Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand

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Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand

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ABSTRACT: Conservation initiatives are typically constrained by economic circumstances, a factor certainly true for marine mammal conservation in New Zealand. Most research in this field has been conducted following concerns over anthropogenic impacts on populations and has therefore been funded and/or driven by stakeholder interest. Bottlenose dolphins *Tursiops truncatus* are classified as ‘Nationally Endangered’ in New Zealand waters. Here, we present the first study on occurrence, site fidelity and abundance of this species off Great Barrier Island (GBI), a previously overlooked region within the home range of the North Island population. Dedicated boat-based photo-identification surveys were conducted monthly from 2011–2013, resulting in 1412 sighting records of 154 individuals. Dolphins were recorded during all months of the year, with a higher probability of encounter in deeper waters during summer and shallower waters during winter and spring. Group sizes (median = 35, mean = 36) were higher than previously reported for this population in other regions. Individual re-sighting patterns were variable; however, overall site fidelity was high (mean monthly sighting rate = 0.33). A Robust Design approach resulted in seasonal fluctuations in abundance and temporary emigration. Based on a super-population estimate, 171 dolphins (CI = 162–180) visited the area during 2011–2013. Our data suggest that GBI is a potential hotspot for bottlenose dolphins of the North Island population rather than a corridor to reach other destinations. We highlight the need for researchers, managers and funding agencies to consider the entire range of a population when conducting or funding research.

KEY WORDS: Photo-identification · Site fidelity · Home range · Hotspot · Population abundance · Mark-recapture · Survival · Robust Design · User-pays research · *Tursiops truncatus*

INTRODUCTION

Worldwide conservation efforts employed to date have typically relied on a triage system, whereby a species/population only receives protection after it has been demonstrated that there is an urgent requirement to do so (Hooker & Gerber 2004). Often, management efforts instigated to conserve these endangered populations subsequently focus on the protection of key areas and habitats (e.g. Komdeur 1996, Clapham et al. 1999, Wright et al. 2008). However, optimal protection would need to encompass the population’s year-round distribution, assuming that this is even known.

Most conservation initiatives are constrained by economic circumstances. In New Zealand, the major-
ity of scientific evaluation of marine mammal species and populations has historically been driven by concerns about either incidental fisheries bycatch (common dolphin *Delphinus* sp.: Thompson et al. 2013; Hector’s dolphin *Cephalorhynchus hectori hectori*: Slooten & Lad 1991, Slooten 2007, Rayment & Webster 2009; Maui’s dolphin *Cephalorhynchus hectori maui*: Slooten et al. 2006; New Zealand sea lion *Phocarctos hookeri*: Chivers et al. 2005, Chivers 2008) or tourism effects (bottlenose dolphin *Tursiops truncatus*: Lundquist et al. 2003, Constantine et al. 2004; common dolphin: Neumann & Orams 2006, Stockin et al. 2008a; dusky dolphin *Lagenorhynchus obscurus*: Lundquist et al. 2012; Hector’s dolphins: Bejder et al. 1999, Martinez et al. 2010; sperm whale *Physeter macrocephalus*: Richter et al. 2006). We use the term ‘user-pays research’ to refer to the type of system illustrated by these examples, whereby a stakeholder provides research funding to address specific conservation or management needs. As such, research objectives are often specifically based on industry-driven requirements. Although the appropriate feedback can be directly provided to industry stakeholders regarding any potential impacts, the system can be flawed if funding motives become limited over time towards certain research interests, populations or geographic regions.

Although the global conservation status of bottlenose dolphins is low risk ‘Least Concern’ (Hammond et al. 2012), the Mediterranean Sea and Fiordland (New Zealand) populations have been recognised as ‘Vulnerable’ (Bearzi et al. 2012) and ‘Critically Endangered’ (Currey et al. 2011), respectively. Coastal bottlenose dolphins occur in 3 geographically discrete populations in New Zealand waters (Baker et al. 2010), with low levels of gene flow among them (Tezanos-Pinto et al. 2009). Under the New Zealand Threat Classification System, the species was listed as ‘Not Threatened’ up until 2002 (Hitchmough 2002) and subsequently uplisted to ‘Range Restricted’ in 2005 (Hitchmough et al. 2007). A further reclassification to ‘Nationally Endangered’ in 2009 (Baker et al. 2010) was based on apparent declines in abundance in 2 of the 3 coastal populations, coupled with reports of high calf mortality (Currey et al. 2009, Tezanos-Pinto et al. 2013).

The coastal bottlenose dolphin population of the northern North Island (hereafter referred to as the North Island population) primarily ranges from Doubtless Bay to Tauranga (see Fig. 1) (Constantine 2002); although infrequent sightings of known individuals outside of these areas have more recently extended the known range to the west coast of the North Island (Tezanos-Pinto et al. 2013). A decline in abundance has been reported for the Bay of Islands (BOI) (Tezanos-Pinto et al. 2013), where studies on bottlenose dolphins have formed the basis of our understanding of the North Island population. Research on the species in this region has primarily been driven by funding generated from dolphin tourism levies through the Department of Conservation (DOC), the government agency responsible for managing New Zealand’s marine mammal species (e.g. Constantine & Baker 1997, Constantine et al. 2003, Hartel et al. 2014). As such, research on this population has not only been heavily focused on tourism effects (e.g. Constantine 2001, Constantine et al. 2004), but perhaps more importantly, primarily restricted to the specific areas in which tourism is highly developed (BOI in the case of the North Island population). Consequently, while the North Island population has been extensively studied within the confines of BOI, there remains only one species-specific study published to represent other regions (i.e. the inner Hauraki Gulf; Berghan et al. 2008) within the greater home range of this population.

Great Barrier Island (GBI) is situated in the outer Hauraki Gulf and within the home range of the North Island population (Constantine 2002); however, previous marine mammal research efforts in the GBI region have been limited to large whale acoustics (Kibblewhite et al. 1967, Helweg 1998, McDonald 2006). No dedicated delphinid studies have been conducted in the GBI area, likely due to a combination of an absence of direct interest from stakeholders and the logistical constraints of fieldwork in this comparatively remote location. As such, no information is presently available within the scientific literature describing bottlenose dolphins or indeed any other delphinid off GBI.

