

## Humpback whales off Namibia: occurrence, seasonality, and a regional comparison of photographic catalogs and scarring

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Humpback whales (*Megaptera novaeangliae*) from a breeding ground off Gabon (0–4°S) and a migratory corridor/feeding ground on the west coast of South Africa (WSA; 33°S) differ genetically and in catch histories. Interpretation of the population structure is hampered by the lack of data from the intervening 3,500 km of coastline or to the north of Gabon. Here we collate all relevant nongenetic data on humpback whales from Namibia (~23°S) from 2005 to 2012 and compare these with corresponding data from Gabon (2000–2006) and WSA (1983–2008). Data from Namibia include photographic catalogs of dorsal fin and tail fluke images, seasonal presence, and a photographic assessment of scarring and wounds from cookiecutter sharks (*Isistius* sp.). No confirmed photographic identification matches could be made between Namibia and Gabon and only 2 potential matches were made between Namibia and WSA from dorsal fins. Humpback whales in Namibia show a bimodal seasonality in occurrence, with a primary peak in austral winter (July) and a secondary peak in spring (September), but generally low directionality of movement. Whales were never recorded to sing, competitive groups were rarely sighted, and very few calves were observed, making it unlikely that this is a breeding area. The prevalence of killer whale bite scars on flukes was similar at all sites. Fresh bites from cookiecutter sharks were highest in Namibia, intermediate in Gabon, but almost nonexistent in WSA. We propose that animals seen in Namibia in winter are on their northward migration and have intercepted the coast from farther offshore (where cookiecutter sharks occur), whereas animals seen in WSA in spring–summer, where they are feeding during their southward migration, have followed a slow coastwise route within the cold Benguela Ecosystem, thus allowing time for cookiecutter bites to heal.

Key words: cookiecutter shark, humpback whale, *Isistius*, killer whale, mark–recapture, migration, Namibia, Gabon, South Africa, scarring

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In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) feed in circumpolar Antarctic waters and migrate northward to relatively discrete breeding grounds in coastal tropical waters (Clapham 1993, 2000; Stevick et al. 2003; Rasmussen et al. 2007). Seven breeding populations or “management areas,” labeled as Breeding Stocks A–G (International Whaling Commission [IWC] 1998), are recog-

nized by the IWC in the Southern Hemisphere. These populations are assigned with varying confidence to 6 summer feeding areas (IWC Areas I–VI) in the Antarctic (Donovan



1991). Some movement between these feeding areas is probable, but the extent of such exchange remains largely unknown (Clapham 2009). Humpbacks that migrate and breed off the west coast of Africa belong to IWC Breeding Stock B (BSB) and are thought to feed in Areas II ( $60^{\circ}$ – $0^{\circ}$ W) and III ( $0^{\circ}$ – $70^{\circ}$ E—Barendse et al. 2010).

In 1982 the IWC agreed to a moratorium on commercial whaling, which took effect in 1986. Part of this agreement was the commitment to undertake a comprehensive assessment of the effect of the moratorium on all whale stocks. By 2005, sufficient data were believed to be in hand to begin the Comprehensive Assessment of Southern Hemisphere humpback whales. Progress has been made on some fronts and includes new estimates of abundance and estimates of rates of increase for some stocks, but has been hampered by a lack of a good catch-series data for many breeding areas (Gales et al. 2011). The assessments of stocks B and C (the west and east coasts, respectively) around Sub-Saharan Africa were undertaken from 2007 to 2011.

Genetic evidence from 2 sampling sites in BSB, off Gabon ( $0$ – $4^{\circ}$ S) and west South Africa (WSA;  $33^{\circ}$ S), and the history of catches in the 2 areas (Best and Allison 2010) indicated some population substructure (Rosenbaum et al. 2009), which has been interpreted to mean that whales from these localities may belong to 2 distinct substocks (named B1 and B2, respectively). However, although the number, sex ratio, and behavior of humpback whales encountered off Gabon unambiguously confirm this region to be a breeding area (Carvalho et al. 2014), WSA functions as both a migration corridor and a seasonal spring–summer feeding ground for a small number of humpbacks, but not as a breeding area (Barendse et al. 2010, 2011). Even though genetic evidence of population substructure exists, 11 individuals have been identified genetically or photographically, or both, in both localities, indicating some degree of physical mixing between these 2 sites (Barendse et al. 2011; Carvalho et al. 2014). Several alternate models of population structure were considered by the IWC in its assessment of the size and recovery rate of BSB, although none was considered to entirely capture the apparent complexity within the population (Müller et al. 2011). Interpreting stock structure and identifying the location of any additional breeding grounds are hampered by the almost total lack of individual genetic or photographic identification (photo-ID) data available from the  $\sim 3,500$ -km region between Gabon and WSA, including the waters of Angola and Namibia (Barendse et al. 2010; Gales et al. 2011; Müller et al. 2011; IWC 2012b), and to the north of Gabon (Hazevoet et al. 2010, 2011; Van Waerebeek et al. 2013).

