



# Demographic characteristics of Australian humpback dolphins reveal important habitat toward the southwestern limit of their range

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**ABSTRACT:** The paucity of information on the recently described Australian humpback dolphin *Sousa sahulensis* has hindered assessment of its conservation status. Here, we applied capture-recapture models to photo-identification data collected during boat-based surveys between 2013 and 2015 to estimate the abundance, site fidelity and residence patterns of Australian humpback dolphins around the North West Cape (NWC), Western Australia. Using Pollock's closed robust design, abundance estimates varied from 65 to 102 individuals, and POPAN open modelling yielded a super-population size of 129 individuals in the 130 km<sup>2</sup> study area. At approximately 1 humpback dolphin per km<sup>2</sup>, this density is the highest recorded for this species. Temporary emigration was Markovian, suggesting seasonal movement in and out of the study area. Hierarchical clustering showed that 63 % of individuals identified exhibited high levels of site fidelity. Analysis of lagged identification rates indicated dolphins use the study area regularly, following a movement model characterised by emigration and re-immigration. These density, site fidelity and residence patterns indicate that the NWC is an important habitat toward the southwestern limit of this species' range. Much of the NWC study area lies within a Marine Protected Area, offering a regulatory framework on which to base the management of human activities with the potential to impact this threatened species. Our methods provide a methodological framework to be used in future environmental impact assessments, and our findings represent a baseline from which to develop long-term studies to gain a more complete understanding of Australian humpback dolphin population dynamics.

**KEY WORDS:** *Sousa sahulensis* · Abundance · Survival · Emigration · Capture-recapture · Site fidelity · Residency

## INTRODUCTION

Understanding the dynamics of wildlife populations, particularly those exposed to disturbance from anthropogenic activities, is fundamental to successful conservation and management. Quantifying these

dynamics can present particular challenges for taxa that are cryptic or otherwise difficult to study and whose populations overlap with human activities. Coastal cetaceans embody this challenge; they are long-lived, slow to reproduce, highly mobile and occupy ecosystems subject to changes as a result of

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human activities (Lotze et al. 2006, Halpern et al. 2008). As a result, many coastal cetacean populations are exposed to multiple stressors associated with anthropogenic activities (Davidson et al. 2012, Parsons et al. 2015), with some species facing extinction (see e.g. Dawson et al. 2001, Jaramillo-Legorreta et al. 2007, Mei et al. 2014).

The ability to implement appropriate conservation and management actions to better protect coastal cetaceans is often limited by the lack of information on local population dynamics and the extent of any threats (e.g. Parra et al. 2006a, Brown et al. 2016). Two of the 3 species of tropical inshore dolphins inhabiting the northern Australian coastline, the Australian snubfin dolphin *Orcaella heinsohni* and the Australian humpback dolphin *Sousa sahalensis* are endemic to the region, and coastal development has been identified as a major threat to the species' persistence (DE-WHA 2010, Parra & Cagnazzi 2016). The Australian humpback dolphin (hereafter 'humpback dolphin') inhabits the tropical/subtropical waters of the Sahul Shelf across northern Australia and southern Papua New Guinea (Jefferson & Rosenbaum 2014). In Australia, they occur mainly in shallow (<30 m), inshore waters from the Queensland–New South Wales border to Shark Bay in Western Australia (WA) (Parra & Cagnazzi 2016). Comprehensive studies on their ecology have been carried out in selected areas of eastern Queensland; however, information is still scarce for most populations in the Northern Territory and WA (see reviews in Hanf et al. 2016, Parra & Cagnazzi 2016). These studies have shown that humpback dolphins typically occur in small populations of approximately 50 to 150 individuals (Parra et al. 2006a, Cagnazzi et al. 2011, Palmer et al. 2014), exhibit high site fidelity and relatively small home ranges (<300 km<sup>2</sup>; Parra 2006, Parra et al. 2006a, Cagnazzi et al. 2011), and relatively fine-scale population structure (Cagnazzi et al. 2011, Brown et al. 2014). The ecological characteristics of humpback dolphin populations render them sensitive to the cumulative impacts associated with human activities (Parra et al. 2006b, Cagnazzi et al. 2013). Their conservation status was recently assessed as Vulnerable using the International Union for Conservation of Nature (IUCN) Red List criteria (Parra & Cagnazzi 2016). However, this assessment has not yet been officially approved by the IUCN, and *S. sahalensis* is currently listed under Near Threatened as *S. chinensis*-type (Reeves et al. 2008). Under Australia's national environmental law, the Environment Protection and Biodiversity Conservation Act 1999, sufficient data is unavailable to allow assessment against the criteria for listing as a threat-

ened species (i.e. Vulnerable, Endangered or Critically Endangered) under that legislation.

In WA waters, less than 1% of the distribution of humpback dolphins has been surveyed adequately enough to assess their abundance (Hanf et al. 2016). A lack of information on their ecology and population status has hindered adequate environmental impact assessments along WA's changing coastline (Allen et al. 2012, Bejder et al. 2012). Results of a 2010 pilot study around the North West Cape (NWC) suggested that the region might represent an important area for the species (Brown et al. 2012). The NWC is part of one of Australia's fastest growing regions, the Pilbara (Fig. 1; WAPC 2012), with major construction and exploration activities associated with oil, gas and mineral extraction industries still occurring or planned for this region (Hanf et al. 2016), despite a recent downturn in this sector. Although much of the NWC is part of Ningaloo Marine Park (NMP), a World Heritage listed Marine Protected Area (MPA), current and projected coastal developments in the adjacent (non-protected) Pilbara region equate to potential cumulative pressures on humpback dolphins likely increasing in the future. Given the preliminary evidence of a sizeable dolphin population, accessibility and prospects of major developments in the locality, the NWC was considered by the Australian Government Department of Environment as one of the key priority areas in northern Australia for conducting research into the ecology of data deficient humpback dolphins (DoE 2015).

In this study, we present the results of the first comprehensive population assessment of humpback dolphins around the NWC and, indeed, the first in the Pilbara region. We used boat-based surveys and photo-identification techniques to collect sighting histories of naturally marked individuals to estimate abundance, apparent survival, temporary emigration, site fidelity and residence patterns of humpback dolphins. We discuss the implications of our findings for humpback dolphin conservation in the region and suggest areas for further research on this data-poor, threatened species. This research contributes towards a more complete understanding of humpback dolphin population dynamics as a basis for future management of this species in Australian waters.

## MATERIALS AND METHODS

### Study site

The NWC study site encompasses the northern part of Ningaloo Reef, Australia's largest fringing

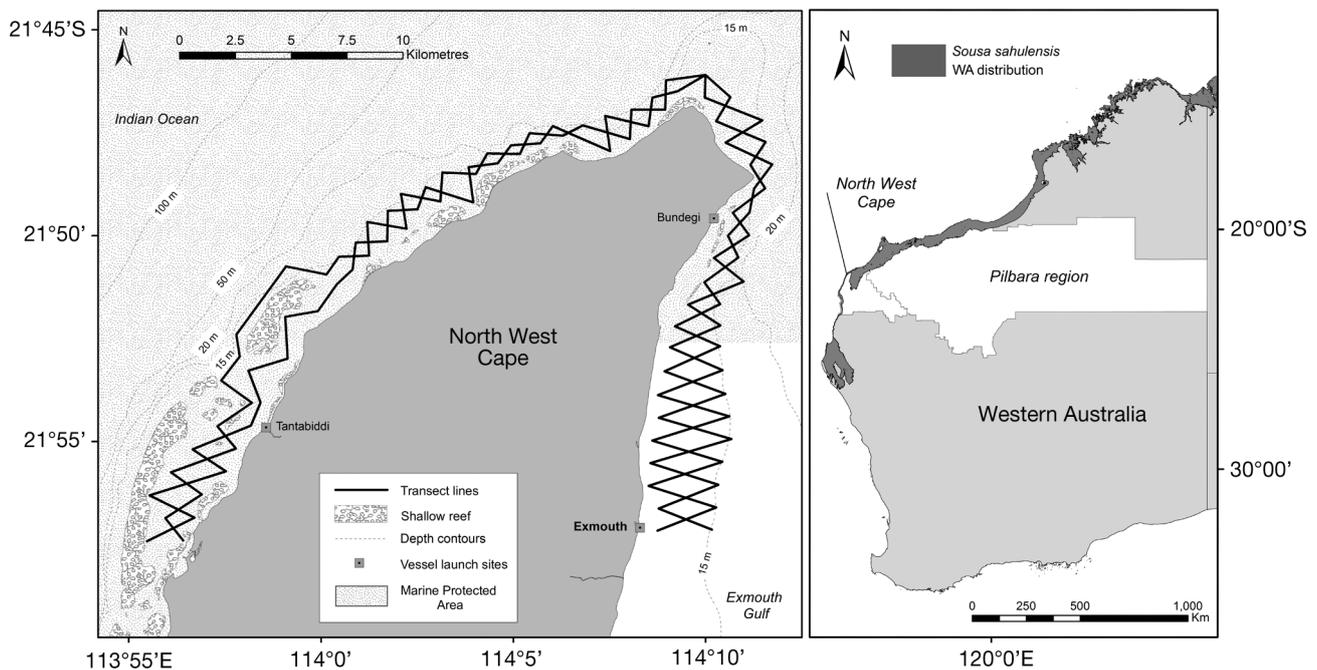


Fig. 1. Left: North West Cape (NWC) study site, including vessel launch sites (Tantabiddi, Bundegi, and Exmouth) and opposing zigzag line transect sampling design ( $2 \times 93$  km in length). Right: Western Australia, indicating the location of the NWC, Pilbara region, and Australian humpback dolphin distribution

