

Estimates of abundance for humpback whales in Gabon between 2001 - 2006 using photographic and genotypic data

T. COLLINS^{1,2}, S. CERCHIO¹, C. POMILLA³, J. LOO^{3, 4}, CARVALHO. I.³, S. NGOUSSONO^{1,6}, H.C. ROSENBAUM^{1,3}

¹WCS/AMNH Cetacean Conservation and Research Program, Marine Program, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460-1099, USA.

²Oman Whale and Dolphin Research Group, PO Box 2531, CPO 111, Muscat, Sultanate of Oman

³Sackler Institute for Comparative Genomics, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

⁴Department of Biology, New York University, 1009 Silver Center, 100 Washington Square East, New York, NY 10003-6688, USA

⁵Faculdade de Ciências do Mar e Ambiente – Universidade do Algarve, Campus Gambelas, 8000-139 Faro, Portugal

⁶Agence Nationale des Parcs Nationaux, Ministère du Tourisme et des Parcs Nationaux, Libreville, Gabon

Introduction

IWC breeding Stock B extends along the west coast of Africa from South Africa (Olsen 1914; Matthews 1938) to the Gulf of Guinea (Budker and Collignon 1952; Gambell, 1976; Best 1994; Walsh *et al.* 2000; Findlay 2001; Rosenbaum and Collins 2004). The precise geographic area utilized by the stock remains uncertain (see Figure 1). There are reports of whales (with a southern hemisphere seasonality) from the northern Gulf of Guinea westwards to Ghana and Cote D'Ivoire (Rosenbaum and Mate 2009, Van Waerebeek *et al.* 2001, 2003 and 2009), Guinea (Bamy *et al.* 2010) and other areas of West Africa (Slijper *et al.* 1964). High densities of whales and breeding have been documented for the coasts of Gabon (Walsh *et al.* 2000; Rosenbaum and Collins 2006; Collins *et al.* 2008), Sao Tome (Carvalho *et al.* 2007) and Angola (Best *et al.* 1999, WCS unpublished data). The west coast of Southern Africa was originally believed to serve only as migratory corridor, but surveys during the austral spring and summer have identified the presence of non-migrating whales in west South Africa and evidence of feeding (Best *et al.* 1995, Barendse *et al.* In Press).

There is some evidence for sub-structure in Breeding Stock B (Carvalho *et al.* SC/62/SH8, Pomilla *et al.* 2006, Rosenbaum *et al.* 2009) and two nominal sub-stocks are currently recognised: The B1 sub-stock winters (June-November) along the coasts of the Gulf of Guinea south to Angola. The B2 sub-stock is thought to utilize the coasts of Namibia and western South Africa, although only feeding and migratory behaviours have been observed in these areas (Best *et al.* 1995; Barendse *et al.* In Press). Considerable uncertainty remains over the definition of these sub-stocks (Rosenbaum *et al.* 2009) and current practice is to align them to discrete geographic areas, likely simplifying a more complex reality. The area of the Walvis Ridge (18°S) is a proposed line of division (Pomilla *et al.* 2006, Rosenbaum *et al.* 2009). The Benguela/Angola frontal zone is also a permanent oceanographic feature of this region and is strongly demarcated by cold and warm water masses (Lass *et al.* 2000; Lutjeharms & Ansorge, 2007). The latitude of this frontal zone varies (6°S-14°S), being at its most northerly extent during the austral winter.

The majority of available data for the B1 sub-stock was collected from field sites in Gabon. Preliminary abundance estimates for Gabon have included aerial survey data and mark recapture data (Strindberg *et al.* in press; Collins *et al.* 2008). Here we present a population abundance estimate for whales utilizing the coastal waters of Gabon using individual identification photographs and genetic multi-locus genotypes.

