



Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) in Adelaide's coastal waters, South Australia

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ABSTRACT

Little is known about the ecology and behavior of southern Australian bottlenose dolphins (*Tursiops* sp.). This hinders assessment of their conservation status and informed decision-making concerning their management. We used boat-based surveys and photo-identification data to investigate site fidelity, residency patterns, and the abundance of southern Australian bottlenose dolphins in Adelaide's coastal waters. Sighting rates and site fidelity varied amongst individuals, and agglomerative hierarchical cluster analysis led to the categorization of individuals into one of three groups: occasional visitors, seasonal residents, or year-round residents. Lagged identification rates indicated that these dolphins used the study area regularly from year to year following a model of emigration and reimmigration. Abundance estimates obtained from multisample closed capture-recapture models ranged from 95 individuals (SE \pm 45.20) in winter 2013 to 239 (SE \pm 54.91) in summer 2014. The varying levels of site fidelity and residency, and the relatively high number of dolphins found throughout the study area highlights the Adelaide metropolitan coast as an important habitat for bottlenose dolphins. As these dolphins also appear to spend considerable time outside the study area, future research, conservation, and management efforts on this population must take into account anthropogenic activities within Adelaide's coastal waters and their adjacencies.

Key words: photo-identification, capture-recapture, agglomerative hierarchical clustering, closed population model, population size, Gulf St Vincent, metropolitan coast, anthropogenic impacts, bottlenose dolphin.

Coastal ecosystems are largely impacted by anthropogenic activities due to increasing population growth in these areas and the associated expansion of urban development (Bulleri and Chapman 2010). Consequently, coastal dolphins are subject to a variety of potential anthropogenic threats. These threats, coupled with the dolphins'

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long life span, low reproductive rates, and high trophic level, render coastal dolphins particularly vulnerable to anthropogenic impacts. For example, heavy boat traffic puts dolphins at risk of boat strikes and increased noise pollution (Nowacek *et al.* 2001), while local fishing activities can bring dolphins into direct contact with fishing gear, causing injury or mortality to individuals through boat interactions, entanglement, or ingestion (Kemper *et al.* 2005, Powell and Wells 2011). Depending on the levels of mortality, this may lead to population declines (*e.g.*, Burkhart and Slooten 2003). Dolphin watch and swim-with tour activities can also lead to adverse behavioral changes and displacement from critical habitats (Bejder *et al.* 2006, Filby *et al.* 2014), while toxins from heavy metal emissions and runoff from wastewater treatment plants can be bio-accumulated and lead to health issues, including compromised immune systems (Lavery *et al.* 2008, Van Bresseem *et al.* 2009, Balmer *et al.* 2011). Effective management and mitigation of human impacts on coastal dolphin populations requires robust information on their site fidelity, residency patterns, population size, and habitat use (Parra *et al.* 2006, Balmer *et al.* 2013). Such data provide the basis for management decisions in environmental impact assessments, species conservation assessments, protected area design, conservation and research investment, and management intervention.

Bottlenose dolphins (*Tursiops* spp.) are distributed along the entire Australian coast (Ross and Cockcroft 1990). It was previously thought that only two species of bottlenose dolphins were present in Australian waters; the Indo-Pacific bottlenose dolphin (*T. aduncus*) and the common bottlenose dolphin (*T. truncatus*) (Rice 1998, Leduc *et al.* 1999, Möller and Beheregaray 2001). However, a third species, the Burrnun dolphin (*T. australis*), was recently described in southern Australian waters based on morphological and genetic evidence (Charlton-Robb *et al.* 2011). Burrnun dolphins are found in inshore and coastal waters of southern Australia, including regions of Victoria, Tasmania, and South Australia (Möller *et al.* 2008, Charlton-Robb *et al.* 2011). The validity of this new species, however, remains under debate (Committee on Taxonomy 2015, Perrin *et al.* 2013), and thus we refer to the dolphins in our study as southern Australian bottlenose dolphins (*Tursiops* sp.).

Studies of southern Australian bottlenose dolphins have been conducted in Victoria on two resident populations; one inhabiting Port Phillip Bay, and the other, Gippsland Lakes (Dunn *et al.* 2001, Scarpaci *et al.* 2003, Filby *et al.* 2014). Due to their genetic distinctiveness (Charlton-Robb *et al.* 2011), small population size (approximately 120 individuals in Port Phillip Bay) and year-round residency (Dunn *et al.* 2001), they are currently listed as threatened in Victoria under the Victorian Flora and Fauna Guarantee Act 1988.

Very little is known about southern Australian bottlenose dolphin (here after referred to as bottlenose dolphin) populations outside of Victoria. A resident population of approximately 30 bottlenose dolphins inhabits the Port River estuary and Barker Inlet, Gulf St Vincent (GSV) in South Australia (SA) (Steiner and Bossley 2008, Cribb *et al.* 2013). This area is also known to be used by a larger number of nonresident dolphins (Steiner and Bossley 2008). Within GSV, boat surveys indicate that sightings of bottlenose dolphins occur across the majority of gulf waters (Kemper *et al.* 2008). It is likely that individuals sighted within the Port River estuary and Barker Inlet form part of a larger population within GSV. Unfortunately, systematic boat-based survey efforts have not extended past the estuarine boundaries of the Port River and Barker Inlet and, consequently, the demography of bottlenose dolphins inhabiting SA coastal waters is largely unknown.

Bottlenose dolphins within GSV live adjacent to Adelaide's metropolitan coast, Australia's fifth largest city. Individuals within this semiopen and highly urbanized coastal area are at potential risk from several anthropogenic activities, including interactions with recreational fishing and dolphin-swim boats (Peters *et al.* 2012, Byard *et al.* 2013), intentional killings (Kemper *et al.* 2008), habitat loss and degradation (Edyvane 1999), and pollution (Lavery *et al.* 2008). Furthermore, bottlenose dolphins within this area were recently subjected to an outbreak of cetacean morbillivirus, resulting in the death of at least 36 individuals (Kemper *et al.* 2013). These threats, coupled with their population characteristics, highlight the need for baseline information on their demographic parameters to aid management and conservation efforts in the region.

In this study we used boat-based surveys and photo-identification data collected along Adelaide's metropolitan coast from December 2012 to August 2014 to estimate site fidelity, residency patterns, and the abundance of bottlenose dolphins. Our results provide important information on the population ecology of bottlenose dolphins in Adelaide's coastal waters for the implementation of future conservation and management strategies.

MATERIALS AND METHODS

Study Site and Data Collection

Monthly boat-based surveys were conducted between December 2012 and August 2014 inclusive within GSV, a relatively shallow and large inverse estuary in the southern coast of Australia (Fig. 1). No surveys were carried out in spring (September to November) due to generally poor weather conditions during this time of the year. Surveys covered a total of 40 km of coastline from North Haven to Hallett Cove, and extended up to 7 km offshore, covering approximately 195 km² of the metropolitan coastal waters of Adelaide. Surveys were conducted on-board two vessels: (1) *Tom Thumb*, a 6.5 m rigid hull inflatable boat with twin 80 hp outboard motors and (2) *Tethys*, a 6.1 m aluminum boat with one 100 hp outboard motor. All surveys were conducted in Beaufort sea state <3 and swell ≤1 m. Surveys followed a predetermined zigzag line transect layout (*ca.* 100 km) at speeds of approximately 13–17 km/h. In good weather conditions, the whole study area was covered in one day. Only surveys in which all transects were completed in one day were included for data analyses.

