Worldwide Decline in Tonal Frequencies of Blue Whale Songs

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Abstract: Blue whale (*Balaenoptera musculus*) songs can be divided into at least ten types worldwide, each type retaining the same units and similar phrasing over decades, unlike humpback whale song which changes substantially from year to year. Historical acoustic recordings dating back as far as the 1960's were examined, measuring the tonal frequencies of 1000's of blue whale songs. Within a given year individuals match the song frequency (related to "pitch" in musical nomenclature) to within less than 3 percent. The best documented song type, that observed offshore California, now is sung at a frequency 31% lower than it was in the 1960's. Data available for seven of the worlds' ten known song types show they are all shifting downward, though at different rates. Any ecological, oceanographic or anthropogenic change hypothesis seeking to explain the observed shifts should account for the worldwide occurrence and a near linear shift. Hypotheses examined consider increasing ocean noise, increasing whale body size post whaling, global warming, interference from other animal sounds and post whaling increases in abundance. None of the commonly suggested hypotheses were found to provide a full explanation, however, increasing population size post whaling provides an intriguing and testable hypothesis that recovery is altering the sexually selected tradeoff for singing males between song intensity (the ability to be heard at a greater distance) and song frequency (the ability to produce songs of lower pitch).

INTRODUCTION

Blue whales (*Balaenoptera musculus)* are an endangered species worldwide, having been commercially hunted until 1972 (Clapham et al. 1999; Branch et al. 2004). During the past several decades, blue whale abundance appears to be increasing in most if not all regions, although the data is sparse and uncertain in most areas (Reeves et al. 1998; Calambokidis & Barlow 2004; see Branch et al. 2007 for a review of worldwide blue whale distribution and abundance).

Blue whales migrate over large distances while producing songs year around, at their tropical breeding grounds, during migration, and on their feeding grounds (Stafford et al. 1999, Širovic et al. 2004). The function of whale song, even the better studied song of the humpback whale, remains a mystery (Darling et al. 2006). Limited observations of singing blue whales suggest different usage patterns than that of humpback whale song and an even greater mystery (Oleson et al. 2007). All singers for which sex has been determined have been males, although both sexes produce non-song calls (Oleson et al. 2007). Singers have always been found to be travelling at relatively high speed, whereas non-song calls are commonly produced by milling or feeding blue whales (Oleson et al. 2007). Blue whale song has a distinctive character and can be classified into at least 10 geographically distinct song types worldwide. McDonald et al. (2006a) describe nine types and recent recordings from near South Georgia Island show an additional type.

McDonald et al. (2006a) have argued the value of division of blue whale populations based on the geographical distribution of each of the 10 song types, though the relationship of these populations and the current blue whale subspecies remains an area of confusion (Reilly et al. 2008). Genetic studies of blue whales have not yet resolved the many questions with regard to subspecies and populations (LeDuc et al. 2007) and questions regarding how subspecies may relate to song type is a topic in recent studies (Samaran et al. 2008). The song types are stable over 10's of years in terms of the number of units, the character of the units and the phrasing, but not the frequency (related to pitch in music) of the song units. The presence of this frequency shift first became apparent to the authors when developing automated blue whale song detectors as used in Burtenshaw et al. (2004). The detector needed to be shifted lower in frequency each year to match the song produced at that time.

Technological advancements in automated long term recording systems are increasing the importance of acoustic recordings as a whale monitoring tool (Mellinger et al. 2007). Acoustic monitoring provides a complimentary approach to conventional visual line transect surveys. Long term acoustic recordings covering much of the world's oceans are becoming freely available from a variety of sources, such as the nuclear test monitoring network (www.rdss.info). What is needed now is development of the methods and understanding to use these acoustic data to improve our knowledge of blue whale migration patterns, population divisions, abundance and behavior.

METHODS

Spanning the last 40 years, blue whale calls have been documented by underwater hydrophones deployed for both whale research and military use, by seafloor seismometers studying regional earthquakes, and more recently by dedicated whale acoustic recording packages. See the electronic supplementary material (ESM) for details of recording dates, locations, number of songs measured, measurement confidence intervals and the locations of archived recordings. Recordings from published reports, archival data, and from on-going projects to monitor blue whales worldwide were examined. When multiple songs from multiple animals were measured the standard deviations and 95 % confidence intervals as well as mean frequencies of song units were computed.

Songs separated substantially by time (generally more than 24 hours) and/or distance are considered separate encounters. Statistical arguments regarding the likelihood of separate encounters being from different individuals based on travel speeds from tag data, time between encounters, population abundance, detection range and geographic range are not developed here, as individual status is not a critical assumption to the focus of this study. The whale encounter category is useful nonetheless in allowing a measure of frequency change within an individual song sequence versus other song sequences from different encounters within the same region and year.

In regions outside the Eastern North Pacific, early raw acoustic recordings were rarely available and the data points have been measured from published spectrograms or waveforms and from published descriptions of the dominant frequency. In some instances only a single song was available. Archival data from the 1960's and 1970's used analog tape recording whereas more recent data are based on digital recordings. Analog tape recordings were calibrated using pilot tones included on the tape, compensating for slight differences in tape speed. Frequency corrections for analog tape speed variance were on the order of a few percent.

Choice of frequency measurement points is illustrated in Figure 1. Taking the eastern North Pacific song as an example, the first unit of the song is pulsed and lasts for about 20 sec, with a fundamental frequency of about 16 Hz and overtones at five additional frequencies. It is difficult to precisely measure the frequency of pulsive sounds, thus these types of sounds are not analyzed. The second unit of the song is nearly tonal and lasts for about 20 sec, with a series of harmonically related frequencies. The harmonic frequencies are precise integer multiples of the fundamental. The frequency of the tonal calls was measured with an accuracy of 0.1 Hz or better using the computer cursor on a spectrogram plot. For the eastern North Pacific song type the frequency of the 3rd harmonic tonal unit at its temporal mid-point was measured because greater precision is obtained at this integer multiple (Figure 1).

Song frequency measurements occasionally require assumptions regarding which song phrase, if any, should be used as most song types show variants in phrase order and occasional changes in character (Edds 1982; Mellinger & Clark 2003). Each song component shifts proportionately, thus typically the frequency of only one (the clearest) is listed in Table 1 of the ESM. The exception in this study is the southeast Indian Ocean song type, where additional averaging of the frequency shift using multiple song components was deemed appropriate, there being only two recordings available to this study.

