

TITLE

Population Size Estimate of Indo-Pacific Bottlenose Dolphins in the Algoa Bay Region, South Africa

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ABSTRACT

This study estimates the population size of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Algoa Bay region on the Eastern Cape coast of South Africa. Mark-recapture analyses were performed on photo-identification data collected on 54 occasions during a three-year study period. Using a photographic dataset of over 10,000 ID-images, 1,569 individuals were identified, 131 of which were photographed on more than one occasion. Using the POPAN formulation in the software program MARK, a total population of approximately 28,482 individuals (95% CI = 16,220 - 40,744; CV = 0.220), was estimated (estimate corrected for the proportion of distinctive individuals in the population). This is the largest population estimate to date for this species along the South African coast, suggesting that the bottlenose dolphins inhabiting the Algoa Bay region represent part of a substantially larger population that ranges along a considerable length of the South African coast.

KEY WORDS: Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, mark-recapture analyses, population estimate, Algoa Bay – Eastern Cape – South Africa

INTRODUCTION

Bottlenose dolphins (genus *Tursiops*) inhabit tropical and temperate zones of all oceans and peripheral seas (Rice 1998) and are among the most-studied cetaceans (Wells and Scott 1999, 2002). Two species are currently recognized, the common bottlenose dolphin (*Tursiops truncatus*) with world-wide distribution, and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) that inhabits coastal waters of the Indian and western Pacific Oceans (Rice 1998; Wells and Scott 1999, 2002). In the southern African region, *T. aduncus* (hereafter the 'bottlenose dolphin') has an apparently continuous distribution from Cape Agulhas eastwards to southern Mozambique, and apparently similarly so further north along the East African coast and off the Indian Ocean islands (Best 2007).

Earlier studies of bottlenose dolphins in South Africa addressed the species biology (Cockcroft *et al.* 1989, Cockcroft and Ross 1990a, 1990b), population genetics (Smith-Goodwin 1997, Natoli *et al.* 2008) population ecology (L. Karczmarski, unpublished data), and incidental mortality in shark nets off the KwaZulu-Natal coast (Cockcroft 1990, Peddemors 1995). Local abundance assessments, based on aerial surveys, have been produced for the KwaZulu-Natal coast, but not confirmed by further more-detailed research. Aerial surveys along 80 km of coast from Durban northwards, conducted in 1984, 1985 and 1989, delivered counts of 367, 433 and 520, respectively, however, only the last estimate was corrected for groups missed due to over-flying, (Cockcroft *et al.* 1992). A survey encompassing 100 km of the coast south of Durban produced uncorrected counts of 219-249 dolphins in 1985 (Ross *et al.* 1989) and 98-132 dolphins in 1990 (Cockcroft *et al.* 1991).

Despite several previous attempts, until recently, nowhere in the southern African region have mark-recapture techniques been used to produce population estimates for this species. The one exception is a recent work by Phillips (2006), where, based on a 2-year photo-identification dataset, a population inhabiting Plettenberg Bay, on the South African south coast, has been

estimated to be between 1,099 and 9,492 bottlenose dolphins. In the study reported here, we performed mark-recapture analyses of photo-identification data collected by L. Karczmarski over a 3-year period, between 1991-1994, in the Algoa Bay region on the southeast coast of South Africa.

METHODS

Study Area and Survey Procedure

Algoa Bay, flanked on the western side by Cape Recife (34°02'S, 25°42'E) and on the eastern side by Cape Padrone (33°46'S, 26°28'E) is located on a generally exposed coastline of Eastern Cape (Fig. 1). Most of the bay is < 50 m deep, with mean spring and neap tidal ranges of 1.61 m and 0.51 m respectively (for more details see Karczmarski *et al.* 1999a).

Boat-based photo-identification surveys were conducted along approximately 55 km of coastline of the southwestern region of Algoa Bay using a small motorized boat, as described in Karczmarski (1999) and Karczmarski *et al.* (1999a and 1999b). Once dolphins were located, they were approached at low speeds (generally < 2 knots), and dorsal fin images were taken using a motorized camera equipped with a variable length (70-210 mm zoom) lens and 100 ISO color positive film. A conscious effort was made to take the photographs at random, photographing every individual in a shooting range of the camera, independent of the size and distinctiveness of individual marks, and irrespective of whether or not the individual appeared to be already photographed. Subsequently, all images were rigorously examined for their quality and individual distinctiveness, similarly as described in detail in Karczmarski *et al.* (2005). Each photograph (color transparency) was projected onto a screen, and its quality was assessed independent of the markings on the individual. Only photographs that were well exposed, in focus, the entire dorsal fin was visible above the water, and the fin filled generally not less than one-quarter of the frame with either none or only moderate cases of parallax were used for further analyses.

