

Humpback whales in Namibia 2005-2012: occurrence, seasonality and a regional comparison of photographic catalogues and scarring rates with Gabon and West South Africa.

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ABSTRACT

Southern Hemisphere humpback whales are divided by the IWC into seven breeding populations or stocks. Breeding Stock B (BSB) off the west coast of Africa is further divided into two substocks referred to as BSB1 and BSB2, based primarily on genetic evidence of population separation (mtDNA & nuDNA) between study locations in West South Africa (WSA at ~33°S) and Gabon (~0-4°S). However, very little data are available in the ~3500km between WSA and Gabon and the location of BSB2's breeding ground remains unknown. Here we collate all available data on humpback whales in Namibia (~23°S) from 2005-2012 and compare these with existing data and catalogues from Gabon (2000-2006) and WSA (1983-2007), including a photographic catalogue of dorsal fin and tail fluke images, seasonality and a photographic assessment of scarring and wounds from cookiecutter sharks (*Isistius brasiliensis*) and killer whales (*Orcinus orca*). The Namibian catalogue consisted of 132 individuals (69 by tail flukes only) photographed between 2008 and 2012. Only two possible matches were made to the WSA catalogue by dorsal fin ID, none to Gabon. Probability of resighting animals between these catalogues is reduced by their size and relative ages. The bimodal seasonality, with a lack of singing and low number of calves observed during the smaller secondary peak, suggest the central Namibian coast acts primarily as a migration route to areas further north, although the lack of directionality and low numbers suggest it is not a major stream and many animals are further from shore on their southward migration. The proportion of killer whale bite scars on humpback flukes was similar in all sites. Healed scars from cookiecutter sharks were highest in Gabon and similar between Namibia and WSA, while fresh bites were highest in Gabon, intermediate in Namibia but almost non-existence in WSA. These results support the hypothesis of multiple migration streams within BSB with animals seen in NAM striking the coast directly from offshore warmer waters (where cookiecutter sharks are prevalent) on their northward migration, while animals encountered in WSA, where they were feeding after the southward migration, were likely to have followed a slow coastwise migration southwards within the cold Benguela Ecosystem, allowing time for cookiecutter bites to heal. These results do not support the concept of BSB2 lying within Namibian waters to the south of the Walvis Ridge.

HUMPBACK WHALES, BREEDING STOCK B, MARK-RECAPTURE, MIGRATION, PHOTO-ID, KILLER WHALE, COOKIE CUTTER SHARK, ISISTIUS

INTRODUCTION

Background

In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) feed in circumpolar Antarctic waters and migrate northwards to relatively discrete breeding grounds in tropical waters (Clapham, 1993, 2000; Stevick *et al.*, 2003; Rasmussen *et al.*, 2007). Seven breeding populations or 'management areas', labelled as Breeding Stocks A-G (IWC, 1998), are recognized by the International Whaling Commission (IWC) in the Southern Hemisphere. These populations are assigned with varying confidence to six summer feeding Areas (I-VI) in the Antarctic (Donovan, 1991). Some movement between these feeding areas is very 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 Breeding Stock B (BSB) and are thought to feed in Areas II (60° W-0°) and III (0°-70° E) (Barendse *et al.*, 2010).

The IWC agreed to a moratorium on commercial whaling, which took effect in 1982. Since this agreement, one goal has been to perform a comprehensive assessment of all whale stocks. The comprehensive assessment of southern hemisphere humpback whales has been on the agenda of the IWC since at least 1997 with progress made on some fronts such as estimates of abundance and rate of increase for many stocks, but hampered by a lack of a good catch series data for many areas (Gales *et al.*, 2011). By 2005, sufficient data were felt to be in hand to begin the Comprehensive Assessment of Southern Hemisphere humpback whales. Five years (2007-2011) were dedicated to assessing stocks B and C around Africa.

During the Comprehensive Assessment process, it was concluded that Breeding Stock (BS) B was further divided into two breeding sub-stocks, based primarily on genetic evidence of population sub-structuring (Rosenbaum *et al.*, 2009) between study sites in Gabon (~0-4°S) and west South Africa (33°S). BSB1 and BSB2 (IWC, 2010) were thought to have partially overlapping distributions in migration routes and breeding ground, however existing data were insufficient to assess the degree of overlap or mixing between these populations (Gales *et al.*, 2011) and the actual geographical location of this breeding ground for BSB2 is unknown (Barendse *et al.*, 2010). Some have proposed the Walvis Ridge or the frontal region between the Angola and Benguela currents (between 14°-17° S) as a possible boundary between the two grounds (IWC 2010, Fig. 1), although the female biased sex ratio of catches (Best, 2011) and the oceanography of the area south of Angola-Benguela front is inconsistent with any other known humpback breeding ground (see discussion in Best and Allison 2010).

Moreover, recent studies suggest that the west coast of South Africa, which should function largely as a migration corridor given its latitude (cf. east coast: Findlay, Best, & Meyer, 2011; Findlay & Best, 1996), also serves as a seasonal spring/summer feeding ground for a small number of humpbacks, some of which have also been identified in Gabon (Barendse *et al.*, 2010). During the Comprehensive Assessment of BSB, several potential stock structure models were proposed (Müller *et al.*, 2011), although a conclusive definition of sub-stock boundaries within BSB is hampered by the almost total lack of genetic or individual ID data available in the ~3500km between Gabon and west South Africa, including the waters of Angola and Namibia. Further, the extent and nature of the breeding grounds north and west of Gabon may be more complex than previously thought, with Southern Hemisphere humpbacks possibly reaching as far as the Cape Verde Islands (Hazevoet *et al.*, 2011).

One of the views of the structure within BSB is provided by Best and Allison (2010). From their analysis of historical whaling catch data and the occurrence and timing of distinct seasonal peaks in catches (which represent northward or southward migrations) at various locations between west South Africa and Gabon, they concluded that the coastal waters of southern Angola, Namibia and west South Africa all function as a migratory corridor to a single breeding ground further north. They argue that differences observed between GAB and WSA in the mtDNA may be a result of a maternally inherited site fidelity to specific feeding grounds with different components of the BSB population using alternative routes to move between the coastal breeding grounds in Gabon, and southern feeding grounds, using both offshore and more inshore routes (Best and Allison, 2010), where they become available to current research efforts.

