

1 **Two unit analysis of Sri Lankan pygmy blue whale song over a decade**

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18 **ABSTRACT**

19 Sri Lankan pygmy blue whale song consists of three repeated units: 1) low frequency pulsive  
20 unit, 2) frequency modulated (FM) upsweep, and 3) long tonal downsweep. The Unit 2 FM unit  
21 has up to three visible upsweeps with energy concentrated at approximately 40 Hz, 50 Hz, and  
22 60 Hz, while the Unit 3 (~100 Hz) tonal downsweep is the most distinct unit lasting 20-30 sec.  
23 Spectral characteristics of the Unit 2 and Unit 3 song elements, along with ocean sound levels,  
24 were analyzed in the Indian Ocean from 2002-2013. The peak frequency of the tonal Unit 3 calls  
25 decreased from approximately 106.5 Hz to 100.7 Hz over a decade corresponding to a 5.4%  
26 decrease. Over the same time period, the frequency content of the Unit 2 upsweeps did not  
27 change as dramatically with only a 3.1% change. Ambient sound levels in the vocalization  
28 bands did not exhibit equivalent patterns in amplitude trends. Analysis showed no increase in  
29 the ambient sound or compensated peak amplitude levels of the tonal downsweeps, eliminating  
30 the presence of a Lombard effect. Here it's proposed that each song unit may convey different  
31 information and thus may be responding to different selective pressures.

32

33 **KEY WORDS**

34 Sri Lankan pygmy blue whale, song, ambient sound, selection

35

36 **I. INTRODUCTION**

37 Animal songs are relatively complex, often species-specific signals that are given in the  
38 context of intra- or intersexual selection (Tyack, 2000; Beecher and Brenowitz, 2005). Different  
39 song types in a repeated display are often seen as parts of the overall display giving an indication  
40 of a singer's fitness. However, many song types consist of more than one unit, each of which can  
41 have a different function. For example, European starlings (Eens *et al.*, 1993) and greater white-  
42 lined bats (Davidson and Wilkinson, 2004) have more tonal units in their songs when singing to  
43 females than when singing to males. In chaffinches, the end flourish of songs is more important  
44 for mate attraction (Riebel and Slater, 1998) while the trill functions in competition between  
45 males (Leitao and Riebel, 2003). In canaries, females only show a copulation solicitation display  
46 to so called 'sexy syllables', which have a more complex structure than other units of the song  
47 (Vallet and Kreutzer, 1995). When units have different functions as illustrated above, changes in  
48 unit structure over time are often not the same among units because the selection pressures  
49 driving change or maintaining stability can be different (Janik and Slater, 2003). Such changes  
50 can therefore be used as an indicator of functional diversity in units.

51 Multiple species of baleen whales produce song. Whale song ranges from simple  
52 repeated single units as observed in fin whales (Watkins *et al.*, 1987) to more complex,  
53 hierarchical song structure as observed in humpback song (Payne and McVay, 1971; Winn and  
54 Winn, 1978). Blue whale song is of intermediate complexity and typically thought to be  
55 produced by males (Oleson *et al.*, 2007). The exact behavioral function of any baleen whale  
56 song remains unknown, but it is generally agreed that song functions in both intra- and  
57 intersexual selection within the context of mating (Tyack, 2000).

58 Blue whale song structure also provides information useful for characterizing population  
59 distribution and delineation worldwide. Song is a reliable population identifier because the song  
60 structure has shown to be stable over decades for many populations (McDonald *et al.*, 2009).  
61 Where traditional genetics, morphology, and osteology studies have not succeeded in producing  
62 a clear picture of blue whale population structure, song is a reliable population identifier that  
63 appears to be stable over time and has provided another indicator of structure and behavioral  
64 grouping. Yet, the internal characteristics of the song units themselves have not been stable over  
65 time. There has been a worldwide decline in the tonal frequencies of portions of blue whale  
66 songs for at least 7 different populations across all oceans (McDonald *et al.*, 2009; Gavrilov *et*  
67 *al.*, 2011, 2012). McDonald *et al.* (2009) described a decrease in the most salient unit of the Sri  
68 Lankan pygmy blue whale song from 116 Hz in 1984 to 106 Hz in 2002. The theories posed in  
69 an effort to explain the observed worldwide decrease in tonal song components included: cultural  
70 conformity and directional synchrony, response to changing environmental sound levels,  
71 increasing body size post whaling, changing ocean sound absorption and propagation related to  
72 global warming, post whaling abundance increases, sexual selection, and biological interference;  
73 however, none of the proposed hypotheses fully explained the observed trends (McDonald *et al.*,  
74 2009; Gavrilov *et al.*, 2011).

75 Sri Lanka pygmy blue whales are vocally and biogeographically distinct from other  
76 pygmy blue whale and true blue whale subpopulations in that they are largely resident in the  
77 northern Indian Ocean and appear to constitute a unique acoustic population (Alling *et al.*, 1991;  
78 McDonald *et al.*, 2006; Stafford *et al.*, 2011; Samaran *et al.*, 2013). Stereotyped and repeated  
79 phrases of Sri Lankan pygmy blue whale song consist of three components: 1) a low frequency  
80 pulsive unit, 2) a frequency modulated (FM) upsweep unit, and 3) a long tonal downsweep unit

81 (Figure 1). Energy in the pulsive Unit 1 component peaks at approximately 30 Hz and can often  
82 not be reliably detected above the background noise. The Unit 2 FM component has up to three  
83 visible upsweeps with energy concentrated at approximately 40 Hz, 50 Hz, and 60 Hz. The Unit  
84 3 (~100 Hz) tonal downsweep is the most distinct of the call units and lasts 20-30 sec. This  
85 salient Unit 3 song component has been used in previous studies as an indicator of whale  
86 presence to gain a better understanding of the Sri Lanka pygmy blue whale distribution and  
87 behavioral ecology (e.g. Samaran *et al.*, 2013). Year-round acoustic presence of the Sri Lanka  
88 pygmy blue whale in the northern Indian Ocean, as indicated by the detection of the Unit 3  
89 component, has been observed in recordings from the island of Diego Garcia (north and south)  
90 and to the northeast of Amsterdam Island (Stafford *et al.*, 2011; Samaran *et al.*, 2013).

91 In this study, we investigated multiple Sri Lankan song units in two dimensions: time and  
92 frequency structure. We simultaneously consider Unit 2 and Unit 3, as opposed to the one most  
93 salient unit (Unit 3) assessed in previous studies, to allow us to look for differential changes in  
94 elements. Unit 1 was not included in this analysis because it was not consistently visible above  
95 the background noise. We hypothesize that if different units of blue whale song have different  
96 functions, we could expect divergent changes in units over time related to different selection  
97 pressures.

