

Where is the breeding ground for humpback whales from Breeding Stock B2?

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Abstract

Genetic data and catch histories suggest some sub structuring within the population of humpback whales that over-winters off the west coast of the southern Africa, or Breeding Stock B, with whales sampled off Gabon (B1) differing from those sampled off the west coast of southern Africa (B2). However the latter locality is a feeding ground/migratory corridor rather than a breeding ground, leaving open the question of where the breeding ground for B2 is located. This note reviews information pertinent to this question.

Introduction

Assessments of the southern hemisphere humpback whale breeding stock B, or that which over-winters on the west coast of Africa, have indicated some population structure, namely, that whales sampled in Gabon are genetically different from those sampled in St Helena Bay on the west coast of South Africa, about 3,000 km to the south. This heterogeneity is supported by the catch histories, which indicate very different patterns of exploitation for whales in Gabon and those taken on the west coast of South Africa (Best and Allison, 2010).

One interpretation of these differences is that they reflect two separate breeding populations, one (B1) centred on Gabon and other (B2) somewhere else. Knowledge of the whereabouts of the latter, and the migratory routes taken to and from it, is critical for the construction of a feasible population dynamics model and the appropriate allocation of catches to it. This note is intended to provide some rationale for making a decision based on the balance of the available evidence. Suggestions to date for natural features that separate the two breeding populations include the Angola/Benguela Front (IWC, 2007) and/or the closely associated Walvis Ridge (Rosenbaum and Mate, submitted).

The Angola-Benguela Front as a barrier between B1 and B2

The Angola-Benguela Front is the convergence region between the southward-flowing (warm) Angola Current and the northward-flowing (cold) Benguela Current. It is a permanent feature at the sea surface and is maintained throughout the year between 14 and 16° S, or just north of the Angola/Namibia border, with a general west to east orientation (Meeuwis and Lutjeharms 1990). The position of the front shifts seasonally, being furthest north in winter and early spring (coincident with the humpback breeding season) when sea surface temperatures at the middle of the front average between 19.5 and 21.5° C (Fig. 1). The sharpest temperature gradients are within 250 km of the coast, and the average gradient is about 1° C per 72 km. It would seem to represent at least a theoretical “barrier” between populations.

However this should be viewed in the context of Rasmussen et al.’s (2007) survey of humpback whale breeding grounds worldwide in relation to sea surface temperature. Information provided for 24 locations in both Northern and Southern Hemispheres indicated that prevailing sea surface temperatures on humpback whale breeding grounds ranged from 21.1 to 28.3° C, and if Southern Hemisphere breeding grounds only are concerned, the range contracts to 23.2 - 28° C. Rasmussen et al. also cite reported temperatures at humpback breeding grounds of 24-28° C, and indicate a similarity between the west coasts of South America and Africa, where coastal upwelling and cold tongue development extending into the equatorial region displace the breeding ground for humpback whales across the equator.

The proposal that the breeding ground for B2 lies south of the Angola-Benguela Front would imply that prevailing sea surface temperatures would average less than 19.5 - 21.5° C, making it the coldest known breeding ground for the species.

Other evidence for the possible existence of a breeding ground south of the Angola-Benguela Front needs to be considered.

The sex ratios of animals sampled north and south of the Front are radically different. North of the Front males predominated in the historic catch, averaging 56.9% (Table 1), while in recent genetic sampling off Gabon 66% of the animals were male, although mother-calf pairs were under-represented (Pomilla and Rosenbaum, 2006). South of the Front females predominated in the historic catch, with males averaging 45.9% (Table 1): Namibia alone had catches where males formed 44.9% of the catch (n = 372). Recent genetic sampling off West South Africa indicated an overall percentage (excluding calves) of 41.5% male (Barendse et al. 2010). Historic exploitation and current genetic sampling of humpback whale breeding grounds has usually indicated a predominance of males (Clapham, 2000), so that the composition of the samples from south of the Front would not be consistent with the presence of a breeding ground.

