

RESEARCH ARTICLE

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Long-Term and Seasonal Changes of Large Whale Call Frequency in the Southern Indian Ocean

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Key Points:

- The call frequency of five populations of whales in the southern Indian Ocean steadily decreases by few tenths of hertz per year since 2010
- Seasonal frequency shifts also occur, particularly for the Antarctic blue whale, and correlate with seasonal changes in the ambient noise
- The interannual frequency decline may reflect growing whale abundances and/or changing acoustic properties of the ocean

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Abstract In the past decades, in the context of a changing ocean submitted to an increasing human activity, a progressive decrease in the frequencies (pitch) of blue whale vocalizations has been observed worldwide. Its causes, of natural or anthropogenic nature, are still unclear. Based on 7 years of continuous acoustic recordings at widespread sites in the southern Indian Ocean, we show that this observation stands for five populations of large whales. The frequency of selected units of vocalizations of fin, Antarctic, and pygmy blue whales has steadily decreased at a rate of a few tenths of hertz per year since 2002. In addition to this interannual frequency decrease, blue whale vocalizations display seasonal frequency shifts. We show that these intra-annual shifts correlate with seasonal changes in the ambient noise near their call frequency. This ambient noise level, in turn, shows a strong correlation with the seasonal presence of icebergs, which are one of the main sources of oceanic noise in the Southern Hemisphere. Although cause-and-effect relationships are difficult to ascertain, wide-ranging changes in the acoustic environment seem to have a strong impact on the vocal behavior of large baleen whales. Seasonal frequency shifts may be due to short-term changes in the ambient noise, and the interannual frequency decline to long-term changes in the acoustic properties of the ocean and/or in postwhaling changes in whale abundances.

Plain Language Summary In the past decades, a progressive decrease in the frequencies of blue whale vocalizations is observed worldwide. Its causes, of natural or anthropogenic nature, are unclear. Based on 7 years of widespread acoustic records in the southern Indian Ocean, we show that the call frequency of five populations of large baleen whales decreases at a constant rate of tenths of hertz per year. We also found that seasonal shifts in the whale call frequency follow seasonal changes in the ambient noise in the same frequency band. Wide-ranging changes in the acoustic environment have thus a strong impact on the vocal behavior of large whales in the short term, but, paradoxically, not in the long term.

1. Introduction

The advent of passive acoustic monitoring of the ocean in the last decades has improved our knowledge of the oceanic acoustic environment. Along with the abiotic (e.g., sea surface process, earthquakes, and volcanic activity) and anthropogenic (e.g., shipping and seismic exploration) sources, the biotic sources, and especially the marine mammal sounds, greatly contribute to this oceanic acoustic environment (Menze et al., 2017; Miksis-Olds et al., 2013; Tsang-Hin-Sun et al., 2015; Wenz, 1962; Wilcock et al., 2014). Vocalizations of large baleen whales dominate the low-frequency range of many recordings in various areas (Dziak et al., 2015; Haver et al., 2017; McDonald, Hildebrand, et al., 2006; Menze et al., 2017; Širović et al., 2013; Tsang-Hin-Sun et al., 2015). Blue and fin whales indeed emit stereotyped calls of low frequency (<100 Hz) and high intensity (~180 dB re 1 $\mu\text{Pa}^2/\text{Hz}$; McDonald et al., 2001; Samaran, Guinet, et al., 2010; Širović et al., 2007) that propagate over long distances (up to several hundreds of kilometers; Gavrilov & McCauley, 2013; Samaran et al., 2010a; Širović et al., 2007). Because of their high vocal activity, passive acoustic monitoring is currently one of the most successful way to study these endangered animals, especially in remote areas where visual observations are poorly efficient (Mellinger et al., 2007). Blue and fin whale calls differ among populations (McDonald, Mesnick, et al., 2006; Oleson et al., 2014; Stafford, 2003; Stafford et al., 2001, 2011; Weirathmueller et al., 2017) but are known to be highly stereotypic and to have constant shape over time.

However, it has been observed that the frequency (Hz) of blue whale calls is decreasing worldwide (Gavrilov et al., 2011, 2012; McDonald et al., 2009; Širović, 2016). The reasons for this long-term decline are unclear.

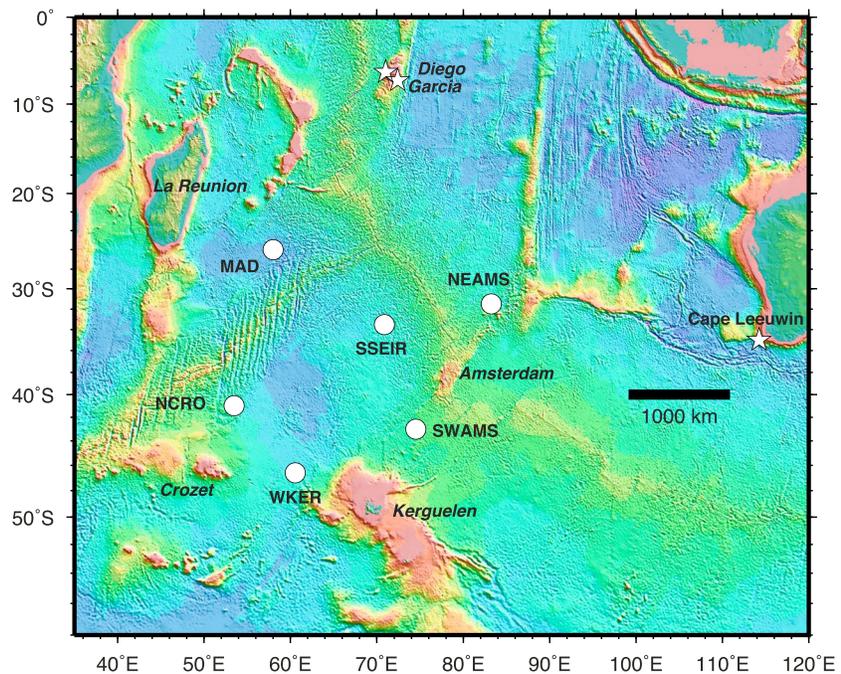


Figure 1. Hydrophone locations (circles) in the Indian Ocean, whose records are analyzed in this paper; stars outline the permanent hydroacoustic stations of the Comprehensive Test-Ban Treaty Organization, whose data have been investigated by other authors (e.g., Gavrilov et al., 2011, 2012; Stafford et al., 2011). MAD = Madagascar Basin; NCRO = north of Crozet Island; NEAMS = northeast of Amsterdam Island; SSEIR = northern Crozet Basin; SWAMS = between Kerguelen and Amsterdam islands; WKER = between Crozet and Kerguelen islands.

