Red shift, blue shift: Doppler shifts and seasonal variation in the tonality of Antarctic blue whale song

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ABSTRACT

The song of Antarctic blue whales (*Balaenoptera musculus intermedia*) comprises repeated, stereotyped, low-frequency calls. Measurements of these calls from recordings spanning many years have revealed a long-term linear decline as well as an intra-annual pattern in tonal frequency. While a number of hypotheses for this long-term decline have been investigated, including changes in population structure, changes in the physical environment, and changes in the behaviour of the whales, there have been relatively few attempts to explain the intra-annual pattern. An additional hypothesis that has not yet been investigated is that differences in the observed peak-frequency from each call are due to the Doppler effect. The assumptions and implications of the Doppler effect on whale song are investigated using 1) vessel-based acoustic recordings of Antarctic blue whales with simultaneous observation of whale movement and 2) long-term acoustic recordings from both the subtropics and Antarctic. Results from vessel-based recordings of Antarctic blue whales indicate that peak frequency variation between calls produced by an individual whale was greater than would be expected by the movement of the whale alone. Furthermore, analysis of intra-annual frequency shift at Antarctic recording stations indicates that the Doppler effect is unlikely to fully explain the observations of intra-annual pattern in the frequency of Antarctic blue whale song. However, data do show cyclical changes in frequency in conjunction with season, thus suggesting that there might be a relationship among tonal-frequency, body condition, and migration to and from Antarctic feeding grounds.

KEYWORDS: ANTARCTIC BLUE WHALE, WHALE SONG, DOPPLER, TONAL FREQUENCY

INTRODUCTION

Antarctic blue whales (*Balaenoptera musculus intermedia*) sing repeated, stereotyped, low-frequency song with calls comprising three units: an approximately 10 second tonal unit with a peak-frequency around 28-26 Hz and two shorter frequency-modulated downsweeps (Rankin et al. 2005). The vocalisations of which these songs are comprised have been named z-calls because of their characteristic shape when viewed as a spectrogram (Figure 1). Comparison of z-calls recorded in different years has revealed both long-term (McDonald et al. 2009, Gavrilov et al. 2012) and seasonal (Gavrilov et al. 2012) patterns in the spectral frequency of these sounds. Gavrilov et al. (Gavrilov et al. 2012) report an inter-annual decline of the tonal component of these calls of 0.135 Hz/year (R^2=0.99), and an intra-annual decline between 0.4-0.5 Hz from March to December (R^2>0.8; Figure 2).

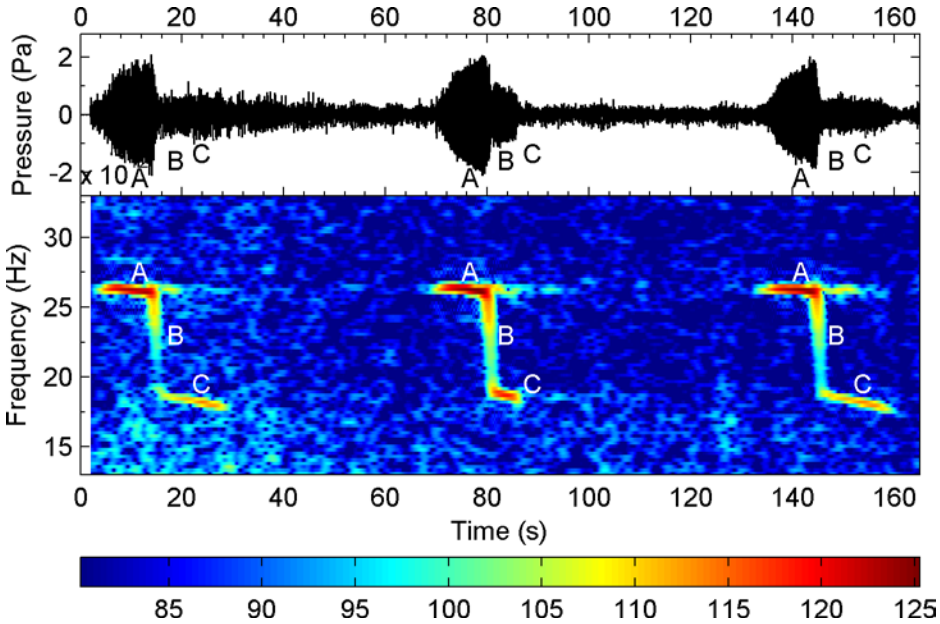

Figure 1 – **Visualisation of Antarctic blue whale song.** Pressure waveform and spectrogram of Antarctic blue whale "z-calls" recorded off Antarctic ice-edge during February 2013. The call is divided into 3 units labelled A, B, and C. Spectrogram was produced using a sample rate of 250 Hz, 1024 point FFT, and 87.5% overlap between time slices. Colors indicate received power spectral density (dB re 1 μPa/Hz).

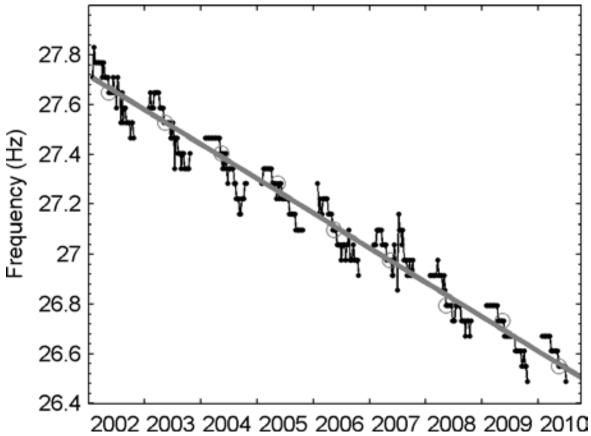

Figure 2 – **Long-term and intra-annual trends in tonality of Antarctic blue whale song.** Long-term trend and intra-annual pattern in tonal frequency of Antarctic blue whale calls. Reprinted with permission from. Gavrilov et al. (2012). Copyright 2012 Journal of the Acoustical Society of America, American Institute of Physics.

McDonald et al. (McDonald et al. 2009) discussed a number of hypotheses for the long-term inter-annual decline including changes in population structure, ambient noise, physical environment, and behaviour of the whales. They concluded that the most likely explanation of the trend is increasing population density, and suggested that the tonal decline is an anatomical constraint of the mechanism of sound production that also yields a decreased source level of calls. A key driver of this theory is that decreased source levels would be required for whales to keep in acoustic contact with a constant number of conspecifics, given an increasing population density. However, presently there are not enough estimates of the source level of calls (let alone population density) of Antarctic blue whales to test whether the source levels have decreased in a manner similar to that predicted by McDonald et al. (McDonald et al. 2009).

Gavrilov et al. (Gavrilov et al. 2012) proposed that the mechanism behind the intra-annual pattern may be explained by a gradual decrease in the depth at which songs are produced. They suggested that this decrease in depth could arise from changes in the dive behaviour over the length of each season, or that it could be due to other factors such as variations in the water temperature or change in the blubber mass. However, they considered that such an explanation is not likely to apply to the long-term trend and suggest that changes in whale vocal behaviour remain the most parsimonious explanation for the long-term decline.

