Line transect estimates of humpback whale abundance and distribution on their wintering grounds in the coastal waters of Gabon

SAMANTHA STRINDBERG*, PETER J. ERSTS[+], TIM COLLINS*, GUY-PHILIPPE SOUNGUET[#] AND HOWARD C. ROSENBAUM*[+^]

Contact e-mail: sstrindberg@wcs.org

ABSTRACT

There have been few recent estimates of abundance for humpback whales (*Megaptera novaeangliae*) in the eastern South Atlantic Ocean. The first distance sampling survey of the coastal waters of Gabon was conducted in 2002. The difficult logistics of covering a large survey region with limited time, effort and refuelling opportunities required a line transect survey design that carefully balanced the theoretical demands of distance sampling with these constraints. Inshore/offshore zigzag transects were conducted to a distance of up to approximately 50 n.miles from the coast of Gabon corresponding to the 1,000m depth contour, from the border with Equatorial Guinea to a point south of Mayumba, near the Congo border representing 1,488 n.miles of survey effort. Seventy-nine different groups of humpback whales were observed throughout the survey area comprising a northern (Equatorial Guinea to Cap Lopez) and southern (Cap Lopez to Gamba) survey stratum. Relatively large numbers of whales were encountered throughout the southern stratum; encounter rates and densities were considerably lower in the northern stratum. The initial abundance estimate from a distance sampling analysis suggests that more than 1,200 humpback whales were present in Gabon's coastal waters during the survey period. This estimate does not account for either availability or perception bias. In addition, this instantaneous snapshot of the number of whales occupying Gabon's coastal waters is likely to correspond to only a portion of the population that uses these waters over time. However, the abundance estimate derived from the aerial survey are consistent with those based on photographic and genetic capture-recapture techniques. A continuing research programme in this area will help refine estimates of humpback whale abundance and using genetic and photographic data also establish the relationships between this and other populations. This is important given the potential overlap of humpback whales in large numbers throughout this region and the current extent and continued expansion of hydrocarbon exploration and extraction activities throughout the Gulf of Guinea.

KEYWORDS: ABUNDANCE ESTIMATE; SURVEY–AERIAL; AFRICA; ATLANTIC OCEAN; SAMPLING STRATEGY; G(0); MODELLING; HUMPBACK WHALE

INTRODUCTION

Early last century populations of Southern Hemisphere humpback whales declined markedly as a result of intense whaling on both the Antarctic feeding and tropical breeding grounds (Townsend, 1935). The first substantial recorded catches of humpback whales in the Southern Hemisphere date back to the 18th and 19th Century American pelagic whaling period (Mackintosh, 1942; Starbuck, 1878). Modern commercial whaling began in 1904 and terminated in 1963, although substantial illegal catches occurred after the 1963 moratorium (Yablokov, 1994). It is estimated that humpback whales were severely depleted, and reduced to perhaps as little as 5% of their original population sizes, during the last century (Chapman, 1974; Findlay, 2000). Though substantially depleted, these populations now appear to be undergoing recovery on certain wintering grounds.

The Gulf of Guinea and neighbouring waters experienced extensive whaling activity during the 18th and 19th centuries. In addition, the West Coast of Africa was host to an intensive episode of humpback whaling in the early 20th Century (the population in this region is currently termed Breeding Stock B[1] by the IWC). Shore based stations and factory ships moored at sites along the coast, including Saldanha Bay, South Africa and Cap Lopez, Gabon, caught an estimated 17,000 humpback whales between 1909 and 1914 (Best, pers. comm.; Findlay, 2000). Annual catches tended to be larger nearer the equator (Findlay, 2000) with a peak in catch in late July/early August, whereas at the southernmost whaling stations in Africa there were two clear peaks about four months apart. This catch pattern is indicative of a northern migration in autumn and a southern migration in spring (Budker and Collignon, 1952).

Several cycles of intense commercial exploitation during the middle of the 20th century also contributed to the depletion of this stock (Findlay, 2000). The humpback whale fishery in this region reopened in 1949 at Cap Lopez, Gabon, with an initial catch level of 1,356 whales, which had plummeted to only 264 whales when the fishery was abandoned in 1952 (Aguilar, 1985). Only 160 whales were caught during a failed attempt to restart the fishery in 1959. During this period mean humpback whale length declined substantially according to catch records (Budker and Roux, 1968; Tønnessen and Johnsen, 1982), both cited in Aguilar (1985). The abandonment after only one year of a commercial fishery initiated in São Tomé, and the reduction of the artisanal catch on the island of Annobón (Pagalu), are further evidence that the Gulf of Guinea stock had been greatly depleted (Aguilar, 1985).

A series of small boat-based, limited aerial surveys, and some shore-based studies have been conducted along the west coast of South Africa, Angola, and Gabon and have

* *Wildlife Conservation Society, Global Conservation, 185th Street and Southern Blvd., Bronx, NY 10460, USA.*
[+] *Center for Biodiversity and Conservation, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.*
[#] *Aventures Sans Frontière, B.P. 7248, Libreville, Gabon.*
[^] *Sackler Institute for Comparative Genomics, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024, USA.*

[1] Within Breeding Stock B, there are currently two sub-stocks termed B1 and B2. The boundary dividing these two sub-stocks currently lies in Angola, and is being re-evaluated (Pomilla *et al.*, 2006; Rosenbaum *et al.*, 2009).

been published (Walsh *et al.*, 2000) or reported to the IWC's Scientific Committee (Best *et al.*, 1999; 1995; Collins *et al.*, 2010; 2006; Pomilla *et al.*, 2006; Rosenbaum and Collins, 2006; Rosenbaum *et al.*, 2009). Beginning in 2001, pilot surveys were undertaken off Gabon with the objective of obtaining data for genetic and photographic mark-recapture estimates of abundance for humpback whales wintering off its coast (Collins *et al.*, 2010; 2006). In 2002, an extensive and systematic set of aerial line transect surveys were flown off Gabon's coast in order to provide the first seasonal abundance estimate for the Southern Hemisphere humpback whale breeding assemblage in wintering sub-Region B1. The estimate generated from these aerial surveys, as well as those reported in Collins *et al*. (2010; 2006) should provide a basis for evaluating future trends in the population migrating to this region.