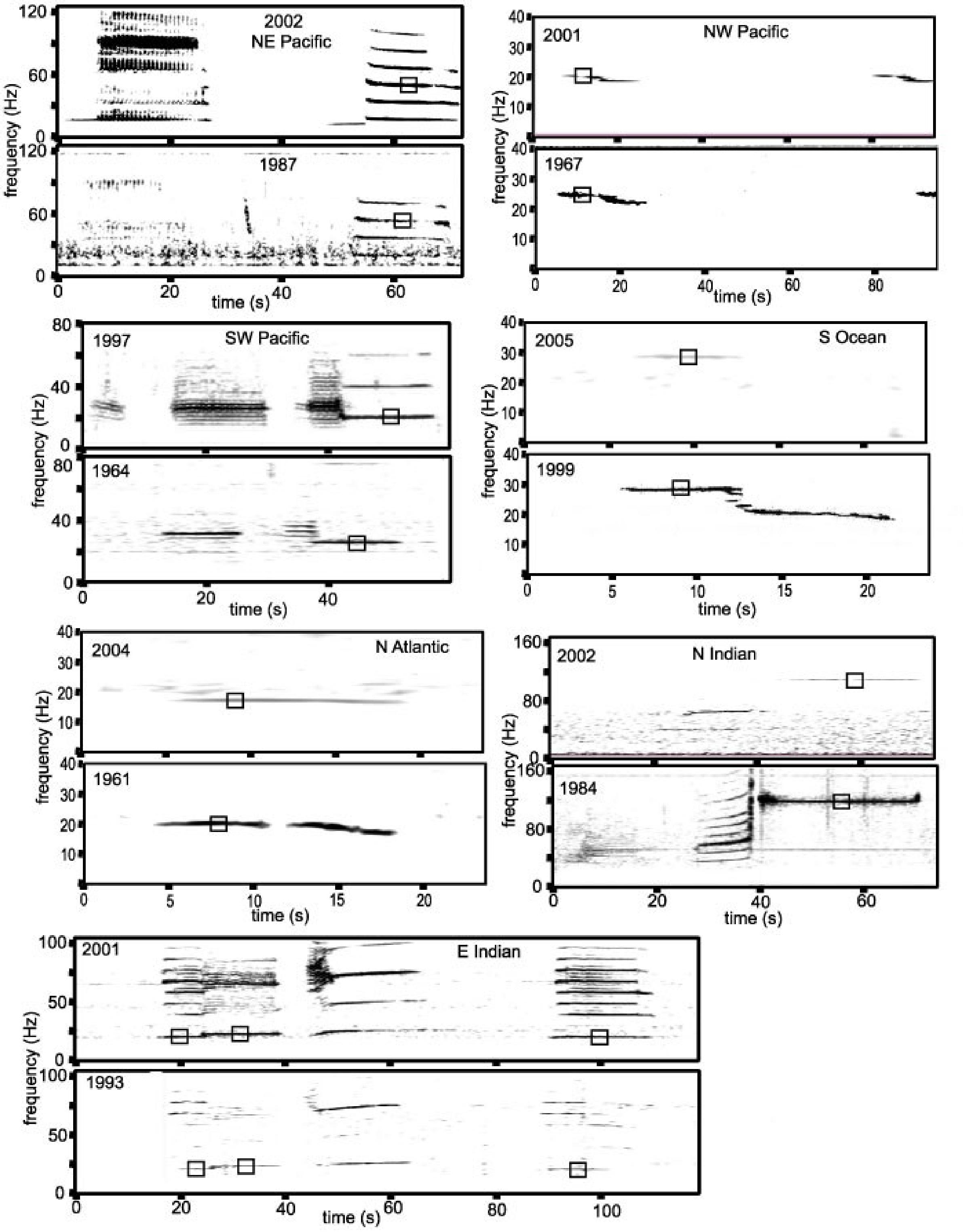

Fig. 1. *Balaenoptera musculus.* The frequency shift in song from each region is illustrated on spectrograms, with the temporal mid-point measurement points used in this study marked with squares.

RESULTS

The standard deviation of the Eastern North Pacific song type at the third harmonic within a whale encounter is 0.1 - 0.4 Hz with an average standard deviation of 0.2 Hz (typical n=10 songs each from 10 separate encounters, similar deviations from one year to the next). Likewise, when calls from multiple encounters are averaged in a given year, the standard deviation is less than 0.4 Hz from the mean frequency (typical n = 1000 calls within one season). Doppler frequency shifts due to swim speed can account for about 0.1 Hz standard deviation at the third harmonic.

The frequencies of blue whale song types for seven of the ten song types for which multiple years of data are available are all shifting downward (Table 1), although these frequencies are different for each song type. The best documented eastern North Pacific blue whale song exhibits a 0.4 Hz per year long-term linear downward frequency shift as measured at the third harmonic, with a downward trend that is surprisingly linear (correlation coefficient r = -.99). In 1963 the song had a mean frequency at the third harmonic of 66 Hz, whereas in 2008 the song had a frequency of 45.5 Hz (Figure 2). Equivalently, the fundamental frequency shifted from 22 Hz in 1963, to 15.2 Hz in 2008. In the eastern North Pacific, the tonal part of a blue whale's song today is 31% lower in frequency than it was 44 years ago.

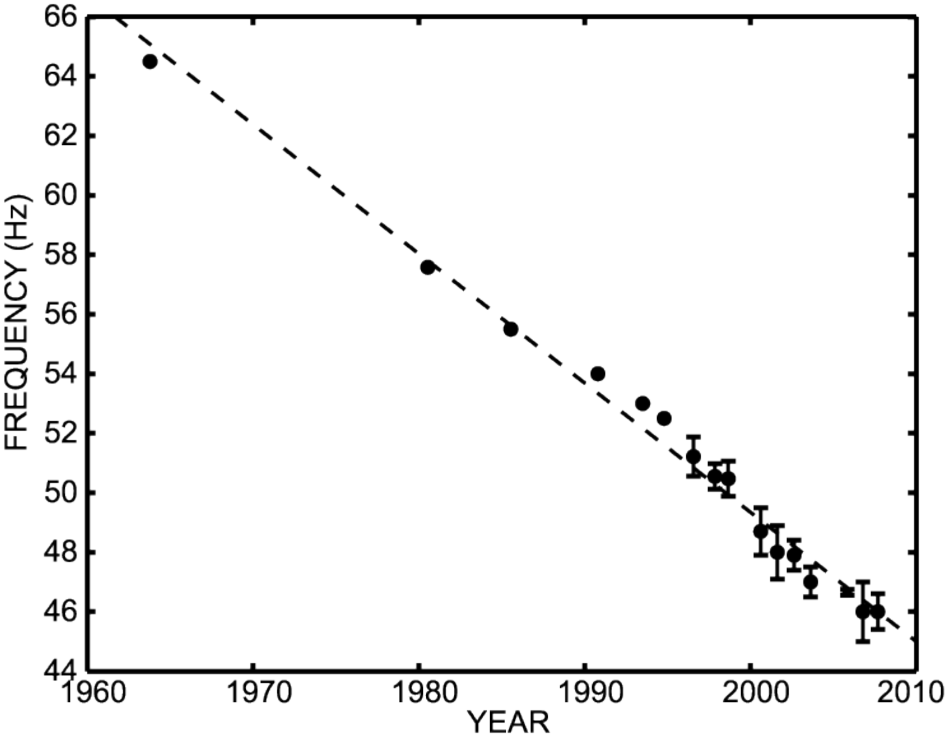

Fig. 2. *Balaenoptera musculus.* Northeast Pacific third harmonic tonal frequencies are shown with 95% confidence limits. The dashed line is the least squares linear trend. Where no confidence limits are shown, there were insufficient data points to compute confidence intervals. The larger confidence intervals are from published records for which raw data were not available and may represent different measurement methods.