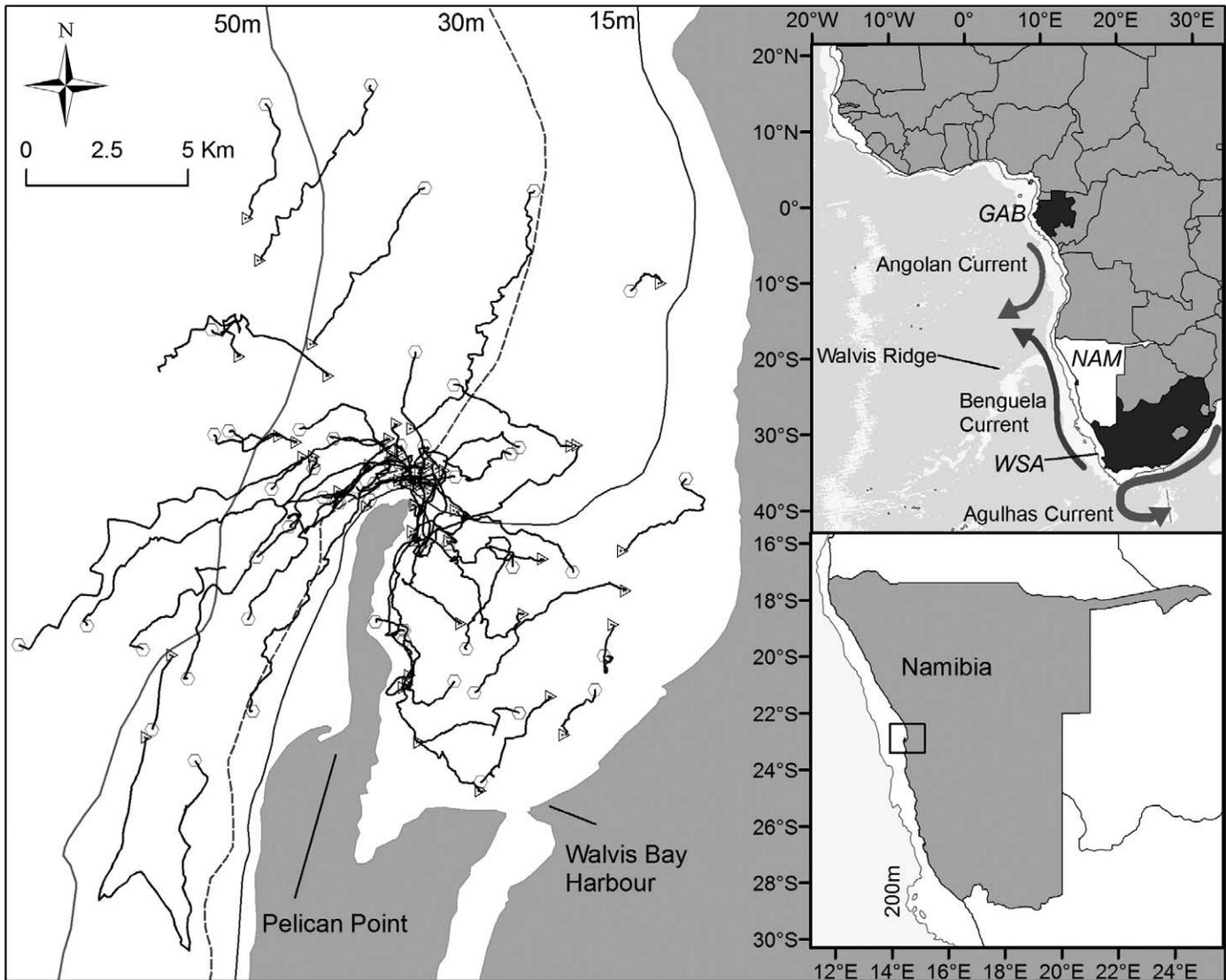
In this paper we describe the seasonality, movement patterns, and behavior of humpback whales observed in the nearshore waters around Walvis Bay, central Namibia ( $22^{\circ}57'$ S,  $14^{\circ}30'$ E), and present an interregional comparison of the differences in the prevalence of scars and wounds caused by killer whales (*Orcinus orca*) and cook-icutter sharks (*Isistius* sp.). In addition, we report on the results of the 1st complete comparison of the Namibian photo-

ID catalog with the Gabon and WSA databases, using tail fluke and dorsal fin images to investigate movements of individuals between study sites. Our objective is to contribute to a better understanding of how humpback whales off Namibia fit into the overall movement patterns and stock structure within BSB, especially the suggested existence of 2 substocks and specifically to evaluate the potential role of the Namibian coast as a breeding ground for substock B2.

## MATERIALS AND METHODS

*Namibian data collection.*—In Namibia, identification images of humpback whales were collected in Walvis Bay ( $23^{\circ}00'$ S,  $14^{\circ}30'$ E) during boat surveys focusing on Heaviside's dolphins (*Cephalorhynchus heavisidii*) and bottlenose dolphins (*Tursiops truncatus*) during the austral winter (June–August) and late summer (February–March) of the years 2008–2012 (Fig. 1). Surveys were focused within the bay and at Pelican Point (northwestern corner of the bay) and search effort in the open ocean and water deeper than 30 m was limited. Humpback whales were rarely encountered but sighting rates were increased due to communication with multiple whale-watching boats operating within the bay. During all encounters of humpback whales made by the research team, data were collected on the group size and composition, relative body size, number of calves in the group, surface behavior, depth, and sea surface temperature at the beginning and end of encounters. A global positioning system track of the route followed during the encounter was automatically recorded. Photographs were taken of the dorsal fins and flanks of whales as well as the tail flukes when exposed. Individuals within a group were identified in the field from fin and fluke characteristics and later through examination of photographic sequences of diving animals. Whenever possible, skin samples were collected from whales using standard biopsy techniques (results to be published elsewhere). Acoustic data were collected during a concurrent study investigating bottlenose dolphin vocal behavior (Kriesell et al. 2014). Recordings were made using a Zoom H4n digital recorder (Zoom Corporation, Tokyo, Japan) with a single HTI-96-MIN hydrophone (sample rate 96 kHz, frequency response  $2$ – $30$  kHz  $\pm$  1dB; High Tech, Inc., Longbeach, Mississippi) deployed from the research boat when stationary or idling. Collection of field data conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Animal Use and Care Committee of the University of Pretoria (AUCC: EC061-09 to SHE).

Seasonal variation in the presence of humpback whales within Walvis Bay, Namibia, was investigated using 2 data sets: our research survey data (expressed as the number of individuals seen per research day on the water) and data from marine tour operators operating in Walvis Bay. Whale-watching data were available from tours conducted year-round and included digital photographs ( $n = 146$ ) of whales collected opportunistically predominantly by a single tour company, many of which have been included in the Namibian catalog;



**FIG. 1.**—Top right: Location of study sites in Gabon, Namibia, and west South Africa (WSA) as well as a simplified representation of the major ocean currents in the region and the 3,000-m isobath highlighting the Walvis Ridge. Bottom right: Location of Walvis Bay and study area within Namibia as well as 200-m isobath highlighting width of shelf. Left: Tracks of humpback whales (*Megaptera novaeangliae*) encountered by the Namibian Dolphin Project research team in and around Walvis Bay, Namibia. Tracks (black lines) are shown with start (triangles) and end (octagons) points to show directionality of movement. Depth contours are shown.

and records of whales present in the bay kept by 2 companies, Eco-Marine Kayak Tours (Walvis Bay, Namibia) from 2005 to 2007, and Catamaran Charters (Walvis Bay, Namibia) from 2010 to 2012. Data from marine tour operators are not corrected for effort: boats are in the water effectively every day of the year but the number of trips (and number of boats on the water) are highest in July–December and lowest in January–May, with August being the busiest month and February the quietest.

*Photographic catalog development for Namibia and comparison with west South Africa and Gabon.*—A photo-ID catalog for Namibia was developed consisting of 339 identification images collected on research trips (2008–2012) and donated from marine tour operators (2007–2012). Sorting and matching of duplicate pictures yielded 132 individual

humpback whales, 98 identified by dorsal fins (110 left and 132 right side images) and 63 by tail flukes (92 images), representing a considerable increase over the smaller preliminary catalog of 35 individuals (tail flukes only) used in Barendse et al. (2011).

