

Ranging and diving behaviour of two ‘offshore’ bottlenose dolphins, *Tursiops* sp., off eastern Australia

Peter. J. Corkeron*[†] and Anthony R. Martin[†]

*Institute of Marine Research, Tromsø branch, Post Box 6404, N-9294, Tromsø, Norway; and School of Tropical Environment Studies and Geography, James Cook University, Townsville, QLD 4811, Australia. [†]NERC Sea Mammal Research Unit, University of St Andrews, Fife, KY16 8LB, UK. Present address: British Antarctic Survey, High Cross, Madingley Rd, Cambridge, CB3 0ET, UK. [†]Corresponding author, e-mail: peter.corkeron@imr.no

This paper describes a study of the ranging and diving behaviour of two ‘offshore’ bottlenose dolphins, *Tursiops* sp., in the waters off south-east Queensland, determined using satellite-linked time-depth recorders attached to two animals. Animal 1’s tag transmitted for 30 days, Animal 2’s for 143 days. Immediately after tagging, Animal 1 swam south, reaching a point 146 km south of the point of tagging, then swam generally northwards until the tag ceased working. Animal 2’s observed range covered 778 km², with a core area of 86 km². The greatest north–south distance between all locations for Animal 2 was 43 km. The manner in which maximum dive depth was related to dive duration was analysed using constrained principal curves. These analyses indicated that for both animals, short dives were to less than 5 m, and there was no clear relationship between dives of greater duration and depth. These dolphins appear to behave differently from ‘offshore’ bottlenose dolphins studied elsewhere.

INTRODUCTION

Bottlenose dolphins, *Tursiops* spp. are among the best-studied cetaceans (Connor et al., 2000). Currently, the genus *Tursiops* includes two species, *T. truncatus* and *T. aduncus*, with separate geographical ranges, but *Tursiops* taxonomy at both the specific and generic level remains uncertain (Le Duc et al., 1999). Both species recognized currently occur as two morphotypes, ‘inshore’ and ‘offshore’ (Hoelzel et al., 1998). Much of the research on bottlenose dolphins has concentrated on the inshore morphotype in bay, estuarine and inshore coastal habitats (Connor et al., 2000). The biology of ‘offshore’ bottlenose dolphins remain poorly understood. Satellite telemetry studies of ‘offshore’ bottlenose dolphins have been based on animals rehabilitated after stranding (Wells et al., 1999), or animals released after capture during a drive fishery (Tanaka, 1987). The movement patterns of these animals may not be representative of the normal behaviour of animals from the areas where they were released.

In the waters off south-east Queensland, Australia, ‘inshore’ Indo-Pacific bottlenose dolphins, *T. aduncus*, have been the subject of ongoing studies since the late 1970s (e.g. Chilvers & Corkeron, 2001). Little is known of the biology of ‘offshore’ bottlenose dolphins in the region, other than that they can occur in near-shore oceanic waters, and are morphologically distinguishable from local ‘inshore’ animals (Hale et al., 2000). Here we describe a study of the ranging and diving behaviour of ‘offshore’ bottlenose dolphins in the waters off south-east Queensland, when satellite-linked time–depth recorders (SLTDRs) were attached to two animals. Given the uncertainty regarding the taxonomy of bottlenose dolphins, we refer to these animals as *Tursiops* sp.

MATERIALS AND METHODS

Study area and animal capture

Dolphins were caught off the east coast of North Stradbroke Island (approximately 27°40’S 153°30’E, Figure 1), using a breakaway hoop net while animals were bow riding. After capture in the net, dolphins were winched aboard a research vessel in a purpose designed sling. Dolphins were held in foam-lined fibreglass boxes that were constantly flushed with fresh seawater. After tag attachment, dolphins were hoisted from the box and released at or near the capture site.

Instrumentation and data collection

Transmitters were built by Wildlife Computers (Redmond WA, USA) using a Telonics (Mesa, AZ, USA) 0.25 watt ST-10 radio transmitting stage. Transmitter packages included a sensor to measure ambient pressure. The packages were potted in epoxy, measured approximately 12×5×2 cm, and were glued to PVC-impregnated belting that had an inner lining of neoprene. Belting and neoprene were cut to shape after each dolphin was captured to ensure a snug fit on each dolphin’s dorsal fin. Holes were cut in the leading edge of the belting to ensure that water could flow under the belting, so the dorsal fin remained flushed by fresh seawater.

