



Broad-scale study of the seasonal and geographic occurrence of blue and fin whales in the Southern Indian Ocean

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ABSTRACT: The southern Indian Ocean is believed to be a natural territory for blue and fin whales. However, decades after commercial and illegal whaling decimated these populations, little is known about their current status, seasonal habitat or movements. Recent passive acoustic studies have described the presence of 4 acoustic populations of blue whales (Antarctic and 3 'pygmy' types), but are generally limited temporally and geographically. Here, we examine up to 7 yr of continuous acoustic recordings (2010–2016) from a hydrophone network of 6 widely spaced sites in the southern Indian Ocean, looking for the presence of Antarctic and pygmy blue and fin whales. Power spectral density analyses of characteristic and distinct frequency bands of these species show seasonal and geographic differences among the different populations, and the overall patterns for each display interannual consistencies in timing and occurrence. Antarctic blue and fin whales are recorded across the hydrophone network, mainly from austral autumn to spring, with peak intensity in winter. Pygmy blue whales show spatial variation: Madagascar pygmy blue whales are mainly present in the west of the network, while the Australian call type is heard at the eastern sites. Both populations share a common seasonality, with a presence from January to June. Finally, the Sri Lankan call type is recorded only on a single site in the northeast. These results confirm the importance of the southern Indian Ocean for several populations of endangered large whales and present the first long-term assessment of fin whales in the southern Indian Ocean.

KEY WORDS: Pygmy blue whales · Antarctic blue whales · Fin whales · Southern Indian Ocean · Passive acoustic monitoring · Sympatry

INTRODUCTION

The Indian Ocean is inhabited by several species and subspecies of large whale, including the Antarctic blue whale *Balaenoptera musculus intermedia*, the pygmy blue whale *B. m. brevicauda* and *B. m. indica*, and the fin whale *B. physalus* (Stafford et al. 2004, 2011, Samaran et al. 2010a, 2013, Balcazar et al. 2015, Tripovich et al. 2015, Tsang-Hin-Sun et al.

2015). During the 20th century, populations of both blue and fin whales in the Southern Ocean were severely decimated by commercial and illegal whaling, particularly in the Indian Ocean (Branch et al. 2004). As a response, in 1979, the International Whaling Commission established the Indian Ocean Sanctuary to protect them from further exploitation (IWC 1980). North of the Equator, this sanctuary comprises the waters from the coast of Africa to 100°E and

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includes the Red and Arabian Seas and the Gulf of Oman; south of the Equator, it extends from 20° E to 130° E and down to 55° S (IWC 1980, see also Fig. 1 in Stafford et al. 2011). The post-whaling and present status of these populations remains poorly understood with no recent abundance estimates for the Indian Ocean (Branch et al. 2007), and most current knowledge of their distribution coming from passive acoustic monitoring (PAM) studies (e.g. Stafford et al. 2004, 2011, Samaran et al. 2013, Tripovich et al. 2015). According to a recent study on genetic differentiation of blue whale subspecies, those sampled in the Indian Ocean were distinct from Antarctic and Pacific blue whales, but no within-Indian Ocean divisions were evident, possibly due to small sample sizes (Leduc et al. 2017). Further, genetic diversity within the Indian Ocean was relatively low (Attard et al. 2016, Barlow et al. 2018). As a conservative measure, the International Union for Conservation of Nature Red List classifies the Antarctic blue whales as 'Critically Endangered', fin whales as 'Endangered', and pygmy blue whales as 'Data Deficient' (Cooke 2018). The unknown status of the pygmy blue whale is largely due to its late identification in 1961 as a distinct species from Antarctic blue whales (Ichihara 1966). Therefore, the impact of whaling on this species is not known (Clapham et al. 1999), although Branch et al. (2007) concluded that whaling likely caused a decrease in the number of pygmy blue whales. The occurrence of acoustically distinct populations of pygmy blue whales in the Indian Ocean further complicates their observation (Stafford et al. 2011, Samaran et al. 2013).

Monitoring whale populations over large geographic and temporal scales is a challenge, especially in the southern Indian Ocean. Visual observations require dedicated ship time and are restricted to periods of daylight, good weather, and accessibility, all of which can be difficult to meet in temperate waters, but even more so in extreme environments such as the Southern Ocean, particularly in the remote Indian sector.

Over the past 15 years, PAM has proved to be an efficient and relatively low-cost method to monitor baleen whales year-round by recording their vocal activity (Mellinger et al. 2007), and has greatly improved our understanding of the distribution of vocally active large baleen whales. Both blue and fin whales produce sounds year-round, although fin whales tend to be more vocally active from fall to spring (e.g. Stafford et al. 2001, Širović et al. 2009, Nieuwkerk et al. 2012, Thomisch et al. 2016). PAM takes advantage of the active vocal behavior of

large whales, which produce easily recognizable and low-frequency calls that can be heard over tens or hundreds of kilometers (Mellinger et al. 2007, Širović et al. 2007, Samaran et al. 2010b). Furthermore, these species produce sounds in long, stereotyped patterns (song) during many months of the year. In the Indian and Southern Oceans, distinct vocal signatures have been documented for at least 5 species or subspecies: fin whales, Antarctic blue whales, and 3 acoustic populations of pygmy blue whales (known as the Madagascan, Australian (or eastern Indian Ocean) and Sri Lankan types) (Stafford et al. 2004, 2011, Samaran et al. 2010a, 2013, Tsang-Hin-Sun et al. 2015).

