Distribution of blue whale populations in the southern Indian Ocean based on a decade of acoustic monitoring

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Abstract :

Globally, the Indian Ocean appears to have the greatest blue whale (Balaenoptera musculus ssp) acoustic diversity, with at least four acoustic populations from three defined sub-species. To understand how these different populations use this region as habitat, we first need to characterize their spatial and seasonal distributions. Here, we build on previous passive acoustic monitoring studies and analyze a passive acoustic dataset spanning large temporal (9 years) and spatial (3 to 9 sites covering more than 12 million km2 of potential acoustic habitat in the southwest Indian Ocean) scales. A novel detection algorithm was employed to investigate the long-term presence of Antarctic blue whale and SEIO and SWIO pygmy blue whale calls. We found that Antarctic and pygmy blue whales have completely different spatial and seasonal distribution in the southern Indian Ocean. Antarctic blue whales are heard almost year-round on the whole array, with great inter-annual variability. The two pygmy blue whales share a highly stable seasonal acoustic presence, but their geographical distributions overlap at only a few central Indian Ocean sites. However, Antarctic and pygmy blue whale acoustic co-occurrence is common, especially in sub-tropical waters. These temporal and spatial distributions strengthen our understanding of seasonal occurrence and habitat use of distinct populations of blue whales in the southern Indian Ocean. A better comprehension of the ecology of Indian Ocean blue whales will require interdisciplinary studies to examine the drivers of the variability seen from passive acoustic studies.

Keywords : Antarctic blue whale, pygmy blue whale, passive acoustics, population distribution

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$_{34}$ 2 Introduction

- ³⁵ The Indian Ocean, particularly its southern extent, is one of the oceans with the greatest blue
- ³⁶ whale acoustic diversity (McDonald et al., 2006). As a response to extensive commercial whaling
- 37 in both the Southern and Indian Oceans which greatly depleted numbers of blue whales, in
- ³⁸ 1979 the International Whaling Commission (IWC) created the Indian Ocean Whale Sanctuary
- ³⁹ (IOWS), the first ever region where commercial whaling was banned for all species(IWC, 1980).
- 40 Three blue whale subspecies are seasonally present in the Indian Ocean: the Antarctic blue
- ⁴¹ whale (Balaenoptera musculus intermedia) and the pygmy blue whales (B. m. brevicauda

indica). Antarctic and pygmy blue whales are genetically distinct and differ in and B. m.42 body size and acoustic signatures (Ichihara, 1966; LeDuc et al., 2007; Ljungblad et al., 1998). 43 Furthermore, at least three distinct populations of pygmy blue whales have been identified: 44 the Northwestern (NWIO), Southwestern (SWIO) and Southeastern (SEIO) pygmy blue whale 45 populations (Stafford et al., 2011). Whereas the Antarctic blue whale has been declared as 46 an endangered species by the IUCN (International Union for the Conservation of Nature), 47 the status of the pygmy blue whales is unknown and therefore considered 'data deficient' by 48 the IUCN (Cooke, 2019). Monitoring blue whales remains a challenge due to the scarcity of 49 individuals and to the extent and location of their habitat, largely encompassing remote and 50 inaccessible regions of the ocean. Moreover, identifying pygmy from Antarctic blue whales by 51 visual observation is very difficult, as they look almost identical, despite the smaller length of 52 pygmy blue whales (Ichihara, 1966). Thus, most of the knowledge about blue whales in the 53 Indian Ocean comes from whaling data (Branch et al., 2007, 2009), and from passive acoustic 54 monitoring (Samaran et al., 2010a; Stafford et al., 2011; Samaran et al., 2013; Leroy et al., 2016; 55 Dréo et al., 2018). Blue whales are particularly good candidates for this type of observation, 56 because of their repetitive, long (more than 15 seconds), loud (more than 180 dB ref 1 uPa at 57 1m) and low frequency (20-100 Hz) calls (Cummings and Thompson, 1971). Blue whale calls 58 vary from one region to another and have been used to tell apart different blue whale sub-59 species and acoustic populations (McDonald et al., 2006). In the southern Indian Ocean, calls 60 of Southeastern Indian Ocean (Figure 1 a) and Southwestern Indian Ocean (Figure 1 b) pygmy 61 blue whale populations as well as Antarctic blue whale calls (Figure 1 c) have clear distinct 62 characteristics that are readily observed in the spectogram (McCauley et al., 2000; Samaran 63 et al., 2010a; Stafford et al., 2011). 64

⁶⁵ Whaling data depicted baleen whale migration as being a consistent movement between ⁶⁶ productive feeding grounds at high latitudes in summer, and breeding grounds at lower latitudes ⁶⁷ in winter (Kellogg, 1929; Mackintosh, 1942, 1966). However, year-round captures and sightings ⁶⁸ of Antarctic blue whales in whaling grounds at high or low latitudes suggest more complex ⁶⁹ migratory behaviors (Harmer, 1931; Branch et al., 2007). In agreement with these findings, ⁷⁰ evidence of year-round acoustic presence of Antarctic blue whales off Antarctica (Širović et al., ⁷¹ 2014; Thomisch et al., 2016) and Namibia (Thomisch et al., 2019), and observations of foraging

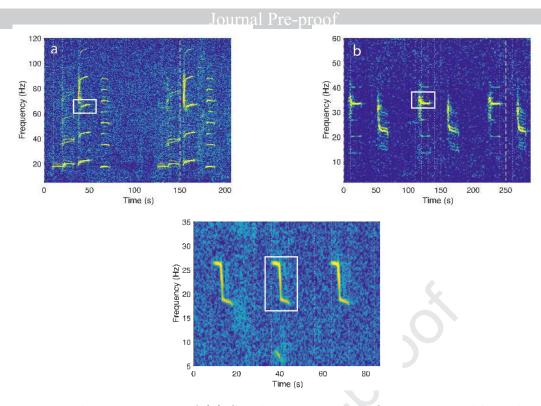


Figure 1: Typical spectrograms of (a) Southeastern Indian Ocean pygmy blue whale calls (b) Southwestern Indian Ocean pygmy blue whale calls, and (c) Antarctic blue whale calls from the Southern Indian Ocean

behavior en route towards summer feeding grounds (Visser et al., 2011) supports the idea of a 72 more complex migratory pattern. For instance, skipping migration to remain at feeding grounds 73 may benefit individuals to maximize their growth and body mass (Shaw and Levin, 2011). In 74 the southern Indian Ocean, Antarctic blue whale calls are detected year-round, with a lesser 75 presence during austral summer and a shift from subantarctic locations in austral autumn 76 to subtropical locations in the austral winter and back to subantarctic locations in spring 77 (September to November) (Stafford et al., 2004; Samaran et al., 2010a, 2013; Leroy et al., 78 2016). This seasonal pattern is generally stable over the years, but some variations suggest 79 that the migration routes are flexible (Samaran et al., 2010a, 2013; Leroy et al., 2016). In 80 contrast, pygmy blue whales present a totally different migration pattern. Short-term (Stafford 81 et al., 2011; Samaran et al., 2013) and broad-scale acoustic studies based on the chorus intensity 82 (intensity within the call frequency band) depict a longitudinal differentiation of the SEIO and 83 SWIO pygmy blue whale populations. The former are mainly present in the eastern Indian 84 Ocean and the latter in the western Indian Ocean. Yet, they seem to share a common seasonality 85 with an acoustic presence during all seasons except spring (Stafford et al., 2011; Samaran et al., 86 2013; Leroy et al., 2018b). 87

Despite their different distribution, SEIO and SWIO pygmy blue whales have both been 88 recorded near the Crozet archipelago (46°24'41" S, 51°45'22" E) (Samaran et al., 2010a) and 89 southwest of Amsterdam Island (37°50'00" S, 77°31'00" E)(Samaran et al., 2013), at the fringes 90 of their respective habitat (see map in Figure 2). Similar co-occurrence of pygmy blue whales 91 (SEIO and southwestern Pacific populations) has been reported in the Bass Strait, between 92 mainland Australia and Tasmania (McCauley et al., 2018), which marks the geographical barrier 93 between these two populations Balcazar et al. (2015). Sympatric acoustic presence of Antarctic 94 and pygmy blue whales has also been observed off southern Australia (Tripovich et al., 2015), 95 near the Crozet archipelago (Samaran et al., 2010a), in the Madagascar Basin, north and south 96 of Amsterdam Island (Samaran et al., 2013) and in the north of the Mozambique Channel 97 (Cerchio et al., 2018). 98

