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Distribution and habitat use of Indo-Pacific bottlenose dolphins *Tursiops aduncus* along the south coast of South Africa

OA Vargas-Fonseca^{1,2*}, SP Kirkman³ , D Conry^{1,2}, GM Rishworth^{2,4} , V Cockcroft¹ and PA Pistorius^{1,2} 

¹ Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa

² Marine Apex Predator Research Unit (MAPRU), Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa

³ Branch: Oceans and Coasts, Department of Environmental Affairs (DEA), Cape Town, South Africa

⁴ DST/NRF Research Chair: Shallow Water Ecosystems, Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa

* Corresponding author, e-mail: alejandra7979@hotmail.com

The distribution and habitat use of the Indo-Pacific bottlenose dolphin *Tursiops aduncus* along the south coast of South Africa was investigated using bi-monthly boat-based surveys, from 2013 to 2016, over a distance of 145 km between the Goukamma and Tsitsikamma marine protected areas (MPAs). Survey effort totalled 6 239 km and 750.6 hours. Encounters occurred throughout the area ($n = 200$) and more frequently during winter. Pod sizes ranged from 1 to 350 animals (mean = 45), with calves mostly associated with larger groups. During 70% of the encounters, at least a single calf was present (up to 80 calves; mean = 5) and calves were more prevalent during summer. Encounters occurred mostly in shallower (mean = 11.3 m) and warmer (mean = 17.4 °C) waters. Groups aggregated in larger sizes in colder waters. Most encounters were in Plettenberg Bay and the Goukamma MPA, both of which are characterised by sandy bottoms and sheltered areas. Encounter rates were lowest in rocky and exposed areas, but dolphin groups in such locations were larger and usually travelling. There was a relatively low association of *T. aduncus* groups with MPAs, except for a sandy area in the Goukamma MPA in particular, suggesting some mismatch between favourable *T. aduncus* habitat and habitat protection.

Keywords: conservation, generalised linear mixed-effects models, Goukamma, habitat preference, line-transect survey, marine protected area, Plettenberg Bay, Tsitsikamma, western Indian Ocean

Online supplementary material: Generalised linear mixed-effects model diagnostic plots for *Tursiops aduncus* occurrence, group size, and calves group size (Supplementary Figure S1) are available at <https://doi.org/10.2989/1814232X.2018.1547221>

Introduction

The distribution of marine species is dynamic in nature, as it responds to variability in the seascape. Marine habitats are generally spatially heterogeneous and are often perceived as a mosaic of patches, a spatial gradient, or some other geometric patterning quantified with respect to either benthic or pelagic environments (Boström et al. 2011). The distribution of marine animals is likely to be influenced by the physical environment, distribution of their predators and prey and other biological requirements (Booth et al. 2013). Species home ranges need to encompass a minimum amount of their preferred habitat—especially key or critical habitats that meet dietary or ontological needs (Karczmarski et al. 2000).

Studies of the distribution or movements of organisms are key for determining their habitat preferences and spatial needs (Karczmarski et al. 1998). Many studies have assessed the spatial distribution and habitat preferences of cetaceans by describing the habitat where animals are encountered according to physiography, such as depth, slope and benthic substrate (Cañadas et al. 2002). To relate

the distribution of cetaceans to habitat, habitat-selection models are increasingly being used (Cañadas et al. 2005; Bailey et al. 2013; Brookes et al. 2013; Marini et al. 2015). These models can provide a tool for assessing areas of high relative density and determining which factors influence the distribution of animals (Garaffo et al. 2011). Such information can assist planners or managers in decision-making, such as with regard to prioritising areas for protection.

A key outcome of the 2002 World Summit on Sustainable Development was the commitment to establish a representative network of marine protected areas (MPAs) to safeguard marine biodiversity and ecosystem integrity. However, opinion is divided regarding the value of MPAs for cetacean conservation (e.g. Boersma and Parrish 1999). Due to the highly mobile and dynamic nature of cetaceans, most MPAs may be too small to contribute to their protection (Hoyt 2005; Bearzi 2012), while many may not encompass the habitat needs of cetaceans. Identifying critical habitats that meet all ontological requirements where cetaceans can feed, rest and reproduce is perhaps the first step towards effective

MPA design for this group of species (Hoyt 2005). Many cetaceans are considered by conservation practitioners to be umbrella species as their spatial protection will likely support the health of other species and support ecosystem processes (Bearzi 2012).

For nearshore dolphin species such as the Indo-Pacific bottlenose dolphin *Tursiops aduncus*, which is generally restricted to waters no deeper than 30 m (Cockcroft and Ross 1990a), knowledge of spatial distribution and habitat preferences is especially relevant for conservation management. This is because such species are susceptible to multifarious anthropogenic pressures associated with coastal areas. These include high levels of pollution, coastal developments, dredging, anti-shark gillnets, overfishing of prey species, accidental capture in fisheries, disturbance from commercial marine tourism activities, noise and ship strikes (Cockcroft and Ross 1990b; Karczmarski et al. 1998; Elwen et al. 2011). The longevity and relatively low reproductive rate of this species furthermore aggravates the effects of habitat degradation and other threats. Globally, *T. aduncus* has been listed as a Data Deficient species in the IUCN Red List of Threatened Species since 1996 (Hammond et al. 2012). However, there is evidence of population decline in some areas. Comparison of mark–recapture population estimates at Plettenberg Bay, South Africa, between 2002–2003 (Phillips 2006) and 2013–2015 (Vargas-Fonseca 2018) showed a decline of 70%, highlighting the potential need for management measures to conserve this potentially threatened population.

Like other bottlenose dolphins, *T. aduncus* is highly social and lives in a fission–fusion society, wherein short- or long-term relationships between individuals within a society may form and dissolve over time (Connor et al. 2000). The size and composition of groups are influenced by extrinsic factors such as seascape complexity, prey availability and predation risks, in addition to intrinsic factors such as the presence or absence of preferred associates (Lusseau et al. 2006). Sex, age, reproductive condition, familial relationships and affiliation histories can further dictate group size (Wells et al. 1987). When food resources are limited, animals will tend to spread out in smaller groups to reduce intraspecific competition, and will aggregate in larger groups when food is abundant, predation risks are high or there is a high proportion of neonates (Connor et al. 2000; Heithaus and Dill 2002; Möller et al. 2002; Parra et al. 2011). All of these factors can affect patterns of spatial distribution and habitat utilisation.

Location data of individuals is, of course, the foremost requirement for studies of the distribution and habitat preferences of species. In the case of species such as *T. aduncus*, where distribution is mostly limited to nearshore areas, boat-based or alternatively aerial surveys are useful approaches for locating individuals or groups in what is almost a linear dimension, as opposed to the wider-scale distributions of more-oceanic species. By recording the locations of encounters during multiple surveys, the pattern of distribution can be related to physical or environmental habitat variables, to determine habitat preferences and utilisation.

The south coast of South Africa, although it is near the western limit of the range of *T. aduncus*, is known to support a relatively high abundance of this species (Reisinger and

Karczmarski 2010). Because the coastline of this area is characterised by having a diversity of habitat types and a network of well-established MPAs, it is well-suited to studying the habitat utilisation and preferences of this species, taking into account the location of MPAs. Whereas recent proposals for new MPA designations or re-zonation within existing MPAs in South Africa have been based strongly on scientific evidence including habitat type and species distributions (Sink 2016), most of the existing MPAs were proclaimed without sufficient information or monitoring programmes to assess whether they adequately address protective needs (Attwood et al. 1997).