While all blue whales share the common traits of producing very long, low-frequency signals that are frequency and/or amplitude modulated, the units that make up these songs differ by region in overall duration, frequency content, and number of components. Because these differences are stable over many decades, the acoustic signatures of blue whales have been used to designate 'acoustic populations' (e.g. Stafford et al. 2001, 2011, Mellinger & Clark 2003, McDonald et al. 2006, Buchan et al. 2014). At present, only 4 subspecies of blue whale are recognized worldwide (Rice 1998), while at least 12 geographically distinct acoustic signatures have been identified. Acoustic studies revealed the importance of the Indian Ocean for Antarctic and pygmy blue whales as a migrating, wintering, and likely feeding area (Stafford et al. 2004, 2011, Samaran et al. 2010a, 2013, Tsang-Hin-Sun et al. 2015). However, most of these studies were limited to 1 or 2 yr of observation. Moreover, at present, there are no post-whaling data on the distribution of fin whales in the area, although there is acoustic evidence of their presence (Tsang-Hin-Sun et al. 2015).

Since the end of 2009, a network of hydrophones has been deployed in the southern Indian Ocean to continuously monitor the low-frequency sounds produced by the seismic and biological activity (Royer 2009, Tsang-Hin-Sun et al. 2016). This acoustic observatory, called OHASISBIO (Observatoire Hydro Acoustique de la SISMicité et de la BIODiversité), now comprises 7 yr of acoustic records at 6 sites spanning an area of 9 000 000 km². The analysis of this dataset shed light on the seasonal and geographic distribution of Antarctic blue whales in the southern Indian Ocean from 2010 to 2016 (Leroy et al. 2016). In this paper, we extend this analysis to pygmy blue whales and fin whales, based on coarser power spectral density (PSD) analyses.

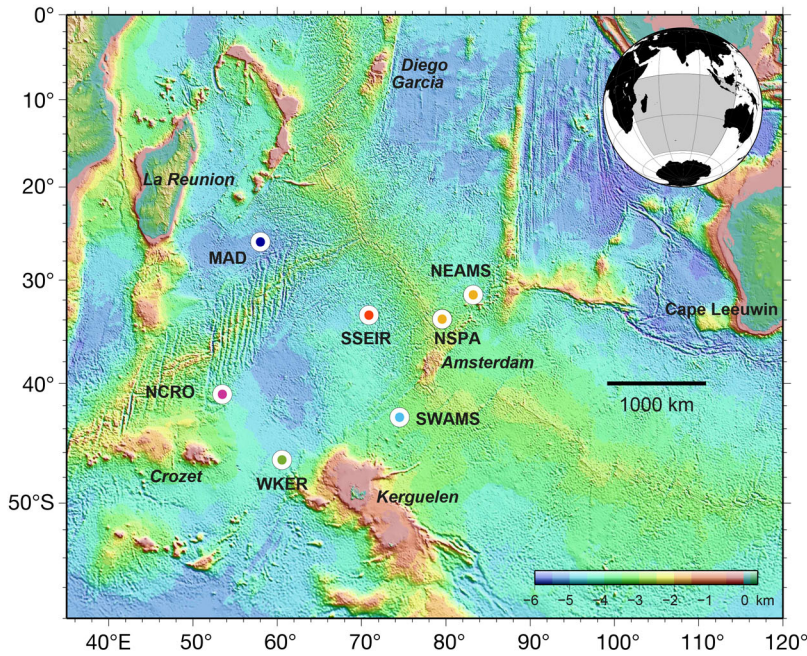


Fig. 1. Hydrophone locations of the OHASISBIO network in the Indian Ocean (circles). Color scale indicates depth. See ‘Data acquisition’ for a description of the sites

MATERIALS AND METHODS

Data acquisition

The acoustic data were collected by a hydrophone network in the framework of the OHASISBIO hydroacoustic experiment (Royer 2009). This network, initially deployed in December 2009 at 5 sites in the southern Indian Ocean, was designed to monitor low-frequency sounds produced by seismic and volcanic events (Royer et al. 2015, Tsang-Hin-Sun et al. 2016), and by large baleen whales. Instruments were deployed south of La Reunion Island in the Madagascar Basin (MAD), northeast of the St Paul and Amsterdam plateau (NEAMS), mid-way between the Kerguelen and Amsterdam islands (SWAMS), north of Crozet Island (NCRO) and west of Kerguelen Island (WKER) (Fig. 1). In 2014, a new site was

established in the northern Crozet Basin (SSEIR). All moorings were recovered and redeployed annually, except in January 2016 when poor weather conditions prevented the recovery of the hydrophones at the WKER and NEAMS sites. Instead, a new mooring was deployed at the WKER site, and a provisional mooring was deployed at 35° S, 079° E (NSPA). Each mooring consists of an expandable anchor, an acoustic release, and an autonomous hydrophone programmed to record acoustic waves continuously at a rate of 240 Hz with a 24-bit resolution and a sensitivity of -163.5 dB re: $1\text{V } \mu\text{Pa}^{-1}$ (see D’Eu et al. 2012 for instrumental details). Hydrophones are deployed in the axis of the sound fixing and ranging (SOFAR) channel, from 500 to 1300 m below sea surface depending on the site. Data are retrieved every year during the annual voyages of the R/V ‘Marion Dufresne’ to the French Southern and Antarctic Territories. The database comprises nearly continuous acoustic data over 7 yr (2010–2016), barring

a few months or years depending on the site, due to battery failures or instrument losses (see Leroy et al. 2016 for more details). Data recorded at the NCRO site in 2010 and 2013 were excluded from the analyses since those records were hindered by high noise levels likely due to the strumming of the mooring line. Deployment periods are summarized in Fig. 2 and listed in Table S1 in the Supplement at www.int-res.com/articles/suppl/n037p289_supp.pdf.

