# Area utilization patterns of humpback dolphins (*Sousa plumbea*) in Richards Bay, KwaZulu-Natal, South Africa

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**Abstract** Geographically referenced data on humpback dolphin (*Sousa plumbea*) distribution and behaviour were collected in Richards Bay, South Africa, between 1998 and 2006. Utilization distributions presented a clear pattern in the distribution of dolphin activities and use of various locations within the study area. The 50 % kernel density estimate (core area) for foraging/feeding (2.1 $km^2$) was clustered around the harbour mouth (including the shark net installation). The core areas for resting, socialising and travelling were more widespread (>2.95 $km^2$). A mixed effects model indicated that location (longitude and latitude), distance from shore, year and group size are important variables in predicting foraging/feeding behaviour as opposed to other behaviours. The resting core was found in the southern part of study area and socialising was less clustered. This indicates preferential use of certain areas for specific behaviours. The overlap of foraging/feeding areas with stationary fishing gear (shark nets) and boat traffic are a major concern due to the risk of human-induced incidental mortalities. Any future alteration of the coastal area of Richards Bay, particularly development in the harbour, should be considered carefully, as further intrusion into areas critical to humpback dolphins, such as their foraging grounds, will inevitably carry negative implications for this already severely impacted population.

**Keywords** Kernel density estimates · Behavioural habitat preference · Humpback dolphins · Coastal conservation management · Richards Bay harbour

## Introduction

Natural environments consist of diverse patches of habitat that frequently vary in size and structure and the amount of resources they provide for the daily needs of animals. This mosaic of habitats generates conditions that can facilitate or limit daily activities of animals, leading to predictable patterns of distribution and habitat use (Mysterud and Ims 1998). On a larger scale, the distribution of resources can affect the daily activities of animals to an extent that shapes their spatial ecology and structure of populations (Gowans et al. 2008). Among cetaceans, several species are known to exhibit a preference for particular sites that are used more frequently and for specific behaviours. One such example are humpback dolphins (*Sousa* spp.); their preferences for sites corresponding with areas of good food source or good conditions for prey capture, hospitable environment for nursing young and sheltered sites for resting have been seen across several studies and

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populations (Saayman and Tayler 1979; Karczmarski et al. 2000; Parra et al. 2006a, b; Guissamulo 2008).

Humpback dolphins inhabit coastal waters of tropical and subtropical West Africa, the Indian Ocean, and the western Pacific Ocean. Their taxonomy remains unresolved, with between one and five nominal species proposed (Ross et al. 1994). Currently, most researchers recognise either two (Jefferson and Karczmarski 2001) or three species of *Sousa* (Rice 1998). The 3-species taxonomy recognises *S. teuszii* off West Africa, *S. plumbea* in the western Indian Ocean, and *S. chinensis* off southeast Asia and in the western Pacific Ocean. When 2-species taxonomy is considered (e.g. the current IUCN classification), *S. chinensis* and *S. plumbea* are combined into one species—*S. chinensis*—ranging across the Indian Ocean and western Pacific. In this study, we follow the 3-species taxonomy of Rice (1998), and the study animal is the Indian Ocean humpback dolphin *S. plumbea* (hereafter the 'humpback dolphin').

Off southern Africa, humpback dolphins occur in a variety of coastal marine environments (Jefferson and Karczmarski 2001); with the isobath of ~25 m representing the critical depth limiting their offshore range (Karczmarski et al. 2000). Their population ecology has been studied mainly in Algoa Bay (Karczmarski 1999; Karczmarski et al. 1999a, b, 2000), Richards Bay (Atkins and Atkins 2002; Keith et al. 2002; Atkins et al. 2004) and Maputo Bay (Guissamulo and Cockcroft 2004; Guissamulo 2008), and their population numbers have been reported to be low across the region. The regional Red List for South Africa classifies *S. plumbea* as Vulnerable (Friedman and Daly 2004), as does the global IUCN Red List assessment (Reeves et al. 2008). Population declines have been inferred over much of their discontinuous range due to continuous and increasing incidental mortality in fishing gear, ongoing environmental degradation and habitat loss. Coastal and estuarine areas are of particular concern as these are the areas where humpback dolphins live.

This study focuses on the Richards Bay population of humpback dolphins, on the subtropical east coast of South Africa. In this area, there is a mosaic of coastal habitats including sandy beaches, estuaries with mangrove swamps, and an enclosed bay with an industrialised harbour bordered by a moderate-sized urban settlement. The Richards Bay area appears to be a particularly important area for humpback dolphins in KwaZulu-Natal (KZN), with sighting rates reported to be higher than in other areas in KZN (Durham 1994). The Richards Bay harbour is known for large volumes of boat traffic, dredging and pollution, all of which are known threats to humpback dolphins (Cockcroft 1989, 1990; Karczmarski 2000; Karczmarski et al. 1998; Friedman and Daly 2004; Reeves et al. 2008). There are also stationary shark nets situated at the eastern side of the harbour mouth to reduce the risk of shark attacks on bathers; these nets are a well-known cause for concern for humpback dolphins (Cockcroft 1990). The Richards Bay shark nets catch many more humpback dolphins than would be predicted by the number of nets alone and are responsible for 62 % of the KZN catch in only 5 % of the fishing effort (Atkins et al. 2013). This high capture rate is of concern as population size estimates for the KZN region and Richards Bay area estimated to be below 287 individuals (Durham 1994; Atkins and Atkins 2002; Keith et al. 2002).

Earlier work by Durham (1994), Keith et al. (2002) and Atkins et al. (2004) indicates that the Richards Bay area is preferred by humpback dolphins, with foraging/feeding occurring predominantly close to shore. To gain greater insights into the population ecology of humpback dolphins at Richards Bay, it is important to understand their spatial use in the environment where several potential threats are concentrated within a spatially-limited area. In the current study, we uncover the patterns of area utilisation of humpback dolphins at Richards Bay, providing baseline evidence for consideration in current and future plans for the area's development and management. Specifically, our aims included: (1) to plot the utilisation distribution of humpback dolphin behaviour at Richards Bay; (2) to investigate annual and seasonal differences in the utilisation distributions; and (3) to identify factors that influence the occurrence of feeding behaviour.

We also provide a base for further studies where the animal–habitat relationship can be investigated in greater detail benefiting from long-term individual sighting history data collected at Richards Bay between 1998 and 2006 (S. Atkins, M. Keith and L. Karczmarski, study in progress).