In light of the above, the aims of this study were to identify habitat preferences of *T. aduncus* and the relative importance of factors influencing their spatio-temporal distribution, including physiographic, environmental, seasonal and behavioural factors. The study also assessed the efficacy of the current placement of MPAs (comprising 66% of the coastline in the study area) and the habitat that they protect in relation to habitat preferences of the species. Although the local MPAs were not designed specifically for *T. aduncus*, we examine overlap between the habitat used by *T. aduncus* and the placement of MPAs to determine whether there is evidence that the MPAs may provide direct or indirect benefits for the species. Recommendations are made to inform conservation management towards effective habitat protection.

Materials and methods

Study area

Data were collected during repeated, standardised line-transect surveys along 145 km of coastline, using boat-based methods. In addition to investigating distribution and habitat use, the surveys were designed to generate a mark-recapture-based abundance estimate (Vargas-Fonseca 2018). The research area extended from the western border of the Goukamma MPA to the eastern boundary of the Tsitsikamma MPA, on the south coast of South Africa (Figure 1). The area is characterised by a diversity of features, including a large bay (Plettenberg Bay) bordered by a peninsula (Robberg Peninsula) to the southwest, and a long stretch of rugged, mainly rocky, coastline to the east. The inshore benthic substrate types include 57% rocky, 27% sandy and 16% mixed coastline (Sink et al. 2011). The area is highly influenced by the Agulhas Current which transports warm water from the Mozambique Channel southwards along the coast (Lutjeharms et al. 2000). Wind-driven upwelling results in high levels of primary productivity, and associated high prey-fish biomass for higher predator species frequently occurs (Hutchings et al. 2009).

Survey design

The surveys were designed as a transect line running parallel to the coast (approximately 100 m from the coastline), thereby corresponding with the known coastal preferences of bottlenose dolphins (Ross et al. 1987; Cockcroft et al. 1990; Photopoulou et al. 2011). Bi-monthly boat surveys were conducted between July 2013 and June 2016. Surveys were performed at a speed of eight knots in order to locate dolphins and conduct detailed observations.

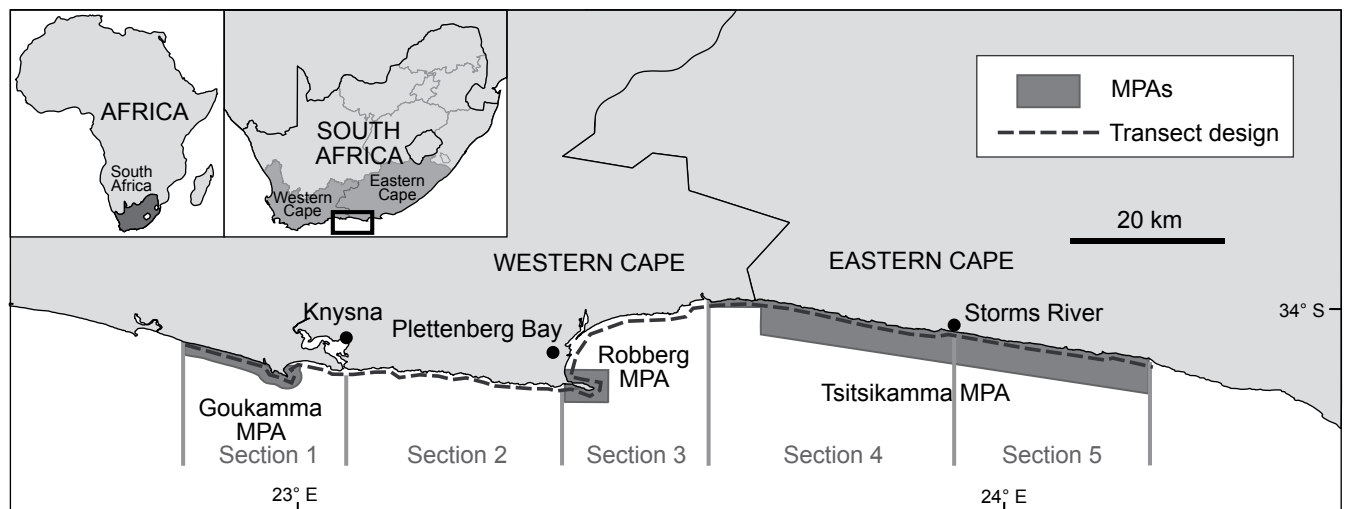


Figure 1: Extent of the study area covered during boat surveys of *Tursiops aduncus* between the Goukamma and the Tsitsikamma marine protected areas (MPAs), South Africa. The transect-line surveys were conducted parallel to the coast, which was divided into five sections according to the launch site (at Knysna, Plettenberg Bay or Storms River) and survey effort

Due to the large extent of the study area, three different launch sites (Knysna, Plettenberg Bay and Storms River) and vessels were used. The study area was divided into five sections according to launch site, and these were generally surveyed on different dates (Figure 1): Section 1 was from the western boundary of the Goukamma MPA to the Knysna Heads (length 24 km); Section 2 from the Knysna Heads to the western boundary of the Robberg MPA (34 km); Section 3 from the western boundary of the Robberg MPA to the western boundary of the Tsitsikamma MPA (29 km); Section 4 from the western boundary of the Tsitsikamma MPA to the Storms River mouth (31 km); and Section 5 from the Storms River mouth to the eastern boundary of the Tsitsikamma MPA (27 km). Surveys in Sections 1, 2 and 3 were conducted using chartered vessels (7.9 m) equipped with two motors (ranging from 115 to 150 hp). For Sections 4 and 5, a rigid inflatable boat (5.5 m or 7.6 m) equipped with two outboard engines (70 hp or 100 hp) was used.

Data collection

All encounters with individuals or groups of dolphins were recorded. A group is defined as two or more animals within a 100-m radius of each other, with coordinated activities (Irvine et al. 1981). When an encounter occurred, a coordinate reading was taken with a handheld device (Garmin GPS-72H). Photographs were taken using a DSLR camera equipped with a 300- or 600-mm lens (for mark-recapture abundance estimates). The time, group size (minimum, maximum and best estimate), composition (numbers of newborns, calves, juveniles and adults), and behaviour were recorded. Calves were defined as individuals that were one-half to two-thirds the length of an adult, whereas newborns were individuals with visible foetal folds and that were less than half the size of an adult; in both cases the animals were swimming in close association with an adult (Möller et al. 2002). Hereafter the term ‘calves’ includes both newborns and calves. Five behavioural categories

were defined, according to Shane et al. (1986): travelling, foraging, socialising, milling and resting. After an encounter was finalised, the transect line was usually resumed at the same place where dolphins were initially encountered.

Survey effort was measured as the number of kilometres and hours travelled in sea conditions not exceeding 3 on the Beaufort scale and with good visibility (e.g. no thick fog). Survey effort was discontinued when the Beaufort sea state was above 3, and also during encounters or while the boat was in transit. Wind speed and direction were recorded using a Kestrel wind meter, and the water depth and sea surface temperature (SST) were recorded using the boat’s fish-finder system (recreational SONAR) or (with regard to the latter) a handheld digital thermometer. The SST, depth and GPS coordinates of the encounters were recorded when the boat was either at the exact location of the encounter or as close to it as possible.

