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Estimating abundance of a small population of Bryde's whales: a comparison between aerial surveys and boat-based platforms of opportunity

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Abstract

Accurate abundance estimates are essential for the development of effective conservation management strategies, yet they are difficult to produce for small populations that are elusive and sparsely distributed throughout their range. For such populations it is challenging to collect a representative dataset sufficient for robust estimation of detectability and abundance. Over a one-year study, we used two methods to estimate abundance of a Nationally Critical, widely dispersed Bryde's whale population in the Hauraki Gulf, Aotearoa/New Zealand; (i) distance sampling from systematic line-transect aerial surveys ($n = 22$ surveys, 9,944 km, total sightings 21–24 whales), and (ii) mark-recapture (MR) using photo-identification images collected from a platform-of-opportunity and small-boat surveys (218 sampling occasions, 27 whales). From the aerial surveys, we estimated an average of 15 whales (95% CI = 6, 30; CV = 37%) at the sea-surface at any time. For the boat-based surveys, we developed a custom MR model to address seasonal and individual heterogeneity in capture probabilities and obtained an estimate of 72 distinct whales (95% CI = 38, 106; CV = 24%) in the population. These two approaches provide different perspectives on the abundance and dynamics of Bryde's whales. The aerial surveys estimate the average number of individuals present at any one time, whereas the MR model estimates the total number of animals that used the Gulf during the study. Although neither sampling method is optimal for estimating the abundance of this small, dispersed population, the use of two complementary approaches informs conservation managers about patterns of abundance and distribution over different temporal and spatial scales. It is common to have limited resources for marine research where model assumptions cannot be met. Here, we highlight pragmatic strategies showing how models can be customized to the population of interest to assist with monitoring species of conservation concern.

Introduction

Abundance estimates are vital for managing wildlife populations. Many species of conservation concern require inferences about their population status; for example, to generate threat classifications (IUCN, 2012; Baker *et al.*, 2019). However, when there are few animals available for detection within a large area, it is challenging to produce abundance estimates using methods designed for more accessible species or projects with long-term funding (Evans & Hammond, 2004; Thompson, 2004). In locations where species are dispersed or rarely sighted and there are resource limitations on the survey methods or duration, the resulting survey design may violate the assumptions required for a robust abundance estimate. Therefore, a more pragmatic and flexible approach is needed to ensure the availability of at least some information about the abundance and distribution of a population, knowledge which is at the core of informing conservation management decisions (e.g. blue whales *Balaenoptera musculus* Williams *et al.*, 2011; gorillas *Gorilla* *beringei* Granjon *et al.*, 2020). This often applies to marine species such as sharks, pinnipeds, and whales, as individuals are sparsely distributed, range widely, and can be difficult to observe (Huveneers *et al.*, 2018; Stern & Friedlaender, 2018; Hindell *et al.*, 2020).

Methods for estimating abundance rely upon statistical procedures for estimating detection probabilities to account for those animals that were unseen (Schwarz & Seber, 1999; MacKenzie *et al.*, 2002). Various techniques are available for survey sampling and analysis. The choice of method depends on the objectives of the study, the characteristics of the environment and the population, and the availability of resources and funding (Pollock *et al.*, 2002).

Line-transect distance sampling and mark-recapture (MR) are two commonly used sampling techniques for estimating abundance (e.g. Carbone *et al.*, 2001; Pollock *et al.*, 2006; Morley & van Aarde, 2007). In distance sampling, detected animals are counted and the detection probability is estimated as a function of distance from the animal to the observer (Buckland *et al.*, 1993). Aerial and small-boat line-transect surveys are used for a range of large marine animals (e.g. Hines, Adulyanukosol, & Duffus, 2005; Certain & Bretagnolle, 2008; Williams & Thomas, 2009; Lauriano *et al.*, 2011). In contrast, MR techniques require animals to be individually recognisable, and they require a minimum of two capture occasions (Eberhardt & Seber, 1975; Chao, 2001). MR studies of marine vertebrates commonly use photo-identification (photo-ID) of natural markings, with examples including spot patterns (Arzoumanian, Holmberg, & Norman, 2005) or fluke markings (Katona *et al.*, 1979).

For nearshore cetacean populations, small-boat line-transect surveys are a popular research method (Williams & Thomas, 2009), largely due to accessibility and cost effectiveness. However, there is increasing interest in exploiting observations from platforms of opportunity, such as whale-watching operations (Ingram *et al.*, 2007), seismic survey vessels (de Boer, 2010), and cruise ships (Williams, Hedley, & Hammond, 2006), especially where financial resources are limited (Evans & Hammond, 2004). Commercial whale-watch operations spend more time on-water than is possible for most research boats, but they also have some limitations as a source of research data. The survey is operator-led, and the primary goal is to ensure a good experience for customers, which dictates the survey course, effort, and number of animals that are encountered (Evans & Hammond, 2004). These decisions may violate core assumptions of abundance estimation techniques (Pollock *et al.*, 2002). Nevertheless, whale-watching vessels and other platforms of opportunity have potential to provide valuable data (Matear *et al.*, 2019; Robbins *et al.*, 2020).