## Materials and methods

### Study area

Richards Bay (28.808731°S, 032.089663°E) is located on the KwaZulu-Natal coast, South Africa (Fig. 1). Within the study area, the coastline comprises sandy beaches and there are no rocky outcrops. In 1972, a single large, relatively undisturbed estuarine system was developed into a harbour, dividing the estuary system into two independent systems. The southern Mhlathuze Estuary is managed as a Marine Protected Area but is too shallow to be accessible by boat and did not form part of the study area. The northern section was developed into a harbour and the wide, deep (continually dredged) mouth. The mouth is approximately 900 m wide and is flanked by two breakwaters that extend out to sea. Within the mouth and harbour there are a variety of marine and estuarine habitat types (Weerts and Cyrus 2002): intertidal sandbanks, sub-tidal mud flats, mangrove

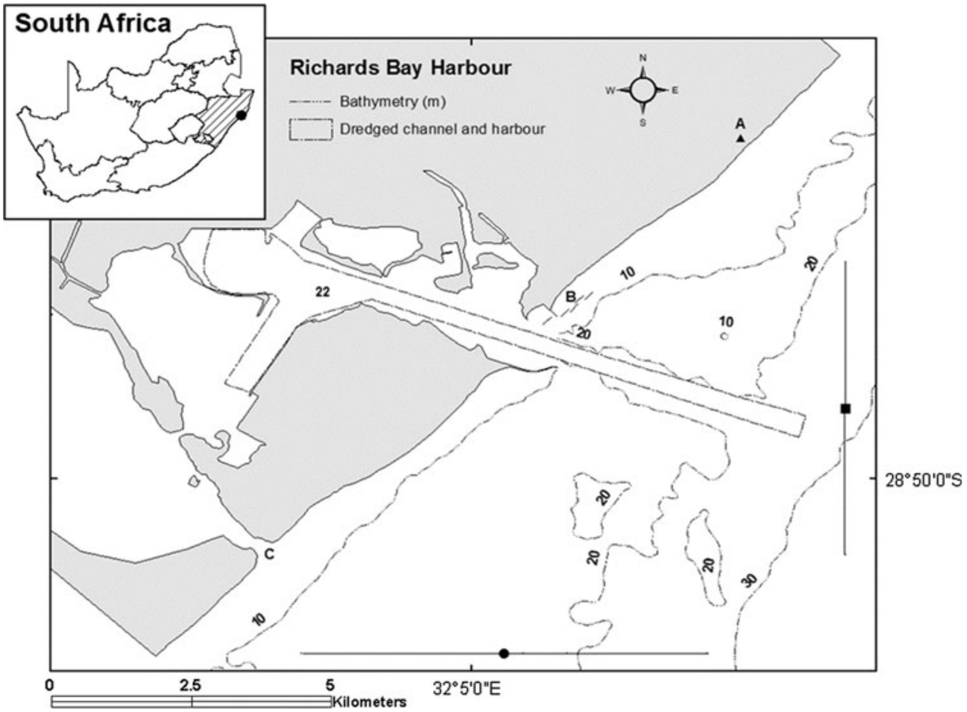


**Fig. 1** The Richards Bay study area, from the lighthouse (*A*) in the north, the harbour mouth and shark nets (*B*) and the Mhlathuze Estuary mouth (*C*) in the south west. Bathymetry indicate the dredged channel and depth at 10-m intervals; bathymetry and coastline GIS layers supplied by the South African Navy Hydrological Office (SANHO). Mean distribution of humpback dolphins (*Sousa plumbea*) GPS points, X (*filled circle*) and Y (*filled square*) coordinates (±SD) denoted at *bottom* and *right axes* of the figure

fringes and dredged channels (up to 20 m deep). The harbour contains both marine and estuarine fish (Weerts and Cyrus 2002), and the larger areas is characterised by very high water turbidity (Durham 1994).

## Field data collection

Field research was performed from April 1998 to March 2006. Boat surveys were conducted in sea conditions of Beaufort Scale <3, using a 5.5-m inflatable boat at ±10 km/h, beginning inside the Richards Bay harbour, exiting the harbour mouth and proceeding along parallel to the shore (at a distance of 0.5 km, and returning at 1.5 km, from the beach) and/or along the dredged channels of the harbour. Once dolphins were sighted, they were approached at low speeds and their location was recorded using a Garmin II-Plus Global Positioning System (GPS) with point localities recorded every 5 min thereafter. While the boat remained in close proximity to animals (referred to hereafter as a 'sighting'), dolphin behaviour was recorded at 5 min intervals as the predominant behaviour of the majority of the group members. These behaviours were grouped into four broad categories (see further) that represented behavioural states (i.e. behaviour patterns of relatively long duration) and are consistent with similar studies of humpback dolphins elsewhere (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000; Atkins et al. 2004; Parra 2006), and other similar work elsewhere (e.g. Heithaus and Dill 2002; Lusseau and Higham 2004).

The behavioural categories used were as follow:

### *Foraging/feeding*

Irregular, often steep and/or fast dives (including rapid accelerations) in varying directions with short swimming distances between dives; sometimes fish were seen at the surface or in the dolphin's mouth.

### *Resting*

Low level of activity, with regular long dives covering a short distance either in one direction or in a localised circular pattern, similar to what other studies term "resting" (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000; Atkins et al. 2004) or "milling" (Lusseau and Higham 2004; Parra 2006).

### *Socialising*

Irregular dive durations with irregular distances and obvious interactions between individuals; frequent energetic displays, leaps and somersaults, lob-tailing and spy-hopping.

### *Travelling*

Movement in one persistent direction with long dive durations and regular surfacing pattern.

A fifth category, 'undetermined', was used to classify behaviours that that could not be clearly assigned to any of the above categories, yet not used in spatial or temporal analysis.

### Data processing

Geographic coordinates (GPS positions) recorded during dolphin follows, along with associated behavioural data were used to investigate potential spatial patterns using ESRI® ArcMap™ 9.3.1.

Two methods to estimate utilisation distributions (UDs) were used: the minimum convex polygon (MCP) and kernel density estimate (KDE) using the Home Range Estimate extension tool (Rodgers et al. 2005) in ArcMap. The MCP and 95 % kernel were used for the overall occurrence estimations and the 50 % kernel was used for the core area of occurrence estimation. Area calculations were based on a Universal Transverse Mercator (UTM) 36S-WGS 84 datum projection, using XTools 7.1 Trial version (Data East 2003) in ArcMap. Coastal and bathymetry GIS spatial layers were supplied by the South African Navy Hydrological Office (SANHO; agreement HYD/B/514/3), and depth data for analysis were extracted from the SANHO spatial layers, using the maximum depth from the depth layer.

The adaptive kernel method with least-squares cross-validation techniques (LSCV) to estimate the smoothing parameter $h$ was used to create a core 50 % kernel and 95 % kernel UD (Rodgers and Carr 1998). The smoothing parameter controls the amount of variation in each component of the UD estimate. Small $h$ values reveal the fine details of the data while large $h$ values obscure all but the most prominent features (Worton 1989).