Data processing and analysis

Physiographical features, encounter rate and dolphin behaviour

The distance of dolphin encounters from the coast, river mouths and reefs was determined by overlaying a coastline map and isobath vector layers with the locations of encounters, using QGIS 2.18.4 (QGIS Development Team 2016). The benthic substrate types were obtained from the benthic and coastal habitat map provided by the National Biodiversity Assessment 2011 (Sink et al. 2011). Broadly, the study area includes three types of benthic substrate, namely rocky, sandy and mixed coast (e.g. rock and sand). Using the Spatial Join tool in QGIS, the substrate types were clipped to an overlaid grid that extended 2 km from the coastline across the entire study area (in order to include all dolphin encounters). The 2-km zone was bisected by perpendicular lines from the coast that were at 2-km intervals from each other, resulting in 73 grid cells of 2 km² along the coast (Minton et al. 2011). Each cell was

characterised according to benthic substrate type, slope, encounter rate (ER) and average group size (for all animals and for calves). The slope for each grid cell was calculated using the formula:

$$\text{Slope ratio} = \frac{\text{Depth}}{\text{Distance}}$$

where depth is the maximum depth in the grid cell and distance is 2 km. The ratio was expressed as meters per km (Cañadas et al. 2002).

To account for variable survey effort over the study area, the encounter rate in each 2-km² grid cell was calculated as the number of encounters (during survey effort time) per 100 km surveyed (Garaffo et al. 2011), with the formula:

$$\text{ER} = \left(\frac{\text{Number of encounters}}{\text{km of survey effort for each cell}} \right) \times 100$$

Behavioural differences in relation to the substrate types and seasons were assessed using Pearson's chi-square (χ^2) tests or the Cochran–Mantel–Haenszel (M^2) test for the interaction between season and substrate. To account for differing area sizes of the three broad benthic substrate types, frequencies were first weighted by the total coastal areas of each substrate type, such that:

$$\text{Weighted behaviour} = \text{frequency of behaviour} \times \left(\frac{\text{Total coastal area of study area}}{\text{Area of substrate type}} \right)$$

Habitat-preference modelling

Generalised linear mixed-effects models (GLMMs) are an extension of generalised linear models (GLMs) and incorporate confounding elements in the data, such as temporal or spatial autocorrelation and repeated measures (Zuur et al. 2009). Three separate GLMMs were used to model: (a) the occurrence of dolphins (calculated as the presence/absence of dolphins per 2-km² grid cell during each transect); (b) their group size; and (c) the number of calves per group, to determine the effects of different predictor variables. Analyses were conducted using the 'lme4' package (Bates et al. 2015) in the freeware RStudio 1.0.136 (R Development Core Team 2017).

Occurrence (presence/absence) and animal group size were modelled using a binomial distribution (family: binomial, link function: logit) and Poisson distribution (family: Poisson, link function: log), respectively. The Poisson distribution, which assumes that the variance is equal to the mean, is often used when modelling count data (McCullagh and Nelder 1989) and it has been used in multiple studies on different dolphin species (Cañadas et al. 2002; Garaffo et al. 2011; Photopoulou et al. 2011).

Predictor variables considered for the models were 'inshore benthic substrate type,' 'situation in relation to MPA boundaries' (inside or outside), 'season,' 'SST,' 'depth,' 'distance to coast,' 'distance to reef,' 'distance to river mouth,' 'calf presence,' 'behaviour,' 'slope,' and the interaction between 'inshore benthic substrate type' and 'MPAs.' Seasons were defined as: (i) summer = December–February; (ii) autumn = March–May; (iii) winter = June–August; and (iv) spring = September–November.

The models were fitted by restricted maximum likelihood (REML) and the random effect variables in each model, whereby autocorrelation effects in the data were accounted for, included the 2-km² grid cell along the coast, and season. Subsequently, season was omitted because it resulted in less-parsimonious models.

Collinearity between all covariates was tested. The variance inflation factor (VIF) scores were calculated for each predictor variable using the 'vifcor' function of the 'usdm' R package (Naimi et al. 2014). Only uncorrelated covariates (VIF < 3) were included to avoid misinterpretation of the model (Redfern et al. 2006). Correlated variables that were excluded were the ones that resulted in a higher Akaike information criterion (AIC) score.

The validity of all model assumptions was assessed visually in terms of normality and homogeneity of residuals. Model selection was based on the AIC score, whereby all realistic permutations of predictor covariates were fitted to separate models under maximum likelihood (ML) estimation using the 'dredge' function in the 'MuMIn' package (Barton 2013). The model with the lowest AIC was selected as the best-fitting model, except when $\Delta\text{AIC} \leq 1$ (ΔAIC reflects the difference in AIC scores between the most-parsimonious model and other comparable models), which reflects analogous models (Zuur et al. 2009). In such cases, the model with the most explanatory variables was selected. These most-parsimonious models were then re-fitted under REML estimation and the significance of predictor coefficients was assessed (Zuur et al. 2009). Conditional R^2 values were calculated as a measure of the goodness-of-fit for each model, which explains the proportion of variance attributable to the fixed and random factors (Nakagawa and Schielzeth 2013).

Results

Survey effort and encounters

A total of 223 boat surveys (performed over 174 days), comprising 750.6 h and 6 239 km of survey effort, were conducted between July 2013 and June 2016. Total duration of the dolphin observations was 89 h and the encounters were distributed throughout the study area (Figure 2). A total of 200 encounters were recorded (Appendix), of which nine were excluded from the analysis because they were sighted outside survey effort.

The average ER was 3.1 encounters per 100 km surveyed. During 40% of the surveys there was at least one dolphin encounter. The pod sizes ranged from 1 to 350 animals (mean = 45 [SD 57]; median = 27); during 70% of the encounters there was at least one calf present. The mean number of calves was 5 (SD 9, median = 1, range 0–80). The mean distance of each encounter to the coast was 356 m (SD 199, median = 332 m, range 7–1 289 m). Mean depth corresponding to encounters was 11.3 m (SD 7.3, median = 10 m, range 2–50 m) and mean SST was 17.4 °C (SD 2.1, median = 16.9 °C, range 11.3–22.7 °C).

Dolphin behaviour

The most common behaviours observed during the encounters were travelling (31%), foraging (21%), socialising (17%), milling (12%) and resting (11%), with 8% of

