Initial assessment of exchange between breeding stocks C1 and C3 of humpback whales in the western Indian Ocean using photographic mark-recapture data, 2000-2006.

SALVATORE CERCHIO[1,2], KEN FINDLAY[3], PETE ERSTS[1,4], GIANNA MINTON[5,6], DAANIE BENNET[7], MIKE MEŸER[7], YVETTE RAZAFINDRAKOTO[1,8], DEON KOTZE[7], HERMAN OOSTHUIZEN[7], MATT LESLIE[1,9], NORBERT ANDRIANARIVELO[1,8] AND HOWARD ROSENBAUM[1,9]

[1]WCS and AMNH Cetacean Conservation and Research Program, c/o Marine Conservation, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460-1099, USA.
[2]Evolutionary Biology Program and Bioacoustics Research Program, Cornell Laboratory of Ornithology 159 Sapsucker Woods Rd. Ithaca, NY 14850, USA.
[3]University of Cape Town, Oceanography Department, Rondebosch 7701, South Africa
[4]Center for Biodiversity and Conservation, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.
[5]Environment Society of Oman P.O. Box. 3955, P.C. 112, Ruwi Sultanate of Oman
[6]University of Malaysia Sarawak, Piasau 70, Miri 98009, Sarawak
[7]Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa
[8]Madagascar Country Program, Wildlife Conservation Society, B.P. 8500, Antananarivo, Madagascar.
[9] Sackler Institute for Comparative Genomics, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) in the southern hemisphere are distributed in circumpolar high latitudes during the austral summer and migrate to discrete or semi-discrete low latitude breeding areas in the austral winter. The International Whaling Commission (IWC) currently designates seven breeding stocks (populations) labeled A through G, ranging from the western South Atlantic eastward to the eastern South Pacific (IWC 1998). The breeding population that winters in the western Indian Ocean is considered Breeding Stock C, and has a winter distribution which ranges from the eastern coastal waters of South Africa to Kenya, off the islands of the Mozambique Channel, and the coastal waters of Madagascar.

Best et al. (1998) proposed three potential subpopulations and migratory corridors of humpback whales in the western Indian Ocean, based upon historical whaling records, land based observations of migrations, and shipboard surveys. The IWC delineation of Breeding Stock C is consequently divided into three sub-regions: C1, wintering off the east coast of South Africa to Mozambique; C2, a group that potentially migrates up the Mozambique Channel to winter grounds in the Comoros Archipelago; and C3, wintering in the coastal waters of Madagascar (Best et al. 1997, 1998, Rosenbaum et al. 1997). At the recent intercessional meeting of the IWC for the Comprehensive Assessment of Southern Hemisphere Humpback Whales (CA SH) in Hobart, Australia 2006, it was proposed that C1 be further delineated into C1S and C1N, with the division at Mozambique Island (IWC 2006). At least the southern portion (the east South African) of C1S is generally considered to be a migratory corridor, although breeding behaviors (such as singing) have been observed, in the Mozambique portion of C1S and in C1N (Findlay and Best 1996, Findlay et al. 1994, in press).

Regarding the relationships between these sub-regions, recent findings suggest that C1 and C3 exhibit significant genetic differentiation, whereas C2 and C3 do not (Rosenbaum et al. 2006, Pomilla 2006). Furthermore, mark-recapture of photographically and genetically identified individuals suggest there may be substantial exchange or overlap between C2, sampled off Mayotte and the Geyser-Zélée Reef

Complex, and C3, sampled off Antongil Bay, Madagascar (Ersts et al 2006). Pomilla (2005) reported one across-year genetic match between C1, sampled off east coast of South Africa, and C3, sampled off Antongil Bay. Thus, although these two sub-regions may be utilized by potentially genetically differentiated sub-populations, there is clearly some degree of exchange between them that is as yet un-quantified due to the lack of adequate sample size and systematic comparison. The purpose of this study is to use individual identification photographs of humpback whales collected from Breeding Stocks C1 and C3 during the years 2000 to 2006 to assess the degree of exchange and overlap between these two sub-populations.

METHODS

Data collection

East African Mainland (C1)

East African Mainland (C1) data were contributed by whale watch tourism operations and collected during research cruises. Generally the data collection sites can be deliniated into six coastal areas as defined in Figure 1: South Coast of South Africa (SC), South Eastern South Africa (ES), North Eastern South Africa (EN), South Mozambique (MS), Central Mozambique (MC), and North Mozambique (MN). Data used in this analysis come from four of these regions, ES, EN, MS and MC (Table 1), and thus are entirely from sub-region C1S, with the vast majority (93%) collected off northern KwaZulu Natal and the Eastern Cape, South Africa in the migration stream portion of the southern C1 range (Table 1).