Data were collected by sensors every ten seconds, stored in transmitter memory and subsequently transmitted to Service Argos (Toulouse, France) via low-orbit satellites. Information on the maximum depth of dive, dive duration, and the length of time that a dolphin spent within predetermined depth ranges (time-at-depth) was summarized and transmitted on surfacing. Data were summarized

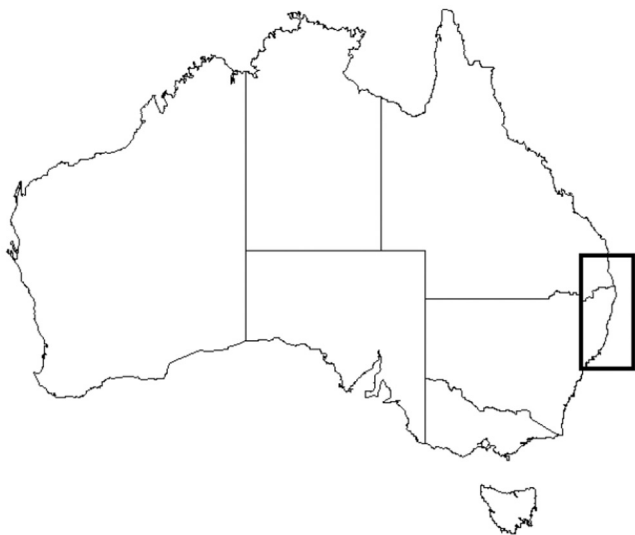


Figure 1. Map of Australia, with a box showing the study area.

by being stored in six programmable depth ranges (histogram bins). Bins were incremented over a 6-h period. Bin ranges for each animal are shown in Table 1. As Animal 1’s maximum dive depth data indicated almost no dives over 50 m, Animal 2’s maximum dive depth data bins were set differently. Other bin ranges were kept constant for comparison with Animal 1. Tags were scheduled to transmit eight hours in every 24.

Analyses

Data were downloaded from Service Argos and manually decoded. Constrained principal curves (CPCs, De’ath, 1999) were used to examine the relationship between maximum depth and maximum dive time for each animal. The CPCs are a technique by which two multivariate datasets can be analysed relative to each other, analogous to canonical correspondence analysis (De’ath, 1999). The manner in which maximum dive depth was related to dive duration was tested, as dive duration bins were the same for both animals. Analyses were carried out in R 1.4.0 (Ihaka & Gentleman, 1996) running under Windows 2000, using the pcurve library (version 0.5–4). Position fixes were imported onto charts of the area (AUS813 and AUS814) digitized into ArcView 3.0 (ESRI Inc, Redlands, CA USA). Ranges were calculated using Hooge & Eichenlaub’s (1997) Animal Movement extension of ArcView.

RESULTS

Transmitters were deployed on two female dolphins: Animal 1 was adult, Animal 2 a juvenile (determined by length and mass). Animal 1 was tagged on 19 October 1996; final transmission from this tag was 17 November.

