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METHODS & TECHNIQUES

Using accelerometers to determine the calling behavior of tagged baleen whales

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ABSTRACT

Low-frequency acoustic signals generated by baleen whales can propagate over vast distances, making the assignment of calls to specific individuals problematic. Here, we report the novel use of acoustic recording tags equipped with high-resolution accelerometers to detect vibrations from the surface of two tagged fin whales that directly match the timing of recorded acoustic signals. A tag deployed on a buoy in the vicinity of calling fin whales and a recording from a tag that had just fallen off a whale were able to detect calls acoustically but did not record corresponding accelerometer signals that were measured on calling individuals. Across the hundreds of calls measured on two tagged fin whales, the accelerometer response was generally anisotropic across all three axes, appeared to depend on tag placement and increased with the level of received sound. These data demonstrate that high-sample rate accelerometry can provide important insights into the acoustic behavior of baleen whales that communicate at low frequencies. This method helps identify vocalizing whales, which in turn enables the quantification of call rates, a fundamental component of models used to estimate baleen whale abundance and distribution from passive acoustic monitoring.

KEY WORDS: Acceleration, Acoustics, Whale

INTRODUCTION

A major challenge in studying acoustic behavior and its ecological context is determining the source of an acoustic signal and assigning the emitted sound to an individual. These data are critically needed to relate movements and physiology to call production, and also to quantify individual call rates for acoustic monitoring. Discerning sender and potential receivers is also important for a wide range of communication and behavioral ecology studies, including the effects of anthropogenic sounds. Identifying call-producers is particularly challenging for whales because they are rarely in view and often vocalize without any visual cue, such as opening the mouth or releasing bubbles. Passive acoustic monitoring using hydrophone or seismometer arrays can localize sound-producing whales over relatively large spatial scales (Soule and Wilcock, 2013; Stanistreet et al., 2013; Weirathmueller et al., 2013; Wilcock, 2012). At finer scales, animal-borne tags equipped with hydrophones provide acoustic information with simultaneous information on orientation, depth and acceleration (Johnson et al., 2009; Johnson and Tyack, 2003). Sounds recorded by these multi-sensor tags have been assigned to either the tagged whale itself or nearby conspecifics based on the angle of arrival (Johnson et al., 2009; Johnson et al., 2006; Madsen et al., 2013; Oliveira et al., 2013) or a combination of consistent received level, high signal-to-noise ratio and apparent isolation of the tagged animal (Janik, 2000; Jensen et al., 2012; Oleson et al., 2007; Parks et al., 2011). Most of these methods are problematic for analyzing baleen whale sound production when conspecifics are present because tagged whale sounds cannot be easily distinguished from those of nearby animals given the typical long-range propagation of low-frequency calls. Another potentially complicating factor is that individuals may vary the source level of generated sounds (Au et al., 2006; Parks et al., 2011), making received level an unreliable indicator of range to the caller. However, recent increases in the sampling capacity of digital recording tags provide new opportunities to assess the calling behavior of individual whales. In particular, the low-frequency signals of large baleen whales could be detected using high-resolution accelerometry from tags attached to vocalizing individuals. Here, we tested this hypothesis in fin whales, *Balaenoptera physalus* (Linnaeus 1758), because they generate some of the lowest frequency calls (~30–20 Hz downsweeps) among aquatic animals (Watkins et al., 1987), making them an ideal model system to study calling behavior with high-resolution, multi-sensor acoustic tags.

RESULTS AND DISCUSSION

For two tagged fin whales, calls as low as 20 Hz were simultaneously recorded on both accelerometers and hydrophones (Figs 1, 2). The acoustic signals exhibited durations of 1.00±0.27 s, and the corresponding accelerometer signals had similar features with respect to duration (0.99±0.03 s). The accelerometer responses that coincided with acoustic signals were largely anisotropic (Fig. 3), exhibiting differences in magnitude among the three accelerometer axes within each deployment. This variation could be related to differences in tag location on each whale, given the inconsistent directionality of the anisotropic accelerometer responses between deployments, but we were unable to resolve this relationship conclusively because of our limited sample size. Nevertheless, the magnitude of accelerometer signals increased with the received sound pressure level of calls recorded on the tag during both tag deployments [acoustic received levels for whale bp12_294a acoustic calls (mean ± 1 s.d.): 184±6 dB

