

Gray whales hear and respond to signals from a 21–25 kHz active sonar

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Abstract

Shore-based theodolite tracking of eastern gray whale (*Eschrichtius robustus*) movements was conducted to test for potential whale responses to a high-frequency sonar system. Southbound migrating whales were observed from two California shore observation stations as the whales swam past the source vessel that was moored in their migration path. The sonar transducer was deployed from the vessel during all observations, broadcasting 21–25 kHz sweeps for half of each day, the other half remaining silent. The order of control and experimental periods was randomized. No readily apparent response to sonar transmissions was observed in the field or in the visual data. Statistical analysis of tracking data indicates that, compared to control data, gray whales deflected inshore at ranges of 1–2 km from the vessel during sonar transmissions at a received sound pressure level of approximately 148 dB re 1 μPa^2 (134 dB re 1 $\mu\text{Pa}^2\text{s}$). These data suggest that the functional hearing sensitivity of gray whales extends to at least 21 kHz.

KEYWORDS

behavioral response, context, hearing, playback, sonar, theodolite

1 | INTRODUCTION

As concern over the potential impacts of anthropogenic sounds on marine animals increases, it becomes more important to understand their auditory capabilities. There are a number of ways that hearing can be described. Auditory or hearing thresholds are the lowest level of sound at which an animal can detect a sound, in the absence of noise. Audiograms are composed of a series of thresholds obtained at different frequencies that can provide a more

complete description of an animals' hearing ability. However, animals, especially those in the wild, can have persistent noise levels in their environment that might exceed hearing thresholds. Any hearing measurement conducted in such an environment should be considered a "noise limited" value. Even higher thresholds can be associated with behavioral changes or physiological damage. Lucke et al. (2016) provide a review of these and related issues.

Traditionally, hearing sensitivity has been investigated with captive animals trained to indicate their perception of a sound (e.g., Kastelein, Hoek, De Jong, & Wensveen, 2010). Such studies are often considered to be the best approach to measuring hearing ability but require potentially lengthy training times with the experimental subjects (Sisneros, Popper, Hawkins, & Fay, 2016). More recently, the use of auditory brainstem response (ABR) or auditory evoked potential (AEP) methods has become more common. These are based on detection of neural activity when the animal is presented with an auditory stimulus. Historically, ABR and AEP methods have tended to produce auditory thresholds that were higher than those produced through behavioral studies (e.g., Szymanski et al., 1999). However new signal processing techniques can now produce threshold estimates using ABR data that are closer to those obtained with trained animals (Finneran, Mulsow, Jones, Houser, & Burkard, 2017b; Houser & Finneran, 2006a; Supin, 2001; Yuen, Nachtigall, Breese, & Supin, 2005). One advantage of ABR methods is that they can be used with untrained animals, reducing the amount of time needed to measure hearing ability. Therefore, this approach has the potential to increase the number of animals for which hearing data are available.

A limitation of both ABR and behavioral methods is that they require that the animal be at least temporarily restrained. This requirement makes it more difficult to obtain hearing data for larger animals. Efforts to create rapid deployment teams to measure the hearing of stranded individuals or large numbers of captive cetaceans in short time periods are beginning to produce usable results (Finneran, Houser, Mase-Guthrie, Ewing, & Lingenfeller, 2009; Houser & Finneran, 2006b; Mann et al., 2010). Attempts to measure the hearing ability of a captive gray whale calf did not provide definitive hearing measurements. However, the data suggested that hearing ability between 3 and 9 kHz was better than that at lower frequencies (Ridgway & Carder, 2001).

There have been attempts in the past to obtain data on the hearing capabilities of large, wild cetaceans. These have typically been behavioral response thresholds (i.e., the minimum level of sound necessary to elicit an observable reaction), as opposed to auditory detection thresholds (i.e., the minimum level of sound necessary for the animal to detect the sound; Frankel, Mobley, & Herman, 1995). There is likely to be a variable offset between behavioral response and detection thresholds, where the value of this offset is thought to be related to the information encoded into the signal (e.g., Deecke, Slater, & Ford, 2002) and the context of exposure (Ellison, Southall, Clark, & Frankel, 2012). Biologically important signals, such as the calls of a predator, are expected to have a very small to zero difference between these two thresholds. The behavioral response of gray whales to playbacks of killer whale (*Orcinus orca*) calls at a 0 dB signal-to-noise ratio (SNR) supports this assertion (Malme, Miles, Clark, Tyack, & Bird, 1983). When presenting novel stimuli to animals, it is reasonable to expect a difference between the auditory and behavioral threshold, i.e., the level of a novel stimulus has to be louder than just detectable in order to elicit a response. However, it is important to note that while the difference between behavioral and auditory thresholds is uncertain, behavioral responses clearly indicate that the animal perceived the signal, and as such provides information about the animal's frequency detection range.

Dahlheim and Ljungblad (1990) investigated gray whale hearing ability by projecting one-second-long tones between 200 Hz and 2.5 kHz to free-swimming whales. The source level of these tones increased with their frequency. Behavioral responses were detected following presentation of tones between 800 and 1,500 Hz with source levels ranging from 95 to 135 dB re 1 $\mu\text{Pa}^2\text{m}^2$. Tones from 1,800 to 2,500 Hz were projected at source levels of 145 dB re 1 $\mu\text{Pa}^2\text{m}^2$, but no responses were observed to these signals. Precise distances from the transducer were not reported. Therefore, no estimates of the received level when responses were provided.