For all images that met quality criteria, a ratio was calculated relating the number of dorsal fins that could be reliably identified to the total number of photographed fins. This calculation was performed for each photo-identification survey, and subsequently an overall ratio was calculated that represents the ratio of individuals that were reliably marked; it is referred to further as the 'proportion of identifiable individuals'.

All individually distinctive dolphins were identified and catalogued following procedures described in Karczmarski and Cockcroft (1998). Only individuals with deep distinctive deformations and notches on the trailing and/or leading edge of the dorsal fin were considered as sufficiently marked and identifiable for the purpose of individual identification, which allowed comparisons of images taken from either side of an individual and minimized the possibility of an existing mark/notch being obscured by new marks.

Analytical Treatment

Mark-recapture analyses of the sighting histories of recognizable individuals were performed using the software program MARK (White and Burnham 1999), which uses Maximum Likelihood models to estimate population parameters (Cooch and White 2006). Due to the length of the study, population closure was not a reasonable assumption. Population parameters were estimated using the open-population POPAN parameterization (Schwarz and Arnason 1996, 2006) which includes the parameter N , denoting the size of a superpopulation. N can be thought of as either the total number of animals available for capture at any time during the study, or, alternatively, as the total number of animals ever in the sampled area between the first and last occasion of the study (Nichols 2005). The parameter Φ represents apparent survival rate, p is the probability of capture and b denotes the probability that an animal from the superpopulation enters the sub-population (sub-population referring to the animals occurring in the study area). In model notation, the subscripts t and $.$ represent time-dependent and constant parameters, respectively (after Lebreton *et al.* 1992). The initial analysis is based on the fully time-dependent/Cormack-Jolly-Seber (CJS) model $\{\Phi_t, p_t, b_{ij}\}$. The first step in the analysis involves

Goodness-of-Fit (GOF) tests for the CJS model using the program RELEASE GOF to validate model assumptions. Based on the biology of the species and consideration of the sampling method, a further 11 models were constructed, including models allowing variation of parameters by season (s). The most appropriate model was selected using the Akaike Information Criterion (AIC, Burnham and Anderson 1998). AIC weighs the deviance (quality of fit) and the precision (via number of estimable parameters) to select a model that best describes the data (Lebreton *et al.* 1992). Based on the result of TEST 2 + TEST 3 in program RELEASE a post-hoc variance inflation factor (\hat{c}) may be estimated to adjust for over-dispersion in the data, resulting in a quasi-Akaike Information Criterion (QAIC). Median \hat{c} and bootstrap GOF are not available in the POPAN parameterization. The mark-recapture population estimates apply only to the population of marked animals. These estimates were expanded to include the entire population by dividing N by the proportion of identifiable individuals, yielding total population size (N_{total}). Variance was estimated using the delta method as

$$\text{var}(N_{\text{total}}) = N_{\text{total}}^2 \left(\frac{\text{var}(N)}{N^2} + \frac{1 - \theta}{n\theta} \right)$$

where n is the total number of dorsal fins from which θ was calculated. Confidence intervals for N_{total} assumed the same error distribution as the mark-recapture estimates (Wilson *et al.* 1999).

RESULTS

During 54 encounters with dolphins over the study period, over 10,000 ID images were taken. Dolphin groups were generally large, ranging from 25 individuals to over 500 individuals per group, with 52% of the observed groups larger than 100 individuals. Consequently, photographic coverage of the group (the number of identifiable individuals photographically “captured”) varied substantially between encounters, ranging from less than 15% to almost 70% of the estimated group size. Very seldom were more than two photographs of a suitable quality taken per identifiable individual per encounter. A total of 1,569 individuals were identified including 62 juveniles; no calf was sufficiently marked to be included into the ID-catalogue. From these, over