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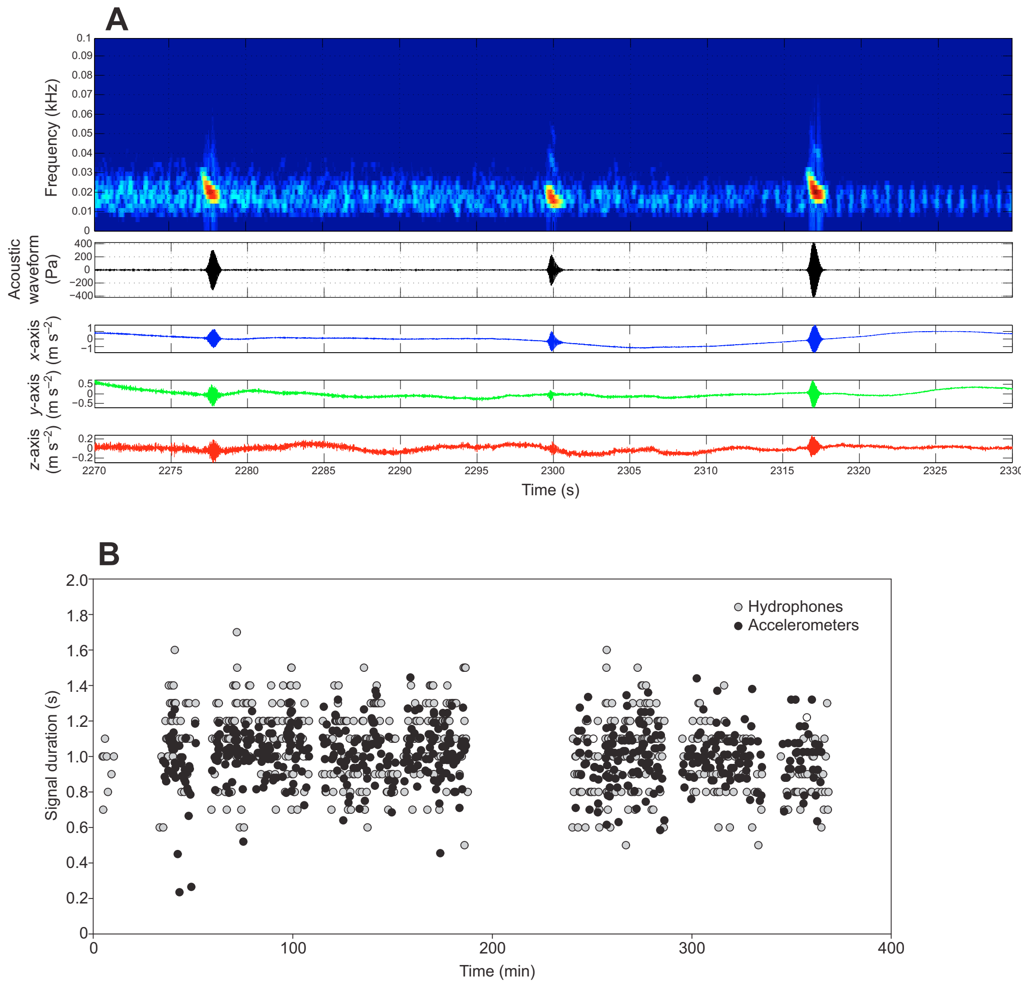

Fig. 1. Detection of fin whale calls from tag data. (A) Acoustic detection of 20 Hz signals were simultaneous with all three orthogonal axes (*x*,*y*,*z*) of the accelerometer. Signal has been adjusted for the tag's analog high-pass filter, filtered (2nd order Butterworth bandpass filter between 10 and 60 Hz) and downsampled (1200 Hz sampling rate). Spectrogram fast Fourier transform (FFT) size 512, 98% overlap. Accelerometer data were mean-subtracted and the linear trend removed, but data were not filtered apart from a one-pole analog anti-alias filter at 50 Hz. (B) Time series of acoustic and accelerometer signal detections (for whale bp12_294a). The cessation and resumption of calling in bp12_294a demonstrated the reliability of this method to assess calling behavior in the context of a controlled exposure experiment (see Materials and methods).

re. 1 μPa peak–peak (p–p), 170±7 dB re. 1 μPa root mean square (rms), and for whale bp13_258b acoustic calls: 177±5 dB re. 1 μPa p–p, 162±5 dB re. 1 μPa rms; Fig. 4]. We also note that we recorded acoustic signals that had no corresponding accelerometer signals for both tag deployments. This may be due to masking of accelerometer signals by greater body movements during these times. The rms noise levels on the accelerometer data in a 1 s window preceding each detected acoustic call supported this hypothesis, with levels higher near calls that were not detected on the accelerometers than near those detected (grand means of 0.21±0.18 and 0.13±0.10 m s^{-2}, respectively).