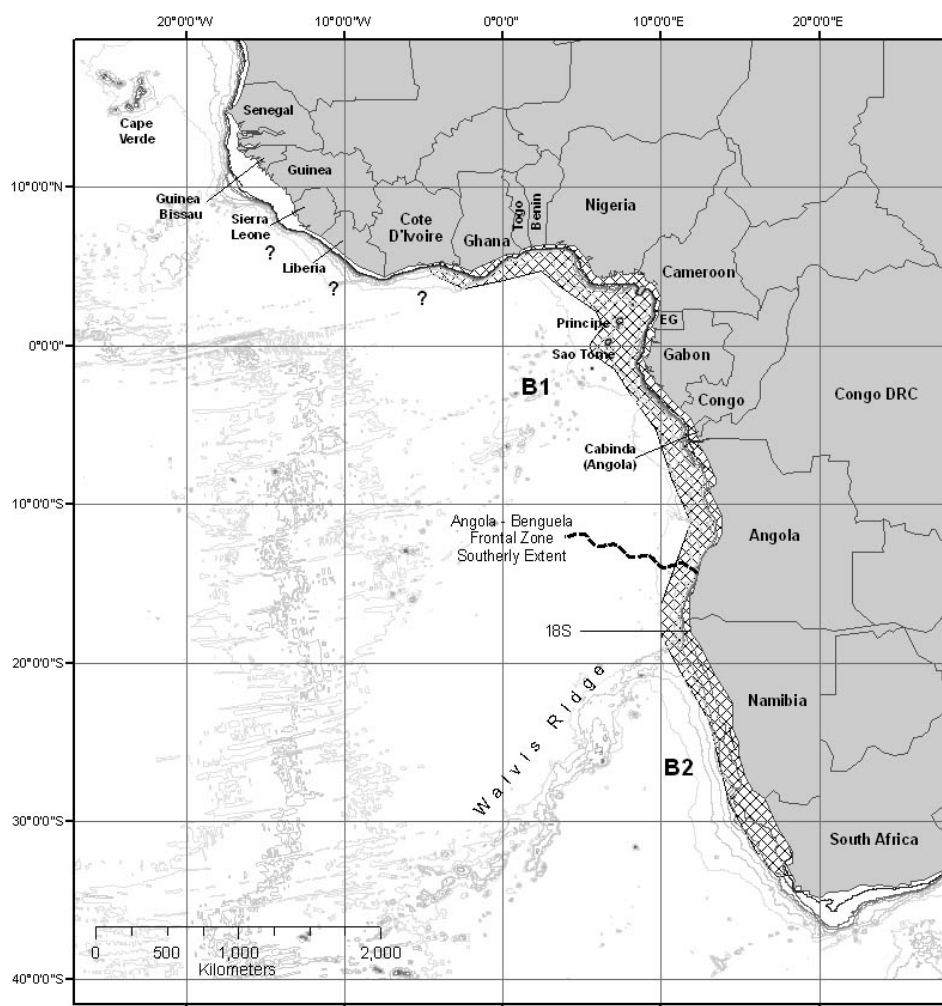


Figure 1: African West Coast and possible extent of Breeding Stock B. Hatched area indicates nominal area of BS B (B1&B2). '?' indicates uncertain but possible distribution

Methods

Photographs and biopsies used in this study were collected from the coastal waters of Gabon during the austral winter (July – October) in each year between 2000 and 2006. Although 4 field sites were worked (see Figure 2), data analysed here were collected between 2001-2006 from two fieldsites; Iguela (1°51'S, 9°20'E) and Mayumba (3°22'S, 10°38'E). These field sites are separated from each other by 200km and were worked concurrently (two boats) during 2005. Effort at each site was not consistent between years and survey periods varied considerably (Table 3), largely due to local logistical constraints. In particular effort at Iguela during 2005 was frequently constrained by limited boat availability. Weather permitting, surveys were conducted on a daily basis and waters extending to a maximum of 50km offshore were the typical focus of effort. Recorded depths never exceeded 100m. Groups of whales were sampled as they were encountered, with a minimal attempt made to evenly distribute sampling effort. Standard procedures were used for identification photography (digital) and biopsy collection (crossbow). Photographs were collected of both sides of the dorsal fin as well as the ventral aspect of the tail flukes. Images were sorted in the field to resolve within day recaptures. These images were imported into a Microsoft Access database to facilitate within and between year matching.



Figure 2: Field sites within Gabon. Iguela and Mayumba data are assessed here

Photographic comparison procedure.

