Humpback whale singing activity off northern Angola: an indication of the migratory cycle, breeding habitat and impact of seismic surveys on singer number in Breeding Stock B1

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ABSTRACT

Passive acoustic monitoring was used to document the temporal and spatial distributions of singing humpback whales off the coast of Northern Angola, off the Congo River outflow, and test for impacts of seismic survey activity on the number of singing whales. Four Marine Autonomous Recording Units (MARUs) were deployed between March and December 2008, two in the near-shore environment (ca. 2-3 km offshore) and two in the offshore environment (at 15 km and 24 km offshore). Song was first heard in mid June and continued through the remaining duration of the study until 1 December (when recording ended). Very few singers were recorded on the near-shore MARUs, but song was a dominant feature of the acoustic environment in the offshore region. Numbers of singers per hour were counted on the offshore MARUs for the period from 24 May to 1 Dec, sampling at least every other day, and in the case of periods containing seismic survey pulses, every day. Distinct seasonal variation was documented, with a rapid but steady increase in singing activity during June, relatively consistent singing from July through October, and a steady decline in singing activity through November to near zero levels by 1 December. Diel variation was also documented, as on other breeding grounds, with a peak in singing activity at night and a low in the afternoon. Comparison of singing activity at the two offshore MARU regions indicated a clear offshore distribution of singers, with many more singers heard on the 24 km MARU, and an analysis of delay times for singers heard on both MARUs indicated a skewed spatial distribution offshore (with >40% of singers locate >20km offshore). Application of General Additive Mixed Models (GAMMs) indicated significant seasonal and diel variation, and muli-modal seasonal distributions for both offshore MARUs that were markedly different. Taken together, the data on temporal and spatial distribution suggests utilization of this region as active breeding habitat and the presence of potentially multiple migratory streams, and has implications for the discussion of sub-stock structure of Breeding Stock B. Seismic survey activity was heard regularly during two separate periods during the deployments, during July and later in the season during mid-October/November. Assessment of a measure of received level (RL), Peak Power, on the number of singers yielded a significant impact: in GAMMs for both MARU 1 and MARU 2, the number of singers significantly decreased with increasing RL of seismic survey pulses. This suggests that the breeding display of humpback whales is disrupted by seismic survey activity, and thus merits further attention and study.

KEYWORDS: PASSIVE ACOUSTIC MONITORING, HUMPBACK WHALE, ANGOLA, SONG, MIGRATION, SEISMIC SURVEY, OCEAN NOISE

INTRODUCTION

The coasts and pelagic regions of Africa support a diverse assemblage of marine life, including populations of large whales in variable states of recovery from commercial whaling. However, in terms of cetaceans, these are among the most poorly understood and documented regions on the globe, with many open questions regarding species presence, distribution, timing of migrations and importance of habitat to critical life functions. At the same time, offshore development (oil and gas exploration and extraction, mining and recent naval manoeuvres) along the African coast is increasing rapidly, and occurring in the absence of sound baseline information about regional cetacean populations, their behaviour, and their response to anthropogenic acoustic stress. This region is both a focal area for new offshore development activities that will generate underwater noise and includes globally important breeding, migratory, and nursery areas for several key cetacean species, making it an important research frontier in the effort to understand, plan for, and mitigate anthropogenic acoustic stress on cetaceans.

Humpback whales (*Megaptera novaeangliae*) in the southern hemisphere are distributed in circumpolar high latitudes during the austral summer and migrate to semi-discrete low latitude breeding areas in the austral winter. The International Whaling Commission (IWC) currently designates seven breeding stocks (populations) labeled A through G, ranging from the Southwest Atlantic eastward to the Southeast Pacific (Gambell 1976). The population that winters in the Southeast Atlantic Ocean is considered Breeding Stock B, and has a winter distribution along the western coast of Africa from Namibia to Nigeria and the Gulf of Guinea.

Whaling data for the Breeding Stock B region includes ~15,350 documented humpback catches between 1909 and 1959 (Townsend 1935; Allison 2006). Humpback whales have been described from South Africa (Olsen 1914; Matthews 1938) to the Gulf of Guinea (Budker and Collignon 1952; Gambell, 1976; Findlay 2000; Rosenbaum and Collins 2006). This population has received comparatively limited study and existing data indicates a potentially complex subpopulation structure (Carvalho et al. 2009, Pomilla et al. 2006, Rosenbaum et al. 2009). The west coast of southern Africa was originally believed to serve only as migratory corridor, but surveys during the austral spring and summer have identified the presence of non-migrating whales and evidence of feeding (Best et al. 1995, Barendse et al. in press). High densities of whales and breeding have been documented for the coasts of Gabon (Walsh et al. 2000; Rosenbaum and Collins 2006; Collins et al. 2010), Sao Tome (Carvalho et al. 2007) and Angola (Best et al. 1999; Weir 2008). Two nominal sub-stocks are thus currently recognized: the B1 sub-stock winters (June-November) along the coasts of the Gulf of Guinea south to Angola, and the B2 sub-stock is thought to utilize the coasts of Namibia and western South Africa (Best et al 1995; Barendse et al in press). Questions remain over whales identified further west in Africa (Van Waerebeek *et al.* 2001, Bamy *et al.* 2010).

Humpback whales are well known for their elaborate acoustic breeding display, male song (Payne and McVay 1971). Songs are organized into a stereotyped, hierarchical pattern of units, phrases and themes, all males within a population share a common set of themes, and songs gradually change over months and years (Payne and McVay 1971, Payne et al. 1983, Guinee et al 1983, Noad et al. 2000, Cerchio et al. 2001). Singing occurs in breeding regions and is believed to be important to male reproductive success (Tyack 1981, Cerchio et al. 2005, Cholewiak 2008, Smith et al. 2009); males also sing to a lesser extent in feeding regions (Mattila et al. 1987, McSweeny et al. 1989, Clark and Clapham 2004) and during migration (Clapham and Mattila 1990, Noad et al 2000). Thus passive acoustic monitoring for the presence of song is a useful indicator of breeding habitat and migratory timing and behaviour. Furthermore, since song is an important breeding display, the impact of anthropogenic activities, either by disturbing singing males or acoustically masking song display, can have potentially negative effects on the reproductive success of individuals and populations.

The Wildlife Conservation Society (WCS) recently conducted an assessment of cetaceans off the coast of Angola, at the outflow of the Congo River. As part of this assessment, we collected nine months of continuous passive acoustic data from two locations in the offshore environment (15 and 24 km offshore). This study reports on the presence of humpbacks whales in the offshore environment between the months of June and December 2008, as indicated by recorded singing males, and provides insight on the migration, breeding habitat and impact of noise introduced by seismic surveys on singing activity in this region.

METHODS

Field Site and Data collection

Work was conducted in northern Angola off the Congo River mouth outflow (Figure 1) at about 6ºS in the South Atlantic Ocean. Passive acoustic monitoring was one component of a larger project to assess marine mammal presence around the construction site of the Angola Liquefied Natural Gas (ALNG) plant. Marine Autonomous Recording Units (MARUs) used in this study were developed by the Cornell Bioacoustic Research Program (www.birds.cornell.edu/brp) and have been applied as a cost-effective means of surveying whales (including blue, fin, humpback, right, and sperm whales) in a variety of coastal, shelf edge, and deep water habitats (Cholewiak 2008, Sousa-Lima and Clark 2008, Di Iorio and Clark 2009). A MARU consists of a glass sphere (capable of withstanding pressures at up to 4,000 m depth) encapsulating an amplifier, frequency filter, programmable computer, software that schedules, records, and stores acoustic data and a disk drive to store the data, and is attached to an external hydrophone. MARUs were programmed and deployed to the sea floor, and then recovered by means of an acoustic communication circuit that signals the unit to release from its anchor and float to the surface. Between March 2 and December 1, 2008, four MARUs were deployed in two pairs in the offshore and inshore environment, respectively, off the Congo River mouth (Figure 1).

Data analyzed in this study were recorded from the offshore MARU locations (labelled MARU 1 and MARU 2 in Figure 1). The MARUs were deployed at approximately 100 meters depth, 24 km and 15 km offshore the Sereia Peninsula, on the edge of the Congo River Submarine Canyon, and separated by 9.65 km (at coordinates 6.080ºS, 12.057ºE and 6.046ºS, 12.137ºE). For these locations, MARUs were configured to record continuously for approximately 90-100 days with an effective bandwidth of 1,000 Hz (2,000 Hz sampling rate), targeting the sounds of baleen whales. Frequency response of the MARUs was 15-1,000 Hz (within approx. 3 dB), and flat from 55-585 Hz with an effective sensitivity of -151.2 +/- 1 dB and nominal dynamic range of 63.2 dB. The offshore MARUs were deployed three times for a continuous period of nine months. After the first deployment of 81 days, the retrieval system of MARU 1 malfunctioned and only MARU 2 was retrieved. The second and third deployment recorded for 88 and 101 days, respectively, and both MARUs were retrieved successfully. Recovered data includes between 1,900 and 2,425 hours of continuous recordings from each unit amounting to approximately 11,016 hours of data from the offshore locations from March 2 to December 1, 2008, with only two breaks of two days each for retrieval, refitting and redeployment. Simultaneously to the offshore deployments, two additional MARUs were deployed at two of three inshore locations (labelled 3, 4 and 5 in Figure 1), approximately 2-3 km from the coast and Congo river outflow at approximately 20-30 m depth. These units were sampling at 32,000 Hz for an effective bandwidth of 16,000 Hz, targeting delphinids; due to the higher sample rate, these units were configured to record on a ¼ duty schedule, recording for 1 hour and off for 3 hours. These were reviewed for the presence of humpback whales but detailed analysis is not reported here.