coral reef (CALM & MPRA 2005) (Fig. 1). The western and northern side of the NWC adjoin the Indian Ocean and NMP, the latter region is characterized by shallow (<10 m depth) lagoon waters, with primarily sandy substrate and coral communities within the fringing (sub-tidal) coral reef system (CALM & MPRA 2005, Cassata & Collins 2008). Water depth drops sharply outside the reef towards the continental shelf (Fig. 1), and the reef is exposed to considerable wave and swell energy (>2 m) (CALM & MPRA 2005, Cassata & Collins 2008). The eastern side of the NWC faces Exmouth Gulf, an area dominated by sub-tidal limestone and coral reef/sandy-bottomed habitat, exposed to low wave energy, that slopes to 20 m depth less than 5 km from the shoreline (Fig. 1; Bancroft & Sheridan 2000, Kobryn et al. 2013). Approximately two-thirds of the study area is within the MPA of NMP (Fig. 1).

### Data collection

Boat-based surveys for humpback dolphins were conducted across the study area during May to October 2013, April to October 2014 and May to October 2015. Surveys were conducted following a systematic line transect sampling design ( $2 \times 93$  km in length, following opposing, evenly-spaced zigzag

lines; Fig. 1). The 2 pre-determined transect routes covered an area of  $\sim 130$  km<sup>2</sup> and included waters between 1 and 20 m deep.

Surveys were conducted on board a 5.6 m research vessel powered by a 100 HP outboard motor at speeds of 10 to 12 km h<sup>-1</sup> and only in good sighting conditions (Beaufort Sea State  $\leq 3$  and no rain). Survey effort was continuous from 07:00 to 18:00 h, depending on suitable conditions. A crew of 3 to 5 (mode = 4) observers systematically searched for dolphins forward of the vessel's beam with the naked eye and 7  $\times$  50 binoculars. Once a school of dolphins was sighted, on-transect effort was suspended and dolphins were approached slowly (<5 knots) to within 10 to 30 m to record GPS location, species identification, school size, school age composition (calf, juvenile, adult), predominant school behaviour (as per Mann 1999) and to collect photo-identification data. Schools were defined as dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) involved in similar (often the same) behavioural activities (modified from Connor et al. 1998). Age class categories used in school composition were those defined by Parra et al. (2006a). Photographs of individual animals were taken using Nikon digital SLR cameras (D600 and D70S) fitted with Nikkor telephoto zoom lenses (80 to 400 mm and 70 to 300 mm). After all or most individ-

uals in the school were photographed, or we lost sight of the dolphins, transect effort resumed from the location on the transect line where the dolphins were first sighted.

### Photo-identification

Individual humpback dolphins were identified based on the unique natural marks on their dorsal fins (Würsig & Jefferson 1990). All photographs taken were examined and subject to a strict quality (Q) and distinctiveness (D) grading protocol (modified from Urian et al. 1999, 2015) to minimise misidentification. Only high quality photographs of distinctive individuals were used in analyses. For full details of the photo-identification protocol used in this study see Supplement 1 at [www.int-res.com/articles/suppl/n032p071\\_supp.pdf](http://www.int-res.com/articles/suppl/n032p071_supp.pdf).

### Estimating abundance, survival and temporary emigration

Capture-recapture records of distinctive individuals were used to estimate abundance, apparent survival and temporary emigration under Pollock's closed robust design (PCRD) (Pollock 1982, Kendall & Nichols 1995, Kendall et al. 1995, Kendall 1997) implemented in program MARK v6.1 (White & Burnham 1999). Under PCRD, photographic 'captures' occur within a hierarchical sampling design, including: (1) primary periods (P-periods) between which the population is considered open to gains and losses, and (2) several secondary periods (s-periods) per P-period, in which the population is assumed closed to

demographic change. Closed population models can be used to estimate capture probabilities and abundance within each P-period, while the open-population portion allows the accommodation of temporary emigration and apparent survival between P-periods (Pollock et al. 1990, Kendall 1997). The PCRD for this study consisted of a total of six ~3-month P-periods (37s-periods), separated by a minimum of 21 d (Table 1). s-periods were defined as the time required to complete a single replicate of the 93 km transect (Fig. 1) within a P-period, which ranged from a minimum of 3 d to a maximum of 31 d (median = 11).

In this study, inference about population abundance ( $\hat{N}$ ), and demographic processes were based on a multi-model-inference capture-recapture paradigm (Burnham & Anderson 2002). Specifically, we averaged parameter estimates based on posterior model probabilities, as approximated by weights of Akaike's Information Criterion with the small sample-size correction (AICc) (Link & Barker 2006). Model averaging is advantageous because a PCRD analysis typically involves considerable model uncertainty in the form of many plausible parameterisations of survival ( $\phi$ ), capture probability ( $p$ ), recapture probability ( $c$ ), probability of becoming a temporary migrant ( $\gamma''$ ), and the probability of remaining a temporary migrant ( $\gamma'$ ). Many of the more complex PCRD models are desirable in order to incorporate ecologically realistic process variation, such as time-varying survival  $\phi(t)$  versus time-invariant survival  $\phi(\bullet)$ . Unfortunately, such complex models are data-demanding and often yield unreliable estimates (especially singularities and boundary-value estimates; Rankin et al. 2016). Part of the post-modelling exercise was to find a candidate set of models with reliable maxi-

Table 1. Survey effort, number of schools of Australian humpback dolphins sighted and number of individual marked animals identified per primary sampling period (P) around the North West Cape in Western Australia during the 2013 (May to October), 2014 (April to October) and 2015 (May to October) survey periods. Dates are shown as (dd/mm/yyyy). Values for total effort are approximate to the nearest kilometre

Primary period (P)	Time period	Length (d)	Total effort (km)	Survey effort (h)	No. of secondary sampling periods	Average ( $\pm$ SD) length of secondary sampling periods (d)	Schools sighted	Individual animals identified
P1	28/05/2013–05/08/2013	22	374	37.6	4	15.75 $\pm$ 10.37	21	34
P2	26/08/2013–21/10/2013	35	465	44.3	5	18.40 $\pm$ 3.9	20	38
P3	09/04/2014–06/07/2014	38	747	70.4	8	9.88 $\pm$ 4.49	34	52
P4	31/07/2014–07/10/2014	39	746	69.9	8	8.13 $\pm$ 3.48	30	47
P5	03/05/2015–05/07/2015	28	466	42.6	5	8.80 $\pm$ 2.39	16	43
P6	29/07/2015–26/10/2015	33	652	65.5	7	12.14 $\pm$ 3.67	24	39
Total		195	3450	330.3	37	11.57 $\pm$ 5.71	145	98

$$\begin{array}{cccc}
 \text{Survival}^a & \text{Temporary migration}^b & \text{Capture \& recapture} & \text{Capture} \\
 & & \text{probabilities}^f & \text{heterogeneity}^h \\
 \left\{ \begin{array}{l} \phi(\bullet) \\ \phi(t) \end{array} \right\} & \times \left\{ \begin{array}{l} \gamma''(\bullet) = \gamma'(\bullet)^c \\ \gamma''(\text{season}) = \gamma'(\text{season})^c \\ \gamma''(t) = \gamma'(t)^c \\ \left( \begin{array}{l} \gamma''(\bullet) \\ \gamma''(\text{season}) \\ \gamma''(t) \end{array} \right) \times \left( \begin{array}{l} \gamma'(\bullet) \\ \gamma'(\text{season}) \\ \gamma'(t) \end{array} \right)^d \\ \gamma'' = \gamma' = 0^e \end{array} \right\} & \times \left\{ \begin{array}{l} \rho(\bullet, \bullet) = c(\bullet, \bullet) \\ \rho(t, \bullet) = c(t, \bullet) \\ \rho(t, s) = c(t, s) \\ \left( \begin{array}{l} \rho(\bullet, \bullet) \\ \rho(t, \bullet) \\ \rho(t, s) \end{array} \right) \times \left( \begin{array}{l} c(\bullet, \bullet) \\ c(t, \bullet) \end{array} \right) \\ \left( \begin{array}{l} \rho(\bullet, \bullet) \\ \rho(t, \bullet) \end{array} \right) \times c(t, s) \\ \text{logit}(\rho) = \text{logit}(c(t, s)) + z^g \end{array} \right\} & \times \left\{ \begin{array}{l} \pi = 1 \\ \pi(\bullet) \\ \pi(t) \end{array} \right\}
 \end{array}$$

