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Relationship between visual counts and call detection rates of gray whales (*Eschrichtius robustus*) in Laguna San Ignacio, Mexico

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Daily acoustic calling rates of Eastern North Pacific (ENP) gray whales were measured on 6 days during 1 mo of their 2008 breeding season in the sheltered coastal lagoon of Laguna San Ignacio in Baja California, Mexico. Visual counts of whales determined that the numbers of single animals in the lower lagoon more than tripled over the observation period. All call types showed production peaks in the early morning and evening with minimum rates generally detected in the early afternoon. For four of the five observation days, the daily number of "S1"-type calls increased roughly as the square of the number of the animals in the lower lagoon during both daytime and nighttime. This relationship persisted when raw call counts were adjusted for variations in background noise level, using a simple propagation law derived from empirical measurements. The one observation day that did not fit the square-law relationship occurred during a week when the group size in the lagoon increased rapidly. These results suggest that passive acoustic monitoring does not measure gray whale group size directly but monitors the number of connections in the social network, which rises as roughly $M^2/2$ for a group size M.
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I. INTRODUCTION

A. Background on acoustic census efforts

Population estimates of marine mammals are currently performed by visual surveys, which are restricted to daylight hours and relatively calm weather conditions and can be costly when conducted in the open ocean. By contrast, passive acoustic monitoring can be an effective, cost-efficient technique for monitoring inaccessible habitats where visual studies are difficult (Baptista and Gaunt, 1997). The use of autonomous passive acoustic recorders to detect the seasonal presence of marine mammals in various ocean basins has become a popular technique, with a large accompanying literature (e.g., Stafford *et al.*, 1998; Mellinger *et al.*, 2004a; Mellinger *et al.*, 2004b; Moore *et al.*, 2006; Mellinger *et al.*, 2007a; Mellinger *et al.*, 2007b; Munger *et al.*, 2008). A natural question that arises is whether passive acoustic methods can be used to estimate the relative or even absolute abundance of marine mammal groups or population density—an "acoustic census."

Previous studies have used passive acoustic monitoring to supplement traditional methods of estimating population densities for terrestrial and aquatic organisms such as birds (Dawson and Efford, 2009; Adi *et al.*, 2010), elephants (Payne *et al.*, 2003; Thompson *et al.*, 2010; Venter and Hanekom, 2010), and marine mammals (McDonald and Fox, 1999; Douglas, 2000; Noad and Cato, 2000; Marques *et al.*, 2009; Moretti *et al.*, 2010; Kyhn *et al.,* 2012). A practical acoustic censusing method needs to overcome multiple challenges, including compensating for fluctuations in background noise levels, changing acoustic propagation characteristics, and variations in animal behavior with respect to age, sex, and multiple time scales. Perhaps the greatest challenge required to establish the efficiency of any acoustic censusing method on marine mammals is the difficulty in determining an accurate independent estimate of population density over appropriate spatial and temporal time scales. Despite the increasing popularity of acoustic censusing, few empirical studies exist that directly measure the functional relationship between call detection rates and population density due to the practical problem of independently verifying the acoustic population predictions. Most previously published acoustic censuses of marine mammals assume proportionality between sound detection rates and population size (e.g., (Marques *et al.*, 2009; Kyhn *et al.*, 2012), although one study on beluga whales claimed to find that the acoustic detection rate increased as the square of the number of animals present (Simard *et al.*, 2010).

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Here a simple acoustic census has been conducted at a unique location that permits accurate visual surveys of a non-captive marine mammal population. Between January and March 2008, acoustic recordings of gray whales (*Eschrichtius robustus*) were collected in Laguna San Ignacio (LSI), Baja California, Mexico, during the winter breeding season (Fig. 1). LSI is an enclosed coastal lagoon where gray whales gather to breed and give birth during the northern hemisphere winter. This study examines relationships between month-long visual counts of gray whales and both raw and noise-adjusted call detection rates for 6 days of acoustic recordings, over daytime and nighttime, measured throughout February/March in the lower region of the lagoon (Fig. 1). The instruments have been deployed in the same location every year since 2008, and some data collected in 2010 are used to estimate acoustic propagation conditions in the area.

There are three reasons why LSI provides an excellent laboratory for investigating the expected complex relationships between sound production rates, group size, ambient noise levels, and time of day. First, the lagoon's restricted geography, combined with the short dive times of the animals, enables frequent visual surveys to be conducted economically and accurately. Second, breeding individuals residing in the mouth of the lagoon (the "lower zone" marked in Fig. 1) travel frequently from one location to another, never loitering in one place for extended periods of time. Thus the spatial distribution of whale acoustic activity

in the lagoon is expected to be relatively homogenous, such that measurements of relative changes in acoustic activity on a single hydrophone may represent relative changes in the acoustic activity across the lower lagoon as a whole, which in turn may be related to the total group size in the lower zone. Finally, the ambient noise levels in the lagoon are relatively steady over time; over the entire month, the hourly noise levels varied by only 8–10 dB across the frequency range of interest in this study. Therefore relatively simple models can be used for adjusting sound detection rates for changes in detection range arising from the ambient noise fluctuations.

The rest of this introduction provides relevant background on the population trends and acoustic behavior of Eastern North Pacific gray whales. Section II describes the acoustic equipment, deployment location, visual survey procedures, and acoustic analysis methods, including methods for adjusting call detection rates for changes in ambient noise levels. Section III presents data manually analyzed from 6 days of acoustic data collected over a 4-wk period off Punta Piedra (Fig. 1), a prominent landmark in the lagoon. These 4 wk captured the middle portion of the breeding season between February 10 and March 8, 2008, during which the number of animals in the lower lagoon roughly tripled. The section discusses sound detection rates for three gray whale call types, the number of tourist boat transits, month-long trends in raw call rates, changes in the ambient noise background during the study, and measurements of the acoustic propagation characteristics of the monitoring area. Section IV discusses the diel patterns observed in two different call types and interprets the long-term nonlinear relationship observed between the visual counts and both the raw and noise-adjusted daily detection counts for the most common call type ("S1") detected.

B. Population trends of gray whales

Eastern North Pacific (ENP) gray whales seasonally migrate from their summer feeding grounds in the Bering, Chukchi, and (possibly) Beaufort Seas to coastal lagoons in Baja California, Mexico. Historically, gray whale population numbers have dramatically risen and fallen due to human exploitation and fluctuations in environmental conditions affecting their food supply. Throughout the 19th century commercial whalers harvested gray whales in major breeding lagoons and bays of Baja California, killing an estimated 7,000–8,000 gray whales (Henderson 1984). Continued hunting into the 20th century reduced the population to critically low numbers, and the gray whale finally received international protection from commercial whaling by the International Whaling Commission in 1946. By the 1960s, the gray whale population was estimated to be 15,000 whales (Rice and Wolman, 1971), and three decades later, in 1998, the population had recovered to an estimated historical level of around 21,000 whales. Following a range-wide mortality event from 1998 to 2000, a 2002 census indicated the population had been reduced to 16,000 whales; however, as of 2006–2007, the gray whale population was estimated to have recovered to approximately 19,000 whales
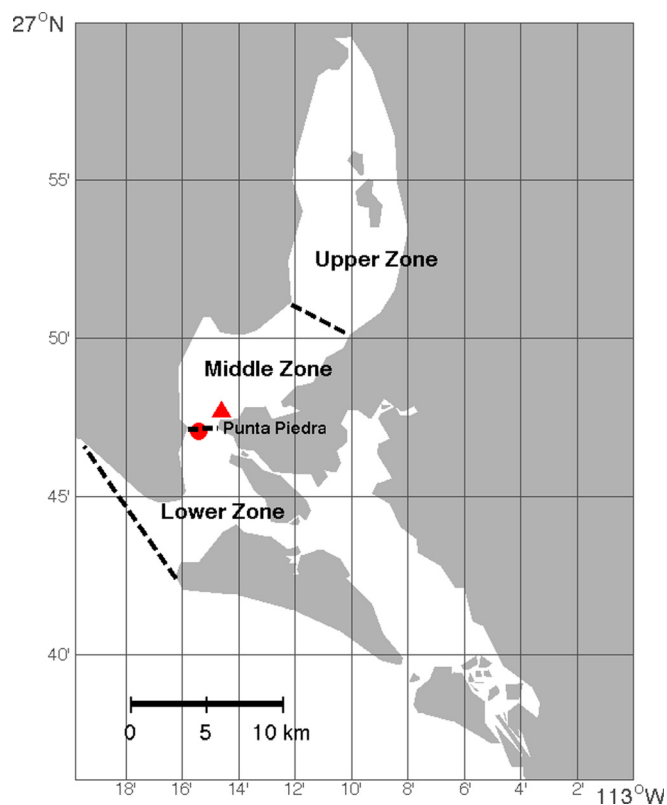

FIG. 1. (Color online) Map of Laguna San Ignacio (LSI), including 2008 and 2010 deployment location of acoustic hydrophone (solid triangle), which is similar to the cabled hydrophone location used by (Dahlheim, 1987). Visual surveys of gray whale population studies are subdivided into three zones indicated by dashed lines. An additional site in 2010 (filled circle) was deployed 1.5 km away to evaluate propagation conditions.

