

Abundance and degree of residency of humpback dolphins *Sousa plumbea* in Mossel Bay, South Africa

BS James^{1,2}, MN Bester¹, GS Penry¹, E Gennari^{2,3} and SH Elwen^{1*}

¹Mammal Research Institute, University of Pretoria, Hatfield, South Africa

²Oceans Research, Mossel Bay, South Africa

³South African Institute for Aquatic Biodiversity, Grahamstown, South Africa

*Corresponding author, e-mail: simon.elwen@gmail.com

Indian Ocean humpback dolphins *Sousa plumbea* inhabit nearshore waters from South Africa to eastern India. Humpback dolphins are vulnerable to conservation threats due to their naturally small population sizes and use of nearshore habitats, where human activities are highest. We investigated the abundance and residency of this species inhabiting Mossel Bay, South Africa, using photographic mark-recapture. Data were collected during 81 surveys in Mossel Bay between 2011 and 2013. Open population modelling using the POPAN parameterisation produced a 'super-population' estimate of 125 individuals (95% CI: 61–260) and within-year estimates of between 33 and 86 individuals (2011: 71 [95% CI 30–168]; 2012: 33 [15–73], 32 [15–70]; 2013: 46 [20–108]). Although less appropriate, closed capture models were also run for comparison with previous studies in the region and generated similar, but slightly smaller, population estimates within each year. We compared our catalogue with opportunistic data collected from East London, Plettenberg Bay, De Hoop and Gansbaai. The only catalogue matches attained were between Plettenberg Bay ($n = 44$ identified) and Mossel Bay ($n = 67$ identified), separated by 140 km. Population exchange was moderate, with nine individuals resighted in multiple years between these two areas. This study supports previous findings of long-range movements for this species and provides a baseline from which to assess future impacts on the population.

Keywords: mark-recapture, open population modelling, photo-identification, Plettenberg Bay, POPAN, *Sousa chinensis*

Introduction

Indo-Pacific humpback dolphins *Sousa* spp. inhabit warm, shallow, coastal waters (<30 m deep) of the Indo-Pacific region between South Africa in the west and Australia and China in the east (Reeves et al. 2008). The western limit of the species' range is currently considered to be False Bay (34°8' S, 18°30' E) on the south-west coast of South Africa, with further range extension being constrained by the cold waters of the Benguela Current (Findlay et al. 1992; Jefferson and Karczmarski 2001; Best 2007). A global study of the genus (Mendez et al. 2013) reported strong genetic and morphometric variation, suggesting three extant species of Indo-Pacific humpback dolphins. The new nomenclature described them as Indian Ocean humpback dolphin *S. plumbea*, Indo-Pacific humpback dolphin *Sousa chinensis* (with the boundary between them occurring in the region of the Bay of Bengal, India) and Australian humpback dolphin *S. sahuensis* off northern Australia (Reeves et al. 2008; Jefferson and Rosenbaum 2014). We have thus chosen to follow this new species designation and hereafter refer to the study species (and all previous literature pertaining to the *plumbea* 'form') as *S. plumbea* or simply 'humpback dolphins' [Given that there are several different species of humpback dolphin I have suggested standardising on '*S. plumbea*' rather than 'humpback dolphins'].].

Available abundance estimates indicate there may be <10 000 individuals of *S. chinensis* and *S. plumbea* combined, worldwide (Reeves et al. 2008), and <1 000 *S. plumbea* are thought to occupy the entire South African coastline (Karczmarski 1996). Their low abundance, discontinuous distribution and high exposure to human impacts, including coastal fisheries, shipping, pollution, entanglement in bather protection nets, and coastal development throughout their global range categorise *S. plumbea* (reported as the *plumbea*-type of *S. chinensis*) [I have suggested the additional wording because a species search on the Red List website doesn't find *S. plumbea*.] as Vulnerable on the IUCN Red List of Threatened Species (Reeves et al. 2008). During the most recent update of the South African National Red List Assessment (June 2014), *S. plumbea* were recognised as Endangered based on a number of criteria, primarily their small range, population fragmentation and low population size (Endangered B1 ab (ii iii v)/Vulnerable D1) (Atkins et al. in press). [Does the SA Red List use the same categories and criteria as the IUCN Red List? Also, why are two categories provided – Endangered and Vulnerable?]. *Sousa plumbea* was the only marine mammal in South Africa to be moved to a higher category of conservation concern and the only dolphin listed as Endangered (Atkins et al. in press). It is one of the better-studied cetacean species on the southern African coastline; however, the majority

of studies are over 10 years old (Elwen et al. 2011). Given the national and international recognition of the conservation status of this species, it is imperative that information on the status of the species in South African waters is updated.

Photographic mark-recapture, using photo-identification, is a powerful and versatile technique widely used to assess the abundance, residency, social interactions and individual behaviours of a number of cetacean species (Calambokidis and Barlow 2004; Baird et al. 2009; Barendse et al. 2010; Reisinger and Karczmarski 2010). Photographic mark-recapture studies assessing *S. plumbea* abundance and residency patterns have been conducted in four locations in southern Africa: on the east coast in Maputo Bay (32°45' E, Guissamulo and Cockcroft 2004) and on the KwaZulu-Natal (KZN) coastline, with a focus on Richards Bay (32°05' E, Durham 1994; Atkins and Atkins 2002; Keith et al. 2002), and on the Cape south coast in Algoa and St Francis bays (25°40' E, Karczmarski et al. 1999); and in Plettenberg Bay (23°23' E, Saayman and Tayler 1973; Jobson 2006) (Figure 1). In all cases, population estimates were <600 individuals and mostly <200 individuals, and population connectivity between these study sites is not well understood.

In South African waters, *S. plumbea* is concentrated in two main areas, the KZN north coast and the Cape south coast (Figure 1). Off the KZN coast, *S. plumbea* is more common in the shallow waters of the Tugela Bank area (which extends roughly 60 km north and 80 km south of Richards Bay), where it appears to be associated with the four major river mouths in the area (Durham 1994). The species is rare along the southern KZN and Transkei (i.e. northern part of the Eastern Cape) coastline as is evident from the low encounters (Durham 1994; Keith et al. 2002), low number of strandings (Findlay et al. 1992), low sightings during aerial surveys (Ross et al. 1989) and low captures in bather protection nets (Atkins et al. 2013). This hiatus in distribution appears to functionally separate South Africa's east and south coast populations. This is supported further by (i) a lack of matches found during a comparison of photo-identification catalogues from Algoa Bay and KZN, which are 1 060 km apart (Karczmarski et al. 1999) and (ii) the existence of two distinct mitochondrial DNA (mtDNA) haplotypes from individuals sampled on the northern KZN coast and the Cape south coast, including Algoa Bay and False Bay (Smith-Goodwin 1997), although sample size from the Cape south coast was limited. Therefore, it appears that the populations of *S. plumbea* on the Cape south coast and on the KZN coast are essentially separate (Figure 1) [See comment below, about populations.]