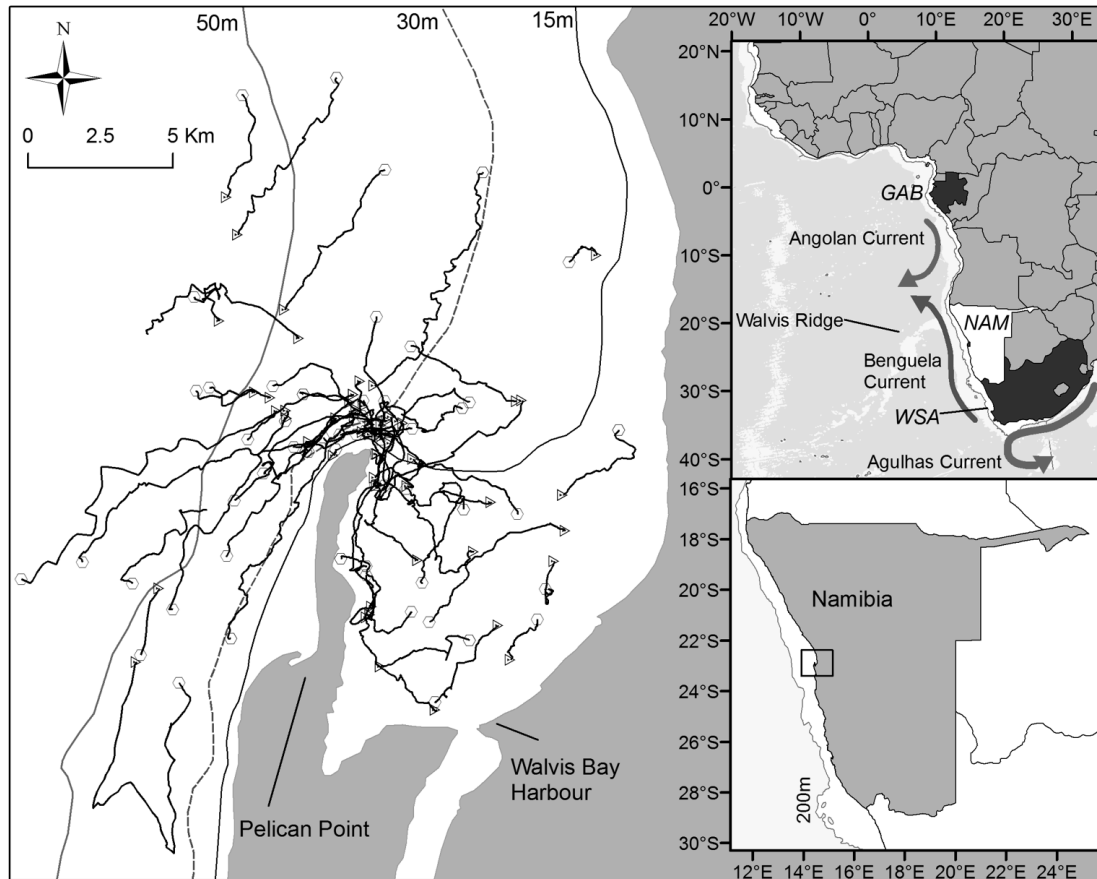


Fig 1. Top Right: Location of study sites in Gabon (GAB), Namibia (NAM) and west South Africa (WSA) as well as a simplified representation of the major ocean currents in the region and the 3000m isobath highlighting the Walvis Ridge; Bottom Right: location of Walvis Bay and study area within Namibia as well as 200m isobath highlighting width of shelf; Left: Tracks of humpback whales 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 as grey lines.

More recent information on the distribution and seasonality of humpback whales in (primarily northern) Angolan waters is available in Weir (2007, 2010), while whaling catches and opportunistic sightings from this area up until 1998 are reviewed in Best and Allison (2010). The majority of evidence shows humpback whales in Angola to have a clear bimodal seasonality in presence with a northward migration peak in May-July and a southward migration peak in August-November. More recent (2004-2009) sightings by Weir (2011) in northern Angola show only a single peak (June-October), but migration direction data are not provided. It is plausible that the population has increased sufficiently that the numbers alone mask the pattern of northward and southward migration peaks, as was observed in the very first years of catch data from Angola before populations started to collapse (Best and Allison 2010). The current distribution of humpback whales off Angola shows them to be distributed from the coast out to a depth of almost 4000 m, although the majority of sightings were on the shelf (<200m; Weir 2011) supporting earlier observations from whaling catch data (Townsend, 1935; Budker and Collignon, 1952; Best and Allison, 2010). The presence of singing (Cerchio et al., 2010) and the high proportion of calves (Best et al., 1999) off northern Angola (Cabinda Province, north of the Angola-Benguela Front) suggest that this area is an active breeding habitat.

Humpback whales were caught commercially off Namibia from shore-based stations from 1912 to 1914 and from 1923 to 1930 (Best and Allison, 2010). Catches showed a clearly bimodal pattern in the seasonal presence of humpback whales in Namibia, reflecting peaks in the northern (Jun-Jul) and southern (Oct-Nov) migration streams. Apart from some images (n=35 individuals from tail flukes only) from Walvis Bay that were compared to West South Africa (Barendse et al., 2011), no more recent published data are available. Namibia has been identified by the International Whaling

Commission as an area of importance from which data are urgently needed to help assess population structure and abundance of southern hemisphere humpback whale stocks (IWC, 2010).

This paper reports the results of the first complete comparison of the Namibian photo-ID catalogue with the Gabonese and South African databases, using tail fluke and dorsal fin images to investigate intra-regional movements of individuals, which will hopefully contribute to a better understanding of the movements and stock structure within BSB. In addition, we have also undertaken a regional comparison of the differences in the prevalence of scars and wounds caused by killer whales (*Orcinus orca*) and cookiecutter sharks (*Isistius* sp.) and describe the seasonality of humpback whales observed in the near-shore waters around Walvis Bay, central Namibia (22°57'S, 14°30'E).