(Laake *et al.*, 2009). Only a small fraction of the total gray whale population winters at LSI. This lagoon remains protected from commercial whaling and most industrial development as a federal marine protected area and whale refuge, and it lies within Mexico's Vizcaino Biosphere Reserve. As a protected wildlife reserve, the lagoon and its gray whales attracted the development of eco-tourism camps along its southern shore. There remains considerable scientific and socio-economical interest in monitoring gray whale numbers in the lagoon each winter as an indicator of the general status of the ENP gray whale population.

The lagoon's relatively small size, high density of adult whales and calves, and cooperative efforts with the local eco-tourism industry has attracted research attention for decades. The lagoon has also attracted researchers due to its relatively isolated location, low levels of commercial development, and restrictions on the levels of tourist activity permitted in the lagoon. These factors provide a relatively undisturbed environment to study whale behavior, and the lagoon thus boasts a long history of visual and acoustic studies of gray whales dating back to the mid-1970s. After an initial period of annual surveys during the period 1977–1982 (Jones and Swartz, 1984), regular visual censuses of the whales in the lagoon were conducted only between 1996 and 2000. Regular systematic visual surveys were resumed in 2006, by the Laguna San Ignacio Ecosystem Science Program (LSIESP; *www.lsiecosystem.org;* last accessed Jan 30, 2012). The LSIESP team also documents individual whales using photographic identification (photo-ID) methods.

C. Gray whale acoustic behavior

The acoustic repertoire of gray whales has been primarily studied in the breeding-calving lagoons of Baja California (Dahlheim, 1987; Wisdom 2000; Ollervides, 2001), with less extensive efforts along the North American Pacific coast (Cummings *et al.*, 1968; Crane and Lashkari, 1996), and arctic waters (Moore *et al.*, 2006; Stafford *et al.*, 2007). In this paper, we restrict our review to sounds collected in LSI, where studies of gray whale acoustics have a relatively long history.

During winter seasons between 1981 and 1984, Dahlheim *et al.* (Dahlheim *et al.*, 1984; Dahlheim, 1987) conducted the first gray whale recordings in LSI by deploying an omni-directional hydrophone near Punta Piedra (Fig. 1). Her findings, distilled from a cumulative 565 hours of underwater recordings, discerned six types of calls, of which three are discussed in this paper. Over a decade later, Wisdom *et al.* (Wisdom, 2000) collected gray whale recordings from hydrophones deployed from a small 4-m boat, locally referred to as a panga.

Both studies have revealed that LSI gray whales produce sounds ranging from rapid, rhythmic pulses to FM signals. Gray whales produce an assorted collection of pulsed calls, with the so-called "S1" pulsed calls being predominant [Fig. 2(a)]. Individual pulses range in frequency between 100 and 1600 Hz and are grouped in sets of 3–18 pulses per call. Peak frequencies range between 300 and 800 Hz, and call durations average 1.8 s (Dahlheim *et al.*, 1984). A sec-

ond type of pulsed call, the "S4" [Fig. 2(b)], is characterized by clustered pulses with intervals much smaller than the S1 call, frequency content between 100 and 800 Hz, with peak frequencies between 150 and 300 Hz, and durations averaging between 0.5 and 1.5 s. A third call type, "S3", is an FM signal typically averaging 1.5 s per call [Fig. 2(c)]. This call is characterized by relatively low frequencies, ranging between 100 and 300 Hz. Wisdom (2000) reported the S3 as being the least common call type, comprising only 3% of her recorded calls. She also defined two additional call types: 1 b and the "rumble." Sound type 1 b is a pulsed signal, whereas "rumble" is a sound that Wisdom recorded in the presence of active calves.

Most researchers have concluded that gray whale sounds are not sonar signals but fill a social function (Wisdom, 2000). Previous studies suggest that these sounds might be used for communication purposes such as contact calling (Fish *et al.*, 1974; Norris *et al.*, 1977), species recognition (Dahlheim *et al.*, 1984), and providing behavioral context (Crane and Lashkari, 1996).

Three of the six call types identified by Dahlheim (S1, S3, S4) are used in this study, because these three calls were commonly found in the 2008 acoustic data set and were also easy to identify and distinguish from each other. Other call types, although present, were relatively uncommon, making conclusive identification difficult, based only on the descriptions and examples in Dahlheim's and Wisdom's theses.

II. MATERIALS AND METHODS

A. Acoustic recording equipment

Acoustic data were collected by a cylindrical, bottom-mounted recorder that contained a Persistor CF2 microprocessor, 60 GB hard drive, 4 GB flash memory chip, D-cell batteries, and a HTI-96-MIN hydrophone with sensitivity of -171.4 dB re 1 V/μPa. These electronics were packed inside a 12 cm diameter by 75 cm long acrylic pressure housing and then deployed from a small boat. In 2008, acoustic data were sampled at 6.125 kHz, and after recording for 67 h to flash memory, the device halted audio sampling for 1.75 h to transfer the data to hard disk. That year, the instrument recorded for 29 days before the batteries discharged. Deployments were also conducted in 2010, with a sampling rate of 12.5 kHz.

As shown in Fig. 3, during both years, two recorders were strapped to a 100 m polypropylene rope, which was deployed horizontally on the lagoon floor, with 10 kg anchors attached on both ends. The second recorder was intended as a backup system, so data from only one recorder are used in this study. The system was recovered using grappling hooks to avoid the use of surface buoys that could entangle whales. A HOBO weather station was also deployed onshore Punta Piedra to help determine relationships between local wind speed and ambient noise levels.

B. Field site

Visual surveys were conducted by LSIESP, and divided the lagoon into three zones: upper, middle, and lower. The
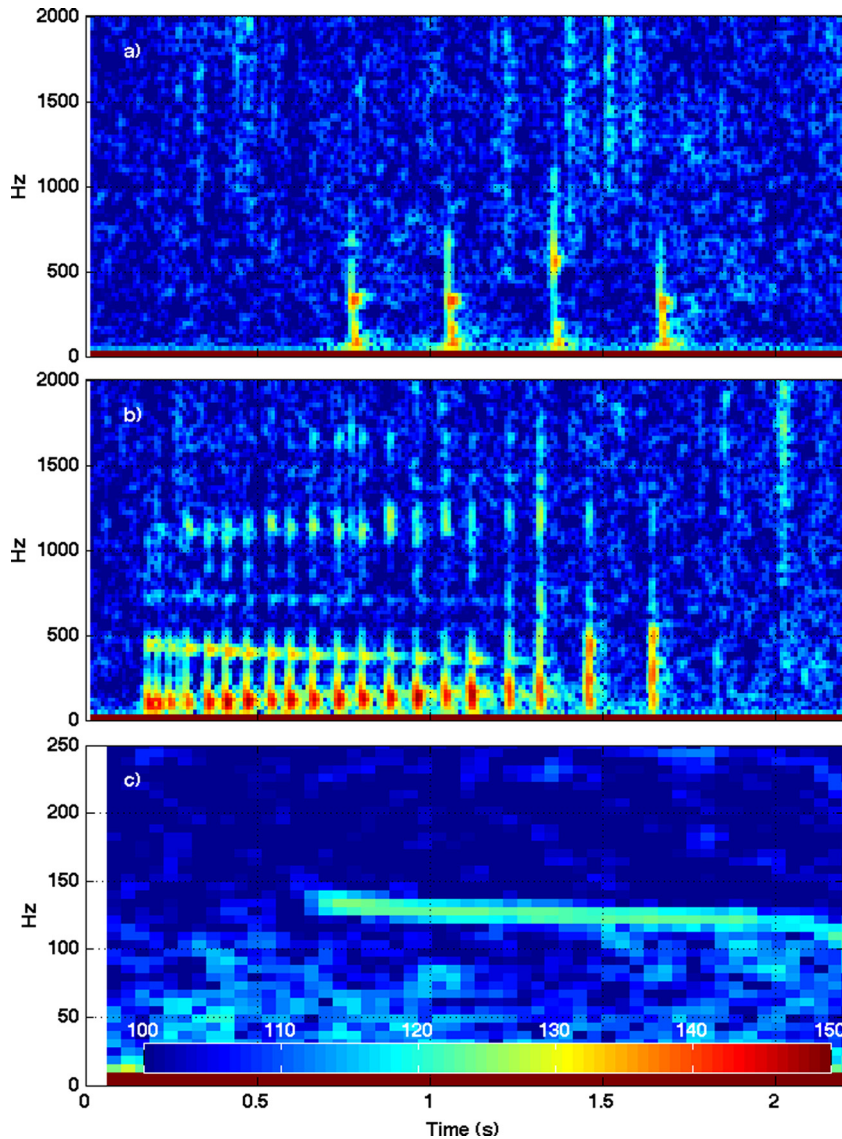
FIG. 2. (Color online) Example spectrograms of gray whale signals in Laguna San Ignacio recorded in 2008. (a) S1 call, showing a train of pulses with energy between 100 Hz and 1 kHz with peak frequencies between 300 and 800 Hz; (b) S4 call, with pulse bandwidth between 100 and 1500 Hz, with peak frequencies between 150 and 300 Hz, and total durations between 0.5 and 1.5 s; (c) S3 call, ranging between 90 and 300 Hz and with call durations between 1 and 2 s. The S1 and S4 call spectrograms are imaged using a 256 pt FFT with 75% overlap on a Hanning-windowed time series sampled at 6.25 kHz; the S3 spectrogram uses a 1024 pt FFT. Image intensity is in units of power spectral density (dB re 1 μPa^2/Hz).