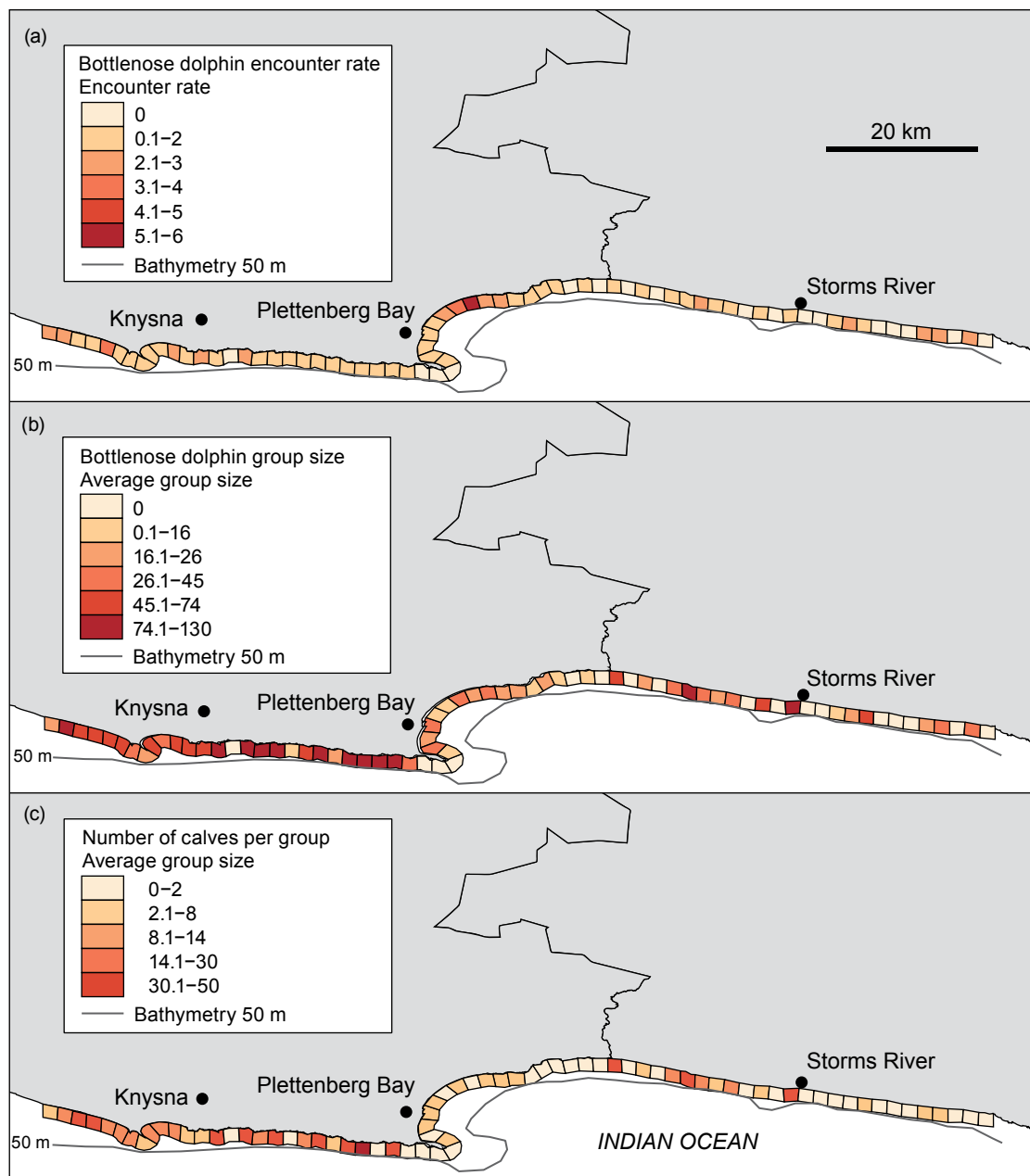


Figure 2: (a) The encounter rate of *Tursiops aduncus* (no. encounters-100 km⁻¹), (b) average group size of individuals, and (c) average group size of calves per 2-km² polygon within the study area

the behaviours recorded as unknown (Figure 3). Dolphin behaviour was influenced by the broad substrate type only ($\chi^2 = 19.4$; $p = 0.01$; $df = 8$) and not by season ($\chi^2 = 14.2$; $p = 0.3$; $df = 12$) or the interaction of season with substrate type ($M^2 = 10.7$; $p = 0.8$; $df = 15$). Between all substrate-type pairings, behaviour proportion durations differed significantly (*post hoc*: mixed vs rocky, $p < 0.001$; mixed vs sandy, $p < 0.002$; sandy vs rocky, $p < 0.001$). Animals tended to engage in milling, resting, socialising and feeding, most frequently in sandy habitat followed by in mixed habitats. Travelling, followed by foraging, were the behaviours most frequently associated with rocky habitat (Figure 3), although

travelling was just as frequently encountered in association with the other two main substrate types.

Effort-weighted density grid analyses

The effort-weighted density-grid (2 km²) analyses (Figure 2) indicated that the areas of highest ER (4–6 encounters-100 km⁻¹ surveyed) of *T. aduncus* were along the east section of Plettenberg Bay followed by in the Goukamma MPA. Both areas were characterised as having predominantly sandy bottoms (Appendix) and gentle slopes as compared with the other areas (Table 1). Encounter rates in the eastern boundary area of the Goukamma

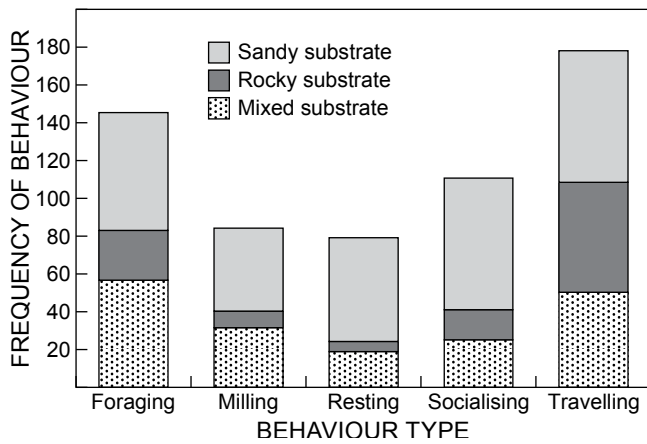


Figure 3: Frequency of *Tursiops aduncus* behaviour types encountered per inshore benthic substrate type (standardised by the total coastal areas of each substrate type)

MPA and in parts of the Tsitsikamma MPA were moderate (ER 2–4). The Tsitsikamma MPA was also characterised by patches of lower ER (1–2), similar to the region from Knysna to the western section of Plettenberg Bay, including the Robberg MPA. For both the Robberg and Tsitsikamma MPAs there were frequent sections with no encounters or a low ER (1–2). Lower occurrences were typical at exposed rocky coasts with steeper gradients, such as the coastline between Knysna and the Robberg Peninsula and most of the coastline within the Tsitsikamma MPA.

Habitat-preference modelling

A summary of the raw data in terms of survey effort and encounters along each section of the study area is presented in Table 1; group size according to season, depth, distance to coast, SST and slope-ratio category are summarised in Table 2. The likelihood of encounter occurrence (presence/absence) of *T. aduncus* was best explained by the GLMM model {Occurrence ~ inshore benthic substrate type * situation in relation to MPA boundaries (inside or outside) + season + slope + SST + 2-km² grid cell (random variable)} (Model PA2 in Table 3; Model 1 in Table 4). The average group size of *T. aduncus* was best explained by the model {Average group size ~ season + SST + depth + distance to coast + calf presence + behaviour + 2-km² grid cell (random variable)} (Model G1 in Table 3; Model 2 in Table 4). The calves group size was best predicted by the model {Calves average group size ~ season + depth + distance of encounter to coast + 2-km² grid cell (random variable)} (Model C2 in Table 3; Model 3 in Table 4). Variables that were excluded from all the models on the basis of AIC scores (compared under ML estimation) were distance of the encounters to reefs and to river mouths. Model diagnostic plots are presented in Supplementary Figure S1. In terms of the R^2 (conditional) values of the models, the model fits for occurrence and for calves group size (Models 1 and 3 in Table 4) were relatively weak (0.12 and 0.20, respectively), and that for overall group size (Model 2 in Table 4) was moderate (0.37) (cf. Nakagawa and Schielzeth 2013).