Acoustic and Song Analysis

Data were downloaded to hard drives, the acoustic data from the pair of MARUs were synchronized for each deployment, and a continuous stream of multichannel sound files was created using custom software developed by Cornell BRP. Recordings were analyzed using software Raven Pro 1.3 or 1.4 (www.birds.cornell.edu/brp/raven/RavenOverview). Spectrograms (1024pt FFT, 75% overlap) were browsed for 50% of all data, visually scanning every other week for the entire nine month duration. It was determined through this browsing that no humpback whale song was heard during the first deployment (2 March to 22 May 2008), and that singers were first recorded on the second deployment (24 May to 20 August 2008), starting sometime in June, and continued through the third deployment (22 August to 1 December 2008). A sampling protocol was then developed to assess the number of singing whales recorded throughout the migration and breeding season.

Sub-sampling of the entire second and third deployment periods was completed in order to assess the number of singers present in the first ten minutes of every hour, for every other day from 24 May to 1 December 2008. First, the song typical of the population and year was characterised in terms of phrases and themes using several high signal/noise recordings for whales that sung near a MARU uninterrupted for >1 hour. Printed spectrograms of these songs were used to help identify phrases and count singers during the analysis. Spectrograms (512pt FFT, 75% overlap) and waveform envelops of each ten minute period were viewed on Raven, with each MARU represented as a different channel in temporally aligned, horizontal panels; the entire ten minute period was scanned to determine a 1 minute interval in which the most overlapping singers were audible. The number of singers was then counted using directly overlapping units, as well as overlapping phrases (since singers in different themes were readily identified) and amplitude differences between singers at varying distances from the MARUs. Singers audible on both MARUs were identified by recognizable phrases on both MARUs, offset in time as a result of time of arrival differences of the signal at each MARU (Figure 2). Each singer in a 10 minute section was assigned a relative amplitude score on a four point scale for each MARU (receiving two scores): 0 - not audible on that MARU (but present on the other MARU); 1 - singer with faint signal detectable on spectrogram, but with no corresponding amplitude detectable on waveform; 2 - singer with distinct signal detectable on spectrogram, and small corresponding amplitude detectable on waveform; and 3 - singer with strong, dark signal detectable on spectrogram, and intense corresponding amplitude on waveform. If a ten minute period was encountered that contained a passing boat that raised the noise floor and potentially masked singers, the next ten minute frame in the hour was reviewed until a ten minute frame without boat noise was found for measurement.

During the review for singers, several periods were encountered where offshore seismic survey pulses were detected on a daily basis (Figure 3). Seismic survey pulses were also logged for each MARU when encountered and care was taken to select a single pulse in the series that did not overlap with other signals in order to measure Received Level (RL) at the MARU. As a measure of RL, the Peak Power measurement in Raven 1.4 was used, with a 1024 point FFT and a 75% overlap. This measure was chosen because for many of the lower amplitude pulses, there where higher amplitude sounds in the same time slice, and thus peak-to-peak amplitude or RMS measurements would not be a representative of pulse RL. The Peak Power measurement provided a spectrogram-based measure of the highest power frequency bin in dB re: 1 dimensionless sample unit; this unreferenced measurement was converted into a RL using a calibration constant for the MARU to yield a measurement in dB re: 1 µPa in a 1 Hz frequency bin. The frequency at which the Peak Power occurred, the Peak Frequency, was also recorded, and both measurements were constrained to a minimum low frequency of 15 Hz,; thus, if the frequency of peak power actually occurred below 15 Hz, only the portion of the pulse above 15 Hz was considered and measured. This was done to account for a conservative bottom range of baleen whale hearing (estimated at about 20 Hz for humpback whales and 15 Hz for blue and fin whales). Once the analysis was completed for every other day across the two deployments, it was determined that all seismic survey activity occurred during two extended periods, from 4 July to 30 July, and from 14 October to 1 December. In order to perform a more rigorous assessment of impact of seismic survey on singing activity, the intervening days not reviewed during these periods were analysed so that we acquired a complete record for all hours of all days during the periods when seismic surveys were active.

Statistical Analysis

Several variables were statistically assessed to determine their effect on singing activity. The dependent variable was the number of singers present each hour, treated separately for each MARU. It was expected that number of singers would vary on a daily basis across the entire period due to timing of the seasonal migration, and that the pattern of this seasonal variation would provide insights as to whether this region represents active breeding habitat or solely a migratory corridor. Seasonality was captured by the Survey Day variable, the number of days since the first singing activity was recorded on 9 June 2008, ranging from 0 to 174. It was also expected that number of singers would vary across hours of the day in a diel cycle (represented by the Hour variable ranging from 0 to 23); singing activity has been shown to peak during the night and reach a trough at midday in other breeding regions (Au et al. 2000, Cholewiak 2008, Sousa-Lima and Clark 2008). Similarly, it has been shown that moon phase significantly influences singing activity (Sousa-Lima and Clark 2008), hence, Moon Phase was included as a factor variable (New Moon, First Quarter, Full Moon, Last Quarter). The potential interaction between Hour and Moon Phase was also considered (as reported in Sousa-Lima and Clark 2008), since diel variation is potentially a function of reduced light levels at night that could be affected by lunar phase. In addition, we wanted to investigate the potential impact of seismic survey activity and considered two variables, namely Peak Power RL in dB re: 1 µPa in a 1Hz bin, and Power Score a categorical variable 0-5 where each category corresponds to intervals of increasing received levels (0 = Seismic survey pulse not detected during the 10 min sample, 1 = 65-75 dB, 2 = 75-85 dB, 3 = 85-95 dB, 4 = 95-105 dB and 5 = >105 dB). A default value of 60 dB was used for Peak Power to represent the background noise level in those cases where there was no seismic signal. We also considered a subset of the data corresponding to the first period of seismic activity 5-31 July 2008. The data set covering the entire period comprised 3,096 data points, whereas this reduced set had 648 data points.

Generalized Additive Mixed Models (GAMMs) were used given their flexibility and capacity for non-linear responses (clearly evident in these data) and options for dealing with temporal correlation (due to the dependence of counts close in time) (Zuur et al. 2009). The auto-correlation function (*ACF*) in R (RDCT 2010) allowed us to visually ascertain the degree of temporal correlation in the data and an autoregressive model of order one (AR-1) was used to deal with it (from the *nlme* library by Pinheiro and Bates 2002). The models were fit in R using the *gamm* function in the *mgcv* library (Wood 2006), which calls the appropriate routine in the *MASS* library (Venables and Ripley 2002). Model selection was based on model diagnostics such as plots (residuals vs. linear predictor, histogram of residuals, response vs. fitted values, etc.), the statistical significance of the terms in the model (based on the approximate p-values produced by *gamm*), Akaike's Information Criterion (AIC) and the adjusted R-squared value were also considered. Cubic regression splines were used to fit the smooth functions (a cyclic smooth was used for the Hour variable to ensure that the first hour matched up with the last hour). A Poisson distribution and log link were assumed. The natural variation in singing activity over an entire season is expected to be much larger than that associated with diel and lunar phase cycles, and potentially also that associated with anthropogenic disturbance. Not only are GAMMs able to capture nonlinear and complex relationships, they are also able to detect significant effects for variables with a large range in explanatory power; thus teasing apart natural cycles or human influences that are seasonal, monthly, daily or almost instantaneous.

RESULTS

Humpback whale singer numbers and seasonal variation

Humpback whale song was first detected on the offshore MARUs 1 and 2 on 9 June 2008. Thus analysis for this study was restricted to the second and third deployments from 26 May to 1 December 2008. Exhaustive review of the inshore MARU data collected at MARU locations for 4, 5 and 6 (Figure 1) revealed relatively little singing activity. During the second deployment (1/4 duty cycle for 79 days between 25 May and 12 August) there were no instances of complete songs being recorded from a singer near the MARU; very faint song, consisting of units from incomplete phrases of distant singers were detected on 2 days, once in the 06:00 block on 22 July, and throughout the 06:00, 10:00 and 14:00 blocks on 23 July. During the third deployment (1/4 duty cycle for 89 days between 24 August to 21 November), singing was somewhat more frequent, with distant units and phrase fragments being detected on 20 days between 26 August and 16 September, present in nearly every hour block (6 hours per day) between 2 and 16 September; however complete phrases, themes or songs where never recorded. While the lack of consistent near-shore singing activity has implications that will be discussed, the data from the inshore MARUs was uninformative for a detailed assessment of singing activity, and is not considered further.

For the offshore MARUs 1 and 2, a total of 3,264 one-hour periods on 136 days were examined and scored between 24 May and 1 December. Unlike the inshore data, once singers were detected on the offshore MARUs, whales were heard consistently singing on a daily basis throughout the season, and typically there were multiple singers. Song was first heard when a single singer was detected on 9 June for every hour between 04:00 and 07:00 on MARU 1, and then again a single singer was detected for every hour between 15:00 and 19:00 on both MARUs. No singing was detected on the following 9 days, and then from 19 June thereafter, singing was recorded on every day examined until the final deployment was retrieved on 1 December.

Considering the total number of singers detected in the overall region (i.e., the combined total of singers heard on both MARUs. counting singers heard on both only once) there were a total of 6,069 individual singer events logged during 3,106 one-hour periods scored after the onset of singing. This value does not represent different individuals because some singers were likely singing during several hours and were thus counted in multiple hours. There was a mean of 1.95 (+/- SD 1.27) singers/hr from the start of singing activity to last day (9 June to 1 Dec), and a maximum of 7 singers detected in a single hour. During the primary singing months from 1 July to 31 October (excluding the ramp up in June and the fall off in November), there was a mean of 2.45 (+/- SD 1.07) singers/hr, and only on 38 hour periods were no singers detected. At least one singer was heard 98% of all hours examined, 82% of hours had two or more singers and 46% of hours had 3 or more singers.

Seasonal variation in singing activity is evident when examining the mean number of singers per hour on a daily basis (Figure 4). There is a very clear increase over the course of June, some fluctuation in the number of singers through the end of October, and then a decline in activity over the course of November (Figure 4a). Two abrupt drops in singing activity are evident when considering total number of singers on both MARUs (Figure 4a) in mid August and mid October, and an abrupt peak in early October. There is a very subtle indication of a bimodal distribution due to a slight depression in singer number from mid August to mid September, however it is not pronounced. When considering the daily mean of number singers on each MARU separately, the seasonal variation on MARU 1 closely follows that of the total number of singers (Figure 4b). However, MARU 2 is distinctly different with overall fewer singers and more erratic fluctuations in daily mean number of singers/hour across the season (Figure 4c).

