

Abundance estimates of an isolated population of common bottlenose dolphins *Tursiops truncatus* in Walvis Bay, Namibia, 2008–2012

SH Elwen^{1*}, R Leeney² and Tess Gridley³

¹*Mammal Research Institute, University of Pretoria, c/o Sea Search Research and Conservation, Cape Town, South Africa*

²*Protect Africa's Sawfishes & Namibian Dolphin Project, Walvis Bay, Namibia*

³*Centre for Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, c/o Sea Search Research and Conservation, Cape Town, South Africa*

**Corresponding author, e-mail: Simon.Elwen@gmail.com*

ABSTRACT

The coastal population of common bottlenose dolphins *Tursiops truncatus* found in Namibia is regionally isolated and unique. This population faces several potential anthropogenic threats, especially in Walvis Bay, including boat-based tourism, a commercial harbour undergoing expansion, and aquaculture for oysters and mussels. Between 2008 and 2012, 238 boat-based surveys were conducted, resulting in 170 encounters with bottlenose dolphins. Group size varied from 1 to 45 individuals (mean = 10.7). Encounter rates, group size and total number of animals identified were higher in winter than summer seasons. The number, and survival and immigration parameters, of dolphins using Walvis Bay was investigated using robust design and Huggins closed population mark-recapture models. The highest numbers estimated were in the first and last years of the study, with estimates of 74 to 82 and 76 to 77 (number identified and upper 95% confidence interval, respectively). The only previously available data from an incomplete study in the early 1990s suggested that the population was between 100 and 150 individuals at that time. Although no linear trend in population size was obvious during this study, the clear evidence of isolation, small population size, low annual birth rate, and potential long-term decrease in numbers since the early 1990s is concerning. Further work to collect data on demographic parameters is urgently recommended with a view to obtaining increased protection.

Keywords: Africa, cetacean, conservation, mark-recapture

Introduction

Populations or species of animals which are isolated from conspecifics are amongst those at highest risk of extinction. Common bottlenose dolphins *Tursiops truncatus* are classified globally as 'Least Concern' on the IUCN Red List (Hammond et al. 2012). However, many small coastal populations of bottlenose dolphins have been documented (Vermeulen and Bräger 2015) and there is a growing recognition of the uniqueness and value of these populations, as well their role in local environments. For example, many show genetic and behavioural traits that differ from other populations of the same species, are important ecologically and are often of high value to local tourism (Amir and Jiddawi 2001; Hu et al. 2009; O'Connor et al. 2009; Leeney 2014). Consequently, several small and isolated populations of bottlenose dolphins have been assessed under IUCN Red List criteria for populations, resulting in generally higher levels of classification such as 'Vulnerable' or 'Critically Endangered' (Currey et al. 2009, 2013; Bearzi et al. 2012; Pusineri et al. 2014).

The common bottlenose dolphins found in the coastal waters of Namibia appear to form a small, isolated population limited to the very shallow waters of the central Namibian coast. Earlier work has described their range as approximately 200 km alongshore between Sandwich Harbour (23°22' S) in the south and Cape Cross (21°46' S) in the north, which are either side of Walvis Bay (Findlay et al. 1992; Best 2007). This is the only known coastal population of common bottlenose dolphins in southern Africa (defined as Namibia, South Africa and Mozambique), with the nearest populations of the same species being in pelagic waters (Hoelzel et al. 1998; Best 2007) and in the Namibe Province in southern Angola (Weir 2010), 800 km to the north of the current study area. The only published data on the size of the Namibian population of bottlenose dolphins dates from the early 1990s (Praetsch in Best 2007, reported in Best [2007]). In that study, 83 individuals were identified over 20 months, with few new animals identified in the final 6 months of the project, indicative of a closed population. The 'great majority' of animals were reported as identifiable and Best (2007) suggested that the overall population was likely between 100 and 150 animals.

Since that study, anthropogenic activities that overlap with the known range of this population on the Namibian coast have increased markedly, particularly in Walvis Bay. Notably, the commercial harbour in Walvis Bay and the aquaculture industry for oysters and mussels have both grown substantially, and a large boat-based tourism industry (comprising 27 motorboats in 2010; Leeney 2014) has developed. Such activities have been shown to have negative impacts on the behaviour and habitat use of dolphins in other areas (Lusseau 2003; Watson-

Capps and Mann 2005; Ribeiro et al. 2007; Stockin et al. 2008), raising concerns about potential impacts on this apparently isolated population in Namibian waters.

Boat-based photographic mark-recapture combined with focal follows is a widely used approach for studying the abundance, survival, distribution, behaviour and other aspects of populations of coastal cetaceans (Wilson et al. 1999; Stockin et al. 2008; Vermeulen and Bräger 2015). For our study, this approach was preferred to line-transect sampling as it allowed for the collection of multiple datasets from this little-studied population. Effective application of mark-recapture analysis is contingent on a number of caveats including a knowledge of the focal population's range, equal probability of capture of individuals and stability of identifying marks. All existing knowledge about the biology of this population supports the concept that it is small, geographically isolated and restricted to the shallow coastal waters of the central Namibian coastline (de Rock al. 2019, Best 2007). Data collection for this study took place in and around Walvis Bay, as no launch sites are available anywhere else in the species' known range. Walvis Bay is the only large embayment within the species' known range, is in the centre of that range, and appears to act as core habitat for the population. In this study, we aim to provide a first mark-recapture assessment of the abundance and degree of residency of bottlenose dolphins in Walvis Bay, Namibia, to provide baseline data against which future changes and threats can be assessed and as a first step towards assessment using IUCN Red List population criteria (IUCN 2013).