METHODS

Description of the study area and survey design

The study area included the entire coastline of Gabon, approximately 486 n.miles, which extends from Equatorial Guinea (1°N) to the Republic of Congo (4°S), and a section of the Congolese coastline until just beyond Conkouati lagoon mouth. The coastal waters of Gabon are characterised by a continental shelf 50–60 n.miles wide that gently slopes to 100m depth with a rapid depth increase thereafter. The 1,000m depth contour was used as a guideline in defining the outer limit of the study area to permit the observation of humpback whale distribution with respect to considerable changes in bathymetry and at varying distances from the coast, while still being feasible in terms of the available survey effort. The inner limit was defined by the coastline; large river inlets were excluded, as were areas in the vicinity of Libreville and Port Gentil to avoid air traffic in those areas.

The study area was split into two strata, namely a northern and southern stratum of 4,706 n.miles^2 and 12,868 n.miles^2, respectively (Fig. 1). This was done to permit the estimation of separate abundance estimates by stratum and due to the survey logistics given available refueling stations in Libreville, Port Gentil, Iguela, Omboué and Gamba. The northern stratum was delimited by the border with Equatorial Guinea and the tip of Cape Lopez; the southern stratum extended south from Cap Lopez until just beyond Conkouati lagoon mouth. Due to persistent fog, the last seven transects legs in the southern stratum were only partially completed in unfavourable sighting conditions. The observations and effort associated with these transect legs were excluded during analysis and the southern stratum was redefined to exclude the partially surveyed region, reducing this stratum to 9,667 n.miles^2.

The definition of two separate survey strata also facilitated the survey design process, as their shape characteristics allowed for a zigzag design, giving an efficient survey plan with no off-effort time between transects (except that required to travel to and from transects at the start and end of each survey day). In addition, it made it possible to orient

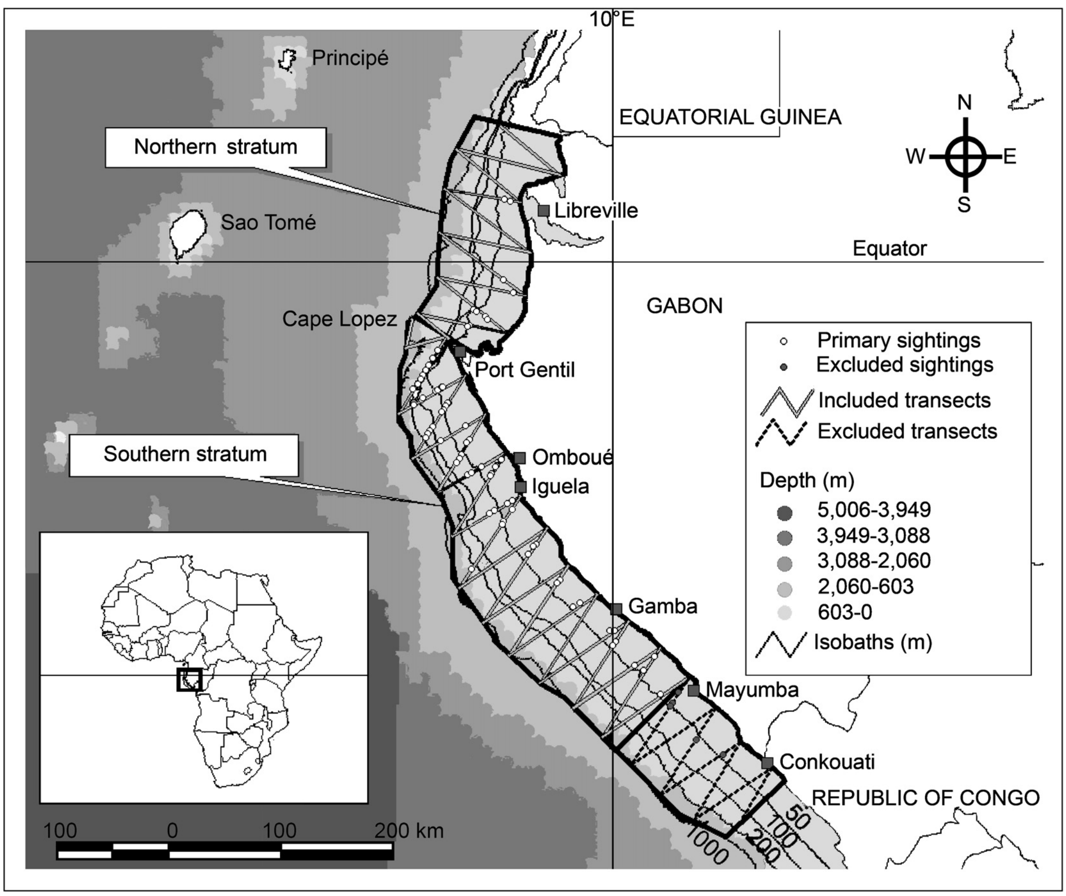

Fig. 1. The study region (bold line) off the Gabon coast delimited by the 1,000m depth contour. The completed line transects in the northern and southern survey stratum are shown as a double line (transects only partially completed and excluded from the analysis are shown as dotted lines). The observations of humpback whale groups made along the survey transects are also shown. The redefined southern stratum that excludes the transects only partially completed due to fog with their five associated observations can also be seen.

Table 1

Details of the study area, survey design with the number of planned/surveyed line transects (k) and planned effort (L_p), as well as the number of observations before truncation (n_{bt}). Also shown are the number of observations (n), the amount of effort (L) and the estimate of encounter rate (n/L) for each stratum with the corresponding standard error (SE), percent coefficient of variation (%CV) and 95% confidence interval (95% CI).

Region	Area (n.m^2)	k	L_p (n.m)	n_{bt}	n	L (n.m)	n/L (n.m^{-1})	SE	(%CV)	95% CI
Study area	14,373	33	1,488.20	74	53	1,348.45	–	–	–	–
Northern stratum	4,706	11	468.83	10	5	446.62	0.011	0.005	44.63	(0.004 – 0.029)
Southern stratum	9,667	22	1,019.37	64	48	902.83	0.053	0.013	24.94	(0.032 – 0.089)
Excluded	3,201	7	298.96	5	–	–	–	–	–	–

the transect legs approximately perpendicular to a suspected density gradient running out from the coast in order to minimise variation in encounter rate and improve the precision of the density estimate. A design axis was used to orientate the line transects and its bearing was defined with respect to an x-axis running in an east-west direction. To orientate the transect legs of the zigzag design approximately perpendicular to the coastline and parallel to the suspected gradient in density, the design axis was set at an angle of 65 and 135 degrees in the northern and southern stratum, respectively.