<sup>a</sup>  $\phi$  apparent survival between primary periods

<sup>b</sup>  $\gamma''$  probability of leaving study area between primary periods;  $\gamma'$  probability of staying outside study area

<sup>c</sup> Random temporary emigration  $\gamma'' = \gamma'$

<sup>d</sup> Markovian temporary emigration  $\gamma'' \neq \gamma'$

<sup>e</sup> No temporary emigration  $\gamma = 0$

<sup>f</sup>  $p$  initial capture probability;  $c$  recapture probability

<sup>g</sup>  $z$  "additive offset" modelling recapture probability as a function of capture probability

<sup>h</sup>  $\pi$  two-point finite mixture parameter, allowing heterogeneity in  $p$  and  $c$ ;  $\pi = 1$  enforces no heterogeneity

Fig. 2. Idealised full set of Pollock's closed robust design (PCRD) models considered for multi-model inference of demographic characteristics of Australian humpback dolphins around the North West Cape, Western Australia. The models are represented as different combinations of parameter specifications, accounting for temporal variation, behavioural responses, and variation among individuals. The notation ' $\bullet$ ' indicates that a given parameter was kept constant, ' $t$ ' indicates that a given parameter was allowed to vary with primary period, ' $season$ ' indicates a temporary migration parameter was allowed to vary by austral seasons 'Autumn-Winter' (April to July) and 'Winter-Spring' (August to October), and ' $s$ ' indicates that capture ( $p$ ) and/or recapture ( $c$ ) probability was allowed to vary by secondary period within primary periods. Parameterisations in grey consistently resulted in singularities and boundary-value estimates for  $p$  and  $c$ , and were discarded from the model-averaging exercise

mum-likelihood estimates (MLEs), and then use this set for AICc-based averaging. Candidate models were screened based on parameter counts, singularities and boundary-value estimates before averaging, so that unreliable parameter estimates were not included. The PCRD models considered for multi-model inference of humpback dolphin abundance, apparent survival and temporary emigration, while taking into account different combinations of parameter specifications, are summarised in Fig. 2.

Given that mortality and permanent emigration are confounded (Pledger et al. 2003), we estimated apparent survival ( $\phi$ ) (Lebreton et al. 1992), and considered time-varying and time-invariant alternatives (Fig. 2). The intervals between P-periods were specified in decimal years between their mid-dates to obtain consistent per annum estimates of apparent survival (as per Tezanos Pinto et al. 2013, Palmer et al. 2014).

For temporary emigration, we considered: constant migration probabilities  $\gamma(\bullet)$ , probabilities varying by P-periods  $\gamma(t)$ , and probabilities varying by austral seasons 'Autumn-Winter' (April to July; P-periods P1, P3 & P5) and 'Winter-Spring' (August to October; P2, P4, & P6), or  $\gamma(season)$  (Fig. 2). Note that P1 is not

considered in PCRD temporary emigration (or apparent survival) parameter estimates since it is the first sampling occasion with no previous sampling occasion from which to derive an estimate. P1 is considered in abundance estimation. For each of these specifications, we also considered: random movement ( $\gamma'' = \gamma'$ ), when the probability that an animal temporarily emigrates is independent of its state during the previous occasion, and Markovian movement ( $\gamma'' \neq \gamma'$ ), when the probability that an animal temporarily emigrates is dependent on its state during the previous occasion (Kendall et al. 1997). Finally, we also considered a no movement model ( $\gamma'' = \gamma' = 0$ ).

For the capture ( $p$ ) and recapture ( $c$ ) probabilities, we considered a large variety of specifications (Fig. 2) given the large influence that such decisions have on abundance estimates (Carothers 1973, Burnham & Overton 1978, Rankin et al. 2016). In particular, the agglomerative hierarchical clustering analysis suggests there may be heterogeneity in migration and resighting patterns, which motivates the *a priori* consideration of individual heterogeneity models. Unfortunately, the data did not support complex models with independent capture and recapture proba-

bilities ( $p \neq c$ ), or individual heterogeneity in capture probabilities using 2-point finite mixture models (Pledger 2000). Models with equality in capture probabilities ( $p = c$ ) were supported (Fig. 2).

We used AICc to rank models (Burnham & Anderson 2002). To account for model selection uncertainty (Buckland et al. 1997), weighted model averaging was applied across all suitable models (i.e. models with cumulative AICc weight >99.9%) to produce model-averaged estimates of population parameters. All model outputs generated used the full parameterisation of maximum likelihood available in MARK.

### Estimating super-population size

To determine the total number of animals that theoretically used the study area during the course of the study we used the Schwarz & Arnason (1996) 'super-population' parameterisation of the Jolly-Seber model (i.e. POPAN) as implemented in MARK. Beside the estimation of a super-population parameter, POPAN models also provide estimates of apparent survival, capture probabilities per sampling period, and the probability of entry of animals from the super-population into the sampled population between sampling periods (Arnason & Schwarz 1995). For POPAN models, each s-period within a P-period was pooled to form a single capture event, for a total of 6 sampling periods. Per annum estimates of apparent survival were derived (as per PCRDR models). A total of 6 POPAN models were examined to allow for fixed ( $\bullet$ ) or time-varying ( $t$ ) effects on apparent survival rates ( $\phi$ ), capture probabilities ( $p$ ), and entry probabilities ( $pent$ ) of humpback dolphins in the study area throughout the survey period. As for the PCRDR models, we applied weighted model averaging by AICc across suitable models to produce model-averaged estimates of population parameters.

### Proportion of marked individuals in the population

Abundance estimates from capture-recapture models were adjusted to take into account the proportion of marked (i.e. distinct) individuals in the study population (Williams et al. 2002). The proportion of marked individuals in the population ( $\hat{\theta}$ ) was estimated using a school sightings-based method (modified from Nicholson et al. 2012). Marked proportion, total population size, associated standard errors and log-normal 95% confidence intervals were calculated using formulas in Supplement 2.

### Goodness-of-fit tests and validation of model assumptions

There is no formal goodness-of-fit (GOF) test for PCRDR. By collapsing the s-periods we determined the GOF across the 6 primary sampling periods using program RELEASE in MARK (Lebreton et al. 1992) and the software U-CARE V2.3.2 (Choquet et al. 2009). We estimated the variance inflation factor  $\hat{c}$  (a measure to quantify over-dispersion) by using the chi-square statistic divided by its degrees of freedom.

PCRDR and POPAN models have a number of assumptions; the violation of which can lead to bias in population estimates (Pollock 1982, Pollock et al. 1990, Williams et al. 2002). We used information on the biology of humpback dolphins and specific tests to validate assumptions of PCRDR and POPAN analyses (Supplement 3).

### Site fidelity

We investigated the tendency of humpback dolphins to return to the study site by calculating the following descriptive statistics of resighting rates: (1) monthly sighting rate: the number of months a given dolphin was identified as a proportion of the total number of months of survey effort, (2) P-sighting rate: the number of P-periods in which a given dolphin was identified as a proportion of the total number of P-periods, and (3) yearly sighting rate: the number of calendar years when a given dolphin was identified as a proportion of the total years surveyed. Monthly sighting rates could range between 0.05 (i.e. animals sighted in only 1 month out of 19 surveyed) and 1 for an individual sighted in all months. Similarly, P-sighting rates could range between 0.17 and 1, and yearly sighting rates could be 0.33, 0.66 or 1 (i.e. sighted in 1, 2 or all 3 years of study). Additionally, site fidelity indices were calculated as the ratio between the number of recaptures for each individual and the number of s-periods from an individual's first capture to its last capture (modified from Simpfendorfer et al. 2011, Bond et al. 2012). A site fidelity index value of 1 indicates an individual was captured in all sampling periods from its first capture to its last capture. Conversely, a value of zero indicates an animal was only sighted once during the sampling period.

