
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

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. breviceauda*

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

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

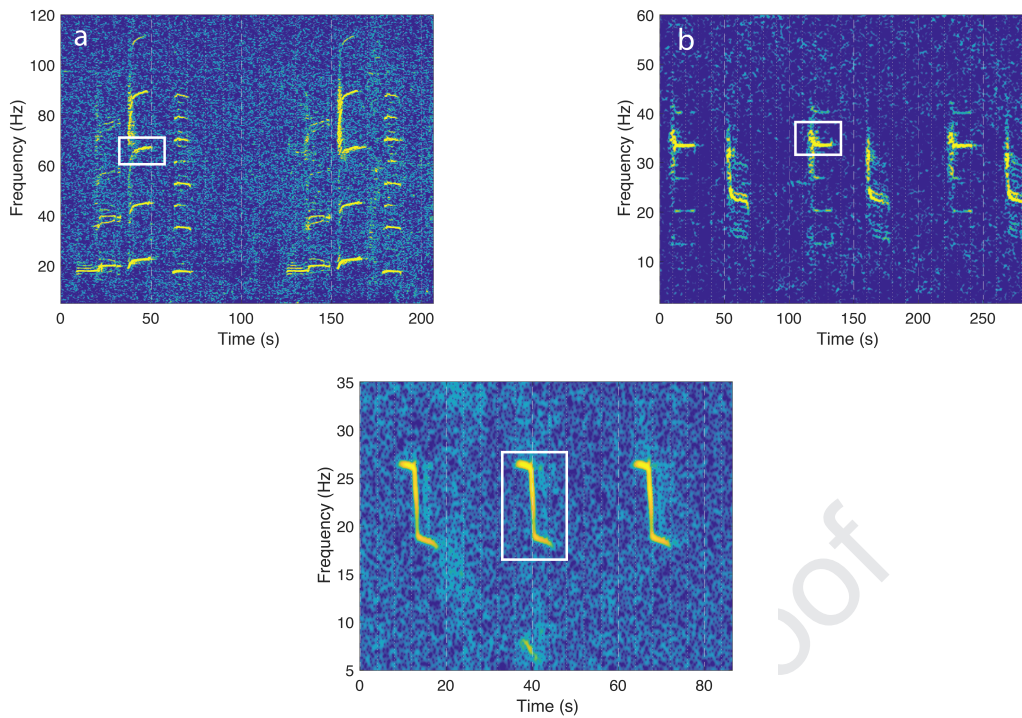


Figure 1: Typical spectrograms of (a) Southeastern Indian Ocean pygmy blue whale calls (b) Southwestern Indian Ocean pygmy blue whale calls, and (c) Antarctic blue whale calls from the Southern Indian Ocean

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

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

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

113 To progress in our understanding of these concepts, this work presents a detailed analysis
114 of the seasonal and spatial presence of Antarctic and pygmy blue whales, based on 9 years of
115 continuous acoustic recordings (2010-2018) at multiple sites across the southern Indian Ocean.
116 Relative to previous analyses, we provide a longer time series and new recording locations. We
117 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.

3 Material and methods

3.1 Data acquisition

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

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 1000m and 1300m depth, corresponding to the local sound fixing and ranging (SOFAR) channel axis. The SOFAR works like a waveguide, where low frequency sounds can propagate over very long distances (Lurton, 2002). The instruments record continuously at a sampling rate of