Here we present the first information about bottlenose dolphins off the west coast of GBI. We describe occurrence, examine factors affecting the probability of encountering bottlenose dolphins at GBI, and assess group dynamics. Using individual photo-identification (Würsig & Jefferson 1990) we investigate site fidelity and estimate abundance, demographic parameters and temporary emigration rates. Our overall objective was to assess the importance of GBI, an overlooked area within the home range of a nationally endangered species, in order to inform current conservation management strategies.
MATERIALS AND METHODS

Study area

GBI (36° 10’ S, 175° 23’ E), situated approximately 80 km northeast of Auckland city (36° 51’ S, 174° 46’ E), is located within the outer Hauraki Gulf, North Island, New Zealand (Fig. 1, inset). The west coast of GBI, adjacent to Cradock Channel in the north (36° 12’ S, 175° 11’ E) and Colville Channel in the south (36° 23’ S, 175° 25’ E), is characterised by numerous shallow embayments and a predominantly rocky shoreline. The study site included all waters up to a distance of 10 km offshore between Miners Head in the north and Ross Bay in the south (Fig. 1) and therefore encompassed ~500 km². Water depths in the study area are relatively shallow and reach a maximum of 90 m (Chart NZ 522, Land Information New Zealand). With a land area of 285 km², GBI is the largest of New Zealand’s northern offshore islands, but has a low human population density, and 68% of the land is administered by DOC (Norgrove & Jordan 2006). Most of the west coast remains uninhabited and there are currently no commercial marine mammal tourism operations at GBI.

Data collection

Survey data were collected across all austral seasons between January 2011 and January 2013. When possible (i.e. when weather and sea conditions permitted), monthly research trips averaging 4 d in duration were made to GBI. Boat-based surveys were conducted on the research vessel ‘Te Epiwhania’, a 5.5 m aluminium boat powered by a 100 hp 4-stroke
outboard engine. A non-systematic survey design was employed, with survey tracks selected based on prevailing weather, sea conditions, and on the extent any particular area had been previously surveyed within that month. Where possible, routes were selected to achieve equal survey coverage of the west coast and to include both nearshore and offshore waters up to 10 km from land within any given month. Efforts were also made to survey the latitudinal extent of the GBI west coast in order to cover both northern and southern regions in any given day. Surveys were conducted in conditions of Beaufort Sea State 3 or less. Time spent travelling along survey tracks searching for dolphins, with vessel speed maintained at ~10 knots, was classified as 'on effort'.

Whilst on effort, 2 experienced observers continuously scanned to the horizon. Dolphins were detected by naked eye and/or binoculars (10 × 50 magnification) using scanning methodology (Mann 1999). Visual cues to indicate dolphin presence included splashing, water disturbance and sighting of dorsal fins (Stockin et al. 2008b). Once the research boat left the survey track to approach a group of dolphins, the survey mode switched to 'off effort' until returning to the track to resume searching for dolphins. Off-effort mode also included all other occasions when the research vessel was away from the survey track (e.g. returning to harbour due to deteriorating sea conditions).

When a dolphin group was detected, the research vessel approached to within 50 m and commenced data collection. Water depth (±0.1 m) was measured using an on-board depth sounder at the location where the group was first sighted. All observational and environmental data were collected using an XDA Orbit II Windows Mobile device. CyberTracker version 3 software (Steventon et al. 2002) was programmed for logging observational data (e.g. group size) and to record the GPS position every 60 s throughout the survey day.

A group of dolphins was defined as any number of individuals observed in apparent association, moving in the same general direction and often, but not always, engaged in the same activity (Shane 1990). Group size was recorded at sea using minimum, maximum and best estimate counts and was later confirmed or amended using photo-identification data. If all individuals in the group were not photographed (e.g. due to time constraints), the best estimate was selected for group size.

Age class definitions follow those previously described for the North Island population (Constantine 2002, Tezanos-Pinto 2009):

- Neonate: presence of obvious white dorso-ventral foetal folds and often uncoordinated upon surfacing to breathe; typically observed up to 3 mo old
- Calf: approximately half or less the size of an adult, closely associated with an adult and often swimming in the ‘infant position’
- Juvenile: approximately two-thirds the size of an adult and frequently observed in association with the mother but not in the ‘infant position’
- Adult: fully grown dolphin of >3.0 m in length.

The number of neonates, calves and juveniles was estimated visually at sea using minimum, best and maximum counts and was later confirmed or amended using photo-identification data.

Photo-identification of individual bottlenose dolphins was conducted for all groups following standard methods (Würsig & Jefferson 1990) using a Canon 7D or 400D camera fitted with 100–400 or 70–300 mm lenses, respectively. Attempts were made to photograph all individuals in the group, regardless of the degree of mark distinctiveness of the fin. Both left and right sides of the dorsal fin were photographed where possible.

After observational data were logged and photo-identification completed, the research vessel returned to the survey route and resumed on-effort searching for independent groups (i.e. groups separated spatially and temporally as confirmed by no photographic matches). Multiple independent groups could therefore be observed during any one given survey.

Data analysis

Austral seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) in accordance with previous studies on this population (Constantine 2002, Berghan et al. 2008, Tezanos-Pinto 2009). Both on- and off-effort sighting data were included in analyses unless otherwise stated. Statistical analyses were carried out using SPSS v.20 for investigations into group composition and seasonal patterns in occurrence according to depth. Since data were not normally distributed, Kruskal-Wallis and Mann-Whitney U-tests were used to test for significance at p < 0.05.

Probability of encounter

Logistic regression was used to model the probability of encountering a bottlenose dolphin. A grid
of 27 cells of 5 × 5 km (Fig. 1) was created in ArcGIS v.10.0, and presence or absence of dolphins was recorded for each cell sampled per survey day. Only on-effort sightings were considered for the analysis, which was carried out in R version 3.0.1 (R Development Core Team 2013). Search effort was calculated as on-effort km per grid cell per survey day using Geospatial Modelling Environment version 0.7.2.0 tools (Beyer 2012). Depth data for cells where dolphins were recorded (i.e. presence) were collected using the onboard depth sounder and within 100 m of the position of the group when first sighted. For cells where dolphins were not encountered (i.e. absence), depth was retrieved at the midpoint of the track segment in each cell surveyed using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012). Daily sea surface temperature (SST) data were obtained from the Physical Oceanography Distributed Active Archive Centre (PO.DAAC, NASA Jet Propulsion Laboratory, Pasadena, California, USA) at a 1 km spatial scale and subsequently averaged over each grid cell. Depth (in m), SST, season (a factor with 4 levels), time of day of the survey, effort (km traversed in the grid) and Beaufort sea state were fit as covariates in the initial model. Variables were dropped or retained from the initial model by comparing the reduction in deviance using a chi-square test. Confidence intervals for each parameter were calculated assuming asymptotic normality.