The photo-ID database for WSA is described in Barendse et al. (2011), and contains 1,820 identification images comprising 510 views of tail flukes, 616 lateral views of left dorsal fins, and 694 lateral views of right dorsal fins representing 289 individual whales. These represent 154 different individuals identified by tail flukes, 230 by left dorsal fins, and 237 by right dorsal fins. The images were collected between 1983 and 2008 in the area west of Cape Agulhas between about 29°S and 34°S, mostly in the St. Helena Bay and Saldanha Bay areas.



**FIG. 2.**—Example photograph of a humpback whale (*Megaptera novaeangliae*) in Namibia bearing both fresh wounds (highest on dorsal hump and 2 most anterior bites) showing clear color differentiation and pinkness in the center and the pale uniform color of healed scars (2 closest to the water line) resulting from predation attempts by cookiecutter sharks (*Isistius* sp.). Photograph by Alice Affatati, Namibian Dolphin Project.

The Gabonese photographic catalog includes images of humpback whales collected from 4 coastal field sites (Port Gentil, Iguela, Gamba, and Mayumba) during 7 field seasons (July–October) from 2000 to 2006. The version of the catalog used in this study contains 5,896 identification images of whales, of which 2,089 tail fluke images represent 1,297 unique individuals, and a further 1,935 lateral views of right dorsal fins and 1,872 of left dorsal fins. The Gabon database, area of collection, and matching procedures are fully described by Collins et al. (2008).

Tail fluke and dorsal fin images from the Namibian catalog were systematically compared to the WSA (tail fluke and dorsal fin) and Gabonese (tail flukes only) humpback whale catalogs. Because the objective was to identify as many matches as possible, images of all quality, including those showing partial flukes and trailing edges, and distinctiveness were reviewed. Potential matches were identified and checked by at least 3 authors to establish whether they were possible or definite matches.

*Identification of scars and wounds from cookiecutter sharks and killer whales and interregional comparison.*—We recorded the presence–absence of cookiecutter shark bites on the dorsal fin and upper back area of the body (hereafter “dorsal flank”) of humpback whales as well as the presence–absence of killer whale bites on the tail flukes (Fig. 2). We did not consider the presence or extent of cyamids, lesions, or anthropogenic-induced scarring (such as that caused by entanglement in fishing nets or ropes) due to lack of lateral photographs of the tail stock needed to assess entanglement scarring (Robbins and Mattila 2004).

For analysis of scarring, all photographs were visually graded as being of acceptable quality based on the quality of the picture (namely focus, graininess or pixel definition, and lighting) and the amount of body or fluke visible. For dorsal flanks, at least 2 or more times the height of the dorsal fin and hump had to be visible above the water, to account for differences in cropping factor between catalogs and the surfacing position of the whale. For flukes, the entire trailing

edge had to be visible above the water and only good-quality images with both left and right sides of the ventral surface of the tail shown were considered for analysis (i.e., no partial flukes were considered). The angle of flank or fluke relative to the camera was not considered as a factor affecting the ability to see bites or scars.

All the dorsal flank identification images in the Namibia, WSA, and Gabon catalogs were checked for the presence of cookiecutter shark bites. Although these marks are found on tail flukes too, the shape and appearance of bite marks on flukes are more easily confused with those of barnacles due to the higher incidence of the latter on flukes and the high rate of unsuccessful attacks (i.e., partial bites) by cookiecutters on this more turbulent part of the whale’s body (Best 2007).

Cookiecutter shark bites are easily recognized by the unique shape of the wounds left after each attack. The oval open pits (fresh wounds) are of a scooped-out nature, about 7 cm long, 4–5 cm wide, and 3 cm deep, with the long axis usually parallel to the body of the whale (Jones 1971; Best 2007). Some have flabby discs of grayish or brown tissue attached to their center, part of the process of healing, whereas others are only crescent-shaped wounds of varying depths of penetration but with no tissue removed (Best 2007; Dwyer and Visser 2011). We have differentiated between fresh or partially healed wounds (wounds) and old, fully healed bite scars (scars). Fresh wounds were identified from the presence of the flesh coloration of the dermal tissue within the pit as well as the integrity of the crater itself (i.e., clean edges and clear pit shape), and the dual coloration of the wound being pink–dark in middle and paler on outside. Healed bites or scars were identified as depressed scars or “divots” of a similar size to fresh wounds, being most commonly uniformly white or gray with distinctive radiating dark lines that occur due to the healing process (Best 2007). Sometimes the dark lines were missing, probably because of different healing processes among individuals. In some cases, the cookiecutter wounds and scars hosted the whale louse (*Cyamus boopis*), which masked the coloration of the tissue underneath. In these cases the recognition of the mark and definition as either wound or scar relied more on the shape and size of the scar than on the coloration alone.

Both wounds and scars from cookiecutter sharks are easily differentiated from those of barnacles (e.g., *Coronula* sp.), because the latter appear either as thick black or white rings (Fertl and Newman 2009; Dwyer and Visser 2011) or solid gray, black, or white circles. Although we cannot confirm that the bite marks discussed here originate from *Isistius* sp., evidence is accumulating that cookiecutter sharks are the source of many of the wounds and scars on cetaceans (Jones 1971; Shevchenko 1971; Shirai and Nakaya 1992; Moore et al. 2003). Bites from sea lampreys (*Petromyzon marinus* and *Lampetra tridentata*) cannot be ruled out as a source for some of the bite marks observed (Dwyer and Visser 2011). Sea lampreys have been observed elsewhere attached to cetaceans, but the resulting wounds appear different because they are much shallower than wounds attributed to cookiecutter sharks,

often barely breaking the skin (Jones 1971; Shevchenko 1971; Dwyer and Visser 2011).

The relative frequency of individuals with cookiecutter shark wounds or scars was compared between sites using chi-square tests, with left and right dorsal fin data combined. Because of the large size of the Gabon catalog, dorsal fin images had not been assigned a unique identification within the database for all animals and multiple images of the same animal may have been included within and between years. To determine whether this could cause a bias, we analyzed a subset of 791 individuals in the Gabon catalog for which individual dorsal fin identifications were available. This revealed that 62% of these animals were represented by a single image for left or right and 33% had 2 images within the database. Individual repeat rates were higher but similar for Namibia (99% of whales had a maximum of 2 photographs per side) and WSA (75% right dorsal fin and 90% left dorsal fin had a maximum of 2 images per side). Inclusion of more than 1 image for dorsal identification was random with respect to scarring, and resightings within and between the databases were low. Thus, we calculated frequency of wounds and scars and performed analysis on all dorsal fin photographs for each population treating these as a random sample of individuals with some internal repetition, rather than as a catalog of unique individuals. This is similar to the approach used by Steiger et al. (2008) for their analysis of killer whale bite scars on tail flukes. Analysis was done for all 3 regions and each pair of regions, with the *P*-value adjusted using a Bonferroni correction.