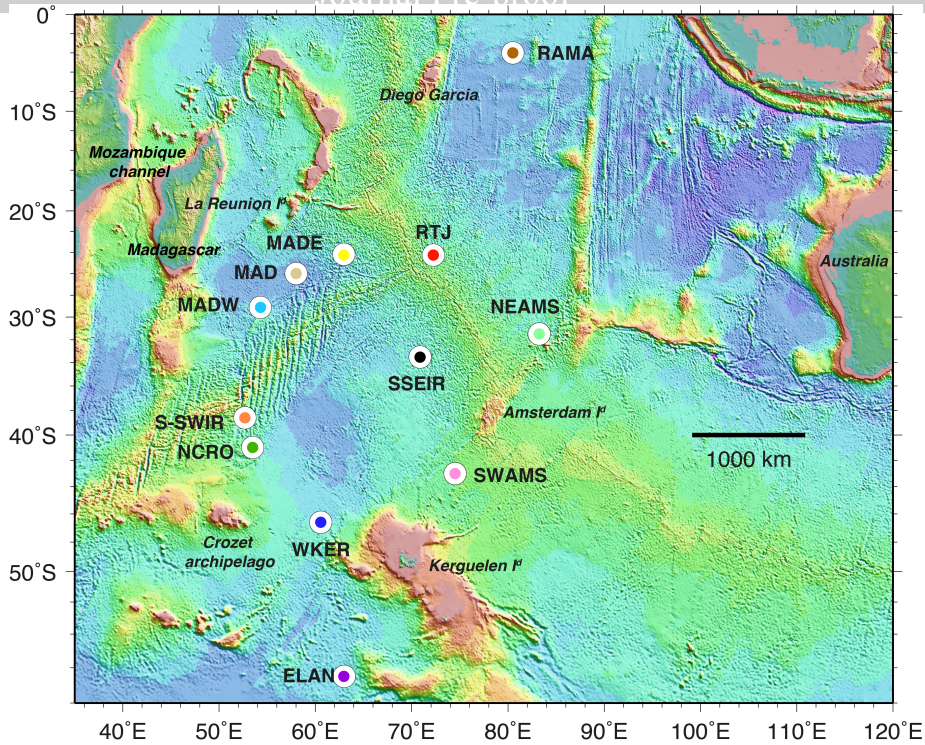


Figure 2: The OHASISIBIO hydrophone network in the Southern Indian ocean. Colored dots represent mooring sites.

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).

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

154 3.2 Acoustic data processing

155 The metrics used here to assess blue whale acoustic presence are the number of calls detected
 156 per week, month or year. For pygmy blue whale calls with multiple units, a single unit was
 157 detected, either because it was the loudest unit of the call or because its frequency did not
 158 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. Coord.	2010		2011		2012		2013		2014		2015		2016		2017		2018	
		Start	Stop	Start	Stop	Start	Stop	Start	Stop	Start	Stop	Start	Stop	Start	Stop	Start	Stop	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	x	x	x	x
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	x	x	x	x	x	x	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	x	x	11/01/14	11/01/15	11/01/15	08/01/16	08/01/16	06/06/16	x	x	x	x
SWAMS	42°59'S, 74°35'E	x	x	x	x	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	x	x	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	x	x	x	x	05/05/12	-	-	11/12/13	x	x	x	x	x	x	x	x	x	x
RTJ	24°15'S, 72°15'E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	11/02/18	10/02/19
MAD-E	24°11'S, 63°01'E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	07/02/17	13/02/18	13/02/18	21/07/18
MAD-W	29°03'S, 54°16'E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	06/01/17	06/01/18	06/01/18	3/11/18
S-SWIR	38°33'S, 52°53'E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	08/01/17	22/12/17	09/01/18	14/01/19
ELAN	56°28'S, 62°59'E	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16/01/18	23/01/19

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

165 3.2.1 Automated call detection

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

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

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

196 **3.3 Detection results analysis**

197 Recordings with a small number of annual detections were manually double checked to assess
198 whether or not these few detections accurately illustrated a blue whale acoustic presence. For
199 SEIO pygmy blue whale calls, ELAN, MAD, SSEIR, MAD-E, MAD-W, NCRO, RTJ, S-SWIR
200 and RAMA sites were double-checked ; for SWIO pygmy blue whale calls, ELAN, SSEIR, RTJ
201 and RAMA sites were double-checked ; for Antarctic blue whale calls only RAMA site was
202 double checked. If most of the detections were false alarms, the annual number of detections
203 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

