Migratory movement of photo-identified humpback whales *Megaptera novaeangliae* along the southeastern coast of Africa

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Abstract

The global conservation of humpback whales *Megaptera novaeangliae* relies on continuous assessments of the populations' post-whaling status, which in turn require information on population mixing and movements. One of the seven breeding stocks in the Southern Hemisphere, breeding stock C and its associated four substocks (C1–C4), utilises the western Indian Ocean in several discrete breeding grounds. However, information on the mixing of stocks across breeding grounds is limited. This study utilises photo-identification methods applied to the first multi-regional catalogue of fluke images available for substock C1S (the southern component of substock C1) which uses the southern portion of the breeding ground, developed as part of this study, to investigate the whales' movements along the southeastern coast of southern Africa. The identification of 1 746 unique individuals, including 11 withinyear matches and 48 between-year matches of 45 individuals, provides new insight into the intra-regional migration patterns, fidelity and structure of substock C1S. The within-year match results confirmed that individual humpback whales are broadly seasonally present for extended periods and visit multiple subregions along this coast, while the between-year matches revealed long-term fidelity to this coastline. Moreover, five of the between-year matches between subregions in South Africa and Mozambique linked the South African migration corridor to the breeding ground in southern and central Mozambique. These findings provide valuable insights into the movement patterns of substock C1S and significantly address the challenges of effective population management, which includes difficulties associated with the whale-watching industry on the east coast of South Africa.

Keywords: breeding ground; fluke images; migration corridor; migration patterns; Mozambique; photo-identification catalogue; substocks

Introduction

The movement behaviour of animals has been of long-standing research interest, particularly among conservationists concerned with the management and protection of a species. Such information provides insight into a species' behaviour in terms of migration patterns, habitat selection, territoriality, foraging and mating, and assists in evaluating how animals respond to environmental changes (Gurarie et al. 2016; Miller et al. 2019). This information is also essential for accurately assessing the current and probable future status of populations, especially in terms of structure and abundance, which is crucial for adequate management and protection of a species (Minton et al. 2011; Bortolotto et al. 2017). Specifically for baleen whales, such as the humpback whale *Megaptera novaeangliae* which has been heavily impacted by historical whaling (e.g. Clapham and Baker 2018), a thorough understanding of their movement behaviour is vital for management purposes.

The movement behaviour of humpback whales has been examined and documented for many years, whereby the earliest evidence of the species' distribution and general movement patterns was obtained from the seasonal information in historic whaling catch records (Risting 1912; Harmer 1931; Mackintosh 1965; Dawbin 1966) and from the introduction of lethal mark-recapture techniques during the RRS Discovery whale-marking efforts in the 1930s (e.g. Rayner 1940). Data so far acquired indicate that humpback whales undertake one of the most-extensive seasonal migrations of all known mammals as a behavioural trade-off between breeding and feeding requirements (Corkeron and Connor 1999; Rasmussen et al. 2007; Clapham et al. 2009; Kettemer et al. 2022).

During austral summer, humpback whales are primarily dispersed throughout high-latitude polar regions in the Southern Hemisphere where feeding occurs; with the onset of winter, they initiate their migrations to low-latitude tropical waters where breeding and calving take place (Mackintosh 1942; Dawbin 1966; Clapham and Mead 1999; Clapham 2000; Clapham et al. 2009). Assessments carried out by the International Whaling Commission's (IWC) Scientific Committee (IWC 1990, 1997, 1998) defined seven distinct migratory breeding stocks of humpback whales in the Southern Hemisphere, with each linked to distinct feeding grounds in the Antarctic, corresponding to the IWC's historically assigned management areas I–VI. These breeding stocks are labelled A–G, with breeding stock C confined to the southwestern Indian Ocean (IWC 1998).

Breeding stock C is suggested to be composed of four distinct substocks (labelled C1–C4), each defined as having a distinct migratory pathway and breeding ground in the southwestern Indian Ocean (SWIO) (IWC 2006; Barendse et al. 2010). Substock C1 further consists of northern (C1N) and southern (C1S) components; the breeding range of C1N extends from the Island of Mozambique (15°S) to southern Kenya (4°S), and that of C1S from the Island of Mozambique (15°S) to South Africa (24°S) (Berggren et al. 2001; IWC 2006; Jackson et al. 2014). However, for practical management purposes, the IWC Scientific Committee refers to C1S and C1N as one breeding substock (IWC 2011).

The most-prevalent migratory pattern exhibited by substock C1 follows the path of individuals travelling northwards from management area III (0 to 60°E) in the Southern Ocean (IWC 1998) to around Knysna (33°S, 23°E) on the south coast of South Africa. From there, the whales continue their migration journey northeastwards along the southeast African corridor until they reach breeding grounds spanning between Mozambique (24°S) and southern Kenya (Wamukoya et al. 1996; Best et al. 1998; Berggren et al. 2001; O'Connor et al. 2009; Findlay et al. 2011). Although valuable insights on the migration patterns followed by substock C1 have been reported, supporting evidence for this alleged migratory route is limited (e.g. Banks et al. 2010; Ersts et al. 2011). For adequate present and future management strategies of breeding substock C, more-contemporary evidence on the migration route, temporal and spatial distribution patterns, and geographic structure of the stock is needed.

The procedures and methods used to monitor and gather information from migrating marine mammal populations has advanced considerably in recent years. Compared with the historic, lethal mark-recapture method, the development of non-invasive research techniques, such as individual identification through natural markings (including photographic identification), are creditable for obtaining key information on species' migration patterns, as well as providing information on the structure of stocks and the levels of connectivity between stocks and substocks (e.g. Baker et al. 1986; Constantine et al. 2007; Araujo et al. 2017).