The automated survey design component of the *Distance* 4 software (Thomas *et al.*, 2010) was changed to produce an amended version of the systematic 'Equal Spaced Zigzag' design with a random start (Strindberg and Buckland, 2004a; 2004b). The amendment to the design included generating the line transects within each survey stratum rather than within a convex hull of each of the survey strata. Given the shape of the strata this led to a more efficient design without any discontinuity in the line transects, which would not have been the case if the usual convex hull were used when generating the transects. It also provided fairly even coverage probability (i.e. the probability of sampling any location in the study area) for this particular survey area, which avoided potentially biased estimates through uneven sampling intensity as described below (Strindberg, 2001). For some other non-convex regions this design might lead to inaccessible areas with zero coverage probability within the study region; whether or not this is the case can be investigated via a coverage probability simulation. When there are inaccessible areas one can revert back to using the convex hull based design. There was insufficient information to attempt an improvement in precision by allocating effort approximately in proportion to abundance in each stratum. Thus, the same equal spacing of 10 n.miles was used to generate the amended 'Equal Spaced Zigzag' designs in each of the strata thereby allocating effort in proportion to stratum size.

The spacing of 10 n.miles in conjunction with the orientation of the design axis was chosen to ensure sufficient replicate transects per stratum for the purposes of estimating variance in encounter rate. The survey design originally comprised 40 transect legs for a combined length of 1,787.16 n.miles with 11 legs (468.83 n.miles) covering the northern stratum and 29 legs (1,318.33 n.miles) covering the southern stratum. The removal of the seven southernmost legs from this analysis, due to the unfavourable survey conditions near the Congolese frontier, resulted in a total survey length of 1,488.2 n.miles with only 22 legs (1,019.37 n.miles) covering the southern stratum. A Transverse Mercator projection was used while generating the design and when calculating the surface areas and line transect lengths (the design is shown in Fig. 1 and details are given in Table 1).

The trade-off between theoretical rigour and difficult logistical constraints

By using an automated survey design algorithm to randomly locate the line transects, a key assumption underlying distance sampling was fulfilled, namely that transects are located randomly with respect to the distribution of the animals (see Thomas *et al*. (2007) for another example of automated survey design use). A random design that also gives even coverage probability is crucial for valid statistical inference using a standard distance sampling analysis. If standard analysis methods are applied when coverage probability is uneven, then biased density estimates may result. To avoid this potential problem when differences in coverage probability are extreme, the Horvitz-Thompson-like (or other) estimator that allows coverage probability to vary by observation can be applied, even if this is likely to lead to an increase in the variance of the estimator (Strindberg, 2001; Strindberg and Buckland, 2004b).

The random zigzag survey design used for this survey was generated by passing the zigzag through equally spaced points on opposite sides of the stratum boundary. This type of design does not provide completely even coverage probability (Strindberg, 2001; Strindberg and Buckland, 2004b). However, the height[2] of the survey strata does not vary dramatically with respect to the design axis used to randomly locate and orientate the zigzag in each survey stratum (the variation in height across each transect causes the potential unevenness in coverage probability). Thus, the variation in coverage probability will also be limited and the design a reasonable alternative to a more complex zigzag design (Strindberg and Buckland, 2004b). This was confirmed by simulating the design 1,000 times over the locations of the sightings and using a χ^2 goodness-of-fit test to examine whether the coverage probability was even at these points (Strindberg, 2001)[3].

A zigzag survey design is an efficient systematic design, as no flight time is wasted moving between survey legs, which was critical for this survey due to limited refuelling opportunities. In addition, with systematic designs, the line transects are evenly spread throughout the study area. Even spatial spread of sampling units tends to improve estimator precision; it ensures that a more representative sample is selected from the population giving less variable estimates (Strindberg, 2001). During aerial surveys, systematic parallel transects are frequently used. Although the latter design gives a more even spatial spread than a zigzag design, it was not an option given the vast extent of the survey area and the limited survey effort available.

[2] The height of the survey stratum at any point is the length of the line that runs perpendicular to the design axis and is delimited by the points at which this line intersects the survey stratum boundary.

[3] The index-of-dispersion used for this purpose (Strindberg, 2001) had a value of 75.10, which did not exceed the value of the distribution with 78 degrees-of-freedom at the 5% significance level, namely 104.98. Thus the null hypothesis of even coverage probability was accepted.

Executing the surveys

The aerial survey was conducted in a single-engine Cessna 182 provided by the Wildlife Conservation Society (WCS). During the survey the aircraft flew at an average altitude of 740ft at an average speed of 104 knots/hr. A data collector was located in the co-pilot seat and primary observers on each side of the plane made observations by scanning an area perpendicular and forward of the plane. Once a sighting was made, a clinometer measurement to the centre of the group, GPS location of the aircraft and altitude reading were taken as the animals passed abeam. The clinometer reading and altitude were used to calculate the perpendicular distance to each observation, except for four of the observations included in the analysis where it was not possible to obtain a clinometer reading (a GPS location of the group was recorded instead in order to estimate perpendicular distance to the transect line). After passing the sighting, the aircraft left the transect line and circled until the two backseat observers and the front seat recorder were each able to independently identify the species and estimate group size. Each person made three estimates of group size: minimum; maximum; and best.

The aerial survey took place between 5–9 August 2002 (excluding the bad weather survey days), corresponding to a likely peak in the migration and abundance in Gabonese coastal waters, as inferred from field surveys (Collins *et al.*, 2010; 2006) and historical catch information (Budker and Roux, 1968; Townsend, 1935). The line transects were completed from north to south in an attempt to minimise systematically double counting individual humpback whales migrating northwards and artificially inflating the estimate of density and abundance.