98

## 99 **II. METHODS**

100 A decade of data (2002-2013) from the Indian Ocean Comprehensive Nuclear-Test-Ban  
101 Treaty International Monitoring Station (CTBTO IMS) at Diego Garcia (6.3421 S, 71.0143 E)  
102 was accessed from the AFTAC/US NDC (Air Force Tactical Applications Center/US National  
103 Data Center) and analyzed to detect Sri Lankan pygmy blue whale vocalizations. The Diego

104 Garcia CTBTO IMS (H08) consists of a triad of hydrophones deployed on each side of the island  
105 and positioned in the deep sound channel. All data in this study were recorded off the north side  
106 of the island from hydrophone N1 which was at a depth of 1248 m. Data were sampled  
107 continuously at a 250 Hz sampling rate and 24 bit A/D resolution. The hydrophones were  
108 calibrated individually prior to initial deployment in January 2002 and re-calibrated while at-sea  
109 in 2011, and there was no measured change in hydrophone sensitivity during the re-calibration of  
110 the H08 N1 hydrophone. Hydrophone H08 N1 had a flat (3 dB) frequency response from 8-100  
111 Hz. Information from individual hydrophone response curves was applied to the data to obtain  
112 absolute values over the full frequency spectrum (5-115 Hz). Data less than 5 Hz and from 115-  
113 125 Hz were not used due to the steep frequency response roll-off at these frequencies.

114         Phrase Units 2 and 3 (Figure 1) were selected for analysis in this study, as these were the  
115 most salient signals consistently recorded at high amplitude and visible above the ambient sound.  
116 The maximum estimated range of signal detection for the peak frequencies of the two analyzed  
117 units from Diego Garcia North was 600-1000 km depending on frequency and bearing. Seasonal  
118 transmission loss was modelled along 360 bearings at 1° resolution using the OASIS Peregrine  
119 parabolic equation model for a receiver in the deep sound channel and a source position  
120 extending over the upper 300 m of the water column to determine the maximum estimated range  
121 of signal detection along each bearing (Miksis-Olds *et al.*, 2015). The estimated range of signal  
122 detection in this region is significantly greater than the 50-150 km range estimated by Širović *et*  
123 *al.* (2009) and Samaran *et al.* (2010) required for individual signal classification of pygmy blue  
124 whale calls off Antarctica and Crozet Islands, respectively, but it is consistent with blue whale  
125 song detection reported by Stafford *et al.* (1998) in the northeast Pacific Ocean and by Harris  
126 (2012) in the Indian Ocean. The dominant factor influencing the propagation loss associated

127 with estimated detection range north of Diego Garcia in this study was bathymetry (Miksis-Olds  
128 et al., 2015) and is also likely to be the factor limiting detection range in the other referenced  
129 studies.

130 Spectral characteristics of the ~ 100 Hz tonal downsweep (Unit 3) and the 60 Hz FM  
131 upsweep (Unit 2), along with long-term patterns of ambient ocean sound, were assessed from  
132 weekly plots of average power spectral density (PSD). Weekly average PSDs were used instead  
133 of measuring characteristics from individual calls to reduce the effect of short-term variations  
134 due to the differences in call characteristics of each whale and are reflective of the characteristics  
135 of the regional population. This methodology is consistent with the analysis methods of  
136 Gavrilov *et al.* (2012) that documented the steady decrease in vocalization frequency of  
137 Antarctic blue whales. Weekly average PSD was calculated to identify frequency peaks and  
138 peak sound pressure levels within targeted frequency bands associated with the calling  
139 population of Sri Lankan pygmy blue whales at approximately 110-100 Hz and 57-63 Hz (Figure  
140 2). A 3 dB signal-to-noise threshold was implemented within the targeted bands of each unit to  
141 identify whale presence and vocal contribution above the background sound. PSD was  
142 computed for each 2 hour period with a 15000-point DFT and Hanning window with no overlap,  
143 corresponding to an approximate resolution of 0.02 Hz, and averaged over each week.

144 PSD of ambient ocean sound was averaged weekly over the targeted 7-Hz frequency  
145 bands of 100-107 Hz for the tonal Unit 3 component and analogous 56-63 Hz band for the Unit 2  
146 component to capture the full band of whale calls over the decade. Weekly average PSD was  
147 also computed in adjacent 93-100 Hz and 107-114 Hz bands around Unit 3 and 49-56 Hz and 63-  
148 70 Hz bands around Unit 2 where there were no contributions from whales. A second-order  
149 polynomial curve created from points in the adjacent sound bands that did not contain whale call

150 energy was fit to the two targeted bands of the weekly average PSD that contained the peak in  
151 whale calling. A polynomial fit allowed a more accurate estimation of ambient sound without  
152 whale contributions because the sound pressure level was not flat across the frequency range  
153 (Figure 2). The spectral level of ambient sound at the peak calling frequency was interpolated  
154 from the fitted curve and is representative of the sound level with no whale contributions. To  
155 determine the contribution of sound in the targeted bands from whales alone for each of the song  
156 units, the peak level of the weekly average PSD was corrected or compensated for the PSD of  
157 ambient sound from the fitted sound level estimate. Recording periods saturated with natural  
158 seismic signals from underwater earthquakes were excluded from this analysis. The full  
159 spectrum sound levels including the natural seismic signals (5-115 Hz) were computed as part of  
160 a previous study (Miksis-Olds *et al.*, 2013).

161 Frequency peaks from the weekly PSD estimates from Weeks 21 and 22 for each year  
162 and both units were included in a linear regression analysis conducted in R software vs. 3.3.1 (R  
163 Core Team, 2016) Frequency was the response variable, and year and unit were included as  
164 explanatory variables (unit was included as a factor). An interaction term between year and unit  
165 was included as part of model selection, conducted using an F-test, to investigate whether the  
166 rate of frequency change significantly differed between the two units. Model fit was visually  
167 assessed using a quantile–quantile (Q-Q) plot. Model assumptions of linearity, constant error  
168 variance, error independence and normality were tested in R software through diagnostic plots  
169 and relevant hypothesis tests. Linear regression analyses were also used to assess any trends in  
170 the noise level measurements. Two models were fitted: one using the weekly average PSD levels  
171 and the other using the compensated (whale-only) peak PSD levels. In each model, PSD level  
172 was the response variable, and year and frequency band (56-63 Hz and 100-107 Hz) were



173 included as explanatory variables (frequency band was included as a factor). Data from Weeks  
174 21 and 22 only were used to be consistent with the frequency analyses. Model fit and  
175 assumptions were tested in the same way as the frequency analyses.

176

### 177 **III. RESULTS**

178 Sri Lankan pygmy blue whale vocal presence, as detected from peaks in the weekly  
179 averaged PSDs, was seasonal (Figure 3). The week of peak calling activity was variable within a  
180 year across the decade and likely related to oceanographic variability driving whale distribution  
181 (Branch *et al.*, 2007a; Stafford *et al.*, 2011). Vocal activity was detected nearly year round at  
182 this location. Peak periods of vocal activity (based on the number of hours per week with calls  
183 present) averaged over the decade occurred during Weeks 21 and 22 corresponding to the  
184 months of May-June in the austral fall.