Methods

Data were collected in Walvis Bay, Namibia (23°00' S, 14°30' E) over several austral summer (February–March) and winter (June–August) field seasons, between 2008 and 2012. Walvis Bay is a shallow (mostly <15 m deep), sandy-bottomed bay, approximately 10 × 10 km, protected from the open ocean by a sandspit ending at Pelican Point (Figure 1). Walvis Bay is the largest embayment along the exposed Namibian coastline and provides one of the few refuges from the open sea. The commercial harbour lies in the south-eastern corner of the bay, just to the north of the entrance to a shallow unsurveyed lagoon, which is a Ramsar protected wetland (Wearne and Underhill 2005) and is inaccessible to motorised vessels.

Local weather conditions are dominated by south-easterly winds and the land-sea breezes that collectively drive the upwelling of the Benguela ecosystem (Robertson et al. 2012). These wind patterns result in generally calm mornings, with stronger winds in the afternoons (usually generating sea states of Beaufort 4 or higher). For this reason, boat surveys were mostly carried out in the mornings when weather conditions were more conducive to finding and

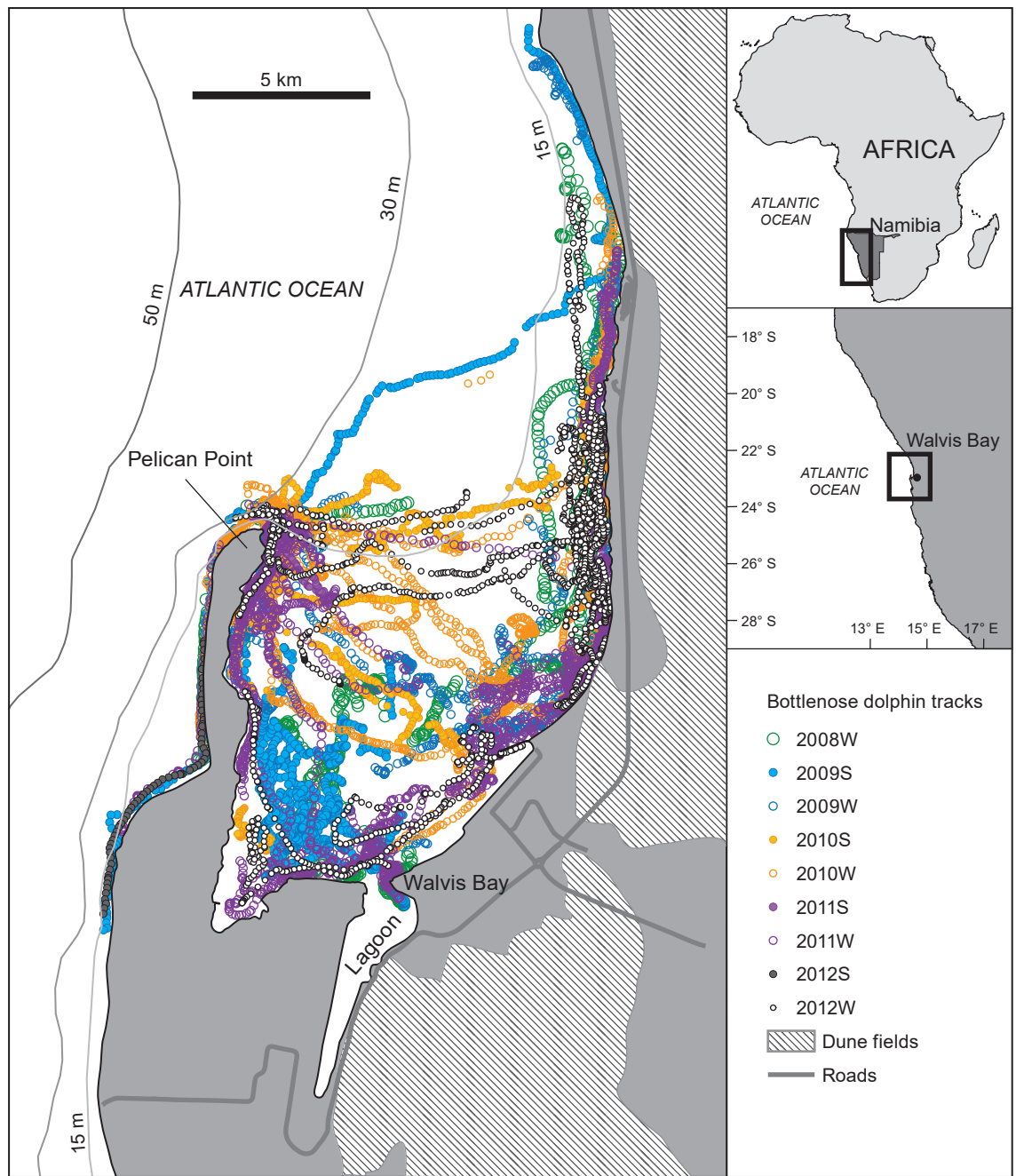


Figure 1: Survey tracks collected during 'follows' of common bottlenose dolphins in Walvis Bay, Namibia; colour-coded dots denote 1-min intervals, collected by GPS, shaded by field season (W = winter, open circles; S = summer). Although dolphins use the lagoon in the southeast, the area was unsurveyed by boat because of very shallow water and a prohibition on motorised vessels within the Ramsar site

photographing dolphins. Research surveys followed a non-systematic route starting and ending at the yacht club in the south-eastern corner of the bay. Communication with and observation of tour boats with animals sometimes artificially increased sighting rates with dolphins. Effort was made to survey in all areas of the bay and surrounds although there was considerable effort expended near Pelican Point, an area regularly frequented by high numbers of Heaviside's dolphins *Cephalorhyncus heavisidii*, which were a secondary focal species of the broader research project.

Surveys were conducted using an 8 m catamaran ski-boat fitted with twin 90 HP 4-stroke engines (2008 and summer 2009) and a 5.8 m rigid-hulled inflatable boat with twin 50 HP 2-stroke engines (winter 2009 onwards). Upon sighting a group of dolphins, the animals were approached and an estimate of group size made. The group behaviour, composition (calves, adults) and the number and type of tour boats present (ski-boat or sailing catamarans under power). Depth and sea surface temperature were recorded at the beginning and end of each encounter using an onboard Garmin GPS/fishfinder. We attempted to photograph both sides of the dorsal fins of all animals in the group, irrespective of the level of scarring or identifiability. Photographs were taken using a Canon EOS 400D camera with a 70-200L lens or a Canon 50D with the same lens and a 1.4× extender. Photo-identification data were collected until all animals observed had been photographed or contact with the group was lost.