When possible a single photograph was chosen to represent the flukes of an individual for a single day. Photographs were compared within each year to determine a within year sample size and the number of within year recaptures. Between-year comparisons were made starting with the first two years and sequentially comparing each subsequent year to a unified catalogue. All photographs used in the comparison were rated for quality on a five level scale: excellent, good, fair, poor, and not useable. Quality was rated separately for each of three categories: *photographic*, which includes focus, exposure, contrast and pixilation of digital images; *orientation*, which includes angle of the flukes in the horizontal and vertical planes, amount of the flukes above water, and obstruction by splash; *distinctiveness*, which was a characteristic of the fluke involving the uniqueness of the pattern and degree of scarring (although this was inevitably influenced by photographic and orientation quality). Flukes were also rated on the proportion of the fluke that was showing above the water plane as whole, left fluke only, right fluke only, trailing edge or leading edge. The latter four orientation categories could only receive a fair, poor or not useable quality.

Several researchers with appropriate experience matched the raw dataset, with a single matcher working at any time. All potential matches were independently verified. Flukes of all quality criteria were compared and used for assessment of within season recapture rates. For mark-recapture estimates of population abundance we used only flukes with quality of fair or better in photographic and orientation. All partial flukes (halves, leading and trailing edges) were also eliminated.

Genotypic procedure.

The genetic capture-recapture approach is based on the resolution of unique genetic profiles to permit unambiguous identification of individuals (Palsboll et al. 1997). Total genomic DNA was

extracted from the epidermal layer of biopsies or sloughed skin, using standard Phenol - Chloroform extraction method or using DNAeasy tissue kit (Qiagen). The samples were genotyped using 10 cetacean microsatellite markers selected from literature. A detailed description of molecular methodology, quality control protocols and statistical analyses of genetic variation can be found in Pomilla & Rosenbaum (2006).

Duplicate samples were detected from genotype identity using the Microsoft Excel add-in GENALEX package version 5.1 (Peakall and Smouse, 2001). The average probability of two different individuals sharing the same multilocus genotype by chance (probability of identity, PI) was estimated to evaluate the reliability of genetic tagging based on the number of loci used. Additionally, for all samples with matching genotypes that represented putative recaptures between years, genotype probability (GP) was generated separately for the specific genotype. The genotype probability estimates the probability of a random match to a given specific genotype in the given population. PI and GP were estimated using the Microsoft Excel add-in mentioned above.

Genotyping error was assessed by the replicate processing of 220 samples, accounting for 13.0% of the total sample (N=1696). Locus-specific error rates were estimated by the proportion of single locus genotypes with at least one allelic mismatch in the replicate sample, for each locus. Genotypic error rate was estimated in two manners: the observed genotypic error rate, or proportion of multi-locus genotypes with an allelic mismatch at one or more loci; and the predicted genotypic error rate, based upon locus specific error rates (Pompanon *et al.* 2005)

Abundance estimation procedures.

Abundance estimates were generated using several combinations of sample years and estimation models. Pair-wise estimates for flukes were generated using the Chapman's modified Petersen model (Begon 1979, Hammond 1986). The program MARK (White & Burnham 1999) was used to generate closed model estimates for both flukes and genotypes. The closed models in MARK allow for a relaxation of the assumption of equal capture probability but data combinations were also varied in an attempt to assess this issue. Population estimates for flukes were generated using a simple closed model based on Otis *et al.* (1978). They are based on the full likelihood parameterization of three parameters; p_i is the probability of first capture, c_i is the probability of recapture, and N is abundance. Photographic datasets assessed in MARK included two different data combinations for Iguela, 2001-2004 and 2001-2005, all data for Mayumba 2005-2006 and an analysis of all data (combined sites) for two non-overlapping periods, 2001-2003 and 2004-2006.

Program MARK incorporates a set of closed population models that allow for estimates of misidentification of marks, in this case attributable to genotypic error (based on the models of Lukacs and Burnham 2005). For each closed model there are two additional parameters, alpha, α , the probability that a genotype is correct ($1 - \text{genotypic error probability}$), and f_0 , the number of individuals never captured, whereas abundance, N , is estimated as a derived parameter. We ran all model variations fixing α at 1.0 (no genotyping errors and therefore no misidentifications) and using the observed and predicted genotypic error rate to assess the effect of error on abundance estimation. For estimation of abundance we ran only the models that fixed α , thus incorporating genotyping error, and generated a weighted average for the derived parameter, N , as described above. Genotypes were run both as a sex-aggregated dataset (males and females) and a male-only dataset. The latter was to address potential heterogeneity as introduced by females potentially having a lower capture probability. Only those sampling occasions for which sex was positively assigned and all subsequent re-samplings of that animal were used; all females and unknowns were excluded and no attempt was made to assign sex retrospectively.