The function of songs for blue whales is not unanimously agreed upon. The fact that 99 only males are thought to sing (Oleson et al., 2007; Lewis et al., 2018) as well as the seasonal 100 repetition, high source levels (McDonald et al., 2001; Sirović et al., 2007; Samaran et al., 2010b) 101 and the long durations of the calls, point to a reproductive purpose (McDonald et al., 2001; 102 Oleson et al., 2007). Acoustic co-occurrence of different sub-species may therefore indicate 103 potential inter-subspecies breeding areas or the use of song to isolate different populations 104 from interbreeding (Stafford and Moore, 2005). However, the year-round detection of songs at 105 high-latitude feeding areas (Stafford et al., 2001; Širović et al., 2004, 2009; Thomisch et al., 106 2016) suggests that the calls may play additional roles, such as assisting in navigation and 107 prey detection (Clark and Ellison, 2004), or promoting the formation of pairs (Lewis et al., 108 2018; Oleson et al., 2007). Acoustic co-occurrence of multiple sub-species may also simply 109 reflect differing ecological strategies and/or habitat use by each subspecies, such as off Southern 110 Australia, which would be a migratory corridor for Antarctic blue whales and a feeding ground 111 for the SEIO pygmy blue whales (Tripovich et al., 2015). 112

To progress in our understanding of these concepts, this work presents a detailed analysis of the seasonal and spatial presence of Antarctic and pygmy blue whales, based on 9 years of continuous acoustic recordings (2010-2018) at multiple sites across the southern Indian Ocean. Relative to previous analyses, we provide a longer time series and new recording locations. We also base our analysis on the systematic detection of pygmy blue whale calls, when former stud-

ies only looked at the chorus power to describe their acoustic presence. The comparison between these two passive acoustic monitoring metrics is then discussed. These data yield a clearer picture on the seasonal acoustic presence of pygmy and Antarctic blue whales and spatially how they share the IWC IOWS. This information is essential for improving the management and conservation of the world's largest animal.

¹²³ **3** Material and methods

¹²⁴ 3.1 Data acquisition

The acoustic data used in this study were recorded by the OHASISBIO (Observatoire Hydro-125 Acoustique de la SISmicité et de la Biodiversité; Royer (2009)) hydrophone network, located in 126 the southwest Indian Ocean (see Figure 2). The network was deployed in December 2009 and is 127 still recording as of the date of publication. Between 2009 and 2016, it comprised 5 permanent 128 mooring sites, located south of La Réunion Island (MAD), north of Crozet archipelago (NCRO), 129 west of Kerguelen Island (WKER) and southwest and northeast of St Paul and Amsterdam 130 islands (SWAMS and NEAMS). In 2012-2013, a mooring was temporarily deployed near the 131 Equator, in the Central Indian Basin, east of Diego Garcia archipelago (RAMA) and since 132 2014, a new site was instrumented, south of the southeast Indian Ridge (SSEIR). In 2017, 133 the network geometry was slightly modified to improve the coverage of the northern areas and 134 refine the location of blue-whale wintering grounds, with three new sites RTJ, MAD-W and 135 MAD-E, the latter two on either side of the initial MAD site. The new site S-SWIR, south of 136 the southwest Indian ridge, replaced the NCRO site and an additional mooring (ELAN) was 137 installed at 56°S, south of Kerguelen plateau, to complete the spatial coverage southward. The 138 MAD and NCRO moorings are no longer deployed. 139

Each mooring is composed of an anchor, an acoustic release, an adjustable length of line and a submerged buoy containing the recording system. The instruments are moored between 1400m and 1300m depth, corresponding to the local sound fixing and ranging (SOFAR) channel 143 axis. The SOFAR works like a waveguide, where low frequency sounds can propagate over very 144 long distances (Lurton, 2002). The instruments record continuously at a sampling rate of

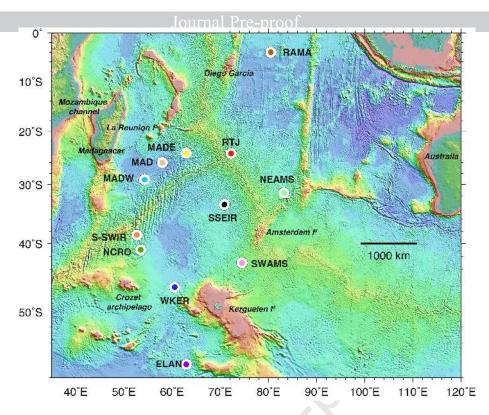


Figure 2: The OHASISIBIO hydrophone network in the Southern Indian ocean. Colored dots represent mooring sites.

¹⁴⁵ 240 Hz using a 24-bit analog-to-digital conversion and the recorded data are archived on the
¹⁴⁶ instrument (d'Eu et al., 2012).

The moorings are turned around annually and the data are collected every January/February during the annual scientific cruise of R/V Marion Dufresne to the French Southern and Antarctic Territories in the southern Indian Ocean. The current database comprises almost continuous acoustic records over 9 years (from 2010 to 2018), with some gaps mostly due to unexpected battery exhaustion. Table 1 summarizes the site coordinates and the recording periods of the data used in this study. The first six lines correspond to the long-term monitoring sites, and the last six lines to the short-term monitoring sites.

154 3.2 Acoustic data processing

The metrics used here to assess blue whale acoustic presence are the number of calls detected per week, month or year. For pygmy blue whale calls with multiple units, a single unit was detected, either because it was the loudest unit of the call or because its frequency did not overlap with that of other blue whale calls (selected units are outlined by white rectangles in

Table 1: Details of the OHASISBIO deployments with: mooring name; latitude and longitude ; starting and ending recording date. A "-" indicates continuous recording without data recovery ; an "x" sign indicates absence of data.

Site	Geo. Coor.	2010		20	2011		2012		2013		2014		2015		2016		2017		2018	
Site	Geo. Coor.	Start	Stop																	
MAD	26°05'S, 058°08'E	20/12/09	19/02/11	19/02/11	09/03/12	10/03/12	09/03/13	09/03/13	16/02/14	16/02/14	18/01/15	18/02/15	28/01/16	29/01/16	09/01/17	х	x	х	х	
NEAMS	31°35'S, 083°14'E	13/02/10	-	-	25/11/11	04/03/12	04/03/13	04/03/13	10/02/14	x	x	4/02/15	25/08/15	x	x	31/01/17	05/02/18	05/02/18	29/01/19	
SSEIR	33°30'S, 70°30'E,	x	x	х	х	х	х	х	х	13/02/14	04/02/15	05/02/15	18/01/16	25/01/16	04/02/17	04/02/17	08/02/18	08/02/18	23/12/18	
NCRO	41°00'S, 52°49'E	x	x	20/01/11	30/01/12	29/01/12	10/02/13	х	x	11/01/14	11/01/15	11/01/15	08/01/16	08/01/16	06/06/16	х	х	х	х	
SWAMS	42°59'S, 74°35'E	х	х	х	х	29/02/12	27/02/13	28/02/13	07/02/14	07/02/14	27/01/15	27/01/15	20/01/16	21/01/16	01/08/16	х	х	31/01/18	30/01/19	
WKER	46°38'S 60°07'E	28/12/09	24/01/11	25/01/11	03/02/12	04/02/12	14/02/13	15/02/13	15/01/14	15/01/14	01/01/15	16/01/15	01/08/16	12/01/16	20/01/17	20/01/17	19/01/18	19/01/18	28/07/18	
RAMA	03°50'S, 80°30'E,	х	х	х	х	05/05/12	-	-	11/12/13	х	х	х	х	х	х	х	х	х	х	
RTJ	24°15'S 72°15'E	x	x	x	x	x	х	x	x	x	x	x	х	x	x	x	x	11/02/18	10/02/19	
MAD-E	24°11'S, 63°01'E	x	x	х	х	х	x	х	x	х	х	x	х	х	х	07/02/17	13/02/18	13/02/18	21/07/18	
MAD-W	29°03'S, 54°16'E	х	х	х	х	х	х	х	х	х	x	х	х	x	x	06/01/17	06/01/18	06/01/18	3/11/18	
S-SWIR	38°33'S, 52°53'E	x	x	х	х	х	х	х	х	х	x	х	х	x	х	08/01/17	22/12/17	09/01/18	14/01/19	
ELAN	56°28'S, 62°59'E	x	x	х	x	x	х	x	х	x	x	x	x	x	x	x	x	16/01/18	23/01/19	