We present utilisation distributions (UDs) based on a subsampled dataset, using only the first location point of each behaviour per sighting, to reduce spatial autocorrelation (e.g. Wilson et al. (1997); see Rooney et al. (1998) and further for more detail). We also present UDs where we relaxed the frequently asserted requirement for independence of observations to maximise sample size and hence the precision and accuracy of the UDs for our analysis (see further for more detail) and used all points per behaviour per sighting.

### Mixed effects modelling

We used generalised linear mixed-effects models in order to understand which of the explanatory variables might influence behaviour. Distribution patterns, and in particular preferred areas, are frequently linked to feeding/foraging behaviour and opportunities (Hastie et al. 2004), and therefore feeding behaviour was singled out for further investigation. Foraging/feeding and other behaviours were treated as binomial response variable (foraging/feeding = 1, and all other behaviours clumped = 0). Analysis was conducted of the explanatory variables and the response variable (behaviour) suitable for logistic regression analysis where a generalised linear model (logit link function) was fitted using maximum likelihood techniques (McCullagh and Nelder 1989). Mixed effects models were applied using lme4 package (Bates and Maechler 2010) in R (v.2.14; R Development Core Team 2011) to account for the dependency of behaviours within specific dolphin sightings.

The probability of dolphins foraging/feeding was modelled by including the following continuous explanatory fixed effect variables into a global model: location coordinates in the UTM coordinate system X and Y, depth, distance to shore (distance), year, month, hour, group size (group) and season. Seasonal variance was included by defining wet season (October–April) and dry season (May–September) seasonal data for the Maputaland Coastal Belts and Maputaland Wooded Grassland regions (Mucina et al. 2006). To test whether location coordinates, distance to shore and depth affected the probability of dolphin foraging/feeding, different iterations of interaction terms between the four variables were also included in the global model (e.g. latitude:longitude:depth).

To account for the dependency of behaviours within certain variables, different random factors were included into the global model. We included sighting (1|SIGHTING), running day (continuous variable), hour of day (HRD), and hour of day nested within sighting (HRD|SIGHTING). A set of ecologically relevant alternative simplifications of the global model was then composed (Burnham and Anderson 2002), and fitted against restricted maximum likelihood (REML) estimation to assess the effects of different random factors. In order to investigate the effects of the fixed effects variables, the models were fitted against maximum likelihood (ML) estimation (Bolker et al. 2009).

### Model selection by use of the Akaike's Information Criteria (AIC)

To compare alternative nested models, the principle of Akaike's information criteria (AIC) was applied (Akaike 1973; Burnham and Anderson 1998). In particular, the AIC-weight criteria ($w$) was applied which reflects the relative performance of models and can be interpreted as the probability that a given model is the best model, i.e. the model that minimises the Kullback–Leibler discrepancy (Burnham and Anderson 2002; Wagenmaker and Farrell 2004). In the evaluation of alternative models, the evidence ratio expressed as a normalised probability as was used in:

$$w_{\mathrm{m}}(\mathrm{AIC})/w_{\mathrm{n}}(\mathrm{AIC})$$

where model $m$ is the best fitting model compared to model $n$ (see Wagenmaker and Farrell 2004). As all models had the same structure and sample size, their respective AIC values were comparable (Burnham and Anderson 1998). We also report on the Bayesian information criterion (BIC).

To check for multicollinearity among explanatory variables, the inter-correlation among the explanatory variables was investigated with Pearson correlation test, and since none of the variables were highly collinear (>0.54; see Table 4, below), no variables were removed from the mixed effect models (Zuur et al. 2010).

### Data independence

Autocorrelation (both spatial and temporal) and/or pseudoreplication are an inherent part of ecological studies (Legendre and Fortin 1989; Dormann et al. 2007; Cushman 2010), and in particular non-randomised non-transect photo-identification/behavioural boat-based cetacean research (Corkeron et al. 2011), such as this study. Autocorrelation/pseudoreplication can increase Type I errors, decreasing the reliability of estimates obtained from independent variables (Diniz-Fihlo et al. 2003; Millar and Anderson 2004; Økland 2007). Data dependence can be reduced by appropriate experimental design and subsequent appropriate statistical techniques, such as filtering data, subsampling, etc. (see Hurlbert 1984; Legendre et al. 2002; Millar and Anderson 2004; Crawley 2007; Corkeron et al. 2011; Cushman 2010). Subsampling of datasets is often used to reduce autocorrelation, although De Solla et al. (1999) finds this to be less effective than alternative approaches, and Cushman et al. (2005) and Cushman (2010) indicate that trying to attain statistical independence through subsampling "incurs heavy costs in terms of information loss". Mixed effect models are said to be a better choice when dealing with lack of independence in the data (Millar and Anderson 2004; Dormann et al. 2007; Chaves 2010; Hegel et al. 2010), and the random factor structure accounts better for autocorrelated error variances (Økland 2007) and reduces overall variance (Hegel et al. 2010). Random factors deals better with unbalanced sample designs, such as this study (Hegel et al. 2010), and it has been frequently emphasised that one should only conclude general interpretations from the predictions derived from these mixed effect models (Millar and Anderson 2004; Venables and Dichmont 2004; Økland 2007; Chaves 2010). Following this line of argument, the mixed effect models were applied in this study.

Since data independence ultimately affects the output of mixed effect models, we investigated the effect of the non-independence of our data. The full dataset used in the spatial statistical analysis was highly spatially autocorrelated ((Moran's I index: 0.07; $Z$ score = 22.65; $P < 0.001$) (derived from spatial statistics tools in ArcMap). Adopting an approach in eliminating non-independence, we subsampled the original dataset. Only in subsamples representing <5 % of the full dataset did we achieve no autocorrelation. We constructed five subsets of data with no autocorrelation using Hawth's Analyasis Tools (v.3.27; Beyer 2007) extension for ArcMap, using sighting as the subset selection for randomised subsampling. Using these five subsampled datasets, we subsequently ran mixed effect models, with the full suite of fixed effect variables and sighting as the random variables, to see if any of the fixed effect variables were influenced by non-independence in the original dataset.

## Results

Across the 9 years of study, 453 boat-based surveys were conducted, presenting a total of 915.7 survey hours and 401.35 h spent with dolphins (Table 1). For the spatial analysis, we used 226 sample days with 249 dolphin sightings and 4,348 GPS points (Table 2). In 1998, there were 64 sightings, with 1,343 GPS data points collected; every other year had fewer than 1,000 GPS records (see Tables 1, 2). On average, the sighting events consisted of 17 (±14.38 SD) 5-min point locations/observations; although in one case (27 August 1999), one continuous sighting contributed 94 observations. The behaviour regarded as Resting was infrequently recorded ($n$ = 399), constraining the calculations of utilisation distributions.