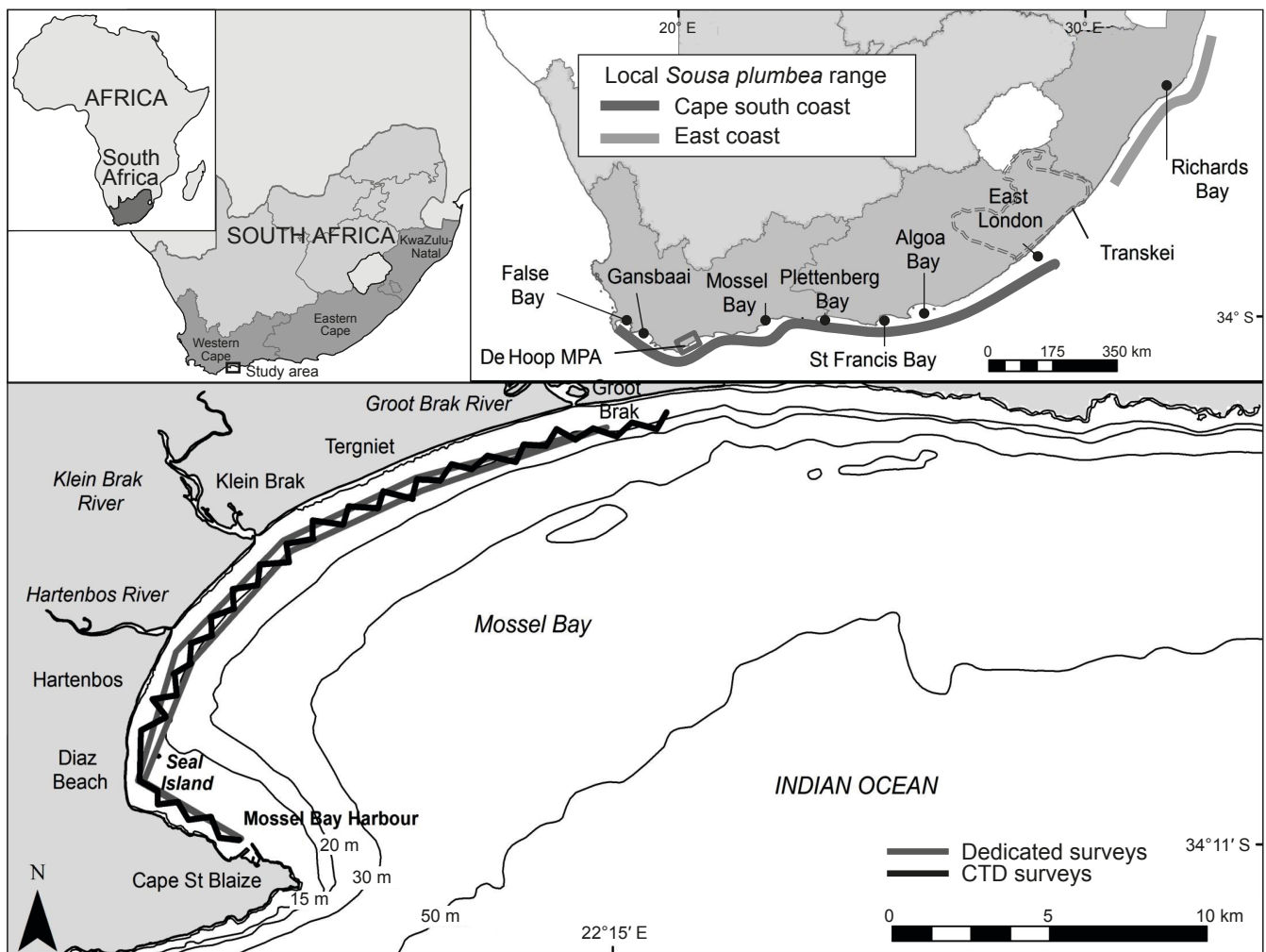


Figure 1: Map of the study area, Mossel Bay, and the names and locations of sites mentioned in the text. Also shown are the typical tracks for dedicated and oceanographic CTD surveys conducted between 20 April 2011 and 14 November 2013. The range of *Sousa plumbea* in South African waters is shown

Despite being adjacent to a populated and accessible stretch of coastline with relatively high numbers of whale-watching companies and research organisations, the Cape south coast population of *S. plumbea* is particularly poorly studied. There are few published data for the approximately 1000 km of coastline between East London and False Bay, other than from Algoa Bay, which was the subject of a multi-year study in the early 1990s (Karczmarski and Cockcroft 1998; Karczmarski 1999; Karczmarski et al. 1999). In the current study we provide a mark-recapture estimate of abundance for Mossel Bay, South Africa (34°11' S, 22°08' E), which represents the most westerly abundance estimate available for *S. plumbea* (500 km from the known western limit of the species). Further, we investigate individual movement patterns by comparing the photo-identification data collected in this study with opportunistic dorsal fin photographs available from four sites along the southern South African coastline. For purposes of comparison, wherever possible we have used the same or similar definitions and methods used in earlier studies in the region.

This study thus provides important baseline information on the population which uses Mossel Bay, which may be useful for broader species conservation and management initiatives.

Material and methods

Data collection

Data were collected a minimum of once per month from 2011 to 2013 in Mossel Bay, except in August 2011 when no surveys were undertaken due to logistical constraints (Table 1). Mossel Bay is a large semi-enclosed embayment on the south coast of South Africa (Figure 1). The bay is shallow, with the 20 m depth contour ~1.2 km from the shore, and is moderately sheltered from the prevailing westerly wind and swell by the Cape St Blaize peninsula to the west of the bay. The sea floor is characterised by areas of both sandy bottom and exposed nearshore reefs (Jackson and Lipschitz 1984). The small Seal Island, on the western side of the bay, is occupied by a rookery of Cape fur seals *Arctocephalus pusillus pusillus* (Johnson et al. 2009). Three rivers enter the bay; the Klein Brak River mouth was permanently open during the study period, the Hartenbos River was closed by a large sandbar (described by Swartz et al. 2000) and the Groot Brak River was opened mechanically (by bulldozer) between September and April each year (Anchor Environmental 2012).

Table 1: Summary of survey effort in Mossel Bay between 2011 and 2013, including number of surveys and encounters, survey time, number of photographs of *Sousa plumbea* and those of quality $\geq Q3^1$ [The legend states that the table lists (i) the total number of photographs and (ii) the number of photographs of quality $\geq Q3$. The table itself, however, lists (i) the total number of photographs and (ii) the number of photographs (or should that be individual dolphins?) of distinctiveness $\geq D3$. Which is correct?]

Month	Number of surveys	Number of encounters	Total survey time (h)	Number of photographs	Number of $\geq Q3^1$ photographs
2011					
April	1	1	5.2	382	274
May	3	1	19.5	358	257
June	6	2	22.8	1 545	838
July	3	0	7.5	0	0
August	0	0	0.0	0	0
September	1	1	5.6	109	95
October	1	0	7.3	0	0
November	3	1	11.6	75	42
December	3	0	12.1	0	0
2012					
January	1	0	5.5	0	0
February	3	2	18.1	272	176
March	4	3	28.2	1 014	764
April	1	0	5.0	0	0
May	1	0	5.0	0	0
June	2	0	13.8	0	0
July	1	1	8.5	123	99
August	4	2	31.1	102	30
September	2	1	13.3	127	14
October	3	1	23.0	64	30
November	2	0	8.8	0	0
December	3	2	18.4	371	206
2013					
January	3	1	15.5	28	7
February	4	1	21.7	528	467
March	3	2	23.0	278	226
April	4	3	29.0	551	335
May	3	1	21.7	28	9
June	2	1	13.8	36	12
July	5	1	26.5	26	16
August	3	1	24.6	15	5
September	3	1	23.1	3	0
October	1	1	9.0	151	133
November	2	1	12.5	6	2
Total	81	32	490.7	6 192	4 037

Q – quality of photograph; D – individual distinctiveness of dolphin

Boat-based surveys were conducted from a 6-m fibreglass catamaran-type skiboat with two 90-HP two-stroke engines. Data were collected during (i) dedicated photo-identification surveys and (ii) line-transect surveys conducted for the collection of physical oceanographic data (conductivity, temperature and depth), hereafter referred to as CTD surveys. Both survey types covered a similar search area between the Groot Brak River mouth and the Mossel Bay harbour (Figure 1). Dolphins were approached and photographed in the same manner during both survey types, allowing for the compilation of a single catalogue.

Dedicated photo-identification surveys were conducted in both directions between the limits of the search area (Figure 1). A searching speed of 7 knots was maintained, with a minimum of three observers searching continuously using the naked eye and binoculars.

During CTD surveys, data collection began in the Groot Brak area and ended at the Mossel Bay harbour, following a predefined inshore-offshore zigzag route between 200 and 1 000 m from the shore (Figure 1). During these surveys, the boat came to a complete stop at the end of each transect line to collect CTD data. A single observer conducted continuous 360° scans during the CTD deployment, as well as when the boat was in transit between sampling stations. If any cetaceans were sighted between stations, the animals would immediately be approached. However, if animals were sighted while on station, they would be approached only after the completion of the CTD data collection.

On both types of survey, standard data collected were as follows: (i) time and location of the encounter; (ii) estimates of group size (minimum, best and maximum); (iii) group composition (calves, juveniles and adults) and (iv) behaviour. A group was defined as a number of individual *S. plumbea*, observed together at the same time, often engaged in the same or a similar behaviour (Karczmarski 1999). Dolphin groups were approached slowly and from behind to minimise disturbance. We attempted to photograph all individuals in the group, regardless of markings or age. Photographs were taken using a digital SLR camera equipped with a 70–300 mm zoom lens and polarising filter. Individuals encountered more than once on the same day were recorded as a single encounter. Residency of animals within Mossel Bay was explored for all animals in the catalogue, with those animals encountered at least four times during the study period considered as 'resident', those seen only once classified as 'transient' and the remainder classified as 'semi-resident', following the definitions of Keith et al. (2002). Seasonality of presence was investigated by determining the number of individuals encountered during each

survey day within the two defined seasons; winter (May–October) and summer (November–April), following Karczmarski et al. (1999).