Materials and methods

Study area

The study area represents the known migration corridor (34°S to 24°S) and breeding grounds (24°S to 15°S) of Southern Hemisphere humpback whales in substock C1S (as described by Findlay et al. 1994; Best et al. 1998). The area extends from Knysna on the south coast of South Africa (34°S) to the Island of Mozambique (15°S), a small coral island connected to the mainland on the northern coast of Mozambique (Figure 1a). The migration corridor and breeding grounds were divided into five subregions by Cerchio et al. (2008a): south coast of South Africa (SC), southeastern coast of South Africa (ES), northeastern coast of South Africa (EN), southern coast of Mozambique (MS), and central coast of Mozambique (MC) (Figure 1b); these represent subregional migration pathways, breeding ground areas and connectivity between regions.

Photo-identification data

A catalogue of fluke images representing substock C1S was compiled by first collating the available photographs in two independent datasets: one containing 4 457 fluke images from independent South African collections obtained between 1988 and 2019, and the other comprising 74 fluke images collected in 2018 and 2019 as part of this study (Supplementary Table S1). The photographed sightings were collected through systematic research surveys (RS), boat-based whale-watching (BBWW) operations, and other platforms of opportunity along the coast of southeastern Africa (see Table 1).

Next, several features of these fluke images were evaluated to select optimal images for inclusion in the catalogue and their usability for analysis. In photo-identification analysis, image quality is a key feature influencing the accurate identification of individuals (e.g. Friday et al. 2000). Quality was assessed based on four image features, following Friday et al. (2000): (i) clarity, in regard to resolution, sharpness and focus of the fluke displayed, and the visibility and clarity of the fluke details; (ii) contrast, relating to the colour ratio and brightness level of the image, as well as distinguishability of the different colours on the fluke; (iii) angle/orientation of the fluke in relation to the field plane; and (iv) completeness, meaning the proportion of the fluke that is clearly visible in the image. The quality of each image feature was scored on a scale of 1–5 (1 = very poor; 2 = poor; 3 = fair; 4 = good; 5 = excellent). Images that scored '1' in any of the image quality features were considered not usable for further analysis and were discarded from the dataset in this study. For each of the usable fluke images, an overall image-quality score was calculated as the mean of the quality criteria. Subsequently, the best-quality image was selected for each individual humpback whale encounter per day to be included in the catalogue.

Furthermore, the fluke colouration was also scored on a scale of 1–5 (following the methods of Katona et al. 1979 and Carlson et al. 1990), where: 1 = 0–20% black; 2 = >20–40% black; 3 = 40–60% black; 4 = >60–80% black; 5 = >80–100% black.

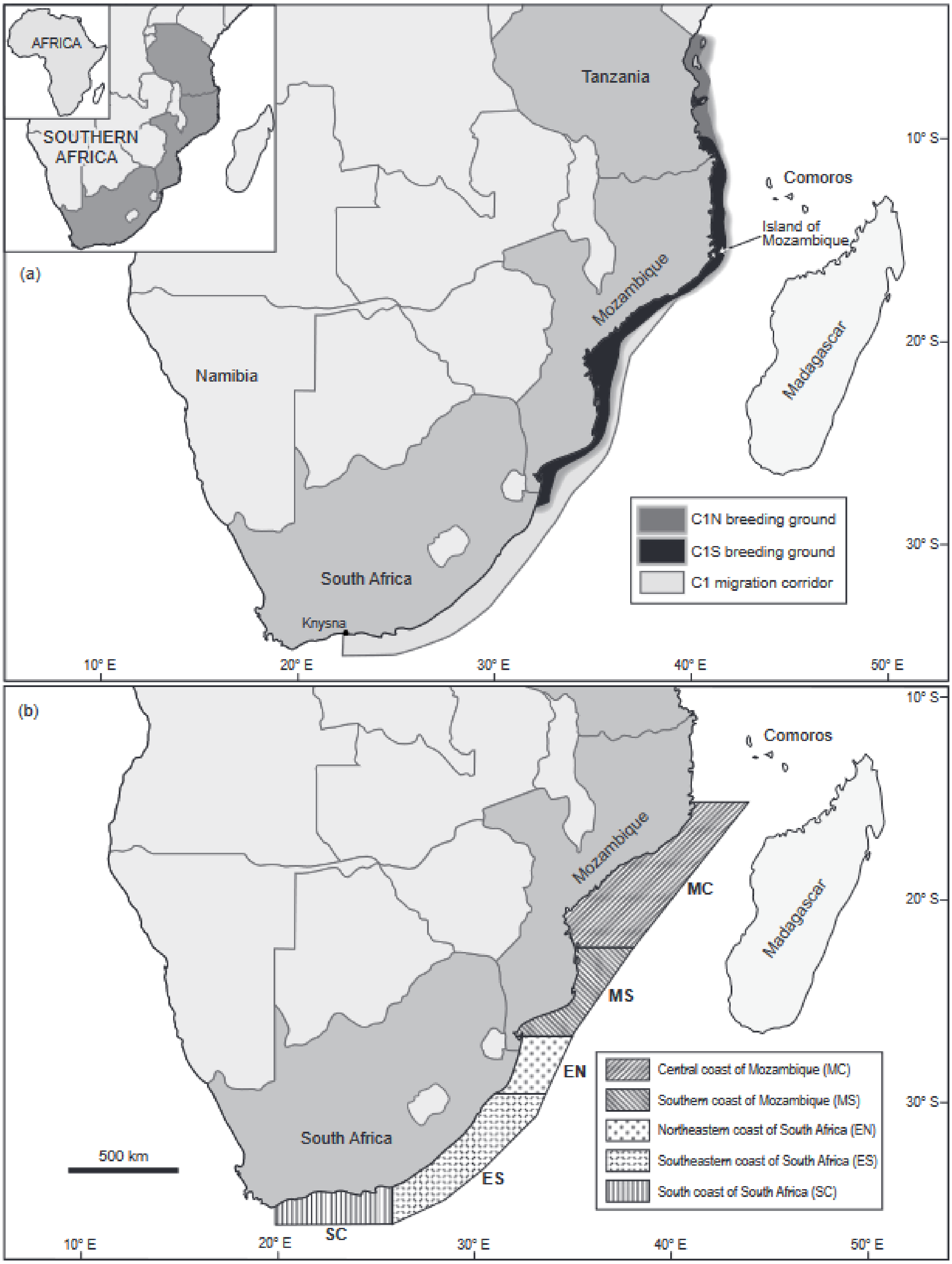
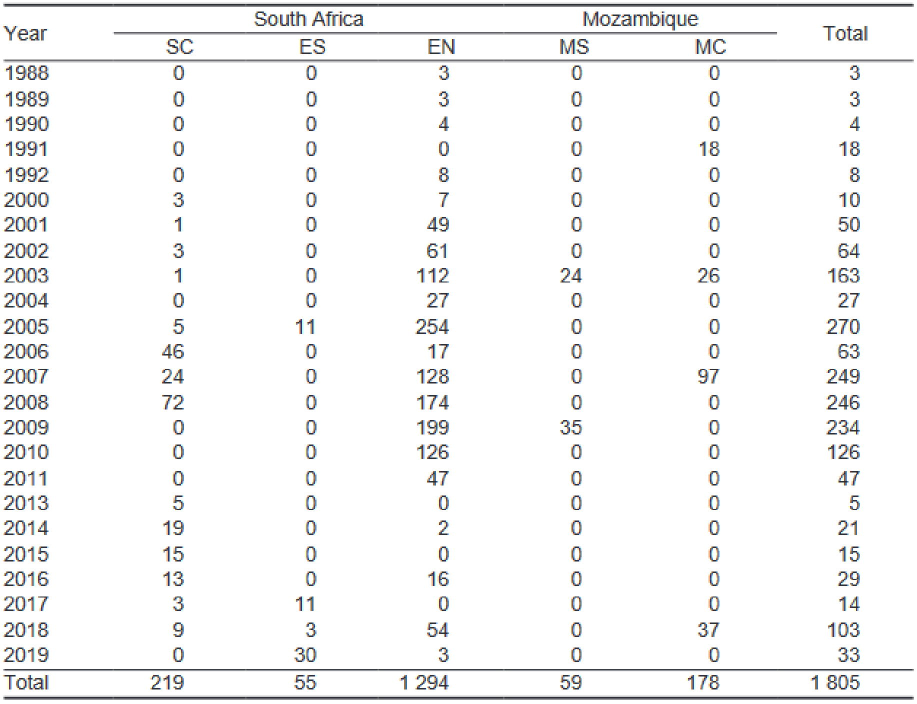