Frankel et al. (1995) reinterpreted playback of biologically meaningful Alaskan humpback whale feeding calls to Hawaiian humpback whales (*Megaptera novaeangliae*; Mobley, Herman, & Frankel, 1988). Typical responses of the whales were overt changes in course and rapid approach toward the playback vessel, often to within meters of the source. The behavioral response threshold was estimated as the predicted received level at the animal. These feeding

calls ranged from 400 Hz to 550 Hz and elicited responses at received broadband levels as low as 102 dB re $1 \mu\text{Pa}^2$ (RMS). While the original paper reported that this level represented 16 dB SNR, a comparison of the received sound levels with more recent and thorough ambient noise estimates for the same area (Frankel & Clark, 1998) suggest that the whales were responding at SNRs close to 0 dB. This is consistent with the observation of a 0 dB SNR response threshold of gray whales to killer whale vocalizations (Malme et al., 1983).

A subsequent study examined the response of migrating gray whales to low-frequency signals from the U.S. Navy's SURTASS-LFA sonar (Clark, Tyack, & Ellison, 1999; Tyack & Clark, 1998). That study used a 160–330 Hz signal, composed of six downsweeps and three CW tonals. The source was sequentially placed at two locations. The first was directly in the migration path. It was later on the offshore edge of the migration corridor. The source level was increased by 15 dB when the source was moved offshore, to maintain the same range of received levels within the migratory corridor. Gray whales responded strongly to signal presentation when the source was in the migration path at received levels of 138–144 dB re $1 \mu\text{Pa}^2$ (Buck & Tyack, 2000). Despite the increased source level, the animals exhibited no response when the source was moved to the offshore edge of the migration corridor, strongly indicating the importance of acoustic context in predicting behavioral response (Ellison et al., 2012). Much of the design and methodology of that earlier experiment were used in this study to test if gray whales would respond to a high-frequency (21–25 kHz) sonar. Any meaningful response would indicate acoustic sensitivity in this frequency range.

2 | METHODS

This study was designed to track the movements of migrating gray whales that might be exposed to short duration (20–880 ms) sonar chirp from 21 to 25 kHz with a source level of 215 dB re $1 \mu\text{Pa}^2\text{m}^2$. Gray whales migrate close to shore where they are easily observed (Shelden & Laake, 2002). All whales are migrating southward during January, ensuring a new set of experimentally naïve subjects each day.

Two shore-based observation teams used theodolites to locate gray whales when they surfaced as they swam past the sonar source vessel (Würsig, Cipriano, & Würsig, 1991). Individual theodolite location estimates of the same whale groups were combined to form whale tracks. These were examined for any potential response to the sonar signal and used in a separate study to provide ground-truth data for comparison with sonar data location estimates (Lucifredi & Stein, 2007).

2.1 | Field site

The study site was located offshore of Point Buchon, north of San Luis Obispo, California (Figure 1). Two shore stations were set two km apart. Gray whales swam southward past these shore observation stations during the January 2004 migration. The R/V *New Horizon* deployed the Integrated Marine Mammal Monitoring and Protection System (IMAPS) sonar source. The sonar transmitter was a vertical line array that produced a vertically directional (6° beamwidth) and horizontally omnidirectional signal every 5 s (Lucifredi & Stein, 2007). The source ship was moored at two different mooring locations that were placed between the two shore stations and in the migration path of the gray whales. The initial position of the mooring was 35.214°N , 120.902°W . On January 21, the mooring was moved inshore and slightly north of the original mooring. The new mooring location of 35.225°N , 120.903°W was used for the remainder of the study.

2.2 | Data collection methods

The use of two observation stations allowed the whales to be tracked for a longer period of time and distance than would have been possible with a single station. The two shore stations were designed to allow the northern shore observers to

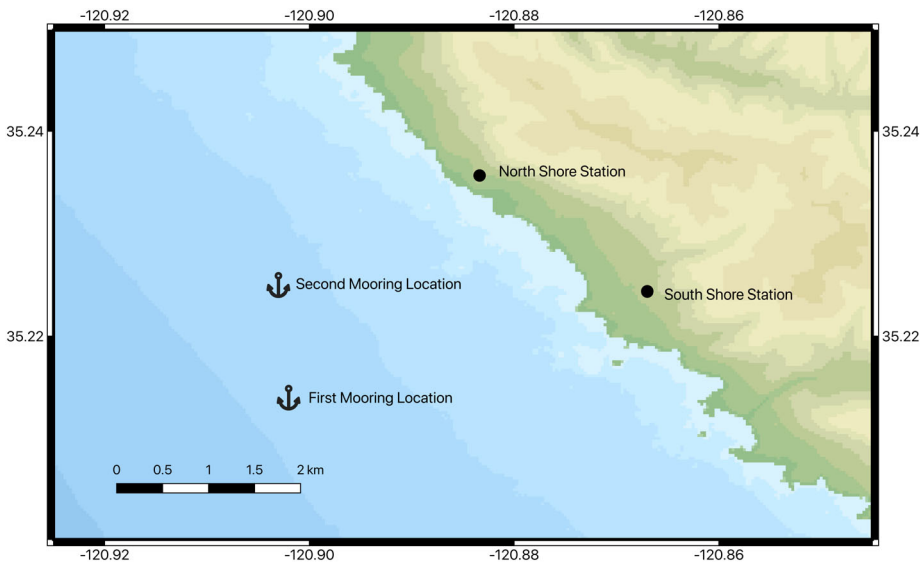


FIGURE 1 Study location. The two shore stations are shown along with the two mooring locations from which the acoustic source was deployed.