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

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

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

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

225 4 Results

226 4.1 Spatial distribution and long term trends

227 Figure 3 displays the number of detected calls per year for the long-term recording sites (rows)
228 and the three blue whale calls (columns). Since blue whale acoustic presence is highly seasonal,
229 normalizing the number of detections per year by the number of days of recording could lead to
230 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 hydrophone only lasted 6 months in 2018, from January to mid-July. Usually SWIO pygmy blue whale calls are detected during the first 6 months of the year, so the number of calls at WKER in 2017 and 2018 is similar. If the number of detections had been normalized, it would have appeared that more calls were detected in 2018 than in 2017. Instead of normalizing the number of calls per year by the recording duration, we show the actual detection number (color bars) and the number of days of recording per year (black dots). For the short-term recording sites, the results are given in Table 2 and in Appendix 1, except for RAMA which did not contained any detections.

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.

	RTJ				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	3 008	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 RAMA (Figure 3, Table 2). Overall, higher numbers of detections per year occurred at MAD-W and NEAMS sites, with the highest number of detections at NEAMS in 2013 ($n = 47\,097$). The annual number of detections was also very high at SWAMS and WKER, whereas fewer detections were reported at SSEIR, NCRO and MAD ($n < 21\,000$), except in 2014 when the number of detections at MAD doubled ($n = 43\,110$). Number of detections were reduced at RTJ, MAD-E and ELAN ($n < 12\,000$), although only one or two years of data were available. At NEAMS, the annual number of detections increased from 2010 to 2013, and then appeared to have reached a plateau of about 40 000 calls per year. At WKER, the annual number of detections per year was steady, with two small peaks in 2012 and 2014. At SWAMS and NCRO, the number of detections does not follow any obvious trend. At MAD, the annual number of detections was steady, except for peak in 2014 with almost twice as many detections as for any of the other years. There were no peaks in detections at the other sites. Globally, the annual number of Antarctic blue whale call detections did not follow any clear systematic trend or pattern.