Statistical analyses

In line transect distance sampling observers traverse lines of aggregate length L. The number n of animals of interest are counted and the perpendicular distance to each is recorded. If the animals of interest occur in groups, as humpback whales do, then the perpendicular distance to the centre of the group is recorded instead. If all animals located on the line were detected with certainty, then the density of humpback whale groups in the study area surveyed (D_s) is estimated as (Buckland *et al.*, 2001):

$$\hat{D}_s = \frac{n\hat{f}(0)}{2L} \quad (1)$$

where $f(0)$ is the probability density function of the perpendicular distances evaluated at zero. Thus density estimates are obtained from estimates of $f(0)$ and encounter rate (n/L). $f(0)$ can be interpreted as $\frac{1}{\mu}$, where μ is referred to as the effective strip half-width and corresponds to the perpendicular distance from the transect line within which the number of undetected groups is equal to the number of groups detected beyond it. Twice the effective strip half-width multiplied by L gives the effective area surveyed. Humpback whale density is obtained by multiplying the estimated whale group density by the estimated expected group size $\hat{E}(s)$. The densities of groups or individual whales are multiplied by the surface area of the study area or survey stratum to obtain the corresponding abundance estimate.

The Distance software was used to analyse the data (Thomas *et al.*, 2010). A number of different groupings of and truncation points for the observational data, as well as different combinations of key function (Half-normal, Uniform, Hazard rate) and series expansion (cosine, simple polynomial, hermite polynomial) were considered as candidate models when estimating the detection function. During analysis the data were grouped and also right truncated to improve model fit, as it is difficult to obtain accurate clinometer measurements, especially at larger distances where a small change in angle relates to a large change in distance. To account for the fact that observers were not able to see directly beneath the aircraft a left truncation distance for the data was selected by inspecting a histogram of detection frequencies plotted against distance from the transect line. Subsequently only data at distances greater than the left truncation distance were used to fit the detection function, which was then extrapolated back to distance zero. Akaike's Information Criterion (AIC) (Akaike, 1973) was used for model selection. The variance of encounter rate was estimated empirically using the replicate transect lines as samples, while maximum likelihood methods were used to estimate the variance of the effective strip width.

An estimate of expected group size $\hat{E}(s)$ was obtained by pooling all the data and calculating the mean of the average best group size estimated independently by the observers for each detection. Group size was regressed against detection distance to determine whether there was any indication of size bias in the group size estimate.

The estimates of whale or whale group density or abundance are clearly negatively biased, as some animals on the line (or at the left truncation distance) are not detected (i.e. $g(0) \neq 1$). This is an unavoidable consequence of the fact that these species spend the majority of their time underwater, where they are difficult or impossible to detect from the air. The risk of biased estimates is particularly hard to quantify in wintering areas such as the coast of Gabon, where detection probabilities are largely unknown and may vary significantly across group types with different behavioural characteristics. This availability bias is compounded by a perception bias that is due in part to the relatively high speed at which the observers are travelling during an aerial survey by plane, but also influenced by observer fatigue, experience or changing weather conditions (Fleming and Tracey, 2008; Marsh and Sinclair, 1989). Given that survey specific data to apply independent observer methods (Laake and Borchers, 2004) for estimating $g(0)$ were not available, the correction factor proposed by Barlow *et al.* (1988) for aerial surveys of harbour porpoise was used. The probability that an animal is visible given that it is on the transect line is given by:

$$\hat{g}(0) = \frac{t+v}{t+d} \quad (2)$$

where t is the average time an animal stays on the surface, v is the amount of time the animal is within the observer's visual range and d is the average time the animal spends submerged while diving. Unlike some of the independent observer methods that account for availability and perception bias, this method accounts for the former type of bias, but does not permit the estimation of the proportion of groups available for detection that were missed. One of the implicit assumptions is that animals who surface have a $g(0)$ of 1 (if $v > d$, then on average this happens at least once during the time they are under observation). The corrected density estimate of humpback whales is then obtained as follows:

$$\hat{D} = \frac{n\hat{f}(0)\hat{E}(s)}{2L\hat{g}(0)} \quad (3)$$

The estimation of $g(0)$ was based on a small sample of 14 humpback whale groups observed off Iguela in a small sub-region within the aerial survey study area in September 2003. Data on the surfacing, ventilation and dive patterns were recorded by observing groups for as close as possible to 60min each during boat-based surveys. The correction factor was calculated by using the mean values for average surface time t and dive time d, or the lower or upper extreme of their 95% confidence interval (95% CI) ranges (note that the method uses means rather than full distributions and there is no way to evaluate variance or to take account of the patterns of animal availability).

RESULTS

A total of 1,488 n.miles of survey effort consisting of 33 individual transect legs were completed. Combining the northern and southern stratum, the total study area consisted of 14,373 n.miles^2 (see Table 1). Across all strata, average conditions on the Beaufort scale equalled two; however higher Beaufort conditions were encountered in the northern stratum compared to the southern stratum. A total of 74 on-effort group sightings were made across both strata, but the majority of the sightings ($n = 64$) were made in the southern stratum, which covers the region from Cap Lopez to areas south of Gamba (Fig. 1).

The data were left truncated at 450m (0.243 n.miles) from the transect line (Fig. 2). The data were right truncated at 2,350m (1.269 n.miles), pooled across both survey strata and grouped to estimate detection ($\hat{f}(0)$ = 2.106 (n.miles^{-1}), percent coefficient of variation (%CV) of 16.38, and a 95% CI = 1.519–2.919) and the effective strip width ($E\hat{S}W$ = 0.475 n.miles and a 95% CI = 0.343–0.658), while the analysis was stratified for encounter rate (Table 1). The encounter rate was considerably higher for the southern stratum compared to the northern stratum (0.053 n.miles^{-1} vs. 0.011 n.miles^{-1} with a corresponding %CV of 25% vs. 45%, respectively).

Using AIC for model selection, a half-normal model with no adjustment terms was selected. The AIC value for the selected model was 219.43, while the difference in AIC values for the uniform with a cosine adjustment term and the hazard-rate with no adjustment terms that were ranked second and third was 0.16 and 2.46, respectively. The density estimates of the half-normal and uniform model with cosine adjustment terms were identical to the second decimal place, and the fit of the former model was marginally better; hence it was selected as the final model. The detection function for the half-normal model fit to the grouped observation data is shown in Fig. 2 (according to the goodness-of-fit test, the probability of a χ^2 greater value, $p = 0.97099$). The estimates of humpback whale group density and abundance for the northern and southern stratum, as well as the study area as a whole are given in Table 2. The global density estimate was calculated by taking the mean of the stratum estimates weighted by stratum area. The estimate of humpback whale group density over the entire study area was 0.041 n.miles^{-2} with an abundance of 597 (95% CI = 342–1,042). Although the detection probability in the northern stratum may have been somewhat decreased due to an increase in Beaufort sea state, there were clear differences in densities between the strata.