When running multiple sample closed population models in MARK, genotypic data were assessed using both simple closed population models and those that incorporate mis-identification of marks. All data from both sites were assessed independently (Iguela was assessed without data for 2005) and data from both sites was unified, split into two non overlapping datasets (2001-2003 and 2004-2005) and assessed with and without Iguela 2005 data. It should be noted that biopsy acquisition at Iguela during 2005 was less constrained by limited boat availability than fluke photography. Biopsies are more readily acquired, being less dependent on individual behaviour and time.

Model selection in each case was completed using comparison of Akaike's Information Criteria values (Akaike 1985, Burnham & Anderson 2002). Models that vary probability of capture and recapture periods (behavior, M_b) generally failed to run or provided nonsensical outputs and are not provided.

Assessment of individual fluking rate

Fluking rates can vary according to individual or group behaviour, or may be a function of sex or social status (Felix 2004) and this heterogeneity represents a source of possible bias. For instance quality control criteria for flukes in the South Pacific may remove a disproportionate number of females from the sample, reducing estimates. We assessed fluking rates for individuals in two group types, competitive groups and pairs, at Mayumba during 2006. Individual whales (N=43) were observed for a minimum of 8 min and a maximum of 76 min, with a mean of 22 min. Activity levels were categorized as low, medium, or high based on speed of swimming and surface activity.

Results

Photographic recaptures.

A total of 1365 flukes collected between 2001 and 2006 were analysed. These represented 1323 individuals. Within-year sample sizes of captured flukes are consistently small (Table 2). Yearly effort periods ranged from 47 to 69 days (Table 1). However day-to-day efficiency within these periods varied considerably, largely due to weather or other constraints. The within-year recapture rate of individuals at Iguela was extremely low, ranging from 0.0% to 3.5%, and no individuals were encountered on more than 2 days (Table 1). The within-year recapture rate of individuals at Mayumba was higher but remains poor, ranging from 1.89% to 2.37% (Table 2). Intervals between within season recaptures varied widely at all sites ranging from 1 to 27 days, with a mean ranging from 1 to 8.33 days and median values ranging from 1 to 6 days (Table 1). Filtered sample sizes and recapture events are presented in Table 4a. At Iguela a total of 26 individuals were recaptured, accounting for 40 pair-wise recapture events (Table 4b). At Mayumba total of 6 individuals were recaptured between 2005 and 2006 (Table 4c). Although some periodicity was evident for particular individuals at Iguela, no clear pattern could be discerned.

Genetic recaptures.

A total of 1696 biopsies collected between 2000 and 2006 in Gabon were analysed. Based on genotype identity ($PI=2.5 \times 10^{-12}$), the samples were assigned to 1404 unique individuals. Eighty-four individuals (6.0%) were encountered in multiple years and there was a total of 100 (7.1%) recaptures between pairs of years. For individual pairs of samples with matching genotypes, GP ranged from 2.3×10^{-19} to 1.3×10^{-10} , therefore there is strong support for the assumption that the samples came from the same individuals. In addition all genotypic matches were supported by sex and mtDNA haplotypes. Yearly sample sizes ranged from 90 to 332 with a resample rate of 7%-17% (Table 6a) and the number of recaptures between each pair of years ranged from 0 to 11 (Table 6b).

Replication of 220 samples (12.9%) revealed 13 samples that had at least one allelic mismatch in at least one locus, yielding an observed error per genotype of 5.91%. As some genotypes had more than one locus and allelic mismatch, there were a total of 16 single-locus mismatches and 19 allelic mismatches for a mean allelic error rate of 0.4%. Locus-specific error rates ranged from 0.45% (1 mismatch) to 2.27% (5 mismatches). Two loci had no observed mismatches, and error was estimated at 10% of the minimum observable (one mismatch), or 0.455%. Mean error per locus was 0.74%, and summation of the ten locus-specific error rates yielded a predicted genotypic error rate of 7.14%. This is the probability that any genotype will have one locus in error, and would cause a misidentification. For the purposes of abundance estimation both the observed error rate (5.91%) and the predicted error rate (7.14%) were used to bracket minimum and maximum genotypic error in the dataset.