lower zone begins from the entrance of the Pacific Ocean and extends to the narrow channel, next to Punta Piedra (Fig. 1). The lower zone typically contains a high density of breeding adult ("single") whales and is open to regulated
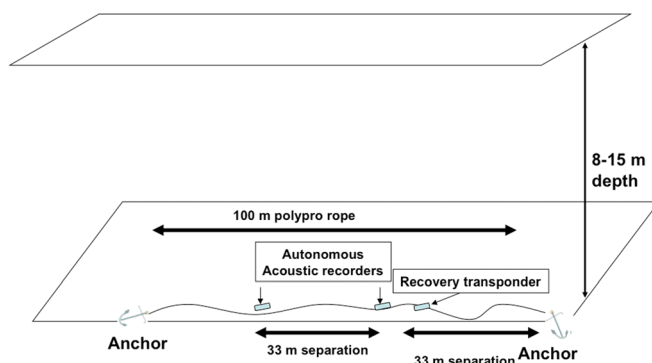

FIG. 3. (Color online) Deployment configuration of bottom-mounted acoustic recording station. Recorders are anchored at 8–15 m below the surface, separated by 33 m of polypropylene rope. An acoustic transponder is attached between a recorder and anchor to facilitate recovery. The second recorder was intended as a backup, so data from only one recorder is used in this study.

whale-watching tours. The shallower middle and upper zones are restricted to a few fishermen and researchers only, as mothers with calves generally occupy this region at the start of the winter season. As the season progresses and the calves grow larger, the mother/calf pairs transition to the lower zone nearest the open ocean.

To collect acoustic data consistent with Dahlheim's field work two decades earlier, the system shown in Fig. 3 has been deployed at 26°47.682′N 113°14.603′W, near Punta Piedra, also known as Rocky Point in (Dahlheim, 1987). Because Punta Piedra is the most elevated site along the lower zone, it is a popular location to view whales. Depending on the lagoon's tidal patterns, the local water depth at the deployment site varied between 8 and 15 m. In 2010 an additional station was deployed 1.5 km southwest from the Punta Piedra site (Fig. 1, circle) to gain insight into the detection range of the sensors.

C. Visual survey procedure

A primary objective of the LSIESP gray whale program is to record the abundance and distribution of whales across

all three spatial zones, from the north end of the lagoon (upper zone) to the lagoon's entrance (lower zone). During the 2008 breeding season, visual counts were conducted every 4 days from January 25 to April 3. Visual surveys were canceled on days when wind conditions exceeded 18 km/h.

All visual surveys started at the north end of the lagoon (upper zone). Survey boats follow a GPS survey trackline down the center of the lagoon, parallel to both shorelines, at a constant boat speed of 11 km/h (Jones and Swartz, 1984; Urban *et al.*, 1997; Urban *et al.*, 2003). On average, the dive time of a whale in the lagoon is rarely more than 4–5 min, while the swimming speed was an average of about 7–9 km/h, thus this particular boat speed was selected to minimize the likelihood of double-counting the same whale surfacing twice. As the surveyors navigated through the lagoon, both shorelines were visible at all times, allowing complete visual coverage of the lagoon. The survey placed two observers on the port and starboard, each looking for "blows" or "spouts" across a 120° scan sector, centered on the beam of the vessel. When whales were found swimming alongside a calf, the sighting was logged as a mother-calf pair, while a single whale was marked as a "single" of unknown sex.

During the early years of the survey, the entire process was then repeated by reversing the boat's course, traveling from the lagoon mouth to the shallow end and repeating the count. A comparison of the two counts found agreement within 10%, so in the 21st century the surveys have only been conducted once a day.

On days where visual surveys are not conducted, the LSIESP team performs photo-identification studies, which allow researchers to estimate the residence time of individuals in the lagoon, and calving rates for known female whales. Typically, singles are estimated to reside in the lagoon for about 7–14 days, while mother-calf pairs reside in the lagoon for up to 3 mo (Urban *et al.*, 2003).

D. Acoustic data analysis procedure

1. Manual analysis

The long-term autonomous recorder was deployed between February 9 and March 8, 2008, yielding 29 recording days. Seventeen days covered a full 24-h period, while 12 days contain 1.75 h gaps in the record when the device was transcribing data to hard disk. Six days (144 hours) that overlapped the visual survey dates were selected for manual analysis: February 10, 15/16, 22, 28, and March 4, 7/8. The two dates that contain two consecutive days, (i.e., February 15/16 and March 7/8), indicate dates when recordings lacked a complete 24-h period, and thus the analysis period was shifted 2 h back into the previous evening to ensure a continuous 24-h analysis period.

During the manual review, each gray whale sound was examined both aurally and visually using a custom-coded MATLAB program for viewing spectrograms and logging calls. Gray whale sounds were classified as "S1", "S3," and "S4" calls, according to Dahlheim's original scheme. Acoustic parameters logged for each call included date, time, frequency range, maximum power spectral density, frequency of the maximum power spectral density, peak ambient noise inten-

sity level, and call duration. In the case of pulsed signals like the S1 call, the number of pulses was logged as well. Pulse sets that occurred less than 2 s apart were clumped together and logged as one call. Also logged were the duration of tourist boat transits and the presence of fish sounds.

The lagoon hosts a variety of acoustically active species, including bottlenose dolphins, fish, and invertebrates. Gray whale sounds share acoustic bandwidth with groupers, sea bass, croakers (D'Spain and Batchelor, 2006) and snapping shrimp (Everest *et al.*, 1948), but their temporal characteristics are sufficiently different from these other species that misclassification is unlikely. Because even the deepest central channel of the lagoon is a relatively shallow environment (10–20 m depth), any multipath reflections of a gray whale sound at the recording station would arrive within a few milliseconds of the primary path and would not be distinguishable on a spectrogram, thus eliminating any risk of "double-counting" calls from multipath as often occurs at a deep-water monitoring site.

2. Diel distribution analysis

For each day analyzed, the logged call times for each call type were converted into detection rates per hour. The hourly detection rates for all 6 days were stacked as a histogram to examine whether a diel distribution for each call type could be discerned. To negate the null hypothesis that the hourly detection rates are independent of the time-of-day, 1000 bootstrap simulations for each call type were conducted. If a total of N calls was detected across all 6 days, then for each simulation, N random times were generated from a uniform distribution between 0 and 24 h and then converted into hourly detection rates. The distribution of the simulated rates was then compared to the observed hourly rates to determine the probability that a uniform distribution could have generated the actual observed hourly detection rate pattern. When analyzing the S3 and S4 calls, certain days (e.g., Feb 15 and 22) produced extremely high call detection rates over a couple of hours, possibly indicative of a single animal generating many calls next to the hydrophone, biasing the data. In this case, the statistical hypothesis testing was conducted both with and without these questionable observational periods.

3. Long-term comparison of call rates with visual census

As noted in Sec. I, there are multiple factors besides group size that influence call detection rates, and various assumptions or data adjustments must be made before comparing trends in call detection rate with visual counts.

a. Sex and age class. The two largest assumptions made in this study are that the age and sex distributions of single breeding animals in the lagoon either remain stationary over the observation period or that the age and/or sex of an animal does not influence its call production rate. While the visual surveys can identify a mature female when she is accompanied by a calf, the surveys cannot identify the age or sex of single whales sighted alone or in breeding groups.