Here we investigate the Doppler effect (Ballot 1845) as an additional explanation for some of the intra-annual patterns in observations of tonal frequency. Doppler shift is the change in frequency of a wave that arises from relative motion between the source and the receiver of the wave. The equation for Doppler shift can be written as the ratio of the measured frequency to the true frequency:

$$\frac{f_m}{f_w} = \frac{\mathrm{v} + c}{c} \qquad 1$$

where v is the relative speed between the whale and the receiver, and c is the speed of sound along the path between source and receiver. If observations are made at a fixed receiver, such as the hydrophone array used by Gavrilov et al. (Gavrilov et al. 2012), then any potential shift in frequency due to the Doppler effect must arise from movement of the sound source, namely vocalising Antarctic blue whales.

Seasonal movements of Antarctic blue whales are not well described; however it has been proposed that they, like most baleen whale species, migrate between high latitude summer feeding grounds and low-latitude wintering grounds (Mackintosh 1966). There is strong evidence that Antarctic blue whales have a circumpolar Antarctic distribution during the Austral summer (Branch et al. 2007). In contrast, there are very few observations of Antarctic blue whales during Austral winter. However, acoustic detections of z-calls (distinctive to Antarctic blue whales) provide some of the most compelling evidence that these animals do migrate to mid-or low latitudes in Austral Winter (Stafford et al. 2004, Samaran et al. 2010a, 2013, Gavrilov et al. 2012).

The temporal aspect of these acoustic detections suggests a mid or low-latitude winter destination for Antarctic blue whales. Stafford et al. (Stafford et al. 2004) report that low and mid-latitude detections begin in April, and continue through November in the South Pacific, South Atlantic, and Indian Oceans. Samaran et al. (Samaran et al. 2010a) found year-round acoustic detections of Antarctic blue whale calls at a mid-latitude site in the Indian Ocean (46°S, 53°E), but proportionally more days with detections in Austral winter. Gavrilov et al. (Gavrilov et al. 2012) also reported near-year round acoustic detection of Antarctic blue whales at Cape Leeuwin, a mid-latitude Indian Ocean site (35°S, 114°E; Figure 3) with detections having highest intensities from May to September.

The peak in intensity in May at Cape Leeuwin could potentially represent the point of closest approach for the majority of the migrating whales, or it could potentially arise from a peak in the number of whales calling. Samaran et al. also found that the month with the highest proportion of days with detected Antarctic blue whale calls was May, off Crozet Island, another mid-latitude location (Samaran et al. 2010a). This peak in calling in May at two widely separated locations is further evidence that at this time of year (vocalising) whales are either migrating through to mid-latitudes or calling more frequently, or quite possibly a combination of the two.

One implication of the Doppler effect could be the ability to track migrating whale populations using recordings made from widely spaced hydrophones located along a latitudinal gradient. For example, at mid latitudes there should be an increase in frequency early in the migration season as the animals approach the hydrophone and a drop late in the season as the animals move away. Such recordings, especially when combined with amplitude information (eg (Gavrilov et al. 2012)) acoustic propagation models (eg (Samaran et al. 2010b)) and/or acoustic bearings to the sound source (Greene et al. 2004) could potentially allow for passive acoustic tracking of the migration of populations of vocalizing whales (Sullivan et al. 2006).

Here we investigate whether Doppler shift could potentially explain the intra-annual pattern in tonal frequency reported by Gavrilov et al. (Gavrilov et al. 2012). We first examine a situation where whale movements were observed and z-calls were recorded simultaneously in order to test whether the Doppler effect on tonal frequencies was measurable for small-scale movements. We then re-examine the intra-annual pattern observed by Gavrilov et al. off Cape Leeuwin (Gavrilov et al. 2012), and supplement this analysis with year-long recordings from two sites in the Antarctic (Figure 3). Next, we examine whether intra-annual changes in frequency fit with existing knowledge of large-scale Antarctic blue whale migration patterns. Finally, we discuss additional observations and continued data collection that may further test hypotheses to explain the changes in tonal frequency of blue whale song.

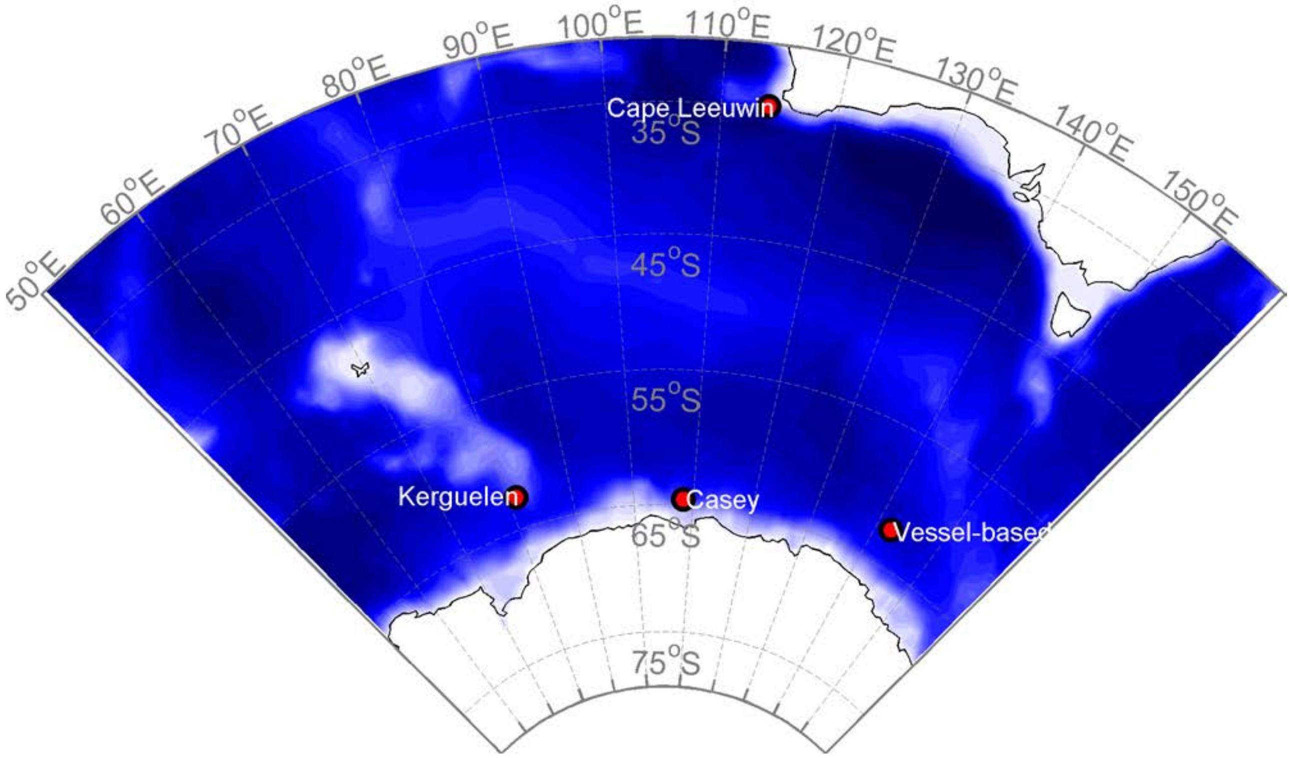

Figure 3 – **Map of recording sites.** Locations of long-term and vessel-based recording stations used in this manuscript for investigation of tonal frequency of the song of Antarctic blue whales. The data from Gavrilov et al. (Gavrilov et al. 2012) (*ie*. Figure 2) were observed at Cape Leeuwin.