Table 1: Summary of survey effort and encounters with *Tursiops aduncus* along line transects in the five different sections of the study area off the south coast of South Africa

	Section 1	Section 2	Section 3	Section 4	Section 5	Total
No. of surveys	58	53	71	25	16	223
Survey effort (km)	1406	1437	2250	730	416	6239
Survey effort (h)	175	158.1	266.4	95.3	55.8	750.6
No. of encounters	65	24	74	18	10	191
Average group size (SD, range)	55 (69, 1–350)	89 (79, 1–300)	24 (24, 1–100)	43 (31, 2–125)	28 (21, 1–60)	45 (57, 1–350)
Average calves group size (SD, range)	8 (13, 0–80)	10 (9, 0–30)	1 (2, 0–15)	6 (7, 0–20)	0.2 (0.6, 0–2)	5 (9, 0–80)
Encounter's SST (°C) (SD, range)	17.6 (2.2, 11.3–22)	16.9 (1.6, 14.5–22)	17.3 (2.6, 12.7–22.7)	17.0 (1.3, 15–18.8)	16.5 (0.9, 15.5–18.9)	17.4 (2.1, 11.3–22.7)
Encounter's depth (m) (SD, range)	9.6 (5.6, 3–42)	14.2 (6.1, 3–30)	10.8 (7.2, 2–41)	12.8 (9.6, 5–50)	13.6 (3.2, 10–19)	11.3 (7.3, 2–50)
Encounter's distance to coast (m) (SD, range)	383 (130, 19–764)	316 (114, 140–577)	394 (246, 7–1289)	209 (217, 96–1066)	254 (162, 125–675)	356 (199, 7–1289)
Slope ratio (m) (SD, range)	1.5 (0.5, 1.0–2.0)	2.5 (0.2, 2.0–2.5)	2.0 (0.4, 1.0–2.5)	2.1 (0.3, 1.5–2.5)	2.3 (0.3, 1.5–2.5)	2.0 (0.5, 1.0–2.5)
Inshore substrate types (%): rocky/sandy/mixed	23/62/15	92/0/8	44/39/17	94/0/6	100/0/0	70/21/10

Table 2: Summary of *Tursiops aduncus* group size according to season, depth, distance of the encounters to the coastline, sea surface temperature (SST) and slope-ratio category. DC = distance of encounter to the coastline; ER = encounter rate; GS = group size; NE = number of encounters

	NE/Average ER (SD, % of encounters with calves)	Average GS (SD, median)	GS range	Average calves GS (SD, median)	Calves GS range
Autumn	56/3.0 (1.5, 61%)	33.7 (42.5, 20)	1–250	5.3 (8.8, 2)	0–50
Spring	42/2.5 (1.5, 69%)	40.9 (59.2, 20)	1–350	4.9 (7.4, 1)	0–30
Summer	31/2.8 (1.2, 52%)	47.9 (56.6, 35)	1–300	4.6 (14.3, 1)	0–80
Winter	62/2.6 (1.4, 56%)	55.6 (64.9, 40)	1–300	5.2 (8, 1)	0–30
Depth 2–7 m*	47/3.1 (1.6, 60%)	29.1 (25.5, 20)	2–104	3.7 (6.2, 1)	0–30
Depth 7–10 m*	48/2.8 (1.4, 65%)	47.4 (63.9, 30)	1–300	6.0 (12.7, 1.5)	0–80
Depth 10–14 m*	45/2.7 (1.1, 62%)	54.8 (67.0, 35)	1–300	6.2 (10.0, 2)	0–50
Depth 14–50 m*	51/2.3 (1.4, 53%)	47.7 (59.2, 30)	1–350	4.5 (7.3, 1)	0–30
DC 2–252 m*	48/2.0 (0.9, 60%)	38.4 (29.3, 30)	1–125	5.3 (8.0, 2)	0–30
DC 252–332 m*	48/2.9 (1.6, 65%)	58.2 (83.5, 25)	1–350	5.3 (12.4, 1)	0–80
DC 332–414 m*	47/3.2 (1.4, 51%)	38.2 (45.2, 25)	1–250	5.1 (9.6, 1)	0–50
DC 414–1 289 m*	48/2.8 (1.5, 63%)	43.8 (54.0, 27.5)	1–250	4.6 (6.8, 1)	0–30
SST 11.3–16 °C*	37/2.7 (1.3, 68%)	63.0 (75.3, 40)	2–300	4.5 (5.2, 3)	0–20
SST 16–16.9 °C*	58/2.6 (1.5, 62%)	44.9 (37.8, 35)	2–190	5.3 (7.9, 2)	0–30
SST 16.9–18.8 °C*	45/2.7 (1.4, 56%)	37.6 (63.9, 15)	1–350	4.2 (7.2, 1)	0–30
SST 18.8–22.7 °C*	51/2.9 (1.5, 55%)	37.6 (50.8, 25)	1–300	6.0 (13.9, 1)	0–80
Slope ratio 1	37/3.2 (1.2, 68%)	54.9 (75.4, 25)	1–350	9.5 (16.1, 3)	0–80
Slope ratio 1.5	80/3.2 (1.5, 54%)	36.7 (50.3, 20)	1–250	3.0 (5.7, 1)	0–30
Slope ratio 2	36/2.3 (0.8, 67%)	50.5 (61.6, 37.5)	1–300	5.3 (7.3, 3)	0–30
Slope ratio 2.5	38/1.6 (1.0, 58%)	46.1 (41.4, 37.5)	1–190	5.0 (6.9, 2)	0–20

*Categories according to quartiles

Table 3: Model diagnostics for generalised linear mixed-effects models (GLMMs) of *Tursiops aduncus* effort-corrected occurrence (presence/absence), group size, and calves group size. The best models are shown; all others had $\Delta AIC > 5.7$. Black dots and 'NA,' respectively, indicate variables incorporated or not incorporated in the models, whereas dashes indicate that the variable was not considered. Selected models are indicated in bold font

Model	Substrate type	MPA (in/out)	Season	Slope	SST	Depth	Distance to coast	Calf presence	Behaviour	Substrate type: MPA	AIC	ΔAIC	Model selected
<i>Occurrence (presence/absence)</i>													
PA1	•	NA	•	NA	•	–	–	–	–	•	1 664.2	0.0	No
PA2	•	•	•	•	•	–	–	–	–	•	1 665.0	0.8	Yes
PA3	•	NA	•	•	•	–	–	–	–	•	1 665.3	1.1	No
PA4	•	•	•	NA	•	–	–	–	–	•	1 665.5	1.4	No
PA5	•	•	•	NA	•	–	–	–	–	•	1 666.0	1.9	No
PA6	•	•	•	•	•	–	–	–	–	•	1 666.8	2.7	No
<i>Group size</i>													
G1	NA	NA	•	–	•	•	•	•	•	–	4 882.3	0.0	Yes
G2	NA	•	•	–	•	•	•	•	•	–	4 884.0	1.7	No
G3	•	NA	•	–	•	•	•	•	•	–	4 886.2	3.9	No
G4	•	•	•	–	•	•	•	•	•	–	4 888.0	5.7	No
<i>Calves group size</i>													
C1	NA	NA	NA	–	–	•	•	–	–	–	1694.9	0.0	No
C2	NA	NA	•	–	–	•	•	–	–	–	1695.5	0.6	Yes
C3	NA	•	NA	–	–	•	•	–	–	–	1696.9	2.0	No
C4	NA	•	•	–	–	•	•	–	–	–	1697.5	2.6	No
C5	•	NA	NA	–	–	•	•	–	–	–	1697.5	2.6	No
C6	•	NA	•	–	–	•	•	–	–	–	1698.4	3.5	No

Table 4: Generalised linear mixed-effects models (GLMMs) of *Tursiops aduncus* effort-corrected occurrence (presence/absence) (Model 1), group size (Model 2), and calves group size (Model 3), as a function of the most-parsimonious predictor variables. Model coefficients (C) for predictor variables with standard errors (SE) and significance levels (p) for test results (z) are shown, with significant values indicated. Season, inshore benthic substrate type, marine protected area (MPA), and dolphin-behaviour predictor coefficients are shown relative to the reference categories 'autumn,' 'mixed,' 'MPA-outside' and 'foraging,' respectively