As the average residence time of breeding individuals is on the order of days (Urban *et al.*, 2003), the group of individuals recorded at the end of the study is likely not the same group of individuals at the start of the study. Thus we must assume that the sex and age ratios of the single animal groups in LSI do not systematically change over the course of the observational study or that any such change is irrelevant to the acoustic behavior of the group.

b. Behavioral state and time-of-day. The types and rate of acoustic vocalizations made by animals can vary with its behavioral state, which in turn depends on a variety of factors, including time of day and mean group size. The presence of a diel pattern in call detection rate is an example of the former factor. To compensate for these effects, the total number of each type of call detected over each contiguous 24-h period defined in Sec. II D 1 is computed and is defined here as the "raw" daily call count. By summing call detections over a full 24-h period to generate a raw count, we attempt to remove diel effects, as well as effectively average over the acoustic behavioral states a gray whale displays over the time scale of a day. Changes in individual behavior that arise from changes in group size (or "density-dependent effects") over longer time scales will not be compensated by using daily counts, with consequences that will be seen in Sec. III.

c. Anthropogenic effects. While LSI remains a relatively undisturbed environment, it does host a vibrant whale-watching tourism industry that uses small boats to carry tourists for encounters with whales. If the number of daily boat tours was to change substantially over the course of the month-long observation period, then one cannot discount the potential effects of this boat activity on either the sound production rates of the animals or the ability of the sensor to detect gray whale sounds.

Fortunately, no tourism (or any human activity) takes place on the lagoon between 1 h before sunset and 1 h after sunrise. Thus one can compute not only a daily call count but also a "daytime" call count (computed between 08:00 and 18:00) and a "nighttime" call count (computed from 18:00 to 08:00 the following day), which also represent time periods with and without boat noise, respectively. If the long-term trends of the daytime and nighttime counts are similar, then the impact of tourist activity on long-term call counts can be discounted (unless the potential diel effects and tourist effects cancel each other out perfectly; an unlikely situation, given that both effects would be expected to *decrease* call detection rates during the daytime; Sec. IV A discusses how diel patterns observed for other marine mammals tend to show lower detection rates during the day).

d. Background noise levels. A crucial factor affecting call detection rates is the level of background noise present during a particular observation time. If the background noise levels increase, then hourly call detection rates would be expected to fall if all other factors remain constant. As discussed in Sec. I, the variation in ambient noise levels in LSI is relatively mild compared to open-ocean acoustic condi-

tions; however, it will be shown that fluctuations of "only" 3 dB in background noise levels can still translate into a factor of two change in call detection rates, depending on the propagation environment. Therefore an essential step for *any* acoustic census study, including this one, is estimating the impact of background noise variations on results derived from acoustic data.

In this study "raw" call counts are distinguished from "noise-adjusted" call counts. Raw call counts are counts obtained directly from the data, and the noise-adjusted counts are raw counts adjusted for variations in background noise levels over hourly time scales. The next subsection introduces the noise-adjustment model in detail.

4. Adjusting raw call rates for differences in background noise levels

The noise-adjustment model applies a simplified version of the sonar equation to translate changes in background noise level into an adjusted hourly detection rate. The cost of simplicity is the necessity of making several significant assumptions about the distribution of animals, their acoustic behavior, and the propagation environment.

The first assumption in the model states that a relative change in the number of vocalizing animals, measured within the small area being monitored, matches the relative change of all vocalizing animals in the lower zone of the lagoon. The key assumption here is not detection range but whether animals are evenly distributed throughout the lower zone to ensure a subsample of a small region is considered representative of the whole. Observations of the LSIESP photo ID team, along with VHF and satellite tagging data, indicate that single animals do frequently traverse across and exit from the lower lagoon area, never remaining in one place for long (Mate *et al.*, 2003; Urban *et al.*, 2003), suggesting that this assumption is reasonable.

Second, the model assumes the lagoon is sufficiently shallow for there to be a proportional relationship between the volume of water accessible to the sensor and the square of the detection range (area of coverage), instead of the cube of the detection range (as would be the case in deep waters of the open ocean). Under this assumption, the detection range of the sensor must be less than the width of the lagoon at Punta Piedra (Fig. 1). In a situation where the detection range of a single sensor is larger than this geographic spatial scale, the detection area would become a highly non-linear function of detection range, due to the presence of the opposite shoreline and shadowing features related to dramatic bathymetry profiles present in the lagoon. The fact that the sensor is positioned near a peninsula and is effectively blocked from detecting sounds from all azimuths does not violate this assumption, as a circular wedge increases as the square of detection range. Section III D discusses experimental measurements and numerical simulations of the detection range around the sensor to support this assumption.

Third, the model assumes that the source level distribution of calls and potential diel acoustic behaviors remain invariant with changes in background noise level. There is evidence that baleen whales increase their source levels to

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compensate for increases in background noise levels (e.g., Parks *et al.*, 2007), so this assumption may be invalid. However, if gray whales do adjust their source levels in response to changes in ambient noise level, then the appropriate call detection counts would be expected to lie somewhere between the raw call counts (which effectively assume that whales compensate perfectly for ambient noise level changes) and the noise-adjusted counts derived here (which assume that whales do not compensate for ambient noise level changes). Thus in the Secs. III and IV, both the raw and noise-adjusted counts are presented, and the relative importance of assuming a constant source level distribution can be judged by comparing the relative differences in the raw and noise-adjusted counts.

The fourth assumption is that all calls above a certain signal-to-noise ratio (SNR) threshold are assumed detected by a manual analyst. The actual value of the SNR threshold where this fall-off occurs is not relevant to the derivation.

Finally, a very simple propagation model is assumed, where the square-pressure of a discrete acoustic signal from a compact source is assumed to fall off with horizontal range r as $r^{-\alpha}$. Another way of stating this assumption is that the dB transmission loss of an acoustic field falls off as $10\alpha\log_{10}(r)$. Note that this assumption, like the second assumption, requires that the effective detection range of the sensor be significantly smaller than the width of the lagoon at Punta Piedra. Section III D discusses simulations and field measurements of the sound propagation factor α.

From these assumptions, the following expression can be derived for adjusting a daily raw call count for differences in ambient noise levels:

$$C_{j,adj} = \sum_{i=1}^{24} C_{ij,raw} \left(\frac{N_{ij}}{N_{ref}} \right)^{2/\alpha}. \tag{1}$$

Here $C_{ij,raw}$ is the number of calls manually detected on hour i of date j, and N_{ij} is the noise level measured over that same hour, integrated over the bandwidth of the call type in question. Note that N is expressed in *linear* units and not decibel units. To obtain daytime and nighttime adjusted call counts, the summation in Eq. (1) is conducted only over the appropriate hours of the day discussed in Sec. II D 3. The quantity in parentheses, raised to the power of $2/\alpha$, is defined here as the "call multiplier."

N_{ij} is computed by first integrating a set of instantaneous power spectral densities (PSD) between 350 and 750 Hz, using a 1024-pt FFT, overlapped 50%. Every 2 min, the minimum integrated PSD value encountered is retained, providing 30 values an hour. These values are averaged in the linear (not dB) domain to obtain N_{ij}. Consequently, the average of a set of *minimum* background noise levels is captured, instead of a simple average of all PSD estimates, to exclude numerous impulsive events like snapping shrimp from the noise calculation, under the reasoning that moderate amounts of impulsive noise do not reduce the ability to detect an S1 call. N_{ref} is a particular reference noise level; here $N_{ref} = 104$ dB re 1 μPa (rms), integrated between 350 and 750 Hz, is used as a representative value for non-pulsive

ambient noise conditions in the lagoon. Equation (1) can also be derived from the density estimation formalism of Eqs. (3), (5), and (6) in (Marques *et al.*, 2009), assuming a Heaviside "step" function for $g(y)$ with detection range w determined by SNR.

A glance at Eq. (1) shows that call counts on relatively noisy days are adjusted upward under the assumption that more calls would have been detected at the (quieter) reference noise level. For α equal to 2 (spherical spreading), the adjusted call counts become proportional to background noise values, such that a 3 dB increase (doubling) in noise level will result in a doubling of the adjusted call count, relative to the raw call count, over that hourly measurement. The larger the value of α, (i.e., the worse the propagation conditions), the less sensitive the call-adjustment formula becomes to fluctuations in ambient noise.

To permit direct comparison, acoustic and visual counts are occasionally presented in relative terms with respect to the first visual census day. For example, the raw and noise-adjusted daily call counts are divided by the raw and noise-adjusted call counts from the first day. Similarly, the visual census counts are divided by the visual census count on the first day, permitting the normalized acoustic and visual measurements to be plotted together. As the acoustic data were collected on the boundary between the lower and middle zones, visual data from both the lower zone and the combined middle and lower zones will be presented.

III. RESULTS

A. Diel pattern in call rates

Figure 4 shows the hourly raw call distributions for the S1, S3, and S4 sounds detected near Punta Piedra, stacked over 6 days. The total raw call counts across all days were 4757 S1 calls, 705 S4 calls, and 520 S3 calls. The horizontal solid lines in Fig. 4 display the average raw call rate computed over the entire 6-day period, while the dashed lines indicate the 5th and 95th percentiles of the mean hourly call rate derived from the bootstrap simulations discussed in Sec. II D 2. Hourly call rates that lie between the dashed lines cannot reject the null hypothesis that they were generated from a uniform (time-independent) calling distribution.