Figure 1). For Antarctic blue whales, the whole call was used for detection (Figure 1 c). For the SEIO pygmy blue whales, we selected the most powerful harmonic at 70 Hz (Figure 1 a). For the SWIO pygmy blue whales, we selected the 35 Hz unit (Figure 1 b), to avoid overlap with the Antarctic blue whale chorus. The chorus is the elevation of the noise in specific frequency bands produced by the accumulation of numerous distant calls overlapping (Širović et al., 2009; Thomisch et al., 2016).

¹⁶⁵ 3.2.1 Automated call detection

To facilitate the time-consuming and tedious task of manually detecting calls, an automated 166 detection algorithm based on dictionary learning and sparse representation of blue whale vo-167 calizations was used (Socheleau and Samaran, 2018). The principal asset of this method lies 168 in the alliance of large dictionaries, which take call variability into account, with linear combi-169 nations of several elements of those dictionaries, to reflect call complexity. The detector does 170 not require an *a priori* fixed template, but works with dictionaries built from temporal call 171 signals directly extracted from the data. It then tries to reconstitute the observed signal with 172 sparse combinations of the waveforms contained in the dictionary. The better the signal is re-173 constructed, the higher the resemblance metric (Socheleau and Samaran, 2018; Guilment et al., 174 2018). 175

¹⁷⁶ In such an endeavor, the difficulty is to avoid the detection of interfering signals and therefore

to avoid a time-consuming double check of each detection - while keeping a reasonable recall, at 177 least for high Signal to Noise Ratio (SNR) calls which are more likely to come from whales close 178 to the hydrophone. To achieve this goal, the algorithm was tested on a large manually annotated 179 data subset containing recordings from different seasons and locations of the OHASISBIO array. 180 A threshold corresponding to one false positive detection per hour was set and the corresponding 181 recall reached 90% for positive SNR calls (Torterotot et al., 2019). The detector was then tested 182 on an entire year of data (2015) at WKER site and every detection was manually double checked, 183 to characterize any interferences that could fool the algorithm and to re-evaluate the false alarm 184 rate in case of call absence. Most interferences are due to chorus, especially for SWIO pygmy 185 blue whale calls. Other interference categories include ship noise and unknown continuous 186 noise within the call frequency band. The number of false positive detections was stable across 187 different abundance scenarios (i.e. periods of high and low call presence) and was far below the 188 theoretical one-false-positive-detection-per-hour rate initially defined. The different annotation 189 procedures (i.e. manual annotation then automated detection versus automated detection then 190 manual double-check) might explain these variabilities. To account for the annual linear pitch 191 decrease of blue whale calls (Gavrilov et al., 2011, 2012; Leroy et al., 2018a), a new dictionary 192 was built for every year from the detector outputs based on a dictionary from a contiguous year. 193 The performance evaluation of the algorithm on the same data used in this paper is thoroughly 194 discussed in Torterotot et al. (2019). 195

¹⁹⁶ **3.3** Detection results analysis

Recordings with a small number of annual detections were manually double checked to assess whether or not these few detections accurately illustrated a blue whale acoustic presence. For SEIO pygmy blue whale calls, ELAN, MAD, SSEIR, MAD-E, MAD-W, NCRO, RTJ, S-SWIR and RAMA sites were double-checked ; for SWIO pygmy blue whale calls, ELAN, SSEIR, RTJ and RAMA sites were double-checked ; for Antarctic blue whale calls only RAMA site was double checked. If most of the detections were false alarms, the annual number of detections was set to 0, otherwise, all the detections were left as is.

²⁰⁴ Seasonal occurrence is presented as the absolute number of detections per week, for every

week with more than 6 days of recording. Weeks with fewer than 6 days are considered as 205 incomplete and the results are not presented. To study the inter-annual variability of the 206 acoustic seasonal pattern, we used the Pearson correlation coefficient, a non-parametric test 207 that is used to measure whether or not a correlation (*i.e.* linear relationship) exists between 208 call distribution from two consecutive years. To assess quantitatively how the different sub-209 species share a recording site, we compared their seasonal pattern using Spearman's correlation 210 coefficients. This statistic tests whether or not a correlation (*i.e.* monotonic relationship) exists 211 between the seasonal presence of two blue whale acoustic populations. For both correlation 212 tests (Pearson's and Spearman's), only the results with a p value < 0.05, meaning that the null 213 hypothesis cannot be rejected, will be reported. 214

Sympatry is defined as the number of hours per month with multiple acoustic blue whale populations detected normalized by the total number of recorded hours that same month over the whole recording period (2010-2018). To avoid taking too many false detections into account, a call type is considered detected when there was more than one detection within an hour.

Austral seasons are defined as follows: summer (December, January, February), autumn (March, April, May), winter (June, July, August), and spring (September, October, November).

Results at sites NCRO and S-SWIR are combined in the same figure for the sake of space: from 2011 until 2016 they refer to NCRO data and for 2017 and 2018 to S-SWIR data. Results for the long-term sites are illustrated in Figures 3 and 4, whereas results for the short-term sites are given in Table 2 or in the appendices.

225 4 Results

²²⁶ 4.1 Spatial distribution and long term trends

Figure 3 displays the number of detected calls per year for the long-term recording sites (rows) and the three blue whale calls (columns). Since blue whale acoustic presence is highly seasonal, normalizing the number of detections per year by the number of days of recording could lead to some misinterpretation, especially regarding pygmy blue whales. For example, at site WKER

the number of SWIO pygmy blue whale calls is similar in 2017 and in 2018. However the 231 hydrophone only lasted 6 months in 2018, from January to mid-July. Usually SWIO pygmy 232 blue whale calls are detected during the first 6 months of the year, so the number of calls at 233 WKER in 2017 and 2018 is similar. If the number of detections had been normalized, it would 234 have appeared that more calls were detected in 2018 than in 2017. Instead of normalizing the 235 number of calls per year by the recording duration, we show the actual detection number (color 236 bars) and the number of days of recording per year (black dots). For the short-term recording 237 sites, the results are given in Table 2 and in Appendix 1, except for RAMA which did not 238 contained any detections. 239

Table 2: Number of detected calls per year for each blue whale acoustic population at the short term OHASISBIO sites. The effort is in days per year with recordings.

