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INTERNATIONAL
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ABSTRACT

Species conservation depends on robust population assessment. Data on population abundance, distribution, and connectivity are critical for effective management, especially as baseline information for newly documented populations. We describe a pygmy blue whale (*Balaenoptera musculus brevicauda*) population in New Zealand waters with year-round presence that overlaps with industrial activities. This population was investigated through a multidisciplinary approach, including analysis of survey data, sighting records, acoustic data, identification photographs, and genetic samples. Blue whales were reported during every month of the year in the New Zealand Exclusive Economic Zone, with reports concentrated in the South Taranaki Bight (STB) region, where foraging behavior was frequently observed. Five hydrophones in the STB recorded the New Zealand blue whale call type on 99.7% of recording days (January-December 2016). A total of 151 individuals were photo-identified between 2004 and 2017. Nine individuals were resighted across multiple years. No matches were made to individuals identified in Australian or Antarctic waters. Mitochondrial DNA haplotype frequencies differed significantly between New Zealand (n = 53 individuals) and all other Southern Hemisphere blue whale populations, and haplotype diversity was significantly lower than all other populations. These results suggest a high degree of isolation of this New Zealand population. Using a closed capture-recapture population model, our conservative abundance estimate of blue whales in New Zealand is 718

(SD = 433, 95% CI = 279-1926). Our results fill critical knowledge gaps to improve management of blue whale populations in New Zealand and surrounding regions.

KEYWORDS: Blue whale, New Zealand, Photo-identification, Abundance, Acoustics, Genetics, Population connectivity, Conservation

INTRODUCTION

Efficacy of species conservation efforts is contingent upon robust knowledge of population status. Without information on the spatial and temporal distribution, residency patterns, connectivity, and abundance of populations, conservation efforts will be ineffective. When new species and populations are first described, it is critical that data on these fundamental population parameters are collected to promote ecological understanding, as well as timely and effective management plans.

Blue whales (*Balaenoptera musculus*) were severely exploited by the commercial whaling industry (Clapham et al. 1999, Branch et al. 2007, Torres 2013). For example, model estimates indicate that Antarctic blue whale (*B. m. intermedia*) populations were reduced to less than 1% of their original population size by commercial whaling (Branch et al. 2004). As a result of such broad scale exploitation, blue whale populations around the world typically remain diminished and are poorly understood. While blue whales are no longer hunted, such reduced population sizes can increase their vulnerability to threats from modern anthropogenic activities.

Three subspecies of blue whales are currently recognized in the Southern Hemisphere: Antarctic (*B. m. intermedia*), pygmy (*B. m. brevicauda*), and Chilean blue whales (recognized as a subspecies by the Society for Marine Mammalogy Committee on Taxonomy, but not yet named (Galletti Vernazzani et al. 2017, Committee on Taxonomy 2017). The pygmy blue whales found in the Indian Ocean and off Australia appear to have diverged from Antarctic blue whales around the last glacial maximum and are genetically, acoustically, and morphologically distinct from Antarctic and Chilean blue whales (Branch et al. 2007, LeDuc et al. 2007, Miller et al. 2014, Attard et al. 2015). Under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, Antarctic blue whales are classified as "critically endangered" (Reilly et al. 2008), and pygmy blue whales are listed as "data deficient" (Cetacean Specialist Group 1996).

The International Whaling Commission (IWC) has recognized the significant data gaps regarding pygmy blue whale populations by highlighting pygmy blue whale population assessment as a "top priority", with an emphasis on estimating the abundance of populations in New Zealand, Indonesia, Australia, and the Southeast Pacific (International Whaling Commission 2017a). Currently, no reliable abundance estimates exist for pygmy blue whales in any region (Clapham et al. 1999, Attard et al. 2015). Baseline data on population abundance, distribution patterns, and connectivity are fundamental to assess and mitigate impacts from industrial activity and longer-term environmental shifts.

Blue whales (*B. m. brevicauda* and *B. m. intermedia*) in New Zealand are currently listed as 'Migrant' species under the national threat classification system (Baker et al. 2016). Yet, Torres (2013) hypothesized that the South Taranaki Bight (STB) region of New Zealand is an important foraging ground for blue whales (Fig. 1) based on (1) opportunistic blue whale sightings in the STB recorded during seismic surveys, (2) observations of blue whales in the STB from Soviet and Japanese whaling records, (3) stranding records of blue whales around New Zealand, and (4) oceanographic studies in the STB documenting regional upwelling events that cause high productivity (Shirtcliffe et al. 1990) and lead to large aggregations of krill (*Nyctiphanes australis*), a known blue whale prey item in the Australasian region (Gill 2002). However, a dedicated study of blue whales in New Zealand had not been conducted. As it is difficult to distinguish between the Antarctic and pygmy blue whale subspecies based on morphology alone, and the distinction is rarely made in sighting and stranding records, Torres (2013) used "blue whale" to refer to both subspecies and recommended that future work identify the subspecies of blue whale occupying the STB region.

The potential use of the STB region by blue whales is of management concern as the area sustains New Zealand's highest concentration of marine industrial activity. The oil and gas industry has a strong presence in the region, with active extraction platforms and ongoing seismic survey efforts to explore for more oil and gas reserves and new drilling locations (Torres 2013). Vessel traffic frequents the STB, with multiple major ports in the region and the neighboring major shipping channel in the Cook Strait (Rawson & Riding 2015). The recent approval of the country's first seabed mine in the STB, slated to extract 50 million tons of iron sands per year for a 35-year period, will likely mean increased anthropogenic pressure on blue whale habitat in the future (Environmental Protection Authority 2017). Due to pressure from the commercial whaling industry all blue whale populations are likely already depleted (Branch et al. 2007, Torres 2013), and may therefore be especially vulnerable to modern threats from the aforementioned anthropogenic sources.

In this study, we apply a multidisciplinary approach to describe a New Zealand blue whale population, including dedicated surveys, acoustic monitoring, genetic assessment, distribution analysis, and photo-identification. Our objectives are to (1) describe spatial and temporal patterns of blue whale presence within New Zealand waters, (2) quantify patterns of individual resighting events in New Zealand and within the STB region, (3) genetically identify the subspecies of New Zealand blue whales and describe connectivity to other southern hemisphere blue whale populations, and (4) estimate the abundance of blue whales in the STB region and in New Zealand. This baseline population assessment of New Zealand blue whales will contribute to the revision of their national threat classification status and enable informed management decisions for mitigating impacts from industrial activity.

METHODS

Data sources

Dedicated fieldwork

Vessel-based surveys for blue whales were conducted in the STB region (Fig. 1) in January and February of 2014, 2016, and 2017. A 14-m jet-propelled catamaran equipped with a flying bridge (height ~4 m) for observational work was used as the research platform for the 2014 and 2016 field seasons. In 2017, the research platform was a 19.2-m vessel outfitted with a comparable flying bridge and equipped with a secondary small rigid-hull inflatable boat for closer approach to the whales. Prior to each survey day, daily images of remotely sensed sea surface temperature and chlorophyll-*a* concentration were assessed to locate areas of upwelled water and high surface productivity; survey tracklines were not standardized, but rather directed toward productive or previously unsurveyed areas.

