Aquatic Mammals 2019, *45*(6), ###-###, DOI 10.1578/AM.45.6.2019.###

Interpreting Fin Whale (*Balaenoptera physalus*) Call Behavior in the Context of Environmental Conditions

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Abstract

A seven-year time series of fin whale (*Balaenoptera physalus*) acoustic detections in the Equatorial Pacific Ocean was examined in combination with regional environmental parameters to better understand fin whale seasonal distribution and behavioral ecology in a traditionally undersampled ocean region. Ecological modeling of environmental variables related to fin whale vocal presence indicated that median sound pressure spectral density level in the 5 to 115 Hz band, chlorophyll concentration, and sea surface temperature (SST) were the strongest predictors of fin whale presence. Fin whale vocal presence increased with increasing median sound level and decreased with increasing SST. Variation in seasonal fin whale call density and estimated animal density varied annually with one of the largest estimates occurring in the only year of the study when both the El Niño–Southern Oscillation and Pacific Decadal Oscillation were in a positive phase. This work illustrates the feasibility and value of applying knowledge of call detection bearings and received levels from long-term, sparse array recordings to estimate animal density of marine mammals in the context of regional environmental conditions.

Key Words: acoustics, density estimation, environmental modeling, fin whale, *Balaenoptera physalus*

Introduction

Passive acoustic recordings are increasingly being used to provide insight into marine mammal behavioral ecology, communication, distribution, and migration patterns. Compared to traditional visual observation methods of stock assessment from ships, remotely deployed passive acoustic sensors are non-invasive, provide high temporal resolution data from long-term deployments, and allow for consistent monitoring of isolated and offshore regions. The value of passive acoustic monitoring of large whales producing loud, low-frequency vocalizations detected in U.S. Navy Sound Surveillance System (SOSUS) recordings was first demonstrated by Watkins et al. (2000), which provided previously intractable information on blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whale seasonal presence and calling patterns in the offshore waters of the North Pacific. Multiple long-term passive acoustic studies combined with synoptic measurements of environmental parameters extended the knowledge base of large whale behavioral ecology in both coastal and offshore environments by linking vocal behavior to local, regional, and ocean basin scale oceanographic features (Moore et al., 2002; Stafford et al., 2005, 2009; Širović et al., 2015).

Sea surface temperature (SST) was observed to be the best predictor of fin whale call detections in the North Pacific by Stafford et al. (2009). At the time of publication, this was the largest spatio-temporal study examining the relationship between oceanographic features and whale vocal behavior. Peak vocal periods occurred during the fall and winter months following a 3 to 4 mo lag in peak SST when waters were cooling. As SST is strongly correlated with primary production, and secondary production of zooplankton tracks in time with phytoplankton blooms by several weeks to months (Longhurst, 2007), it logically follows that the peak vocal periods lagging peak SST by 3 to 4 mo likely corresponds with peaks in zooplankton abundance for foraging fin whales. In the North Atlantic Ocean, Visser et al. (2011) reported the peak in fin whale visual sightings lagging behind the spring phytoplankton bloom by 3 to 4 mo and connected the lag to the time required for zooplankton abundance to increase following the spring phytoplankton bloom.

An acknowledged limitation of the interpretation of the results by Stafford et al. (2009) was that the changes in vocal behavior could not be conclusively linked to changes in number of whales, as was accomplished by Visser et al. (2011) with daily visual surveys. Seasonal increases in vocal detections could be a result of an increase in the number of vocalizing whales, but it could also be a result of changing vocal behavior due to increasing call production rate or variations in ambient sound levels impacting detectability. The behavioral context is also crucial in interpreting increases in call activity as whales have been observed to increase call rate following productive feeding periods (Payne & Webb, 1971).

In two Northeast Pacific long-term studies (Stafford et al., 2009; Širović et al., 2015), overall fin whale calling activity was observed to increase over the duration of the multi-year study, suggestive of population recovery post-whaling. However, in both cases, it was again not possible to correlate the increasing trend with actual number of whales. Interpretation of the vocal activity increase in these studies was augmented by the concurrent visual surveys, which were consistent with an increase in visual sightings consistent with observations of population recovery post-whaling (Barlow & Forney, 2007; Campbell et al., 2015).

Comparing passive acoustic monitoring studies with dedicated visual survey effort in the same region is one way to make a direct link between changes in vocal detections and animal abundance to address management and conservation concerns related to population status or correlations to biophysical oceanographic features. However, methods in passive acoustic density estimation have also been developed to estimate absolute animal density from acoustic recordings. Acoustic density methods have been used to estimate densities of fin whale (McDonald & Fox, 1999; Harris et al., 2018b), several species of beaked whale (Marques et al., 2009; Moretti et al., 2010; Küsel et al., 2011; Hildebrand et al., 2015), right whale (*Eubalaena japonica*; Marques et al., 2011), sperm whale (*Physeter macrocephalus*; Barlow & Taylor, 2005; Ward et al., 2012), minke whale (*Balaenoptera acutorostrata*; Marques et al., 2012; Martin et al., 2013), harbor porpoise (*Phocoena phocoena*; Kyhn et al., 2012), and finless porpoise (*Neophocaena phocaenoides*; Kimura et al., 2010). A variety of passive acoustic density estimation methods were employed across this set of studies and included distance sampling (Marques et al., 2011), spatial capture-recapture (SCR, also known as spatially explicit capture-recapture; Marques et al., 2012; Martin et al., 2013), census/strip transect methods (Moretti et al., 2010; Ward et al., 2012), and a variety of methods using auxiliary data (Marques et al., 2009; Kimura et al., 2010; Küsel et al., 2011; Harris et al., 2018b). The selection of method was study-specific and dependent on the information available from which the probability of detection, a key parameter in density estimation, could be estimated (see the review by Marques et al., 2013, for a detailed explanation of method details and assumptions).

Of the 13 studies cited above, seven took place on U.S. Navy ranges instrumented with a cabled system of 14 to 82 bottom-mounted hydrophones. Access to instrumented ranges is relatively rare, and the more commonly employed sparse arrays often do not meet the data requirements of density estimation methods achievable using recordings from a range. In particular, the sparse three-sensor array configuration of the hardware available in the Harris et al. (2018b) 3-mo pilot study did not meet the requirements of distance sampling or SCR methods, so a new method was developed to estimate detection probability and, ultimately, animal density for which only horizontal bearings to calling animals were estimable. The horizontal bearings method also requires knowledge of auxiliary information, including the call signal-to-noise ratio (SNR—a ratio of mean-square pressure of the signal to the mean-square pressure of the noise), source level, sound propagation, and call production rate. It is this method that the present study employs to estimate seasonal fin whale density from recordings by the Comprehensive Nuclear-Test-Ban Treaty Organization International Monitoring System (CTBTO IMS) hydrophones at Wake Island in the Pacific Ocean.