METHODS

Vessel-based measurements of frequency and whale speed

During the 2013 Antarctic Blue Whale Voyage of the Southern Ocean Research Partnership, acoustic recordings of Antarctic blue whales were collected along with simultaneous visual tracking (Double et al. 2013). Upon approach, the location of surfacing whales was measured using a video-photogrammetric system (described by Leaper (Leaper & Gordon 2001)) to determine their range and bearing relative to the ship. Acoustic recordings were made during approach using DIFAR sonobuoys (Miller et al. 2013).

While over the course of the voyage there were dozens of high-quality audio recordings and visual tracks of Antarctic blue whales, there was only one instance (an encounter on 7 February 2013) of simultaneous video and audio recordings where the whale produced z-calls. This data set was used to investigate whether there was a relationship between whale movements and the received tonal frequency of calls (*ie.* whether our observations were sensitive enough to detect the Doppler effect). We re-arrange Equation 1 in order to obtain the expected linear relationship between received tonal frequency and velocity yielding:

$$f_m = av + b \qquad (2)$$

where $a = f_w/c$ and $b = f_w$. It should be noted that the velocity, v, corresponds only to the component of movement in the direction of the acoustic wavefront such that:

$$v = \|v_w\| \cos\theta \qquad (3)$$

where $\|v_w\|$ is magnitude of the velocity of the whale, and θ is the difference in angle between the direction of motion of the whale and the bearing from the sonobuoy to the whale.

Locations of Antarctic blue whales obtained via video tracking were assumed to correspond to the “true” location of the whale (at the surface) due to the high accuracy and precision of photogrammetric video tracking (Leaper & Gordon 2001). Average heading and whale speed were then computed between successive photogrammetric locations. All z-calls in this data set were produced when the whale was out of sight underwater, and linear interpolation between successive photogrammetric locations was used to estimate the locations of the whale at the times when z-calls were received.

Sonobuoys were assumed to drift in a constant direction at a constant speed. The direction and speed of drift were estimated by measuring acoustic bearings to the research vessel (*ie.* a source with a known location), and solving for the direction and speed that maximised the likelihood of these measurements.

Acoustic analysis was restricted to the duration over which there were high-quality photogrammetric measurements. Songs originating from the tracked whale were identified and used for further analysis, while songs that were believed to be from other whales were discarded. Several criteria, including the type of call, temporal pattern of calling, and received level, were used in addition to the acoustic bearing to the song (from the DIFAR sensors) to determine whether or not the call should be included for further analysis.

Measurements of peak-frequency were made from audio recordings of z-calls that were selected for analysis. Peak-frequency measurements were made in the frequency domain by computing the power-spectral density (PSD) for acoustic data spanning the duration of the first tonal unit of the Z-calls, which we refer to as unit A. Measurements of peak-frequency were restricted to the band between 25 and 27 Hz in order to exclude potential sources of tonal noise (eg. engine and/or generator noise from vessels).

The frequency resolution (*ie.* bin-width) of the PSD is equal to the inverse of the duration of the signal. Due to the relatively short duration of the calls compared to the desired frequency resolution, acoustic waveforms were extended with zeros before the start and after the end of the signal to allow for a sufficiently large number of samples in order to obtain frequency resolution of 0.001 Hz when computing the spectrum via Fast-Fourier Transform (FFT). Before padding each end with zeros, a Hanning window was applied to the acoustic waveform in the time domain in order to minimise any spectral distortion that might arise from the impulsive discontinuity that would otherwise occur at the interface between zeros and acoustic signal.

Long-term measurements of frequency

In contrast to the vessel-based observations, analysis of the intra-annual pattern in frequency relied solely upon the PSD with no attempt to measure individual whale calls. Thus, our analysis methods were identical to those employed by Gavrilov et al., (Gavrilov et al. 2012). Measurements of peak-frequency in the Antarctic blue whale band, f_m, were digitized from Figure 5 in Gavrilov et al., (Gavrilov et al. 2012). The long-term trend described by Gavrilov et al., (Gavrilov et al. 2012):

$$f_w(t) = -0.135t + 27.666; \text{ (}R^2\text{=0.99, 95\% CI }\pm0.003\text{ Hz/year)} \qquad 4$$

was defined to be the ‘true’ (*ie.* non-Doppler shifted) frequency, $f_w(t)$, emitted by Antarctic blue whales. Here t represents the number of years since the start of the dataset: 12 Mar. 2002. For each weekly observation reported by Gavrilov et al. (Gavrilov et al. 2012), the frequency ratio of measured frequency, f_m to f_w (*ie.* the left side of equation 1) was computed. The relative speed of the source, *ie.* the population of whales emitting z-calls, was computed by re-arranging equation 1 to obtain:

$$\text{v} = \text{c}\left(\frac{f_m(t)}{f_w(t)} - 1\right) \qquad 5$$

where positive speeds indicate that the direction of travel is towards the observer and negative speeds indicate the direction of travel is away from the observer. The sound speed was assumed to be 1500 m/s.

A similar analysis of peak-frequency was also performed on two data sets recorded off Antarctica: data recorded from ARPs off Casey Station over 2004 to 2005, and the Kerguelen Plateau from 2005 to 2007. These data were recorded near the sea floor at approximately 1800 m depth at a sample rate of 500 Hz. Before analysis, these data were filtered and re-sampled to 100 Hz in order to increase frequency resolution while maintaining small memory footprint for computations. PSD was averaged daily and the FFT size was 16384 samples (chosen to obtain 0.01 Hz frequency resolution). Portions of the recordings that contained strong broadband noise sources (eg. large storms) were excluded from the PSD analysis. For each daily PSD, the frequency with maximum energy was selected as the peak-frequency. Monthly mean and standard deviation of these daily peak-frequencies were computed for each station.

All vessel-based work and long-term acoustic recordings were carried out in strict accordance with the approvals and conditions of the Antarctic Animal Ethics Committee for Australian Antarctic Science projects 2683 and 4102.

RESULTS AND DISCUSSION

A. Vessel-based observations

Results

During the recording session on 7 February 2013, the whale passed within a kilometre of a sonobuoy (Figure 4). Maximum received levels of whale calls correlated well with the estimated point of closest approach. This provided confidence that the calls were produced by the photogrammetrically-tracked whales, and that estimates of direction and speed of drift of the sonobuoy (170 degrees; 0.93 m/s respectively) were consistent. Song was recorded both as the whale was approaching the sonobuoy, and as the whale moved away from the sonobuoy (Figure 5a).