Figure 1: (a) The known extent of the migration corridor and breeding grounds used by humpback whales comprising substock C1 (C1S = south component; C1N = north component). (b) Subregions within the migration corridor and breeding grounds used by substock C1S (modified from Cerchio et al. [2008a])

Table 1: Total number of humpback whale fluke images in the newly developed catalogue for each calendar year containing data, by collection country and coastal subregion. SC = south coast of South Africa; ES = southeastern coast of South Africa; EN = northeastern coast of South Africa; MS = southern coast of Mozambique; MC = central coast of Mozambique



Year	South Africa			Mozambique		Total
	SC	ES	EN	MS	MC	
1988	0	0	3	0	0	3
1989	0	0	3	0	0	3
1990	0	0	4	0	0	4
1991	0	0	0	0	18	18
1992	0	0	8	0	0	8
2000	3	0	7	0	0	10
2001	1	0	49	0	0	50
2002	3	0	61	0	0	64
2003	1	0	112	24	26	163
2004	0	0	27	0	0	27
2005	5	11	254	0	0	270
2006	46	0	17	0	0	63
2007	24	0	128	0	97	249
2008	72	0	174	0	0	246
2009	0	0	199	35	0	234
2010	0	0	126	0	0	126
2011	0	0	47	0	0	47
2013	5	0	0	0	0	5
2014	19	0	2	0	0	21
2015	15	0	0	0	0	15
2016	13	0	16	0	0	29
2017	3	11	0	0	0	14
2018	9	3	54	0	37	103
2019	0	30	3	0	0	33
Total	219	55	1 294	59	178	1 805

Finally, each fluke image chosen for the catalogue received a unique identification code, which included the photographer's identification (initial and surname), the area of encounter, the survey vessel name, and the sighting date (in the format YYYYMMDD); these were summarised with an individual alphanumeric code, for example: B. TREE_DURBAN_PHAKISA_20190601_A3. Finally, the fluke images in the catalogue were grouped by year.

Photographic matching

Using the newly developed C1S photo-identification catalogue, we attempted within-year and between-year matching of the fluke images to identify intraseasonal and interseasonal site fidelity, temporal and spatial migration patterns, intra-regional migration connectivity, and the overall stock structure of substock C1S within their migration corridor and breeding grounds. Matching of the catalogued fluke images was performed with a modified Microsoft Office Access database matching system

specifically developed for this study. The catalogued fluke images and associated data (whale ID number; survey name and survey vessel; quality/distinctiveness/fluke type and encounter location/date/time) were imported into the Access system through a standardised Excel spreadsheet, and then the matching process was performed in a stepwise manner, described below.

A 'master catalogue' within the system served as the core dataset. Additional datasets comprising images for each year (for within-year matches) and images from the following year, one year at a time (for between-year matches), were imported as a 'new dataset'. These images were individually compared/matched (visually) to images in the master catalogue dataset using the fluke-type value assigned to each image for comparison; for this step, each fluke image was compared to other images with the same fluke-type value and to those with one value lower and one value higher. Matches were identified visually by the data submitter and subsequently recorded as 'matched' within the system. All identified matches were confirmed by at least two of the authors.

All image matches were then evaluated according to the temporal distance (number of days) and spatial distance (number of kilometres) between the matched images of photographed sightings (discussed below in terms of photo-identification 'capture-recapture'). Within-year matches could be used to calculate an individual humpback whale's approximate migration rate (kilometres per day), and also revealed information on an individual's travelled direction (north or south), intra-seasonal site fidelity trend, migration route, and migration connectivity between subregions. For between-year matches, the calculated temporal and spatial distributions could similarly reveal information on the inter-seasonal site fidelity trends, migration routes and migration connectivity of the population.