Survey effort was conducted at vessel speeds of 8 to 12 knots in suitable weather conditions (Beaufort Sea State <5). During the surveys, one observer was posted on the port and another on the starboard sides of the flying bridge, and additional observers surveyed the entire area. At all whale sightings, survey effort was stopped, and the date, time, and location were recorded. The animal(s) were then approached for photo-identification (photo-id) effort with concurrent behavioral observation. Photographs of the left and right sides of each blue whale were captured whenever possible for identification of individuals based on unique body pigmentation patterns and dorsal fin shape (Sears et al. 1990). Unmanned aerial system (UAS) flights were also conducted, which allowed for non-disturbing, closer approach and the additional aerial perspective to enhance our observational power for establishing behavior state. Based on surface observations, behavior states were classified as travel, forage, social, rest, or unknown. Travel was defined as directional movement and regular surfacing. Indications of foraging included surface lunges and staying in one area for a prolonged period with irregular surfacings or fluke-out dives. Social behaviors included mother-calf nursing, prolonged coordinated surfacing such as racing, and tactile contact between individuals. Resting behavior consisted of logging near the surface with minimal forward movement. All behaviors that did not fit within these classifications were considered unknown. These data describe blue whale behavior patterns in the STB, but are not necessarily indicative of a behavioral budget.

Once photo-id effort was complete, tissue biopsy sampling effort was initiated. Skin and blubber biopsy samples were collected using a lightweight biopsy dart (cutting head size 7 mm x 19 mm) fired from a Paxarms biopsy rifle (Krutzen et al. 2002). A fine-mesh (300-µm) dip net attached to a long pole was used to collect opportunistic fecal samples from surface waters. Biopsy and fecal samples were stored in sterile containers and frozen at -20°C until genetic analysis.

To assess the spatio-temporal patterns of blue whale vocalizations in the STB region, Marine Autonomous Recording Units (MARUs) (Calupca et al. 2000) were deployed at five sites (Fig. 1). Each MARU hydrophone had a flat frequency response (± 2.0 dB) in the 15-585 Hz band and recorded continuous acoustic data 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 23 January-30 June 2016, and 11 July-29 December 2016 (MARU refurbishment occurred during the brief interim period). While a New

Zealand blue whale call type has been documented and described (McDonald 2006), the source level is unknown. The estimated source level for pygmy blue whale song in the eastern Indian Ocean is 179 ± 2 dB re 1μPa at 1 m (Gavrilov et al. 2011), and the estimated maximum acoustic detection range was 50-200 km (Gavrilov & McCauley 2013), depending on the recorder capabilities, ambient noise levels, and sound propagation conditions. We expect that the detection range of our hydrophones is comparable; thus, all acoustic detections of blue whales were from within the New Zealand Exclusive Economic Zone (EEZ).

Opportunistic data sources

Opportunistic blue whale photographs and sightings were compiled for analysis. Data sources include incidental blue whale sightings confirmed, collated, and administered by the New Zealand Department of Conservation; reports from marine mammal observers during seismic surveys; opportunistic sightings reported during surveys for other marine mammals, and sightings from whale watch vessels (Table S1). The blue whale sub-species of these sightings are unknown. Replicate reported sightings were identified and removed from the dataset prior to analysis. Photographs of blue whales suitable for individual identification were provided from 19 sources (Table S2), including contributions from within the New Zealand EEZ (15 sources), from Australian waters (3 sources), and from Antarctic waters (1 source).

Analytical methods

Distribution of reported sightings

All reported blue whale sightings (from dedicated surveys and opportunistic sources) were compiled to assess their spatial and temporal distribution in New Zealand. The total number of blue whale sighting reports in each month of the year was tabulated within the STB region and within the New Zealand EEZ. Given the non-systematic data collection, this synthesis describes the temporal pattern of sighting reports, not necessarily the temporal distribution of blue whales.

To assess the spatial distribution of sighting reports, all sighting locations within the New Zealand EEZ were plotted in ArcMap 10.4.1 (Esri 2016) and converted to a point density map using a search radius of 50 km. The resulting map is an assessment of available sighting reports, not a complete depiction of the spatial distribution of blue whales in the New Zealand EEZ.

Acoustics

Acoustic data were examined for the occurrence of blue whale song (McDonald et al. 2006) using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, USA). While blue whales produce several different vocalizations, song is understood to be produced only by males and likely serves a reproductive function, although the year-round occurrence of blue whale song may suggest a broader function of the call than exclusively reproduction (Oleson et al. 2007). Other blue whale vocalizations, including D-calls, were not analyzed. Data were visually reviewed in consecutive 15-minute spectrograms, with a 10-250 Hz frequency bandwidth (512 point Hann window; 50% overlap). Each recording day was manually reviewed in its entirety by an experienced analyst, and the daily acoustic presence of the New Zealand blue whale call type was annotated for each MARU recording site. Percent monthly presence for each site was normalized for recording effort by dividing the number of days containing the New Zealand blue whale call type by the number of recording days analyzed within the month.

Photo-identification

Photographs of blue whales from dedicated surveys in the STB region were reviewed and grouped by individual within each sighting event, and individuals were then compared between events. Using standard methods (Sears et al. 1990), individuals were identified using unique body pigmentation patterns and dorsal fin shape. Photo quality was assigned a rating on a scale of 1-5 (with 1 representing the lowest quality and 5 the highest quality), based on the angle of the photographer to the whale, amount of the whale that was visible in the photo, sharpness of the image, and glare from the sun. Photos of quality 1 and 2 were discarded to minimize error in the identifying individuals. Using the individuals identified from the dedicated surveys, a discovery curve was generated by plotting the cumulative number of identified individuals versus the cumulative number of days of survey effort. It should be noted that while for most individuals both sides of the whale were photographed, for some only left-side or right-side photos were obtained. Therefore, it is possible that some individual whales are counted twice and this can only be reconciled with further data collection in future work.

Subsequently, images of the whales identified during the dedicated surveys within the STB region were compared to the 19 other sources of opportunistically collected photo-id data (Table S2). Individuals resighted in multiple years were examined in greater detail, and the sighting locations of resighted animals were plotted in ArcMap 10.4.1.