detect and track the southbound whales and then “hand off” each group to the southern observers. The handing off procedure began by staff communicating via radio between the two stations describing the location and behavior of the animals. Ideally, teams from both stations took a simultaneous theodolite measurement (fix) on the group to confirm that the two half-tracks were linked properly. Mean total track duration was 42 min and had a length of 4.1 km.

Shore-based observations began early in the morning and continued throughout the day. Observations were made when wind speeds were <25 knots and when the visual tracking area was not obscured by fog. Each shore station was manned by five personnel: a theodolite operator, a computer operator, a note-taker, an observer/spotter, and a radio operator. Observers used naked eye and Fujinon 7 × 50 binoculars equipped with reticles and a magnetic compass to detect and track whales. Leitz/Sokkisha theodolites (models DT-5a and DT-500) were used to locate whale groups. Both theodolites were calibrated immediately prior to the field effort. Groups were defined as one or more whales within five body lengths of each other and engaged in coordinated swimming behavior. When animals surfaced, the declination and bearing angles from the shore station to the whales were measured with the theodolite. These data were transmitted electronically to Dell Inspiron 8500 computers running Pythagoras software (Gailey & Ortega-Ortiz, 2002) that recorded the angles and the time of data collection. The computer operators then entered a text label that identified the group.

The shore observers were blind to experimental condition, i.e., whether the sonar was on or off. A balanced randomized transmission schedule was used. As shown in Figure 2, the sonar transmitted for one half of each day, either during the morning or the afternoon. The schedule was predetermined by the transmit team, although occasionally deviations from schedule were needed. The portion of the day when the sonar was transmitting was referred to as experimental condition, while the other half of the day without sonar transmission was considered the control condition.

The R/V *New Horizon* motored from the harbor at the start of each day, attached to the mooring and deployed the IMAPS sonar. The sonar transducer was deployed for the entire day during both control and transmission periods. This was done so that the only difference between control and experimental periods was whether the signal was being transmitted. This controlled for any effect of the transducer being in the water and the vessel being located in the migration path and prevented cueing the observers to the experimental condition.

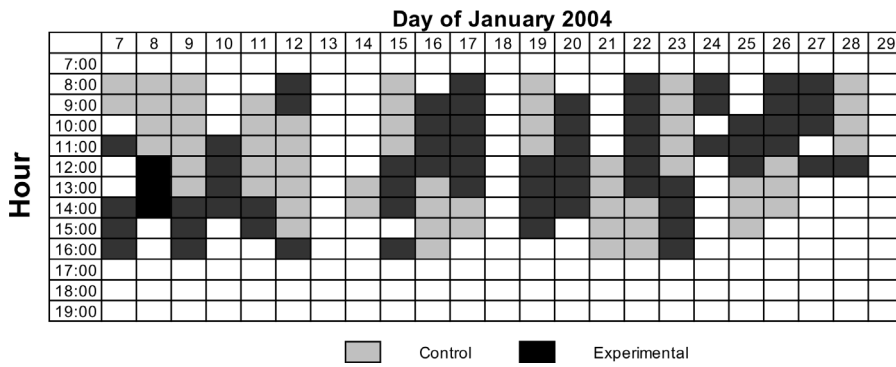


FIGURE 2 Graphical representation of data collection efforts. Control and experimental blocks are in gray and black. White blocks are hours without data collection.

Two marine mammal mitigation observers were stationed on the vessel to detect any marine mammals that approached within 100 m. If any marine mammal was seen within this distance, the sonar was shut down for 15 min, or until the animal was seen again farther away from the vessel. The shipboard observers also assisted with the handing off procedure between the two shore stations. Sonar transmissions were also halted when weather prevented adequate visual observation.

2.3 | Track fusion

The two shore stations collected data on independent computers. While the observers made their best efforts to communicate the correct identification of the groups to the other station during the handing off procedure, errors inevitably occurred. The two theodolite data files for each day were checked in the evening, and identifiable errors were corrected.

A MATLAB program was written to combine the daily north and south station data files into a single file. The program took the measured locations of whales from each shore station and calculated new theodolite data for a single “virtual” theodolite station located between the two stations. These transformed theodolite data were exported as a single file in Aardvark data format (Mills, 1996). Aardvark data visualization tools were used to detect misidentified groups and other errors in the data. If two theodolite fixes were taken on the same group and were separated in time by <60 s, then one fix was deleted since descriptive statistics calculated from such a pair of measures were more likely to be strongly affected by measurement error.

The fused and edited theodolite tracks were then analyzed with the Aardvark statistics package (Mills, 1996), which creates a variety of descriptive statistics for the track of each group as well as the relative distance and position of the group from the source vessel. Finally, the experimental condition for each group was determined by whether the sonar signal was being transmitted during the observed whale track. There were three conditions: control, where the entire track was recorded without sonar transmissions; transitional, when a portion of the track was recorded during control and a portion during transmission; and experimental, when the entire track was recorded during sonar transmission. Transitional tracks were deleted from the analysis, and the remaining control and experimental tracks were compared statistically.