PSD analysis

As noted above, baleen whales emit stereotyped calls, patterned in sequences with regular inter-call intervals (i.e. song). These acoustic signatures are readily distinguishable among the different acoustic

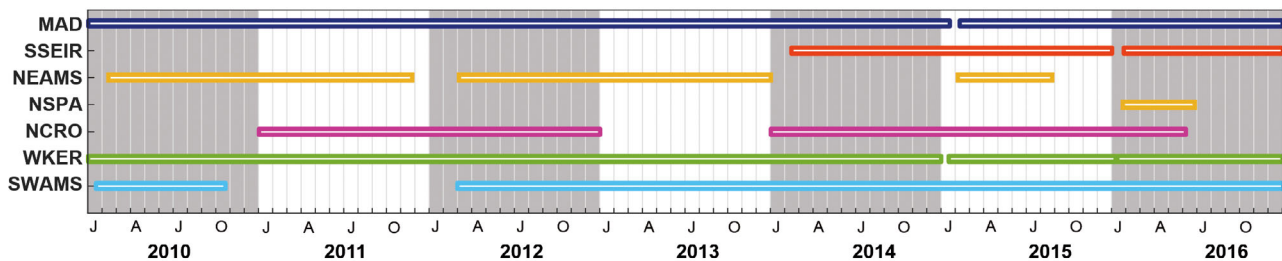


Fig. 2. Periods of continuous acoustic recordings analyzed at each site (color coded as the circles in Fig. 1)

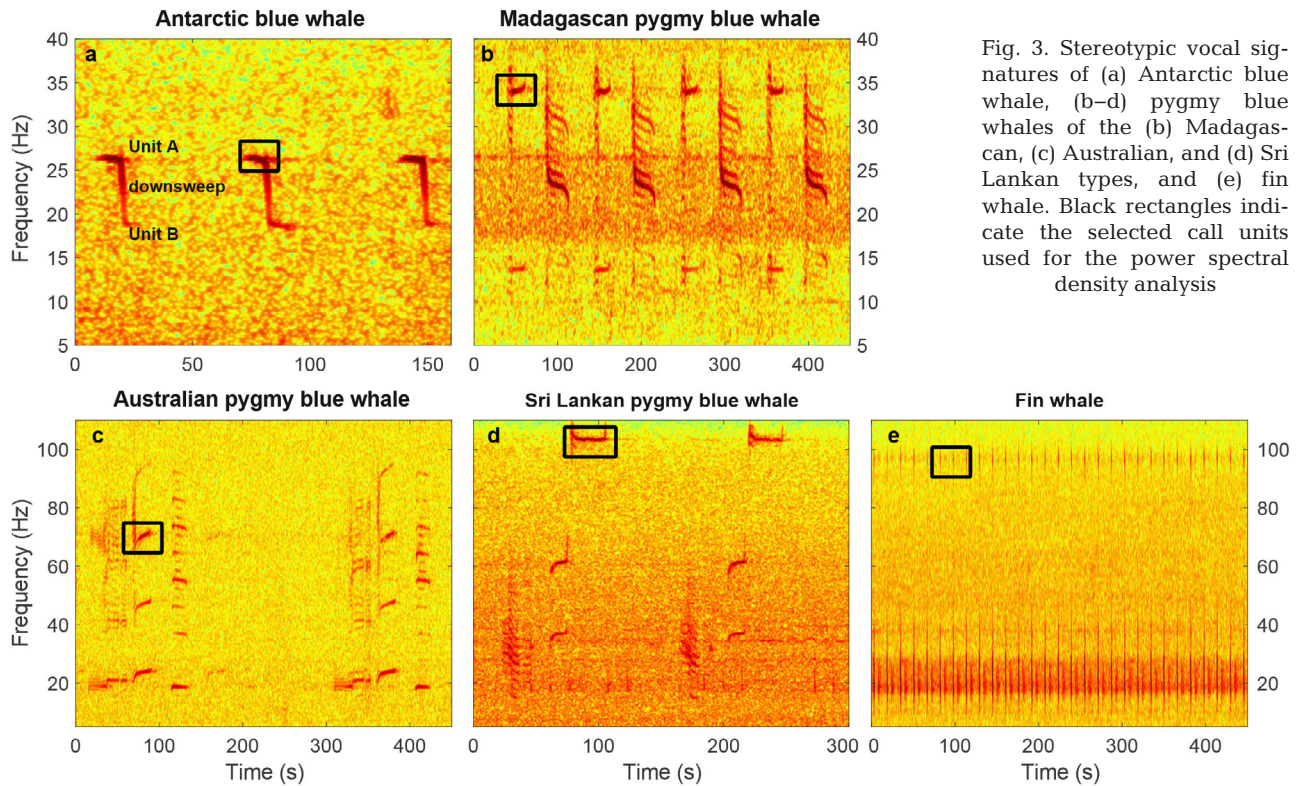


Fig. 3. Stereotypic vocal signatures of (a) Antarctic blue whale, (b–d) pygmy blue whales of the (b) Madagascar, (c) Australian, and (d) Sri Lankan types, and (e) fin whale. Black rectangles indicate the selected call units used for the power spectral density analysis

populations, based on their time-frequency characteristics. The signals of Antarctic and Indian Ocean blue whales (Fig. 3) are now well described in the literature (Alling et al. 1991, Ljungblad et al. 1998, Stafford et al. 2004, 2011, Rankin et al. 2005, Samarán et al. 2010a, 2013).

Worldwide, fin whales emit short duration, broadband pulses (<1 s) often called ‘20 Hz pulses’ (Watkins et al. 1987), ranging from ~15 to 30 Hz; in the Southern Hemisphere, they simultaneously produce an upper note near 89–99 Hz (Širović et al. 2009, Gedamke & Robinson 2010, Fig. 3e). The upper note produced by Antarctic fin whales varies geographically; this pulse occurs at 89 Hz off west Antarctica and at 99 Hz off east Antarctica (Širović et al. 2009). Long-term spectral averages of our data show that, in the southern Indian Ocean, fin whales also produce a pulse at ~99 Hz.

One way to assess the broad-scale presence of vocalizing whales is to compare the acoustic power in the frequency bands of their vocalizations to the acoustic power in adjacent frequency bands (Gedamke et al. 2007, Širović et al. 2009). This method, known as PSD analysis, is commonly used to determine the seasonal presence of blue and fin whales in large acoustic datasets (Curtis et al. 1999, Širović et al. 2004, 2009, Gavrillov et al. 2012, Nieukirk et al. 2012, Leroy et al. 2016, Thomisch et al. 2016, Menze et al. 2017).