Fluking rates

Analyses were limited to competitive groups and pairs due to small sample sizes. A distribution curve indicates potential skew in individual fluke rate (Fig. 3). Some individuals never fluked during the observation period, while others fluked more frequently (0.57 flukes/min). The mean fluke rate of individuals in competitive groups was significantly lower than fluking rates in pairs (t -test: $t_{25} = -3.51$, $P = 0.002$). Fluke rate differences for groups with low, medium, and high activity levels were significant (Chi-Square: (df:2, $N=2$) = 6.41, $P=0.041$).

Photographic abundance estimates.

Estimates for flukes were calculated using Chapman's modified Petersen estimator in a logical pair-wise fashion, yielding estimates for Iguela that ranged from 3225 (CV=0.39) for 2001-2002 and 5827 (CV=0.49) for 2004-2005 (Table 7). Given few recaptures the photographic data are very sensitive to minor changes in sample size (for instance minor reassessment of photographic quality criteria yields marked changes in resultant estimates). A single Chapman's estimate was calculated for Mayumba, 2590 (CV=0.33) for 2005-2006. It should be noted that estimates from different sites do not represent distinct estimates of different populations; there is clear overlap, with recaptured individuals sighted and biopsied at both sites. The potential for individual site fidelity still requires assessment.

Fluke estimates generated in MARK suggest selection of the M_t model in each case when using the AIC selection procedure. Various data combinations were used and provide a means to assess possible closure violations. This possible affect may be seen when data are either combined for both sites (2001-2003 and 2004-2006) and 2005 is either included or excluded (Tables 10 & 11), or when sites are assessed independently (Tables 12 & 13). Estimates in general are smaller than genotypic estimates for the same data combinations (see below). M_t estimates were predominant in a weighted average of all models for two non overlapping datasets (2001-2003 & and 2004-2005) based on AICc weights (Table 10).

The sex-aggregated genotypic data (both males and females) were run for both three-year datasets as described above using models that include mis-identifications and the more simple closed models used for the flukes (Tables 15,16 & 19, 20). The genotypic data was also restricted to males, to assess the possibility of heterogeneity introduced by a lower capture probability of females (Tables 17, 18). Differences between combined site estimates that allow for mis-identification are less different than would be expected. An explanation might be found in sampling period differences; field seasons in 2001 and 2002 started earlier in July and it is possible that shifting sex ratios or differences in predominant behaviours (for instance formation of competitive groups) might lead to a sampling bias.

Genotypic Abundance Estimates.

In order to assess the potential effect of genotyping error on abundance estimation, we ran all closed models on the genotypic recapture data fixing α at 1.00 (no error), 0.9409 (observed error rate per genotype of 5.19%) and 0.9285 (predicted probability of error per genotype of 7.15%). The sex-aggregated genotypic data (both males and females) were run for 2 three-year datasets that incorporated Iguela only (2001 – 2003) and Iguela and Mayumba combined (2004-2006). Model outputs are provided in tables 15 to 20. There was a clear trend of reduction in the abundance estimates that was very similar for all models. Estimates that account for error are substantially reduced when genotype error is incorporated. Assuming that the true probability for mismatches is somewhere between the observed and predicted genotypic error rates, all closed models were run for each value of α .

Discussion

The small numbers of recaptures between sampling periods are an important consideration with this dataset. Data collected at Iguela between 2001 and 2004 and at Mayumba 2005-2006 are considered more reliable given more consistent effort. However recapture probabilities are low (2-4%), suggesting small sample sizes relative to the apparent population size, resulting in poor precision and increased bias. This problem may be compounded when sampling periods are different between years, or when individuals display non-random movement, introducing potential negative biases simply because animals are unavailable. Estimates generated using data from all sites and all years (2001-2006) are considered less reliable due to evident closure violations; estimates generated using data that is limited to specific sites are markedly smaller. Datasets that span fewer years also produce smaller estimates, an indication of possible closure violations when more years are grouped.

Pairwise Chapman's estimates of photographed flukes are generally smaller than MARK estimates for genotypes. This likely reflects larger sample sizes and more recaptures for genotypes. Differences may be motivated by differential sex biases in capture probability for the two sampling methods (eg. sex-specific fluking rates, availability on breeding ground). Capture uncertainty in photo-identification and genotype data of this kind is likely to be focused on females, which have a more variable probability of capture and possibly shorter residency times on the breeding grounds than males. This pattern is clear in current analyses of samples from B1 (see SC62SH8), with an almost 2:1 male to female sampling ratio. Other analyses have shown that some females are non-migratory (eg. Brown *et al.* 1995, Clapham *et al.* 1996, Mattila *et al.*, 1998), and brings into question probability of capture as well as the difference between availability on migratory routes and breeding grounds. Excluding females allows use of a male-only model as a sensitivity analysis against a non-structured model (IWC 2009). Some of the differences in genotypic estimates may also be attributed to some portion of the population avoiding biopsy. If animals do exhibit a 'trap response', resulting in different capture and recapture probabilities, then the number of recaptures would be systematically reduced (particularly relative to photographic data) introducing a positive bias into abundance estimation.