2.4 | Transmission loss measurements and acoustic recording

On two occasions, a portable recording system was deployed from a small inflatable boat that moved away from the R/V *New Horizon* on a linear transect in order to measure the received sound level of the sonar pings as a function of

range. The received level (RL) data were used to create an empirical transmission loss (TL) curve that was then used to predict sound exposure at the animal locations. These measured RLs were found to agree well with predictions from the OASES propagation model (Lucifredi & Stein, 2007).

Additionally, two bottom-mounted autonomous recorders (MARU pop-ups) were deployed approximately one and two kilometers away from the R/V *New Horizon* (Clark, Calupca, Charif, Corzilius, & Fristrup, 1998). These units recorded continuously for five days at a sampling rate of 64 kHz. After retrieval of the units, the spectral characteristics of the sonar signals were examined and used to evaluate the acoustic characteristics of the transmission, i.e., the presence or absence of low-frequency artifacts.

2.5 | Sonar signal characteristics

The IMAPS sonar had a maximum RMS source level of 215 dB re $1 \mu\text{Pa}^2\text{m}^2$. The frequency ranged from 21 to 25 kHz. Pulse duration ranged from 20 to 80 ms with a ping interval of 5 s (Figure 3). The spectrogram was made with a 512 point FFT, Hann windowing, and 93.5% overlap. The continuous spectral line at 26.3 kHz is an artifact of the recording system.

2.6 | Statistical methods

2.6.1 | Movement segment length and duration

A pair of successive whale group locations is referred to as a movement segment. The length and duration of these segments were compared between control and experimental conditions using a Wilcoxon rank-sum test since the distribution of speeds and durations was skewed toward lower values. Earlier studies had shown that humpback whales respond to low-frequency sound by increasing the length and duration of these movement segments (Frankel & Clark, 1998, 2000).

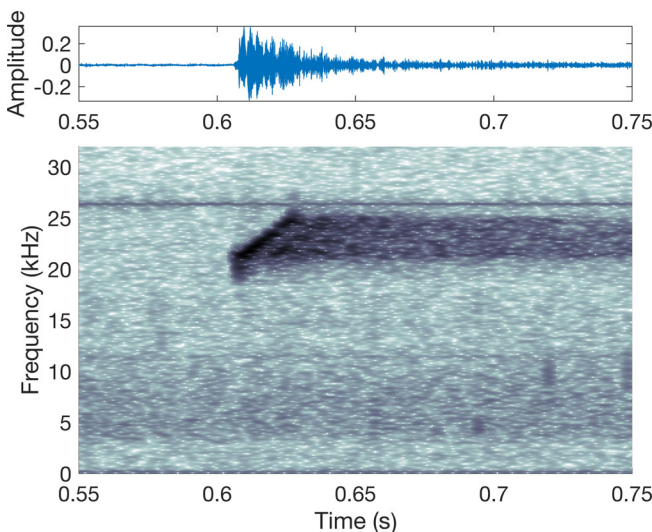


FIGURE 3 The waveform and a spectrogram of the IMAPS ping recorded with a pop-up MARU recorder. The tone at 26.3 kHz is an artifact of the recording system. Apparent reverberation of the sonar chirp is seen as well.

2.6.2 | Swimming speed

Swimming speed was measured by dividing the distance between successive whale locations by the elapsed time. It was possible that different individuals in the group would be “fixed” at different surfacings. Therefore, only one location estimate was taken per surfacing to minimize the potential effect of fixing different individuals. The mean speed for each group was calculated. A one-way ANOVA was used to test for differences in speed between control and experimental conditions.

2.6.3 | Relative orientation score (ROS)

The relative orientation score (ROS) was defined by Bowles, Smultea, Würsig, Demaster and Palka (1994) as:

$$\text{ROS} = \cosine(\text{orientation of a whale relative to the vessel} - \text{relative bearing to the vessel})$$

The values of ROS range from +1, which indicates a whale swimming directly toward a vessel, to -1, which indicates a whale swimming directly away from a vessel. Therefore, the higher the value of this metric, the more directly an animal is swimming toward the vessel. A mean ROS was determined for each group. The distribution of the ROS was non-normal, so a Wilcoxon rank-sum test was used to compare the scores between control and experimental conditions.

2.6.4 | Offshore distance analysis

Earlier gray whale noise experiments created an analysis method to measure the offshore distance of the whales both upstream and downstream of the position of the source vessel along the migration path. (Malme et al., 1983; fig. 7.1). This is accomplished by translating whale positions to a new coordinate system. The first axis is migration axis, which is a regression line of the coastline in the study area. The second axis is the offshore distance. This coordinate system is designed so that most whales will travel along the migration axis with minimal deflection in the offshore direction (Figure 4). As in Malme et al. (1983), eleven ranges (-4, -3, -2, -1, -0.5, 0, 0.5, 1, 2, 3, 4 km) along the migration axis were selected. Measured whale tracks were linearly interpolated to estimate the offshore distance at each of the migration axis ranges. Because these offshore distances of control and experimental groups are repeated measures of the same group of whales, the overall effect of sonar transmission was first examined with a generalized estimating equation (GEE) approach (Hanley, Negassa, Edwardes, & Forrester, 2003). The “geeglm” function from the R package “geepack” was used (Højsgaard, Halekoh, & Yan, 2005) with an autoregressive correlation model. One-way ANOVAs would be used as post hoc tests if an effect of sonar transmission was found. Differences would indicate changes in swimming path due to the sonar transmissions.

