



Temporal occurrence of three blue whale populations in New Zealand waters from passive acoustic monitoring

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Describing spatial and temporal occurrence patterns of wild animal populations is important for understanding their evolutionary trajectories, population connectivity, and ecological niche specialization, with relevance for effective management. Throughout the world, blue whales produce stereotyped songs that enable identification of separate acoustic populations. We harnessed continuous acoustic recordings from five hydrophones deployed in the South Taranaki Bight (STB) region of Aotearoa New Zealand from January 2016 to February 2018. We examined hourly presence of songs from three different blue whale populations to investigate their contrasting ecological use of New Zealand waters. The New Zealand song was detected year-round with a seasonal cycle in intensity (peak February–July), demonstrating the importance of the region to the New Zealand population as both a foraging ground and potential breeding area. The Antarctic song was present in two distinct peaks each year (June–July; September–October) and predominantly at the offshore recording locations, suggesting north-bound and southbound migration between feeding and wintering grounds. The Australian song was only detected during a 10-day period in January 2017, implying a rare vagrant occurrence. We therefore infer that the STB region is the primary niche of the New Zealand population, a migratory corridor for the Antarctic population, and outside the typical range of the Australian population.

Key words: blue whale, bioacoustics, distribution, ecology, marine mammals, New Zealand, passive acoustic monitoring, populations, vocalizations

Over time, species and populations diverge along separate evolutionary paths. One way that groups of animals delineate is through separate life-history strategies and interactions with the environment, carving out distinct ecological niches (De Queiroz 2007). Blue whales (*Balaenoptera musculus*) are a long-lived mammalian species with a cosmopolitan distribution composed of distinct subspecies and populations across different ocean basins (Branch et al. 2007a; LeDuc et al. 2007). In the Southern Hemisphere, three blue whale subspecies are recognized: Antarctic (*B. m. intermedia*), pygmy (*B. m. brevicauda*), and Chilean (officially recognized by the Society for Marine Mammalogy Committee on Taxonomy but yet unnamed; Committee on Taxonomy 2021). Beyond these subspecies that can be distinguished morphologically and genetically (Branch

et al. 2007b; Attard et al. 2015), separate blue whale populations are acoustically distinct from one another (McDonald et al. 2006; Leroy et al. 2021). Enhancing our knowledge of the spatial and temporal occurrence patterns of these distinct populations has implications for our understanding of their evolution and ecological niche specialization, and consequences for relevant and effective management.

Throughout the world, blue whales sing songs composed of a limited number of sound types that are produced in succession to form a recognizable pattern (McDonald et al. 2006). These songs are presumed to be signals produced exclusively by males and likely play a role in reproduction (McDonald et al. 2006; Oleson et al. 2007; Lewis et al. 2018). Furthermore, these songs are highly stereotyped and stable over decadal scales,

with characteristics that are distinct between acoustic populations. Therefore, differences in blue whale songs between areas can be used as a hypothesis about population structure (McDonald et al. 2006; Samaran et al. 2013; Balcazar et al. 2015). In these long-lived animals that have a late age of sexual maturity and exhibit a low reproductive rate, vocalizations may evolve more rapidly than traditional markers such as genetics or morphology, and therefore patterns of acoustic dissimilarity may reflect more immediate discontinuities in movement and behavior, making songs a useful tool to differentiate distinct populations (McDonald et al. 2006).

Despite the general rule of thumb that population-specific blue whale songs are recorded in separate geographic regions, there are examples throughout the Southern Hemisphere where songs from different populations are detected in the same location (Samaran et al. 2010, 2013; Tripovich et al. 2015; McCauley et al. 2018; Buchan et al. 2020; Leroy et al. 2021). These examples may represent instances where separate populations partition their ecological use of the same area despite overlapping in space or time. For example, temporal differences in the peak occurrence patterns may minimize overlap by alternating which population predominantly occupies the region (Leroy et al. 2018). Alternatively, populations may overlap spatially and temporally, but occupy different ecological niches at the same site, thus reducing interaction between them. In this case, an area may simultaneously be a migratory corridor for one population and a foraging ground for another (Tripovich et al. 2015).

The South Taranaki Bight (STB) region, which lies between the North and South Islands of Aotearoa New Zealand, is an important foraging ground for pygmy blue whales (Torres 2013; Barlow et al. 2018). A wind-driven upwelling system drives elevated primary productivity and aggregations in the krill prey that blue whales depend on (Bradford and Chapman 1988; Chiswell et al. 2017; Barlow et al. 2020, 2021). The New Zealand blue whale song (also referred to as the southwest Pacific Ocean song, SWPO) is detected acoustically in the area year-round (Barlow et al. 2018; Warren et al. 2021), and genetic analysis of tissue samples collected in the summer months revealed that the blue whales foraging in the STB are from a New Zealand population that is genetically distinct from all other known populations in the Southern Hemisphere (Barlow et al. 2018).

Antarctic blue whales are also detected acoustically around New Zealand (McDonald 2006; Warren et al. 2021). While the precise migratory routes of Antarctic blue whales are unknown, acoustic evidence suggests that at least some portion of the population travels between foraging grounds around Antarctica during the summer and low-latitude areas ($\sim 7\text{--}30^\circ\text{S}$) in the winter, but without a singular or definitive wintering destination (Stafford et al. 2004; Leroy et al. 2016). Therefore, acoustic detection of the Antarctic blue whale song around New Zealand may occur during migration periods between high and low latitudes (Warren et al. 2021).