Behavioural criteria used for identifying a humpback whale wintering area have included observations of small calves, the presence competitive groups of adults and singing by males (Rasmussen et al. 2007). Off Gabon, recent observations are consistent with previous descriptions of wintering grounds, where most of the groups encountered are male-female pairs or large competitive groups, although the prevalence of females suggests that some animals might still be migrating through the area to a breeding ground further north (Pomilla and Rosenbaum 2006). Singing also occurs commonly in the area (Darling and Sousa-Lima, 2005). Off Cabinda (Angola), 21.1% of groups encountered contained a calf, and 21.1% of groups exhibited marked social interactions, including high-speed swimming, head lunges, tail swipes and much breaching (Best et al. 1999): singing has also been recorded from mid-June to 1 December, indicating active breeding habitat (Cerchio et al. 2010). Off west South Africa there have been no observations of competitive groups (Barendse, pers. comm.), only a few small calves have been seen and no singers were detected in dedicated acoustic monitoring – although there is a single incidental record of singing (Barendse et al. 2010). Off Walvis Bay, Namibia, the few current observations of humpback whales have been of slowly-moving animals with no indication of competitive behavior: no reports of singing are available although there has been no dedicated acoustic monitoring (Elwen, pers. comm.).

In summary, there are a number of lines of evidence that suggest that if there is a boundary between the breeding grounds for B1 and B2, it does not correspond with the position of the Angola-Benguela Front, and is likely to be to the north of it.

Relationship of whales from Angola with those off West South Africa or Gabon

The history of exploitation of humpback whales off Angola includes a pulse of catching pre-WWI, with an estimated 9,840 whales taken between 1909 and 1914, followed by a collapse and resumption of catching only in 1923, after which annual humpback catches were extremely low (<50 per annum), and the industry switched to other species. This pattern was followed in Namibia and the SW Cape, but not in Gabon, where catches resumed after WWI at a level of 500-700 humpback whales a year, at least initially. This suggests that the whales off Gabon were somehow less vulnerable to exploitation than whales to the south, including off Angola.

This contrast between the whaling histories for humpbacks in Gabon and other whaling grounds on the west coast of southern Africa has been noted by other authors. Tønnessen and Johnsen (1982), for instance, state that while the presence of migrating whales past the Angolan coast would lead one to suppose that stocks of whales existed to the north off Gabon, and the more stationary nature of the whales there (without evidence of a pause between northward and southward migrations) would suggest that this was the terminus of the migration, “it was undoubtedly incorrect to believe that whales off the Congo were the same (humpback) stocks as those that proceeded past Angola”. As apparent evidence in support of this they cite research showing that there were separate stocks of humpback in the Antarctic, each proceeding north to its own particular area.

Of six humpback whales that were satellite-tagged off Gabon in August/September and subsequently moved south past Angola, only two remained close to shore (< 50 km from the coast). The remaining four travelled far

offshore (>200 km from the coast): two of these continued on south past Namibia and South Africa at even greater distances (1,000 km or more) from the coast. Such an offshore migratory route, if utilized on both north and south migrations by the same cohort of animals, would effectively shield them from exposure to exploitation from coastal whaling at other sites in West South Africa, Namibia and even Angola. This might be sufficient to produce the different catch histories seen.

Unfortunately only a small number of whales from Angola have been photo-identified ($n = 14$) or biopsied ($n = 13$) to date (Best et al, 1999): there have been no matches with whales in either Gabon or West South Africa. Grouping of the Angolan genetic samples with either those from Gabon or those from WSA produced a significant difference from WSA or Gabon respectively, both for mtDNA and microsatellites, although the values of *FST* were higher for both markers when Angola was grouped with Gabon (Carvalho et al. 2009). One interpretation of this could be that the Angolan sample represents some mixing between whales from B1 and B2: the sampling site off Angola (at $6^{\circ} 52'S$) was only some 400 km from the southernmost sampling site in Gabon (Mayumba, at $3^{\circ} 25'S$).