	C	SE	z-value	p-value
<i>Model 1: Occurrence (presence/absence)</i>				
(Intercept)	-4.65	0.95	-4.91	**
Substrate-rocky	-0.74	0.30	-2.42	*
Substrate-sandy	-0.18	0.31	-0.58	0.56
MPA-inside	-1.70	0.81	-2.11	*
Season-spring	0.02	0.21	0.09	0.93
Season-summer	-0.20	0.23	-0.84	0.40
Season-winter	0.77	0.22	3.49	**
Slope ratio	-0.38	0.23	-1.67	0.10
SST	0.12	0.04	2.78	*
Substrate-rocky: MPA-inside	1.52	0.84	1.80	0.07
Substrate-sandy: MPA-inside	1.81	0.84	2.16	*
<i>Model 2: Group size</i>				
(Intercept)	2.91	0.19	15.25	**
Season-spring	-0.01	0.05	-0.13	0.90
Season-summer	0.62	0.05	13.64	**
Season-winter	0.62	0.04	14.86	**
SST	-0.04	0.01	-4.18	**
Depth	0.04	0.00	20.96	**
Distance encounter to coast	-0.001	0.00	-12.12	**
Calf presence	1.08	0.04	30.09	**
Behaviour-milling	-0.29	0.06	-4.54	**
Behaviour-unknown	-0.26	0.09	-3.03	*
Behaviour-resting	0.18	0.05	3.56	**
Behaviour-socialising	0.87	0.04	21.28	**
Behaviour-travelling	-0.04	0.04	-0.90	0.37
<i>Model 3: Calves group size</i>				
(Intercept)	1.11	0.23	4.82	**
Season-spring	-0.03	0.11	-0.28	0.78
Season-summer	0.24	0.12	2.08	*
Season-winter	0.00	0.10	0.01	0.99
Depth	0.02	0.01	3.75	**
Distance encounter to coast	0.00	0.00	-3.95	**

* $p < 0.05$; ** $p < 0.001$

Dolphins were observed less often in rocky habitats and inside MPAs, but when inside the MPAs the tendency was to find them along sandy bottom (see Figure 2; Appendix); hence, there was a significant interaction (Model 1 in Table 4) between inshore benthic substrate type (sandy coast) and MPA (inside). Of the three MPAs, the ER was highest in Goukamma, where sandy-bottom substrate is predominant, whereas the other two MPAs have predominantly rocky coastlines (Figure 2a; Appendix).

Winter months were characterised by high dolphin occurrence (Model 1 in Table 4). Larger groups were found in both winter and summer (55.6 [SD 64.9] and 47.9 [SD 56.6] dolphins per group, respectively, as compared with 33.7 [SD 42.5] and 40.9 [SD 59.2] in autumn and spring), more often in deeper waters (>7 m) and nearer the coastline (<332 m) (Table 2; Model 2 in Table 4). Presence

of calves was more likely to be associated with larger groups (Model 2 in Table 4), and the largest groups of calves were encountered mostly during summer, although group size was highly variable and low on average during this time (Model 3 in Table 4; see Table 2 for a summary of calves group sizes and ranges). Within the seasons, there was a relatively high occurrence of dolphins in warmer waters (Model 1 in Table 4), but when SST decreased they tended to form bigger groups (Model 2 in Table 4) (median group size of 40 in waters with SST of 11.3–16 °C, as compared with median group sizes of between 15 and 35 in three quantiles of SST from 16 to 22.7 °C; Table 2). Larger pods were observed when animals were resting or socialising, and smaller aggregations formed when milling (Model 2 in Table 4).

Discussion

This study made use of systematic boat-based surveys conducted at monthly intervals to assess spatial distribution of *T. aduncus* in relation to substrate type, season and other factors along the south coast of South Africa. There was obvious variability across the study area in terms of where dolphins occurred and their group size. The ER was highest in Plettenberg Bay and the Goukamma MPA, which are characterised by a higher proportion of sandy habitats (Table 1). These habitats were associated with foraging, resting and socialising behaviours. The dolphins' preference for sandy habitat when engaging in these behaviour types accounts for the relatively high ER in these areas. Larger groups were found in different areas: between the western borders of the Goukamma and Robberg MPAs and some patchy areas along the Tsitsikamma MPA (Figure 2). These areas had predominantly rocky habitats and were associated with travelling behaviour.

Larger groups were formed within deeper waters during both summer and winter, as well as when dolphins were socialising and resting and when calves were present. Records of social behaviour in larger groups have been found in other *Tursiops* species (Vermeulen et al. 2015). In addition, large nursery groups are possibly related to calf protection and might favour social learning (Bearzi et al. 1997; Gibson and Mann 2008; Vermeulen et al. 2015). Similar to findings for dolphins off KwaZulu-Natal on the east coast of South Africa (Cockcroft and Ross 1990b), calves and newborns were more often observed during summer months. This potentially provides a physiological advantage to the mother and calves by reducing their energetic demands because of less-extreme internal-ambient temperature gradients (Bearzi et al. 1997). During summer, larger groups might also be formed in order to protect the high proportion of calves, while during winter, groups might form for protection from predators, such as white sharks *Carcharodon carcharias*, which are known to prey upon dolphins (Hussey et al. 2012) and occur more often in the area during these months (Rycklief et al. 2014). Winter is also characterised by the sardine run, where dolphin groups from the study area or those that move through the study area pursue the large schools of sardines *Sardinops sagax* that move northwards along the east coast of South Africa at this time (O'Donoghue et al. 2010). That

bottlenose dolphins tend to form larger groups when food is abundant, for safety reasons, or when there is a high proportion of neonates, has been previously documented in other studies (Connor et al. 2000; Heithaus and Dill 2002; Möller et al. 2002; Parra et al. 2011).

Modelling showed that, apart from being more commonly encountered in association with sandy habitat, dolphins were more likely to be encountered during winter months and outside rather than inside of the MPAs. This finding was influenced by the fact that two of the three MPAs were characterised mainly by rocky, steeply sloping benthic habitat, whereas sandy habitat was preferred. This emphasises that substrate type, rather than the protection level of an area, influenced the distribution of dolphins. The Goukamma MPA therefore includes preferred dolphin habitat and the northeastern section of Plettenberg Bay, which is not part of an MPA, is another key area that could benefit dolphins if there were some form of protection there (e.g. as a controlled ecotourism zone to minimise disturbance).

The current local MPA network was not specifically designed for cetacean protection and therefore any benefit accrued would be incidental. The efficacy of spatial protection of *T. aduncus* as a conservation tool—should the MPA network be more consistent with the habitat needs of the species, or if it were larger—is debatable. Indeed, opinion is divided regarding the value of MPAs for cetacean conservation, given the animals' wide-ranging behaviour (Boersma and Parrish 1999; Hoyt 2005). Nevertheless, multiple studies have contributed to the identification of key areas for whales and dolphins, and have assisted in the creation or expansion of MPAs (e.g. Bearzi 2012). Concurrently, some existing MPAs have been shown to be beneficial for the protection of cetaceans (Hooker and Gerber 2004). Identifying critical habitats where cetaceans can feed, rest and reproduce is the first step towards being able to include cetacean needs into MPA design (Hoyt 2005).