There are no published records of acoustic detection of the Australian blue whale song (also called the southeast Indian

Ocean song, SEIO) in New Zealand waters to date, despite the relative proximity ($\sim 2,400$ km) to documented acoustic recordings, sightings, and genetic sampling of the Australian pygmy blue whale population (Attard et al. 2010; Balcazar et al. 2015; Tripovich et al. 2015; McCauley et al. 2018). Evidence from satellite tracking (Double et al. 2014) and acoustic monitoring (McCauley et al. 2018) shows that this population migrates northward along the west coast of Australia to Indonesian waters seasonally, suggesting that their typical distribution and movements do not overlap with the New Zealand population. However, recordings of the Australian blue whale song in Chilean waters demonstrate their capability to travel great distances, including far beyond their expected range (Buchan et al. 2020).

As blue whale populations can be morphologically similar but acoustically divergent (Tripovich et al. 2015), the use of passive acoustic monitoring to distinguish populations by their songs can shed light on population separation or overlap, and ecological niche segregation. In this study, we harness continuous acoustic recordings from five hydrophones deployed in the STB of central New Zealand for a 2-year period. By examining the hourly presence of blue whale songs, we investigate the temporal occurrence of multiple blue whale populations in the region. We predict that there are ecological implications associated with their seasonal use of New Zealand waters.

MATERIALS AND METHODS

Acoustic data collection.—Acoustic data were recorded using five Marine Autonomous Recording Units (MARUs; Calupca et al. 2000) deployed in the STB region at depths ranging from 66 to 278 m (Fig. 1). The hydrophones had a flat frequency response (± 2 dB) in the 15–585 Hz frequency band, and recorded continuously at a 2-kHz sampling rate with a high-pass filter at 10 Hz and a low-pass filter at 800 Hz. Acoustic data were collected between 23 January 2016 and 3 February 2018, with brief gaps in recording approximately every 6 months for hydrophone refurbishment.

Blue whale song detection.—Blue whale songs can be identified based on their stereotypical spectral characteristics (McDonald et al. 2006). All recordings were analyzed using the acoustic analysis program Raven Pro, versions 1.6 and 2.0 (Center for Conservation Bioacoustics 2019). Spectrogram template correlation detectors (Mellinger and Clark 2000) were implemented to automatically identify putative New Zealand and Antarctic songs in the recordings. Five templates were selected for the New Zealand song, and four templates were used for the Antarctic song. Putative song detections were compared against the template with the highest spectrogram correlation score, and a detection threshold of 0.75 was applied for both.

Detector performance was evaluated by comparison to a subset of 26 days, representing one randomly selected day per month over the total recording period between January 2016 and February 2018. This ground-truth data set was manually reviewed in consecutive 15-min spectrograms within the 0–50

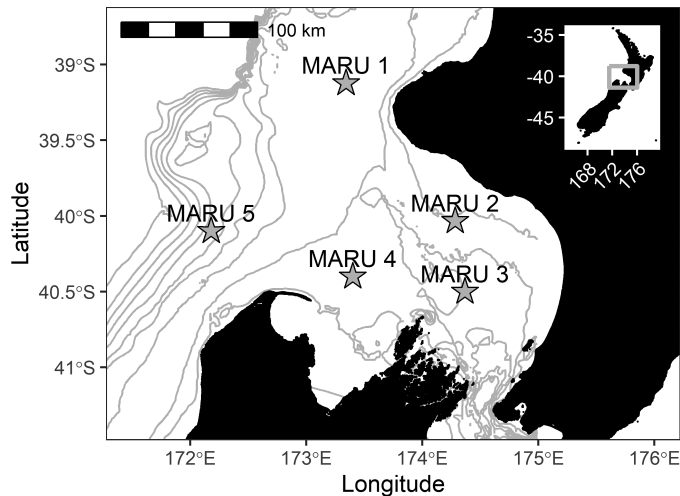


Fig. 1.—Map of the study area in the South Taranaki Bight region, with hydrophone locations denoted by the stars. Gray lines show bathymetry contours at 50-m depth increments, from 0 to 500 m. Location of the study area within New Zealand is indicated by the inset map.

Hz frequency bandwidth (3,000 point Hann window; 50% overlap) by an experienced analyst (DRB), and annotated for the occurrence of vocalizations that matched the known spectral characteristics of the New Zealand and Antarctic songs (McDonald et al. 2006). Detections were considered true positives if they overlapped with a manually annotated song in the ground-truth data set by at least 50% in time and frequency. Three evaluation metrics were calculated using custom MATLAB scripts: *precision* represents the proportion of detections that were true positives, *recall* is the proportion of true songs that were detected, and the *false alarm rate* is computed as the number of false positives per hour (Mellinger et al. 2016).

After running the New Zealand and Antarctic song detectors on the full data set, detection events were manually reviewed by an experienced analyst (MHC) in Raven Pro in consecutive 15-min spectrograms within the 0–50 Hz frequency bandwidth (3,000 point Hann window; 50% overlap). Detection events that did not match the spectral characteristics of the blue whale song being examined were removed. This additional manual validation step was taken to ensure that false-positive detections (e.g., low-frequency ship noise) were not included in the analysis.