*Identification of killer whale bite marks.*—Killer whale bite scars were defined as a set of 3 or more white or black parallel scars in close proximity (Fig. 3), following the definition used by Steiger et al. (2008). Because it is impossible to differentiate between the scars resulting from false killer whale (*Pseudorca crassidens*) bites and those of small killer whales from a photograph alone and there is no clear evidence that false killer whales kill or consume large whales (Best 2007; Mehta et al. 2007), we have assumed for the purpose of this analysis that all “killer whale–like” scars are generated by killer whales and not false killer whales. Because of the small sample sizes we did not differentiate between the degree of damage to flukes (categories 1–3 of Steiger et al. [2008]), but did include a category for possible killer whale–inflicted wounds (equivalent to category 4 of Steiger et al. [2008]) where scars did not meet the definitions above (e.g., there were only 2 parallel scars, or chunks were missing from the fluke but no rake marks were apparent [Fig. 3]).

To calculate the proportion of flukes with rake marks, only a single identification image from each animal in each catalog was used. We investigated differences in the presence of killer whale bite scars on flukes among regions using a chi-square test.

## RESULTS

*Presence and seasonality in Namibia.*—All data were collected in nearshore waters mostly within or just to the

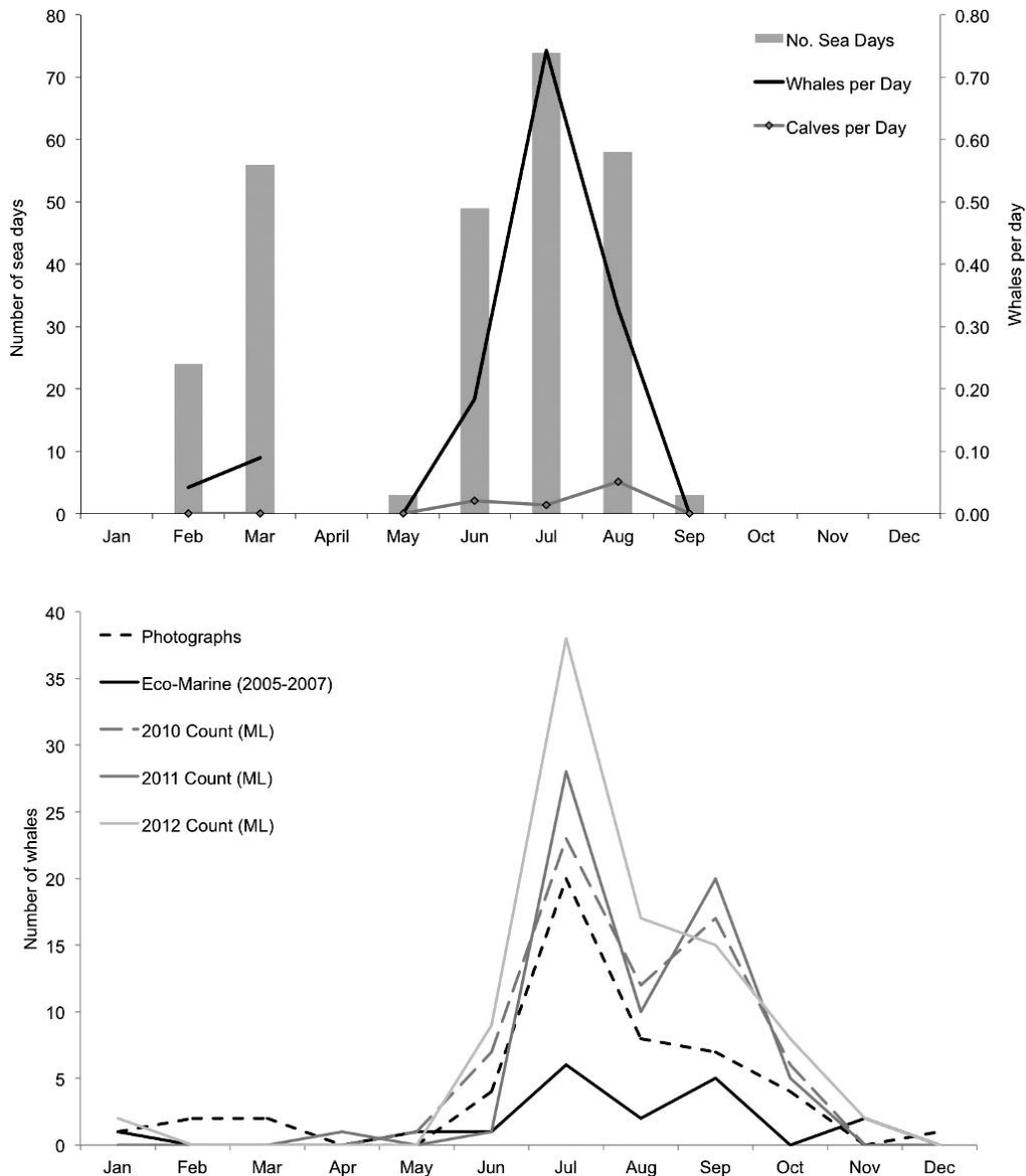


FIG. 3.—Top: Example photographs of humpback whale (*Megaptera novaeangliae*) flukes showing definite killer whale (*Orcinus orca*) rake marks. Bottom: Scars possibly caused by killer whales but not meeting the criteria of 3 parallel rake marks. Photographs by Tess Gridley (top) and Simon Elwen (bottom).

northwest of Walvis Bay and thus represent only a very small part of the area where humpback whales are known to occur off Namibia. Seasonal (monthly) presence of humpback whales in the Walvis Bay area from research survey records and marine tour operators is shown in Fig. 4. Systematically collected records were limited primarily to June–August and show a single clear peak in numbers of whales seen per sea day during July (Fig. 4). Records of calves ( $n = 5$ ) were highest in August ( $n = 3$ ). Two of the encountered calves (28 July 2008 and 9 August 2012) were extremely small and light gray in color, suggesting they had been born very recently.