A potential limitation of this work is the lack of reef habitat identified for the study area. Elsewhere it has been shown that *T. aduncus* preferred feeding in areas that include both reefs and soft substrate (Cockcroft and Ross 1990a; Amir et al. 2005). While several reefs are known to occur especially within the Tsitsikamma MPA, they are patchily distributed and appear to be underrepresented in the national habitat map that was used, most likely because of the scale at which the map was produced. However, the presence of reefs may account for patches with a higher ER of *T. aduncus* within this MPA, which was otherwise less-utilised than sandy areas of Plettenberg Bay and the Goukamma area. To the west of the study area, the habitat map shows an area that consists primarily of reef habitat but this could not be included in the boat-based surveys of this study for logistical reasons. Use of aerial surveys to cover a greater area could allow greater coverage of habitat types and associated dolphin distribution, although this would not enable collection of the photo-identification data that are necessary for population modelling based on mark-recapture. Another potential limitation of this study is the movement of the animals along the study area, either within a survey day or across different days. Some of the surveys (22%) were conducted in different sections on the same day, and animals could have potentially moved between those areas during the survey time-frame, thereby

creating duplicate counts. However, this situation might help to reinforce the observed preference by *T. aduncus* for certain habitats on same-day surveys.

Ideally, the distributions of both predators and prey of *T. aduncus* need to be taken into account in habitat-use models. In the absence of complete information on such distributions or habitat preferences, the models were limited mainly to environmental and physical variables, which can serve as proxies for biological variables. However, the models explained limited variability in *T. aduncus* distributions (R^2 values between 0.12 and 0.37), and would likely have been more informative if biological variables could have been taken into account. For example, the apparent avoidance of the Robberg MPA area might be associated with the abundance of white sharks attracted to this area because of the growing resident colony of Cape fur seals *Arctocephalus pusillus pusillus* that is present all year round (Huisamen et al. 2011). However, the possible effect of the predators would be difficult to distinguish from the effect of substrate type, given that the Robberg Peninsula is characterised by mainly rocky habitat, which was not favoured across the study area. Winter is the time of year when young seals are most vulnerable to white shark predation and is therefore the time of year when white sharks are most prevalent in the vicinity of seal colonies (Ryklief et al. 2014). The fact that there was no interaction in the models between MPA (inside) and season (winter) does suggest that it is the substrate type, rather than the predator presence, that influences the dolphins' avoidance of the Robberg area.

Conclusions

This study has shown that Indo-Pacific bottlenose dolphins associate closely with a sandy-substrate habitat type. Rocky habitats appear to serve as corridors as they were used primarily as transient areas by dolphins. Sandy habitats were clearly the substrate type associated with non-travelling behaviours, and therefore represent an important feature for *T. aduncus* along South Africa's south coast. The south coast of South Africa is characterised by exposed rocky shores with isolated and scattered sandy habitats along the coastline. Sandy substrate types are known to support many of the preferred prey species of *T. aduncus* (Cockcroft and Ross 1990a; Amir et al. 2005). *Tursiops aduncus* is also known to feed on reefs along the coasts of KwaZulu-Natal (east coast of South Africa) and Tanzania (Cockcroft and Ross 1990a; Amir et al. 2005), but this substrate type was underrepresented in the habitat map of the study area, highlighting that further assessments in reef habitat should be undertaken. Although not directly or originally designed for this purpose, the Goukamma MPA is ideally placed for dolphin protection as it encompasses both sandy and rocky-reef substrate types and is highly utilised by *T. aduncus*. The northeastern section of Plettenberg Bay is an unprotected dolphin hotspot and therefore creation of a controlled-use zone to minimise dolphin disturbance in this area should be considered.

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ORCID

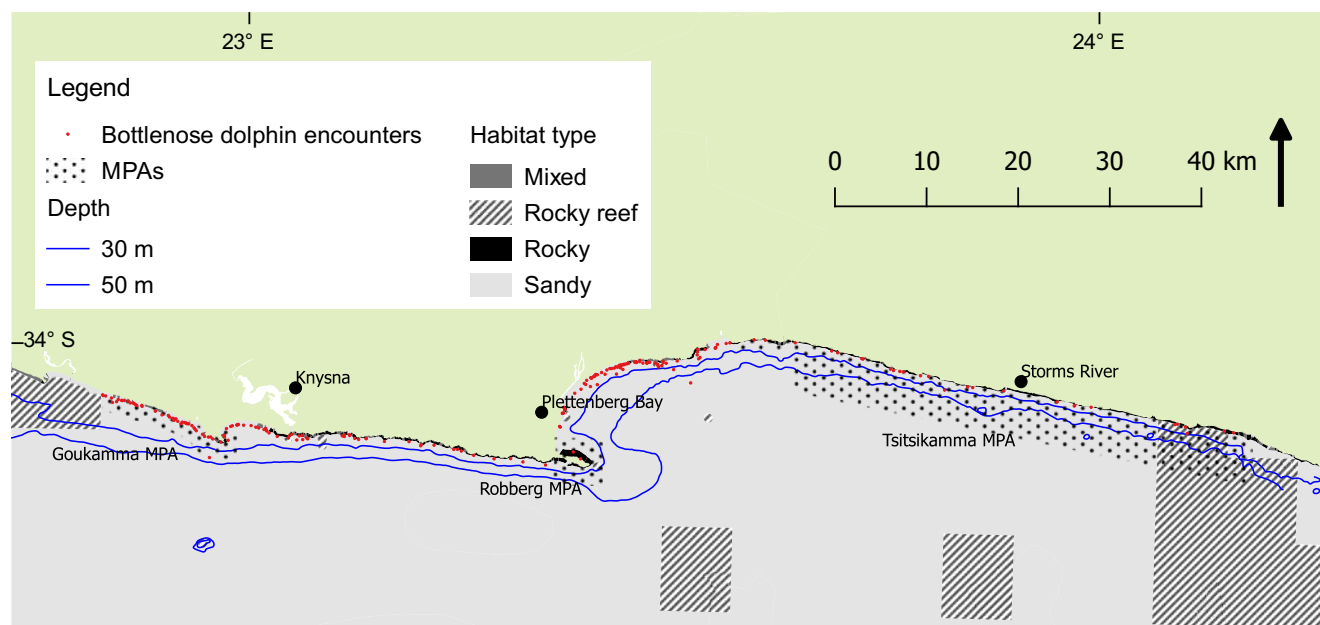
Stephen Kirkman  <https://orcid.org/0000-0001-5428-7375>
 Pierre Pistorius  <https://orcid.org/0000-0001-6561-7069>
 Gavin Rishworth  <https://orcid.org/0000-0003-1148-0081>