To assess if distinctive clusters of individuals with similar degrees of site fidelity could be identified based on monthly and yearly sighting rates, and site fidelity indices, we used agglomerative hierarchical clustering (AHC; Legendre & Legendre 2012) to

construct a dendrogram using Euclidean distance as our dissimilarity measure and Ward's method (minimum variance) as our clustering algorithm due to its robustness (Ward 1963, Cao et al. 1997, Singh et al. 2011, Murtagh & Legendre 2014). Approximately unbiased (AU)  $p$ -values were generated for each cluster using a multiscale bootstrap resampling technique (1000 bootstrap replications per cluster; Suzuki & Shimodaira 2006). High AU  $p$ -values indicate high confidence in the clusters and were used to specify a cut-off point along the dendrogram (a dissimilarity threshold) to represent the most appropriate number of clusters (as per Singh et al. 2011). To test the overall efficiency of the clustering we calculated the cophenetic correlation coefficient (CPCC). This is a measure of how faithfully clusters in the dendrogram represent the dissimilarities among observations (Sokal & Rohlf 1962), with a CPCC-value  $>0.8$  indicating a reliable representation of the data (Bridge 1993). AHC analysis was performed in Excel add-in software 'statistXL' v1.11 (Roberts & Withers 2009) and in R (R Core Team 2015) using the 'pvclust' package (Suzuki & Shimodaira 2009).

Finally, to explore long-term site fidelity, we cross-checked the 54 distinctive individuals identified around the NWC during the 2010 pilot study (Brown et al. 2012) with our photo-identification catalogue from this study (as per protocol described above).

### Residency

To estimate residency patterns, we calculated lagged identification rates (LIR), i.e. the probability that, if an individual was identified in the study area at any time, it was identified during any single identification made in the area some time lag later (Whitehead 2001). We compared observed LIR rates to expected LIR from exponential mathematical models of no movement, emigration/mortality, emigration + re-immigration, and emigration + re-immigration + mortality (Whitehead 2001, 2009). To consider movements within yearly survey periods, (and hence exclude the ~6 month time period between these yearly survey periods) a maximum time lag (Whitehead 2009) was set at 177 d. This period was the longest possible time between the first capture and last capture of an individual in any yearly survey period. Applying this restriction allowed the models to consider overall residency patterns across the 3 years surveyed while removing consideration of movement patterns between yearly survey periods. LIR models were set to 1000 bootstrap replications, and start parameters

were explored against default values for each model to check the fit and test suitability of model parameter outputs (Whitehead 2009). Model selection was based on the Quasi-Akaike Information Criterion (QAIC) value, with the most supported model having the lowest QAIC value. Computation of LIR and model fitting was carried out using the computer software SOCPROG 2.6 (Whitehead 2009).

## RESULTS

### Survey effort, photo-identification and proportion of marked individuals

A total of 330 h of survey effort (~3450 km) was completed across our 6 P-periods and 37 s-periods (Table 1). A majority (79%) of the survey effort across the study period occurred in Beaufort Sea State (BSS) 2 (153 h) and 3 (108 h), and to a lesser extent in BSS 1 (65 h, 20%) and BSS 0 (4 h, 1%). Similarly, the majority (66 to 87%) of survey effort within each P-period occurred in BSS 2 and 3. Differences in BSS are likely to cause differences in capture probability, which, if unaccounted for, would increase the error in abundance estimates. We accommodate such differences, to a certain extent, in the  $p(t,s)$  models.

Our surveys resulted in a total of 145 sightings of humpback dolphin schools with an encounter rate of 0.04 schools, or 0.17 individuals (including calves) per km of transect surveyed. Schools varied in size from 1 to 19 animals, with a mean school size ( $\pm$  SD) of  $4.6 \pm 3.2$ . A total of 98 marked individuals (86 adults and 12 juveniles) were identified, of which 26 (27%) were sighted once and 49 (50%) were sighted 4 or more times (mean  $\pm$  SD  $4.1 \pm 3.0$ , range 1 to 15). The cumulative number of marked individuals identified (Fig. 3) over the study period showed a steady increase, indicating that not all individuals using the study area had been identified.

### Estimates of abundance, survival and temporary emigration

In this section, we detail the model-selection and model-averaging techniques used to estimate abundance, survival and temporary emigration by capture-recapture. The models considered are detailed in Fig. 2. Some ecologically desirable specifications were excluded (finite mixture models and  $p \neq c$  models) because of severe symptoms of over-parameterisation, including MLEs at boundary values ( $\hat{p} = 0$ , or

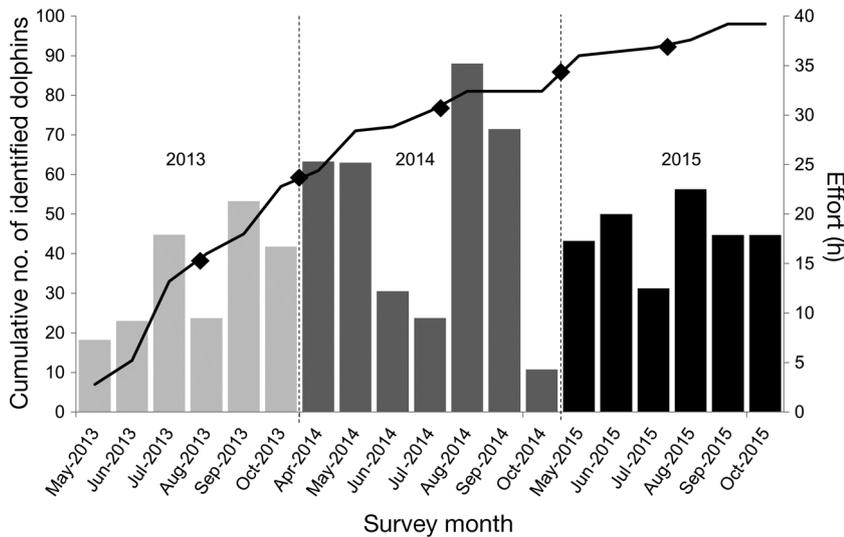


Fig. 3. Cumulative discovery curve of identified Australian humpback dolphins ( $n = 98$ ) within the North West Cape study area over the 2013 (May to October), 2014 (April to October) and 2015 (May to October) survey periods (total 195 d). Vertical bars represent the number of survey effort hours during each month of study. Diamond symbols indicate separation of the 6 primary periods throughout the entire survey period. Vertical dotted lines indicate separation of yearly survey periods

Table 2. Summary of most supported Pollock's closed robust design (PCRD) models fitted to the capture histories of Australian humpback dolphins to estimate population size ( $N$ ), apparent survival rate ( $\hat{\phi}$ ), emigration ( $\gamma''$ ,  $\gamma'$ ) and capture probability ( $p$ ). The top 10 models shown account for >96% cumulative AICc weight. The notation ' $\bullet$ ' indicates that a given parameter was kept constant, ' $t$ ' indicates that a given parameter was allowed to vary with time, and ' $season$ ' indicates that emigration parameters were allowed to vary by seasons Autumn–Winter (Primary sampling periods P1, P3 and P5) and Winter–Spring (P2, P4 and P6). Capture probability was allowed to vary with time among and within primary sampling periods ( $t,s$ ). Recapture probability ( $c$ ) was set equal to  $p$  and therefore is not included in the model description. The top 3 ranked models are shown in **bold**. For details of the full 22 (reduced) PCRD model set see Table S2 in Supplement 4