To test the hypothesis that accelerometer signals coincident with pressure indicate that the calls come from the tagged whale, we attached a DTAG to a drifting buoy deployed at 30 m depth, within 1000 m of calling fin whales. We recorded fin whale calls on the DTAG hydrophone, but no evidence of calls on the accelerometers was resolvable on the associated data stream (Fig. 2D). An opportunistic test also occurred with deployment bp12_294a, when the tag fell off the whale and recorded a call 3 s after detachment. At an estimated distance of less than 10 m from the whale, assuming a fin whale steady swimming speed of less than 3 m s^{-1} (Goldbogen et al., 2006), there were no concomitant accelerometer signals when the call was recorded acoustically on the tag (Fig. 2B). Our measurements of clear accelerometer signals for tags attached to calling animals and the absence of such signals on tags close to calling whales suggest that the body vibrations associated with calling played a substantial role in generating the coincident accelerometer signals.

However, most acoustic signals do consist of particle acceleration as well as pressure. In the far field of a sound source, sound pressure and the associated particle acceleration are related by known physics, expressed by the linearized conservation of the momentum equation. We tested the null hypothesis that the tag accelerometer signals could represent the particle accelerations associated with incoming calls of fin whales in the far field of the tagged whale by applying these models to each data stream (see Appendix). The magnitude and phase of the pressure and accelerometer data did not conform to these predicted far-field relationships, suggesting that calls were recorded in the near field. In addition, acceleration and pressure magnitudes in the far field are proportional to each other with the constant equal to $2\pi f/\rho c$, where f is frequency (Hz), ρ is seawater density (g cm^{-3}) and c is the speed of sound in water (m s^{-1}). Given the sound pressure levels of the calls on the tag (Fig. 4), accelerometer magnitudes on our tag recordings were much higher than expected. For example, the ~1000 Pa p–p pressure signal recorded in Fig. 1A should produce an acceleration magnitude of ~0.08 m s^{-2}. The levels we recorded on tags coupled to calling animals were close to an order of magnitude higher than this prediction. This evidence further supports the hypothesis that tagged animal body vibrations were contributing to these surprisingly high accelerometer values. It is important to note that because the details of the fin whale sound production mechanism are unknown, the boundary that defines the transition from near field to far field is also unknown, and could be anywhere from 15 to 150 m, or less than a whale length to