The quality of an identity photograph can impact the ability to recognise animals, especially poorly marked ones, and it is recommended practice in the field of photographic mark-recapture to remove poor-quality images prior to analysis (Friday et al. 2008; Urian et al. 2014). All fin images were rated for quality purely on the characteristics of the image and not the degree of distinctiveness of the fin. Image quality was rated out of six: Q1 – barely identifiable; Q2 – poor; Q3 – average, contains information but is too small (<200 pixels tall), unfocused or poorly angled; Q4 – good image, fin >200 pixels, well lit; Q5 – good image, fin >200 pixels but backlit or poorly lit so scarring and colouration is not clearly visible; Q6 – excellent, big, focused, well lit, perpendicular to camera. A catalogue was created and identifiable animals in acceptable quality images from each day were matched against the catalogue and given a new identification number if not contained therein. Each animal in the catalogue was then given a rating for 'distinctiveness' (following Elwen et al. 2009) out of five: D1 – no mark or scarring only; D2 – one small mark on fin edge or clear scarring only; D3 – one large or two or more smaller marks; D4 – multiple fin edge marks or mutilations; D5 – large, extremely obvious fin mutilations. Where possible, animals within the catalogue were assigned a confirmed or probable sex based on visual assessment of the genital area of an identified dolphin in images (usually a series of photographs of a jump), or consistent close association with a calf within

and across encounters. Animals that were initially identified as adults in 2008 but were never observed associating with a calf (including in opportunistic data collected between 2013 and 2015) were identified as possible males.

For mark-recapture analysis, we used a subset of the photographic dataset with only animals of distinctiveness rating D3, D4 or D5 (referred to as D345) and photographs of good to excellent quality (Q4, Q5 or Q6, referred to as Q456). This produced a set of photographs in which we could confidently identify all individuals considered marked. This compromise between mark distinctiveness and image quality is widely accepted in the field and recommended as the optimal way to make the most of the data (e.g. Read et al. 2003, Friday et al. 2008, Urian et al. 2014).

The logistical inability to survey the entire geographic range of a dolphin population is typical of most studies using small-boat photographic identification (for example: Parra et al. 2006; Reisinger and Karczmarski 2010; Cheney et al. 2014; Vermeulen and Bräger 2015; Hunt et al. 2017). Animals being unavailable for 'capture' (by being outside the survey area during any given survey) does not introduce any bias into capture-recapture analysis, as long as presence in the study area on any sampling occasion is effectively random (Seber 1982; Hammond 1986). The location of the study area at the centre of the known range of the population and the shallow water preference of the animals means that all individuals should pass through the survey area at some point, making them available for capture. Combined with the high encounter rates in the bay, and other indicators of closure the population being closed we are confident that the population meets the assumption of geographic closure over short time-periods and the use of closed-population models is appropriate in this population. The results of a closed capture-mark-recapture model in a situation like this can best be interpreted as the number of individuals using the study area over the study duration, a useful number for management and conservation purposes. That said, it is likely that some level of heterogeneity in capture probability occurs in all wild populations, although this can be accounted for to some extent through use of appropriate models (Hammond 1986; Urian et al. 2014).