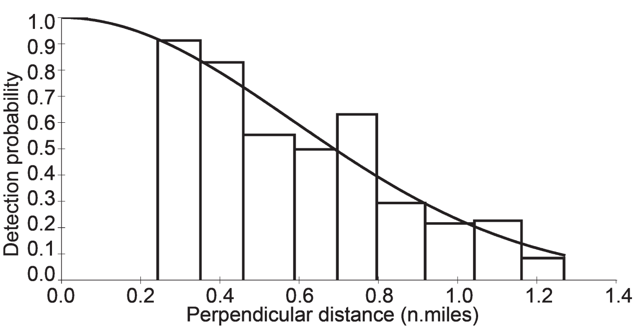

Fig. 2. Detection function for the half-normal model fit to the perpendicular distances of observations of humpback whale groups. Observations with a perpendicular distance of less than 450m (0.243 n.miles) or greater than 2,350m (1.269 n.miles) from the transect line where truncated. To improve model fit the data were grouped for analysis to deal with inaccuracies in the clinometers measurements and the interval cutpoints were also selected to deal with some potential heaping in the data.

The estimate of expected group size $\hat{E}(s)$ was 2.109 with a %CV of 6.86 and a 95% CI of 2.074–2.143. Percentage distribution of estimated group size[4] from one to seven is 30.82, 42.77, 11.95, 7.55, 4.40, 1.89, 0.63, respectively. Using detections beyond 450m from the transect line and only those sightings whose distances had been obtained by means of a clinometer reading, the estimate of group size did not vary significantly from that obtained by regressing group size against detection distance (the p-value was equal to 0.321).

The estimates of humpback whale density and abundance for the northern and southern stratum, as well as the study area as a whole, were calculated using $\hat{E}(s)$. The overall humpback whale density was estimated as 0.09 n.miles^{-2} with a resulting abundance for the study area of 1,259 whales with a 95% CI of 710–2,333 (see Table 2). The stratified estimates of humpback whale density and abundance are also shown in Table 2.

The average surface and dive time were calculated for each of the 14 groups[5] and then the overall averages were calculated across all groups to obtain the mean surface time t and dive time interval d of 2.58 and 3.25 minutes with 95% CIs of 1.77–3.40 and 2.15–4.37, respectively. The smallest clinometer readings taken during the survey were 3 degrees, which at an average altitude of 740ft implies that the observers were scanning for whales out to a distance of approximately 2.3 n.miles. Given that the aircraft flew at an average speed of 104 knots hr^{-1}, this distance would be covered in about 1min, thus this is the time value used for v. The correction factor was calculated by using the mean values for t and d, or the lower or upper extreme of their 95% CI ranges resulting in values between 0.45 and 0.79 with a value of 0.61 using the means (Table 3). Adjusting the overall abundance estimate of 1,259 humpback whales using these extreme values for $\hat{g}(0)$ would alter the result considerably, giving estimates that range between 1,594 and 2,798 with 2,064 corresponding to the value of 0.61. The estimate of availability bias should be interpreted with caution, as it was not possible to collect data at the time of the survey and hence the group size, composition and behaviour might have been different than for those in the area at the time of the survey. Dive times are likely to vary by group type and behaviour, with larger groups or groups displaying certain types of behaviour (e.g. competitive behaviour, repeated breaching, tail lobbing) being on the

[4] Includes all group size estimates made independently by the observers for those sightings where group size was recorded.

[5] There were 4 mother-calf pairs, 3 other pairs, 5 singletons (3 of which were singing) and 2 other groups (of which one was an unusually large group of about 12 whales that split into four groups of 6, 3, 2, and 1 individual(s) about 18 minutes into the 50 minute observation period).

Table 2

Global (area weighted mean of the stratum estimates) and stratified estimate of humpback whale group density ($\hat{D}_s$) in numbers per n.m^2 and abundance ($\hat{N}_s$), as well as humpback whale density ($\hat{D}$) in numbers per n.m^2 and abundance ($\hat{N}$), with the corresponding standard error (SE), percent coefficient of variation (%CV) and 95% confidence interval (95% CI). These are the unadjusted results that do not account for $g(0)<1$.

Region	Area (nm^2)	Group estimates		SE	(%CV)	95% CI	Individual estimates		SE	(%CV)	95% CI
Study area	14,373	$\hat{D}_s$	0.042	0.012	28.24	(0.024–0.073)	$\hat{D}$	0.088	0.025	29.06	(0.049–0.155)
		$\hat{N}_s$	597	168.59		(342–1,042)	$\hat{N}$	1,259	365.87		(710–2,233)
Northern stratum	4,706	$\hat{D}_s$	0.012	0.006	47.54	(0.004–0.031)	$\hat{D}$	0.025	0.012	48.04	(0.009–0.067)
		$\hat{N}_s$	55	26.15		(21–147)	$\hat{N}$	117	56.20		(44–314)
Southern stratum	9,667	$\hat{D}_s$	0.056	0.017	29.84	(0.031–0.101)	$\hat{D}$	0.118	0.036	30.62	(0.064–0.216)
		$\hat{N}_s$	541	161.42		(300–977)	$\hat{N}$	1,142	349.64		(623–2,091)

Table 3

The estimated values for $\hat{g}(0)$ given a range of values (mean, lower and upper limit of their 95% confidence intervals) for the average time (in minutes) an animal stays on the surface (t) and the average time the animal spends submerged diving (d), assuming the amount of time the animal is within the observer's visual range (v) is approximately 1 minute.

t	d	$\hat{g}(0)$
2.58	3.25	0.61
1.77	3.25	0.55
3.40	3.25	0.66
2.58	2.15	0.76
1.77	2.15	0.71
3.40	2.15	0.79
2.58	4.37	0.52
1.77	4.37	0.45
3.40	4.37	0.57

surface for a larger proportion of time or more visible. Availability for detection is also likely to be different from the air versus from the boat used to collect data to compute ventilation and dive patterns (for example, individual singing males tend to spend more time underwater and are thus less available for detection during an aerial survey).