Here, we estimate the abundance of the Aotearoa/ New Zealand-listed, Nationally Critical Bryde's whale (*Balaenoptera edeni brydei*) (Baker *et al.*, 2019) in the Hauraki Gulf/ Tīkapa Moana/ Te Moananui-a-Toi (hereafter the Gulf). The Gulf is a core part of the Bryde's whale range along the northeastern coast of the North Island/ Te Ika-a-Māui (Baker & Madon, 2007). Whales are sighted year-round (Wiseman *et al.*, 2011; Constantine *et al.*, 2015), comprising a mixture of frequently and infrequently sighted individuals, with the structure and composition of the mixture unstable over time. Bryde's whales range widely throughout the ~12,000 km^2 Gulf waters, occur at low densities, and their distribution is dynamic in time and space, which is now being further influenced by changes in prey availability from overfishing and increasing sea-surface temperature (Baker & Madon, 2007; Colbert, 2019; Gostischa, Massolo, & Constantine, 2021). A previous photo-ID study estimated 135 whales in the Gulf (CI = 100, 183) at some time during the sampling period between 2011 and 2013 (Tezanos-Pinto *et al.*, 2017). Given the challenges associated with abundance estimation for small, dispersed populations (Southwell *et al.*, 2008; Nykanen *et al.*, 2018), and the conservation status of Bryde's whales in New Zealand (Baker *et al.*, 2019), we investigate two methods of abundance estimation, and the effectiveness of each method for improving our understanding of these whales.

Surveys of Bryde's whales were conducted over the same time-period using (i) aerial line-transect distance sampling surveys, and (ii) photographic MR from small boats and platforms of opportunity. The aerial surveys were dedicated systematic research surveys implemented in a double-observer framework, also known as mark-recapture distance sampling. The photo-ID data were collected predominately on a whale-watch vessel and supplemented by dedicated but unsystematic small-boat research surveys and were analysed using a seasonally structured MR model customized to the target population, a common approach for situations where standard model assumptions are unable to be met. Abundance estimates from the two protocols are not directly comparable; rather they are complementary. The distance sampling method we used delivers estimates of the average number of individuals at the sea-surface at any one time, whereas the MR method provides estimates of the cumulative total number of individuals that used the area over the study period (Pollock, 1990; Buckland *et al.*, 2001). We compare the outputs from the two methods and consider the relative merits of the two approaches in the study of this widely distributed, small population of Bryde's whales with limited resources for population monitoring. Informing conservation managers about the number of whales in the Gulf over different spatial and temporal scales will support conservation management decisions around past and emerging threats.

Materials and methods

Sightings and photo-ID data were collected in the Hauraki Gulf, New Zealand (36° 10′–37° 10′ S; 174° 40′–175° 30′ E) during systematic aerial surveys and non-systematic small boat surveys, respectively (Fig. 1).

Aerial line-transect surveys

Double-observer aerial line-transect surveys were conducted approximately twice a month from November 2013 to October 2014, totalling 22 surveys. Surveys followed a