Whale-Watch Tourism Operations

Two licensed South African whale-watch operators voluntarily collected photo-identification images and data from humpback whales migrating through the East Coast waters of South Africa, particularly along the northern KwaZulu Natal coast. Such whale-watch operations are limited in their approach to pods of whales by permit and "code of conduct" conditions, and the timing and scope of "survey effort" may be biased by market forces.

Apart from a single image collected within the ES sub-region, all data collected by whale-watch operators was collected by DB within the EN sub-region. This whale-watch operation targets the apparent coastal migratory stream during both the northward and southward migration, and lies some 30 km to the south of Cape Vidal from where shore-based observations of migration characteristics have been undertaken (Findlay and Best 1996 a, b, Findlay and Best, 2006ms). All images collected by whale-watch operations prior to and including 2004 were collected by film camera, while digital images were collected after 2004. Film images were digitally scanned by KF for comparison to digital images and compilation of final catalogue.

Research Cruise Operations

Images and associated data have been collected from research initiatives as follows:

1. 2002 ISACH (Indo-South Atlantic Humpback Whale Consortium) cruise.

Ship-based surveys of humpback whales were planned from the South African Department of Environment Affairs and Tourism fisheries research vessel *FRS Algoa* over the period 4 July to 25 July 2002 within sub-region EN. Surveys were aimed at providing verification of the offshore distribution, migration speeds and group sizes of humpback whales for comparison with shore based survey work at Cape Vidal, as well as the collection of photo-identification and genetic data for the purpose of population and individual movement analyses. Both inclement weather conditions and failure of the vessel transmission after 16 July resulted in the vessel-based component being severely compromised and all research after 16 July was carried out by small boat excursions from Richards Bay harbor. Both the left and right aspects of the dorsal fins and the ventral surface of the tail flukes (if exposed upon dive) were photographed using motor - driven SLR cameras and 80 - 200 mm or 200 – 400 mm lenses using both digital (Nikon D1) or film (Nikon 801) systems.

2. 2003 Mozambique Cruise

A one-month survey of humpback whales in Mozambique waters was carried out in August / September 2003. While the northward transit of the survey area incorporated a line transect survey between Cabo Inhaca and Mozambique Island, the southward leg of the survey intercepted humpback whales for collection of identification samples (both genetic and photographic) across sub-region MC and MS. This was carried out over the period 12 to 18 September, and a series of seven way-points were established at approximately equidistant points between Beira and Cabo Inhaca. Research was initiated at each of these way-points at the start of the seven available days. Two or three small boats were deployed from the *FRS Algoa* each morning and dispatched to humpback whale sightings made by observers from the upper bridge as the *FRS Algoa* proceeded southwards at a slow speed of usually less than 5 knots. At times when no whales were visible for interception, the small boats ran alongside the *FRS Algoa* until whales were observed. High densities of whale groups encountered, meant that the *FRS Algoa* often suspended steaming to remain in the vicinity of the small boats while sampling occurred. Sampling was terminated and the small boats were recovered at between 16h00 and 17h00 each day. Daily progress towards the next way-point was consequently determined by whale densities, and distances between way-points not covered during the day, were steamed at night.

Photographs of both the left and right aspects of the dorsal fins (and the ventral surface of the tail flukes if exposed) of as many individual whales as possible in each intercepted group were taken with a hand-held digital SLR camera (Nikon D1 or DX1) and 70-200 mm lens.

3. 2005 Ship based survey

Identification photographs of humpback whales were collected from the *FRS Algoa* in a similar manner as the above two cruises in the sub-region ES over the period 25 June to 30 June 2005.

Madagascar (C3)

Madagascar (C3) data were collected on the breeding area of Antongil Bay, Madagascar (Fig. 1). Antongil Bay, in the northeastern corner of Madagascar, is a shallow, semi-protected bay that extends approximately 80km inland from the mouth of the bay and is on average approximately 30km in width. Humpback whales can be observed in Antongil generally from June to October with the highest concentrations occurring in July through early September (Rosenbaum et al. 1997). Behaviors widely accepted to indicate breeding activity are regularly observed in Antongil Bay, as are females with young calves, and thus the bay is considered a breeding area within the western Indian Ocean (Rosenbaum et al. 1997). The degree to which the bay represents an endpoint "destination" for migratory whales with high residency, versus a "stopover" point with relatively transient residency is debated and under study, although recent evidence suggests short residency times and fluid movements (Cerchio et al 2006).