Hypotheses range from physiological causes, such as genetic selection or postwhaling increase in the whale body size, to behavioral causes, such as interferences between whale species or postwhaling increase in whale abundance, to environmental causes, such as increasing oceanic noise levels due to anthropogenic activities or changes in the oceanic acoustic properties due to climate change and ocean acidification (McDonald et al., 2009). At present, the most plausible (but speculative) reason for this long-term frequency decrease is an increase of the population density, leading to a decrease of the call intensity, involving a nonintentional decrease of the call frequency (Gavrilov et al., 2011; McDonald et al., 2009; Miller et al., 2014). In addition to this long-term frequency decrease, variations are observed on a seasonal scale (Gavrilov et al., 2012; Miller et al., 2014). Among potential explanations, seasonal changes in dive behavior (Gavrilov et al., 2012), Doppler effects as whales pass by recording hydrophones (Miller et al., 2014) or changes in body conditions after feeding periods (Miller et al., 2014) have been explored but ruled out.

To broaden the observation to the southern Indian Ocean and to further investigate these open questions of the interannual and intra-annual frequency variations of blue whale calls, we analyzed 7 years of passive acoustic data collected at up to six widespread sites in this region (Figure 1). Results show a long-term frequency decrease for the call of the Antarctic blue whale (*Balaenoptera musculus intermedia*), three acoustic populations of pygmy blue whales (*Balaenoptera musculus breviceauda* and *Balaenoptera musculus indica*)—known as the Madagascan, Australian, and Sri Lankan populations (Samaran et al., 2010b; Stafford et al., 2011)—and the fin whale (*Balaenoptera physalus*). This frequency decline is described for the first time for the Madagascan pygmy blue whales and the fin whales in the Southern Ocean, confirming a recent observation of fin whale 20 Hz-call frequency decrease in the North-East Pacific Ocean (Weirathmueller et al., 2017). There is still no explanation for this long-term decrease other than that explored by previous authors (Gavrilov et al., 2011, 2012; McDonald et al., 2009; Miller et al., 2014). However, in addition to this long-term phenomenon, our data clearly outline intra-annual frequency variations, particularly for the Antarctic blue whale calls, based on high-resolution frequency measurements on a large number of calls, and for fin whale calls, based on a lower resolution analysis (frequency measurements extracted from power spectral density [PSD]). These short-term frequency changes follow the seasonal changes in ambient noise levels at surrounding frequencies.

2. Material and Methods

2.1. Data Acquisition

This study is based on two data sets. The first set was acquired in 2007 during the DEFLOHYDRO hydroacoustic experiment (Royer, 2008) that deployed three autonomous hydrophones in the southern Indian Ocean from October 2006 to April 2008. The instruments, 1,500 to 2,500 km apart, were located south of La Reunion Island in the Madagascar Basin (MAD), midway between the Kerguelen and Amsterdam islands (SWAMS), and north-east of the St Paul and Amsterdam volcanic plateau (NEAMS) (Figure 1). Moorings consisted of an anchor, an acoustic release, and a hydrophone moored in the axis of the sound fixing and ranging channel, at a depth of 1,000 to 1,300 m below sea surface. Data were continuously sampled at 250 Hz (see Royer et al., 2015, for a complete description of the recorder specifications). The second set comes from the OHASISBIO hydrophone array (Royer, 2009), which was installed in December 2009 in the same area and is still operational as of July 2018. The array comprises the three previously instrumented sites (MAD, NEAMS, and SWAMS) and additional sites north of Crozet Island (NCRO) and between Crozet and Kerguelen islands (WKER). In 2014, a new site was established in the northern Crozet Basin (SSEIR) (Figure 1). Moorings are similar to those of the DEFLOHYDRO array. The data are continuously sampled at a rate of 240 Hz (see D'Eu et al., 2012, for instrument details) and are collected every year during the annual voyages of the R/V Marion Dufresne to the French Southern and Antarctic Territories. The records are almost continuous for the past 6 years (2010–2015), except for a few months or years depending on the site, due to battery failures or instrument losses (see Leroy et al., 2016, for details). The whole 6-year-long data set was analyzed in this study, except the NCRO site in 2010 and 2013, hindered by high noise levels likely due to strumming of the mooring line.

2.2. Frequency Measurement of Baleen Whale Calls

Baleen whales emit stereotyped calls (i.e., song), regularly repeated over time, with one or several units and overtones at specific frequencies (Figure 2). With a sampling rate of 240 Hz, our records captured calls from three (sub)species of large whales: fin whales (Figure 2b), Antarctic blue whales (Figure 2e), and pygmy blue whales of three acoustically distinct populations, the Sri Lankan (Figure 2a), Australian (Figure 2c), and Madagascar populations (Figure 2d) (Samaran et al., 2010b, 2013; Stafford et al., 2011). In each vocal signature, we selected specific units, either because they occurred consistently and loudly or for their distinctiveness from the other species units: near 26 Hz (unit A) for the Antarctic blue whale, near 35, 70, and 108 Hz for the Madagascar, Australian, and Sri Lankan pygmy blue whales (respectively), and the 99 Hz-pulse for the fin whale. These selected units are outlined by black rectangles in Figure 2.

For the Antarctic blue whale call, hereinafter referred to as Z-call due to its Z-shape in the time/frequency domain (Figure 2e), we measured the peak frequency (i.e., at maximum power) of the unit A on more than 1,000,000 previously automatically detected calls (Leroy et al., 2016), with a precision of 0.035 Hz. Frequencies were averaged per day and then per week, and over all sites. Note that since the Antarctic blue whale Z-calls are present year-round in our study area; although in smaller number during the austral summer (Leroy et al., 2016), the frequency measurements are available year-round for this call type.

The other whale calls are more complex. In order to assess their frequency evolution, a PSD of the signal was computed for each file (~6h28 duration) of the entire data set (2007 and 2010 to 2015), over 300s windows, 50% overlap, and with a frequency resolution of 0.0018 Hz. For each targeted species, frequency ranges were defined to encompass the frequency of the selected unit for the call of interest (Table 1 and Figure 2, black rectangles). We then extracted the frequency associated to the peak of energy in the considered bandwidths, leading to pairs of frequency/power for each file and each considered whale acoustic population.