The histograms suggest that S1 and S4 calling activity levels are greatest around dawn and twilight hours. By contrast, by mid-morning and mid-afternoon, these call types are detected at rates at least 40% below the 24-h averaged calling rate. For example, the S1 call [Fig. 4(a)] shows an obvious decrease in calling activity between 10:00 and 15:00 hours in comparison to the rest of the day. For the S1 call, the high rates at dusk and dawn and the low rates during mid-morning and mid-afternoon lie outside the 5th and 95th percentile lines for the uniform distribution, indicating that the null hypothesis of a uniform (non-diel) distribution can be rejected. In addition to the bootstrap simulations, two-sample *t*-test and Welch's approximate *t*-test were also conducted on the S1 data comparing daytime detection rates (between 08:00 and 18:00) with nighttime rates. The two-sample *t*-test and Welch's test yielded P values of 1.85×10^{-4} and 2.47×10^{-4}, respectively, for the S1 data,
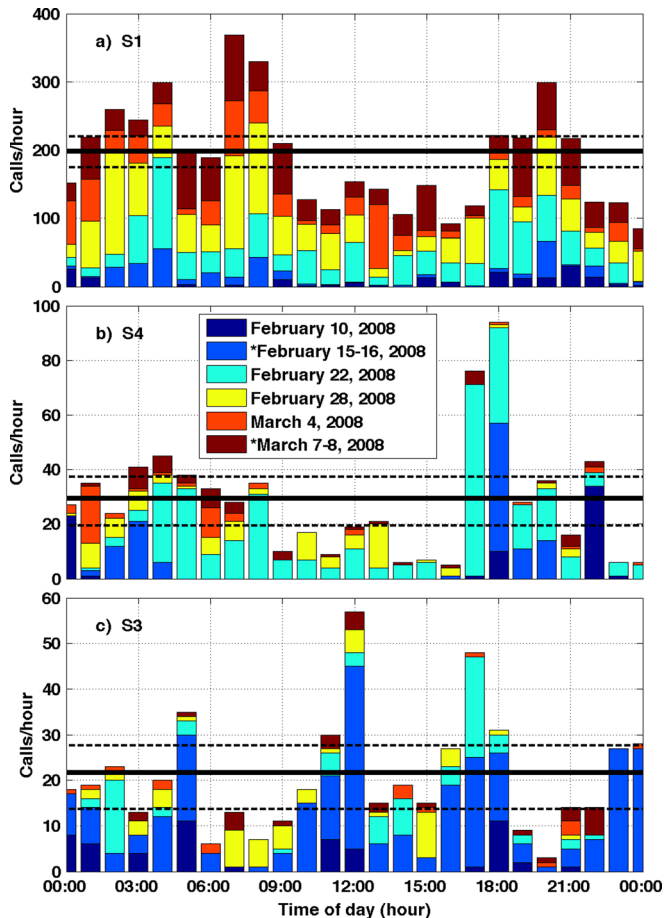
FIG. 4. (Color online) Cumulative histograms of gray whale call type distributions over a 24-h period using six non-consecutive days of data between February 10 and March 10, 2008. The solid line indicates the mean call rate per hour, averaged over the 6 days. The dashed lines indicate the 5 and 95% confidence limits of the mean hourly call rate synthesized from 1000 simulations of N random times drawn from a uniform 24-h distribution, where N is the total number of calls observed in each subplot. (a) S1 calls, with a mean hourly rate of 198 calls per hour (solid line) and confidence limits of 174 and 220 calls per hour; (b) S4 calls, with a mean hourly rate of 29 calls per hour and confidence limits of 19 and 37 calls per hour; (c) S3 calls, with a mean hourly rate of 21 calls per hour and confidence limits of 13 and 27 calls per hour.

providing further evidence that the mean detection rate for the S1 call type differs between night and day.

The bootstrap analysis of the S4 call is more ambiguous. Both the sunset and mid-day call rates lie outside the 5th and 95th bootstrap percentiles; however, the very high calling rates during the 2 h of sunset are generated on only 2 days and may thus be biased by a single individual. A Welch's t-test performed on the entire S4 data set yielded P values of only 0.85, because the low detection rates during the day were effectively cancelled out by the high detection rates at 17:00 and 18:00, which are still "daytime" hours. Once these questionable hours of data from Feb. 15–16 and Feb. 22 were removed, a Welch's t-test conducted on the remaining data yields a P value of 0.0014, indicating that the low detection rates measured for the S4 call during the day are significantly different from the evening values.

Finally, the S3 call sample size in Fig. 4(c) is so much smaller than the other two call types that the bootstrap simulations cannot reject the null hypothesis of a uniform distri-

bution. Furthermore, a Welch's t-test performed on the daytime and nighttime hours yielded a P value of 0.73. Even if suspicious times of high activity during the noon and sunset hours are removed, the resulting P value drops to only 0.49. Therefore, a diel cycle cannot be positively identified in the S3 call, potentially due to its small sample size.

B. Boat transit activity

Noise from boat transits in the lagoon was regularly present between 09:00 and 15:00 for every day studied, although a couple of transits per hour are observed as early as 07:00. Figure 5 displays the boat transit rate observed as a function of date and time of day. A couple of weeks after the start of the tourism season, boat traffic in the lagoon rapidly increased, beginning February 15–16, with the number of transits increasing as the season progresses. High numbers of transits are observed between 11:00 and 14:00 hours, although the noontime hour has fewer transits as all tourists return to shore for a lunch break. The maximum number of transits detected per hour was 18 passes on March 4 at 14:00 hours. As discussed in Sec. II, acoustic call counts have been divided into daytime and nighttime counts, which coincide with windows of time of presence and absence of boat traffic, to determine whether this increasing trend in boat traffic is a factor behind the changing call detection counts over the course of the month.

C. 2008 visual counts and raw call counts

Figure 6(a) displays the visual counts of single animals and mother-calf pairs observed in both the middle and lower zones of LSI over six dates. For example, on Feb. 10, at the beginning of the breeding season, 21 single whales and 10 mother-calf pairs were observed in the lower zone, while an additional 16 singles and 16 mother-calf pairs were sighted in the middle zone. By the end of the acoustic monitoring period, the total number of whales in the lower zone had
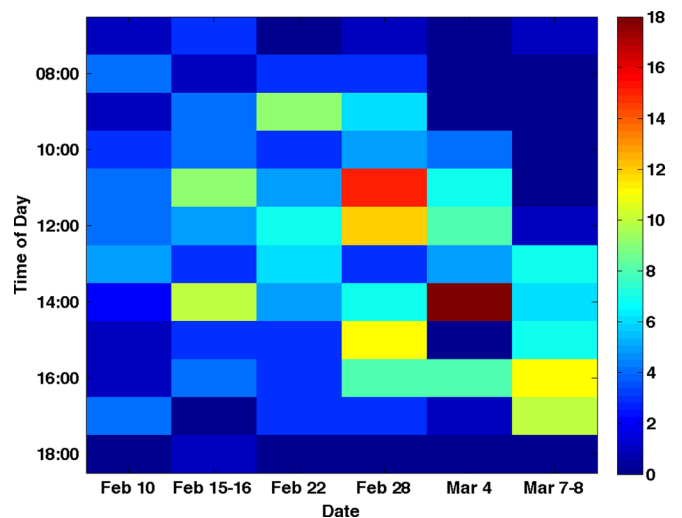

FIG. 5. (Color online) 2D matrix quantifying boat transits detected by the recorder during daylight hours over the 6 days analyzed. The intensity scale indicates the transits detected during that hour and day. The maximum number of transits per hour (18) occurred on March 4 at 14:00 and then slightly less on February 28 at 11:00.

