Local abundance, apparent survival and site fidelity of Bryde's whales in the Hauraki Gulf (New Zealand) inferred from long-term photo-identification

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ABSTRACT: Bryde's whales *Balaenoptera edeni* in New Zealand are classified as 'nationally critical' according to the New Zealand Threat Classification System. In the Hauraki Gulf, Bryde's whales occur year-round and are subject to ship-strike mortality events. Photo-identification surveys were conducted to estimate local abundance, apparent survival and site fidelity during 2 periods from 2004 to 2006 (261 daily surveys) and from 2011 to 2013 (382 daily surveys). The photo-identification database contained a total of 364 sighting records of 72 Bryde's whales. Overall, 20 whales were sighted across the 2 survey periods, indicating long-term site fidelity. Local abundance was estimated using the robust design (RD) and POPAN mark-recapture approaches for each period, including upward adjustment for the proportion of unmarked whales. RD seasonal abundance estimates varied from 17 to 43 whales between 2004 and 2006, and from 13 to 31 whales between 2011 and 2013. Temporary emigration followed a random pattern ($\gamma' = \gamma''$) and was estimated at 0.557 between 2004 and 2006, and 0.610 between 2011 and 2013. POPAN seasonal abundance ranged from 38 to 74 whales for the 2004 to 2006 period and from 42 to 68 whales for 2011 to 2013. Apparent survival was estimated across periods at 0.878 (95% CI = 0.811–0.923). From the 'super population' estimate of the 2011 to 2013 survey period ($\hat{N}_{super}$ = 135 whales, CI = 100–183), we calculated a potential biological removal (PBR) of 1 whale yr^{-1}. Given the impact of ship strikes on this local unit, it is important to continue long-term photo-identification of Bryde's whales. This technique provides valuable demographic information for a poorly known species.

KEY WORDS: Mark-recapture · Pollock robust design · POPAN · Residency · *Balaenoptera* · Cetacean

INTRODUCTION

Bryde's whales *Balaenoptera edeni* are the least known of the large whales (Kato 2002) and are distributed worldwide in tropical and temperate waters, usually between latitudes 40°N and 40°S. They have been widely hunted during the past century and are still exploited in the North Pacific (Kasuya 2002, Baker et al. 2006). The taxonomic status of Bryde's whales remains uncertain. Three species have been proposed: *B. edeni*, *B. brydei* and *B. omurai* (Kato 2002, Wada et al. 2003, Kershaw et al. 2013). The

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Society of Marine Mammalogy's Committee on Taxonomy recognizes *B. omurai* but considers the other 2 forms (*B. edeni edeni* and *B. edeni brydei*) as subspecies (Committee on Taxonomy 2016). Based on genetic analysis, New Zealand Bryde's whales have been identified as *B. edeni brydei*, the so-called 'offshore form' (Wiseman 2008).

In New Zealand, Bryde's whales are reported only for the north-eastern coast of the North Island (Baker & Madon 2007, Wiseman 2008) and occur year-round in the Hauraki Gulf (Behrens & Constantine 2008, Wiseman et al. 2011). The whales have been observed throughout the inner Gulf in water depths ranging from 12 to 60 m (Wiseman et al. 2011). Some whales have been resighted regularly over multiple years, including reproductive females accompanied by their calves (Wiseman 2008).

In New Zealand, there is currently no information on long-range or seasonal movements along the coast. In the Hauraki Gulf, it appears that there is a higher occurrence of whales during the austral winter (Wiseman et al. 2011), although seasonality was not detected in a more recent study (Dwyer 2014). Bryde's whales in the Hauraki Gulf are subject to a high level of anthropogenic mortality, as evidenced by records of ship strikes and entanglements (Stockin et al. 2008, Wiseman 2008, Riekkola 2013, Constantine et al. 2015). From 1996 to 2014, a total of 44 whales were reported dead. The cause of mortality was determined for 20 carcasses, of which vessel strike was a contributing factor to mortality in 85% of cases (n = 17), while 3 others died as a consequence of entanglement in mussel aquaculture spat lines (n = 2) and unidentified fishing gear (n = 1; Constantine et al. 2015). On average, a minimum of 2.3 whales are estimated to be killed by vessel strikes in the Hauraki Gulf every year (Constantine et al. 2015).

The International Union for Conservation of Nature (IUCN) classified this species as Data Deficient (Reilly et al. 2008). In New Zealand, Bryde's whales are classified as 'nationally critical' by the New Zealand Threat Classification System because of the apparent small size of the local population in the Hauraki Gulf and the high incidence of ship strikes (Baker et al. 2010, 2016).

Here, we implemented mark-recapture techniques through individual photo-identification using both open models and the robust design. Temporal changes in abundance are considered a function of births, deaths, immigration and emigration. Examining population dynamics is not possible without considering immigration and emigration in the subpopulations.

Pollock's robust design (hereafter referred to as RD; Pollock 1982), allows considerable flexibility in estimating a number of demographic parameters, including apparent survival, abundance and temporary emigration. In addition, POPAN or the 'super population' ($\hat{N}_{super}$, the total number of whales that used the area during the entire course of the study) parameterization of the Jolly-Seber open population model (Crosbie & Manly 1985, Schwarz & Arnanson 1996) provides abundance estimates while allowing entries (i.e. birth, immigration) and losses (i.e. death, permanent emigration) in the population under study. This method estimates the abundance of all animals that visited the area during the study period (Williams et al. 2002), providing an estimate of $\hat{N}_{super}$. This is particularly useful in open populations that are connected to larger metapopulations or where local use is variable over time, as has been hypothesized for Bryde's whales (Wiseman 2008). It appears that a small local population unit of Bryde's whales regularly uses the Hauraki Gulf, although it is considered unlikely that the New Zealand local population would be isolated from a larger (yet unknown) population in the South Pacific (Wiseman 2008).

Monitoring of Bryde's whales in the Hauraki Gulf has primarily been conducted via aerial surveys (Baker & Madon 2007, Behrens 2009). While this technique provides valuable information on distribution, habitat use and abundance, it does not allow detection of individual changes in site fidelity over time or estimation of population parameters such as apparent survival and temporary emigration. Here, we used photo-identification records collected between 2003 and 2006 and between 2011 and 2013 in the Hauraki Gulf to analyse and compare site fidelity patterns between periods. A subset of this dataset collected during 2004 to 2006 and 2011 to 2013 was further used to estimate local abundance, apparent survival and temporary emigration with the RD and POPAN approaches.