Since the presence of these other acoustic populations is highly seasonal (Leroy, 2017; Samaran et al., 2013; Stafford et al., 2011), we estimated a chorus-to-noise ratio (CNR) to sort the noise from the actual calls. This metric measures the ratio between the noise power in the frequency range of the calls and the noise power in surrounding frequency bands. The latter is estimated by averaging the noise level above and below the call frequency range (Table 1). For the Sri Lankan pygmy blue whale, we proceeded differently because the selected call unit near 100 Hz is very close to the fin whale 99 Hz-pulse. Furthermore, at these frequencies (>80 Hz), the PSD decreases rapidly with the frequency. To estimate the CNR, we fitted the power of the noise level in the 102–106 Hz to a straight line and extrapolated linearly the noise level to the frequency range of interest for the call and then subtracted it from the call power level. We then only considered frequencies whose power exceeded a given threshold of CNR (set to 1, 0.7, and 1.0–1.5 dB for the Madagascar, Australian, and Sri Lanka pygmy blue whales, respectively, and 0.6 dB for the fin whales). The remaining frequency values

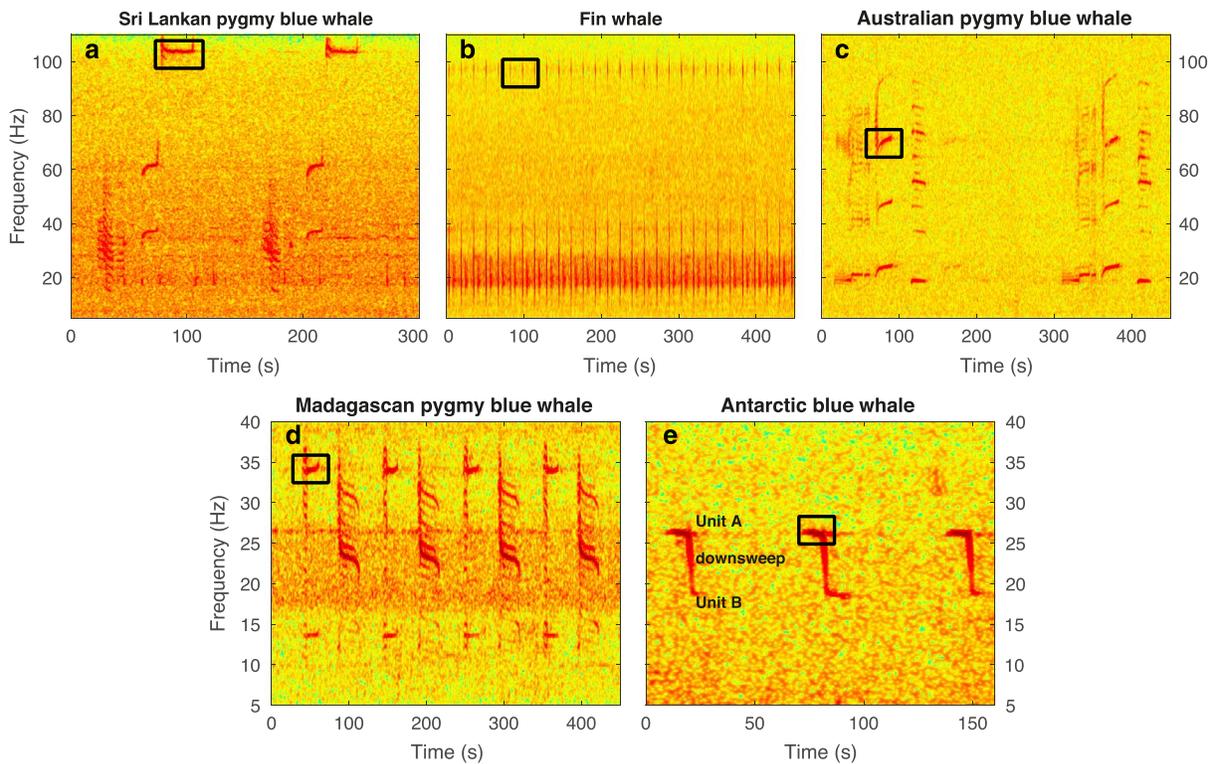


Figure 2. Stereotypic vocal signatures of pygmy blue whale of the (a) Sri Lankan type, (b) fin whale, (c) pygmy blue whale of the Australian and (d) Madagascan types, and (e) Antarctic blue whale. Black rectangles indicate the selected units in the calls.

were then averaged per week, with the additional condition that the considered week had at least 12 values (i.e., the frequency was detected in at least 12 files = 3 days for that week). Finally, we averaged these weekly means over the sites where each population is found: all sites except NEAMS for the Madagascan pygmy blue whale, only SWAMS and SSEIR sites for the Australian pygmy blue whale, and all sites for the fin whale. Note that the Sri Lankan pygmy blue whales were only recorded at NEAMS site. Earlier measurements from the Indian Ocean using a similar approach (Gavrillov et al., 2011, 2012) were also included.

2.3. Ambient Noise Levels

Ambient noise levels were calculated in frequency bands near the whale vocal signatures: for the Antarctic and Madagascan call types we measured the level in the 10- to 13-Hz and 30- to 33-Hz bands. For the Australian, Sri Lankan, and fin whale call types, we used the noise measurements made to calculate the CNRs; i.e., we averaged the noise levels of the upper and lower noise windows surrounding these calls (see Table 1). Noise levels were estimated file by file over 300s windows in 0.0018-Hz bins, averaged per week and month, and reported in decibels (dB re 1 $\mu\text{Pa}^2/\text{Hz}$).

Table 1

Frequency Band of the Computed PSD for the Call Units of Interest in Each Vocal Signature and for the Lower and Upper Noise Windows

	Call-unit frequency band		Noise window	
	2007 (Hz)	2010–2015 (Hz)	Lower (Hz)	Upper (Hz)
Sri Lankan PBW	102.4–105	98.9–102.1	N/A	102–106
Fin whale	96–99	95.2–97.8	91–93	99–101
Australian PBW	69–71	67.1–70	64–66	71–73
Madagascan PBW	34–35	33.5–34.5	30–32	36–38

Note. PBW = pygmy blue whale; PSD = power spectral density.

2.4. Detrended Variations of Frequency and Ambient Noise

To study the intra-annual variations in the call frequencies and ambient noise level, described in section 3.2, interannual trends were removed from the time series. A linear trend with a slope of -0.14 and -0.21 Hz/year was subtracted from the Z-call and fin whale call frequencies, respectively. A polynomial curve was fit to the noise data and subtracted from the noise curves at 30–33 Hz and at 91–93/99–101 Hz.

