±16.2 (N=87)	74.8±26.5 (N=87)	98.6±18.2 (N=87)	50.2±15.1 (N=87)	1.3±0.4 (N=87)	15.6±10.6 (N=87)
Accelerometer-detected D calls	59.6±9.2 (N=38)	65.0±7.9 (N=38)	97.5±14.3 (N=38)	45.2±8.4 (N=38)	1.16±0.2 (N=38)	12.1±7.3 (N=38)
Intra-correlated D calls	59.4±10.0 (N=10)	60.8±5.4 (N=10)	92.2±13.2 (N=10)	41.4±7.7 (N=10)	1.2±0.2 (N=10)	10.2±4.4 (N=10)

Characteristic frequencies, durations and depths of all D calls in the tag record. Calls that registered signals on the accelerometers are reported separately because these typically corresponded to the strongest detections. The 10 D calls with highly intra-correlated acceleration signals in deployment bm15_054a are also reported separately. All values are reported as means±s.d.

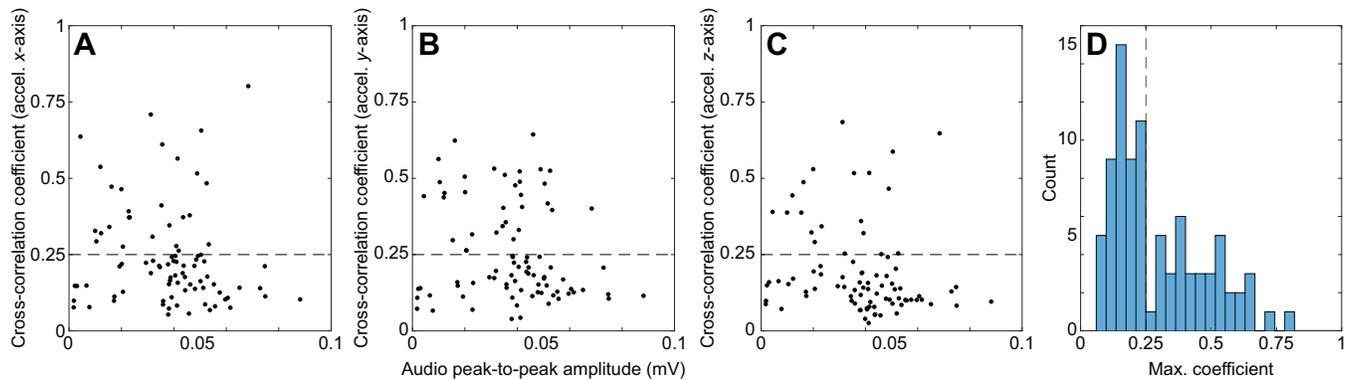


Fig. 4. Distributions of cross-correlation coefficients between concurrent D call audio and tri-axial accelerometer signals. Normalized peak coefficients from the cross-correlation of concurrent audio and accelerometer (accel.) signals as a function of call amplitude. (A) x-axis; (B) y-axis; (C) z-axis. (D) Histogram of the maximum cross-correlation coefficient values across the three axes for each D call. A bimodal distribution separates calls into those that do and those that do not register detectable accelerometer signals. In all four panels, dashed lines at coefficient values of 0.25 indicate the minimum threshold identified for an audio signal to be associated with a detectable acceleration signal. Many D calls only registered associated signals on a subset of the accelerometer's three orthogonal axes.

depths ranging from 1 to 36 m (mean 12 m). However, calls were recorded by the tag hydrophones at depths as great as 48 m. The deployment in which most of the D calls were recorded also contained 57 detected feeding lunges, largely grouped into two rounds of shallow foraging (Fig. 6).