Individual identification photographs used in this analysis were collected from 2000 to 2006 during yearly research field seasons of the Wildlife Conservation Society's Cetacean Conservation and Research Program (WCS/CCRP). Effort was relatively consistent each year from July to September (Table X) with the exception of 2002, which was an anomalously short season due to political upheaval in Madagascar. Standard procedures were used for identification photography using primarily Nikon D1 digital cameras. Photographs were collected of both sides of the dorsal fin as well as the ventral tail flukes whenever possible, however recapture analysis of only tail flukes are reported here.

<u>Photographic comparison procedure</u>

Photographs were analysed on a computer screen, and the best representative photograph for each individual whale was chosen for each single survey day. Scanned and digital images were referenced with relevant sighting data in a tailor-designed MS Access database (consider copyright for CCRP?). Tailor designed forms and queries allowed for comparison of on-screen digital images to conduct within-year and between year matching. Each region was treated separately to compile two separate regional catalogues for C1 and C3, respectively, as follows. Photographs were first compared within each year to establish within-year sample size of individuals and within-year recaptures. All coastal areas described above for C1 were lumped in creating the yearly C1 samples. Between-year comparisons were then conducted starting with the first two years and sequentially comparing each subsequent year to the reconciled catalogue of all previous years. The finalized catalogues for each region, consisting of the best quality photograph of each individual identified, were then merged into an interregional database, which allowed for on-screen comparison of images between regions. Within-year, between-year, and between region matching were all conducted by individuals with considerable experience in humpback whale photo-identification. All recaptures detected by matchers were confirmed by SC or one other representative of the matching team. Forms included an option to designate "possible matches", which could be examined and either verified or discounted by a second matcher.

All photographs used in the comparison were rated for quality on a five-level scale: excellent, good, fair, poor, and not useable. Quality was rated separately for three categories: *photographic*, which included focus, exposure, contrast and pixilation of digital images; *orientation*, which included angle of the flukes in the horizontal and vertical planes, amount of the flukes above water, and obstruction by splash; and *distinctiveness*, which was an intrinsic characteristic of the fluke involving the uniqueness of the pattern and degree of scarring (although this was inevitably influenced by photographic and orientation quality). Flukes were also rated on the proportion of the fluke that was showing above the water plane as whole, left fluke only, right fluke only, trailing edge or leading edge. By defined protocol the latter four categories (essentially partial flukes) could only receive a fair, poor or not useable quality rating in orientation. Flukes of all qualities were compared and used for assessing recapture rates of individuals within season and temporal characteristics of individual captures. Capture-recapture statistical procedures for assessment of exchange between C1 and C3 only included flukes with quality rating of fair or better in photographic and orientation categories. Photographs of only the right or left fluke were also eliminated from the sample since they cannot be compared to each other.

Assessment of exchange between sub-regions

Inferential tests were performed under the null hypothesis that C1 and C3 represent a single randomly mixing population. Hypotheses and predictions are as follows:

H_0: C1 and C3 represent a single randomly mixing population.

H_1: C1 and C3 represent at least partially segregated subpopulations, with non-random mixing between sub-regions.

P_{1a} – If C1 and C3 represent different subpopulations, we expect to observe more within regional recaptures (C1->C1, and C3->C3) then predicted at random.

P_{1b} – If C1 and C3 represent different subpopulations, we expect to observe fewer across regional recaptures (C1->C3, and C3->C1) then predicted at random.

In order to test whether there was equal likelihood for animals captured in each sub-region to be recaptured in the same vs. the other sub-region, a randomized permutation analysis was carried out, using the software R. For each pair of years, Year1 = Capture Year, Year2 = Recapture Year, the region of the Recapture Year was randomly permuted among all individuals captured in the Recapture Year. This provided a distribution with equal likelihood of movement while preserving the actual number of recaptures from each region and accounting for sample size differences in the Recapture Year. After 10,000 iterations of the permutation, a random distribution was created for the number of expected recaptures in the four possible directional categories: C1->C1, C3->C3, C1-C3, C3->C1. The actual number of recaptures for each directional category in each pair of years was tested against the random distributions.