The greatest relative change is observed in the two North Pacific song types and the least change in the south Indian Ocean song type (Figure 3). The rate of downward frequency shift, expressed as a percentage, differs by as much as a factor of two between song types, but all units of each song type are shifting linearly such that a tonal at one half the highest frequency will shift with a slope of one half that of the highest frequency. The southwest Indian Ocean and eastern South Pacific song type are not plotted because the available data are insufficient to measure any potential shift.

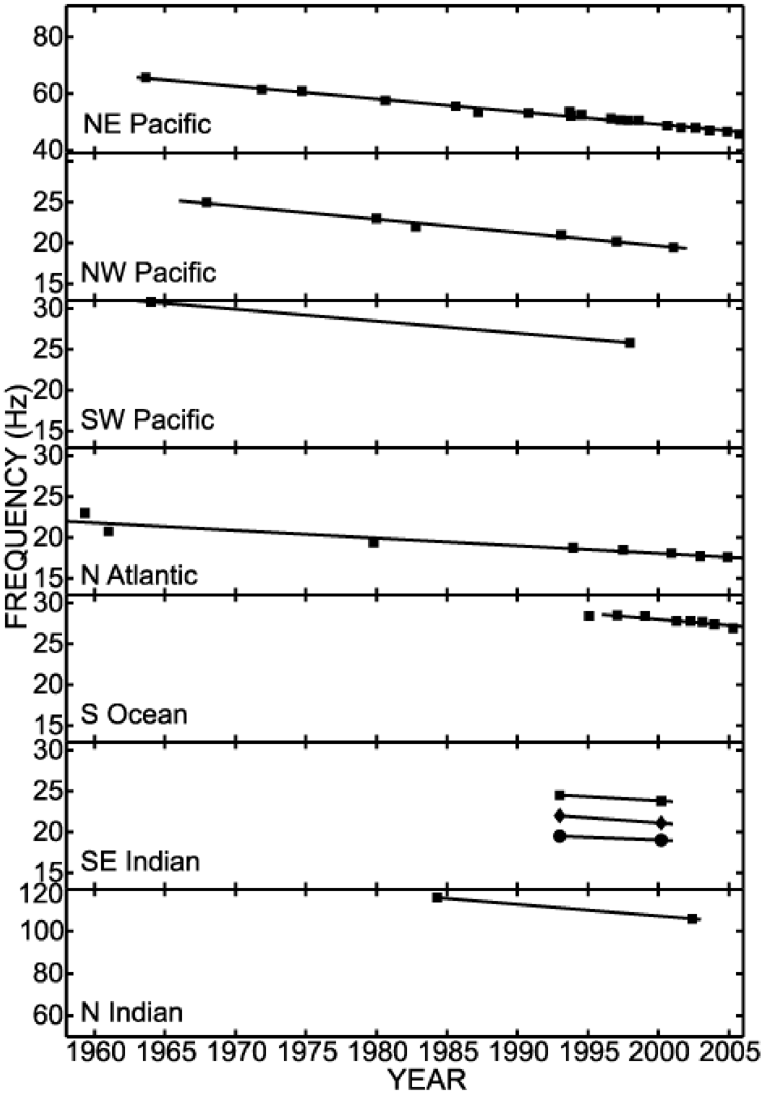

Fig. 3. *Balaenoptera musculus.* The frequency shift for seven song types, labeled as to region following McDonald *et al*. (2006). The lines are least squares linear trends. The frequency scales were chosen to allow comparison of the slopes (e.g. a 100 Hz measurement point should have a frequency axis five times compressed relative to a 20 Hz point). The mean 95 % confidence interval is 0.6 Hz and the individual values are in the ESM.

DISCUSSION

Any hypothesis seeking to explain the observed shifts should account for long term change, near worldwide occurrence and a relatively linear shift. First we discuss why blue whales may choose to synchronize their songs in frequency during a given season and the possible significance of lower frequency songs. Next, we review a list of hypotheses seeking to explain the global pattern and our conclusions regarding the validity or promise of each.

Cultural conformity within populations and global synchrony in the direction of the pitch shift. When new behavioral variants spread rapidly through a population over time scales of less than a generation and when there is no obvious environmental driver, social learning (culture) may be operating (Rendell and Whitehead 2001). While the calls of many marine mammals are known to vary geographically, variation is best known among the songs of male humpback whales (*Megaptera novaeangliae*). At any one time, male humpbacks in a region sing nearly the same song but the song changes noticeably over the breeding season and substantially over subsequent years (Payne & McVay 1971; Payne et al., 1983). Cerchio (1993) suggests that the variation in humpback song can be likened to temporal dialects in which conformity may be socially significant, as in birds (Payne 1982). While humpback song was once thought to be a unique example among non-human animals of a continuously evolving conformist culture in a large and dispersed population (Rendell & Whitehead 2001; Payne 2006), the worldwide coverage and time span of data on blue whales exceeds even that of humpback whales. Conformist cultures – in which individuals adopt the most common form of behavior present in the population - can lead to the structuring of a population into culturally marked groups (Boyd and Richerson 1985, Whitehead 2008). While it is unclear why cultural conformity would drive blue whale song frequencies lower, it is clear that all regions in the world are experiencing the same direction of change. This leads to the question, without resolution, of whether there are cultural linkages among blue whale populations worldwide.

Does sexual selection favor lower frequency song? Male song typically has two functions: species recognition and intraspecific competition for mates either through female choice or male-male competition. Although blue whale songs occur year around, they are known only in males, thus it is likely that there is some direct relationship between singing and breeding success. The maximum intensity at a given frequency is controlled by the whale's air volume (size) as per Aroyan et al. (2000). Sexual selection is well known to cause directional selection in male traits either as an indicator of "good genes", runaway selection, or sensory exploitation (Ryan et al. 1990, Andersson 1994). Blue whales are widely dispersed during the breeding season, and while it is reasonable to assume that songs function to advertise the species and location of the singing whale, it is not known to what extent blue whale song is also under selection as a form of inter and/or intra-sexual display. In addition to pitch, several other attributes of song may be under selection by females as well, such as loudness, duration, repertoire and song complexity (Searcy & Andersson 1986).

In terrestrial species, many females are shown to prefer males whose acoustic attributes are correlated with large body size (low frequency calls, higher intensity calls; Searcy 1996, Gerhardt & Huber 2002) and that sing longer and more complex songs (Rand & Ryan 1981, Catchpole & Slater 1995). In blue whales (the largest animal on the planet), an honest indicator of large body size as indicated by their ability to sing songs of a given pitch at a greater loudness may be favored in mate selection by females. Ascertaining the traits that females in either terrestrial or marine species may use to locate and assess singers is by no means straightforward however, and several additional factors such as female sensory biases, other components of male fitness, and the costs and benefits of choosiness are likely to play an important role. The role that blue whale song may play in male-male interactions is also unknown. Future work to examine the relative complexity of blue whale calls among geographic regions may provide additional insights into the differences in the intensity of selection and density of individuals among regions as predicted by studies of birds (Catchpole 1980, Kroodsma 1983, Price 1998).

