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# **Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops* sp.) off Useless Loop in the western gulf of Shark Bay, Western Australia**

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## **Abstract**

Capture–recapture models were used to provide estimates of abundance, apparent survival and temporary emigration of Indo-Pacific bottlenose dolphins (*Tursiops* sp.) in a 226-km<sup>2</sup> study area off Useless Loop in the western gulf of Shark Bay, Western Australia. Photo-identification data were collected during boat-based surveys in Austral autumn to early spring (April–September) from 2007 to 2011. Abundance estimates varied from 115 (s.e. 5.2, 95% CI 105–126) individuals in 2008 to 208 (s.e. 17.3, 95% CI 177–245) individuals in 2010. The variability in abundance estimates is likely to be a reflection of how individuals used the study area, rather than fluctuations in true population size. The best fitting capture–recapture model suggested a random temporary emigration pattern and, when coupled with relatively high temporary emigration rates (0.33 (s.e. 0.07) – 0.66 (s.e. 0.05)) indicated that the study area did not cover the entire ranges of the photo-identified dolphins. Apparent survival rate is a product of true survival and permanent emigration and was estimated annually at 0.95 (s.e.

0.02). Since permanent emigration from the study area is unlikely, true survival was estimated to be close to 0.95. This study provides a robust baseline for future comparisons of dolphin demographics, which may be of importance should climate change or increasing anthropogenic activity affect this population.

**Additional keywords:** capture-recapture, demographic parameters, photo-identification, Pollock's closed robust design.

## **Introduction**

Shark Bay has been listed as a World Heritage Area since 1991, in recognition of its natural beauty, biological diversity and ecological processes. The marine ecosystem is considered relatively pristine, because of its remote location and relatively low levels of anthropogenic activity (Heithaus *et al.* 2007). Bottlenose dolphins (*Tursiops* sp.) have been studied in the eastern gulf of Shark Bay for three decades (Connor and Smolker 1985). This ongoing research has a strong focus on behaviour, ecology, genetics, communication and social structure, making it one of the most well renowned dolphin-research sites in the world (Connor *et al.* 2000b). Shark Bay's bottlenose dolphins live in a fission-fusion society with a complex social organisation (Connor *et al.* 1992, 2000b, 2011; Smolker *et al.* 1992) and exhibit a remarkable variety of foraging strategies within a population (Smolker *et al.* 1997; Connor *et al.* 2000a; Mann and Sargeant 2003; Allen *et al.* 2011). The density of the dolphin population may well drive such behavioural complexity. There are, however, no dedicated, robust abundance or density estimates available for bottlenose dolphins in the region.

Prior information on bottlenose dolphin abundance and density in Shark Bay resulted from a study designed to estimate the abundance and distribution of dugongs. Using aerial surveys that covered an area of 14 906 km<sup>2</sup>, Preen *et al.* (1997) estimated dolphin abundance to be 2888 (s.e. 434), with a

density of 0.19 dolphins km<sup>-2</sup>, in 1989, and 2064 (s.e. 267) dolphins, with a density of 0.14 dolphins km<sup>-2</sup>, in 1994. These estimates were corrected for perception bias (animals are visible, but missed by the observer), but not for availability bias (animals are missed because they are not visible). They are, therefore, likely to be substantial underestimates. In another study investigating the effect of ecological and anthropogenic factors on dolphin home-range sizes, Watson (2005) estimated the density of bottlenose dolphins in the eastern gulf study area (250 km<sup>2</sup>) to be 2.4 dolphins km<sup>-2</sup>. However, this estimate was derived from information on the number of individuals identified within a defined, unsystematically sampled area and should, therefore, be interpreted with caution (Watson 2005). For both empirical and applied reasons, there is a need for robust estimates of bottlenose dolphin abundance in Shark Bay, such that a baseline exists for future comparisons.

Bottlenose dolphins, like many cetacean species, can be individually identified from natural marks on the trailing edge of their dorsal fin (Würsig and Jefferson 1990). These unique marks, documented in photographs, provide a means of identifying individuals and establishing records of sightings and associations over time. The photo-identification method is widely applied with capture–recapture methods to estimate abundance and other demographic parameters, such as survival and temporary emigration rates, of small cetaceans (e.g. Wilson *et al.* 1999; Read *et al.* 2003; Parra *et al.* 2006; Silva *et al.* 2009). The main advantage of using photo-identification data for capture–recapture analyses is that animals do not need to be physically captured to be marked (Hammond 1986, 1990). In addition, this allows capture–recapture data to be collected in such a way as to minimise behavioural responses to capture, which can complicate population parameter estimation (Pollock *et al.* 1990; Williams *et al.* 2002).