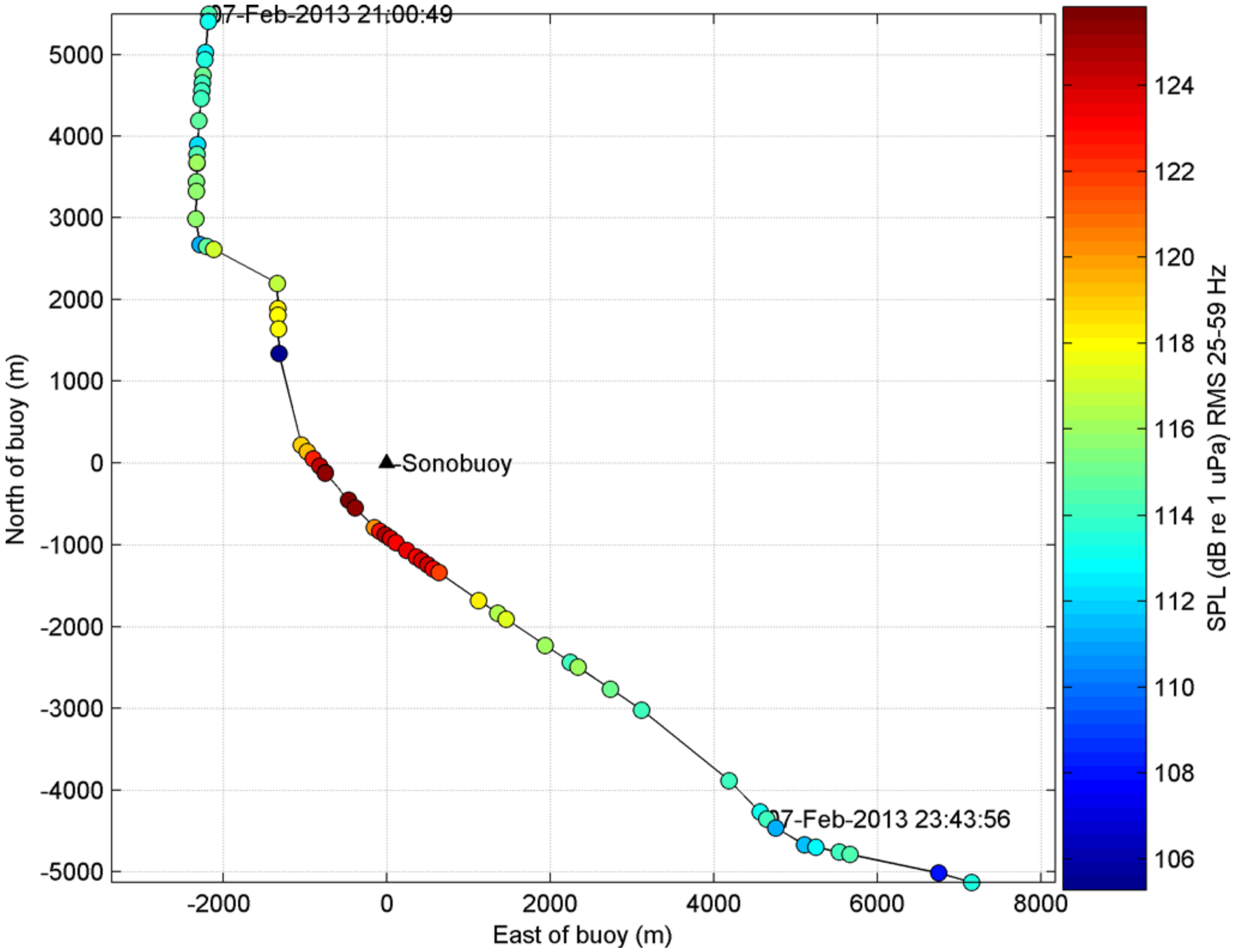

Figure 4 – **Whale track near a sonobuoy.** Whale positions obtained by photogrammetric video tracking (solid black line). All positions are relative to the location of the drifting sonobuoy. Filled circles show the estimated location of the whale, relative to the receiver, when z-calls were detected. Color of the circle indicates the received root-mean-square (RMS) sound pressure level (SPL) of call unit A measured in the 25-29 Hz band.

The average speed of the whale between photogrammetrically-derived positions was approximately 2 m/s throughout the encounter. With respect to the buoy, the velocity of the whale ranged from just above 1 m/s to nearly -2 m/s (with negative sign denoting whale movements away from the sonobuoy; Figure 5b). Whale velocity components along the direction of the acoustic wavefront ranged from 1 to -1 m/s (Figure 5c). Measured peak-frequencies ranged between 26.050 and 26.325 Hz, while frequencies predicted from the Doppler effect ranged between 26.160 – 26.220 Hz.

The velocity, v, explained only a very small proportion of the variability in observed peak-frequency in the multiple calls produced by this individual, f_m ($R^2 = 0.07$; $p = 0.039$; Figure 6). The intercept of the measured peak-frequencies was 26.182 Hz and the standard deviation of the raw data was 0.0814. Applying the Doppler ratio derived from the whale velocity, we obtained a base (*ie.* non-shifted) frequency of 26.181 Hz, and a standard deviation of 0.0784.