Genetics

Biopsy and fecal samples collected in the STB during 2014, 2016, and 2017 were analyzed along with tissue samples held at the New Zealand Cetacean Tissue Archive (NZCeTA) at the University of Auckland. The NZCeTA included samples previously collected from beachcast blue whales (see Torres 2013 Fig. 2, Table S2 for details) and biopsy samples of three live individuals: one from the Hauraki Gulf (2006) and two from the Cook Strait (2011 and 2013) (Fig. 1). Total genomic DNA was extracted from skin tissue following standard proteinase K digestion and phenol/chloroform methods (Sambrook et al. 1989), modified for small samples (Baker et al. 1994). Fecal samples were first filtered through a 0.4-µm cyclopore polycarbonate track etched membrane filter (GE Healthcare Life Sciences). The filter was transferred to a 2-ml tube and frozen in 800 µl of Longmire's buffer (Longmire et al. 1997) until extraction. Total genomic DNA was extracted from the filtered samples using the phenol/chloroform method described above for skin samples with an extended mixing period during the first PCI step to ensure the filter had completely dissolved. Initial attempts to amplify DNA from some fecal samples failed, suggesting the presence of PCR inhibitors. Affected DNA was cleaned with a OneStep™ PCR inhibitor removal kit (Zymo Research). In some cases, two applications were necessary to remove all inhibitors.

A standard DNA profile, including molecular sex, amplification and sequencing of 410 bp of the mitochondrial DNA (mtDNA) control region, and microsatellite genotyping of up to 15 loci, was generated for all samples following methods described Sremba et al. (2012). An additional two microsatellite loci, DlrFCB17 and GATA98 were genotyped following methods described in LeDuc et al. (2007). Control region sequences were visualized and manually reviewed using the program Sequencher v4.6 (Gene Codes Corporation). Individual haplotypes were aligned with previously published blue whale haplotypes (LeDuc et al. 2007, Sremba et al. 2012, Torres-Florez et al. 2014, Attard et al. 2015) downloaded from GenBank. Microsatellite alleles were analyzed using Genemapper v4.0 (Applied Biosystems), and peaks were visually inspected. Samples that amplified at less than 12 loci were considered to be poor quality and were removed from the dataset.

Replicate samples of individual whales were identified using CERVUS v3.0.3 (Kalinowski et al. 2007) and probability of identity ($P_{(ID)}$) was calculated for pairs of samples showing exact matches. Mismatches of up to three loci were allowed to prevent false exclusion due to allelic dropout and other genotyping errors (Waits et al. 2001). Electropherograms from mismatching loci were reviewed and corrected or repeated.

An exact binomial test implemented in Program R version 3.4.0 (R Core Team 2017) was used to test whether the sex ratio of males to females differed from 1:1, after removing replicate samples. ARLEQUIN v3.5.1.2 (Excoffier & Lischer 2010) was used to calculate haplotype diversity and to test for mtDNA haplotype differentiation between (1) STB and NZCeTA samples, and (2) pairwise between the combined New Zealand samples and three other populations: Antarctic blue whales in the Southern Ocean (n = 183, Sremba et al. 2012), Chilean blue whales in the Southeast Pacific including the Chilean coast (n = 113, Torres-Florez et al. 2014), and pygmy blue whales from the south and west coasts of Australia (n = 89, Attard et al. 2015) that included sequences previously published by LeDuc et al. (2007). The significance of differences in haplotype diversity between the New Zealand dataset and the other blue whale populations was tested using a permutation procedure implemented in Program R, Genetic_diversity_diffs v1.0.4 (Alexander et al. 2016). Analysis of molecular variance (AMOVA) implemented in ARLEQUIN was used to estimate mtDNA differentiation of the New Zealand blue whales from the other populations, using both F_{ST} based on haplotype diversity and Φ_{ST} based on nucleotide diversity.

Abundance estimates

The three years of survey effort were used to generate a within-year capture-recapture abundance estimate for the STB region for each year and a conservative abundance estimate for blue whales in New Zealand. A Bayesian closed population model was used, which was fitted using Markov chain Monte Carlo in the R package multimark (McClintock 2015). Models in multimark allow for the inclusion of multiple “mark types”. Here, our two mark types were left- and right-side photographs. It is possible that some individuals were counted twice if left- and right-side photos were not obtained simultaneously at one encounter, and this is accounted for by the population models implemented in multimark. The use of multimark avoids the need for separate right-side and left-side abundance estimates, and increases our overall sample size. We assumed no behavioral response to the capture events (i.e., captured individuals were no less likely to be re-photographed on a subsequent occasion), equal probability of type one and type two encounters (i.e., we were equally likely to obtain a left-side photograph as a right-side), a conditional probability of obtaining both mark types simultaneously (i.e., for some animals we had only left-hand or right-hand side photographs, and for some we were able to obtain both during the encounter), and allowed for temporal variation in detection probability.

For each within-year abundance estimate, three capture periods were designated as groups of consecutive survey days separated by breaks in survey activity due to poor weather conditions (Table S3). Therefore, if an individual was seen multiple times in the same day or on consecutive days, it was not counted as a resighting to avoid pseudo-replication that would bias the abundance estimate.

An abundance estimate for blue whales in New Zealand was generated using the three survey years as three separate capture periods (Table 3). For this estimate, we also used a Bayesian Markov chain Monte Carlo closed-population model in multimark. A complete lack of information on population parameters such as immigration and emigration rates as well as the inability for multimark to compute abundance estimates for open populations incorporating multiple mark types inhibited the application of an open-population abundance model. We provide this closed-population model abundance estimate for New Zealand blue whales as a conservative estimate, and further justification of this approach is provided in the discussion. The same detection probability parameters were assumed as for the within-year estimates with the addition of an “effort” covariate, which accounted for the difference in survey length between the three capture events. Survey length was measured by kilometers of survey effort in each year.

RESULTS

Distribution of sightings

Three dedicated surveys were conducted in the STB region in 2014 (n = 7 days between 24 Jan and 3 Feb), 2016 (n = 11 days between 23 Jan and 8 Feb), and 2017 (n = 9 days between 5 and 20 Feb). This survey effort resulted in a total of 64 blue whale sightings. The most frequently observed known behavior was foraging (32.8% of sightings), followed by travel (6.3%), socializing (4.7%), and rest (0%). Behavior was unknown for 56.3% of sightings. Eight mother-calf pairs were observed, including documentation of nursing behavior through UAS (video in Supplementary Materials). Combining observations from these dedicated surveys with the opportunistic sightings data, a total of 740 blue whale sightings have been reported in New Zealand waters between 1900 and 2017. Of these, 704 had precise sighting coordinates, while regional sighting locations were provided for the remainder. The sightings without precise location data were used for the temporal distribution assessment, but not for the spatial distribution analysis.

Blue whale sightings were reported during every month of the year (Fig. 2), both in the STB region and elsewhere in the New Zealand EEZ. Fewer sightings were reported during the austral winter months, between May and September. For nearly every month, the majority of reported blue whale sightings within the New Zealand EEZ occurred in the STB region. The spatial distribution of blue whale observations illustrates a predominant concentration of sightings in the STB region (Fig. 3). Additional areas with slightly elevated densities of blue whale sighting reports include Kaikoura, Hauraki Gulf, and Bay of Islands regions, which could be an artifact of elevated marine observations in these areas (i.e., whale watch and research vessels).