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

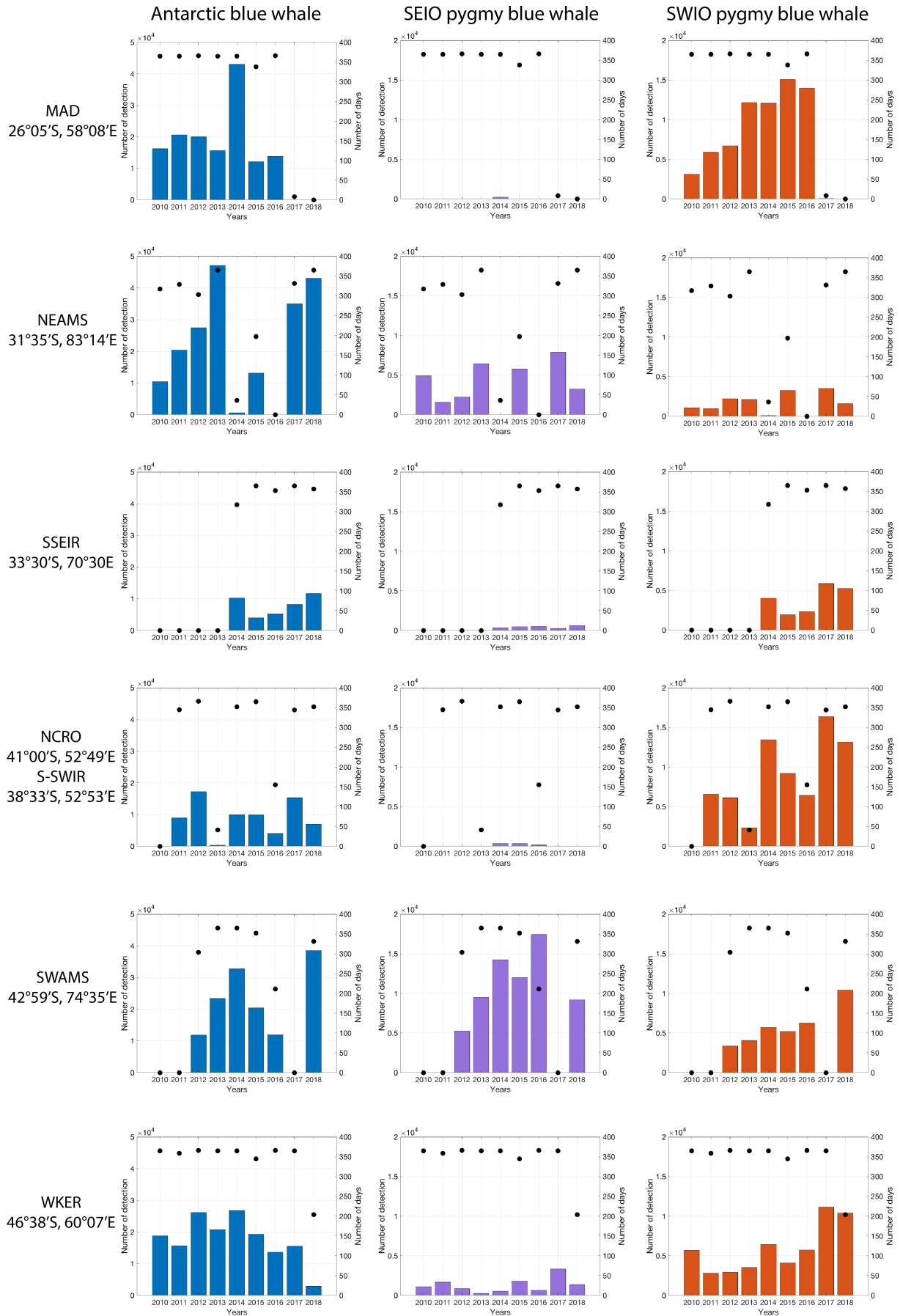


Figure 3: Number of detected calls per year (left y-axis). Each row corresponds to a different site and each column to a different call type. The sites are displayed from north to south. Black dots represent the number of days of recording for each year (right y-axis).

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

266 SWIO pygmy blue whale calls were recorded at all the OHASISBIO sites except at RTJ,
267 with only a few barely detectable calls (i.e. with very low SNR) in the chorus, and RAMA
268 (Figure 3, Table 2). At MAD-W, even though only two years of data are available, the number
269 of detections per year ($n > 28\ 000$) was almost double that of any other site. The long-term sites
270 where SWIO pygmy blue whale calls were most commonly detected were MAD and NCRO,
271 at the western side of the OHASISBIO hydrophone array. Conversely, NEAMS and SSEIR
272 displayed fewest detections per year ($n < 6\ 000$). At MAD site, the annual number of detections
273 steadily increased from 2010 to 2015, from fewer than 3000 calls per year to more than 15 000.
274 At SWAMS, the annual number of calls was more modest but also increased, doubling from
275 3387 calls in 2012 to 6279 in 2018. At the other sites, NCRO, NEAMS, SSEIR and WKER,
276 there was no clear trend in the annual number of SWIO pygmy blue whale detections.

277 4.2 Seasonal distribution and inter-annual variability

278 The seasonal acoustic presence of Antarctic and both pygmy blue whales is shown in Figure
279 4 for the six long-term monitoring sites. The observations for the short-term monitoring sites
280 are presented in Appendix 2.