Observations of bottlenose dolphins were made by 3–5 (mode 4) observers by naked eye and with the aid of 7 × 50 Fujinon binoculars. Dolphins were defined as part of the same group if they were within a 100 m radius of each other, and heading in the same direction if traveling (Irvine *et al.* 1981). Once a dolphin group was sighted, survey effort was ceased and the dolphins were approached to a distance of approximately 30 m to record data on location (using a hand-held Global Positioning System), time, group size and age composition. These data were recorded every 5 min thereafter or when there was a change in behavior, group size and/or composition. Individuals were assigned to one of three age classes (adults, juveniles, and calves), according to body size, and degree of independence from an adult individual. Adults were defined as fully grown individuals of approximately 2.5–3 m in body length, juveniles were defined as individuals of approximately 1.5–2.5 m in body length, and calves were defined as individuals up to 1.5 m in body length and in close association with an adult (adapted from Peters *et al.* 2012).

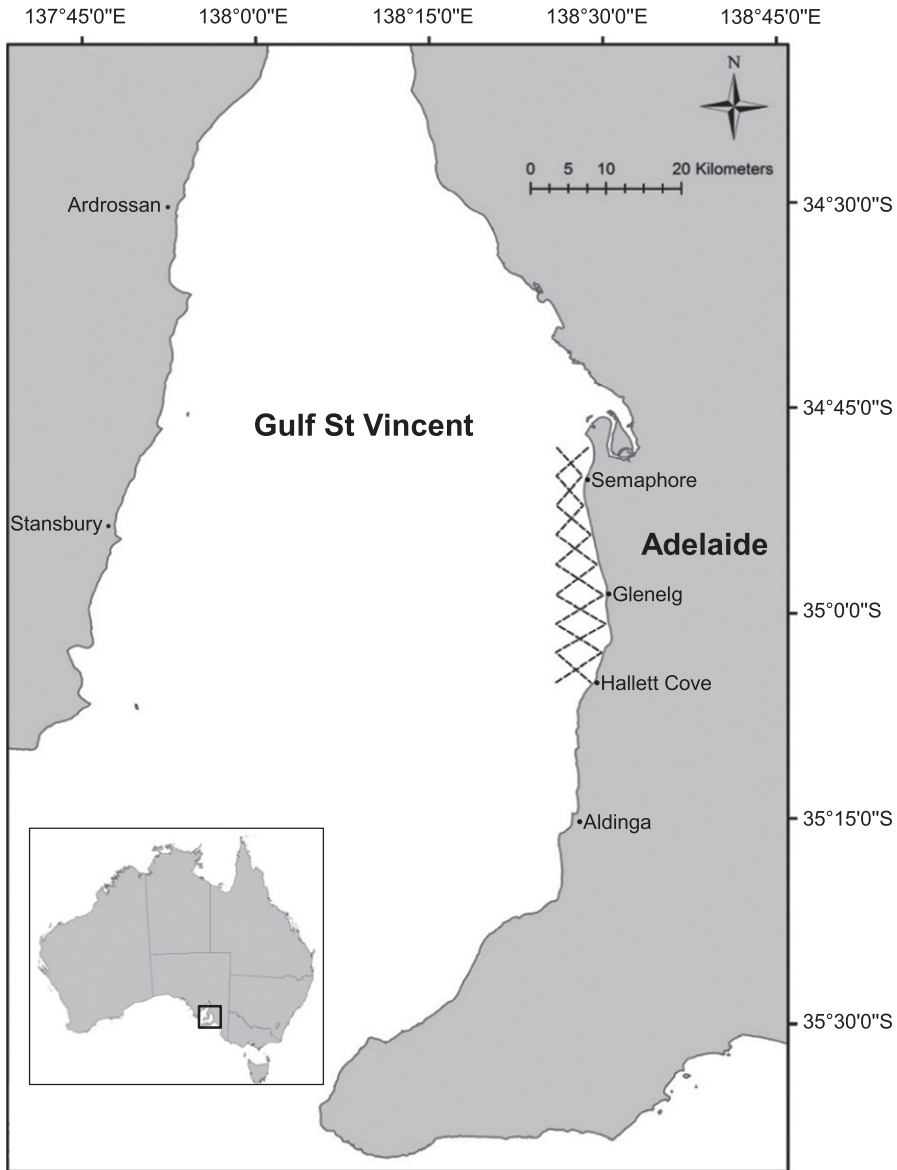


Figure 1. Map of the study area in South Australia. Boat surveys took place in Adelaide's coastal waters (transects are located along the dashed line).

After the initial encounter, we approached the group to a distance of approximately 10 m for photo-identification of individual dolphins. Photographs were taken using a digital SLR with a 70–300 mm zoom lens. We aimed to photograph all individuals within the group irrespective of their age and/or distinctiveness. Once photographs of all individuals in the group were taken, the boat moved away from the group and the survey recommenced along the transect line where the group was first observed.

Photo-Identification

Photographs containing dorsal fins were assigned to three categories (excellent, good, and poor) based on photo quality. Photo quality was assessed according to focus, contrast of the dorsal fin to the background, and the angle and size of the dorsal fin relative to the frame (Urian *et al.* 1999). Individual dolphins were primarily identified using the unique and natural marks on their dorsal fins (Würsig and Jefferson 1990), including nicks and notches on the leading and trailing edges. Secondary features (pigmentation, scarring, and peduncle marks) were also used for photo-identification. Distinctiveness was used as a measure of how identifiable an individual is, based on the number of marks on both leading and trailing edges of the dorsal fin. Individuals with very distinct fins were given a distinctiveness rating of D1; those with an average amount of information were given a rating of D2; and nondistinctive individuals were given a rating of D3 (criteria based upon the Sarasota Dolphin Research Program, 2006, adapted from Urian *et al.* 1999). Only excellent and good quality images containing distinguishable individuals (D1 and D2) were used to identify individuals and develop an identification catalogue for analysis (Würsig and Jefferson 1990, Read *et al.* 2003). This approach ensures that marks of distinguishable individuals and any changes occurring to them over time can be tracked and correctly identified, which minimizes misidentification and heterogeneity in capture probabilities. Calves were excluded from analysis as they generally lack identifiable marks and remain in close association with their mothers.

Site Fidelity

In this study, an individual “capture” was defined as a photograph of sufficient quality and distinctiveness to be added to the photo-identification catalog. To investigate the tendency of animals to remain in, or return to, and reuse the study area (*i.e.*, site fidelity), we used the total number of captures for each individual to calculate three measures of site fidelity: (1) seasonal sighting rates (the number of seasons a dolphin was identified in as a proportion of the total number of seasons surveyed), (2) monthly sighting rates (the number of months a dolphin was identified in as a proportion of the total number of months surveyed) (Parra *et al.* 2006), and (3) site fidelity indices. Site-fidelity indices were calculated as the ratio between the number of recaptures for each dolphin and the number of survey days (defined as the number of survey days from an individual’s first capture to its last capture) (Simpfendorfer *et al.* 2011, Daly *et al.* 2014, White *et al.* 2014). A site fidelity index value of one indicates that the individual was captured on all survey days from an individual’s first capture to its last capture, and a value of zero indicates that it was never recaptured after its first capture. This measure allows the comparison of site fidelity indices between dolphins sighted over different time periods (*e.g.*, Daly *et al.* 2014).

To distinguish groups or “clusters” of individuals with similar degrees of site fidelity, we incorporated seasonal and monthly sighting rates, and site fidelity indices into an agglomerative hierarchical cluster analysis performed in XLStat V 5.01 (Addinsoft, Addinsoft Deutschland, Andernach, Germany). Agglomerative hierarchical clustering (AHC) is a bottom-up clustering method that starts with each observation as an individual cluster. These clusters are then successively combined based on similarity until all clusters have been combined into one (Legendre and Legendre 2012). AHC requires two components: (1) a measure to calculate the dissimilarity between individuals being clustered, and (2) an agglomerative clustering algorithm.