The idea of capture–recapture is to capture and mark a sample of individuals in the population during a defined sampling period and use the proportion of recaptured, marked individuals in subsequent samples to estimate the proportion of marked individuals in the population at large (Lincoln 1930; Le

Cren 1965; Seber 1982). The length of the study relative to the life-history characteristics of the study species usually determines whether the population can be considered closed or open to additions and deletions and is the basis for choosing which modelling approach to use for parameter estimation. Closed population, open population and robust design models, which combine closed and open population models, have been developed (Otis *et al.* 1978; Pollock *et al.* 1990; Williams *et al.* 2002).

Pollock's closed robust design (Pollock 1982; Kendall and Nichols 1995; Kendall *et al.* 1995, 1997), which has been increasingly used for estimating cetacean abundance and other demographic variables (e.g. Silva *et al.* 2009; Speakman *et al.* 2010; Cantor *et al.* 2012), combines the use of closed and open population models under a nested sampling framework. Short bursts of sampling, with longer gaps in between the bursts, mean that closed models can be used for the bursts, whereas open models are needed for the whole study. Open population models are used to estimate apparent survival and temporary emigration rates, while closed population models are used to estimate abundance in an integrated framework. Although a more complex design, Pollock's closed robust design brings more biological reality into the analysis by taking into account the possibility that animals may temporarily emigrate and then return, unlike standard open models, which do not allow for temporary emigration (Kendall and Nichols 1995; Kendall *et al.* 1997).

In this study, we applied Pollock's closed robust design models to photo-identification data collected over 5 years to estimate abundance, apparent survival and temporary emigration rates of bottlenose dolphins off Useless Loop in the western gulf of Shark Bay. These estimates are the first robust estimates for any region in Shark Bay and provide baseline information for future comparisons, which may become of increased importance if climate change or other anthropogenic activities influence this population.

## Materials and Methods

### *Study area*

Shark Bay is a ~15 000-km<sup>2</sup> semi-enclosed bay divided by Peron Peninsula into two north-facing gulfs (Fig. 1). Seagrass, covering more than 4000 km<sup>2</sup> (Walker *et al.* 1988), forms the foundation of the marine ecosystem in Shark Bay. This study was conducted in the Denham Channel, off Useless Loop, in the western gulf of Shark Bay (26°03'S, 113°26'E) (Fig. 1). Ten loosely parallel transect lines, each ~11 km in length and 2 km apart, covering an area of 226 km<sup>2</sup>, were designated across depth contours. The study area covers shallow seagrass habitat, as well as five channels of <16-m water depth, disrupted by shallower sand flats (Tyne *et al.* 2012). Previous research in the western gulf study area has concentrated on assessing the factors that drive tool use in bottlenose dolphins (Bacher *et al.* 2010; Tyne *et al.* 2012).

### *Field Methods*

Boat-based surveys were conducted from Austral autumn to early spring (April–September) between 2007 and 2011. Sampling was restricted to this time of year because the weather conditions (primarily high heat and winds) between November and March are considered unsuitable for effective data collection. Transect lines were sampled in a random order, with each transect line sampled five times in 2007, 2008 and 2010, 10 times in 2009 and three times in 2011. A 5.4-m research boat with a 100-hp outboard was driven at speeds of 7–8 knots along each transect line. The number of transect lines surveyed in a day was dependent on weather conditions, varying between one and six. Transects were conducted only in Beaufort sea states of two or less, because the presence of white caps (Beaufort sea state three) makes surfacing small cetaceans difficult to detect (Evans and Hammond 2004).

A survey was conducted on each individual or group encountered within 300 m of the transect line, thus allowing for a 600-m 'survey zone' (Sargeant *et al.* 2007). A group was defined using the '10 m

chain rule', where animals within 10 m of any other group member were considered to be part of the same group (Smolker *et al.* 1992). When a dolphin group was sighted, the transect was paused and the dolphin/s were approached for surveying. Surveys lasted a minimum of 5 min, during which dolphin identities, group composition and predominant behavioural activity were recorded, along with information on location, depth and environmental conditions. If possible, all individuals in the group were photographed, using digital cameras fitted with telephoto zoom lenses, for later identification from the unique nicks and notches on the trailing edge of the dorsal fin (Fig. 2) (Würsig and Würsig 1977; Würsig and Jefferson 1990). As the exact age of individuals could not be determined, encountered individuals were assigned to one of three mutually exclusive age classes (adults, juveniles and calves) according to body size and degree of ventral speckling (Sargeant *et al.* 2007). A survey was considered completed once photographs of all individuals in a group were obtained. This could not always be achieved, because of either evasive behaviour of animals, when there was uncertainty over how many animals were present, or when there were several unmarked individuals in a group and distinguishing among them was considered impossible.