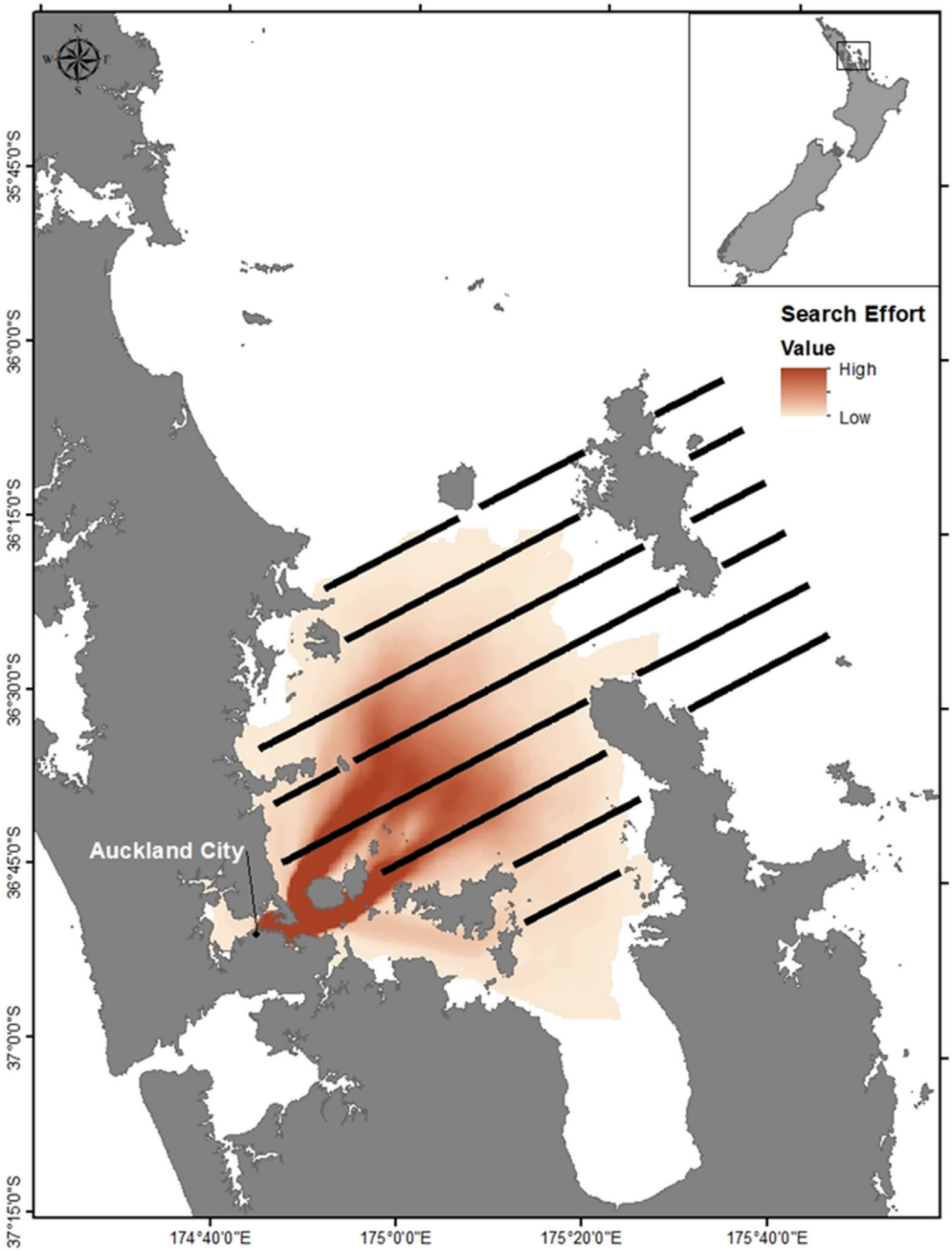

Figure 1 The Hauraki Gulf, New Zealand, showing (i) the line-transect grid flown during systematic aerial surveys (black lines), and (ii) the density of search effort from the *Dolphin Explorer* vessel (red heatmap, produced using a selection of trips from August 2000 to June 2019 and reflect this study; adapted from Colbert, 2019).

systematic line-transect course of eight parallel transects spaced at 10 km intervals, covering a range of environmental conditions, surveying less-researched areas in the outer Gulf, and following distance sampling methodology where we did not break the track (Buckland *et al*., 2001) while remaining within aircraft flight capability and budget. The systematic grid remained fixed for all surveys, with a start point randomly chosen in accordance with design-unbiased sampling (Buckland *et al*., 2004; Fewster, 2011). Some transects were not continuous as their path overlapped with islands, resulting in 16 sub-transects (Fig. 1).

Surveys commenced when the Beaufort Sea-state was ≤3, there was no rain or fog, and there was sufficient light to complete the ~4.2 hr survey. The grid was surveyed from the north or south, depending on the weather forecast, using a Cessna 207 aircraft at an altitude of 152.4 m (500 ft) and a speed of 100 kt (185.2 km/hr). Double-observer line-transect surveys followed the protocols of MacKenzie & Clement (2014), detailed in Hamilton *et al*. (2018). Briefly, there were four experienced observers on each flight, two on each side, divided into two teams; the two front observers and the two rear observers, so each side of the aircraft was monitored by one observer from each team. Observers did not communicate while on effort and searched independently of each other. A group was defined as any number of Bryde's whales in apparent association, moving in the same direction, and often (but not always) engaged in the same activity (Shane, 1990). During surveys, common (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) were also observed but did not interfere with data collection on Bryde's whales as they were rarely observed together.

For every detected whale group, observers recorded the time, the downward angle from the transect line, and the group size. The time and declination angle were taken when the group was perpendicular to the plane using synchronized digital clocks and hand-held inclinometers. Sighting locations were determined after the survey using the recorded sighting times and the aircraft's GPS tracks. While our analysis accounted for perception bias, with only few whale sightings we were unable to account for availability bias, in which some whale groups are not available to observers because they are beneath the sea-surface. We expect availability bias to be minimal for Bryde's whales, which spend over 90% of their time within 12 m of the surface (Constantine *et al*., 2015). Therefore, our distance sampling methods produce an estimate of the average number of whales at the surface, rather than the absolute abundance. Minimum abundance estimates are nonetheless valuable, especially for rare species, and are informative for conservation monitoring (e.g. Williams *et al*., 2011).

Distance sampling analysis

Bryde's whales were encountered at low densities during surveys. As a result, there was little uncertainty around matching duplicate sightings, that is, deciding which of the sightings made by both observers on one side of the plane corresponded to the same whale group. Duplicates were primarily reconciled using the fixed tolerance protocol described by Hamilton *et al*. (2018). Reconciliations were conducted using three combinations of angle (A) and time (T) tolerances: A = 10°, T = 5 s; A = 15°, T = 5 s; A = 15°, T = 10 s. Within each setting, all sightings made by observers on the same side of the plane, within the specified time and angle tolerances of each other, were classified as duplicates. The three settings created three different reconciled datasets, from which the abundance estimates were compared to ensure they were robust to the choice of tolerances. For additional verification, we also ran the fully probabilistic method of duplicate identification described by Hamilton *et al*. (2018).