Photographic mark-recapture of humpback whales

Photographic identification of individual humpback whales, for the purpose of mark-recapture, is a well-established technique. Humpback whales may be identified from either the shape, scarring and colour patterns on their tail fluke (Katona et al., 1979; Mizroch, 2003); or lateral views of the dorsal fin and back where shape, knuckles and scarring or pigmentation may be individually distinctive (Kaufman et al., 1987; Barendse et al., 2011). Although the use of dorsal fins and lateral body markings has yielded successful matches (Gill et al., 1995), the more distinctive flukes are preferred for photo-identification purposes in most studies (Barendse et al. 2011). The exposure of flukes, however, can vary between individual whales and across regions, which may affect individual capture probability (Perkins et al. 1984, 1985), whereas dorsal fins are always exposed and more easily photographed (Gill et al., 1995). Off West SA less than 60% of whales had flukes photographed presumably due to their behaviour (Barendse et al., 2011), a feature in common with humpbacks in Namibian waters (S. Elwen pers. obs.); therefore we included both tail flukes and dorsal fins as matching features in this study.

Use of scars to investigate population structure.

Scars and marks on either the dorsal fins or tail flukes may result from attacks by predators, anthropogenic activities (Jensen and Silber, 2003; Fleming and Jackson, 2011; Meyer et al., 2012) and the hosting of various parasites or epibionts such as barnacles, fungal or viral infections (Bossart et al., 1996; Higgins, 2001; Flach et al., 2008). Variation in the prevalence of scarring or parasite loads can provide insight into the structure within a population due to geographic or temporal variation (Best, 1969, 1977; Smith et al., 1999; Steiger et al., 2008).

The killer whale is the most common predator of humpback whales (Jefferson et al., 1991), although attacks are rarely observed in the field (Clapham, 1996; Naessig and Lanyon, 2004). Most attacks are largely confined to young calves and predation may thus have a significant influence on survival during the first years of life (Mehta et al., 2007; Steiger et al., 2008) while scarring on adult animals is likely to be relatively constant between years. Instances of survived predation attempts can be inferred by the presence of the distinctive parallel tooth “rake” marks of killer whale teeth on the flukes and fins of prey species including humpback whales (Shevchenko, 1975). Scarring rates vary in frequency between areas and provide insight into the level of killer whale predation on a population, within a region or migration route (Mehta et al., 2007; Steiger et al., 2008). False killer whales (*Pseudorca crassidens*) may also attack humpback whales (Best, 2007) including possibly in Gabon (Weir et al. in review). Due to the inability to differentiate between the scars resulting from a bite of false killer whales and those of small killer whales from a photograph alone, and the inconclusive evidence of actual killing and consumption of marine mammals (Best, 2007; Mehta et al., 2007), we have chosen to disregard possible predation by this species in further analysis.

Attacks from the cookiecutter shark are also very common on humpback whales worldwide (Mikhalev, 1997; Mattila and Robbins, 2008; Fleming and Jackson, 2011). Two species are known to occur; *Isistius brasiliensis* which is relatively common and *Isistius plutodens* which appears to very rare globally (Kiraly et al., 2003). Due to the rarity of *I. plutodens*, we have assumed from here on that the majority of bites on cetaceans are thus likely to have been caused by *I. brasiliensis* and refer exclusively to this species from here on. *Isistius brasiliensis* is a small squaloid shark found in the pelagic waters of tropical and sub-tropical oceans (Jahn and Haedrich, 1987; Nakano and Nagasawa, 1996; Dwyer and Visser, 2011). Although known to dive deeply (up to 3700m depth, Compagno, Dando, & Fowler, 2005) within its pelagic habitat, its range appears to be restricted by water temperature, with distribution records limited to area with SST between 18° and 26° (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 (NOAA Office of Satellite and Product Operations¹). Records of cookiecutter sharks in the South Atlantic reach as far south as ~40°S (V. Shevchenko, 1974, FishBase²), supporting the temperature limited distribution of this species (Nakano and Nagasawa, 1996). Cookiecutter sharks have a unique parasitic foraging strategy that enables them to prey on animals much larger than themselves (Papastamatiou et al., 2010), this involves biting off plugs of flesh from large predators such as tunas, swordfish and cetaceans (Best, 2007). Evidence of this comes from the crater-shaped wounds found on fish and cetaceans which match the plugs of flesh found in the stomachs of cookiecutter sharks, as well as the unusual nature of their dentition (Shevchenko, 1974; Heithaus, 2001; Best, 2007). Forty-nine species of cetaceans have been reported in the literature with cookiecutter shark bites (Dwyer and Visser, 2011).

The entire Namibian coastline and the WSA study site lie within one of the world's major eastern boundary upwelling systems, the Benguela ecosystem (Hutchings et al., 2009): a cold water (mostly <15°C) wind-driven upwelling system which stretches along the west coast of southern Africa from 34°S (Africa's southernmost tip) to as far north as approximately 14°S at the Angola-Benguela Front; and from 200 to 750 km offshore (Ansorge and Lutjeharms, 2007; Hutchings et al., 2009). Cookiecutter sharks have a tropical to sub-tropical distribution and are thus unlikely to occur within the Benguela Ecosystem (Compagno et al., 2005).

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). Humpback whales within the BSB area have been estimate to migrate at 63-79 km per day (Best and Allison, 2010), making the NAM field site at Walvis Bay (23° S) roughly 9.5-16 days travel time (750-1000 km) from the Angola-Benguela Frontal region (14-17° S). It is thus likely that a whale observed with fresh bites in the near-shore waters of the NAM study site has either a) recently migrated into coastal waters or b) moved recently southwards from tropical waters north of the Angola-Benguela Front rather than having migrated slowly along the coast from the WSA study site and cooler waters to the south, where the water temperature conditions are well below the presumed tolerance of cookiecutter sharks.

MATERIAL AND METHODS

Namibian data collection and catalogue comparison with WSA and GAB

In Namibia, identification images of humpback whales were collected in Walvis Bay (23°00'S, 14°30'E) during boat surveys focussing on Heaviside's (*Cephalorhynchus heavisidii*) and bottlenose dolphins (*Tursiops truncatus*) during the austral winter (June - August) and summer (January - March) of the years 2008-2012 (Fig 1.). Humpback whales were rarely encountered but sightings were increased due to communication with multiple whale watching boats operating within the bay. Additional photographs were added to the NAM catalogue through donation of opportunistically taken images from several tour operators from the period 2007-2012. The Namibian catalogue, to date, consists of 339 identification images. Sorting and matching of duplicate pictures yielded 132 individual humpback whales, 98 identified by dorsal fins (247 images) and 63 by tail flukes (92 images) representing a considerable increase on the smaller preliminary catalogue of 35 individuals (tail flukes only) used in Barendse *et al.* (2011).