3. Results and Discussion

3.1. Long-Term Trend

All selected whale tonal units clearly show a constant long-term decrease in frequency over the years, here documented for the first time for Madagascan pygmy blue whales and fin whales in the Southern Ocean (Figure 3): From 2007 to 2016, the frequency of the Antarctic blue whale call decreased by -0.14 Hz/year ($R^2 = 0.98$), consistent with an earlier estimate based on data from 2002 to 2010 at one station (Gavrilov et al., 2012). The two data sets overlap between 2007 and 2010, showing that different approaches (power spectra (Gavrilov et al., 2012) vs. individual call measurements) agree for tonal units (Figure 3e). For the pygmy blue whales, the frequency decreased by -0.12 Hz/year ($R^2 = 0.98$) for the Madagascan type, -0.54 Hz/year ($R^2 = 0.96$) for the Sri Lankan type, and -0.32 Hz/year ($R^2 = 0.72$) for the Australian type, similar to -0.35 Hz/year measured from individual calls (Gavrilov et al., 2012). The shift between the two data sets is likely due to the nonmonotonal nature of the unit whose frequency can be measured from different parts (Figure 3c). Note that the -0.32 or -0.35 Hz/year decline corresponds to a decrease of about -0.11 Hz/year for the fundamental frequency of the considered call-unit. Finally, for the fin whale 99 Hz-pulse, the frequency decreased by -0.21 Hz/year ($R^2 = 0.82$). These frequency declines correspond to 0.51% of the mean frequency of Antarctic blue whale calls; 0.35%, 0.46%, and 0.55% for the Madagascan, Australian, and Sri Lanka pygmy blue whale calls (respectively); and 0.22% for the fin whale call.

Similar long-term frequency decreases have been observed worldwide for blue whales (McDonald et al., 2009), sometimes based on very sparse data (few measurements several years apart), and in the Indian Ocean, for Antarctic blue whales and Australian pygmy blue whales off western Australia (Gavrilov et al., 2011, 2012). The reason for such long-term frequency decline, which appears to be relatively linear, should also be long term and worldwide (McDonald et al., 2009). A number of explanations have been hypothesized, such as changes in the vocal behavior, either cultural or in response to sexual selection; physiological changes like an increase in body size; a response to changes in environmental conditions (e.g., ocean acidification); an adaptation of the frequency to overcome anthropogenic noises or biological interferences (McDonald et al., 2009); or a change in the average depth of the vocalizing whales (Gavrilov et al., 2011).

Among worldwide environmental changes, global warming and ocean acidification may contribute to modify the acoustic properties of the ocean. According to McDonald et al. (2009), the induced changes either in the sound-speed velocity (temperature changes, e.g., Bindoff et al., 2007) or in the acoustic absorption of sounds (acidification, e.g., Hester et al., 2008) are small compared to the observed frequency shifts in whale calls. However, postindustrial projection of regional changes in pH, and thus sound absorption, predicts increasing propagation ranges for low-frequency sounds (<200 Hz), enabling large whales to communicate over longer distances (Ilyina et al., 2010), or for a given distance, to lower their level of emission and hence their call frequency, as discussed below. The observed steady frequency decline since the 1960s may thus reflect the progressive ocean acidification.

It has also been observed that the ambient noise levels are rising in most of the oceans (Hildebrand, 2009; Matsumoto et al., 2014; McDonald, Hildebrand, et al., 2006; McDonald et al., 2009; Miksis-Olds et al., 2013). Lowering a call frequency would be a way to increase its propagation range (Dziak et al., 2017; McDonald et al., 2009). However, lowering a fundamental frequency by a few tenth of hertz would neither significantly reduce the signal attenuation nor significantly shift the signal relative to the ambient noise. Furthermore, as explained below, a lowered call frequency is predicted to result from a lowered call emission level and thus cannot compensate for increasing ambient noise (McDonald et al., 2009).

In the southern Indian Ocean, however, unlike in other parts of the world ocean, the ambient noise level tends to slightly decrease over the years, at the different frequency bands bracketing the targeted call units (Figure 4; see also Miksis-Olds & Nichols, 2016). This observation could suggest that in the southern Indian Ocean, the long-term call frequency decline is caused by a decrease in the ambient noise level. But two arguments counter this hypothesis: First, the decrease in the ambient noise level in the study area is neither

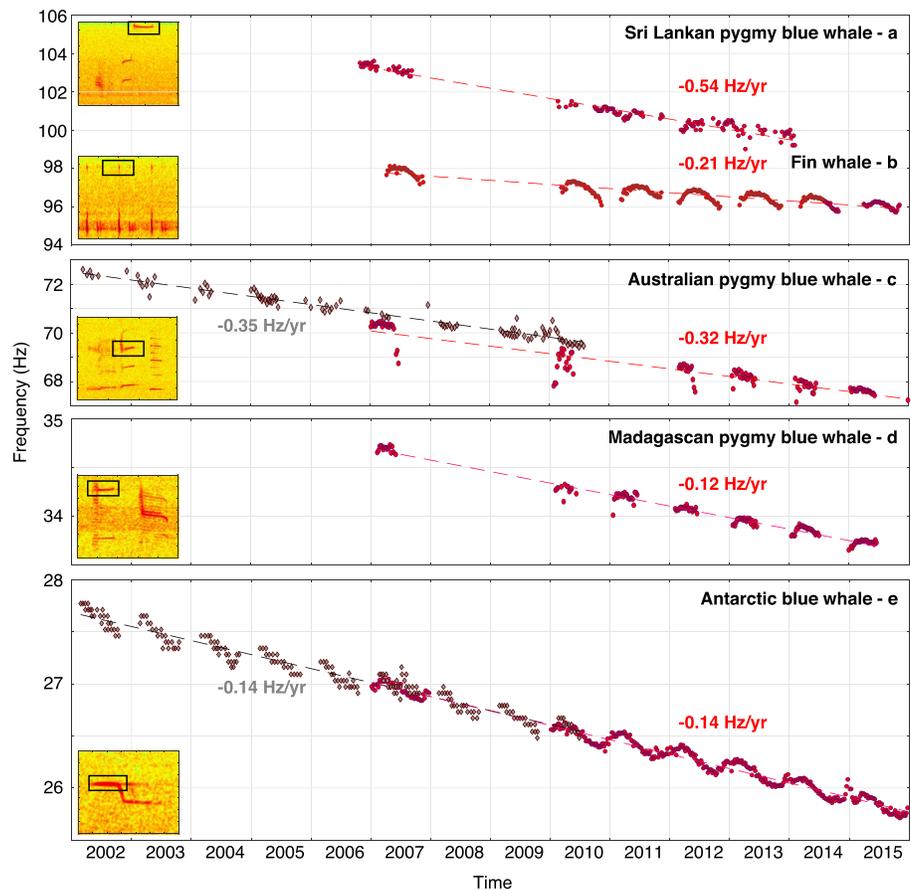


Figure 3. Fin and blue whale call-frequency decline over the years in the southern Indian Ocean. Symbols (red, this study; black diamonds, data digitized from Gavrilov et al., 2012) are weekly averaged peak frequencies measured for selected units in the calls (black rectangles in the time-frequency diagrams). The rates of frequency decrease in hertz per year are the slopes of the fitted dashed lines. Spectrogram insets are zoomed-in in Figure 2.

linear nor monotonous, for instance in the frequency band near 70 Hz (Figure 4c). In addition, while the noise level does not change or even increases slightly (e.g., 2015 in Figure 4), the call frequency is still linearly decreasing. Second, it is unlikely that a worldwide long-term frequency decline would have different causes in different oceans.