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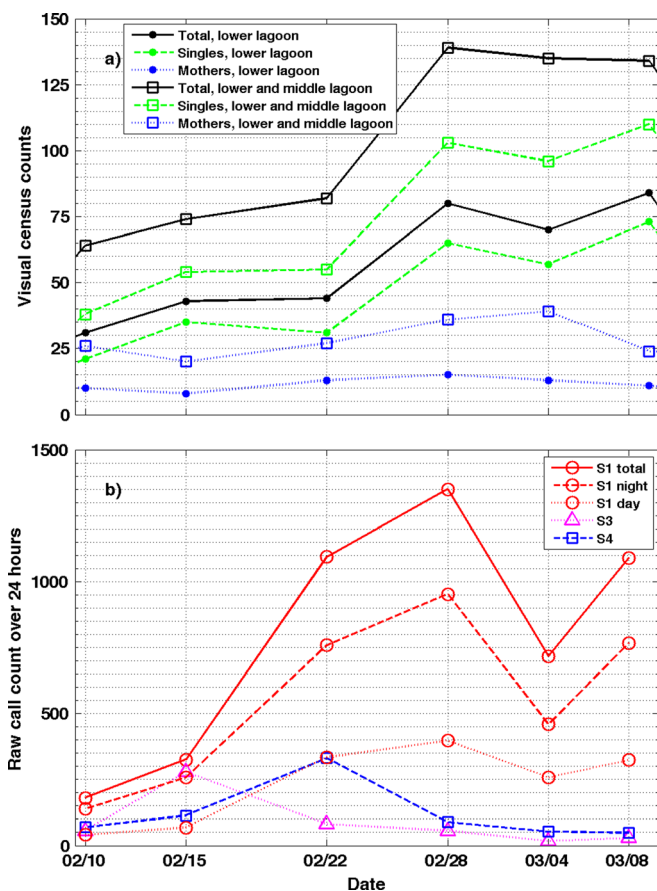Ponce *et al.*: Gray whale acoustic census   2707

FIG. 6. (Color online) Visual and raw acoustic call counts of Eastern Pacific gray whales in LSI in 2008, measured on 6 days over 30 days. (a) Visual counts of mother-calf pairs (dotted), single animals (dashed), and total animals (solid) in the lower and middle zones of the lagoon. Solid dots indicate census counts from the lower zone only, while open squares show the combined counts from the lower and middle zones. (b) Raw call detection counts over 24 h periods that encompass times of visual surveys. Three types of calls are plotted: S1 (circle), S4 (square), and S3 (triangle). The S1 counts are further subdivided into daytime only (dotted line), nighttime only (dashed line), and total daily count (solid line).

increased by a factor of 2.7 with a final count of 73 singles and 11 mother-calf pairs. This increase was primarily due to a tripling of single animals in the lower zone with a large influx of single individuals taking place over a single week (Feb. 22–28).

Figure 6(b) shows the daily, nighttime, and daytime raw call counts for S1 calls and the daily call counts for S3 and S4 calls. Throughout Feb. 10, 180 S1 calls, 70 S4 calls, and 57 S3 calls were detected. By Feb. 28, the total number of S1 calls increased by over a factor of 6 with most of the increase arising from increased detection rates during nighttime. Unlike the S1 call, the counts of the other two less-frequent call types peak early and then decrease over the course of the month. By the last observational date on Mar. 7/8, the raw S1 call count completely dominates the acoustic repertoire, so the remaining discussion will focus on the S1 calls.

D. Background noise variations, sound propagation estimates, and noise-adjustment factors

Figure 7 displays both numerical simulations and empirical measurements of the sound propagation factor α shown
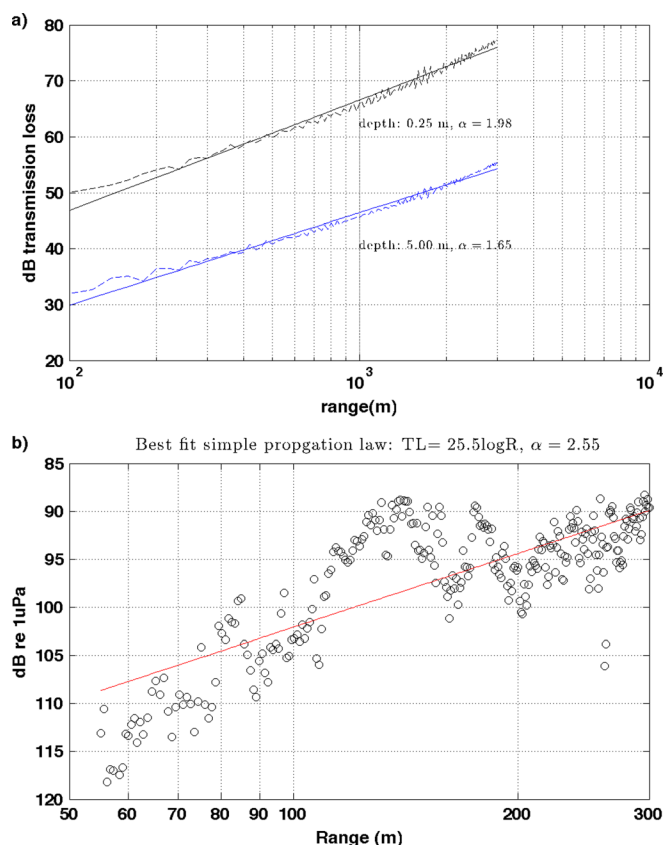

FIG. 7. (Color online) Modeling and measurements of propagation loss factor α in Eq. (1): (a) Modeled transmission loss (dashed lines) as a function of propagation range, averaged over 25 frequencies evenly spaced between 350 and 750 Hz. Two source depths of 0.25 and 5 m are shown along with the transmission loss modeled by the best-fit α value (solid lines). The modeled environment was a 10 m deep Pekeris waveguide with 1650 m/s bottom speed and 1.5 g/cc density, typical values for sand. The receiver depth was 10.25 m, simulating a buried instrument. (b) Empirical measurements of integrated received levels between 100 and 500 Hz during a direct approach by a motorboat toward the recorder during a 2010 deployment. A single point in this plot was estimated by averaging four 4096 point FFT snapshots, overlapped 50%, which translates into 1.15 s of data using the 12.5 kHz sampling rate. The power spectral density was integrated between 100 and 500 Hz (the dominant frequency band of the boat) and then converted to logarithmic units, yielding units of dB re 1 μPa. The best-fit logarithmic propagation law is shown as a solid line. Beyond 300 m range the boat noise was buried in the background.

in Eq. (1). The top subplot shows the modeled transmission loss between 350 and 750 Hz (typical frequency ranges detected for an S1 call on the sensor) and between 100 and 3000 m range for two sources at 0.25 m and 5 m depth in a 10 m deep Pekeris waveguide, using a normal mode propagation code. Figure 7(a) shows the transmission loss averaged across frequency in the linear domain (because the S1 call is broadband pulsive, the equal weighting was chosen). A least-squares fit of a transmission loss in the form of $r^{-\alpha}$ was then applied to yield the effective α. The receiver depth is modeled as being 0.25 m underneath the ocean floor because the tidal cycles in the lagoon bury the instruments (but not the polypropylene grappling rope) during the course of the deployment.

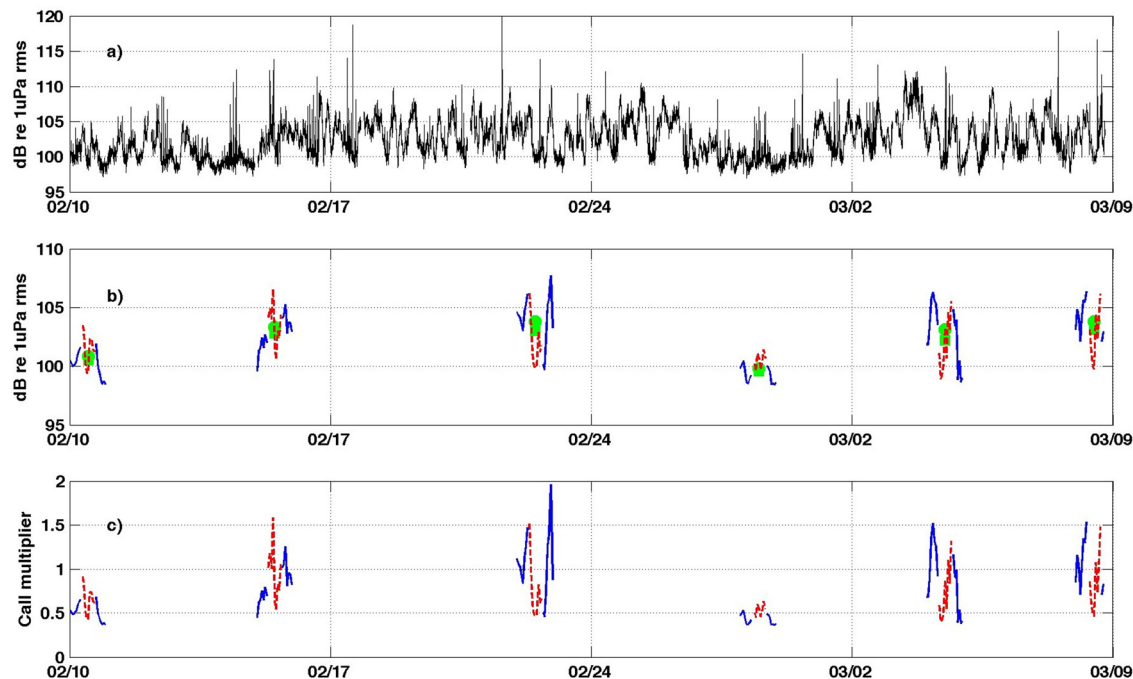Source depth has a major impact on α. The 0.25 m source depth was selected to model expected transmission

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FIG. 8. (Color online) Background noise levels in the lagoon, with resulting call multiplier factors. (a) Background noise levels in dB re 1 μPa rms, integrated between 350 and 750 Hz, using a 1024-pt FFT, overlapped 50%, and retaining the minimum level detected every two minutes, to suppress effects of impulsive noise. The diel effects of land and sea breezes are readily apparent. (b) Hourly averages of the data shown in (a), during days of visual surveys. Dashed lines indicate daylight hours, solid lines nighttime hours. The dots indicate the geometric and arithmetic mean of the ambient noise over a 24-h period. (c) Resulting hourly call multiplication factors ($[N/N_{ref}]^{2/\alpha}$) used in Eq. (1), with $\alpha = 2.55$ and $N_{ref} = 104$ dB re 1 μPa (rms), using the same pattern scheme as (b) for indicating daytime and nighttime.

loss from cavitation noise from small boats or animals vocalizing at or near the surface, while the 5 m source depth was selected to represent a potential deeper depth for whale vocalizations. The shallow depth yields a value of α close to that expected by free-space spherical spreading; at a shallow depth, the source excites mostly higher-order propagating modes that suffer high attenuation loss through strong interaction with the ocean bottom. By contrast, sound from a deeper source propagates more effectively through the water, yielding a smaller value of α. Modeling sloping bathymetries using gradients measured around Punta Piedra did not substantially change the value of α, but the simulations did not incorporate potential acoustic backscatter from extremely steep bathymetry gradients.