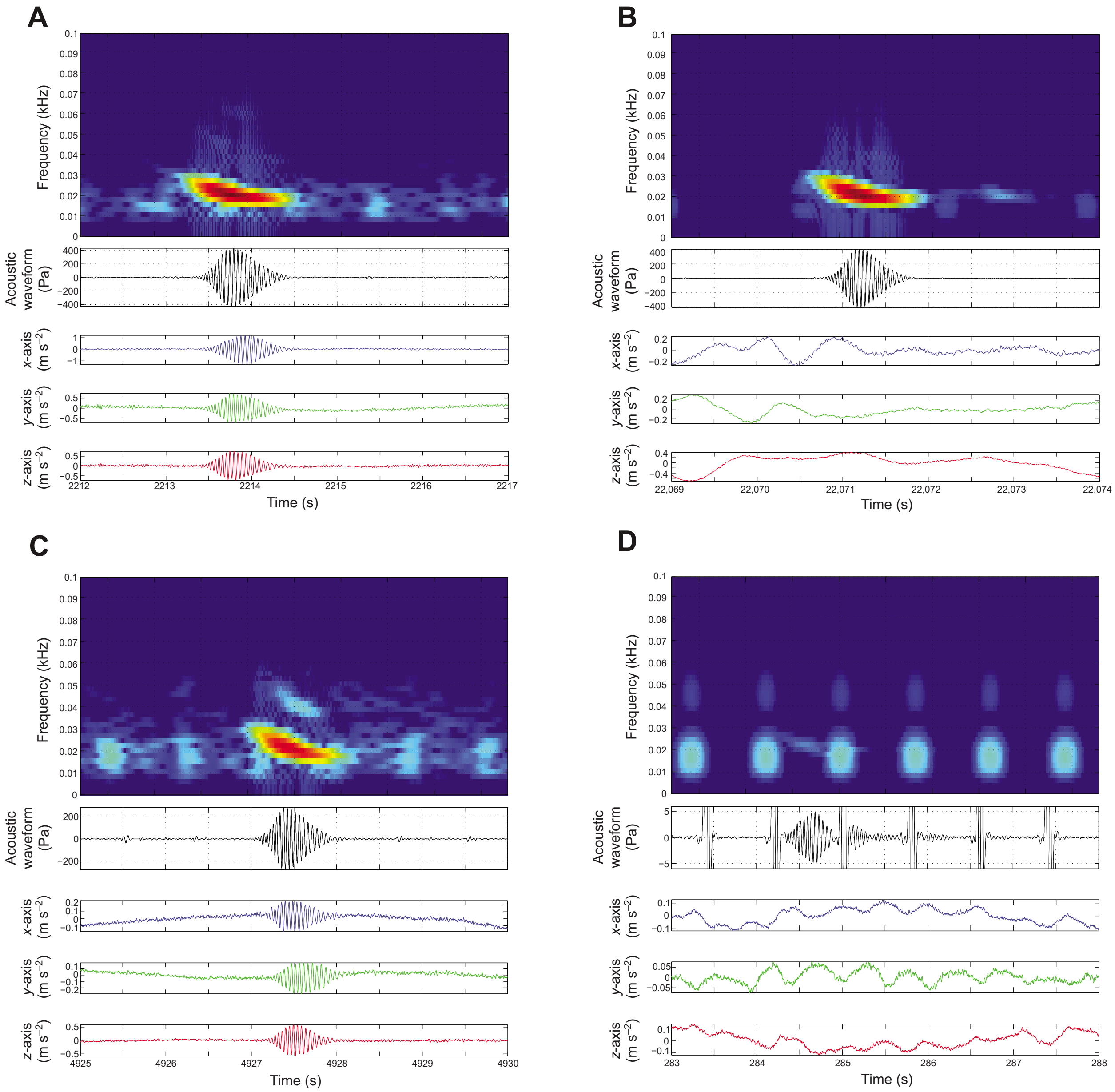

Fig. 2. Different tag deployment scenarios and their effect on accelerometer signal detection. Spectrogram parameters, acoustic signal processing and accelerometer processing as in Fig. 1. (A) Tag attached to whale bp12_294a. (B) Tag just moments after detachment from whale bp12_294a. (C) Tag attached to whale bp13_258b. (D) Tag attached to floating buoy in vicinity of calling fin whales. Impulsive spikes in the acoustic record are interference from the tag's VHF radio transmissions.

approximately eight whale lengths away (see Appendix). Thus, although the modeling described above suggests that calls were recorded in the near field, there remains a small chance they were produced by a whale closely and consistently associated with the tagged whale. However, considering the clear results of our opportunistic experiments, the most likely explanation for our observations is that the acoustic and accelerometry signals originate from each call produced by the tagged whale.

Using high-resolution accelerometry to detect low-frequency call production will significantly increase our ability to study baleen whale communication systems, including the contexts in which a particular sender signals, and how individuals acoustically respond to other animals or anthropogenic sound. The method we propose here offers a breakthrough in identifying when a tagged whale produces a sound. Although acoustic tags equipped with high-resolution accelerometry may make it possible to confirm caller identity in other species, the applicability of this method will be limited by sensor capacity and resolution. For these reasons, our approach may be limited to large baleen whales that generate low-frequency signals, or toothed whales that exhibit lower frequency body movements associated with emission of sounds (Johnson et al., 2009). This method also enables the quantification of individual calling rates, a fundamental input parameter for models that use passive acoustic monitoring to estimate the abundance and distribution of animals (Marques et al., 2013). Lastly, characteristics of these accelerometer signals may prove useful in future investigations of baleen sound production (Adam et al., 2013).