3 | RESULTS

3.1 | Acoustic stimuli

Because the signal broadcast to the gray whales was expected to be near or above the projected upper range of their hearing, the MARU pop-up recordings were examined for any low-frequency artifacts. Relative (uncalibrated) sound pressure levels were compared between and during sonar transmissions (Figure 5). Spectral parameters were FFT size = 256, Hamming window, and 87.5% overlap. The spectrum between pings is shown as a dotted line while the spectrum of the ping is a solid line. Note that there is a recorder-generated acoustic artifact at 26.3 kHz that occurs throughout the recording.

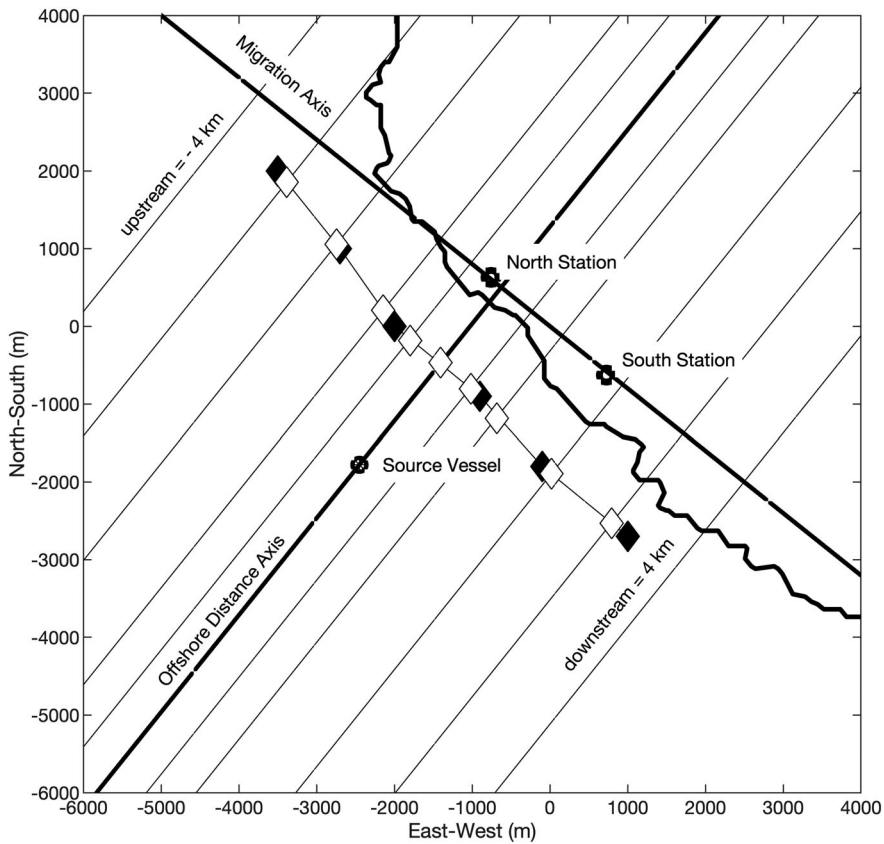


FIGURE 4 Actual locations (black diamonds) are shown for a sample whale track. The distance offshore from the migration axis was interpolated at the reference distances (e.g., -4 km upstream, 4 km downstream) as shown by the thick black lines. The interpolated positions are shown as white diamonds.

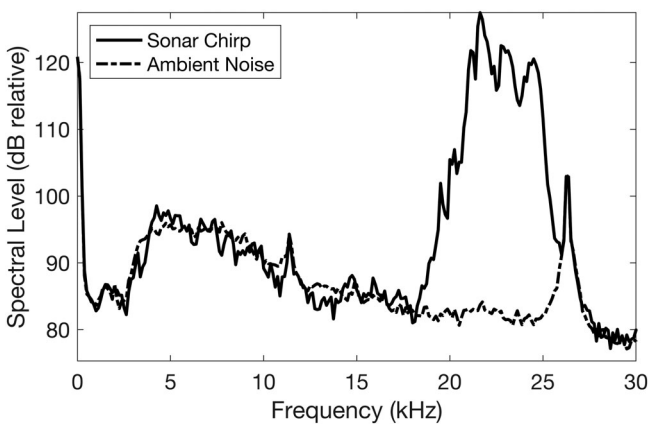


FIGURE 5 The spectrum of ambient noise and a ping. Ping energy is limited to the 21–25 kHz region. The peak at 26.3 kHz is an artifact of the recording system.

The background noise level between 2 and 10 kHz was elevated relative to frequencies above and below. This elevated noise level occurred on all recordings, including when the vessel was not present. These data show that the projected energy was solely within the intended frequency range and that the IMAPS transducer did not transmit any low-frequency signals that could be responsible for an observed response.