Existence of breeding ground to the north of Gabon

It has been suggested that the breeding ground for B2 might lie north of Gabon, or in the Gulf of Guinea. In recent years there have been a number of sightings and strandings of humpback whales in Nigeria, Benin, Togo, Ghana and Ivory Coast during the austral winter that have given rise to the suggestion of a “Bight of Benin” or “Gulf of Guinea” substock (Van Waerebeek et al. 1981, 2009). Records even further to the west and north with an austral seasonality have come from Guinea (Bamy et al. 2010) and the Cape Verde Islands (Havevoet et al. 2011). While the abundance of humpback whales in these areas and their relationship to those further south are unknown, seven whales (all females, including two with calves) that were satellite-tagged in waters off Gabon in August/September 2002 subsequently travelled northwards into the Gulf of Guinea, visiting areas off Cameroon, Nigeria, Togo, Benin and Ghana (Rosenbaum and Mate, submitted). As only 13 whales were effectively satellite-tagged in Gabon, this suggests a strong physical linkage between Gabonese waters and the northern Gulf of Guinea.

However there are no genetic data yet available from the northern Gulf of Guinea to establish how reproductively distinct the whales there may be from those off Gabon, Angola or WSA, or whether in fact they simply represent a geographical extension of the breeding grounds off Gabon.

There is also the enigma of why there was little if any interest in whaling north of Gabon, either in the 19th century (Fig. 2) or in the early 20th century. In modern whaling, humpback whales were hunted briefly at the island of Fernando Po (Bioko), 32 km off the coast of Cameroon, in 1914, when 280 whales (unspecified, but believed to be mostly humpbacks) were taken. Otherwise catches in both eras were concentrated off Gabon and Angola. Although there may be logistic, sampling or other reasons why this was so, it is possible that there was an insufficient concentration of cow-calf pairs in particular along the northern rim of the Gulf to attract whalers on a regular basis.

Summary

There seems little doubt that there is some substructure to the humpback whale population in Breeding Stock B, but the data that might resolve the nature of this substructure are not available at the necessary spatial scale. What can be concluded is that if there is some accompanying geographical separation between the postulated BSB1 and BSB2 substocks then it very probably lies not at but to the north of the Angola/Benguela Front. Inspection of the satellite tracking data for whales moving south suggests a bifurcation in the vicinity of the Congo River mouth, or around $6-7^{\circ}S$: whether this feature should be considered a revised “boundary” between BSB1 and BSB2 is a moot point, but its location would not be inconsistent with the differing catch histories of humpback whales from Gabon and Angola.

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Table 1: Sex ratios in humpback whales caught off African west coast (data from IWC) – bold = significantly more males, italics = significantly more females

Season	Gabon/Angola		Namibia/WSA	
	Number sexed	Propn male	Number sexed	Propn male
1913			65	<i>0.353846</i>
1914			33	0.545455
1918			4	0
1919			14	0.571429
1920			40	0.375
1922	613	0.747145	13	0.53846
1923	685	0.563504	212	0.457547
1924	566	0.530035	96	0.604167
1925	472	0.50847	69	<i>0.304348</i>
1926	321	0.501558	19	0.578947
1927	3	1	39	0.333333
1928	37	0.513514	24	0.624999
1929			40	0.35
1930	578	0.633218	36	0.527777
1934	722	0.635734		
1935	1236	0.58495		
1936	841	<i>0.42925</i>	27	0.407407
1937	299	0.568562	28	0.5
1947			5	0
1948			14	0.714286
1949	1356	0.644543	15	0.466667
1950	1403	0.575196	7	0.428571
1951	1104	0.484601	9	0.555556
1952	264	<i>0.420455</i>	15	0.266667
1953			9	0.666667
1957			3	0.666667
1958			2	1
1959	160	0.56875	7	0.428571
1960			4	0.5
1961			4	0.75
1962			9	0.444444
1963			3	0.666667
Total	10660	0.5689	865	<i>0.4589595</i>