### ***Photo-identification process***

All photographs containing a dorsal fin were graded for quality so as to minimise misidentification and heterogeneity in capture probabilities (Friday *et al.* 2000; Gowans and Whitehead 2001). The photographic quality-grading protocol used in this study was modified for the Sarasota Dolphin Research Program (2006) from a protocol developed by Urian *et al.* (1999). Accordingly, all photographs were given an absolute value score for clarity and focus (2, 4 or 9), degree of contrast (1 or 3), angle of the dorsal fin to the camera (1, 2 or 8), whether the dorsal fin was fully visible (1 or 8) and the proportion of the frame filled by the fin (1 or 5). The individual scores for each category were summed to obtain an overall quality score (QS). Scores from 6 to 7 were considered excellent quality, 8 to 11 good quality and >11 poor quality. Scores for each category, apart from contrast and the

proportion of the frame filled by the fin, were weighted in a way that inadequate quality in one category alone could push the photograph over the poor-quality threshold.

The degree of distinctiveness varies among dorsal fins of individuals and some are not sufficiently marked to be included in capture–recapture analyses, which only pertain to the distinctly marked population (Wilson *et al.* 1999; Read *et al.* 2003). Each individual in the catalogue was therefore given a distinctiveness score, based on the amount of information contained on the leading and trailing edges of the dorsal fin. Only marks visible from both sides of the dorsal fin were used for identification, so that identifications made from photographs from either side of the dorsal fin could be included in the analyses. Urian *et al.*'s (1999) distinctiveness protocol was used to grade dorsal fins. Very distinct fins with features evident from distant or poor-quality photographs were given a score *D1*; fins with an average amount of information (one larger or several smaller nicks) were given a score of *D2*; and fins with no, or very little, information a score of *D3*. Every individual was compared with all others in the catalogue before being assigned with a unique identification code and included in the catalogue.

### ***Statistical methods***

In this study, a 'capture' was defined as a photograph of sufficient quality of an individual's distinctly marked dorsal fin. Only excellent- and good-quality ( $\leq 11$ ) photographs and distinctly marked (*D1* and *D2*) individuals were included in capture–recapture analyses, so as to ensure that more distinctly marked individuals would not have a higher probability of being captured (Gowans and Whitehead 2001) and to reduce errors in data as a result of misidentification. Capture histories, consisting of 1s and 0s, corresponding to whether or not an individual was captured within a sampling period (a run through all 10 transects), were compiled for each identified individual remaining after the photographing process, except calves. Capture–recapture models were then applied to these data by using program MARK (White and Burnham 1999).



The photo-identification data were collected in a way that allowed for Pollock's closed robust design to be used for estimating abundance, apparent survival and temporary emigration rates (Pollock 1982; Kendall and Nichols 1995; Kendall *et al.* 1995, 1997). This design consists of two levels of sampling, namely, primary periods and secondary periods. Secondary periods are temporally close sampling occasions within primary periods, which are separated by a longer interval. The population is assumed to be closed within and open between primary periods. In the model, data within each primary period are essentially pooled to estimate apparent survival and temporary emigration rates using an open population model, whereas data from the secondary sampling periods are used to estimate abundance for each primary period. In this study, secondary periods consisted of individual sampling occasions within the winter of each year, whereas primary periods were years.

The assumptions of our particular implementation of Pollock's closed robust design (Pollock 1982; Pollock *et al.* 1990; Williams *et al.* 2002) were that (1) all individuals have equal probability of being captured within a sampling occasion, (2) capture and recapture probabilities are equal (no trap response), (3) marks are unique, permanent and identified correctly, (4) the sampling interval for a particular secondary sample is instantaneous, (5) the population is closed within primary periods, (6) all individuals have equal probability of survival and (7) each individual's probability of capture is independent of all others. Our methodology and information on the biology of the species were considered to evaluate how well assumptions were validated.