Increase in body size post whaling. With the cessation of commercial whaling, it is reasonable to consider that the size of blue whales has increased over time. However, lung and vocal tract volume changes over the past 40 years are at most a secondary factor. During the whaling era, large animals were selectively removed from the population, both because of whaling regulations limiting the catch to large animals (>70 feet for north Pacific blue whales), and because of the economic value of large animals. Indeed, whaling data for the northeast Pacific suggest a reduced body length for blue whales harvested during 1960-65, the final decade of whaling (Gregr et al. 2000). Following the cessation of whaling, body size would be expected to return to the pre-whaling distribution due to the removal of hunting pressure on mature animals. Since blue whales reach sexual maturity and have 95% of their mature body weight at age 8 (Lockyer 1978), it seems likely that body size distributions have returned to near pre-whaling values in less than the 40 years since the cessation of whaling. The continued linear shift in pitch and calculations relative to lung volume changes suggest this is not a primary factor in the observations presented here.

Global climate change and ocean acidification. It is recognized that average global temperatures are increasing, causing higher average sound velocities in the uppermost ocean inhabited by these whales (Levitus et al. 2005). However, the average warming of the ocean's uppermost 700 m over the last 40 years is estimated to be 0.1 °C (Bindoff et al. 2007), or equivalently 0.3 m/sec sound velocity increase in the mid-latitude Pacific. As a percentage of average surface sound velocity (~1500 m/sec), these changes are small, less than 0.02%, compared to the 31 % change in blue whale tonal frequencies. It is not clear how or why the whale sound generation source would change in concert with the changing sound velocity.

Acidification of the oceans with climate change is predicted to result in better sound propagation via a lowering of the acoustic absorption coefficient (Hester et al. 2008). At reasonable ranges for whale communications (out to several hundred km), acoustic absorption is a small component of propagation losses and the predicted changes appear small relative to a 31% shift in blue whale frequency. The potentially more significant impact of the predicted change in absorption would be better basin wide propagation of shipping noise over 1000's of km, a topic discussed below.

Biological interference. Interactions between blue whales and other marine mammals may be another factor affecting call frequency. The other species which commonly produces substantial sounds in the blue whale frequency band is the fin whale. Fin whales use short (<1 sec) pulsed calls. When blue and fin whales are producing songs or calls in close proximity, interference between their respective calls may encourage the blue whales to change the fundamental frequency of their calls to avoid overlap with the frequency band of the fin whale calls. Fin whale calls and songs however change with season and/or geographic region and blue whale songs occur above, below and within the fin whale frequency bands (McDonald et al. 2008), so it is unclear how this hypothesis would cause the blue whale songs to all shift down in frequency.

Anthropogenic noise. Blue whales may modify their call frequencies to adapt to increasing anthropogenic noise. The dominant low frequency noise in the deep-water northeast Pacific is due to commercial shipping traffic, which occurs primarily in the same 10-100 Hz frequency band as blue whale songs. In the northeast Pacific, an approximately 12 dB increase in ambient noise is reported over the past 4 decades (Andrew et al. 2002; McDonald et al. 2006b). The shipping noise increase is likely less in the Antarctic where shipping traffic and noise levels are low and is likely greater in the northern Indian Ocean where shipping traffic and noise levels are high (Wagstaff & Aitkenhead 1979, Širovic et al. 2009).

Have blue whales decreased their call frequencies to compensate for ambient noise increases due to shipping? A lowered fundamental frequency in the band near 20 Hz would not significantly lower the intrinsic attenuation of these acoustic signals, as spreading loss far outweighs signal attenuation at all practical propagation distances (e.g. 0 – 1000 km). Likewise, a change of a few Hz would not substantially shift the blue whale signal relative to ambient noise (McDonald et al. 2006b). A lowered fundamental call frequency is predicted to result in lower blue whale call source levels (as discussed below), counter to the expectation that call source levels would increase to compensate for increased noise. The frequency shift plot looks nearly linear in frequency and time. This is not the relationship to be expected if the animals were shifting away from a linear increase in ambient noise, as it becomes exponentially more difficult to physiologically shift down one Hz as the frequencies become lower (ESM appendix equation 1). A quantitative assessment of the likely non-linear increase in sound source level to compensate for increased masking noise is a complex topic (Gelfand 2004). While ambient noise increase in the world's oceans may be an important factor, it appears not to be the dominant factor, as the expected frequency shift owing to increasing noise would be up rather than down.

Population recovery from whaling. Increasing population size is hypothesized to allow a lowering of song frequency (pitch) while still achieving communication with the same number of conspecifics. This hypothesis can be divided into three parts, the first being that there exists a trade-off between song frequency and sound intensity as derived in the appendix based on the physics of sound production. Physical acoustics argues that a higher song frequency corresponds to potentially higher intensity (louder) songs and greater acoustic propagation distance. The blue whale call source level is argued to be limited by lung volume and vocal tract efficiency. As more source level measurements become available from more song types, the song intensity versus song frequency relationship can be tested.

The second part of this hypothesis is the assumption that changes in population density can be sensed by the animals. One possibility is that population density would be acoustically sensed in terms of the number of other singers the whales hear, allowing the whales to change their song in response. Male blue whales that lived in areas with low population densities at the end of commercial whaling may have needed to sing higher frequency and correspondingly louder songs to adequately communicate in some form of mate competition. During recovery, increasing population size has two likely influences on singing males. First, more males are singing, which potentially increases the intensity of sexual selection and may be driving song lower, and second, there are more whales (both males and females) in the same area which decreases selection on song loudness and corresponding detection range. Lower frequency sounds will be produced at lower intensity and have shorter detection ranges, making this a costly shift in terms of optimizing communication potential (see ESM appendix). With higher population densities, however, selection may not be as intense on males for long distance communication and thus the whales can afford to shift to lower frequencies. Our records of blue whale song begin coincident with the end of commercial whaling, when population densities were dramatically reduced in many parts of the world.

The third and most notional portion of this hypothesis is why blue whales would choose to sing at the lowest frequency possible that still allows sufficient communication range. This may relate to sexual selection (see above), as a lower frequency call is part of the mating strategy for a broad range of species (e.g. Gerhardt & Huber 2002). From the first two parts of the hypothesis above, the change in frequency is related to a change in maximum acoustic source level and therefore distance at which the song can be heard. The distance a song can be heard is then related to the population density of the animals producing that song type. The relative population densities and changes in population densities with time can be theoretically calculated (Table 1). These results are likely confounded by changing ocean ambient noise in ways that are not yet understood. Nonetheless, the relative density and source level calculations in Table 1 appear to coincide with what is known of source level and density differences for whales of each song type (see further discussion in ESM).

Table 1. The theoretical source levels in dB re 1 µPa @ 1 m are calculated for the earliest and most recent data points for each song type and the dB per year change is calculated between these two points. Population density index is derived from the change in area ensonified at equal dB level assuming 17.5 log (range) losses. The percent change in population density index over time is a proxy for population growth rate. Relative density index is referenced to the NE Pacific song type because this source level was used as an arbitrary reference point for the calculations. Potential size differences between populations would contribute second order corrections.