To quantify the occurrences of the Australian song type, all recordings were manually reviewed in Raven Pro in consecutive 15-min spectrograms with a 0–150 Hz frequency bandwidth (2,048 point Hann window; 50% overlap) by an experienced analyst (DRB), and instances of the Australian blue whale song that matched the spectral characteristics described in the literature (Gavrilov et al. 2011; Balcazar et al. 2015; Tripovich et al. 2015) were selected. Occurrence of all three song types was summarized as hourly presence or absence, and the number of hours per day with each song type was tabulated. Temporal occurrence of all three song types was then evaluated across the full, 2-year recording period for all five hydrophone locations.

Detection area calculation.—The area over which blue whale song could be detected by each hydrophone unit was estimated using the range-dependent acoustic model (RAM) (Collins 1993). RAM is well-suited for calculating detection areas in low-frequency soundscapes and shallow water environments like the STB, and does so by simulating song propagation from a whale to a hydrophone under the conditions at the time. The model incorporates several aspects that impact the detection range for singing blue whales, including sound speed profile through the water column, depth of the hydrophone receiver, seafloor substrate characteristics, depth of the singing whale, the source level, and frequency of the vocalizations of interest, and ambient noise.

Sound speed profiles were based on the World Ocean Atlas (WOA 2009), bathymetry was extracted at a 1-arc minute resolution from the ETOPO1 data set (Amante and Eakins 2009), and geo-acoustic parameters for fine sand (Wentworth 1922; Bostock et al. 2019, grain size $\phi = 3$) were used in the propagation model. The depth of the singing whale was set to 25 m. The source levels and dominant frequency band differ by song type, and therefore can influence detection area. We obtained these parameters from the literature for application in the models. For the New Zealand song, the source level has not been estimated, so the source level of 179 dB re 1 μ Pa at 1 m estimated for pygmy blue whales from the Australian population was used as a proxy (Gavrilov et al. 2011), and the dominant frequency band used was 17–50 Hz. For the Antarctic song, we applied a source level of 189 dB re 1 μ Pa at 1 m (Širović et al. 2007; Bouffaut et al. 2021) and a frequency band of 25–30 Hz (Bouffaut et al. 2021). Finally, we used a source level of 179 dB re 1 μ Pa at 1 m (Gavrilov et al. 2011) and frequency band of 65–71 Hz (Balcazar et al. 2015; Tripovich et al. 2015) for the Australian song. Ambient noise levels were considered the 1st percentile levels of the dominant frequency band for each song type. Songs were simulated across a grid of points at 1-arc minute resolution (~ 2.25 km²) at varying distances surrounding each hydrophone, and detection area was estimated given the ambient noise recorded at the hydrophone. For each song type, the detection areas were calculated for the months during which songs were detected. To summarize the modeled detection distances, we calculated the mean and standard deviation of the detection area and effective radius ($\sqrt{\text{area}/\pi}$) for each song type at each hydrophone across the entire recording period and by season.

RESULTS

We detected and identified blue whale songs from the New Zealand, Antarctic, and Australian populations in our 2-year acoustic recording data set (Fig. 2). The detector evaluation for the New Zealand song yielded a *precision* score of 0.927, *recall* of 0.960, and a *false alarm rate* of 8.18 false positives per hour. For the Antarctic song, the detector evaluation produced a *precision* score of 0.819, *recall* of 0.972, and a *false alarm rate* of 0.36 false positives per hour. False positives were subsequently removed through manual validation. Since the Australian song

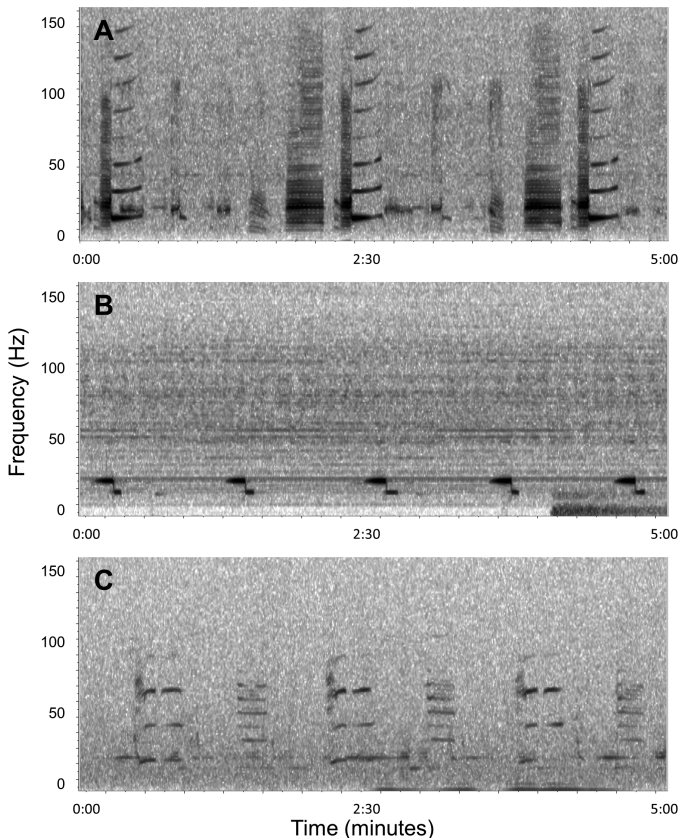


Fig. 2.—Example spectrograms of the three song types recorded in New Zealand waters. (A) New Zealand song on 31 May 2016, (B) Antarctic song on 26 August 2017, and (C) Australian song on 22 January 2017. Spectrograms are configured with a 2048-point fast Fourier transform, Hann window, 50% overlap.

was entirely manually evaluated, there were presumed to be no false-positive or false-negative detections.