90% of individuals were seen only once (Fig. 2). The cumulative number of identified individuals (discovery curve, Fig. 3) continued to increase throughout the study period, showing no signs of approaching an asymptote. Of the 12 models tested, numerical convergence of the parameter estimates was not reached for two models, $\{\Phi, p_t, b\}$ (capture rate varies with time while survival and probability of entry are constant) and $\{\Phi_s, p_t, b_s\}$ (capture rate varies with time while survival and probability of entry vary with season). Violation of certain model assumptions was evident in the results of TEST 2 + TEST 3, and a variance inflation factor of $\hat{c} = 2.51$ was estimated and applied. Closer examination of TEST 2 and TEST 3 results indicated overdispersed data and thus potential reasons for model violation, as discussed below. Results of program RELEASE are presented in Table 1. The most appropriate model was then selected using QAIC. According to QAIC, the most supported model was $\{\Phi_s, p_t, b_t\}$ (survival and probability of entry vary with time and capture rate varies with season). Model details, as well as population estimates, are presented in Table 2. No models had a $\Delta\text{QAIC} < 2$ units, which would have indicated that they were also good descriptions of the data (Burnham and Anderson 1998). The proportion of identifiable individuals (all marked adults and juveniles) was 0.896 (SE = 0.0985) and based on model $\{\Phi_s, p_t, b_t\}$'s population estimate, total population size was estimated at 28,482 (95% CI = 16,220 - 40,744; CV = 0.220). Average probability of entry for this model was 0.034 (SE = 0.010) and survival rates of 0.992 (SE = 0.002) and 1.000 (SE = 0.010) were estimated.

DISCUSSION

Discovery Curve and Sighting Rates

The increasing (non-asymptotic) discovery curve (Fig. 3) indicates that the sampling effort was not sufficient to identify all or most of the individuals that use this region; the bottlenose dolphin population is open, with individuals leaving and entering the Algoa Bay region, causing new individuals to be sighted throughout the study period. The overall large number of identified individuals, low re-sighting rate (8.35%) and large proportion of individuals seen only once (91.65%, Fig. 2) suggest that the animals seen in the Algoa Bay region form part of a much larger

population that ranges along a substantial length of the South African coast, an idea put forward by Karczmarski (1996). Larger sampling effort, over a longer period and a larger spatial scale, could have lead to the discovery curve becoming asymptotic, but such research effort would likely have needed to continue for several more years; even then, recruitment could make it unlikely for the discovery curve to become asymptotic.

The results of a mark-recapture study of bottlenose dolphins in Plettenberg Bay (over 300km to the west) by Phillips (2006), similarly show a low re-sighting rate. Many of the individuals seen in Plettenberg Bay during Phillips's studies are the same as photographed several years earlier by Karczmarski in Algoa Bay (G.L. Phillips, pers. comm.), supporting further the notion of long-range movements and the dynamic nature of the bottlenose dolphin population along the South African southeast coast.

Assumptions: Validation and Violations

As discussed by Begon (1983), validation of the assumptions underlying mark-recapture methods is critical in providing relatively unbiased estimates of population parameters. As nicks and other dorsal fin mutilations are long-lasting, mark loss in this study was considered negligible. Sampling periods were days, and sampling effort was similarly distributed between marked and unmarked animals, although heterogeneous capture probabilities due to differences in the behavior of individuals were unavoidable (e.g., Hammond 1986). Any further violations of equal capture probabilities were minimized by careful laboratory procedures (quality and distinctiveness criteria).

During the course of the analyses, TEST 2 and TEST 3 in program RELEASE (Table 1) were useful for identifying lack-of-fit in the data. TEST 2 and TEST 3 examine the assumptions of equal capture probabilities and survival, respectively (Cooch and White 2006). The result of TEST 2 + TEST 3 indicates overdispersion in the data, but if \hat{c} values are ≤ 3 , the lack-of-fit is acceptable and models can be confidently corrected with such an inflation variance factor (\hat{c} ,

Lebreton *et al.* 1992). More detailed examination of the results of RELEASE indicates slight overdispersion in TEST 2 (capture heterogeneity), which could have been expected, given the differences in the behavior of individuals. TEST 3 (loosely referred to as the “survival test”), shows marked lack-of-fit. The components of TEST 3 more specifically reveal the potential source of this lack-of-fit. TEST 3.SR, in simple terms, deals with whether animals are seen again. Of the possible explanations for this lack-of-fit (Cooch and White 2006), the presence of transients (migratory individuals leaving the sampling area shortly after capture) and/or heterogeneity in capture rates are biologically the most plausible explanation; while cautious laboratory procedures make marking effects (unequal catchability due to inconsistent quality and distinctiveness criteria) unlikely.