Among other possible explanations, McDonald et al. (2009) concluded that the most likely one is a postwhaling increase of the large whale population density. Indeed, an increasing density of individuals would require lower call source levels to keep in acoustic touch amid conspecifics, due to a reduced interindividual distance. For anatomical reasons, the call source level and its frequency are likely linked, whereby low-level calls have lower peak frequencies than high-level calls (McDonald et al., 2009). If this hypothesis is true, a long-term density increase can thus cause a long-term decrease in the call source levels, leading to the observed decline in the call peak frequency (McDonald et al., 2009). The potential link between call frequency and call intensity has yet to be rigorously tested, given that the mechanisms of large-whale sound emission are still an open question (Adam et al., 2013; Cazau et al., 2013; Dziak et al., 2017; Reidenberg & Laitman, 2007), though this hypothesis would fit the worldwide character of the phenomenon. Here we observe that the decline rate (Hz/year) differs among species and subspecies, from 0.22% to 0.55%, which, as suggested by McDonald et al. (2009), could reflect a different rate of population recovery for each subspecies.

3.2. Seasonal Variation

3.2.1. Intra-Annual Variations in Antarctic Blue Whale Call Frequency

Our dense set of observations also shows intra-annual shifts in call frequency with regular and yearly patterns, particularly clear for the Antarctic blue and fin whales (Figures 3e and 3b). They are best documented for the Antarctic blue whale, based on precise measurements of more than 1,000,000 individual calls detected

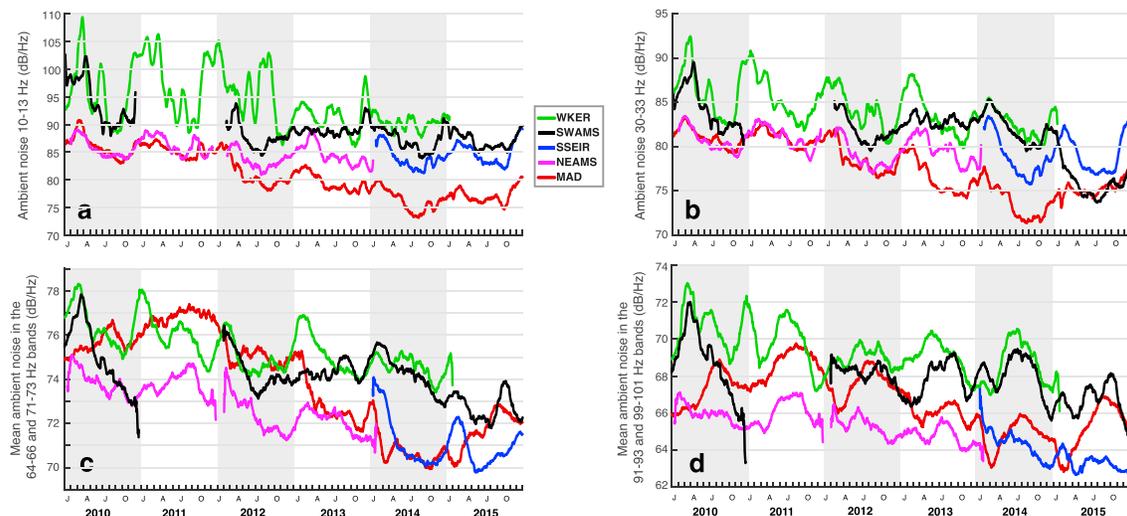


Figure 4. Long-term decrease of the ambient noise level in the (a) 10- to 13-Hz, (b) 30- to 33-Hz, (c) 64- to 66-Hz and 71- to 73-Hz, and (d) 91- to 93-Hz and 99- to 101-Hz frequency bands at all sites except the north of Crozet Island. Frequency bands (a) and (b) bracket the Antarctic blue whale calls, (c) the Australian pygmy blue whale calls, and (d) the 99-Hz fin whale pulses. MAD = Madagascar Basin; NEAMS = northeast of Amsterdam Island; SSEIR = northern Crozet Basin; SWAMS = between Kerguelen and Amsterdam islands; WKER = between Crozet and Kerguelen islands.

year-round over the network (Leroy et al., 2016). These short-term changes in the Antarctic blue whale call frequency were first documented off western Australia by Gavrilov et al. (2012), based on PSD measurements. This methodology measures the acoustic power generated by the presence of numerous and/or high received level whale calls and is thus subjected to the seasonality of the Antarctic blue whale presence in the recording area. Hence, the intra-annual frequency was described as declining by about 0.4–0.5 Hz from March to December and then resetting, the following March, to the mean value of the previous season (Gavrilov et al., 2012). Miller et al. (2014) explored these intra-annual changes on a composite data set, of limited duration, and showed that this sharp reset results from a lack of acoustic observations during January and February, while there is, in fact, a gradual increase in frequency. Here we show that this seasonal change occurs continuously and yearly, throughout 6 years of observation and at all sites, and is superimposed on the long-term frequency decline (Figure 5).

As noted in section 2, the frequency of Antarctic blue whale Z-calls were measured at the maximum of energy for unit A (Figure 2e). One may argue that the observed shift in frequency over time is an artifact due to two possible causes: different noise environment or propagation losses at different range, which may shift this maximum to a slightly lower or higher frequency, or, depending on the noise level surrounding individual

whales, their level of emission may differ and induce a slight shift in frequency (louder calls having a higher frequency than lower calls; McDonald et al., 2009). Averaging individual call frequencies by day or week might conceal such variability and bias the observation. The consistency of the observed seasonal shifts at six distant sites, based on more than a million samples, covering six continuous years (Figure 5), suggests that the frequency changes over time are not measurement artifacts; the largest dispersion occurs in the austral late spring and summer, when the Antarctic blue whale presence is the lowest at the site latitudes. In addition, different approaches provided independent evidence for this seasonal shift (Gavrilov et al., 2012; Miller et al., 2014).