Singer spatial distribution

When comparing singer detections between the two MARUs, very strong distinctions were noted. During July to October, on MARU 1 (located 24 km offshore) there was a mean of 2.25 (+/- SD 0.98) singers/hr, at least one singer was heard 97% of all hours examined, 80% of hours had two or more singers and 38% of hours had 3 or more singers, similar to the overall totals. However on MARU 2 (located 15 km offshore), there was a mean of 0.91 (+/- SD 0.87) singers/hr, only 63% of all hours examined had at least one singer, 22% of hours had two or more singers and only 4% of hours had 3 or more singers. This relationship is further emphasized when considering the proportion of singers heard on only one MARU; of the total detected (6069) 62.9% where only heard on MARU 1, whereas 27.3% were heard on both, and 9.8% were heard only on MARU 2 (Figure 5a). The distribution of loudness scores assigned to singers was roughly similar on each MARU with the exception of “0” scores assigned to singers heard only on the other MARU (Figure 5b).

The 1,655 singers detected on both MARUs allow a rough assessment of geographic distribution of singing whales. By assessing at which MARU the signal arrives at first, it can be determined to which MARU the singer is closer. Moreover, the delay in arrival of the signal at each MARU can be measured, and for any given delay the source of the signal with coordinates (x, y) must lie upon a hyperbola described by the equation:

$$(x^2 / a^2) - (y^2 / (c^2 - a^2)) =$$

where the foci (the MARUS) are separated by 2c, and the constant range difference (the delay multiplied by the speed of sound) is 2a. This relationship is used to localize a signal source when more then two hydrophones are used, at the intersection of hyperbolae generated by all pair-wise combinations of hydrophones. With only two MARUs, we cannot localize singers, but we can assess zones of detection described by ranges of delays. The delay hyperbolae for a set of specific delays ranging from 6 sec to -6 sec have been plotted on Figure 1. These were created using a speed of sound of 1.484 km/sec, which was the minimum speed measurement at the seafloor obtained from oceanographic survey work in the vicinity of the MARUs (Kelly 2006). This speed predicted a maximum delay of 6.50 sec at the distance between the MARUs (9.647 km from GPS readings at the surface at moment of deployment), which was largely congruent with our maximum observed delay of 6.55 sec, allowing for error related to location and synchronization. A delay of 0 sec indicates a singer that is equidistant from both MARUs and would lie on a straight line perpendicular to the axis of the MARUs (see Figure 1); any other value would lie in a zone defined by two of the hyperbolae plotted on Figure 1. The frequency distribution of measured delays for all singers is strongly skewed to positive delays in the offshore region (Figure 6), with 81.8% being greater than 0 (and thus closer to MARU 1) and only 18.2% being less than 0 (and thus closer to MARU 2). Moreover, fully 42.8% of singers had a delay greater than 4 sec (Figure 6) and thus were located in the distinctly offshore range defined west of the 4 sec hyperbola (Figure 1), whereas only 7.5% of singers had a delay less than -2 sec (Figure 6) and thus were located in the distinctly inshore range defined east of the -2 sec hyperbola (Figure 1). Examining the distribution of delays by month reveals a distinct shift in the distribution of singers across the season (Figure 7). The earliest few singers detected in the month of June were predominantly in the offshore region, whereas by July and August the distribution takes on the shape observed overall, with a strong mode in the offshore region defined by 5 to 6 sec delays, and a tail trailing into inshore zones (Figure 7). By September this distribution starts to shift inshore, with an increase in the proportion of delays in the middle zones (e.g., between delays of 1 to 2 sec), and by November the mode has shifted fully to the zone define by 0 to 1 sec delays (Figure 6). Thus we can conclude that while the predominant distribution of singers is offshore, greater than 15 to 20 km, there is a clear shift of singer distribution more inshore late in the season.

Diel variation

A subtle diel variation in singing activity was evident, congruent with studies from other breeding grounds. Considering data from the primary months of activity (July through October) there was a slight peak in the mean number of singers at 05:00 in the morning, and a depression in singing activity around 17:00 in the early evening (Figure 8). The pattern was similar for all singers considered together, and when treating each MARU separately. The cycle was slightly more pronounced in August and September, but all months were largely similar.

Seismic survey detections

Seismic surveys were detected in a total of 449 hour periods during 50 days. These were divided into two distinct periods, with surveys detected on all 27 days between 4 July and 30 July, on 33 days between 14 October and 1 December, and never outside of these periods (Figure 9). During the July surveys, pulses were detected during 7 to 13 hours each day and were fairly consistent across the 27 day period; during the longer late season period the occurrence was more variable and sporadic, with pulses heard during 0 to 15 hours each day across the 49 day period (Figure 9). Surveys were more frequent on MARU 1, detected during 444 hours compared to 243 hours on MARU 2. The measured Peak Power in a 1 Hz bin ranged from 65.5 to 133.2 dB re: 1 µPa, with a mean of 88.4 (+/- SD 8.7) dB re: 1 µPa. Peak Frequency ranged from 15.6 to 406 Hz, with a mean of 123.8 (+/- SD 68.2) Hz. Pulses received at MARU 2 tended to have Peak Power at the higher end of the frequency range, greater than 100 Hz (mean of 165.5 +/- SD 60.2), whereas pulses with Peak Power between 15 and 100 Hz were detected predominantly on MARU 1 (mean of 101.0 +/- SD 61.2 Hz) (Figure 10 and 11). The loudest pulses were heard on MARU 2 during a single day, from 11:00 to 14:00 on 14 October, when a survey vessel was apparently operating particularly close to the location at 15 km offshore. Despite these somewhat outlier measurements (see Figure 10), mean peak power measured at the MARUs was relatively similar, 87.3 (+/- SD 9.2) dB re: 1 µPa for MARU 1, and 90.4 (+/- SD 9.2) dB re: 1 µPa.

GAMM Results

The value of ACF at different time lags indicated significant auto-correlation in the data. All models showed a significant reduction in AIC value and improvement in diagnostic plots when this temporal correlation was dealt with using AR-1, thus all top-ranked models according to AIC, include the AR-1 correlation structure. Models including either the variable Peak Power or Power Score gave almost identical results in terms of AIC value, significance of the variable, adjusted R-squared and thus we omit the results for Power Score and only discuss those for Peak Power. Including the interaction between Moon Phase and Hour by conditioning the Hour smooth on the Moon Phase factors did not lead to any significant improvements in the models.

Table 1 shows the top five models for each hydrophone. For MARU 1 and 2 for the top model, the correlation between residuals separated by one time unit is 0.513 and 0.475, respectively; by two it is 0.513^2=0.263 and 0.475^2=0.226, respectively. The value of the correlation between residuals is fairly similar across all models considered. For each of these models in Table 1, all the model covariates turned out to be significant (at the 5% level). Models with a difference in AIC value less than two are plausible candidates for best fitting model (Burnham and Anderson 2002). Thus, for MARU 1 the model with Survey Day, Hour and Moon Phase has approximately equal weight in the data to the model that also includes Peak Power. Although, seasonality (Survey Day) explains the largest proportion of the variation in the number of humpback singers and to a lesser extent time of day (Hour) and moon phase, the Peak Power variable is significant and indicates that singer numbers are reduced with an increase in received noise levels due to seismic survey activity. For MARU 2 the top ranked model included only Survey Day and Moon Phase with a much larger difference in AIC values between the top-ranked and the remaining models. Although the Peak Power (and the Hour) variable were significant they were not in the top-ranked model. For Peak Power this may be explained in part by the fact that most of the seismic activity seemed to occur offshore and a smaller proportion of seismic signals were received by MARU 2, which was inshore.

Figure 12 shows the estimated smoothers for the GAMM models for number of humpback whale singers with covariables Survey Day, Hour, Peak Power and Moon Phase (although for MARU 2, this model differed considerably in terms of AIC value from the top-ranked model, its results are shown to permit a contrast between the hydrophones; also the results it gives for Survey Day and Moon Phase are almost identical to the top-ranked MARU 2 model). As can be seen from the Figure 12, the Survey Day variable was highly significant for both MARUs, showing a bimodal distribution in singer density across the season for MARU 1 and a slightly different trimodal distribution for MARU 2. There was significant diel variation for both MARU 1 and MARU 2. The peak singing activity was estimated to occur around 4 am for both hydrophones, whereas the lows in singing activity was estimated at slightly different times – around noon for MARU 1 and a lag of quite a few hours for MARU 2. There was a significant trend for fewer singers during periods with higher received seismic survey activity levels at both MARUs. The estimated reduction in number of singers was greater for MARU 2, possibly due to the couple of outlier values corresponding to unusually high readings for received levels. Using “New Moon” as a reference level, for MARU 1 the model results indicated that there was a significant reduction in singers during the “First Quarter” and “Full Moon” (less so for the former), and the “Last Quarter” was not significantly different. For MARU 2 the “First Quarter” and “Last Quarter” were not significantly different to the “New Moon” in terms of number of singers, but there was a significant reduction in singers during the “Full Moon”.

The models considered for the reduced data set, corresponding to the first period of seismic activity, included all combinations of the Survey Day, Hour, Peak Power and Moon Phase variables. Namely, the full model with all four variables, models with one of these removed, models with two variables and finally single variable models (see Table 2 for the top-ranked models). In contrast to models over the full data set, with the reduced data set Survey Day and Moon Phase were frequently not significant. The former probably because the period corresponded to a period of relative stability in singer numbers and the latter possibly due to the lack of replication for this variable over the shorter time period. Due to dramatic improvements in AIC values, all models included the AR-1 correlation structure. For MARU 1 the top-ranked model includes Hour, Peak Power and Moon Phase, and for MARU 2 the top model includes only Peak Power. Figure 13 shows the smoothers for Peak Power for these models again showing a significant trend for fewer singers during periods with higher received seismic activity levels at both MARUs. The estimated reduction in number of singers was again greater for MARU 2, possibly due to the outlier values.