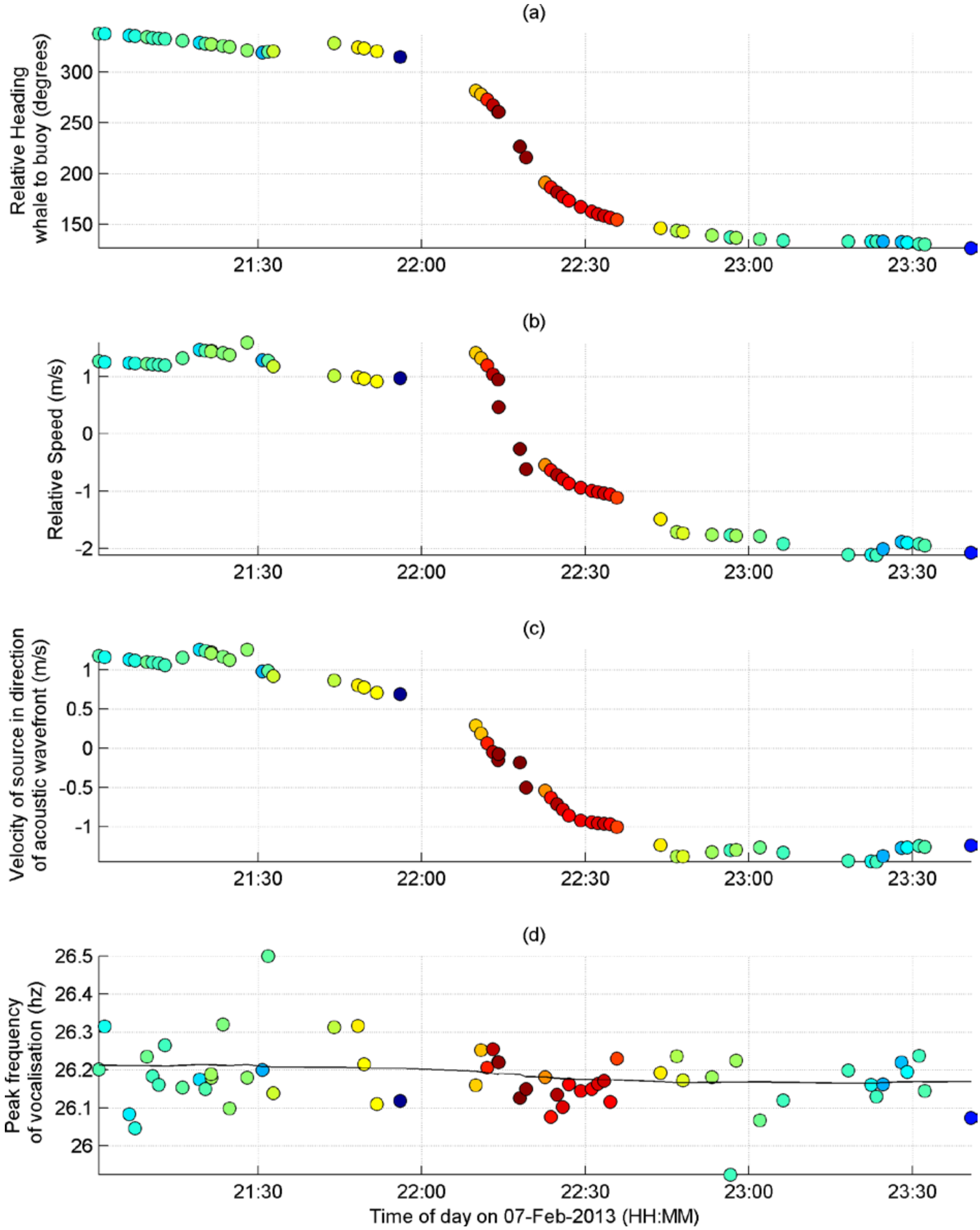

Figure 5 – **Time series of whale movements.** Time series of whale movements shown at the times when z-calls were detected (filled circles). (a) Bearing from sonobuoy to whale. (b) Relative speed between the whale and the buoy. (c) The component of whale velocity in the direction of the acoustic wavefront; (d) Peak-frequency of whale call. The black line in (d) corresponds to the prediction from Equations 2 and 4. Colour of circles corresponds to received level of call as per Figure 4.

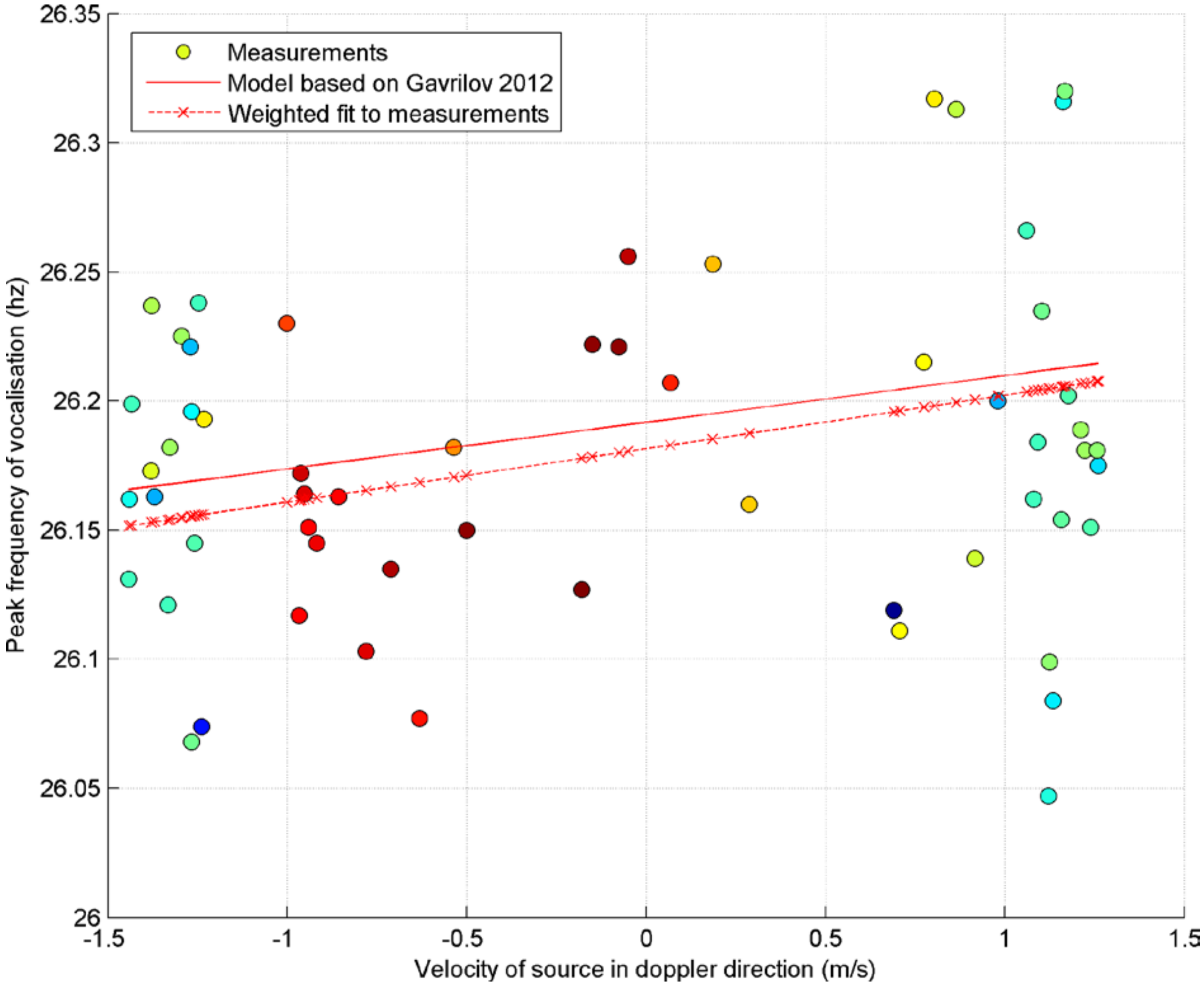

Figure 6 – **Relationship between observed frequency and movements.** Peak-frequency as a function of the velocity of the whale in the direction of the receiver. Filled circles show measured values and colours indicate received level as per Figure 4. Solid line represents the expected frequency shift derived from Equations 2 and 4 (f_w = 26.192; slope = 0.018). Dashed line represents a linear fit to the measurements (f_w = 26.182; slope = 0.021; R^2 = 0.07 (p = 0.039).

Discussion

Simultaneous observation of whale movement and acoustic recordings provided an opportunity to test the degree to which the Doppler effect was responsible for frequency variation in calls recorded from an Antarctic blue whale. The observed relationship between speed and peak-frequency (0.021 Hz m^{-1} s) was significant (p = 0.039) and was also very similar to that predicted by the Doppler effect (0.018 Hz m^{-1} s). Furthermore, by ‘correcting’ the raw observations of peak-frequency for Doppler effects, the standard deviation of the data was reduced from 0.0814 to 0.0784 Hz demonstrating that we were able to remove the Doppler effect in order to better estimate the ‘true’ peak-frequency emitted by the whale. However, the variance in measured peak-frequency was greater than would be expected to occur from only Doppler effects due to motion of the whale. This suggests that factors in addition to Doppler shift were responsible for the variation in peak-frequency between independent calls and that these factors dominated the variance.

Change of tonal frequency in blue whale calls may occur from a number of physical factors that are not mutually exclusive. Urick (1983) indicated that both frequency shift and dispersion arise not only from Doppler shift, but also from reverberation of sound as it reflects off the moving sea surface (Urick 1983). He further noted that there appeared to be a complex relationship among reverberation, frequency shift, frequency dispersion and wind-speed. Thus whilst the small amount of Doppler shift did undoubtedly occur from the motion of the whale, it appears that it is but one of several factors that contribute to frequency variation between individual calls.