Humpback whale distribution was negatively associated with increasing water depth (see Fig. 1). Observations were predominantly made in shallow waters of less than 50m depth (52 observations, including all 10 observations made in the northern stratum and most of the observations in the southern portion of the southern stratum). In the northern portion of the southern stratum only a single sighting was made beyond the 200m depth contour, while 12 observations fell in the 50–100m depth range (spread across different transects) and 14 fell in the 100–200m depth range[6] (occurring just south of Cape Lopez where the depth contours are close together due to the precipitous slope of the continental shelf). Thus, 65.82%, 15.19%, 17.72%, 1.27% of the observations were made within the depths ranges 0–50m, 50–100m, 100–200m, 200–1000m, respectively, corresponding to 35.23%, 18.13%, 13.30%, 33.33% of the surface area of the study region[7]. These results are based on fairly coarse GEBCO Digital Atlas[8] (GEBCO Digital Atlas, 2003) bathymetry data, so should be interpreted with some caution.

[6] Nine of these observations where made almost exactly along the 200m contour as the third transect south of Cape Lopez followed this contour unlike other transects that tended to cut across all depth contours (see Fig. 1).

[7] Not surprisingly, a test that combines the last two depth categories, due to the single sighting in the 200–1000m depth range, gives $p < 0.001$.

[8] Contours compiled and digitized from the International Bathymetric Chart of the Central Eastern Atlantic (Sheets 1.08–1.12) published by the Service Hydrographique et Oceanographique de la Marine (Paris, France) at a scale of 1:250,000 (datum WGS84).

DISCUSSION

Even with the uncorrected conservative abundance estimate of 1,259 whales (%CV = 29.06; 95% CI = 710–2,333), the results indicate that the humpback whale population utilising the coastal waters of Gabon has undergone some degree of recovery following the cessation of whaling in the 1960s. Correcting for animals on or near the line that are not seen increases estimates of abundance. The estimate of $g(0)$ gives some indication of how the abundance estimate might change. However given that it was not possible to account for perception bias these numbers are still likely to be negatively biased.

Another contributor to the potentially negatively biased abundance estimates is the fact that these surveys provide only an instantaneous snapshot of the number of whales occupying Gabon's coastal waters. There are reports of humpback whales in other areas throughout the region from west South Africa to the Bight of Benin (Best *et al.*, 1999; Van Waerebeek *et al.*, 2001) with some proportion of the population potentially visiting localities in the region where humpback whales are know to congregate, including São Tomé, Bioko and the coasts of Equatorial Guinea, Cameroon, Congo and Angola (Aguilar, 1986; Best *et al.*, 1999; Pomilla *et al.*, 2006; Rosenbaum and Collins, 2006; Rosenbaum *et al.*, 2009; Van Waerebeek *et al.*, 2001). This indicates that the wintering grounds for humpback whales in the Gulf of Guinea extend beyond the coastal waters of Gabon, and thus the likelihood that all whales in the population or populations[9] of interest will occupy these waters at the same time is low. In addition, certain classes of animals such as calving females are likely to have different occupancy periods based on reproductive condition. Recent evidence suggests that some animals (particularly females and juveniles) may not even make the full migration to equatorial waters every year (Corkeron and Connor, 1999). From satellite tagging results of 15 whales in 2002, there is clearly differential use and movement of humpback whales through Gabon's waters (Rosenbaum and Mate, Submitted), demonstrating that this area is an important wintering ground in the Gulf of Guinea.

These considerations suggest that the number of humpback whales actually using Gabon's coastal waters at some point in their life cycle is probably larger than indicated by the transect estimates presented here. Determining exactly how much larger, especially with a corrected estimate that ranges between 1,594 and 2,798, will require additional surveys at different time periods and also using other methods for estimating abundance, such as those described in Collins *et al.* (2010). Following 277 days of boat-based survey effort off the coast of Gabon (primarily in the

[9] See Section 3.2.4 of IWC (2011b).

southern stratum), between 2001 and 2006, 1,323 different individuals were identified photographically from tail flukes and 1,404 different individuals were identified from genotyped biopsy samples. Capture-recapture analyses from the photographic identification and genetic studies yield a consistent set of abundance estimates of 4,300–7,200 individuals (Collins *et al.*, 2010; 2006)[10]. As the capture-recapture abundance estimates are carried out through a large portion of the breeding season and likely include animals moving through Gabon's waters to other areas in the Gulf of Guinea, the abundance estimate derived from the distance sampling is consistent with a substantial portion of the entire population being encountered during this period.

The 1,000m depth contour was chosen as the outer limit of the survey region because of both safety and refuelling limitations of the aircraft, in addition to expectations of whale distribution being negatively associated with increasing water depth for this species on their breeding grounds. As the waters on the continental shelf have relatively uniform depths, but depth progressively increases toward the shelf edge, there was some appreciable decrease in encounter rate as the observers approached the 1,000m depth contour along most transects. Consistent with patterns observed in other breeding grounds where humpback whales tend to spend most of their time in coastal waters over the continental shelf, with very limited occurrence in deeper waters (Andriolo *et al.*, 2006; Best *et al.*, 1996; Ersts and Rosenbaum, 2003; Findlay *et al.*, 1994; Zerbini *et al.*, 2004; Zerbini *et al.*, 2006), the vast majority of observations were made on the continental shelf out to a depth of approximately 200m.

The abundance estimates presented here and the distribution of the observations suggest that large numbers of humpback whales use the inshore waters between Cap Lopez and the Congo Frontier (southern survey stratum) during the austral winter breeding season. Given the overlap between this important breeding habitat for humpback whales and extensive ongoing and planned hydrocarbon activities, risks to this population need further investigation. The scientific and conservation community has expressed concern about the negative effects of noise exposure on whale populations and other cetaceans (Clark *et al.*, 2009; IWC, 2011a); seismic surveys occurring in breeding grounds, feeding regions, and restricted migratory corridors may have a negative impact on critical life functions of these species (Cerchio *et al.*, 2010; IWC, 2007). Potential impacts to whales include acoustic disturbance due to geophysical seismic surveys (Cerchio *et al.*, 2010; Di Iorio and Clark, 2010), as well as disturbance associated with vessel traffic and oil production operations (Richardson *et al*., 1995; IWC, 2007; NRC, 2005). In addition, industrial activities within and pollution of the marine environment in Gabon are also causes for some general concern (Findlay *et al.*, 2004). On several occasions during this aerial survey, oil slicks were seen to be emanating from oil production facilities and were relatively large, stretching a kilometre or more from their source across the water's surface.