A majority of previous acoustic density estimation studies reflected the development and validation of methods in focused, short-term pilot investigations lasting from an hour of data collection (Marques et al., 2012) to less than a year in most cases. In four instances, data collection periods exceeded a year and were applied to pressing questions related to abundance and seasonal distribution of two endangered species and three protected species. Marques et al. (2011) analyzed a year of data over two separate time periods from 2001 to 2002 and 2005 to 2006 to provide tentative estimates of total North Pacific right whale population size along the eastern Bering Sea shelf. Kimura et al. (2010) applied density estimation results for Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) to an examination of seasonal migration behavior. Multi-year abundance estimates of Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) were made on two U.S. Navy ranges to contribute knowledge of beaked whale population trends in relation to range activities (DiMarzio et al., 2018). DiMarzio et al. (2018) reported abundance estimates in absolute numbers of animals each month, which can easily be converted to animals per unit area given the areas of the two ranges. Finally, Hildebrand et al. (2015) estimated the density of Cuvier's beaked whales and Gervais' beaked whales (*Mesoplodon europaeus*) in the Gulf of Mexico between 2010 and 2013. To our knowledge, the present study is the first study to use passive acoustic density estimation methods outside of instrumented military ranges to assess regional baleen whale density over multiple, contiguous years in the context of oceanographic features.

The goal of this study was to determine the best environmental predictors of the endangered fin whale vocal behavior in the Equatorial Pacific around Wake Island, and then to relate this knowledge to the interpretation of seasonal animal density estimates over a 7-y time period. The first phase of the study consisted of compiling time series of ocean sound statistics, satellite estimates of chlorophyll concentration, SST, primary productivity, and regional shipping levels as explanatory variables to best explain patterns of fin whale vocal presence using the 20-Hz song unit as a proxy for fin whale presence. Detections of individual fin whale 20-Hz calls were then translated into seasonal estimates of fin whale density in an attempt to relate changes in animal density to regional environmental conditions and large-scale oceanographic features such as the El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO).

Methods

Data for the local- and basin-scale respective analyses of fin whale vocal presence and density estimation were obtained from the CTBTO IMS hydrophones at Wake Island (19° 18' 30.7872" N, 166° 37' 51.6432" E) in the Pacific Ocean. Data from the three hydrophones of the northern triangular array (H11N1, H11N2, and H11N3, spaced 2 km apart) where the average water depth was 1,425 m (estimated from Amante & Eakins, 2009) were used in this study. Hydrophones were suspended in the deep sound channel at depths of 731 m (H11N1), 721 m (H11N2), and 746 m (H11N3). Recording was continuous at a sampling rate of 250 Hz and 24 bit analog-to-digital (A/D) resolution (see Lawrence, 2004, and Miksis-Olds et al., 2013, for details on CTBTO IMS monitoring stations and recording characteristics). "Hourly fin whale vocal presence" from 2007 to 2012 was used as the response variable in the analysis to determine the best environmental predictors of local fin whale vocal presence. Seasonal density was then estimated from all fin whale calls automatically detected when the animals were seasonally present from November to March in this region from 2007 to 2013 (Mizroch et al., 1984; Soule & Wilcock, 2013).

Predictors of Fin Whale Vocal Presence

Acoustics—The hourly presence/absence of the fin whale 20-Hz song unit was manually assessed over the duration of the H11N1 dataset and represented the number of hours of vocal presence within the active acoustic space of the hydrophone per day. Hourly presence for this portion of the study was only assessed on hydrophone H11N1; localization of individual calls necessary for density estimation was not required for this portion of the study, so it was not necessary to run redundant analyses on all hydrophones in the array triad due to their close spacing. Protocol guiding the manual detection of 20-Hz fin whale call presence within an hour marked the top of each hour as the starting point. Manual scanning of the data continued until either a fin whale call was detected or 60 min without calls was achieved indicating vocal absence. When a call was detected, it was logged, and the review progressed to the start of the next hour. "Hourly vocal detection" was the response variable in the models developed to assess the best environmental predictors of fin whale presence.

Full spectrum mean-square sound pressure spectral density levels were averaged over each minute of the dataset (5 to 115 Hz), and all occurrences of the terms *sound levels* and *noise levels* throughout the rest of this work refer to mean-square sound pressure spectral density levels. Full spectrum mean-square sound pressure spectral density levels were considered because fin whales produce vocalizations across the entire spectrum of the 5 to 115 Hz band available in the CTBTO IMS data even though only the 20-Hz call was used in the environmental and density estimation analyses. Frequencies below 5 Hz and above 115 Hz were not included due to the steep roll-off of hydrophone response at these frequencies. Mean-square sound pressure spectral density levels were calculated using a Hann windowed 15,000 point Discrete Fourier Transform with no overlap to produce sequential 1-min spectral density estimates over the duration of the dataset. "Sound levels" were included as predictor variables in the models in addition to being used to assess signal detection area directing the acquisition scale of the satellite products (see below). A note of importance, the "sound level" predictor variables included more than just the fin whale contribution to the soundscape, capturing the acoustic input of other biological, geological, and anthropogenic sources present.

Daily percentile parameters for each frequency (P1, P50, and P99) were identified from the 1-min spectral density estimates (Miksis-Olds et al., 2013; Miksis-Olds & Nichols, 2016). P1 is indicative of the soundfloor (i.e., quietest periods) with characteristics of underlying geologic processes (geophony) created by wind and waves (Pijanowski et al., 2011); P50 is the median and includes sound produced by biologic (biophony), geologic, and distant anthropogenic (anthrophony) sources; and P99 represents the loudest periods of the day which were most often dominated by loud sources very close to the hydrophone either of biologic or human origin (Miksis-Olds & Nichols, 2016).

Shipping—The "level of regional shipping" was a predictor parameter of interest. The number of ship movements, an indicator of regional shipping activity, was recorded quarterly and was acquired from Lloyd's List Intelligence (London, UK). The data contained the number of ship movements in and out of Pacific Ocean ports; the "total ship movements" parameter used in the statistical modeling included the combined total movements of container, dry bulk, gas, general cargo, tanker, and other vessels. The data were acquired from the first quarter of 2002 (coinciding with the earliest CTBTO observations) to the end of the third quarter in 2011 (the time that the data were requested). However, the data recording methods of Pacific Ocean ship movements changed in the fourth quarter of 2010, precluding the remainder of the shipping observations in the analysis due to the data no longer representing the same measurement parameter.