Acoustics

The total number of recording days ranged between 295-331 days for each MARU site. New Zealand blue whale calls (Fig. 4; McDonald et al. 2006) occurred regularly at all five sites in the STB region (Fig. 5; mean daily occurrence 86.6% across all sites). Calls occurred most frequently at sites MARU 5 and MARU 1, with 99.7% and 96% daily acoustic presence, respectively. All sites had 100% daily acoustic presence during March, April, and May 2016, and ≥90% daily acoustic presence in June and July. While no blue whale calls occurred at site MARU 3 in January 2016, this hydrophone was only recording for six days of the month (Fig. 5). Percent daily acoustic presence of calls was less at sites MARU 2 (44.8%) and MARU 3 (44.8%) during February 2016, and for all sites during September 2016 (Fig. 5). No acoustic data were collected at site MARU 4 during December 2016.

No Antarctic blue whale vocalizations (McDonald et al. 2006) were recorded during times when vessel-based data collection was underway (January and February 2016). We therefore consider it highly unlikely that any photos obtained during the dedicated fieldwork in the STB are of Antarctic blue whales.

Photo-identification

A total of 89 individual blue whales were identified during dedicated surveys in the STB region over the three survey years. These identifications included 64 for which both left- and right-side identification photos were obtained, 12 left-side only IDs, and 13 right-side only IDs; we acknowledge that the true number of unique individuals observed may be slightly lower than 89. The discovery curve depicts a consistently upward trend and does not appear to be reaching an asymptote (Fig. 6), indicating we are still in the discovery phase and not yet nearing identification of the entire population.

Opportunistic photos of New Zealand blue whales identified between 2004 and 2017 were compiled and a total of 322 photographs were deemed suitable for identification and comparison. This opportunistic photo dataset yielded 78 sightings for the identification of 62 individuals, and when combined with the STB region survey sightings, a total of 151 unique individuals were identified (93 left- and right-side, 36 left-side only IDs, 22 right-side only IDs). This collection represents the most comprehensive photo-id catalog of blue whales in New Zealand waters.

Nine blue whales were resighted across multiple years in the New Zealand EEZ (Fig. 7). For all of these inter-annual resightings, at least one of the sightings was in the STB region. For four of these resightings, both observations occurred in the STB region within the same monthly period of different years (NZBW004, NZBW018, NZBW008, NZBW023), indicating consistent temporal use of this area by individuals. The maximum number of resightings for an individual was four times over a seven-year period, and this individual (NZBW031) was observed with a calf at three out of four observations. No blue whales identified anywhere in the New Zealand EEZ matched to any photo in the Australian collection (n = 197) or Antarctic collection (n = 65).

Genetics

A total of 72 samples were available for genetic analysis. This included 43 biopsy samples and 14 fecal samples collected in the STB in 2014, 2016 and 2017. Additionally, the NZCeTA contained samples from 12 beachcast whales from around New Zealand and biopsy samples collected from two live whales in the Cook Strait and one in the Hauraki Gulf. Six of the fecal samples and two skin samples collected from beachcast whales failed to amplify for 12 or more loci and were considered poor quality. The six poor quality fecal samples were removed from further analysis. As the two poor quality skin samples obtained from beachcast whales were collected before any biopsy effort, they represent two unique individuals that were not present for potential resampling during survey effort, and as such, they were retained in the genetic dataset.

Genotype matching identified 10 whales sampled multiple times in the STB region by biopsy and/or fecal sample; these samples show sufficiently low $P_{(ID)}$ values (1.17×10^{-9} to 7.65×10^{-8}) to support that the matches are not due to random chance. After removing within-year replicates, genotypes were compared between STB individuals and samples from the NZCeTA. This comparison identified one individual sampled in the STB in both the 2014 and 2016 field seasons ($P_{(ID)} = 5.63 \times 10^{-9}$). All genotype matches were confirmed by photo-id. With all replicates removed, the New Zealand blue whale genetic catalogue contains 53 individuals. Twenty-nine individuals are females, 17 are males, and the sex could not be determined for 7 individuals due to degradation of the DNA. The sex ratio of 17:29 did not differ significantly from 1:1 (exact binomial test, $p = 0.104$).

Control region haplotypes were sequenced from 52 individuals, which included all but one of the NZCeTA samples (Table 1). After control region sequences were trimmed to a 410 bp consensus region and compared with published sequences on GenBank, seven haplotypes were identified in the New Zealand dataset: four previously described by LeDuc et al. (2007), one previously described by Attard et al. (2015), and two previously undescribed. The two new haplotypes presented here are referred to as BmuNZ18 and Bmu17NZf1. The majority of the samples in the New Zealand dataset (75%) were haplotype d (LeDuc et al. 2007).

The haplotype diversity of the New Zealand dataset was 0.406 ± 0.085, which is significantly lower than any of the other blue whale populations tested ($p < 0.001$ for all comparisons; Table 2). There was no significant differentiation in mtDNA haplotypes between the STB and NZCeTA collections ($F_{ST} = 0.000$, $p = 0.684$), so they were combined for comparison to the other areas. The combined New Zealand collection showed highly significant differentiation from the Southern Ocean and Southeast Pacific populations for both F_{ST} and Φ_{ST} (Table 2). The New Zealand collection of samples was most similar to the Australian pygmy blue whale population Yet, these two blue whale populations show a low level of differentiation, indicated by F_{ST} (0.04, p = 0.009) but not Φ_{ST} (0.013, p = 0.075).

Abundance

The 2017 survey yielded the highest number of individually identified whales, even though the 2016 survey covered the most distance (Table 3). Within-year abundance estimates of blue whales in the STB region were relatively similar for each survey year (Table 3), with a mean of 140 (SD = 28). Using all survey years of photo-id captures, our abundance estimate for New Zealand blue whales from a closed population model is 718 (SD = 433, 95% CI = 279-1926) individuals. While the uncertainty around this estimate is large, the point estimate of 718 is likely an underestimate of total population size.

DISCUSSION

Our multidisciplinary study demonstrates that a genetically distinct blue whale population occurs in New Zealand waters year-round. This finding is of significant conservation importance considering the history of exploitation and current anthropogenic threats.

Given that blue whales in New Zealand waters are not solely 'Migrant,' revision of the current threat classification status of blue whales in New Zealand is warranted. We estimated the abundance of this population to be 718 (SD = 433) individuals, determined that they are genetically most similar to the pygmy blue whale subspecies (*B. m. brevicauda*) found off Australia, described multiple individual resightings within New Zealand waters across multiple years and in multiple seasons, highlighted a lack of photo-id matches between New Zealand blue whales and photo collections from neighboring regions, and documented year-round presence in the STB region where foraging was frequently observed during surveys. These results lead us to hypothesize that this newly documented blue whale population may be largely resident to New Zealand, although we recognize that excursions beyond New Zealand waters may occur. Individual movement data are needed for hypothesis confirmation.