Photo-identification

Photographs included in analysis and in the subsequent Great Barrier Island Bottlenose Dolphin Catalogue (S. L. Dwyer unpubl. data) were selected based on 4 criteria described in Berghan et al. (2008), to account for angle, focus, relative size and contrast of the fin. Following Tezanos-Pinto et al. (2013), only excellent and good quality photographs were included in the analyses. Nicks and notches in the dorsal fin were used in conjunction with secondary features (i.e. scarring, including tooth rake marks) to identify and match individuals (Würsig & Jefferson 1990). All matching of images was performed by S. L. Dwyer and cross-checked by 2 experienced researchers. Sighting information was recorded in a database for each identified individual. Mother–calf associations were confirmed using photographs from at least 2 independent encounters (Tezanos-Pinto 2009).

Site fidelity

Site fidelity at GBI was investigated using monthly (MSR) and seasonal sighting rates (SSR), a methodology described by Parra et al. (2006). These were calculated by expressing the number of months a dolphin was identified as a proportion of the total number of months in which at least 1 survey was conducted, and the number of seasons a dolphin was identified as a proportion of the total seasons surveyed, respectively (Parra et al. 2006, Cagnazzi et al. 2011). MSR could therefore range between 0.05 and 1.0, for individuals sighted in only 1 survey month or in all 20 survey months, respectively; similarly, SSR could range between 0.25 and 1.0 for individuals sighted in only 1 season or in all 4 seasons, respectively. To minimise the chance of dependence in the data, only 1 sighting record per individual per day was used (Parra et al. 2006, Cagnazzi et al. 2011). Based on previously published high and low mean MSR values for dolphins (e.g. high MSR = 0.26: Cagnazzi et al. 2011; low MSR = 0.10: Parra et al. 2006), individuals were subsequently and conservatively (i.e. using higher minimum values than those previously reported) classified into 1 of 3 categories based on MSR and SSR: (1) occasional visitors (MSR ≤ 0.15, irrespective of SSR), (2) moderate users (0.15 < MSR < 0.35, SSR ≥ 0.5), or (3) frequent users (MSR ≥ 0.35, SSR ≥ 0.75). Therefore, frequent users were defined as animals sighted on average at least once every 3 mo and observed during at least 3 seasons of the year. A weighted ratio of the total number of sighting records per unique individual was calculated for each category to assess the relative changes by season.

In order to assess whether dolphins sighted at GBI were also recorded outside the study area, each individual in the Great Barrier Island Bottlenose Dolphin Catalogue was cross-referenced (using standard photo-identification methods described herein) with images and published records of bottlenose dolphins photographed in 3 other regions of the North Island population home range (Fig. 1, inset): (1) Inner Hauraki Gulf (south of GBI). All waters south of a line between Takatu Point on the mainland and Kaitiri Point on the Coromandel Peninsula. Data from 2000 to 2006 (Hauraki Gulf Bottlenose Dolphin Catalogue, HGBDC) were combined with data from 2009 to 2013 (S. L. Dwyer unpubl. data).

2 Hauraki Gulf Bottlenose Dolphin Catalogue: J. Berghan, K. Algie, K. Stockin, N. Wiseman & G. Tezanos-Pinto, unpubl. data
(2) Bay of Plenty (south of GBI). Coastal Tauranga region up to 40 km offshore. Photographs were analysed from data collected during dedicated surveys conducted between 2010 and 2013 (A. M. Meissner unpubl. data).

(3) Whangarei Coast (north of GBI). Coastal waters between Tutukaka and Ruakaka, including the Poor Knights Islands located 20 km offshore. Bottlenose dolphins were photographed opportunistically on 20 occasions between 2002 and 2011 (I. N. Visser unpubl. data).

Abundance, temporary emigration and survival estimates

Mark-recapture techniques using the Robust Design (Pollock 1982, Kendall et al. 1997) were used to estimate abundance, demographic parameters and temporary emigration rates. The Robust Design incorporates open sampling events called ‘primary periods’ within which are a number of closed ‘secondary periods’ (Pollock 1982). Closure is assumed within primary periods but not between them. To fulfil this assumption, the Robust Design relies on secondary periods being close together temporally (Kendall 2004). Bottlenose dolphins along the North Island have variable patterns of residency and home ranges (Constantine 2002, Tezanos-Pinto 2009) that may result in unequal capture probabilities between individuals (Tezanos-Pinto et al. 2013). The Robust Design allows for temporary emigration, resulting in a useful model to estimate abundance for species that move in and out of the study area. The Schwarz and Arnanson ‘super-population’ parameterization of the Jolly-Seber model (Schwarz & Arnanson 1996, Williams et al. 2002) was implemented to estimate the total number of dolphins that used the area during the course of the study (the super-population) by considering one sighting per season for each dolphin (Williams et al. 2002, Nichols 2005), meaning that the dolphin was either absent (0) or present (1) during that season.

Robust Design model

Pollock’s Robust Design models were run in MARK version 5.1 (White & Burnham 1999). The intervals between seasons were specified in decimal years between their mid dates to obtain consistent estimates of survival. For each season, we estimated the capture probability ($p$) and abundance ($N^*$) of dolphins at GBI. From the intervals between seasons, we estimated the apparent survival probability ($\phi$), the probability that an animal is outside the study area on a sampling occasion given that it was inside the study area on the previous occasion ($\gamma^*$), and the probability that an animal is outside the study area on a sampling occasion given that it was inside the study area on the previous occasion ($\gamma^\prime$; Kendall et al. 1995, 1997). Models were considered with temporal variation in capture probabilities between ($s$ = seasons or primary samples), within ($t$ = daily surveys within a season, secondary samples), and both between and within primary periods ($s*t$). Recapture probabilities were constrained to equal capture probabilities on each occasion for all models because there was no evidence of a behavioural effect. We fitted models with no temporary emigration ($\gamma^* = \gamma^\prime = 0$), random ($\gamma^* = \gamma^\prime$) and Markovian temporary emigration ($\gamma^* \neq \gamma^\prime$) (Huggins 1991, Kendall et al. 1997). To provide
parameter identifiability for the Markovian models, we either constrained apparent survival ($\phi$) to be constant or added a constraint (session $k = session k - 1$) resulting in the last 2 parameters in the time series set to equal (Kendall et al. 1997). We used Akaike’s Information Criterion (AIC) to evaluate model fit. The best fitting model was identified as having the lowest AICc (Burnham & Anderson 2004).