Satellite Products—Signal detection areas around Wake Island were estimated seasonally using the passive sonar equation and ranged from 2,000 to 8,000 km^2 over the winter and spring seasons for frequencies from 20 to 50 Hz (Miksis-Olds et al., 2015). Satellite products were assessed over the same spatial scale to be as comparable as possible with the scale of acoustic area sampled. The standard NASA satellite imagery Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua Level 3 products were used to assess 8-d "chlorophyll concentration" ([Chl]), "primary production" (kg C/m^2), and "SST" at 9 × 9 km spatial resolution within the study region as fin whale vocal presence predictor variables. Eight-day temporally binned data were chosen to reduce the number of missing data points due to cloud coverage while still allowing for enough information at scales relevant to whale response. Primary production from the Vertical Generalized Production Model (VGPM) (Behrenfeld & Falkowski, 1997) was obtained from the NASA MEaSUREs Ocean Color Product Evaluation Project website (http://wiki.icess.ucsb.edu/measures/Main_Page); SST and [Chl] were obtained from the NASA Ocean Color website (http://oceancolor.gsfc.nasa.gov); and SST observations were acquired at night in the 4 micron nighttime microwave band. The NASA standard chlorophyll imagery product for [Chl] was utilized in each region (O'Reilly et al., 1998, 2000). All imagery time series were compiled from the start of the mission in June 2002 through the end of 2012. Pixels were extracted that were within the season-specific signal detection area for fin whale song units within the 10 to 30 Hz band detected around Wake Island. Any pixels within a water column less than 50 m deep were eliminated to ensure there were no inaccuracies in the satellite products caused by bottom impacts.

Statistical Modeling—The temporal resolution of the response and predictor data sources differed. The acoustical metrics (sound pressure level [daily percentile levels] and vocal presence [# h/d]) were daily, shipping was quarterly, and satellite products were 8 d. All data were merged to match the 8-d resolution of the satellite imagery. All daily ocean sound levels for a given 8-d period were averaged for that period. The hourly whale detection data were summed for each 8-d period and, thus, could range from 0 to 192 (8 × 24) for each 8-d period. The quarterly ship movements were divided equally between each 8-d period of a quarter.

Generalized linear and additive models (GLM and GAM) were used to investigate the relationship between the number of hours per 8-d period that fin whales were manually detected vocally (response variable) and the predictor variables. The predictor variables of the initial models included "total ship movements," "SST," "[Chl]," "primary production," and "P1," "P50," and "P99" for full spectrum noise. Data were initially checked for outliers by removing data points that were greater than three standard deviations (SDs) away from the mean. Collinearity was evaluated and was found between "primary production," "SST," and "[Chl]," which is not surprising given "SST" and "[Chl]" are used in the calculation of "primary production," thus "primary production" was removed from the list of predictor variables. There was also collinearity found between the sound level parameters P1 and P50. However, rather than removing one of the sound measures, both were included in different models. This was because the P1 and P50 levels were considered to be representative of different soundscape components, and, therefore, it was of interest to assess whether either was a significant predictor of fin whale calling.

GLM and GAM were fit in *R*, Version 3.5.1 (R Core Team, 2018), with a quasi-Poisson distribution (due to overdispersion in the data) and log link function. Predictor variables were removed in a step-wise process, based on a significance criteria of $p < 0.05$ using an F-test until all variables in the model were considered significant. QAIC (quasi-Akaike Information Criterion) scores were used to select whether the GLM or GAM was the preferred model, as well as choosing between models containing P1 or P50 sound levels. An upper limit of 3 kts was set for each smooth function in the GAM to prevent overfitting. The number of knots in a GAM determines the dimension of the basis function used in the GAM and can affect the flexibility of the smooth function (Wood, 2006). Model assumptions of linearity, appropriate mean-error variance, error independence, and normality were tested for the final model in *R* through diagnostic plots and relevant hypothesis tests.

Estimating Fin Whale Density

Harris et al. (2018b) described the automatic detection of fin whale calls in a pilot study from December 2007 through February 2008 in which fin whale density and distribution were estimated using acoustic bearings derived from the Wake Island CTBTO IMS sparse array data. The same methods were used here to estimate density across several years (2007 to 2013) during the peak calling period as identified from the hourly presence data (November-March). A summary of the density estimation method is given below; full details are included in Harris et al. (2018b).

Animal density can be estimated from acoustic cues (e.g., animal calls) using the following equation (from Marques et al., 2009):

$$\hat{D} = \frac{n_c(1-\hat{c})}{K\pi w^2 \hat{P}_a T\hat{r}} \qquad \text{(Eqn 1)}$$

where $\hat{D}$ = animal density, n_c = number of detected cues, $\hat{c}$ = false positive proportion, K = number of monitoring points, w = maximum detection range, $\hat{P}_a$ = average probability of detection of a cue within radius w of the sensor, T = total monitoring time, and $\hat{r}$ = cue, or call, production rate.

In Harris et al. (2018b), detection probability, $\hat{P}_i$, is estimated for each detected cue, which combine to estimate the abundance of cues, $\hat{N}_c$, accounting for those cues missed during the detection process:

$$\hat{N}_c = \sum_{i=1}^{n_c} 1/\hat{P}_i \qquad \text{(Eqn 2)}$$

Therefore, the density estimator becomes

$$\hat{D} = \frac{\widehat{N_c}(1-\hat{c})}{K\pi w^2 T\hat{r}}$$

There are several steps to estimate density from bearing data, with many stages required to estimate detection probability:

1. A subset of the recordings is manually checked for correct detection of the 20-Hz fin whale call. SNR of a sample of calls is measured, as well as noting whether the calls were automatically detected or not. SNR of the call was calculated using a noise level (NL) measured from the second of data preceding the call (in the same frequency bandwidth as the measured call rms received level [RL]) (Harris et al., 2018b). The probability of automatically detecting a call is then modeled as a function of SNR using a GAM. The resulting model, known as the *detection characterization curve*, can then be used to predict the detection probability, P(SNR), for each detected call across the whole dataset.

2. The monitored area is estimated using elements of the passive sonar equation: source level (SL) and NL distributions are used with a transmission loss (TL) model to determine ranges at which calls are expected to be masked from the automated detection process (i.e., P(SNR) is expected to be very low). These masked areas are then excluded from further analysis. Herein, the methods in Harris et al. (2018b) were altered so that the 99th and 1st percentiles from the SL and NL distributions across the entire datasets, respectively, were used as thresholds to define a loud call in quiet noise, and areas where the probability of detecting such a call were less than 0.0025 (i.e., 0.25%) were considered to be masked. This was due to the fact that initial thresholds (taking the 90th and 10th percentiles from the SL and NL distributions, respectively, and using a detection probability of 0.1) were found to be too conservative, potentially excluding areas in which animals could, in theory, be detected (Harris et al., 2018a).