Despite the paradigm that baleen whales migrate seasonally between high-latitude feeding grounds to low-latitude breeding grounds, there are several exceptions (Geijer et al. 2016). It has been noted that blue whales may not always fit this rigid categorization and that migration patterns may also change over time (Calambokidis et al. 2009, Leduc et al. 2017). Furthermore, it has been established that there is a year-round resident population of Northern Indian Ocean blue whales (*B. m. indica*) in Sri Lanka (*e.g.* de Vos et al. 2014) based only on observations of blue whales in the waters surrounding Sri Lanka during every month of the year (Ilangakoon & Sathasivam 2012). We similarly present evidence of blue whale sighting reports in New Zealand waters during every month of the year, which is corroborated by acoustic detections of the New Zealand blue whale call on 99.7% of recording days by at least one hydrophone during 2016. These findings highlight the importance of relying on applicable scientific data for conservation management rather than on paradigms.

While blue whale sightings and vocalizations were reported during every month of the year, fewer sightings were reported during the winter months, which could indicate that a proportion of the population migrates to other waters, including a yet unknown breeding ground. However, during the winter months with fewer visual sightings, we recorded a high daily acoustic presence in 2016, indicating that decreased visual sightings may be an artifact of observer effort. In contrast, recordings from Australian waters show a stronger seasonal pattern of blue whale acoustic detections, including a drop-off or complete absence during the winter months (Balcazar et al. 2015). Although the breeding and calving locations of this New Zealand population are currently undetermined, our hydrophones often recorded blue whale song, which is thought to be associated with breeding behavior, during every month of the year. Additionally, we observed multiple mother/calf pairs, including documentation of nursing behavior. At this stage we have only assessed acoustic presence, and we recognized that this does not account for call density. Further analysis of our acoustic dataset will elucidate the spatial and temporal occurrence patterns of blue whales in the STB region for a multiple-year recording period.

While the concentration of blue whale sightings in the STB region (Fig. 3) is influenced by both dedicated and seismic survey observer effort in the area, we believe the STB region to be critical habitat for New Zealand blue whales. If Kaikoura, the Hauraki Gulf, and the Bay of Islands were occupied by blue whales with the same frequency as the STB region, sighting reports in these areas would likely be greater due to relatively high observation effort by marine mammal scientists and the whale watching tourism industry. Furthermore, while feeding blue whales have occasionally been reported in the Hauraki Gulf and Kaikoura, oceanographic conditions there are different than in the STB region, which is characterized by a wind-driven upwelling system that produces a plume of cold, productive water associated with high concentrations of *N. australis* (Shirtcliffe et al. 1990, Torres 2013). These oceanographic conditions are unique within New Zealand, and are consistent with well-documented blue whale habitat in Australia (Gill 2002), Chile (Buchan & Quiñones 2016), and California (Croll et al. 1998). We therefore posit that, even in the absence of New Zealand-wide systematic survey effort for blue whales, we have substantial evidence to indicate that the STB region is an important area for blue whales within the New Zealand EEZ, particularly for foraging.

The resighting of nine individual whales between years within the New Zealand EEZ demonstrates site fidelity to New Zealand waters. In addition, Olson et al. (2015) reported one other photo-identification match between years, sighted in the Cook Strait and Oamaru (Fig. 1). Of all these inter-annual resightings, at least one of the sightings was made in the STB region (Fig. 7), further emphasizing the likely importance of the region for blue whales in New Zealand. It is also noteworthy that three of the inter-annual resightings were made in different seasons, indicating that at least some individuals make use of the region in both winter and summer.

Genetically, our samples of New Zealand blue whales are most similar to the Australian pygmy blue whales, but differ significantly in haplotype frequencies and diversity. We described two new mtDNA haplotypes in the New Zealand population, and the genetic samples are characterized by very low haplotype diversity. This is significantly lower than that of the pygmy blue whale population found in southern Australia that was described as having the lowest genetic diversity of any blue whale population (Attard et al. 2015). As hypothesized by Attard et al. (2015) for the southern Australian pygmy blue whale population, the low genetic diversity of the New Zealand population may reflect a relatively recent founding event. While there was significant differentiation for F_{ST} based on haplotype diversity, there was no significant differentiation for Φ_{ST} based on nucleotide diversity, between the New Zealand and Australian populations. This indicates that the New Zealand population is most closely related to the Australian population, and likely corroborates the hypothesis of a more recent founding event as it takes longer for population separation to be reflected in Φ_{ST}. The low genetic diversity makes these populations potentially vulnerable to future climate change and other anthropogenic impacts (Attard et al. 2015). The vulnerability of the New Zealand population may be exacerbated by their year-round occupancy of the STB region, where they are frequently exposed to anthropogenic activities.

The IWC has prioritized the need for population assessments of pygmy blue whales (International Whaling Commission 2017a). We present the first abundance estimate for any pygmy blue whale population to date. Although our conservative abundance estimate for pygmy blue whales in New Zealand is based only on photos captured during dedicated survey effort in the STB region, we considered this estimate representative because (1) the majority of all reported blue whale sightings occurred in the STB region (Fig. 2), (2) individuals re-occur in the STB region across multiple years, with some evidence of individual movement between the STB region and other parts of New Zealand (Fig. 7), (3) no matches have been made between individual blue whales identified in New Zealand and those identified in Australia or Antarctica, and (4) the New Zealand population has significant genetic differentiation from all other known southern hemisphere blue whale populations. In the absence of any known immigration/emigration between New Zealand and other regions, this last point also justifies our application of a closed population model. However, we recognize that there are several caveats that must accompany this population abundance estimate. The New Zealand blue whale call has infrequently been recorded outside New Zealand waters (in Tonga and eastern Australia; Balcazar et al., 2015). We also acknowledge that births and deaths likely occurred between 2014 and 2017 creating some degree of bias in the estimate. However, this bias is expected to be minimal given the short duration of the study period relative to low pregnancy rates (Lockyer 1984) and high survival probabilities for blue whales (Ichihara 1966). The rates of individual movement between the STB and other areas of New Zealand are not well understood at this time, and therefore could not be accounted for in our abundance model. The result of the closed population model using our three survey years as discrete capture periods, therefore, represents a conservative abundance estimate (N = 718, SD = 433) for the blue whale population occupying New Zealand waters. This New Zealand estimate is qualified as a Category 2 abundance estimate under the standards set by the IWC, described as "an underestimate, suitable for 'conservative' management but not necessarily reflective of total abundance" (International Whaling Commission 2017b). The upward trend of the discovery curve indicates that we are not yet nearing full identification of the whole population. Additionally, the low rate of resightings resulted in wide confidence intervals around the estimate, which may be reduced with subsequent years of data collection and analysis.

In this study, we document a unique New Zealand blue whale population through a comprehensive population assessment that determined evidence of year-round presence, individual resightings across years, and genetic differentiation from other regions. These multidisciplinary results align and lead us to hypothesize that this blue whale population may be mostly resident within New Zealand waters. The concentration of blue whales in the STB region is of significant management importance due to the high industrial presence in this area. Further investigation into potential space-use conflict between blue whales and industrial activity such as seismic surveys, oil and gas drilling and extraction, seabed mining, and vessel traffic is warranted. A vital first step in any impact assessment is baseline information on population distribution, connectivity, and abundance, which we have provided here. We recommend that subsequent analyses build on these findings to investigate blue whale spatial and temporal habitat use patterns and assess the potential cumulative effects of industrial activity on the behavior and health of the population.