In addition to physical factors in the environment that may have affected the peak-frequency itself, measurement error could potentially add to the masking of the contribution of the Doppler effect. Given our careful consideration to use only calls with high-signal-to-noise ratio, the largest source of measurement error is likely to arise in estimation of velocities of the whale and sonobuoy. Velocities were estimated by interpolation of surface positions and thus are only an average rather than instantaneous representation of the underwater speed and course of the vocalising whale. Compounding this issue is the fact that the observed swim speeds were all in the same narrow range of approximately 1–2 m/s. Measurement errors in estimating the velocity would be expected to increase the deviation of the measured peak frequency from that predicted by Doppler, but would not necessarily be expected to yield the level of variation observed in the vessel-based measurements. Furthermore, our observed slope of 0.021 Hz m s^{-1} was very similar to that of 0.018 Hz m s^{-1} predicted to arise from Doppler shifts, indicating that measurement errors in both speed and peak-frequency were reasonably small and relatively unbiased.

Lastly, the inherent precision of the whale's sound production was a likely a substantial source of variability in peak-frequency. While physical factors and acoustic measurement errors may also contribute to variability, a whale's inherent inability to produce exactly the same frequency from one call to the next is potentially the largest driver of variation in peak-frequency. While the range of observed peak-frequencies was very small (approximately 0.25 Hz) this range of peak-frequencies is nearly twice as large as the inter-annual decline of 0.135 Hz described by (Gavrilov et al. 2012). Neither the degree to which whales can control the pitch of their song (nor the ability of the intended recipient to perceive differences in pitch of said song) have been quantified to date, but further discussion of models of sound production and perception can be found in the following section on seasonal factors.

Despite these limitations, our results highlight the benefits of combined visual and acoustic observations and demonstrate that we are able to describe the variance in peak-frequency having removed the effect of Doppler shift on the received signals. To our knowledge, the data presented here represent a first attempt to measure the Doppler effect in any cetacean vocalisation, let alone the long-duration, low-frequency songs of baleen whales.

Obtaining more underwater tracks, ideally of higher accuracy and over a wider range of velocities, could help to reduce these confounding effects. Time-depth recorders with yaw-pitch-roll sensors, and acoustic recording capability such as the DTAG or Acousonde could provide one such way to obtain more accurate underwater tracks, and these instruments would also allow comparison of recordings from an instrument moving on the whale with a stationary one. Alternatively, data fusion algorithms could be used to combine position information from video-tracks, DIFAR sonobuoys, time-differences-of-arrival of sound, and possibly multipath (Nosal & Frazer 2007, Valtierra et al. 2013) in order to obtain more accurate tracks from the existing data set.

B. Long-term observations

1. Results

The three long-term recording sites (Figure 3) that were utilized to examine intra-annual variation in frequency ratio (Equation 1) all showed similar results. Across all three recording sites the mean frequency ratio was 1.0006 with 95% interval between 0.9955 and 1.0050. However, it is important to note that the distribution of frequency ratios varied cyclically over the year, with ratios greater than one more likely to occur from March through June; ratios remaining near one in July and August, and ratios less than one occurring in September and October (Figure 7; Table I).

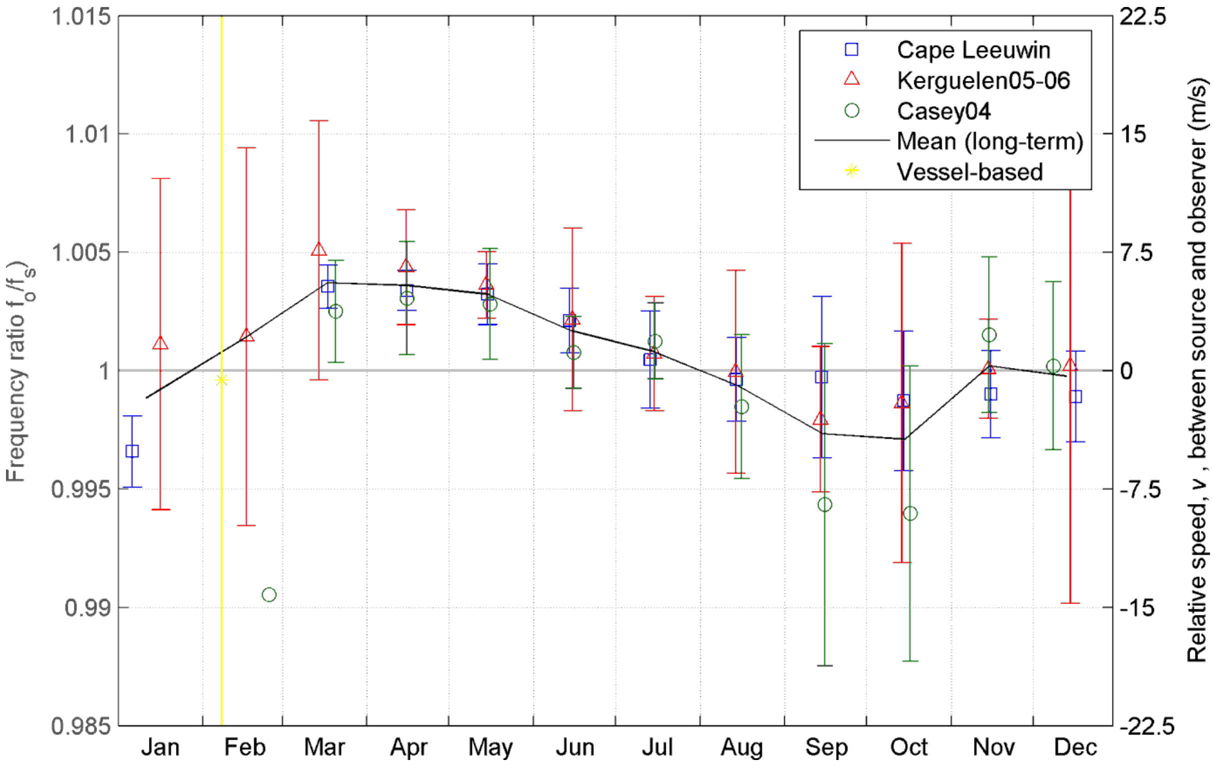

Figure 7 – **Monthly observations of frequency shift.** Markers show the ratio of measured to 'true' frequency of Antarctic blue whale song. Measured frequency and 'true' frequency are calculated from the data from (Gavrilov et al 2012) and monthly means are pooled from 9 years of acoustic observations (blue dots). The Antarctic recording stations Kerguelen (red triangle), and Casey (green circle) comprise 2 and 1 years of acoustic observations. Error bars show the monthly standard deviation. The black line connects the mean of all montly observations from all of the long-term recording stations. The yellow star shows the mean of the vessel-based measurements with error bars denoting one standard deviation (note that error bars for the vessel-based observations extend well beyond the range of the vertical axis for this figure).