Model	Rank	$\Delta AICc$	AICc weight	Cumulative AICc weight (%)	No. of parameters
<b><math>\phi(\cdot) \gamma''(season) \neq \gamma'(\bullet) p(t,s)</math></b>	<b>1</b>	<b>0.0</b>	<b>0.33</b>	<b>33.1</b>	<b>47</b>
<b><math>\phi(\cdot) \gamma''(season) \neq \gamma'(season) p(t,s)</math></b>	<b>2</b>	<b>0.1</b>	<b>0.32</b>	<b>64.9</b>	<b>48</b>
<b><math>\phi(\cdot) \gamma''(season) = \gamma'(season) p(t,s)</math></b>	<b>3</b>	<b>1.5</b>	<b>0.15</b>	<b>80.3</b>	<b>46</b>
$\phi(t) \gamma''(season) = \gamma'(season) p(t,s)$	4	4.0	0.05	84.9	50
$\phi(\cdot) \gamma''(t) \neq \gamma'(\bullet) p(t,s)$	5	4.6	0.03	88.2	50
$\phi(t) \gamma''(\bullet) = \gamma'(\bullet) p(t,s)$	6	4.7	0.03	91.4	49
$\phi(\cdot) \gamma''(\bullet) \neq \gamma'(\bullet) p(t,s)$	7	6.0	0.02	93.1	46
$\phi(t) \gamma''(season) \neq \gamma'(\bullet) p(t,s)$	8	6.5	0.01	94.3	51
$\phi(t) \gamma''0 = \gamma'0 p(t,s)$	9	6.6	0.01	95.5	48
$\phi(t) \gamma''(\bullet) \neq \gamma'(\bullet) p(t,s)$	10	7.2	0.01	96.5	50

$\hat{p} = 1$ , or  $\hat{N}_t = M_t$  where  $M_t$  = no. of captured individual dolphins per P-period). Among the models used for estimation, some estimates of apparent survival and temporary emigration were likewise at boundary values (e.g.  $\hat{\phi} = 1$  or  $\hat{\gamma}'' = 0$ ). These results indicate data sparseness and over-parameterisation, and are common among temporary-emigration models (see Discussion). The full reduced set of 22 PCRD models is shown in Table S2 in Supplement 4.

The PCRD model most supported by AICc included Markovian temporary emigration, where  $\gamma''$  varied by season, and  $\gamma'$  and apparent survival were constant (Table 2). The next 2 models with high support (AICc weight = 0.47) were: (1) Markovian temporary emigration, whereby the only difference from the top model was that  $\gamma'$  varied by season, and (2) random emigration, where apparent survival was constant throughout the survey period, and both  $\gamma''$  and  $\gamma'$  varied by season (Table 2). All 22 PCRD models were averaged by AICc weights to obtain estimates of abundance and apparent survival (Table 3), temporary emigration parameters (Table 4), and capture probability (Table S3 in Supplement 4). The proportion of distinctively marked individuals within the study population ( $\hat{\theta}$ ) was estimated at 0.83 and estimates of abundance were adjusted accordingly. Original parameter estimates from the top 3 PCRD models are given in Tables S4–S6 in Supplement 4.

Model-averaged capture probabilities were variable across the survey period (per s-period), ranging from 0.01 to 0.40, with a mean value of 0.17 (95% CI 0.00 to 0.55; Table S3). Effective detection probability per P-period ranged from 0.50 to 0.86, with a mean value of 0.67 (Table S3). Model-averaged estimates of the total number of humpback dolphins using the study area ranged from 65 to 102 with comparatively higher

Table 3. Model-averaged estimates of abundance ( $N$ ) and apparent survival ( $\phi$ ) of Australian humpback dolphins for 22 Pollock's closed robust design (PCRD) models. P-period: primary sampling period; AW: Autumn–Winter season, WS: Winter–Spring season;  $N_m$ : estimate of number of marked animals in the population;  $N_{total}$ : estimate of total population size after correcting for proportion of identifiable individuals (= 0.83). Note that P1 values for  $\phi$  cannot be obtained since there is no previous sampling occasion from which to derive an estimate. For details of the 22 PCRD models averaged see Table S2 in Supplement 4

P-period (season)	$N_m$ (95% CI)	$N_{total}$ (95% CI)	$\phi$ (95% CI)
1 (AW)	62 (33–90)	75 (47–118)	–
2 (WS)	57 (41–73)	69 (51–91)	0.9 (0.09–1.00)
3 (AW)	73 (58–87)	88 (72–107)	0.97 (0.11–1.00)
4 (WS)	54 (47–62)	65 (56–75)	0.93 (0.11–1.00)
5 (AW)	85 (58–112)	102 (74–140)	0.97 (0.09–1.00)
6 (WS)	55 (40–69)	66 (51–86)	0.86 (0.05–1.00)

abundance estimates ( $N = 75$  to  $102$ ) in Autumn–Winter (i.e. P1, P3 and P5) than in Winter–Spring ( $N = 65$  to  $69$  in P2, P4 and P6; Table 3).

Model-averaged apparent survival rates across all P-periods were high, with estimates ranging  $0.86$  to  $0.97$  (95% CI  $0.05$  to  $1.00$ ). Temporary emigration rates ( $\gamma''$  and  $\gamma'$ ) were variable but values were consistent across season (i.e. Autumn–Winter vs. Winter–Spring; Table 4). The probability of an individual emigrating out of the study area ( $\gamma''$ ) was low, while the conditional probability of an individual staying out of the study area ( $\gamma'$ ) was relatively high (Table 4). Estimates of  $\gamma'$  in Autumn–Winter indicate that if an animal was outside the study area in the previous season, there is a  $\sim 50\%$  probability that it will re-enter the study area (Table 4). The top 4 models all considered temporary emigration parameters by season, and accounted for 85% of AICc weight, with the top 2 models supporting Markovian emigration and accounting for 65% of AICc weight (Table 2).

### Estimate of super-population size

The POPAN model with most support was one in which probability of capture of individuals remained

Table 4. Model-averaged estimates of temporary emigration ( $\gamma''$ ,  $\gamma'$ ) rates of Australian humpback dolphins for 22 Pollock's closed robust design (PCRD) models fitted to capture-recapture data.  $\gamma''$  is the probability of emigration from the study area given an individual was present in the previous primary (P) period, and  $\gamma'$  is the probability of staying out of the study area given an individual was absent in the previous P-period. Temporary emigration patterns considered were either random ( $\gamma'' = \gamma'$ ), Markovian ( $\gamma'' \neq \gamma'$ ), or no temporary migration ( $\gamma'' = \gamma' = 0$ ), and were either kept constant ( $\bullet$ ), allowed to vary with time ( $t$ ), or by 'season', i.e. Autumn–Winter (P3 & P5) or Winter–Spring (P2, P4, & P6). Note that emigration parameters for P1 cannot be obtained since it is the first sampling occasion with no previous sampling occasion from which to derive an estimate.  $\gamma'$  for P2 cannot be estimated given there are no animals to be considered in P2 that were also outside the study area in P1 (i.e. they had not been captured yet). For details of the 22 PCRD models averaged see Table S2 in Supplement 4

P-period	Season	Temporary emigration $\gamma''$ (95% CI)	Temporary emigration $\gamma'$ (95% CI)
P2	Winter–Spring	0.3 (0.15–0.51)	–
P3	Autumn–Winter	0.01 ( $1.2 \times 10^{-5}$ –0.94)	0.52 (0.06–0.94)
P4	Winter–Spring	0.3 (0.15–0.50)	0.73 (0.09–0.99)
P5	Autumn–Winter	0.01 ( $6.6 \times 10^{-6}$ –0.96)	0.52 (0.06–0.94)
P6	Winter–Spring	0.29 (0.11–0.56)	0.71 (0.08–0.99)

constant, and the apparent survival rate and probability of individuals entering the study population varied across all 6 sampling periods (Table S7 in Supplement 4). The next model with high support (AICc weight = 0.40) differed from the top model only in that  $p$  varied across all 6 sampling periods (Table S7). The top 4 models with most support were weight-averaged to obtain estimates of super-population size ( $N_{super}$ ), apparent survival ( $\phi$ ), capture probabilities ( $p$ ) and entry probabilities ( $pent$ ). The total super-population size estimate was 129 humpback dolphins (95% CI 117 to 141; Table 5). Estimates of apparent survival varied from 0.45 to 0.96, with capture probability relatively high (range 0.56 to 0.80), and probability of entry generally low (range 0.03 to 0.22; Table 5).