The presence of transients agrees with the notion that the dolphins observed in Algoa Bay represent part of a much larger population that ranges along the South African coast. Unfortunately, it is currently impossible to separate and quantify the effects and sources of the abovementioned violations. A technique developed by Whitehead (1990), allows for estimating population parameters where individuals may emigrate from, and later return to, the population; continued photo-identification over a substantially longer time period could have made such analyses possible.

Population Size Estimate

The total population estimate of 28,482 (95% CI = 16,220 - 40,744; CV = 0.220), using the model $\{\Phi_s, p_t, b_t\}$ that best describes our data and taking into account the proportion of identifiable individuals, is the largest to date for *T. aduncus* along the South African coast. This model allows for variation in capture probability (p) and probability of entry (b), and allows survival (Φ) to vary seasonally (summer and winter). Along the southeast coast of South Africa, bottlenose dolphins occur sympatrically with Indo-Pacific humpback dolphins (*Sousa plumbea*). The abundance of the latter species in Algoa Bay varies seasonally, apparently related to the abundance and distribution of inshore prey resources (Karczmarski 1999, Karczmarski *et al.* 1999a, 1999b). A

similar seasonal pattern has been observed for bottlenose dolphins in the same geographic region (L. Karczmarski, unpublished data), and is likely due to similar ecological causes. The incorporation of this factor into the model thus takes into account this seasonal movement, which affects the local or apparent survival of the population. Due to overdispersed data, heterogeneous capture rates, and hence a potential violation of some of the mark-recapture assumptions, the population size estimate presented here might be biased downwards; although missed capture opportunities due to large group sizes could argue for just the opposite. For comparison, Phillips's (2006) estimates of 1,099 – 9,492 individuals do not include an open population estimate, and are probably substantial underestimates.

Although there are many cases where bottlenose dolphins have relatively small ranges, these animals are also known to range over several hundred kilometers in areas with patchy distribution of inshore prey resources (Ballance 1990, Defran and Weller 1999, Defran *et al.* 1999). A similar situation seems likely for bottlenose dolphins along the exposed Eastern Cape coastline, where potentially restricted prey resources have been suggested to influence the site fidelity of Indo-Pacific humpback dolphins (Karczmarski 1999; Karczmarski *et al.* 1999a, 1999b). Studies along the KwaZulu-Natal coast suggest the existence of at least two populations of bottlenose dolphins: coastal “resident” dolphins that occur all year round, and a “migratory” population that occurs in the coastal waters only during the annual winter migration of sardines (*Sardinops ocellatus*) into the coastal waters (Peddemors 1999). Large schools of “migratory” individuals follow sardines northwards into the KwaZulu-Natal region, travelling from at least as far south as Plettenberg Bay, Western Cape (Natoli *et al.* 2008); passing through the Algoa Bay region on their way.

Considering that the population estimate reported here was produced using the open-population POPAN parameterization (Schwarz and Arnason 1996, Schwarz and Arnason 2006), which estimates the total number of animals available for capture at any time during the study; and considering the likely long-range movements of bottlenose dolphins along the coast, it is possible that the estimate reported here represents the total number of animals moving along a substantial

length of, possibly even the entire, South African coast. If this assumption is correct, management implications are considerable, as any localized anthropogenic impact along the coast does not carry only local implications for bottlenose dolphins. Although local effects might be weaker due to long-range movements of individuals within a larger population, the entire population is subjected to local management decisions, which further enforces the notion of a need to exercise perspective, precautionary thinking at every step of coastal management planning.

While this study improves our knowledge of the population status of *Tursiops aduncus* in South African waters, it does not address issues related to the details of movement and population structure as a whole. Further work investigating site fidelity at various locations, movement and individual ranging pattern, habitat relationships, population connectivity and stock structure, using photo-identification and other techniques, is very much needed.

ACKNOWLEDGEMENTS

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Figure 1

Algoa Bay study area on the Eastern Cape coast, South Africa.

Figure 2

Sighting frequency distribution of Indo-Pacific bottlenose dolphins during 54 surveys in the Algoa Bay region from 1991 to 1994.

Figure 3

Discovery curve showing the cumulative number of identified individuals of Indo-Pacific bottlenose dolphins during 54 surveys in the Algoa Bay region from 1991 to 1994.

Table 1

Program RELEASE goodness-of-fit results for the fully time-dependent/Cormack-Jolly-Seber model tested in a mark-recapture analysis of individual sighting histories of Indo-Pacific bottlenose dolphins in the Algoa Bay region, using the open-population POPAN parameterization in program MARK.