Discussion

SWIMMING SPEEDS

If we assume that these shifts in frequency are due to the Doppler effect, we can apply equation 5 to convert these ratios to a mean speed of 0.93 m/s with 95% interval between -6.68 and 7.45 m/s (Table I). The swimming speeds estimated from frequency shift were within the range of plausible speeds for blue whales during the Austral summer and winter at all three locations. However for the Doppler effect to account for all of the frequency variation, speeds in the Austral spring and autumn would be higher at all three locations than mean speeds measured for Northern hemisphere blue whales (Oleson et al. 2007, Bailey et al. 2009).

Bailey et al., found mean speeds for non “foraging” whales to be around 1 m/s (Bailey et al. 2009), while Oleson et al., found that blue whales off California (*Balaenoptera musculus musculus*) making repetitive AB calls (*ie.* song) were most often travelling at speeds between 1.9 and 4.5 m/s, which they referred to as fast travelling (Oleson et al. 2007). However, Sears and Perrin suggest travelling speeds for blue whales (*Balaenoptera musculus* ssp.) of 8.3 m/s, and suggest that whales being chased (by whalers), or interacting with conspecifics may travel at speeds of 9.7 m/s (Sears & Perrin 2009). Furthermore, preliminary results from satellite telemetry tracks of two tagged Antarctic blue whales indicate swimming speeds of Antarctic blue whales do, at least sometimes, approach 10 m/s (Andrews-Goff et al. 2013). This indicates that the potential source speeds calculated here could conceivably be achieved, though it is highly unlikely that the majority of vocalising whales travel at these speeds for the duration of migrations.

DIRECTION OF TRAVEL AND MIGRATION

The Doppler effect occurs due to the relative speed between the source and the receiver in the direction of the acoustic wavefront, not the absolute speed of the source. This implies that the maximum frequency shifts will occur at the whale's top speed only when the whale's course is directly towards or away from the receiver.

Positive frequency shifts occurred from March to June at all receivers. If the Doppler effect alone was responsible for this change in frequency, then this would indicate that whales are moving towards all three of these widely spaced receivers during these months. Similarly negative frequency shifts occurred during August to November. Again, if the Doppler effect was the cause then this would suggest movement away from all three of these sites at this time of year. From July through September, there was no net frequency shift at Cape Leeuwin or the Kerguelen plateau, and strong negative shift at Casey. Assuming that these shifts are due to the Doppler effect and that movement patterns are similar between different recording years, we could conclude that the population of vocalising Antarctic blue whales had no net movement towards or away from Cape Leeuwin or the Kerguelen plateau during these months, yet moved rapidly away from Casey. While frequency shifts observed at Cape Leeuwin yield speeds and directions of travel that are broadly consistent with the proposed migration, this is not the case at Casey and the Kerguelen Plateau, even when assuming that whales are detected from very far away.

Consequently, we believe that it is highly unlikely that the intra-annual pattern in frequency is primarily a result of the Doppler effect during migration. The swimming speeds required to achieve observed Doppler shifts are generally too high to be maintained, and if they were maintained, then the migration would be completed in a matter of days. Additionally, the direction of travel (simultaneously towards both Antarctic and sub-tropical receivers) is not consistent with any plausible or likely migration route.

Intensity of sound and/or call counts may provide better indicators of migration than frequency shifts. Maximum received levels at a hydrophone could potentially arise from proximity to the hydrophone. However, a maximum in the PSD, as reported by Gavrilov et al. (Gavrilov et al. 2012) could also arise from a maximum in the number of whales calling without an increase in proximity. Samaran et al., found that the months of May and June had the highest proportion of days with detected Antarctic blue whale calls off Crozet Island, Cape Leeuwin, and Diego Garcia, and found peaks in PSD at these times off Casey Station and the Kerguelen Plateau (Samaran et al. 2013). That these maximums in PSD with peaks in calling co-occuring at such widely separated locations (Samaran et al. 2013) may further strengthen the hypotheses that whales are either calling more frequently at this time of year, calling more intensely, or some combination of the two.

Gavrilov et al., presented correlation between the frequency shift and received levels off Cape Leeuwin with maximums of both values occurring over March to May (Gavrilov et al. 2012), and McDonald et al., proposed that calls with lower peak-frequencies would have lower source levels and should also occur when population density is high (McDonald et al. 2009). Our results suggest that peak-frequency was higher on the high-density feeding grounds. Notwithstanding the discovery of an even higher-density breeding ground, our observations suggest that the intra-annual change in frequency may not be driven by the same factors that have been proposed by McDonald et al., to cause long-term decline (McDonald et al. 2009). However, further data on source-levels, locations and density of whales on breeding grounds, and whale behaviour would be required to test these hypotheses.

SEASONAL FACTORS

Gavrilov et al., described the intra-annual frequency pattern as declining from March to December and then "resetting" next March (Gavrilov et al. 2012). This sharp "resetting" may have resulted from lack of acoustic observations and measurements at Cape Leeuwin during January and February. By including data from the Kerguelen plateau, we observed a more gradual increase in frequency over January and February that leads to this apparent "reset." This gradual increase in frequency over the Austral summer fleshes out the overall intra-annual pattern with a more sinusoidal rather than sawtooth appearance.

After removing the long-term trend, the highest frequencies are produced by whales in March, while the lowest frequencies are produced in October. Upon arriving at the feeding grounds in the Antarctic between November and January, peak-frequency increases until maximum is achieved in March. By April, most singing whales are believed to have departed the feeding grounds for winter migration (Mackintosh 1966). Peak-frequency decreases at all sites from mid-autumn through mid-spring as singers are presumably away from their main feeding grounds until the cycle begins anew in November.

While we have demonstrated a clear seasonal pattern in tonal-frequency of Antarctic blue whale calls, it remains to be seen whether these intra-annual patterns, like the long-term decline (McDonald et al. 2009), also occur in other populations of blue whales. While there are hints that similar intra-annual variation in frequency may occur in southeast Indian ocean pygmy blue whales (*Balaenoptera musculus brevicauda*) (Gavrilov et al. 2011), further investigation and quantification of these patterns for other populations of blue whales is warranted. Comparative studies across different populations may yield insights into the cause(s) of these seasonal variations.

While we cannot rule out a purely behavioural reason for the intra-annual change in frequency, throughout the year the mean variation by month rarely exceeds 0.5% of the “base” frequency for that year. At such low frequencies it is unknown if blue whales, like bottlenose dolphins (Thompson & Herman 1975), can perceive a difference in frequency of 0.5% despite indications that they have a hypertrophied cochlea indicative of acute low-frequency hearing (Ketten 1997). However the change in the mean-monthly peak-frequency throughout the year is less than variation between calls observed during an hour of vessel-based measurements of a single whale. If an individual exhibits this much variability between calls in such a short period of time, it seems unlikely that the observed longer term seasonal pattern of such small shifts in peak-frequency is a result of intentional behavioural changes by all vocalising whales.

Instead, the gradual variation in mean frequency from month-to-month and the increased variability as whales return to the Antarctic could suggest a link between intra-annual frequency patterns and whale anatomy (*ie*. body condition). One avenue for further investigation into this link would be to test whether there is a relationship between body condition and tonal frequency. Interestingly, the cyclical intra-annual pattern in tonal frequency appears to match that of blubber thickness for male blue whales (Mackintosh et al. 1929), especially those less than 19 m in length (Figure 8). While there is admittedly a temporal disparity between these two data sets and presently a lack of understanding of a causal mechanism linking blubber thickness to tonal frequency, this correlation is intriguing and worthy of further investigation.