**POPAN super-population models**

A ‘super-population’ approach was applied in POPAN as implemented in MARK, to estimate the abundance of the ‘larger’ population that used the area during the course of the study. The approach is based on a re-parameterization of the Jolly-Seber (JS) model with an additional parameter $N_{super}$ that denotes the size of the ‘super-population’. Models were considered with constant (.) and temporal variation (t) in capture probabilities between seasons. We added a constraint to the first 2 and the last 2 capture probabilities to provide parameter identifiability for all models (Cooch & White 2011).

**Mark ratio**

As with other wild populations of dolphins, not all individuals bear sufficient marks for individual recognition. To account for these unmarked dolphins at GBI, we estimated a mark ratio (Jolly 1965). High quality photographs (only excellent and good quality) were counted including all age-classes to estimate the ratio of individually identifiable dolphins (i.e. marked animals) during 2011–2013. Only those encounters in which all dolphins, irrespective of their marks, were photographed several times were included for this estimate. The proportion of marked dolphins ($P_m$) was estimated (Gormley et al. 2005) as the ratio between the number of marked dolphins and the total number of dolphins observed on each survey, averaged over all surveys (Cantor et al. 2012). $P_m$ and its variance (Gormley et al. 2005) were estimated as follows:

$$\hat{P}_m = \frac{\sum I_i}{k}, \text{ var}(\hat{P}_m) = \left( \frac{\sum_{i=1}^{k} \hat{P}_m (1 - \hat{P}_m)}{T_i} \right) / k^2$$

where $I_i$ is the number of identifiable (i.e. marked) dolphins per survey, $T_i$ is the total number of dolphins sighted during the $i^{th}$ survey day and $k$ is the total number of survey days for which $I/T$ was calculated ($k = 34$), for each $\hat{P}_m = I_i / T_i$. Abundance estimates were scaled by the mark-ratio to obtain the total abundance $\hat{N}_{total}$ (Williams et al. 1993) as follows:

$$\hat{N}_{total} = \hat{N}_m / \hat{P}_m$$

where $\hat{N}_m$ is the abundance of marked dolphins. The variance (var) and standard error (SE) of $\hat{N}_{total}$ were calculated (Wilson et al. 1999) as follows:

$$\text{var}(\hat{N}_{total}) = \left( \hat{N}_{total} \right)^2 \left[ \text{var}(\hat{N}_m) / \hat{N}_m^2 + \text{var}(\hat{P}_m) / (\hat{P}_m)^2 \right],$$

$$\text{SE}(\hat{N}_{total}) = \sqrt{\text{var}(\hat{N}_{total})}$$

Log-normal confidence intervals were calculated (Burnham et al. 1987) as follows:

$$\hat{N}_{lower} = \hat{N}_{total} / C \text{ and } \hat{N}_{upper} = \hat{N}_{total} \times C,$$

where $C = \exp\left( z_{\alpha/2} \sqrt{\log_e \left\{ 1 + \left[ \text{cv}(\hat{N}_{total}) \right]^2 \right\} } \right)$

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.

**RESULTS**

Between January 2011 and January 2013, over 4000 km were surveyed off the west coast of GBI (Fig. 1) during 71 survey days across 20 mo. A total of 44 independent groups of bottlenose dolphins were recorded, 36 encountered on effort and 8 off effort (Table 1). Photo-identification effort at GBI totalled 78.2 h during 37 survey days across all seasons. A total of 1412 sighting records (i.e. sighting of an identified individual on a discrete day) of 154 individuals photographed at GBI were used in the analyses. Individual sighting frequencies ranged from 1 to 27 (mean = 9.17, SD = 7.93).


Table 1. Summary of bottlenose dolphin *Tursiops truncatus* encounters and survey effort by season (Summer: Dec–Feb; Autumn: March–May; Winter: Jun–Aug; Spring: Sep–Nov) and depth category at Great Barrier Island, New Zealand, between January 2011 and January 2013. Groups encountered: on-effort totals for all years combined (off-effort totals in parentheses); sighting records: total number of individual dolphin sighting records for a discrete day, as confirmed by photographic matches; unique individuals: number of unique individuals identified in that season. Survey effort includes on-effort km spent actively searching for dolphins; time spent with dolphins and transiting while off-effort is not included.

<table>
<thead>
<tr>
<th>Season</th>
<th>Groups encountered</th>
<th>Sighting records</th>
<th>Unique individuals</th>
<th>Survey effort (km) per depth category (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0–9</td>
</tr>
<tr>
<td>Summer</td>
<td>10 (3)</td>
<td>524</td>
<td>100</td>
<td>26.4</td>
</tr>
<tr>
<td>Autumn</td>
<td>9 (2)</td>
<td>217</td>
<td>116</td>
<td>31.4</td>
</tr>
<tr>
<td>Winter</td>
<td>7 (2)</td>
<td>237</td>
<td>77</td>
<td>36.3</td>
</tr>
<tr>
<td>Spring</td>
<td>10 (1)</td>
<td>434</td>
<td>98</td>
<td>33.7</td>
</tr>
<tr>
<td>Total</td>
<td>36 (8)</td>
<td>1412</td>
<td>154</td>
<td>127.8</td>
</tr>
</tbody>
</table>

**Occurrence**

Bottlenose dolphins were sighted at GBI during all months of the year. Despite extensive effort up to 10 km offshore (Fig. 1), dolphins were found within 1 and 2 km of the coast for 84 and 96% of encounters, respectively. Groups were encountered across a range of water depths from 2 to 57.4 m (mean = 22.88, SD = 15.88, n = 44), with surveys conducted in depths of up to 86 m (Table 1, Fig. 2). Since areas with water depths of >60 m were only available for surveying in the northern region of the study area, these depths received less effort. There was a significant difference in depth according to season (Kruskal-Wallis $H = 19.10$, df = 3, $p < 0.001$, n = 44), with shallower waters used during spring (median = 6.60, IQR = 4.6–20.2) and winter (median = 11.50, IQR = 5.4–26.1) and deeper waters used during summer (median = 39.40, IQR = 29.1–43.9).