Following duplicate reconciliation, the abundance (N) of Bryde's whales was estimated using mark-recapture distance sampling (MRDS). Due to the nonstandard configuration of the aircraft, we implemented a custom MRDS formulation as described by Hamilton *et al*. (2018). Briefly, this involved estimating three detection functions corresponding to (i) the probability of detection by the rear team, (ii) the conditional probability of detection by the front team given detection by the rear team, and (iii) the conditional probability of detection by the front team given non-detection by the rear team. The three detection functions $p_k(y)$ for $k = 1, 2, 3$ were formulated as functions of the perpendicular distance y of an animal from the transect line, as follows:

$$p_k(y) = \text{logit}^{-1}(\alpha_k + \beta_k y) \text{ for } l_k \le y \le w,$$

where α_k and β_k denote parameters to be estimated; w is the right-truncation distance of sightings from the transect line; and l_k is the minimum sighting distance possible for the observer team corresponding to detection function k, which accommodates the specific configuration of the front observer's flat window in the aircraft deployed (MacKenzie & Clement, 2014; Hamilton *et al*., 2018), such that l_k is 0 m for the rear team $(k = 1)$, and 60 m for the front team $(k = 2, 3)$. The inverse logit function is $\text{logit}^{-1}(x) = \exp(x)/\{\exp(x) + 1\}$.

For each set of reconciled data, the three detection functions were estimated and combined into a function $p.(y)$ giving the probability of overall detection as a function of y, which was then averaged over y to estimate the overall probability of detection for any whale group, $E(p.)$. The abundance $\widehat{N}^c$ of individual whales in the area covered by the line transects, totalled over all 22 surveys, was then obtained from the Horvitz-Thompson estimator:

$$\widehat{N}^c = \frac{n\bar{s}}{E(p.)},$$

where n is the total number of whale groups seen, and $\bar{s}$ is the average size of detected groups, across the 22 surveys in the reconciled dataset being analysed.

The final MRDS abundance estimate for the Gulf for a given reconciled dataset was:

$$\widehat{N} = \frac{A\widehat{N}^c}{2wL},$$

where $A = 4352.37$ km^2 is the total area of the survey region, and L is the on-effort distance flown across all 22 surveys, measured in km. Thus, the MRDS procedure estimates the average number of surface-visible whales in the surveyed region at any time-point, where the average is understood to be taken over time.

We obtained standard errors using a bootstrap procedure with 500 bootstrap replicates. For each iteration, 22 replicate surveys were selected from the original 22 surveys at random with replacement to create a new dataset, which was analysed using the same scheme as the real data to obtain a bootstrap sample of abundance estimates. The mean and standard deviation of these bootstrap estimates were taken as the final abundance estimate and standard error, and 95% confidence intervals were gained from the corresponding percentiles of the bootstrap sample.

Small-boat photo-identification surveys

Photo-ID data were collected primarily from the 19.9 m MV *Dolphin Explorer* and supplemented by dedicated non-systematic research surveys aboard a University of Auckland 15 m vessel and a 5.5 m Massey University vessel. To establish a comparable research period to the aerial surveys, we analysed photo-ID data collected between November 2013 and October 2014. Data were collected by researchers and experienced crew aboard *Dolphin Explorer* and the university vessels. *Dolphin Explorer* followed an unsystematic route with the initial bearing depending on the prevailing weather conditions and information regarding recent whale sightings. A typical trip lasted 4.5 hours with the vessel rarely leaving the inner Gulf (Fig. 1). Research vessels also followed a non-systematic path, but effort was concentrated in the outer Gulf. When a Bryde's whale was encountered, observers took dorsal fin photographs using digital SLR cameras equipped with 70–400 mm zoom lenses. While on *Dolphin Explorer*, the duration of the encounter was at the discretion of the captain. While on the university research vessels, an encounter ended once the whales had been photographed.

Photograph grading and matching

Photographs were graded based on the quality of the images and the distinctiveness of the nicks and marks to minimize misidentification of individuals (Stevick *et al.*, 2001). Four elements were used for grading image quality: focus, contrast, angle, and visibility of the dorsal fin and back. All fin images were rated from 1 (excellent) to 4 (poor) (Table 1). Image quality categories 1–3 were further assessed for the distinctiveness of markings ranging from 1 (highly recognisable) to 4 (no marks present) (Table 1). All images with quality and distinctiveness scores of 1–3 were matched to an established photo-ID catalogue. Any new individuals were checked independently by at least two experienced researchers, then given an accession number in the catalogue and the database was updated when a match was made. Only images with scores of 1–3 and distinctiveness scores of 1–3 were included in the MR analysis.

Mark-recapture photo-identification dataset

Each day of survey effort represented a single capture occasion, from 1st November 2013 to 28th October 2014, totalling 218 capture occasions. The sightings effort for each capture occasion was the sum of on-effort hours among all vessels that conducted surveys that day. Given that most trips were conducted on *Dolphin Explorer*, we established the unit of effort for all vessels relative to their average daily trip time of 270 min (4.5 hr) which we took to represent one block of effort.

If a Bryde's whale was sighted more than once a day, it was counted as a single sighting. This could arise if there were two trips, or if an individual whale was encountered more than once in a trip, or if more than one vessel was operating at the same time and photographed the whale. A capture history was built for each distinctive whale, where for each sampling occasion the whale was allotted 1 for a capture, that is, a photographic record, and 0 for a non-capture. This resulted in a 27×218 matrix of capture records for 27 distinctive whales over the 218 sampling occasions.