The dataset was thoroughly investigated visually and analytically to assess growth of the catalogue and the impact of field-season effort and duration on the number of animals identified (linear regressions, discovery curves), seasonal and sexual differences in use of the bay, and the inclusion of sex and capture heterogeneity to improve model performance. Field effort was lower and inconsistent in summer periods and fewer individuals were identified, so only the five winter field seasons were used in the analysis of survival and abundance. As sex was unknown for 57% of the adult population, it was not informative in the mark-recapture models

and resulted in a high number of parameters within models and low model convergence, so was excluded from final analyses.

This seasonal approach to data collection allowed for the effective application of the Pollock's robust design (RD) capture-recapture modelling approach (Kendall 2016). The RD approach effectively combines open and closed population models and thus allows for the estimation of apparent survival (S) and temporary emigration (γ'') and immigration (γ') between primary periods (annual field seasons in this study), and treats each primary period as a temporally closed sampling period consisting of secondary sampling occasions (days in this study), from which population abundance (\hat{N}) and the probability of capture and recapture (p and c) can be calculated. Thus, the population can be open to births, deaths, immigration and emigration between primary periods but assumes demographic and geographic closure within these periods. Analysis within primary periods (field seasons) was performed using Huggins closed-population models. The log-likelihood methods developed by Huggins (Huggins 1989) are recommended due to their flexibility and ability to include covariates (e.g. sex, season) to account for variation in capture probability (Manly et al. 2005; Conn et al. 2011). In the absence of covariates, Huggins and full-likelihood models provide equivalent results (Lukacs 2016). Analysis was conducted in the program MARK (White and Burnham 1999; Cooch and White 2016) using the RMark interface (La Rosa and Rexstad 2010). Days were used as capture occasions. As there is no biological reason to expect a behavioural change between initial and later captures, as in the case of physically trapped animals, c (recapture probability) was set equal to p (initial capture probability) throughout (Parra et al. 2006; Nicholson et al. 2012). Similarly, capture probability was assumed to vary between occasions as environmental conditions were not constant and only a portion of the population was captured on any occasion; thus models with constant capture probability were not considered, with the exception of running a null model for comparative purposes.

A series of models were fitted to explore which combination of parameters best described the data. Survival was modelled as both fixed $S(.)$ and time varying $S(t)$ between primary seasons. Three types of temporary emigration were explored: (i) no emigration or immigration ($\gamma'' = \gamma' = 0$); (ii) random immi(e)migration ($\gamma'' = \gamma'$) where the probability of an animal being present in the study area is independent of its status in the previous primary occasion, and (iii) Markovian (γ'', γ) where the probability of an animal being present in the study area is conditional on its presence or absence in the previous sampling period. Emigration parameters were both held constant $\gamma''(.)$ and allowed to vary between sessions $\gamma''(t)$. Model fit was assessed using the Akaike information criterion corrected for small samples sizes (AICc) within MARK. The

difference between the AICc values of models is referred to as ΔAIC and allows for comparison between the most-parsimonious model and others. Models with $\Delta\text{AIC} < 2$ are considered to have equivalent fit (Burnham & Anderson, 2002). Initial modelling was conducted within the full heterogeneity framework of the Huggins model design, which allows for the calculation of abundance, capture probability and the inclusion of capture heterogeneity as two 'mixtures' within the population (i.e. heterogeneity effects are partitioned into two groups with a homogenous capture probability within each group [Pledger 2000]). The best-fitting model (by a factor of 19.01 ΔAICc) was extremely complex with over 200 parameters and allowed p to vary for each secondary capture occasion in two heterogeneity mixtures. Although this model produced reasonable parameter estimates for S and \hat{N} , a significant number of γ and p parameters did not converge. As model results for key parameters were similar to those of simpler models, we conducted the RD analysis with closed models that did not take into account capture heterogeneity. Nicholson et al. (2012) report a similar problem with their use of the 'robust design'. Following their approach, we have presented the simpler model for the entire dataset and then separately explored the impact of capture heterogeneity by conducting closed-model within-season estimates for each winter season.

The mark-recapture estimates only apply to the number of well-marked animals in the population (D345), termed \hat{N} (Wilson et al. 1999). The estimate was extrapolated upwards by the proportion of marked animals in the population (termed θ) to generate an estimate of the entire population size (N_{total}) following Wilson et al. (1999). Due to the small number of animals identified in each season, we were confident of identifying all individuals photographed during the season because all animals seen had at least some form of identifiable colouration or subtle scarring. Thus, we calculated θ as being the proportion of well-marked individuals to total individuals identified that season. A separate θ value for each field season was used for extrapolation as it varied slightly by year. Errors for N_{total} were calculated using the delta method following Wilson et al. (1999).