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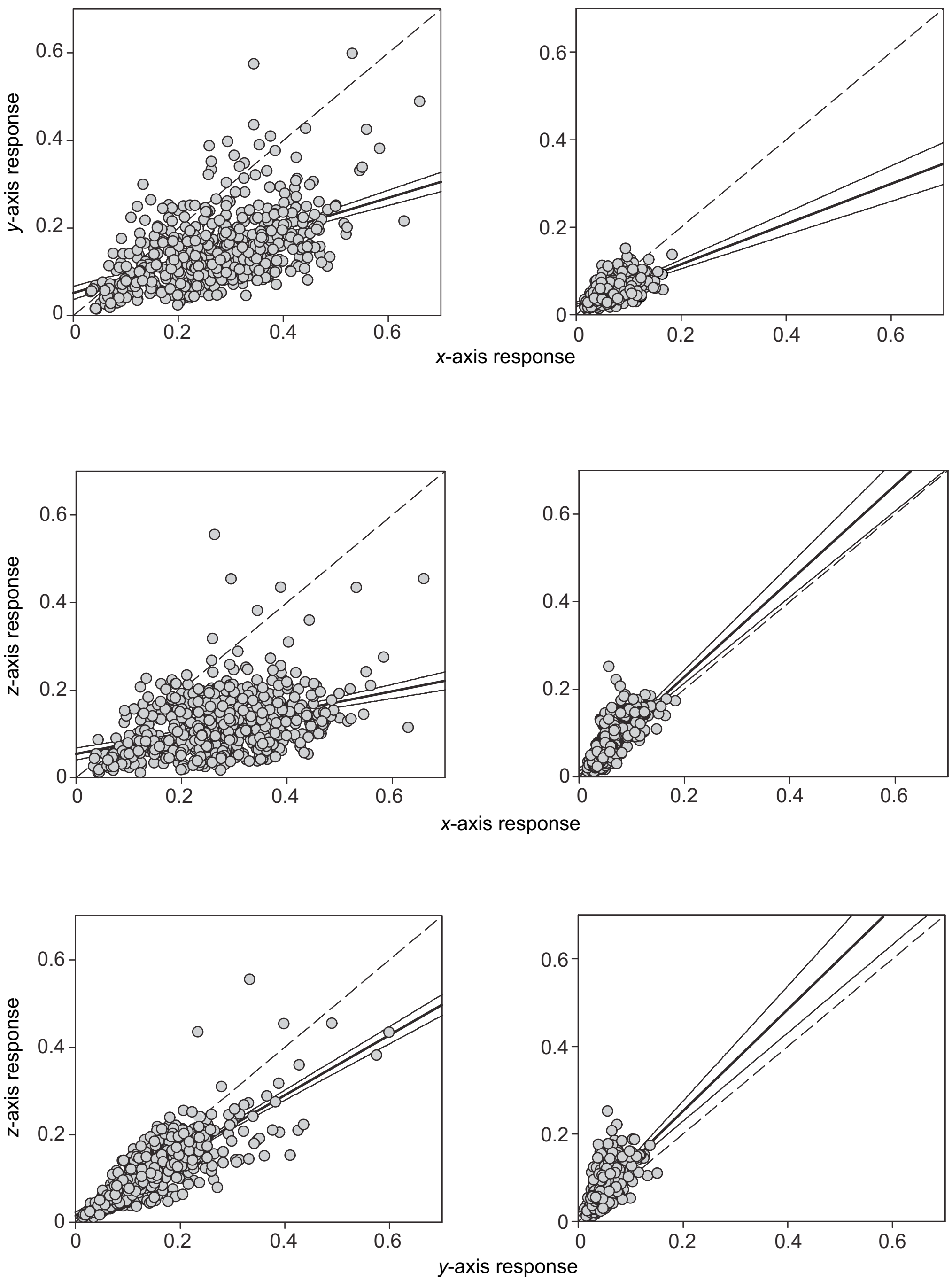

Fig. 3. Accelerometer response during fin whale calls. The acceleration measurements along each axis represent peak-to-peak magnitudes for each tag deployment (bp12_294a, left panels; bp13_258b, right panels). Ordinary least-squares linear regressions (solid thick lines) and 95% confidence intervals (solid thin lines) for each pairwise comparison were used to illustrate a general departure from isometry (dashed lines) for bp12_294a (*x*–*y*, r^2=0.26; *x*–*z*, r^2=0.15; *y*–*z*, r^2=0.64) and bp13_258 (*x*–*y*, r^2=0.32; *x*–*z*, r^2=0.56; *y*–*z*, r^2=0.42).