Results

Photo-identification data

The largest component of the catalogued fluke images was collected along the South African coastal migration corridor (86.9%; *n* = 1 568 images), and predominantly within subregion EN (71.7%). Fluke images from the Mozambique coast (*n* = 237) were mainly collected within subregion MC. The sample size varied substantially among years, with most years (62%) having ≤50 fluke images. The largestbcomponent of the catalogued fluke images (82%; *n* = 1 481)bwas collected between 2003 and 2010, or in 2018; no flukebimages were available for the years 1993–1999 and 2012.

Photographic matches

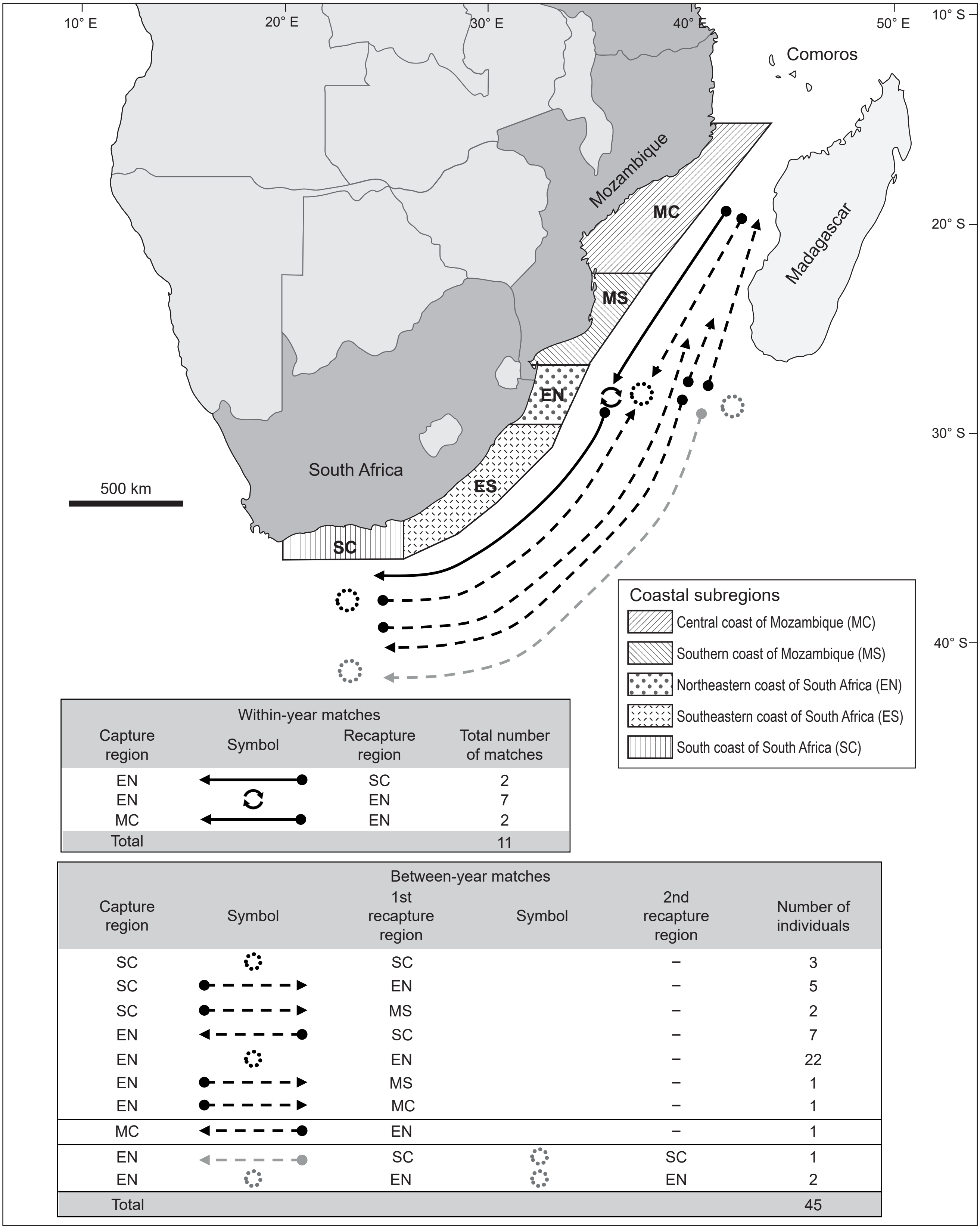
Table 2 provides an overview of the within-year and between-year fluke image matches; Figure 2 illustrates the numbers of within-year and between-year matches between photo-identification 'capture and recapture' locations or dates. Eleven within-year matches were obtained: 5 matches (45%) in 2005, 2 (18%) in 2007, 2 (18%) in 2008, 1 (9%) in 2002, and 1 (9%) in 2003. All within-year matched individuals were those captured and recaptured (i.e. photographed) just twice within a season, with the shortest time interval between a given match being a single day and the longest interval 114 days; the distance between a given match ranged from 0 to 1 200 km (Table 2). The capture and recapture locations of seven individuals (64%) were within the same coastal subregion (i.e. EN); of these, one capture-recapture was between Richards Bay and St Lucia (~65 km apart), whereas six captures-recaptures were in the same location (St Lucia) (Table 2; Figure 2). The one individual that was matched between Richards Bay and St Lucia was marked and recaptured in July, 1 day apart. Of the six individuals captured-recaptured at St Lucia, the capture-recapture of two individuals occurred within the same month (2 days apart in July, and 1 day apart in September), two other individuals were captured- recaptured between July and October (65 and 72 days apart, respectively), one between August and October (75 days apart), and another between September and October (32 days apart). Two of the individuals were captured-recaptured between South African subregions EN and SC (~1 200 km apart): one in October and November 2005 (45 days apart) and the other in August and December 2008 (114 days apart). Two other individuals were captured-recaptured between a subregion in Mozambique (MC) and another in South Africa (EN) (~900 km apart), both between September and October (22 and 39 days apart, in 2003 and 2007, respectively).