Opportunistic photographs of *S. plumbea* were available from locations to the east and west of Mossel Bay. These were collected from commercial whale-watching boats operating in Plettenberg Bay (34°3' S, 23°23' E) and Gansbaai (34°37' S, 19°24' E), during scientific research in East London (33°0' S, 27°55' E) and Plettenberg Bay, and during aerial patrols in the De Hoop Marine Protected Area (34°37' S, 20°18' E) (Table 2).

Data selection and processing

Photographs were graded for quality (Q) on a scale of 1–6 (Q1 being the worst and Q6 the best), based on the level of focus, exposure of the dorsal fin and hump, lighting, and angle to the camera (Elwen et al. 2009). Using only photographs with a grade of Q3 or higher, individuals were then graded on a distinctiveness (D) scale of 1–5, D1 being not distinctive and D5 very distinctive (Elwen et al. 2009). Individual identification was determined using several criteria, including: (i) dorsal fin tears; (ii) nicks and notches; (iii) deformities; (iv) colouration; (v) scratches; (vi) scars and wounds; and (vi) distinctive fin shapes (Karczmarski and Cockcroft 1998; Wilson et al. 1999; Mansur et al. 2011). Multiple dorsal-edge marks and body scars were used to identify or confirm the identity of catalogued individuals, and all matches were confirmed by at least two authors (BJ and SE). On account of the small group sizes and high frequency of markings (body and dorsal markings), it was possible to distinguish all individuals on any given day. However, not all individuals were sufficiently distinctive to allow for confident re-sighting between days or over longer time periods. Calves and juveniles were defined based on their sizes and the closeness of their associations with adults that were assumed to be their mothers (Karczmarski 1999). Only a small proportion of calves and juveniles had distinguishing body marks that enabled confirmation of their identity. Although adult individuals in Q3 photographs were included in the photo-identification catalogue, only individuals of distinctiveness D3–D5 in photographs of quality Q4 and above were used in mark-recapture analyses to ensure consistent identification between encounters. Opportunistic photographs were evaluated in the same manner, with the best photograph ($\geq Q3 \geq D3$) of each identifiable individual placed into a working catalogue for each of the four locations (East London, Plettenberg Bay, De Hoop and Gansbaai). Individuals were then compared between each catalogue and that of Mossel Bay, with all catalogues consisting of animals $\geq Q3 \geq D3$ identified in each location. Of the 69 animals identified in the various locations only 58 were $\geq Q3 \geq D3$ and thus used for comparison between

Table 2: Summary of opportunistic photo-identification data for *Sousa plumbea* from various locations along the South African coast and from different sources [Would the data be unpublished, from each source?]

Location	Number of photographs	Time period	Number of surveys	Total number of dolphins identified	Source
East London	115	2012	1	6	GSP
Plettenberg Bay	622	2006–2010, 2013	15	44	GSP; Orca Foundation (2009, 2010)
De Hoop MPA ¹	22	2007	3	8	P Chadwick (WWF-SA)
Gansbaai	62	2007, 2008	7	11	Dyer Island Conservation Trust

¹ MPA – marine protected area. Of the 69 animals identified only 58 were >Q3 >D3

areas. For all locations individuals photographed in close association with a calf on three or more sampling occasions were assumed to be female (Karczmarski 1999; Keith et al. 2002).

Estimating abundance of marked individuals

Capture histories for each individual were compiled using survey days on which *S. plumbea* was encountered as the capture period. A visual inspection of the discovery curve of newly captured individuals was used to investigate whether the population could be considered 'open' or 'closed' relative to the study area and period (Williams et al. 2002). The presence of an asymptote would indicate that most animals had been captured and the population could effectively be treated as closed, whereas the absence of an asymptote would indicate that a relatively large number of individuals in the population were yet to be captured, so the population should be treated as open (e.g. Keith et al. 2002; Williams et al. 2002; Reisinger and Karczmarski 2010).

To enable comparability with previous studies in the region, we analysed our mark-recapture data using both open and closed population models. The different assumptions and analytical methods employed by the two approaches (Jolly 1965; Otis et al. 1978; Chao 2001; Chao and Huggins 2005; Cooch and White 2012) mean that the results are not directly comparable, but using both can provide a more comprehensive assessment of the number of *S. plumbea* in the study area and also allows for direct comparisons to other studies where closed models have been used. Here, we have used both closed and open population models to estimate annual abundance for each of the three consecutive years (2011–2013). Closed models provide an estimate of the number of individuals using the study area during each of the three years whereas open population models provide an estimate of the super-population for the entire study period, which accounts for births and deaths occurring within that period and also assume that some animals may be outside the area (immigration and emigration) during the period. Given that the mark-recapture estimates apply only to the proportion of the population that is distinctively marked (see below), it must further be assumed that the behaviour and capture probability of the marked individuals is representative of the entire population (Cooch and White 2012). Calves and juveniles were excluded from the mark-recapture analysis due to the low incidence of permanent/reliable dorsal fin markings on young animals (Hammond et al. 1990). Our abundance estimates therefore are representative of the adult population. All mark-recapture analyses in our study were conducted in the programme MARK (White and Burnham 1999; Cooch and White 2012) using the RMark interface (Laake 2013).

Closed population models

Annual estimates of abundance of *S. plumbea* in Mossel Bay were calculated for 2011, 2012, and 2013, respectively, by means of a series of closed capture models using the Huggins log-likelihood method (Huggins 1989, 1991). Model fit was compared using the penalised Akaike Information Criterion (AICc) value to determine the best-fitting model in each model set, with AICc values >2 regarded as significant (Burnham and Anderson 2002). We implemented models that allowed for variations in capture probability over time and for differences in capture probability (heterogeneity) within the population using a two-mixture approach (Pledger 2000). For models that included capture heterogeneity, the probability that an individual occurs in a specific mixture (π) was fixed at a value of 0.475, based on a series of successful model runs, to improve model convergence. We did not include models that investigated a behavioural response to capture (as might occur when animals are trapped or physically captured) and set initial capture probability equal to subsequent recapture probability ($p = c$).

Open population models

Open population modelling was conducted using the POPAN parameterisation (Schwarz and Arnason 1996) in the Jolly-Seber (JS) framework (Jolly 1965; Seber 1965). Parameters calculated were the super-population size (defined here as N_s [Could this be written as N_s ? If so, need to check all occurrences. Note that N_{total} uses a subscript.]), apparent survival (ϕ), capture probability (p) and the probability of entry from the super-population (b) (Cooch and White 2012). Additionally, open population models were also run for each year [In addition to being run for the entire period, as indicated above?] and were compared with annual abundance estimates produced using closed models. Because only adults were used in analyses, no estimates of birth rate or recruitment were available. Model fit was compared using the quasi-penalised Akaike Information Criterion (QAICc) (Cooch and White 2012).

Goodness-of-fit testing

Goodness-of-fit testing was performed to produce a variance inflation factor (\hat{c}), which would indicate whether the data were over- or underdispersed compared to a fully time-dependent Cormack-Jolly-Seber model with perfect fit (Cormack 1964; Jolly 1965; Seber 1965), and by how much the data violate the model assumptions (Cooch and White 2012). The factor was then used to produce a QAICc [Should this be QAICc?] to provide a means for model selection. For this study, \hat{c} was determined using 1 000 simulations in a bootstrap goodness-of-fit test in

the programme MARK and using the standalone programme RELEASE (Burnham et al. 1987). RELEASE also provided results of TEST 2, TEST 3.SR and TEST 3.Sm which test for capture homogeneity, survival homogeneity and potential variation in survival over time, respectively.. Values of \hat{c} larger than 1.0 indicate overdispersion in the data. To be conservative, the greatest \hat{c} value produced by means of these tests was used to correct the AICc prior to model selection using the QAICc for all open population models (Cooch and White 2012).