RESULTS

Sample size by sub-region and year varied among years and sub-region (Table 1). The C1 sample comes predominately from coastal area EN, and thus is primarily from the southern portion of C1S in the apparent migratory corridor. Sample size in C1 varied substantially among years, with sample sizes of less than 50 individuals (after filtering for quality) in four of the seven years. Effort is reported as the range of dates (date of first and last photo in a year) and the number of days in each year during which photographs were collected (C1: Table 2a; C3: Table 3a). Date ranges are a very coarse assessment of effort, but demonstrate the non-consistent and only partially overlapping sampling in some years for C1 (Table 2a). Sampling in C3 was largely consistent in timing and magnitude of effort among years, with the exception of 2002 which represented an abbreviated field season (Table 3a). Yearly sample size of identified individuals before and after filtering for quality are reported for C1 in Table 2b and for C3 in Table 3b, and reflect the effort limitations noted above. Very few recaptures across years were made in C1 (Table 2c), with only 6 of 21 pairs of years containing a recapture, and only one with 2 individuals. In C3, recaptures across years were also limited, but more abundant than in C1 with number of recaptures per pair of years ranging from 0 to 4.

Comparison of finalized catalogues from each region revealed 2 recaptures between C1 and C3 (Table 4). Of these, 1 match involved a C1 photo of poor quality, and thus was not included in the analysis of exchange. Interestingly, both recaptures were from the same years and temporal direction; captured in C1 in 2003 and recaptured in C3 in 2006. The low incidence of recaptures between C1 and C3 on first assessment suggests little overlap between the populations utilizing the two regions. However, examination of the with-region C1 recapture table reveals that there is generally a low recapture rate for C1 individuals. In most years this is clearly due to the small sample sizes in C1; however, in those years with larger sample sizes comparable to those in C3, the recapture numbers were still low.

Random permutation analysis indicated that there were no statistically significant deviations in observed number of recaptures from random expectations in any individual pair of years. This was true both for within sub-region comparisons which did not have more recaptures than expected at random (Table 5), and for between sub-region recaptures, which did not show fewer than expected recaptures (Table 6). The tests between individual pairs of years lack power due to small numbers of recaptures, and moreover did not suit the dataset as indicated by the many cells at a probability of 1.0 (typically due to there being 0 recaptures for that cell and therefore only 1 possible outcome in the permutation analysis, "0"). Thus a combined analysis was conducted combining the observed values for all years and generating combined expected distributions for each directional category. This overall test resulted in highly significant values for all categories, despite the generally low number of recaptures (Table 7). Since many years from C1 contain small samples, the test was repeated using only the three years with larger samples sizes from both sub-regions (2003, 2005 and 2006) to assess potentially stochastic effects in the small sample years, as well as the power of the test with reduced data. Recaptures from C3 remained significantly different from random mixing expectations in both directions, with greater than expected return recaptures to C3, and fewer than expected across sub-region recaptures to C1 (Table 8). However, the recaptures from C1 were no longer significantly different than expected at random (Table 8). This may be due to the reduction in the sample size of recaptures from C1, or alternatively may indicate a stronger site fidelity among the whales that migrate to the C3 region.

DISCUSSION

In evaluating and interpreting these results, it is important to first consider the sampling effort for the study and inherent limitations that result. Data from C3 was conducted during a single research effort over several field seasons that were targeting the collection of a representative sample over the seasonal duration of whale concentrations in Antongil Bay. This proved to be of critical importance for the C3 population due to residency and migratory characteristics of that population. Cerchio et al. 2006, 2008 report short residency times and highly significant consistency in timing of individual recaptures in Antongil Bay, with 76% of pair-wise recaptures occurring within 10 days of the Julian date of initial year capture. It therefore appears that individuals are moving through the area at roughly the same time each year, and spending a relatively short time in the sample area. In such a structured migratory flow, it is imperative to have consistent temporal field effort each year spanning the entire period of whale concentrations in order to obtain a representative sample for capture-recapture analysis. Not doing so would result in a biased sample that introduces heterogeneity of capture probability, the character of which would be determined by the nature of the sampling bias and could introduce either a negative or positive bias in population parameter estimation (see Cerchio et al. 2008 SC/60/SH32).

In contrast to the consistent and systematic C3 sampling effort, the C1 sample was derived from several sources, some opportunistic in nature and spanning a large geographic region. Temporal coverage varied from year to year and among sample locations, so that effort in some pairs of years was entirely non-overlapping in time (Table 2a, Fig. 2). Sampling was equally inconsistent geographically, so that different years were represented by data from different sub-regions within C1 (Table 1, Fig. 2). This presents problems for application of these data to capture-recapture analyses on several levels. Any parameter estimation using capture-recapture data makes the assumption of equal capture probabilities among individuals in the population; this assumption can be relaxed in some cases when the nature of the variation in capture probability is understood and the appropriate model is applied. Since some spatial heterogeneity might exist within the C1 sub-region, the spotty geographic nature of the C1 sample is reason for concern, particularly in light of the temporal variation of sampling in sub-regions. Furthermore the majority of C1 samples in this analysis come from the migratory portion of the C1S range. The nature of individual movements in this migration is entirely unknown; there is good reason to suspect that the temporal characteristics of individuals may be similar to that described for C3 above. Furthermore, some temporal age or reproductive class segregation may occur (as found by Dawbin 1966). For example, Findlay (1994) found the migration to comprise co-incident waves each year, although the composition of such waves are unknown. In such a scenario it would be imperative to have even and consistent temporal coverage in each year, and thus the temporal inconsistency in sample effort is also a reason for considerable concern. We do not recommend the use of the C1 photographic data for capture-recapture parameter estimation, due to the non-representative nature of the sample and the unpredictable biases that could result.