Table 1 Criteria used to grade all photographs including a Bryde's whale dorsal fin

Photo quality categories		Criteria
1	Excellent	All attributes comply. Dorsal fin and back clearly visible allowing assessment of mark distinctiveness. Animal perpendicular with whole dorsal fin visible plus a portion of the back, excellent focus and exposure
2	Good	One attribute failed to comply. The whole dorsal fin and back is visible with image less than 45°, in focus, good exposure. May be partially obscured by spray but not impeding assessment of the marks
3	Average	Two attributes failed to comply; but information not compromised by photographic quality. Image may be partially blurred but outline of dorsal fin and back is visible; some over or under exposure but details and outline are visible
4	Poor	Identification marks visible but the back and fin is not visible, or focus and exposure too poor to determine details, and/or poor angle of the dorsal fin (>45°)
Distinctiveness categories		**Criteria**
1	High	Large fin nicks and/or damage on the back region of the whale. Makes whale easily recognisable
2	Medium	More subtle fin nicks and distinctive shaped fin and/or marks on the whale's back. Recognisable due to permanence of the marks
3	Low	No fin nicks but distinctive fin shape as a primary feature. Temporary marks on the dorsal fin, for example, scratches and subtle scarring or marks on the back were secondary features (see Elliser, van der Linde, & MacIver, 2022)
4	Absent	No markings (no photo quality categories)

Photo quality criteria assess the quality of the images, and distinctiveness categories assess the quality of the markings following Tezanos-Pinto *et al.* (2017).

Mark-recapture model

Abundance (N) was estimated with a custom-formulated capture-recapture model under the following assumptions: (1) no deaths or births, which is reasonable given the one-year period of the study relative to the lifespan of long-lived animals (Williams & Thomas, 2009), (2) no mark change or loss, which we controlled for by including only good quality photographs of distinctive animals in the analysis (Stevick *et al.*, 2001), and (3) no behavioural response to capture, which is a reasonable assumption for photo-ID techniques where images can be taken at distance from the whale.

The custom-devised model allowed capture probabilities to vary due to: (i) survey effort, (ii) time at a coarse temporal scale, and (iii) individual heterogeneity. First, capture probabilities were modelled as probabilities per block of effort. The realized capture probability for any capture occasion was the capture probability per block of effort, multiplied by the number of 270-minute effort blocks that took place on that capture occasion.

Second, inspection of the capture history matrix revealed that there were three distinct panels within the study period, that is, stretches of time with stable capture behaviour within each panel separated by abrupt changes between panels, based on the number of sightings per capture occasion (Fig. 2). These were handled by allowing for three distinct sets of capture probabilities, one for each temporal panel.

Third, within each temporal panel we allowed for unequal capture probability among individuals using a two-point mixture model (Pledger, 2000). We assumed that whales belong to one of two discrete groups within each time panel, one with lower capture probability and one with higher capture probability. This parsimonious formulation allows for individual heterogeneity in capture probability without introducing many additional parameters for estimation (Horsup *et al.*, 2021). For convenience, we defined the first group to have lower capture probability, namely p_i per effort-block in temporal panel i $(i = 1, 2, 3)$, and the second group to have higher capture probability of q_i per effort-block in temporal panel i. The probability that a whale belonged to the lower-probability group was defined as π_i for $i = 1, 2, 3$. One further constraint was applied, that $p_2 = 0$. This was imposed due to the very low sighting rate in panel 2 (Fig. 2), and it corresponds to an assumption that a portion of whales temporarily emigrated outside of the sampling area for the duration of this panel.

The capture probability of an individual whale within panel i, on capture occasion t for which the number of effort-blocks was e_t, was therefore:

$$\pi_i p_i e_t + (1-\pi_i) q_i e_t,$$

where π_i, p_i, and q_i are parameters to be estimated for each temporal panel $i = 1, 2, 3$, except for p_2 which was set to be $p_2 = 0$. A whale was assumed to maintain its status in the low- or high-capture group for the duration of each panel, but its group membership was considered independent between panels, so it could potentially be in the high-capture group for one panel and the low-capture group for another panel. However, the model does not attempt to assign group membership to individuals, instead focusing on estimating the proportion of whales in each group during each panel, via the parameters π_i for $i = 1, 2, 3$.