Results

Between 2008 and 2012, 238 surveys of Walvis Bay (Figure 1) were conducted, resulting in 170 encounters with bottlenose dolphins. The number of surveys conducted per field season ranged from 22 to 55 with bottlenose dolphins encountered on 59% to 83% of surveys (Table 1). Group size from photo-identification results often exceeded field estimates of group sizes and was thus preferred for accuracy. Overall group size varied from 1 to 45 individuals (mean = 10.7) with group sizes being larger in winter seasons than summer seasons (Table 1).

Table 1: Summary of survey effort, encounters, group sizes, and number of common bottlenose dolphins photographically identified in all field seasons (S = austral summer, W = austral winter), in Walvis Bay, Namibia. The numbers photographically identified are for the total number of animals identified including calves (ID.all), and for only those well-marked adult or juvenile animals (ID.D345) used in the analysis. Encounter rate is the number of bottlenose dolphin groups encountered per survey in each season. Newly identified calves are listed only for winter seasons, for consistency across years

Season	No. of surveys	No. of encounters	Encounter rate	Average group	ID.all	ID.D345	New calves
2008W	30	24	0.80	14.75	74	54	2
2009S	23	15	0.65	5.24	24	18	–
2009W	22	18	0.82	12.89	56	49	3
2010S	34	20	0.59	3.62	22	18	–
2010W	36	30	0.83	9.10	54	42	3
2011S	12	5	0.42	6.00	14	11	0
2011W	55	40	0.73	10.36	63	55	3
2012S	3	2	0.67	10.00	19	17	0
2012W	38	23	0.61	17.36	76	57	7

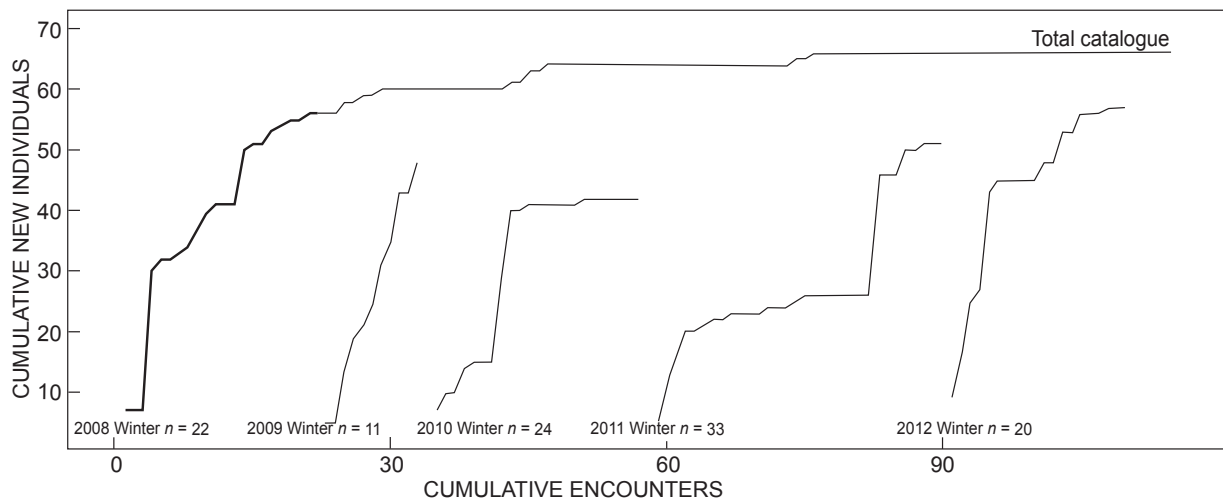


Figure 2: Discovery curves showing growth of the catalogue of photographically identified common bottlenose dolphins in Walvis Bay, Namibia. Curves (cumulative newly identified individuals per encounter day) are shown separately for each winter field season, as well as for the total growth of the catalogue over the study period. The sample sizes given only reflect days with dolphin encounters, not the total number of survey days (see Table 1), and are thus slightly truncated (steeper) in comparison to the total survey effort

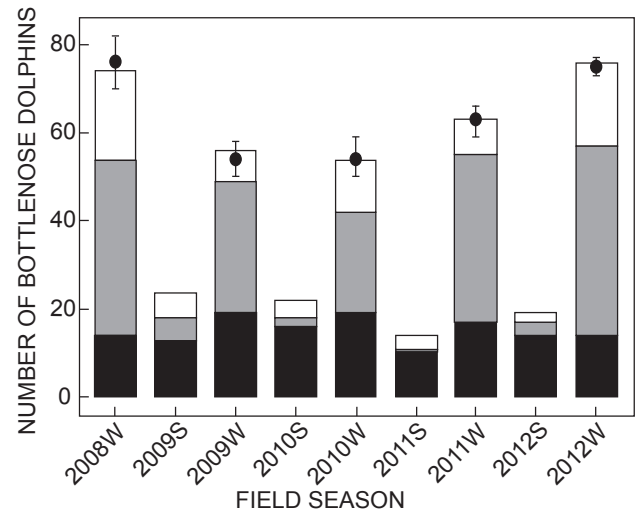


Figure 3: Estimated total abundance estimates of common bottlenose dolphins in Walvis Bay, Namibia, from 2008 to 2012, for winter (W) and summer (S) field seasons. Bars show the total number of individuals identified in each season (full bar, including white), the total number of well-marked animals used in the mark-recapture analysis (bars up to grey portion), and the proportion of identified animals in each season that were made up of the resident 'summer dolphins' (black portion). Mark-recapture abundance estimates extrapolated to total population size (N_{total}) shown as dots, with whiskers showing 95% confidence intervals