### ***Validation of model assumptions***

Regardless of sampling methods used, the assumption of all individuals having equal probability of capture is rarely met for any cetacean population (Hammond 1986). Capture probabilities may be heterogeneous because of age, sex or social status of the animal. Home ranges may also vary in response to transect location or individual preference for certain areas can affect the probability of capture (Pollock *et al.* 1990). All this may lead to a negative bias in abundance estimates. Another

cause of heterogeneity in capture probabilities when using photo-identification is that some individuals may be more distinctly marked than others, resulting in those individuals having a higher probability of being captured. Heterogeneity resulting from mark distinctiveness was minimised by including only captures from excellent- and good-quality photographs and by including only sufficiently marked individuals in analyses. The assumption of the first capture ( $p$ ) and recapture ( $c$ ) probabilities being equal is considered valid, because photo-identification methods do not require physical capture or handling of animals (Parra *et al.* 2006). We also included additional analyses to address our concerns over heterogeneity (see Supplementary Material, available on the web).

Coastal bottlenose dolphin populations are socially structured in a way that capturing a particular individual increases the chance of its closest associates being captured over other individuals (Connor *et al.* 2000b). The assumption of captures being independent may have therefore been violated. This is unlikely to cause a bias in our estimates; however, standard errors are likely to be underestimated to some extent (Williams *et al.* 2002).

The assumption of equal probability of survival is also difficult to fully satisfy, because survival rate can vary by age. So as to minimise violation of this assumption, only adults were included in our analyses. However, survival may still vary within this broad (artificial) age class, consisting of the majority of independent individuals.

Correct identification of individuals is a requirement for unbiased parameter estimates (Evans and Hammond 2004; Yoshizaki *et al.* 2009). To ensure this, only excellent- and good-quality photographs and distinctly marked dorsal fins were used for individual identification. Misidentification can occur in the following two ways: one individual is identified as two (false negative error) or two individuals are identified as one (false positive error). False negative errors, which may lead to positive bias in

abundance estimates, are more likely to occur when identifying individuals from natural marks because marks can evolve over time (Yoshizaki *et al.* 2009). However, the nicks and deformities on the dorsal fins of bottlenose dolphins are persistent (Wilson *et al.* 1999). Thus, mark changes, if they occurred, were detected as a change for the same animal.

Validating the assumption of instantaneous sampling was not achievable because of logistics, available resources, weather conditions and the nature of our study species. On average, it took 19 days to complete a sampling occasion (a set of 10 transects). Finally, we assumed that the population was closed (constant) over the secondary sampling periods within a primary period. This sampling was carried out over periods of between 47 and 104 days and, therefore, the assumption of closure was not strictly satisfied. The implications of this violation are discussed later.

### ***Estimating population demographic parameters of distinctly marked individuals***

We define the temporary emigration parameter ( $\gamma''$ ) as ‘the probability of an individual being a temporary emigrant, given it was alive and present in the study area in the previous sampling period’. The other temporary emigration parameter ( $\gamma'$ ) is ‘the probability of an individual being a temporary emigrant, given it was a temporary emigrant in the previous sampling period’. Apparent survival rate ( $\phi$ ) is the probability of surviving and staying in the study area and is the product of true survival and fidelity to the study area. All rates are on an annual basis. A set of 14 models, composed of parameters for population size ( $N$ ) apparent survival rate ( $\phi$ ), temporary emigration rates ( $\gamma'', \gamma'$ ) and capture probability ( $p = c$ ), were fitted to the data and estimated under the full parameterisation of maximum likelihood available in program MARK.

The following three temporary emigration patterns were considered in the model set: (1) no temporary emigration ( $\gamma'' = \gamma' = 0$ ), where there is no temporary emigration at all; (2) random ( $\gamma'' = \gamma'$ ), where the

probability of an individual being present in the study area is independent on whether or not it was present in the study area in the previous sampling period; and (3) Markovian ( $\gamma''$ ,  $\gamma'$ ), where the probability of an individual being present in the study area is conditional on whether it was present or not in the study area in the previous sampling occasion (Kendall and Nichols 1995; Kendall *et al.* 1997; Williams *et al.* 2002). The resulting parameter estimates from these models were for the distinctly marked population; however, we assumed that all demographic parameters are homogeneous over the distinctly marked and unmarked population.

Combinations of models, where parameters were either constant or were allowed to vary with time, were fitted for each temporary emigration pattern. Capture probability was allowed to vary with time for each sampling occasion, both between and within primary periods. Models with constant capture probability were not fitted to the data, because environmental conditions were not constant over the sampling periods and, therefore, the probability of capture varied among them. For all fitted models, recapture probability ( $c$ ) was set equal to first capture probability ( $p$ ), because capture should not affect recapture when using photo-identification methods. The Akaike's information criterion ( $AIC_c$ ) with small sample-bias adjustment was used as a measure of relative model fit. The model with the lowest  $AIC_c$  was selected as the most parsimonious; however, models within two  $AIC_c$  units have support from the data and should not be dismissed (Burnham and Anderson 2002).