The New Zealand song was the most frequently occurring blue whale song type recorded, with presence nearly every hour of every day between February and August, followed by a decrease between September and January (Fig. 3). The New Zealand song, therefore, occurs year-round at all five recording locations, following a seasonal cycle of intensity whereby peak song production occurs in the austral fall. The Antarctic song illustrates a punctuated seasonal occurrence pattern, with detections during two short and distinct peaks per year (Fig. 3). In 2016, the first peak occurred in late June to July, followed by a decrease in August and a subsequent second peak in late September to mid-October. In 2017, the same pattern of two peaks was shifted in time, with the first peak in late July and the second peak between late August and mid-September. Antarctic song was detected at all five hydrophones, but more songs were detected at MARU1 and MARU5, which are the westernmost, offshore recording locations. The Australian song was detected only between 15 January 2017 and 25 January 2017, and exclusively at the two offshore hydrophones (MARU1 and MARU5; Fig. 3).

Detection ranges varied considerably by song type, hydrophone, and season (Table 1). The ambient noise levels were highest within the New Zealand song band and lower within the

Australian and Antarctic song band (Supplementary Data SD1). Across all seasons and recording locations, New Zealand song had the smallest mean daily detection range (79.21 ± 19.09 km), followed by the Australian song (147.57 ± 20.62 km, computed for January), and the Antarctic song had the largest detection range (253.55 ± 116.60 km, computed for June–November). The large detection range of the Antarctic song indicates overlapping detection areas among the hydrophones, and therefore songs produced by the same whales may be detected at multiple recording locations (pseudoreplication); this is not necessarily the case for the New Zealand song. Although the sound propagation analysis indicated that detection ranges could occasionally overlap among hydrophones, the recording units were not time-synchronized, which prohibited measuring the difference in arrival time of song that may be detected at multiple hydrophones for localization. Additionally, the frequent occurrence of overlapping song further limited any ability to identify instances of the same song detected at multiple recording locations. Therefore, the data are analyzed strictly as the hourly presence or absence of each song at each hydrophone, acknowledging the possibility of some overlap.

DISCUSSION

In this study, we evaluate and quantify the acoustic presence of blue whale song from three populations in central New Zealand over a 2-year period. The contrasting acoustic occurrence patterns provide evidence that the three populations are distinguishable as resident, migrant, and vagrant in the region. As predicted, these acoustic occurrence patterns reflect their evolution and ecology, and can inform conservation management. The New Zealand song was by far the most prevalent, with year-round detections and a seasonal cycle in intensity, demonstrating the ecological importance of the STB region to the New Zealand blue whale population as both a foraging ground and potential breeding area. The Antarctic song was present in two distinct peaks each year (generally, June–July and August–September) and predominantly at the offshore recording locations, possibly representing the occurrence of migrating whales to and from their foraging and wintering grounds along the west coast of New Zealand. The Australian song was only detected during a brief period, indicating a rare vagrant appearance. We therefore infer that the STB region is the primary niche of the New Zealand population, a migratory corridor for the Antarctic population, and outside the typical range of the Australian population aside from the occasional visitor (Fig. 4).

The New Zealand population occupies the STB region during all times of the year. This year-round presence makes them vulnerable to the pressures of anthropogenic activities in this region, including petroleum and mineral exploration and extraction, and vessel traffic (Torres 2013; Barlow and Torres 2021), all of which contribute noise to the soundscape of the STB (Supplementary Data SD2). The detection range for the New Zealand song was smaller than for the other two song types examined (Table 1), which likely reflects the higher background noise levels in their population-specific song frequency band