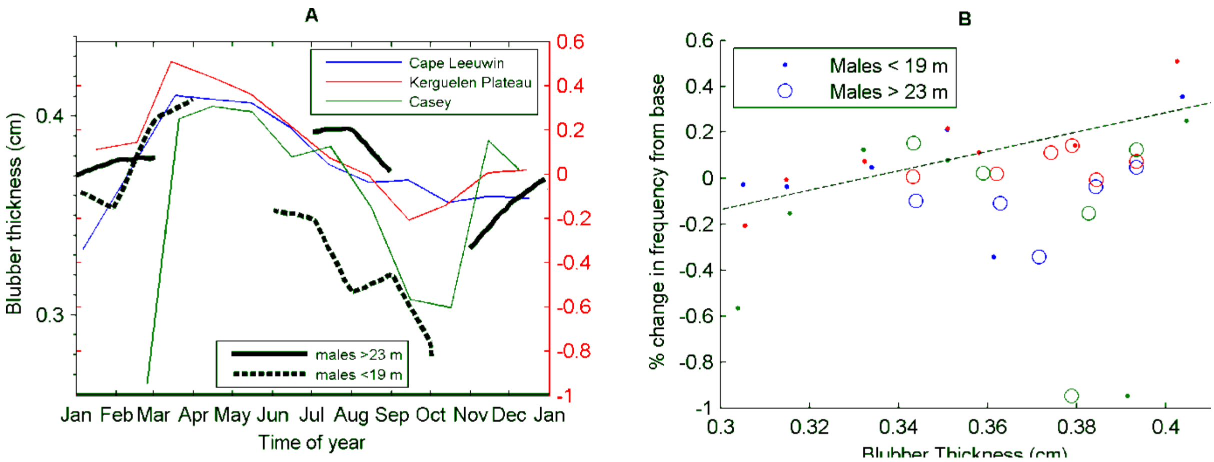

Figure 8 – **Relationship between blubber and tonal frequency.** Seasonal changes around the base frequency measured in this study correlate with seasonal changes in blubber thickness measured by Mackintosh and Wheeler (1929), particularly for males less than 19 m. (**A**) Time series of intra-annual variation in frequency ratio and blubber thickness. Colored lines represent the frequency ratio measured at each recording site (left vertical axis), while black solid and dashed lines (right vertical axis) are a summary blubber thickness measurements digitised from Mackintosh et al., (1929). (**B**) Relationship between blubber thickness and intra-annual measurements of peak-frequency. Open circles represent whales greater than 23 m in length, while dots represent whales less than 19 m in length again with blubber thickness digitised from Mackintosh et al., (1929). The colors of each symbol correpsond to the recording locations (*ie.* blue: Cape Leeuwin; red: Kerguelen Plateau; green: Casey). Dashed line shows the least-squares fit at all locations to males less than 19 m weighted by the inverse variance of the frequency ratio (intercept = -1.44; slope = 4.32; R^2 = 0.71; p = 0.001). Males greater than 23 m did not have a significant relationship, so no trend line is shown (intercept = -0.53; slope = 1.35; R^2 = 0.10 p = 0.74).

Sound production in blue whales is not well understood, and initial theories (Aroyan et al. 2000, Thode et al. 2000) do not appear to satisfactorily describe the mechanism, observed frequency content, and source levels of blue whale sounds (Reidenberg & Laitman 2007). New models of sound production have recently been proposed for mysticetes (Reidenberg & Laitman 2007) and tested for humpback whales (Adam et al. 2013), but remain untested on blue whales. Without additional testing of anatomical models or additional collection of vessel-based behavioural, anatomical, and acoustic data, the cause of cyclical intra-annual variation in tonal frequency of Antarctic blue whale song may remain poorly understood.

CONCLUSIONS

Variation in the peak-frequency of Antarctic blue whale calls was measured from vessel-based recordings in the Antarctic. This variation was significantly correlated with, but also much greater than, the level that would be predicted by the Doppler effect. This suggests that, at least at low speeds, factors other than the Doppler effect are likely to be the predominant driver of the seasonal variation in peak-frequency of Antarctic blue whale calls. Furthermore, the fact that the same intra-annual pattern was observed off Cape Leeuwin, Casey Station, and the Kerguelen Plateau makes it unlikely that Doppler shifts coincident with migration are responsible for the intra-annual variation in blue whale peak frequencies. However, this same fact also makes it unlikely that the physical environment (eg. water temperature, salinity, etc.) is responsible for the pattern, barring extremely long-range acoustic propagation. Thus changes in whale behaviour, or more likely body condition, remain the most parsimonious explanations for the observed intra-annual pattern.

Our results indicate that seasonal patterns in tonal frequency may also yield biological insight into the life-history of Antarctic blue whales complementary to historical (Stafford et al. 2004, Gedamke et al. 2007, Širović et al. 2009, Samaran et al. 2010a, 2013) and ongoing ("SORP Acoustic Trends Project" 2014) studies of the spatial variation and seasonality of acoustic detections. Future studies of intra-annual variation in tonal frequency of blue whale song should consider correcting for Doppler effects, but may only need to do so in situations where whales are moving at high speeds. Further acoustical studies of whale migration should focus on more precise estimates of the number of calling whales, measurements of the intensity (as well as propagation loss and source level of calls) and supplementing acoustical data with anatomical measurements such as length, girth and body condition.

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TABLES

Table I - Mean monthly speeds (m/s) estimated at Cape Leeuwin assuming that intra-annual frequency change is caused by doppler shift.

	Cape Leeuwin	**Kerguelen**	**Casey**
Jan	-5.1 ± -2.2 (n= 2)	1.7 ± -10.5 (n= 19)	N/A
Feb	N/A	2.2 ± -12.0 (n= 65)	-14.2 ± NaN (n= 1)
Mar	5.3 ± -1.4 (n= 8)	7.6 ± -8.2 (n= 67)	3.8 ± -3.2 (n= 22)
Apr	5.1 ± -1.3 (n= 14)	6.6 ± -3.7 (n= 44)	4.6 ± -3.6 (n= 30)
May	4.8 ± -1.9 (n= 21)	5.4 ± -2.1 (n= 37)	4.2 ± -3.5 (n= 31)
Jun	3.2 ± -2.0 (n= 20)	3.3 ± -5.8 (n= 58)	1.2 ± -2.3 (n= 30)
Jul	0.7 ± -3.1 (n= 23)	1.1 ± -3.6 (n= 62)	1.9 ± -2.4 (n= 29)
Aug	-0.5 ± -2.6 (n= 25)	-0.1 ± -6.4 (n= 37)	-2.3 ± -4.6 (n= 28)
Sep	-0.4 ± -5.1 (n= 26)	-3.1 ± -4.6 (n= 32)	-8.5 ± -10.2 (n= 30)
Oct	-1.9 ± -4.4 (n= 22)	-2.0 ± -10.1 (n= 35)	-9.0 ± -9.3 (n= 26)
Nov	-1.5 ± -2.8 (n= 20)	0.1 ± -3.1 (n= 33)	2.3 ± -4.9 (n= 19)
Dec	-1.6 ± -2.9 (n= 8)	0.3 ± -15.1 (n= 33)	0.3 ± -5.3 (n= 6)