Discovery curves (Figure 2) showed asymptotes in **most** winter field seasons and a clear asymptote in the overall catalogue growth, supporting the use of closed-population models within seasons. Survey effort was substantially lower during summer field seasons meaning we could not generate abundance estimates based on these data. However, photographic analysis of data collected in the summer was informative as we identified a core of 19 individuals common to both summer (identified in at least two summers) and winter seasons. We refer to these as the 'summer dolphins' and their contribution to the overall population is represented graphically in Figure 3. The number of dolphins identified (all distinctiveness categories) was not affected by the number of surveys per season (slope of linear regression = 0.095, $r^2 = 0.013$) or encounters per season (slope = -0.173 , $r^2 = 0.021$) suggesting that adequate surveys were completed in each time-period to capture a representative sample of the population. Of the 77 well-marked individuals identified across the five winters, 18 were females, four were probable females, eight were males with a further three probable males. The majority of individuals were seen in multiple years (23 were seen in all five winters, 16 in four winters, 15 in three winters, 13 in two winters and only 10 animals were encountered in a single winter season). Encounter rates (no. encounters/no. surveys) for winter field seasons showed a general decline from 0.80 in 2008 to 0.61 in 2012 (Table 1) but there was no significant relationship between measures of effort and the number of animals identified in each season suggesting sufficient survey effort was conducted in each year. The number of calves was similar between years with two or three calves observed most years, except in 2012 when seven newly identified calves were documented (Table 1). Birth rate (percentage of total population N_{total}) thus averaged 5.5% for the population (range: 2.6-9.3).

Models

Robust design models that allowed for capture heterogeneity within primary periods had a high number of parameters that did not converge and were thus not included here. The two best-fitting robust design models ($\Delta\text{AICc} < 1$) that did not allow for capture heterogeneity had constant survival $S(\cdot)$ and allowed capture probability to vary with time throughout the study $p(\text{session}:\text{time})$, but provided a contradictory influence of emigration and immigration (Table 2). \hat{N} were identical in these two models. Survival was calculated as 0.965 (SE 0.02) in the best-fitting model and 0.940 (SE 0.03) in the second-best-fitting model. Temporary emigration rates for 2008 to 2011 were 0.16 (SE 0.058), 0.018 (SE 0.062), 0.20 (SE 0.076) and dropping to 0.06 (SE 0.055) as would be expected given the high number of animals identified in the last field season (i.e. 2012, for which an emigration rate cannot be calculated). As capture heterogeneity could not be included effectively into the robust design models, we investigated its effect on abundance estimates within each of the five winter field seasons from 2008 to 2012. In all years, the model allowing for heterogeneity in capture probability (two mixtures)

Table 2: Results for six best-fitting robust design models ($\Delta AICc < 10$) and the null model, used to estimate the size and population dynamics of an isolated population of common bottlenose dolphins in Walvis Bay, Namibia, over five winter field seasons (2008–2012). Models shown in bold were the two best-fitting models selected using the AICc value

Model	No. of parameters	AICc	$\Delta AICc$	Weight	Deviance
S(~1) $\gamma^{**}(\sim 1)$ $\gamma'(\sim 1)$ $p(\sim \text{session:time})c()$	115	5434.155	0.000	0.428	6038.803
S(~1) $\gamma^{**}(\sim \text{time})$ $\gamma'(\sim \text{time})$ $p(\sim \text{session:time})c()$	120	5434.216	0.060	0.416	6026.540
S(~1) $\gamma^{**}(\sim \text{time})$ $\gamma'()$ $p(\sim \text{session:time})c()$	117	5437.074	2.919	0.100	6036.807
S(~time) $\gamma^{**}(\sim 1)$ $\gamma'(\sim 1)$ $p(\sim \text{session:time})c()$	118	5438.790	4.635	0.042	6036.058
S(~time) $\gamma^{**}(\sim \text{time})$ $\gamma'(\sim \text{time})$ $p(\sim \text{session:time})c()$	123	5441.483	7.328	0.011	6026.357
S(~time) $\gamma^{**}(\sim \text{time})$ $\gamma'()$ $p(\sim \text{session:time})c()$	120	5443.932	9.777	0.003	6036.256
[Null model] S(~1) $\gamma'(\sim 1)$ $\gamma^{**}(\sim 1)$ $p(\sim 1)c()$	5	5894.151	459.99	0.0	6743.590

Table 3: Mark-recapture model outputs of the estimated number of well-marked and identifiable common bottlenose dolphins (\bar{N}) in Walvis Bay, Namibia, and calculated total population size (N_{total}), which extrapolates to account for unidentifiable dolphins. Huggins log-likelihood closed models were used for all mark-recapture analyses. The robust design approach calculates all seasons as one analysis, taking into account demographic changes between seasons, but does not account for capture heterogeneity (see text). For closed models run on each winter season (W) independently, the model allowing for two mixtures of capture heterogeneity and time-varying capture probability was the best-fitting in all seasons. Model coding in RMark: $\text{pi}(\sim 1)p(\sim \text{time} + \text{mixture})c()$. Final estimates of total population size for each season were calculated from the closed-model results by extrapolating upwards for the proportion of marked animals in each season (θ), with standard error (SE) calculated using the delta method (see text)