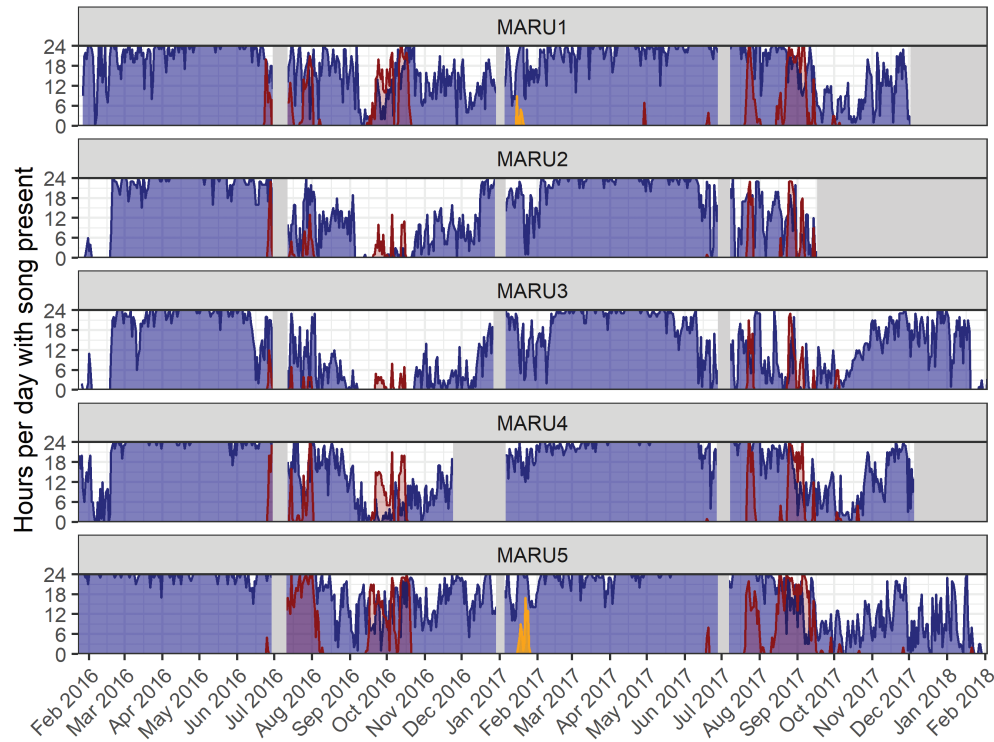


Fig. 3.—Temporal occurrence pattern of New Zealand (dark blue), Antarctic (red), and Australian (yellow) blue whale song detections at each of the five hydrophones. The y-axis represents the number of hours per day that blue whale song was detected, and the x-axis represents the recording period. Grayed out sections represent gaps in recording due to hydrophone refurbishment.

Table 1.—Mean \pm standard deviation of the detection area and effective radius for each blue whale song type over the recording period, by season and hydrophone (MARU) location in the South Taranaki Bight. Detection ranges were computed for the predominant months during which calling was present for each song type: year-round for the New Zealand song, June–November for Antarctic song, and January for the Australian song. Periods with NA values indicate times when detection ranges were not computed because they were outside of the period when the song type was recorded.

Season	Hydrophone	New Zealand		Antarctic		Australian	
		Area (km ²)	Radius (km)	Area (km ²)	Radius (km)	Area (km ²)	Radius (km)
Spring (September–November)	MARU1	23,232 \pm 8,489	84.08 \pm 18.04	264,115 \pm 178,690	271.86 \pm 100.79	NA	NA
	MARU2	24,812 \pm 7,195	87.95 \pm 12.74	392,544 \pm 273,190	330.98 \pm 124.11	NA	NA
	MARU3	19,293 \pm 5,647	77.17 \pm 13.60	299,191 \pm 298,051	272.08 \pm 145.64	NA	NA
	MARU4	32,506 \pm 13,569	99.05 \pm 23.11	128,302 \pm 112,858	182.77 \pm 86.21	NA	NA
	MARU5	20,546 \pm 13,602	75.39 \pm 29.25	287,555 \pm 210,540	277.82 \pm 119.79	NA	NA
Summer (December–February)	MARU1	18,531 \pm 8,063	74.14 \pm 20.04	NA	NA	75,678 \pm 22,826	153.30 \pm 24.22
	MARU2	22,909 \pm 5,788	84.73 \pm 10.57	NA	NA	63,495 \pm 12,885	141.50 \pm 13.65
	MARU3	17,837 \pm 5,006	74.31 \pm 12.45	NA	NA	52,237 \pm 21,831	126.47 \pm 25.15
	MARU4	25,275 \pm 12,429	86.49 \pm 23.75	NA	NA	58,684 \pm 9,030	136.23 \pm 10.90
	MARU5	14,081 \pm 10,950	61.78 \pm 25.77	NA	NA	10,4858 \pm 31,467	180.35 \pm 29.16
Fall (March–May)	MARU1	19,579 \pm 6,110	77.70 \pm 13.94	NA	NA	NA	NA
	MARU2	21,608 \pm 4,711	82.45 \pm 8.91	NA	NA	NA	NA
	MARU3	16,406 \pm 5,377	70.89 \pm 14.02	NA	NA	NA	NA
	MARU4	20,958 \pm 11,084	78.61 \pm 22.16	NA	NA	NA	NA
	MARU5	14,020 \pm 9,039	63.09 \pm 21.95	NA	NA	NA	NA
Winter (June–August)	MARU1	21,537 \pm 8,281	80.82 \pm 17.97	200,943 \pm 137,151	236.99 \pm 88.30	NA	NA
	MARU2	25,439 \pm 8,217	88.60 \pm 15.68	384,945 \pm 272,575	323.44 \pm 133.87	NA	NA
	MARU3	19,021 \pm 6,271	76.26 \pm 15.43	312,407 \pm 325,794	272.04 \pm 159.50	NA	NA
	MARU4	31,416 \pm 13,362	97.25 \pm 23.27	106,380 \pm 104,078	164.21 \pm 83.05	NA	NA
	MARU5	14,253 \pm 11,282	61.89 \pm 26.56	158,483 \pm 150,020	199.55 \pm 103.09	NA	NA

(Supplementary Data SD1). Although the New Zealand song is detected nearly every day of the entire recording period, there is a cyclical intra-annual pattern in the amount of song detected, with the peak in song between February and July (Fig. 3). Other

acoustic monitoring studies also document occurrence of the New Zealand song around New Zealand yet with lower rates of acoustic presence (McDonald 2006; Miller et al. 2014; Warren et al. 2021), indicating that the STB region is an area of high