The photographic database for west South Africa (WSA) is described in Barendse *et al.* (2011a), and contains 1820 identification images of ventral flukes and dorsal fins, namely 510 views of tail flukes (TF), 308 lateral views of left dorsal fins (LDF) and 321 lateral views of right dorsal fins (RDF), representing 154 different individual humpback whales identified by TF, 230 by LDF and 237 by RDF. The images were collected between the years 1983 and 2008 in the area west of Cape Agulhas between about 29-34° S mostly at St Helena and Saldanha Bays.

The Gabonese (GAB) photographic catalogue includes images of humpback whales collected from four coastal field-sites in Gabon (Port Gentil, Iguela, Gamba and Mayumba) during seven field seasons

¹ <http://www.ospo.noaa.gov/Products/ocean/sst/contour/index.html>

² <http://www.fishbase.org/summary/isistius-brasiliensis.html#>

(July-October) in 2000 to 2006. The latest version of this catalogue used in this study contains 6640 identification images of whales, of which 2089 TF images represent 1297 unique individuals, and a further 1935 lateral views of RDF and 1872 of LDF. The GAB database, area of collection and matching procedures are fully described by Collins *et al.* (2008).

All images in the NAM catalogue were systematically compared to the tail fluke and dorsal fin images of the WSA humpback whales as well to the tail flukes from the GAB catalogue. Images of all quality, including those showing partial flukes and trailing edges were reviewed. Any possible matches were reviewed by at least 3 authors.

Defintion of scar and wound types from cookiecutter sharks and killer whales and regional comparison

We recorded the presence/absence of cookiecutter shark bites on the dorsal fin and upper back area of the body (hereafter 'dorsal fin') 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 human induced scarring (such as that caused by entanglement in fishing nets or ropes) due to the large number of poor quality photographs (especially the older black and white images from the WSA catalogue) and the lack of lateral photos of the tail stock needed to assess entanglement scarring (Robbins and Matilla, 2004).

Identification of cookiecutter shark bites and scars

The three main study sites considered here used slightly different methods in the collecting, processing and organising of photographs which had to be accounted for to allow for an unbiased assessment. The majority of images from WSA prior to 2004 were scanned black and white film, after which colour digital photography was used (see Barendse *et al.* 2011). All images from GAB and NAM were colour digital photographs from a variety of camera and lens combinations (Nikon and Canon). Dorsal fin images in the GAB catalogue were cropped in tighter to the dorsal hump than those in the other two catalogues, thus a smaller proportion of the body was available to inspect potentially biasing the estimate downwards. To minimise the effects of this and any other image specific biases, photos were graded as being of acceptable quality based on 1) the quality of the picture (namely focus, graininess, lighting, pixel definition) 2) the amount of body visible, which had to be at least two or more times the height of the dorsal fin and hump (to account for differences in cropping factor between catalogues and the surfacing position of the whale). The angle of whale relative to the camera was not considered as a feature affecting the ability to see cookie cutter shark bites or scars.



Fig 2. Example photograph of a Namibian humpback whale bearing both fresh wounds showing clear colour differentiation and pinkness in the centre and pale uniform colour, healed scars (two closest to the water line) resulting from cookiecutter sharks predation attempts. Photo by Alice Affatati.

Cookie -cutter shark bites are easily recognised by the unique shape of the wounds left after each attack. The 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 greyish or brown tissue attached to their centre, part of the process of healing, while others are only crescent-shaped wounds of varying depths of penetration but with no tissue removed (Best, 2007; Dwyer and Visser, 2011). In this study we differentiated between fresh or partially healed wounds (wounds) and old, healed scars (scars). Fresh wounds were identified from the presence of the flesh colouration of the dermal tissue within the pit as well as the integrity of the crater itself (i.e. clean edges, clear pit shape), and the dual colouration 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 white or grey with distinctive radiating dark lines which occur due to the healing process (Best, 2007); sometimes the dark lines were missing probably owing to different healing processes among individuals. In some cases, the cookiecutter wounds and scars hosted the parasite 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 integrity of the scar than on the colouration alone. Moreover, when considering black and white photographs, the determination of a fresh vs. old bite relied on the overall scarring appearance.

Both wounds and scars from cookiecutter sharks are easily differentiated from those of barnacles (e.g. *Coronula spp*), since the latter appear either as thick black or white rings (Fertl, 2008; Dwyer and Visser, 2011) or solid grey, 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, 1974; 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 attached to cetaceans, however, the resulting wounds appear different as they are much shallower than wounds attributed to cookiecutter sharks, often barely breaking the skin (Jones, 1971; Shevchenko, 1974; Dwyer and Visser, 2011).

All the identification images of the Namibian, West South African and Gabonese catalogues were checked in order to compare the scarring rates of the three databases. We only considered photographs of dorsal fins for the detection and assessment of cookiecutter shark bites, although these marks are found on tail flukes too. However, the shape and appearance of bite marks on tail flukes are more easily confounded with those of barnacles due to the higher incidence of barnacle scars on the flukes and the low rate of successful attacks (i.e. partial bites) by cookiecutters on this more turbulent part of the whale's body (Best, 2007).

Comparison of proportions of individuals with cookiecutter shark bites between sites was performed using Chi-squared tests, with left and right dorsal fins combined (these are shown separately in Fig 4.). Due to the large size of the GAB catalogue, dorsal fin images were not assigned a unique ID within the database for all animals and it was thus not possible to control for individual identity or multiple images of the same animal within and between years. All three catalogues frequently included more than one, but never more than 6 photographs of an individual to best capture the entire dorsal flank (or fluke) of the animal. An analysis of a subset of 791 individuals in the GAB catalogue for which individual dorsal fin IDs were available revealed that 62% of these animals were represented by a single image for left and/or right and 33% had 2 images within the database with similar rates for WSA and NAM. Since inclusion of more than one image for dorsal ID was random with respect to scarring and resightings within and between the databases were low, we thus calculated frequency of bites 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 a catalogue 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 three sites and each pair of sites, with the p-value adjusted using a Bonferroni correction.

Identification of killer whale bite marks

We defined a killer whale bite mark or scar as a set of three or more white or black parallel scars in close proximity (Fig 3) following the definition used by Steiger *et al.* (2008). Due to the small sample sizes involved we did not differentiate between the degree of damage to flukes (Categories 1-3 in 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).