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

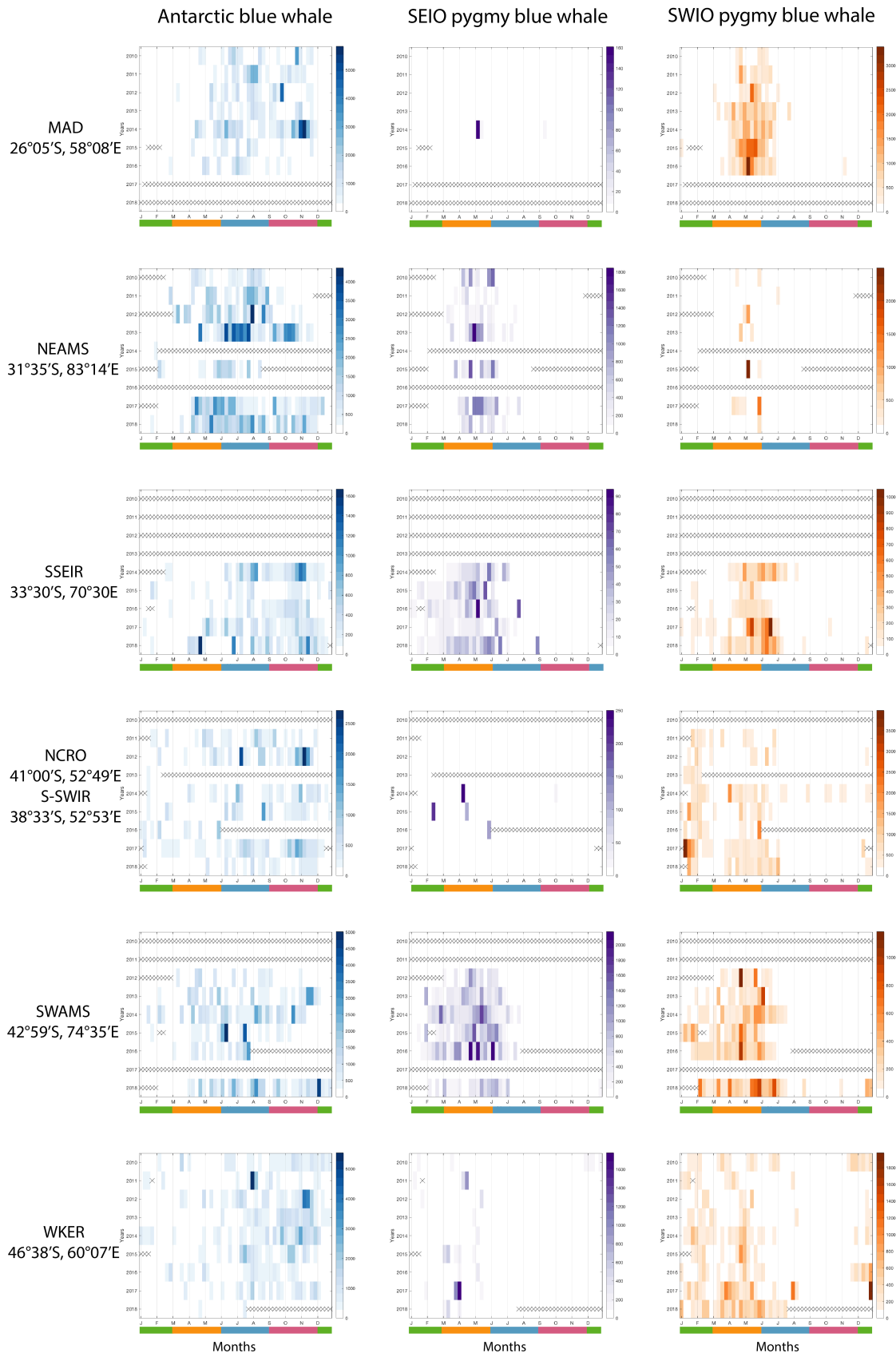


Figure 4: Blue whale weekly acoustic presence. Each row corresponds to a recording site and each column to a blue whale call type. Each graph shows the density of calls per week (color intensity) for every month (x-axis) of the year in the y-axis. Note that the color scale is different for every graph). 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).