There were 48 between-year matches involving 45 individuals (Table 2). Of these, 42 individuals were seen twice (recaptured once), and the remaining 3 individuals were seen three times (recaptured twice). In descending order, the highest number of recaptures was obtained in the years 2011 (8.5%), 2006 (7.9%), 2004 (7.4%) and 2001 (6%). An average between-year recapture rate of 3.9% was

Table 2: Summary of information pertaining to the within-year and between-year matches of fluke images of humpback whales in breeding substock C1 south component (C1S), obtained from the photo-identification catalogue. Subregions: SC = south coast of South Africa; ES = southeastern coast of South Africa; EN = northeastern coast of South Africa; MS = southern coast of Mozambique; MC = central coast of Mozambique

Match number	Capture date (year and month)	Capture location (area and coastal subregion)	1st recapture date (year and month)	1st recapture location (area and coastal subregion)	Interval between captures (d = days; y = years)	Approximate distance between capture locations (km)	2nd recapture date (year)	2nd recapture location (area and coastal subregion)	Interval between 1st and 2nd capture (years)	Distance between 1st and 2nd recapture locations (km)
Within-year matches										
1	2002 (Jul)	Richards Bay (EN)	2002 (Jul)	St Lucia (EN)	1 d	65	-	-	-	-
2	2003 (Sept)	Bazaruto (MC)	2003 (Oct)	St Lucia (EN)	22 d	900	-	-	-	-
3	2005 (Jul)	St Lucia (EN)	2005 (Oct)	St Lucia (EN)	72 d	0	-	-	-	-
4	2005 (Jul)	St Lucia (EN)	2005 (Oct)	St Lucia (EN)	65 d	0	-	-	-	-
5	2005 (Aug)	St Lucia (EN)	2005 (Oct)	St Lucia (EN)	75 d	0	-	-	-	-
6	2005 (Oct)	St Lucia (EN)	2005 (Nov)	St Lucia (EN)	32 d	0	-	-	-	-
7	2005 (Oct)	St Lucia (EN)	2005 (Nov)	Knysna (SC)	45 d	1 200	-	-	-	-
8	2007 (Jul)	St Lucia (EN)	2007 (Jul)	St Lucia (EN)	2 d	0	-	-	-	-
9	2007 (Sep)	Bazaruto (MC)	2007 (Oct)	St Lucia (EN)	39 d	900	-	-	-	-
10	2008 (Aug)	St Lucia (EN)	2008 (Dec)	Knysna (SC)	114 d	1 200	-	-	-	-
11	2008 (Sep)	St Lucia (EN)	2008 (Sep)	St Lucia (EN)	1 d	0	-	-	-	-
Between-year matches										
1	1988	Cape Vidal (EN)	2006	Knysna (SC)	18 y	1 224	-	-	-	-
2	2000	St Lucia (EN)	2001	St Lucia (EN)	1 y	0	-	-	-	-
3	2000	St Lucia (EN)	2001	St Lucia (EN)	1 y	0	-	-	-	-
4	2000	Knysna (SC)	2001	St Lucia (EN)	1 y	1 192	-	-	-	-
5	2001	St Lucia (EN)	2002	Richards Bay (EN)	1 y	66	2009	St Lucia (EN)	7	66
6	2001	St Lucia (EN)	2003	Knysna (SC)	2 y	1 192	2006	Knysna (SC)	3	0
7	2001	St Lucia (EN)	2006	St Lucia (EN)	5 y	0	-	-	-	-
8	2001	Knysna (SC)	2007	St Lucia (EN)	6 y	1 192	-	-	-	-
9	2001	St Lucia (EN)	2008	St Lucia (EN)	7 y	0	-	-	-	-
10	2001	St Lucia (EN)	2008	St Lucia (EN)	7 y	0	-	-	-	-
11	2002	St Lucia (EN)	2003	St Lucia (EN)	1 y	0	-	-	-	-
12	2002	Richards Bay (EN)	2003	St Lucia (EN)	1 y	66	2007	St Lucia (EN)	4	0
13	2002	St Lucia (EN)	2004	St Lucia (EN)	2 y	0	-	-	-	-
14	2002	St Lucia (EN)	2005	St Lucia (EN)	3 y	0	-	-	-	-
15	2002	St Lucia (EN)	2007	Knysna (SC)	5 y	1 192	-	-	-	-
16	2002	Richards Bay (EN)	2007	St Lucia (EN)	5 y	66	-	-	-	-
17	2002	Richards Bay (EN)	2009	Ponta Mamoli (MS)	7 y	258	-	-	-	-
18	2003	St Lucia (EN)	2004	St Lucia (EN)	1 y	0	-	-	-	-
19	2003	St Lucia (EN)	2007	Knysna (SC)	4 y	1 192	-	-	-	-
20	2003	St Lucia (EN)	2008	Knysna (SC)	5 y	1 192	-	-	-	-
21	2003	St Lucia (EN)	2008	Knysna (SC)	5 y	1 192	-	-	-	-
22	2004	St Lucia (EN)	2005	St Lucia (EN)	1 y	0	-	-	-	-
23	2004	St Lucia (EN)	2006	Knysna (SC)	2 y	1 192	-	-	-	-
24	2005	Knysna (SC)	2006	Knysna (SC)	1 y	0	-	-	-	-
25	2005	St Lucia (EN)	2007	St Lucia (EN)	2 y	0	-	-	-	-
26	2005	St Lucia (EN)	2007	St Lucia (EN)	2 y	0	-	-	-	-