DISCUSSION

Call characterization

SEP2 calls

The Southeast Pacific type 2 (SEP2) call appears to be much more common than the Southeast Pacific type 1 call (SEP1, described by Cummings and Thompson, 1971 and Stafford et al., 1999) during the February to March period of this study. The tag record contained no SEP1 calls, although they have been occasionally found in passive acoustic recordings from the same region during June to August (Buchan et al., 2014; Colpaert et al., 2016). SEP2 calls recorded on DTAGs have similar frequency and timing characteristics to SEP2 calls recorded using passive acoustic methods (Stafford et al., 1999; Buchan et al., 2014). However, the C2 and D2 components in the DTAG records have more stereotyped peak frequencies and a lower frequency emphasis than the same components recorded using towed hydrophones (Table 1). The lower variability, however, may simply indicate that our smaller sample of SEP2 calls was recorded from a smaller group of whales than in previous studies. B2 components recorded on DTAGs also tended to have higher peak frequencies than were seen in passive acoustic recordings; B2 components containing energy as high as 500 Hz were occasionally found in DTAG recordings (Fig. 2B). Two-tailed unpaired *t*-tests indicated that the peak frequency differences between this study and Buchan et al. (2014) were statistically significant for the B2, C2, pre-D2 and D2 components ($P < 0.01$). The recordings described by Buchan et al. (2014) were made in 2012–2013, so these differences may reflect frequency shifts occurring over time. Blue whale song frequency shifts have been described globally, although over much longer time scales (McDonald et al., 2009). Alternatively, differences could result from differing frequency responses of recording equipment, differences in analysis methods, and/or individual variability in call parameters. The latter seems somewhat less likely at least for the frequency differences seen in the C2 and D2 call components, given the extremely low variability found in this study.

D calls

Downswept (D) calls are part of the vocal repertoires of blue whale populations around the world. We offer the first description of D calls for blue whales off the coast of Chilean Northern Patagonia, which are quite variable but tend to range from about 100 Hz to below 50 Hz (Table 3). D calls recorded on two tagged whales in this population tended to be substantially higher in frequency than calls recorded for the blue whale population off the coast of California, which range from about 60 to 45 Hz (McDonald et al., 2001), and in the North Pacific, which range from about 76 to 40 Hz (Oleson et al., 2007). Similarly, downsweeps produced by Antarctic blue whales range from about 76 to 40 Hz (Rankin et al., 2005). D calls in our tag record are closest in frequency to calls from pygmy blue whales in the Indian and Southwest Pacific Oceans, which sweep downward from 70–100 to 20–50 Hz (Gavrilov et al., 2011). Thus our data did not support the hypothesis that the acoustic parameters of Chilean blue whale vocalizations are intermediate to those of other Southern Hemisphere populations.

Use of tag accelerometers to identify calls from the tagged whale

SEP2 calls

Given that SEP2 calls recorded using passive acoustic methods are typically powerful sounds, probably used by blue whales for long-distance communication (Payne and Webb, 1971), we were surprised that all of the SEP2 calls in our tag record appeared significantly fainter than many of those recorded on towed and moored hydrophones (Buchan et al., 2014; Colpaert et al., 2016). Therefore we suspect that none of the SEP2 calls we recorded were produced by the tagged animals. Thus, based on recent studies (Goldbogen et al., 2014; Stimpert et al., 2015) suggesting that accelerometer signals may be used to identify calls produced by the tagged whale, we did not expect these calls to register on the tags' accelerometers, yet many did. Several additional lines of evidence point to these calls being produced by whales other than the tagged whale. First, many SEP2 calls were interrupted by the whale breaking the surface (Fig. 2B). It would seem counter-productive for a blue whale to engage in long-distance calling behavior while surfacing due to destructive interference from the surface. Second, many SEP2 components overlapped with other call types, and biphonation has not been reported for blue whales. In some of these