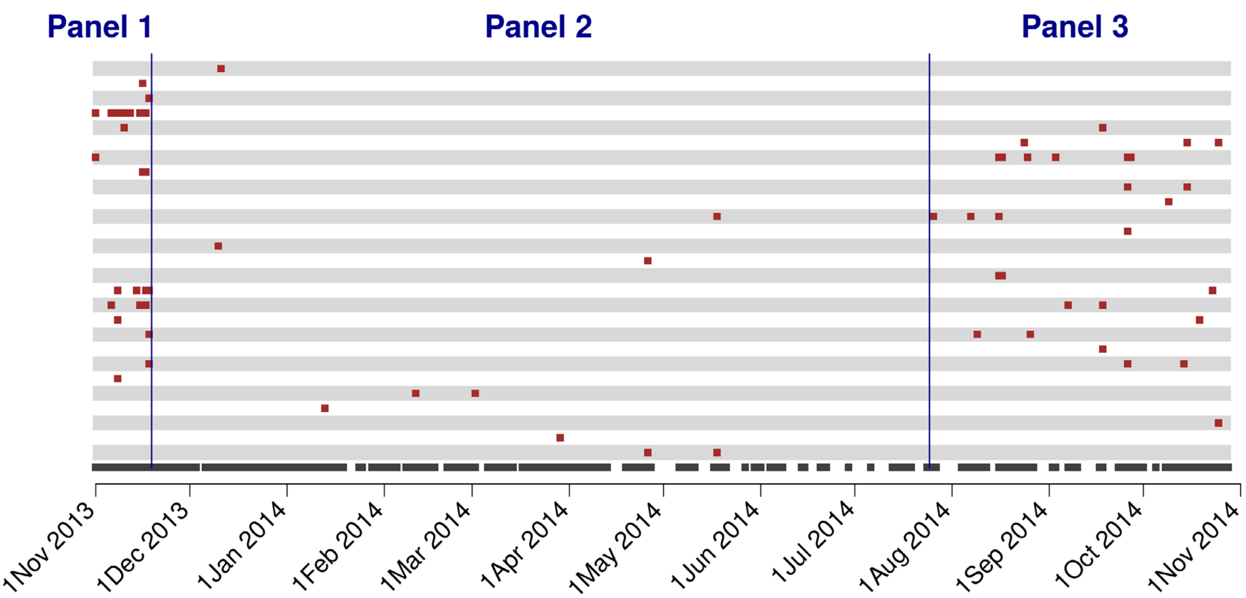

Figure 2 Capture histories of $n = 27$ distinct Bryde's whales by calendar day. Each row corresponds to one whale, where rows are distinguished by alternating pale grey and white shading. Columns correspond to calendar dates. The first and last day in the plot are 1st November 2013 and 28th October 2014, respectively, and the black horizontal bar at the base of the plot shows days that survey trips took place. Brown blocks on each row indicate days the corresponding whale was sighted. The vertical blue lines show the division between the three panels in the selected model.

Implementing the three-panel model required selection of the panel boundaries. Optimal boundaries were selected by fitting the model with several different combinations of k_1 and k_2, the number of sampling occasions included in temporal panels 1 and 2, respectively. The Akaike Information Criterion (AIC) was used to select the combination of k_1 and k_2 corresponding to the best-supported model.

Parameters were estimated using maximum likelihood. The full set of parameters was N: abundance (number of individual distinctive whales exposed to capture during the study period); p_1 and p_3: probability of capture per effort-block for the low-capture group in panels 1 and 3 respectively; q_1, q_2, and q_3: probability of capture per effort-block for the high-capture group in panels 1, 2, and 3; and π_1, π_2, and π_3: probability of belonging to the low-capture group in panels 1, 2, and 3.

Variance was estimated using a non-parametric bootstrap procedure, by resampling entire capture histories of whales with replacement and refitting the model to each replicate of 27 resampled whales. As for the previous analysis, the bootstrap procedure also provided an alternative final estimate of abundance based on the mean of the bootstrap replicates, which we considered more robust due to reduced reliance on the capture histories of individual whales.

We assessed goodness-of-fit of the model two ways. First, we checked that the distribution of the number of sightings per whale agreed with the distribution predicted by the fitted model, using one chi-squared test for each panel and another test for all three panels combined. The combined test was used to check the assumption that the high or low catchability status of each whale was independent between the three panels. Second, we checked that the maximized log-likelihood for the real data was within the null distribution predicted by the fitted model.

The abundance estimate for distinctive whales was finally scaled by an estimate of the mark ratio, defined as the proportion of whales in the population that were sufficiently distinctive to be included in the MR study. The estimated mark ratio was taken from a previous study (Tezanos-Pinto *et al.*, 2017) and verified against a subset of our own data (University of Auckland, unpublished data).

Results

Distance sampling analysis from aerial line-transect surveys

Line-transect surveys covered a cumulative total of $L =$ 9,944 km on 22 days between 15th November 2013 and 10th October 2014, averaging just under two surveys per month. Bryde's whale groups ($n = 27$) were observed within the truncation distance of $w = 0.4$ km determined in a larger concurrent analysis (Hamilton *et al.*, 2018). The average group size per sighting was 1.2 whales (SD = 0.40) across all sightings by both observer teams, that is, with duplicates counted twice. Three sightings were mother–calf pairs, none of which were duplicates under any of the fixed tolerance settings. After duplicate reconciliation under the three fixed-tolerance settings, the reconciled datasets ranged from 16 to 19 whale groups and from 21 to 24 individual whales, with little difference in these results across the three settings.

The minimum abundance estimates under the three fixed-tolerance settings for duplicate reconciliation were: (i) $\widehat{N} = 15$ whales (CV 37%) for tolerances A = 10°, T = 5 s; (ii) $\widehat{N} = 15$ whales (CV 42%) for tolerances A = 15°, T = 5 s; and (iii) $\widehat{N} = 14$ whales (CV 36%) for tolerances A = 15°, T = 10 s, where $\widehat{N}$ estimates the average number of individual whales present at any given time, averaged over the one-year period. Results from the verifying probabilistic analysis were $\widehat{N} = 14$ whales (CV 38%). The fixed tolerance setting A = 10°, T = 5 s was selected for reporting, since it provided a representative result with simple specifications and gave the most similar output to the more complicated probabilistic verification analysis.