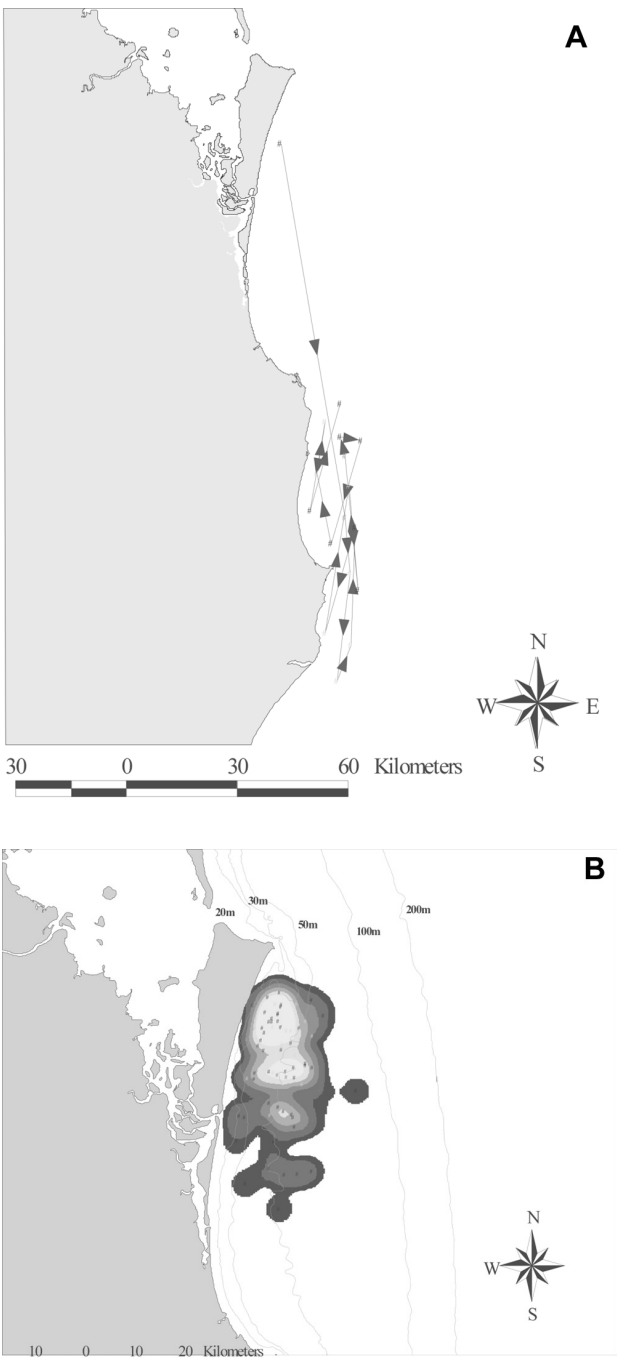


Figure 2. (A) Plot of the movement of Animal 1 during the period over which the SLTDR was operational, as revealed by satellite-derived locations of quality Class 0 or better. Arrow heads indicate direction of movement. Hash marks indicate satellite-derived locations. (B) Plot of the home range of Animal 2, during the period over which the SLTDR was operational, as revealed by satellite-derived locations of quality Class 1 or better. This animal’s range was modelled using a fixed kernel home range algorithm; 50% (lighter) to 95% (darker) probability isopleths from this analysis are shown. Hash marks indicate satellite-derived locations.

Table 1. Summary statistics (means \pm standard deviations) for maximum dive time bins, both animals.

	to 1 min	1 to 2 min	2 to 3 min	3 to 4 min	4 to 8 min	over 8 min
Animal 1	78.7 \pm 42.01	20.7 \pm 12.01	21.9 \pm 10.99	12.8 \pm 8.50	4.1 \pm 4.17	0.2 \pm 0.52
Animal 2	85.9 \pm 44.00	15.7 \pm 10.60	15.3 \pm 9.70	15.7 \pm 7.84	11.8 \pm 9.98	0.3 \pm 0.73

Animal 2 was tagged on 24 April 1997; final transmission from this tag was 14 September. After release, both animals were observed returning to the school of dolphins from which they had been caught. Satellite-derived locations were not obtained every day during the tracking period, making it impossible to detect and remove poor quality locations based on unrealistically rapid rates of travel, so poor quality satellite uplinks were discarded from analyses.

Ranging

Figure 2A shows the movements of Animal 1 over the 30 days during which the tag functioned, revealed by 19 positions of Class 0, 1, 2 or 3 that were received. Immediately after tagging, Animal 1 swam south for eight days, reaching a point 146 km south of the point of tagging (all distances estimated are Great Circle distances). In the first two of these days, Animal 1 swam 102 km. Over the following 21 days Animal 1 swam generally northwards until the tag stopped, 72 km from the point of tagging, and 75 km from the southernmost point recorded.

Figure 2B shows the home range of Animal 2 over the 143 days during which the tag remained functional, revealed by 69 positions of Class 1, 2 or 3 that were received. Animal 2's range was modelled using a fixed kernel home range algorithm, giving a home range over the period of tagging of 778 km² (95% isopleth), with a core area (50% isopleth) of 86 km². The greatest north-south distance between all locations for Animal 2 was 43 km. Given the small scale of Animal 2's movements, Class 0 locations were not included in Animal 2's ranging analyses as they would introduce measurement error of a scale that we considered unacceptable.

Diving

Only data were selected where the number of dives allocated to the histogram bins of dive duration and dive maximum depth for a 6-h period was equal (to within two dives). This gave 3184 dives from 23 uplinks for Animal 1 and 18,221 dives from 126 uplinks for Animal 2. For time-at-depth, only data were used where the summed time at depth equalled 360 min (± 2 min). This gave 14 uplinks for Animal 1 and 71 uplinks for Animal 2.

Time-at-depth data demonstrated that both dolphins spent nearly two-thirds of their time within 5 m of the water surface in each 360 min segment: Animal 1, 227.5 \pm 223–236.5 min; Animal 2, 235 \pm 220.5–245 min (medians \pm 1st and 3rd quartiles). There was no diurnal variation in the time that Animal 2 spent within 5 m of the surface (Kruskal-Wallis test, $\chi^2=5.3227$, $P=0.15$). There were too few data to test for diurnal patterns of Animal 1's time at depth. Animal 1 made maximum dives to over 150 m, but Animal 2 did not. Neither animal made many dives of over eight min (Table 1). For both animals, dives recorded in the '4 to 8 min' and 'over 8 min' bins were combined for further analysis, as were dives in the two greatest depth bins.