Given that Gabon's coastal waters are probably a significant wintering area for humpback whales in the southeastern Atlantic Ocean, additional measures for protection and mitigation of impacts to this population on their breeding grounds should be considered.

[10] The authors propose use of a combination of photographic and error corrected genotypic results for males only to define naïve lower and upper bounds for estimates of population size. A suggested lower bound is 4,314 (%CV = 19) individuals based on the 2001–2004 fluke data. A suggested upper bound is 3,567 (%CV = 23) based on the 2004–2006 genotypes for males only, giving a corrected estimate of 7,134 whales.

ACKNOWLEDGMENTS

We thank Peter Ragg for his expert piloting, navigating, and logistical skills that made this survey feasible. We greatly appreciate the work done by Solange Nguessono, Hannalore Ragg and Francois Horrent to collect the data used in the preliminary estimation of *g*(0). We are grateful for the support provided Lee White, the WCS Gabon Country Program, Operation Loango and thank the Government of Gabon for their support of this work. We thank Rombout Swanborn, Piet van Leuven, Mireille Meersman and the staff of Loango Lodge for their support and hospitality at Iguela. Finally, we are thankful for the generous support of numerous individuals, foundations, and organisations primarily through grants to HCR that have helped make this project possible.

REFERENCES

Aguilar, A. 1985. Compartmentation and reliability of sampling procedures in organochlorine pollution surveys of cetaceans. *Residue Rev.* 95: 91–114.

Aguilar, A. 1986. A review of old Basque whaling and its effect on the right whales (*Eubalaena glacialis*) of the North Atlantic. *Rep. int. Whal. Commn (special issue)* 10: 191–99.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp.267–81. *In*: Petran, B.N. and Csaáki, F. (eds). *International Symposium on Information Theory*. Akademia Kiado, Budapest, Hungary. 451pp.

Andriolo, A., Martins, C.C.A., Engel, M.H., Pizzorno, J.L., Mas-Rosa, S., Freitas, A.C., Morete, M.E. and Kinas, P.G. 2006. The first aerial survey to estimate abundance of humpback whales (*Megaptera novaeangliae*) in the breeding ground off Brazil (Breeding Stock A). *J. Cetacean Res. Manage.* 8(3): 307–11.

Barlow, J., Oliver, C.W., Jackson, T.D. and Taylor, B.L. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. *Fish. Bull.* 86(3): 433–44.

Best, P.B., Reeb, D., Morais, M. and Baird, A. 1999. A preliminary investigation of humpback whales off northern Angola. Paper SC/51/CAWS33 presented to the IWC Scientific Committee, May 1999, Grenada, WI (unpublished). 12pp. [Paper available from the Office of this Journal].

Best, P.B., Sekiguchi, K. and Findlay, K.P. 1995. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Marine Ecology. Progress Series* 118(1–3): 1–12.

Best, P.B., Sekiguchi, K., Rakotonirina, B. and Rossouw, A. 1996. The distribution and abundance of humpback whales off southern Madagascar, August–September 1994. *Rep. int. Whal. Commn* 46: 323–31.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK. vi+xv+432pp.

Budker, P. and Collignon, J. 1952. Trois campagnes baleinieres au Gabon (1949–1950–1951). *Bulletin Institut d'Études Centrafricaines* 3: 75–100. [In French].

Budker, P. and Roux, C. 1968. The 1959 summer whaling season at Cape Lopez (Gabon). *Norsk Hvalfangsttid.* 6: 141–5.

Cerchio, S., Collins, T., Strindberg, S., Bennett, C. and Rosenbaum, H.C. 2010. Humpback whale singing activity off northern Angola: an indication of the migratory cycle, breeding habitat and impact of seismic surveys on singer number in Breeding Stock B1. Paper SC/62/SH12 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 21pp. [Paper available from the Office of this Journal].

Chapman, D.G. 1974. Status of the Antarctic rorqual stocks. pp.218–38. *In*: Schevill, W.E. (eds). *The Whale Problem, A Status Report*. Harvard University Press, Massachusetts. x+419pp.

Clark, C.W., Ellison, W.T., Southall, B.L., Hatch, L., van Parijs, S.M., Frankel, A. and Ponirakis, D. 2009. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Mar. Ecol. Prog. Ser.* 395: 201–22.

Collins, T., Cerchio, S., Pomilla, C., Loo, J., Carvalho, I., Ngouessono, S. and Rosenbaum, H.C. 2010. Estimates of abundance for humpback whales in Gabon between 2001–2006 using photographic and genotypic data. Paper SC/62/SH11 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 23pp. [Paper available from the Office of this Journal].

Collins, T., Cerchio, S., Pomilla, C., Ngouessono, S., Mbadinga, N., Dushane, J., Murray, A., Weber, D. and Rosenbaum, H.C. 2006. An estimate of abundance using mark-recapture data for breeding stock B1: Gabon. Paper SC/A06/HW10 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006 (unpublished). 8pp. [Paper available from the Office of the Journal].

Corkeron, P. and Connor, R.S. 1999. Why do baleen whales migrate? *Mar. Mammal Sci.* 15: 1228–45.

Di Iorio, L. and Clark, C.W. 2010. Exposure to seismic survey alters blue whale acoustic communication. *Biol. Letters* 6: 334–35.

Ersts, P.J. and Rosenbaum, H.C. 2003. Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *J. Zool., London.* 260: 337–45.

Findlay, K.P. 2000. A review of humpback whale catches by modern whaling operations in the Southern Hemisphere. *Mem. Queensl. Mus.* 47(2): 411–20.

Findlay, K.P., Best, P.B., Peddemors, V.M. and Gove, D. 1994. The distribution and abundance of humpback whales on their southern and central Mozambique winter grounds. *Rep. int. Whal. Commn* 44: 311–20.