		RT	J		MAD-E					MAD-W			ELAN			
	Antarctic	SEIO	SWIO	Effort	Antarctic	SEIO	SWIO	Effort	Antarctic	SEIO	SWIO	Effort	Antarctic	SEIO	SWIO	Effort
2017	0	0	0	0	11 707	507	8 292	324	44 551	0	28 130	359	0	0	0	0
2018	$11 \ 567$	198	0	324	3008	460	$9 \ 394$	197	36 569	0	34 888	302	$11 \ 352$	124	7 481	345

Antarctic blue whale calls were detected at all the OHASISBIO recording sites except at 240 RAMA (Figure 3, Table 2). Overall, higher numbers of detections per year occurred at MAD-241 W and NEAMS sites, with the highest number of detections at NEAMS in 2013 (n = 47097). 242 The annual number of detections was also very high at SWAMS and WKER, whereas fewer 243 detections were reported at SSEIR, NCRO and MAD (n < 21000), except in 2014 when the 244 number of detections at MAD doubled (n = 43 110). Number of detections were reduced at 245 RTJ, MAD-E and ELAN (n < 12000), although only one or two years of data were available. 246 At NEAMS, the annual number of detections increased from 2010 to 2013, and then appeared 247 to have reached a plateau of about 40 000 calls per year. At WKER, the annual number of 248 detections per year was steady, with two small peaks in 2012 and 2014. At SWAMS and NCRO, 249 the number of detections does not follow any obvious trend. At MAD, the annual number of 250 detections was steady, except for peak in 2014 with almost twice as many detections as for any 251 of the other years. There were no peaks in detections at the other sites. Globally, the annual 252 number of Antarctic blue whale call detections did not follow any clear systematic trend or 253 pattern. 254

²⁵⁵ SEIO pygmy blue whales were present at all sites of the hydrophone array, except at RAMA

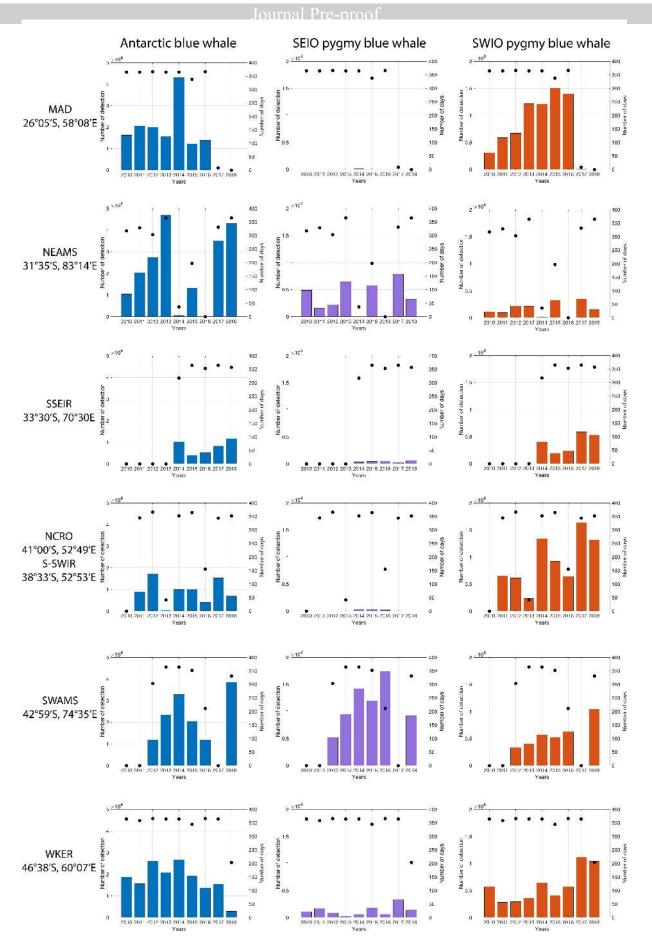


Figure 3: Number of detected calls per year (left y-axis). Each row corresponds to a different site and each column to a different call type. The sites are displayed from north to south. Black dots represent the number of days of recording for each year (right y-axis).

and MAD-W (Figure 3, Table 2). However, for some sites, detections were scarce and limited 256 to specific years; for instance calls were only detected in 2014 for MAD and in 2014, 2015, 257 and 2016 for NCRO. The site with the highest number of detections was SWAMS, followed 258 by NEAMS and then WKER. The SSEIR site had detections of SEIO pygmy blue whale calls 259 every year, but in very small numbers (from 258 in 2017 to 627 in 2018). Similarly, only a 260 few calls were detected at RTJ, MAD-W and ELAN. Over the years, for NEAMS, WKER and 261 SSEIR, the number of calls detected per year does not follow any particular trend. However, at 262 SWAMS, the number of detections significantly increased from 2012 to 2016 (5226 up to 17453, 263 resp.) and diminished in 2018 (9188), although the number of recording days was less in 2016 264 (Figure 3). 265

SWIO pygmy blue whale calls were recorded at all the OHASISBIO sites except at RTJ. 266 with only a few barely detectable calls (i.e. with very low SNR) in the chorus, and RAMA 267 (Figure 3, Table 2). At MAD-W, even though only two years of data are available, the number 268 of detections per year $(n > 28\ 000)$ was almost double that of any other site. The long-term sites 269 where SWIO pygmy blue whale calls were most commonly detected were MAD and NCRO, 270 at the western side of the OHASISBIO hydrophone array. Conversely, NEAMS and SSEIR 271 displayed fewest detections per year (n < 6000). At MAD site, the annual number of detections 272 steadily increased from 2010 to 2015, from fewer than 3000 calls per year to more than 15 000. 273 At SWAMS, the annual number of calls was more modest but also increased, doubling from 274 3387 calls in 2012 to 6279 in 2018. At the other sites, NCRO, NEAMS, SSEIR and WKER, 275 there was no clear trend in the annual number of SWIO pygmy blue whale detections. 276

4.2 Seasonal distribution and inter-annual variability

The seasonal acoustic presence of Antarctic and both pygmy blue whales is shown in Figure 4 for the six long-term monitoring sites. The observations for the short-term monitoring sites are presented in Appendix 2.

Antarctic blue whale calls were detected year-round in the monitored area. Nonetheless, they were mostly detected from April to November at the northernmost sites (MAD-W, MAD, MAD-E, RTJ, NEAMS, SSEIR, SWAMS). At WKER and ELAN, the peak acoustic presence

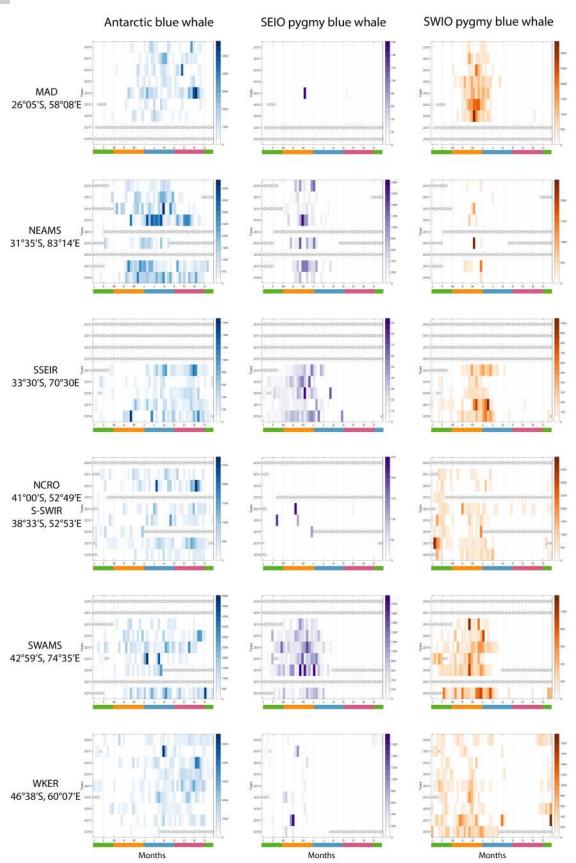


Figure 4: Blue whale weekly acoustic presence. Each row corresponds to a recording site and each column to a blue whale call type. Each graph shows the density of calls per week (color intensity) for every month (x-axis) of the year in the y-axis. Note that the color scale is different for every graph). Weeks with fewer than 6 days of recordings are shown by X. Seasons are shown below the x-axis in different colors (summer: green, autumn: orange, winter: blue, spring: pink).

was shifted and occurred from July until December/January. The seasonality was less clear at
S-SWIR and NCRO where the calls were detected almost all year long.