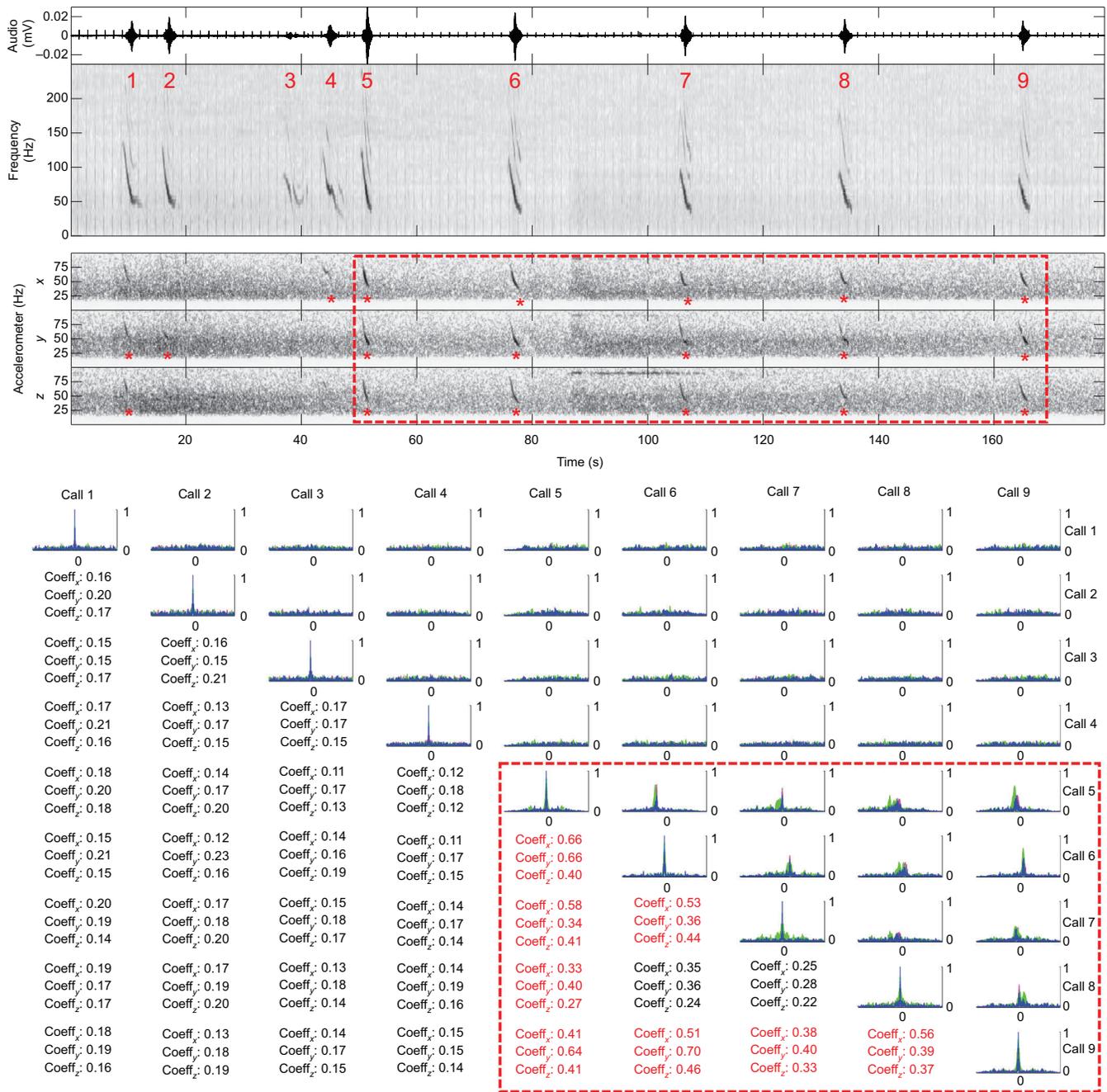


Fig. 5. Cross-correlation analyses of a series of downswept calls. A series of nine D calls are numbered in red on the audio spectrogram (256-point FFT, Hamming window, 99% overlap). Of these nine calls, eight register a concurrent accelerometer signal on at least one of the tag's orthogonal axes (three lower panels). Only call 3 registered no detectable acceleration signals. Red asterisks indicate acceleration signals that yielded peak coefficients of at least 0.25 when cross-correlated with aligned audio signals. Below the accelerometer spectrograms, the acceleration vectors of all nine calls were cross-correlated with one another. Cross-correlation functions for all three axes are shown in the same plots, with x-axis functions in magenta, y-axis functions in green, and z-axis functions in blue. Normalized cross-correlation coefficients are displayed in red for pairs of signals that were highly (≥ 0.25) correlated along all three axes. The red boxes indicate that calls 5 to 9 all have highly correlated acceleration signatures, which suggests that they were produced by the tagged whale. There were no significant correlations among the acceleration signals of calls 1 to 4, suggesting that they were produced by another whale (or whales) whose orientation relative to the DTAG was not fixed.

cases the SEP2 component and the overlapping call type both registered signals on the accelerometer (Fig. 2C). Finally, often only a subset of the call that was detected on the hydrophone was detected on the accelerometer. This seems unlikely if the tagged whale was producing the call. Together, these lines of evidence suggested to us that calls from other nearby (non-focal) whales are

capable of registering acceleration signals in the tagged (focal) animal's DTAG record.