Other authors (e.g. Dawbin 1966, Findlay and Best 1996, Findlay and Best, 2006, Cerchio *et al.* 2009) have observed a marked consistency in the resighting dates of particular individuals in other datasets, and although not detected here, it may be a confounding factor, particularly when sampling periods and sampling effort are also inconsistent. This is of particular concern for 2005 data at Iguela; although many days were worked, the effort was itself compromised by constraints set on boat use. Surveys were typically restricted to short working periods in near shore areas.

A major concern for these data in general is that the degree of regional sub-structure for Breeding Stock B has not yet been adequately determined and in the absence of additional work in under-

sampled areas, these issues may not be resolved for some time yet. New evidence presented at SC60 presented in Santiago suggested that the degree of population structure is more complex than previously suspected (see SC/60/11 and SC/60/44). Additionally, the total extent of B1 remains undefined, other areas under-sampled and if a proportion of animals from the provisional B2 region are also visiting Gabon then these estimates could be biased high. These estimates should not therefore be adopted for the B1 region as a whole and moreover not for B1/B2. This may be more of a concern if whales visiting the Gulf of Guinea have regional site preferences, a concern raised elsewhere (Hammond, 1990).

Findlay (2000) identified four independent and substantial recoveries of the Gabon 'stock' following declines in catches and subsequent closures of whaling operations. These recoveries were at odds with grounds elsewhere (Angola, Namibia and West South Africa), and he suggests a degree of segregation of this stock as a plausible cause, suggesting that some whales used alternate migration routes and thus avoided capture. Telemetry data indicate that some proportion of whales migrating north past Iguela in late August and early September in 2002 continued northwards into the Gulf of Guinea and stayed there until late in the breeding season (Rosenbaum and Mate, *submitted somewhere*). If a southbound route similar to that used during the northbound migration is presumed, late-season whales would likely avoid capture once they turned south; our data collection season ended in mid-September during the first two years, and continuing into early October in the four later years.

Sources of possible negative bias

Photographic estimates are at risk of heterogeneity due to varying fluking rates. Individual fluking rates may vary, or rates may vary depending on group type or activity level. If certain groups or individuals show a tendency to fluke more often (non random), certain individuals might be preferentially photographed and thus negatively bias resultant estimates. Our limited study suggests that we may have inadvertently biased our sampling effort to groups that were more readily sighted, but that exhibited lower fluking rates.

Surveys in Gabon may represent area-bound density estimates, so are likely to under-estimate the size of the stock. Biases to the C1 estimate are dependent on area coverage relative to the extent of the habitat that the whales use. If heterogeneity exists, and there is non-random visitation of the sampling areas such that mixing is not equal throughout sub-stock C3, then the closed model estimates will be biased low. Problems associated with low recapture rates may be compounded when sampling periods do not strictly overlap, or when individuals display non-random movement, introducing potential negative biases simply because animals are unavailable.

Sources of possible positive bias

There is an inherent positive bias in the photographic estimates introduced by the presence of "false negatives" or matches (marks) that are not recognized in the photographic comparison process. The use of only high quality photographs should control for this (all poor quality photos were eliminated in this comparison), and conducting redundant independent comparison can be used as a check for this. Stevick *et al.* (2001) note that 'In practice, matching protocols are generally risk averse to false positives. Identifications are made by experienced individuals, use restrictive criteria, and (or) are confirmed by at least two individuals, substantially reducing the probability of errors.' All of the identifications described here were checked by at least two experienced staff. No instances of disagreement were recorded.

When eliminating the fair in addition to poor quality photographs and only using good and excellent photos in the comparison, there was an observed reduction in the abundance estimates, with an associated loss of precision. However, the small number of recaptures in this dataset

makes the estimates very sensitive to small changes in sample size and recaptures. Therefore, we interpret the reduction of estimates when limited to the highest quality photos to be more a function of reduction in sample size and stochastic processes, and does not necessarily imply an increase in accuracy.