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

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

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

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

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

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
Antarctic blue whale	2010-2011	*	0.38	X	X	X	*
	2011-2012	0.37	0.43	X	*	X	*
	2012-2013	*	*	X	*	*	0.50
	2013-2014	0.28	*	X	*	*	0.57
	2014-2015	*	X	0.43	*	*	*
	2015-2016	0.29	X	0.40	*	*	*
	2016-2017	X	X	*	*	X	*
	2017-2018	X	*	*	0.31	X	*
SEIO pygmy blue whale	2010-2011	X	*	X	X	X	*
	2011-2012	X	*	X	X	X	*
	2012-2013	X	0.53	X	X	0.65	*
	2013-2014	X	*	X	X	0.50	*
	2014-2015	X	X	0.40	*	0.52	*
	2015-2016	X	X	0.41	*	*	*
	2016-2017	X	X	0.35	X	X	0.43
	2017-2018	X	0.33	*	*	X	*
SWIO pygmy blue whale	2010-2011	0.78	*	X	X	X	*
	2011-2012	0.49	*	X	*	X	*
	2012-2013	0.49	*	X	X	*	*
	2013-2014	0.81	*	X	X	0.56	0.56
	2014-2015	0.76	X	*	*	0.31	0.68
	2015-2016	0.83	X	0.69	*	0.59	0.31
	2016-2017	X	X	0.57	*	X	0.40
	2017-2018	X	0.90	0.71	0.66	X	*

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.

4.3 Sympatry

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

328 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	*	X	0.49	X	0.30	0.65	X	0.77	0.51
Antarctic - SWIO populations	*	0.11	-0.34	*	0.17	-0.24	-0.21	*	-0.33
Antarctic - SEIO populations	*	X	-0.37	X	0.40	-0.40	X	*	-0.23

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

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

345 5 Discussion

346 5.1 Using passive acoustics to monitor blue whale populations

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

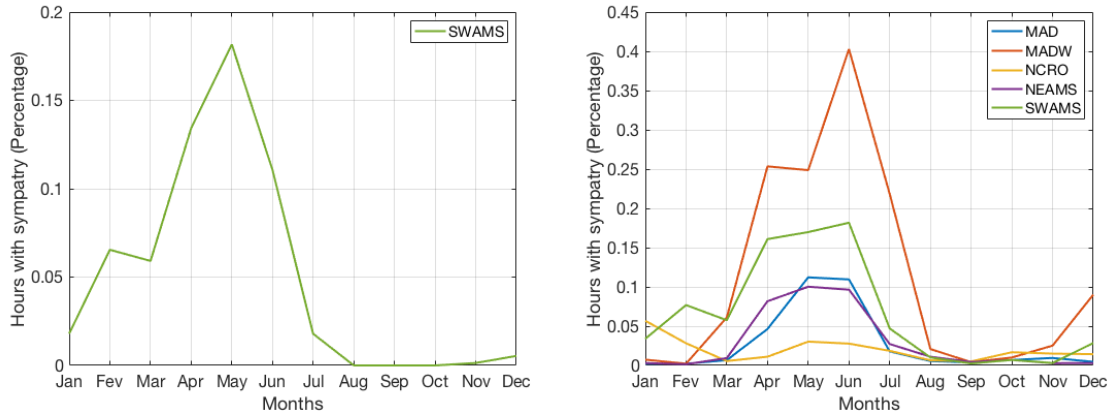


Figure 5: Number of hours per month with sympatric detections of blue whale calls a) SEIO and SWIO pygmy blue whales b) Antarctic blue whales and SEIO or SWIO pygmy blue whales. The number of detections is normalized by the number of hours of recording available for each month, over the total duration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

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

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

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

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

382 **5.2 Spatial distribution of blue whale populations in the southwest** 383 **Indian Ocean**

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

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

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

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

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

441 **5.3 Seasonal distribution of blue whale populations in the southwest** 442 **Indian Ocean**

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

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).

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

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

484 and frequented twice a year (from May to July and from November to January) (Cerchio et al.,
485 2018). The absence of call from August until October both in the Mozambique channel (Cerchio
486 et al., 2018), and in the OHASISBIO array suggest a migration in the northern Indian Ocean.
487 However, there is no evidence of their presence in the north of the Indian Ocean during this
488 period.

489 **5.4 Long term and seasonal variability**

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

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

512 can not be generalized to the entire population.