### Spatial analysis

The MCP approach estimated considerably large areas of the dolphin use for different behaviours within the study area (one point per sighting: 17.71–43.65 km$^2$, Table 3a; all points for each behaviour per sighting 32.49–72.99 km$^2$,

**Table 1** Survey intensity (number of surveys, total survey duration and total sighting duration) during 1998–2006 for humpback dolphins (*Sousa plumbea*) in Richards Bay

| Years | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Surveys ($n$) | 84 | 52 | 72 | 95 | 36 | 40 | 41 | 28 | 5 | 453 |
| Total survey (h) | 199.3 | 111.8 | 159.7 | 177.9 | 66.7 | 65.5 | 70.4 | 56.7 | 7.93 | 916 |
| Total sighting (h) | 120.4 | 70.13 | 85.53 | 38.8 | 7.55 | 26.5 | 26 | 22.9 | 3.5 | 401.4 |

**Table 2** Number of GPS points recorded during 1998–2006 ($n = 4{,}348$) for all 249 sightings used in spatial statistical analysis for all apparent behaviours

| Years | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | Total (b) |
|---|---|---|---|---|---|---|---|---|---|---|
| Sightings (*n*) | 64 | 30 | 45 | 32 | 9 | 27 | 18 | 20 | 4 | 249 |
| Foraging/feeding | 713 | 205 | 268 | 92 | 39 | 105 | 81 | 55 | 13 | 1,571 |
| Resting | 111 | 91 | 96 | 43 | 3 | 28 | 14 | 13 | – | 399 |
| Socialising | 322 | 281 | 167 | 87 | 26 | 81 | 86 | 73 | 21 | 1,144 |
| Travel | 197 | 169 | 366 | 198 | 21 | 84 | 103 | 88 | 8 | 1,234 |
| Total (year) | 1,343 | 746 | 897 | 420 | 89 | 298 | 284 | 229 | 42 | 4,348 |

Totalled columns include the total number of points recorded for each year, *total (year)*, and the total number of points for each categorised behaviour, *total (b)*

**Table 3** Calculated areas (km$^2$) for minimum convex polygon (*MCP*), kernel density estimate (*KDE*) at *95 %* and *50 %* utilisation distributions (*UD*) for (a) first point behaviour and (b) all behavioural points per sighting observed during 1998–2006 for humpback dolphins in Richards Bay (see "Materials and methods" for the description of behaviours)

| | MCP | KDE 95 % UD | KDE 50 % UD | *h* | href | No. points | Moran's *I* index |
|---|---|---|---|---|---|---|---|
| (a) First point behaviour | | | | | | | |
| Foraging/feeding | 43.65 | 19.41 | 1.87 | 0.06 | 0.43 | 149 | $0.03^{1.32\text{ns}}$ |
| Resting | 17.71 | 41.79 | 7.26 | 0.40 | 0.54 | 40 | $-0.04^{-0.19\text{ns}}$ |
| Socialising | 33.71 | 21.27 | 3.95 | 0.13 | 0.45 | 117 | $0.002^{0.22\text{ns}}$ |
| Travelling | 36.45 | 24.81 | 4.36 | 0.13 | 0.42 | 162 | $0.02^{0.51\text{ns}}$ |
| (b) All behavioural points | | | | | | | |
| Foraging/feeding | 72.99 | 19.26 | 1.92 | 0.03 | 0.29 | 1,571 | $0.07^{13.6***}$ |
| Resting | 32.49 | 17.54 | 2.95 | 0.07 | 0.37 | 399 | $0.47^{7.26***}$ |
| Socialising | 52.61 | 16.40 | 3.10 | 0.05 | 0.31 | 1,144 | $0.19^{23.2***}$ |
| Travelling | 54.68 | 28.29 | 4.86 | 0.08 | 0.30 | 1,234 | $0.01^{0.81\text{ns}}$ |

The number of points used in KDE UD estimation for each behaviour as well as Moran's *I* index for spatial autocorrelation (Moran's *I* value, *Z* score, and *P* value, where *ns* not significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) are reported

**Table 4** Pearson correlation values for the fixed effect variables: the hour of the day when observations in sighting occurred, wet–dry season (see description in text), month of year, year, average group size, distance to shore of locality during the recorded point within the sighting, the depth of locality during the recorded point within the sighting *X*, *Y*

| | Hour | Wet–dry | Month | Years | Group | Distance | Depth | *X* |
|---|---|---|---|---|---|---|---|---|
| Wet–dry | −0.16 | – | | | | | | |
| Month | −0.04 | −0.15 | – | | | | | |
| Year | −0.06 | 0.26 | −0.29 | – | | | | |
| Group | 0.07 | −0.08 | 0.12 | −0.05 | – | | | |
| Distance | 0.02 | −0.1 | 0.11 | −0.19 | 0.28 | – | | |
| Depth | 0.09 | −0.05 | 0.08 | −0.11 | 0.08 | 0.39 | – | |
| *X* | −0.13 | 0.24 | 0.05 | −0.05 | −0.08 | 0.08 | 0.17 | – |
| *Y* | 0.004 | 0.15 | −0.07 | 0.14 | −0.24 | −0.5 | −0.08 | 0.53 |

Table 3b). Using the more conservative KDE utilisation distributions (UD) resulted in estimates of different space use for the different behaviours, which was smaller than MCPs.

The subsampled data, based on the single point per behaviour/sighting, were not autocorrelated (Table 3a; Moran's *I* index −0.04–0.03; *Z* score = −0.19–1.31; *P* = not significant), whereas for the full dataset, travelling behaviour was not spatially clustered (Moran's *I* Index = 0.01, *Z* score = 0.81; *P* = ns) yet Foraging/feeding, Resting and Socialising were highly clustered (see Table 3b).

The UD for Foraging/feeding behaviour for the full dataset was widespread within the study area (95 % KDE: 19.26 km$^2$; Table 3b), including most of the harbour (Fig. 2a). The 50 % KDE UD (1.92 km$^2$) was clustered in the harbour mouth and around the breakwaters (77.07 % of core 50 % KDE UD foraging/feeding area); the remaining 22.92 % of core 50 % KDE UD foraging/feeding area was found across the study area and across a range of depths, even inside the harbour. The 50 % KDE UD derived from the full dataset for foraging/feeding behaviour was clustered, yet this UD was only marginally larger than the 50 % KDE UD calculated (1.87 km$^2$) from the first point

**Fig. 2** Kernel density estimates (KDE) for each of four behaviours of humpback dolphins in the Richards Bay area for the period of 1998–2006. *Dark grey shading* 50 % KDE, *hatched* area 95 % KDE. **a** Foraging/feeding (KDE *h* value: 0.03, 1,571 points). **b** Resting (KDE *h* value: 0.07, 399 points). **c** Socialising (KDE *h* value: 0.05, 1,144 points). **d** Travelling (KDE *h* value: 0.08, 1,234 points)