We chose Euclidean distance as our dissimilarity measure and Ward's method (minimum variance) as our clustering algorithm due to its known robustness (Ward 1963, Cao *et al.* 1997, Singh *et al.* 2011). AHC results are displayed in a dendrogram that provides the suitable clusters into which the data could be grouped. The dissimilarity threshold, or truncation, specifies a cut-off point along the dendrogram and represents the most appropriate number of clusters. We selected automatic truncation as it is based on the entropy criterion to define homogenous clusters; automatic truncation stops aggregating clusters when it finds a strong increase in dissimilarity levels (Li *et al.* 2004). To check the validity of the dendrogram, we calculated the cophenetic correlation coefficient (CCC), using the AHC method (selecting Euclidean distance and Ward's method) in StatistiXL V 1.11 (StatistiXL, Nedlands, Western Australia). The CCC is the correlation between the observed distance among pairs and the level at which they are joined on the dendrogram (Bridge 1993), where the closer the value of the CCC is to 1 the more accurately the clustering solution reflects the structure in the data.

Residency

Rates of movement into and out of the study area, and residency patterns (*i.e.*, amount of time identified individuals reside within the study area) were investigated using lagged identification rates (LIR). LIR is the probability that if an individual is identified within the study area at any particular time, it is identified in the study area some time lag later (Whitehead 2001). Plots of lagged identification rates against time provide an indication of the temporal use of the area by individual animals. If the population is closed, and identifications are independent, the LIR should remain constant and the probability is the inverse of the population size (Whitehead 2001). If there is emigration and or mortality, the LIR will typically fall with time lag. When the LIR drops off after a certain time lag and continues to level off above zero, this indicates that some individuals may remain resident and/or other individuals re-immigrate into the study area (Whitehead 2001). LIR were calculated only for individuals that were observed on at least five occasions; the average number of sightings for individual in our photo-identification catalog. This cut off point was selected to ensure a reliable representation of the data. Different models of no movement, emigration/mortality, and emigration + mortality (Whitehead 2001) were then fitted to the observed LIR data. Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc), was used for model selection (Burnham and Anderson 2002). LIR and model fitting was carried out using the computer software SOCPROG 2.1 (Whitehead 2009).

Abundance

Capture-recapture histories were compiled for each identified dolphin and abundance was estimated separately for each of the austral seasons: summer (December to February), autumn (March to May) and winter (June to August) (the number of sampling occasions per month is listed in Table 1). We considered the population to be likely closed to gains (births or immigration) and losses (deaths or emigration) during each season as sampling was completed over a relatively short period of time when considering the longevity of the study species (Hammond 2009). We estimated abundance using multisample closed capture-recapture population models, including Pledger's mixture models (which use two mixtures of

Table 1. Total number of survey days, per month, conducted along Adelaide's metropolitan coast between December 2012 and August 2014.

Year Season	2013									2014								
	Summer			Autumn			Winter			Summer			Autumn			Winter		
Months No.	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
survey days	2	10	0	7	5	6	4	0	0	4	10	2	13	5	0	4	5	6

capture probabilities to model individual heterogeneity) (Pledger 2000), in the program MARK (White and Burnham 1999). Capture probabilities were either set as constant (M_o), to vary with time (M_t), to be heterogeneous (M_b), or to be heterogeneous and vary with time (M_{tb}). Models including a behavioral response were not used as we found no significant influence of trap-dependence (see Results), which is expected with photo-identification, as animals are unlikely to be subjected to any stress due to the noninvasiveness of this technique. To measure over-dispersion of the data, the median of the variance inflation factor (\hat{c}) was estimated in MARK. Where over-dispersion was present (when median \hat{c} is > 1), models were adjusted accordingly and QAICc was used for model selection (Burnham and Anderson 2002). We chose to use multisample closed capture-recapture models for our analysis instead of open (*e.g.*, POPAN, Schwarz and Arnason 1996) or open-close population models (*i.e.*, Pollock's Robust Design; Pollock 1982) due to the following reasons: (1) when considering the longevity of this study species (30–40+ yr), our study period is of too short a duration (2 yr) to yield robust estimates of apparent survival; (2) our sampling periods were of reasonably short duration (austral seasons, 3 mo each) for population gains and losses to likely be minimal; and (3) our data showed evidence of heterogeneity of capture probabilities, suggesting that population models incorporating heterogeneity would be more appropriate (*e.g.*, Pledger's mixture models).

Validation of Capture-recapture Analysis

Violation of capture-recapture model assumptions can lead to biases in population estimates. Closed population models assume that (1) there are no births, deaths, emigration or immigration; (2) individual marks are retained and identified correctly; and (3) the sampling interval is instantaneous. Additionally, closed models that do not allow variation of capture probabilities also assume that (1) capture probabilities are homogenous among individuals, and that (2) there is no behavioral (trap) response from individuals (Begon 1983, Pollock *et al.* 1990). We used biological information about the species to investigate the potential for bias and goodness-of-fit tests to test for departures from the model assumptions.

Assumptions of homogenous capture probabilities are rarely met for cetacean populations (Read *et al.* 2003). Considering the longevity of the study species and the short sampling periods selected for analysis, we considered births, deaths and migration to be minimal. Furthermore, closure within each season was tested using program CloseTest (Stanley and Burnham 1999). To minimize incorrect identification of individuals, photographs were catalogued by a minimum of two independent researchers and only excellent and good quality photographs were used for analysis.

Analyses were also restricted to adult individuals with distinctive and long lasting marks that could be monitored over time. The assumption of instantaneous sampling was likely satisfied as the sampling periods were completed within a given day. Further, capture rates can be influenced by age, sex, and/or behavior as individuals may become trap “happy” or trap “shy.” Capture rates can also be influenced by an individuals’ site fidelity to an area, where higher and lower capture rates can be associated with resident and transient individuals, respectively. To test for heterogeneity in capture probabilities and trap-dependence we implemented goodness-of-fit tests (TEST 2 and TEST 3) in program U-CARE (Choquet *et al.* 2009) and RELEASE (implemented within MARK).

Total Population Size

Abundance estimates obtained from the capture-recapture procedure only account for the distinctly marked proportion of the population (individuals categorized as D1 or D2, described above). To estimate the size of the total population, estimates were adjusted to account for the proportion of unmarked individuals following (Wilson *et al.* 1999):

$$\hat{N}_t = \frac{\hat{N}_m}{\hat{\theta}},$$

where \hat{N}_t is the estimated total population size, \hat{N}_m is the estimated marked population size and $\hat{\theta}$ is the estimated proportion of distinctly marked individuals in the population. $\hat{\theta}$ was estimated using only groups where all individuals were photographed with sufficient quality, irrespective of distinctiveness (group score of 1, Nicholson *et al.* 2012). The total number of distinctive (D1 and D2) individuals was then divided by the total number of dolphins encountered within these groups (Nicholson *et al.* 2012). Standard errors for the total population size were derived from the variance of N following Williams *et al.* (2002) and modified according to Urian *et al.* (2015):

$$SE(\hat{N}_t) = \sqrt{N_t^2 \left[\frac{SE(\hat{N}_m)^2}{\hat{N}_m^2} + \frac{SE(\hat{\theta})^2}{\hat{\theta}^2} \right]}$$

and log-normal 95% confidence limits of the total population size were calculated by either multiplying or dividing the total abundance by a factor C (Burnham 1987), Williams *et al.* (2002):

$$\hat{N}_t^{\text{Lower}} = \frac{\hat{N}_t}{C} \text{ and } \hat{N}_t^{\text{Upper}} = \hat{N}_t \times C,$$

where

$$C = \exp \left(1.96 \sqrt{\ln \left\{ 1 + \left[\frac{SE(\hat{N}_t)}{\hat{N}_t} \right]^2 \right\}} \right).$$

RESULTS

Survey Effort and Photo-identification

A total of 83 survey days were completed (approximately 545 h of survey effort, covering a distance of approximately 8,134 km) between December 2012 and August 2014 (Table 1). Survey effort varied between months and seasons due to restrictions from weather conditions. A total of 244 distinctly marked individuals were identified, with 69 individuals (28%) sighted only once and 175 (72%) sighted on more than one occasion. The maximum number of resightings for any one individual was 16 (Fig. 2). The discovery curve (cumulative number of identified animals; Fig. 3) began to plateau toward the end of the study period, suggesting that the majority of the identifiable individuals in the study area had been identified. Our analysis of high quality photos (excluding calves) revealed that 0.85 (SE \pm 0.01) of individuals within the population were distinctively marked.