References

- Amir OA, Berggren P, Ndaro SGM, Jiddawi NS. 2005. Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. *Estuarine, Coastal and Shelf Science* 63: 429–437.
- Attwood CG, Mann BQ, Beaumont J, Harris JM. 1997. Review of the state of marine protected areas in South Africa. *South African Journal of Marine Science* 18: 341–367.
- Bailey H, Corkrey R, Cheney B, Thompson PM, Station F. 2013. Analyzing temporally correlated dolphin sightings data using generalized estimating equations. *Marine Mammal Science* 29: 123–141.
- Barton K. 2013. MuMIn: multi-model inference. R package version 1.40.0. Available online at <http://CRAN.Rproject.org/package=MuMIn>.
- Bates D, Maechler M, Bolker BM, Walker S. 2015. Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software* 67: 1–48.
- Bearzi G, Notarbartolo-di-Sciara G, Politi E. 1997. Social ecology of bottlenose dolphins in the Kvarnerić (northern Adriatic Sea). *Marine Mammal Science* 13: 650–668.
- Bearzi M. 2012. Cetaceans and MPAs should go hand in hand: a case study in Santa Monica Bay, California. *Ocean and Coastal Management* 60: 56–59.
- Boersma PD, Parrish JK. 1999. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* 31: 287–304.
- Booth C, Embling C, Gordon J, Calderan S, Hammond P. 2013. Habitat preferences and distribution of the harbour porpoise *Phocoena phocoena* west of Scotland. *Marine Ecology Progress Series* 478: 273–285.
- Boström C, Pittman SJ, Simenstad C, Kneib RT. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps and challenges. *Marine Ecology Progress Series* 427: 191–217.
- Brookes KL, Bailey H, Thompson PM. 2013. Predictions from harbor porpoise habitat association models are confirmed by long-term passive acoustic monitoring. *The Journal of the Acoustical Society of America* 134: 2523–2533.
- Cañadas A, Sagarminaga R, Garcia-Tiscar S. 2002. Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Research II* 49: 2053–2073.
- Cañadas A, Sagarminaga R, De Stephanis R, Urquiola E, Hammond PS. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15: 495–521.
- Cockcroft VG, Ross GJB. 1990a. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In: Leatherwood S, Reeves R (eds), *The bottlenose dolphin*. San Diego, California: Academic Press. pp 295–308.
- Cockcroft VG, Ross GJB. 1990b. Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of southern Africa. *Fishery Bulletin [US]* 88: 289–302.
- Cockcroft VG, Ross GJB, Peddemors VM. 1990. Bottlenose dolphin *Tursiops truncatus* distribution in Natal's coastal waters. *South African Journal of Marine Science* 9: 1–10.
- Connor RC, Wells RS, Mann J, Read AJ. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds), *Cetacean societies: field studies of dolphins and whales*. Chicago, Illinois: The University of Chicago Press. pp 91–126.
- 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.
- Garaffo GV, Dans SL, Pedraza SN, Degradi M, Schiavini A, González R, Crespo EA. 2011. Modeling habitat use for dusky dolphin and Commerson's dolphin in Patagonia. *Marine Ecology Progress Series* 421: 217–227.
- Gibson QA, Mann J. 2008. The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour* 76: 389–405.
- Hammond PS, Bearzi G, Bjørge A, Forney KA, Karczmarski L, Kasuya T et al. 2012. *Tursiops aduncus*. The IUCN Red List of Threatened Species 2012: e.T41714A17600466. Available at <http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T41714A17600466.en> [accessed 25 May 2018].
- Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83: 480–491.
- Hooker SK, Gerber LR. 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *BioScience* 54: 27–39.
- Hoyt E. 2005. *Marine protected areas for whales, dolphins, and porpoises: a world handbook for cetacean habitat conservation*. London: Earthscan.
- Huisamen J, Kirkman SP, Watson LH, Cockcroft VG, Pistorius PA. 2011. Re-colonisation of the Robberg Peninsula (Plettenberg Bay, South Africa) by Cape fur seals. *African Journal of Marine Science* 33: 453–461.
- Hussey N, McCann H, Cliff G, Dudley S, Wintner S, Fisk A. 2012. Size-based analysis of diet and trophic position of the white shark, *Carcharodon carcharias*, in South African waters. In: Domeier ML (eds), *Global perspectives on the biology and life history of the white shark*. Boca Raton, Florida: CRC Press. pp 27–50.
- Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Bartholomae HCH, van der Plas AK et al. 2009. The Benguela Current: an ecosystem of four parts, with boundary zones. *Progress in Oceanography* 83: 15–32.
- Irvine AB, Scott MD, Wells RS, Kaufmann HJ. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* 79: 671–688.
- Karczmarski L, Cockcroft VG, McLachlan A, Winter PED. 1998. Recommendations for the conservation and management of humpback dolphins *Sousa chinensis* in the Algoa Bay region, South Africa. *Koedoe* 41: 121–129.
- Karczmarski L, Cockcroft VG, McLachlan A. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *Marine Mammal Science* 16: 65–79.

- Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM et al. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology* 75: 14–24.
- Lutjeharms JRE, Cooper J, Roberts M. 2000. Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737–761.
- Marini C, Fossa F, Paoli C, Bellingeri M, Gnone G, Vassallo P. 2015. Predicting bottlenose dolphin distribution along Liguria coast (northwestern Mediterranean Sea) through different modeling techniques and indirect predictors. *Journal of Environmental Management* 150: 9–20.
- McCullagh P, Nelder JA (eds). 1989. *Generalized linear models*. London, UK: Chapman and Hall.
- Minton G, Peter C, Tuen AA. 2011. Distribution of small cetaceans in the nearshore water of Sarawak, East Malaysia. *The Raffles Bulletin of Zoology* 59: 91–100.
- Möller L, Allen S, Harcourt R. 2002. Group characteristics, site fidelity and seasonal abundance of bottlenosed dolphins (*Tursiops aduncus*) in Jervis Bay and Port Stephens, south-eastern Australia. *Australian Mammalogy* 24: 11–22.
- Naimi B, Hamm NA, Groen TA, Skidmore AK, Toxopeus AG. 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37: 191–203.
- Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142.
- O'Donoghue SH, Whittington PA, Dyer BM, Peddemors VM. 2010. Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. *African Journal of Marine Science* 32: 361–374.
- Parra GJ, Corkeron PJ, Arnold P. 2011. Grouping and fission–fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. *Animal Behaviour* 82: 1423–1433.
- Phillips G. 2006. Bottlenose dolphins (*Tursiops aduncus*) in Plettenberg Bay, South Africa: population estimates and temporal dynamics of groups. MSc thesis, Nelson Mandela Metropolitan University, South Africa.
- Photopoulou T, Best PB, Hammond PS, Findlay KP. 2011. Movement patterns of coastal bottlenose dolphins in the presence of a fast-flowing, prevailing current: shore-based observations at Cape Vidal, South Africa. In: Kirkman SP, Elwen SH, Pistorius PA, Thornton M, Weir CR (eds), *Conservation biology of marine mammals in the southern African subregion*. *African Journal of Marine Science* 33: 393–401.
- QGIS Development Team. 2016. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Available online at <http://qgis.osgeo.org> [accessed 15 January 2017].
- R Development Core Team. 2017. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J et al. 2006. Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series* 310: 271–295.
- 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, Butterworth DS. 1987. Offshore distribution of bottlenosed dolphins in Natal coastal waters and Algoa Bay, Eastern Cape. *South African Journal of Zoology* 22: 50–56.
- Rycklief R, Pistorius PA, Johnson R. 2014. Spatial and seasonal patterns in sighting rate and life-history composition of the white shark *Carcharodon carcharias* at Mossel Bay, South Africa. *African Journal of Marine Science* 36: 449–453.
- Shane S, Wells RS, Würsig B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science* 2: 34–63.
- Sink K, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T et al. 2011. *National Biodiversity Assessment 2011: technical report, volume 4: marine and coastal component*. Pretoria, South Africa: South African National Biodiversity Institute (SANBI).
- Sink K. 2016. The marine protected areas debate: implications for the proposed Phakisa Marine Protected Areas Network. *South African Journal of Science* 112: Art. #a0179.
- Vargas-Fonseca OA. 2018. Population ecology of Indo-Pacific bottlenose dolphins along the southeast coast of South Africa. PhD thesis. Nelson Mandela University, South Africa.
- Vermeulen E, Holsbeek L, Das K. 2015. Diurnal and seasonal variation in the behaviour of bottlenose dolphins (*Tursiops truncatus*) in Bahía San Antonio, Patagonia, Argentina. *Aquatic Mammals* 41: 272–283.
- Wells RS, Scott MD, Irvine AB. 1987. The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed.), *Current mammalogy*. New York: Plenum Press. pp 247–305.
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. *Mixed-effects models and extensions in ecology with R*. New York: Springer New York.

Appendix



Appendix: Locations of encounters with *Tursiops aduncus* in the research area, between the Goukamma and the Tsitsikamma marine protected areas (MPAs), South Africa, overlaid with the benthic substrate types