Estimating total population size

To account for the poorly marked individuals not used in the mark-recapture analysis, the mark-recapture estimates (\hat{N}) from both closed and open population models were extrapolated upwards to calculate the total population size (N_{total}), with variance calculated using the Delta method (Wilson et al. 1999). The proportion of marked individuals (θ) was calculated as the number of distinctly marked animals ($\geq D3$) in good-quality photographs (Q4–Q6, $n = 1\,321$) expressed as a proportion of the number of animals identified during each survey, averaged over all surveys.

Results

In all, 491 hours of boat-based surveys, during 81 survey days, were conducted between 20 April 2011 and 14 November 2013 (66 dedicated photo-identification and 15 CTD surveys). *Sousa plumbea* individuals were encountered on 32 surveys (26 dedicated, 6 CTD) and successfully photographed on 31 of them. The total time spent with the dolphins during all encounters was 30 hours. During this time, 6 661 photographs were taken, of which 1 321 (20%) were of acceptable quality (Q4 and above) for use in mark-recapture analyses. Nine individuals were rated with a distinctiveness of D2, 11 of D3, 33 of D4 and 14 of D5, with no adult individuals rated as D1 (unidentifiable) in reasonable quality photographs. In all, 67 distinctive animals were identified and used to develop a photo-identification catalogue (with 87% of catalogued animals at least D3 in $\geq Q3$ photographs).

Of the catalogued individuals, 44% were encountered within the first three months of the study. About half ($n = 33$, 49%) were sighted only once, with only two being encountered more than 10 times (Figure 2). Most individuals ($n = 44$, 66%) were present in only a single year; some ($n = 20$, 33%) were present in two years and only three (1%) were present in all three years of the study. Group sizes varied between one and 15 (mean 4.9 ind. [SD 3.5]), with only four encounters of

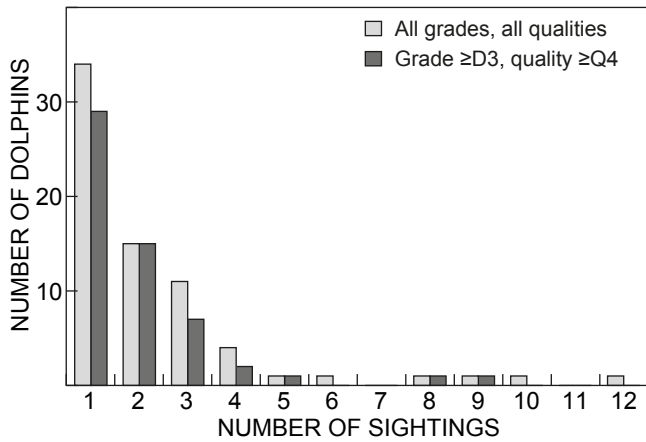


Figure 2: Frequency distribution of sightings of *Sousa plumbea* of all distinctiveness grades in photographs of all qualities, and only distinctive animals ($\geq D3$) in photographs of good quality ($\geq Q4$) in Mossel Bay between April 2011 and November 2013

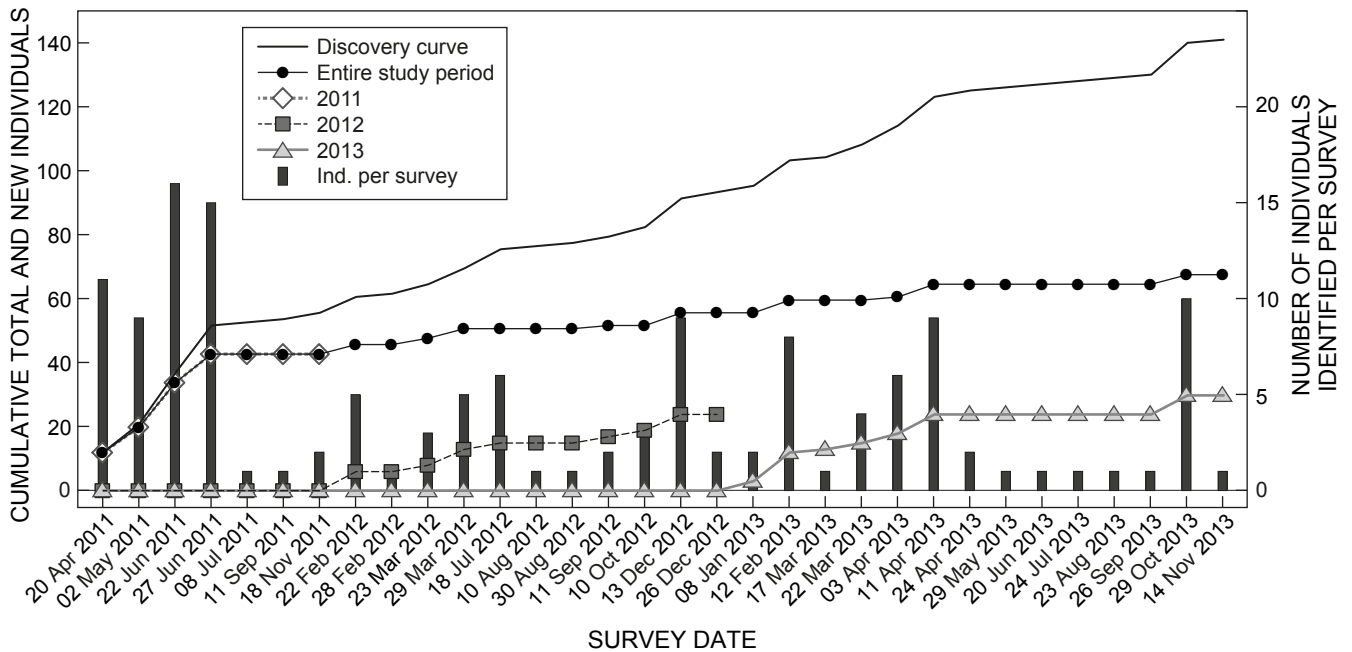


Figure 3: Comparison of the discovery curve of the cumulative individuals identified with the newly identified animals per encounter for 2011, 2012, 2013 and the entire study period. The bars denote the number of individuals identified per survey for the study period (April 2011–November 2013)

lone adults. Larger group sizes were observed in 2011 than during other years, and groups tended to be larger in summer (Figure 3)

Abundance estimate: closed population models

Closed capture models corrected by the proportion of marked individuals in the population produced the following within-year population estimates (N_{total}): 2011 – 71 ind. (95% CI 30–167); 2012 – 35 ind. (14–86) and 28 ind. (14–55); and 2013 – 43 ind. (19–98) and 54 ind. (19–154). For 2011, the best-fitting model allowed for variation in capture probability with time. In 2012, the null model and the model allowing for capture heterogeneity fitted the data equally well. In 2013, the model allowing for variation in capture probability over time and the model allowing for capture probability to vary both over time and with heterogeneity were the best fitting models (Table 3). Model averaging of the real parameter value of p was undertaken for the two best-fitting models in 2012 and 2013, respectively, but no significant difference was found between model results (Student's t -test), and results from both models are presented for each year.

Abundance estimate: open population models

Goodness-of-fit testing suggested slight overdispersion in the super-population data, with $\hat{c} = 1.197$ based on bootstrapping in MARK and $\hat{c} = 1.04$ in RELEASE based on TEST 2 and TEST 3 (Table 4). The more conservative value of \hat{c} (1.197) was used to correct the AICc for model selection. The best model (QAICc = 399.1) produced a super-population abundance estimate (N_{total}) of 125 ind. (95% CI: 112–140) and included time-dependent survival, constant capture probability and time-dependent probability of entrance of an animal from the super-population into the population $\{\phi(t)p(.)b(t)Ns(.)\}$ (Table 5). Open population estimates (N_{total}) were fairly consistent between models and varied between 104 ind. for the model with constant survival and recapture probabilities and constant entrance into the super-population $\{\phi(.)p(.)b(.)Ns(.)\}$ and 127 ind. for the model that included constant survival and capture probabilities with time dependent entrance into the super-population $\{\phi(.)p(.)b(t)Ns(.)\}$ (Table 5). Open population modelling was also conducted within each year. The best model for 2011 (QAICc = 85.1) produced an abundance estimate of 71 ind. (95% CI: 30–168) and included time-dependent survival, constant recapture probability and entrance into the population. For 2012, two models fitted the data equally well (QAICc = 94.5 and 95.2), producing population estimates of 33 ind. (95% CI: 15–73) and 32 ind. (95% CI: 15–70), respectively. Both models included constant survival and recapture probabilities but the models differed in time dependence and constant entrance into the super-population respectively. For 2013, the best-fitting model (QAICc = 99.1)