With these caveats and limitations in mind, our photographic comparison indicates that there is clearly some exchange between the two breeding stocks, C1 and C3. It is important to note that the limitations of the C1 sample described above, along with the small sample size and sparse recaptures overall, make it inadvisable to estimate an "index of exchange" or similar population parameter with these data. However, as a preliminary conclusion, our inferential permutation analysis indicates that exchange between the two is less than would be expected if it was a randomly mixing single stock. This corroborates the findings of population genetic analyses of both mtDNA (Rosenbaum et al 2006) and microsatellite nuDNA (Pomilla et al 2006). There is some suggestive indications that there may be greater exchange from C1 to C3, given that the only 2 interregional matches were in that direction, despite a very low incidence of within region recapture in C1. We might speculate that this could be in part due to the sampling of C1, in that it is was almost entirely in the migratory corridor portion of C1S and thus might represent individuals on migration to both C1 and C3 breeding areas. However, it is important to recognize that the recaptures detected were across a four year span (2003 to 2006), and thus provide no insight in regards to migratory pathway. Any number of scenarios can be constructed for the actual movement patterns of the recaptured individuals during these years. Furthermore, our sample is insufficient to assess whether the individuals involved have a higher probability of capture in either sub-region, and thus any inference regarding regional affinity or interchange directionality are ill-advised. We can only conclude that there is some degree of exchange between these sub-regions, the character of which remains unknown. Until further information is available, care should be taken in the interpretation of population abundance estimates from the two regions, as any estimates derived from C1S capture-recapture data collected off South Africa may overlap to some degree with those from C3, and combining such estimates could result in a positive bias.

We do not believe the data presented here to be sufficient or adequate to estimate a parameter of overlap. However, we believe our data indicate that the structure is neither one of a single randomly mixing population, nor one of two distinct and non-overlapping breeding stocks. We recommend that there be further discussion regarding values for proportion of overlap for use in assessment models, that bracket reasonable possibilities within the polar extremes of "no overlap" and "complete overlap". Note also, that the lack of data from C1N, as well as from C2, in this analysis may present other complicating factors, although probably less so than the fact that most of the C1 data used in this analysis comes from the migratory corridor of C1S. In this context we must assess the relationship between C1N and C1S. The C1N sub-region is more closely situated by latitude and longitude to C2 and the sample site of C3. There has already been documentation of greater exchange between C3 (Antongil Bay) and C2 (Mayotte; Ersts et al. 2006), then presented here between C3 and C1S. Given the very close proximity of C1N, C2 and our C3 sample site, it is conceivable that these three sub-regions may have more exchange as breeding assemblages than any of them have with C1S (which within its currently proposed boundaries encompasses both a migratory corridor and breeding area). Therefore, the actual picture of exchange and overlap of these sub-populations is likely to be very complex and require greater MRR sampling that currently available to fully elucidate.

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Table 1. Sample of fluke identification photographs used for interchange analysis between C1 and C3, broken down by sub-regions that were sampled (indicated in Figure 1). Totals were tabulated after filtering photos by quality, and thus represent only photos of fair or better quality used in the exchange analyses.

Sample by Sub-Region	2000	2001	2002	2003	2004	2005	2006	Total
North Eastern South Africa (EN)	3	24	48	82	21	125	112	415
South Eastern South Africa (ES)	0	0	1	0	0	9	0	10
Central Mozambique (MC)	0	0	0	8	0	0	0	8
South Mozambique (MS)	0	0	0	25	0	0	0	25
Total C1 Sample (all C1S)	3	24	49	115	21	134	112	458
Madagascar, C3, Antongil Bay (AB)	89	159	16	126	151	143	158	842

Table 2. Eastern Africa Mainland (EAM), C1 sample. (a) Effort by date ranges and number of days on which photographs were collected, (b) sample of individual identifications, ***n***, before and after filtering for quality, and (c) within region recaptures, ***m***, for each pair of years, with values in () indicating number of matches excluded due to filtering of poor quality photographs. Shaded cells indicate years of low sample size.