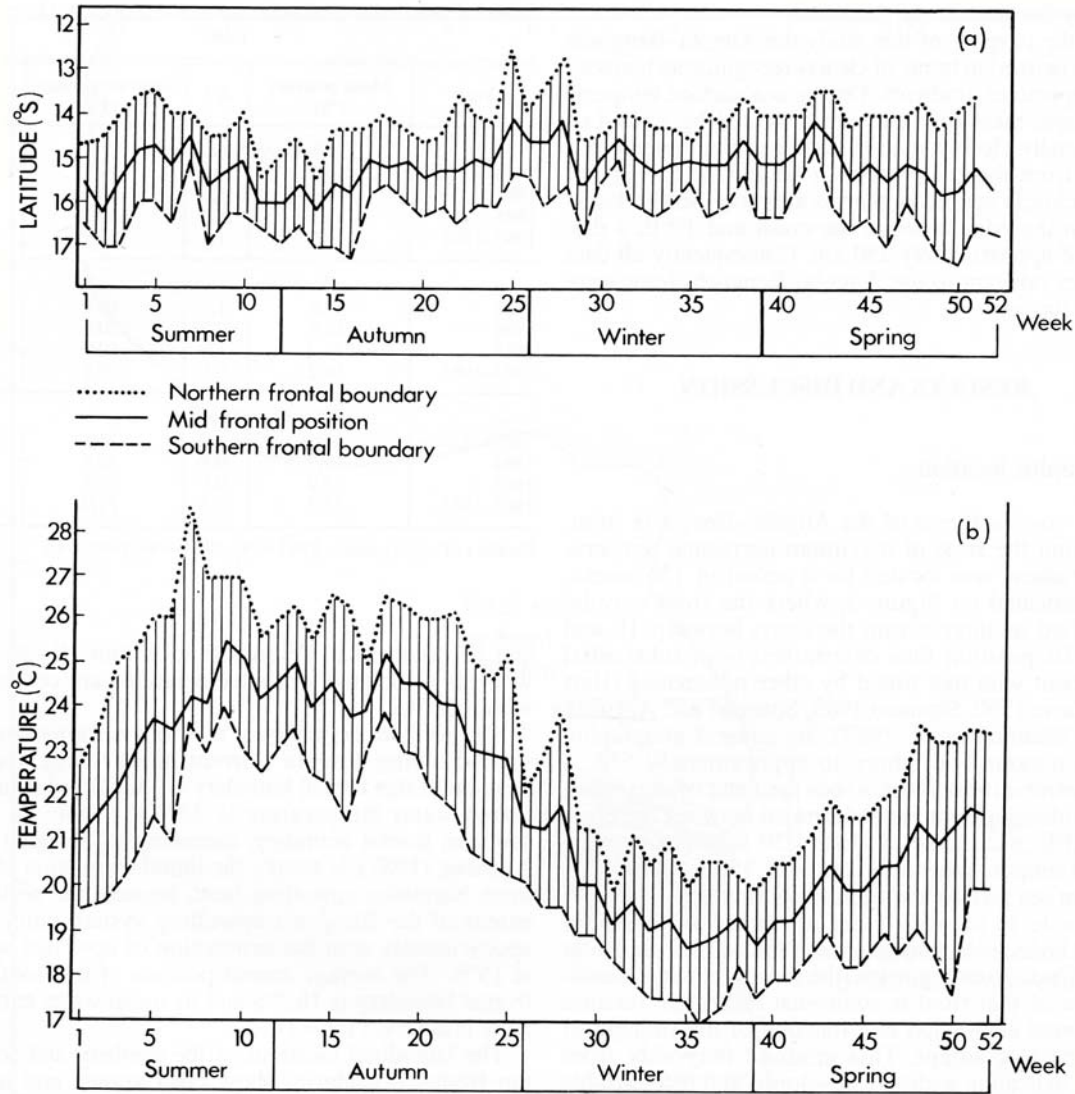


Fig. 1: (a) Average latitude at the coast of the mid front and the northern and southern frontal boundaries of the Angola-Benguela Front, 1982-1985; (b) average sea surface temperatures of the mid front and its northern and southern boundaries (from Meeuwis and Lutjeharms, 1990)