Season	Robust design		Closed models			Total population			
	\bar{N}	SE	No. of parameters	\bar{N}	SE	θ	N_{total}	Low 95% CI	High 95% CI
2008W	55.25	0.51	24	56.27	2.36	0.74	76	70	82
2009W	48.07	1.12	14	48.21	1.77	0.89	54	50	58
2010W	41.44	0.69	26	43.31	1.98	0.80	54	50	59
2011W	52.02	0.13	35	53.69	1.46	0.86	63	59	66
2012W	59.05	0.22	22	59.57	0.79	0.79	75	73	77

and for capture probability to vary with time were the best-fitting models. \hat{N} estimates increased by less than two individuals for each field season, but estimates became less precise as standard errors increased by up to a factor of 10 (Table 3).

The results from the stand-alone closed models above were used to generate total population abundance estimates. Upon extrapolation to total population size (N_{total}), using a field season-specific value for θ (proportion of marked animals), we generated estimates of between 50 and 82 adult individuals documented in Walvis Bay over each of the winter field seasons. No linear increasing or decreasing trend in population trajectory was obvious, as the largest estimates occurred in the first and last field seasons. These estimates were very similar to the total number of adults, juveniles and calves photographically identified in each season from good-quality photographs (Table 1 and 3).

Discussion

Bottlenose dolphins are large-bodied, highly mobile top predators, which can move rapidly over long distances, and undergo seasonal or long-term directional movements at the individual (Robinson et al. 2012) or population level (Wilson et al. 2004; Cheney et al. 2014). The goal of this study was to assess the bottlenose dolphin population that uses Walvis Bay, a highly impacted but biologically important embayment on the Namibian coastline. We present information on the size of the total population, and the number of individuals using the bay in summer and winter seasons using a combination of photographic mark-recapture and summary statistics of surveys. Walvis Bay is the only area along the Namibian coastline where this population can be studied effectively, as there are no other launch sites and the extreme near-shore habitat of the animals prohibits the effective use of larger vessels. However, this is also the area with the greatest need for information as it is the most impacted by human activities, including a large and growing harbour and a growing marine-tourism industry (Leeney 2014). The results of this study are thus highly relevant to the conservation of the population as a whole.

The published range limits of this population (Best 2007) are Sandwich Harbour (~50 km south of Walvis Bay) and Cape Cross (~200 km north), spanning a total distance of ~250 km, but observer effort beyond these locations has historically been extremely low. Opportunistic records since 2010 and photographs collected by our research team in Lüderitz in 2012 (~400 km south of Walvis Bay) confirm that animals from the study population range at least that far south, but with survey effort beyond this limited by a lack of human settlements for a further ~400 km and a very restrictive access policy in the Sperrgebiet National Park. The northern

limit of the population remains unclear but reports of sightings at Möwe Bay (~400 km north of Walvis Bay) by long-term resident rangers in between 1982 and 2008 were 'extremely rare' (R Braby and J Paterson pers. comm.), suggesting that the effective range limit is somewhere south of this. Broadscale changes in environmental conditions such as sea surface temperature and chlorophyll concentration have been linked to genetic population structure and limitations of dispersal in both franciscana dolphins *Pontoporia blainvillei* (Mendez et al. 2010) and Indian Ocean humpback dolphins *Sousa plumbea* (Mendez et al. 2011). Very strong and persistent wind-driven upwelling cells occur to the south of Lüderitz and at Angra Point to the north of Möwe Bay. These areas of upwelling are central to the oceanographic and biological function of the Benguela ecosystem (Robertson et al. 2012a), and may play a role in limiting the dispersal of this population, but prey type and availability, and social factors, are also likely to play a role. The nearest known neighbouring coastal population of bottlenose dolphins occurs in Namibe Province in southern Angola, roughly 800 km north of Walvis Bay (Weir 2010). Little is known about this population and further research on connectivity and relatedness would be informative. With no known coastal populations of common bottlenose dolphins to the south of Lüderitz, or along the eastern African coast (Best 2007), the balance of evidence thus supports the suggestion that the Namibian population is effectively isolated and lives in a narrow strip of habitat between the coast and a maximum of 30 m depth along the central Namibian coast.