Table 3: Huggins full heterogeneity closed model outputs including: number of parameters (N_{par}); penalised Akaike Information Criterion (AICc); difference between the selected candidate model and the top ranked model ($\Delta AICc$) [Is this insertion correct?]; the model's deviation from a perfect fit (Deviance); [What is 'Weight'?] estimate of the number of marked animals (\hat{N}); standard error (SE); lower and upper limits of the 95% confidence interval (LCL and UCL); and estimated total population (N_{total}). The proportion of marked individuals (θ) was calculated as the number of distinctly marked animals ($\geq D3$) in good quality photographs (Q4–Q6, $n = 1\ 321$) expressed as a proportion of the number of individuals identified during each survey within each year, resulting in values of 0.85, 0.80 and 0.99 for 2011, 2012 and 2013, respectively

Model	Model selection criteria					Marked population				Total population			
	N_{par}	AICc	$\Delta AICc$ [Edit Ok?]	Deviance	Weight	\hat{N}	SE	LCL	UCL	N_{total}	SE	LCL	UCL
2011													
$\pi(.)p(t)c()$	6	160.3	0.0	179.9	0.9	60	15	42	106	71	33	30	167
$\pi(.)p(.)c()$	1	170.0	9.7	200.0	0.0	65	17	44	116	76	35	32	182
2012													
$\pi(.)p(.)c()$	1	153.7	0.0	150.1	0.5	22	4	19	35	35	17	14	86
$\pi(.)p(mix)c()$	2	153.7	0.1	148.1	0.5	28	8	20	57	28	10	14	55
$\pi(.)p(t + mix)c()$	11	159.0	5.3	133.7	0.0	28	8	20	56	35	17	14	84
$\pi(.)p(t)c()$	10	159.4	5.7	136.4	0.0	22	3	18	33	27	9	14	53
2013													
$\pi(.)p(t)c()$	8	178.8	0.0	176.3	0.6	43	8	33	68	43	19	19	98
$\pi(.)p(t + mix)c()$	9	179.6	0.8	174.9	0.4	53	18	35	115	54	31	19	154
$\pi(.)p(.)c()$	1	188.4	9.7	200.6	0.0	45	9	34	73	45	20	20	105
$\pi(.)p(mix)c()$	2	189.2	10.5	199.4	0.0	57	20	36	128	57	34	19	169

The parameters used to build the models in these sets are: the probability of being captured initially (p); the probability of recapture given that the animal has been captured before (c), which for our models was set equal to p ; and the probability that an animal occurs in a specific mixture (π). Each parameter may be designated as time dependent (t) or constant over time ($.$). Mixture (mix) was included as a heterogeneity parameter to determine if capture probability varies between individuals with π set at 0.475 for these models

Table 4: Program RELEASE goodness-of-fit test results of the fully time-dependent Cormack-Jolly Seber model within a POPAN parameterisation in the program MARK, of sighting histories of *Sousa plumbea* in Mossel Bay during the period April 2011 to November 2013 for the super-population and for each year. Parameters for goodness-of-fit testing are designated as follows: variance inflation factor (\hat{c}); Chi-squared statistic (χ^2), degrees of freedom (df) and statistical significance (p value). NA denotes no data

Test	Super-population				2011				2012				2013			
	\hat{c}	χ^2	df	p	\hat{c}	χ^2	df	p	\hat{c}	χ^2	df	p	\hat{c}	χ^2	df	p
TEST 2+ TEST 3	1.04	34.27	33	0.41	0.55	1.64	3	0.65	1.02	6.12	6	0.41	0.22	1.32	6	0.97
TEST 2	1.61	29.04	18	0.05	0.55	1.64	3	0.65	1.32	3.97	3	0.26	0.33	1.32	4	0.86
TEST 3	0.35	5.24	15	0.99	NA	NA	NA	NA	0.72	2.15	3	0.54	0.0	0.0	2	1.0
TEST 3.SR	0.25	2.27	9	0.99	NA	NA	NA	NA	1.08	2.15	2	0.34	0.0	0.0	2	1.0
TEST3.Sm	0.50	2.97	6	0.81	NA	NA	NA	NA	0.0	0.0	1	1.0	0.0	0.0	0	1.0

produced an abundance estimate of 46 ind. (95% CI: 20–108) and included time-dependent survival, constant recapture probability and time-dependent entrance into the super-population. Model selection for each year was based on corrected AICc values using the more conservative \hat{c} values (Table 4)

Residence

The time between resightings varied from five days to 22 months. Very few animals ($n = 7$, or 10% of the population) were ‘resident’ in Mossel Bay during the study period, as defined by Keith et al. (2002). Of those considered resident, five were female (based on repeated close association with a calf), of which two were seen more frequently when they were accompanied by a small calf and less frequently when the calf was older. Half of the animals identified in Mossel Bay would be classified as ‘transient’ and 40% as ‘semi-resident’.

Seasonality

There were no consistent seasonality patterns in Mossel Bay in terms of either number of animals encountered or individual presence. Within each year there were multiple months when no new individuals were captured. More groups and more individuals were encountered during April and June 2011 (summer and winter), March and December 2012 (summer 2) and April and October 2013 (summer and winter) compared to other times of the year (Figure 3).

Population links

The catalogue of *S. plumbea* identified in Mossel Bay was compared to images taken opportunistically at four locations over a 7-year period (2006–2013; Table 2). No individuals identified at East London, De Hoop or Gansbaai were common to any of the other locations, whereas nine (15%) individuals from 58 used to evaluate movement between areas [I am not sure where the number 58 comes from. In Table 2 there are 69 animals from the other four locations, added to which are your Mossel Bay animals.] were found to be common to both Mossel Bay and Plettenberg Bay. Four of the nine were observed in multiple years in Mossel Bay but during only a single year in Plettenberg Bay, and one individual was seen during multiple years in both locations (Table 6). Two individuals were seen during multiple years in Plettenberg Bay and in only a single year in Mossel Bay. Two individuals were seen during only a single year in both locations. The only year in which data were collected at both locations was 2013. Five identified individuals were determined to be female, based on close association with a

Table 5: Open population (POPAN) model outputs for the super-population and for each year, including: number of parameters (N_{par}); quasi-penalised Akaike Information Criterion (QAICc); difference between the selected candidate model and the top ranked model ($\Delta QAICc$); indication of the model's deviation from a perfect fit (Qdev); [What is 'Weight'?] number of distinctive *Sousa plumbea* (\hat{N}); standard error (SE); lower and upper limits of the 95% confidence interval (LCL and UCL); and estimated total population (N_{total}). The QAIC and Qdev were corrected for overdispersion based on the bootstrapped goodness-of-fit using \hat{c} values of 1.197 (super-population), 1.039 (2011), 1.235 (2012) and 1.0 (2013). The proportion of marked individuals (θ) was calculated as the number of distinctly marked animals ($\geq D3$) in good-quality photographs (Q4–Q6, $n = 1\ 321$) of the number of animals identified during each survey over the entire time period, resulting in a θ value of 0.872, 0.85, 0.80 and 0.99 (over the three year period and in 2011, 2012 and 2013 respectively)