MATERIALS AND METHODS

This project was conducted under the terms of US National Marine Fisheries Service (NMFS) research permit numbers 14534 and 16111 [as well as Channel Islands National Marine Sanctuary (CINMS) permit number 2010-004 for operations within the boundaries of the CINMS].

We attached multi-sensor acoustic recording tags, or DTAGs (Johnson et al., 2009; Johnson and Tyack, 2003), to fin whales off the coast of southern California in the summer months of 2012 and 2013. These tagging operations took place in the context of a behavioral response study, where tagged whales were exposed to controlled sounds (DeRuiter et al., 2013; Goldbogen et al., 2013; Southall et al., 2012). The tags contained a pressure transducer, stereo hydrophones sampling at 240 kHz, and tri-axial accelerometers and magnetometers sampling at 200 Hz for whale bp12_294a and at 500 Hz for bp13_258b. DTAGs were equipped with flotation, four small suction cups for attachment and a VHF transmitter for tag retrieval.

The tag acoustic record was manually audited by visual inspection of a spectrogram [Hamming window, fast Fourier transform (FFT) size 512, 75% overlap]. The auxiliary sensor data (accelerometers, magnetometers, pressure) were separately visually inspected for corresponding signals, and the time, duration and peak-to-peak magnitude of those signals was recorded over a manually determined window. Acoustic call start times were marked by an analyst, and received levels were automatically calculated in Matlab using these user-defined time cues as a starting point. Calls were low-pass filtered (6th order Butterworth filter at 100 Hz) before level measurement, and both the waveforms and reported levels have been adjusted for measured tag sensitivity (based on laboratory calibration at 10 Hz to 20 kHz) to account for reduced hydrophone response at low frequency and the effects of the tag's analog high-pass filter. Reported peak-to-peak and rms received levels for acoustic calls were calculated over the full reported signal duration based on a 97% energy criterion for signal duration (Madsen et al., 2004).

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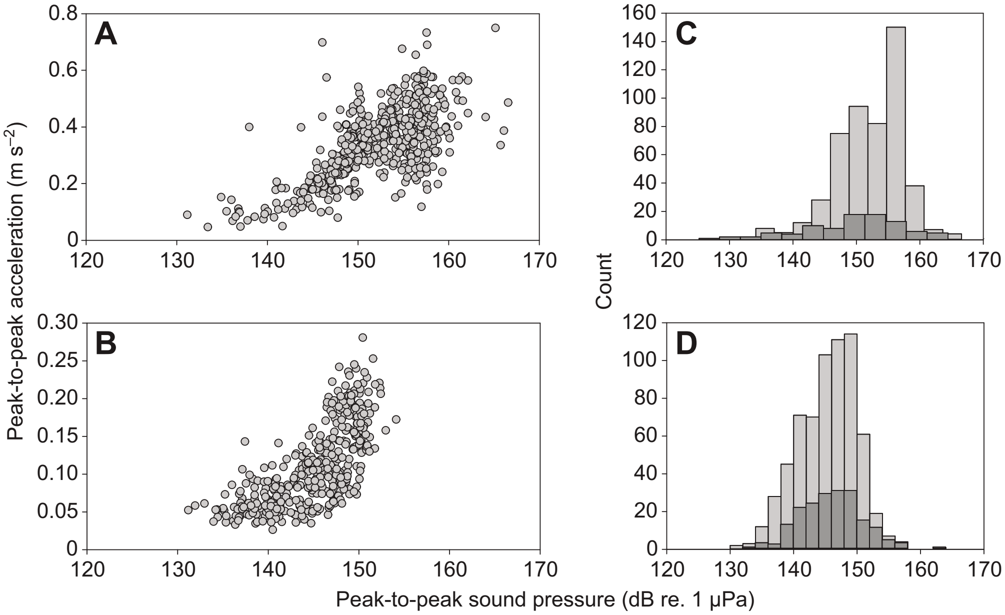

Fig. 4. Relationship between accelerometer magnitude and the received level of sound. (A,B) Received levels of sound (peak-to-peak sound pressure levels) were correlated with peak-to-peak accelerations for both bp12_294a (r_s=0.614, P<0.005; A) and bp13_258a (r_s=0.654, P<0.005; B). (C,D) Distributions for bp12_294a (C) and bp13_258a (D) of received sound levels with (light gray bars) and without (dark gray bars) concomitant acceleration signals.