Site Fidelity

Seasonal sighting rates of bottlenose dolphins ranged from 0.17 (individuals sighted in one season only) to 1.00 (individuals sighted in all seasons) (mode = 0.17)

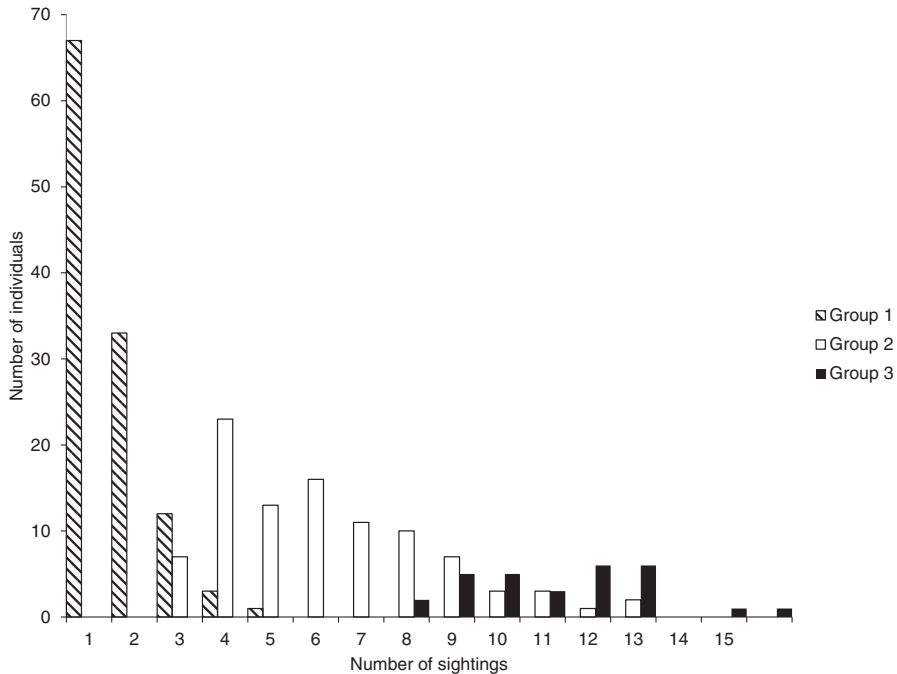


Figure 2. Number of sightings of southern Australian bottlenose dolphins along Adelaide's metropolitan coast between December 2012 and August 2014 according to the three clusters of site fidelity identified by the agglomerative hierarchical cluster analysis (group 1, patterned; group 2, not shaded; and group 3, shaded).

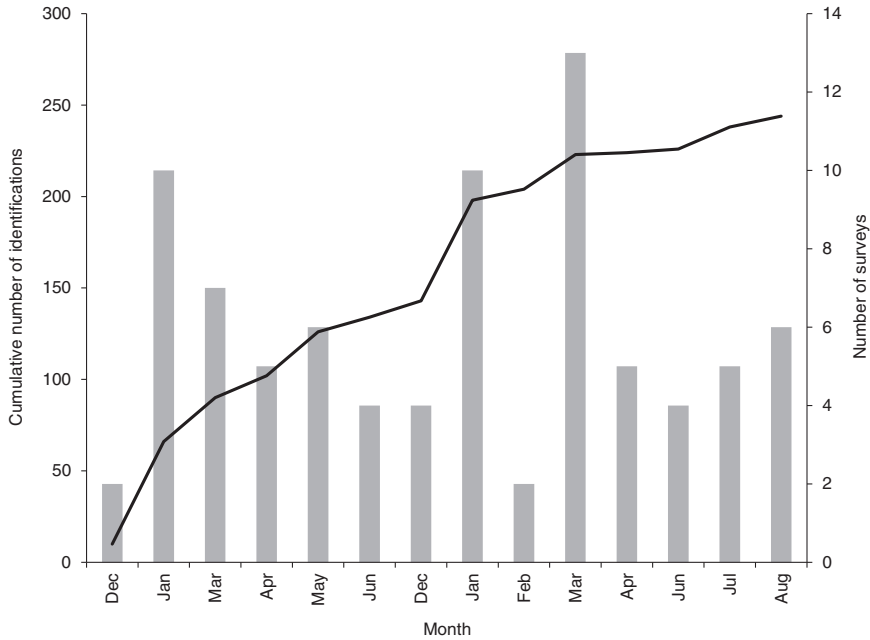


Figure 3. Discovery curve of the cumulative number of southern Australian bottlenose dolphins identified along Adelaide's metropolitan coast between December 2012 and August 2014. Vertical bars represent the number of identifications per survey day.

(Table 2). Monthly sighting rates ranged from 0.07 (individuals sighted in 1 mo only) to 0.71 (individuals sighted up to 10 mo) (mode = 0.07). Site fidelity indices ranged from 0 to 0.5 (mode = 0).

The AHC analysis provided a reasonable separation of individuals into clusters based on the three measures of site fidelity (Fig. 4a); the AHC CCC was 0.71, indicating the dendrogram is a reasonable representation of the dissimilarities among

Table 2. Average sighting rates and site fidelity indices (SF) of southern Australian bottlenose dolphins in groups 1, 2, and 3 as determined by agglomerative hierarchical cluster (AHC) analysis. SD = standard deviation of mean and IR = interquartile range.

Sighting rate	Mean	SD	Mode	Median	25%–75% IR
Group 1					
Seasonal	0.22	0.08	0.17	0.17	0.17–0.33
Monthly	0.11	0.05	0.07	0.07	0.07–0.14
SF Index	0.06	0.13	0	0	0.00–0.07
Group 2					
Seasonal	0.58	0.08	0.50	0.50	0.50–0.67
Monthly	0.32	0.09	0.21	0.29	0.21–0.36
SF Index	0.11	0.04	0.13	0.10	0.08–0.13
Group 3					
Seasonal	0.87	0.07	0.83	0.83	0.83–0.83
Monthly	0.55	0.09	0.50	0.57	0.50–0.64
SF Index	0.15	0.03	0.11	0.15	0.14–0.18

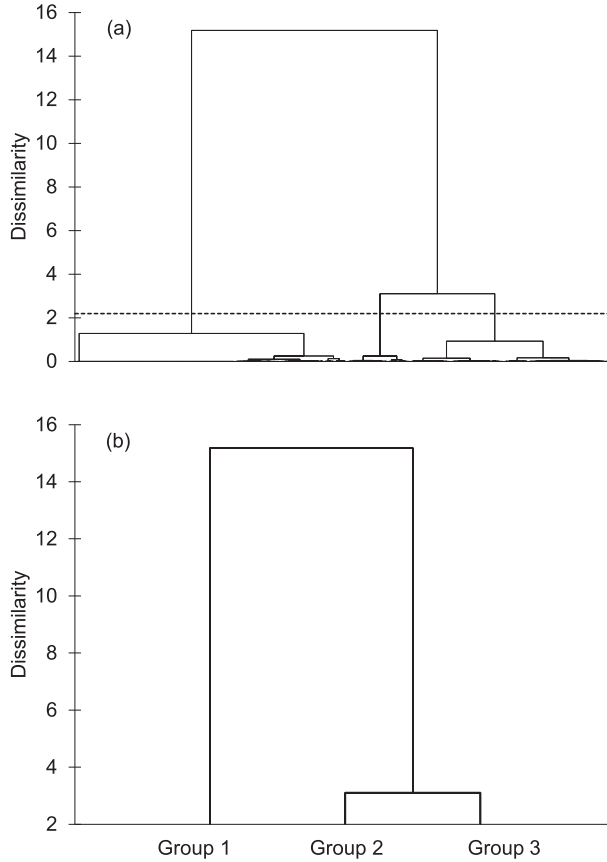


Figure 4. Dendrogram of the agglomerative hierarchical clustering (AHC) analysis separating clusters of southern Australian bottlenose dolphins based on three measures of site fidelity: seasonal sighting rate, monthly sighting rate and site fidelity indices. Dissimilarity threshold (cut-off point) was 2.19, resulting in three clusters; group 1: occasional visitors, group 2: seasonal residents, and group 3: year-round residents.