To assess this ratio, hereinafter called the ‘chorus-to-noise ratio’ (CNR), we first selected specific units of each vocal signature, either because they occurred consistently and loudly, or for their distinctiveness from the other species units (units outlined by black rectangles in Fig. 3a–e). For the pygmy blue whales, we selected the 35 Hz unit of the Madagascar-type call (Fig. 3b), the 70 Hz harmonic of the Australian-type call (Fig. 3c), and the 105 Hz unit of the Sri Lankan-type call (Fig. 3d). Finally, to avoid the overlap between the fin whale 20 Hz pulse and the Antarctic blue whale Z-call, we used the 99 Hz component of the fin whale vocal signature (Fig. 3e). To consistently study all the blue whale subspecies recorded by the OHASISBIO array with the same PSD metric, we applied the same weekly PSD analyses to Antarctic blue whale calls, based on the unit A of a Z-call, near 26 Hz (Fig. 3a). Note that the selected frequency band for analyzing the presence of Antarctic blue whale calls is extremely narrow and focuses on Z-call unit A, hence avoiding any energy from other calls in the 18–28 Hz frequency range (e.g. fin whale 20 Hz pulses, Madagascar pygmy blue whale 25 Hz unit). In a previous analysis (Leroy et al. 2016), the geographic and seasonal distribution of Antarctic blue whales was inferred from individual calls, automatically detected using a subspace projection algorithm (Socheleau et al. 2015). Comparing these results provides a way to cross-validate the 2 approaches.

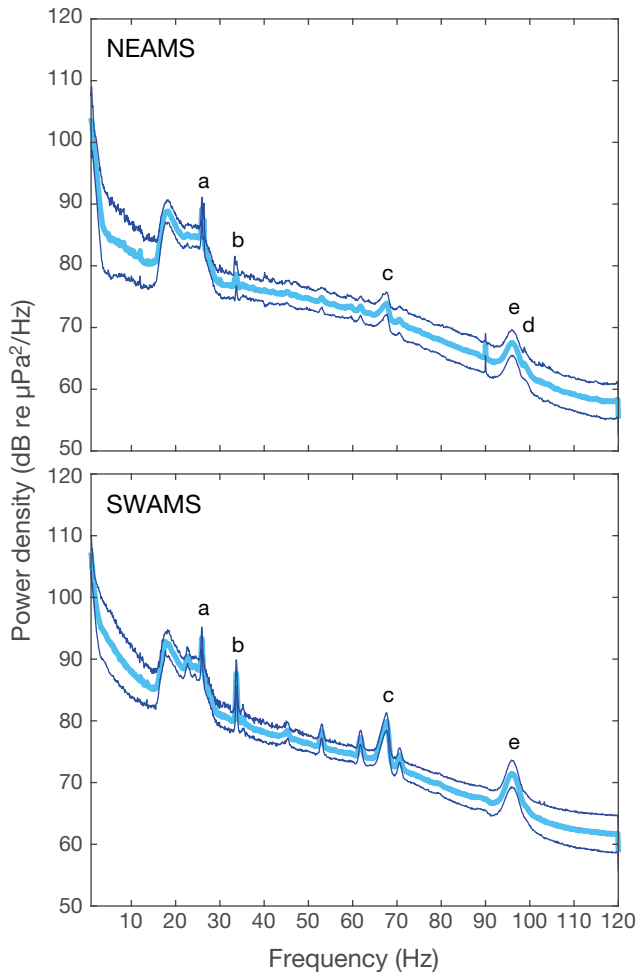


Fig. 4. Power spectral density of the data for sites NEAMS and SWAMS (see Fig. 1) for April 2015 (mean level and standard deviation). The letters refer to the selected frequencies for the Antarctic blue whale (a), the Madagascan pygmy blue whale (b), the Australian pygmy blue whale (c), the Sri Lankan pygmy blue whale (d) and the fin whale (e) (see Table 1)

The PSD for each acoustic file (~6 h 28) was computed using the P-welch Matlab function, over 300 s windows, with 50% overlap and a frequency resolution of 0.0018 Hz. The averaged power (in dB Hz⁻¹ re: 1 µPa) was then calculated (1) in the frequency range that encompassed each unit selected to characterize the vocal signature of each species or subspecies (Fig. 4, Table 1), and (2) in adjacent frequency bands of noise above and below these units (upper and lower noise windows in Table 1). Finally, following Širović et al. (2009), the average power density of the lower and upper noise windows was subtracted from the power of the selected unit frequency band. Note that for the Antarctic blue whale and the Sri Lankan pygmy blue whale, we only used an upper noise window since a

lower noise window would have fallen into the frequency range of fin whale calls; a lower noise band relative to Antarctic blue whale Z-calls would overlap with fin whale 20 Hz pulses and that relative to the selected Sri Lankan frequency would overlap with the fin whale 99 Hz pulse. In addition, since the PSD rapidly decreases with frequency, we fitted the power density of the noise level in the 102–106 Hz range to a straight line, and then extrapolated and subtracted it from the call power level between 99 and 102 Hz to estimate the CNR of the Sri Lankan-type call.

The resulting CNR values for all species were then averaged by week for each call type and each recording site. The mean seasonality for each species is estimated by averaging the weekly CNR values over the available years of data. The peak seasonality of the CNR values corresponds to the dates of the upper quartile of the cumulative distribution of CNR ranked by week.

RESULTS

Geographic distribution

The vocal signatures of the different species were not recorded uniformly across the study area, reflecting differences in the geographic distribution of these acoustic populations across the basin. Antarctic blue whales and fin whales were recorded at all sites (Fig. 5). Madagascan pygmy blue whales were recorded at every site except NEAMS, while Australian pygmy blue whales were only recorded at SSEIR, SWAMS, and NEAMS. Lastly, Sri Lankan pygmy blue whales were only recorded at the NEAMS site, but with very low CNR (Fig. 6c). The NEAMS site is mostly dominated by fin and Antarctic blue whale choruses. In contrast, the SWAMS and SSEIR sites show the greatest acoustic diversity, with 3 blue whale call types and fin whales.