Match number	Capture date (year)	Capture location (area and coastal subregion)	1st recapture date (year)	1st recapture location (area and coastal subregion)	Interval between captures (d = days; y = years)	Approximate distance between capture locations (km)	2nd recapture date (year)	2nd recapture location (area and coastal subregion)	Interval between 1st and 2nd capture (years)	Distance between 1st and 2nd recapture locations (km)
27	2005	St Lucia (EN)	2008	Knysna (SC)	3 y	1 192	-	-	-	-
28	2005	Knysna (SC)	2009	Ponta Mamoli (MS)	4 y	1 377	-	-	-	-
29	2005	St Lucia (EN)	2009	St Lucia (EN)	4 y	0	-	-	-	-
30	2005	St Lucia (EN)	2011	St Lucia (EN)	6 y	0	-	-	-	-
31	2005	St Lucia (EN)	2011	St Lucia (EN)	6 y	0	-	-	-	-
32	2006	Knysna (SC)	2007	Knysna (SC)	1 y	0	-	-	-	-
33	2006	Knysna (SC)	2008	Knysna (SC)	2 y	0	-	-	-	-
34	2006	Knysna (SC)	2009	Ponta Mamoli (MS)	3 y	1 377	-	-	-	-
35	2006	Knysna (SC)	2011	St Lucia (EN)	5 y	1 192	-	-	-	-
36	2007	St Lucia (EN)	2008	St Lucia (EN)	1 y	0	-	-	-	-
37	2007	St Lucia (EN)	2009	St Lucia (EN)	2 y	0	-	-	-	-
38	2007	Knysna (SC)	2009	St Lucia (EN)	2 y	1 192	-	-	-	-
39	2007	St Lucia (EN)	2009	St Lucia (EN)	2 y	0	-	-	-	-
40	2007	Bazaruto (MC)	2010	St Lucia (EN)	3 y	891	-	-	-	-
41	2008	Knysna (SC)	2009	St Lucia (EN)	1 y	1 192	-	-	-	-
42	2008	St Lucia (EN)	2009	St Lucia (EN)	1 y	0	-	-	-	-
43	2008	St Lucia (EN)	2010	St Lucia (EN)	2 y	0	-	-	-	-
44	2008	St Lucia (EN)	2018	Bazaruto (MC)	10 y	891	-	-	-	-
45	2010	St Lucia (EN)	2011	St Lucia (EN)	1 y	0	-	-	-	-



Within-year matches

Capture region	Symbol	Recapture region	Total number of matches
EN	◀——●	SC	2
EN	⟳	EN	7
MC	◀——●	EN	2
Total			11

Between-year matches

Capture region	Symbol	1st recapture region	Symbol	2nd recapture region	Number of individuals
SC	◌	SC		–	3
SC	●- - -▶	EN		–	5
SC	●- - -▶	MS		–	2
EN	◀- - -●	SC		–	7
EN	◌	EN		–	22
EN	●- - -▶	MS		–	1
EN	●- - -▶	MC		–	1
MC	◀- - -●	EN		–	1
EN	◀- - -●	SC	◌	SC	1
EN	◌	EN	◌	EN	2
Total					45

Figure 2: Graphic representation of the numbers of within-year and between-year matches obtained between humpback whale capture-recapture locations (through photo-identification) for the Southern Hemisphere breeding substock C1

estimated. The intervals of the between-year capture–recapture events ranged from 1 year to 18 years. Of the 42 individuals recaptured once, 12 individuals (28.6%) were recaptured after 1 year, 9 individuals (21.4%) after 2 years, and 21 individuals (50%) after ≥3 years (among the latter, two whales were recaptured after ≥10 years). Of the 3 individuals recaptured twice, 2 were first recaptured after 1 year, and then recaptured again 4 and 7 years later (i.e. 5 and 8 years from their initial capture), respectively; the third individual was first recaptured after 2 years, and then recaptured again 3 years later (i.e. 5 years from its initial capture).

As mentioned, 42 of 48 individuals were seen twice (recaptured once) between years: of these, 37 were captured-recaptured along the coast of South Africa, and 5 between South Africa and Mozambique. Of those 37 between-year matches obtained off South Africa, 25 individuals (64.6%) were captured-recaptured in the same subregion (22 within EN; 3 within SC), 5 (13.5%) were between SC–EN, and 7 (18.9%) between EN–SC. Of those 5 individuals captured-recaptured between South Africa and Mozambique, 2 had moved between SC–MS, and one each had moved between EN–MS, EN–MC, and MC–EN. Finally, the remaining 3 of 45 individuals in the between-year matches were seen three times (recaptured twice) between years, and all movements were within South Africa (EN–EN–EN = 1; EN–SC–SC = 1).

Discussion

This study provides valuable and novel information on the intraseasonal and interseasonal occurrence and movement patterns of Southern Hemisphere humpback whales migrating and breeding along the southeastern coast of Africa (i.e. breeding substock C1) and identifies the value of photo-identification as a cost-effective research tool.

To determine the distribution and migration patterns of humpback whales, it is necessary to investigate their movement over broad temporal and spatial scales. Opportunistic data collections, such as cetacean observations and photo-identification records produced by citizen science during activities such as land- or boat-based whale watching, collectively often extend over broad temporal and spatial scales, frequently beyond ranges achievable through traditional scientific research (Brossard et al. 2005; Dickinson et al. 2010; Salgado Kent et al. 2012; Cigliano et al. 2015; Embling et al. 2015; Earp and Liconti 2020; Kelly et al. 2020; Sandahl and Tøttrup 2020). The large component of citizen science data represented in our catalogue of fluke images shows the value of exploiting opportunistic information to fill data gaps arising from the limitations of traditional scientific research. Here, we demonstrate that such data can contribute importantly to our understanding of humpback whale movements along the southeastern coast of Africa.

Performing the image-quality analysis to determine the distinctive nature of an individual's photo-identified features was important for reliable and unbiased analyses of data that were largely collected in an unsystematic fashion. Also, it is essential to consider the limitations of the data contained in this photo-identification catalogue in terms of accurate information about key population parameters through capture-recapture analyses. A key assumption of open-population capture-recapture analyses is that all individuals in the population have an equal chance of being captured (Hammond 1990; Lettink and Armstrong 2003). Several studies on the temporal and spatial migration patterns of humpback whales have reported that their migration is typically segregated by sex (Dawbin 1966, 1997; Craig et al. 2003) and that the Julian date when some individuals or groups are present in certain areas can be consistent between seasons (Félix and Haase 2001; Craig et al. 2003; Cerchio et al. 2005, 2008a, 2008b). For example, during migration northwards towards the breeding grounds, non-pregnant females tend to be the first to arrive, and pregnant females the last; also, mother–calf pairs tend to be the last to depart the breeding grounds when heading southward to the feeding grounds

(Chittleborough 1965; Dawbin 1966). It is therefore crucial to understand the temporal and spatial migration patterns displayed by different groups and individuals within a population, and to ensure that the data collection effort spans temporal and spatial scales representative of the entire population and migration period and remains consistent between seasons (Felix and Haase 2001; Cerchio et al. 2005, 2008a, 2008b; Constantine et al. 2012; Banks 2013) if a full understanding of the migration parameters is to be met.