These levels are not source levels, and cannot be compared directly with fin whale call levels measured using other methods.

APPENDIX

Acoustic modeling

The tag accelerometer measures the vibration of the body of a calling fin whale as well as the particle accelerations of both incoming and outgoing sounds. Therefore, proper delineation of an accelerometer signal that coincides with a sound pressure signal exhibiting the spectral characteristics of a fin whale call from a tag needs to be based on known physical laws governing underwater acoustics. Further than a wavelength away from the non-linear and highly irregular near field of a sound source, sound pressure and the associated particle acceleration are related by known physics, expressed by the linearized version of Newton's second law (conservation of momentum). Thus, to delineate, we can use the null hypothesis that the tag accelerometer signals are the particle accelerations associated with incoming calls of fin whales in the far field of the tagged fin whale. Our argument is that if signals exhibiting the spectral characteristics of fin whale calls do not satisfy this known relationship, then they are likely associated with vocalizations of the tagged fin whale itself.

Notation

In this paper, we use the following notation: ρ is the density of seawater (1000 kg m^{-3}), c is the speed of sound (in seawater, about 1500 m s^{-1}), $\vec{a}$ is the acceleration vector, p is acoustic pressure, f is frequency (20 Hz), $\lambda=c/f$ is the acoustic wavelength, $\omega=2\pi f$ is the angular frequency and $k=\omega/c$ is the spatial wavenumber.

Expectations under the far-field assumption

We begin with Newton's second law for conservation of momentum, $F=ma$ or, for acoustics [see Medwin et al. (Medwin et al., 2005), chapter 1 for details],

$$-\nabla p = \rho\vec{a}\,. \qquad (1)$$

Because the tag has only a single hydrophone measuring pressure and not pressure gradient, it is necessary to make an adequate assumption about the wavefront shape. A locally plane wavefront in the vicinity of the hydrophone is assumed. This is a good approximation of signal coming in from a distance.

For the purposes of argument, we here assume far-field plane wave propagation; in other words, r>λ (or equivalently, kr>>1), where r is the range between source and receiver. Assuming a planar wavefront shape, the direction of propagation of a call in the far field can also be estimated based on Eqn 1 for conservation of momentum. If the propagation direction were variable, that would indicate the calls were coming from several other animals in different locations, or a separate animal moving its position relative to the tagged animal. If the propagation direction were consistent, it could indicate the direction of the sound source inside the whale, or a consistently located separate whale.

Estimation of the propagation direction (given a plane wave front) is discussed below. In order to use the accelerometer data to determine the direction of call propagation, two conditions (below) need to be satisfied. If these conditions are not satisfied, it could be because the sound is not propagating as a plane wave and the tag may be in the near field of the sound.

The conditions that must be satisfied are: (1) the magnitude of $\vec{k}=\{k_x,k_y,k_z\}$ (propagation vector) should be equal to the wave number:

$$\sqrt{k_x^2+k_y^2+k_z^2}=\frac{2\pi f}{c} \qquad (2)$$

and (2) k should be real (or its imaginary parts relatively small).

Because we would like to calculate pressure and accelerometer magnitudes for a given frequency, namely the frequency of fin whale calls, we will ultimately operate on the FFT of the pressure and acceleration data. We therefore introduce some additional notation: $\vec{A}$ =FFT($\vec{a}$) and P=FFT(p). Below, $\vec{A}$ and P for a given frequency are written as $\vec{A}_p$ and P_p, and are complex numbers. Further note that $\vec{A}$ is a vector with x, y and z components (so calculations would be done three times, once for each element).

To estimate propagation direction, we again begin with Eqn 1. Assuming plane wave propagation, writing the pressure and acceleration amplitudes as complex exponentials, and assuming that both pressure and acceleration are measured at a single sensor location (r=0, neglecting propagation loss and range dependence for the purposes of convenience), we know that:

$$p = pe^{i(\omega t-\vec{k}\cdot\vec{r})} \qquad (3)$$

and

$$\vec{a} = \vec{a}e^{i(\omega t - \vec{k}\cdot\vec{r})}, \quad (4)$$

where $\vec{k}$ is the propagation vector and $\vec{r}$ is the position vector for the tag (assumed to be 0 for this initial calculation, though it would change as the wave propagates).