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TABLES AND FIGURES

Table 1. Frequencies of mitochondrial DNA haplotypes for individual pygmy blue whales sampled in the South Taranaki Bight (STB) region and from beachcast animals around New Zealand held at the New Zealand Cetacean Tissue Archive (NZCeTA). Haplotype codes follow Le Duc et al. (2007) except for Haplotype 15 (Attard et al. 2015) and the two newly identified haplotypes (BmuNZ18 and Bmu17NZfl).

	GenBank code	**STB**	**NZCeTA**	**Total NZ**
Haplotype d	EU093921	30*	10	39
Haplotype e	EU093922	1	2	3
Haplotype ii	EU093952	2	1	3
Haplotype mm	EU093956	1	1	1
BmuNZ18		2	0	2
Haplotype 15	HQ130731	1	0	1
Bmu17NZf1		1	0	1
Total		**38**	**14**	**52**

*One sample was heteroplasmic for haplotype d and an undescribed haplotype, and was excluded from further analysis.

Table 2. Pairwise comparisons of mitochondrial DNA control region differentiation using haplotype (F_{ST}) and nucleotide (Φ_{ST}) diversity between New Zealand pygmy blue whales and three other blue whale populations: The Southern Ocean, the Southeast Pacific, including Chile, Ecuador and Peru, and Australia.

Dataset	**Sample size**	**# Haplotypes**	**Haplotype diversity (h)**	**Nucleotide diversity (π)**	**F_{ST}**	**P value**	**Φ_{ST}**	**P value**
New Zealand	52	7	0.406 ± 0.085	0.001 ± 0.001	-	-	-	-
Southern Ocean	183	52	0.969 ± 0.004	0.014 ± 0.007	0.257	< 0.001	0.333	< 0.001
Southeast Pacific	113	19	0.904 ± 0.012	0.014 ± 0.006	0.310	< 0.001	0.381	< 0.001
Australia	89	14	0.680 ± 0.053	0.003 ± 0.002	0.040	0.009	0.013	0.075

Table 3. Within-year abundance estimates for the South Taranaki Bight region for each survey year.

Year	Survey effort (km)	Unique IDs	Abundance estimate	SD	95% CI
2014	315	22	109	97	29-379
2016	2,759	26	145	99	47-417
2017	1,677	42	166	80	75-367

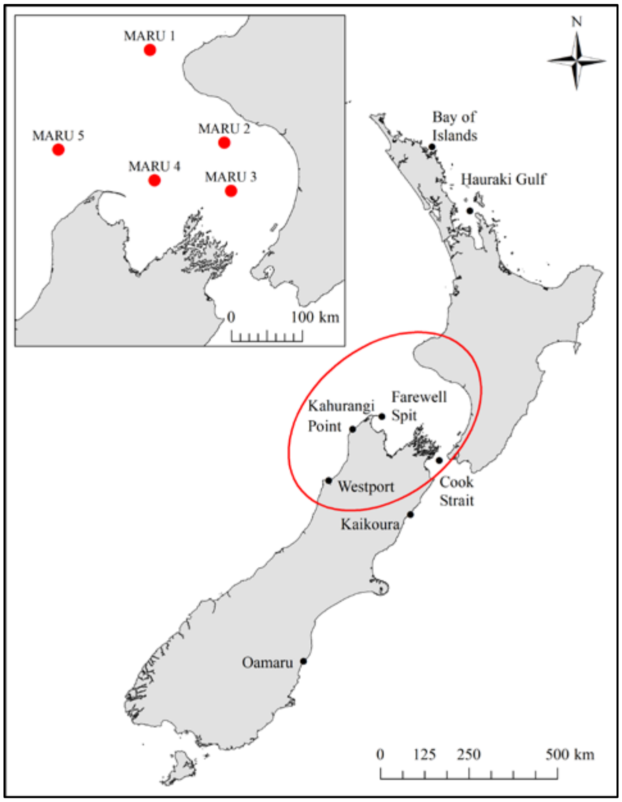

Figure 1. A map of New Zealand indicating the location of the South Taranaki Bight (STB) region (marine area within the red circle). Locations of the five marine autonomous recording units (MARUs) deployed in the STB region to assess blue whale vocalization patterns are shown in the inset.

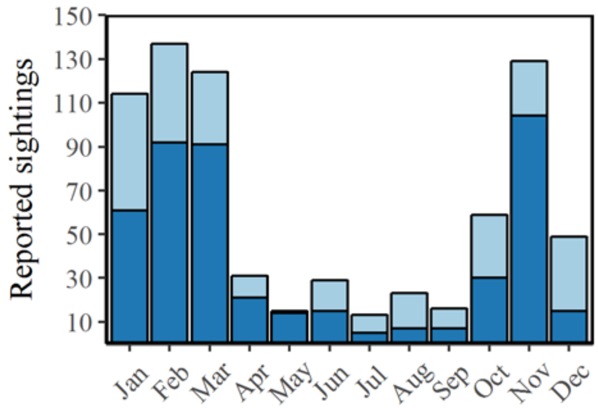

Figure 2. Blue whale sighting reports by each month of the year between 1900 and 2017, including systematic survey and opportunistic data sources (n = 740). Light blue bars represent all reports from within the New Zealand Exclusive Economic Zone (EEZ), and dark blue bars represent reports from the South Taranaki Bight (STB) region.

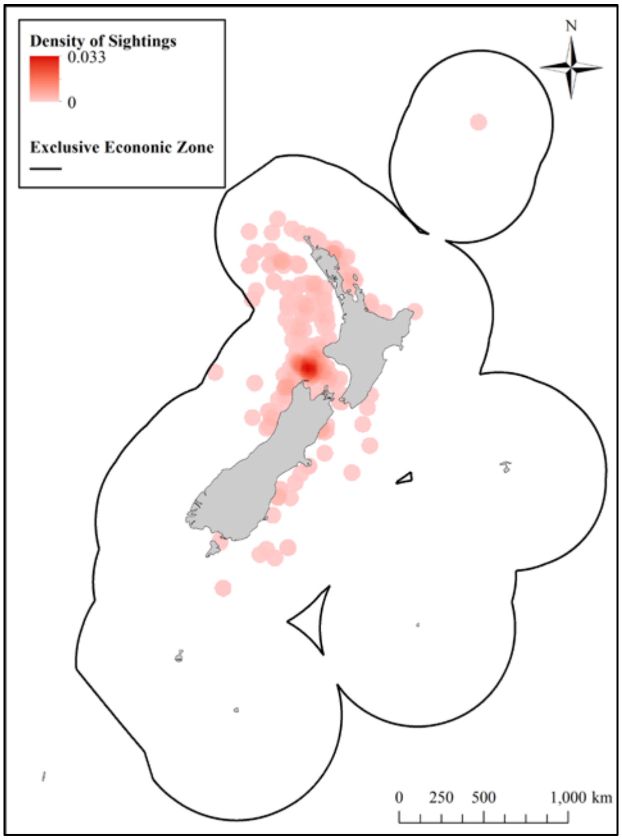

Figure 3. Point density map of blue whale sighting reports that provided geographic coordinates within the New Zealand Exclusive Economic Zone between the years 1980 and 2017 (n = 704). Densities are calculated as the number of blue whales per km^2 with a 50 km search radius. A minimum-maximum stretch type with a gamma stretch of 1.5 was applied for visualization.