	Observed change		Change in source level (model)	Change/year (model)		Relative density (model)
Region	Year	Frequency	dB	dB	Den. %	%
NE Pac	1960-2008	22.2 to 15.2	188.4-185.3	.067	1.8	100
SW Pac	1964-1998	30.8/25.3 to 25.8/20.1	190.7-188.8	.027	0.8	47
NW Pac	1968-2001	25/23 to 19.45/17.9	187.1-184.9	.066	1.8	126
N Atl	1959-2004	23 to 17.6	196.3-193.9	.053	1.4	11
S Ocean	1995-2005	28.5 to 26.9	196.2-195.7	.050	1.3	7
N Ind	1984-2002	116 to 106	199.8-199.0	.04	1.2	3

SE Ind	1993-2000	19.5 to 19.0	186.9-186.6	4.043	1.2	82

CONCLUSIONS

The demonstrated global trend in blue whale song frequency shift begs explanation. Changing demographics herald changes in the density of whales and the intensity of sexual selection. Coupled with a strong cultural component, we suggest that shifts in song frequency may be related to changes in a density index as these populations recover from commercial whaling, modified by global increases in ambient noise owing to shipping, and trade-offs between short-distance and long-distance communication. Blue whale song frequencies cannot continue to shift downward indefinitely and we suggest that song frequencies will stabilize as the population densities become stable.

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Electronic Supplementary Material for

"Worldwide Decline in Tonal Frequencies of Blue Whale Songs"

by McDonald, Hildebrand and Mesnick

Table 1. Origins of the blue whale song data used in Figures 2 and 3 of article. When data sets were effectively limitless, we chose to measure 10 songs from each of 10 individual whale encounters. We show all call frequency data in an attempt to be complete and unbiased, such that the reader may judge for themselves the significance of any anomalous data, even though these points may be the result of differences in methods when the raw data were not available for this study.

Index #	date	region	calls #	whales #	mean freq. (Hz)	95% confid. (Hz)	references
1	9-08	NE Pac.	100	10	45.5	.21	this study
2	8-07	NE Pac.	100	10	46.0	0.6	this study
3	9-06	NE Pac.	100	10	46.0	1.0	this study
4	9-05	NE Pac.	100	10	46.6	0.1	this study
5	7-03	NE Pac.	89	10	47.0	0.4	this study
6	7-02	NE Pac	97	10	47.9	0.5	this study
7	7-01	NE Pac	85	7	48.0	0.9	this study
8	7-00	NE Pac	100	8	48.7	0.8	this study
9	7-98	NE Pac	63	2	50.5	0.6	this study
10	10-97	NE Pac	88	7	50.5	0.4	McDonald et al. 2001
11	3-97	NE Pac	318	10	50.7	2.4	Stafford et al. 1999
12	7-96	NE Pac	47	5	51.2	0.7	this study
13	6-94	NE Pac	1	1	52.5	--	CNAWC 1994
14	6-93	NE Pac	1	1	52.5	--	pers. comm. Dave Clark
15	9-93	NE Pac	22	3	52.2	1.5	Rivers 1997
16	8-93	NE Pac	295	NA	53.7	2.0	Stafford et al. 1998
17	9-90	NE Pac	25	1	53.1	0.6	McDonald et al. 1995
18	2-87	NE Pac	23	2	53.4	2.8	Thompson et al. 1996
19	7-85	NE Pac	1	1	55.5	--	Jacobson et al. 1987
20	7-80	NE Pac	1	1	57.6	--	Riedesel et al. 1987
21	8-74	NE Pac	40 hr	NA	60.9	--	Morris 1978

22	10-71	NE	25	2	61.4	0.8	Cummings 2002
23	7-63	NE	24	3	65.7	0.5	Cummings 2002
24	12-67	NW Pac.	2	1	25		Northrop et al. 1971
25	1-80	NW Pac.	8	2	23		Thompson & Friedl 1982
26	9-82	NW Pac.	43	1	22		Duennebeir et al. 1987
27	1-93	NW Pac.	39	5	20.2	0.25	McDonald & Fox 1999 & this study
28	1-97	NW Pac.	7	2	20.1	0.29	this study (data near Wake Island)
29	1-01	NW Pac.	26	1	19.45	0.20	this study (data near Hawaii)
30	?-64	SW Pac.	1	1	25.3		Kibblewhite et al. 1967 & Cummings 2002
31	12-97	SW Pac.	20	2	20.0	0.29	McDonald 2006 & this study
32	4-59	N Atl.	many	?	23		Weston & Black 1965
33	?-61	N Atl.	8	1	20.7	0.16	Payne 1977
34	9-79	N Atl.	7	1	18.95		Edds 1982
35	12-93	N Atl.	3816	?	18.4	0.27	Mellinger & Clark 2003
36	6-97	N Atl.	12	1	18.5		Clark & Charif 1998
37	11-00	N Atl.	52	5	18.07	0.12	PMEL data, this study
38	12-02	N Atl.	33	4	17.7	0.22	PMEL data, this study
39	11-04	N Atl.	11	1	17.6	0.08	PMEL data, this study
40	1-95	S Ocean	18	2	28.4	0.12	D. Demer recordings, this study
41	1-97	S Ocean	4	1	28.5		Ljungblad et al. 1998
42	1-99	S Ocean	1	1	28.4		Matsuoka et al. 2000
43	3-01	S Ocean	100	10	27.8	0.16	this study
44	3-02	S Ocean	100	10	27.8	0.29	this study & Širovic et al. 2004
45	2-03	S Ocean	100	10	27.7	0.20	this study
46	12-03	S Ocean	20	5	27.4	0.24	this study
47	4-05	S Ocean	48	5	26.9	0.16	this study
48	4-93	E Indian	6	2	24.25 21.42 18.96	0.37 0.25 0.18	McDonald et al. 2006 & L. Hall pers. comm.
49	2-00	E Indian	235 35 134		23.9 21.1 18.95		McCauley et al. 2001
50	3-84	N Indian	2	?	115.5		archival tape, British Library, J. Gordon
51	4-02	N Indian	1	1	106		this study, data near Diego Garcia

Data Sources: recording methods, media, recording locations, archives & synopsis of related publications

While Table 1 provides a numerical tabulation of the data, a written synopsis of each data source is provided here as referenced to the index numbers in Table 1. Where the data were not available in raw form, some explanation is provided with regard to why the data is considered valid or at least worthy of plotting.

Index numbers 1-9: For the years 2000-2008 offshore Southern California, the data set is practically limitless. We selected 834 blue whale calls categorically assumed to be from 77 different individuals as recorded on digital recorders custom built by Scripps Institution of Oceanography. The digital data is archived at Scripps. The recorders are described in Wiggins (2003) and Wiggins and Hildebrand (2007). All data used were recorded offshore Southern California. Frequency measurement errors are negligible. These 834 calls were selected to provide a statistically valid sample of 10 calls from each of 10 assumed individuals. In some cases fewer than 100 calls were measured because the effort required to access and search more of the archived data was not deemed worth the gain achieved by adding more calls to the statistics for that year. The assumption of the whales recorded on different days in different locations being individuals can be argued statistically as we have good estimates of the population size (~2500), average travel rates (3 km/hr), detection range in this setting (10's of km) and frequency of singing, but it is not a critical assumption to this study. Some of the 77 individuals reported here may be repeat recordings of the same animal but this is not expected to bias the overall trend in frequency shift.