To explore the effects of heterogeneous capture probabilities on resulting estimates, additional models within Pollock's closed robust design were fitted to the data. These models, with two-point finite mixtures (Norris and Pollock 1996; Pledger 2000) allow for capture probabilities to vary among individuals ( $M_h$ ) and between individuals and time ( $M_{th}$ ). Under the two-point finite mixtures approach, animals may belong to one group of animals with a capture probability  $p_1$  or another group of animals with a capture probability  $p_2$ .

### ***Proportion of distinctly marked individuals in the population***

To estimate the proportion of distinctly marked individuals in the population, all surveys were given a score to identify the thoroughness of the photographic coverage of a given survey. A score of one was given if all individuals in the group were photographed with sufficient quality ( $QS \leq 11$ ) and all individuals were either identified or confirmed as unmarked ( $D3$ ) individuals. A score of two was given when there were individuals with distinct dorsal fins, but the photographic quality was considered insufficient ( $QS > 11$ ) to include them in analysis. A score of three was given when photographic coverage was incomplete because all individuals were not approached for photographs, no photographs were taken or photographs taken were not suitable to be included in the grading process.

Only surveys with photographic coverage score of one were used to estimate the proportion of distinctly marked individuals ( $\theta$ ) in the population. The number of distinctly marked animals ( $D1$  and  $D2$ ) encountered was divided by the total number of animals encountered on transect, in surveys with photographic coverage score of one, during the whole study period (2007–2011). Only surveys with photographic coverage score of one were used for this estimation because when only a proportion of group members is photographed, there may be a tendency to focus on more distinctly marked individuals, causing a bias in the proportion of distinctly marked individuals. Calves, being dependent individuals, were excluded from this estimation. The total population-size estimate is therefore also exclusive of calves.

### ***Total population size***

The population-size estimates from the capture–recapture model relate to the distinctly marked population. To estimate the total population size at a particular time, these estimates need to be

adjusted to take into account the proportion of individuals in the population that are unmarked, as follows:

$$\hat{N}_{total} = \hat{N}_m / \hat{\theta},$$

where  $\hat{N}_{total}$  is the estimated total population size,  $\hat{N}_m$  the estimated distinctly marked population size and  $\hat{\theta}$  the estimated proportion of distinctly marked individuals in the population. The approximate variance for the estimated total population size was derived using the following formula for the standard error of a ratio:

$$SE(\hat{N}_{total}) = \sqrt{\hat{N}_{total}^2 \left( \frac{SE(\hat{N}_m)^2}{\hat{N}_m^2} + \frac{1 - \hat{\theta}}{n\hat{\theta}} \right)},$$

using the delta method (Williams *et al.* 2002). Log-normal 95% confidence intervals were calculated, with a lower limit of  $\hat{N}_{total}^L = \hat{N}_{total} / C$  and upper limit of  $\hat{N}_{total}^U = \hat{N}_{total} \times C$ , where

$$C = \exp \left( 1.96 \sqrt{\ln \left( 1 + \left( \frac{SE(\hat{N}_{total})}{\hat{N}_{total}} \right)^2 \right)} \right)$$

(Burnham *et al.* 1987).

## Results

### *Photo-identification and proportion of distinctly marked individuals*

The study periods varied in effort and spanned different lengths of time each year (Table 1). In total, 685 surveys were conducted on transect between 2007 and 2011. Of all surveys, 45% were given a photographic coverage score of one, 23% a score of two and 32% a score of three. Surveys resulted in the identification of 435 individuals, of which 96 were identified as calves and five as juveniles at first capture. The photographic quality-grading process resulted in the removal of 18 individuals from the dataset. These individuals were distinctly marked animals, of which no photographs of sufficient quality were obtained during the study. Scoring for distinctiveness of dorsal fins resulted in the removal of 17 individuals from the dataset. These individuals were identified from scarring and marks other than the nicks and notches on the trailing edge of the dorsal fin, but were not sufficiently marked for capture–recapture analyses. Altogether, 304 independent individuals from a total of 1499 captures remained for inclusion in the capture–recapture analyses. The proportion of distinctly marked individuals using the study area was estimated to be 0.93 (s.e. 0.01).

### *Model selection and abundance of distinctly marked individuals*

The best-fitting model to our data, determined by the lowest  $AIC_c$  value, was that with constant apparent survival rate, time-varying random temporary emigration and time-varying capture probabilities (Table 2). The estimated abundance of distinctly marked individuals ( $\hat{N}_m$ ) varied between 107 and 194 among the years (Table 3). The second model in the set (Table 2), with  $\Delta QAIC < 2$ , also fitted the data adequately. For this model, the parameter for apparent survival rate was kept constant, emigration parameter  $\gamma''$  was allowed to vary with time, emigration parameter  $\gamma'$  was kept constant and capture probability was allowed to vary with time. All parameter estimates from this model were very similar to the estimates from the first model and will not be discussed separately.