To assess the frequency of killer whale rake marks on flukes, we looked at all images of tail flukes in the catalogue and classified these as suitable for analysis based on 1) focus, lighting, exposure and pixel definition in photographs and 2) the amount of fluke displayed in the frame due either to angle to the camera or proportion of the tail out of water. Only good quality images with both sides of the tail shown were considered for analysis. To calculate the proportion of flukes with rake marks, only a single identification image from each animal in each catalogue was used. We investigated differences in the presence of killer whale bite scars on flukes among regions using a Chi-squared test.



Fig 3. Example photographs of humpback whale flukes showing definite killer whale rake marks (top) and scars possibly caused by killer whales but not meeting the criteria of three parallel lines rake marks. Photos by Tess Gridley (top) and Simon Elwen (bottom)

Seasonality of humpback whales in Namibia

Seasonal variation in the presence of humpback whales within Walvis Bay, Namibia was investigated by collating sightings from two primary sources: 1) Encounters by the Namibian Dolphin Project research team (including a known level of search effort, group composition, group number and the water depth and surface temperature at sightings), 2) data (daily summaries and opportunistic photographs) recorded by commercial marine tour operators working in Walvis Bay. Tour operator data are available from 1) digital photographs (n=146) of whales collected opportunistically by tour operators, predominantly a single company, many of which have been included in the NAM catalogue; 2) records of whales present in the bay kept by Jeanne Meintjies (Eco-Marine Kayak Tours) from 2005-2007, including those encountered by or reported to her and 3) records of whales present in the

bay kept by Mike Lloyd (Catamaran Charters) from 2010-2012, including those encountered or reported to him, records are shown separately for each year.

Data collected by the NDP is seasonally limited to Feb-Mar and Jun-Aug. Data from marine tour operators is not corrected for effort but trips (and number of boats at sea) are higher in Jun-Dec than Jan-May, with Aug being the busiest month and Feb the quietest, although boats are on the water effectively every day of the year.

RESULTS

Relatedness between populations and resightings between and within sites for GAB and WSA are discussed in detail by: Barendse et al. (2011); Collins et al. (2008) and Pomilla & Rosenbaum (2006).

Inter-regional photo-ID catalogue comparisons.

NAM-WSA catalogue comparison

No confirmed matches could be made between NAM and WSA on any identity feature. Two possible matches were made between the two sites using dorsal fins, with photograph quality and low distinctiveness of the individuals being the main factor limiting confirmation. Animal NAM-070 was photographed on 26 September 2008 in Walvis Bay and ZAW-275 on 24 November 2005 in St Helena Bay. NAM-078 was photographed on the 07 July 2011 in Walvis Bay, Namibia and ZAW-141 on the 19 July 2002 in Saldanha Bay, South Africa.

NAM-GAB catalogue comparison

No matches were found between the tail fluke catalogues from Namibia and Gabon.

Comparison of scarring rates between GAB-NAM-WSA

The prevalence of cookie cutter shark bites on the dorsal fins of humpback whales was calculated separately for left and right sides and for fresh bites and healed scars (Fig. 4). Due to the similarity between sides at each location, sides were combined for statistical analysis. The short duration of field seasons in GAB and NAM 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 sites ($\chi^2 = 66.6, p < 0.0001$). The prevalence of scars was highest in GAB while WSA and NAM did not differ significantly ($\chi^2 = 4.96, p = 0.08$). The prevalence of fresh cookiecutter shark bites differed significantly between sites ($\chi^2 = 148.72, p < 0.0001$). All sites were significantly different from each other when compared in a pair-wise fashion with the highest prevalence of fresh bites seen in NAM, followed by GAB. Only two dorsal fin photographs (one left side, one right side) from WSA contained a 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 (GAB: 29%; NAM: 24%, WSA: 35%; Fig. 5) and did not differ significantly between sites ($\chi^2 = 4.3107, p = 0.3656$).

Seasonality in Namibia

All Namibian data presented here is collected in nearshore waters mostly within or just to the north-west of Walvis Bay and thus only represents a very small part of the area known to be used by humpback whales. Seasonal (monthly) presence of humpback whales in the Walvis Bay area from NDP records and marine tour operators are shown in Fig 7.

NDP winter records are limited primarily to June-August and show a single clear peak in numbers of whales seen per sea day during July (Fig. 7). NDP records of calves (n=5) are highest in August (n=3). Two of the encountered calves (28 July 2008 and 09 August 2012) were extremely small and light grey in colour suggesting they had been born very recently.

Records from marine tour operators show a similar peak in July with a clear secondary peak in Sep (all sources except photographs). Data from marine tour operators are not effort-corrected, although Jul-

Dec 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 north west of Walvis Bay will be spotted during this season. Consistent records of calf presence were not available from marine tour operators.