3. The range of each detected cue is not known, but the distribution of possible ranges for each cue can be estimated via the passive sonar equation using the measured received level (RL), the bearing of each cue, and the associated bearing-specific TL, as well as the assumed SL distribution. The probability density function (pdf) of ranges for each cue can then be estimated. This probabilistic approach is used rather than estimating a single range because (1) SL for each cue does not have to be assumed known, instead

coming from a probability distribution; and (2) TL does not increase monotonically with range, so even if SL was known, a detected cue with a given RL could correspond to more than one range.

4. Account for missed cues by scaling each cue using the predicted detection probability from the detector characterization curve given the cue's SNR. In other words, each cue, i, on average corresponds to $1/P(SNR_i)$ cues within the monitored area.

5. Sum the number of estimated cues at each range and bearing step to give a total estimated abundance and use a generalized estimating equation (GEE) to produce a smooth spatial map of cues across the monitored area, taking into account spatial autocorrelation.

6. Use an appropriate density estimator (i.e., include additional multipliers) to estimate density. Multipliers will include false positive proportion (which may also include false cues caused by multipath and other types of multiple arrival, although in this study, a 1 s buffer was included in the automatic detection process to eliminate multiple arrivals), time spent monitoring (excluding periods of high ambient noise that cause masking), and cue rate. The method also allows a final step for which density is only estimated over a restricted area (determined using a simulation) where results may be more reliable due to detection probabilities generally being higher at smaller ranges. Further, the monitored area specified in Step 2 may be initially overestimated; therefore, density estimates averaged across this defined area may be underestimated. By restricting the area of inference further, any bias caused by the initial overestimation of the monitored area is reduced.

7. Estimate variance of detection probability using a bootstrap approach (n = 250 in this study) and use the delta method (Seber, 1982) to combine the variance contributed by separate components of the density estimator.

Characterizing the Automatic Detector—Approximately 52,560 h of data (6 y × 365 d × 24 h) were processed from April 2007 through March 2013, capturing six full annual migration cycles (November-March) annually, totaling 21,600 h over the six migration cycles. An automatic detector was run across the entire H11N1 dataset. The detector used a synthetic detection kernel and spectrogram cross correlation to detect target cues and was run in *Ishmael* software (Mellinger, 2002). The optimal detection threshold had a 0.1 false positive proportion and 0.56 to 0.6 false negative proportion over the 6-y time period, which is similar to the detector performance of the 3-mo study in Harris et al. (2018b). The detector output fed custom *MATLAB* (Mathworks, 2016) scripts to determine the root-mean-square (rms) RL and SNR of each detected call. Every 155th half-hour segment of data was analyzed manually for fin whale calls. With this sampling scheme, a half-hour was analyzed approximately every 3 d for a total of 680 analyzed 30-min data segments over the study period. This method of subsampling data prevented the analyzed data segment from consistently falling on the same day of the week or same time of day, limiting potential bias introduced by consistent anthropogenic noise sources. The SNR of all manually detected calls was measured (using the rms RL and the NL in the 1 s preceding the call), and whether the automatic detector has successfully detected the call was also noted. Detector performance was assumed not to change by year; therefore, a single detector characterization curve was fit in *R*, Version 3.3.1 (R Core Team, 2016).

Propagation Loss, Source Level, and Noise Level for Density Estimation—The propagation loss model used in the density analysis (both for the SL estimates and range distribution estimation) was the OASIS Peregrine Parabolic Equation (PE) model (Heaney & Campbell, 2016) following the methods in Miksis-Olds et al. (2015). The seasonal TL for a 20-Hz cue was modelled along 360 bearings at 1° resolution. Seasonal (November-March) sound speed profiles were obtained from *The World Ocean Atlas* (https://www.nodc.noaa.gov/OC5/indprod.html), and the bathymetry was taken from the global bathymetry database ETOPO1 (Amante & Eakins, 2009). Surface loss was negligible due to the low frequency of cues, and sea floor parameters of soft sand sediment were used representing a global average of deep ocean sediment. Details of the geoacoustic parameters in the specific regions were not known but should not affect propagation in these environments due to direct path/sound channel propagation. Whales were assumed to be calling at a depth of 15 m (following results in Stimpert et al., 2015).

Mean-square sound pressure spectral density levels were measured every minute as described above but were restricted to the 10 to 30 Hz band to more closely align with the target 20-Hz call. These NL values were used to assess when the ambient NL exceeded the maximum 1-min NL value in which a manually checked fin whale call was detected, therefore defining time periods that were likely to be masked by noise.

Given the array configuration at Wake Island, it was possible to localize a sample of calls within 10 km of the array, enabling SL to be estimated using time difference of arrival (TDOA) and two-dimensional (2D) hyperbolic methods. RLs (rms) were measured from which SL estimates were back-calculated together with propagation loss estimates. Bearings of calls were also estimated where possible using TDOA methods.

Other Density Estimator Inputs—Call production rate was estimated from Stimpert et al., (2015) and was the same value used in the pilot study (45.08 calls h^{-1}; standard error: 22.31) given the little data available about this parameter from any region. False positive proportion was also estimated from the manual checks described above and was assumed to stay constant across years, so a single parameter was estimated.

Results

The 20-Hz fin whale song component was detected in the region surrounding Wake Island with regularity. The time series of hourly fin whale detections summed over each week of the dataset identified the seasonal vocal presence of fin whales at this location as November through March (Figure 1E). This information then directed the density estimation analysis. A seasonal pattern was also observed in fin whale vocal presence, which lagged the warmest SST observed from July through October by 3 to 4 mo. Peak vocal detections occurred when waters were cooling (Figure 1D). This is consistent with peak fin whale detections following a 3 to 4 mo lag in SST in the North Pacific (Stafford et al., 2009) and 3 to 4 mo lag of the spring phytoplankton bloom in the North Atlantic (Visser et al., 2011). The most striking observation from the ocean sound-level time series was an increase in the P99 parameter occurring in conjunction with