Pollock's closed robust design model, allowing for heterogeneous and time-varying capture probabilities for individuals, with constant apparent survival rate, time-varying random temporary emigration and time-varying capture probabilities also fitted the data. This model was very complex, with 71 parameters. Resulting parameter estimates were also very similar to those estimated by the best fitting model in a set in which no model accounted for heterogeneity in individual capture probabilities (see Supplementary Material). For this reason, we focussed on the model that did not account for heterogeneity in capture probabilities.

### ***Total abundance***

During the 5-year study period, the total number of bottlenose dolphins using the study area ( $\hat{N}_{total}$ ) varied from the lowest estimate of 115 in 2008, to the highest estimate of 208 in 2010 (Table 3).

### ***Apparent survival and temporary emigration***

The model that best fitted the data gave a constant annual apparent survival-rate estimate of 0.95 (s.e. 0.02, 95% CI 0.87–0.98). The model also suggests a random temporary emigration pattern, in which the probability of an individual being present in the study area in a given study period is independent on whether or not it was present in the study area in the previous sampling period. Temporary emigration rates were estimated to be 0.66 (s.e. 0.05) in 2007–2008, 0.33 (s.e. 0.04) in 2008–2009, 0.33 (s.e. 0.07) in 2009–2010 and 0.5 (s.e. 0.08) in 2010–2011.

## **Discussion**

The presented estimates of abundance and rates of apparent survival and temporary emigration represent the first available estimates for bottlenose dolphins in Shark Bay and in Western Australia. Abundance estimates varied among years, from the lowest estimate of 115 (95% CI 105–125)



individuals in 2008 to the highest estimate of 208 (95% CI 174–242) individuals in 2010. Since each capture–recapture estimate of abundance reflects the number of animals using the study area during the study period, the variability in our abundance estimates is unlikely to be indicative of fluctuations in the true population size. Rather, it represents how individuals used the study area during each study period. Inter-annual variation in sampling effort may affect the precision of each abundance estimate, but is unlikely to cause bias in the estimates. Simple density estimates calculated from our results ( $\hat{N}/\text{area}$ ) were between 0.53 (s.e. 0.02) and 0.92 (s.e. 0.02) individuals per km<sup>2</sup> for our 226-km<sup>2</sup> study area, being higher than the density estimates of 0.19 and 0.14 individuals per km<sup>2</sup> reported in Preen *et al.* (1997) for all of Shark Bay. However, our density estimates are likely to be overestimates, because the size of the study area does not take into account those individuals' home range that may lie partially outside the study area (Williams *et al.* 2002). More robust home-range information for animals in the study area should be a priority of future research.

Comparisons of bottlenose dolphin-abundance estimates among populations are difficult, given the variety of methods used to obtain information on population abundance or density. In subtropical Moreton Bay, Queensland, the bottlenose dolphin population is thought to be considerably larger than many other bottlenose dolphin populations in subtropical and tropical climates, most likely attributable to the high productivity in the bay (Lukoschek and Chilvers 2008). Bottlenose dolphin abundance was assessed for a part of Moreton Bay, ~350 km<sup>2</sup>, using both capture–recapture and line-transect methods (Lukoschek and Chilvers 2008). Capture–recapture estimates (mean ± s.e.) were 512 ± 98.8 and 622 ± 116.7 individuals in 1997 and 1998, respectively, and a line-transect estimate was 407 ± 113.5 individuals in 2000 (Lukoschek and Chilvers 2008). Simple density estimates calculated from these results are 1.46 (s.e. 0.28) and 1.78 (s.e. 0.33) individuals per km<sup>2</sup> for the capture–recapture estimates and 1.16 (s.e. 0.28) individuals per km<sup>2</sup> for the line-transect estimate. Comparing densities, dolphin abundance in the Moreton Bay study area appears to be higher than that in the Shark Bay study area. However, the location of the study area (when not covering the range of the entire population) and time of sampling may affect the resulting abundance estimates because the

density of animals is not necessarily spatially or temporally uniform, but can vary across habitat types because of predation pressure and/or prey availability (Heithaus and Dill 2002). This further complicates comparisons among populations. To overcome some of the difficulties in comparing abundance estimates among populations, dedicated studies in which sampling is designed for the purpose of estimating abundance are needed. Photo-identification protocols should also be standardised in capture–recapture studies for this purpose.