Unfortunately, high-quality empirical measurements of propagation loss in the lagoon over the S1 call frequency range are not available. While controlled playbacks of sounds have been conducted in the lagoon by other researchers (Dahlheim, 1987, Appendix A), the playbacks occurred at frequencies 1 kHz and higher, above the primary frequency range of interest for the gray whale S1 call. Instead empirical estimates of α have been obtained by using data collected in 2010 to measure how the cavitation noise from a research boat increases with decreasing range [Fig. 7(b)], as the vessel directly approaches a recorder at the site with a constant engine turnover. Figure 7(b) shows a value of α on the order of 2.55, a value greater than the spherical spreading prediction. This situation could arise if the source were intrinsically directional or if a complicated bathymetry (such as sand bars) created shadow zones and thus strong gradients in transmission loss with range. To cover the full range of possible α values in the LSI environment, propagation factors of 1.6 (from simulation, deeper whale call) and 2.55 (from boat measurements) will be used in the subsequent sections.

Figure 8 shows how the background noise environment of the lagoon, combined with $\alpha = 2.55$, translates into the effective call multiplier in Eq. (1). Note that the background noise levels of the lagoon are quite noisy with rms levels between 95 and 110 dB re 1 μPa (rms), integrated between 350 and 750 Hz, using the procedure described in Sec. II D 4 to suppress impulsive noise. A diel cycle in the noise pattern is apparent; this correlates well with the strong land and sea breezes that are characteristic of this flat, desert environment. The portions of the ambient noise record that overlap the days of visual surveys are shown in Fig. 8(b), where one sees that the hourly average noise levels (large dots) vary by around 8 dB across the 6 days analyzed. This relatively mild variation, along with the relative high propagation loss factors, yields call multipliers [Fig. 8(c)] ranging between 0.5 and 2 or within a factor of three of each other. As expected, days with low background noise levels (e.g., Feb. 28) have small call multiplier factors and vice versa.

The high background noise levels ($\sim$100 dB re 1 μPa rms) suggest that even if the more favorable propagation factor of 1.6 was used (a $16\log_{10}r$ propagation law), a gray whale call with an estimated source level of 140–150 dB re 1 μPa @ 1 m (Cummings et al., 1968) would decay to ambient levels at ranges between 300 and 1400 m from the source. This detection range estimate is supported by the observation that in 2010 few matching whale calls were detected between the Punta Piedra sensor and a second
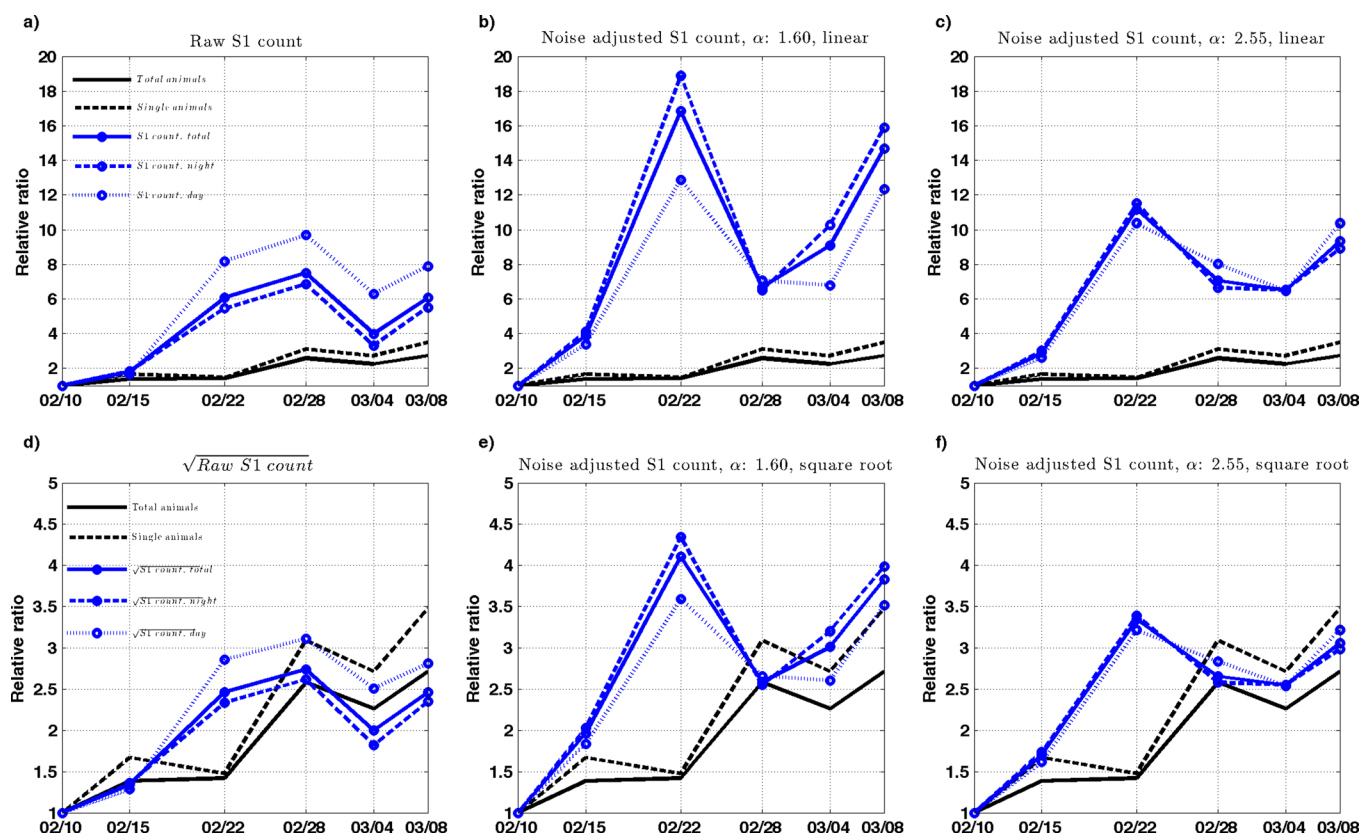
FIG. 9. (Color online) Relative changes in visual survey counts, raw S1 acoustic call counts, and noise-adjusted S1 call counts over the observation period. The normalized lower-zone single animal visual count (dashed line) and total lower-zone animal count (solid line) are identical on all plots, and show the number of animals sighted in the lower zone on a given date, divided by the count on Feb. 10, the first observation date. The top row (a, b, c) shows the relative changes in the S1 acoustic call count during daytime (dotted line with circles), nighttime (dashed line with circles) and over the entire 24-h period (solid line with circles). The bottom row (d, e, f) plots the relative changes in the *square root* of the S1 acoustic call count. The first column (a, d) plots the raw acoustic count data, the second (b, e) and third columns (c, f) show the noise-adjusted call counts using $\alpha = 1.65$ and 2.55, respectively.

sensor placed 1.5 km away (Fig. 1). Thus the assumption that the detection range of the sensor is not greater than the width of the lagoon at Punta Piedra seems justified.

E. Comparison between relative increase in visual sightings, raw and noise-adjusted acoustic counts

Figure 9 shows a detailed comparison of the normalized S1 call counts and normalized visual counts. The solid and dashed lines (without circles) represent the relative changes in the lower zone visual count for the total number of animals and single animals, respectively. The top row of plots [Figs. 9(a)–9(c)] show the linear ratio between the acoustic call count and acoustic count observed on Feb. 10. Each column shows the use of a different noise-adjustment model with the first column showing the raw counts only. The second and third columns apply noise-adjusted counts derived from α-values of 1.6 and 2.55, respectively. In every plot, the call counts for daytime and nighttime hours are broken down separately, along with the total 24-h call count.