185 Annual rate of decrease of both units was estimated from the regression analysis using  
186 the average peak frequencies in Weeks 21 and 22 from 2002-2012 to reflect the measured shift  
187 during the peak in vocal activity. The QQ plot (not included here) suggested an adequate model  
188 fit and all model assumptions were met.

189 The peak frequency of both units of the Sri Lankan pygmy blue whale call significantly  
190 decreased across years ( $F_{1,36} = 395.69$ ,  $p < 0.001$ ). Unit 3 tonal calls peak frequencies measured  
191 in Weeks 21 and 22 decreased from 106.5 Hz to 100.7 Hz over a decade corresponding to a 0.54  
192 Hz/year rate of decrease (Figures 4, 5, 6). This is an approximate 13% decrease from 1984 when  
193 the peak frequency was reported at 115.5 Hz (McDonald *et al.*, 2009), and a 5.4% decrease over  
194 the past decade. Over the same time period, the frequency content of the ~ 60 Hz Unit 2 FM  
195 upsweeps measured in Weeks 21 and 22 did not change as dramatically. The regression model

196 predicted a 0.18 Hz/year rate of decrease (Figures 4, 5, 6) corresponding to only an approximate  
197 3.1% decrease over the past decade. The interaction term between year and unit was selected in  
198 the model ( $F_{1,36} = 92.66$ ,  $p < 0.001$ ), indicating that the rates of frequency change across years  
199 differed significantly between the two units. A series of simple linear regressions showed a  
200 weak within-season trend in the Unit 3 call with six of the eleven seasons having a significant  
201 progressive decrease at the 95% significance level in tonal frequency over one annual season  
202 (Figure 7). However, with the application of the Bonferroni correction for multiple tests ( $n=11$ ),  
203 (applying a significance level of  $0.0045 = 0.05/11$ ), the only significant seasonal trend was  
204 observed in 2005 (Figure 7).

205 Both weekly noise level measurements displayed a visible seasonal trend in the two  
206 targeted frequency bands (56-63 Hz and 100-107 Hz) associated with the migratory presence of  
207 vocalizing whales (Figure 8). The frequency decrease observed in the whale call units over the  
208 decade did not appear to be related to increasing ambient sound. The linear regression models  
209 fitted to the Week 21 and 22 data had adequate fit and the model assumptions were met. The  
210 average spectrum level in both frequency bands actually showed a decreasing annual trend over  
211 the same decadal time period ( $F_{1,41} = 10.238$ ,  $p = 0.003$ ) (Figure 8a-b), which is consistent with  
212 decadal trends over similar frequencies in particular percentiles (Miksis-Olds *et al.*, 2013). The  
213 maximum spectrum level reflecting the seasonal whale contribution to the ambient sound  
214 showed no significant decadal trend ( $F_{1,41} = 0.1664$ ,  $p = 0.685$ ) (Figure 8c-d).

215

#### 216 **IV. DISCUSSION**

217 In this ten-year dataset from Diego Garcia, the Sri Lankan blue whale song was a  
218 prominent feature of the soundscape. Analysis of weekly PSDs revealed calling nearly year-

219 round, peaking in the austral fall (May-June). The advantage of the analysis approach used in  
220 this study is that the frequency parameters obtained from weekly PSDs in the annual analysis  
221 reflect the vocal activity of the subpopulation as a whole, as opposed to measured call  
222 characteristics from individual whales assuming that the weekly PSD peak is not the result of a  
223 single singing whale. This eliminated the need for extrapolation of information from individual  
224 singers, which can be age-, sex-, and reproductive status-dependent and related to segregation in  
225 migration of the general subpopulation (Craig *et al.*, 2003; Stevick *et al.*, 2003). We analyzed  
226 two units in the blue whale song and found that the previously reported frequency decrease over  
227 time occurs more strongly in the Unit 3 call compared to the Unit 2 call. The Unit 2, ~60 Hz  
228 component of the call is more stable over time than Unit 3 at ~100 Hz, showing that the reported  
229 decrease in peak frequency in blue whale song does not affect the entire song uniformly.

230         The timing of singing and the fact that documented baleen whale singers are males  
231 implies that at least parts of song are a mating display (Tyack, 2000). The seasonal peak of Sri  
232 Lankan pygmy blue whale vocal activity occurs at Diego Garcia between April and June  
233 (Stafford *et al.*, 2011; Samaran *et al.*, 2013, this study), which corresponds to the subpopulation's  
234 breeding cycle. Although the distribution of the Sri Lankan population extends widely into the  
235 southern hemisphere, their reproductive cycle is offset from other southern Indian Ocean  
236 populations by six months, aligning with a northern hemisphere breeding cycle (Mikhalev, 2000;  
237 Branch *et al.*, 2007b). In addition, in other populations it is blue whale males that produce song  
238 (McDonald *et al.*, 2001; Oleson *et al.*, 2007) and peak song production by Sri Lankan pygmy  
239 blue whales occurs during the breeding season; it logically follows that song is connected to  
240 reproductive behavior as is proposed for other baleen whale species such as humpback whales  
241 (reviewed in Herman, 2017) and fin whales (Croll *et al.*, 2002; Oleson *et al.*, 2014).

242           The most salient feature of this multi-part blue whale song is Unit 3, the long, ~ 100Hz  
243 tonal downsweep. Like McDonald *et al.* (2009), who reported a 10 Hz decrease between 1984  
244 and 2002 (Table 1 in McDonald *et al.*, (2009)) we also observed a gradual, almost linear  
245 decrease in the frequency of this sound, from 106.5 Hz in 2002 to 100.7 Hz in 2012, or about  
246 0.54 Hz/yr. Unlike other studies examining blue whale calls (e.g. Gavrilov *et al.*, 2012) we did  
247 not observe any significant “resetting” of the Unit 3 frequency each year. Unit 2 of the song  
248 showed a less dramatic change in frequency over time, potentially making this unit a more  
249 stable, attractive cue for passive acoustic monitoring applications such as density estimation.

250           Many interesting theories about the mechanism driving this continual frequency decrease  
251 of blue whale song units have been proposed (McDonald *et al.*, 2009). Changes in the physical  
252 and chemical properties of the ocean over time or changes in calling depth hardly affect  
253 frequency parameters and can therefore be excluded as possible explanations. Frequency  
254 changes to compensate for noise from an anthropogenic source has been observed in other  
255 species, but the expected frequency shift in response to increasing ocean noise would be an  
256 increase in tonal frequency (McDonald *et al.*, 2009), as observed in belugas (Lesage *et al.*, 1999)  
257 and right whales (Parks *et al.*, 2007), rather than a decrease, as observed in blue whale  
258 populations. Furthermore, we did not observe an increasing trend in weekly sound pressure  
259 levels in blue whale vocalization bands, indicating background noise levels did not increase  
260 significantly over the course of this decadal study and did not contribute to a Lombard effect (see  
261 also Miksis-Olds *et al.*, 2013; Hotchkyn and Parks, 2013). Potential biological interference or  
262 masking from other vocalizing marine mammals in the frequency range below 100 Hz is  
263 predominantly restricted to other baleen whale species. In the Indian Ocean, this would include  
264 vocalizations from fin, humpback, Bryde’s, sei, and other blue whale subpopulations (i.e.

265 Antarctic, Madagascar, Australian) (McDonald *et al.*, 2006, 2009; Ballance and Pitman, 1998;  
266 Best *et al.*, 1998). At the Diego Garcia location over the time period examined, there were no  
267 other whale calls detected that overlapped the Sri Lankan Unit 3 song component. Hence,  
268 biological and anthropogenic noise is not a viable explanation for the observed frequency shift in  
269 this subpopulation.

270 Increase in blue whale body size post whaling has also been suggested as a source of  
271 decadal frequency decrease because body size sets the lower limit of the frequency of sound  
272 production (Bradbury and Vehrencamp, 1998). Accurate historical records of blue whale body  
273 size are difficult to obtain due to lack of measurement standards and deliberate misreporting of  
274 species during commercial whaling (Best, 1989; Branch *et al.*, 2007c). McDonald *et al.* (2009)  
275 hypothesized that present day body size distributions of blue whales have returned to pre-  
276 whaling values based on the rationale that blue whales reach sexual maturity and have 95% of  
277 their mature body weight at 8 yrs (Lockyer, 1984). If we assume that the present day blue whale  
278 body size distribution has remained stable at pre-whaling levels while tonal frequencies of song  
279 components continue to decrease, an increase in whale body size post-whaling driving the  
280 observed frequency shift is not supported. Sexual selection has also been eliminated as a  
281 potential driver of song frequency decrease within blue whale populations as the change we are  
282 observing is too fast for genetic sexual selection. McDonald *et al.* (2009) felt the most plausible  
283 explanation for the decline in tonal frequencies of blue whale song was that of increasing  
284 population size post whaling contributing to a sexually selected tradeoff for singing males  
285 between amplitude and frequency. This explanation might be expected to apply equally to all  
286 song units, which is not case here with different rates of change. Additionally, to date there is no  
287 definitive evidence of decreased amplitude of blue whale calls (Gavrilov *et al.*, 2011), but the

288 acoustic technology in ocean observing systems is evolving and may allow us to fully investigate  
289 this theory in the future.

290         Given the data currently available, what new can we say about this tonal frequency  
291 decrease of blue whale vocalizations? The analysis of two stereotyped blue whale song units in  
292 this study, compared to the single unit analyses of previous studies (McDonald *et al.*, 2009;  
293 Gavrilov *et al.*, 2011), provides additional information critical to developing a plausible theory  
294 explaining the mechanistic driver behind the observed trend; however, it should be noted that it  
295 is unknown whether the observed tonal decreases are detectable or significant to the blue whales,  
296 because so little is known about the hearing capabilities of this species. Because Unit 2 and Unit  
297 3 are changing differently over time, it is possible that different units of blue whale song,  
298 particularly Sri Lankan song, might serve different functions and carry different information.  
299 Songs or calls of numerous species have multiple parts that apparently serve different functions  
300 and change differently over time (Janik and Slater, 2003). In killer whales (*Orcinus orca*),  
301 biphonic and monophonic calls vary in diversity and are thought to convey different information  
302 such as group and individual identification (Filatova *et al.*, 2012). In white crowned sparrows  
303 (*Zonotrichia leucoophrys*), the trill, which encodes dialect identity, changes faster than other  
304 units of the song (Nelson *et al.*, 2004). Riebel and Slater (1998) found that the end flourish in  
305 chaffinch (*Fringilla coelebs*) song is the part that attracts the females, and hypothesize that the  
306 start of the song gives different information, and both parts would therefore be subject to  
307 different kinds of selection pressures. The Savannah sparrow (*Passerculus sandwichensis*) has a  
308 relatively simple four-part song with segments that convey different information. During a 30-  
309 year study, the introductory notes and buzz segments of Savannah sparrow song changed little  
310 over time and are believed to identify the species. The middle segment was quite variable and

311 might distinguish individuals. The fourth segment, the terminal trill, decreased in both. Each  
312 segment is therefore likely to communicate different types of information (Williams *et al.*, 2013).

313         Perhaps Unit 2, the more stable portion of the Sri Lankan blue whale song, conveys  
314 information such as species identification or draws attention to the caller before it produces Unit  
315 3 thereby priming listeners to pay attention. The reduced rate of change in Unit 2 in the Sri  
316 Lankan population reinforces the fact that simplistic explanations such as change in body size  
317 may not be the sole explanation for the song frequency decrease. The observed differential  
318 frequency shift of the Unit 3 song component, while the Unit 2 song remained more stable by  
319 comparison, suggests possible voluntary and purposeful control of the song units. Parks *et al.*  
320 (2007) point out that the upward shift in right whale calls to compensate for increased noise in  
321 the environment must be a behavioral change as opposed to a sexually selected response because  
322 the long term shift occurred within the known lifespan of individual whales. Similarly here, the  
323 continuing decrease is occurring within the lifespan of individual whales. However, in this study  
324 increased environmental noise was not identified as a potential driver as in right whales (Parks *et al.*  
325 *al.*, 2007). There remains the possibility that the decrease in frequency of the Sri Lankan pygmy  
326 blue whale Unit 3 call, as well as the tonal frequency decrease observed in other blue whale  
327 populations, may be voluntary to increase the range of effective communication.

328         The high apparent conformity and change in unison within the Sri Lankan population to  
329 sing the same song suggests that whales can hear one another within the Indian Ocean and may  
330 likely be changing this part of their song via social learning and cultural transmission. Such song  
331 synchrony has been observed in other baleen whales such as fin whales (Oleson *et al.*, 2014;  
332 Širović *et al.*, 2017), humpback whales (Payne and Payne, 1985; Cerchio *et al.*, 2001) and other  
333 populations of blue whales (Gavrilov *et al.*, 2012). However, numerous blue whale populations

334 are in acoustic contact in the Indian Ocean, yet there is no evidence of song hybridization such as  
335 that seen in humpback whales (Noad *et al.*, 2000).

336 One of the most intriguing aspects of the blue whale song unit decrease is that it is  
337 happening worldwide (McDonald *et al.*, 2009). McDonald *et al.* (2009) thoroughly explored  
338 potential causes for this global decrease in frequency, and predicted a stabilization of frequency  
339 as populations continue to recover from exploitation. Recent work by Monnahan *et al.* (2015)  
340 estimates that the eastern North Pacific population of blue whales is close to carrying capacity  
341 (97% carrying capacity, 95% CI 62%-99%), which provides an ideal opportunity to explore the  
342 prediction of McDonald *et al.* (2009) in future years. Frequencies have also continued to  
343 decrease in the Sri Lankan, Australian pygmy (Gavrilov *et al.*, 2011) and Antarctic (Gavrilov *et*  
344 *al.*, 2012) populations of blue whales possibly indicating that these populations may have not yet  
345 approached carrying capacity and continue to grow. At some point, whale anatomy and  
346 physiology cannot continue to support the observed frequency decrease. Investigating other units  
347 of song in other populations of blue whales may provide additional insight into this phenomena  
348 and overall blue whale song function.

349

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499

500 **FIGURE CAPTIONS**

501 **Figure 1.** Sri Lankan pygmy blue whale call recorded from the CTBTO IMS station at Diego  
502 Garcia. The Unit 1 pulsive (1), Unit 2 frequency modulated upsweep (2), and Unit 3 tonal  
503 downsweep (3) components are labelled. (color online)

504 **Figure 2.** Weekly average spectrum from Week 3 in year 2004 recorded from the CTBTO IMS  
505 station at Diego Garcia. The arrows indicate the spectral peaks corresponding to the two salient  
506 components (60 Hz Unit 2 and ~ 100 Hz Unit 3 from Figure 1) of the Sri Lankan pygmy blue  
507 whale call analyzed as part of this study. The red line shows the polynomial curve fit to a  
508 portion of the PSD for the 60 Hz Unit 2 target frequency band spanning 56-63 Hz. (color online)

509 **Figure 3.** Annual time series and decade average of hourly vocal presence detected per week.  
510 Average decadal vocal activity peaked during Weeks 21-22, and data from these two weeks were  
511 used in further power spectral density trend analyses. (color online)

512 **Figure 4.** Long term spectral average from the Diego Garcia H08 N1 location in the Indian  
513 Ocean. The decadal spectral image was constructed using a 1-hour window and 0.25 Hz  
514 resolution. A decrease in the Sri Lankan blue whale call is observed over time in the 110-100 Hz  
515 range. (color online)

516 **Figure 5.** Peak frequency of Sri Lankan whale vocalizations determined from weekly PSD sound  
517 averages. The blue circles are the weekly peaks measured throughout the season when whales  
518 were vocally present. The trend line is related to the red circles that are peak frequency from  
519 Weeks 21 and 22 of each year. The greyed regions designate the 95% confidence intervals for  
520 the trend. (color online)



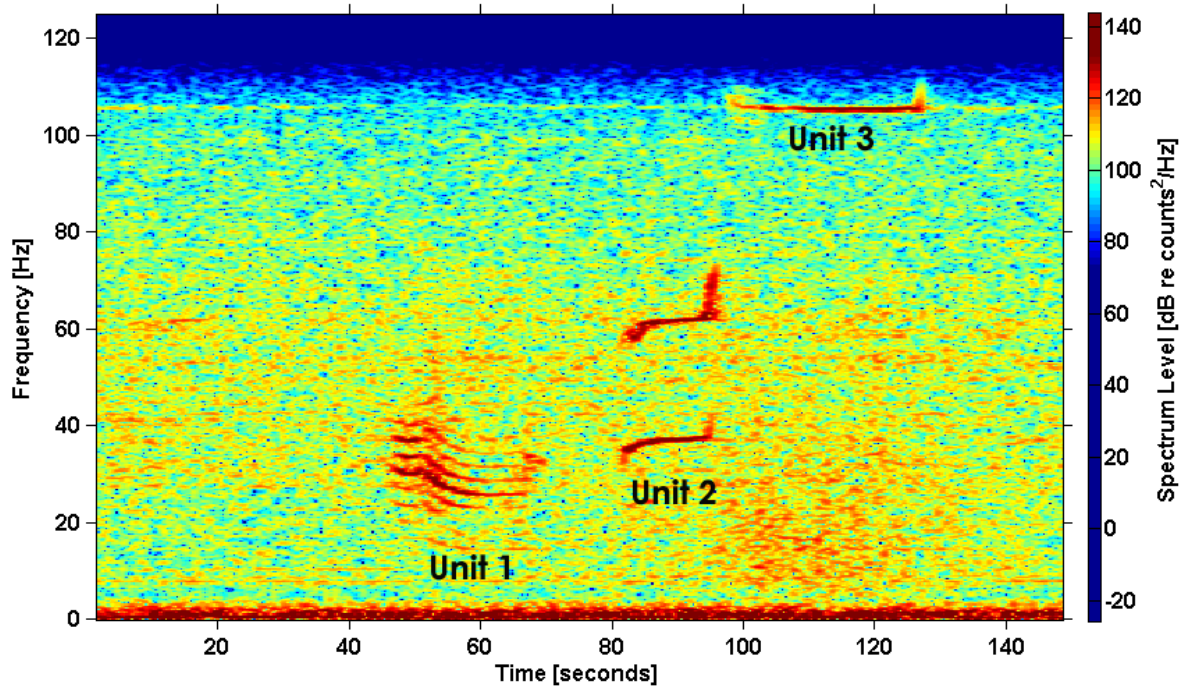
521 **Figure 6.** Power spectral density of ambient ocean sound averaged over Week 22 (28 May – 3  
522 June) in 2002, 2008, and 2012. The indicated peaks reflect the tonal peak of Sri Lankan blue  
523 whale calls. (color online)

524 **Figure 7.** Within season average rate of frequency change of the ~ 100 Hz Unit 3 song unit. The  
525 \* denotes significant frequency decreases over a single season (p-value < 0.05 for annual linear  
526 regression analysis) for six of the eleven years analyzed. The \*\* denotes the single year showing  
527 a significant seasonal decrease after the application of a Bonferroni correction (p-value < 0.0045).  
528 (color online)

529 **Figure 8.** Average and compensated maximum spectrum levels in the 56-63 Hz (a, c) and 100-  
530 107 Hz (b, d) frequency bands. The blue circles are the weekly PSD levels throughout the full  
531 dataset. The trend line was fitted to data from Week 21 and 22 of each year (red circles). The  
532 greyed regions designate the 95% confidence intervals for the trend. Band compensated  
533 spectrum levels reflect the contribution of whales alone corrected for the PSD of ambient sound  
534 from the fitted sound level estimate. (color online)

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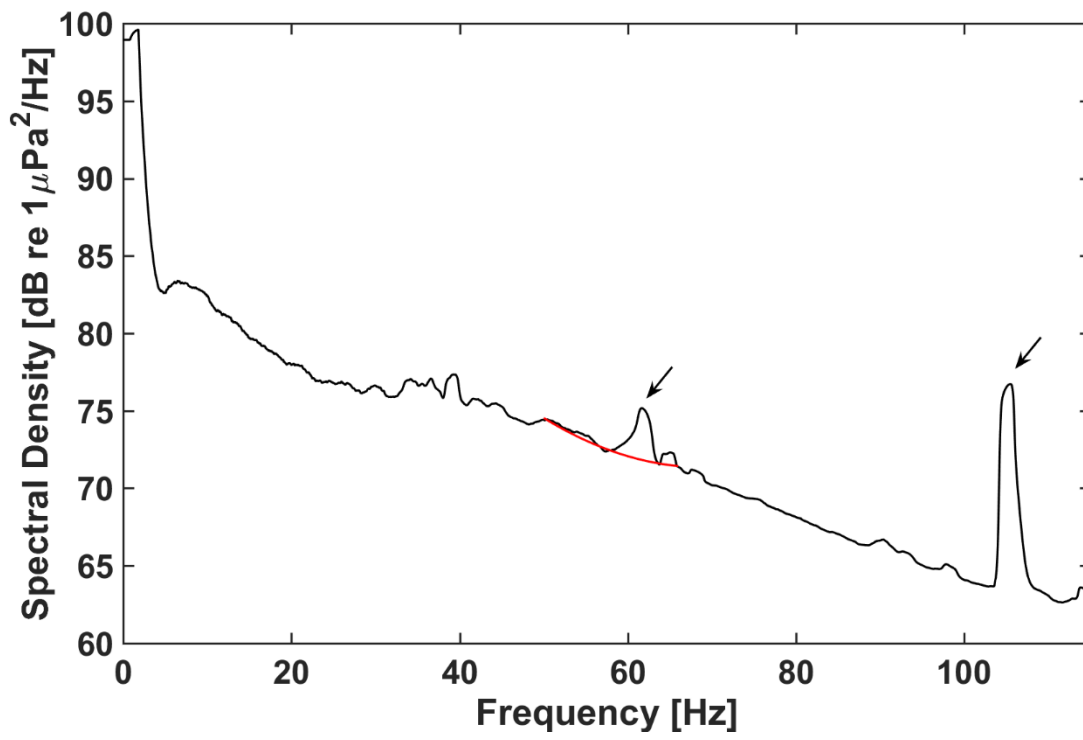
536 Figure 1.



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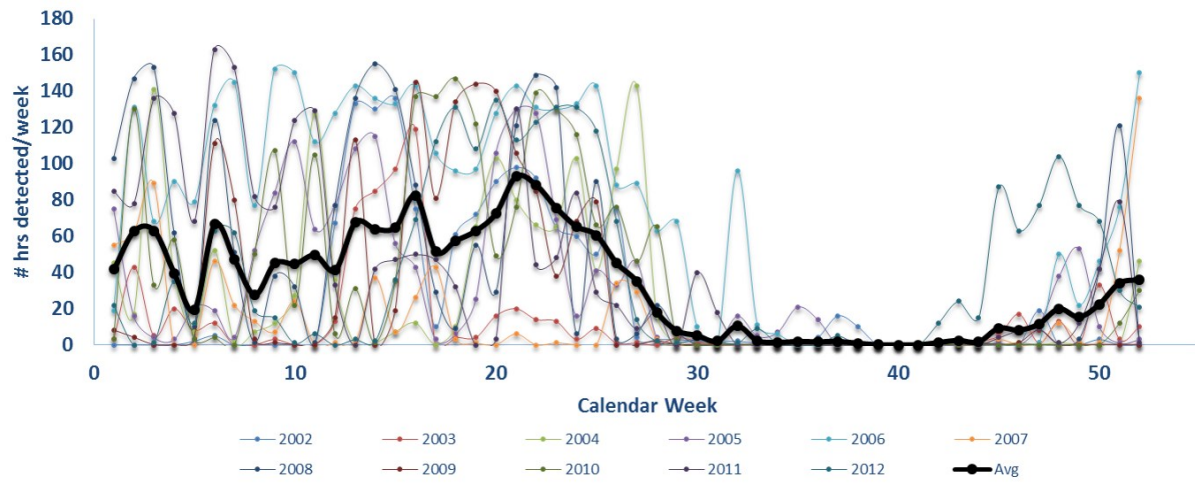
539 Figure 2.



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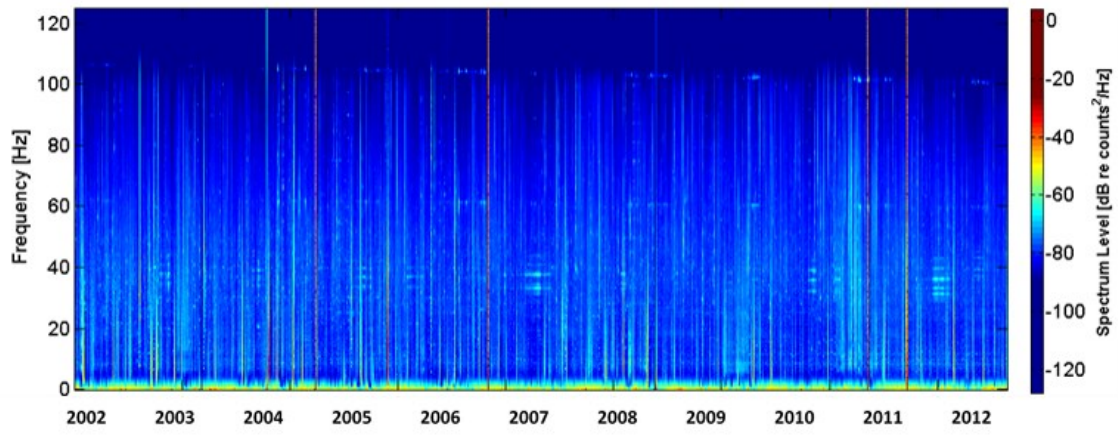
542 Figure 3.