MATERIALS AND METHODS

Data collection

From March 2003 to February 2006, sighting and photo-identification records were collected mainly from a commercial whale watch vessel, a 19.9 m diesel-powered catamaran (hereafter referred to as 'Dolphin Explorer') and several other smaller independent research platforms (Wiseman 2008). Daily surveys typically lasted 5 h following a non-system-

atic survey route primarily determined by the prevailing weather conditions (further details in Wiseman et al. 2011).

From August 2011 to December 2013, surveys were conducted in the Hauraki Gulf using 'Dolphin Explorer' and 2 independent research vessels, 'Te Epiwhania' and 'Aihe II'. Both research vessels were 5.5 m Stabicrafts powered by a 100 and 120 hp 4-stroke engine, respectively. Dedicated surveys followed a methodology consistent with Wiseman (2008).

Surveys on 'Dolphin Explorer' were conducted in good visibility (≥1 km), swell < 1 m, and Beaufort sea state (BSS) ≤ 4. When onboard the research vessels, surveys were also carried out in good visibility (≥1 km) and swell < 1 m, but in lowered BSS ≤ 3. The direction of travel was based upon sea state and wind direction, with survey vessel speed maintained at 19 knots for 'Dolphin Explorer' and 11 knots for the research vessels. A survey was discontinued when weather conditions deteriorated (visibility < 1 km, swell > 1 m, BSS ≤ 4 for the tour boat; BSS ≤ 3 for the research vessels).

Trip Encounter Rate (TER) was calculated following Wiseman et al. (2011) as the number of trips per month during which whales were observed, expressed as the proportion of the total number of trips undertaken that month. TER provided a monthly index of Bryde's whale occurrence. Only 1 trip d^{-1} was considered in the analyses to avoid pseudo-replication. (Hurlbert 1984). Seasonal analyses were based on austral seasons: spring (September to November), summer (December to February), autumn (March to May) and winter (June to August).

Photo-identification evaluation

From 2003 to 2006, dorsal fin photographs were collected from Bryde's whales in the Hauraki Gulf using Cannon 20D and EOS5 cameras fitted with a Tamron 200 to 400 mm lens. During 2011 to 2013, dorsal fin photographs were collected using a Nikon D7000 fitted with a Tamron 200 to 400 mm lens. Attempts were made to photograph both sides of the dorsal fin.

The photographic quality of the images and the distinctiveness of nicks used for individual identification were evaluated using a quality scale (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n034p061_supp.pdf). Each image was classified into 5 categories of photo quality (excellent, good, fair, average or poor) according to focus, exposure (contrast between dorsal fin and background), size of the dorsal fin relative to the frame (definition) and relative angle of the camera to the whale (Blackmer et al. 2000, Friday et al. 2000, Stevick et al. 2001). Photographs of each individual were graded according to a scale of nick distinctiveness, ranging from 1 (very distinctive dorsal fin) to 5 (non-distinctive dorsal fin; see Table S2 in the Supplement). Images were matched to the catalogue, and when a match was found, records were updated accordingly. New individuals were cross-matched by 2 experienced researchers, given a new access number and added to the catalogue.

Overall, 28 whales (and their associated sighting data) were excluded from these analyses. Deleted data were included in a former study conducted by Wiseman (2008). Of these, 8 presented poor quality images and 20 were classified as having a non-distinctive dorsal fin. Wiseman (2008) included 'fin shape' and scars as attributes to identify whales. While fin shape and scarring may be used as secondary features to assist with the identification of whales (Penry 2010), they cannot be considered sufficient to identify individuals over time. This is because fin shape can be easily distorted by the angle at which the image has been taken, as observed in whale carcasses examined post-mortem (K. A. Stockin unpubl. data). In addition, the stability of scarring is unknown for this species. As such, we deemed identification of whales based solely on fin shape and/or scarring to be unreliable, especially for a long-term study that includes comparisons over an 8 yr period.

Site fidelity

Site fidelity of Bryde's whales in the Hauraki Gulf was examined using photo-identification sighting records collected between 2003 and 2006, and between 2011 and 2013. Monthly (MSR) and seasonal sighting rates (SSR) were calculated by expressing the number of months a whale was identified as a proportion of the total number of months in which at least 1 survey was conducted and the number of seasons in which a whale was identified as a proportion of the total seasons surveyed (Parra et al. 2006, Cagnazzi et al. 2011). MSR could therefore range between 0.015 for a whale sighted in only 1 survey month, to 1 for an individual observed in all 65 survey months. Similarly, SSR could range between 0.04 for a whale sighted in only 1 season out of 23, to 1 for an individual recorded in all 23 seasons across the study.

Mark ratio

As with other cetacean populations, not all whales exhibited sufficient marks for individual recognition. To account for these unmarked individuals, we estimated a mark ratio (Jolly 1965). High quality photographs (only photos categorized 'excellent' and 'good quality') from each encounter were counted to estimate the proportion of whales with distinctive marks (mark ratio). Total abundance was estimated as follows:

$$\hat{N}_{total} = \hat{N}_{m} / \hat{P}_{m} \tag{1}$$

where $\hat{N}_{m}$ is the abundance of marked whales and $\hat{P}_{m}$ is the proportion of marked whales. The variance was estimated using the delta method (Wilson et al. 1999) as follows:

$$var\left(\hat{N}_{total}\right) = \hat{N}_{total}^{2}\left[\frac{Var\left(\hat{N}_{m}\right)}{\hat{N}_{m}^{2}} + \frac{1-\hat{P}_{m}}{n\hat{P}_{m}}\right] \tag{2}$$

where n is the total number of occasions from which $\hat{P}_{m}$ was estimated. The standard error was calculated as follows:

$$SE\left(\hat{N}_{total}\right) = \sqrt{var\left(\hat{N}_{total}\right)} \tag{3}$$

Log-normal confidence intervals for each estimate of abundance were calculated (Burnham et al. 1987) as follows:

$$\hat{N}_{lower} = \frac{\hat{N}_{total}}{C} \tag{4}$$

and

$$\hat{N}_{upper} = \hat{N}_{total} \times C \tag{5}$$

where

$$C = \exp\left(z_{\alpha/2}\sqrt{\log_{e}\left\{1 + \left[CV\left(\hat{N}_{total}\right)\right]^{2}\right\}}\right) \tag{6}$$

where $\hat{N}_{lower}$ is the lower bound of the confidence interval, $\hat{N}_{upper}$ is the upper bound of the confidence interval, $Z_{\alpha/2}$ is the normal deviate, $\alpha = 0.05$ and CV is the coefficient of variation.