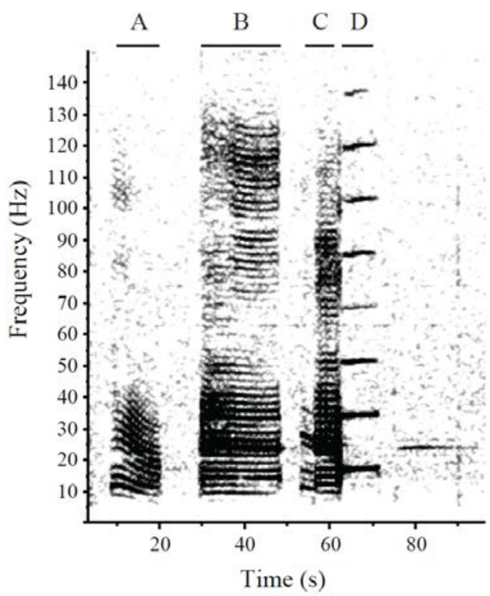

Figure 4. Spectrogram of New Zealand blue whale call type recorded on 25 February 2016 at Marine Autonomous Recording Unit (MARU) 4. Call type consists of 3 pulsed calls (A-C), followed by a tonal call (D). Spectrogram visualized with a 1024 point fast Fourier transform, Hann window, 90% overlap, 0.488 Hz frequency resolution, and 204 ms time resolution.

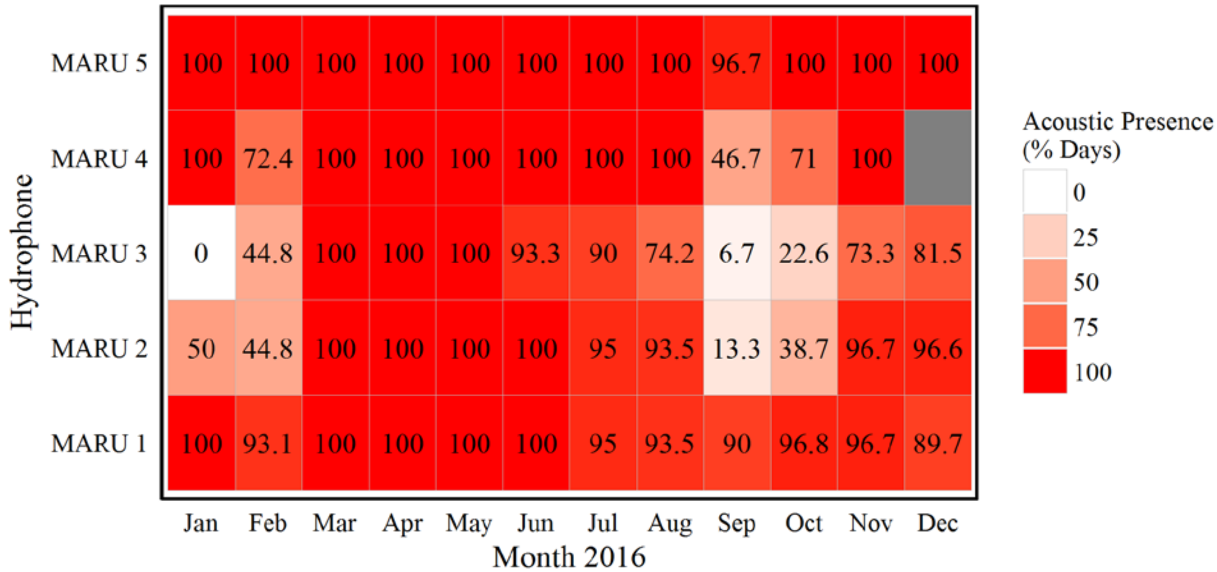

Figure 5. Percent of recording days with acoustic detection of the New Zealand blue whale call type, by each month of 2016 at each hydrophone location (MARU 1-5). No data were collected at site MARU 4 during December 2016.

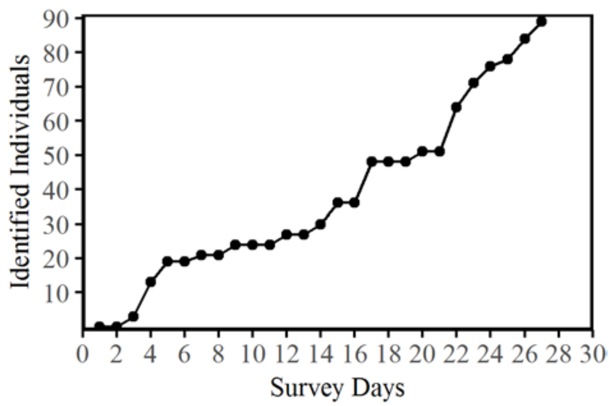

Figure 6. Blue whale photo-identification discovery curve of the cumulative number of unique individuals identified versus the cumulative number of days of survey effort. Data were derived from dedicated survey effort in the South Taranaki Bight (STB) region during 2014, 2016, and 2017.