Model	Model selection criteria					Marked population				Total population			
	N_{par}	QAICc	$\Delta QAICc$	Qdev	Weight	\hat{N}	SE	LCL	UCL	N_{total}	SE	LCL	UCL
<i>Super-population</i>													
$\phi(t)p(.)b(t)N_s(.)$	9	399.1	0.0	68.7	9.8^{-1}	109	19	73	146	125	48	61	260
$\phi(t)p(.)b(.)N_s(.)$	8	407.3	8.2	79.3	1.6^{-2}	94	11	72	116	108	35	58	200
$\phi(.)p(.)b(t)N_s(.)$	8	414.2	15.1	86.2	5.2^{-4}	111	20	72	150	127	50	60	269
$\phi(.)p(.)b(.)N_s(.)$	4	416.2	17.0	97.2	2.0^{-4}	91	11	70	112	104	33	56	192
<i>2011</i>													
$\phi(t)p(.)b(.)N_s(.)$	3	85.1	0.0	0.0	9.5^{-1}	60	15	31	90	71	33	30	168
$\phi(.)p(.)b(.)N_s(.)$	3	93.4	8.2	0.0	1.5^{-2}	72	20	33	110	84	41	34	206
$\phi(.)p(.)b(t)N_s(.)$	6	93.4	8.3	0.0	1.5^{-2}	74	20	35	112	86	41	36	210
$\phi(.)p(t)b(.)N_s(.)$	8	94.9	9.8	0.0	7.7^{-3}	68	24	20	116	79	44	29	219
<i>2012</i>													
$\phi(.)p(.)b(t)N_s(.)$	6	94.5	0.0	23.3	4.4^{-1}	27	6	15	38	33	14	15	73
$\phi(.)p(.)b(.)N_s(.)$	4	95.2	0.7	30.0	3.1^{-1}	26	5	15	37	32	13	15	70
$\phi(t)p(.)b(t)N_s(.)$	8	97.0	2.5	18.6	1.3^{-1}	26	6	15	38	32	14	14	71
$\phi(t)p(.)b(.)N_s(.)$	6	97.0	2.6	25.8	1.2^{-1}	26	5	16	36	32	13	15	69
<i>2013</i>													
$\phi(t)p(.)b(t)N_s(.)$	10	99.1	0.0	0.0	8.2^{-1}	45	10	27	64	46	21	20	108
$\phi(t)p(.)b(.)N_s(.)$	6	103.4	4.3	0.0	9.8^{-2}	46	9	28	65	47	21	20	108
$\phi(t)p(t)b(.)N_s(.)$	11	104.0	4.9	0.0	7.1^{-2}	38	6	27	50	39	15	19	80
$\phi(.)p(.)b(t)N_s(.)$	6	109.6	10.5	0.0	4.3^{-3}	68	20	30	107	69	37	26	184

Table 6: Catalogued *Sousa plumbea* found in both Mossel Bay (MB; 2011–2013) and Plettenberg Bay (PB; 2006–2013, excluding 2011 and 2012). A value of 1 represents a year in which an individual was captured in a surveyed area and 0 when that individual was not seen

Individual ID	Sex	Plettenberg Bay						Mossel Bay		
		2006	2007	2008	2009	2010	2013	2011	2012	2013
MB_Sp_026/PB_Sp_006	Unknown	0	1	0	0	0	0	1	0	1
MB_Sp_027/PB_Sp_029	Unknown	0	0	0	0	0	1	1	0	1
MB_Sp_034/PB_Sp_024	Unknown	0	0	1	1	0	0	1	0	0
MB_Sp_043/PB_Sp_013	Female	0	1	0	0	0	0	0	1	1
MB_Sp_048/PB_Sp_050	Unknown	0	0	0	1	0	0	0	1	0
MB_Sp_050/PB_Sp_010	Female	0	1	0	0	1	0	0	1	1
MB_Sp_053/PB_Sp_027	Female	0	0	0	0	0	1	0	1	1
MB_Sp_055/PB_Sp_014	Unknown	0	1	0	0	0	1	0	0	1
MB_Sp_059/PB_Sp_054	Unknown	0	0	0	0	0	1	0	0	1

calf on three or more occasions, with three of these individuals common to Mossel Bay and Plettenberg Bay.

Discussion

This study presents the most westerly published abundance estimate for *S. plumbea* and the first within southern Africa in over 11 years. Here we applied closed and open population models to generate within-year abundance estimates of *S. plumbea* using Mossel Bay over three consecutive years, and open population models to determine the size of the super-population over a 3-year period. Additionally, we explored individual movement patterns over a 1000 km stretch of coastline using photographs collected opportunistically. During the study period, 67 individuals were identified in Mossel Bay, and mark-recapture analysis yielded an open population estimate of <130 individuals. The confidence intervals in this study were large as a result of the low number of resightings of animals. However, even the upper confidence limit was below the abundances estimated for other populations on the Cape south coast, namely Algoa Bay and Plettenberg Bay (see below). Certain individuals were observed in both Mossel Bay and Plettenberg Bay (140 km apart), suggesting that abundance estimates for these populations cannot be treated in isolation. We discuss below the limitations and implications of our results and place them within the context of what is known about *S. plumbea* biology in southern Africa.

Photo-identification is a widely used research technique and full rationalisation of assumptions of this approach to studying dolphins has been discussed in detail elsewhere (e.g. Wilson et al. 1999; Read et al. 2003; Elwen et al. 2009). Briefly, to assess abundance or survival rates accurately, both closed and open population mark-recapture models are reliant on the fulfilment of several key assumptions, namely that marks are unique, do not change between sampling periods, and are correctly identified, and that marking does not affect the capture probability of the individual. Additionally, sufficient time must pass between sampling periods to allow for complete mixing of the population, sampling periods should be instantaneous, and all animals must have an equal chance of being captured (Cooch and White 2012). The frequency of our surveys and the use of multiple marks for individual recognition reduced the probability of a mismatch occurring as a result of marks changing. The relatively high number of animals that were encountered only once, and the lack of a complete asymptote in the discovery curves for 2012 and 2013, suggest that some animals spend the majority of their time outside the study

area. Although this does not necessarily violate the assumptions of closed population models, provided their use of the study area is effectively random, it reduces the probability of recapturing individuals and can reduce model accuracy and precision. We included closed models primarily to improve comparability with other studies along the South African coastline that have used these models (Durham 1994; Keith et al. 2002; Atkins and Atkins 2002; Jobson 2006), and because they allow heterogeneity of capture probability to be accounted for analytically (Pledger 2000). Ultimately, the abundance estimates obtained using both open and closed models within each year were very similar, lending confidence to the results and confirming the low number of animals using Mossel Bay.

Mark-recapture methods have been used to estimate the abundance of *Sousa plumbea* in seven previous studies at four other sites along the southern African coast (see Table 7). All were similar to the current study in spatial extent (except that of Durham [1994] that investigated almost the entire KZN coastline) and duration, and applied either open population models only or a combination of both open and closed models (Table 7). Slight differences in the methods used among the studies make direct comparisons of results difficult, but there are several marked similarities. For most studies, estimates of abundance were ~100 individuals using each study area, although open population models generated higher estimates for Algoa Bay (465 km to the east of Mossel Bay; Karczmarski et al. 1999) and Plettenberg Bay (140 km to the east of Mossel Bay; Jobson 2006) on the Cape south coast (Table 7). These generally low estimates are supported by the small number of animals identified in each location, ranging from 52 ind. in Maputo Bay (Guissamulo and Cockcroft 2004) to 181 ind. in KZN (Keith et al. 2002). Low encounter rates in most studies (Table 7), lack of complete asymptotes in discovery curves where available (Durham 1994; Karczmarski et al. 1999b; Keith et al. 2002; Jobson 2006), and high proportions of individuals seen only once, collectively suggest that these studies represent only a proportion of the range of the population(s) under study, with many individuals spending at least some time outside of the areas under study. From a conservation and management perspective, it is valuable to know to which area or population an estimate applies, and whether there is any population overlap between estimates from adjacent areas. Hence it is important to determine individual ranging patterns and population structure within southern African waters.

The definition of resident or transient individuals in studies of *Sousa plumbea* is somewhat arbitrary and typically is based on the number of times animals are photographed successfully, rather than a known behavioural distinction, as observed in some bottlenose dolphin

Table 7: Summary of study design and mark-recapture results obtained from previous studies on *Sousa plumbea* in southern Africa: Maputo Bay (MapB, ¹1992 and 1995–1997), KwaZulu-Natal (KZN, ²1991–1993), Richards Bay (RB, ³1998, ⁴1998–2000), Algoa Bay (AB, ^{5,6}1991–1994), and Plettenberg Bay (PB, ⁷2002 and 2003) and in the present study in Mossel Bay (MossB, ⁸2011–2013). Values not reported are shown as NA; *mean closed population size [Please check additions in red font]