D calls

Although calls from nearby animals appear to register on the tags' accelerometers, we sought to determine whether criteria could be

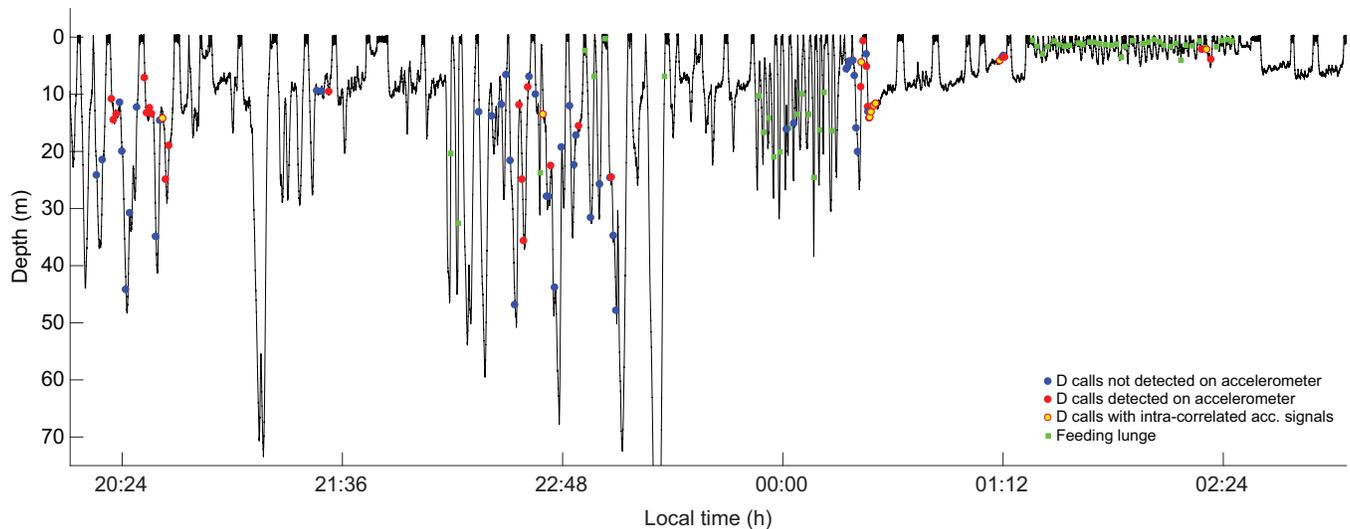


Fig. 6. The occurrence of D calls on a dive profile. Eighty-one D calls from deployment bm15_054a are mapped on the tag's depth profile, with the 36 calls registering detectable acceleration (acc.) signals shown in red and the 10 calls with highly intra-correlated acceleration signals marked in yellow. Calls shown in blue did not register detectable accelerometer signals. Green squares indicate feeding lunges identified in the DTAG record.

developed to distinguish between calls produced by the tagged whale and calls produced by nearby whales. As SEP2 call components seemed unlikely to be produced by the tagged whales, we focused our study of accelerometer signals on D calls. As accelerometer responses are very sensitive to tag placement on the animal (Goldbogen et al., 2014), we were fortunate to have one deployment (tag bm15_054a) with 81 D calls not separated by discernible tag slips. Consistent with previous studies, we found that accelerometer signals associated with low-frequency calling were often masked in the accelerometer record by noise due to larger-scale body movements (Goldbogen et al., 2014; Stimpert et al., 2015). Efforts to use peak-to-peak and root mean square amplitude-based criteria, as were used in previous studies, were hindered by our small sample size of calls with positive signal-to-noise ratios in the accelerometer record. We were able to find no strong correlation between acoustic and accelerometer signal amplitudes because so many of our signals were dominated by higher-amplitude non-acoustic accelerometer noise. To mitigate this issue, we used cross-correlation to analyse the phase match of concurrent audio and acceleration signals (Figs 3 and 4). Cross-correlating audio and accelerometer signals across all three axes offers a quantitative way of determining whether or not an acoustic signal is associated with a vibration of the DTAG; however, it does not address whether or not the audio signal was produced by the animal to which the accelerometer is anchored. Of the 81 D calls picked up by the hydrophone in a single tag deployment, 36 calls registered concurrent signals along at least one of the accelerometer axes. However, because of the substantial variability in acoustic and accelerometer signal characteristics, and because of the suspected recording of non-focal SEP2 calls on the accelerometers, we were hesitant to assign all 36 of these calls to the focal blue whale.