Under the selected setting, the final minimum estimate was $\widehat{N} = 15$ individual whales (95% CI = 6, 30; CV = 37%). The estimate of overall detection probability, averaged across distance, was 0.93 (CV = 16%). The estimated detection curves yielded roughly certain overall detection at distances beyond 60 m that were visible to both observer teams, while detection ranged from 0.55 to 0.58 within the 60 m zone that was visible only to the rear team.

Mark-recapture estimate from photo-identification

Collectively, 229 trips were conducted on 218 days from 1st November 2013 to 28th October 2014. The majority ($n = 220$ trips) were conducted from *Dolphin Explorer*. On 11 days there was more than one trip per day.

The AIC procedure selected $k_1 = 16$ sampling days in panel 1, and $k_2 = 152$ sampling days in panel 2 (Fig. 2). The bootstrap procedure estimated 45 whales (95% CI = 33, 71; CV = 22%) in the population over the study period. This is to be interpreted as the estimated total number of distinctive Bryde's whales present in the Gulf across the whole year. The alternative (non-bootstrap) estimate, and precision based on asymptotic maximum likelihood theory was very similar, estimating 44 whales (95% CI = 28, 68; CV = 23%) present in the Gulf across the whole year. The estimated single-occasion capture probabilities per effort-block in panels 1, 2, and 3 were respectively 0.025, 0.001, and 0.014 (CV = 40%, 31%, 39%). Goodness-of-fit diagnostics were very favourable, returning $P > 0.9$ for each of the four chi-squared tests, and $p = 0.57$ for the log-likelihood test.

The estimate of abundance was adjusted by an estimated mark ratio to account for individuals that did not meet the distinctiveness criteria and were not used in the estimate. We used the mark ratio of 0.63 (SE = 0.04) from Tezanos-Pinto *et al.* (2017). This was comparable to the mark ratio derived from a sample of the dataset used in our study but had greater precision as it covered a two-year period. Our final estimate of abundance, adjusted for the mark rate, was 72 whales (95% CI = 38, 106; CV = 24%) present in the Gulf over the one-year study period.

Discussion

The simultaneous use of aerial line-transect distance sampling and photo-ID MR from boat-based platforms of opportunity has provided a nuanced understanding of the dynamics of Bryde's whales using the Gulf. This is valuable given their Nationally Critical status (Baker *et al*., 2019) where even small changes to their distribution and mortality rates could have a large impact. Until late 2014, Bryde's whales had high levels of ship-strike mortality in the Gulf, but this is now mitigated with a voluntary protocol to reduce ship speeds (Constantine *et al*., 2015; Ebdon, Riekkola, & Constantine, 2020). Abundance is the most important system state variable to monitor to inform conservation decisions of past and emerging threats. Here we provide a valuable baseline against which to assess future population trends.

Before examining the efficacy of using two techniques to estimate Bryde's whale abundance, we note the differences in what is being measured by the two approaches. The aerial distance sampling surveys provided an estimate of the average number of surface-visible whales in the Gulf at any one time (Buckland *et al*., 2004), whereas the boat-based MR surveys estimated the total number of individual whales that used the Gulf over the year. Consequently, the two estimates are complementary, and should be interpreted in the context of the population and study site (Calambokidis & Barlow, 2004). The aerial distance sampling surveys estimated an average of 15 (6–30) surface-visible whales present at any one time, whereas the boat-based MR estimate was a cumulative total of 72 (38–106) whales during the study period.

In the case where the entire population range is sampled, and animals exhibit a high degree of residency, results from the two techniques should be similar, as found for bottlenose dolphins in southern Brazil (Daura-Jorge & Simoes-Lopes, 2017), and killer whales (*Orcinus orca*) in British Columbia (Williams & Thomas, 2009). In our study, all surveys were in the Gulf which covered only part of the species' wider range (Baker & Madon, 2007), highlighting one of the challenges with estimating the abundance of highly mobile species and designating their threat status. Some Bryde's whales are frequent users of the Gulf with individuals observed regularly over 20+ years, while others are occasional visitors. Temporary emigration is an important feature of this population, but the frequency and duration of movements in and out of the Gulf by individual whales is unknown (Wiseman, 2008; Tezanos-Pinto *et al*., 2017). The population is genetically diverse, suggesting extant pathways to gene-flow (Wiseman, 2008). Our estimates further support this scenario, suggesting that the average number present at any time is less than one-quarter of the total number of whales that visit the Gulf over a year.

Despite the larger-scale, systematic design of our aerial line-transect surveys, only 27 groups were detected, which was fewer than the 60–80 detections recommended by Buckland *et al*. (2001) for reliable inference, and was reflected in the wide confidence interval and high CV. This outcome is not surprising, given that the population size is small, individuals occur at low densities, and only some of the population is present at any one time. Nevertheless, our distance sampling surveys provided valuable insight into how whales are using the Gulf and how this may vary in an ecosystem increasingly under stress. Bryde's whale distribution in the Gulf aligns with patterns of seasonal upwelling and productivity (Stephenson *et al*., 2023). These may vary annually as the whales shift their use of the Gulf in years with anomalously warm water (Colbert, 2019), a phenomenon predicted to increase in frequency (Stevens *et al*., 2022). Because whales have shifted their diet to zooplankton with a decline in fish prey, there has been considerable disruption to multi-species communities where Bryde's were a key species (Gostischa *et al*., 2021). Additionally, whales moving to the outer Gulf in warm-water years sees them inhabiting areas where there is no protection from ship-strike. There is a trend towards ecosystem-based management, including in the Gulf where a holistic marine spatial plan aims to reverse degradations due to multiple anthropogenic pressures (https://www.doc.govt.nz/our-work/sea-change-hauraki-gulf-marine-spatial-plan/). Large predators are often the best indicators of change, and with clear shifts in ecosystem function in the Gulf, conservation managers are concerned not only about immediate threats to the whales but also their role in ecosystem function.