Study site	Duration of study (months)	Number of surveys	Number of encounters	Group size (ind.; range [mean])	Max individual distance travelled (km)	Catalogue size (ind.)	Animals seen more than once (ind.)	Distinct animals (%)	Closed model abundance estimate (ind. [95% CI])	Open model abundance estimates (ind. [95% CI])	Reference
MapB	24	146	37	2–25 (14.9)	NA	52	23	52	NA	105 (31–151)	1
KZN (entire)	18	136	56	1–18 (6.7)	120	96	45	68	165 (134–229)	161 (81–240)	2
RB	18	41	30	1–20 (5.1)	70	45	23	31	NA	38 (19–56)	2
	7	73	56	1–20	140	24 (181 KZN)	56	76	NA	74 (60–88)	3
	25	125	NA	NA	NA	92	56	54	244 (217–287)	170 (112–230)	4
AB	36	60	104§	3–24 (7)	110	70	37	92	NA	466 (447–485)	5, 6
PB	24	87	35	2–20 (mode = 5)	32	63	36	77	112 (75–133)	727	7
MossB	32	81	31	1–15 (4.9)	139	67	34	94	46* (38–56)	125 (112–140)	8

§The high number of encounters made in Algoa Bay compared to other studies can be attributed to differences in survey methods, as the research boat was launched only in response to shore-based sightings of *S. plumbea* (Karczmarski et al. 1999). References: 1 – Guissamulo and Cockcroft (2004), 2 – Durham (1994), 3 – Keith et al. (2002), 4 – Atkins and Atkins (2002), 5 – Karczmarski (1996), 6 – Karczmarski et al. (1999), 7 – Jobson (2006), 8 – Current study

populations (e.g. Conn et al. 2011). Given that the number of times individuals will be photographed depends heavily on the level of survey effort and the area searched, it is difficult to compare these parameters directly between studies. Within South Africa, the majority of *S. plumbea* appear to be transient within both the Tugela Bank region of KZN (Durham 1994; Keith et al. 2002) and on the Cape south coast including in Algoa Bay, Plettenberg Bay and Mossel Bay (Karczmarski et al. 1999; Jobson 2006; this study). The relative proximity of locations on the Cape south coast suggests there is likely to be some degree of population overlap between study areas. However, data on alongshore movements of *S. plumbea* in southern Africa is limited. The longest stretch of southern African coastline that has surveyed in a single study on humpback dolphins to date is the 550 km of the KZN coastline (Durham 1994). Multiple launch sites along the coast were used to cover the area. The longest range movement by an individual detected during that study was 120 km. However, 59% of individuals (and 80% of identified mothers) were always sighted within the vicinity of their first sighting (i.e. in the same 'search area' [Was a search area defined in that study in terms of being accessed from a given launch site?]), with maximum recorded alongshore movements of between 17 and 70 km, suggesting high site fidelity within the population (Durham 1994). A more recent study supports these findings, with 181 individuals identified off KZN but only a single long-distance movement of 150 km detected (from Durban to Richards Bay) (Keith et al. 2002). On the Cape south coast, all individuals identified from two surveys of St Francis Bay were resighted in the adjacent Algoa Bay, some 100 km away; however, only 10% of the identified population was seen frequently, with females comprising 80% of these animals (Karczmarski et al. 1999). Of animals identified in Plettenberg Bay, three individuals were also seen in Buffalo Bay, approximately 32 km to the west (Jobson 2006).

In the current study, we found matches between Mossel Bay and Plettenberg Bay (140 km away), the closest site from which data were available and also the site with the largest quantity of data. Several of the nine individuals identified in both bays were identified in multiple years and they were found to move in both directions. These nine individuals represent 13% of the animals in the Mossel Bay catalogue and 20% of the 44 animals identified opportunistically in Plettenberg Bay, suggesting a moderate degree of overlap between these two sites and supporting previous suggestions that humpback dolphins on the Cape south coast probably form one large population (Karczmarski 1996). It has been suggested that mother-calf pairs would have higher site fidelity to an area (Durham 1994; Karczmarski et al. 1999); however, three of the nine animals seen to undertake these long-distance movements were females with

calves. The movement of individuals back and forth between multiple locations over a number of years suggests that both areas are within the home range of these animals and that this is not an artefact of a seasonal movement or gradual shift in range over time.

In Mossel Bay, a peak in relative abundance of *S. plumbea* was observed in the number of individuals encountered during summers (November–April) of 2011-2012 and 2012-2013, although the largest groups were seen in winter (May–October) of 2011. In Algoa Bay, the population of *S. plumbea* exhibited strong seasonal fluctuations with higher abundance during summer and late winter (Karczmarski et al. 1999), whereas in Plettenberg Bay, Jobson (2006) found humpback dolphins were present year-round (Jobson 2006). The observed seasonality, combined with the resightings between these study sites, is consistent with the notion of a single continuous population that exhibits some level of alongshore seasonal movement, westward from Algoa Bay at the end of summer/beginning of autumn and eastward from Mossel Bay towards Algoa Bay during mid-winter, with Plettenberg Bay being a core-use area.

Previous studies reported higher resightings of female than male animals, suggesting that high residency to localised areas was possibly a result of females adjusting their travelling speed and distances to the capacity of the calf (Durham 1994; Keith et al. 2002). In our study, only two of five identified resident females were seen more frequently when accompanied by a small calf, while at least three were observed moving between Mossel Bay and Plettenberg Bay, including a single animal photographed in Mossel Bay with a calf and then in Plettenberg Bay five months later (from where no photograph of the calf was available). These observations suggest that this pattern of higher female site fidelity may not hold for all study areas.

Conclusion

The abundance estimates produced in this study represent the most westerly population data available for *Sousa plumbea* and indicate that a small number of these dolphins use Mossel Bay and the adjacent coast. Although both closed and open population models were used in this study to improve comparability to earlier work, the wide-ranging nature of the animals suggest that open population models are more appropriate for this species along the South African coast. Placing our estimated numbers within the context of the entire Cape south coast is confounded by the lack of good data on the alongshore range of individuals and on any possible sex- or age-related differences. To date, almost all studies of *S. plumbea* in southern African

waters have been conducted in relatively small survey areas (10s of km long) and, when comparisons have been made with studies from other locations, they have often relied on older or limited data. In order to address this gap in the data and to determine accurately the total population size and structure of *S. plumbea* along the Cape south coast, we recommend that a wide-scale, multi-site, mark-recapture study be undertaken. Ideally such a study should include a genetic component, and pollutants and other threats should be investigated. Although satellite telemetry would be a powerful tool, consideration should be given to ethical issues associated with the use of an invasive technique on this potentially endangered population. If such a wide-scale estimate of the entire Cape south coast population can be achieved, it would allow for a thorough regional threat assessment to be conducted, such as the one undertaken for the critically endangered bottlenose dolphin *Tursiops truncatus* population in Doubtful Sound, New Zealand (Currey et al. 2009). Until this can be achieved, the available information suggests that the *S. plumbea* population of the Cape south coast is small, numbering in the hundreds to low thousands at most. Also, it is largely isolated from populations farther east, making the population particularly vulnerable to further impacts.

Acknowledgements — We thank Oceans Research for the provision of logistical support by way of volunteers, boats, running costs and skippers. A special thank you to Oceans Research skippers, Rob Lewis, Dorien Schröder, Riley Elliott, Dylan Irion, Andre Faul, John Wiley, Mike Barron, Chris Henderson, Dan Dawson, Jeremy Frimond, Natalie Graham, Dave van Beuningen and Curtis Young. Thanks are also due to the following: Monica Betts for providing additional humpback dolphin photographs from Mossel Bay, taken between May and November 2013; Renae Logston who helped with photography during 2011 and 2012 and allowed us additional boat time during her CTD surveys; the volunteers that helped in data collection and the sorting of photographs during 2011, 2012 and 2013; the Centre for Dolphin Studies and Tracey Meintjies of the Orca Foundation in Plettenberg Bay; Dyer Island Conservation Trust in Gansbaai and Peter Chadwick, formerly of WWF-SA, for providing additional photographs of humpback dolphins. Tess Gridley, Pedro Fruet and an anonymous reviewer provided useful and valuable comments on an earlier draft of this manuscript. This research was conducted under a series of permits issued to the Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, by the Department of Environmental Affairs. The methods used were approved by the Animal Ethics Committee of the University of Pretoria (ec061-09, ec019-12).

References

Anchor Environmental. 2012. Great Brak estuary situation assessment. Unpublished report. Prepared for Cape action for people and the environment (C.A.P.E) regional estuaries management

programme and the Mossel Bay Municipality by Anchor environmental, Suite 8, Steenberg House, Steenberg Office Park, Steenberg Rd, Tokai 7945, South Africa [More detail needed. Who was it prepared for? Report number, if available? Geographical location of Anchor Environmental?]