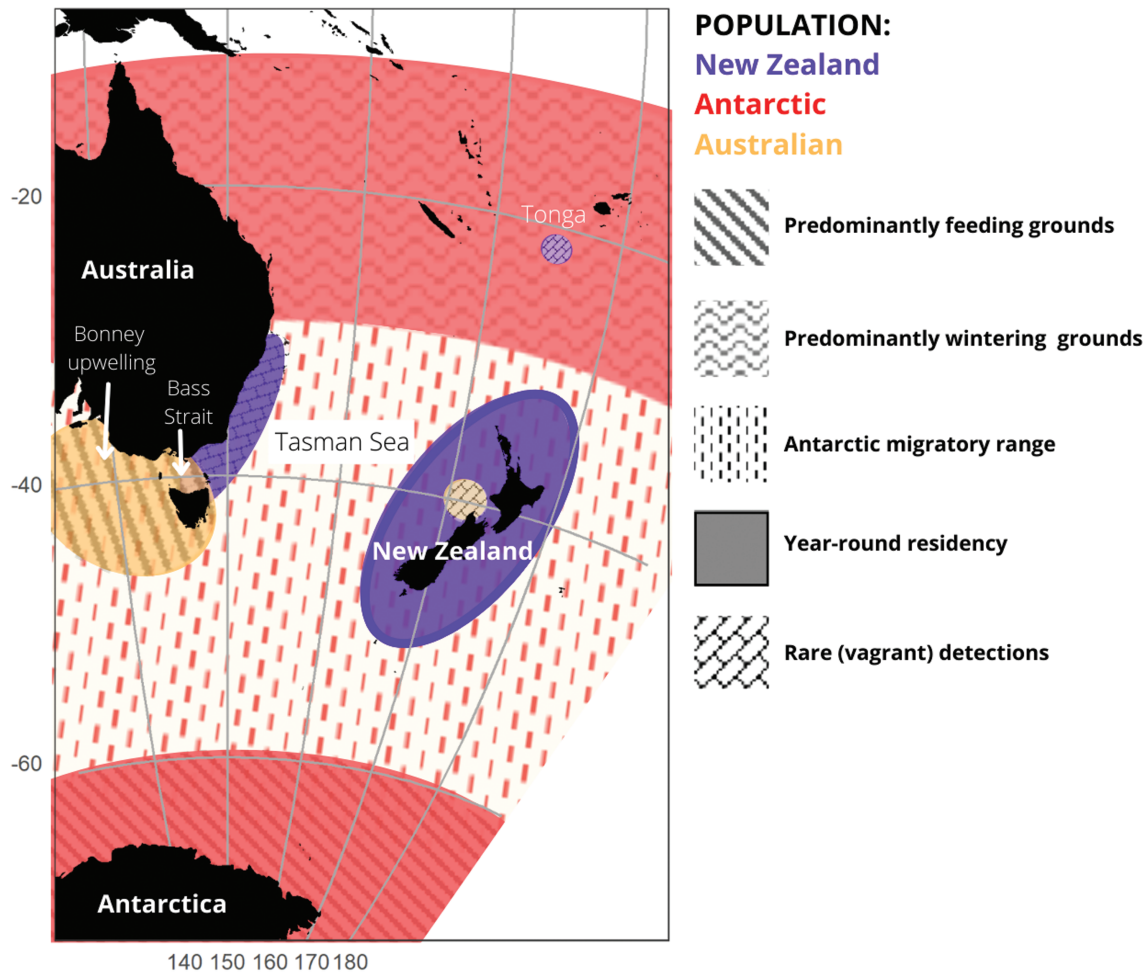


Fig. 4.—Conceptual map illustrating the current understanding of the approximate typical range of each blue whale population. Colors indicate the song type, and patterns represent inferred ecological use of each region. Distribution and occurrence patterns are synthesized from acoustic research published in the literature (e.g., Stafford et al. 2004; Balcazar et al. 2015, 2017; Tripovich et al. 2015; McCauley et al. 2018; Warren et al. 2021), and findings presented in this study.

importance for this population within their broader use of the waters surrounding New Zealand. It is important to note that blue whales also produce downswept vocalizations known as “D calls,” which are produced by both males and females and potentially serve to attract other blue whales to feeding areas or maintain group cohesion during feeding (Oleson et al. 2007; Lewis et al. 2018; Cade et al. 2021). D calls are recorded in the STB region during the spring and summer months when song occurrence is reduced, and are correlated with feeding opportunities from upwelling-driven productivity (Barlow et al. 2021). Future investigation into the seasonality and environmental drivers of the two call types may further elucidate blue whale habitat use in the STB region, particularly since song is only produced by the males and therefore only partially representative of the population.

In contrast to the year-round presence of the New Zealand song, the Antarctic population was only recorded at discrete and relatively short intervals each year. The punctuated seasonal detection of Antarctic song likely reflects their use of New Zealand waters as a migratory corridor, further supporting what is known about migration patterns based on detections of

Antarctic blue whale song at other times of the year and in different locations (Širović et al. 2004; Stafford et al. 2004; Leroy et al. 2016; Balcazar et al. 2017). The Antarctic song is detected across all five hydrophones, although to a lesser extent at the recording locations within the STB. The detection range results indicate overlapping detection areas between hydrophones for this song type, and it is therefore likely that many calls are detected at multiple locations simultaneously. This explanation is further supported by the concurrent peaks in calling across hydrophones (Fig. 5). The calls detected within the STB most likely originated further offshore in the western portion of the study region rather than from the east where landmasses reduce transmission of acoustic signals (Figs. 1 and 3, Table 1). Acoustic monitoring across a broad latitudinal range in the Southern Hemisphere supports the hypothesis of Antarctic blue whale migration between polar feeding grounds in the summertime and low-latitude areas in the wintertime (Širović et al. 2004; Stafford et al. 2004; Leroy et al. 2016; Balcazar et al. 2017). Off the east coast of New Zealand, a similar pattern of seasonal occurrence as we document in this study is observed, with peaks at the beginning and end of the winter (Warren et

al. 2021). Off the south coast of Australia at a comparable latitude to the STB, Antarctic blue whale song is similarly detected between June and October (Tripovich et al. 2015). Therefore, while Antarctic blue whales are seasonally present in New Zealand waters, they exhibit relatively low residence time and seem to rely on the region as a migratory area rather than for other functions such as foraging or breeding.