Table 1. Frequency bands of the computed power spectral density for the call units of interest and the bracketing noise bands. BW = blue whale, PBW = pygmy blue whale, na = not applicable

	Call-unit frequency band (Hz)	Lower noise window (Hz)	Upper noise window (Hz)
Antarctic BW	25.5–26.8	na	30.0–33.0
Madagascan PBW	33.5–34.5	30.0–32	36.0–38.0
Australian PBW	67.1–70	64.0–66.0	71.0–73.0
Sri Lankan PBW	98.9–102.1	na	102.0–106.0
Fin whale	95.2–97.8	91.0–93.0	99.0–101.0

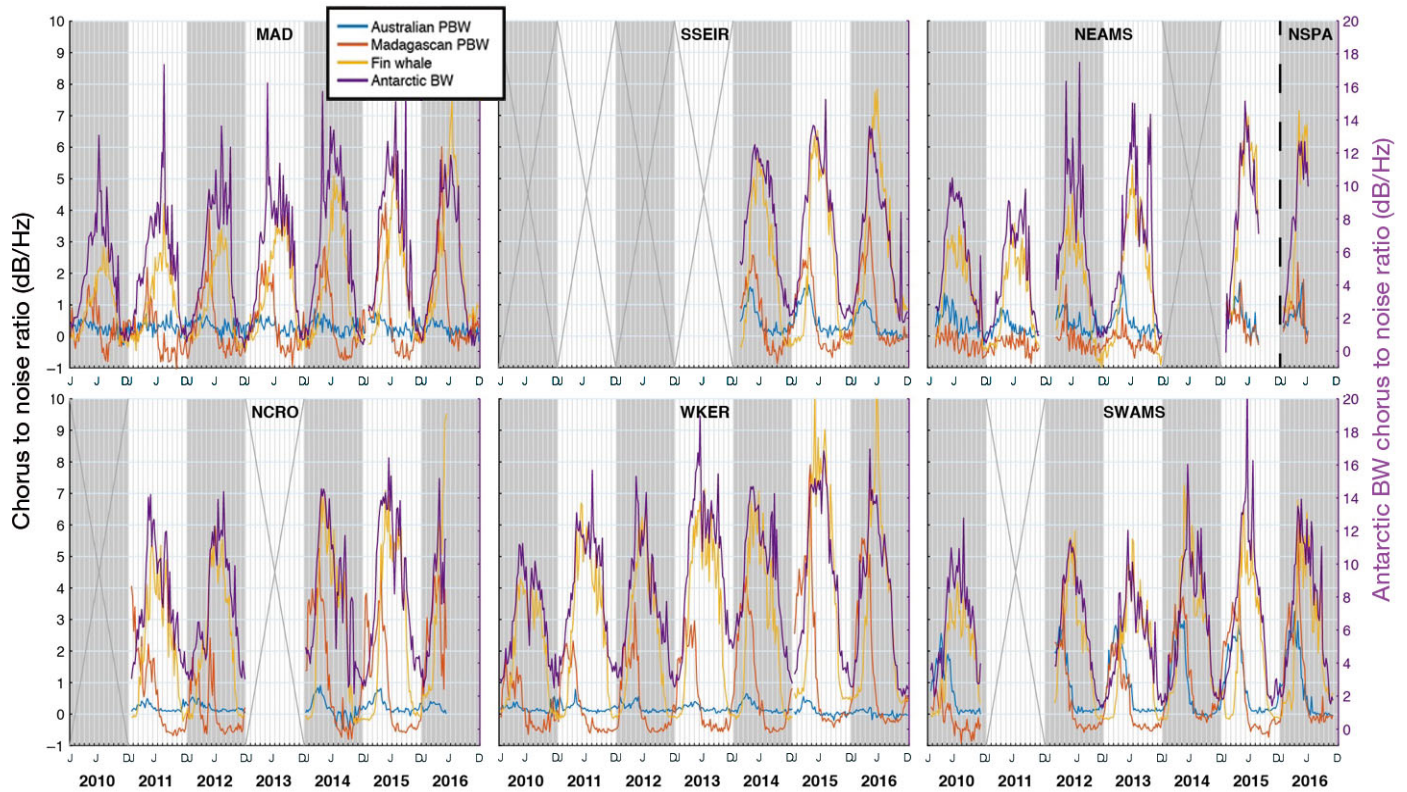


Fig. 5. Weekly means of chorus-to-noise ratio of each acoustic population for every recording site of the OHASISBIO hydrophone network. NSPA results are displayed with NEAMS, since this hydrophone was deployed temporarily in 2016 to replace the NEAMS site. Sri Lanka pygmy blue whale calls are only detected at NEAMS and have a very low chorus-to-noise ratio level compared with the other call types; for sake of clarity, their seasonality is only shown in Fig. 6c. Data are given for January, June, and December (DJ: December/January). For location of sites see Fig. 1. BW = blue whale, PBW = pygmy blue whale

Seasonal distribution

The presence of the studied whale species in the OHASISBIO array is highly seasonal and this seasonality is consistent over the 3 to 7 yr of data analyzed per site (see Fig. S1 in the Supplement). Furthermore, the seasonality of the different call types varies among species and locations (Figs. 5 & 6).

Pygmy blue whales

Madagascan pygmy blue whales. The presence of the pygmy blue whale Madagascan call type is strongly seasonal and occurs almost exclusively from January to June (austral summer to autumn) at the southernmost stations (NCRO, WKER, SWAMS, and SSEIR). The CNR level is low everywhere outside of this 6 mo period. At the northernmost station MAD, its seasonality is shorter, from the end of March to

June (austral autumn), and the peak CNR is delayed by about 2 mo relative to the other sites (Fig. 6a). The peak CNRs for the Madagascan chorus are highly variable among sites (Table 2) and occur as early as mid-January at NCRO and as late as the third week of March at MAD. For all sites but MAD, the CNR rapidly decreases after the end of May. For all sites, however, there is no CNR chorus from July to December (Fig. 6a).