Figure 9(a) shows that the relative raw call count increases much faster than the relative number of animals for all dates; by the date of the last survey (March 8), the total number of raw S1 calls per day has increased by nearly a factor of six, and the daytime raw S1 call count has increased by a factor of 8. By comparison, over the same time interval, the visual count of single animals increased by

only a factor of 3.2. From Sec. II C, the uncertainty of the visual estimates (10% for the raw count, or 15% for the relative count) cannot account for the discrepancy between relative call and visual counts. When the simple noise-adjustment model is applied, the discrepancy worsens, with the relative number of total noise-adjusted calls increasing by a factor between 9 and 15. As expected, more favorable propagation conditions (lower α) increase the absolute and relative call counts.

The second row shows the result of plotting the *square root* of the normalized call count ratio against the relative visual count ratio. The raw acoustic count data in Fig. 9(d) immediately show a much better correspondence with the visual counts on four of the five measurement days, for all times of day, and the relative call counts lie within the uncertainties of the visual counts. The effect of applying the noise-adjustment model is relatively subtle; it increases the discrepancy on Feb. 22, but the adjustment using the higher propagation factor causes the relative daytime and nighttime call counts to converge [Fig. 9(f)]. There is apparently a slight systematic difference in background noise levels between daytime and nighttime throughout all measurement dates, which is visible in Fig. 8(b). Unfortunately, given the 15% uncertainties in the relative visual estimates, one cannot say whether the acoustic data match best with the total visual count (singles plus mother/calf pairs), or the single animal count only.

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Using the combined visual counts from the lower and middle zone of the lagoon, instead of just the lower zone, does not significantly change any of these results.

IV. DISCUSSION

A. Diel patterns in calling behavior

Bootstrap simulations and Welch's *t*-tests have determined that S1 and S4 call detection rates are not uniformly distributed over time (i.e., one can reject the null hypothesis that the calls are generated uniformly and independently with respect to time) and that the mean detection rates during the day are lower than during the evening. To obtain these conclusions for the S4 data, anomalously high call detection rates between 16:00 and 18:00 on 2 days had to be removed.

One possible interpretation of this result is that gray whales display a diel calling pattern for S1 and S4 calls—which would be an unsurprising conclusion, given that considerable literature already exists on diel patterns observed in baleen whale call rates in ocean basins, including sei (Baumgartner and Fratantoni, 2008), right (Munger *et al.*, 2008), humpback (Au *et al.*, 2000), and blue whales (Stafford *et al.*, 2005; Oleson *et al.*, 2007). The peaking of call rates at sunrise and sunset is also reminiscent of croaker fish choruses along the eastern Pacific coast (D'Spain and Batchelor, 2006; Sirovic *et al.*, 2009). The reason behind this pattern is unknown; gray whales are not believed to feed during the winter months in the lagoon.

Another potential contributing factor to the observed diel pattern is that gray whales might become less vocal whenever whale-watching tourist boat noise increases in the lagoon (Ollervides, 2001) or from acoustic masking caused by boats. For instance, the detection rates of S1 and S4 calls dropped by 40% between 09:00 and 15:00 hours, which coincide with the times of peak whale-watching activity (Fig. 5). The next section examines this question in some detail as well.

B. Relationship between acoustic call counts and visual counts during 2008

Of the three call types studied, only the S1 call seems to show a potential correspondence with the visual count, and Fig. 9 shows that the correspondence must be nonlinear in that only the square root of the relative raw [Fig. 9(d)] and noise-adjusted [Figs. 9(e) and 9(f)] daily call counts correlates with the relative visual count of animals in the lower zone, for four of the five data points available. A previous study found a similar relationship between whistle detection rate and beluga group size, but the plotted relationship was tenuous (Simard *et al.*, 2010). All values of α examined are relatively large, and this, combined with the relatively high ambient noise levels in the lagoon, seemed to ensure that the detection range of the sensor was less than the width of the lagoon, thus validating a couple of key assumptions used in the noise model.

This square root relationship seems robust to several assumptions. First, the relationship is visible in the raw call count as well as for various noise-corrected counts. As argued in Sec. II D 4, the raw call count can also be interpreted as a situation where gray whales perfectly compensate their source levels for changes in background noise level, and thus the relationship cannot be explained by a simple change in source level distribution. Second, as the relationship remains visible in all noise-corrected call counts, it cannot be explained as arising from changes in the background noise level over the observation period. Finally, the square-root relationship also persists when only nighttime hours are used, and thus the increasing boat traffic during the season cannot be responsible for the relatively large increases in call detection rates. Thus an explanation for the discrepancies shown in the first row of Fig. 9 must arise from a long-term change in the call production rate of the population in the lagoon and not changes in source level distributions, ambient noise levels or tourist boat effects.

From Sec. II D 3, two likely explanations exist for these results: (1) different subsets of the single population, related to sex or age, call at different rates, and the relative proportion of these subsets changes over time in the lagoon or (2) the individual call production rate of all single animals increases over time. Note the emphasis on single animals instead of mother/calf pairs because the visual count of the latter group remains fairly steady over the course of the month.

The second interpretation has an appealing theoretical explanation for why the call detection rate increases as the square of the number of animals. Marine mammal calls that are essentially one-way communication—such as echolocation signals, or sexual, and conspecific advertisements that do not stimulate a response from listeners—would indeed yield a proportional relationship between population size and acoustic call rate (Marques *et al.*, 2009; Moretti *et al.*, 2010). If, however, the calls in question serve a "social" purpose, such that conspecifics would generate similar calls in response (a "two-way" or "countercalling" communication), then a quadratic relationship between group size and call rates would be expected. Specifically, for a given group size M, there exist $M(M-1)/2$ possible unique pairings within the group, so that if call rates are related to the number of pairwise social connections (relationships), then the number of calls will effectively increase as $M^2/2$ once M exceeds 10. The appropriate interpretation of Fig. 9 would be that an acoustic census measures the number of connections in the social network and not the nodes (number of animals). This relationship should be robust to changes in age and demographic composition of the group. This nonlinear relationship, or "density-dependent" effect, between acoustic call rate and group size might be a general feature of social calls in multiple taxa, and censuses that assume a proportional relationship between call rate and population size for social sounds might risk significantly overestimating the number of individuals present.

If this interpretation has merit, why would there be a breakdown in this relationship on February 22? Figure 6 indicates that on that date the group size in the lagoon was increasing rapidly; over 7 days, the single animal population in the lagoon essentially doubled. Additionally, Fig. 4 suggests that the increase in call rate appeared throughout the

day, so the discrepancy cannot be explained by an increase in call rates in the afternoon or evening, once the visual survey had been completed, or by a single whale persistently vocalizing next to the hydrophone for several hours. Our tentative interpretation is that whenever group size changes rapidly, individuals within the group become even more vocally active than under "equilibrium" conditions. Once the group size stabilizes, calling rates would gradually return to the observed "square-root" equilibrium pattern. There is some basis to this speculation; close-range acoustic and visual observations of orcas in the Pacific Northwest found unusually heavy levels of acoustic activity from A-pod members, when joined by resident whales from outside the same pod (Ford, 1989).

V. CONCLUSION

A manual analysis has been conducted of acoustic call rates of ENP gray whales residing in Laguna San Ignacio, during 6 days over the course of the 2008 breeding season. The analysis found evidence of a diel effect in call rates for two call types, but it cannot be determined whether this cycle arises from natural behavior or from peaks in noise from boat activity during the afternoon.

The enclosed geography of the lagoon, combined with the relatively short dive times of the animals, provided excellent conditions for visual group size counts. The relatively steady levels of ambient noise throughout the month, combined with a large change in group size during the month, permitted demonstration that over 4 of the 5 days analyzed both the raw and noise-adjusted calling rates of a specific type of call (S1) were related to the square of the number of animals in the lower zone of the lagoon. However, it was not possible to flag whether the relationship is related to both demographic groups or just single, breeding animals. The same relationship appeared during daytime and nighttime hours, so an increase in tourism effects could not be responsible for the observed relationship. We also note that while this relationship is visible even without the noise-adjustment model, the use of the model created greater consistency between the relative increases predicted from call counts measured during daytime and nighttime [Fig. 9(f)].

We interpret the observed nonlinear relationship as suggesting that passive acoustic monitoring of social (two-way communication) calls in gray whales does not measure population size directly but instead measures the number of social connections in the group. The exception to the observed relationship occurred during a time of rapid increase in the whales' group size in the lagoon, and it is speculated that acoustic social calling rates will be poorly correlated with group size during times of rapid change in whale group size.

The relationship between call rate and group size is speculated to be a general feature of social sounds in multiple taxa. Future work includes applying automated analysis to all days of the acoustic record, repeating the analysis at several locations around the lagoon, between years as well as within years, and adding biopsy sampling to the LSIESP research group, to allow quantifying the potential influences of sex and age distribution on acoustic censusing efforts.

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