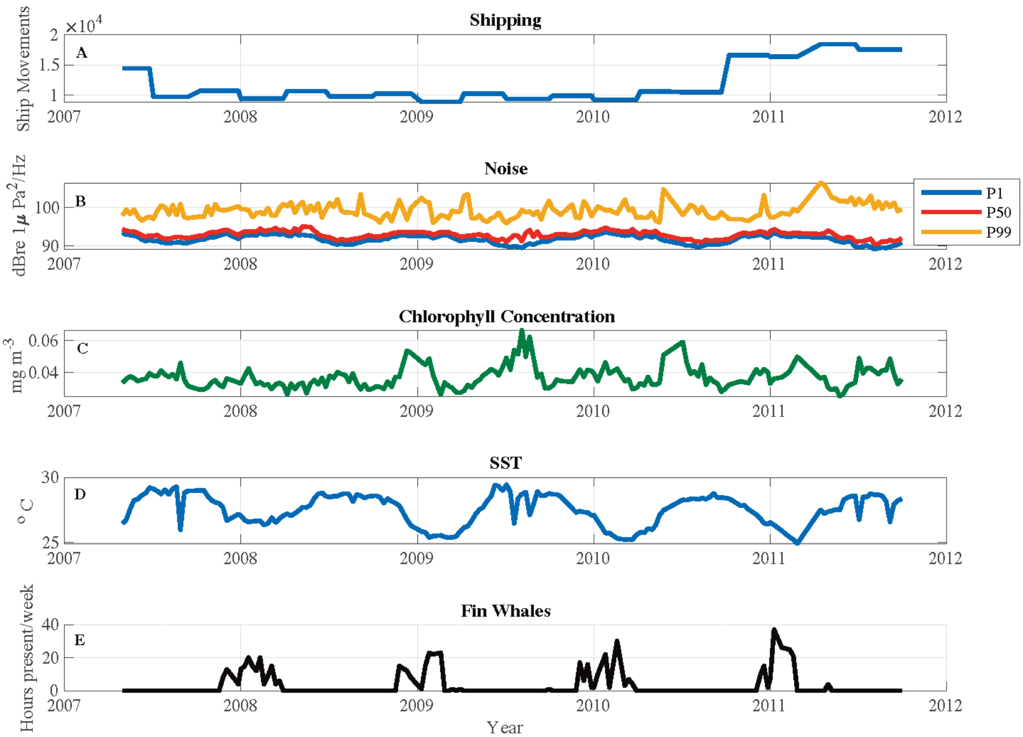

Figure 1. Time series of (A) shipping movements*; (B) P1, P50, and P99 mean-square sound pressure spectral density levels in the 5 to 115 band; (C) satellite-estimated chlorophyll concentration [Chl]; (D) satellite-estimated sea surface temperature (SST); and (E) fin whale vocal detection in hours per week from the Wake Island H11N1 hydrophone. *The data recording methods of Pacific Ocean ship movements changed in the fourth quarter of 2010, precluding the remainder of the shipping observations in the statistical analysis due to the data no longer representing the same measurement parameter.

an increase in shipping (Figure 1A & B). There was no observed trend on the P50 and P1 times series. The observed P99 increase over the duration of this study period is consistent with an increased P99 trend in Miksis-Olds & Nichols (2016). Similarly, the relatively unchanging P1 and P50 values over time is consistent with the slightly negative linear regression coefficients expressed as slopes in Miksis-Olds & Nichols (2016) for the same time period. No salient patterns or trends were observed in the [Chl] (Figure 1C).

The final selected model was a GAM (with a ΔQAIC score of 32 between the two candidate GLM and GAM models). Both P1 and P50 sound levels were consistently retained in candidate models, but P50 was the preferred predictor. Significant single predictors of fin whale vocal detections in the final model were P50 sound levels, [Chl], and SST. Smooth plots depicting the relationship between the predictors and the response are given in Figure 2. Fin whale detections increased with increasing P50 sound levels and decreased with increasing SST. Fin whale detections showed a slight increase from low to medium values of [Chl], with a slight decrease at higher [Chl] values. The final model explained 60.2% of the deviance, and all model assumptions were met.

Fin Whale Density Estimation

Detector Characterization—A total of 602 fin whale calls were manually detected: 336 calls were not automatically detected, while the remaining 266 calls were detected. SNR values ranged between -0.83 and 26.8; the mean SNRs (and SDs) of undetected calls and detected calls were 4.49 (1.51) and 13.32 (5.29), respectively. The fitted GAM predicted that the majority of calls with an SNR greater than 10 dB were certain to be detected (Figure 3).

Source Level and Noise Level Estimates—SL was estimable from 727 calls across the multiple years. The sample size enabled a SL distribution by year to be described. There was slight variability between the SL distributions (assumed to be normally distributed and summarized on the dB scale); annual means of the SL distributions ranged between 162.59 dB re 1 μPa m (SD: 4.57, $n = 130$) in 2010/2011 and 164.43 dB re 1 μPa m (SD: 6.06, $n = 134$) in 2012/2013. The annual means of the NL distributions in the 10 to 30 Hz band (also assumed to be normally distributed and summarized on the dB scale) measured in association with manually detected calls also showed annual variation, ranging between 88.11 dB re 1 μPa^2/Hz