In contrast to the models over the full data set where the better models for MARU 1 and 2 had an adjusted R-squared value of between 0.471-0.484 and 0.156-0.190, respectively, this value plummets to between 0.041-0.091 and 0.014-0.144, respectively. This highlights the explanatory power of the Survey Day variable in particular in the full data set. Although the proportion of variance explained is considerably better for the models on the entire data set, especially for MARU 1, there is still quite some room for improvement indicating that certain key variables are missing. One of these may correspond to the disturbance due to boat passes (as reported by Sousa-Lima and Clark 2008) and will be included in a future analysis once the data have been processed.

DISCUSSION

Breeding behaviour and migratory cycle

This study represents the first acoustic assessment of humpback whale breeding activity off the coast of Angola, and moreover the first comprehensive documentation of the migratory timing and seasonal presence of Breeding Stock B in the Gulf of Guinea. As documented here, the use of passive acoustic techniques to monitor singing behaviour of humpback whales provides an effective and efficient means of obtaining detailed data over an extended timeframe. Even the modest application of two sensors has provided important information on migratory timing, habitat utilization, and behavioural disturbance by anthropogenic noise sources.

Our sampling timeframe effectively captured the entire migratory cycle, despite the last retrieval date perhaps missing the final tail of the temporal distribution of singers returning to feeding grounds after 1 December. Singing activity was prevalent for a full six month period, suggesting a potentially protracted breeding season; more northerly breeding areas might be expected to have a shorter duration, and comparisons would be informative. After a relatively short and rapid increase in the number of singers over a two to three week period in June, singing activity was relatively constant for four months from early July to early November, and was followed by a rapid drop off in singing during November. If this region represented solely a migratory corridor, we might expect to see a strongly bimodal distribution of singers represented by an early season northward migratory pulse, and a late season southward migratory pulse. Conversely if the region was an end point destination for breeding whales, we might expect to see predominantly normal distribution with a broad, flattened top. Our data indicates a combination of these expectations; for the total number of singers, and singers detected on the further offshore MARU 1, there was an indication of a mid-season dip in singing activity between mid-August and mid-September (Figure 4a, b), and the smoothed spline of the GAMM captured this distinctly with a bimodal humped shape (Figure 12). This dip does not fall to the low levels of singing indicative of the early season ramp up or late season fall off. Therefore, the temporal distribution is better described as the consistent presence of singing whales through the four months with a swelling of numbers early in the season during July, and late in the season from mid-September to late-October, with the latter peak being more pronounced. This is suggestive of a dual utilization of the region, both as an active breeding destination as well as a corridor for whales potentially moving to destinations further north and then back again.

There were distinct spatial patterns evident in the comparison of the different monitoring stations. Most noteworthy is the dramatic differences between the offshore MARUs and the inshore sites of MARUs 3, 4 and 5, located approximately 2-3 km off the Sereia Peninsula and the Congo River outflow. Singers were never documented close to these sites. There is likely reduced sound propagation in this shallower environment (at 20-30 m vs 100 m of the offshore sites); however even faint song was only detected on a very small percentage of days, whereas offshore song was prominently heard throughout the day on a daily basis. Considering only the offshore MARUs, all data indicated that the spatial distribution of singers was strongly skewed toward the further offshore MARU. During the peak singing months, the mean number of singers per hour detected on MARU 1 at 24 km was more than twice that on MARU 2 at 15 km. Furthermore, in fully 37% of hours examined, there was no singing detected on MARU 2, compared to only 3% of hours on MARU 1. Perhaps the most informative analysis conducted for spatial distribution was the assessment of time of arrival differences, or delays, for the proportion of singers heard on both MARUs. Plotting this on the “delay zones” mapped out on Figure 1 suggests that over 40% of singers were located greater than 20 km offshore (west of the 4 sec delay hyperbola) whereas only 7.5% were located inshore of about 10-15km (east of the -2 second delay hyperbola). Temporal assessment of these delay distributions provided further insights into habitat utilization, with a distinct shift inshore towards MARU 2 late in the season. This could be indicative of different preferences for depth or offshore distance for animals on the opposing migratory streams, and possibly related to currents or other oceanographic conditions. There is also the trimodel nature of the seasonal distribution of singers on MARU 2, with the third pulse in numbers late in the season that is not evident on the further offshore MARU 1, suggestive of differences in the utilization of the offshore environment.

There are several implications that these results have regarding the current knowledge and questions on stock structure. If there are multiple stocks within BS B1 (Best et al. 1995, 1999; Barendse in press), the trends we are seeing may result from the passage of one sub-stock in migration in the further offshore waters off Angola, whereas the second sub-stock, may be utilizing the nearer shore waters as breeding habitat, and consequently be fewer in number. The mechanism separating B1 and B2 remains unclear; the migratory behaviour and breeding destinations of B2 are as yet unstudied. Furthermore, it is possible that the stock structure of B1 may be more complex, with further subdivision of groups of animals with different behavioural and migratory patterns; a multi-substock structure (and/or presence of multiple migratory streams) would be a potential explanation both for nature of the temporal and spatial singer distributions reported here, as well as the complexities encountered with the estimation of abundance for B1, Collins *et al.* 2010).

Impact of seismic surveys on singing activity

The presence of oil and gas exploration activities in this region and globally, and the potential acoustic impact that seismic survey operations may have on sensitive species is an increasing area of study and concern for marine mammal biologists and conservationists (Weller *et al.* 2002). The loud pulses produced by seismic surveys have the potential of both disturbing animals and altering their behaviour as well as masking acoustic signals and negatively effecting communication. We have demonstrated in our GAMM analysis that the seismic surveys recorded during our study period had a negative impact on the number of singers in this region, with singing activity declining with the presence of and increase in received levels of seismic survey pulses at the MARUs. It appears that whales are ceasing to sing, or moving to other areas to sing when seismic surveys are operating. The influence of the variable in the model was not as strong or pronounced as the influence of Survey Day or Hour; however, given the natural variation due to migration expected over the course of season, and the diel trends that have been noted in other studies, it is not surprising that these natural cycles would have a more prominent effect. Moreover, this study was not designed to test the influence of or disturbance caused by these anthropogenic signals; without the ability to locate the singers, nor the knowledge of the location of the seismic survey vessel, the source level of the pulses, or the distance between the source and potentially impacted singers, the design was far from ideal and hardly optimal for testing and detecting an effect. Therefore, that a significant effect was in fact detected, is rather remarkable and suggests that it could be more pronounced than indicated by this analysis.

Di Iorio and Clark (2009) reported a significant impact of seismic survey activity on the calling behaviour of blue whales in the St. Lawrence Estuary, however the effect was in the opposite direction. Blues whales in the region had a significant tendency to call more frequently during days when seismic surveys were present compared to not present, as well as within days during hours when surveys were present. They interpreted this to be a response on the part of blue whales to compensate for the increased noise levels with greater repetition and redundancy in their signalling, in accordance with expectations from information theory. The difference in response observed in Di Iorio and Clark (2009) and our study may be related to differences between social communication (calls recorded in the blue whale study) and song (the subject of our study); congruent with this, blue whales have been reported to cease singing in response to seismic survey activity (MacDonald et al. 1995).

It is impossible from this study to determine whether the documented decrease in number of humpback whale singers would translate into detrimental impacts on individuals or the population. We can only report that the impact exists. Songs of humpback whales are breeding displays, and there is good evidence indicating that singing is important in male breeding strategy (Smith et al. 2008, Cholewiak 2008), so it is likely a critical component of male reproductive success (Cerchio 2003, Cerchio et al . 2005). Thus it is possible that disruption of this breeding display could have significant adverse impacts on individual males and at some threshold of numbers of impacted individuals, this could translate into adverse impacts at the population level. Our finding therefore underscores the need for further investigation and testing for effects of such disturbance, particularly as seismic exploration continues during baleen whale breeding seasons in documented breeding regions.

ACKNOWLEDGEMENTS

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Table 1: Results for Generalized Additive Mixed Models fit to data from each of the hydrophones MARU 1 and 2. The stars indicate which variables were included in each model and also their significance level ('***' < 0.001, '**' < 0.01, '*' <0.05, and 'ns' indicates non-significant terms at the 5% level in the models). The hashes indicate models where Hour was conditioned on the Moon Phase factor variable. The AIC, the difference in AIC between the model under consideration and the model with the minimum AIC (Delta AIC) and the adjusted R-squared value (R-sq (adj)), which is the proportion of variance explained, is shown. All models include the AR-1 correlation structure.

MARU	Model No.	Survey Day	Hour	Peak Power	Moon Phase	AIC	Delta AIC	R-sq (adj)
1	1	***	**		***	4586.99	0.00	0.482
	2	***	**	*	***	4588.59	1.61	0.484
	3	***			***	4593.16	6.18	0.471
	4	***		*	***	4594.79	7.80	0.473
	5	***	*** - #	**	***	4596.15	9.16	0.485
2	1	***			***	9019.85	0.00	0.156
	2	***		**	***	9034.08	14.24	0.159
	3	***	*** - #	**	***	9093.03	73.18	0.184
	4	***	***		***	9097.59	77.75	0.187
	5	***	***	**	***	9112.22	92.38	0.190

Table 2: Results for the top Generalized Additive Mixed Models fit to data from each of the hydrophones MARU 1 and 2 for the first period of seismic activity 5-31 July 2008. The stars indicate which variables were included in each model and also their significance level ('***' < 0.001, '**' < 0.01, '*' <0.05, and 'ns' indicates non-significant terms at the 5% level in the models). The AIC, the difference in AIC between the model under consideration and the model with the minimum AIC (Delta AIC) and the adjusted R-squared value (R-sq (adj)), which is the proportion of variance explained, is shown. All models include the AR-1 correlation structure.