Our results indicated that the probabilities of animals being temporary emigrants were quite high (0.33–0.66) in different years and were likely to be random in nature. Research in the eastern Shark Bay estimated average home-range size to be 47.8 km<sup>2</sup> (s.e. 5.7) for female dolphins and 101.71 km<sup>2</sup> (s.e. 3.7) for males (Watson 2005; Randić *et al.* 2012). Both of these estimates were considered conservative and true home-range sizes may be much higher. Although we did not expect many new animals to have entered the western gulf study area through recruitment or immigration from other populations, we conclude that it was small (226 km<sup>2</sup>) in comparison to the likely home ranges of some dolphins. The study area was also unlikely to encompass the entire range of many individuals, with animals moving in and out of the study area because their home ranges extend beyond its limits. Therefore, we could not assume population closure over the duration of each primary period. However, if individuals are randomly moving in and out of the study area, as indicated by the random temporary emigration pattern, no bias should be introduced to the abundance estimates from closed population models; although the estimates may be less precise (Kendall 1999).

Should precise estimates of abundance and density be required in the future, study design will have to balance the need for a larger sampling area with practical issues, such as research costs and logistics. To better understand how individuals use the defined study area and determine the range of the larger meta-population, further investigation into movement patterns of individuals is required. This could be addressed by using multi-state models (Schwarz *et al.* 1993; Williams *et al.* 2002) applied to data

that are collected in multiple states, here referring to multiple areas. As animals move from one discrete location to another, sampling multiple locations will allow for better description of population status. This sampling design allows for estimation of location-specific survival rates and transition probabilities among states (e.g. locations).

Our estimate of apparent survival (0.95) is the product of true survival and permanent emigration and can be used only as an estimate of true survival if it can be assumed that permanent emigration is zero. If permanent emigration and fidelity ( $1 - \text{permanent emigration}$ ) can be estimated separately from, say, a telemetry study, then true survival can be estimated by taking the ratio of apparent survival, divided by fidelity. This was not possible in our study; however, permanent emigration from the study area seems unlikely, given that bottlenose dolphins in Shark Bay use their natal range as part of their adult home range (Krützen *et al.* 2004). We therefore expect true annual survival to be at least 0.95 for this population.

There are several special considerations when using photo-identification data for population demographic capture–recapture analyses (Gowans and Whitehead 2001; Friday *et al.* 2008; Hammond 2010). First and foremost, individuals should be photographed so as to ensure sufficient quality to confirm identification, as well as to ensure the photograph passes the quality-grading process. This will increase the captures available for inclusion in the analyses. Second, because most cetacean studies span a relatively long period of time and it is common for numerous personnel to be involved in the photo-identification process, protocols should be designed to ensure repeatability and consistency over time.

Heterogeneity of capture probabilities is ubiquitous in capture–recapture studies and any violation of the assumption of equal probability of capture means that abundance estimates may be biased

downward (Pollock *et al.* 1990; Williams *et al.* 2002). In this study, however, extra analyses allowing for individually heterogeneous capture probabilities suggest that any such bias is small because those estimates of population abundance were almost identical to estimates from a model that did not allow for heterogeneity (see Supplementary Material).

So as to reduce misidentification and heterogeneity in capture probabilities, photographs should be graded for quality and fins graded for distinctiveness. As a general rule, the least distinctly marked individual included in the dataset should be identifiable from the lowest-quality photograph included in the analyses. We deemed misidentification due to mark change to be minimal in this study. Data were collected in consecutive years and the majority of individuals were captured, although not necessarily on transect effort, each year. This, together with the longevity of marks used for identification (Wilson *et al.* 1999), means that mark changes were likely to be tracked successfully.

Because some individuals in the population are not marked, it is important to estimate the proportion of marked individuals in the population. A high proportion (0.93) of individuals in our study area were distinctly marked, indicating that most weaned individuals in the study area have acquired sufficient marks for capture–recapture analyses. To ensure a relatively unbiased estimation, only surveys in which all individuals were photographed with sufficient quality were used for estimating the proportion of marked individuals in the population.

When using photo-identification data, collected for other purposes, for capture–recapture analyses it is important to consider how, or if, model assumptions can be satisfied to ensure that resulting estimates are not biased. Further research is needed to develop existing protocols and models to better meet the requirements for capture–recapture analyses when studying cetaceans. The approach and analytical techniques employed for abundance and other population demographic-parameter estimations in this

study are applicable to other study sites beyond Shark Bay, as well as to other marine megafauna species that are individually identifiable.