### Goodness-of-fit tests and model validation

GOF tests for the 6 primary sampling periods conducted in program RELEASE and U-CARE indicated

Table 5. Model-averaged POPAN estimates of Australian humpback dolphin super population size, apparent survival ( $\phi$ ), capture probability ( $p$ ) and probability of entry into the study area ( $pent$ ) for the 4 most supported POPAN models.  $N_m$ : estimate of number of marked animals in the population;  $N_{super}$ : estimate of total population size over the study period after correcting for proportion of identifiable individuals (= 0.83); AW: Autumn–Winter season; WS: Winter–Spring season. Note that first sampling period parameters of  $\phi$  and  $pent$  cannot be obtained since there was no previous sampling occasion from which to derive an estimate. In fully time-dependent models, (i.e.  $\phi(t)$   $p(t)$   $pent(t)$ ), the final  $\phi$  and  $p$ , and the initial  $pent$  parameters are confounded. Parameter estimates provided are those averaged where the fully time-dependent model has been removed.

For details of all POPAN models averaged see Table S7 in Supplement 4

Models averaged	Sampling period (season)	$N_m$ (95% CI)	$N_{super}$ (95% CI)	$\phi$ (95% CI)	$p$ (95% CI)	$pent$ (95% CI)
$\phi(t)$ $p(\bullet)$ $pent(t)$ (Rank 1)	1 (AW)	107 (98–116)	129 (117–141)	–	0.8 (0.26–0.98)	–
$\phi(t)$ $p(t)$ $pent(t)$ (Rank 2)	2 (WS)			0.5 (0.15–0.84)	0.57 (0.40–0.72)	0.22 (0.06–0.55)
$\phi(\bullet)$ $p(t)$ $pent(t)$ (Rank 3)	3 (AW)			0.96 (0.30–1.00)	0.65 (0.50–0.78)	0.08 (0.01–0.52)
$\phi(\bullet)$ $p(\bullet)$ $pent(t)$ (Rank 4)	4 (WS)			0.69 (0.32–0.92)	0.63 (0.50–0.75)	0.03 (0.00–0.52)
	5 (AW)			0.93 (0.38–1.00)	0.56 (0.44–0.70)	0.13 (0.05–0.29)
	6 (WS)			0.45 (0.09–0.88)	0.58 (0.44–0.71)	0.05 (0.01–0.24)

a  $\hat{c}$  value of 0.92 and 1.33, respectively; suggesting there is not strong evidence of lack of fit. Results from the Otis et al. (1978) closure test indicated no strong evidence of gains (births or immigration) or losses (deaths or emigration) of individuals from the population for all primary periods in the PCRD analysis ( $p$ -values > 0.11). GOF tests run in U-CARE showed some suggested difference ( $p$ -value = 0.05) in expected time of first recapture between 'new' and 'old' individuals seen at least once (TEST 3.SM), but in general showed no strong evidence of 'trap-happy' or 'trap-shy' behaviour (TEST 2.CT), transience effect (TEST 3.SR) or overall heterogeneity in capture probabilities (Test 2 + 3) (Table S1 in Supplement 3).

### Site fidelity

Mean ( $\pm$ SD) monthly and yearly sighting rates indicated individuals were sighted in 3 separate months ( $0.18 \pm 0.12$ ) and over 2 separate years ( $0.65 \pm 0.27$ ) across the study period. The P-period sighting rate was  $0.43 \pm 0.25$ , indicating that individuals were typically sighted in 3 out of 6 P-periods. Site fidelity indices ranged from 0 to 0.5, with a mean value of  $0.15 \pm 0.12$ , indicating that most individuals were not captured in all sampling periods from their first capture to their last capture, but had at least 3 recaptures

spread over more than 2 consecutive P-periods (i.e. 1 to 2 yr).

AHC analysis separated individuals into 3 main clusters (dissimilarity threshold = 2.5) according to monthly and yearly sighting rates, and site fidelity indices (Fig. 4; Table 6). The values of CPCC (0.82) and AU  $p$ -values (0.89 to 0.97) indicated clusters in the dendrogram are a good representation of the dissimilarities among observations. Group A ( $n = 30$ ) consisted of individuals sighted in the study area over all 3 years and a minimum of 3 separate months (mean = 6 months; Table 6), and were thus considered long-term residents. Group B ( $n = 32$ ) consisted of individuals sighted in the study area in 2 separate years and a minimum of 2 separate months (mean = 3 months; Table 6), and were considered part-time residents. Group C ( $n = 36$ ) were considered occasional residents, and were comprised of individuals sighted in a single year of the study and a minimum of 1 separate month (mean = 1 month; Table 6). Group A and B individuals displayed stronger levels of site fidelity to the study area than those in Group C (Table 6). This finding was further supported by their primary cluster being derived from the same 'root' in the dendrogram tree (AU  $p$ -value = 0.76; Fig. 4).

Of the 54 humpback dolphins identified in the study area in 2010, 34 individuals (65%) were re-sighted during this study, indicating long-term site fidelity of some individuals to the study area. The

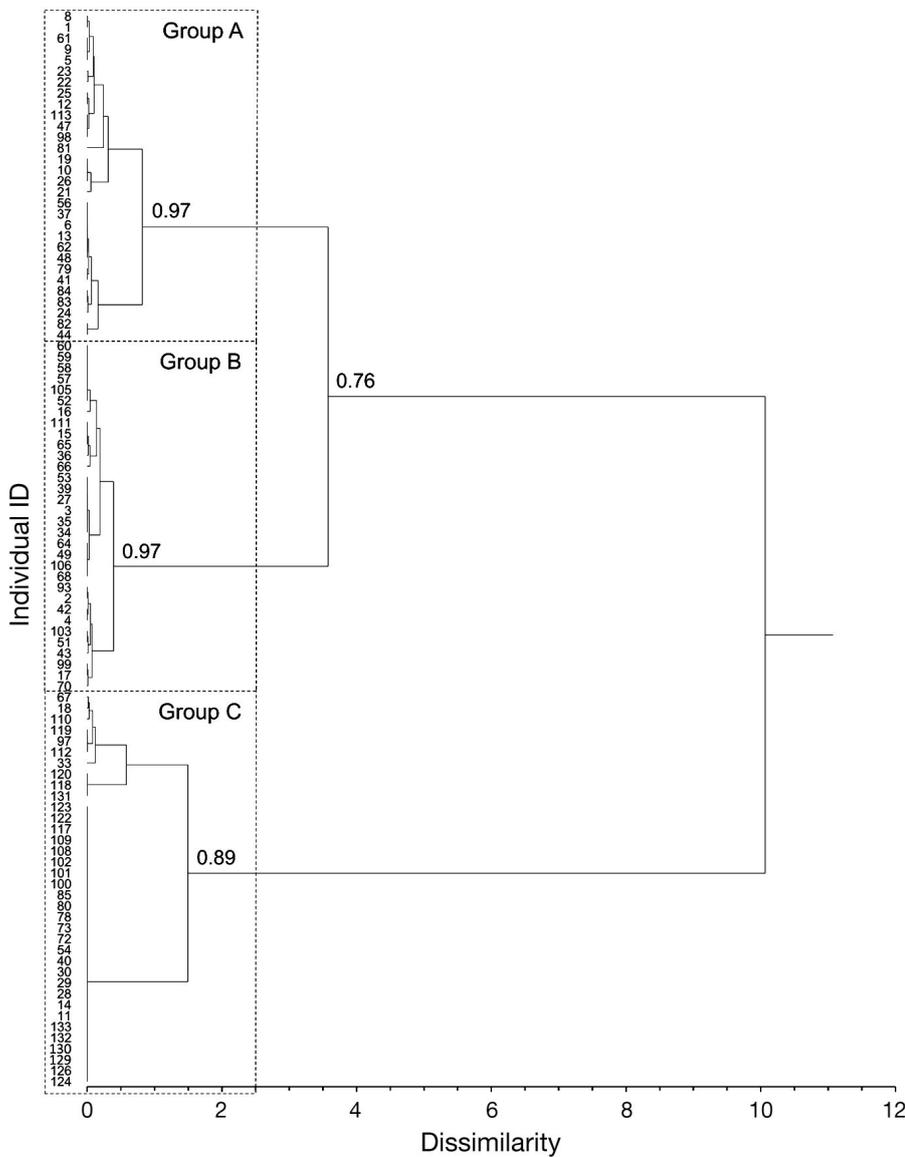


Fig. 4. Dendrogram of the agglomerative hierarchical clustering (AHC) analysis separating clusters of Australian humpback dolphins based on 3 measures of site fidelity: monthly sighting rate, yearly sighting rate, and site fidelity indices. Dashed rectangles indicate 3 clusters (dissimilarity threshold = 2.5): Group A (long-term residents), Group B (part-time residents) and Group C (occasional residents). Approximately unbiased (AU) probability values for each group and main cluster are indicated on the dendrogram

majority of individuals (n = 30) were resighted across 2 or more years of this study, and 4 individuals were resighted in 2015 only.