MARU	Model No.	Survey Day	Hour	Peak Power	Moon Phase	AIC	Delta AIC	R-sq (adj)
1	1		**	*	***	571.74	0.00	0.0903
	2	**	**			572.65	0.91	0.0914
	3		**			572.86	1.12	0.0407
	4	**	**	*		573.00	1.26	0.0983
	5		**	*		573.34	1.59	0.0455
	6[1]			*	***	573.60	1.85	0.0498
2	1			**		1476.30	0.00	0.0138
	2			**	ns	1484.39	8.08	0.0148
	3	ns				1485.61	9.31	0.0304
	4	ns			ns	1494.38	18.07	0.0373
	5	ns		**	ns	1494.42	18.12	0.0521

[1] Six rather than the top five models are shown for MARU 1, as these all have a Delta AIC value of less than 2.

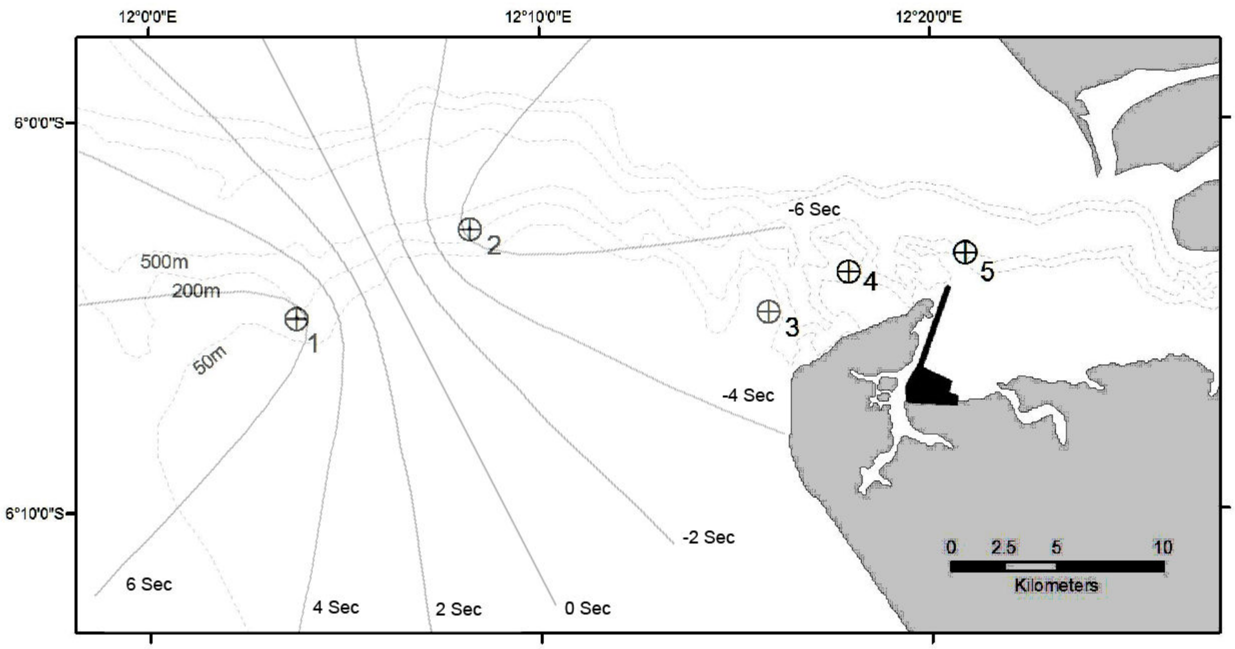


Figure 1. Positions of Marine Autonomous Recording Units (MARUs) deployed off Angola at the Congo River outflow (crosshairs 1-5). Data reported here come from MARUs 1 and 2, deployed ca. 24km and 15km offshore, respectively, near the edge of the Congo River Submarine Canyon, and recorded continuously at a sample rate of 2,000Hz, during three months from 2 March to 1 December 2008, in three deployments of 81, 88 and 101 days. Also depicted are "delay hyperbolae" representing the line on which a signal source (e.g., a singing whale) would lie if received at both MARUs with the specified delay in arrival indicated, for delays of 6, 4, 2, 0, -2, -4, and -6 seconds.

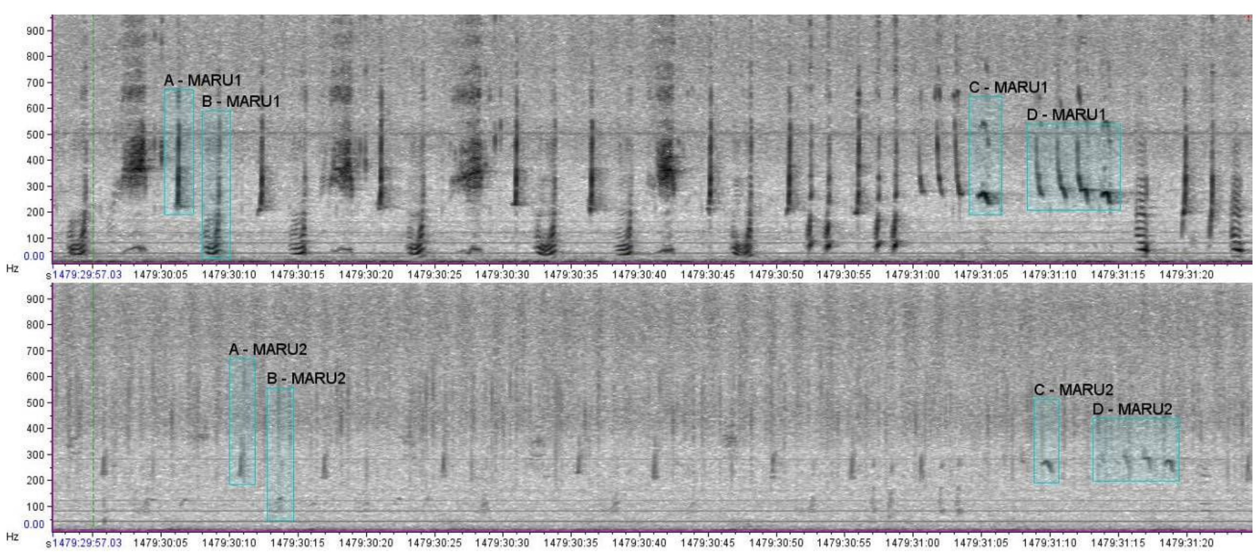


Figure 2. Example of humpback whale song recorded on the MARUs. The top row is MARU 1 and the bottom row is the MARU 2, separated by 9.7km, temporally synchronized. The singer is audible on both MARUs, closer (and louder) on MARU 1. The different patterns, or "phrases" of humpback whale song evident. Four different features in the song are noted (A, B, C and D), illustrating the delay in the arrival of the sound at MARU 2.

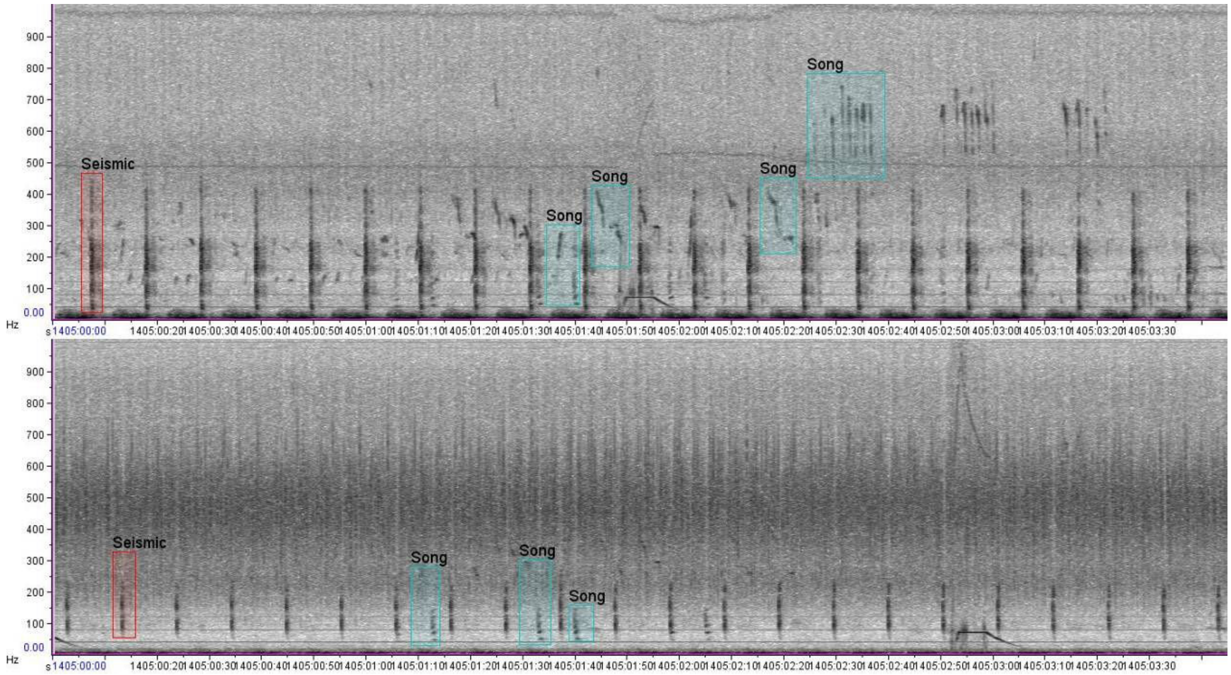


Figure 3. Example of a seismic survey recorded on the MARUs on July 22nd at 12:00AM. The seismic survey impulses are evident on both MARU 1 (top row) and MARU 2 (bottom row), outlined in red, and a humpback whale is also observed singing, outlined in blue.