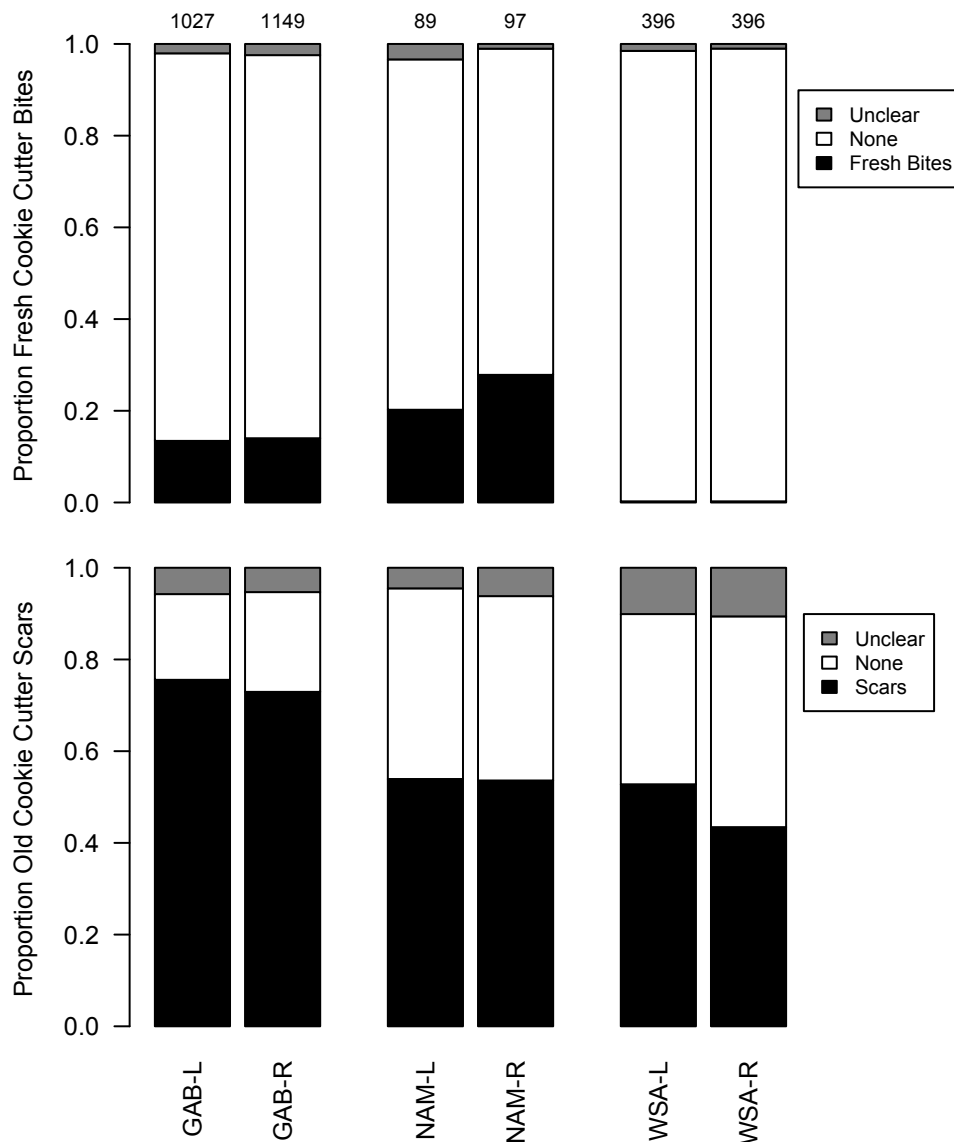


Fig 4. Prevalence of fresh wounds (top) and healed scars (bottom) from the bites of cookie sharks on the dorsal fins and flanks of humpback whales in Gabon, Namibia and west South Africa. Left and right flanks are shown separately, sample sizes are shown above the bars. Note that for WSA, a single record of a fresh bite was observed in both the left and right side databases (difference individuals).

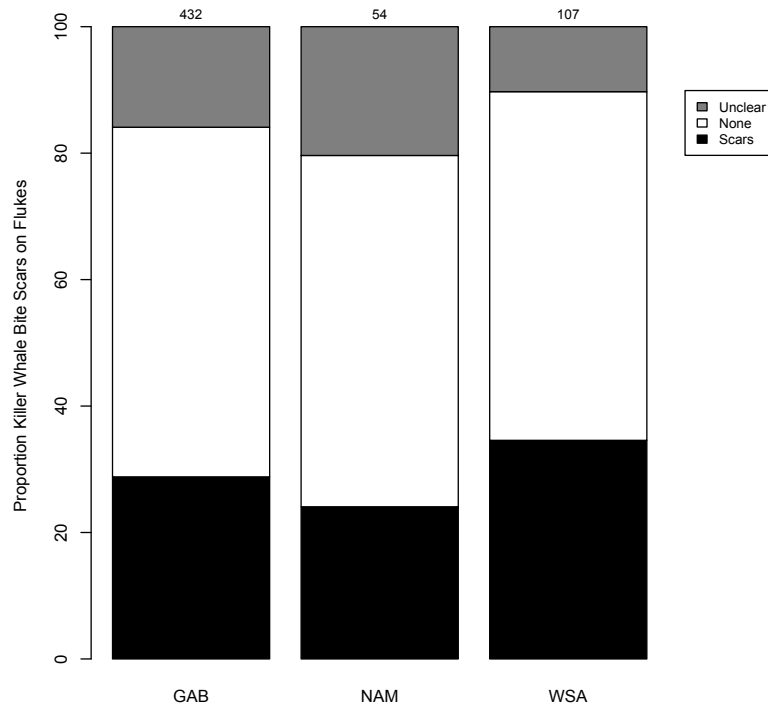


Fig 5. Prevalence of killer whale bite scars on the tail flukes of humpback whales in Gabon, Namibia and west South Africa.

Behaviour and directionality of movement of whales in Namibia

Other than a general tendency to move along a track in a south west to north east direction (or vice versa, rather than directly along a line north to south or coast-wise), there was no overwhelming 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 Jun-Aug), 28 tracks ended north of where they started, while 27 ended more southwards; 17 animals moved eastwards during tracking and 38 westwards.

Animals were most frequently encountered in the area directly north of Pelican Point, where search effort by both the research vessel and marine tour operators was highest and then tended to head west or south-west once approached. The majority of whales approached by the research team were initially spotted by marine tour operators and had been in the presence of several tour boats (up to 11 being the highest recorded simultaneously) prior to contact and tracking. Avoidance of this level of harassment may play a role in the general movement pattern away from the bay, rather than general northward migration movement as is expected in July-August in Namibia.