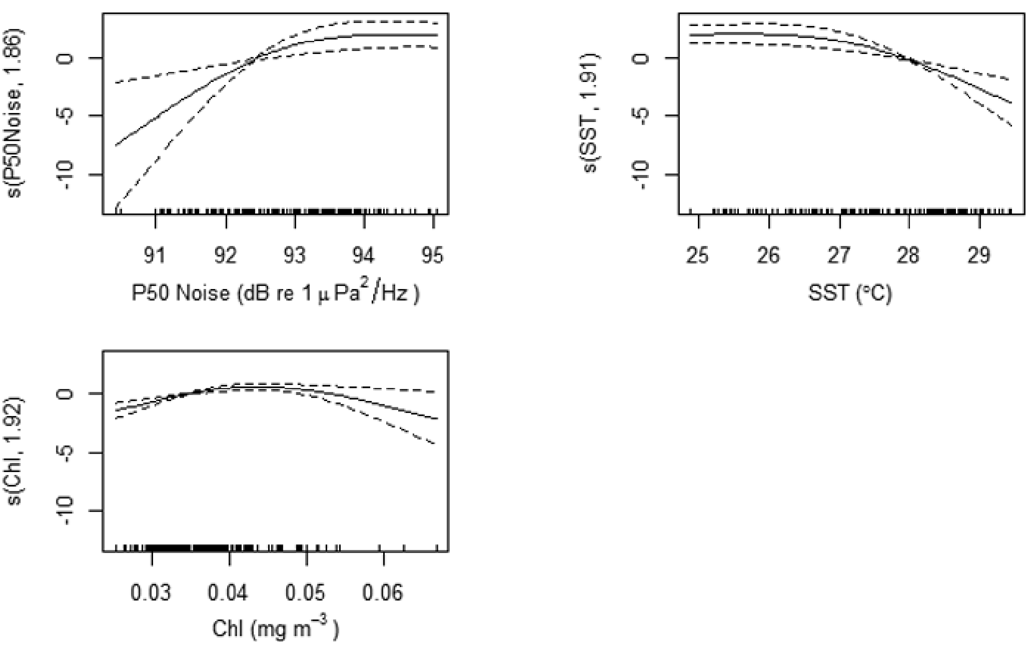

Figure 2. Plots of smooth functions (on the scale of the linear predictor) for significant predictors of fin whale temporal vocal patterns at Wake Island H11N1 in the Pacific Ocean. Dotted lines depict two standard errors above and below the smooth estimate. A rug plot (small vertical black lines on each x-axis) show the data for each predictor variable. The effective degrees of freedom used for each smooth function is shown in parentheses in the y-axis labels.

(SD: 1.4, n = 75) in 2008/2009 and 91.39 dB re 1 µPa^2/Hz (SD: 2.82, n=42) in 2007/2008.

Other Density Estimator Inputs—A total of 82,681 cues were detected across all datasets. The SNR of 3,128 detections was below the lowest SNR of an automatically detected call included in the detector characterization analysis (SNR = 2.33). Therefore, these calls were removed from the dataset to prevent extrapolation of the detector characterization curve, which could lead to extremely small predicted detection probabilities. Of the remaining 79,553 detections, 39,126 detections (49%) had measured bearings, ranging between 0.35° and 359.60° (Figure 4).

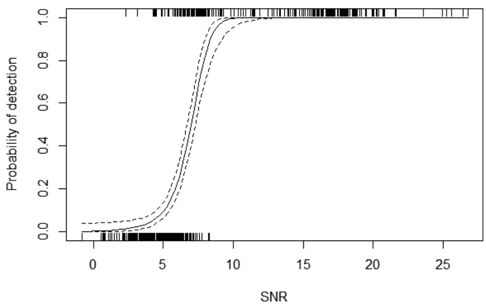

Figure 3. Logistic regression model of detection probability as a function of SNR; 95% confidence intervals (CIs) are shown.

Each 5-mo season had continuous monitoring over 3,648 h. Based on the 1-min ambient NL measurements across the whole dataset, very few minutes (n = 35) were omitted from the analysis due to potential masking caused by high noise. The false positive proportion, $\hat{c}$, was estimated to be 0.14 (standard error: 0.05). Finally, like the pilot study, the initial maximum detection radius, where detection probability was assumed to be negligible, was set to 1,000 km.

Density Results

Like the pilot study, the annual density surfaces demonstrated that the ranges at which the automatically detected calls were predicted to occur were small compared to the initially considered 1,000 km. Further, the monitored area was fragmented, driven by the fluctuating transmission loss patterns as a function of range (Figure 4). Total estimated detection area varied widely by year; the minimum was 729 km^2 in 2010/2011 and the maximum was 7,262 km^2 in 2012/2013.

The average estimated call densities (before the call production rate parameter was applied) ranged between 0.003 calls h^{-1} km^2 in 2008/2009 to 0.011 calls h^{-1} km^2 in 2009/2010. When the call production rate from the Southern Californian Bight was applied, average fin whale densities ranged from 0.07 animals/1,000 km^2 in 2008/2009 to 0.25 animals/1,000 km^2 in 2009/2010. However, the results were re-analyzed to restrict the area of inference to 10 km, following simulation results

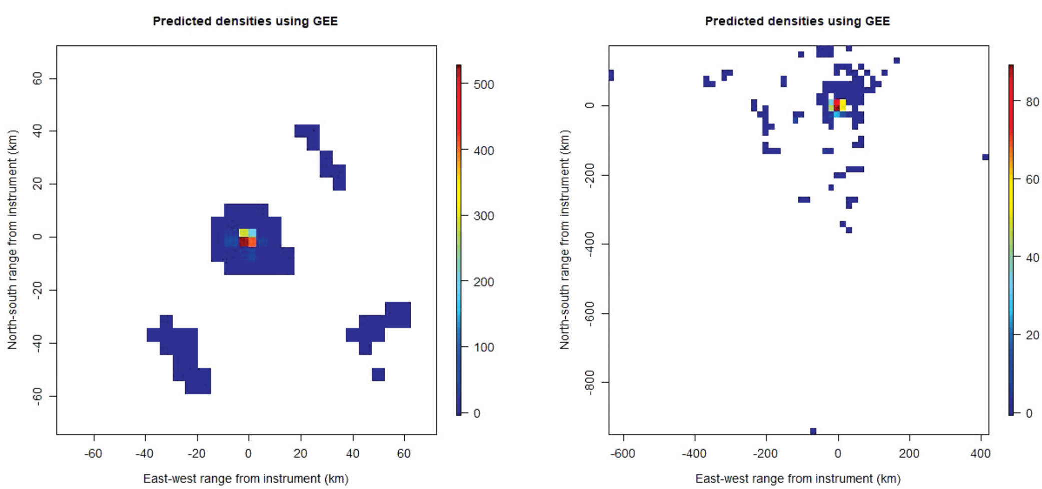

Figure 4. Two estimated georeferenced plots from the 2010/2011 season (left) and 2012/2013 season (right) showing the irregular and patchy estimated monitored area given assumptions based on measurements of SL, NL, TL, and detector performance. The colors depict the estimated call density (calls/km^2). Note, however, that the apparent low density at larger ranges from the instrument may be due to overestimation of the monitored area, and, thus, these areas are omitted from the final part of the analysis.

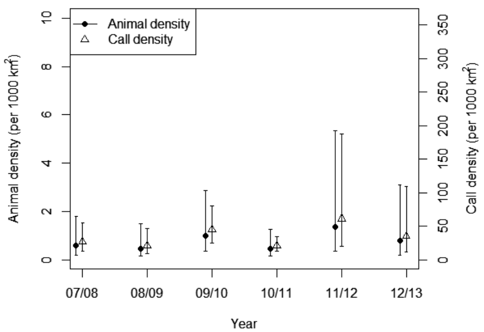

Figure 5. Predicted fin whale animal and call densities by season with associated 95% CI. Note that the call density values in the figure are per 1,000 km^2 as opposed to the call density numbers presented in the text per km^2. These results were generated after restricting inference to within 10 km of the instrument (H11N1, in this case). Detector performance, false positive proportions, and call production rate were assumed to remain constant across years in the animal and call density estimations.

in Harris et al. (2018b) that suggested that results may be robust when restricted to this smaller range. In this case, call densities increased, ranging between 0.020 calls h^{-1} km^2 in 2010/2011 to 0.061 calls h^{-1} km^2 in 2011/2012 (Figure 5). Applying the call production rate resulted in annual animal density estimates ranging between 0.5 animals/1,000 km^2 (in 2008/2009 and 2010/2011) and 1.4 animals/1,000 km^2 in 2011/2012 (Figure 5). Coefficient of variation (CV) estimates for the animal density estimates ranged from 0.56 to 0.80. Due to the call rate parameter and detector false positive performance being kept constant across years, the call density estimates followed the same patterns as the animal density estimates but had smaller CVs (0.27 to 0.63) due to the removal of the call rate parameter from the estimated variance.