Differentiating Eqn 3 in three dimensions to get $-\nabla p$, then substituting the result and the complex exponential expression for $\vec{a}$ (from Eqn 4) in Eqn 1, we have:

$$\rho\vec{a}e^{i(\omega t - \vec{k}\cdot\vec{r})} = -(-i\vec{k}pe^{i(\omega t - \vec{k}\cdot\vec{r})}). \quad (5)$$

Dividing by the complex exponential term that appears on both sides of the equation and simplifying, we obtain:

$$\rho\vec{a} = i\vec{k}p, \quad (6)$$

or, in the frequency domain and for a given single frequency:

$$\rho\vec{A}_p = i\vec{k}P_p, \quad (7)$$

so:

$$\vec{k} = \frac{\rho A_p}{iP_p}. \quad (8)$$

Calculating pressure and acceleration magnitudes for a frequency of 20 Hz produced results that did not satisfy these relationships: the magnitude of $\vec{k}$ was not equal to the wave number, and the imaginary parts of $\vec{k}$ were not substantially smaller than its real parts. This supports the idea that the call was recorded in the near field.

We can also consider a simple comparison of the relative magnitudes of the pressure and accelerometer signals under the far-field, plane wave assumption. Expressing the pressure as a complex exponential as in Eqn 3, we can rearrange Eqn 1 to show that in the far field, acceleration and pressure are proportional to each other with the proportional constant equal to $2\pi f/\rho c=\omega/\rho c=k/\rho$.

Summary and conclusions

The direction of call propagation could not be determined because the above conditions were not satisfied, suggesting that the tag is in the near field of the produced call. In addition, magnitudes of acoustic calls measured on the tags should have corresponded to accelerometer magnitudes of the order 10^{-2} m s^{-2}, if the recording were made in the far field and accelerometer signals were caused by particle acceleration. In fact, accelerometer values were generally 10^{-1} m s^{-2}, an order of magnitude higher than expected, indicating the accelerometer readings are being enhanced in some way, which could be extreme near-field phenomena and/or tagged animal body vibration.

Modeling the near field requires an understanding of the mechanics of how a fin whale projects sound, which at this point is limited. For simple-geometry piston transducers, one of the best-studied sources of acoustic waves in a fluid, the transition range to the far field is approximately the area of the piston divided by the acoustic wavelength (Clay and Medwin, 1977). A hypothetical fin whale sound source could be approximated by a circular piston of approximately 5 m diameter, which when transmitting at the low frequency of 20 Hz will act as a monopole. In this case the far field begins at ~1/5λ, or 15 m. If this is the case, it is unlikely that even a very close associate fin whale (average fin whale length 17 m) could produce a call whose pressure/accelerometer relationship would act as in the near field. However, for other source types, the near field can theoretically begin greater than 150 m away (~2λ); 150 m would be approximately eight adult fin whale lengths away. It is therefore possible that the tag could still be in the near field of calls produced by an associate whale within a few whale lengths of the tagged whale.

However, it is unlikely that a tag would drift even 15 m away in less than 3 s after detachment, and yet a call produced at that time registered no signal on the accelerometer record (Fig. 2). In addition, an associate whale, bp13_258a, was tagged shortly before bp13_258b, whose tag record is described here. The acoustic record of bp13_258a was scanned for acoustic calls and none were found, even though this whale maintained a close spatial relationship with bp13_258b for a portion of the tag attachment period. It is possible that the flow noise and associated body movements of that whale were enough to obscure the calls of its associate, despite their proximity to one another. Signal-to-noise ratio for the calls on the tag attached to a drifting buoy were low and did not allow accurate measurements of those calls. Because of this and the lack of calls on the record of bp13_258a, we were unable to test whether these physical relationships would in fact hold for calls known to be in the far field.

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Competing interests
The authors declare no competing financial interests.

Author contributions
J.A.G., A.K.S. and S.L.D. analyzed data and wrote the paper. All authors contributed with fieldwork, experimental design, manuscript editing and/or theory.

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