These results represent the first robust abundance estimates for bottlenose dolphins in any part of Shark Bay and provide an important baseline for future comparisons in the study area. In the face of climate change and the direct and indirect effects of increased coastal development, seagrass ecosystems have been identified among the most threatened ecosystems on the planet (Waycott *et al.* 2009). Furthermore, coastal development has been identified as ‘the major threat’ to coastal dolphin populations around Australia (DEWHA 2010). Shark Bay’s seagrass-centric ecosystem would be markedly altered by changes in sea temperature and sea level, as well as by modifications to habitat by anthropogenic activity. Accordingly, proposed increases in anthropogenic activity (e.g. dredging to accommodate larger ships and more shipping traffic) should be carefully scrutinised in terms of their potential impacts on coastal dolphins and their critical habitats, before approvals are granted (Bejder *et al.* 2012). Baseline data on the marine megafauna that rely on this productive ecosystem will prove critical for the ongoing conservation management of the Shark Bay World Heritage Area.

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Fig. 1. The study area covered an area of approximately 226 km<sup>2</sup> off Useless Loop in the western gulf of Shark Bay, Western Australia. Solid lines indicate 10 parallel transect lines, each ~11 km in length and 2 km apart, which were surveyed for dolphins by using boat-based photo-identification techniques.



Fig. 2. Photo-identification photograph of an adult bottlenose dolphin with a distinctly marked dorsal fin suitable for individual identification for capture–recapture analyses.



Table 1. Field effort to estimate abundance and other demographic parameters of bottlenose dolphins in the western gulf of Shark Bay, Western Australia

Year	Study period	Effort (days)	Effort (h)	Repeats of transects
2007	29 June–3 September	28	98	5
2008	9 August–24 September	23	90	5
2009	4 April–23 July	51	176	10
2010	15 April–25 July	31	94	5
2011	17 May–28 August	22	58	3

Table 2. Capture–recapture models fitted to the capture histories of bottlenose dolphins to estimate parameters for population size ( $\hat{N}$ ), survival (?), emigration ( $\gamma''$ ,  $\gamma'$ ) and capture probability ( $p$ )

Model	Restrictions	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	AIC <sub>c</sub> weight
$\varphi(\cdot)\gamma''(t)\gamma'(t)p(t)$	$\gamma'' = \gamma'$	805.7765	0.0000	0.40186
$\varphi(\cdot)\gamma''(t)\gamma'(\cdot)p(t)$		805.8964	0.2199	0.36002
$\varphi(\cdot)\gamma''(t)\gamma'(t)p(t)$		808.6124	2.8359	0.09733
$\varphi(t)\gamma''(t)\gamma'(t)p(t)$	$\gamma'' = \gamma'$	808.6448	2.8683	0.09577
$\varphi(t)\gamma''(t)\gamma'(\cdot)p(t)$		811.0240	5.2475	0.02915
$\varphi(t)\gamma''(t)\gamma'(t)p(t)$		812.2458	6.4693	0.01582
$\varphi(t)\gamma''(\cdot)\gamma'(t)p(t)$		826.3089	20.5324	0.00001
$\varphi(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma'$	826.5702	20.7937	0.00001
$\varphi(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$		827.1846	21.4081	0.00001
$\varphi(\cdot)\gamma''(\cdot)\gamma'(t)p(t)$		827.5092	21.7327	0.00001
$\varphi(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$		828.7547	22.9782	0.00000
$\varphi(t)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma' = 0$	829.1983	23.4218	0.00000
$\varphi(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$	$\gamma'' = \gamma' = 0$	999.6622	193.8857	0.00000
$\varphi(\cdot)\gamma''(\cdot)\gamma'(\cdot)p(t)$		1002.0314	196.2549	0.00000

Table 3. Capture–recapture estimates of abundance of distinctly marked individuals and corrected abundance estimates taking into account the proportion of unmarked individuals within the study area  $n$  = number of individuals captured,  $\hat{N}$  = estimated markable population size, s.e. = standard error, CI = confidence interval,  $\hat{N}_{total}$  = estimated total population size after correcting for the proportion of distinctly marked individuals

Year	$n$	Distinctly marked population			Total population		
		$\hat{N}$	s.e.	95% CI	$\hat{N}_{total}$	s.e.	95% CI
2007	105	112	3.5	108–123	120	5.0	111–130
2008	99	107	3.8	103–118	115	5.2	105–126
2009	186	193	2.9	189–201	207	5.0	197–217
2010	132	194	15.4	170–232	208	17.3	177–245
2011	96	160	20.0	131–212	172	22.0	134–221