Table 2

Model choice criteria, population size estimate (N) and total population size estimate (N_{total} , corrected for the proportion of identifiable individuals) for 12 models tested in a mark-recapture analysis of individual sighting histories of Indo-Pacific bottlenose dolphins in the Algoa Bay region, using the open-population POPAN parameterization in program MARK.

Table 1. Program RELEASE goodness-of-fit results for the fully time-dependent/Cormack-Jolly-Seber model tested in a mark-recapture analysis of individual sighting histories of Indo-Pacific bottlenose dolphins in the Algoa Bay region, using the open-population POPAN parameterization in program MARK.

| Test | \hat{c} |
|-----------------|-----------|
| TEST 2 + TEST 3 | 2.51 |
| TEST 2 | 1.74 |
| TEST 3 | 3.51 |
| TEST 3.SR | 4.44 |

Table 2. Model choice criteria, population size estimate (N) and total population size estimate (N_{total} , corrected for the proportion of identifiable individuals) for 12 models tested in a mark-recapture analysis of individual sighting histories of Indo-Pacific bottlenose dolphins in the Algoa Bay region, using the open-population POPAN parameterization in program MARK.

| Model | Model Choice Criteria | | | | | Identifiable Individuals | | | | Total Population | | | |
|------------------|-----------------------------------|---------------|-------------|-----|---------|--------------------------|-------|-----------------|-------|--------------------|-------|-----------------|-------|
| | QAICc | Δ QAIC | QAIC Weight | NP | QDEV | N | SE | 95% CI | CV | N_{total} | SE | 95% CI | CV |
| $\Phi_s p_t b_t$ | 1021.27 | 0 | 0.99 | 61 | 0 | 25,520 | 5,602 | 14,538 - 36,502 | 0.220 | 28,482 | 6,256 | 16,220 – 40,744 | 0.220 |
| $\Phi_t p_t b_t$ | 1030.16 | 8.89 | 0.01 | 60 | 0 | 23,047 | 4,722 | 13,792 - 32,302 | 0.205 | 25,722 | 5,274 | 15,386 – 36,059 | 0.205 |
| $\Phi_t p_t b_t$ | 1076.69 | 55.42 | 0 | 114 | 0 | 20,715 | 4,734 | 11,436 - 29,994 | 0.229 | 23,119 | 5,287 | 12,758 – 33,481 | 0.229 |
| $\Phi_t p_t b_t$ | 1094.50 | 73.23 | 0 | 19 | 0 | 13,528 | 1,636 | 10,321 - 16,736 | 0.121 | 15,098 | 1,830 | 11,512 – 18,684 | 0.121 |
| $\Phi_t p_s b_t$ | 1095.21 | 73.94 | 0 | 25 | 0 | 14,101 | 1,768 | 10,634 - 17,568 | 0.125 | 15,738 | 1,977 | 11,863 – 19,612 | 0.126 |
| $\Phi_s p_s b_t$ | 1096.86 | 75.60 | 0 | 26 | 0 | 14,380 | 1,930 | 10,597 - 18,162 | 0.134 | 16,049 | 2,158 | 11,820 – 20,278 | 0.134 |
| $\Phi_t p_t b_t$ | 1158.67 | 137.40 | 0 | 74 | 0 | 14,616 | 2,005 | 10,686 - 18,546 | 0.137 | 16,313 | 2,241 | 11,920 – 20,705 | 0.137 |
| $\Phi_t p_t b_t$ | 10861.09 | 9839.82 | 0 | 107 | 5477.10 | 1,569 | 0 | 1,569 - 1,569 | 0 | 1,751 | 14 | 1,725 – 1,778 | 0.008 |
| $\Phi_t p_t b_t$ | 10910.44 | 9889.17 | 0 | 54 | 5643.04 | 1,569 | 0 | 1,569 - 1,569 | 0 | 1,751 | 14 | 1,725 – 1,778 | 0.008 |
| $\Phi_t p_t b_t$ | 14240.30 | 13219.03 | 0 | 3 | 9078.40 | 2,450 | 64 | 2,325 - 2,576 | 0.026 | 2,734 | 74 | 2,588 – 2,880 | 0.027 |
| $\Phi_s p_t b_s$ | Numerical convergence not reached | | | | | | | | | | | | |
| $\Phi_t p_t b_t$ | Numerical convergence not reached | | | | | | | | | | | | |

QAIC = Quasi-Akaike Information Criterion value, NP = number of parameters, QDEV = quasi-deviance, SE = standard error, 95% CI = 95% confidence interval, CV = coefficient of variation.