Goodness of fit

To conduct goodness of fit tests, data were pooled into seasons (rather than months) to avoid sparseness due to low data density (Cooch & White 2011) and analysed in a Cormack-Jolly-Seber (CJS) framework.

This approach provides a goodness of fit test for primary sessions for the RD and seasons for POPAN. The variance inflation factor ($\hat{c}$) was estimated using a median $\hat{c}$ approach as implemented in MARK (Cooch & White 2011). To evaluate potential violations of mark-recapture assumptions, goodness of fit tests (test 2 [2.CT and 2.CL] and test 3 [3.SR and 3.SL]) were run in U-CARE v.2.2 (Choquet et al. 2005) following Tezanos-Pinto et al. (2013).

The RD does not have a specific goodness of fit test. However, data can be evaluated using current open and closed models accordingly. U-CARE was implemented using a CJS framework across primary periods (i.e. seasons) to examine potential violations of assumptions (tests 2 and 3). In addition, CloseTest (Stanley & Burnham 1999) was implemented to examine if data from each secondary period fulfilled the closure assumption.

Mark-recapture dataset

During 2003, there were relatively few photo-identification surveys conducted in the Hauraki Gulf because of a reduced tour schedule for 'Dolphin Explorer'. To minimize heterogeneity (i.e. over-dispersion), data collected during 2003 were excluded from mark-recapture analyses. Photo-identification data collected from 2004 to 2006 and 2011 to 2013 were pooled by austral seasons to estimate apparent survival, abundance and the total number of whales that used the area during the course of the study (i.e. $\hat{N}_{super}$). Monthly and annual periods were considered but not deemed suitable as pooling these resulted in either over- or under-dispersion. Periods were analysed separately to estimate abundance and account for potential differences in the area covered between periods (mostly inner Hauraki Gulf between 2004 and 2006; inner and outer Hauraki Gulf including Great Barrier Island from 2011 to 2013). However, data were combined to estimate apparent survival since it was of interest to examine whale survival across periods.

Population abundance models

RD structure

Mark-recapture data were extracted from the complete photo-identification dataset to fit a sampling structure of closely adjacent secondary samples (i.e. daily surveys: 1 survey d^{-1}) within more widely sepa-

rated primary samples (i.e. seasons). Following this structure, data were stratified by austral seasons to estimate the number of whales present in the Hauraki Gulf, rates of temporary emigration and apparent survival. For each season, we estimated the capture probability (p) and abundance ($\hat{N}_m$) of whales in the Hauraki Gulf. From the intervals between seasons, we estimated apparent survival (Ø) and temporary emigration (γ' and γ''). Capture probability was modelled to vary between seasons (s = seasons or primary samples) and within seasons (t = daily surveys within a season or secondary samples). Recapture probabilities were constrained to equal capture probabilities on each occasion for all models, because there was no evidence of a behavioural effect on capture. Temporary emigration was modelled assuming no emigration (i.e. $\gamma'' = \gamma' = 0$), random (i.e. $\gamma'' = \gamma'$), Markovian temporary emigration (i.e. $\gamma'' \neq \gamma'$) and the even flow model ($\gamma'' = 1 - \gamma'$; Huggins 1991, Kendall et al. 1997).

POPAN design structure

The Schwarz and Arnason 'super population' parameterization of the Jolly-Seber model (i.e. POPAN; Crosbie & Manly 1985, Schwarz & Arnanson 1996) was applied to estimate apparent survival and abundance of whales in the Hauraki Gulf (Williams et al. 2002) during the study period. In addition, this approach allows estimating the probability of entry (β). Models incorporated a seasonal structure in the design matrix to evaluate whether seasonality explained capture probabilities and apparent survival. TER was added into the design matrix to examine if capture probabilities were explained by effort. In order to estimate all parameters in the fully parameterized model, a constraint was added to the first and last capture probabilities (i.e. $p_1 = p_2$ and $p_k = p_{k-1}$; Cooch & White 2011). POPAN provides an estimate of $\hat{N}_{super}$.

Potential biological removal

Any marine mammal population with an estimate of human-induced mortality that is greater than its potential biological removal (PBR) has a level of mortality that could lead

to the depletion of the population (Wade 1998). We conducted a PBR analysis following Wade (1998):

$$\text{PBR} = N_{\text{MIN}} \; \frac{1}{2} R_{\text{MAX}} \; F_{\text{R}} \qquad (7)$$

where N_{MIN} is 20th percentile log-normal total abundance estimate of the stock, R_{MAX} is one-half the maximum theoretical or estimated net productivity rate of the stock at a small population size, and F_{R} = a recovery factor between 0.1 and 1.

RESULTS

Effort

Between January 2004 and February 2006, a total of 261 daily surveys were conducted in the Hauraki Gulf (Fig. 1). Average seasonal TER ranged from a low of 0.33 during spring to a high of 0.51 during summer and winter ($\bar{x}$ = 0.46; Table 1) and did not differ significantly among seasons (Kruskal-Wallis test, H_3 = 10.4, p = 0.693) or across years (Kruskal-Wallis test, H_3 = 4.99, p = 0.08).

Data collected during August 2011 to December 2013 included 382 daily surveys (Fig. 1). Average seasonal TER ranged from a low of 0.44 in autumn to a high of 0.81 in spring ($\bar{x}$ = 0.57) and did not differ significantly among seasons (Kruskal-Wallis test, H_3 = 5.43, p = 0.70) or across years (Kruskal-Wallis test, H_2 = 1.50, p = 0.47). However, there were significant differences when comparing average monthly TER
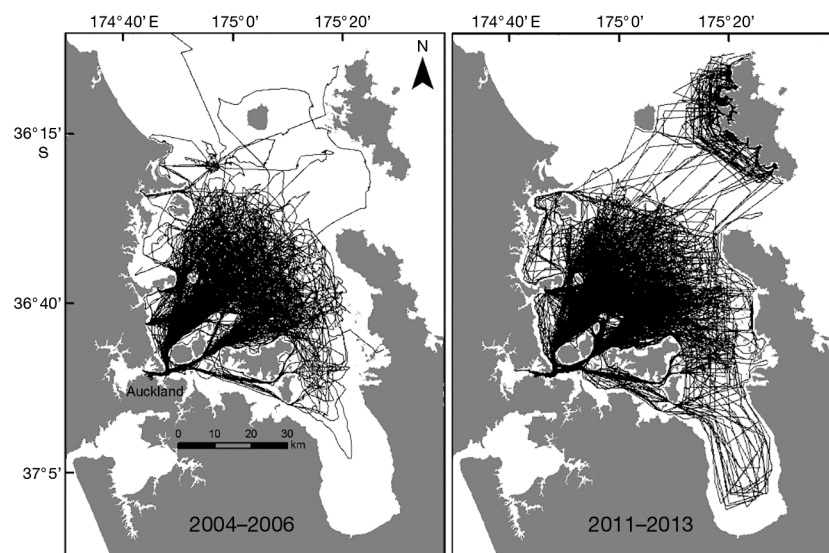