observations. The dissimilarity threshold was estimated at 2.19, which grouped individuals into three main clusters (Fig. 4b). Group 1 consisted of 119 individuals that were sighted only once or sighted across 3 mo (monthly sighting rate = 0.07–0.21), and thus included the occasional visitors to the study site. The remaining individuals were classed as either group 2 (comprising 96 individuals) or group 3 (comprising 29 individuals). The number of sightings for individuals within group 3 (median = 11, SE \pm 0.37) was significantly larger than the number of sightings for individuals within group 2 (median = 6, SE \pm 0.24) (Mann-Whitney, $U = 176.5$, $P < 0.001$, Fig. 2). Seasonal sighting rates, monthly sighting rates, and site fidelity indices were on average larger for group 3 in comparison to group 2 (Table 2). Thus, individuals within group 2 appear to be seasonal residents to the area, while individuals within group 3 appear to be year-round residents.

Residency

The LIR began to fall after periods of approximately 10 to 100 d (Fig. 5). This suggests that the population consists of a mixture of individuals with different degrees of residency. Some individuals may spend short periods of time (10 d) inside the study area, while others stayed up to 100 d before moving outside the area. The lagged identification rate also leveled off above zero (Fig. 5), suggesting that some animals are residents and others re-immigrate into the study area after long time lags.

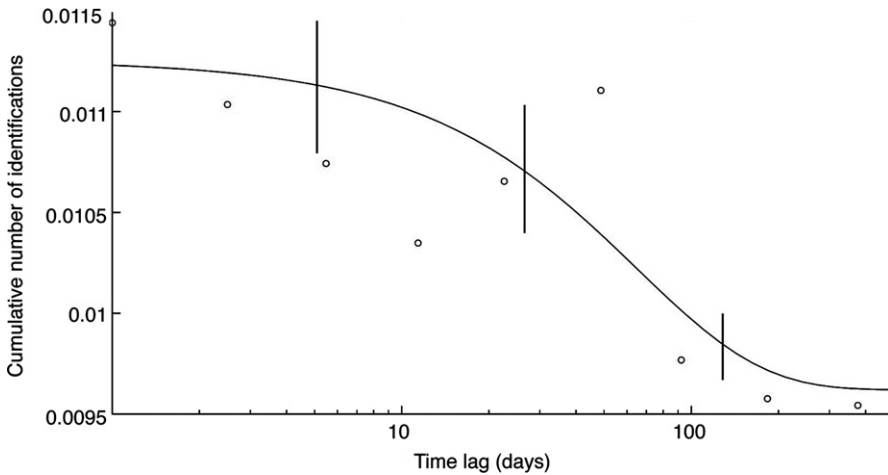


Figure 5. Lagged identification rates (LIRs) of individual southern Australian bottlenose dolphins sighted five or more times along Adelaide's metropolitan coast. Data points are represented by circles with the best-fit model (emigration + reimmigration) fitted to the data.

Table 3. Models fitted to observed lagged identification rate (LIR) data of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. For description of model equations see Whitehead (2001). The model that best fitted the data according to Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc) is shown in bold. Δ QAIC indicates how well the data support the less favored model (Burham and Anderson 2002).

Model equation	Model explanation	QAIC	Δ QAIC
$(1/a1)*\{(1/a3) + (1/a2)*\exp[-(1/a3 + 1/a2)*td]\}/(1/a3 + 1/a2)$	Emigration + reimmigration	3,1039.3	
$a2*\exp(-a1*td)$	Emigration/mortality	3,1042.3	2.9
$(1/a1)*\exp(-td/a2)$	Emigration/mortality	3,1042.3	2.9
$a1$	Closed	3,1042.6	3.3
$1/a1$	Closed	3,1042.6	3.3
$a2 + a3*\exp(-a1*td)$	Emigration + reimmigration	3,1044.6	5.3
$[\exp(-a4*td)/a1]*\{(1/a3) + (1/a2)*\exp[-(1/a3 + 1/a2)*td]\}/(1/a3 + 1/a2)$	Emigration + reimmigration + mortality	3,1044.8	5.4
$a3*\exp(-a1*td) + a4*\exp(-a2*td)$	Emigration + reimmigration + mortality	3,1045.3	5.9

Of the models applied to the data, the model of emigration + reimmigration was of best fit (Table 3). The emigration + reimmigration model estimated that approximately 89 (88.8, SE \pm 22.8) individuals were present within the study area at any one time. Residency time inside the study area was estimated at over one year (446.8, SE \pm 244.3), and time spent outside the study area was estimated at approximately 76 d (75.9, SE \pm 92.6).

Abundance

Results from CloseTest indicated that all seasons could be considered closed with no significant gains (births or immigration) or losses (deaths or emigration) of individuals from the population ($P \geq 0.05$). Goodness-of-fit tests conducted in U-CARE showed no effect of trap-dependence (TEST2.CT: $2 = 3.17$, $df = 3$, $P = 0.36$; TEST2.CL: $2 = 2.61$, $df = 2$, $P = 0.27$). However, we found a significant effect of transience (TEST3.SR: $2 = 35.54$, $df = 4$, $P < 0.001$), which suggests heterogeneity in capture probabilities.

Table 4. Multi-sample closed capture-recapture model selection, and abundance estimates for the marked population (\hat{N}_m) and the total population size accounting for unmarked individuals (\hat{N}_t) of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Capture probabilities were modelled to be constant (M_{ij}), to vary with time (M_t), to be heterogeneous (M_{ij}), or to be heterogeneous and vary with time (M_{ij}). The models that best fitted the data according to Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc) are shown in bold. SE = standard error and CI = 95% confidence intervals.

Season	Model	QAICc	Δ QAICc	Marked population			Total population		
				\hat{N}_m	SE(\hat{N}_m)	95% CI	\hat{N}_t	SE(\hat{N}_t)	95% CI
Summer 2013	Mt	55.16	—	134	26.11	83–186	158	46.76	89–279
	Mo	57.29	2.13	137	27.15	85–191	161	48.16	91–286
	Mh	61.33	6.17	138	27.15	85–191	162	48.35	92–287
	Mth	79.03	23.87	133	26.66	83–183	156	46.99	88–278
Autumn 2013	Mt	209.26	—	151	13.04	131–184	178	42.58	112–282
	Mth	229.56	20.30	149	12.73	130–181	175	41.96	110–278
	Mh	291.49	82.23	232	79.31	145–494	273	111.49	126–589
	Mo	295.32	86.06	154	13.77	134–189	181	43.63	114–289
Winter 2013	Mt	-24.64	—	81	33.88	15–148	95	45.20	39–230
	Mo	-21.43	3.22	87	37.34	14–161	102	49.83	42–252
	Mth	-17.35	7.30	46	14.26	18–74	54	20.69	26–112
	Mh	-17.19	7.45	87	37.34	14–161	102	49.53	42–252
Summer 2014	Mt	323.60	—	203	10.87	186–230	239	54.91	153–373
	Mth	343.69	20.09	203	10.83	186–229	239	54.90	153–373
	Mo	412.69	89.09	206	11.40	189–234	242	55.83	155–378
	Mh	412.83	89.23	230	33.21	188–327	271	72.02	162–452
Autumn 2014	Mt	417.73	—	189	8.61	175–210	222	50.74	143–346
	Mth	439.98	22.25	188	8.58	175–210	221	50.48	142–344
	Mh	572.58	154.85	239	46.84	185–387	281	83.60	159–497
	Mo	574.44	156.71	193	9.36	179–216	227	51.95	146–354
Winter 2014	Mth	502.06	—	158	7.22	147–176	186	42.42	120–289
	Mh	503.01	0.95	275	20.94	149–397	324	76.42	205–511
	Mt	506.53	4.47	157	6.98	147–175	185	42.11	119–287
	Mo	508.62	6.56	157	7.06	147–175	185	42.13	119–287