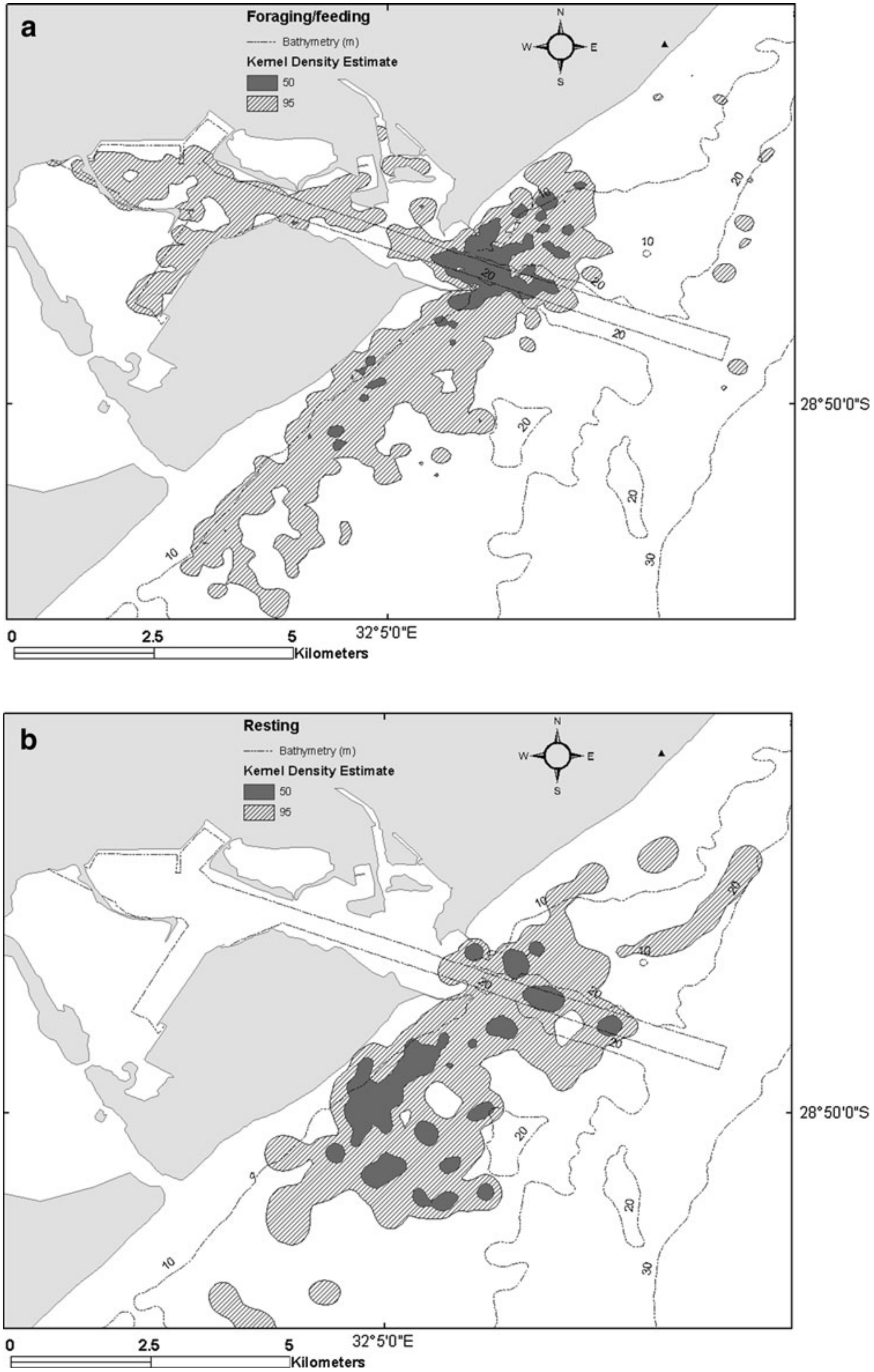
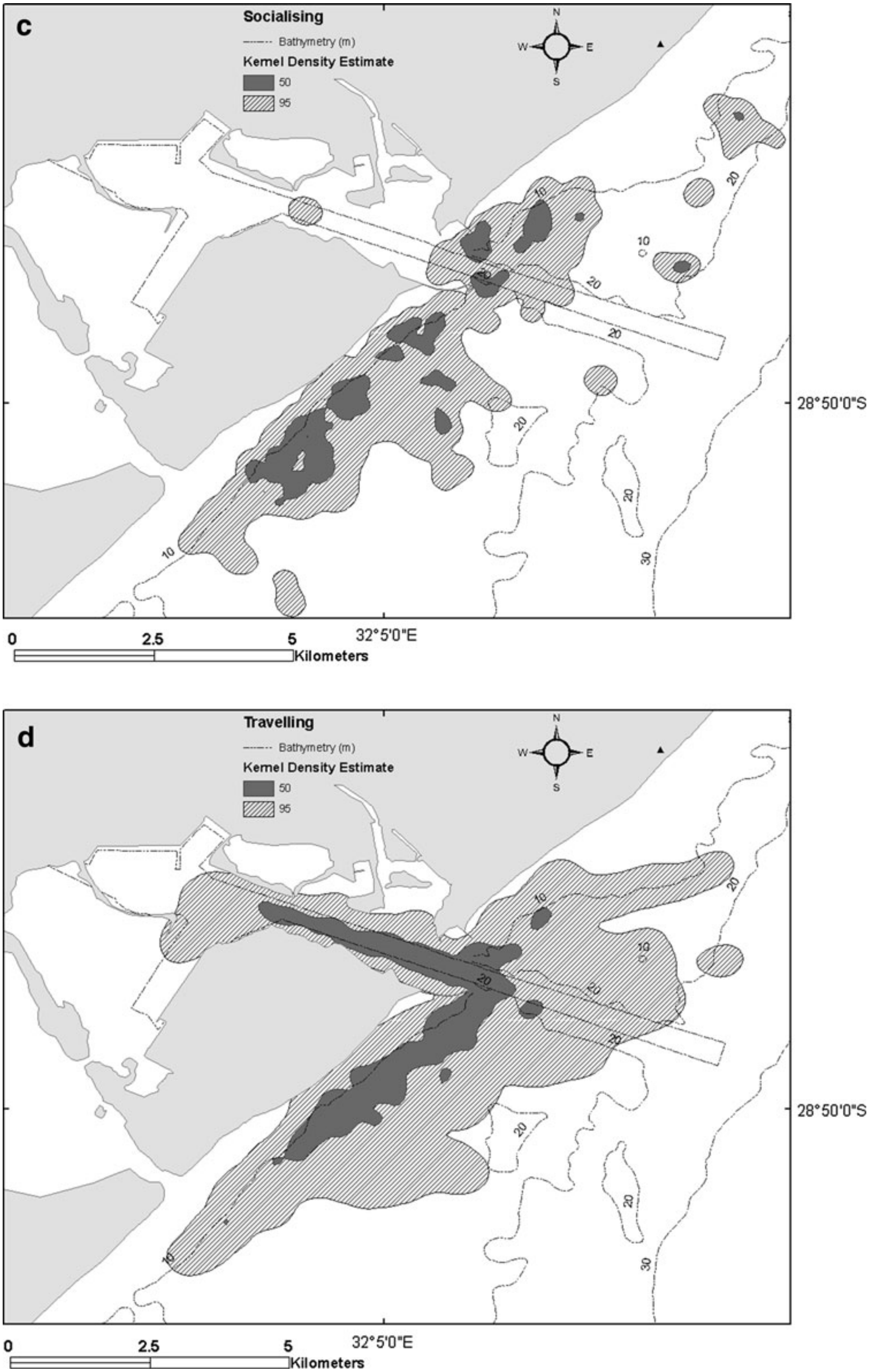


**Fig. 2** continued



per behaviour/sighting data (Table 3a), and these two 50 % KDE UD overlapped by 48 % in the harbour mouth. The centroids for each of the core Foraging/Feeding behaviour UDs were only 284 m apart, indicating similar patterns between full dataset, and data controlled for autocorrelation.

Resting behaviour from the full resting dataset was also recorded along the coastline but never in the harbour (95 % KDE: 17.54 km$^2$; Fig. 2b), extending the UD further offshore than the other behaviours, with the 50 % KDE core areas restricted (2.95 km$^2$), with many patches in the 10–20 m depth range and occasionally even deeper.

Resting KDE UD from all resting points was produced with a considerably smaller number of points compared to other behaviours. By estimating a KDE UD using the first point of resting/sighting for resting, this produced a very large 50 % KDE of 7.25 $km^2$ which extended across the whole study site; mainly the result of only 40 points used for kernel construction.

Socialising behaviour was recorded along the coastline (full dataset 95 % KDE: 16.40 $km^2$), though rarely inside the harbour (Fig. 2c). The full dataset 50 % KDE UD (3.1 $km^2$) was found predominantly to the south of the harbour, generally in water less than 15 m in depth, though not uncommon in the 20 m depth range. This KDE result was supported by the subset-analysis, where the first point of socialising behaviour/sighting dataset produced a 50 % KDE UD of 3.95 $km^2$.

Travel behaviour occurred throughout the study area, including much of the harbour (Fig. 2d), with full dataset 50 % KDE UD estimated to be 4.86 $km^2$. The full dataset travel behaviour points were not spatially auto correlated, and the subsampled dataset produced a slightly smaller 50 % KDE UD of 4.36 $km^2$. The full dataset 50 % KDE UD occurred predominantly within the 15-m isobath and, unlike resting and socialising, extended into the harbour, and the broad UD was mainly due to a larger spread of points across the area.

## Temporal pattern

The wet season points used to derive core utilisation distribution (50 % KDE) yielded an area of 3.51 $km^2$ ($h = 0.03$; href = 0.29; $n = 1{,}649$, Moran's Index = 0.1; $Z$ score 26.9; $P < 0.01$), which was only slightly smaller than core utilisation distribution for the dry season months area of 3.77 $km^2$ ($h = 0.03$; href = 0.26; $n = 2{,}699$, Moran's Index = 0.2; $Z$ score 18; $P < 0.01$).

Yearly comparison between core utilisation distributions (KDE 50 %) produced similar restricted cores for foraging/feeding (0.92 $km^2 \pm 0.75$), resting (1.35 $km^2 \pm 0.47$) and socialising (1.12 $km^2 \pm 0.81$), while travel behaviour produced a consistently larger UD range through the years (4.02 $km^2 \pm 1.68$).

## Mixed effect modelling

The random factor with hour of day nested within sighting (HRD|SIGHTING) presented the model with the lowest AIC using a REML to estimate the model parameters. Subsequently, the model best fitting the data for fixed effect interactions indicated a 71 % likelihood of explaining the occurrence of foraging/feeding, which was compiled from five of the explanatory variables: location coordinates, the distance to shore, year and average group size (fitted with ML to estimate model parameters; AIC = 3,408; Table 5). The estimated effect of fixed factors for the top five models varied with different iterations of location coordinates, distance to shore, depth, and year and average group size per sighting, which all contributed a significant proportion of the variance found in the top five models (Table 5).

In a spatial statistical context, the median/mean locality for $X$ and $Y$ coordinates were just south of the south breakwater (Fig. 1). The probability of foraging/feeding decreased (negative estimate) with an increase in $X$ of the study site. As $Y$ increased, so did the probability to foraging/feeding (Table 6), increasing the probability of foraging/feeding further north, into the harbour/mouth area (Fig. 2a). The collinearity in the $X$ and $Y$ variables (Pearson correlation = 0.53; Table 4) produced a two-dimensional effect on the predicted spatial probability of foraging/feeding in the current study. Distance to shore, with a negative estimate, indicated the probability to feed was closer to shore. No interaction combination between $X$, $Y$, distance to shore and/or depth were found to contribute to the best fit of the top models for the full dataset. The inclusion of year as a factor in the most likely model

**Table 5** Statistical outputs of the five mixed effect model (of 30) according to the lowest Akaike's information criteria (*AIC*), variation in AIC, and AIC-weight criteria (*w*), Bayesian information criterion (*BIC*), explaining the variation in the probability of foraging/feeding behaviour and other behaviours of humpback dolphins in the Richards Bay area

| Model | AIC | ΔAIC | $w_{AIC}$ | BIC |
|---|---|---|---|---|
| $X + Y$ + Distance + Year + Group | 3,408 | 0.00 | 0.71 | 3,509 |
| $X + Y$ + Distance + Depth + Year + Group | 3,410 | 2.00 | 0.26 | 3,520 |
| $Y$ + Distance + Depth + Year + Group | 3,416 | 8.00 | 0.01 | 3,518 |
| $X$ + Distance + Depth + Year + Group | 3,417 | 9.00 | 0.01 | 3,519 |
| $X \times Y$ + Distance + Year + Group | 3,420 | 12.00 | 0.00 | 3,569 |

Fixed effect components featuring in model outputs were: the hour of the day when observations in sighting occurred, wet–dry season (see description in text), month of year, year, average group size, distance to shore of locality during the recorded point within the sighting, the depth of locality during the recorded point within the sighting $X$, $Y$. The hour of day was nested within sighting number (HRD|SIGHTING) and included as a random factor in all models indicated foraging/feeding probability differed between years; however, with small differences around the intercept (1998) as these values are reported in log-odds (Table 6). The largest estimate difference in year was for 2006, log-odds estimate of −12.47, which even though significant effect on probability of foraging/feeding is a small difference in combination with the intercept. Group size estimate suggests that it might influence the probability of foraging/feeding (group = negative log-odds estimate − smaller groups higher probability to feed). A subsequent analysis of group size and behaviours indicated there were significant differences for group size and different behaviours (Kruskal–Wallis $\chi^2_3 = 494.15$, $P < 0.01$), with a multiple comparison test after Kruskal–Wallis (package *pgirmess* in R) suggesting that all behaviours were different from one another, except feeding and travelling. Depth, which was present in some of the models (Table 5), also presented a negative estimate effect on the probability to forage/feed, indicating that humpback dolphins tend to forage/feed in shallower areas.

**Table 6** Mixed effect model selected with the lowest Akaike's information criteria (AIC) value (AIC = 3,408) for analysis on foraging/feeding (1) and other behaviours (0) (FA)

| | Estimate | SE | *Z* value | Pr(> \|Z\|) | *P* |
|---|---|---|---|---|---|
| Intercept | −25,300.00 | 13,430.00 | −1.884 | 0.05 | * |
| *X* | −297.10 | 92.93 | −3.197 | 0.00 | ** |
| *Y* | 3,948.00 | 1,991.00 | 1.983 | 0.05 | * |
| Distance | −2.00 | 0.31 | −6.496 | 0.00 | *** |
| 1999 | −6.02 | 1.62 | −3.729 | 0.00 | *** |
| 2000 | −8.84 | 1.56 | −5.659 | 0.00 | *** |
| 2001 | −10.70 | 2.22 | −4.818 | 0.00 | *** |
| 2002 | −6.12 | 3.19 | −1.920 | 0.05 | |
| 2003 | −8.65 | 1.98 | −4.376 | 0.00 | *** |
| 2004 | −9.41 | 2.23 | −4.218 | 0.00 | *** |
| 2005 | −9.92 | 2.49 | −3.985 | 0.00 | *** |
| 2006 | −12.47 | 5.68 | −2.194 | 0.03 | * |
| Group | −0.09 | 0.02 | −3.94 | 0.00 | *** |

Model variables in the best fit model were as follows: *X*, *Y*, distance to shore, year and mean group size as a factor variable. The hour of day nested within sighting number (HRD|SIGHTING) as a random factor in the model, produced the lowest AIC value fitted on a REML estimate. The number of observations is 4,348 and number of sightings (SIGHTING) = 249. FA ~ *Y* + *X* + Distance + Year + Group + (HRD|SIGHTING)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The mixed effect model analyses undertaken for the five non-autocorrelated 5 % subsampled datasets consistently identified the variables *X*, *Y*, distance to shore, year and group to significantly contribute to the variance explained in the probability of foraging/feeding (Table 7). Depth was also present in two of the models. Two of the five models with the lowest AIC values were constructed out of the same fixed effect variables as the final model based on the complete dataset (Table 6), using hour of day nested within sighting as a nested random effect variable. Interactions between *X* and *Y* consistently influenced the probability of foraging/feeding. Although the estimates for all the subsets varied for each model as was expected, the trend (+ or −) for each estimate of the fixed factors was the same as for the complete dataset.

## Discussion

As might be expected, the more localised behaviours, i.e. foraging/feeding, resting and socialising, tend to occur over smaller areas and have smaller core distributions than travelling. Foraging/feeding was recorded most frequently and, compared to the other two localised behaviours (socialising and resting), it occurred over a large area, yet had a small core area. The small bandwidth (*h*) suggests that the smoothing of the utilisation distribution was conservative and fits tightly around the points for foraging/feeding (Worton 1989). In spite of a difference in the frequency of the recorded socialising and resting behaviours (Table 3), they occurred over similar-sized areas with similar core areas. We recognize that autocorrelation (high autocorrelation: Moran's *I* value; Table 3b) within our full

**Table 7** Mixed effect model AIC outputs for five sub-sampled non-autocorrelated datasets for the best fit model for analysis on the probability of foraging/feeding versus other behaviours

| Model | Subsample 1 $0.04^{1.55\text{ns}}$ | Subsample2 $0.01^{1.02\text{ns}}$ | Subsample3 $0.04^{1.41\text{ns}}$ | Subsample 4 $0.07^{2.78\text{ns}}$ | Subsample 5 $-0.02^{-0.5\text{ns}}$ |
|---|---|---|---|---|---|
| *X* + *Y* + Distance +Year + Group | **262.2** | **254.7** | 223.3 | 232.5 | 232.8 |
| *Y* + Distance + Year + Group | 263.8 | 253.2 | **221.1** | 231 | 232.7 |
| *Y* + Distance + Depth + Year + Group | 264.9 | 256.2 | 223.5 | 232 | **231.6** |
| *X* × *Y* + Distance + Year + Group | 265.4 | 255.1 | 224.6 | 234.7 | 236.2 |
| *Y* + *X* + Distance + Depth + Year + Group | 264.1 | 254.9 | 224.8 | **229.3** | 233 |

AIC scores in bold denote lowest AIC score output. Model variables were *X*, *Y*, distance to shore, depth, year, and mean group size as factor variables. The hour of day nested within sighting number (HRD|SIGHTING) were included as a random factor in the model. Number of observations for all subsample datasets were ±220 and number of sightings ±165 datasets could possibly have contributed to the concentrated utilisation distributions derived; however, the KDE UD for behaviours (other than resting), especially the core foraging/feeding derived from the full datasets, were not much different in size, and foraging centroids were close to one another (Tables 1, 2). Even though the $h$ values were low ($h < 0.40$ of href; Seaman et al. 1998), indicating that the kernels fit well around the points, we likely did not have over-fit of our UD. The area over which travelling occurred was the largest, which is intuitive since part of the definition of travel is the distance the dolphins cover.

Humpback dolphins at Richards Bay display a clear pattern of area preferences, with core foraging/feeding grounds centred at the harbour mouth area, though resting, socialising and travelling were more widespread across the study area. These findings conform to Atkins et al. (2004) and similar studies of other populations (Saayman and Tayler 1979; Durham 1994; Karczmarski et al. 2000; Parra et al. 2006b; Guissamulo 2008), where humpback dolphins were seen foraging/feeding in well-defined areas, whereas resting and socialising occurred in less specific areas.

Conditions for prey capture determine preferred foraging areas (Wilson et al. 1997); the two deciding factors are the quantity of available prey and how conducive an area is to the capture of prey. Humpback dolphins feed predominantly on reef-associated, estuarine and demersal fish (Barros and Cockcroft 1991; Ross et al. 1994), and in KZN, humpback dolphins display a high affinity to estuaries (Durham 1994). As a functioning estuary, the Richards Bay harbour is a source of estuarine fish, and the mangroves within the harbour fulfil a nursery role to diverse fish communities (Weerts and Cyrus 2002; Sheaves and Johnston 2009). Karczmarski et al. (2000) described humpback dolphins in the Algoa Bay region favouring inshore rocky reefs as their key foraging areas. In Richards Bay, the two breakwaters at the harbour mouth act as artificial reefs, attracting reef-associated fish. Furthermore, the breakwaters create an impediment to water flow (longshore currents and water entering and leaving the harbour). Like harbour porpoises (Johnston et al. 2005), humpback dolphins may target specific regions of enhanced relative vorticity as foraging sites. This high concentration of dolphin activities in one area is not unique to the Richards Bay population. Bottlenose dolphins in the Gulf of California (Ballance 1992), as well as bottlenose dolphins at Moray Firth, Scotland, UK (Wilson et al. 1997), are found in higher numbers in the estuary mouth and deeper narrows, respectively. It is suggested that these dolphins are sighted in these areas more often because this is where they will find higher numbers of prey facilitating effective foraging.

There is a clear distinction in where the animals perform their different daily activities, with resting predominantly recorded away from the foraging/feeding area and socialising throughout the study area. This is strikingly similar to findings of Karczmarski et al. (2000) in Algoa Bay, South Africa, where humpback dolphins were seen feeding near rocky reef areas, resting off sheltered sandy bottom areas, and socialising more widely and throughout the different areas. Resting behaviour was seen less frequently than the other behaviours during the study and the 50 % UD was located primarily to the south of the Richards Bay harbour area in a scattered pattern (Fig. 2b). Earlier work by Atkins et al. (2004) in the same study area found that foraging/feeding decrease with distance offshore while resting increases further offshore, which is supported by the GLMM. Guissamulo's (2008) research in Maputo Bay, Mozambique, reports that humpback dolphins rest in deeper water and at low tide, following active feeding sessions that occur in shallow water during the rising and high tide when the dolphins can come closer to the shore. Although there are records of resting in the northern area around the Richards Bay harbour mouth and more offshore (further offshore than the foraging/feeding behaviour), this tends to occur in the southern reaches of our study site (Fig. 2b).

Ecologically, feeding is a particularly important behaviour, and therefore areas where foraging/feeding occur are of primary importance as they facilitate energy intake. For group-living animals such as dolphins, social interactions form the basis of group dynamics and are important in maintaining social cohesion between individuals. Consequently, locations where both feeding and socialising occur are especially important as they facilitate both nutritional and behavioural needs of the animals. In Richards Bay, social behaviour appears to be the next predominant behaviour after feeding (Atkins et al. 2004), and it is not uncommon to see it in the same location as foraging/feeding, near the harbour mouth area. This area is considered to be of high risk due to the shark net installation, which represents a severe threat (Atkins et al. 2013). The detrimental impacts of shark nets has already been well documented since late 1980s (Cockcroft 1989, 1990) and the threat is on-going (Atkins et al. 2013). However, structures such as harbour walls and shark nets attract aggregations of fish and other organisms, and consequently they attract dolphins. This highlights the challenges to management and conservation in disturbed environments where human-generated structures may act as both attractants and life-threatening danger.

In the Eastern Cape, the segregation of behaviours with habitat type was clear with feeding occurring along exposed, rocky coastline and resting and socialising occurring in sheltered, sandy-bottomed areas (Karczmarski et al. 2000; Saayman and Tayler 1979). Presumably, animals choose relatively safe habitats to rest in. The most sheltered area in our study site was inside the harbour where wave energy is low compared to the high energy of the surf along the coastline, yet the dolphins never rested and only rarely socialised there. Like bottlenose dolphins in Shark Bay, they chose unsheltered, deeper water to rest (Heithaus and Dill 2002) where predation risk may be lower (Heithaus and Dill 2006), particularly with respect to the estuarine-tolerant Zambezi shark, *Carcharhinus leucas* (Cliff and Dudley 1991).

Results of the mixed effect model reinforced the importance of location (harbour mouth area) with respect to foraging/feeding behaviour. There was also an annual change in the probability in foraging/feeding which declined slightly over time. This, however, may be due to a decline in research effort over the years. Furthermore, the effect of group size on the probability of foraging/feeding indicate that foraging/feeding occurred in smaller groups. Similarly, in Australia, humpback dolphins groups are smaller when foraging compared to socialising (Parra et al. 2011), and bottlenose dolphin groups in Shark Bay, Western Australia, are smaller when feeding as opposed to resting, which is consistent with the food–safety trade-off (Heithaus and Dill 2002). The trends from the mixed effect model based on the full dataset was supported by subsampled data with reduced autocorrelation. The estimates of the fixed effect variables support the proposed effect of location, year and group size on the probability of foraging/feeding.

As pointed out by Karczmarski et al. (2000), humpback dolphins are highly dependent on limited inshore resources within their restricted shallow-water distribution. This overall pattern is frequently re-occurring, even though the choice of specific habitats might differ between locations and regions in response to varying coastal environments and frequency of habitat patches. Consequently, these animals are particularly susceptible to habitat loss and destruction of near-shore environments (Karczmarski 2000; Karczmarski et al. 2000).

The harbour mouth in particular is an area of importance to humpback dolphins as a feeding area, and it overlaps with some of the major anthropogenic threats. The shark nets are set in the humpback dolphins feeding core. The nets catch a mean (+SE) of 4.36 (+0.52) humpback dolphins per year (Atkins et al. 2013), which may constitute between 5 and 10 % of the population (Durham 1994; Keith et al. 2002), and bycatch mitigation is imperative. All boats entering or leaving the harbour travel through the humpback dolphins' feeding core. The majority of these are cargo and small recreational vessels. Boat traffic disturbs humpback dolphin behaviour and masks their vocalisations (Ng and Leung 2003; Sims et al. 2011; Van Parijs and Corkeron 2001a). Feeding and social vocalisations (specifically burst pulses) are masked by small vessel noise, and disturbance can occur over 1.5 km (Van Parijs and Corkeron 2001a, b), which means that dolphins anywhere in the feeding core are potentially frequently disturbed. Fast-moving vessels elicit strong disturbance reactions (Ng and Leung 2003) and underwater noise levels are largely dependent on boat speed (Spence et al. 2007). Early study of humpback dolphin behaviour in Algoa Bay on the southeast coast of South Africa (Karczmarski et al. 1997) indicated that these animals were particularly disturbed by boating activities and actively avoided the proximity of boats, especially fast-moving recreational boats. Management plans for the Richards Bay coastal region should consider the density and especially the speed of boat traffic in this area. Furthermore, pollution outflow from the harbour constricts at the breakwaters, in the humpback dolphin feeding core, and the animals might be exposed to high levels of contamination. As shown by several studies (e.g. Aguilar et al. 2002; Cockcroft 1989, 1990), such pollutants, including chemical compounds, oil pollution-derived substances, debris, sewerage-related pathogens, excessive amounts of nutrients, and radio-nucleotides, represent a considerable threat to dolphin health and reproduction.

The development of the Richards Bay harbour and destruction of coastal resources, combined with a continued capture of humpback dolphins in shark nets, may prove detrimental to the survival of this population.

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