Fig. 1. Hauraki Gulf, including track effort (black lines) obtained while conducting surveys between 2004 and 2006 (n = 261), and between 2011 and 2013 (n = 382)

Table 1. Total number of daily surveys, total number of observations of Bryde's whales, and trip encounter rate (TER) in the Hauraki Gulf between 2004 and 2006, and 2011 and 2013, with average for each season listed below monthly values

Season	Month	2004–2006			2011–2013		
		Daily surveys	No. obs. whales	TER	Daily surveys	No. obs. whales	TER
Summer	December	16	19	0.51	44	29	0.66
	January	37	16	0.64	24	7	0.29
	February	25	13	0.52	30	10	0.33
Summer average				0.51			0.47
Autumn	March	25	7	0.28	30	8	0.27
	April	25	10	0.42	30	17	0.57
	May	24	12	0.41	21	8	0.38
Autumn average				0.42			0.41
Winter	June	29	13	0.54	29	12	0.41
	July	24	10	0.71	33	20	0.61
	August	14	3	0.27	40	27	0.68
Winter average				0.51			0.58
Spring	September	11	6	0.40	27	22	0.81
	October	15	5	0.31	35	30	0.86
	November	16	5	0.31	39	32	0.82
Spring average				0.33			0.84
Total		261	119	Mean: 0.46	382	222	Mean: 0.58

values per year between periods (2004 to 2006 and 2011 to 2013; Mann-Whitney test, $U_1 = 5.88$, p = 0.01).

Photo-identification

The original photo-identification catalogue from Wiseman (2008) contained 72 unique whales. After the removal of 28 whales and their associated sighting data (see 'Materials and methods'), the catalogue contained 44 unique whales. New photo-identification data collected between 2011 and 2013 resulted in a total of 48 unique whales, of which 28 represented new individuals and 20 were resightings of previously catalogued whales. Overall, the final catalogue contained 352 sighting records of 72 unique whales from 2003 to 2006 and 2011 to 2013. During 2003, there were only 26 sighting records representing 11 unique whales (2 whales were only sighted during 2003); this information was used for site fidelity analyses but excluded from mark-recapture estimates to avoid introducing heterogeneity.

Site fidelity

The majority of whales (n = 43) were sighted during ≤3 months across the 65 surveyed months, 24 whales were sighted during 4 to 10 survey months, and 5 were sighted during 11 to 15 survey months (Fig. 2). Overall, MSR ranged from a low of 1.5% (whales sighted during only one month) to a high of 23.1% (whales sighted 15 out of 65 months), with an overall mean (±SE) of 5.6 ± 0.6%. Similarly, the majority of whales (n = 50) were sighted during ≤3 of the 23 seasons, 20 whales were sighted in 4 to 9 seasons and 2 whales were sighted across 10 and 13 seasons, respectively. Accordingly, SSR ranged from a low of 4.2% (for a whale sighted in only 1 season) to a high of 56.5% (for a whale sighted in 13 of 23 seasons), with an overall mean of 12.4 ± 1.2% (Fig. 2).

Of the 72 unique whales evaluated, 20 were sighted across the 2 periods (2003 to 2006 and 2011 to 2013); however, MSR varied among whales between periods (Fig. 3). For example, whale ID12 (female; Wiseman 2008) was sighted across 11 months (MSR = 16.9%) during 2003 to 2006 but never sighted during 2011 to 2013. Whales ID22 and ID23 (both females) were sighted across 8 and 9 months during 2003 to 2006, respectively. However, during 2011 to 2013 they were observed only during 5 and 2 months, respectively. Whale ID90 (female) was sighted 10 out of 29 months (MSR = 34.5%; Fig. 3) only during 2011 to 2013. These results suggest that some whales changed their site fidelity patterns over time.
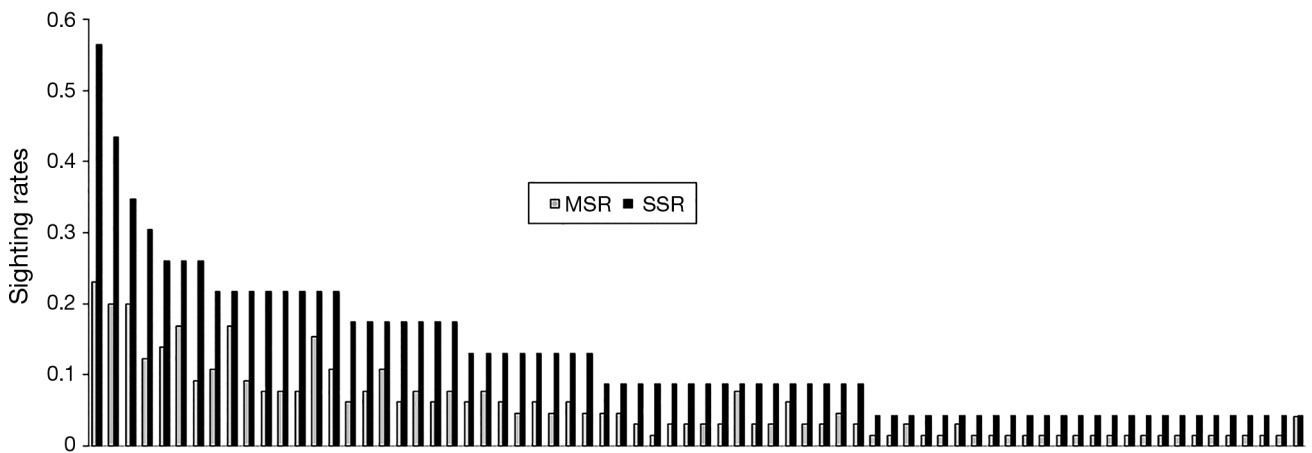
Fig. 2. Monthly (MSR; grey) and seasonal sighting rates (SSR; black) for individual Bryde's whales photo-identified in the Hauraki Gulf from 2003 to 2006 and 2011 to 2013
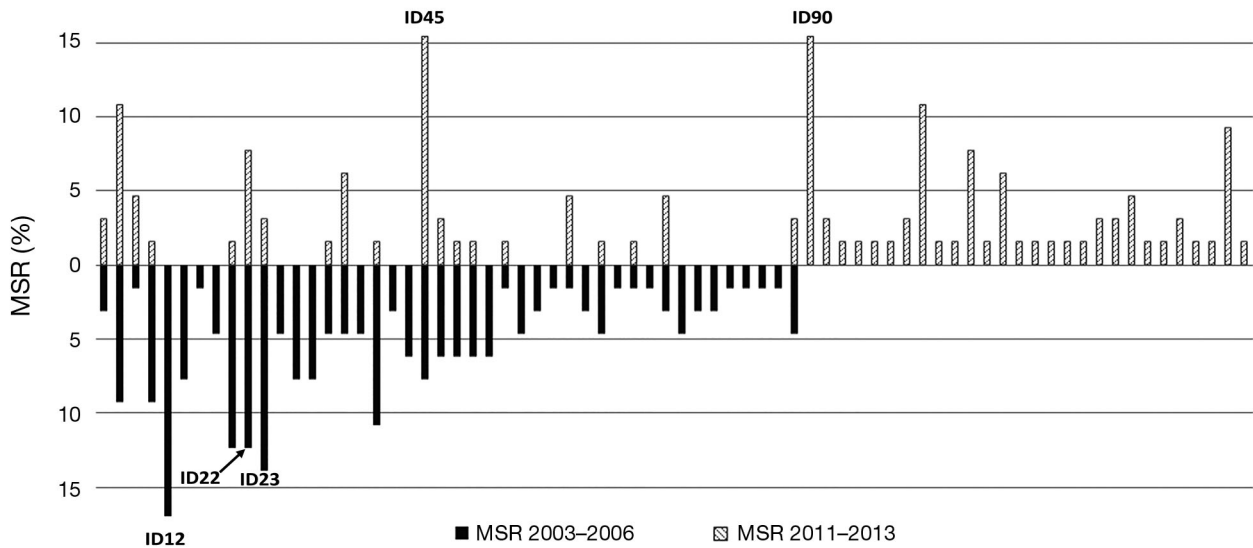

Fig. 3. Monthly seasonal sighting rates (MSR, in percentage) for individual Bryde's whales (each vertical line represents a whale) photo-identified in the Hauraki Gulf from 2003 to 2006 (black) and 2011 to 2013 (hatched). Whales ID12, 22, 23, 45 and 90 are labelled (see 'Site fidelity')

Mark ratio

The mark ratio for 2004 to 2006 was re-estimated excluding individuals that did not meet photo-quality and/or nick distinctiveness criteria. A total of 131 sightings of whales were used, of which 83 were uniquely marked individuals, resulting in a ratio of 0.633 (SE = 0.06). Using the same criteria, the mark ratio for 2011 to 2013 was estimated over 181 sightings, of which 91 were 'marked' whales, resulting in a ratio of 0.497 (SE = 0.04). All abundance estimates presented here were scaled up to their corresponding mark ratio (i.e. 63.3% for 2004 to 2006 and

49.7% for 2011 to 2013). Despite the difference, the mark ratio between periods did not vary significantly ($F = 0.253$).

Goodness of fit

For the 2004 to 2006 dataset, the estimated ĉ was indicative of no over-dispersion (ĉ = 0.987), and was set to 1 as recommended by Cooch & White (2011). Results for the global test in U-CARE were not significant (test 2 + test 3, $\chi^2 = 16.843$, p = 0.470, df = 17). Correspondingly, none of the tests showed signifi-

cant departure from assumptions (test 2.CT, p = 0.143; test 2.CL, p = 0.597; test 3.SM, p = 0.993; test 3.SR, p = 0.768).

For the 2011 to 2013 dataset, the estimated $ĉ$ was indicative of under-dispersion ($ĉ$ = 0.535), and was set to 1 as recommended by Cooch & White (2011). Results for the global test in U-CARE were not significant (test 2 + test 3, χ^2 = 9.627, p = 0.920, df = 18). Correspondingly, none of the tests showed significant departure from assumptions (test 2.CT, p = 0.914; test 2.CL, p = 0.597; test 3.SM, p = 0.709; test 3.SR, p = 0.829).

Population abundance models

Robust design

The 2004 to 2006 dataset included 9 primary periods (seasons) composed of 106 secondary sessions (i.e. days; Table 2). Annual time intervals ranged from 0.234 to 0.277. The best fitting RD model (based on corrected Akaike's information criterion [AICc] score) suggested a population with constant apparent survival, capture probabilities and temporary emigration (Table 3). Abundance estimates correcting for the proportion of unmarked whales between 2004 and 2006 ranged from a low of 17 (95% CI = 10–28; CV = 0.26) to a high of 43 whales (95% CI = 25–73; CV = 0.28; Fig. 4). Temporary emigration was estimated at 0.557 (95% CI = 0.439–0.669) and capture probability at 0.081 (95% CI = 0.070–0.094).

The 2011 to 2013 dataset included 8 primary periods (seasons) composed of 102 secondary sessions (i.e. days; Table 2). Annual time intervals ranged from 0.184 to 0.488. The best fitting RD model (based on AICc score) suggested a population with constant apparent survival, capture probability and temporary emigration (Table 3). However, a second model with constant apparent survival, temporary emigration and seasonal capture probabilities presented a high AICc weight (0.412). Consequently, model averaging was implemented to estimate all parameters (Cooch & White 2011).

Abundance estimates correcting for the proportion of unmarked whales during 2011 to 2013 ranged from a low of 13 (95% CI = 9–18, CV = 0.17) to a high of 32 whales (95% CI = 16–61, CV = 0.11; Fig. 4). Temporary emigration was estimated at 0.610 (95% CI = 0.454–0.747) and capture probability at 0.105 (95% CI = 0.068–0.160).

POPAN analyses

Several models were evaluated, including those that incorporated effort (i.e. TER) in the design matrix, as well as variations in the parameters by time and season; however, only the 6 best fitting models are presented (Table 3).

Table 2. Structure of the robust design (RD) for Bryde's whale data collected in the Hauraki Gulf from 2004 to 2006 and 2011 to 2013, including primary sessions (seasons) and secondary periods (days), start and end of each session, duration, total number of unique whales identified within each session, annual intervals between sessions, number of secondary sessions within each primary session and results from CloseTest (Stanley and Burnham closure test)

Primary session	Year	Season	Start session	End session	Unique whales ID	Annual intervals	Secondary sessions	Close test
1	2003–2004	Summer	04-Jan-04	09-Mar-04	7		5	0.398
2	2004	Autumn	23-Mar-04	13-Jun-04	11	0.240	9	0.362
3	2004	Winter	26-Jun-04	07-Sep-04	9	0.248	5	0.998
4	2004	Spring	22-Oct-04	30-Nov-04	8	0.277	6	0.474
5	2004–2005	Summer	03-Jan-05	13-Mar-05	27	0.241	16	0.312
6	2005	Autumn	26-Mar-05	16-Jun-05	38	0.242	23	0.722
7	2005	Winter	01-Jul-05	14-Sep-05	31	0.256	22	0.790
8	2005	Spring	13-Oct-05	02-Dec-05	12	0.251	6	0.597
9	2005–2006	Summer	07-Jan-06	25-Feb-06	16	0.234	14	0.586
1	2011	Winter	20-Aug-11	09-Sep-11	12		9	0.853
2	2011	Spring	22-Sep-11	19-Dec-11	19	0.184	13	0.286
3	2012	Autumn	28-Mar-12	04-Jun-12	17	0.488	15	0.205
4	2012	Winter	30-Jun-12	19-Sep-12	22	0.275	14	0.115
5	2012	Spring	09-Oct-12	15-Dec-12	21	0.258	10	0.060
6	2012–2013	Summer	10-Jan-13	07-Mar-13	15	0.240	11	0.156
7	2013	Winter	09-Jul-13	28-Aug-13	9	0.485	9	0.236
8	2013	Spring	02-Oct-13	11-Dec-13	49	0.260	21	0.171

Table 3. Model selection for mark-recapture data of Bryde's whales in the Hauraki Gulf. Models displayed include the first 6 best models for the robust design (RD, top) and seasonal POPAN data (bottom) for each period. Ø: apparent survival; p: capture; c: recapture; γ' and γ'': temporary emigration probabilities; β: probability of entry; TER: trip encounter rate (see 'Materials and methods: Data collection'). For the RD: s: seasons or primary samples; t: daily surveys within a season. The lowest corrected Akaike's information criterion (AICc) value represents the model that has the most support from the data. NP: number of parameters. Notation: $\gamma' = \gamma'' = 0$: no temporary emigration; $\gamma = \gamma''(x) = \gamma'(x)$: random temporary emigration; $\gamma''(x) \neq \gamma'(x)$: Markovian temporary emigration; constant parameter $p = c(x)$ = no behavioural effect on capture (following Kendall et al. 1997). ML: model likelihood; QDev: deviance. RD models that incorporated TER in the design matrix scored after model 6 and are not shown here

Models		AICc	ΔAICc	AICc weights	ML	NP	QDev
Robust design							
Dataset 2004−2006							
1	Ø(.) γ(.) p=c(.)	839.177	0	0.81505	1	12	785.293
2	Ø(.) γ(.) p=c(s)	843.481	4.303	0.09479	0.1163	15	782.321
3	Ø(.) γ''(.)≠ γ'(.) p=c(.)	843.606	4.428	0.08904	0.1092	16	779.950
4	Ø(.) γ(.) p=c(t)	854.042	14.865	0.00048	0.0006	20	780.022
5	Ø(.) γ''(.)≠ γ'(.) p=c(.)	854.594	15.417	0.00037	0.0005	21	777.885
6	Ø(.) γ''(t)≠ γ'(t) p=c(t)	855.198	16.021	0.00027	0.0003	29	755.396
Dataset 2011−2013							
1	Ø(.) γ(.) p=c(.)	805.654	0	0.54525	1	11	717.000
2	Ø(.) γ(.) p=c(s)	806.215	0.561	0.41189	0.755	13	712.791
3	Ø(.) γ''(.)≠ γ'(.) p=c(.)	810.767	5.113	0.0423	0.078	19	702.148
4	Ø(t) γ''(.)≠ γ'(.) p=c(.)	819.435	13.780	0.00055	0.001	23	699.875
5	Ø(.) γ''(t)≠ γ'(t) p=c(.)	827.242	21.588	0.00001	0	30	686.752
6	Ø(t) γ''(t)≠ γ'(t) p=c(t)	846.908	41.253	0	0	36	686.395
POPAN							
Dataset 2004−2006							
1	Ø(.) p(.) β(.)	276.394	0	0.84818	1	4	37.184
2	Ø(.) p(s) β(.)	280.162	3.768	0.12891	0.152	7	40.024
3	Ø(.) p(t) β(.)	284.544	8.15	0.01441	0.017	12	48.313
4	Ø(.) p(.) β(t)	285.916	9.522	0.00726	0.0086	11	44.333
5	Ø(t) p(.) β(.)	289.445	13.051	0.00124	0	11	40.804
6	Ø(.) p(TER) β(.)	295.640	19.246	0	0	12	37.217
Dataset 2011−2013							
1	Ø(.) p(s) β(.)	236.671	0	0.7662	1	7	48.365
2	Ø(.) p(.) β(.)	239.987	3.316	0.1460	0.190	4	38.041
3	Ø(.) p(t) β(.)	241.009	4.337	0.0876	0.114	12	57.081
4	Ø(t) p(.) β(.)	254.319	17.645	0.0001	0.0001	11	41.001
5	Ø(.) p(TER) β(.)	258.891	22.219	0	0	12	39.199
6	Ø(t) p(t) β(.)	259.975	23.304	0	0	19	59.985

For the 2004 to 2006 dataset, the model that best explained the data consisted of all constant parameters (Model 1). Parameter estimates from this model resulted in probability of entry = 0.073 (95% CI = 0.044−0.118) and capture probability = 0.288 (95% CI = 0.202−0.392). Seasonal abundance correcting for the proportion of unmarked animals during 2004 to 2006 ranged from 38 (95% CI = 20−73; CV = 0.34) to 75 whales (95% CI = 50−111; CV = 0.20). The abundance of all the whales that visited the area during this period was estimated at 94 (95% CI = 74−120; CV = 0.12).

For the 2011 to 2013 dataset, the model that best explained the data consisted of constant survival and probability of entry and seasonal capture probabili-

ties. Parameters estimated from this model resulted in probability of entry = 0.043 (95% CI = 0.020−0.087). Seasonal capture probabilities ranged from 0.161 during summer (95% CI = 0.084−0.289), 0.203 during autumn (95% CI = 0.070−0.461), 0.278 during spring (95% CI = 0.153−0.451) and 0.282 during winter (95% CI = 0.1723−0.426). Abundance correcting for the proportion of unmarked animals ranged from 42 (95% CI = 27−64; CV = 0.22) to 68 whales (95% CI = 43−106; CV = 0.23; Fig. 5). The abundance of all the whales that visited the area during this period was estimated at 135 (95% CI = 100−183; CV = 0.16).

Apparent survival combining both datasets (2004 to 2006 and 2011 to 2013) was estimated at 0.878 (95% CI = 0.811−0.923).
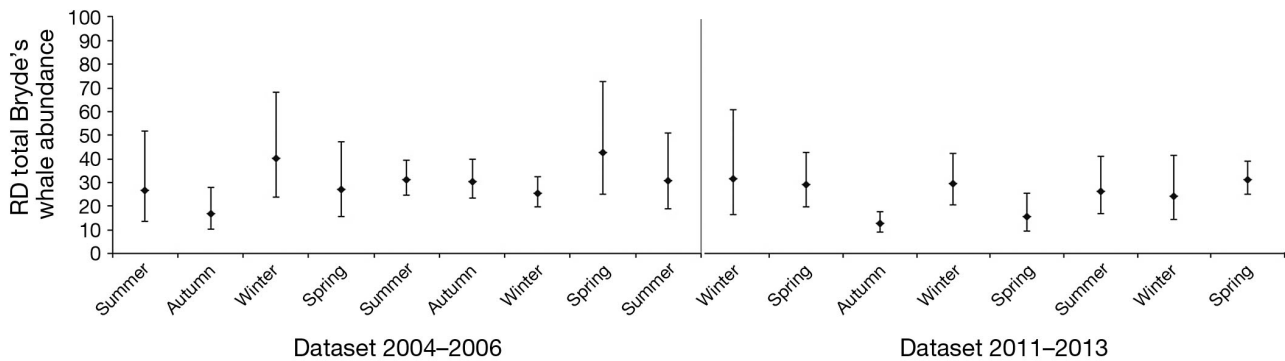
Fig. 4. Seasonal abundance estimates of Bryde's whales in the Hauraki Gulf from 2004 to 2006, and 2011 to 2013 (marked and unmarked animals) obtained using the robust design (RD), including 95% confidence intervals (vertical bars)
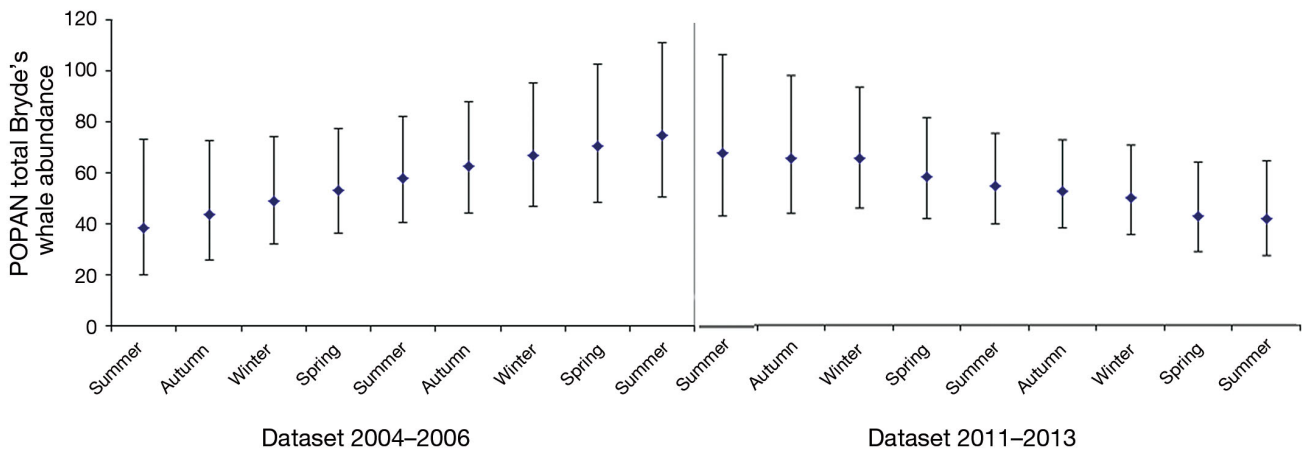

Fig. 5. Seasonal abundance estimates of Bryde's whales (marked and unmarked animals) in the Hauraki Gulf from 2004 to 2006 and 2011 to 2013 obtained using POPAN, including 95% confidence intervals (vertical bars)

PBR

Following Wade (1998), we set the recovery factor at 0.5 and the maximum rate of increase at 0.04. Abundance estimates for $\hat{N}_{super}$. during 2011 to 2013 and its corresponding CV were used ($\hat{N}_{super}$ = 135, CV = 0.16) to calculate N_{MIN}. Results from the PBR analyses indicated that the local unit of Bryde's whales in the Hauraki Gulf could not sustain mortality of more than 1 whale yr^{-1} (abundance of 135 whales [N_{MIN} = 118], CV = 0.16; recovery factor = 0.5, maximum rate of increase = 0.04).

DISCUSSION

In New Zealand, Bryde's whales are listed as 'nationally critical', and globally as Data Deficient (IUCN; Baker et al. 2010). The Hauraki Gulf is an important habitat for the species (Wiseman 2008, Wiseman et al. 2011), but it is also a region of high shipping transit, which results in whale mortality caused by vessel-strike injuries (Stockin et al. 2008, Wiseman 2008, Behrens 2009, Riekkola 2013, Constantine et al. 2015). Our estimates are precise, robust to the assumptions of the models and could be used in the future to examine population trajectories over time and the impact of ship strikes on the long-term persistence of the population.

Site fidelity and occurrence

Examination of individual site fidelity patterns suggested that some whales changed their use of the Hauraki Gulf over time. Overall, 28% of the whales (n = 20) were sighted across the 2 survey periods (8 yr). Most whales presented low MSR and SSR ratios, suggesting low site fidelity, with the exception of a few whales that showed moderate values. This

indicates that the area is an important habitat for some whales. However, site fidelity patterns are not static and change over time, possibly due to responses to environmental conditions, prey availability, age-class and/or reproductive status (Switzer 1993, Hauser et al. 2007, Foote et al. 2010, Barnett et al. 2011). During the course of this study, 13 whales were sexed as females and 3 whales were sexed as males based on molecular identification (Wiseman 2008) and/or on photographs of the whales in close association with young calves. Interestingly, the 3 males identified by Wiseman during 2004 to 2006 were not resighted during 2011 to 2013. It is possible that the whales were in the area but were not identified (i.e. if the notch changed and the whale was misidentified), that they were in the area but not photographed or alternatively, they were absent. Wider genetic sampling of naturally marked whales would allow investigation of potential differences in habitat use by each sex.

The Hauraki Gulf is used by Bryde's whales for both calving and feeding (Wiseman et al. 2011). Approximately the same number of whales visited the area over time; however, the identity of these individuals changed between periods, with the exception of a few whales that continued using the area. It is unknown where these whales go when they leave the area or the reasons that motivate changes in site fidelity over time.

The differences in TER between study periods suggested higher rates in the earlier period during winter months (June to August; Wiseman et al. 2011). However, no significant differences were found among average seasonal TER values, despite higher values obtained during spring 2011 to 2013. In addition, abundance varied between sampling occasions but there was no evidence of seasonality. In contrast, Wiseman et al. (2011) found a seasonal pattern, with higher TER values during winter. Behrens (2009) reported a peak in sightings during autumn and fewer sightings during summer, but this result was not statistically significant. A more recent study found annual but not seasonal changes in the relative density of Bryde's whales in the Hauraki Gulf (Dwyer et al. 2016), and it was noted that inter-annual fluctuations could be explained by climate-driven systems such as El Niño or La Niña. Along the California Bight (USA), Bryde's whale occurrence increased between 2000 and 2010. This increase was driven by changes in prey availability that were affected by seasonal and inter-annual changes in climate and oceanographic conditions (Kerosky et al. 2012). In the southwestern Gulf of California, higher occur-

rences of Bryde's whales were observed during La Niña conditions. In contrast, fewer whales were recorded during El Niño and neutral conditions, suggesting that changes in occurrence in that region relate to El Niño-Southern Oscillation inter-annual variability and are probably mediated by prey availability (Salvadeo et al. 2011). Continued monitoring of Bryde's whale abundance, distribution and site fidelity using photo-identification is required to provide a longitudinal dataset of individual whales to evaluate potential effects of inter-annual climate variability in New Zealand waters. This should be conducted in conjunction with aerial surveys that currently provide abundance, though not site fidelity, information for this local population.

Population abundance, migration and apparent survival

We estimated the number of whales in the Hauraki Gulf across almost a decade of surveys using both the RD and POPAN population models across seasons. The RD approach takes into account temporary emigration, whereas POPAN estimates the total number of animals that visited the area. Both approaches are suited for open populations with heterogeneous data resulting from unequal capture probabilities (Amstrup et al. 2005). Abundance estimates with the RD varied between sampling periods but did not present a seasonal pattern. Temporary emigration rates were fairly consistent between periods (57% during 2004 to 2006 and 61% during 2011 to 2013), indicating that approximately half of the whales leave the Hauraki Gulf every season before subsequently returning.

Wiseman (2008) estimated abundance using closed and open methods. The closed estimates were larger than our estimates and also presented broader confidence intervals (e.g. 128 whales estimated during summer); therefore, the closed estimates are deemed imprecise. Estimates of abundance with open models resulted in 46 whales yr^{-1} (95% CI = 39–53). While this estimate is somewhat comparable to our POPAN estimates (for 2004 to 2006: 38–74 and 2011 to 2013: 42–68 whales), ours are seasonal as opposed to annual estimates.

In our study, the differences between POPAN and the RD estimates may be due to the fact that the RD incorporates an estimate for temporary emigration, allowing individuals to move in and out of the study area between occasions, modelling heterogeneity and resulting in less biased estimates.

The estimated apparent survival for Bryde's whales (0.878) is lower than survival estimates for humpback whales *Megaptera novaeangliae* (0.93–0.98; Chaloupka et al. 1999, Perrin et al. 2009, Ashe et al. 2013). POPAN assumes that animals that left the study area died and/or emigrated (confounded parameter), which may result in an underestimate of apparent survival. Since the Hauraki Gulf represents only a small part of a wider range for the New Zealand Bryde's whale population, it is clear that emigration is significant. Nevertheless, mortality should not be underestimated. Vessel strikes have been reported as a major cause of mortality for Bryde's whales in the area (Constantine et al. 2015), and the lower apparent survival estimated here may be reflecting this mortality.

Constantine et al. (2015) estimated that a minimum average of 2.3 whales yr^{-1} have died as a result of vessel-strike injuries in the Haruaki Gulf since 1996. Results from our PBR analysis suggest that the local unit of Bryde's whales could not sustain the removal of more than 1 whale yr^{-1} combining all sources of mortality. For this reason, it is imperative that appropriate management measures are instigated to avoid mortalities due to anthropogenic causes.

CONCLUSIONS

Individual photo-identification studies allow fine-scale demographic analysis and provide valuable information for the long-term management of populations. Our results provide the first analysis of long-term site fidelity and estimates of apparent survival for Bryde's whales in the Hauraki Gulf using photo-identification methods. We estimated that less than 50 whales visit the Hauraki Gulf during each season (RD estimates), with an estimated apparent survival of 0.88. Despite long-term site fidelity being detected for 20 whales across an 8 yr period, we report individual changes in the use of the region by whales over time that has, until now, gone undetected. While it is acknowledged that the Hauraki Gulf forms only a part of the known home range for Bryde's whales, it still appears that this region is of importance to the local population — especially to those whales that display moderate site fidelity. It is currently unknown where the whales go when leaving the Hauraki Gulf. However, our findings highlight the need for continuous, as opposed to intermittent, photo-identification studies of Bryde's whales in the region so that fluctuations in abundance, movements, female reproductive rates, individual patterns of residency and habitat use can be monitored over time.

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