Index numbers 10: These data were collected using sonobuoys recorded by digital audio tape recorders during a cruise between San Francisco and San Diego by MAM. The focus of the cruise was to photo identify blue and humpback whales in waters further offshore than small boats are able to work, thus the sonobuoy deployments were primarily near the continental shelf, spread along the entire San Francisco to San Diego track. A further description of some of these recordings is provided in McDonald et al. (2001). The digital data are archived in the office of the lead author (MAM).

Index number 11: This data point was reported by Stafford et al. (1999) using data recorded on autonomous digital recorders. The anomalously large confidence intervals reported here presumably relate to measuring something other than the midpoint of the B call, though it is not clear from the manuscript how the measurement was made. The data point is included for completeness and to demonstrate that no matter what measurement differences there may have been, this data point does not contradict the overall trend in frequency shift. The raw data are available on the internet at http://www.pmel.noaa.gov/vents/acoustics/ftpfiles/GetTPDbyDays.html (Jan 23, 2009 verified), though the raw data were not used in this study because of the effort required to do so in relation to the relative importance of one more data point for this song type in this year.

Index number 12: These data were collected using sonobuoys recorded by digital audio tape recorders during a series of 3 day cruises between Santa Rosa Island and Santa Barbara California.

The digital data are archived in the office of the lead author (MAM). Frequency errors associated with sonobuoys and digital audio recorders are thought to be negligible.

Index number 13: This report describes blue whale calls recorded off San Diego with sonobuoys and a military aircraft. A spectrogram of a high signal to noise ratio blue whale call is provided. The frequency measurement reported here was measured on the paper copy of the published spectrogram. Status of the original data is unknown.

Index number 14: This raw recording was provided to the authors by Dave Clark of SPAWAR, San Diego from a Navy study related to ship shock testing. The recording is believed to be from a sonobuoy and a military aircraft. A copy is archived in the offices of the lead author (MAM).

Index number 15: This measurement is as reported by Rivers et al. (1997). Status of the original data is unknown. The data point is included for completeness and to demonstrate that no matter what measurement differences there may have been, this data point does not contradict the overall trend in frequency shift.

Index number 16: This measurement is as reported by Stafford et al. (1998). The recordings were made with a dipping hydrophone and digital audio tape recorder over a range of locations off California from 37 degrees north to 38 degrees north (more details in the published paper). The raw data was not available to the authors.

Index number 17: These recordings are described in McDonald et al. (1995) several hundred miles offshore the Oregon coast. Custom built digital recorders were used, thus there is no frequency measurement error. Copies are archived in the offices of the lead author (MAM).

Index number 18: These recordings are described in Thompson et al. (1996) in the Gulf of California with a dipping hydrophone and analog tape recorder. It is unclear why the confidence intervals reported for these frequency measurements are much larger than seen in other data. Status of the original data is unknown.

Index number 19: These recordings are described in Jacobsen et al. (1987) several hundred miles offshore Oregon. Jacobsen recognized these sounds to have been produced by whales, though the species was unclear at this time. The published paper provides waveform displays of the blue whale calls which allowed clear identification and precise frequency measurement of one call, from the image of the waveform. A digital autonomous hydrophone system was used to make the recordings and is expected to have had negligible frequency error. The raw data was only available to the authors in the paper form as published.

Index number 20: These recordings are described in Riedesel et al. (1987) near the southern tip of Baja California. These sounds were only recognized as coming from blue whales after publication of the paper (pers. comm. Mark Riedesel). The instruments used were digital seismographs, expected to have negligible frequency error. The blue whale calls were plotted in the published paper with both spectra and waveform displays which is effectively as good as raw data for the one call published. Status of the original data is unknown.

Index number 21: These recordings are described in Morris (1978) several hundred miles offshore San Diego. A vertical hydrophone array was recorded with commercial analog scientific recorders.

A prominent frequency line corresponding to that known to be from whales was recognized and reported, though the whale species was not recognized in this publication. We now recognized this frequency peak to be very near the midpoint of the B call of the blue whale. In this case, Morris is reporting the average of many blue whale calls. Status of the original data is unknown.

Index number 22-23: These data are in the form of raw analog tapes at the Hubbs Sea World acoustic library, as donated by William Cummings. The recordings were made with various seafloor cabled hydrophones described in a long list of now declassified Navy reports, particularly those by Wenz and by Thompson. For this study we relied entirely on the raw analog data for which each tape contained frequency calibration tones. The frequency corrections applied were on the order of 1 percent based the tones on the tapes. The spectrograms presented by Wenz, Thompson and others in the now declassified reports serve to confirm the frequency measurements made from the raw analog tapes. Each tape contains a voice introduction describing each recording. Copies are archived in the offices of the lead author (MAM).

Index number 24: These recordings are described in Northrop et al. (1971) several hundred miles offshore Midway Island. A cabled hydrophone and analog recorders would have been used. The sounds were recognized as probable whales, though the species was unclear. The paper provides a study of call frequencies, complete with example waveforms. Status of the original data is unknown.

Index number 25: These recordings are described in Thompson & Friedl (1982) off the north coast of Oahu, Hawaii with a cabled hydrophone and analog tape recorders. The frequencies of the blue whale calls are described in the paper along with example spectrograms. Status of the original data is unknown.

Index number 26: These recordings are described in Duennebeir et al. (1987) from a location several hundred miles northeast of Japan. Whale sounds, now recognized as blue whales are well described in the publication and spectra are presented showing the dominant peaks associated with the two whale calls from this song type. Status of the original data is unknown.

Index number 27: These recordings are described in McDonald & Fox 1999 from one of the same hydrophones used by Thompson and Friedl (1982) off the north coast of Oahu, Hawaii. A digital recording system was used and copies of the data are archived in the offices of the lead author (MAM).

Index number 28: These recordings were acquired from the Comprehensive Test Ban Treaty Organization along with the data described in McDonald (2006) from cabled hydrophones as described in McCreery and Duennebier (1993) near Wake Island. These are digitally recorded at 320 samples per second. Copies of the data are archived in the offices of the lead author (MAM). The data is available on the internet at http://www.rdss.info.

Index number 29: These data were digitally recorded on a seafloor recorder (Wiggins 2003) north of the big island of Hawaii. The data are archived at Scripps Institution of Oceanography.

Index number 30: These data are described in Kibblewhite et al. (1967) and raw analog tapes of these recordings are available from the Hubbs Sea World acoustic library, as donated by William Cummings. For this study we relied entirely on the raw analog data, each tape of which contained frequency calibration tones. The frequency corrections applied were on the order of 1 percent based on the tones on the tape. The spectra presented by Kibblewhite serve to confirm the frequency measurements made from the analog tapes. The tape contains a voice introduction describing the recording. Copies are archived in the offices of the lead author (MAM).

Index number 31: These data were acquired from the Comprehensive Test Ban Treaty Organization and are described in McDonald (2006). These data are digital recordings at 160 samples per second from a cabled near seafloor hydrophone. Copies of the data are archived in the offices of the lead author (MAM). These data are available on the internet at http://www.rdss.info.

Index number 32: These data are described in Weston & Black (1965) from the southern Norwegian Sea. The paper provides a thorough description of the sounds now known as North Atlantic type blue whale songs, though at the time these sounds were termed simply whale moans. The frequencies of the multipart songs are described, but no raw waveforms or spectra are presented. There is little description of the tape recorders or analysis systems and the whereabouts of the original data is unknown.