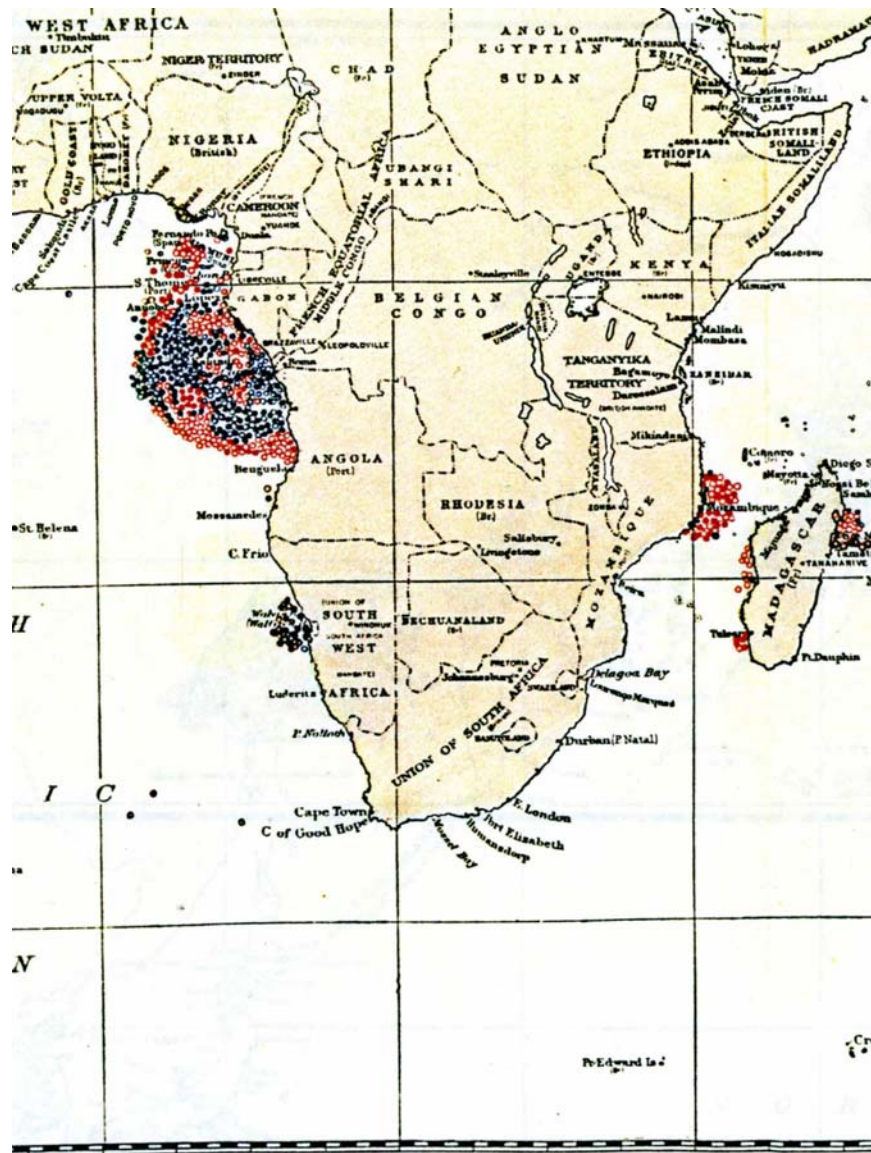


Fig 2: Positions of 19th century whalers on days that they caught humpback whales around southern Africa (from Townsend (1935).

January
February
March
April
May
June
July
August
September
October
November
December