FIGURE 6 Transmission loss measurements and curve fit to the data. The dashed line shows spherical spreading at all ranges.

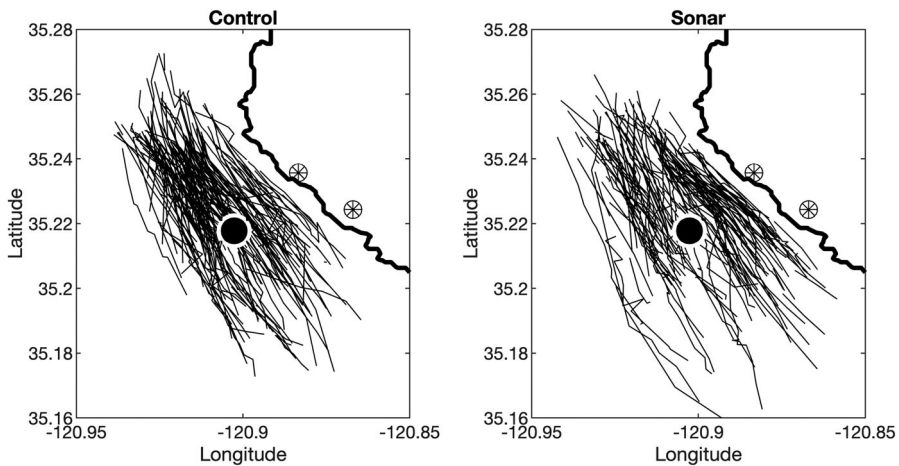
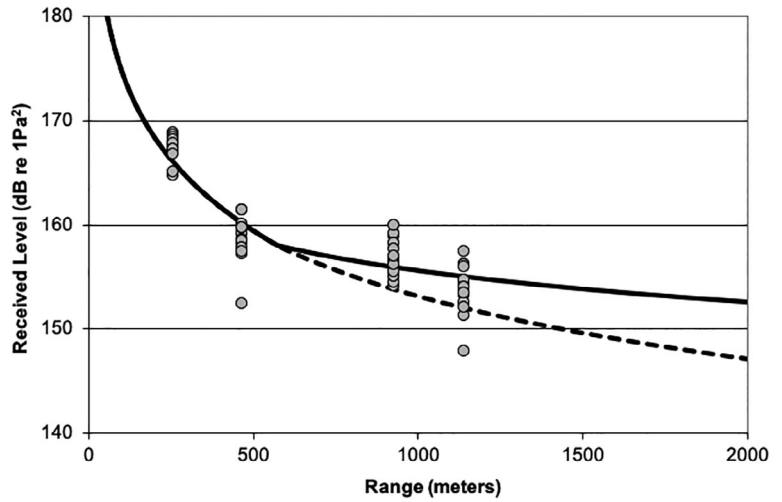


FIGURE 7 Whale tracks collected during control (left) conditions and sonar transmission (right). The gap in the tracks during the sonar condition is clearly visible and is not present in the control condition.

3.2 | Transmission loss

Received level measurements were made over several days at a variety of ranges. An empirical model was fit to these measurements. The empirical model is based upon spherical spreading over the first 572 m of range and then transitioning to cylindrical spreading. An absorption term of 0.0032 dB/m was applied at all ranges (Figure 6). This transmission loss curve was used to predict the received levels at the whales.

3.3 | Whale track data

Data were collected from 7 to 28 January 2004, with a total of 119.7 hr of observation effort for both stations. A total of 532 whale groups were tracked by one or more shore stations. Group sizes ranged from 1 to 10, with a mean

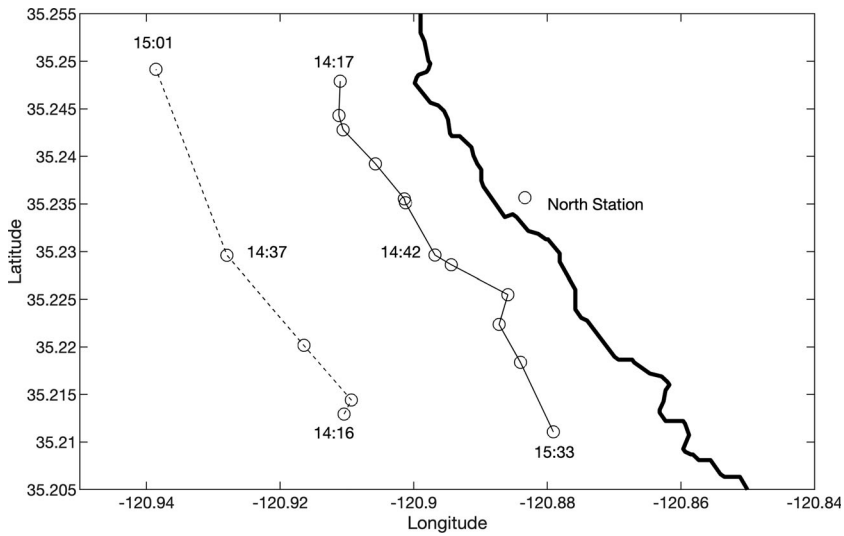


FIGURE 8 Killer whales (dashed track) swimming north as a group of gray whales (solid track) swims south. At about 14:42, the gray whales made an overt turn inshore away from the killer whales. The thick black line is the shoreline.

of 1.75 whales. During the experiment, observers never noted an obvious change in the whales' swimming patterns in response to the presence of the vessel or sonar transmissions. This is in stark contrast to the LFA sonar test conducted in the same area (Clark et al., 1999; Tyack & Clark, 1998), where the deflection of animals in response to the sonar was readily apparent to the shore teams during data collection.