Findlay, K.P., Collins, T. and Rosenbaum, H.C. 2004. Environmental impact assessment and mitigation of marine hydrocarbon exploration and production in the Republic of Gabon. Report of the Wildlife Conservation Society, 2300 Southern Blvd, Bronx, NY 10460, USA.

Fleming, P.J.S. and Tracey, J.P. 2008. Some human, aircraft and animal factors affecting aerial sruveys: how to enumerate animals from the air. *Wildlife Research* 35: 258–67.

GEBCO Digital Atlas. 2003. *Centenary edition of the IHO/IOC General Bathymetric Chart of the Oceans*. British Oceanographic Data Centre, UK. [See *www.bodc.ac.uk.*]

International Whaling Commission. 2007. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 9:227–96.

International Whaling Commission. 2011a. Report of the Scientific Committee. Annex K. Report of the Standing Working Group on Environmental Concerns. *J. Cetacean Res. Manage. (Suppl.)* 12:238–66.

International Whaling Commission. 2011b. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, 4–7 April 2006, Hobart, Tasmania. *J. Cetacean Res. Manage. (special issue 3)*: 1–50.

Laake, J. and Borchers, D. 2004. Methods for incomplete detection at distance zero. pp.108–89. *In*: Buckland, S.T., Anderson, K.P., Burnham, K.P., Laake, J., Borchers, D. and Thomas, L. (eds). *Advanced Distance Sampling*. Oxford University Press, Oxford. 595pp.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197–300.

Marsh, H. and Sinclair, D.F. 1989. Correcting for visibility bias in strip transect aerial surveys for aquatic fauna. *J. Wildl. Manage.* 53(4): 1017–24.

NRC. 2005. *National Research Council – Marine Mammal Populations and Ocean Noise – Determining when Noise Causes Biologically Significant Effects*. The National Academies Press, Washington DC. 142pp.

Pomilla, C., Best, P.B., Findlay, K.P., Collins, T., Engel, M.H., Minton, G., Ersts, P., Barendse, J., Kotze, P.G.H., Razafindrakoto, Y., Ngouessono, S., Meyer, M., Thornton, M. and Rosenbaum, H.C. 2006. Population stucture and sex-biased gene flow in humpback whales from Wintering Regions A, B, C and X based on nuclear microsatellite variation. Paper SC/A06/HW38 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006 (unpublished). 22pp. [Paper available from the Office of this Journal].

Rosenbaum, H.C. and Collins, T. 2006. The ecology, population characteristics and conservation efforts for humpback whales (*Megaptera novaeangliae*) on their wintering grounds in the coastal waters of Gabon. pp.425–33. *In*: Alonso, A. and Campbell, P. (eds). *Natural History of the Gamba Complex*. Smithsonian Press, Washington, DC.

Rosenbaum, H.C. and Mate, B. Submitted. From north of the equator to the Antarctic: unique and unexpected movements for humpback whales off the coast of West Africa and throughout the eastern South Atlantic Ocean. *Proceedings of the Royal Society B* Biological Sciences.

Rosenbaum, H.C., Pomilla, C., Mendez, M.C., Leslie, M.C., Best, P.B., Findlay, K.P., Minton, G., Ersts, P.J., Collins, T., Engel, M.H., Bonatto, S., Kotze, D.P.G.H., Meyer, M., Barendse, J., Thornton, M., Razafindrakoto, Y., Ngouessono, S., Vely, M. and Kiszka, J. 2009. Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Oceans. *PLoS ONE* 4(10): 11pp. [e7318. doi: 10.1371/journal.pone.0007318].

Starbuck, A. 1878. History of the American whale fishery from its earliest inception to the year 1876. Appendix A. pp.1–768+6pls. *Report of the US Commissioner of Fish and Fisheries, Part 4, 1875–76*. Government Printing Office, Washington, D.C. [Reprinted in 1964 in two volumes by Argosy Antiquarian Ltd, New York].

Strindberg, S. 2001. Optimized automated survey design in wildlife population assessment. PhD thesis, University of St. Andrews, St. Andrews, UK.

Strindberg, S. and Buckland, S.T. 2004a. Design of distance sampling surveys and Geographic Information Systems. pp.190–228. *In*: Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (eds). *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, New York.

Strindberg, S. and Buckland, S.T. 2004b. Zigzag survey designs in line transect sampling. *J. Agric. Bio. Env. Stat.* 9: 443–61.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. and Burnham, K.P. 2010. Distance software design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.

Thomas, L., Williams, R. and Sandilands, D. 2007. Designing line transect surveys for complex survey regions. *J. Cetacean Res. Manage.* 9(1): 1–13.

Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling*. C. Hurst and Co., London. i–xx+798pp.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica (NY)* 19(1–2): 1–50+6 maps.

Van Waerebeek, K., Tchibozo, S., Montcho, J., Nobime, G., Sohou, Z., Sehouhoue, P. and Dossou, C. 2001. The Bight of Benin, a North Atlantic breeding ground of a Southern Hemisphere humpback whale population, likely related to Gabon and Angola substocks. Paper SC/53/IA21 presented to the IWC Scientific Committee, July 2001, London. 8pp. [Paper available from the Office of this Journal].

Walsh, P.D., Fay, J.M., Gulick, S. and Sounguet, G.P. 2000. Humpback whale activity near Cap Lopez, Gabon. *J. Cetacean Res. Manage.* 2(1): 63–68.

Yablokov, A.V. 1994. Validity of Soviet whaling data. *Nature, Lond.* 367(6459): 108.

Zerbini, A.N., Andriolo, A., Da Rocha, J.M., Simoes-Lopes, P.C., Siciliano, S., Pizzorno, J.L., Waite, J.M., DeMaster, D.P. and VanBlaricom, G.R. 2004. Winter distribution and abundance of humpback whales (*Megaptera novaeangliae*) off northeastern Brazil. *J. Cetacean Res. Manage.* 6(1): 101–07.

Zerbini, A.N., Andriolo, A., Heide-Jørgensen, M.P., Pizzorno, J.L., Maia, Y.G., VanBlaricom, G.R., DeMaster, D.P., Simões-Lopes, P.C., Moreira, S. and Bethlem, C. 2006. Satellite-monitored movements of humpback whales (*Megaptera novaeangliae*) in the Southwest Atlantic Ocean. *Mar. Ecol. Prog. Ser* 313: 295–304.