Detection of SEIO pygmy blue whale calls was highly seasonal, from from February until 286 June and peaking in autumn (March and April). They were detected a bit later at NEAMS 287 (from March/April). At WKER, SEIO pygmy blue whale calls were recorded every year, during 288 a few weeks between January and May. At MAD and NCRO, SEIO pygmy blue whale call 289 detections only occurred rarely, during one week in March 2014 at MAD and during a few 290 weeks in April 2014, in February and April 2015 and in May 2016 at NCRO. At the short term 291 sites (RTJ, MAD-E and ELAN), SEIO pygmy blue whale calls were briefly detected, with a 292 few calls spread on a small number of weeks, mostly during May and June. 293

The presence of SWIO pygmy blue whale calls was also highly seasonal, especially north of 294 the array, where they were mostly detected from March until July (MAD-W). At MAD-E and 295 MAD, the seasonality was even more restrained, occurring only between April and June. At 296 NEAMS, they were only detected during a few weeks per year in April or May. At SSEIR, calls 297 were mostly detected between May and July, with sometimes a few detections from February 298 until April. At NCRO and S-SWIR, the detection pattern seemed bimodal, with calls detected 299 from January to February and then from April until June. At SWAMS, calls could be detected 300 from January to June although occasionally they were detected as early as December. South 301 of the array, SWIO pygmy blue whale calls were sometimes detected as early as mid-November 302 until July at WKER, and from mid-October until January and then from April to July at 303 ELAN. 304

The inter-annual correlations (Pearson's coefficients) are higher for pygmy blue whale presence than for that of Antarctic blue whales (Table 3). The seasonality of the latter was quite variable, with only a few pairs of years with a high correlation coefficient. Most of the time, the null hypothesis could not be rejected for Antarctic blue whale presence, especially at NCRO where only one pair of years was correlated and SWAMS where no correlation was found. The greatest correlation coefficient (57%) occurred at WKER, between 2013 and 2014.

Pygmy blue whales followed a more stable presence pattern over the years, particularly at sites with a large number of detections (*e.g.* SWAMS for SEIO pygmy blue whales and MAD

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Table 3: Pearson correlation coefficients for each pair of years. X means that no data were
available and * means that the correlation was not significant and therefore that the null
hypothesis could not be rejected $(p>0.05)$

		MAD	NEAMS	SSEIR	NCRO/S-SWIR	SWAMS	WKER
	2010-2011	*	0.38	Х	Х	Х	*
	2011-2012	0.37	0.43	Х	*	Х	*
	2012-2013	*	*	Х	*	*	0.50
	2013-2014	0.28	*	Х	*	*	0.57
Antarctic blue whale	2014 - 2015	*	Х	0.43	*	*	*
	2015-2016	0.29	Х	0.40	*	*	*
	2016-2017	Х	Х	*	*	Х	*
	2017-2018	Х	*	*	0.31	Х	*
	2010-2011	Х	*	Х	Х	Х	*
	2011-2012	Х	*	Х	Х	Х	*
	2012-2013	Х	0.53	Х	Х	0.65	*
CEIO and the second second second	2013-2014	Х	*	Х	Х	0.50	*
SEIO pygmy blue whale	2014 - 2015	Х	Х	0.40	*	0.52	*
	2015-2016	Х	Х	0.41	*	*	*
	2016-2017	Х	Х	0.35	X	Х	0.43
	2017-2018	Х	0.33	*	*	Х	*
	2010-2011	0.78	*	Х	Х	X	*
	2011-2012	0.49	*	Х	*	Х	*
	2012-2013	0.49	*	Х	Х	*	*
SWIO	2013-2014	0.81	*	Х	X	0.56	0.56
SWIO pygmy blue whale	2014-2015	0.76	Х	*	*	0.31	0.68
	2015-2016	0.83	Х	0.69	*	0.59	0.31
	2016-2017	Х	Х	0.57	*	Х	0.40
	2017-2018	Х	0.90	0.71	0.66	Х	*

for SWIO pygmy blue whales). The correlation was smaller or non-significant at less frequented sites (*e.g.* WKER and NCRO for SEIO pygmy blue whales and NEAMS for SWIO pygmy blue whales). The only exceptions were at NEAMS, a site with consistent SEIO pygmy blue whale detections, and at NCRO, a site with consistent SWIO pygmy blue whale detections.

317 4.3 Sympatry

Both pygmy and Antarctic blue whale calls occur at most of the OHASISBIO array sites. The 318 western sites are mostly frequented by Antarctic and SWIO pygmy blue whales and the eastern 319 sites by Antarctic blue whales and SEIO pygmy blue whales. The three acoustic populations 320 are commonly recorded at NEAMS, SWAMS and WKER (Figure 3). Figure 4 shows that 321 blue whales acoustic populations sometimes acoustically co-occured. The results of the Spear-322 man's correlation tests are shown in Table 4. For the sites where both pygmy blue whales 323 were recorded (MAD-E, NEAMS, SSEIR, SWAMS and WKER), Spearman's correlations are 324 positive. In other words, when the number of SWIO pygmy blue whale calls increases, the 325 number of SEIO pygmy blue whale calls increases as well. The only exception is at ELAN, 326 where the correlation is not significant. On the contrary, Antarctic blue whale seasonal presence 327

is generally negatively correlated with the pygmy blue whale presence. Therefore, except at

³²⁹ MAD and NEAMS, their acoustic presence does not match that of the pygmy blue whales.

Table 4: Spearman correlation coefficient by pair of populations. For a given site, a positive value means the two considered populations are jointly present, a negative value means that they are not present at the same times, an X means a lack of calls for one or both populations, and an asterisk (*) means that the correlation was not significant (*i.e.* the null hypothesis could not be rejected (p>0.05)).

	ELAN	MAD	MAD-E	MAD-W	NEAMS	SSEIR	NCRO/S-SWIR	SWAMS	WKER
SEIO - SWIO populations	*	Х	0.49	Х	0.30	0.65	Х	0.77	0.51
Antarctic - SWIO populations	*	0.11	-0.34	*	0.17	-0.24	-0.21	*	-0.33
Antarctic - SEIO populations	*	Х	-0.37	X	0.40	-0.40	Х	*	-0.23

For the sites where both pygmy blue whales were recorded (MAD-E, NEAMS, SSEIR, SWAMS and WKER), there was a positive monotonical correlation. In other words, when the number of SWIO pygmy blue whale calls increase, the number of SEIO pygmy blue whale calls tend to increase as well. The only exception is at ELAN, where the correlation is not significant. On the contrary, Antarctic blue whale seasonal presence often negatively correlated with the pygmy blue whale presence. Therefore, their acoustic presence is offset from that of the pygmy blue whale call types.

Figure 5 shows the number of hours with acoustic co-occurence either from both pygmy blue 337 whales or from Antarctic blue whales and one pygmy blue whale population. We only show 338 sites with at least 5% of hours with sympatry within any month of the year. For pygmy blue 339 whales (Figure 5 a), the only site that meets this condition is SWAMS, with peak co-occurence 340 from March to June. For Antarctic and pygmy blue co-occurence (Figure 5), MAD-W is the site 341 with the greatest co-occurrence, with 40% of hours in June. Other sites with acoustic sympatry 342 include MAD, NCRO, NEAMS and SWAMS. The main period of co-occurence is between April 343 and June except at NCRO, where greatest co-occurence happens in January. 344

345 5 Discussion

³⁴⁶ 5.1 Using passive acoustics to monitor blue whale populations

Passive acoustic monitoring with a wide network of hydrophones is a very effective approach to
detect the presence of blue whales, as in this study. However it cannot be used to determine the

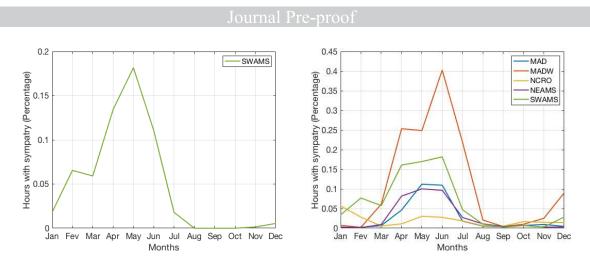


Figure 5: Number of hours per month with sympatric detections of blue whale calls a) SEIO and SWIO pygmy blue whales b) Antarctic blue whales and SEIO or SWIO pygmy blue whales. The number of detections is normalized by the number of hours of recording available for each month, over the total duration of the recordings (from 2010 to 2018)

abundance of whales in the vicinity of an hydrophone based on the number of detected calls. Indeed, several factors can influence the number of blue whale calls present in the data. Some of them are dependent on blue whale behavior (*e.g.* when, where and why they sing and how song structure changes) and others are dependent on sound propagation dynamics that affect the detection ranges of calls.