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

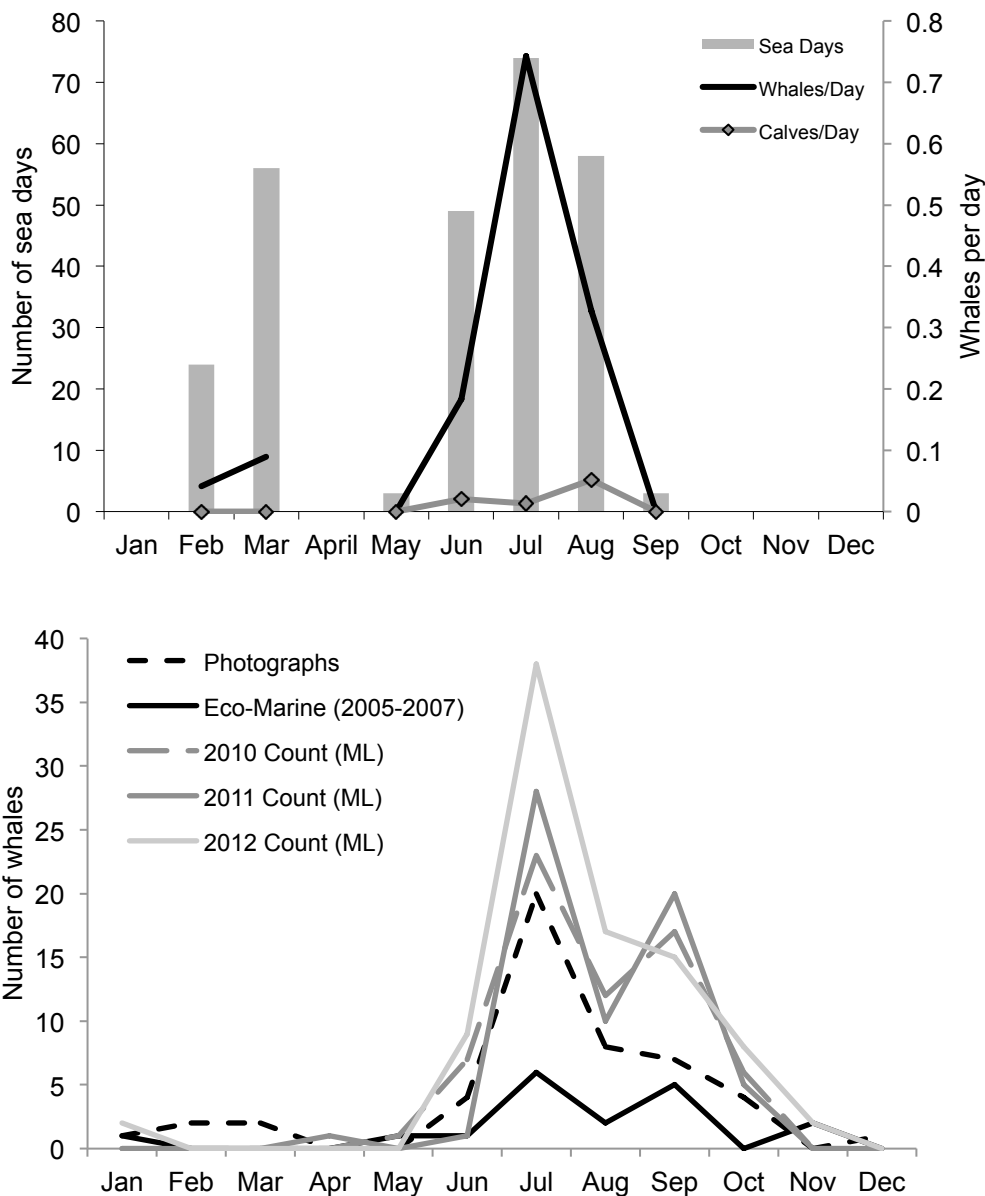


Fig 6. Seasonality of humpback whales seen in Walvis Bay, Namibia by the Namibian Dolphin Project research team (top), showing number of sea days (left axis) and adjusted total number of humpback whales/sea day and calves only/sea day for each month (right axis). Bottom figure shows total monthly counts (uncorrected for effort) of individual humpback whales recorded year round by local whale watching companies from a) photographs donated to catalogue by Catamaran Charters 2008-2010 (Mike Lloyd, Ute von Ludwiger and Orlanda Sardinha) and b) whales seen and reported year round (2005-2007) by Eco-Marine Kayak Tours (Jeanne Meintjies) and c) counts of whales seen or reported to Mike Lloyd of Catamaran Charters 2010-2012. Although not effort corrected, note that due to peaks in tourism, vessel/observer effort is higher in Jun-Dec than Jan-May.

DISCUSSION

Two main alternate hypotheses have been put forward to explain the stock structure of Breeding Stock B on the west coast of Africa: 1) the existence of two separate breeding sub-stocks, named B1 (off Gabon and the Gulf of Guinea) and B2 (an unknown area) (Rosenbaum et al., 2009; IWC, 2010; Müller et al., 2011) and 2) the existence of a single breeding stock within which different maternally directed migration routes create genetic differentiation between animals samples off GAB and WSA (Best and Allison, 2010). The IWC Scientific Committee concluded that while neither model

adequately captured the complexity of the BSB population structure, both were useful for making inferences about the current status of the stock (IWC 2012). Considerable uncertainty remains as to the location of BSB2 (should it exist) with it being shown by various authors as WSA only (Carvalho et al., 2009), 2) northern Namibia/Angola (Barendse et al., 2011), 3) the whole of west Africa from northern Angola to WSA (Rosenbaum et al., 2009) and even 4) north west of Gabon into the Gulf of Guinea (Van Waerebeek et al., 2009; Best, 2011). The lack of clarity (and consensus) on population structure in BSB is due in large part to the lack of post-whaling era data outside of small coastal areas in Gabon and west South Africa.

Irrespective of the one- or two-stock model, it seems from ambient water temperatures and sex-ratios within populations that the Namibian coastline is more likely to be a migratory corridor/temporary feeding ground than a breeding area (Best, 2011). Below we summarise available data from Namibia and place it within the context of the above hypotheses.

No confirmed matches of individuals were found between NAM and GAB (tail flukes only) and only two possible matches were made between NAM and WSA using dorsal fins. The lack of confirmed matches can not be interpreted to mean no interchange and this result has to be interpreted within the context of a number of considerations. The NAM catalogue is small and due to logistic constraints, represents only a very small fraction of the animals passing through Namibian waters (many of which pass well offshore of the study area or outside of the data collection period). In addition, the flukes of many animals were not captured and individual variation in fluking rate may play a role in capture probability.

The number of humpback whales that visit Gabonese waters is considerable, estimated at 9,310 in 2005 under the two-stock hypothesis (IWC, 2012), reducing the probability of any resightings (but see photographic and genetic recaptures reported in Barendse et al. 2011). The NAM catalogue (2008-2012) does not overlap temporally with those of either WSA (1983-2007) or GAB (2000-2006). Humpback whale stocks around the world are increasing in the region of 10% per annum (e.g. Findlay et al., 2011; Zerbini, Clapham, & Wade, 2010) and although direct estimates are not available, BSB is also predicted to be increasing, resulting in a large proportion of young animals in the population, which may never have been captured in the GAB and WSA catalogues. An additional caveat (which applies also to analysis of scarring rates, below) is the known differences in sex and age ratios between feeding, breeding and migratory areas (see Steiger *et al.* 2008 for a more detailed discussion). Thus, even if this is one panmictic population, not all animals may be available for capture at all sites. Given the uncertainties involved, the lack of confirmed matches does not at this stage provide clear evidence for or against any of the existing BSB hypotheses.