Presuming that Antarctic blue whales indeed follow the traditional baleen whale migration paradigm, the difference in timing of the peaks in Antarctic song detections in the STB between years may reflect variability in migration timing of Antarctic blue whales. In 2017, the first peak of Antarctic song started later and had a shorter gap until the second peak, indicating that Antarctic blue whales may have stayed on their southern feeding grounds longer and spent a shorter time at lower latitudes compared to 2016 (Fig. 5). This finding suggests some degree of flexibility in the timing of migration between years, which is also observed for North Pacific blue whales transitioning from feeding to migrating in Monterey Bay, California (Oestreich et al. 2022). Furthermore, we observed subseasonal variations in Antarctic song occurrence within each northbound or southbound peak (Fig. 5). This within-season variability may reflect the migration timing of different cohorts or demographic groups within the population, as is the case for other migratory mysticetes including humpback (Craig et al. 2003) and gray (Melica et al. 2021) whales.

Through acoustic monitoring there is evidence of a geographic boundary between the eastern extent of the Australian population and the western extent of the New Zealand population ranges. Despite extensive acoustic recordings along the east coast of Australia, in the Bass Strait in southeastern Australia, and in waters around Tonga, the New Zealand song has rarely been detected at these locations (Fig. 4; Balcazar et al. 2015; McCauley et al. 2018). Furthermore, the Australian song has not been detected east of the waters off eastern Australia prior to this study. The Bonney upwelling system to the west of Bass Strait off the southern coast of Australia, which bears similarities to the upwelling in the STB region (Barlow et al. 2021), is a known foraging ground for the Australian blue whale population (Fig. 4; Gill et al. 2011). Blue whales feeding in southern Australian waters migrate west and then northward from the foraging grounds. Satellite tags attached to blue whales off western Australia identified a migratory route along the west coast of Australia and into the waters surrounding Indonesia (Double et al. 2014; Möller et al. 2020), which is corroborated by the seasonality in acoustic detections of the Australian song along the south and west coastlines of Australia (McCauley et al. 2018). Furthermore, the Australian song is consistently recorded in regions of the Indian Ocean, and while the precise migratory routes are not well understood, acoustic monitoring suggests the possibility of multiple migratory destinations in the Indian Ocean (Leroy et al. 2018). Thus, current evidence suggests that the occurrence of the Australian song at the offshore hydrophones in New Zealand's STB region is an anomalous event rather than a regular seasonal pattern, though gaps in knowledge remain. Given the detection of the Australian

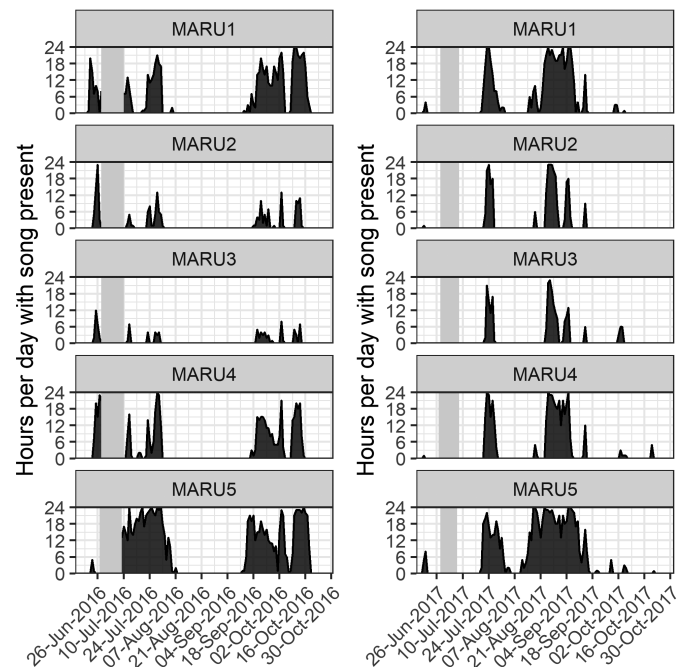


Fig. 5.—Temporal occurrence pattern of the Antarctic blue whale song at each of the five hydrophones during the seasonal periods when the song was recorded in the South Taranaki Bight in New Zealand during 2016 (left panels) and 2017 (right panels). The y-axis represents the number of hours per day during which blue whale song was detected, and the x-axis represents the date. Grayed out sections represent gaps in recording due to hydrophone refurbishment. Synchronous peaks in occurrence between hydrophones and the overlapping detection ranges of the hydrophones (MARU1–5) indicate calls are detected simultaneously at multiple locations.

song only on the offshore hydrophones, these calls most likely originated at the western extent of our study area. Considering the distances blue whales are capable of traveling (average daily travel distance for Australian blue whales during migration ~28–90 km/day, reaching up to 462 km/day; Double et al. 2014) and the relatively low energetic cost associated with locomotion and long-distance movement (Woodward et al. 2006), the span of the Tasman Sea between Australia and New Zealand (~2,400 km) is unlikely to be a barrier to travel. Rather, our detection of the Australian song during a short period (10 days during a 2-year monitoring record) could be an example of the exception proving the rule. While it is possible for the two populations to overlap spatially, the precedent is geographic separation and only rare co-occurrence (Fig. 4).