For instance, a recent study found that the structure of SEIO pygmy blue whale songs 354 shows variations (Joliffe et al., 2019). The usual 3-unit song was sometimes shortened by 355 whales omitting one of the units. If the omitted unit is the one targeted by a detector, then 356 the relationship between the number of call detections and the density of whales in the vicinity 357 of the hydrophone may change. This phenomenon has not been studied in other blue whale 358 populations. In the OHASISBIO data, it is rare to observe the full 3-unit SEIO pygmy blue 359 whale vocalisation (due to loud background noise and and only the loudest unit is used for the 360 automated detection (see Figure 1). Variations in song structure are therefore less straightfor-361 ward to observe, but they may explain some of the inter-annual variations in the number of 362 detections. 363

Acoustic detection ranges of blue whales are way larger than visual observation ranges. The estimated detection range for Antarctic blue whale calls is about 200 km (Širović et al., 2007; Samaran et al., 2010b; Thomisch et al., 2016). Pygmy blue whale call detection range is not well known. There is a tradeoff in that the lower background noise in the higher frequencies used

by pygmy blue whales suggests that their vocalisations could propagate further than Antarctic 368 blue whale ones. However, higher pitched sounds tend to propagate less far and it seems 369 that pygmy blue whale calls have lower source levels than Antarctic blue whale calls (Samaran 370 et al., 2010b). Therefore, their detection range is probably smaller than 200 km (Samaran et al., 371 2010a). Moreover, variability in the annual or seasonal number of calls can arise from seasonal 372 changes in the sound propagation range. This range relies on many environmental parameters 373 (e.g. the sound speed, the bathymetry and the background noise) that can evolve over time. 374 For example, Thomisch et al. (2019) found that depending on the season, the propagation range 375 of blue whale calls can vary from 200 km to 500 km. A greater propagation range increases 376 the hydrophone detection area. This may result in an increase in the number of call detections 377 that is not reflective of a true increase in blue whale numbers in the vicinity of the hydrophone. 378 Computing seasonal detection range variations for our many sites is beyond the scope of this 379 paper. However we assume that our detection patterns are representative of a regional blue 380 whale presence around the hydrophones rather than a very local one. 381

5.2 Spatial distribution of blue whale populations in the southwest Indian Ocean

Ovarian data collected from 1934 to 1972 suggested that 60°S was the northern limit of Antarc-384 tic blue whale distribution (Branch et al., 2009). However, since 2010, acoustic surveys have 385 demonstrated that Antarctic blue whales regularly occur in subantarctic and subtropical lati-386 tudes of the Indian Ocean (Stafford et al., 2004; Samaran et al., 2010a, 2013; Leroy et al., 2016), 387 the Pacific Ocean (Stafford et al., 1999, 2004; Buchan et al., 2018) and even in the equatorial 388 Atlantic Ocean (Samaran et al., 2019). Overall, the Antarctic blue whale acoustic presence 389 results presented here match those reported in Leroy et al. (2016) for MAD, SSEIR, NEAMS, 390 SWAMS, NCRO and WKER sites from 2010 to 2015. A large number of calls detected annually 391 at the additional sites included here confirms the importance of the subtropical and southern 392 Indian Ocean for this sub-species. The most consistently visited site by Antarctic blue whales 393 seems to be MAD-W, suggesting either that this region concentrates many individuals or that 394 their calling rate is higher in this vicinity. Sites MAD-E and RTJ seem less occupied, implying 395

that they may define the northern limits of their distribution in the Indian Ocean. No Antarctic 396 blue whale calls were recorded at RAMA, but only two years of data were available for this 397 site, so it may occasionally be frequented by Antarctic blue whales. For now, the northern 398 limit of their distribution in the Indian Ocean is thus thought to be located around the Diego 399 Garcia archipelago, 7.6°S (Stafford et al., 2004). The longer time series confirms the observa-400 tion of Leroy et al. (2016) that SSEIR, NCRO and and its neighboring S-SWIR site are less 401 used by vocal Antarctic blue whales than the other sites. These regions could be suboptimal 402 for Antarctic blue whales or their call rate is lower there for an unknown reason. This is the 403 first time that Antarctic blue whale acoustic presence is reported at ELAN, the southernmost 404 hydrophone site. It provides additional evidence of Antarctic blue whale presence around the 405 entire Southern Ocean (Širović et al., 2004, 2009; Gedamke and Robinson, 2010; Miller et al., 406 2015; Thomisch et al., 2016). 407

SEIO pygmy blue whale calls have been previously recorded off southern (Gill, 2002; Gavrilov 408 et al., 2011) and western Australia (McCauley et al., 2000, 2018; Stafford et al., 2011; Balcazar 409 et al., 2015). The eastern limit of their distribution is the Bass strait (Balcazar et al., 2015; Mc-410 Cauley et al., 2018) with the exception of a few extralimital detections near the Juan Fernandez 411 Islands in the SE Pacific Ocean (Buchan et al., 2020). Satellite telemetry has revealed SEIO 412 pygmy blue whale distribution along the western Australian coast as far north as Indonesian 413 waters (Double et al., 2014). In the eastern part of the Indian Ocean, SEIO pygmy blue whale 414 calls were recorded as far west as the Crozet archipelago (Samaran et al., 2010a). Our results 415 support the broad scale study in Leroy et al. (2018b) where a strong chorus is observed at 70 416 Hz at the easternmost sites, SWAMS, SSEIR and to a lesser extent at NEAMS. SEIO pygmy 417 blue whale calls are consistently recorded at SWAMS, NEAMS and less so at WKER. Even 418 fewer calls are detected at SSEIR, suggesting that SEIO pygmy blue whales are uncommon 419 at SSEIR. Therefore, the western limit of their general distribution could be located between 420 the sites ELAN/WKER/SSEIR and NEAMS/SWAMS. SEIO pygmy blue whales clearly range 421 far from the west coast of Australia based on the data presented here and in previous studies 422 (Samaran et al., 2010a; Stafford et al., 2011; Samaran et al., 2013; Leroy et al., 2018b). Like for 423 most pygmy blue whale populations globally, breeding grounds are largely unknown. However, 424 SEIO pygmy blue whale calls were neither detected at Diego Garcia Stafford et al. (2011), nor 425

at RAMA. If the calls are only a mating display it would be unlikely that the northern Indian
Ocean is a breeding ground for this population.

Recent analysis using the Chorus to Noise Ratio (CNR) metric revealed that SWIO pygmy 428 blue whale population is distributed at least from 26°S (Leroy et al., 2018b; Dréo et al., 2018) 429 to 46°S and 52°E to 74°E. Overall, it is clear that SWIO pygmy blue whale acoustic presence 430 is stronger in the western Indian Ocean (sites MAD, MAD-W, NCRO) and diminishes when 431 going to the east towards SSEIR and SWAMS sites. The eastern boundary of their distribution 432 may be located at the eastern limit of our hydrophone array, as suggested by Leroy et al. 433 (2016). To the north, a few SWIO pygmy blue whale calls were detected at NEAMS and Diego 434 Garcia (Stafford et al., 2011), which could be the northern limit of SWIO pygmy blue whale 435 distribution. Only chorus was detected at RTJ. Longer time series at RTJ and Diego Garcia 436 could refine the northern limit of this pygmy blue whale population distribution. Consistent 437 detection of SWIO pygmy blue whale calls at WKER and also on the single year of data at 438 ELAN, confirms that they also occupy the subantarctic Indian Ocean as previously observed 439 by (Gedamke and Robinson, 2010). 440

5.3 Seasonal distribution of blue whale populations in the southwest Indian Ocean

The analysis of the first years of the OHASISBIO recordings demonstrated that Antarctic blue 443 whale acoustic distribution is seasonal in the southwest Indian Ocean (Samaran et al., 2010a, 444 2013; Leroy et al., 2016, 2018b). The monthly seasonal pattern is stable over the years but differs 445 among sites, with more detections during autumn and spring (March to May and September to 446 November) at the subantarctic locations and more detections during winter (June to August) at 447 subtropical locations, suggesting the presence of migration routes and of a wintering, possibly 448 breeding, area at northern latitudes (Leroy et al., 2016). Our observations confirm these findings 449 at a finer and longer temporal scale (Figure 4 and Table 3). Generally, the peak of detections 450 occurs during the second part of the year (from March to December) at most of the sites, 451 including the southernmost subantarctic site ELAN. This is complementary to the seasonal 452 acoustic presence recorded in Antarctica (Širović et al., 2004, 2009; Thomisch et al., 2016), 453

⁴⁵⁴ where the peak occurs during the first trimester of the year (January until March/April). This ⁴⁵⁵ suggests a migration pattern from southern latitudes where they are heard from December ⁴⁵⁶ to April to lower latitudes from April to November. However, acoustic presence nearly all ⁴⁵⁷ year round at some subantarctic and subtropical locations (WKER, NCRO and SWAMS) is ⁴⁵⁸ indicative of some animals not migrating every year (Thomisch et al., 2019).