The best fitting models, based on QAICc, varied according to season (Table 4). Model M_t was selected as the best model for all but winter 2014, while model M_{th} was selected as the best model for the latter (Table 4). Abundance estimates, adjusted for proportion of unmarked individuals, varied according to seasons and ranged from 95 individuals (SE \pm 45.20) in winter 2013 to 239 (SE \pm 54.91) in summer 2014.

DISCUSSION

Baseline information on abundance, site fidelity and movement patterns are essential for effective conservation and management of wildlife as they can inform status of populations and the potential impacts of anthropogenic activities. Here, we provide the first estimates of site fidelity, residency, and abundance of southern Australian bottlenose dolphins in Adelaide's coastal waters, the most rapidly developing urban area in South Australia. We found varying patterns of site fidelity and residency for bottlenose dolphins within the study site, with individuals with higher levels categorized as year-round residents and seasonal residents, and individuals with lower levels categorized as occasional visitors. This study suggests that the Adelaide metropolitan coast is an important habitat within their home range. However, the low site fidelity of some dolphins, the emigration and reimmigration movement pattern observed, and the variation in abundance estimates across seasons suggest that animals do range beyond the limits of the fine-scale study area. Given the two years of survey effort for this study, the patterns of abundance, site fidelity, and residency found here might not be entirely representative of the bottlenose dolphins inhabiting Adelaide's metropolitan coast over the long-term. Future systematic, multiple year survey effort should continue for monitoring trends in abundance, and for investigating the potential influences of reproductive status and sex on individual site fidelity and residency.

Comparisons of site fidelity, residency, and abundance estimates among bottlenose dolphin populations should be treated with caution given differences in species, size, and habitat characteristics (*e.g.*, prey and predator availability) of study areas, and variety of sampling and analytical techniques used to estimate population parameters. Varying degrees of site fidelity and residency have been reported for bottlenose dolphin populations in the southeastern United States (Zolman 2002, Balmer *et al.* 2008). These classifications appear to resemble the three clusters defined in this study, where individuals were defined as (1) year-round residents with high site fidelity and sighted frequently across months and years, (2) seasonal residents that are sighted within the same season across years, and (3) transient individuals that are only sighted within one season. Balmer *et al.* (2013) suggested that depending on the length of time spent within the study area, these defined groups may use the habitat differently. Differences in habitat use among resident and transient individuals are also likely to occur along the Adelaide metropolitan coast, as individuals use different areas within the study site and for different periods of time.

High levels of site fidelity and residency suggest that individuals frequently utilize the habitat along Adelaide's coastal waters. A large proportion of individuals used the study area regularly across seasons, with an estimate of 89 individuals present within the study area at any one time, with some individuals residing inside the study area for periods of a year or more. This finding is consistent with previous studies of bottlenose dolphins in the adjacent Port River estuary and Barker Inlet, where

individuals exhibit year-round site fidelity (Steiner and Bossley 2008). High levels of site fidelity are typical for bottlenose dolphins in protected coastal areas, particularly in areas with high prey availability and increased protection from predators (Shane *et al.* 1986, Wells *et al.* 1987). Additionally, calves were also present throughout the year and sighted in the study area (data not shown), suggesting that the area may also provide protected habitat that is an important calving and nursery ground for mother-calf pairs.

On the other hand, low levels of site fidelity are typical of dolphins that show large ranging patterns in areas of lower productivity (Ballance 1992, Defran and Weller 1999). Our modelling of sighting patterns suggested that dolphins in Adelaide's coastal waters follow an emigration and reimmigration movement pattern. The large number of occasional visitors within Adelaide's metropolitan waters also suggests that individuals frequently make use of areas beyond the metropolitan coast. In addition, the dissimilarity threshold obtained in this study would need to increase only slightly (*ca.* 1.0) for a different clustering solution to be obtained. Increased survey effort in the future should elucidate whether the site fidelity patterns obtained in this study are representative of the population in this study area over time.

Abundance Estimates

Abundance estimates of bottlenose dolphins are largely influenced by habitat type. In protected and enclosed habitats bottlenose dolphin abundance is typically smaller (Shane *et al.* 1986, Wells *et al.* 1987) than in semiopen habitats (Ballance 1992, Defran and Weller 1999). For example, in Australia small populations of 34–75 (*Tursiops* spp.) have been documented for the semienclosed Port Essington, Northern Territory (Palmer *et al.* 2014), and 61–108 (*T. aduncus*) for Jervis Bay, New South Wales (Möller *et al.* 2002), compared to a larger population of approximately 700–1,000 (*Tursiops* spp.) in the open coast off North Stradbroke Island, Queensland (Chilvers and Corkeron 2003). Our results support this concept, as abundance estimates of southern Australian bottlenose dolphins for Adelaide's coastal waters are larger than those obtained for the semienclosed coastal areas of Port Phillip Bay (*ca.* 120 individuals) (Filby *et al.* 2014). However, our results are more similar to abundance estimates of 143–160 (*T. aduncus*) in the Port Stephens embayment, NSW (Möller *et al.* 2002), and 115–208 (*Tursiops* sp.) in the semienclosed waters off Useless Loop, Western Australia (Nicholson *et al.* 2012). This suggests that the abundance of bottlenose dolphins along metropolitan Adelaide is somewhat small and more similar to populations in enclosed and semienclosed habitats.

The abundance of bottlenose dolphins in Adelaide's coastal waters was lowest during winter 2013 and highest during summer 2014. Survey effort was also lowest during winter 2013, and thus we exercise caution in interpreting this season as the lowest abundance estimate. On the other hand, the 2014 summer period coincided with a significant increase in the number of individuals seen only once (data not shown). Influxes of individuals during certain periods of the year may represent a seasonal distributional change, possibly due to habitat (*i.e.*, temperature change), prey abundance, predator distribution, breeding requirements, or a combination of these factors (Irvine *et al.* 1981, Wilson *et al.* 1997). Some known prey items of bottlenose dolphins in South Australia include squid (*Sepioteuthis australis*) and small pelagic fish, *i.e.*, trevally (*Pseudocaranx* spp.), garfish (*Hyporhamphus melanochir*), and yellow-eyed mullet (*Aldrichetta forsteri*) (Gibbs *et al.* 2011). In the study area, the influx of

dolphins over the summer period may be associated with the distribution of these species that move into Adelaide's coastal waters during this period (Triantafillos 2002, Bryars 2003, Rogers *et al.* 2008). Similar patterns have been observed in other populations of bottlenose dolphins (Balmer *et al.* 2008). Alternatively, the summer influx may be associated with mating opportunities (as observed by Smith *et al.* 2013 for *T. aduncus* in Bunbury, Western Australia), where individuals with larger home ranges may move into Adelaide metropolitan waters to increase reproductive success.