(a)

Dates of IDs	2000	2001	2002	2003	2004	2005	2006
Min	Jun-00	Jun-01	4-Jul-02	3-Jun-03	1-Sep-04	25-Jun-05	4-Jun-06
Max	Jul-00	6-Nov-01	6-Dec-02	28-Oct-03	30-Sep-04	17-Nov-05	12-Nov-06
Count	3	17	29	52	7	58	48

(b)

n	2000	2001	2002	2003	2004	2005	2006
All	4	38	69	147	28	157	129
Filtered	3	24	49	115	21	134	112

(c)

m	2000	2001	2002	2003	2004	2005	2006
2000	x	0	0	0	0	0	0
2001		x	1	0	0	0	0
2002			x	1	1	0	1
2003				x	0 (1)	0	0
2004					x	1	0
2005						x	2
2006							x

Table 3. Madagascar (MAD), C3 sample. (a) Effort by date ranges and number of days on which photographs were collected, (b) sample of individual identifications, ***n***, before and after filtering for quality, and (c) within region recaptures, ***m***, for each pair of years, with values in () indicating number of matches excluded due to filtering of poor quality photographs. Shaded cells indicate years of low sample size.

(a)

Dates of IDs	2000	2001	2002	2003	2004	2005	2006
Min	17-Jul-00	10-Jul-01	22-Aug-02	11-Jul-03	10-Jul-04	13-Jul-05	16-Jul-06
Max	17-Sep-00	14-Sep-01	11-Sep-02	9-Sep-03	5-Sep-04	5-Seip-05	4-Sep-06
Count	37	35	12	34	34	28	37

(b)

n	2000	2001	2002	2003	2004	2005	2006
All	122	184	24	161	179	170	181
Filtered	89	159	16	126	151	144	158

(c)

m	2000	2001	2002	2003	2004	2005	2006
2000	x	2	1	3	1 (1)	0 (1)	1
2001		x	1	3	3	3	2
2002			x	3 (1)	0	0	0
2003				x	2 (1)	1	3
2004					x	4	3
2005						x	4
2006							x

Table 4. Comparison of C1 and C3 catalogues of humpback whale identification photographs. (a) Sample of photographs used in comparison from Madgascar (MAD) and East African Mainland (EAM) after filtering for photographic quality, and (b) numbers of recaptures found from MAD to EAM, below diagonal, and from EAM to MAD, above diagonal.

(a)

n	2000	2001	2002	2003	2004	2005	2006
MAD	89	159	16	126	151	144	158
EAM	3	24	49	115	21	134	112
Total	92	183	65	241	172	278	270

(b)

m					EAM			
		2000	2001	2002	2003	2004	2005	2006
	2000	0	0	0	0	0	0	0
	2001	0	0	0	0	0	0	0
	2002	0	0	0	0	0	0	0
MAD	2003	0	0	0	0	0	0	0
	2004	0	0	0	0	0	0	0
	2005	0	0	0	0	0	0	0
	2006	0	0	0	1 (1)	0	0	0

Table 5. Random permutation analysis results, testing for higher than expected recaptures within sub-regions. Values represent the probability of a number of recaptures equal to or greater than the observed value for each pair of years; C1->C1: below diagonal; C3->C3: above diagonal. No values are significantly greater than expected at random.

p	2000	2001	2002	2003	2004	2005	2006
2000	x	0.760	0.252	0.141	0.875	1.000	0.586
2001	1.000	x	0.247	0.142	0.683	0.132	0.340
2002	1.000	0.755	x	0.138	1.000	1.000	1.000
2003	1.000	1.000	0.482	x	0.765	0.506	0.196
2004	1.000	1.000	0.118	1.000	x	0.071	0.207
2005	1.000	1.000	1.000	1.000	0.485	x	0.112
2006	1.000	1.000	0.411	1.000	1.000	0.174	x

Table 6. Random permutation analysis results, testing for fewer than expected recaptures between sub-regions. Values represent the probability of a number of recaptures equal to or less than the observed value for each pair of years; C1->C3: below diagonal; C3->C1: above diagonal. No values were significantly less than expected at random.

p		EAM						
		2000	2001	2002	2003	2004	2005	2006
	2000	x	0.760	0.252	0.141	0.875	1.000	0.586
	2001	1.000	x	0.247	0.142	0.683	0.132	0.340
	2002	1.000	0.755	x	0.138	1.000	1.000	1.000
MAD	2003	1.000	1.000	0.482	x	0.765	0.506	0.196
	2004	1.000	1.000	0.118	1.000	x	0.071	0.207
	2005	1.000	1.000	1.000	1.000	0.485	x	0.112
	2006	1.000	1.000	0.411	1.000	1.000	0.174	x

Table 7. Combined permutation analysis for all pairs of years, testing for significant deviations from random expectations in the number of recaptures in each of the four directional categories, C1->C1, C3->C3, C1->C3, and C3->C1.