Atkins S, Atkins BL. 2002. Abundance and site fidelity of Indo-Pacific humpback dolphins (*Sousa chinensis*) at Richards Bay, South Africa. Report No. SC/54/SM presented at the 54th Annual Meeting of the International Whaling Commission, Shimonoseki, Japan, May 2002. Impington, UK: International Whaling Commission.

Atkins S, Cliff G, Pillay N. 2013. Humpback dolphin bycatch in the shark nets in KwaZulu-Natal, South Africa. *Biological Conservation* 159: 442–449.

Atkins SA, Plön S, Conry D, Pistorius P, Cockcroft V, Elwen S. in press. A conservation assessment of *Sousa plumbea*. In: Child MF, Do Linh San E, Raimondo D, Davies-Mostert H (eds), *The national red list of mammals of South Africa, Swaziland and Lesotho*. Pretoria, South Africa: South African National Biodiversity Institute. [any update?]

Baird RW, Gorgone AM, McSweeney DJ, Ligon AD, Deakos MH, Webster DL, Schorr GS, Martien KK. 2009. Population structure of island-associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiian Islands. *Marine Mammal Science* 25: 251–274.

Barendse J, Best PB, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC. 2010. Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *African Journal of Marine Science* 32: 1–22.

Best PB. 2007. *Whales and dolphins of the southern African subregion*. Cape Town: Cambridge University Press.

Burnham KP, Anderson DR. 2002. *Model selection and multi-model inference: a practical information-theoretic approach* (2nd edn). New York: Springer-Verlag.

Burnham KP, Anderson DR, White GC, Brownie C, Pollack KH. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5, part 9. : 387-410

- Calambokidis J, Barlow J. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Marine Mammal Science* 20: 63–85.
- Chao A. 2001. An overview of closed capture-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics* 6: 158–175.
- Chao A, Huggins RM. 2005. Classical closed-population capture-recapture models. In: Amstrup SC, McDonald TL, Manly BFJ (eds), *Handbook of capture-recapture analysis*. New Jersey: Princeton University Press. pp 22–35.
- Conn PB, Gorgone AM, Jugovich AR, Byrd BL, Hansen LJ. 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *The Journal of Wildlife Management* 75: 569–579.
- Cooch E, White G. 2012. *Program Mark – a gentle introduction* (11th edn). Available from <http://www.phidot.org> [place and publisher?]
- Cormack RM. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429–438.
- Currey RJC, Dawson SM, Slooten E. 2009. An approach for regional threat assessment under IUCN Red List criteria that is robust to uncertainty: the Fiordland bottlenose dolphins are critically endangered. *Biological Conservation* 142: 1570–1579.
- Durham B. 1994. The distribution and abundance of the humpback dolphin (*Sousa chinensis*) along the Natal coast, South Africa. MSc thesis, University of Natal, South Africa.
- Elwen SH, Findlay KP, Kiszka J, Weir CR. 2011. Cetacean research in the southern African subregion: a review of previous studies and current knowledge. *African Journal of Marine Science* 33: 469–493.
- Elwen SH, Reeb D, Thornton M, Best PB. 2009. A population estimate of Heaviside's dolphins *Cephalorhynchus heavisidii* in the southern end of their range. *Marine Mammal Science* 25: 107–124.
- Findlay KP, Best PB, Ross GJB, Cockcroft VG. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning*. *South African Journal of Marine Science* 12: 237–270.

- Guissamulo A, Cockcroft VG. 2004. Ecology and population estimates of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique. *Aquatic Mammals* 30: 94–102.
- Hammond PS, Mizroch SA, Donovan GP (eds). 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. *Reports of the International Whaling Commission Special Issue* 12: 57–61.
- Huggins RM. 1989. On statistical analysis of capture-recapture experiments. *Biometrika* 76: 133–140.
- Huggins RM. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47: 725–732.
- Jackson LF, Lipschitz S. 1984. *Coastal sensitivity atlas of southern Africa 1984*. Pretoria: Department of Transport.
- Jefferson TA, Karczmarski L. 2001. *Sousa chinensis*. *Mammalian Species* 655: 1–9.
- Jefferson TA, Rosenbaum HC. 2014. Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. *Marine Mammal Science* 30: 1494–1541
- Jobson AJ. 2006. Insights into population size, group dynamics and site fidelity of humpback dolphins (*Sousa chinensis*) in Plettenberg Bay, South Africa. MSc thesis, Nelson Mandela Metropolitan University, South Africa.
- Jolly GM. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.
- Johnson RL, Bester MN, Dudley SFJ, Oosthuizen WH, Meyer M, Hancke L, Gennari E. 2009. Coastal swimming patterns of white sharks (*Carcharodon carcharias*) at Mossel Bay, South Africa. *Environmental Biology of Fishes* 85: 189–200.
- Karczmarski L. 1996. Ecological studies of humpback dolphins *Sousa chinensis* in the Algoa Bay region, Eastern Cape, South Africa. PhD thesis, University of Port Elizabeth, South Africa.
- Karczmarski L. 1999. Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. *Journal of Zoology, London* 249: 283–293.

- Karczmarski L, Cockcroft VG. 1998. Matrix photo-identification technique applied in studies of free-ranging bottlenose and humpback dolphins. *Aquatic Mammals* 24: 143–147.
- Karczmarski L, Winter PED, Cockcroft VG, McLachlan A. 1999. Population analyses of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, Eastern Cape, South Africa. *Marine Mammal Science* 15: 1115–1123.
- Keith M, Peddemors VM, Bester MN, Ferguson JWH. 2002. Indo-Pacific humpback dolphins at Richard's Bay, South Africa: implications for incidental capture in shark nets. *South African Journal of Wildlife Research* 32: 153–162.
- Laake JL. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Report No. 2013-01, 25 p. Alaska Fisheries Science Centre, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle WA 98115 [Seems to be a mismatch between institution and place?]
- Mansur RM, Strindberg S, Smith BD. 2011. Mark-resight abundance and survival estimation of Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, in the Swatch-of-No-Ground, Bangladesh. *Marine Mammal Science* 28: 561–578.
- Mendez M, Jefferson TA, Kolokotronis SO, Krützen M, Parra GJ, Collins T, Minton G, Baldwin R, Berggren P, Särnblad A, Amir OA, Peddemors VM, Karczmarski L, Guissamulo A, Smith B, Sutaria D, Amato G, Rosenbaum HC. 2013. Integrating multiple lines of evidence to better understand the evolutionary divergence of humpback dolphins along their entire distribution range: a new dolphin species in Australian waters? *Molecular Ecology* 22: 5936-5948
- Otis DL, Burnham KP, White GC, Anderson DR. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62: 1–135.
- Pledger S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics* 56: 434–442.
- Read AJ, Urian KW, Wilson B, Waples DM. 2003. Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. *Marine Mammal Science* 19: 59–73.

- Reeves RR, Dalebout ML, Jefferson TA, Karczmarski L, Laidre K, O'Corry-Crowe G, et al. 2008. *Sousa chinensis*. The IUCN Red List of threatened species. Version 2010.4. Available at www.iucnredlist.org [accessed 14 May 2011].
- Reisinger RR, Karczmarski L. 2010. Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. *Marine Mammal Science* 26: 86–97.
- Ross GJB, Cockcroft VG, Melton DA, Butterworth DS. 1989. Population estimates for bottlenose dolphins *Tursiops truncatus* in Natal and Transkei waters. *South African Journal of Marine Science* 8: 119–129.
- Saayman GS, Tayler CK. 1973. Social organisation of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. *Journal of Mammalogy* 54: 993–996.
- Schwarz CJ, Arnason AN. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860–873.
- Seber GAF. 1965. A note on the multiple-recapture census. *Biometrika* 52: 249–259.
- Smith-Goodwin JA. 1997. A molecular genetic assessment of the population structure and variation in two inshore dolphin genera on the east coast of South Africa. PhD thesis, Rhodes University, Grahamstown, South Africa.
- Swartz CD, Knott M, Malan WM, van Eeden JD. 2000. Biological phosphate removal to meet strict quality requirements for discharge into ecosensitive Hartenbos estuary. Presented at the WISA (Water Institute of South Africa) Biennial Conference, Sun City, South Africa. 28 May–1 June 2000.
- White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (supplement): 120–138.
- Wilson B, Hammond PS, Thompson PM. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9: 288–300.
- Williams BK, Nichols JD, Conroy MJ. 2002. *Analysis and management of animal populations*. London: Academic Press.