The data represented in this fluke image catalogue were obtained from several non-related and non-systematic sources, with inconsistent temporal and spatial extents—meaning that the 'capture' probabilities were unequal among individuals. Furthermore, the temporal and spatial coverage of the catalogue does not encompass the whole breeding season and breeding grounds of substock C1. Despite these limitations, valuable novel information was obtained from the within-year and between-year image-match results.

Within-year matches

The mean temporal occurrence of 43 days revealed by the within-year match results may indicate that humpback whales in the Southern Hemisphere are seasonally present off the coast of southeastern Africa for extended periods. This observation is further supported by the longest known capture-recapture interval of 114 days obtained for a single humpback whale.

Our results are comparable to the sighting intervals obtained from humpback whales photographed along the eastern Australian migration corridor and breeding range between 2003 and 2005, where sighting intervals between captures-recaptures ranged from 5 to 125 days (Burns et al. 2014). Research on the seasonal occurrence patterns of humpback whales from substock C4 off Réunion Island, between 2008 and 2010, revealed a mean re-encounter interval in the range of 22–29 days, and the longest interval for a single whale was 64 days (Dulau-Drouot et al. 2012). Within-year recapture results associated with substock C3 off Antongil Bay, Madagascar, based on data from 2000–2006, ranged from 3 to 8 days (Cerchio et al. 2008a). As indicated, these studies of substocks C3 and C4 were performed over a much shorter time-period than was our study, so the lengthier within-year recapture intervals obtained in the present study would then be expected. In addition, the above-mentioned recapture intervals obtained for substocks C4 and C3 represent only whales within their respective breeding grounds, and do not include whales along the stock's representative migration corridors.

Evaluation of the spatial movements displayed by the within-year recaptured individuals provided valuable information on geographic locations used by these individuals during a migration period. Based on the short recapture intervals obtained from images of the three individuals captured-recaptured in coastal subregion EN within the same month (1 day apart in July 2002; 2 days apart in July 2007; and 1 day apart in September 2008), there is reason to believe that this subregion is a migration transit area, rather than a destination. Since the individual that moved between Richards Bay and St Lucia was captured-recaptured only 1 day apart (in July 2002), and since Richards Bay is situated south of St Lucia, it is assumed that the whale was encountered both times during its northward migration. The timing of this individual's capture-recapture month also falls within the assumed northward migration period of humpback whales in the region (Findlay 1994; Findlay and Best 1996, 2006; Findlay et al. 2011; Wilkinson et al. 2023).

The longer recapture intervals (July–October, August–October, and September–October) obtained for four individuals captured-recaptured in St Lucia suggested that these whales were correspondingly sighted during their northward and southward migrations. This is further corroborated by the months of their captures-recaptures (Findlay 1994; Findlay and Best 1996, 2006; Findlay et al. 2011). Moreover, there is little reason to believe that these extended recapture intervals show continuous occupancy in the region since past studies in the area indicated that most of the humpback whales traversing this region displayed travelling behaviour, suggesting that this area is a transit station during migration rather than a destination (Findlay 1994; Findlay and Best 1996, 2006; Findlay et al. 2011; Wilkinson et al. 2023).

The two within-year fluke image matches of individuals attained between St Lucia (EN) and Plettenberg Bay/Knysna (SC) in 2005 and 2008, respectively, may indicate extensive coastal movement of humpback whales during migration, as well as the migration pathways used by substock C1S. The months of the within-year match in 2005 (October–November) may suggest that on both occasions the individual was encountered during its southward migration. Considering the recapture interval of this individual was 45 days, the approximate distance that it could have travelled per day was ~26.7 km, if the whale maintained its course and travel speed, moving at ~1.1 km h−1. This daily travel distance and speed is significantly lower than other southward migration rates recorded for this substock. Findlay (1994) proposed an estimated average instantaneous swim speed of 5.3 km h−1 for southward migrating humpback whales off Cape Vidal (within subregion EN). However, it was highlighted that these instantaneous swim speeds estimated for southward-migrating whales should be interpreted with caution, since the speeds were recorded from whales travelling in a region of the fast-flowing, southward-moving Agulhas Current during daylight hours (Findlay 1994). It is also well known that humpback whales' migration is not always linear or in a north–south direction, as many whales have been observed to migrate with different trajectories (Fossette et al. 2014). Furthermore, northward migration rates of humpback whale groups recorded in this area during 2018 and 2019 ranged from 0 to 20 km h−1, with average speeds of 7.1 ± 0.27 km h−1 for 2018, and 5.5 ± 0.25 km h−1 for 2019 (Wilkinson et al. 2023).

Investigations of humpback whales migrating southward along the west coast of South Africa indicated that 70% of whale groups sighted moved at net speeds of <1.5 km h−1 (Best et al. 1995). Based on the migration rates suggested by Chittleborough (1953), Best et al. (1995), Jenner et al. (2001) and Jenner and Jenner (2011), it is likely that the individual re-encountered between St Lucia and Plettenberg Bay/Knysna in 2005 was alternately travelling and resting, explaining the longer-than-expected capture-recapture interval. The capture-recapture months in which the within-year match was obtained between these two subregions in 2008 (August–December) suggested that the individual was captured during its northward migration and recaptured during its southward migration. The recapture interval of this individual also indicated that it was present on the coast for at least 3 months, which is within the 10-month period that the species can occur on this coastline during migration and breeding (e.g. Findlay and Best 1996; Dawbin 1997; Banks 2013).