	C1->C1	**C3->C3**	**C1->C3**	**C3->C1**
Observed Recaptures	7	40	1	0
Random Expectations				
mean	3.5	23.9	4.5	16.1
min	0	13	0	6
max	8	34	8	27
Probability of observed in random distributions				
P	0.0099	<0.0001	0.0099	<0.0001

Table 8. Combined permutation analysis for years with large sample in both sub-regions, 2003, 2005, 2006, testing for significant deviations from random expectations in the number of recaptures in each of the four directional categories, C1->C1, C3->C3, C1->C3, and C3->C1.

	C1-C1	**C3-C3**	**C1-C3**	**C3-C1**
Observed Recaptures	2	8	1	0
Random Expectations (10000 iterations)				
mean	1.3	4.6	1.7	3.4
min	0	0	0	0
max	3	8	3	8
Probability of observed values in random distributions				
P	0.3793	0.0108	0.3793	0.0108

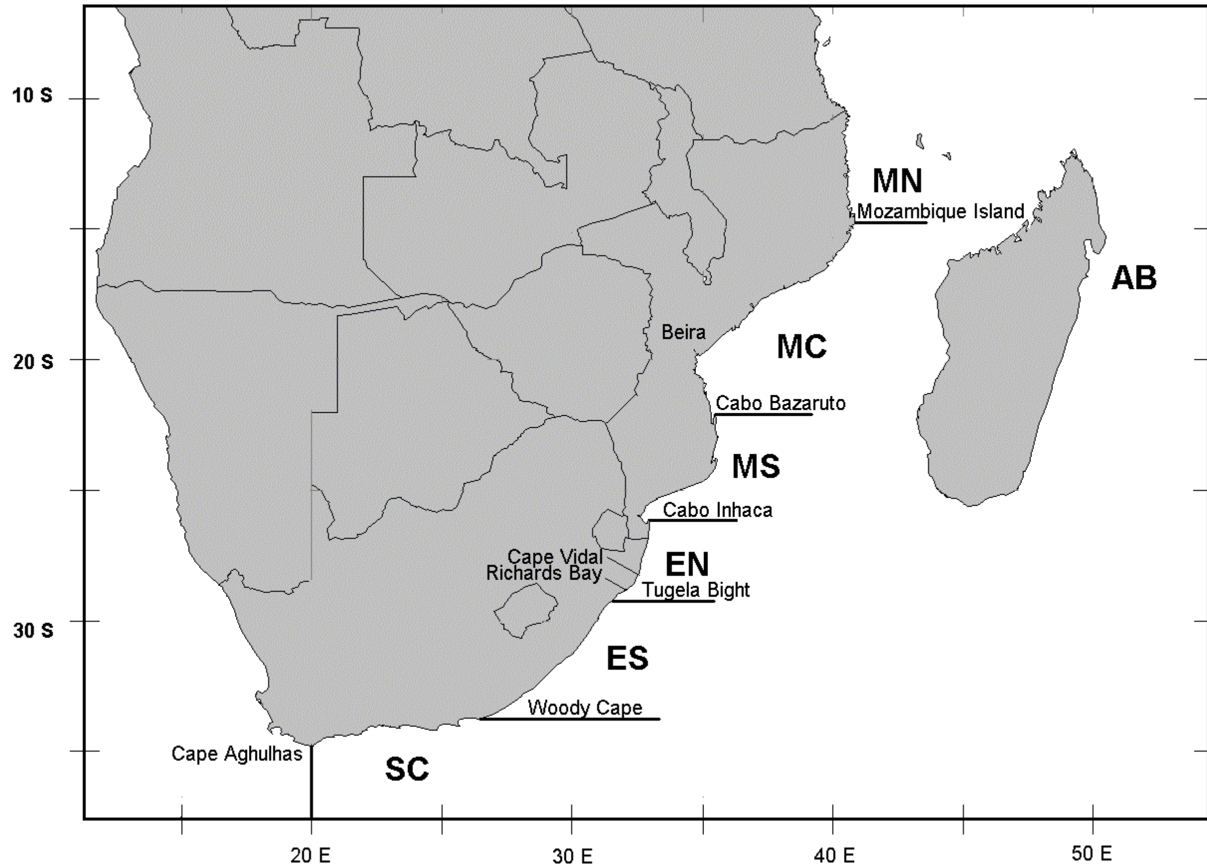

Figure 1. Location of sampling sights and sub-regional localities used in photographic analysis for C1: South Coast of South Africa (SC), South Eastern South Africa (ES), North Eastern South Africa (EN), South Mozambique (MS), Central Mozambique (MC), and North Mozambique (MN); and C3: Antongil Bay, Madagascar (AB).