Nevertheless, tracks collected during control and sonar transmission show a remarkably different pattern. Figure 7 shows that whale tracks during the control period appear to be evenly distributed through the migration corridor. However, the tracks produced during the sonar transmissions show a paucity of whale tracks near the vessel and indications that more whales shifted their paths inshore.

The only strong reaction observed during data collection was an apparent response to a group of killer whales that traveled into the study area from the south on 17 January (Figure 8). A group of gray whales to north of the killer whales altered their course and swam inshore towards shallower waters as the killer whales approached. The closest point of approach between the two groups was 2.2 km.

3.4 | Movement metrics

No significant differences were found in segment distance ($Z = 0.392$, $p = .695$) nor segment duration ($Z = 0.415$, $p = .679$) between the control and experimental conditions. The mean speed of whales during the experimental condition was slightly slower than during the control condition (6.23 v. 6.56 km/hr). This difference was statistically significant ($F = 4.643$, $p = .032$). The relative orientation scores for sonar and control conditions were compared with a one-way ANOVA. ROS scores were significantly higher during control conditions than in the sonar period (0.420 vs. 0.30; $F_{(1,361)} = 4.487$, $p = .038$). This indicates that whales swam more directly toward the source vessel during control conditions. Conversely, the lower ROS score during sonar transmissions indicates that whales were deflecting around the ship transmitting sonar pings.

3.5 | Offshore distance analysis

The linearly interpolated locations and offshore distances at the 11 positions of the migration axis were compared between control and experimental tracks. The mean and standard deviation of the offshore distances are shown in Figure 9. The two positions of the source vessel are shown as green triangles.

Because these are repeated measurements of the same group, a GEE analysis using pod identification as the clustering variable was used to test for the effect of sonar transmission. Table 1 shows that both the position along the migration axis and sonar experimental condition were statistically significant. The interaction term was found to

FIGURE 9 The distance offshore for gray whale tracks 4 km north (negative values) and south (positive values) of the vessel position. Thus, whales are moving from left to right in this presentation. Whale positions were significantly closer to shore from 1 km north to 1 km south of the vessel during sonar transmissions (indicated by larger yellow diamonds).

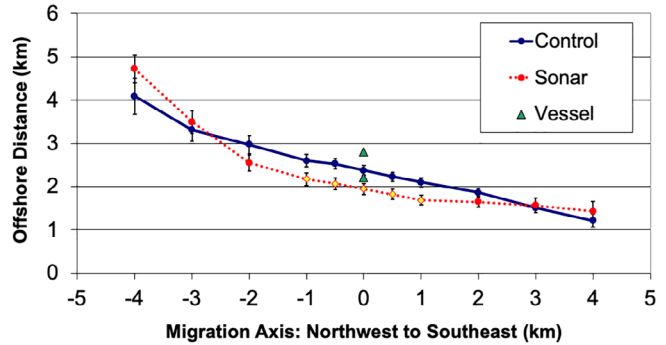


TABLE 1 GEE parameter estimates and significance test results.

Parameter	Coefficient estimate	Standard error	Wald	<i>p</i>
Intercept	2,305.7	80.5	819.65	<2e-16
Migration axis distance	-318.0	12.2	681.27	<2e-16
Sonar transmission	-155.2	60.3	6.62	.01

TABLE 2 *F* values for distance offshore ANOVAs are shown. Control and Sonar represent mean distance offshore followed by the standard error (SE) of the mean; *n* refers to sample size.

North to south distance	Control	Sonar	SE (Control)	SE (Sonar)	<i>n</i> (Control)	<i>n</i> (Sonar)	<i>F</i>	<i>p</i>
-4	4.09	4.72	0.42	0.32	3	5	1.400	0.280
-3	3.31	3.49	0.25	0.27	17	15	0.255	0.617
-2	2.97	2.55	0.21	0.18	30	38	2.374	0.128
-1 ^a	2.60	2.17	0.14	0.15	67	58	4.317	0.040
-0.5 ^a	2.53	2.06	0.12	0.14	84	70	6.425	0.012
0 ^a	2.38	1.94	0.12	0.13	84	70	6.298	0.013
0.5 ^a	2.23	1.82	0.11	0.12	84	70	6.508	0.012
1 ^a	2.10	1.68	0.10	0.11	79	64	7.669	0.006
2	1.86	1.64	0.10	0.11	61	45	2.169	0.144
3	1.51	1.56	0.12	0.17	43	22	0.074	0.787
4	1.21	1.43	0.16	0.22	21	11	1.017	0.320

^aRows with significant differences.

be nonsignificant and removed from the model. The sonar coefficient was found to be -155.2 , confirming the inshore movement during sonar transmissions.