Discussion

Estimates of animal abundance or density are critical to effective management and regulation of marine mammal stocks because they provide a quantitative measure related to tracking population health, recovery, impact, and behavioral ecology. Animal density information has traditionally been obtained from visual sightings through the implementation of distance sampling and mark-recapture methods (e.g., Borchers et al., 2002; Buckland et al., 2004). While effective over small temporal and spatial scales, visual methods used for marine mammals are limited by the proportion of time animals spend at the surface and are available for sighting, sighting conditions (e.g., sea state, darkness, etc.), and cost, constraining a majority of dedicated surveys to coastal or nearshore areas. These constraints have limited the density estimate of fin whales in the North Pacific to specific nearshore regions, and there is currently no population estimate for fin whales in the North Pacific as a whole (Barlow, 1995, 2003, 2010; Forney et al., 1995).

Estimating animal density from passive acoustic recordings provides another method to assess animal abundance by employing detections of species-specific vocalizations. Techniques developed for estimating animal density from acoustic time series expands the geographic, temporal, and spatial scale of visual methods because they are less limited by visibility conditions and cost, hardware can be deployed for long periods of time in remote locations, and underwater propagation conditions extend the detection area of animals compared to visual surveys. Long-time series provided by passive acoustic monitoring supporting density estimation now broaden the application of passive acoustic recordings to questions requiring estimates of absolute animal numbers such as stock assessments, impacts of disturbance, and assessment of risk and appropriate mitigation procedures. However, accurate interpretation of changes in animal density patterns or trends requires an understanding of confounding environmental factors impacting animal behavior, movements, and distribution. The present study is the first multi-year acoustic density estimation time series to be examined in the context of local and basin scale ocean conditions for any baleen whale species.

The multiple regression analysis of environmental parameters most predictive of fin whale vocal presence in the Equatorial Pacific indicated that vocal activity was linked to seasonal trends in SST. Cooler SST is indicative of physical conditions wherein nutrients can be brought into surface waters, increasing primary production rates. In this region, greater numbers of fin whales are detected during periods of cooler SST when primary production also increases. Fin whales are rather cosmopolitan with their diets and eat krill (euphausids), other zooplankton, and schooling fish (Nemoto & Kasuya, 1965). SST and associated primary productivity were also identified as the best oceanographic variables for predicting fin whale presence in the subarctic and Northeast Pacific over a 6-y period from 1997 to 2002 and in the North Atlantic over a 4-y period from 2004 to 2007 (Stafford et al., 2009; Visser et al., 2011), indicating that food is a strong driver of fin whale movements and distribution despite the season, location, or migration phase. The overall distribution of fin whales assessed from visual sightings in summer in the subarctic North Pacific also coincided closely with the distribution of zooplankton biomass (Sugimoto & Tadokoro, 1997), providing further support that the use of vocal detections as a proxy for animal presence is comparable to visual survey results.

An additional relationship was identified between increases in fin whale vocal activity and increases in the regional median sound level indicated through the P50 variable. The result of P50 being a strong predictor of fin whale vocal presence begs the questions as to whether this is a confounding factor capturing distant fin whale song as background noise in the soundscape or whether other sources are driving the corresponding increases. Fin whales are not the only large, low-frequency call producing whales inhabiting the region around Wake Island. Sei (*Balaenoptera borealis borealis*), blue, Bryde's (*Balaenoptera edeni*), and minke whales have been observed to be seasonally present in the region and overlap in time and space with fin whales (Donovan, 1991; Stafford et al., 2001; Oleson et al., 2003; Horwood, 2009). Vocalizing whales were identified as the source category driving soundscape dynamics over the same time period at this location in Miksis-Olds & Nichols (2016). It is likely that multiple species vocalizing at a distance are contributing to the increase in the seasonal median sound levels predictive of fin whale vocal presence as there was no overt seasonal trend observed in shipping activity.

The environmental variables most predictive of fin whale vocal presence provided information on what oceanographic conditions were most closely linked to regional and seasonal fin whale presence, but they did not provide information on whether more or fewer whales were present in the area across years and what may be driving observed differences. Changes in animal abundance are needed to draw any meaningful conclusions on the impact of changing conditions on animal populations. When the acoustically derived fin whale estimates were compared with seasonal averages of the environmental parameters most predictive of whale presence and the larger climatic indices for ENSO and PDO (Table 1), the only striking observation was that one of the largest changes in abundance coincided with phase shifts in both ENSO and PDO. There was a negative to positive ENSO and PDO phase shift from the 2008/2009 season to the 2009/2010 season corresponding to an increase in vocally detected fin whales north of Wake Island. During the 2010/2011 season, the ENSO and PDO reverted back to a negative phase along with a decrease in whale density. The year with the largest estimated fin whale numbers corresponded with the most negative PDO phase observed over the duration of the study. Typically, ENSO and PDO phase shifts are coupled to corresponding changes in the SST, [Chl], and primary productivity of a region (Newman et al., 2003), yet ENSO and PDO values were not observed to be tightly linked to the seasonal averages for these parameters at this location or time. While the current work is suggestive of a relationship between climate patterns and fin whale abundance, and successfully demonstrated the feasibility of such studies, a longer time series more reflective of the ENSO and PDO cycles is needed to be able to draw statistically valid inferences.