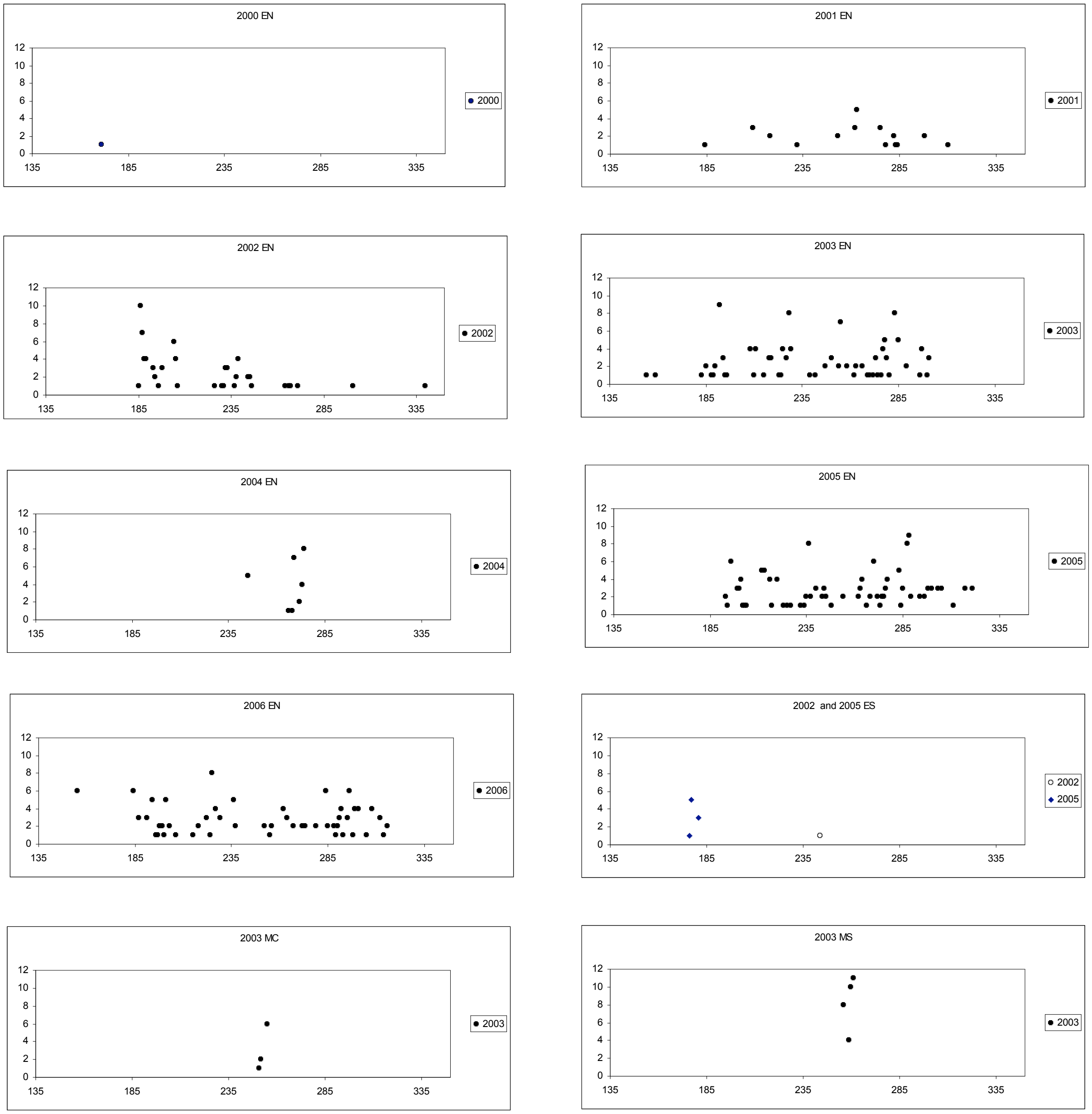

Figure 2. Sampling profiles from sub-regions EN, ES, MC and MS showing dates on which individual photo-identification samples were taken expressed as Julian Days