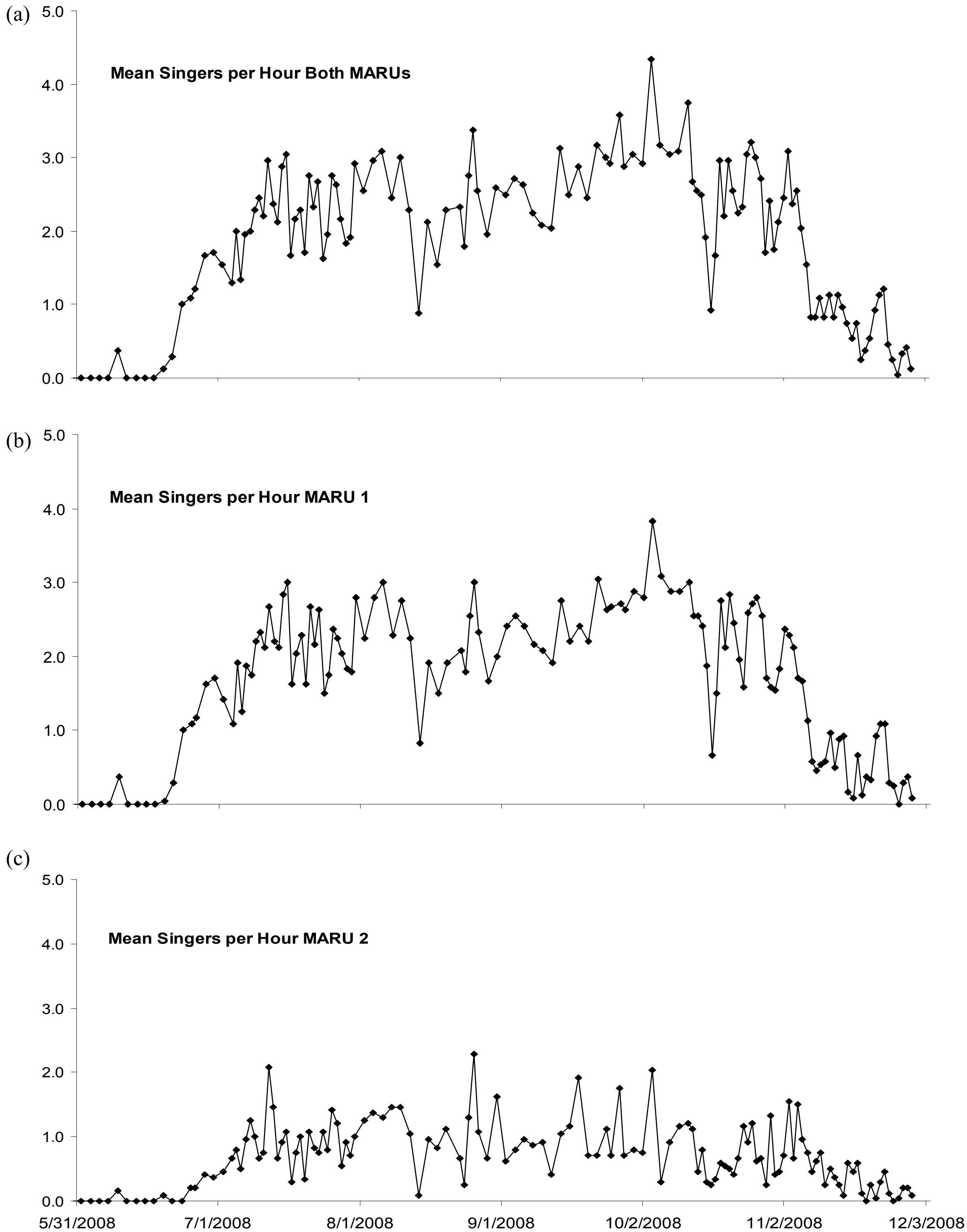
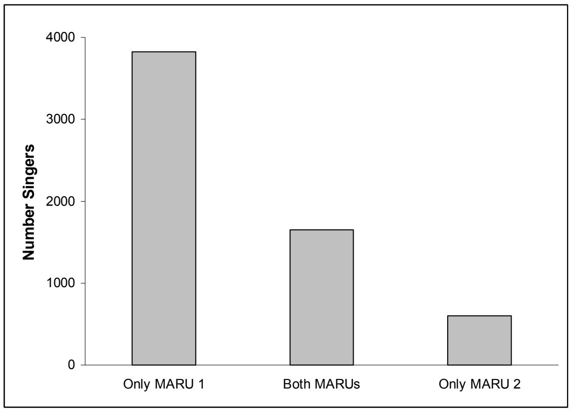
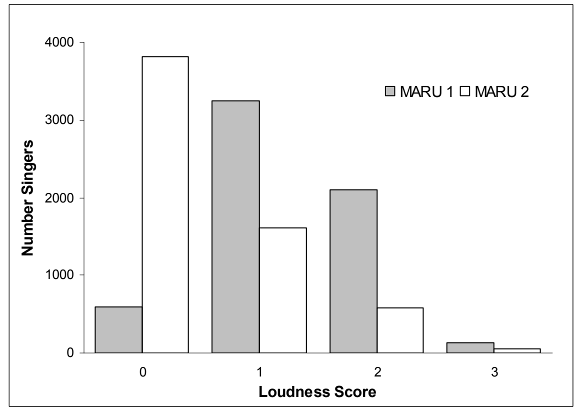


Figure 4. Mean number of humpback whale singers logged per hour for each day, June through November 2008; (a) for both MARUs combined (all singers with those detected on both MARUs counted once), (b) for MARU 1 at 24km offshore and (c) for MARU 2 at 15km offshore.





(a) (b)

Figure 5. (a) Of 6,069 individual singers logged on one or both MARUs, 3,820 (62.9%) were heard only on MARU 1; 594 (9.8%) were heard only on MARU 2; and 1,655 (27.3%) were heard on both. (b) Loudness scores of the 6,069 logged singers; if a singer was audible on a MARU, it received a score of 1-3 from faint to loud; a singer received a score of 0 if it was not heard on that MARU while being heard on the other. Mean loudness scores (including 0 for not present) were 1.29 (+/- 0.67) for MARU 1, and 0.48 (+/- 0.70) for MARU 2.

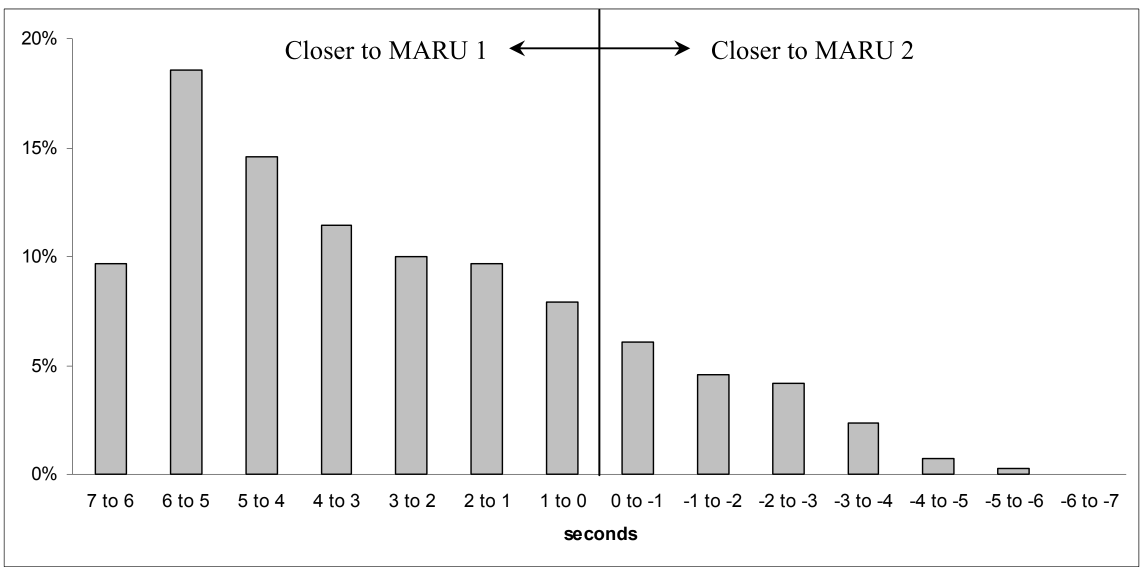


Figure 6. Time of arrival differences at each MARU for 1,655 singers that were recorded on both MARUs. A signal that arrives at both MARUs simultaneously will have a delay of 0 and indicate a singer that is equidistant from the two MARUs, whereas positive delays indicate a singer closer to MARU 1 (24km offshore) and a negative delay indicates a singer closer to MARU 2 (15km offshore).