This year-round acoustic presence is not observed for pygmy blue whales in the array and 459 more broadly, in the Indian Ocean basin. To the west, SEIO pygmy blue whale calls are recorded 460 as far east as the Crozet Archipelago in May and June. In the southwest Indian Ocean, their 461 calls are recorded consistently, with a clear seasonal pattern from February until June, and no 462 detections from July to January. Our results confirm that SEIO pygmy blue whale acoustic 463 presence is highly seasonal in the Indian Ocean, between February and June at SSEIR and 464 SWAMS and from April to June at NEAMS. SEIO pygmy blue whale calls were absent from 465 our recordings from August through December. It is not clear yet whether they stop singing 466 or dwell in a different area during this period, perhaps Indonesian waters, where their presence 467 was revealed by satellite telemetry from July to September (Double et al., 2014). 468

Our results support the previous findings that SWIO pygmy blue whale acoustic presence is 469 highly seasonal (April and/or May) in the northwest of the hydrophone array. They also provide 470 more accurate information on the acoustic presence of SWIO pygmy blue whales further south. 471 SWIO pygmy blue whale calls were detected from November until June or July at WKER 472 and mostly from October until December at ELAN. Their presence at NCRO is bimodal with 473 two peaks, the first from December to February and second from April to June. Similar 474 detection patterns are reported north of the Mozambique channel (from May to July and from 475 November to January) (Cerchio et al., 2018) and implies a possible double migration pattern. 476 A first migration would occur from high latitudes (ELAN, WKER) in summer (December to 477 February) to low latitudes in autumn or winter (MAD-W, MAD) then back again to higher 478 latitudes in the middle of winter (June to August). The absence of call detections during austral 479 spring (from August to October) might indicate a change in SWIO pygmy blue whale vocal 480 behavior or a migratory corridor different from the one they use in autumn to go from south to 481 north, for example along the eastern coast of South Africa (Branch et al., 2007). The second 482 migration pattern would involve a migratory corridor located north of the Mozambique channel 483

and frequented twice a year (from May to July and from November to January) (Cerchio et al.,
2018). The absence of call from August until October both in the Mozambique channel (Cerchio
et al., 2018), and in the OHASISBIO array suggest a migration in the northern Indian Ocean.
However, there is no evidence of their presence in the north of the Indian Ocean during this
period.

489 5.4 Long term and seasonal variability

Long-term monitoring of Antarctic blue whale acoustic presence did not reveal global trends 490 in the number of calls recorded annually over time despite clear seasonal variations in number 491 of detections. It is possible that some areas are more appealing to whales in certain years 492 and attract more individuals than the previous years at the expense of other areas. However, 493 Antarctic blue whale calls were detected every year at all sites, suggesting that they do not 494 all abandon their wintering ground, even if the environmental conditions may not be optimal. 495 Baleen whales were long thought to fast during migrations and at breeding grounds, never-496 theless, the choice of wintering ground for blue whales appears driven by the presence of krill 497 (Branch et al., 2007). Low, or absence of, significant correlation between the weekly presence 498 on two consecutive years emphasizes that Antarctic and pygmy blue whale movements likely 499 rely primarily on environmental conditions. The obvious next step is to examine environmen-500 tal variability during the same decade (via satellite derived data for sea surface temperature, 501 chlorophyll A, upwelling index) to determine how the physical environment might drive changes 502 in blue whale site frequentation in the array. 503

Like Antarctic blue whales, the annual numbers of SEIO pygmy blue whale call detections 504 do not display a global trend in the array, but show inter-annual variations. However, the high 505 correlation between weekly presence over two consecutive years at SWAMS suggests a stable 506 seasonal presence. In the Bass Strait, the annual difference of blue whale call detections was 507 hypothesized to be due to fluctuations in the seasonal occurrence of krill (Tripovich et al., 2015). 508 McCauley et al. (2018) report a 4.3% growth rate for the population visiting the Bass Strait. 509 computed from acoustic analysis of call rates. However, they emphasize that this value applies 510 only to the proportion of the SEIO pygmy blue whale population that occupies this region and 511

can not be generalized to the entire population.

SWIO pygmy blue whale calls are the only ones to show an increasing trend throughout the 513 extent of their distribution in the array. This trend is also visible in the chorus (Leroy et al., 514 2018b), which could suggest a global population growth (McCauley et al., 2018). However, it 515 is impossible to quantify the extent of this growth solely from acoustic data. The NCRO and 516 SSEIR sites do not display similar tendencies. SWIO pygmy blue whale presence here might 517 be more reliant on environmental drivers than elsewhere as suggested for SEIO pygmy blue 518 whales (Tripovich et al., 2015; Garcia-Rojas et al., 2018). SWIO pygmy blue whale seasonal 519 acoustic presence is very stable at MAD, suggesting that they might come here every year, no 520 matter the changing environmental conditions. These observations might indicate that NCRO 521 and SSEIR regions are feeding areas en route to the Madagascar basin, around the site MAD. 522

523 5.5 Use of the southern Indian Ocean by multiple blue whale pop-524 ulations

Antarctic blue whale calls are present year-round in the southern Indian Ocean, but with peaks 525 during winter and spring (from June to November) whereas SWIO and SEIO pygmy blue 526 whales are heard seasonally mostly during summer, autumn and early winter (from January 527 to June). The negative correlation between Antarctic and pygmy blue whale seasonal presence 528 confirms the complementary use of the Indian Ocean by the two subspecies. Moreover, each 529 seems to have different migratory strategies. Antarctic blue whales may not all migrate south 530 annually as indicated by their year-round presence at sub-antarctic locations (Leroy et al., 2016; 531 Thomisch et al., 2019). In contrast, highly seasonal acoustic presence and absence indicates 532 a clear migration pattern for pygmy blue whales. Such differences in geographic and seasonal 533 occupancy of the southern Indian Ocean by Antarctic and pygmy blue whales could reflect prey 534 preference, different habitat use (i.e. breeding or feeding), but also very different life history 535 strategies between a highly mobile sub-species (Antarctic blue whales) and a sub-species that 536 is largely resident to the Indian Ocean (pygmy blue whales). 537

Productive Antarctic waters are the main Antarctic blue whale feeding grounds. This sub species feeds mainly on large Antarctic krill (*Euphausia superba*) (Kawamura, 1980; Miller et al.,

⁵⁴⁰ 2019). Antarctic blue whale migration is guided by the seasonal presence of krill in summer ⁵⁴¹ in high latitudes. Presumably, a part of the population remains year-round at lower latitudes ⁵⁴² (Thomisch et al., 2019).