As seen in previous studies (Goldbogen et al., 2014), accelerometer signals associated with low-frequency sounds were anisotropic, which suggested to us that they might depend on the relative orientation of the sound source to the DTAG. We would then expect that calls originating from a source with a constant relative orientation would generate similar acceleration signals on all three axes of the tag accelerometer. This relationship depends on three key assumptions: (1) that the tag's placement on the whale is

relatively constant during the duration of the deployment, (2) that the properties of vibrating tissues or airspaces of the whale are consistent between individual calls of the same type, and (3) that the DTAG vibrates differently depending on the direction of the sound source. If indeed tag accelerometer signals reflect airspaces or tissues vibrating when sound is either produced or received, then it is plausible that sounds coming from different directions will excite different vibrations resolvable by the tri-axial accelerometer. If the detected vibrations of the tag were instead excited directly by the sound pressure or particle motion from calls, we would still expect the tri-axial acceleration signals to contain information about the relative orientation of the source and the tag (Mooney et al., 2016).

Cross-correlation of acceleration vectors between all possible pairs of D calls in the same deployment revealed a single group of 10 relatively strong calls that had highly correlated acceleration signals across all three accelerometer axes (five of these highly correlated D calls are among the series of nine calls displayed in Fig. 5). Comparison of all cross-correlation pairs yielded no other groups or pairs of highly correlated acceleration signals. When all possible pairs of accelerometer noise signals immediately adjacent to D calls were cross-correlated with one another, no noise signals were found to be highly intra-correlated. This indicates that the high cross-correlation coefficients found between D call acceleration signals were not caused by non-acoustic sources of acceleration shared between call times (behavioral states such as diving or ascending, for instance). When we cross-correlated the acoustic signals between all pairs of D calls, we found that all 81 D calls in the deployment had highly correlated acoustic signals. As the audio signals of the D calls were sufficiently stereotyped to yield high cross-correlation coefficients, we might reasonably expect that their concurrent acceleration signals (whether they reflect body vibrations of the whale or direct excitation of the tag by a sound wave) would also be cross-correlated if the sound sources have a consistent orientation relative to the DTAG. Under this interpretation, the presence of only a single group of 10 D calls with intra-correlated acceleration signals indicates that there is only one source of D calls with a consistent orientation relative to the DTAG. We propose that the most likely source of these calls, which all have a consistent acceleration signature, is the tagged whale.

We used a conservative normalized peak cross-correlation coefficient threshold of 0.25 to identify which pairs of accelerometer signals were highly correlated. Experimenting with less stringent thresholds, we found that the group of calls with highly correlated accelerometer signals expanded to include more calls; however, we also began to include pairs of calls not registering concurrent acceleration signals. We expect that these accelerometer signals probably contained correlated noise due to non-acoustic body movements, and that these calls were therefore unlikely to have been produced by the focal whale. It is important to note that while our negative control of cross-correlating accelerometer noise between call times suggests that our method and threshold is robust against mistakenly including calls that are cross-correlated for non-acoustic reasons, it does not rule out the possibility of excluding calls whose accelerometer record is sufficiently masked by non-acoustic accelerometer noise. In fact, we found that the mean peak-to-peak amplitude of accelerometer noise surrounding the 26 D calls detectable on the accelerometers but not assigned to the intra-correlated group ($0.0151 \pm 0.0080 \text{ m s}^{-2}$) was on average higher than that of the noise surrounding the 10 intra-correlated D calls ($0.0065 \pm 0.0037 \text{ m s}^{-2}$). This might indicate that the high correlation values among the 10 D calls were caused primarily by decreased interference rather than increased similarity in the accelerometer records. However, of the 26 accelerometer-detected but non-intra-correlated D calls, 15 exhibited accelerometer noise peak-to-peak amplitudes well within the range observed for the 10 intra-correlated calls, which suggested to us that decreased masking due to noise does not alone explain the high correlation of accelerometer signals observed among the 10 intra-correlated D calls. Nonetheless it is possible and likely that our stringent correlation threshold excluded a small number of calls that were indeed produced by the focal animal but were sufficiently masked by accelerometer noise.