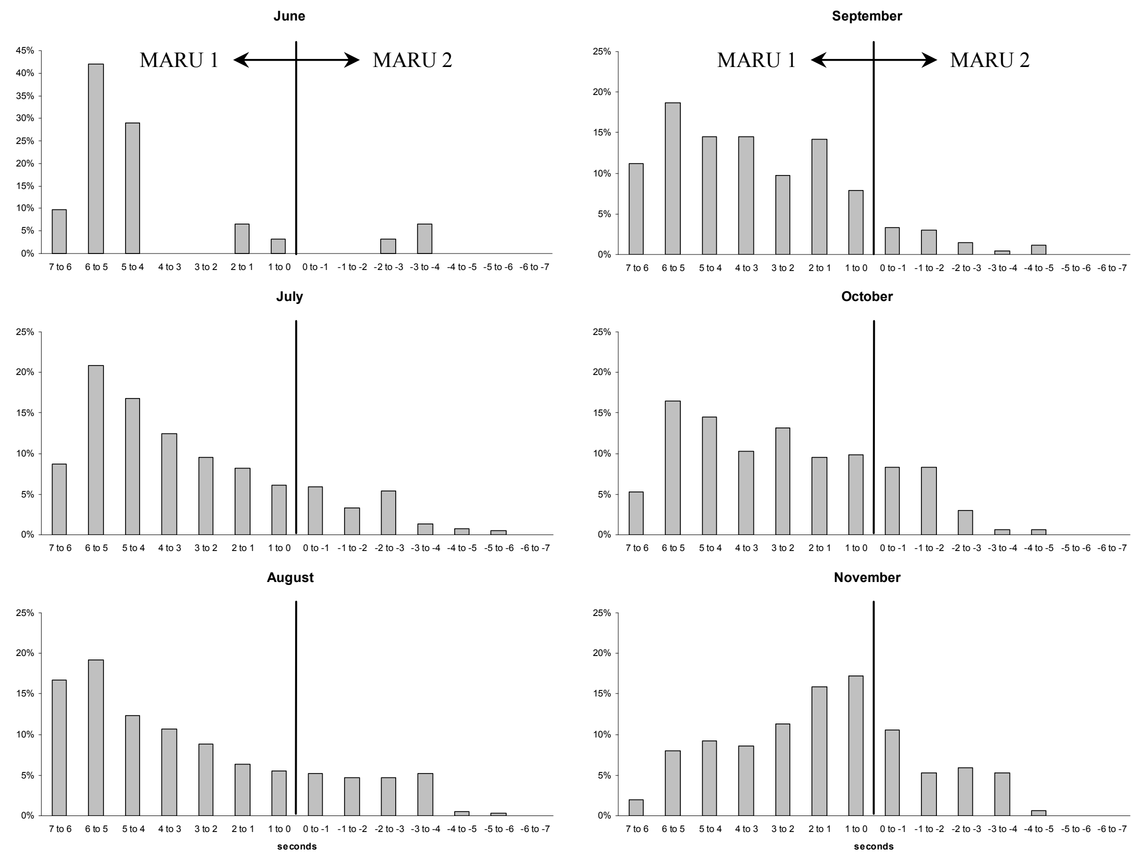


Figure 7. Time of arrival differences for singers that were recorded on both MARUs, broken down by month (see Figure 6 for explanation).

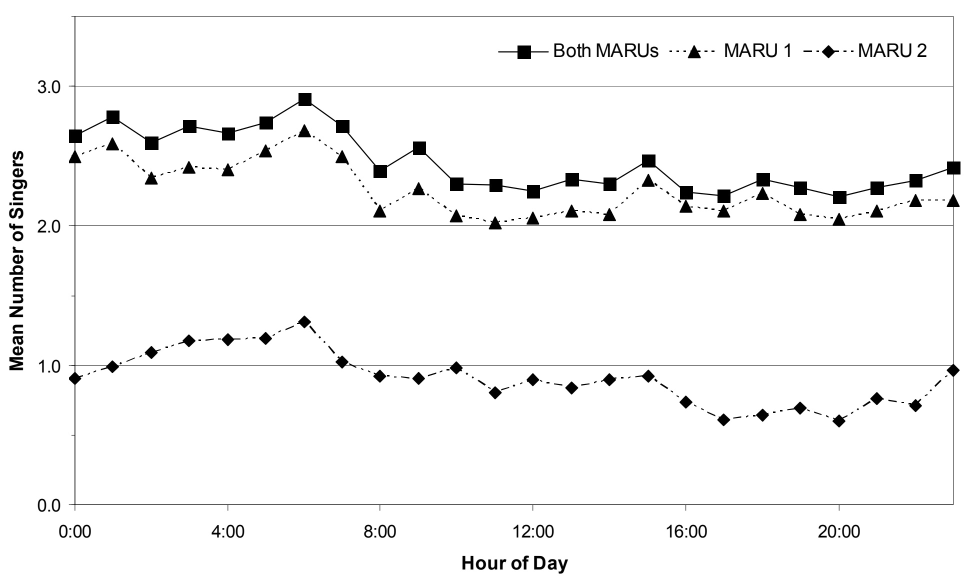


Figure 8. Diel trends in mean humpback whale singers per hour for the primary months of singing activity, July, August, September and October; data are shown for both MARUs combined, MARU 1 at 24km offshore, and MARU 2 at 15km offshore.

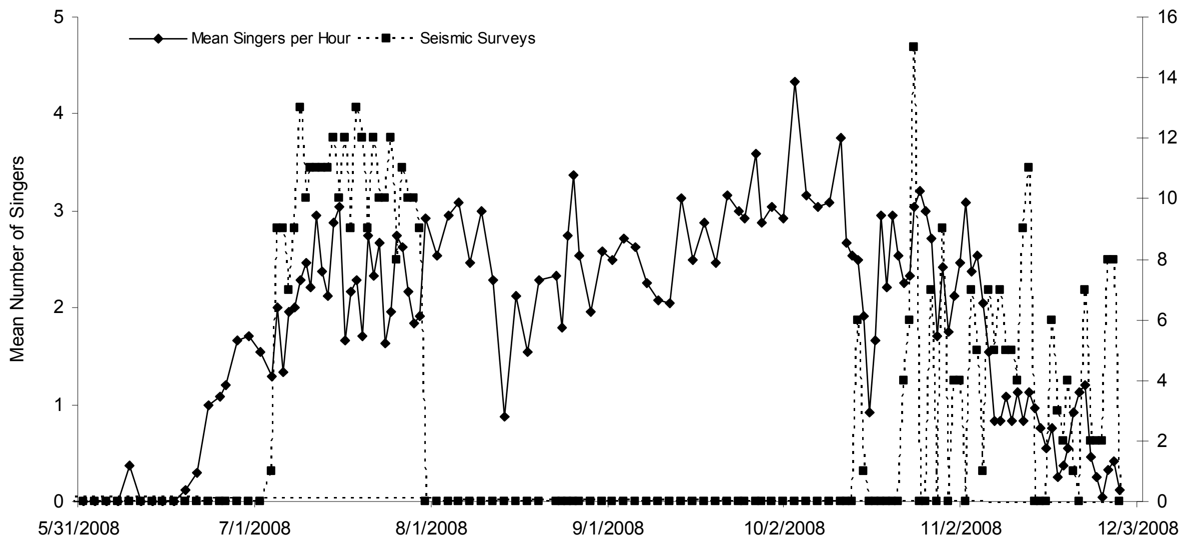


Figure 9. Seismic Survey activity represented as the number of hours in a given day in which pulses were detected on either MARU, overlaid on the mean number of singers per hour for both MARUs combined.

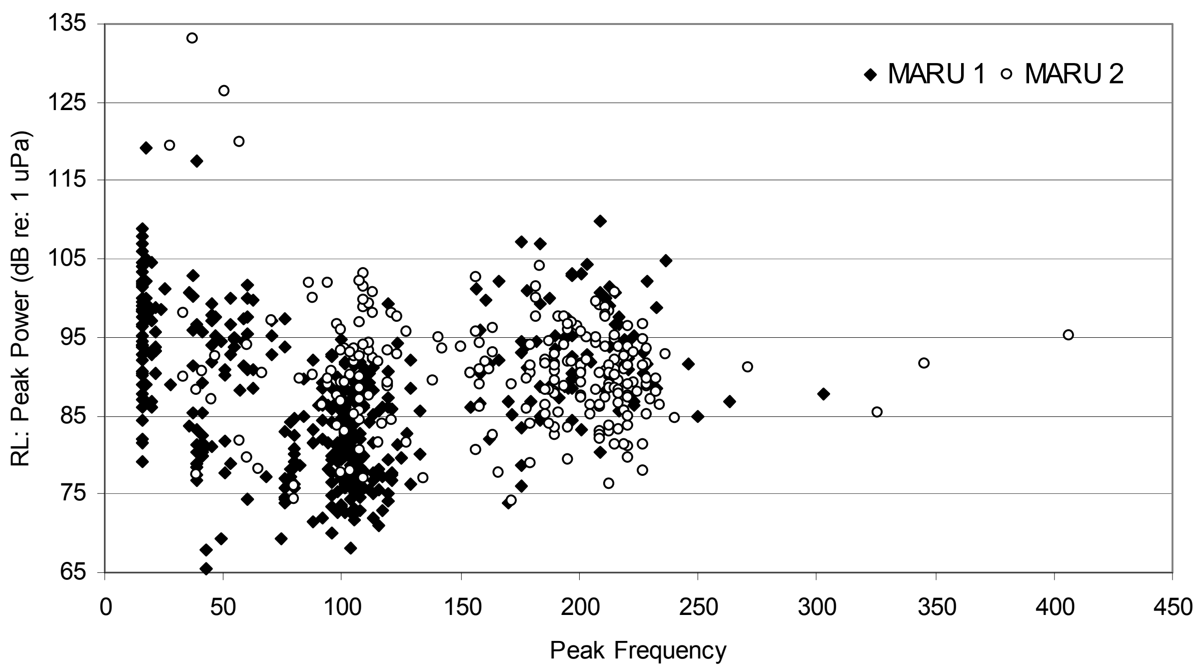
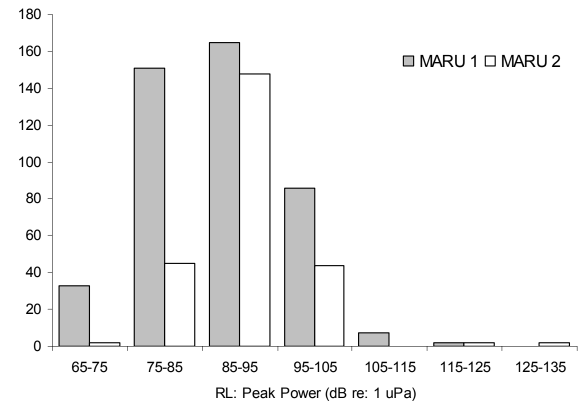
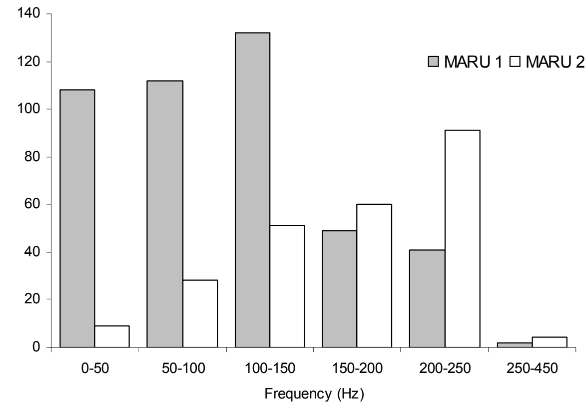


Figure 10. Seismic survey pulses measured in each time block, plotted for the relationship between Peak Power (dB re: 1uPa in a 1 Hz bandwidth) and Peak Frequency, the frequency at which the Peak Power occurs. Measurements were truncated at 15 Hz, to account for likely limitation of baleen whale hearing.