Such a partial migration to the Antarctic feeding ground may be driven by the year-round 543 availability of prey in the subantarctic and subtropical Indian Ocean. The SEIO pygmy blue 544 whale population has been observed feeding on *Nuctiphanes australis* south of Australia during 545 autumn (Gill, 2002). SWIO pygmy blue whale feeding grounds are not precisely known, but 546 stomach contents showed that around Crozet and Kerguelen islands they ate mainly Euphausia 547 frigida and E. vallentini (Nemoto, 1962). Their diet seems to shift in South African waters 548 to E. recurva or E. diomedeae (Kawamura, 1980). These differences in diet might be due to 549 geographic availability of prey. 550

SWAMS is the site with the greatest number of calls from the three acoustic populations 551 studied here. Co-occurrence of Antarctic and SWIO pygmy blue whales happens mostly at 552 the western sites (MAD, MAD-E, MAD-W, NCRO) whereas co-occurrence of Antarctic blue 553 whales and SEIO pygmy blue whales mostly occurs to the east (SWAMS, NEAMS) (Figure 554 5). Hourly acoustic co-occurrence does not necessarily mean that the vocalizing whales could 555 hear each other, as one could be located at one limit of the hydrophone detection range and 556 another one at the opposite limit, for instance. However, it indicates that a relatively small 557 area was occupied by two different blue whale acoustic populations. It is therefore an indicator 558 of a region of high interest for blue whales. Assuming that SEIO and SWIO pygmy blue 559 whales both breed during winter, they might all use the northern Indian Ocean as a common 560 breeding ground with Antarctic blue whales. Attard et al. (2012) reported a case of hybridation 561 between an Antarctic blue whale and a pygmy blue whale from a whale biopsied off Antarctica. 562 The acoustic co-occurrence during late autumn and beginning of winter (April to June) in 563 the northern Indian Ocean could indicate potential co-breeding grounds. MAD-W could be 564 a candidate breeding ground for both Antarctic blue whales and SWIO pygmy blue whales, 565 and NEAMS for both Antarctic blue whales and SEIO pygmy blue whales. Neither pygmy 566 blue whale population appears to co-occur at any northern site of the array (MAD, NEAMS), 567 suggesting that they might have separate breeding grounds. However, sympatry of feeding SEIO 568 pygmy blue whales and migrating or breeding Antarctic blue whales during autumn (March 569

to May) south of Australia (Tripovich et al., 2015) suggest that acoustic co-occurence might also indicate regions used for two different purposes by different acoustic populations of blue whales. Clearly, while passive acoustic monitoring has provided unprecedented information about the seasonal and geographic occurrence of multiple acoustic populations of blue whales in the southern Indian Ocean, it is only through interdisciplinary studies that include visual observations, that we will fully understand the ecology of Indian Ocean blue whales.

576 6 Conclusion

This study documents the presence of three blue whale acoustic populations for nearly a decade 577 in the southern Indian Ocean. Its results are based on a long and continuous time series and on 578 the application of a single algorithm for the detection of the different calls. These results support 579 the spatial and seasonal distribution previously depicted in this region and the additional years 580 and recording locations refine these previous findings, both temporally and geographically. 581 What is immediately clear from the data is that Antarctic and pygmy blue whales use the 582 southern Indian Ocean very differently. The former is acoustically recorded almost year-round 583 whereas the latter are recorded only seasonally. Moreover, Antarctic blue whale migration is 584 highly variable from one year to the next while pygmy blue whale seasonality appears relatively 585 stable. Antarctic and pygmy blue whales co-occur, especially in the north of the OHASISBIO 586 array. SEIO and SWIO pygmy blue whales have a similar seasonality in the southern Indian 587 Ocean, but their distribution only overlaps slightly around SWAMS, where they mostly co-occur 588 mostly from April to June. 589

The next steps to better understand how blue whales use the southern Indian Ocean are 590 multiple. First, additional recording locations could be established, especially along the eastern 591 African coast for SWIO pygmy blue whales and between the OHASISBIO hydrophone array 592 and Australia for SEIO pygmy blue whales. This would refine the limit of distribution and 593 perhaps complete our knowledge about pygmy blue whale migration routes. Second, for all 594 subspecies, additional behavioral information is needed to better understand in which context 595 they produce calls. Finally, comparing seasonal presence, behavior and environmental data 596 would be useful to define preferential Antarctic and pygmy blue whale habitats in the southern 597

⁵⁹⁸ Indian Ocean.

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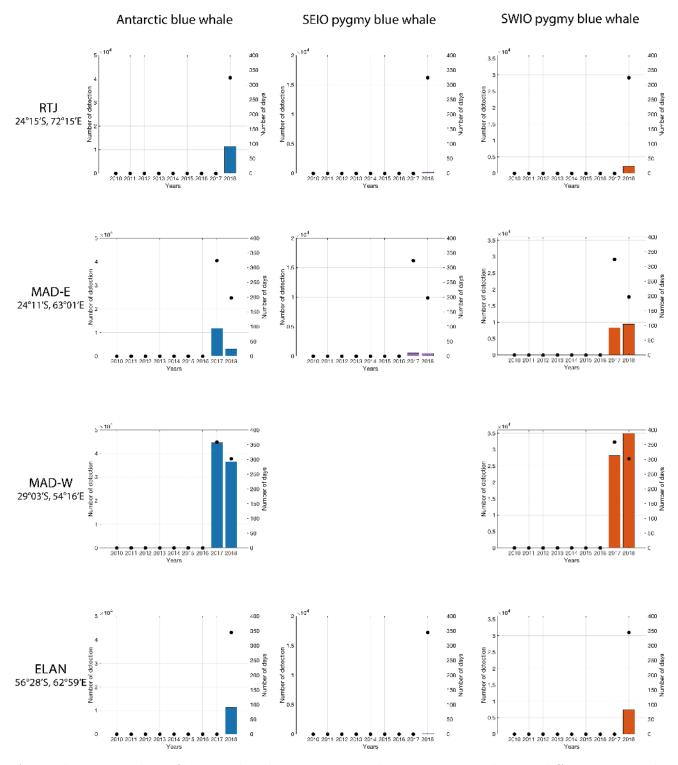
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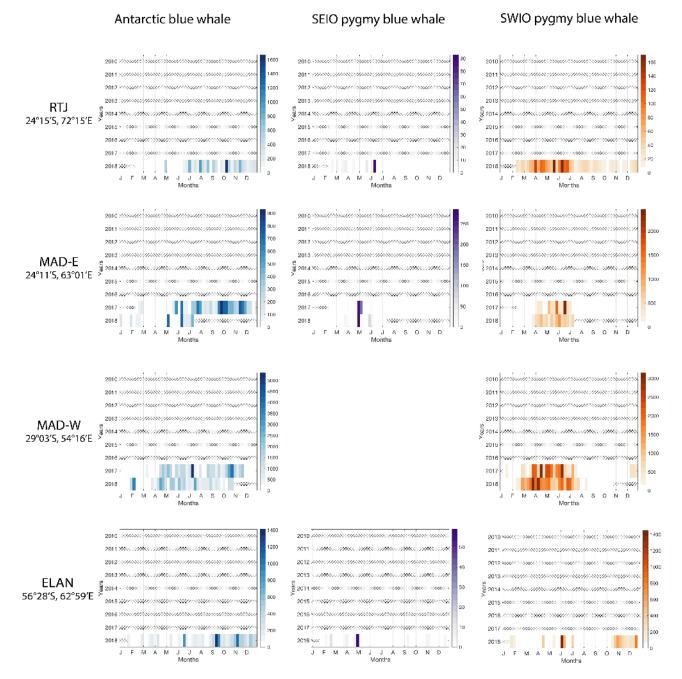
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796 8 Appendices



Appendix 1: Number of detected calls per year. Each row corresponds to a different site and each column to a different call type. Black dots represent the number of days of recording for each year. No SEIO pygmy blue whale calls were recorded at MAD-W, hence the absence of figure.



Appendix 2: Blue whale weekly acoustic presence. Each row corresponds to a recording site and each column to a blue whale call type. Each graph shows the density of calls per week (color intensity) for every month (x-axis) of the year in the y-axis. Note that the color scale is different for every graph). Weeks with fewer than 6 days of recordings are shown by X. Seasons are shown below the x-axis in different colors (summer: green, fall: orange, winter: blue, spring: pink). No SEIO pygmy blue whale calls were recorded at MAD-W, hence the absence of figure.

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Declaration of interests

 \boxtimes The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: