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RESEARCH ARTICLE

Indian Ocean humpback dolphin (*Sousa plumbea*) movement patterns along the South African coast

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Abstract

1. The Indian Ocean humpback dolphin was recently uplisted to 'Endangered' in the recent South African National Red List assessment. Abundance estimates are available from a number of localized study sites, but knowledge of movement patterns and population linkage between these sites is poor. A national research collaboration, the SouSA project, was established in 2016 to address this key knowledge gap. Twenty identification catalogues collected between 2000 and 2016 in 13 different locations were collated and compared.
2. Photographs of 526 humpback dolphins (all catalogues and photos) were reduced to 337 individuals from 12 locations after data selection. Of these, 90 matches were found for 61 individuals over multiple sites, resulting in 247 uniquely, well-marked humpback dolphins identified in South Africa.
3. Movements were observed along most of the coastline studied. Ranging distances had a median value of 120 km and varied from 30 km up to 500 km. Long-term site fidelity was also evident in the data. Dolphins ranging along the south coast of South Africa seem to form one single population at the western end of the species' global range.
4. Current available photo-identification data suggested national abundance may be well below previous estimates of 1000 individuals, with numbers possibly closer to 500. Bearing in mind the poor conservation status of the species in the country, the development of a national Biodiversity Management Plan aimed at ensuring the long-term survival of the species in South Africa is strongly recommended. At the same time, increased research efforts are essential, particularly to allow for an in-depth assessment of population numbers and drivers of changes therein.
5. The present study clearly indicates the importance of scientific collaboration when investigating highly mobile and endangered species.

KEYWORDS

coastal, dispersal, endangered species, humpback dolphin, mammals, photo-identification

1 | INTRODUCTION

The Indian Ocean humpback dolphin (*Sousa plumbea*) has recently been described as a separate species from the Indo-Pacific humpback dolphin (*Sousa chinensis*), based on molecular analysis, skeletal morphology, and external morphology and coloration (Jefferson & Rosenbaum, 2014; Mendez et al., 2013). However, they are not yet officially documented by the IUCN Red List, which still lists both these species as forms of *S. chinensis* (Reeves et al., 2008). More recently, *Sousa plumbea* has been assessed as an independent species by Braulik, Findlay, Cerchio, and Baldwin (2015) using IUCN Red List Criteria, based on the most recent available data across its range. Both assessments agree that, regardless of taxonomic status, Indian Ocean humpback dolphins should be listed as 'Endangered' when considered as a separate species (Braulik et al., 2015) as well as when considered as *S. chinensis* (*cf. plumbea* form) (Reeves et al., 2008).

Globally, Indian Ocean humpback dolphins (hereafter 'humpback dolphins') are distributed in a narrow coastal strip from the Bay of Bengal to False Bay, South Africa (Braulik et al., 2015; Jefferson & Rosenbaum, 2014; Mendez et al., 2013), with strong genetic population structure driven by environmental heterogeneity between putative populations (Mendez et al., 2011). Within this range, the species is thought to number in the low 10s of thousands (Mendez et al., 2011). However, this estimate is based on limited abundance estimates in discrete locations (summary available in Braulik et al., 2015). Considering the poor knowledge on the species movement patterns and fine scale population structures, any in-depth assessment of the species' total abundance, conservation status and management needs remains challenging.

Within its global range, the humpback dolphin has probably been most studied in South Africa (Braulik et al., 2015; Elwen, Findlay, Kiszka, & Weir, 2011; Plön et al., 2016; Plön, Cockcroft, & Froneman, 2015). Studies have been conducted on diet (Barros & Cockcroft, 1991; Cockcroft & Ross, 1990a), growth rates (Cockcroft & Ross, 1990b), distribution (Conry, 2017; Durham, 1994; Karczmarski, Cockcroft, & McLachlan, 1999; Ross, Heinsohn, & Cockcroft, 1994), habitat selection (Conry, 2017; Durham, 1994; Karczmarski, Cockcroft, & McLachlan, 2000), abundance (Atkins & Atkins, 2002; Durham, 1994; James, Bester, Penry, Gennari, & Elwen, 2015; Jobson, 2006; Karczmarski, Winter, Cockcroft, & McLachlan, 1999; Keith, Peddemors, Bester, & Ferguson, 2002), behaviour (Atkins, Pillay, & Peddemors, 2004; Keith, Atkins, Johnson, & Karczmarski, 2013) and long-term temporal variation in group size and sighting rates (Koper, Karczmarski, Du Preez, & Plön, 2015). Based on available abundance estimates for the KwaZulu-Natal coast (Durham, 1994) and Algoa Bay (Karczmarski, Winter et al., 1999), the latter authors estimated in the late-1990s that there were fewer than 1000 individuals in South African waters. In view of the existing knowledge, the species was recently recognized as 'Endangered' in South Africa during a 2014 National Red List Assessment (Plön et al., 2016), and is considered to be the country's most endangered resident marine mammal (Child, Roxburgh, Do Linh San, Raimondo, & Davies-Mostert, 2016).

More recently, abundance estimates have become available from a number of additional sites along the South African coast based on photo-identification analysis (Atkins et al., 2016; Atkins & Atkins, 2002; Conry, 2017; Greenwood, 2013; James et al., 2015; Jobson, 2006; Keith et al., 2002). Although these estimates support the idea of low overall numbers of humpback dolphins in the country (reviewed in James et al., 2015), they have little temporal overlap, and few studies exceeded 24 months in duration, making any national assessment of the abundance and population trends difficult (but see Koper et al., 2015). Additionally, data on spatial movements of individual humpback dolphins suggests regular alongshore movements of up to 150 km (Durham, 1994; James et al., 2015; Jobson, 2006; Karczmarski, Winter et al., 1999; Keith et al., 2002). Therefore, an overlap of identified individuals between assessment areas can be assumed, meaning that summing of local abundance estimates based on photo-identification would provide inflated estimates at the national or regional level. A comprehensive understanding of humpback dolphin movement patterns along the South African coastline is therefore a fundamental requirement to generate an accurate assessment of regional abundance, population dynamics, and the impact of current and future threats to the species' conservation status.

Recognizing this knowledge gap, a consortium of 16 researchers from 12 institutes that were collecting or holding data on humpback dolphins from the South African coast, was established in May 2016 (The SouSA project). The goal of this consortium was to increase collaboration, gather existing and new data on humpback dolphins, and assess the species' national conservation status. This manuscript presents the first results of a collation of photo-identification data gathered between 2000 and 2016, evaluating large- scale movement patterns of humpback dolphins in South African waters. Considering the longevity of the species (estimated to exceed 46 years for both sexes according to Cockcroft, 1989; V. Cockcroft unpublished data), discussion points are raised on national abundance based on the number of individuals in the national photo-identification catalogue.

2 | MATERIALS AND METHODS

2.1 | Data collation

Photo-identification data of humpback dolphins for the period 2000 to 2016 (Table 1) were collated from as many areas as possible along the species distribution range in South Africa. These data were collected from dedicated, small-boat, cetacean-focused surveys ('scientific data') as well as opportunistically obtained photographs from a range of contributors, including platforms of opportunity and citizen scientists ('opportunistic data').

All scientific data were collected in similar ways (for detailed methodologies, see Greenwood, 2013; James et al., 2015; Jobson, 2006). Most of the surveys were multi-species focused, with effort in only three locations being specifically targeted for *S. plumbea* (see Table 2). Scientific data typically included established photo-identification catalogues with full sighting histories (i.e. all of the dates on which each individual was (re)sighted in the same area).

All opportunistic data were verified for date and location. For regions where scientific data already existed, opportunistic data were added to the region's photo-identification catalogue. For any region

TABLE 1 Timeline over which photo-identification data were gathered in each region (listed west to east)

	Study period																
Area	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
False Bay																■	■
Walker Bay												■		■			■
Kleinbaai							■	■	■		■	■		■	■	■	■
Struisbaai																	■
St Sebastian Bay																■	■
Mossel Bay												■	■	■			
Knysna															■	■	■
Plettenberg Bay		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Tsitsikamma														■	■	■	■
Algoa Bay									■	■	■	■	■			■	■
East London													■				
Mdumbi																■	■
Richard's Bay	■	■	■	■	■	■	■										■

where no scientific data were available, opportunistic data were used to create a new identification catalogue for that respective region. In two regions, Kleinbaai and Plettenberg Bay, opportunistic data were already converted to an established catalogue prior to data collation (S. Hörbst pers. comm., James et al., 2015). Table 2 provides a summary.

2.2 | Data selection

Individual humpback dolphins were identified using natural marks present on their dorsal fins and humps (Weir, 2009; Würsig & Jefferson, 1990). The image quality (Q) and distinctiveness (D) of each dorsal fin of all photographs received (regardless of whether they were included in a pre-existing catalogue or not) were assessed independently by two experienced researchers (EV, TB). First, all images were graded for quality (Q), from 1 (excellent quality) to 3 (poor quality) based on clarity, contrast, focus, distance, water spray or other aspects covering/obscuring the dorsal fin, proportion of the frame filled by the fin and angle of the dorsal fin (following Urian, Hohn, & Hansen, 1999; Wilson, Hammond, & Thompson, 1999). Only photographs with a score of Q1 or Q2 were used in further analyses. Q3 photographs were considered unsuitable for detecting marks on less distinctive individuals and were excluded from the dataset. The second phase of grading involved rating the fins for distinctiveness (D). Distinctiveness scores varied between D1 (very distinctive) to D3 (barely distinctive) (following Urian et al., 1999; Wilson et al., 1999). Only very distinctive dorsal fins (D1 and D2) were used in further analysis in order to minimize the risk of false positive and false negative matches (Urian et al., 1999; Urian et al., 2015).

2.3 | Data matching

In regions where more than one photo-identification catalogue was available (Knysna, Plettenberg Bay and Tsitsikamma; Table 2), identification photographs were matched to create one final catalogue for that region (containing the most recent pictures of each individual). Subsequently, re-sightings and matches between regional catalogues were used to assess spatial distribution and movement patterns of humpback dolphins between regions. All possible features were used for matching in order to reduce the possibility of false positives and negatives (Scott, Wells, Irvine, & Mate, 1990; Würsig & Jefferson, 1990). Comparison of all photo-identification catalogues was conducted independently by three researchers experienced with photo-identification (EV, TB, BSJ). All matches found were reviewed by two researchers independently for confirmation (any of EV, TB, BSJ who did not initially find the match). Matches between areas >200 km apart required additional confirmation by at least one other researcher (SE). To assess the extent of movements, distances between different areas were measured along the coast using the measuring tool in QGIS 2.18.4 (Quantum GIS Development Team, 2016).

Movement patterns and re-sighting rates of individual dolphins were further assessed using the available sighting histories of all individuals identified in areas where data were gathered through dedicated surveys. To correct for any bias due to the high variability in dedicated survey effort, an expected sighting rate was calculated for each individual in each area based on the survey effort within each area (Bräger et al., 2002; Silva et al., 2012) using the equation

$$Eij = ni \times \frac{sj}{S}$$

where Eij = the expected sighting rate of humpback dolphin i in study area j, ni = total number of sightings of humpback dolphin i, sj = number of surveys in study area j, and S = total number of surveys. A log-likelihood ratio goodness of fit test was then used to compare the observed sighting rate with the expected sighting rate determined from the effort data.

Sighting histories were further consulted to assess the directional movement of the individuals photographed in multiple regions, as well as the time elapsed between re-sightings.

3 | RESULTS

Fifteen existing catalogues (two from opportunistic data) of eight different locations, created between 2000 and 2016, were collated. A

TABLE 2 Number of surveys (dedicated/opportunistic), research focus, number of sightings (during dedicated surveys / opportunistic sightings), number of identification catalogues available, catalogue size before and after data selection, and availability of full sighting histories for each of the 13 different areas where photo-identification pictures were obtained (listed west to east). Catalogues created from opportunistic data before this study indicated by an *. The area from False Bay to Plettenberg Bay is in the Western Cape Province, Tsitsikamma to Mdumbi in the Eastern Cape Province and Richard's Bay in KwaZulu-Natal Province

Area	No. of surveys	Research focus of dedicated surveys	No. of sightings	No. of identification catalogues (S = scientific data; O = opportunistic data)	No. of identified dolphins in catalogue	No. of identified dolphins in catalogue after data selection	Sighting history available (S = scientific data)
False Bay	34/11	All cetaceans	2/7	1 S	17	11	Yes
Walker Bay	0/3	NA	0/3	1 O	5	3	NA
Kleinbaai	0/843	NA	0/161	1*O	25	19	NA
Struisbaai	0/1	NA	0/1	1 O	1	0	NA
St Sebastian Bay	11/1	*Sousa plumbea*	8/1	1 S	24	18	Yes
Mossel Bay	81/0	*Sousa plumbea*	32/0	1 S	73	47	Yes
Knysna	62/0	*Tursiops aduncus* and *Sousa plumbea*	79/0	2 S	49	40	Yes
Plettenberg Bay	179/573	*Tursiops aduncus* and *Sousa plumbea*	150/358	6 (4 S + 1 O + 1*O)	174	82	Yes (for 2 S)
Tsitsikamma	51/0	*Tursiops aduncus* and *Sousa plumbea*	31/0	2 S	28	24	Yes
Algoa Bay	133/0	All cetaceans	57/0	1 S	58	43	Yes
East London	0/8	NA	0/3	1 O	7	4	NA
Mdumbi	0/2	NA	0/2	1 O	2	2	NA
Richard's Bay	268/8	*Sousa plumbea*	245/8	1 S	63	44	Yes
Total					**526**	**337**	
Number of matches						90	
Number of unique individuals observed in ≥2 regions						61	
Number of unique individuals						247	

further five new catalogues were created from opportunistically obtained photographs that represented five previously unsampled areas. This resulted in a total of 20 identification catalogues from 13 different locations (Table 2), covering approximately 1695 km of coastline (Figure 1).

After matching catalogues within sites, a total of 526 humpback dolphins were identified nationally (sum of all regional catalogues) over the study period. After excluding poor quality images (i.e. insufficient quality for reliable identification; Q3) and animals with indistinct natural markings (D3) that were considered inadequate for matching purposes, 337 humpback dolphins were confidently identified from 12 locations and were used in further analysis (see Table 2). Comparison between these 12 regional catalogues resulted in 90 matches representing 61 individuals (including at least 12 identified females with calves), resulting in 247 unique individual humpback dolphins identified between 2000 and 2016 in South African waters. Between False Bay and Algoa Bay (south coast of South Africa), 198 unique individuals were identified of which the movement of 59 individuals linked all the regional study sites. Individual humpback dolphin movements were observed along the entire coastline studied except between Algoa Bay and East London, and between Mdumbi and Richards Bay (Figure 2). Distances between study sites had a median value of 120 km, ranging from 30 km (Walker Bay to Kleinbaai) up to 500 km (Kleinbaai to Tsitsikamma). The maximum distance covered by known females with calves was 275 km.

Most matches were found between the catalogues of Mossel Bay, Knysna, Plettenberg Bay and Tsitsikamma. Table 3 provides a summary of the number of individuals shared between any two regions.

When accounting for catalogue size, the highest exchange rate (i.e. number of animals moving between two areas vs total of the number of animals identified in both areas) was found between False Bay and Kleinbaai (30%). The exchange rate reduced considerably at distances >200 km (Figure 3a). In order to assess the potential bias in the data due to the limited temporal overlap in which data were collected, the analysis was conducted using only data collected in 2015–2016. Results show a similar trend (Figure 3b), with the exchange rate between sites decreasing at distances >150 km.

Considering only scientific data, the highest encounter rate of dedicated surveys (number of surveys with humpback dolphin sightings / total number of surveys) was observed in Richards Bay (65%) and Saint Sebastian Bay (64%), followed by Knysna (61%), Plettenberg Bay (55%), Tsitsikamma (42%) and Mossel Bay (40%). Lowest values were found in Algoa Bay (31%) and False Bay (12%). The average number of re-sightings of individuals for which a full sighting history was available (165 individuals) was six, ranging between 1 and 52 (sightings in all dedicated study areas combined). The number of re-sightings was highest within the Richards Bay study site (mean: 12, range: 1–52, n = 44 individuals). The number of re-sightings for individuals identified between False Bay and Algoa Bay (n = 121 individuals) was much lower averaging 3.3 and ranging between 1 and 12. Excluding Richards Bay from the analysis, re-sighting rates in a particular study area did not differ between individuals that were only seen in that specific area (average = 1.9, range: 1–12, n = 78) and those individuals that were recorded to move to other study areas (average = 2.0, ranging between 1 and 9, n = 43).

To adjust for any bias due to the uneven distribution of survey effort, expected and observed sighting rates (number of re-sightings/survey) were calculated for all 165 individuals. A log-likelihood ratio test showed that only 10 individuals (6%) had a geographical distribution of sightings that was not explained by the geographical distribution of survey effort. As such, the high re-sighting rate of 10 individuals (average = 0.08 re-sightings/survey) in Richards Bay was unexpected considering the survey efforts. This suggests these 10 individuals show a relatively high residency to the area of Richards

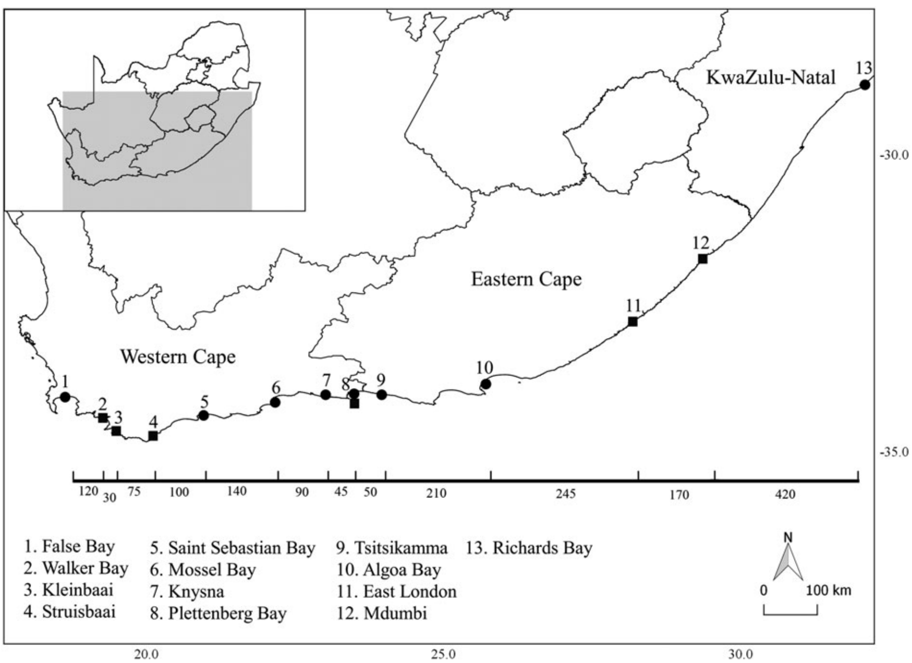

FIGURE 1 Map of South Africa indicating the south-eastern coastline and all localities where Indian Ocean humpback dolphin identification photographs were obtained. Names of the provinces are given in the map. Circles indicate the areas where scientific data were available, squares indicate areas where data were gathered opportunistically. Distances along the coastline between each locality are also indicated (in km)

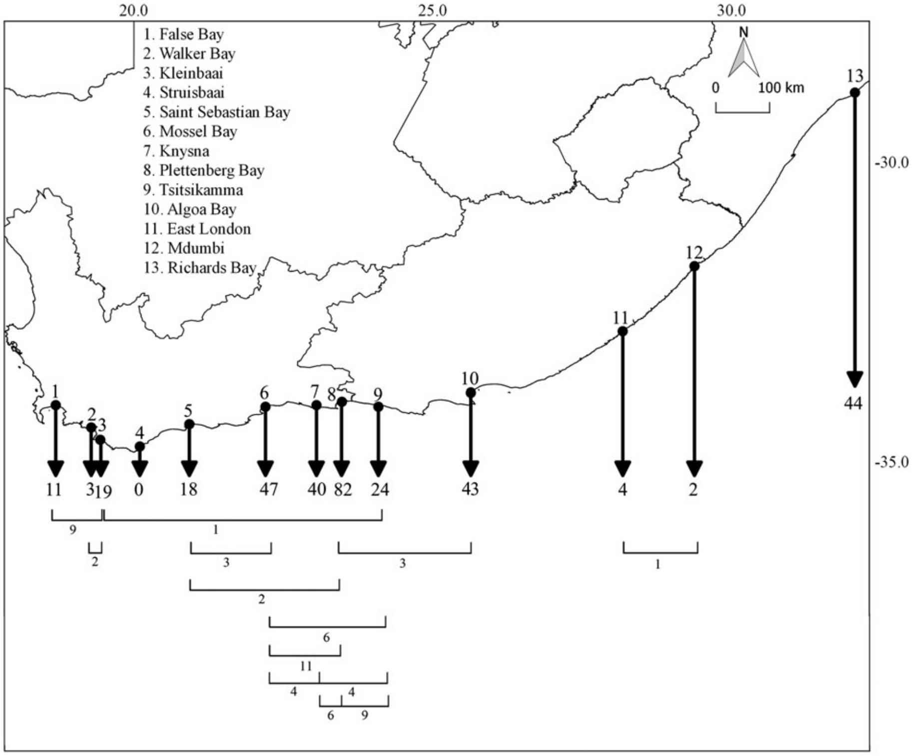

FIGURE 2 Map of the south-eastern coastline of South Africa indicating the number of individuals identified in each region after data selection (number under arrows) as well as the number of individuals moving between the different localities (maximum distances, i.e. irrespective of whether or not they were photographed in the intermediate localities)

TABLE 3 Matrix indicating the number of individuals shared between the catalogues of two specific regions (listed west to east). Note this does not reflect the number of unique individuals, i.e. if one individual was photographed in more than two regions, it will be included multiple times in this matrix. The number in the shaded grey cells represents the total number of individuals identified in each region. FB = False Bay, WB = Walker Bay, KB = Kleinbaai, ST = Struisbaai, SSB = Saint Sebastian bay, MB = Mossel Bay, KN = Knysna, PB = Plettenberg Bay, TK = Tsitsikamma, AB = Algoa Bay, EL = East London, MD = Mdumbi, RB = Richards Bay

	FB	WB	KB	SB	SSB	MB	KN	PB	TK	AB	EL	MD	RB
FB	11												
WB	1	3											
KB	9	3	19										
SB	0	0	0	0									
SSB	0	0	0	0	18								
MB	0	0	1	0	5	47							
KN	0	0	1	0	1	20	40						
PB	0	0	1	0	2	19	24	82					
TK	0	0	1	0	0	7	9	19	24				
AB	0	0	0	0	0	0	0	3	1	43			
EL	0	0	0	0	0	0	0	0	0	0	4		
MD	0	0	0	0	0	0	0	0	0	0	1	2	
RB	0	0	0	0	0	0	0	0	0	0	0	0	44

Bay. These results further suggest a low residency and substantial movement of all the other individuals in the other study areas.

Based on individual sighting histories, no clear overall directional movement (range shift) nor a seasonal or annual trend in directional movement was observed. For example, an individual was observed in early 2012 in Mossel Bay, late 2012 in Plettenberg Bay, back in Mossel Bay in 2013, Knysna in 2014 and 2015 and finally in Saint Sebastian Bay in 2016. For the longest distance covered (500 km between Kleinbaai and Tsitsikamma), the animal was first sighted in Kleinbaai in 2011, Mossel Bay in 2013, and Plettenberg Bay, Knysna and Tsitsikamma in 2014 and 2015. This was the only individual for which an apparent eastward directional movement over time was visible.

Re-sightings of an animal in the same area over several years occurred frequently, indicating a general pattern of site fidelity. The longest time span between all re-sightings of an individual in the same area was the full 16 years (2000 to 2016 for three individuals in

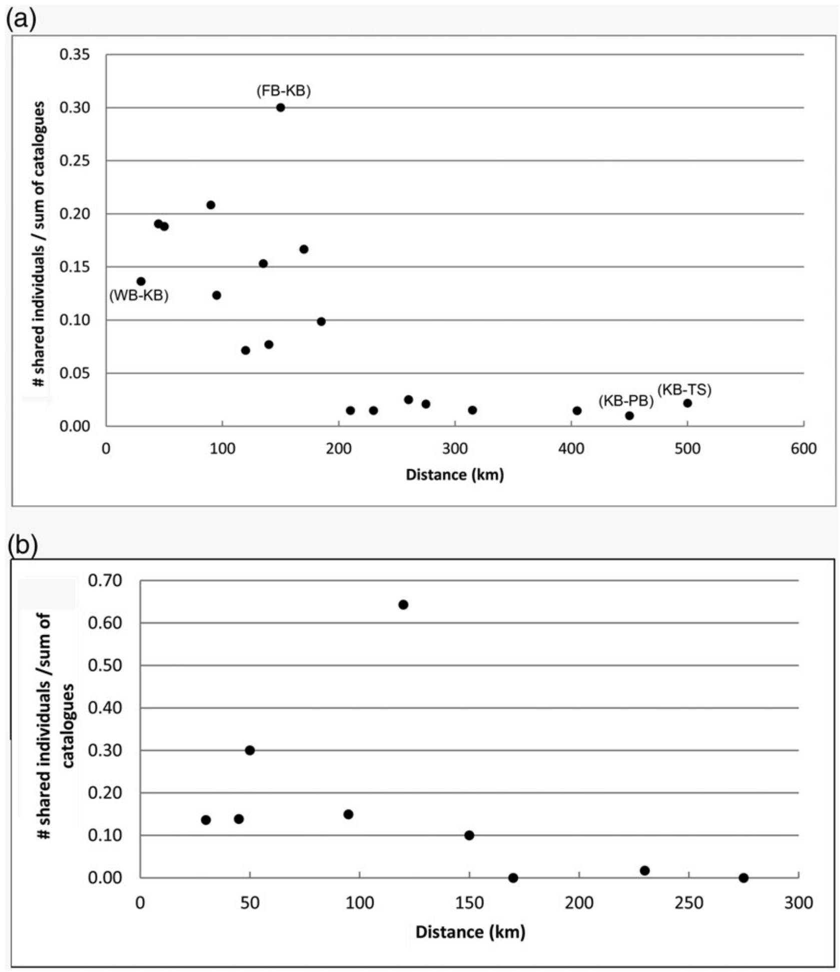

FIGURE 3 Exchange rate among localities expressed as the proportion of individuals shared between catalogues as a function of distance for all data (a) and for data collected in 2015–2016 only (b). Only data points at the extremes of X and Y axis of figure are labelled (WB = Walker Bay, KB = Kleinbaai, FB = False Bay, PB = Plettenberg Bay, TS = Tsitsikamma)

Richards Bay). If data before 2000 had been included, this time span would increase by another 2 years (1998–2016; S. Atkins unpublished data). Four individuals in Plettenberg Bay were resighted over a period of 13 years. The shortest time span between any two re-sightings of an individual in different areas was 1 day during which an animal travelled 45 km between Knysna and Plettenberg Bay, 2 days during which an animal travelled 50 km between Plettenberg Bay and Tsitsikamma and 8 days during which two animals travelled 95 km between Knysna and Tsitsikamma. For distances >100 km, the shortest time span between re-sightings was 24 days and represented a female with calf sighted in Plettenberg Bay on 19 January 2013 and in Mossel Bay on 12 February 2013.

4 | DISCUSSION

Results of the photo-identification matching process of identified humpback dolphins in South Africa clearly show substantial movements of the species along the nation's coastline, as was suggested by Durham (1994), James et al. (2015) and Keith et al. (2002). Maximum distances previously observed (150 km, Keith et al., 2002) were unexceptional in this study, which has shown that several individuals travelled well over 200 km between study sites, up to a maximum of 500 km. Based on available data, no temporal trend could be observed in directional movements. In general, individuals seemed to have low levels of residency (low re-sighting rates, mostly not different from expected), possibly related to the limited geographical range of survey effort in relation to the observed movement patterns of individuals, and the general challenge to collect photo-identification data on the species (usually in small groups which may avoid boats, present in large swells, etc.). Nonetheless, data clearly showed long-term site fidelity within study sites of up to 16 years. However, it is important to take into account the temporal aspect of this study which may have biased some results. Indeed, over the 16 year period, individuals may have died, marks may have changed too much for correct re-identification and young individuals will be recruited into the marked population. In addition, surveys conducted in the different study sites had limited time overlap. Considering these aspects, the observed movement patterns, indications of residency and site fidelity should be considered a minimum rather than a maximum.

Humpback dolphins were observed to move between nearly all regions along the south coast between False Bay and Algoa Bay, suggesting it is a single population. Most matches were found in the central area of the south coast between Mossel Bay and Plettenberg Bay, although this may be an artefact of the higher survey effort in this region. No matches were found with individuals identified in Richards Bay, although this could also be an artefact of data availability considering the large distance (420 km) to the nearest site with (limited) photo-identification data. However, substantial dedicated research effort on coastal dolphins conducted between 2014 and

2016 along the stretch of coastline between East London and Mkambati (approx. 100 km north of Mdumbi) and opportunistic effort of experienced water users (e.g. whale-watching operators) during sardine run tourism activities along the Eastern Cape and KwaZulu-Natal coast, resulted in only rare sightings of the species (O'Donoghue, Drapeau, & Peddemors, 2010) and consequently a lack of photo-identification data in this region (effort data therefore not included in the manuscript; M. Caputo pers. comm.[1]). A hiatus in the distribution of the species along the Eastern Cape coast has been suggested before based on a number of lines of evidence (see James et al., 2015 for further discussion), and a similar gap in distribution of the species of several hundred kilometres is reported in the Sea of Oman and in Tanzania (Baldwin, Collins, Van Waerebeek, & Minton, 2004; Braulik et al., 2015). It is believed that the very narrow shelf and exposed coastlines of these areas may result in unfavourable habitat conditions, driving the formation of population structure (Mendez et al., 2011). It therefore seems that, based on the presented data, we cannot refute the idea that the humpback dolphins along the south coast may be largely separated from those observed off KwaZulu-Natal, as suggested previously by Karczmarski (1996). On the other hand, we cannot substantiate it either, as current available data are too limited. And although there is limited evidence of genetic differentiation between the south and east coast populations (Smith-Goodwin, 1997), the overall genetic population structure of humpback dolphins in South Africa remains poorly understood. It is clear that a more in-depth study on this topic, including increased effort along the larger coast of the Eastern Cape and KwaZulu-Natal and substantial genetic sampling is essential to address these aspects of local and regional population structure, relevant to the species' conservation. Notably, all genetic data of South African humpback dolphins used in global comparisons originated from the coast of KwaZulu-Natal. Therefore, until further data become available, the suggested genetic (maternal) linkage between humpback dolphins of South Africa and Mozambique (Mendez et al., 2013) should be interpreted with caution.

Although there are currently no national abundance estimates for humpback dolphins in South Africa, Karczmarski (1996) estimated in the late-1990s that there were fewer than 1000 individuals in the entire country based on local abundance estimates from photo-identification analysis, ranging between 38 (Durham, 1994) and 466 (Karczmarski, Winter et al., 1999) individuals (see James et al., 2015 for a summary). However, data presented on the dolphins' movement patterns clearly indicate that summing local abundance estimates will provide inflated numbers. In fact, all available photo-identification data from South Africa from 2000 onwards rendered only 247 unique, well-marked individuals, with most discovery curves (of scientific data) tending towards an asymptote (data not shown, but see James et al., 2015 and Atkins et al., 2016 for examples). This suggests that nearly all available individuals in the study areas had been identified. Considering the observed proportion of barely distinctive individuals in the collated photo-identification catalogues not included in the analysis (D3 = 20%), a proportion of unmarked individuals (juveniles and calves) in the population (average of 68% in eight local abundance estimates along the South African coast; James et al., 2015), and a known low density in the least sampled stretch of coastline due to unfavourable habitat (see discussion in the paragraph above), data suggest that the total population size in South Africa may be well below 1000 individuals, with numbers possibly closer to 500. Considering solely the south coast of South Africa, numbers would be even lower.

In their review, Braulik et al. (2015) indicated that most Indian Ocean humpback dolphin populations are small, usually numbering less than 500 individuals. Furthermore, the authors stated that, due to the species' specific habitat preferences and restricted nearshore distribution, they may be one of the least resilient marine megafauna species with a high risk of extinction (Braulik et al., 2015; Davidson et al., 2011; Purvis, Gittleman, Cowlishaw, & Mace, 2000). Karczmarski (2000) suggested the population of humpback dolphins in Algoa Bay seemed to be relatively stable in the early 1990s (estimated annual growth rate of −3% to +2% between 1991 and 1994), and unlikely to be growing. However, nearly two decades later, a land-based monitoring survey conducted in Algoa Bay between 2010 and 2011 showed a significant decline in the frequency of occurrence, group size average (from seven to three animals) when compared with the study in the early 1990s, and a possible decline in the number of calves (Koper et al., 2015). For Plettenberg Bay, Greenwood (2013) suggested a possible decrease in population size of 50% between 2002 and 2012, although based on limited sampling effort. In Richard's Bay, the mortality in bather protection nets continues to contribute to unsustainable loss of humpback dolphins (4.3 individuals or 5–10% of the population per year; Atkins, Cliff, & Pillay, 2013; Atkins et al., 2016). It is clear that, owing to its nearshore distribution, the species is highly vulnerable to anthropogenic activities, such as coastal constructions, bather protection nets, acoustic and chemical pollution and fisheries, leading to risks of direct mortality and/or population fragmentation (Plön et al., 2015). All of these data support the recent up-listing of the species to ‘Endangered’ in terms of South Africa's Red List for Mammals (Plön et al., 2016). Additionally considering that the actual population size is likely to be half of what was previously believed, the conservation status of the species may in reality be in a critical state. We therefore strongly recommend the development of a Biodiversity Management Plan (BMP) focused on the species. Such BMPs are being implemented for the country's most endangered species, e.g. the African penguin *Spheniscus demersus* (DEA, 2013), in terms of the National Environmental Management: Biodiversity Act (2004), and are aimed at ensuring the long-term survival in nature of the species (or ecosystem) to which the plan relates. The BMP must ensure that threats affecting the species are identified and prioritized, and formally coordinate directed and implementable actions and interventions to address the threats, as well as research and monitoring. Various immediate conservation actions can be advised such as, for example an alternative to the shark nets in Richards Bay, which are responsible for the incidental catch of several individuals per year, the prohibition of approaching the species with any type of watercraft at distances <500 m, as well as increased public outreach and education. In addition, increased research efforts (especially in poorly studied areas) are highly recommended to obtain robust estimates of national abundance, in order to better understand and monitor the species' conservation status.

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Overall, humpback dolphins were observed relatively frequently in all study areas. The highest success rate of surveys appeared to be in Richards Bay, and the area between Saint Sebastian Bay and Plettenberg Bay. Although a more in-depth assessment would be needed to accurately indicate priority areas for humpback dolphin conservation in marine spatial planning, these results give some indication of general 'hotspots' for humpback dolphin sightings. However, considering the reported ranging distances, the protection of discrete locations in the form of marine protected areas (MPA) may not be sufficient to protect the species. Indeed, various authors have stated that there is little evidence that MPAs are effective in preserving marine mammal populations which often have high dispersal capabilities (Gormley et al., 2012; Hoelzel, 1994). In fact, it seems important to consider corridors for population connectivity as well, vital to retain the evolutionary potential of small populations. Therefore, the possibility of expanding current existing MPAs along the coastline, and identifying additional conservation actions, should be considered within future marine spatial planning, if we aim to protect and preserve the endangered humpback dolphin.

The present study provides information only attainable through collation of multiple datasets, indicating the significance of scientific collaboration when studying highly mobile marine species. Continued collaboration, both at a national and international level, will be important for a thorough assessment of the species' conservation status within and beyond national borders.

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