The overall combination of low site fidelity, emigration and reimmigration, and variation in abundance estimates, suggests that animals move outside of the study area. A large number of individuals were only sighted in the northern and southern boundaries of the study area suggesting that movements may include areas along the coast to the north and south (known as the "edge effect," Williams *et al.* 2002). Sightings of photo-identified individuals are known to occur in adjacent coastal areas (NZ, personal observations) and may also extend further offshore, to areas within the central and western parts of GSV. Boat surveys indicate that sightings of bottlenose dolphins do occur across central and western GSV waters (Kemper *et al.* 2008), as well as to areas further north of the Gulf (NZ, personal observations). The integration of multiple techniques, such as photo-identification, genetics, telemetry, and stable isotopes (*e.g.*, Ansmann *et al.* 2015, Balmer *et al.* 2014, Browning *et al.* 2014, Ansmann *et al.* 2012) to identify population boundaries, together with survey efforts that cover a larger sampling area, will provide a better understanding of bottlenose dolphin movement patterns and home ranges within GSV.

Implications for Conservation

This study highlights the Adelaide metropolitan coast as an important habitat within the home range of bottlenose dolphins in GSV. This is evident by the relatively high number of dolphins found throughout the study area, and the seasonal or year-round use of the area. Our results suggest, however, that bottlenose dolphins off Adelaide's metropolitan coast move over a larger area within GSV, and adjacent waters may be of similar or higher importance. Thus, efforts to conserve and manage local bottlenose dolphins should not be limited to the metropolitan coast and must take adjacent areas into account.

Current management strategies for dolphins along the Adelaide metropolitan coast are limited to vessel and swimmer approach distances. This study provides a platform for the design of monitoring programs that will assist in the development of future conservation and management initiatives for dolphins along this highly urbanized coastline. The recent outbreak of cetacean morbillivirus in this area (Kemper *et al.* 2013) may have led to a significant local population decline, but unfortunately the long-term impacts remain unknown. The ability to detect significant changes in abundance, trends and survival rates of cetacean populations over time depends largely on long-term, individual-based, photo-identification studies. Therefore, systematic, long-term dolphin monitoring programs will be crucial to assess the impacts of future disease outbreaks and anthropogenic activities. Lastly, it is vital that monitoring programs use information on dolphin distribution to determine preferred dolphin habitat and identify areas of potential risk from anthropogenic activities within this highly urbanized coastline. This could then be used when considering area-based management strategies for this region.

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LITERATURE CITED

- Ansmann, I. C., J. M. Lanyon, J. M. Seddon and G. J. Parra. 2015. Habitat and resource partitioning among Indo-Pacific bottlenose dolphins in Moreton Bay, Australia. *Marine Mammal Science* 31:211–230.
- Ansmann, I. C., G. J. Parra, J. M. Lanyon and J. M. Seddon. 2012. Fine-scale genetic population structure in a mobile marine mammal: Inshore bottlenose dolphins in Moreton Bay, Australia. *Molecular Ecology* 21:4472–4485.
- Ballance, L. T. 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science* 8:262–274.
- Balmer, B. C., R. S. Wells, S. Nowacek, *et al.* 2008. Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *Journal of Cetacean Research and Management* 10:157–167.
- Balmer, B. C., L. H. Schwacke, R. S. Wells, *et al.* 2011. Relationship between persistent organic pollutants (POPs) and ranging patterns in common bottlenose dolphins (*Tursiops truncatus*) from coastal Georgia, USA. *Science of the Total Environment* 409:2094–2101.
- Balmer, B. C., L. H. Schwacke, R. S. Wells, *et al.* 2013. Comparison of abundance and habitat usage for common bottlenose dolphins between sites exposed to differential anthropogenic stressors within the estuaries of southern Georgia, U.S.A. *Marine Mammal Science* 29:E114–E135.
- Balmer, B. C., R. S. Wells, L. H. Schwacke, *et al.* 2014. Integrating multiple techniques to identify stock boundaries of common bottlenose dolphins (*Tursiops truncatus*). *Aquatic Conservation: Marine and Freshwater Ecosystems* 24:511–521.
- Begon, M. 1983. Abuses of mathematical techniques in ecology: Applications of Jolly's capture-recapture method. *Oikos* 40:155–158.
- Bejder, L., A. Samuels, H. Whitehead, *et al.* 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* 20:1791–1798.
- Bridge, P. D. 1993. Classification. Pages 219–242 in J. C. Fry, ed. *Biological data analysis: A practical approach*. Oxford University Press, Oxford, U.K.
- Browning, N. E., S. D. McCulloch, G. D. Bossart and G. A. J. Worthy. 2014. Fine-scale population structure of estuarine bottlenose dolphins (*Tursiops truncatus*) assessed using stable isotope ratios and fatty acid signature analyses. *Marine Biology* 161:1307–1317.
- Bryars, S. 2003. An inventory of important coastal fisheries habitats in South Australia. Fish Habitat Program, Primary Industries and Resources South Australia, Adelaide, Australia.
- Bulleri, F., and M. G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* 47:26–35.
- Burkhart, S. M., and E. Slooten. 2003. Population viability analysis for Hector's dolphin (*Cephalorhynchus hectori*): A stochastic population model for local populations. *New Zealand Journal of Marine and Freshwater Research* 37:553–566.

- Burnham, K. P. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.
- Byard, R., A. Machado, L. Woolford and W. Boardman. 2013. Symmetry: The key to diagnosing propeller strike injuries in sea mammals. *Forensic Science, Medicine, and Pathology* 9:103–105.
- Cao, Y., A. W. Bark and W. P. Williams. 1997. A comparison of clustering methods for river benthic community analysis. *Hydrobiologia* 347:24–40.
- Charlton-Robb, K., L. A. Gershwin, R. Thompson, J. Austin, K. Owen and S. McKechnie. 2011. A new dolphin species, the burrunan dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters. *PLOS ONE* 6:e24047.
- Chilvers, B. L., and P. J. Corkeron. 2003. Abundance of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, off Point Lookout, Queensland, Australia. *Marine Mammal Science* 19:85–95.
- Choquet, R., J. D. Lebreton, O. Gimenez, A.-M. Reboulet and R. Pradel. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* 32:1071–1074.
- Committee on Taxonomy. 2015. List of marine mammal species and subspecies. Society for Marine Mammalogy. Available at <http://www.marinemammalscience.org>, consulted on 2 May 2016.
- Cribb, N., C. Miller and L. Seuront. 2013. Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) habitat preference in a heterogeneous, urban, coastal environment. *Aquatic Biosystems* 9:3.
- Daly, R., M. J. Smale, P. D. Cowley and P. W. Froneman. 2014. Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of southern Africa. *PLOS ONE* 9:e109357.
- Defran, R. H., and D. W. Weller. 1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science* 15:366–380.
- Dunn, W., A. Goldsworthy, D. Glencross and K. Charlton. 2001. Interactions between bottlenose dolphins and tour vessels in Port Phillip Bay, Victoria. Report to the Department of Natural Resources and Environment, Victoria, for the Sustainable Dolphin Tourism Program. 60 pp.
- Edyvane, K. S. 1999. Coastal and marine wetlands in Gulf St. Vincent, South Australia: Understanding their loss and degradation. *Wetlands Ecology and Management* 7:83–104.
- Filby, N. E., K. A. Stockin and C. Scarpaci. 2014. Long-term responses of Burrunan dolphins (*Tursiops australis*) to swim-with dolphin tourism in Port Phillip Bay, Victoria, Australia: A population at risk. *Global Ecology and Conservation* 2:62–71.
- Gibbs, S. E., R. G. Harcourt and C. M. Kemper. 2011. Niche differentiation of bottlenose dolphin species in South Australia revealed by stable isotopes and stomach contents. *Wildlife Research* 38:261–270.
- Hammond, P. S. 2009. Mark-recapture. Pages 705–709 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. Academic Press, New York, NY.
- Irvine, A. B., M. D. Scott, R. S. Wells and J. H. Kaufmann. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* 79:671–688.
- Kemper, C., A. Flaherty, S. Gibbs, M. Hill, M. Long and R. Byard. 2005. Cetacean captures, strandings and mortalities in South Australia 1881–2000, with special reference to human interactions. *Australian Mammalogy* 27:37–47.
- Kemper, C., M. Bossley and P. Shaughnessy. 2008. Marine mammals of Gulf St Vincent, Investigator Strait and Backstairs Passage. Pages 339–352 in S. Shepherd, S. Bryars, I.