Records from marine tour operators showed a similar peak in July with a clear secondary peak in September. Data from marine tour operators are not effort-corrected, although July–December is a consistently busy season for operators. With up to 27 boats operating simultaneously within the bay (Elwen et al. 2011) and communicating sightings to each other, there is a very high probability that any whale within or immediately to the northwest of Walvis Bay will be spotted during this time of the year. Consistent records of calf presence were not available from marine tour operators and so have not been included here.

*Directionality of movement and behavior of humpback whales in Namibia.*—Humpback whales were most frequently encountered in the area directly north of Pelican Point, where search effort by both the research boat and marine tour operators was highest. Many animals encountered by the research boat were either accompanied by or had recently been



**FIG. 4.**—Top: Seasonality of humpback whales (*Megaptera novaeangliae*) seen in Walvis Bay, Namibia, by the Namibian Dolphin Project research team, showing number of sea days (bars, left axis) and adjusted total number of humpback whales per sea day and calves only per sea day for each month (lines, right axis). Bottom: Total monthly counts (uncorrected for effort) of individual humpback whales recorded year-round by local whale-watching companies from photographs donated to catalog by Catamaran Charters 2008–2010 (“Photographs”), whales seen and reported year-round (2005–2007) by Eco-Marine Kayak Tours (“Eco-Marine”), and counts of whales seen by or reported to Mike Lloyd of Catamaran Charters 2010–2012 (“ML”). Although not effort-corrected, note that because of peaks in tourism, boat or observer effort is higher in June–December than January–May.

in contact with tour boats and thus subjected to some level of harassment already. Other than a general tendency to move along a track in a southwest to northeast direction (or vice versa, rather than directly along a line north to south or coastwise), there was no clear pattern observable in the directionality of humpback whale movements in the Walvis Bay region (Fig. 1). The general movement pattern of most whales encountered can be best described as “away from” Walvis Bay. Looking only at the relative latitude and longitude of start and end points (winter tracks only June–August), 28 tracks ended north of where they started, whereas 27 ended

more southward; 17 animals moved eastward during tracking and 38 moved westward.

The majority of the 89 humpback whales encountered in Namibia by the research team were single ( $n = 36$ ) or in pairs ( $n = 19$ ). One mother–calf plus escort was seen, as well as a single occurrence of a possible competitive mating group of 5 individuals that included a very small calf; the 3 escorts in the group displayed some signs of surface-active mating behavior (chases and pushes). No other surface-active or mating groups were ever observed by the research team in the 5 years of the study.

Dedicated acoustic recordings of humpback whales were not made during this study. However, singing was never heard in air (through the hull of the boat) or detected in the background during 79 h of recordings analyzed in detail for a study of bottlenose dolphin vocalizations taking place concurrently in 2009, 2011, and 2012 (Kriesell et al. 2014).

*Interregional photo-ID catalog comparisons.*—Relatedness between populations and resightings between and within sites for Gabon and WSA are discussed in detail by Carvalho et al. (2014), Pomilla and Rosenbaum (2006), and Barendse et al. (2011, 2013).

*Namibia–WSA catalog comparison.*—No definite matches could be made between Namibia and WSA using any identification feature. Two possible matches were made from dorsal fins, with photograph quality and low distinctiveness of the individuals being the main factors limiting confirmation. Animal ZAW-275 photographed on 24 November 2005 in St Helena Bay, South Africa, was possibly matched to animal NAM-070 photographed on 26 September 2008 in Walvis Bay. Animal ZAW-141 photographed on the 19 July 2002 in Saldanha Bay, South Africa, was possibly matched to NAM-078, photographed on 7 July 2011 in Walvis Bay, Namibia.

*Namibia–Gabon catalog comparison.*—No possible or definite matches were found between the tail fluke catalogs from Namibia and Gabon.

*Comparison of scarring rates between regions.*—The prevalence of cookiecutter shark bites on the dorsal flanks of humpback whales was calculated separately for left and right sides and for wounds and healed scars (Fig. 5). Because of the similarity between left and right side results at each location, sides were combined for statistical analysis. The short duration of field seasons in Gabon and Namibia prohibited analysis of seasonal patterns. Scars of old cookiecutter shark bites were present on animals at all study sites but the prevalence differed significantly between regions ( $\chi^2_2 = 66.6$ ,  $P < 0.0001$ ). The prevalence of such scars was highest in Gabon, whereas WSA and Namibia did not differ significantly in scarring rates ( $\chi^2_2 = 4.96$ ,  $P = 0.08$ ). The prevalence of fresh cookiecutter shark bites differed significantly between regions ( $\chi^2_2 = 148.72$ ,  $P < 0.0001$ ). All regions were significantly different from each other when compared in a pairwise fashion, with the highest prevalence of fresh bites seen in Namibia, followed by Gabon. Only 2 dorsal fin photographs (different animals, 1 left side and 1 right side) from WSA contained fresh cookiecutter shark bites.

Scars from killer whale bites on the flukes of humpback whales were seen at a similar prevalence in all study sites (Gabon: 29%; Namibia: 24%, WSA: 35%; Fig. 6) and did not differ significantly between regions ( $\chi^2 = 4.3107$ ,  $P = 0.36$ ).

## DISCUSSION

The current timing of humpback whale presence in central Namibia is very similar to the bimodal peak observed in the commercial catch data in the early part of the 20th century (Best and Allison 2010), supporting the hypothesis that central

Namibia is in the middle of a migration path and not a breeding ground. The smaller secondary peak (southward migration) seen in the current data suggests that many animals may migrate southward farther from shore, or take a more direct transoceanic route toward Southern Ocean feeding grounds than on the northward migration. The existence of an offshore route is supported by evidence from animals fitted with satellite tags in Gabon, which shows southward-migrating animals using either an offshore route (in which they apparently followed the Walvis Ridge offshore from where it strikes the continental shelf around the Namibia–Angola border) or a more coastal migration route remaining on the continental shelf (Rosenbaum et al. 2014).

The scarcity of competitive groups, low number of calves, and lack of singing detected further support the function of the Namibian coastline as a migration route and not a breeding area.

No definite photographic matches of individuals were found between Namibia and Gabon (tail flukes only) and only 2 possible matches were made between Namibia and WSA using dorsal fins. Conversely, 11 individuals have been resighted or biopsied in both Gabon and WSA (Barendse et al. 2011; Carvalho et al. 2014), despite the greater distances involved and the relatively small size of the WSA catalog and population. Possible explanations for this include a higher sampling rate in WSA than in Namibia, or an undersampling of southward-migrating animals off Namibia due to the seasonality of sampling effort.