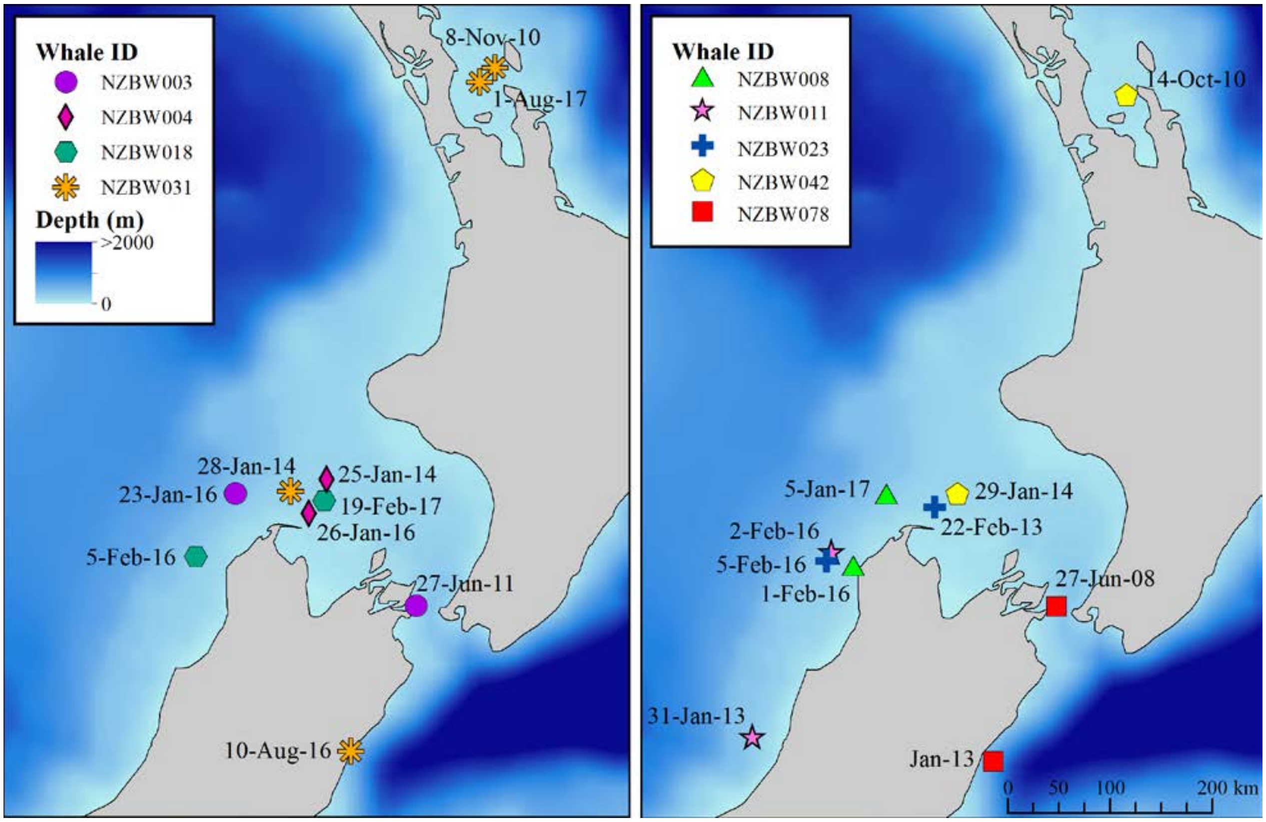

Figure 7. Inter-annual resighting locations for blue whales in the New Zealand Exclusive Economic Zone. Two panels used for visualization clarity. Note: precise sighting coordinates were not given for NZBW031 in August 2016 or for NZBW078 in January 2013; however, approximate locations were provided. The exact date of the sighting was not provided for NZBW078 in January 2013.

SUPPLEMENTARY MATERIALS

Table S1. Sources of blue whale sighting data from within the New Zealand Exclusive Economic Zone.

Contributor	Years	Number of Sightings
Abel Tasman Air	2014, 2015	2
Olive Andrews, Silversea Expeditions	2015	1
Australian Marine Mammal Centre (Double et al. 2013)	2013	19
Geoff Balks, Maui B Oil Platform	2012	1
Blue Planet Marine/OMV Ltd. (Blue Planet Marine 2011)	2011	14
Blue Planet Marine/TGS-NOPEC Geophysical Company	2014	43
Blue Planet Marine/New Zealand Oil and Gas	2010, 2013	3
Blue Planet Marine/Petroleum Geo-Services Seismic Survey	2016, 2017	120
Ian Brown, Trawler “Receiver”	2013	1
Callum Lilley, Department of Conservation	2007, 2013	3
Cawthron Institute/Ministry of Primary Industries, South Island Hector’s Dolphin Survey	2013, 2015	38
Cawthron Institute/OMV Ltd., Taranaki Benthic Survey	2013, 2014	13
Department of Conservation, Cook Strait Survey	2004, 2008, 2011, 2013-2015	11
Department of Conservation, Sightings Database	1900, 1994, 1997-2005, 2007-2016	234
Dolphin Safari	2017	1
Eric De Boer, Department of Conservation, Westport Office	2015	1
Clinton Duffy, Department of Conservation	2014	2
Barry Grovier, Department of Conservation	2007	1
Steve Kelly, Maui B Oil Platform	2014	1
Theresa Kirchner, Texas A&M Dusky Dolphin Survey	2013	1
Massey University	2009-2015	18
Don Neale, Department of Conservation	2015	1
National Institute of Water and Atmospheric Research, Ltd.	2012	2
OMV Ltd., M/V Polarcus Alima	2014	3
Oregon State University, Blue Whale Survey	2014, 2016, 2017	64
Sounds Air	2014	1
Chris Tessaglia-Hymes, Cornell University	2017	2
Todd Energy	2013	85
Transiting ship records (Cawthorn 2009)	1980, 1982-1991, 1998	44
University of Auckland	2010, 2015	3
Whale Watch Kaikoura	2010, 2012-2014, 2016	9
Gary Willison, FPSO Umuroa	2012	1
Wings Over Whales	2016	1

Table S2. Sources of photo-identification data from within the New Zealand Exclusive Economic Zone and from Australian and Antarctic regions.

Contributor	Years	Region	Number of IDs
Olive Andrews, Silversea Expeditions	2015	South Taranaki Bight	4
Australian Marine Mammal Centre (Double et al. 2013)	2013	South Island	14
Cawthron Institute/OMV Ltd., Taranaki Benthic Survey	2013	South Taranaki Bight	2
Department of Conservation, Cook Strait Survey	2004, 2008, 2011, 2013-2015	Cook Strait	14
Dolphin Safari	2017	Hauraki Gulf	1
Eric De Boer, Department of Conservation Westport Office	2015	South Taranaki Bight	4
Theresa Kirchner, Oregon State University	2013	Kaikoura	1
Massey University	2009-2015	Bay of Islands, Hauraki Gulf	12
Don Neale, Department of Conservation Technical Advisor	2015	Westport	1
Petroleum Geo-Services Seismic Survey	2016	South Taranaki Bight	2
Chris Tessaglia-Hymes, Cornell University	2017	South Taranaki Bight	3
Todd Energy Survey	2013	South Taranaki Bight	3
University of Auckland	2010, 2015	Hauraki Gulf, Raoul Island	3
Whale Watch Kaikoura	2010, 2012, 2013, 2014, 2016	Kaikoura	13
Wings Over Whales	2016	Kaikoura	1
Australian Marine Mammal Centre	2012	Bonney Upwelling, South Australia	56
Blue Whale Study, Inc.	1998-2000, 2003-2011	Bonney Upwelling, South Australia	139
Brian Miller, Australian Antarctic Division	2014	East Coast of Australia	2
Australian Marine Mammal Centre (Double et al. 2013)	2013	Antarctica	65

Table S3. Within-year capture periods for each survey year, used to produce capture-recapture abundance estimates for each survey year.

Survey year	Capture period 1	Capture period 2	Capture period 3
2014	24-25 Jan	28-19 Jan	2-3 Feb
2016	23-26 Jan	1-3 Feb	5 Feb
2017	8-11 Feb	16 Feb	18-20 Feb