Index number 33: These data are available as a compact disk (Payne 1977), with liner notes providing the only documentation available to us. The blue whale songs are pitch shifted by a factor of 10 to be better heard by human ears, but these are Atlantic blue whale songs from a recording location unknown to us.

Index number 34: These data are described in Edds (1982) as recorded in the St. Lawrence River with analog tape. The frequencies of individual calls are tabulated in the publication. Status of the original data is unknown.

Index number 35: These data are described in Mellinger & Clark (2003), a subset of which is available in raw digital form on CD with an increased playback speed as Clark (1996). The data was recorded on restricted access military hydrophone arrays. The frequency data presented in the published paper is used here.

Index number 36: The report by Clark & Charif (1998) provides a spectrogram of blue whale song recorded on restricted access military hydrophone arrays. The frequency reported here was scaled off that published image. We presume the raw data are not available without special permission and clearances.

Index number 37-39: The raw digital data used is available on the internet at http://www.pmel.noaa.gov/vents/acoustics/ftpfiles/GetTPDbyDays.html (Jan 23, 2009 verified). The recordings are from custom built digital autonomous hydrophones and are further described in Nieukirk et al. (2004).

Index number 40: These recordings were made with sonobuoys and digital audio tape recorders by Dave Demer while working with the Census of Antarctic Marine Life project near Elephant Island Antarctica. The original audio tapes were made available to the lead author (MAM) and copies of these data are archived in the offices of MAM.

Index number 41: These data were measured from the published spectrograms in Ljungblad et al. (1998). The data were recorded with sonobuoys and digital audio tape. The archival status of the original data is unknown to us.

Index number 42: This frequency measurement was taken from the image of the spectrogram in Matsuoka et al. (2000). The recording was made with an autonomous digital hydrophone system. The archival status of the original data is unknown.

Index number 43-47: These data were recorded on autonomous digital systems as described by Wiggins (2003). Publications which further describe these data include Širovic et al. (2004), Širovic et al. (2007) and Širovic et al. (2009). These data are archived at Scripps Institution of Oceanography.

Index number 48: These data were recorded on a military towed array in the Timor Sea and provided to the authors by Lindsey Hall, then of the New Zealand Defence Research Establishment. The recordings are further described in McDonald et al. (2006). The data are archived in the offices of the lead author (MAM).

Index number 49: The report by McCauley et al. (2001) provides spectrogram examples of blue whale songs for which the frequencies were picked from the paper prints. McCauley & Salgado have also provided a digital example of a high SNR blue whale song. The recordings were made with custom built digital recorders and are presumed to be archived at Curtin University.

Index number 50: These recordings are from an archival tape contributed to the British Library by Jonathan Gordon. These are believed to have been made with a dipping hydrophone and an analog tape recorder near Trincomalee, Sri Lanka. A digital copy was obtained directly from the British Library for this study.

Index number 51: These data were recorded by the Comprehensive Test Ban Treaty Organization near Diego Garcia and are available on the internet at http://www.rdss.info
Note that only the earliest few years of data are available without a password, while the later data are being held confidential except to researchers of the nation within which it was collected and/or by special permission. The data are all from cabled hydrophones and digital recorders.

Population recovery from whaling: assumptions, calculations and tests

Assumptions used in calculating relative population density and change in density:

(a) Although songs occur year around, there is some direct relationship between singing and breeding success, where all singers in a population must sing the same song at the same pitch to be successful. Singing at high source level may be a means for male blue whales to demonstrate fitness for breeding

(b) Male blue whales that live in areas with lower population densities sing louder songs. This could be in order to be heard by a greater number of animals or to be better heard in some form of mate competition.

Producing a blue whale call (song phrase) may require nearly all of the whale's total respiratory volume (Aroyan *et al.*, 2000), with the lowest or fundamental frequency requiring more than 90 percent of the air volume (McDonald *et al.*, 2001). The frequency of the most demanding call and the maximum possible sound pressure level are directly related. Given that song frequency is fixed within any given singing season for each song type, whales with greater air volume (larger whales) will potentially be heard at greater distance and be louder at lesser distances.

While sound intensity allows calculation of maximum communication range; loudness, a measure of hearing perception, is typically not linearly related. It is unclear whether loudness or maximum communication range is more relevant, but maximum communication range is certainly the more easily calculated. To achieve lower (more desirable?) frequencies, the physical constraints of fixed lung volume force blue whales into a trade-off with sound intensity. However, because populations are growing, these whales may still be reaching the same or even a greater number of individuals (Figure 1).

From this rate of frequency shift, a population density increase or population growth rate within some geographic region where song is most important could theoretically be calculated, except for the confounding effect of increasing ocean noise. The calculations follow:

1. Assuming a typical propagation loss, call frequency (f) is related to change in ensonified area, a proxy for change in population density (ΔD) by equation 1, which is derived in the appendix.

$$\Delta f = \left(\frac{1}{\Delta D} \right)^{0.4375} \qquad \text{(eq. 1)}$$

2. The pitch shift calculation

The Hz/year shifts for each song type are translated to an index of population density increases (Table 1), ignoring small corrections for differences in acoustic propagation. Acoustic propagation between near surface whales is expected to be good at high latitudes due to the surface sound channel, good at low latitudes due to the surface sound duct and poorer at temperate latitudes due to a downward refracting environment (Urick 1983). In the Antarctic, Širovic et al. (2007) found losses to be 17.8* log (range). Acoustic absorption is negligible at these distances (0-1000 km) and frequencies (15-150 Hz). The relevant ranges are those at which a listener might practically swim to the caller in a reasonable time, rather than the maximum distance at which a call could be detected in ideal conditions.

3. Predictions of population density based on source levels

The four factors which set the maximum source level of sound which a blue whale can produce throughout a continuous tonal call are 1) call duration (seconds), 2) fundamental frequency (Hz) of the longest duration tonal song phrase, 3) lung volume and 4) resonance factor. We assume a fixed combined lung volume and resonance factor based on 186 dB re 1 μPa @ 1 m source level for the California blue whale calls in 1997 (McDonald et al. 2001) for all blue whales worldwide. The lung volume/resonance factor can be treated as a percentage of lung volume. Given this lung volume/resonance factor, the call duration and call frequency determine the theoretical maximum call source level. Potential differences in lung volume based on average size differences between whale populations may provide a second order correction (Branch *et al*. 2007).

Given the sound production capacity we can predict with the theoretical model what the maximum call source level should be for seven of the nine song types which have been observed worldwide. Our definition of a continuous tonal call for the purpose of this calculation means the whale would not have time between calls to re-circulate the air, a different definition than may be used when dividing blue whale song into units. When two frequencies are present as two continuous phrases in the call we use the weighted mean frequency for the calculation. We apply our calculation to the fundamental tonal frequency when harmonics are present.