At face value, the lack of matches between Gabon and Namibia fails to support the hypothesis that there is panmixia between these regions. Nevertheless, several factors must be taken into account. The Namibian catalog (2008–2012) does not overlap temporally with those of either WSA (1983–2007) or Gabon (2000–2006), so there is a potentially reduced likelihood of recaptures of Gabon animals in Namibia. As a rough estimate of this, the number of humpback whales that visit Gabonese waters was estimated at 9,310 in 2005 under the 2-stock hypothesis (IWC 2012a). If the population has continued to increase at the rate of 3.9–5.3% per annum previously estimated (Müller et al. 2011), it would number 12,170–13,360 in 2012. At the same time, the catalog of known individuals would have declined because of mortality: using the lowest (0.925) and highest (0.984) plausible mean survival rates calculated for humpback whales from Zerbini et al. (2010), the catalog might have shrunk from 1,297 to 752–1,159 individuals by 2012. Assuming the extremes (low catalog survival plus high population increase rate, and high catalog survival plus low population increase rate), between 5.6% and 9.5% of the Gabon humpback whale population in 2012 should have been “marked” in 2012. If there was panmixia between Gabon and Namibia, then the Namibian sample of 63 tail flukes should have contained between 4 and 6 individuals from the Gabon catalogue.

A similar comparison is difficult to make with WSA due to the long time span (> 20 years) over which that catalog has been developed and the mixture of animals encountered there

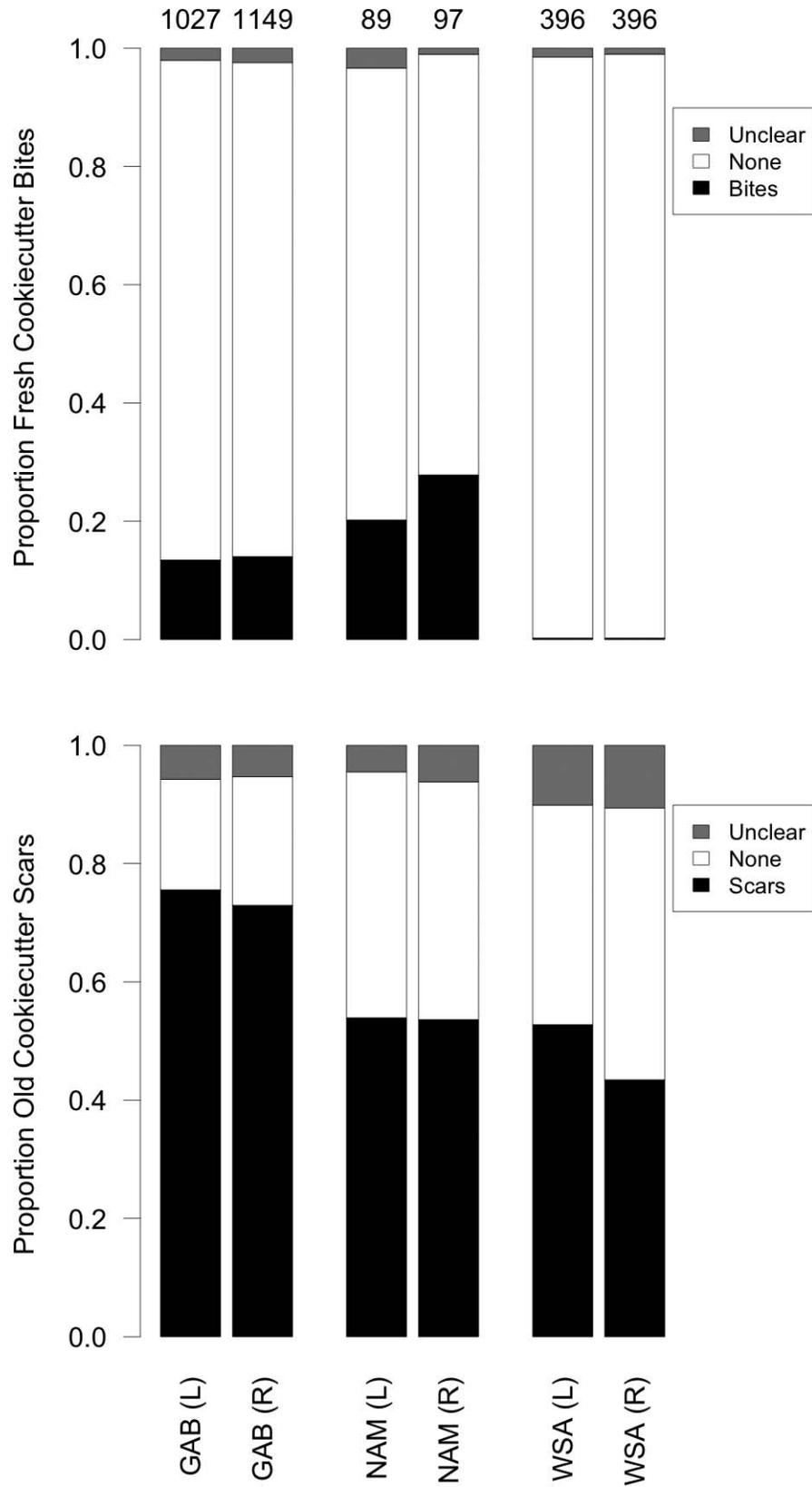


FIG. 5.—Prevalence of fresh wounds (top) and healed scars (bottom) from the bites of cookiecutter sharks (*Isistius* sp.) on the dorsal fins and flanks of humpback whales (*Megaptera novaeangliae*) in Gabon (GAB), Namibia (NAM), and west South Africa (WSA). Left-side (L) and right-side (R) flanks are shown separately; sample sizes are shown above the bars. Note that for WSA, a single record of a fresh bite was observed in both the left- and right-side databases (different individuals).