Further, the density estimates could be produced at a finer temporal resolution to be comparable with the oceanographic data presented in this study. Then, the density estimates could be treated as the response variable and modeled directly with the environmental covariates. This approach has already been demonstrated for cetacean species using acoustic density estimates—for example, for fin whales in the Atlantic (Thomas et al., 2013) and harbor porpoises in the Baltic Sea (Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise [SAMBAH], 2017). Combining density estimation with modeling was outside the scope of this study due to the amount of auxiliary analyses required for the bearing-only density estimation method; it was not feasible to process enough data to allow for independent estimates of all the inputs required for the method, such as SLs and NLs, as well as characterizing the detector, at a reduced temporal scale. The number of auxiliary analyses required for the bearing-only method is a disadvantage of this approach compared to other density estimation methods, such as distance sampling and spatial capture-recapture, both in terms of amount of analysis time needed but also the potential for these estimated inputs to be biased and/or have large uncertainty. However, despite the coarse scale seasonal analysis, the acoustically derived density estimation methods described within this work illustrate the potential for the bearing-only density estimation method to be another valuable tool for assessing the relationship between environmental conditions and animal density/abundance for many marine mammal species in the future.

How comparable are the acoustic density estimates to other abundance estimates of fin whales in the North Pacific? The density estimates derived in this study are over a magnitude higher than the acoustically derived estimates reported by McDonald & Fox (1999) and visual estimates reported by Barlow (2003) in Hawaiian waters. McDonald & Fox (1999) did not use a cue rate multiplier to estimate number of animals from acoustic encounters as was done in the current work (but see the discussion below about the limitations of the cue rate used in this study). Detection

Table 1. Average seasonal (November-March) values of climate indices and environmental parameters most predictive of fin whale vocal presence around Wake Island. PDO index data were obtained from http://research.jisao.washington.edu/pdo/PDO.latest.txt. The Oceanic Niño Index (ONI) is a 3-mo running mean of *ERSST*, Version 5, SST anomalies in the Niño 3.4 region (5° N to 5° S, 120° to 170° W), based on centered 30-y base periods updated every 5 y. It is one measure of ENSO, and data were downloaded from http://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. Blue highlights the maximum value within each parameter column, and green highlights the minimum value within each parameter column.

	PDO	ONI	SST (ºC)	[Chl] (mg m^{-3})	PP	P50 (dB re 1 μPa^2/Hz)	DE (animals/ 1,000 km^2)
2007/2008	-0.83	-1.46	27.03	0.034	110.47	93.8	0.6
2008/2009	-1.33	-0.66	26.06	0.037	127.04	93.4	0.5
2009/2010	0.35	1.32	26.25	0.037	125.27	93.7	1.0
2010/2011	-0.89	-1.32	26.25	0.037	127.64	93.8	0.5
2011/2012	-1.48	-0.80	26.95	0.032	108.72	93.0	1.4
2012/2013	-0.45	-0.22	27.26	0.035	107.47	92.9	0.8

probability was also assumed to be certain within a defined monitored area, and so a minimum population density estimate was derived with the authors noting that more sophisticated future approaches may indeed incorporate cue counting methods. Fin whale density estimates in the current study, however, are consistent with density estimates derived from visual line transects conducted in the early 1990s within 161 km of the California coast (1.1 animals/1,000 km^2; Barlow, 1995; Forney et al., 1995) and within 483 km of the California-Oregon-Washington coastline in 2008 (2.5 animals/1,000 km^2; Barlow, 2010).

In this study, assumptions were made about detector performance and false positive proportions remaining constant across years; such assumptions should be investigated if this study were to be refined and expanded to a longer time series. Further, the variance from the detection probability estimation process was a large component of the overall variance in density for each year and potentially could be reduced through an increased number of bootstrap iterations. Also, the propagation model (used both to estimate SL and as part of the main method) was assumed to be known—no uncertainty was included for the propagation. The method framework could, however, readily be extended to incorporate additional uncertainty regarding propagation loss. Finally, the cue rate parameter was a major limitation of the animal density estimates in this study; along with detection probability, cue rate was another major source of uncertainty in the overall variance estimates as the cue rate information was derived from a study in another part of the Pacific at a different time (Stimpert et al., 2015). Therefore, it is imperative to improve understanding of this parameter and assess how it may vary over space and time. Without this information, and by assuming a constant call production rate, it is possible that observed changes in animal density estimates may actually be caused by the same number of animals altering their vocal behavior.

It is not definitively known which stock of fin whale was recorded at Wake Island. The November-March detection period observed in the study directly overlaps with the peak period of seasonal fin whale detections in the Northeast Pacific and Hawaii (McDonald & Fox, 1999; Stafford et al., 2009). Although the animal densities are similar between the animals recorded in the Equatorial Pacific and Northeast Pacific, the large distance between the two locations does not support the hypothesis that the Wake Island fin whales are from the Northeast Pacific population. It is possible that the animals recorded off Hawaii and Wake Island could be from the same population spread out in range. It is also likely that the whales recorded in the Equatorial Pacific are from a southern hemisphere stock recorded during the breeding period (Mizroch et al., 1984). There is also the possibility that the animals recorded in the Wake Island region are a separate and undocumented population. The tracking of individual animals will be necessary to determine which fin whale stock is being recorded off Wake Island, and the density estimation methods employed herein can then be applied to stock abundance estimates over time as the Wake Island dataset continues to grow in length.

Application of a density estimation method based on the bearing estimates of each detected fin whale call from a sparse three-element array provided seasonal estimates of local fin whale density around Wake Island. While the dataset was not long enough to statistically relate changes in animal abundance to long-term climate patterns, it provides a method for doing so in the future without the use of instrumented military arrays. The methods are also directly translatable to the other five CTBTO IMS locations in the South Atlantic, Indian, South Pacific, and Southern Oceans (Coyne et al., 2012; Haralabus et al., 2017) and any other sparse array that can estimate the bearing to detected calls, making this capability widely accessible where other density estimation approaches cannot be implemented.

Acknowledgments

DVH was funded by the Office of Naval Research (ONR) (Award N00014-14-1-0394). JMO was funded under Awards N00014-11-1-0619, N00014-14-1-0397, and N00014-16-1-2860 from ONR. CM was also funded under ONR Award N00014-14-1-0397. Kevin Heaney (Applied Ocean Sciences, LLC) generously contributed the propagation modelling results for which we extend sincere thanks. The CTBTO data was accessed from the Air Force Tactical Applications Center/U.S. National Data Center. Thanks are extended to James Neely (AFTAC), Richard Baumstark (AFTAC), Mark Prior (formerly CTBTO), Andrew Forbes (formerly CTBTO), Mario Zampolli (CTBTO), and Georgios Haralabus (CTBTO) for their assistance in data transfer and transfer of knowledge of CTBTO data. Thanks also to AFTAC and CTBTO for making the data available (CTBTO Virtual Data Exploitation Centre [vDEC]: https://www.ctbto.org/specials/vdec). Finally, please note that the views expressed in this study are those of the authors and do not necessarily represent the views of the CTBTO Preparatory Commission.

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