3.2.2. Intra-Annual Variations in Low-Frequency Ambient Noise

As mentioned in section 1, there is no satisfactory explanation for this seasonal frequency change (Gavrilov et al., 2012; Miller et al., 2014), other than that it may have a different cause from the long-term decline. Here we notice that the ambient noise, especially in the 10- to 13-Hz and 30- to 33-Hz frequency bands, displays seasonal variations, similar to the frequency variations seen in blue whale Z-calls (Figures 4a and 4b). These

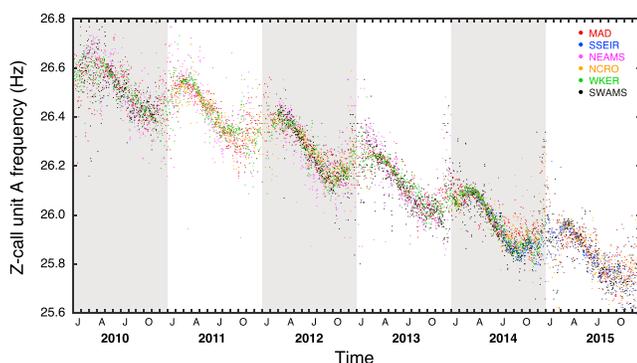


Figure 5. Daily averaged frequency of Z-call units A at each recording site, based on a total of 1,003,988 individual calls. MAD = Madagascar Basin; NCRO = north of Crozet Island; NEAMS = northeast of Amsterdam Island; SSEIR = northern Crozet Basin; SWAMS = between Kerguelen and Amsterdam islands; WKER = between Crozet and Kerguelen islands.

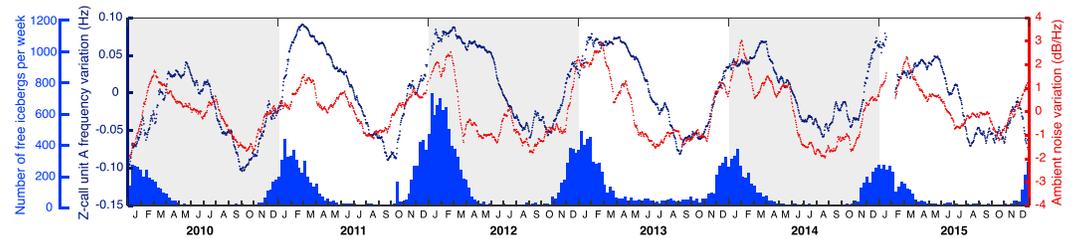


Figure 6. Detrended evolution of Z-call unit A frequency (blue dots) and of the ambient noise level in the 30- to 33-Hz frequency band (red dots), as observed at the Madagascar Basin site (26° S). Each dot represents the averaged frequency or noise level in a moving window of 1 month, based on weekly averaged samples. Histograms show the number per week of free icebergs, smaller than 8 km² (Tournadre et al., 2016). This figure outlines the seasonal correlation between the occurrence of icebergs, the increase in the noise level, and the concomitant shift in the Z-call frequency.

two frequency bands, which bracket the Z-call frequency range, display intra-annual variations within an amplitude of 4 to 10 dB re 1 $\mu\text{Pa}^2/\text{Hz}$. As the 10–13 Hz is more prone to low-frequency natural transient noises (earthquakes, volcanic tremors, and icequakes), we focus on the 30- to 33-Hz band. After removing the long-term trend in the noise level and in the frequency of the Z-call units A, it can be observed that both curves display a clear correlation (e.g., $R^2 = 0.65$ at MAD site; Figure 6). The two curves have the same phase and period of 365 days. An increase in the ambient noise level from October to February co-occurs with an increase in the call frequency, and after February, both the noise level and frequency gradually decrease until next October. There are periods when the two curves clearly mimic one another (e.g., May to November 2014) and periods when the two curves depart. Still, high noise levels match with high-frequency pitch, and conversely.

To further test the correlation between call frequency and noise level, we plotted the frequency of unit A versus the 30- to 33-Hz noise level measured at the MAD, NEAMS, WKER, and SWAMS sites (SSEIR has only 2 years of data available; see Figure 1). Note that here we used the nondetrended measurements. All sites show a general linear increase of the call frequency as the noise level increases (Figure 7); the overall correlation coefficients of linear regressions are $R^2 = 0.8, 0.5, 0.4,$ and $0.4,$ respectively, for MAD, SWAMS, NEAMS, and WKER. The smaller coefficients reflect the fact that these plots also show in a different way that the call frequency and noise level both decrease over the years; they thus combine intra-annual with interannual variations. When data for a single year are correlated, it is worth noting that the rate of frequency increase relative to the noise level is fairly constant between 75 and 90 dB re 1 $\mu\text{Pa}^2/\text{Hz}$, keeping in mind that the frequency varies linearly and the noise level logarithmically (0.2 to 0.5 Hz for a 10 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ increase); excluding few outliers (e.g., MAD or SWAMS 2015), most fitted lines in Figure 7 are parallel to each other. In addition, this seasonal frequency/noise concomitance or dependency seems insensitive to the long-term decline of the frequency. This observation confirms that the intra-annual and interannual changes in call frequency likely reflect two different behaviors.

3.2.3. Call Level Adjustments to the Ambient Noise

Z-call units A show cyclical variations of ± 0.1 Hz about their mean frequency (Figure 6). With such yearly seasonality, it is unlikely that this small frequency variation results from an intentional behavioral change from all vocalizing whales, as pointed out by Miller et al. (2014). For some cetaceans, shifting frequency is indeed a strategy to stand out from an increasing level of noise in their usual frequency bandwidth, but these changes generally reach several or tens of hertz (Ansmann et al., 2007; Erbe et al., 2016; Lesage et al., 1999; Parks et al., 2007). Following the hypothesis of a link between call intensity and call frequency (McDonald et al., 2009), we rather hypothesize that within a year, whales adapt their level of emission to the level of ambient noise, which in turn involuntarily modifies their call frequency. This adaptation to maintain the signal-to-noise ratio of vocalizations is known as the *Lombard effect* (Hotchkin & Parks, 2013; Lombard, 1911) and has been demonstrated for birds (Brumm, 2004; Brumm & Slabbekoorn, 2005), frogs (Halfwerk et al., 2015), and primates (Brumm et al., 2004), but also for right whales (*Eubalena glacialis*; Parks et al., 2011), humpback whales (*Megaptera novaengliae*; Dunlop et al., 2014), and possibly blue whales in the Southern California Bight (*B. m. musculus*; Melcon et al., 2012).