One-way ANOVAs (Table 2) were used as post hoc tests for differences at each location between control and sonar conditions. At the position of -4 km north of the vessel, there is a difference in the mean, but the standard deviation for these measures is so large that it is not significantly different. At the positions of -2 and -3 km to the north, the mean offshore distances are very similar. However, at the positions of -1.0 , -0.5 , 0 , 0.5 , and 1.0 km north and south of the vessel, the animals presented with sonar are significantly inshore of the control animals. At distances of 2 , 3 , and 4 km south, there are again no statistically significant differences between the two groups' positions. Note that the control tracks pass between the two source vessel positions and very close to the inshore vessel position. Conversely the experimental animals swam inshore of both vessel positions.

The tracks in Figure 9 show that whales were deflecting from their baseline migration path as they approached the source vessel when sonar signals were being transmitted. The offshore distance measures are consistent with the change in ROS scores. At the position two kilometers north of the vessel, whales were closer inshore during sonar transmissions, but the difference was not statistically significant. When the whales reached one kilometer north of the vessel, the difference was significant. These data suggest that the deflection reaction began to occur about two kilometers away from the vessel or at a received level of ~ 148 dB re $1 \mu\text{Pa}^2$ (~ 134 dB re $1 \mu\text{Pa}^2\text{s}$).

4 | DISCUSSION

The changes in ROS and differences in the distance offshore clearly indicate that gray whales responded to the IMAPS sonar signal that ranged between 21 and 25 kHz at a received level of approximately 148 dB re $1 \mu\text{Pa}^2$ (134 dB re $1 \mu\text{Pa}^2\text{s}$). The response also demonstrates that their functional hearing range extends higher than 21 kHz. The hearing ability of gray whales has not been completely described, however, a predicted gray whale hearing curve based on ear anatomy, includes detection thresholds from 105 to 120 dB re $1 \mu\text{Pa}^2$ at 21 to 25 kHz (D. R. Ketten, personal communication, November 2005). A more generalized theoretical hearing curve for all mysticetes predicts thresholds between 67 and 76 dB re $1 \mu\text{Pa}^2/\text{Hz}$ for these frequencies (Finneran et al., 2017). While the values of the predicted thresholds vary greatly, both theoretical predictions do agree with the experimental finding that gray whales can hear above 21 kHz.

The current study and the low-frequency sonar (LFA) experiments (Clark et al., 1999; Tyack & Clark, 1998) used similar methods. Furthermore, these are the only two tests of the effects of nonimpulsive noise on gray whale movement behavior employing realistic source levels. However, the source level, as well as spectral and temporal qualities of these two stimuli differed, as did the magnitude of the response.

Gray whales reacted, sometimes overtly and obviously, to LFA sonar signals when the source was located in their migration path. The 50% response threshold was 135 dB re $1 \mu\text{Pa}^2$ (Buck & Tyack, 2003). This value is about 13 dB lower than the response threshold for the IMAPS sonar signal. Furthermore, there were none of the overt and obvious responses seen in the earlier study.

Any one or all of the signal structure differences between LFA and IMAPS might contribute to the difference in observed behavioral response. Motivational-structural rules (Morton, 1977) may apply to these signals to partially explain the differences in response. All signals were tonal. However, LFA was composed of downsweeps and CW tonals, whereas IMAPS was an upsweep. There are some data to indicate that upsweeps can produce stronger reactions than downsweeps (Kastelein, 2014; Nixon, Von Gierke, & Rosinger, 1969). In humans, longer stimuli at the same sound level have been found to be more annoying (Hiramatsu, Takagi, Yamamoto, & Ikeno, 1978; Huang & Griffin, 2014).

Interestingly, the approximate ranges of reaction for both the IMAPS and LFA study was between 1 and 2 km. This suggests there could be a proximity or spatial component involved in mediating the response of gray whales to

unfamiliar or anthropogenic sounds (Ellison, Southall, Frankel, Vigness-Raposa & Clark, 2018). This would also be consistent with the results of the offshore LFA playbacks, which did not elicit overt responses.

Nevertheless, the relatively high received levels of anthropogenic sound required to elicit behavioral responses contrasts with their response to killer whale calls. Malme et al. (1983) played killer whale calls to southbound migrating grays. Responses included cessation of migration, milling and movement toward the shore. These responses began at ranges greater than 2 km from the playback vessel, indicating the whales responded at or near a SNR of 0 dB. High responsiveness to killer whales is a common occurrence (Allen, Schanze, Solow, & Tyack, 2014; Bowers et al., 2018; Curé et al., 2013; Sivle et al., 2015). Indeed, the current study, a group of gray whales overtly turned away from a group of killer whales that passed 2.2 km away. There were no high-frequency recordings collected on this day, so there are no data on potential killer whale vocal production.

The difference in responsiveness among these three stimuli suggests that while gray whales can hear and will respond to IMAPS and LFA, neither the IMAPS nor LFA signals represented clear matches to biologically meaningful templates such as certain sounds from predators or conspecifics.

In conclusion, the response data have clearly shown that gray whales can perceive signals between 21 and 25 kHz, which greatly improves our understanding of their hearing ability. The IMAPS sonar signals produced responses at sound pressure levels much greater than needed for biologically meaningful signals (i.e., killer whales). Differences in the magnitude of response to the sonar signals may be due to differences in the structural characteristics of the two signals. The similarity of response distances between the two sources also suggests a potential proximity or spatial context effect in the response.

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AUTHOR CONTRIBUTIONS

Adam S. Frankel: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing. **Peter J. Stein:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review and editing.

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