It is postulated based on genetic evidence that the Australian blue whale population diverged from the Antarctic population around the last glacial maximum (Attard et al. 2015). During this time the Antarctic blue whale population size was at its largest, as ice sheets around the Antarctic continent were at their greatest extent, maximizing foraging habitat for blue whales that relied on ice edge-associated productivity. Subsequent contraction of the ice sheets reduced their carrying capacity, and a small founder population potentially remained at lower latitudes, evolving to exploit the temperate foraging grounds off of Australia (Attard et al. 2015).

While it is possible that the New Zealand population was founded in a similar way to the Australian population, it is also possible that these populations were once a single founding population when the separation from the Antarctic population occurred, and they have since diverged over time. The geographic proximity between the ocean regions occupied by the New Zealand and Australian populations would indicate that overlap and interbreeding are possible. However, the genetic and acoustic differentiation between the two populations imply that they are distinct and on separate evolutionary trajectories in contemporary times. The genetic diversity of the Australian population is extremely low (Attard et al. 2015) and the New Zealand population has the lowest recorded haplotype diversity of any blue whale population (Barlow et al. 2018), while the genetic diversity of the Antarctic population remains relatively high despite severe exploitation during commercial whaling (Branch et al. 2007a; Sremba et al. 2012). The low genetic diversity in the New Zealand and Australian populations not only indicates their relatively recent founding from a small source population, low genetic diversity can also be interpreted as a warning of increased extinction risk through reduced evolutionary potential, and implies these populations are at increased vulnerability by threats such as anthropogenic activities and climate change (Attard et al. 2015; Barlow et al. 2018).

Large baleen whales, including blue whales, do not always follow the classical paradigm of migrating between high-latitude feeding grounds and low-latitude breeding grounds each year (Geijer et al. 2016). The three blue whale populations examined in this study may represent a spectrum of evolutionary strategies in terms of their migration and residency. The Antarctic population predominantly exploits the seasonally available, highly abundant, and energetically rich krill (*Euphausia superba*) around the ice edges of Antarctica (Miller et al. 2019), and their massive body size enhances their capacity for both energy storage and long-distance migrations. Off New Zealand and Australia, blue whales have adopted a different strategy, feeding on a smaller krill species (*Nyctiphanes australis*) in productive temperate regions for longer periods throughout the year (Gill et al. 2011; Barlow et al. 2020). Their body size is smaller (Branch et al. 2007b; Burnett et al. 2018), and these populations have adopted shorter migration distances in the case of the Australian population and potentially even no migration in the case of the New Zealand population.

Our study demonstrates how acoustic monitoring for blue whale population-specific songs can shed light on their life history, connectivity, and ecology. The STB region of New Zealand supports year-round habitat for the New Zealand blue whale population, a migratory corridor for Antarctic blue whales, and the occasional rare presence of Australian blue whales. These spatial and temporal differences in occurrence patterns between populations provide valuable insights into their evolutionary paths and ecological niche, which can aid population management and conservation efforts.

ACKNOWLEDGMENTS

We thank the New Zealand Department of Conservation for their ongoing support of this research effort. Acoustic data collection and analysis were accomplished thanks to many experts

from the K. Lisa Yang Center for Conservation Bioacoustics at Cornell University: Chris Tessaglia-Hymes and Kristin Hodge supported the acoustic data collection, and Kristin Hodge and Bobbi Estabrook advised on the acoustic detector development and evaluation. Additionally, we are grateful to Kim Bernard, Daniel Palacios, Will White, and Sarah Henkel for their helpful feedback on results and interpretation.

FUNDING

Funding for this study was provided by the New Zealand Department of Conservation, the Aotearoa Foundation, and the Marine Mammal Institute at Oregon State University. Additionally, DRB is supported by ARCS Foundation Oregon and the Hatfield Marine Science Center McNeil Scholarship.

DATA AVAILABILITY

Processed data and analysis code are available via the following Figshare digital repository: <https://doi.org/10.6084/m9.figshare.20022629>.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Hourly ambient noise over the full recording period, using the 1st percentile (p01) noise levels within the bandwidth of each blue whale song: New Zealand (dark blue, 17–50 Hz), Antarctic (red, 25–30 Hz), and Australian (yellow, 65–71 Hz).

Supplementary Data SD2.—Monthly spectral probability density (SPD) plots, by hydrophone location. The y-axes show power spectral density (PSD) in dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$, which is the standardized spectrum of sound levels across frequency. The x-axes show frequency in Hz. The color ramp indicates the SPD, which is the distribution of dB values for a given frequency, with dB values in PSD. The figures show the distribution of spectral values such that the hotter colors indicate where the sound is more concentrated at a given frequency. The location of the warmer bands near the center of the range shows that the recording units were calibrated correctly to accommodate the ambient noise conditions. In some cases, the frequencies bunch up slightly higher than adjacent frequencies, indicating that a sound at that frequency is driving up and dominating the sound there. These instances could be due to vocalizing species or seismic airgun noise. A separate set of SPD plots is shown below for each month of the recording period examined in this study, computed at a 1-s resolution.

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Submitted 6 January 2022. Accepted 18 October 2022.

Associate Editor was Burton Lim.