Frequency changes over the years (approximately -0.1 Hz/year) and within a year (± 0.1 Hz) would both reflect similar changes in call source level. However, if the interannual frequency or call source level decline is a response to an increasing population density (Gavrilov et al., 2011; McDonald et al., 2009), unlikely to vary in yearly cycles, we believe that short-term changes in the call source levels are linked to the low-frequency

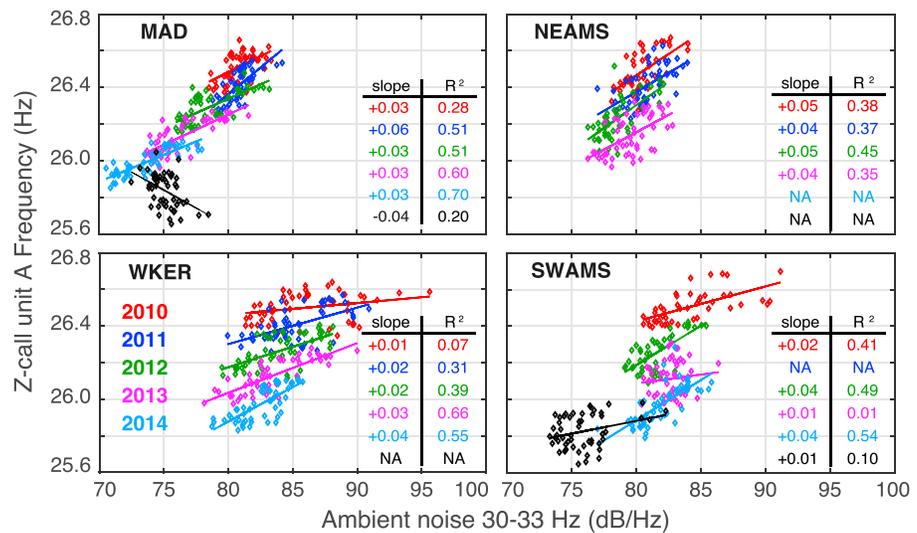


Figure 7. Frequency of Z-call units A relative to the ambient noise level in the 30- to 33-Hz frequency band. Data are color-coded by year. The slopes of the fitted lines are in Hz/(dB/Hz); R^2 is the regression coefficients. MAD = Madagascar Basin; NEAMS = northeast of Amsterdam Island; SWAMS = between Kerguelen and Amsterdam islands; WKER = between Crozet and Kerguelen islands.

ambient noise level. Yet Figure 4 shows that in the southern Indian Ocean, the long-term noise level in the selected bandwidths is decreasing. This leads to a second observation that the seasonal frequency/noise relationship seems independent of the absolute noise level, since, except for 2015, slopes of the fitted lines are similar in the 70–85 dB re $1 \mu\text{Pa}^2/\text{Hz}$ (MAD and NEAMS) and 80–90 dB re $1 \mu\text{Pa}^2/\text{Hz}$ ranges (WKER and SWAMS). Furthermore, this seasonal adaptation of frequency (i.e., call source level) is wide range since, for a given time of the year, the frequency of Z-calls is the same at all observation sites throughout the southern Indian Ocean and the frequency variations have the same amplitude at all sites (Figure 5).

3.2.4. Potential Sources of Seasonal Ambient Noise

Among noise sources that can be detected over great distances in the Southern Hemisphere, the Antarctic ice shelf or drifting icebergs generate low-frequency cryogenic sounds (up to 40 Hz) powerful enough to ensonify the whole Southern Ocean up to tropical latitudes (Chapp et al., 2005; Matsumoto et al., 2014; Tsang-Hin-Sun et al., 2015). The induced noise level is highly seasonal and reaches its peak in the austral summer. This is when most iceberg cracking noises are heard in the subantarctic latitudes (Chapp et al., 2005; Hanson & Bowman, 2005; Royer et al., 2015; Tsang-Hin-Sun, 2016; Tsang-Hin-Sun et al., 2015). As a proxy for the ice-related noise, Figure 6 displays the number per week of free icebergs, smaller than 8 km^2 , detected from satellite altimetry (Tournadre et al., 2016) in the Indian sector of the Southern Ocean ($30^\circ \text{ E} - 110^\circ \text{ E}$, up to 40° S). In a wider geographic window ($30^\circ \text{ E} - 150^\circ \text{ E}$) at a monthly time scale, Matsumoto et al. (2014) measured a correlation coefficient of 0.84 between the 30- and 36-Hz noise at Cape Leeuwin and the iceberg volume (see also Tsang-Hin-Sun et al., 2015). For the whole time series in Figure 6, the Pearson correlation coefficient between the number of icebergs and the 30- to 33-Hz noise level equals 0.6. However, depending on the year, there may be a time lag between the appearance of icebergs and the noise level. With an analysis of yearly time series centered on the middle of the summer (end of January), the correlation coefficient improves to 0.7 for 2011, 2014, and 2015 and over 0.8 for 2012 and 2013, but with a time lag in the order of 50 days for 2011 and 2015, a month for 2013 and 2014, and none for 2012. Such time lags may indicate different oceanic conditions prevailing during the dispersal and subsequent breakup of the icebergs, if one assumes that all the noise is due to drifting icebergs. Alternatively, the large time lags reflect the prevalence of additional noise sources such as icebergs larger than 8 km^2 or the dislocation of the ice shelf off Antarctica, not accounted for in our comparison and artificially shifting the correlation. Using the total surface of the icebergs instead of their number does not change these results (volumes would require additional information on their heights). This analysis emphasizes, as broad-scale analyses (Matsumoto et al., 2014; Tsang-Hin-Sun et al., 2015), the eminent role of icebergs in the generation of low-frequency noise in the Southern Hemisphere. Even though the MAD site is located at a tropical latitude, 5° north relative to Cape Leeuwin (Figure 1), its 30- to 33-Hz noise level starts to rise as the free icebergs appear in the austral spring (October–November), increases up to 5 dB when the number of icebergs peaks in the austral summer (January–February; up to 800/week), and decreases as

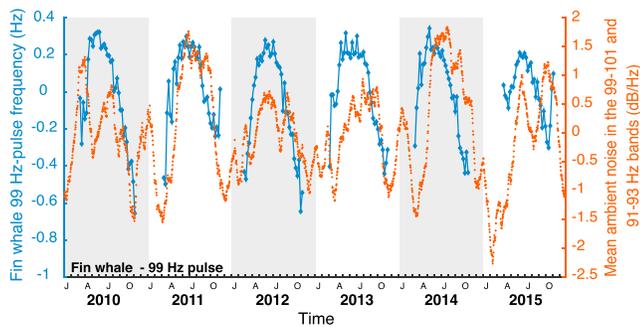


Figure 8. Detrended variations of fin whale 99 Hz-pulse frequency (blue) and ambient noise in the surrounding frequency band (red), as observed at the Madagascar Basin site (26° S).

the icebergs vanish in the fall (April–May; Figure 6). Smaller peaks of noise, the rest of the year, are likely due to other sources, including cryogenic noise from the ice shelf itself (e.g., ice-shelf cracking and iceberg calving). Many ice tremors have been detected and located along the Antarctic shelf in the fall and winter seasons (Chapp et al., 2005; Hanson & Bowman, 2005; Royer et al., 2015).