- Kirkegaard, P. Harbison and J. Jennings, eds. Natural history of Gulf St Vincent. Royal Society of South Australia Inc., Adelaide, Australia.
- Kemper, C., L. Woolford and I. Tomo, *et al.* 2013. Abnormally high dolphin mortalities linked to Morbillivirus in South Australia (SA). Poster presentation for the 21st Biennial Conference on the Biology of Marine Mammals, Dunedin, New Zealand.
- Lavery, T. J., N. Butterfield, C. M. Kemper, R. J. Reid and K. Sanderson. 2008. Metals and selenium in the liver and bone of three dolphin species from South Australia, 1988–2004. *Science of the Total Environment* 390:77–85.
- Leduc, R. G., W. F. Perrin and A. E. Dizon. 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome *b* sequences. *Marine Mammal Science* 15:619–648.
- Legendre, P., and L. Legendre. 2012. Numerical ecology. 3rd edition. Elsevier Science B.V, Amsterdam, The Netherlands.
- Li, T., S. Ma and M. Ogihara. 2004. Entropy-based criterion in categorical clustering. *Proceedings of the 2004 IEEE International Conference on Machine Learning (ICML 2004)*:536–543.
- Möller, L. M., and L. B. Beheregaray. 2001. Coastal bottlenose dolphins from southeastern Australia are *Tursiops aduncus* according to sequences of the mitochondrial DNA control region. *Marine Mammal Science* 17:249–263.
- Möller, L. M., S. Allen and R. Harcourt. 2002. Group characteristics, site fidelity and seasonal abundance of bottlenosed dolphins (*Tursiops aduncus*) in Jervis Bay and Port Stephens, south-eastern Australia. *Australian Mammalogy* 24:11–22.
- Möller, L. M., K. Bilgmann, K. Charlton-Robb and L. Beheregaray. 2008. Multi-gene evidence for a new bottlenose dolphin species in southern Australia. *Molecular Phylogenetics and Evolution* 49:674–681.
- Nicholson, K., L. Bejder, S. Allen, M. Krützen and K. Pollock. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops* sp.) off Useless Loop in the western gulf of Shark Bay. Western Australia. *Marine and Freshwater Research* 63:1059–1068.
- Nowacek, S. M., R. S. Wells and A. R. Solow. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17:673–688.
- Palmer, C., L. Brooks, G. J. Parra, T. Rogers, D. Glasgow and J. C. Z. Woinarski. 2014. Estimates of abundance and apparent survival of coastal dolphins in Port Essington harbour, Northern Territory, Australia. *Wildlife Research* 41:35–45.
- Parra, G. J., P. J. Corkeron and H. Marsh. 2006. Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: Implications for conservation. *Biological Conservation* 129:167–180.
- Perrin, W. F., P. E. Rosel and F. Cipriano. 2013. How to contend with paraphyly in the taxonomy of the delphinine cetaceans? *Marine Mammal Science* 29:567–588.
- Peters, K. J., G. J. Parra, P. P. Skuza and L. M. Möller. 2012. First insights into the effects of swim-with-dolphin tourism on the behavior, response, and group structure of southern Australian bottlenose dolphins. *Marine Mammal Science* 29:E484–E497.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* 56:434–442.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Powell, J., and R. Wells. 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science* 27:111–129.
- Read, A. J., K. W. Urian, B. Wilson and D. M. Waples. 2003. Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. *Marine Mammal Science* 19:59–73.

- Rice, D. W. 1998. Marine mammals of the world: Systematics and distribution. Special Publication Number Four, Society of Marine Mammalogy.
- Rogers, P., W. Dimmlich and T. Ward. 2008. The small pelagic fishes of Gulf St Vincent and Investigator Strait. Pages 353–366 in S. Shepherd, S. Bryars, I. Kirkegaard, P. Harbison and J. Jennings, eds. Natural history of Gulf St Vincent. Royal Society of South Australia, Adelaide. Royal Society of South Australia Inc., Adelaide, Australia.
- Ross, G., and V. Cockcroft. 1990. Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). Pages 101–128 in S. Leatherwood and R. R. Reeves eds. The bottlenose dolphin. Academic Press, San Diego, CA.
- Sarasota Dolphin Research Program. 2006. Manual for field research and laboratory activities. 62 pp. Available at <http://www.sarasotadolphin.org/5187/>.
- Scarpaci, C., N. Dayanthi and P. J. Corkeron. 2003. Compliance with regulations by “swim-with-dolphins” operations in Port Phillip Bay, Victoria, Australia. *Environmental Management* 31:342–347.
- Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52:860–873.
- Shane, S. H., R. S. Wells and B. Würsig. 1986. Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science* 2:34–63.
- Simpfendorfer, C. A., B. G. Yeiser, T. R. Wiley, G. R. Poulakis, P. W. Stevens and M. R. Heupel. 2011. Environmental Influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): Results from acoustic monitoring. *PLOS ONE* 6:e16918.
- Singh, W., E. Hjørleifsson and G. Stefansson. 2011. Robustness of fish assemblages derived from three hierarchical agglomerative clustering algorithms performed on Icelandic groundfish survey data. *ICES Journal of Marine Science* 68:189–200.
- Smith, H. C., K. Pollock, K. Waples, S. Bradley and L. Bejder. 2013. Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PLOS ONE* 8:e76574.
- Stanley, T., and K. Burnham. 1999. A closure test for time-specific capture-recapture data. *Environmental and Ecological Statistics* 6:197–209.
- Steiner, A., and M. Bossley. 2008. Some reproductive parameters of an estuarine population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Aquatic Mammals* 34:84–92.
- Triantafillos, L. 2002. Population biology of southern calamary, *Sepioteuthis australis*, in Gulf St. Vincent, South Australia. Ph.D. dissertation, Northern Territory University, Darwin, Australia. 230 pp.
- Urian, K. W., A. A. Hohn and L. J. Hansen. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-425. 22 pp.
- Urian, K. W., A. Gorgone, A. Read, *et al.* 2015. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science* 31:298–321.
- Van Bresseem, M. F., J. A. Raga, G. Di Guardo, *et al.* 2009. Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Diseases of Aquatic Organisms* 86:143–157.
- Ward, J. H., Jr. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* 58:236–244.
- Wells, R. S., M. Scott and A. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. *Current Mammalogy* 1:247–305.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- White, J., C. A. Simpfendorfer, A. J. Tobin and M. R. Heupel. 2014. Spatial ecology of shark-like batoids in a large coastal embayment. *Environmental Biology of Fishes* 97:773–786.

- Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: Application to sperm whales. *Ecology* 82:1417–1432.
- Whitehead, H. 2009. SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology* 63:765–778.
- Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, London, U.K..
- Wilson, B., P. S. Hammond and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Wilson, B., P. Thompson and P. Hammond. 1997. Habitat use by bottlenose dolphins: Seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 34:1365–1374.
- Würsig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. Report of the International Whaling Commission 12:43–52.
- Zolman, E. S. 2002. Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River Estuary, Charleston Count, South Carolina, U.S.A. *Marine Mammal Science* 18:879–892.

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