**Probability of encounter**

The final logistic model found evidence that the probability of encounter depended only on season and depth (although these 2 variables interacted). There was no evidence that the ‘effort’ variable (km traversed within the grid cell on that sample occasion) was important, however it was retained in the final logistic model. There was strong evidence ($p = 0.0016$) of an interaction between depth and season, with the effect of depth dependent upon season. Corresponding with the results of the non-parametric tests, the model suggested an increased probability of encountering dolphins in deeper water (further from shore) in summer (Fig. 3). Additionally, the probability of encountering dolphins in shallow water (closer to shore) was highest in winter and spring (Fig. 3). Overall, the probability of encountering dolphins was highest in waters of less than 20 m depth (Fig. 3).

**Group dynamics**

Group size ranged from 1 to 82 individuals (median = 35, mean = 36.39, SD = 23.36, n = 44) and varied with depth and season (Fig. 2). A relatively large proportion (32%) of groups consisted of ≥50 individuals, all of which...
were recorded in the southern region of the study area (Fig. 4) and primarily during spring and summer (86%). Conversely, all small groups of <10 individuals (18%) were recorded in the northern region (Fig. 4). A solitary dolphin was encountered during autumn and the largest group size (n = 82, as confirmed by photo-identification) was recorded during spring. Larger groups were sighted more frequently in spring and summer, and smaller groups were more prevalent in autumn and winter (Fig. 2). Two independent groups, confirmed by no photographic matches, were observed on the same survey day on 7 occasions. This included 109 individuals recorded at GBI on 18 February 2012 in 2 groups of 60 and 49 dolphins, separated by a distance of 19.4 km. The majority of groups (82%) contained immature dolphins. Group size (comparing only the number of adults within groups) was significantly higher (Mann-Whitney $U = 384.50, p < 0.001$) in groups containing neonates or calves (median = 40, IQR = 28.5–52.3) than groups containing only adults or adults and juveniles (median = 8, IQR = 3.0–22.0). Groups with neonates and calves were therefore, on average, 5 times the size of groups with only adults or adults and juveniles. All adult-only groups contained <22 individuals (median = 7, SD = 7.42).

Neonates and calves were observed across all seasons in 70% of groups. Where present, the number
of neonates in groups ranged from 1 to 4 (SD = 1.15) and number of calves ranged from 1 to 9 (SD = 2.47). Forty-three percent of groups contained at least one neonate, with the highest proportion of these groups encountered during summer (54%) followed by spring (26%) and autumn (16%). Only one group was recorded with a neonate during winter. Parturition was not directly observed in the field; however, very young neonates were observed at GBI. For example, individual TM027 was recorded 27 times without a calf between 26 January 2011 and 28 December 2012 before being photographed with a neonate on 2 January 2013. During the study, 12 photo-identified adults were recorded consistently associated with neonates.

**Photo-identification**

Bottlenose dolphins were encountered during 19 out of 20 survey months. The discovery curve (Fig. 5) showed a steep ascent during early surveys before reaching a plateau in May 2012, with only 8 new individuals identified after this plateau during the final quarter of the study. Thirty-five dolphins (23%) were sighted only once in the study area; however, a larger proportion of individuals (37%, n = 57) were sighted ≥10 times. Most re-sighted individuals (87%, n = 134) were recorded in the study area in more than 1 year. The total number of individual sighting records in summer and spring were double those of autumn and winter (Table 1), in part due to the higher proportion of large group sizes observed in summer and spring (Fig. 2).

**Site fidelity**

Relative to the total number of months surveyed, bottlenose dolphins showed varying degrees of site fidelity to the west coast of GBI (Fig. 6). Higher proportions of both occasional visitors (41%) and frequent users (40%) and a lower number of moderate users (19%) were observed. Overall, site fidelity was relatively high (mean MSR = 0.33, SE = 0.022, range 0.05–0.85). Over 32% of all identified individuals were sighted in more than 50% of the total survey months. SSR was also high (mean = 0.70, SE = 0.025; Fig. 6), with 117 individuals (76%) sighted in the study area during at least 2 different seasons. Just under half (44%) of all identified individuals were recorded at GBI in all 4 seasons. Using a weighted ratio of the total number of sighting records per unique identified individual, the highest proportion of occasional visitors and frequent users per season were observed during autumn (30%; Fig. 7) and winter (63%; Fig. 7), respectively.

The majority (85%) of individuals identified at GBI were recorded in at least one of the other regions within the North Island home range for which photo-identification data were available (Table 2). Sixteen individuals were recorded in all of these regions. Unsurprisingly, there were a high number of matches (n = 115) to the nearby inner Hauraki Gulf. Since all frequent users of GBI (n = 61) were sighted in at least one neighbouring region, even individuals regularly using GBI waters left the area at least seasonally to visit other regions up to 200 km away.
Our data showed an interesting pattern in which higher numbers of dolphins were counted during summer (n = 524) and spring (n = 434), but a higher number of unique individuals were sighted in autumn (n = 116) than in any other season (Table 1). This was due to seasonal variations in re-sighting patterns and group dynamics, with a larger proportion of occasional visitors present at GBI during autumn (Fig. 7) in overall smaller group sizes (Fig. 2).

### Abundance, temporary emigration and survival estimates

The mark ratio was estimated from a total of 1423 high-quality photographs collected from 34 surveys during 2011–2013. Of these, 1260 images represented identifiable individuals (I). From this, the mark ratio ($P_{m}$) was estimated at 0.885 (SE = 0.012), or 88.5%.

The study population could not be considered geographically closed between seasons as some individuals were captured inconsistently across sampling seasons. Therefore, models that incorporated temporary emigration were included in the set of models. As expected, the likelihood ratio test (LRT) rejected models with no temporary emigration (models 5 & 7; Table 3) when tested against models with random ($\chi^2 = 58.4$, df = 11, $p < 0.0001$) and Markovian ($\chi^2 = 91.2$, df = 10, $p < 0.0001$) temporary emigration.

### Table 2. Number of bottlenose dolphins *Tursiops truncatus* identified at Great Barrier Island (GBI) and sighted in other regions of the North Island population home range. HGBDC: Hauraki Gulf Bottlenose Dolphin Catalogue

<table>
<thead>
<tr>
<th>Region</th>
<th>GBI individuals (n = 154)</th>
<th>GBI frequent users (n = 61)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner Hauraki Gulf</td>
<td>115</td>
<td>47</td>
<td>HGBDC unpubl. data, S. L. Dwyer unpubl. data</td>
</tr>
<tr>
<td>Bay of Plenty</td>
<td>89</td>
<td>49</td>
<td>A. M. Meissner unpubl. data</td>
</tr>
<tr>
<td>Whangarei Coast</td>
<td>51</td>
<td>5</td>
<td>I. N. Visser unpubl. data</td>
</tr>
</tbody>
</table>
We first attempted to simplify the capture probability structure by assuming it constant (.) or varying between seasons (s) but models with fully time-varying (t) capture probabilities were strongly favoured. We then tested models with constant apparent survival probability \( \phi(t) \) (models 1, 7 & 8; Table 3). AICc indicated that models with Markovian temporary emigration (models 1, 2, 4 & 8; Table 3) received more support from the data than models with random emigration (models 3 & 6; Table 3). The best fitting model assumed constant apparent survival, fully time-varying Markovian temporary emigration and fully time-varying capture probabilities (model 1; Table 3) and accounted for 93% of the AICc weight in the model set. Capture probabilities were variable within (range 0.13–0.90) and between (range 0.33–0.70) seasons. Overall, spring and summer presented the highest capture probabilities (0.70, SE = 0.022, and 0.63, SE = 0.034, respectively) when compared to autumn (0.33, SE = 0.024) and winter (0.35, SE = 0.026; Fig. 8). Estimates of abundance also varied; unfortunately, abundance estimates for summer had very low and high standard errors and were deemed unreliable (Fig. 8). Seasonal estimates varied from a low of 60 dolphins (95% CI = 53–67) in winter 2012, to a high of 131 during autumn 2012 (95% CI = 114–151; Fig. 8), including the correction for unmarked dolphins. Overall, seasonal abundances seemed lower during winter (Fig. 8) when compared to autumn.

- **Table 3.** Model selection for sighting data of bottlenose dolphins *Tursiops truncatus* at Great Barrier Island, New Zealand, during 2011–2013. Model results are for seasonal Robust Design data (top), and POPAN (below). The lowest AICc value represents the model that has the most support from the data (in **bold**). Abbreviations: apparent survival \( \phi \), capture \( p \), recapture \( c \) and temporary emigration \( \gamma \) probabilities, probability of entry \( \beta \). ML: maximum likelihood; NP: number of parameters; Dev: deviance. The notation (.) indicates that a given parameter was kept constant, (t) indicates that a given parameter was allowed to vary with time, (s) indicates that a parameter was allowed to vary between seasons, and \( k \) is a constraint (session \( k = k - 1 \)).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
<th>ML</th>
<th>NP</th>
<th>Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Robust Design</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 ( \phi(.) \gamma(t, k = k - 1) \gamma'(t, k = k - 1) c = p(t) )</td>
<td>-765.77</td>
<td>0.00</td>
<td>0.93362</td>
<td>1</td>
<td>51</td>
<td>1618.36</td>
</tr>
<tr>
<td>2 ( \phi(t) \gamma(t, k = k - 1) \gamma'(t, k = k - 1) c = p(t) )</td>
<td>-760.48</td>
<td>5.29</td>
<td>0.06638</td>
<td>0.0711</td>
<td>58</td>
<td>1671.08</td>
</tr>
<tr>
<td>3 ( \phi(t) \gamma(t, k = k - 1) \gamma'(t) c = p(t) )</td>
<td>-730.80</td>
<td>34.97</td>
<td>0.00010</td>
<td>0</td>
<td>52</td>
<td>1714.12</td>
</tr>
<tr>
<td>4 ( \phi(t) \gamma(t) \gamma'(t) c = p(t) )</td>
<td>-711.65</td>
<td>54.12</td>
<td>0</td>
<td>0</td>
<td>42</td>
<td>1755.18</td>
</tr>
<tr>
<td>5 ( \phi(t) \gamma = 0 c = p(t) )</td>
<td>-696.46</td>
<td>69.31</td>
<td>0</td>
<td>0</td>
<td>41</td>
<td>1772.54</td>
</tr>
<tr>
<td>6 ( \phi(t) \gamma = \gamma'(t) c = p(t) )</td>
<td>-696.46</td>
<td>69.31</td>
<td>0</td>
<td>0</td>
<td>41</td>
<td>1772.54</td>
</tr>
<tr>
<td>7 ( \phi(.) \gamma = 0 c = p(t) )</td>
<td>-680.26</td>
<td>85.51</td>
<td>0</td>
<td>0</td>
<td>38</td>
<td>1795.22</td>
</tr>
<tr>
<td>8 ( \phi(.) \gamma(t, k = k - 1) \gamma'(t, k = k - 1) c = p(s) )</td>
<td>-610.49</td>
<td>155.27</td>
<td>0</td>
<td>0</td>
<td>32</td>
<td>1877.83</td>
</tr>
<tr>
<td><strong>POPAN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 ( \phi(.) p(t) \beta(t) )</td>
<td>553.15</td>
<td>0.00</td>
<td>0.87145</td>
<td>1</td>
<td>12</td>
<td>4.46</td>
</tr>
<tr>
<td>10 ( \phi(t) p(t) \beta(t) )</td>
<td>557.91</td>
<td>4.76</td>
<td>0.08067</td>
<td>0.0926</td>
<td>19</td>
<td>0</td>
</tr>
<tr>
<td>11 ( \phi(t) p(t) \beta(t) )</td>
<td>558.99</td>
<td>5.84</td>
<td>0.04705</td>
<td>0.0540</td>
<td>19</td>
<td>0</td>
</tr>
<tr>
<td>12 ( \phi(t) p(t) \beta(t) )</td>
<td>567.09</td>
<td>13.94</td>
<td>0.00082</td>
<td>0.0009</td>
<td>27</td>
<td>0</td>
</tr>
</tbody>
</table>

**Fig. 8.** Seasonal abundance estimates of bottlenose dolphins *Tursiops truncatus* at Great Barrier Island, New Zealand (marked and unmarked dolphins), with the Robust Design including confidence intervals, capture probabilities \( p \) and SE (in parentheses). Note: for summer 2011, SE was unestimable.
The temporary emigration rates of being absent based on the previous period state of being present \((\gamma')\) were low and ranged from 0.00 to 0.04 with a peak in winter 2012 and a mean value of 0.01 (SE = 0.006; Table 4). The temporary emigration rates of being absent based on the previous period state of also being absent \((\gamma)\) were high and ranged from 0.03 to 0.75 with a peak in winter 2012, with a mean of 0.267 (SE = 0.140). The ‘return rate’ of temporary emigrants \((1 - \gamma)\) was lower between winter and spring and higher between summer and autumn (Table 4). Our model yielded an apparent survival estimate of 0.918 (SE = 0.058, 95% CI = 0.70−0.98) for adults and juveniles combined, or 0.950 (SE = 0.081, 95% CI = 0.40−0.99) for adults only.

### POPAN super-population models

The best fitting model incorporated constant apparent survival, time-varying capture probability and constant probability of entry (model 9; Table 3). This model carried 87% of the AICc weight. Model averaging was used to estimate the parameters. However, given that this dataset violated goodness of fit tests (Table A1 in the Appendix), only the ‘super-population’ estimate was considered here. This is because we wanted to estimate the total number of dolphins that used GBI from 2011−2013 regardless of their re-sighting pattern (i.e. occasional visitor, moderate user or frequent user). The super-population (i.e. total number of dolphins that visited GBI during the course of the study) was estimated at 171 dolphins (CI = 162−180) including the correction for unmarked animals.

### DISCUSSION

Considering all regions within the home range of a population is important when determining appropriate conservation management. We suggest GBI, a previously undescribed region for delphinids, is a potential hotspot for bottlenose dolphins of the New Zealand North Island population. We report a high level of individual site fidelity, large average group size and high year-round use of the area by groups that predominantly contain neonates and calves. An estimated total of 171 dolphins used this area during the study period. Even within the narrow scope of this focused study at GBI, it is apparent that many individuals spend extended periods of time outside of what has formerly been recognised as the core home range for this population (i.e. BOI/inner Hauraki Gulf). Additionally, it is clear that the GBI region is not simply being used as a corridor to reach other destinations but instead is a key site for at least a part of the North Island population.

Bottlenose dolphins were recorded at GBI during all months of the year, although the probability of encounter depended upon season and depth. A general seasonal onshore–offshore movement between shallow and deeper waters was found to correspond with the same trend identified in BOI, whereby dolphins were distributed in shallower waters during winter and deepest waters during summer (Constantine 2002). A definitive cause for this seasonal shift could not be determined in BOI due to a paucity of data on prey movements, and the same is true for GBI. This warrants further investigation as it may have implications for the general movement patterns of this population and subsequent management plans.

Until now, our understanding of group dynamics within the North Island population has been based on studies conducted solely in BOI. Median and maximum group sizes for BOI have been reported as 8−12 and 60, respectively (Constantine 2002, Tezanos-Pinto 2009). It was therefore surprising to report considerably larger group sizes at GBI (median = 35, maximum = 82). Group size for bottlenose dolphins worldwide is typically reported as 2 to 15 animals (Shane et al. 1986); however, groups of more than 15 individuals are not uncommon in New Zealand waters (Lusseau et al. 2003, Merriman et al. 2009). Although it is unclear why bot-

### Table 4. Temporary emigration rates for the best fitting model for bottlenose dolphins *Tursiops truncatus*, including return rates of temporary emigrants \((1 - \gamma)\).

<table>
<thead>
<tr>
<th>Season</th>
<th>Temporary emigration rates ((\gamma'))</th>
<th>Temporary emigration rates ((\gamma))</th>
<th>Return rate ((1 - \gamma))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn–Winter 2011</td>
<td>0.003 (0.0001)</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Winter–Spring 2011</td>
<td>0.009 (0.001)</td>
<td>NE</td>
<td>na</td>
</tr>
<tr>
<td>Spring–Summer 2011–12</td>
<td>0.019 (0.005)</td>
<td>0.655 (0.025)</td>
<td>0.345</td>
</tr>
<tr>
<td>Summer–Autumn 2011–12</td>
<td>0.000 (0.0008)</td>
<td>0.029 (0.004)</td>
<td>0.971</td>
</tr>
<tr>
<td>Autumn–Winter 2012</td>
<td>NE</td>
<td>0.112 (0.019)</td>
<td>0.888</td>
</tr>
<tr>
<td>Winter–Spring 2012</td>
<td>0.040 (0.014)</td>
<td>0.752 (0.052)</td>
<td>0.248</td>
</tr>
<tr>
<td>Spring–Summer 2012–13</td>
<td>0.000 (0.0001)</td>
<td>0.047 (0.008)</td>
<td>0.953</td>
</tr>
</tbody>
</table>
Bottlenose dolphins at GBI repeatedly form large groups, one possible explanation may be related to food availability. The south western coast of GBI, where all groups of more than 50 individuals were recorded, is associated with the Colville Channel. This area is characterised by the strongest currents in the Hauraki Gulf (Manigetti & Carter 1999). Strong upwellings occur at GBI and around the Colville Channel under southeasterly winds (Black et al. 2000) and thus the use of the area by large groups of dolphins may be attributed to a localised increase in biological productivity. Alternatively, GBI may act as a social hub where smaller groups fuse for socialising (S. L. Dwyer unpubl. data). Mann et al. (2000) found bottlenose dolphin group sizes were largest for groups with calves up to 3 mo old, which may also in part explain the formation of large groups at GBI given the high frequency of neonates and calves recorded.

Based on the variable patterns of site fidelity and habitat use observed in BOI (Constantine 2002, Tezanos-Pinto 2009, Hartel et al. 2014, Tezanos-Pinto et al. 2013), we anticipated new individuals would continue to be photo-identified for the duration of the study. The discovery curve reached a plateau after 17 mo of field effort, although a further 8 new individuals were added to the catalogue in the final summer season. We expect that a number of individuals that do not frequently use GBI waters have yet to be identified. Similarly, some dolphins may only visit the area rarely (i.e. transient dolphins), something that has also has been noted for BOI (Tezanos-Pinto et al. 2013).

Overall site fidelity \((\text{MSR} = 0.33)\) to the GBI region was high, although re-sighting patterns were variable among individuals. The large proportions of both frequent users and occasional visitors are similar to the variable patterns of residency reported for BOI (Constantine 2002, Tezanos-Pinto 2009). Based on records of GBI individuals outside the study area, it is clear that most bottlenose dolphins recorded at GBI cannot be classified as permanent residents, despite a large proportion of individuals spending considerable periods of time there. Dolphins from BOI are hypothesised to move to the Hauraki Gulf during winter, based on a seasonal low of individuals in BOI (Tezanos-Pinto 2009). However, given the relatively lower abundance and lower number of sighting records for GBI during winter, it seems unlikely that dolphins are congregating there when absent from BOI. Furthermore, peaks in bottlenose dolphin sightings have been reported for autumn in the inner Hauraki Gulf (Berghan et al. 2008). This corresponds with our records of high numbers of occasional visitors at GBI during autumn and the highest return rate for temporary emigrants between summer and autumn. While individuals using BOI are known to frequent GBI waters (Tezanos-Pinto 2011), it is currently unclear what proportion of the North Island population are using GBI waters and to what extent. Future studies should therefore investigate the seasonal movements of North Island bottlenose dolphins across the entire known range to try and discern these apparent trends.

The estimates of temporary emigration were highly variable and sometimes large. Such large fluctuations in abundance and temporary emigration rates indicate variable use of the area through time. Interestingly, our analyses suggested seasonal differences in abundance estimates. Despite the low precision of the summer estimates, our data suggest that abundance is lower during winter and spring. Specifically, abundance estimates varied from a low of 60 dolphins (95% CI = 53–67) during winter 2012 to a high of 131 (95% CI = 114–151) during autumn 2012 (excluding summer estimates). This is comparable to a recent study conducted on a coastal population of bottlenose dolphins in Bunbury, Western Australia, that also implemented the Robust Design (Smith et al. 2013); that population also exhibited a seasonal fluctuation in abundance with peak numbers detected in summer and autumn (139 dolphins in autumn 2009) and lower numbers during winter months (63 dolphins in winter 2007). In BOI, a seasonal fluctuation was also apparent with a lower number of dolphins during winter months (Tezanos-Pinto et al. 2013).

In our analysis, models incorporating Markovian temporary emigration were deemed better than both random temporary emigration and models with no temporary emigration. Temporary emigration rates varied between seasons for the best fitting Markovian model, with higher rates during time intervals when animals had been absent in the previous period \((\gamma')\) than the rates for those present in the previous period \((\gamma)\). This implies that some individuals leave the study area for multiple seasons but subsequently return. Temporary emigration rates estimated in Bunbury \((\gamma' = 0.34–0.97)\) (Smith et al. 2013) were similar to those estimated in this study \((\gamma' = 0.03–0.75)\) and also varied seasonally. The apparent survival estimated here for adults and juveniles combined \((0.918, SE = 0.058)\) is marginally lower than the estimate for adults only \((0.950, SE = 0.081)\). This is consistent with studies conducted in other areas that reported lower survival rates for juveniles (Stolen &
Barlow 2003). Additionally, a recently reported mortality event at GBI involved a fatal boat strike to a juvenile bottlenose dolphin (Dwyer et al. 2014). Adult survival estimates for GBI are slightly higher than those reported for BOI (0.928, SE = 0.008) for 1997–2006 (Tezanos-Pinto et al. 2013) but similar to Bunbury (0.95, SE = 0.02) for 2007–2009 (Smith et al. 2013).

In Bunbury, seasonal fluctuations in abundance were explained by an influx of adult males into the study area during the breeding season (summer/autumn) and their subsequent departure during the non-breeding months (Smith et al. 2013). Breeding is also seasonal in BOI (Constantine 2002, Tezanos-Pinto 2009) so it is possible that a similar situation occurs in GBI waters, where the sex of most dolphins is currently largely unknown, especially males and non-reproductive females.

We believe the importance of the GBI region has likely been overlooked at least partly as a consequence of the user-pays research system. Since core long-term research on the North Island population has primarily focused only on areas where bottlenose dolphins are subject to tourism activities, it remains unclear how long and to what extent GBI and potentially other regions of unstudied coastline have been important for this population. We therefore strongly recommend that other poorly studied areas within the home range be examined so their relative importance in the context of the North Island population can be assessed. We also recommend further studies to estimate abundance, in addition to reproductive and demographic parameters, across the entire range of the North Island population. This is particularly relevant following the decline in local abundance of bottlenose dolphins in BOI, where it is unclear whether the decline is due to mortality, low recruitment, emigration or a combination of these (Tezanos-Pinto et al. 2013).

From a management perspective, we suggest commercial tourism should not be allowed to target marine mammals in the GBI region until further research has been conducted into the relative importance of the area for the North Island population. GBI also offers a unique opportunity as a control site to compare against other regions of the home range that are heavily exposed to tourism.

**CONCLUSION**

For management to be effective, a comprehensive approach including the entire home range of a population is required, especially when considering wide-ranging species such as marine mammals. This is arguably constrained if the majority of field-based research is funded via user-pays systems. We therefore highlight the need for researchers, managers and funding agencies to maintain an open outlook on the population of interest as a whole when conducting or funding research.

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Appendix

Table A1. Results of goodness of fit test conducted in U-CARE 2.02 for the seasonal dataset in a Cormack-Jolly-Seber framework for bottlenose dolphins *Tursiops truncatus* at Great Barrier Island, New Zealand

<table>
<thead>
<tr>
<th></th>
<th>TEST 2.CT</th>
<th>TEST 2.CL</th>
<th>TEST 3.SM</th>
<th>TEST 3.SR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seasonal dataset:</td>
<td>$\chi^2 = 41.2$</td>
<td>$\chi^2 = 14.01$</td>
<td>$\chi^2 = 51.3$</td>
<td>$\chi^2 = 35.1$</td>
</tr>
<tr>
<td></td>
<td>$p &lt; 0.0005$</td>
<td>$p = 0.02$</td>
<td>$p &lt; 0.005$</td>
<td>$p &lt; 0.0005$</td>
</tr>
<tr>
<td>Stat = −5.4</td>
<td></td>
<td></td>
<td></td>
<td>Stat = 4.3</td>
</tr>
<tr>
<td></td>
<td>$p &lt; 0.0005$</td>
<td></td>
<td></td>
<td>$p &lt; 0.0005$</td>
</tr>
<tr>
<td>Sum of tests:</td>
<td>$\chi^2 = 141.8$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p &lt; 0.005$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>