Australian pygmy blue whales. Overall, the Australian call-type chorus shows a similar seasonality to the Madagascan call type, except that there are much greater geographic differences in the CNR levels. At the 3 easternmost sites of the array, SWAMS in particular, the CNRs are very high (Fig. 6b), whereas at the western sites, MAD, NCRO, and WKER, CNRs are almost null. However, the chorus peak of this call type is very similar among sites: from the first to the third week of February until the first to the third week of May (Table 2).

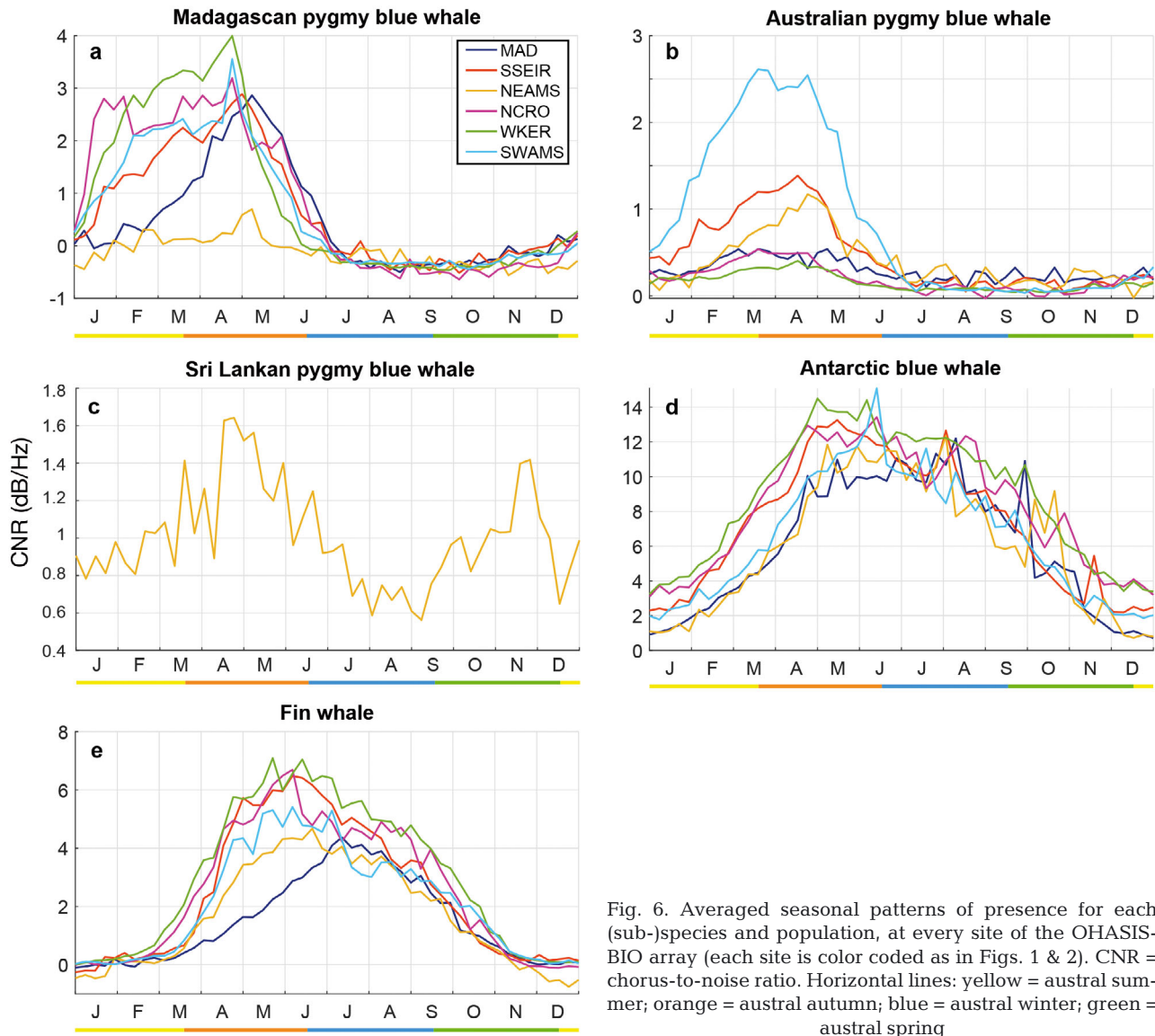


Fig. 6. Averaged seasonal patterns of presence for each (sub-)species and population, at every site of the OHASIS-BIO array (each site is color coded as in Figs. 1 & 2). CNR = chorus-to-noise ratio. Horizontal lines: yellow = austral summer; orange = austral autumn; blue = austral winter; green = austral spring

Sri Lankan pygmy blue whales. This call type is only observed at a single site (NEAMS). Despite a low CNR, a seasonal pattern is distinguishable, with 2 peaks from March to June then in November (Table 2, Fig. 6c).

Antarctic blue whales

Antarctic blue whales are recorded nearly year-round at all sites, from February to November (Fig. 6d). The chorus starts to increase at the 3 southernmost sites in February and roughly a month later at the 3 sites further north (Fig. 6d). The peak CNR for most sites occurs from the middle or end of April to early August. The exception is the MAD site where

the peak CNR occurs mid-May (Table 2). For all sites, however, CNR starts declining steadily after August up to December (Fig. 6d).