In principle, detections of whales could be increased by adopting a tailored sampling design based on stratified sampling (Anderson, 2001; Thompson, 2004; Brown *et al*., 2013). However, in practice, the aerial surveys were designed to examine the wider community of large predators in the Gulf, including other cetaceans and sharks, so adapting the design to meet the needs of one species could have been counterproductive as well as financially demanding (Stephenson *et al*., 2023). This highlights the reality of wildlife conservation and monitoring programmes, in which trade-offs must be made due to financial and logistical constraints often resulting in suboptimal data, which is nonetheless the best available to inform management decisions and conservation action (e.g. Barlow, Gerrodette, & Silber, 1997; Williams *et al*., 2011).

Our MR estimate of 38–106 whales over one year can be compared with the super-population estimates of Tezanos-Pinto *et al*. (2017), corresponding to two periods which estimated 74–120 (2004–2006) and 100–183 (2011–2013) individual whales in the Gulf. The 2011–2013 estimate is somewhat higher than ours, but it was based on a wider survey region as well as a longer time-period, both of which could potentially augment the super-population. Notwithstanding these discrepancies, the overlapping confidence intervals indicate that there is little to no significant evidence of population change between our results and the earlier surveys. Tezanos-Pinto *et al*. (2017) also provided estimates of the total number of whales present in each season, based on a robust-design analysis. Seasonal point-estimates ranged from 17 to 43 whales in 2004–2006, and 13 to 31 whales in 2011–2013. These estimates are comparable with our aerial distance-sampling estimate of an average of 15 surface-visible whales present at any one time.

MR estimates from platform-of-opportunity surveys are prone to bias because of the biased survey design (Scallan & Keller, 1999). While the whale-watch boat in our case prioritizes Bryde's whales, all cetaceans are of interest, and the time spent with other species as well as individual whales depends on the quality of the interaction, creating a potential source of heterogeneity in capture probabilities and additional associated bias (Calambokidis & Barlow, 2004). In these cases, attention is needed to develop a suitable framework to account for unequal capture probabilities. Our proposed finite-mixture model generated a biologically sensible estimate of abundance with good precision (CV = 24%). In addition, combining the opportunistic photo-ID data with the data collected during research surveys improved the precision of the MR abundance estimate, validating the benefits of such an approach.

The two methodologies provided us with different perspectives on the abundance of Bryde's whales during the study period. Under their current design, neither of the sampling methods is optimal, but they are useful. The line-transect surveys systematically covered a considerably larger geographical range, but the density of whales was too low to collect a satisfactory sample under a conventional design. In contrast, sufficient whales were encountered during photo-ID trips to estimate abundance with reasonable precision using MR techniques, but this approach suffers from a biased sampling scheme and the population's unknown usage of the sampled area relative to its wider range. MR estimates could be made more accurate by focusing research effort on the outer Gulf, which would complement data collected from the whale watch boat in the inner Gulf. In addition, research boats could employ a more systematic design in the inner Gulf to improve the quality of estimates.

While data from platforms-of-opportunity are useful, they are dependent on the tourism industry, and vulnerable to disruptions such as the COVID pandemic or economic changes. A more promising option for future surveys may be unmanned aerial vehicles (UAVs/drones), which are now being used to perform aerial surveys of marine mammals, many of which are of conservation concern (e.g. Hodgson, Peel, & Kelly, 2017; Angliss *et al*., 2018; Johnston, 2019). While not yet readily available, long-range drones are potentially a more affordable approach for long-term monitoring and may in future be able to overcome limitations of using manned aircraft, such as auditing of sightings information and safety requirements.

For Bryde's whales in the Gulf, we recommend maintaining and intensifying the programme of systematic aerial surveys which would be more affordable with drones, and extending the spatial coverage of boat surveys, to maximize understanding of the population. This is particularly important as the population is now potentially increasing from previously unsustainable levels of ship-strike mortality (Constantine *et al*., 2015), and simultaneously changing its distribution in response to ocean warming (Colbert, 2019). Re-evaluating the Bryde's whales Nationally Critical status requires robust estimates and an understanding of the population's connectivity to other areas. Our results highlight the gaps in understanding that can arise from a lack of systematic survey coverage. Important questions remain about the overall status of the population, because we were only able to sample part of its wider range. Nonetheless, we have shown how a pragmatic approach can deliver valuable information for conservation managers with limited resources.

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Authors' contributions

ONPH, *RF* and *RC* conceived the ideas and designed the methodology; *ONPH, PL, FJ, CL, KAS, KvdL* and *RC* collected and prepared the data; *ONPH, RF, PL, FJ* and *RC* analysed the data; *ONPH, RF* and *RC* led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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