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

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

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

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

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

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

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

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

576 **6 Conclusion**

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

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

598 Indian Ocean.

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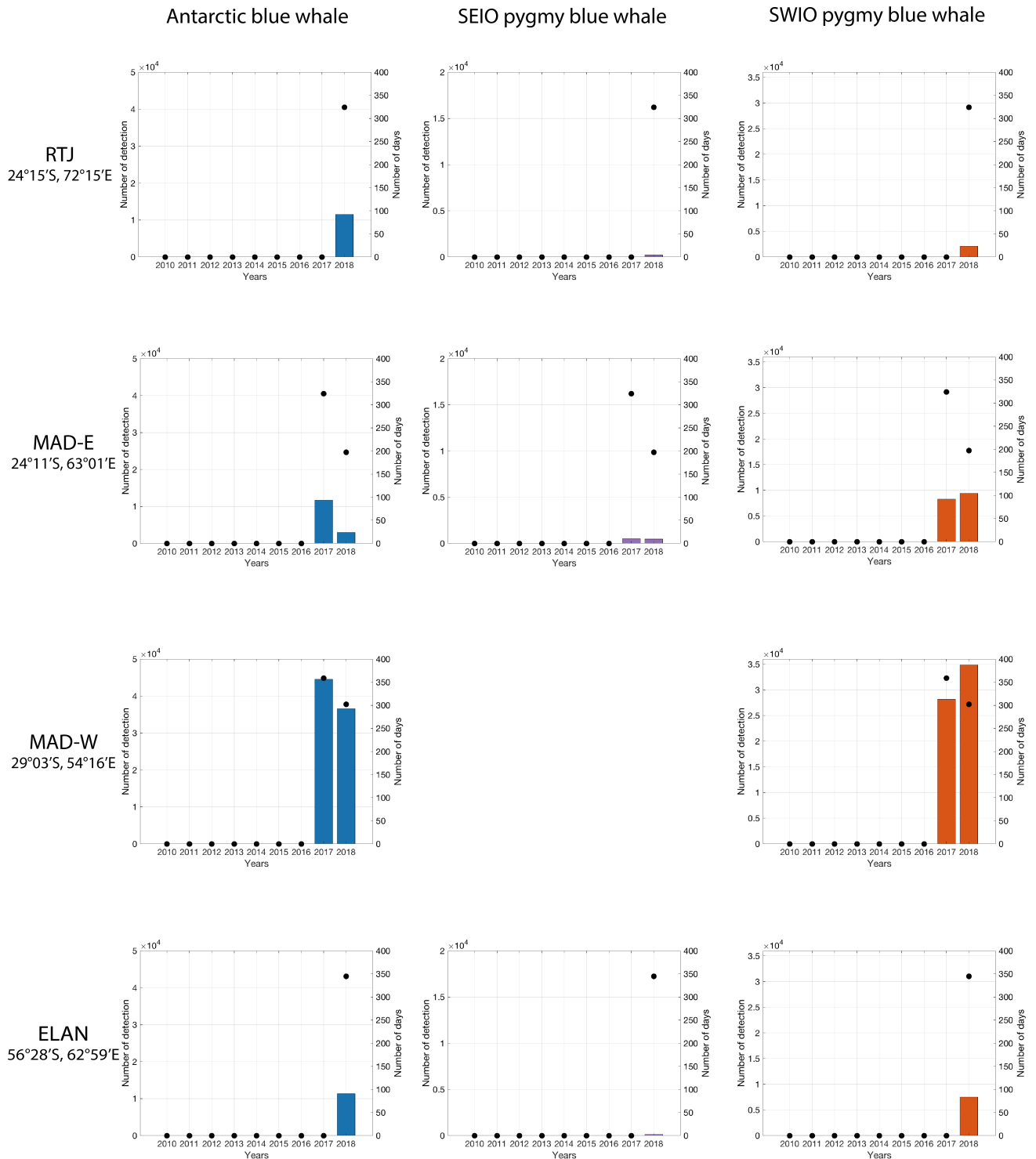
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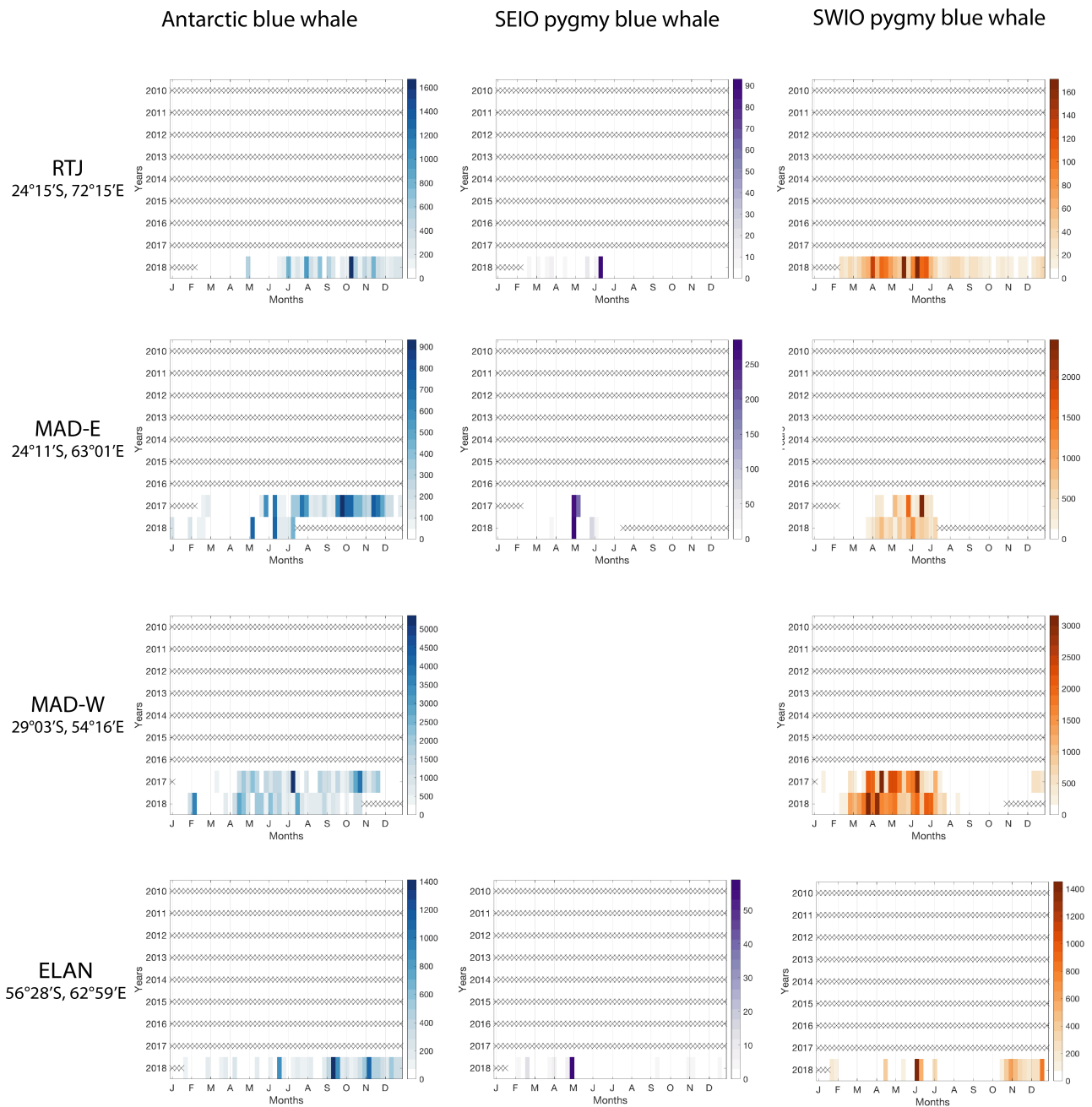
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796 8 Appendices



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

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:

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