Ship traffic is another potential source of noise but is very limited in the southern Indian Ocean, except perhaps at the MAD site located in the traffic corridor between the Cape of Good Hope and the Malacca Strait (Tsang-Hin-Sun et al., 2015). This year-round traffic may contribute to the overall noise level but unlikely to its seasonality. Furthermore, on the long term, the 10- to 13-Hz and 30- to 33-Hz noise levels tend to decrease at MAD, which may be partly due, after 2012, to the rerouting of vessels on their way to or from the northwestern Indian Ocean, following the decline

of piracy attacks off East Africa (Vespe et al., 2015). Although airgun shots from distant seismic surveys can ensonify very large areas of the ocean (as far as 6,000 km away), they are not seasonal. Finally, there is no apparent effect from the powerful low-frequency background noise generated by subsea earthquakes and volcanic activity.

Whale vocalizations can also be considered as seasonal noise sources. It is then possible that whales change their call source level in response to the noise generated by another whale population. However, in such case, the induced changes should vary with the location of the animals and follow the migration pattern of the source of noise.

3.2.5. Further Observations

Similar to Antarctic blue whales, the 99 Hz-pulse of fin whales also displays seasonal frequency variations (Figure 3b). These measurements are based on PSD and not on individual calls and are thus less accurate than for the Antarctic blue whale calls, so this observation remains preliminary. However, when zoomed-in and detrended from the long-term decline of frequency (Figure 8), this seasonal frequency shift appears to follow that of the noise levels in the 91- to 93-Hz and 99- to 101-Hz frequency bands. The main peaks in frequency and noise occur in May–June, 3 months later than for the Antarctic blue whale and the 30- to 33-Hz noise levels. The noise in this higher frequency range thus displays a different seasonality, and its source is yet unknown and most likely unrelated to cryogenic events (of which noise rarely exceeds 50 Hz; Matsumoto et al., 2014; Royer et al., 2015; Tsang-Hin-Sun et al., 2015). Nevertheless, as for the Antarctic blue whale, there is a clear correlation, perhaps with a short time lag, between seasonal frequency changes and relative noise level changes in the surrounding frequency bands. Seasonal frequency shifts seem also to occur for the Australian and Madagascar pygmy blue whales (Figures 3c and 3d) but need to be confirmed by finer analyses.

4. Conclusion

This analysis of whale call frequency from an acoustic data set spanning 6 to 13 years and an area of 9,000,000 km² in the southern Indian Ocean provides robust observations of a long-term linear decrease of the call frequency of five species, subspecies, and/or populations of large baleen whales. This phenomenon had already been partly documented for some blue whale populations and in every ocean (Gavrillov et al., 2011, 2012; McDonald et al., 2009; Širović, 2016). The frequency decline ranges from 0.12 to 0.54 Hz/year, depending on the whale species and the selected call unit. Our continuous set of observations also documents cyclical intra-annual variations, within a 0.2-Hz interval, of the call-frequency for Antarctic blue whales, fin whales, and also for Madagascar pygmy blue whales.

For Antarctic blue whales, frequencies increase and decrease as the low-frequency noise level increases during the austral summer and decreases in the fall and winter. In the absence of anthropic sources of noise in the southern Indian Ocean, the seasonal cryogenic noise, particularly from free icebergs, seems the most plausible cause for the seasonal changes in the frequency of blue whale calls. For the fin whales, the main peaks in frequency and noise level near 99 Hz occur from May to October, showing the same noise/frequency correlation but from another noise source. Although nice correlations do not ascertain a cause-effect relationship, our observation hints that short-term and wide-range changes in the natural acoustic environment may have a strong impact on the vocal behavior of large whales.

The same order of magnitude of the intra-annual and interannual frequency variation suggests a similar physiological explanation such as a link between call intensity and call frequency, where the frequency pitch rises or diminishes by a fraction of hertz with the intensity of the call. Proving this assertion would require measuring a significant number of call source levels, to overcome any dependence on the size or physical conditions of individuals, and over the long-term (year-round and every year), a challenging task for whale species dwelling in such remote areas. The seasonal changes and the long-term decline of the whale call source levels (and peak frequencies) have most probably different explanations. We showed that intra-annual variations mimic that of the noise level in frequency bandwidths near that of the whale calls, suggesting an adaptation of the call source level to the seasonal variations of the ambient noise level. These seasonal adjustments, however, seem insensitive to the absolute noise level, varying among sites (Figure 4), and have the same amplitude (0.2 Hz) relative to the yearly frequency, which does not vary among sites (Figure 5). The long-term decline in frequency, that is, call level, must have a long-term cause, such an increase in density population, which would reduce the need for raising the call level to communicate with conspecifics (McDonald et al., 2009). This decline rate represents 0.20% to 0.50% of the selected frequencies, which may be clues for differentiated population recovery among species. Alternatively or concomitantly, the ocean-wide steady acidification since the industrial era, which results in a decrease in sound absorption and therefore an increase in propagation distance (Ilyina et al., 2010), may facilitate the low-frequency communications among large baleen whales, inducing lower call levels and the observed steady decline of call frequencies.

Although noise levels are rising in some parts of the world ocean (Hildebrand, 2009; Matsumoto et al., 2014; McDonald, Hildebrand, et al., 2006; Miksis-Olds et al., 2013), they seem to have no effect on the worldwide frequency decline (McDonald et al., 2009); yet, in places, they may partly counterbalance the effect of a density growth. There is thus a paradox between the effects of the environmental noise on the short-term acoustic behavior of large whales and its apparent lack of effects on the long term. All these questions warrant additional long-term and continuous passive acoustic monitoring to better document short-term and long-term changes in frequency for other whale species in other parts of the world, particularly in the southern Atlantic or Pacific oceans, along with a joint monitoring of the chemistry (pH) and acoustic properties (sound speed and absorption) of the ocean.

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