Fin whales

The presence of the fin whale chorus is strongly seasonal and occurs from March to November (Fig. 6e). The peak CNR occurs from the end of April to late August (austral autumn and winter, Table 2), except at the northernmost site (MAD) where the peak CNR occurs from the first week of June to the first week of September. The fin whale chorus is first detected in March at all sites, with WKER and NCRO ramping up more sharply from March to April than

Table 2. Peak seasonality (date range for the upper quartile of CNR values) for each call type at each location. BW = blue whale, PBW = pygmy blue whale, na = not applicable. See Fig. 1 for location of sites

Call type	MAD	SSEIR	NEAMS	NCRO	WKER	SWAMS
Madagascan PBW	23 Mar–21 Jun	1 Mar–31 May	22 Feb–24 May	19 Jan–4 May	8 Feb–17 May	16 Feb–18 May
Australian PBW	16 Feb–25 May	8 Feb–11 May	28 Feb–8 Jun	23 Feb–25 May	8 Feb–18 May	16 Feb–18 May
Sri Lankan PBW	na	na	22 Mar–21 Jun and 15 Nov–29 Nov	na	na	na
Antarctic BW	18 May–10 Aug	27 Apr–10 Aug	3 May–3 Aug	20 Apr–24 Aug	20 Apr–10 Aug	27 Apr–10 Aug
Fin whale	8 Jun–7 Sep	27 Apr–27 Jul	11 May–7 Aug	27 Apr–24 Aug	27 Apr–27 Jul	27 Apr–17 Aug

the other sites, followed by SSEIR, SWAMS, and NEAMS (Fig. 6e). At all sites, the chorus declines throughout September and October and reaches a minimum from November to February (austral summer).

DISCUSSION

It is increasingly clear from the OHASISBIO data that the southern Indian Ocean is an important habitat for large whales. The Indian Ocean has the largest variety of blue whale vocal signatures globally including 3 'acoustic populations' of pygmy blue whales (Stafford et al. 2011). Further, the consistent, seasonal presence of Antarctic blue and fin whales throughout the subantarctic Indian Ocean suggests that these species are widespread at mid-latitudes during much of the year. The present study illustrates the regular geographic and seasonal variation in the occurrence of pygmy blue whales, which supports the use of song as a robust means of defining geographic populations and assessing their habitat.

Low-frequency choruses of these species have been hypothesized to be detectable over hundreds to perhaps thousands of kilometers (Cummings & Thompson 1971, Payne & Webb 1971). The estimation of the chorus detection range is beyond the scope of this paper. First, it would require a robust estimation of the call source level, and of the detection range of individual calls. For the southern blue whales, these estimates are scarce and based on a very limited number of calls (Širović et al. 2007, Samaran et al. 2010b, Gavrilov et al. 2011). Second, the detection range is likely to vary with the environmental conditions surrounding the instruments, known to change with latitude, longitude, season, and the depth of the hydrophone or of the vocalizing animals (Helble et al. 2013a,b, Širović et al. 2015). Finally, with these parameters known, a proper esti-

mate of the chorus detection range would require modeling the emission of numerous calls by several individuals at various distances and azimuths around a hydrophone. This question would thus call for an entire dedicated study.

Nonetheless, our records suggest that this range could be only in the order of hundreds up to perhaps 1000 km. Indeed, the CNR seasonality of Australian and Madagascan pygmy blue whales is largely different at SWAMS, NEAMS, and SSEIR, which are all less than 1000 km apart (e.g. in 2015 or 2016 in Fig. S1). This is even more striking for Sri Lankan pygmy blue whales, whose chorus is recorded only at NEAMS and nowhere else. An exception may be the Antarctic blue whales, whose chorus appears relatively identical at every site. However, Leroy et al. (2016) have shown that this chorus at the same geographical sites shows high spatial variability. We thus believe that the CNR is a pertinent proxy to study the presence of vocalizing baleen whales on multi-year and broad-basin scales.

Variation in CNR could also be due to changing propagation conditions, e.g. CNR may increase because of lower noise levels. However, noise level does not follow the CNR pattern (see Tsang-Hin-Sun et al. 2015, Leroy et al. 2016), which rejects this hypothesis. As a result, we do believe that seasonal changes in CNR could be attributed either to calling animals getting seasonally closer to the site, or to more animals calling and contributing to the chorus, or to seasonal changes in their acoustic behavior, or to some combination of these. At present, although we cannot be entirely certain, we do not believe that the changes in CNR are due to changes in acoustic behavior, at least for blue whales. This species appears to produce characteristic song phrases throughout the year (e.g. Širović et al. 2004, Stafford et al. 2004, Samaran et al. 2013, Leroy et al. 2016). Without information on the numbers and distributions of calling whales around the hydrophone, distinguishing

between the first 2 possibilities is difficult. We do know from Leroy et al. (2016), in which both counts of detected calls and CNR for some of the same data were reported, that the number of individually detected calls matches fairly well with the CNR curves. This suggests that, for some sites, increases in CNR are due to animals moving closer to the hydrophones; to be detected automatically, individual calls need to be loud and clear, and therefore relatively close to the hydrophone.

Madagascan pygmy blue whales

The only site where Madagascan pygmy blue whale calls are not recorded is our eastern station (NEAMS), indicating that this population mostly inhabits the western and southern Indian Ocean basin. The Madagascan call type is only recorded during 6 mo (during austral summer to autumn) except at the northernmost station (MAD) where its seasonal presence is shorter (austral autumn only). These geographic and seasonal patterns are consistent with observations from the same area in 2007–2008 (Samaran et al. 2013). A recent study confirms their presence exclusively during autumnal months near our northern site (MAD) (Dréo et al. in press). Similarly, in 2004, Madagascan pygmy blue whale calls were detected near Crozet Island from January to June (Samaran 2008, Samaran et al. 2010a), which is consistent with our observations at the NCRO site. Our analysis thus highlights the robustness of seasonal occurrence and also extends our understanding of the spatial distribution of this population. The Madagascan pygmy blue whale population is distributed in summer and autumn (January to June) between 26° S (MAD) and 46° S (WKER), 52° E (NCRO) and 74° E (SWAMS). The western Indian Ocean is probably not a winter or spring habitat for this population of pygmy blue whales. Where these animals go during these seasons is presently unknown. However, a few instances of this call type were recorded from May to July at Diego Garcia (Stafford et al. 2011) and in the Mozambique Channel, off the northwest coast of Madagascar (S. Cerchio et al. unpubl.), suggesting a migration to northern latitudes at the end of autumn, which may be their wintering area. Visual observations and whaling data suggest that blue whales are found off the coast of South Africa (Branch 2007), and recent acoustic observations also report their presence from mid-October to December in the Mozambique Channel, off the northwest coast of Madagascar (S. Cer-

chio et al. unpubl.). Based on this seasonality, we assume that this population is acoustically active during at least 10 mo of the year. Therefore the absence of calls in our study area during austral winter and spring reflects the absence of individuals and not a change in their acoustic behavior.