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) and to define age categories of Cuvier's beaked whales (*Ziphius cavirostris*) (Mcsweeney et al., 2007). Differences in the prevalence of healed cookiecutter bite scars between study sites can be interpreted as indicating differences in long term exposure to predation by animals using different migratory routes or feeding areas (since cookie cutter sharks do not occur in cold water feeding areas). Conversely, fresh bites are indicative of recent movement patterns (days to weeks) from or through warm tropical or sub-tropical waters where cookiecutter sharks are known to occur.

Whales in NAM and WSA (both within the cool Benguela ecosystem where cookiecutter sharks are not thought to occur) had the same level of scarring suggesting similar levels of long term exposure to predation, while animals in GAB exhibited higher levels of scarring and long term exposure to cookiecutter shark predation. This result shows that firstly, at least some animals seen in WSA spend time in warmer waters further north or offshore where they are exposed to cookie cutter sharks (which was already known from photographic and genotypic matches with GAB – Barendse et al., 2011) and secondly, at least some level of differentiation occurs in the populations between GAB and NAM. This differentiation may occur through some GAB animals spending less time in Benguela Ecosystem as would be expected if they were following an offshore migration route to or from GAB. 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.

The prevalence of fresh cookie cutter shark bites is strikingly different to 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 GAB catalogue 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 NAM catalogue were taken during the expected period of northward migration (Jun-Aug), and the number of fresh bites seen suggests that a large proportion of animals here had moved recently into the coast from warm offshore waters rather than travelled northwards along the coast through the Benguela ecosystem from WSA. The lack of fresh bites in WSA (most images taken during the summer feeding season (Oct-Jan, and after the GAB breeding season, Barendse *et al.* 2011), combined with direct evidence of southern migration from GAB to WSA by several individuals (Barendse *et al.* 2011), suggests that animals encountered here had been resident for extended periods (probably more than the 30 days estimated healing time for a small shallow wound) within the Benguela, possibly following a slow migration southwards along the continental shelf. These data support the concept that many animals on their northward migration to BSB strike the coast well north of the WSA study site as put forward by Olsen (1914) and (Barendse *et al.* (2010) but also suggest that the animals seen feeding there in late spring to late summer may be animals which have completed a southward migration staying mainly within the Benguela ecosystem.

Differences in the prevalence of killer whale bite scarring between populations and feeding or breeding areas of large baleen whales can be 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 and have been seen in all water depths surveyed from the coast to >2600m (Best *et al.*, 2010; Weir *et al.*, 2010; Elwen and Leeney, 2011). Scarring rates on flukes (using only a single image for each whale) are similar among all study sites, suggesting similar levels of predation in 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 three study sites.

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. Acoustic recordings of whales were not made but no singing was ever heard in any of the whales groups approached in Walvis Bay, nor was singing ever detected in the background during a study of bottlenose dolphin vocalisations taking place concurrently in 2009, 2011 and 2012 (NDP, unpublished data). The lack of mating behaviour observed, low number of calves and lack of singing recorded further support this model. The smaller size of the second (southward) peak suggests that many animals may be migrating much further from shore where they are not seen by coastal researchers.

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) while others are almost entirely trans-oceanic (e.g. the western North Atlantic, Stevick *et al.* 2003). Rosenbaum *et al.* (2009) suggest that coastal Namibia may act as a migration corridor for animals moving between the WSA feeding ground and an unsurveyed breeding area further north (but south of sampling sites off GAB) and likely off Angola. The very low numbers and lack of predictable directionality in the movement of whales observed in the coastal waters of central Namibia (surveyed up to ~10km 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 200m isobath being ~100km offshore, thus whales following a migration route along the continental shelf may be spread widely across the shelf and into deeper waters.

Summary and conclusions

The paper provides the only available current information on humpback whale presence, seasonality, movements and scarring in Namibia and the first complete comparison of the photographic ID catalogues between Namibia and regional databases in Gabon and west South Africa. We have collated multiple lines of evidence and discussed them within the framework of the hypotheses regarding population structure within Breeding Stock B off the west coast of Africa.

In summary: we found no definite photographic matches between animals seen in NAM and either GAB or WSA. The size and age of each of these catalogues, relative to the size and likely rapid increase of the overall population of whales in BSB, confound any interpretation of the lack of matches within the context of population structure. Similar levels of killer whale bite scarring on the flukes of humpback whales suggest similar levels of predation risk throughout BSB. The seasonality, behaviour, lack of singing and scarcity of calves seen in NAM support the idea that the area functions primarily as a migration route, although the low numbers of whales and general lack of directionality indicate that the coastal waters around Walvis Bay are certainly not a major migration stream. The smaller secondary peak of the southward migration suggests that the many animals may remain further from shore on their southward migration, possibly following a route along the Walvis Ridge. The prevalence of cookie cutter shark scarring on humpback whales in all study sites shows that some animals from all populations spend time in warmer or offshore waters where they are exposed to these predators and that there is some differentiation in this exposure between NAM and GAB. The striking lack of fresh cookie cutter shark wounds in the WSA study site suggests that the vast majority of animals seen here had not recently moved in from warmer waters further from shore or further north but had spent a considerable amount of time within the inshore Benguela ecosystem, possibly following a slow coastal route southwards. Five whales photographed in Gabon between 14 August and 26 September between 2002 and 2005 were encountered in either the same year off west South Africa between 17 October and 16 December or in the following year between 10 and 18 January, i.e. with individual transit times of 44 – 146 days (average 93 days). This would probably be sufficient time for healing of wounds contracted in or near Gabon to occur (Barendse et al. 2011).

Combined, these data suggest that humpback whales migrating up the west coast of Africa to the BSB breeding ground(s) are not following a single main, high density migration route, as is observed off the east coast of Africa (C1 population, Findlay et al., 2011). Rather, whales on their northward migration are striking the coast/shelf at multiple points mostly north of the WSA study site. The smaller southward migration peak seen in nearshore Namibia (this study; Best and Allison, 2010), known use of the Walvis Ridge route by animals moving south (Best and Allison, 2010), timing of whales in WSA and lack of fresh cookie cutter shark bites in WSA support the concept of at least two different southward migration routes with many of the whales seen in WSA having moved coastwise down from GAB, spending a considerable amount of time in the cold Benguela ecosystem where no fresh bites are likely to have occurred and ones gained in tropical waters to the north may have healed.

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