Relatively few animals were consistently identified in each summer (approximately 1/3 of the population), suggesting that only a component of the population consistently remains in the bay during this period. During summer months, winds are usually weaker in the northern Benguela, resulting in reduced productivity in the ecosystem (Robertson et al. 2012a). In Walvis Bay, this leads to reduced mixing of the water column, anoxic conditions, algal blooms and sulphur blooms, all of which may result in reduced prey availability within the bay (Weeks et al. 2004; Robertson et al. 2012b). Namibian bottlenose dolphins have been observed feeding on South African mullet *Liza richardsonii* (Best 2007) and silver kob *Argyrosomus inodorus* (Namibian Dolphin Project, unpublished data). During summer months, adult silver kob migrate southwards along the central Namibian coastline from the Skeleton Coast National Park to Sandwich and Meob Bays where they spawn (Kirchner and Holtzhausen 2001), thereby crossing the known range of the bottlenose dolphin population, with particularly large fish available on the central coast in the January to April period overlapping the summer field seasons of this study. Although mullet are resident year-round in Walvis Bay, catches in the Benguela by gillnet fishers peak in the summer months (de Villiers 1987), suggesting some seasonality. It is thus likely that, during summer months, at least some dolphins shift to an

alternate foraging strategy, or increased use of sites along the open coasts rather than in the protected waters of Walvis Bay.

Two or three new calves were identified in each winter season with a high of seven in the last year of the study, 2012. This birth rate is similar to that of other similar-sized bottlenose dolphin populations (Wilson et al. 1999; Haase and Schneider 2001; Vermeulen and Bräger 2015). The number of calves may have been underestimated as they are difficult to photograph, often staying very close to shore in the surf zone, and in relatively large and tightly formed groups of adults and calves, when encountered. Additionally, most are born in the summer months, so by the winter field seasons calves already showed some independence from their mothers and could have been identified in the field as juveniles. Calf survival has been linked to maternal experience, size at birth (Cheney et al. 2017), predation (Mann et al. 2000), calf body condition (Mann and Watson-Capps 2005) and even social influences (Stanton and Mann 2012). Further investigation of calf survival rates and the inter-calf intervals of females would provide useful information on demographic parameters of this population.

Fundamental to the application of mark-recapture analysis is the assumption that sufficient survey effort is expended in a large enough area to capture a representative proportion of the population. Encounter rates were lower in summer than winter seasons but there was no relationship between survey effort and either the number of animals identified or calculated abundances within winter seasons, and mark-recapture estimates closely tracked the total number of identified individuals in each season. These results suggest that there was sufficient effort expended in each field season to capture a representative sample of the animals using the bay during the study period, and sufficient recaptures to calculate an accurate abundance estimate, ultimately providing a useful insight into the overall population size. Despite an initial rapid decrease in estimated abundance from 2008 to 2010, annual estimates increased in 2011, and the estimate in 2012 was very similar to that of 2008, resulting in no directional trends in overall numbers of animals using Walvis Bay over the five-year study period. These results suggest that the population was effectively stable over the duration of the study and that variation in abundance estimates between years reflects use of the bay during the field season, and not necessarily overall trends in the population – this is supported by the high survival probability calculated in the best fitting RD models (0.94 to 0.96). The highest numbers estimated were in the first and last years of the study with estimated population sizes of 70 to 82 and 73 to 77 individuals, respectively. It is thus likely that the total number of animals in this population is within this range and certainly less than 100 individuals. Best (2007) reported between 100 and 150 individuals in the population in the early 1990s based on an estimated extrapolation from 83 individuals identified over 20 months. Assuming the proportion of

identifiable animals in the population has not changed over time (average of 0.82 in this study), then the total population in the early 1990s was likely closer to 100 individuals. Although the time-frames of the studies are not directly comparable, this does suggest that there may have been a decrease in total population size since that time.

A population of under 100 individuals is very small, and well below the threshold of 250 mature individuals used by the IUCN (in conjunction with other indicators) to define a population as 'Endangered' (IUCN 2012). Population size estimates are not available for any other cetacean species in Namibia but information from the recently assessed South African populations provides some perspective. The two most endangered resident cetaceans in South Africa are the Endangered Indian Ocean humpback dolphin *Sousa plumbea* (Plön et al. 2016), of which 247 were photographically identified forming a likely total population in the country of around 500 animals (Vermeulen et al. 2017), and the Vulnerable inshore form of the Bryde's whale *Balaenoptera edeni*, which likely numbers between 500 and 1 000 individuals (Penry et al. 2016). Comparisons to terrestrial mammals are challenging as the conservation issues faced (hunting, farmer conflict, poisoning, habitat fragmentation, etc.) and management options (fencing, telemetry, translocation, etc.) are quite different. However, by way of comparison the Namibian Carnivore Atlas (Hanssen and Stander 2004) estimates 355 to 601 wild dogs *Lycaeon pictus* and 562 to 894 lions *Panthera leo* in Namibia, of which 112 to 139 form the partially isolated 'desert lion' population (Standar 2010). It is thus likely that the population of bottlenose dolphins in Namibia is one of, if not the, smallest populations of cetaceans and possibly mammals in Namibia and southern Africa. Although the results of this study showed no trends in the abundance of the species over this relatively short time-period, the small size and apparent isolation of the population make it vulnerable to human impacts, which are growing in the region. We thus strongly recommend that research and monitoring of this population is continued, and the additional data needed for formal classification according to IUCN Red List criteria (trends in population, extent of occurrence, degree of isolation) are attained as soon as possible and a Red List assessment is conducted as a first step in more formal recognition of this unique population.

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