**Residency**

LIR began to fall after periods of 1 to 142 d (Fig. 5), indicating that some individuals spend very short amounts of time in the study area, while others remain within the study area for most of each yearly survey period. LIR, in general, levelled above zero, suggesting that some animals are residents while others re-immigrate into the study area after long time lags. The most supported model was that of emigration/mortality (QAIC = 2437.8; Fig. 5, Table S8 in Supplement 5). The mean number of humpback dolphins in the study area at any one time, derived from this model, was 57 (95 % CI 47 to 69). The mean residence time of individuals in the study area was 288.4 d (95 % CI 162 to 778), with a low emigration rate of 0.003 (95 % CI 0.001 to 0.006). The model of emigration + reimmigration + mortality (QAIC = 2440.0, ΔQAIC = 2.2) was also well supported (Fig. 5, Table S8).

**DISCUSSION**

**Abundance and density**

This study provides the first comprehensive assessment of the population demographics of Australian humpback dolphins inhabiting the

Table 6. Monthly sighting rate, yearly sighting rate and site fidelity (SF) indices of 3 clusters (A, B and C; see Fig. 4) of Australian humpback dolphins in the North West Cape study area as determined by agglomerative hierarchical clustering (AHC) analysis.

Sighting rate	Group A (n = 30)					Group B (n = 32)					Group C (n = 36)				
	Mean	SD	Mode	Median	95 % CI	Mean	SD	Mode	Median	95 % CI	Mean	SD	Mode	Median	95 % CI
Monthly	0.32	0.09	0.26	0.32	0.28–0.35	0.17	0.05	0.21	0.16	0.16–0.19	0.07	0.04	0.05	0.05	0.06–0.08
Yearly	1.00	0.00	1.00	1.00	1.00–1.00	0.67	0.00	0.67	0.67	0.67–0.67	0.33	0.00	0.33	0.33	0.33–0.33
SF Index	0.22	0.08	0.20	0.20	0.19–0.24	0.16	0.06	0.20	0.16	0.14–0.18	0.08	0.16	0.00	0.00	0.03–0.13

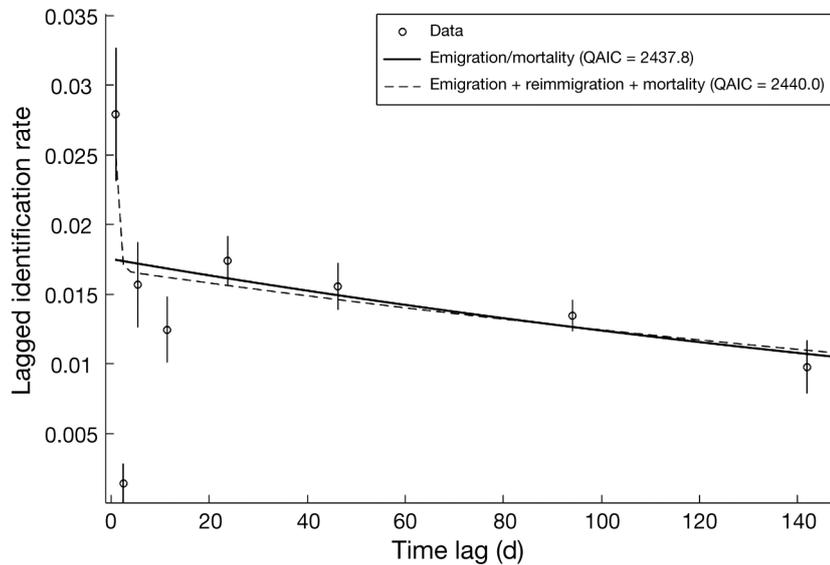


Fig. 5. Lagged identification rates (circles) and estimated standard errors (bars) of individual Australian humpback dolphins sighted in the North West Cape study area, together with the best (emigration/mortality) and second best (emigration + reimmigration + mortality) fitting models of movement. Maximum time lag was set to 177 d (i.e. the longest period of time between the first capture and last capture of an individual in any yearly survey period) in order to consider movements within yearly survey periods (and exclude the ~6 month time period between these yearly survey periods)

waters around the NWC in WA, including the first reported abundance estimate for this species along the ~1000 km Pilbara coastline. Population capture-recapture models are powerful techniques for estimating abundance, rates of apparent survival and temporary emigration, but the validity of the estimates depend on the validation of model assumptions underlying this methodology. We acknowledge there was difficulty in precisely quantifying the survival and migration processes, likely due to the sensitivity of PCRDM to low-detection probabilities, data-sparseness, transience, and individual heterogeneity. Despite these limitations, we believe our estimates are supported by the amount of data that we have (in addition to being backed by the GOF tests), and that the assumptions of the PCRDM and POPAN mark-recapture models were satisfied (Supplement 3).

About 60 to 100 animals used the NWC study area at any one time, with a total of ~129 individuals (95% CI 117 to 141 individuals) using the area over the 3-yr study. These estimates are broadly comparable to those reported for other humpback dolphin populations across northern Australia, which average 54 to 89 individuals and 0.1 to 0.19 individuals  $\text{km}^{-2}$  (see reviews in Brown et al. 2016, Parra & Cagnazzi 2016).

At 0.90 to 1.09 individuals  $\text{km}^{-2}$ , the NWC represents the highest density recorded for this species. This high density, together with the high levels of site fidelity and residence patterns observed, indicates that the NWC represents an important habitat towards the southwestern limit of this species' range.

Abundance estimates on the NWC tended to be slightly higher during the Autumn–Winter (P1, P3, P5) than the Winter–Spring (P2, P4, P6) sampling periods. This variation in abundance suggests some seasonality in movement in and out of the study area. The influx of individuals into the study area during the Autumn–Winter periods is supported by our findings of Markovian temporary emigration from PCRDM analysis, with 50% return rate of temporary emigrants, and marginally higher probability of entry (*pent*) values during Autumn–Winter from POPAN models. This result suggests that the NWC study population is open to

emigration/immigration, and that the NWC study area likely represents a portion of the home range of humpback dolphins in this region. It seems likely that the full extent of the home range of individuals in this population extends further into the Exmouth Gulf and Ningaloo Reef regions, given that representative ranges of humpback dolphins elsewhere range from 190 to 325  $\text{km}^2$  (Parra et al. 2006a, Cagnazzi et al. 2011), and that individually identified humpback dolphins seen in our 130  $\text{km}^2$  study area were also sighted opportunistically beyond that region (T. N. Hunt unpubl. data). Study areas typically cover a subset of inshore dolphins' home ranges; some individuals will have large parts of their home range covered within the study area, and some will be on the peripheral of the study area. These ranges may vary temporally, and be influenced by ecological and social factors (e.g. Balance 1992, Sprogis et al. 2016a). Future capture-recapture studies including simultaneous surveys inside and outside the NWC study area, coupled with genetic analyses and multi-state models (Brownie et al. 1993), could be employed to estimate movement probabilities between areas, individual home ranges, and better define population boundaries and population structure.

### Apparent survival and temporary emigration

Survival is a key demographic process, but is difficult to estimate from capture-recapture data, given that mortality and permanent emigration can be confounded (Pledger et al. 2003). This difficulty is amplified when dealing with short study periods relative to the subject's longevity (in this instance, only a few years for a species that may live to >50 yr). The PCRD apparent survival estimates reported here for humpback dolphins (0.86 to 0.97) are comparable to those reported for other coastal delphinids both around Australia (e.g. Nicholson et al. 2012, Palmer et al. 2014, Brooks & Pollock 2015, Sprogis et al. 2016b) and globally (Currey et al. 2009, Silva et al. 2009, Cantor et al. 2012, Tyne et al. 2014). This estimate suggests low levels of permanent emigration and/or mortality, and high levels of site fidelity and residency of the local population over the study period. Considering the relatively small study area, the variable POPAN apparent survival rates reported are likely a result of movement patterns (e.g. 'transient' animals that are sighted, and then never, or infrequently, seen again; Silva et al. 2009), and do not reflect differences in true survival (see Palmer et al. 2014, Brooks & Pollock 2015).