For both animals, the first two principal components explained most of the variation in the data set (Animal 1, 91.33%, Animal 2, 93.43%). For the CPCs, a linear model was used to relate the two sets of variables (i.e. dive

duration and maximum depth bins); correspondence analysis was used to determine the starting configuration for the principal curve; and the smoother used to fit the principal curves was a Poisson generalized additive model (GAM, $df=4.33$) for Animal 2. Using a poisson GAM to fit the principal curve led to difficulties with convergence for Animal 1, (probably due to small sample size), so a lowess smoother ($df=2$) was used instead.

Most of the sum of squared distances from the centroid of the dive duration data was accounted for by the fitting procedure (Animal 1, 87.98%, Animal 2, 86.2%, this measure is comparable to the variance accounted for in principal components analysis (PCA)). As Animal 2's data set was much greater than Animal 1's further analyses are described for Animal 2's data set only. However, the general pattern observed in Animal 2's data was also found for Animal 1. The principal curve approximated the first principal component, which the eigenvectors of the PCA indicated were mostly influenced by short dives. Partial effects plots (De'ath, 1999) indicated that the strongest depth effect, when adjusted for the effects of other depth values, was that of dives to 5 m. That is, Animal 2's short dives were shallow, but there were no clear patterns in other dive times and depths.

DISCUSSION

Ranging behaviour

Animal 1 and Animal 2 exhibited differing ranging behaviour. Initially, Animal 1 swam a comparatively long distance (146 km) south, including moving at least 100 km in the first two days. After an initial southern excursion, Animal 1 moved generally northwards until tag failure, 30 days after tagging. However, for nearly five months while Animal 2's tag was functional, this dolphin maintained a clearly defined home range, in shallow waters just south of the easternmost point of North Stradbroke Island. The core area of this range lay almost entirely inside the 50 m depth contour (Figure 2B). Animal 2's position fixes very close to shore (Figure 2B) are credible, as 'offshore' bottlenose dolphins have been observed just outside the surf zone in this area (P.J.C., personal observation).

Both animals in this study travelled far less coastline distance, and remained in shallower waters, than did two rehabilitated 'offshore' bottlenose dolphins off the US east coast (Wells et al., 1999), or the 14 bottlenose dolphins released after capture in a drive fishery off Japan (Tanaka, 1987). Unlike 'offshore' bottlenose dolphins tracked elsewhere, neither of these animals moved into waters off the continental shelf, nor did their tracks suggest long-range movements. The data were consistent with these two 'offshore' bottlenose dolphins being resident in relatively small home ranges in waters over the continental shelf.

Diving

The two dolphins in this study engaged in relatively shallow, short dives. Both animals spent approximately two-thirds of their time within the top 5 m of the water column. Despite their relatively shallow dives, both

animals could have dived to the sea-floor. There was no strong relationship between the duration and maximum depth of deep dives for either animal. This may indicate foraging both on the sea-floor and in midwater. Both animals' ranges included areas where six hours' movements could include areas of very different depths, confounding the relationship between dive length and depth, even if all foraging was at the sea-floor. Both animals spent a large proportion of their time in surface waters, and we could detect no diurnal pattern in this for the animal for which we had sufficient data for analysis.

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REFERENCES

- Chilvers, B.L. & Corkeron, P.J., 2001. Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society B*, **268**, 1901–1906.
- Connor, R.C., Wells, R.S., Mann, J. & Read, A.J., 2000. The bottlenose dolphin, social relationships in a fission–fusion society. In *Cetacean societies: field studies of dolphins and whales* (ed. J. Mann et al.), pp. 91–126. Chicago: University of Chicago Press.
- De'ath, G., 1999. Principal curves: a new technique for direct and indirect gradient analysis. *Ecology*, **80**, 2237–2253.
- Hale, P.T., Barreto, A.S. & Ross, G.J.B., 2000. Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans. *Aquatic Mammals*, **26**, 101–110.
- Hoelzel, A.R., Potter, C.W. & Best, P.B., 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proceedings of the Royal Society B*, **265**, 1177–1183.
- Hooge, P.N. & Eichenlaub, B. 1997. *Animal movement extension to ArcView version 1.1*. Anchorage, AK, USA: Alaska Biological Science Center, US Geological Survey.
- Ihaka, R. & Gentleman, R., 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- LeDuc, E.G., Perrin, W.F. & Dizon, A.E., 1999. Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Marine Mammal Science*, **15**, 619–648.
- Tanaka, S., 1987. Satellite radio tracking of bottlenose dolphins *Tursiops truncatus*. *Nippon Suisan Gakkaishi*, **53**, 1327–1338.
- Wells, R.S., Rhinehart, H.L., Cunningham, P., Whaley, J., Baran, M., Koberna, C. & Costa, D.P., 1999. Long distance offshore movements of bottlenose dolphins. *Marine Mammal Science*, **15**, 1098–1114.

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