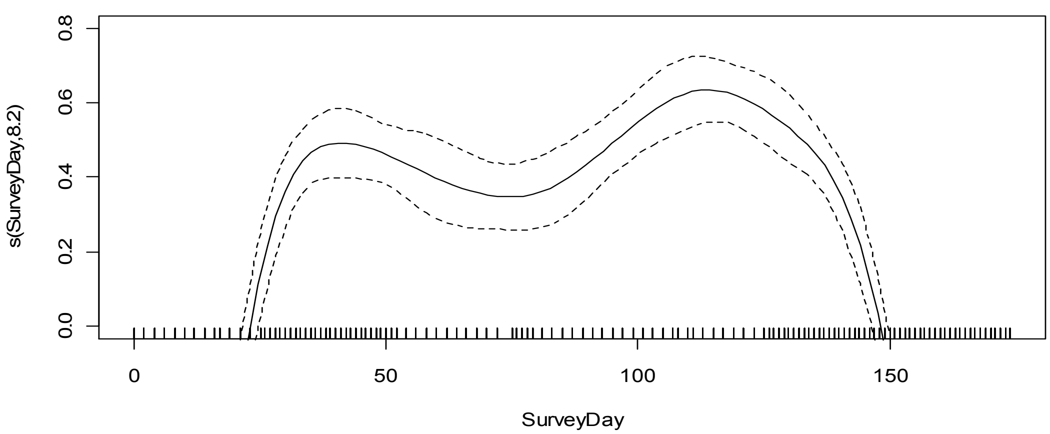


(a)

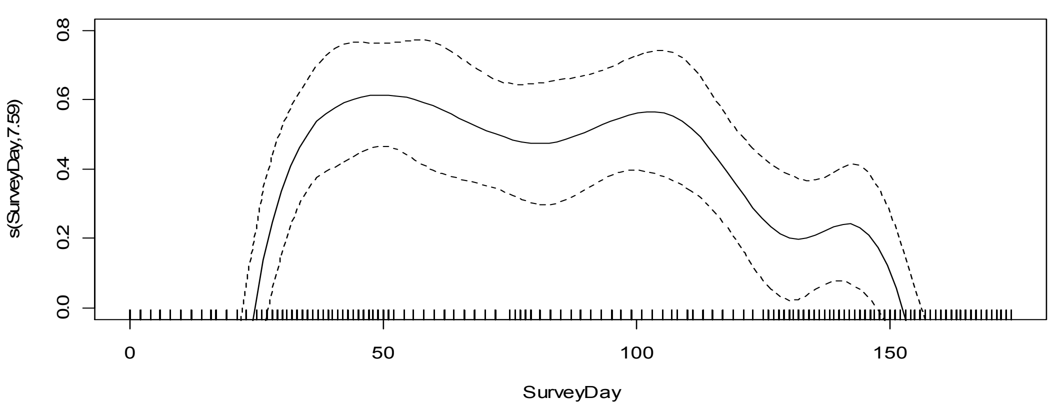


(b)

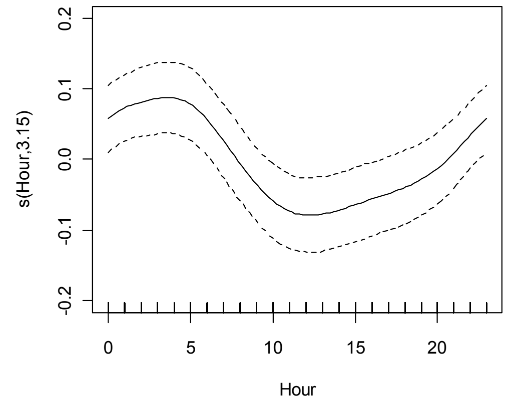
Figure 11. Distribution of (a) Peak Power and (b) Peak Frequency for all seismic survey pulses measured for MARU 1 and MARU 2.



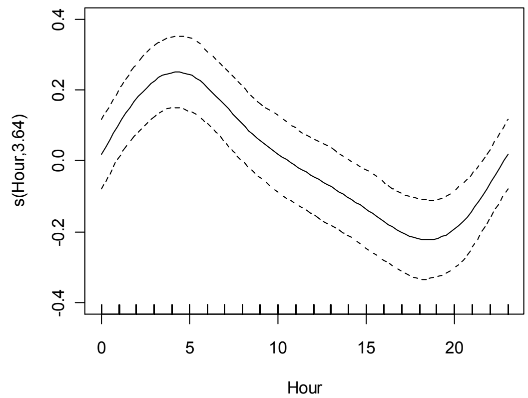
(a)



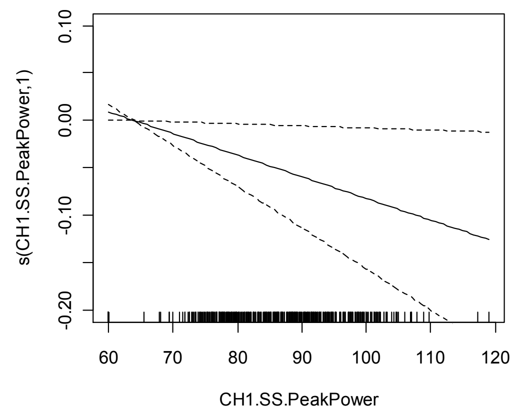
(b) Figure 12. a. and b. Results of GAMM models (caption on next page)



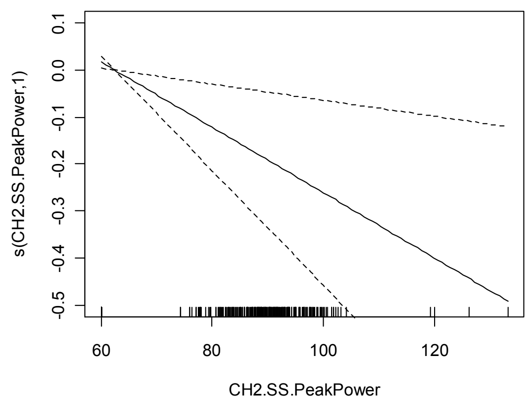
(c)



(d)



(e)



(f)

Figure 12. Results of GAMM models for number of humpback whale singers with covariables including Survey Day, Hour, Peak Power and Moon Phase (separate models were fit for each of the MARUs); the plots above show the estimated conditional dependence of humpback whale singer numbers on: Survey Day, mapping seasonal variation, for (a) MARU 1 and (b) MARU 2; Hour, describing diel variation, for (c) MARU 1 and (d) MARU 2; and Peak Power, describing received level of noise (in dB) for (e) MARU 1 and (f) MARU 2. Estimates (solid lines) and confidence intervals (dashed lines), with a rug plot indicating the covariate values of observations (short vertical bars along each x-axis), are shown. Note that y-axis scale is selected optimally for each covariate.

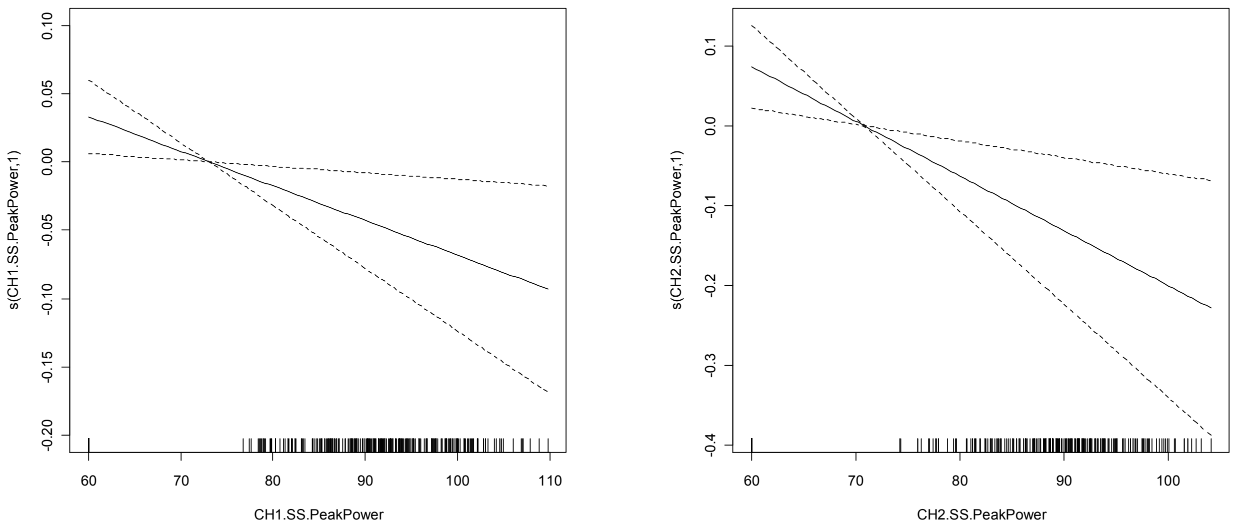


Figure 13. Results of GAMM models for number of humpback whale singers with covariables including Hour, Peak Power and Moon Phase for MARU 1 and only Peak Power for MARU 2, when restricting data to the first period of seismic activity 5-31 July 2008. Shown is the estimated conditional dependence of humpback whale singer numbers on Peak Power (received level of noise in dB) for (a) MARU 1 and (b) MARU 2. Estimates (solid lines) and confidence intervals (dashed lines), with a rug plot indicating the covariate values of observations (short vertical bars along each x-axis), are shown. Note that y-axis scale is selected optimally for each plot.