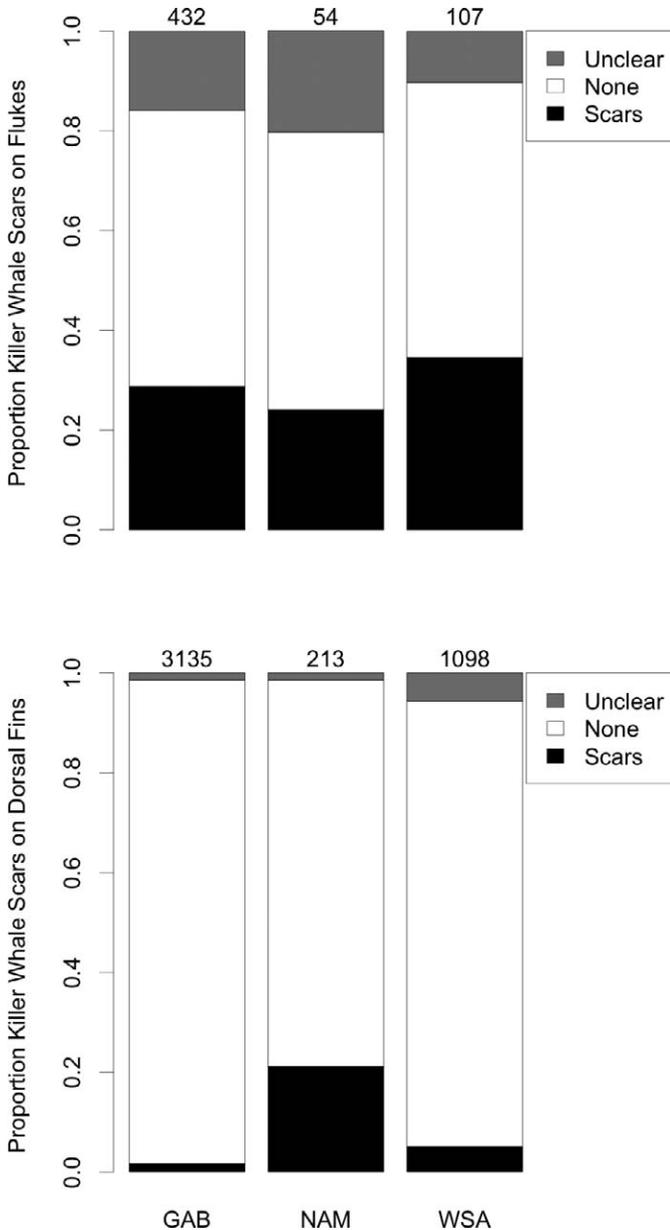


FIG. 6.—Prevalence of killer whale (*Orcinus orca*) bite scars on the tail flukes of humpback whales (*Megaptera novaeangliae*) in Gabon (GAB), Namibia (NAM), and west South Africa (WSA). Sample sizes are shown above bars.

that are considered to be either migrating past or part of a nonmigratory feeding population (Barendse et al. 2013). However several additional factors may have played a role in reducing the probability of resighting animals from Gabon in Namibia, including the known differences in sex and age ratios between feeding, breeding, and migratory areas (see Steiger et al. [2008] for a more detailed discussion), and differential patterns in seasonal attendance by animals of different sex and reproductive state as described for WSA (Barendse et al. 2013; Carvalho et al. 2014). Consequently, the timing of data collection at the 3 study sites may play a role in the lack of resightings and provide further insight into migration patterns.

With the exception of a low photographic sample of the southern migration in Namibia (September), the dates of data collection largely reflect peak whale presence at each of the 3 study sites with peaks of photograph numbers in Namibia in July, in Gabon in August, and in WSA from October to January. Almost all animals photographed in Namibia were on their (presumed) northward migration in August, whereas few of the animals photographed in WSA were captured during the northward migration. It has been suggested that the majority of animals migrating north to Gabon strike the coast well north of the WSA study site (Barendse et al. 2011) and potentially use a transoceanic migration route for most if not all of their migration (Best and Allison 2010). Even if only some of these individuals subsequently follow an offshore migration route southward (thereby avoiding WSA altogether), it would greatly reduce the number of animals likely to feature in both catalogs. Of the 9 whales resighted in both Gabon and WSA (Carvalho et al. 2014), 4 were encountered in the same season (see below) and all had moved from north to south presumably following a “coastal” migration route over the continental shelf that would pass through Namibian waters. However, due largely to logistical reasons, the photographic sample of the southward migration stream in Namibia is very small (3 tail flukes), meaning that undersampling is a distinct possibility.

In summary, although the lack of matches between Gabon and Namibia might suggest a lack of panmixia, the extent and seasonal coverage of sampling in Namibia have been insufficient to reach such a conclusion. Given the limitations and increasing ages of the existing databases, further application of photographic identification data seems to be of limited value without a massive increase in survey effort. Effort ideally needs to focus on areas and periods that have been poorly covered in the past such as the Angolan coast and offshore Namibia and South Africa and the southward migration and summer months in Namibia.

Attacks from the cookiecutter shark are very common on humpback whales worldwide (Mikhalev 1997; Mattila and Robbins 2008; Fleming and Jackson 2011). Three species of *Isistius* are currently recognized, *I. brasiliensis*, *I. plutodus*, and *I. labialis* but because of the apparent rarity of the latter 2 species (Meng et al. 1985; Kiraly et al. 2003), we have assumed that the majority of bites on humpback whales in Namibia are likely to have been caused by *I. brasiliensis*. This shark is found in the pelagic waters of tropical and subtropical oceans (Jahn and Haedrich 1987; Nakano and Nagasawa 1996; Dwyer and Visser 2011), in sea surface temperatures between 18°C and 26°C (Nakano and Tabuchi 1990; Nakano and Nagasawa 1996; Yamaguchi and Nakaya 1997). In the South Atlantic, the 18°C isotherm lies close to 40°S, and outside of the Benguela Ecosystem (National Oceanic and Atmospheric Administration 2013). Records of cookiecutter sharks in the South Atlantic reach as far south as ~40°S (Fishbase 2013), but the Namibian and WSA study sites lie within the Benguela Upwelling System, which stretches along the entire west coast of southern Africa as far north as approximately 14°S at the Angola–Benguela Front, and from 200 to 750 km offshore,

with sea surface temperatures generally  $< 15^{\circ}\text{C}$  (Ansorge and Lutjeharms 2007; Hutchings et al. 2009). Given their oceanic nature and general preference for warmer waters, cookiecutter sharks are unlikely to occur inshore within the cooler waters of the Benguela Upwelling Ecosystem (Compagno et al. 2005).

The prevalence of cookiecutter shark bite scars or wounds varies between populations and scarring has been used previously as a potential population identifier for fin whales (*Balaenoptera physalus*—Moore et al. 2003), sei whales (*B. borealis*—Shevchenko 1977), Bryde's whales (*B. edeni*—Best 1977), and Arabian Sea humpback whales (Mikhalev 1997). Whales in Namibia and WSA (i.e., within the cool Benguela Ecosystem) had the same level of cookiecutter scarring, suggesting similar levels of long-term exposure to predation, whereas animals in Gabon exhibited higher levels of scarring and thus long-term exposure to cookiecutter shark predation. This suggests, firstly, that at least some animals seen in both WSA and Namibia spend time in warmer waters farther north or offshore where they are exposed to cookiecutter sharks (a behavior that was already known for WSA from photographic and genotypic matches with Gabon [Barendse et al. 2011]) and secondly, that at least some level of differentiation occurs between the populations in Gabon and Namibia–WSA. It is difficult to make further conclusions based on these data without better information on the distribution of cookiecutter sharks and the location where most bites occur relative to migration routes, but the higher incidence off Gabon would suggest that these whales spend more time exposed to cookiecutter shark attacks during their annual migrations. Known offshore migratory routes for some of these whales (Rosenbaum et al. 2014) would be consistent with this suggestion.