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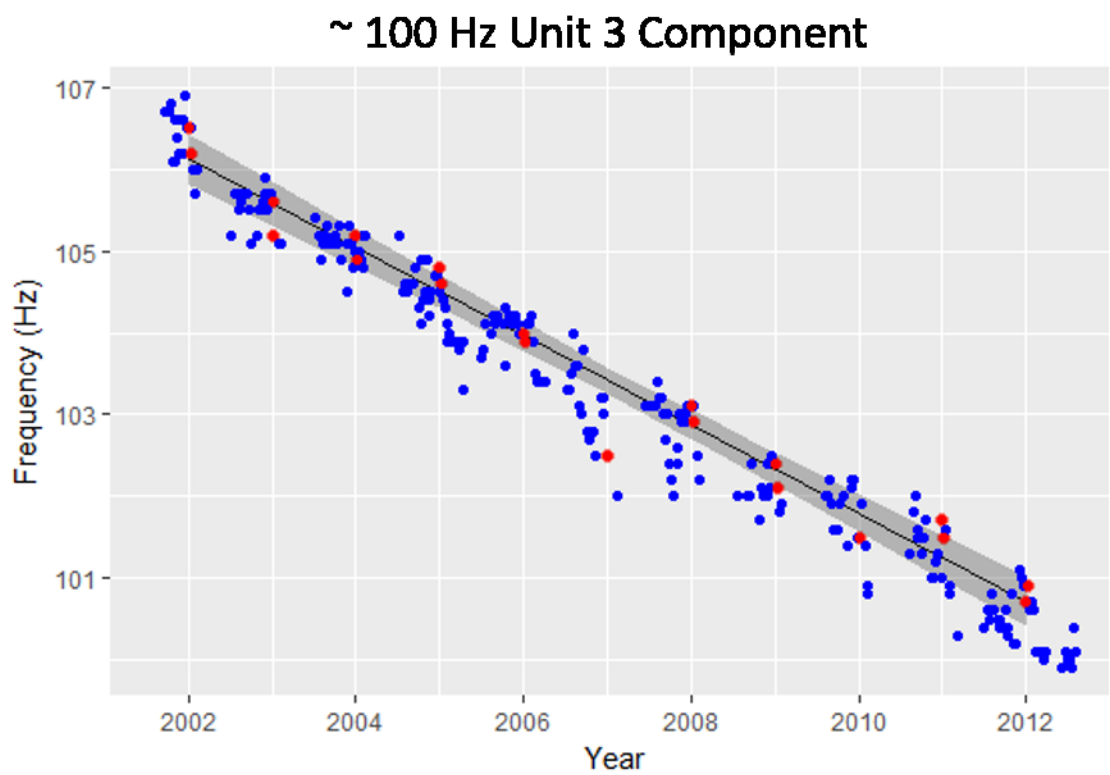
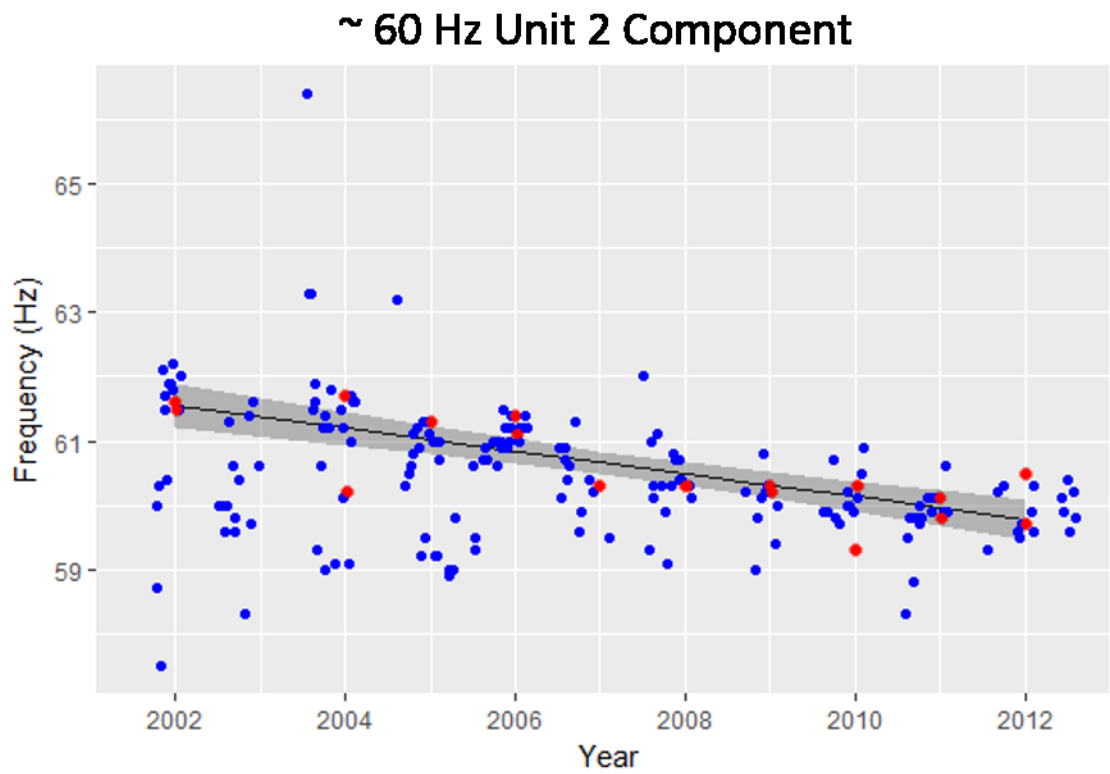
545 Figure 4.



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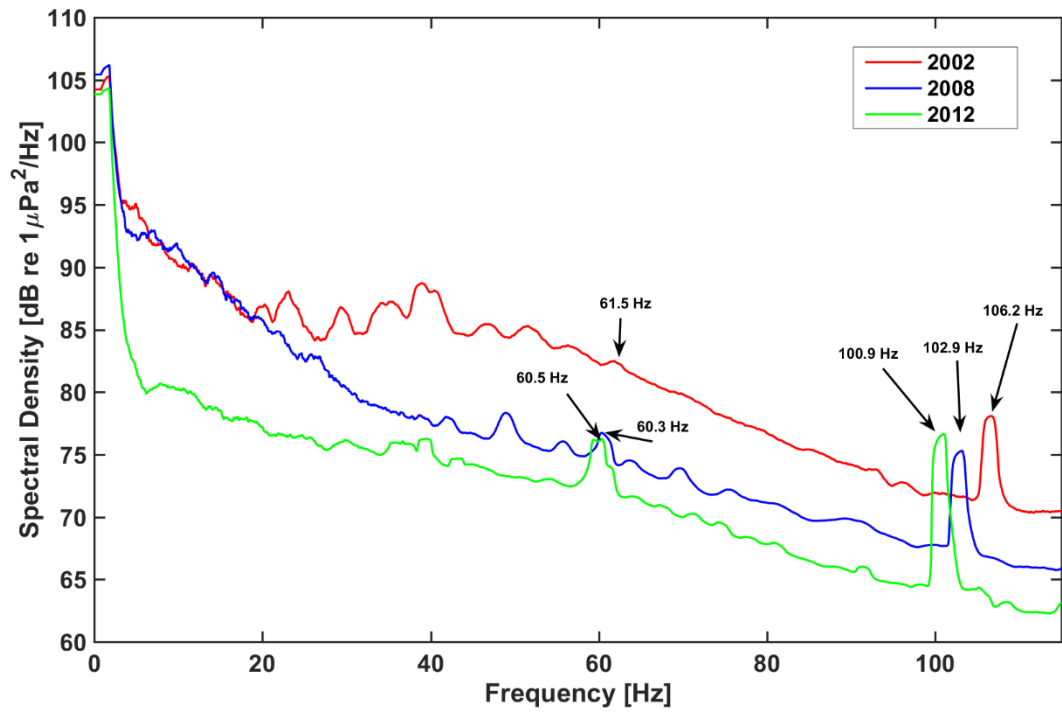
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548 Figure 5.



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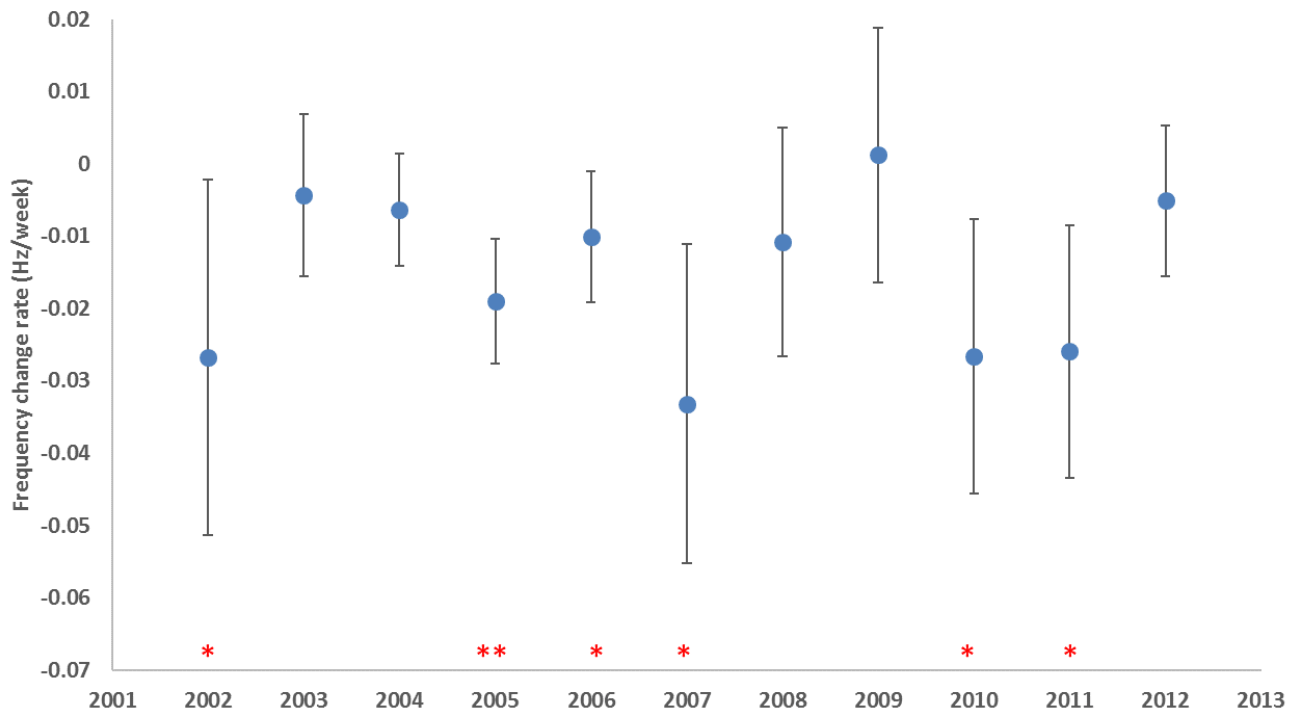
550 Figure 6.



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553 Figure 7.

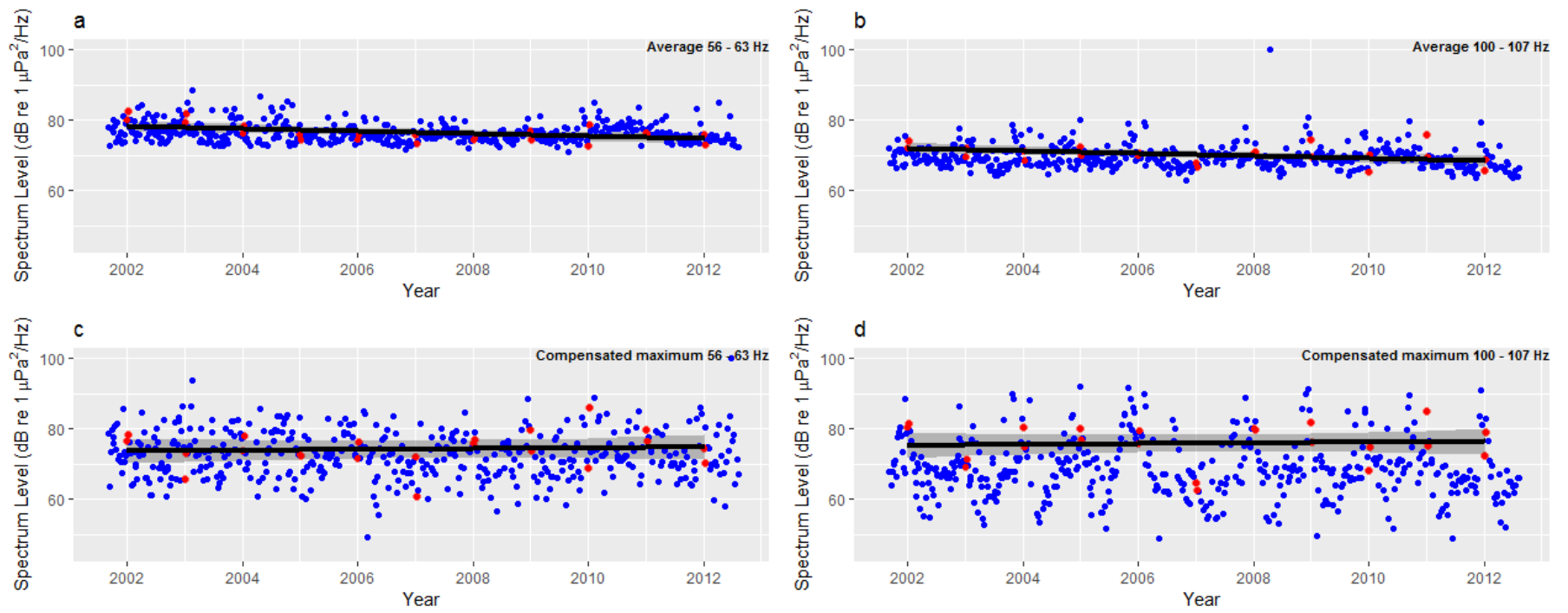


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556 Figure 8.



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