The two within-year matches of fluke images obtained between Bazaruto, Mozambique (subregion MC), and St Lucia, South Africa (subregion EN; October–November 2003 and September–October 2007), links humpback whales breeding in central Mozambique to the migration corridor previously associated with substock C1. The months during which these individuals were observed correspond to the southward migration period for humpback whales along this coastline. Since these animals took 22 and 39 days to move between the two subregions, they travelled at ~1.0 and 1.7 km h−1, respectively, assuming they maintained their course and a continuous swim speed. These speeds also correspond to the resting travel speeds mentioned by Chittleborough (1953), Best et al. (1995), Jenner et al. (2001) and Jenner and Jenner (2011).

Between-year matches

The reason for the highly variable seasonal recapture rates (range 0.7–8.5%) and the resultant low mean (3.9%) obtained from our analysis is unclear. The recapture rate could have been influenced by several factors, including temporal and spatial variation in effort, population size, and variability of photographic 'catchability', which in turn would be highly influenced by the behaviour of different individuals, weather conditions, and the number of photographers (Baker et al. 1986; Calambokidis et al. 2001; Wedekin et al. 2010; Robbins et al. 2011; Burns et al. 2013; Witteveen and Wynne 2017). Nonetheless, the results provide supporting evidence of long-term migration fidelity of substock C1 along the southeastern coast of Africa. For instance, the 3 individuals that were captured-recaptured in three different years had recapture intervals ranging from 5 years (2 individuals) to 8 years (1 individual). The failure to detect any between-year matches of individuals recaptured before 2000, in the period 2012–2017, or in 2019 may be attributable to the low number of fluke images available for those years.

Most of the between-year matches were associated with individuals that were first photo-identified along the coast of South Africa (98%) (Table 2; Figure 2), which might be explained by the fact that the majority (87%) of the images in the built catalogue were collected within South African coastal regions. The matches within/between South African coastal subregions provide further evidence of the use of this region by substock C1S for migrations. Some level of long-term migration fidelity to Plettenberg Bay/Knysna (within region SC) is suggested by four between-year encounters/re-encounters obtained in this area. Additionally, strong long-term fidelity to St Lucia (within subregion EN) is indicated by 22 between-year recaptures of individuals in this area. In addition to 1 within-year match obtained between Richards Bay and St Lucia, the 4 between-year recaptures obtained between these two locations confirm that these areas form part of the migration corridor for this substock. Furthermore, 13 between-year matches (together with the 1 within-year match) obtained between locations within subregions SC (near Plettenberg Bay/Knysna) and EN (Cape Vidal/St Lucia) confirm that these areas are used during migration.

Only a few within-year and between-year matches were obtained for subregions MS and MC, which could be a result of the low availability of fluke images collected in this part of the western Indian Ocean (Figure 2; Table 1). However, since individuals are constantly on the move, often spending only brief periods in some areas, it is possible that the densities of humpback whales during the time of data collection were more concentrated in areas outside the geographic range observed (Mattila et al. 1994; Cerchio et al. 2008a, 2008b; Wedekin et al. 2010; Ersts et al. 2011; Baracho-Neto et al. 2012; Dulau-Drouot et al. 2012; Witteveen and Wynne 2017). Accordingly, this may account for the low number of within-year and between-year matches of individuals in the Mozambique subregions. Nevertheless, the 5 between-year matches obtained with data from subregions MS and MC indicate long-term site fidelity of substock C1 to this coastline and perhaps verify that the migration corridor along the South African coast is linked to the breeding grounds in southern and central Mozambique (subregions MS and MC). Such connection is in agreement with previous findings (e.g. Olsen 1914; Findlay 1994; Findlay et al. 1994; Best and Ross 1996; Best et al. 1998; IWC 2000; Cerchio et al. 2008b; Ersts et al. 2011; Banks 2013).

Conclusions

The photo-identification data obtained from the fluke image catalogue developed during this study represent substock C1S humpback whales over extensive temporal and spatial scales, although large temporal and spatial gaps in the available data prevent a sure assessment or precise illustration of the distribution and migration patterns of this population. It will be possible to expand the temporal and spatial scope of the catalogue through awareness-raising of the significance of fluke images, specifically for the management of the species, and by encouraging voluntary contributions of photographs of whale markings, thereby enabling a more-accurate representation of the

population. In addition, this catalogue provides a valuable, non-invasive means to obtain novel information on the distribution, migration and structure of humpback whale populations in the western Indian Ocean, offering a valuable resource to facilitate international collaborations in humpback whale research. The maintenance and expansion of this catalogue could contribute significantly towards a better understanding of the population ecology of humpback whales throughout the Southern Hemisphere through the examination of the species' movement patterns on both small and broad scales.

Future photo-identification research efforts planned within the western Indian Ocean should include areas of historically poor coverage, most notably the coasts of south and southeastern South Africa and southern and central Mozambique. It is of fundamental importance to acquire a more continuous and accurate representation of the intra-regional population structure, the width and extent of the migration stream, the migration pathways utilised by this species, and connectivity between the migration corridor and breeding areas. Continuous and consistent data-collection efforts are also required to obtain an updated and accurate abundance estimate of substock C1S using systematic photo-identification sampling. It is further suggested that an additional photo-identification catalogue is developed for substock C1N, for comparison with the C1S catalogue compiled as part of this study, to determine the northern migration and breeding limits of the C1S component, the level of intermixing that occurs between components C1S and C1N, and the distribution limit of substock C1 along the coast of northern Kenya. Comparisons against the broad database being built through the citizen science platform 'Happywhale' (www.happywhale.com) (Cheeseman et al. 2022) will further help reveal connections with other breeding grounds and the interchange of individuals among these. We also advise comparison of our fluke image catalogue to the internationally collaborative Antarctic Humpback Whale Catalogue (Allen et al. 2020), particularly the images obtained in management areas II, III and IV, to increase our understanding of the level of connectivity between the feeding and breeding grounds of the different substocks.

Lastly, we also recommend that the information provided by this study is ultimately incorporated into the management and conservation of humpback whales occurring along the coast of East Africa as well as considered in future marine spatial-planning programmes.

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