Temporary emigration of humpback dolphins from the study area seems to follow a Markovian model, indicating it was dependent on animals being absent or present in the previous sampling season. The probability of temporary emigration for dolphins that had been absent in a previous season was higher than the temporary emigration rates of dolphins that were present in the previous season, suggesting that a high proportion (30 to 50%) of individual dolphins return to the study area after being absent for a season. The high probability ( $1 - \gamma = 0.99$ ) of animals being present in the study area in Autumn–Winter if they were present in Winter–Spring, despite there being a ca. 6 month Summer–Autumn period in between (i.e. November to March), suggests dolphins may remain around the NWC during the Summer–Autumn period. Year-round residency with temporary movement in and out of the study area is suspected for humpback dolphins around the NWC based on opportunistic sightings (T. N. Hunt unpubl. data), and studies of this species in eastern Australia (Parra et al. 2006a, Cagnazzi 2010, Cagnazzi et al. 2011). Future studies including surveys over the Summer–Autumn period are needed to confirm year-round residency of this population at the NWC.

Despite the inability of GOF tests to detect heterogeneity, transience and trap-behaviour responses, we

note that there was considerable support for mark-recapture models that included heterogeneity. However, data sparseness prevented us from including these models in our model-averaging set. Therefore, the predictable consequence of not accounting for individual heterogeneity is a slight negative bias in abundance estimates (Carothers 1973, Burnham & Overton 1978, Rankin et al. 2016). Given our data, this is justified by the classic 'bias-variance' trade-off in model selection. By selecting simple models, we deliberately favour slightly biased estimates that are low variance, rather than the unbiased, high variance estimates from more complex models (which suffer singularities and boundary value estimates). Thus our abundance estimates may be slightly downward biased as a result of ignoring individual heterogeneity, but are more likely to be closer to the truth than the wildly varying estimates from the over-parameterised mixture models. Our estimates represent a comprehensive attempt at better understanding the population demographics of humpback dolphins on the NWC. Future studies should prioritise: (1) increasing the number of resightings and the effective capture probabilities at the study design through a targeted increase in survey effort (e.g. use of 2 boats to simultaneously cover the study area), or (2) using recently developed individual heterogeneity Bayesian models to circumvent MLE issues with model fitting, such as parameter singularities (albeit, with more injection of prior information; Rankin et al. 2016), and (3) better accounting for sub-populations with different site-fidelity (as per our cluster analysis).

Sparse data have another immediate consequence for temporary-migration models, in that there is an almost unavoidable correlation between survival and migration parameters. This is particularly true when effective detection probabilities are low within primary sampling periods. These correlations can manifest as boundary value parameter estimates (i.e. 0 or 1) and singularities, and very wide 95% CIs (Rankin et al. 2016). In this study, wide CIs are evident for apparent survival and some temporary emigration estimates (Tables 3 & 4). These are inherent issues of temporary migration models, such that one cannot effectively separate individuals remaining in the 'unobservable state' and death, especially under low capture probabilities (Kendall et al. 1995, Rankin et al. 2016). Limitations are therefore placed on our ability to interpret survival estimates under sparse data and low detection probabilities (Bailey et al. 2010). Despite these limitations, we assert that our PCRD models provide evidence of relatively high levels of site fidelity and regular movement in and

out of the area for humpback dolphins in the NWC population. This was well supported by our site fidelity and residence analysis.

### Site fidelity and residency

Overall, humpback dolphins inhabiting the NWC showed high levels of site fidelity and residency, further emphasising the importance of this area for this population. Most individuals identified were resighted on multiple occasions across all months and years surveyed. Two-thirds (65%) of the individuals identified in 2010 (Brown et al. 2012) were resighted during this study. The site fidelity groups identified from agglomerative hierarchical clustering indicated individual variability in site fidelity, with the majority of individuals (63%, sighted in 2 or more years) considered long-term and part-time residents, and some occasional residents. Individual variability in site fidelity has also been found in other Australian humpback dolphin populations (Parra et al. 2006a, Cagnazzi 2010, Cagnazzi et al. 2011), as well as in other humpback dolphin species elsewhere (e.g. Karczmarski et al. 1999, Stensland et al. 2006, Xu et al. 2012).

Site fidelity patterns are largely influenced by resource availability and predation risks (Greenwood 1980, Switzer 1993). Two-thirds of the study area is within the boundaries of NMP, with the majority (86%) of humpback dolphin sightings occurring within this MPA (T. N. Hunt unpubl. data). We hypothesise that the predominant high site fidelity patterns to the NWC may be driven by high quality, heterogeneous and productive habitat within the MPA. A total of 6 sanctuary zones (no fishing zones) are within the boundaries of the MPA in the study area (see DPaW & DoF 2014). Fitzpatrick et al. (2015) found that, within NMP, fish assemblages at sanctuary zones had higher biomass and abundance than at sites where fishing is permitted. Given that protected areas in general can increase overall abundance and biomass of fish assemblages, and that humpback dolphins are thought to be opportunistic feeders (Parra & Jedensjö 2014), consistent prey availability may be influencing regular use of NMP by humpback dolphins, compared to the adjacent (unprotected) Exmouth Gulf. Tiger sharks *Galeocerdo cuvier* and white sharks *Carcharodon carcharias* are known to occur in the NWC region (T. N. Hunt pers. obs.; see also Fitzpatrick et al. 2006). These sharks are known to prey on dolphins (Heithaus 2001) and likely pose predation risks to humpback dolphins in this region. Future studies on seasonality in prey and predator

abundance and biomass (e.g. Heithaus & Dill 2006, Fearnbach et al. 2012, McCluskey et al. 2016) and sociality (e.g. Smith et al. 2016) are needed to determine their influence on humpback dolphin site fidelity and abundance patterns.

Evidence of Markovian temporary emigration suggests that dolphins do not reside permanently in the study area, but move in and out of the study area regularly. Modelling of sighting patterns support this assertion, with data supporting movement models characterised by emigration/mortality, and emigration + reimmigration + mortality. Similar movement patterns were observed for humpback dolphins in Cleveland Bay, northern Queensland (Parra et al. 2006a). The mortality aspect of the lagged identification rate movement models may be driven by permanent emigration and/or transients, which corresponds to the wide CIs and variable values in our estimates of apparent survival rates. It may also be indicative of a larger temporal scale (years) of temporary emigration, which is supported by the identification of individuals in 2015 that were first sighted in 2010, but not sighted in 2013 or 2014. This evidence of long-term site fidelity further supports the NWC as important habitat for humpback dolphins.

### Implications for conservation and management

The high density, site fidelity and residency of humpback dolphins in our study area highlight the importance of the NWC to this endemic, poorly known species of conservation concern. Reviews of available data from across their range suggest that density is generally lower elsewhere, considerably so in most cases (Brown et al. 2016, Parra & Cagnazzi 2016), suggesting this NWC population is of high conservation value. For example, less than 20 individually identifiable humpback dolphins were recorded in each of five ~130 km<sup>2</sup> study sites across the adjacent Kimberley region of WA (Brown et al. 2016).

The identification of a sizeable humpback dolphin population within a MPA offers 2 potential benefits for this species' conservation: (1) a regulatory management framework on which to base conservation strategies and the management of human activities with the potential to impact this threatened species, and (2) a logistically and ecologically suitable site for long-term research and monitoring, with the potential to provide important information on this species' life history traits and behavioural ecology. Humpback dolphins are already a recognised value within NMP (CALM & MPRA 2005), but the efficacy of this

marine park (and other MPAs) in protecting humpback dolphins (and other marine mammals) is uncertain. Management agencies have a unique opportunity to target research and conservation objectives of a threatened species within this MPA, and to use the knowledge gained to better manage and protect humpback dolphin populations outside MPAs.

Although the NWC area remains relatively undeveloped to date, its proximity to ongoing petroleum interests in the region means that there is potential for it to be affected by exploration and coastal development (Hanf et al. 2016). The cumulative impact of activities associated with exploration and coastal development (e.g. seismic surveys, dredging, pile driving, vessel traffic, and pollution) have been recognised as major threats to this species (Parra & Cagnazzi 2016). The methods presented in the present study provide a methodological framework that should be used by those conducting future environmental impact assessments. Our results provide a robust demographic baseline of inshore delphinids on which to base environmental impact decisions, and a strong platform for the design and implementation of Before-After-Control-Impact studies. Specifically, the NWC study area can serve as a quasi-control site, and we emphasise the importance of surveying adjacent areas to better understand populations that do not occur in protected areas and may be subject to the cumulative pressures associated with future coastal development. Through the development of long-term studies, we can gain a more complete understanding of Australian humpback dolphin population dynamics as a basis for their future management in Australian waters.

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