Testing the model

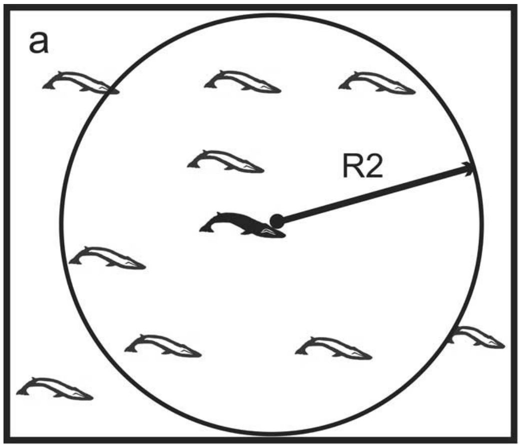
The proposed model could be tested and/or modified by future studies which correlate blue whale song acoustic source level maximum with fundamental song frequency. Maximum blue whale song source level and call frequency are expected to be directly related while lower call frequencies are expected to correlate to higher population densities. Direct measures of call source levels are uncommon, (Cummings and Thompson 1971; McDonald *et al*. 2001; Širovic *et al*. 2007) and care should be taken with such correlations as not every song a whale produces must be at the maximum level possible. For instance, limited data suggests males in male/female pairs sing at a lower source level than single traveling males (Thode *et al*. 2000; Oleson 2005). Antarctic blue whale song maximum sound pressure levels have been measured near 195 dB at 27 Hz (Širovic *et al*. 2007) while Eastern North Pacific blue whale song has been measured at a maximum level near 186 dB at 16.8 Hz (McDonald *et al*. 2001), consistent with the model presented here, both in the frequency-source level correlation and in the relative density index correlation.

Some of the best known blue whale densities are in the northeast Pacific and the Antarctic (Calambokidis & Barlow 2004; Branch *et al*. 2004). The Eastern North Pacific density during the summer is approximately 2500 animals per 2,000,000 km^2 or 1.25 animals/ 1000 km^2 and in the Antarctic, during the summer, is approximately 1900 animals per 20,000,000 km^2 or 0.1 animals/ 1000 km^2, close to the predicted relative densities calculated from song frequencies (Table in article). A review of worldwide blue whale densities and seasonal variability is beyond the scope of this study and differences in site-specific background noise levels and average lung volume differences in the whale populations could be applied as correction factors.

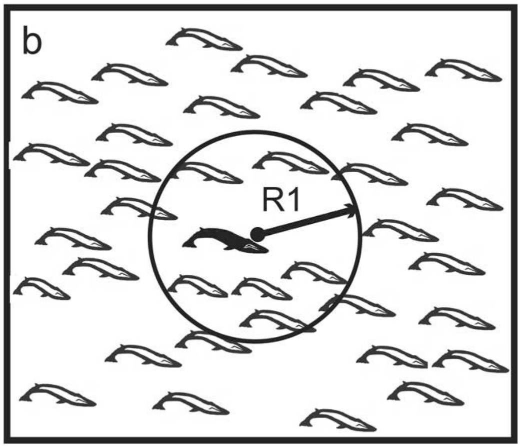
Another test of the proposed hypothesis would be to compare computed relative growth rates from the hypothesis for each song type with growth rates estimated from demographic models. Initial analyses show that the growth rates calculated here are in the same direction and are similar to, but lower than the more or less five percent growth rates anticipated from blue whale biology models (Branch *et al*. 2004). The difference may be because of increases in ambient noise worldwide. Masking noise from increased commercial shipping is expected to result in blue whale songs needing to have higher source levels to be detected by the same number of conspecifics, a topic which needs further development before making quantitative predictions of the ambient noise change effect.

Lastly, analysis of yet-to-be discovered historical recordings of blue whale song may provide additional data points for comparison with our recordings. Additional early recordings of blue whale song in the Antarctic and elsewhere may enable determination of whether the turning point of the song frequency shift corresponds with the end of whaling.

At least one other species, the three wattled bellbird, is known to have a long term linear downward shift in its song frequency and is known to be decreasing in abundance (Kroodsma 2005). This is the opposite trend, however; given the jungle environment and the frequencies involved, frequency dependent attenuation may be the dominant factor in how far the song can be heard, where lower frequencies are being heard further. While the calculations for this species will be different, the concept may still be applicable.



end of whaling, low density



recovery, high density

Figure 1. As the number of whales increases after the cessation of commercial whaling, the intensity of selection on the various aspects of song may change. When whales were scarce, a higher sound pressure level song is received over a larger radius (a). As the number of whales increases, a lower sound pressure level song at lower frequency is associated with a smaller radius (b)

Table 2. The theoretical source levels in dB re 1 μPa @ 1 m are calculated for the earliest and most recent data points for each song type and the dB per year change is calculated between these two points. Population density index is derived from the change in area ensonified at equal dB level assuming 17.5 log (range) losses. The percent change in population density index over time is a proxy for population growth rate. Relative density index is referenced to the NE Pacific song type because this source level was used as a basis for the calculations.

SONG TYPE	DURATION	INITIAL			FINAL			CHANGE / YEAR		RELATIVE DENSITY
REGIO	SECOND	YEA	FREQ	dB	YEAR	FREQ	dB	dB	DENSITY	%

N	S	R	.			.			%	
NE Pac.	19	1960	22.2	188.4	2003	15.9	185.5	.067	1.8	100
SW Pac.	6+12	1964	30.8/25.3	190.7	1998	25.8/20.1	188.8	.027	0.8	47
NW Pac.	12+12	1968	25/23	187.1	2001	19.45/17.9	184.9	.066	1.8	126
N Atl.	8	1959	23	196.3	2004	17.6	193.9	.053	1.4	11
S Ocean	10	1995	28.5	196.2	2005	26.9	195.7	.050	1.3	7
N Ind.	27	1984	116	199.8	2002	106	199.0	.044	1.2	3
SE Ind.	20	1993	19.5	186.9	2000	19.0	186.6	.043	1.2	82

Appendix

Derivation of relationship between call frequency and source level

Assuming a call of fixed duration, the call frequency (f) and sound pressure level at the source (P_o) are limited by the animals' respiratory system volume (V) as follows:

$$V = \frac{P_o}{\rho\pi(f)^2} \qquad \text{(eq. 1)}$$

where, ρ is the density of seawater (Aroyan *et al.*, 2000).

For a fixed respiratory volume, call sound pressure level is increased by increasing the call frequency. Call sound pressure level is physically related to the range at which these calls will be detected by conspecifics. The number of animals which can hear the song, N can be calculated as:

$$N = \pi(r)^2 D \qquad \text{(eq. 2)}$$

where r is the range at which the song can be heard and D is population density index of the animals. The received sound pressure level of the song, P_R declines with range per equation 3

$$P_R = \frac{P_0}{r^{1.75}} \qquad \text{(eq. 3)}$$

The propagation loss coefficient used here (1.75) is an approximation which will vary geographically. Combining equations 1 through 3, eliminating the constants, the relationship between change in frequency and change in population density is:

$$\Delta f = \left(\left(\left(\frac{1}{\Delta D} \right)^{\frac{1}{2}} \right)^{1.75} \right)^{\frac{1}{2}} = \left(\frac{1}{\Delta D} \right)^{0.4375} \qquad \text{(eq. 4)}$$

Equation 4 is used to calculate the change in area per year over which a blue whale call could be heard, given the shift in frequency per year.

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