Australian pygmy blue whales

For the Australian pygmy blue whales, a strong chorus is observed at SWAMS and SSEIR sites, and also at NEAMS but with a lower CNR. As noted by Samaran et al. (2013), their presence is strongly seasonal, with acoustic occurrences in winter and autumn, and no vocal activity from July to January. They also noted relatively fewer calls at NEAMS than at SWAMS. Australian pygmy blue whale calls have also been recorded off the western and southern coasts of Australia from February to July in the Perth Canyon, from February to May in the Bass Strait (Balcazar et al. 2015), from March to June off Portland, Australia (Tripovich et al. 2015), and from February to July as well as November to December at Cape Leeuwin (Gavrilov & McCauley 2013). The latter observation suggests that, like the Madagascan pygmy blue whales, the Australian population is vocally active at least during 8 mo of the year, which supports the idea that the absence of calls in our study area during the austral winter and spring is due to a displacement of the population to another area, and not a change in the whale vocal behavior. Here again, the location of the wintering area is puzzling, although slightly better documented off the West Australian coast thanks to satellite telemetry. Indeed, Double et al. (2014) showed that Australian pygmy blue whales that feed off western and southern Australia travel relatively close to the Australian coastline to reach potential breeding grounds in Indonesian waters by June. Their southward migratory route, from September to December, remains uncertain due to a lack of satellite data for this period, and lack of call detections between July and the end of October. It is also not known whether the whales recorded in the west of our study area share the same wintering areas as the satellite-tracked whales. Based on the recording of these signals in the southwestern Indian Ocean between January and June, it is possible that a part of this population may migrate longitudinally from east to west in the Indian Ocean. This suggests there may be multiple migratory routes for this population of blue whales.

Sri Lankan pygmy blue whales

The chorus of Sri Lankan pygmy blue whales is absent at all sites but NEAMS. It confirms earlier observations in 2007 at NEAMS, although SWAMS also recorded few calls (Samaran et al. 2013), with calls occurring throughout the year with a slight peak in spring. In our study, in contrast, we found a decrease in the level of chorus in spring at NEAMS. Relatively few calls were detected near Crozet in 2004 (Samaran et al. 2010a). This seasonality more closely resembles that reported near Diego Garcia (Stafford et al. 2011), which displays a first peak in March–April and a second peak from November to December. This lack of Sri Lankan chorus in our data and the few detections from previous studies in the same area support the common belief that this population mostly dwells in the northern Indian Ocean, with a limited migration to subantarctic latitudes during the austral summer and autumn, i.e. after the period of high productivity driven by monsoons in the northern Indian Ocean (Branch 2007, Samaran et al. 2013).

Antarctic blue whales

For the Antarctic blue whale, the in-depth analysis of the first 6 yr of data (2010 to 2015) by Leroy et al. (2016) used monthly averages of the CNR instead of weekly averages. Both averages show similar seasonal patterns, but the weekly CNR levels help to refine the picture. They show a progressive arrival of the whales in autumn from the southernmost to the northernmost sites, and their presence throughout the winter and spring.

This south to north migration is consistent with that deduced from individual call numbers (Leroy et al. 2016). This agreement *a posteriori* validates the weekly CNR approach, although coarser than the call detection approach.

Fin whales

The arrival of fin whales at the different sites also follows a latitudinal gradient. This observation provides evidence for a likely south to north migration of the species. Fin whales are first heard south of the array at the end of austral summer, after spending the summer feeding off Antarctica (Širović et al. 2004, 2009), and then move northwards to subantarctic and subtropical latitudes during the winter.

The CNR reaches its peak in May at the southern sites and in July–August at the northernmost site (MAD) and decreases synchronously across all sites toward October–November. The seasonal decrease in CNR may result from a change in acoustic behavior. Fin whale vocalizations, when produced in series, have been attributed to a mating behavior during the period of reproduction, which would explain a weak CNR during the austral summer, when the whales are feeding (e.g. Watkins et al. 1987, Croll et al. 2002, Širović et al. 2009). Furthermore, there is some indication that fin whales do not produce long bouts of 20 Hz pulses year-round but change their vocal behavior (Širović et al. 2013).

CONCLUSIONS

The results of this wide-range and long-term data analysis confirm the importance of the southern Indian Ocean for several populations of large whales, simultaneously, as a possible feeding area, particularly for pygmy blue whales (Samaran et al. 2010a, 2013), and as a wintering area for Antarctic blue whales (Samaran et al. 2013, Leroy et al. 2016) and fin whales. This is also the first broad-scale assessment of the seasonal and geographic distribution of fin whales in the Indian Ocean. Pygmy blue whales do not migrate to the Antarctic waters but appear to spend their lives in subantarctic and subtropical waters. The Madagascan and Australian acoustic populations show similar seasonalities but clearly different distributions. Furthermore, their seasonal occurrence in our hydrophone array is distinct from that of Antarctic blue whales and fin whales. The latter are heard throughout the austral winter with the lowest CNR level in austral summer when they presumably are off Antarctica.

Although the CNR metric does not provide fine-scale information on acoustic behavior or seasonal variations, it is an efficient tool for investigating the broad-scale spatial and seasonal distribution of different whale populations. In our study area, this approach emphasizes the sympatric occurrence of several (sub-)species of blue whales and fin whales over many years and thousands of kilometers. These results call for future studies examining the inter-annual occurrence of each species in the context of oceanographic and environmental variability.

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