The prevalence of fresh cookiecutter shark bites is strikingly different from that of healed scars. Namibian whales had the highest prevalence of fresh bites (24.2%), with Gabon having more moderate levels (13.7%) despite being a warm tropical area where cookiecutter sharks are thought to occur. The tighter cropping factor on dorsal fin images in the Gabon catalog may have led to an underestimate of prevalence in this population. The most striking result of this comparison is the almost total lack of fresh bites observed in WSA. The majority of images in the Namibian catalog were taken during the expected period of northward migration (June–August), and the number of fresh bites seen suggests that a large proportion of animals may have taken a transoceanic route to reach Namibian waters. Most images in the WSA database were taken during the summer feeding season, corresponding to the highest sighting rates (October–January, and after the Gabonese breeding season [Barendse et al. 2011]). Wound healing in large whales is poorly studied, but shallow wounds in dolphins from propeller cuts or shark bites close within 30–45 days and heal to scars within 90–150 days (Orams and Deakin 1997; Elwen and Leeney 2010; Dwyer and Visser 2011). The lack of fresh bites in WSA therefore suggests that animals encountered here had been resident for extended periods (probably a minimum of 30 days) within the Benguela, possibly following

a slow migration southward over the continental shelf, or making extended use of localized feeding opportunities inshore (Barendse et al. 2013). Four whales biopsied in Gabon between 14 August and 26 September between 2001 and 2005 were encountered in either the same year off WSA between 17 October and 16 December or in the following year on 10 January, that is, with individual transit times of 43–123 days (average 82 days—Carvalho et al. 2014). These are likely to be maximum values, because they assume a direct transit, but they seem to be sufficient for healing of wounds contracted in or near Gabon to occur. The cookiecutter shark data support the concept that many animals on their northward migration to BSB strike the coast well north of the WSA study site (including in Namibia) as put forward by Olsen (1914) and Barendse et al. (2010) but also suggest that the animals seen feeding off WSA in late spring to late summer are likely to be animals that have completed a southward migration staying mainly inshore within the Benguela Ecosystem.

Differences in the prevalence of killer whale bite scarring between populations and between feeding–breeding areas of large baleen whales have been used to interpret stock separation and migration routes (Mehta et al. 2007; Steiger et al. 2008). Very little is known about movement patterns, relative density, or stock structure of killer whales off the west coast of Africa and the South Atlantic. We do know that killer whales are present year-round throughout the BSB area from WSA to the Gulf of Guinea where they have a broad diet, including cetaceans. They have been seen in all water depths surveyed from the coast to  $> 2,600$  m depth (Best et al. 2010; Weir et al. 2010; Elwen and Leeney 2011). Scarring rates on flukes (using only a single image for each whale) were similar among all study sites, suggesting similar levels of killer whale predation at all sites or along the migration routes leading thereto. The apparent ubiquity of killer whales in the South Atlantic may explain the similar levels of bite scars seen at the 3 study sites.

The hypothesis that the southern Angolan and entire Namibian coasts may form a breeding ground separated from that to the north (including Gabon) by the Walvis Ridge or Angola–Benguela Front between  $14^{\circ}\text{S}$  and  $17^{\circ}\text{S}$  (IWC 2012b; Fig. 1) is not supported by the findings of this paper, at least so far as the Namibian coast from Walvis Bay southward is concerned. Furthermore, the oceanography of the area south of the Angola–Benguela Front, the bimodal nature and timing of migration peaks from catch data (Best and Allison 2010; this study), and the female-biased sex ratio (Best 2011) are all inconsistent with the characteristics of any other known humpback whale breeding ground (Rasmussen et al. 2007).

The migration routes followed by humpback whales between high-latitude feeding grounds and low-latitude breeding grounds vary widely, with some populations following more coastal routes (e.g., east coast of Africa and Australia—Chaloupka et al. 1999; Findlay et al. 2011), whereas others are almost entirely transoceanic (e.g., the western North Atlantic [Stevick et al. 2003] and western South Atlantic [Horton et al. 2011]). Rosenbaum et al. (2009)

suggested that coastal Namibia may act as a migration corridor for animals moving between the WSA feeding ground and an unsurveyed breeding area farther north (but south of sampling sites off Gabon) and likely off Angola. Since that time, it has been suggested that an unsurveyed breeding area may actually be located to the north of Gabon (Rosenbaum et al. 2014). The relatively low numbers and lack of pattern in directionality of movement of whales observed in the coastal waters of central Namibia (surveyed up to ~10 km offshore) during the current study do not support the hypothesis of this area being a major coastal migration route equivalent to that off Cape Vidal on the east coast of southern Africa (Findlay et al. 2011). The continental shelf at Walvis Bay is very wide with the 200-m isobath located approximately 100 km offshore; thus, whales following a migration route along the continental shelf may be spread widely across the shelf and into deeper waters.

The paper provides the only available current information on humpback whale presence, seasonality, movements, and scarring in Namibia and the 1st complete comparison of the photo-ID catalogs between Namibia and regional databases in Gabon and WSA. We have collated multiple lines of evidence and discussed them within the framework of some existing hypotheses regarding population structure within BSB off the west coast of Africa.

Combined, examination of these data suggests that humpback whales migrating up the west coast of Africa to the BSB breeding ground(s) on their northward migration are converging on the coast at multiple points mostly north of the WSA study site. The smaller southward migration peak seen in nearshore Namibia, known use of the Walvis Ridge route by some animals moving south from Gabon, the timing of whale presence, and lack of fresh cookiecutter shark bites in WSA all support the suggestion of at least 2 different southward migration routes and possibly destinations. Whales seen in the feeding ground off WSA and also documented from the Gabon breeding ground have likely moved there following a coastwise route through the cold Benguela Ecosystem, where no fresh cookiecutter shark bites are likely to have occurred and the ones gained in tropical waters to the north may have healed. The WSA feeding ground is associated with a localized upwelling cell (Barendse et al. 2010). Similar upwelling cells occurring in the northern Benguela Ecosystem in Namibian waters may provide further feeding opportunities for whales.

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