Additional factors not necessarily related to the relative orientation of the sound source to the DTAG, such as the acoustic properties of the D calls, may contribute to high correlations between acceleration signals. The 10 intra-correlated D calls tended to have slightly less variable center, start and end frequencies (Table 3). Furthermore, the 10 intra-correlated D calls exhibited slightly higher correlations among their acoustic records than was observed among the other 26 accelerometer-detectable D calls, although there was substantial overlap between the distributions of correlation coefficients. Higher acoustic similarity between the 10 D calls may further support our claim that the intra-correlated calls were those produced by the tagged whale.

Physiological and behavioral implications

Many of the strongest D calls that we identified as likely produced by the tagged whale exhibited a characteristic offset between the accelerometer signals from the tag's *x*- and *y*-axes (Fig. 3). In particular, we found that the presumed focal D calls were often characterized by a vibration along the tag's *x*-axis slightly before a vibration along the *y*-axis. This offset may be related to the sound-producing physiology of blue whales, which is poorly understood, and/or to the placement of the tag. Unfortunately, further analysis is limited by having only one tag deployment with a substantial number of accelerometer-detected signals.

Previous studies of downswept D calls in other blue whale populations have suggested that blue whales exchange these calls while foraging (McDonald et al., 2001; Oleson et al., 2007). Our tag record includes exchanges of D calls between the presumed focal whale and at least one other non-focal whale (Fig. 5). Plotting the occurrence of these calls on the tag deployment's dive profile (Fig. 6)

reveals that D calls are often produced and received around periods of diving and lunging characteristic of foraging (Goldbogen et al., 2011). Observations of blue whales off the coast of California similarly found that D calls were produced at depths between 10 and 40 m (Thode et al., 2000; Oleson et al., 2004). Although the majority of D calls in our tag record fell within this range, we did record two probable focal calls produced at tag depths of less than 5 m.

Conclusions and future directions

DTAGs deployed on blue whales in the Gulf of Corcovado, Chile, recorded SEP2 and downswept calls in addition to other more variable sounds. Measurements of signal parameters from SEP2 calls recorded on DTAGs were largely consistent with previous studies of this population using passive acoustic methods (Stafford et al., 1999; Buchan et al., 2014). D calls tended to be higher in frequency than those reported for Antarctic blue whales (Rankin et al., 2005) and are more similar to those reported for pygmy blue whales (Gavrilov et al., 2011). Several lines of evidence indicate that vocalizations from non-focal whales can register detectable accelerometer signals on the focal whale's DTAG, which suggests that the amplitude-only criteria for assigning calls to the tagged animal described by Goldbogen et al. (2014) may not be fully reliable if there are other nearby vocalizing whales. We describe a method of cross-correlating concurrent acoustic and accelerometer signals in order to determine which calls are associated with detectable acceleration signals. Furthermore, cross-correlating accelerometer signals between calls of the same type can identify calls with similar acceleration signatures, which may be a characteristic of calls produced by the tagged animal.

Future tagging expeditions will focus on tagging multiple associated blue whales simultaneously in order to determine with certainty if calls from one animal can register accelerometer signals on another animal's tag. Future expeditions will also focus on simultaneously deploying two DTAGs on different locations on the same whale, in order to further examine acceleration patterns associated with vocalizing behavior. Using accelerometer signals to identify vocalizations produced by the tagged whale will enhance studies of blue whale communication, and improve the accuracy of estimates of individual call rates. Individual call rates are a key parameter that can enable population density estimates from passive acoustic data (Marques et al., 2013). Improved understanding of blue whale behavior in the Chiloense ecoregion gained from such studies will aid Chilean policy makers in making more informed decisions regarding conservation efforts in this area, which is one of the most important nursing and feeding grounds for the endangered Southeast Pacific blue whale population (Hucke-Gaete et al., 2004).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.S.S.; Methodology: M.R.S., L.S.S.; Software: M.R.S.; Formal analysis: M.R.S.; Investigation: A.B., L.S.H., G.C., R.L., P.A.B., G.H., P.S.S.; Resources: A.B., L.S.H., G.C., R.L., P.A.B., G.H., P.S.S.; Data curation: M.R.S., L.S.S.; Writing - original draft: M.R.S., L.S.S.; Writing - review & editing: M.R.S., G.C., P.A.B., L.S.S.; Project administration: A.B., G.C., R.L.; Funding acquisition: A.B., G.C., R.L.

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