The use of multiple years of data in closed models can introduce a potentially significant positive bias due to violation of the assumption of closure, a result of recruitment and death (Hammond 1986). Therefore estimates generated using 2001-2006 all site models, may represent overestimates relative to the site specific or more constrained estimates. Larger estimates were generated by longest term data sets, and potential closure violations should be suspected.

There may be a trap response evident in the genotypic captures, introduced by some portion of individuals in the population successfully avoiding biopsy. This would result in different capture and recapture probabilities, and thus systematically reduce the number of recaptures (particularly relative to photographic data) introducing a positive bias into abundance estimation for the genetic data.

If false negatives occurred between years the result would be that some recaptures are missed and m is under represented. In a dataset such as this with a small probability of capture and sparse recaptures, missing even 1 or 2 recaptures will have substantial positive bias on the abundance estimate. If it occurred within a year, the result would be an inflation of the sample size for the year, also resulting in a positive bias on abundance estimation.

In our somewhat limited study fluking rates were also found to be positively skewed according to group type; fluke rate was significantly higher in pairs than competitive groups. This could be of consequence during data collection; surface active groups are more readily sighted at sea, particularly when weather conditions are less than ideal (average sea state in Gabon is 3-4). When combined with low within-season recapture rates and inconsistent effort this could readily lead to a sampling bias. One might reasonably anticipate that fluking rates also differ with activity level. In fact fluking rates in our study were observed at higher rates at low activity levels, but the trend was only observed in pairwise comparisons. This could become significant with a larger sample size. Sex biased differences in fluking rate were not assessed here but are known concern for other datasets, for instance the South Pacific.

Conclusion

These abundance estimates present data from Gabon only but represent an unknown degree of sub-stocks B1 and B2. Winter destinations for B2 animals are unknown but the Gulf of Guinea is clearly a candidate site. The data are considered problematic for a variety of reasons. In addition to the issues related to geographic and sub-stock representation of the abundance estimates, there are other limitations that must be considered before these abundance estimates can be used in assessment models. These include poor precision due to small sample size, the sensitivity of estimates to stochasticity due to few recaptures, the potential for heterogeneity of capture probability due to behavior of individuals, the effects of temporary immigration/emigration, exacerbated by potential of sampling migrating animals from different sub-stocks en route and variation in temporal sampling from year to year, and affect if there exists a temporal structure to migration and sub-populations.

A larger estimate may be more representative for the B1 region (or even B) as a whole but the absence of sampling at other sites makes larger estimates unreliable. Our study population is clearly Gabon; defining the target population is problematic and caution should be exercised when presuming larger estimates are more representative of B1 (or even B1/B2) region as a

whole given the current complexities in population structure (temporal and spatial, see SC/60/SH44), as well as differences identified through connectivity to different feeding grounds (SC/60/11). Pooling data across larger time spans (and multiple sites) more readily violates assumptions of closure.

We propose using a combination of the MARK photographic and error corrected genotypic results for males only to define naive lower and upper bounds for estimates of population size. A suggested lower bound is the Iguela 2001-2004 MARK M_t model for flukes (4314, CV=0.19). Inclusion of our anomalous year at Iguela in 2005 increases this estimate by almost ~40%, an improbable rate of increase. A suggested upper bound is provided by the 2004-2006 MARK M_t genotypes for males only (3567, CV=0.23) for a corrected estimate of 7134 whales. The MARK estimates allow for heterogeneity and time varying capture probability and may be more forgiving of inconsistent effort.

Literature cited

- Akaike, H. 1985. Prediction and entropy. Pages 1-24 in A. C. Atkinson and S.E. Fienberg, (eds.) A Celebration of Statistics: the ISI Centenary Volume, Springer-Verlag, New York, New York, USA.
- Ayres KL, Overall DJ (2004) api-calc 1.0: a computer program for calculating the average probability of identity allowing for substructure, inbreeding and the presence of close relatives. *Molecular Ecology Notes*, **4**, 315-318.
- Barendse J, Best P, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC (*in press*) Migration redefined? Seasonality, movements, and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *African Journal of Marine Science*
- Begon M (1979) Investigating animal abundance: capture-recapture for biologists. University Park Press, Baltimore.
- Best (1994). A review of catch statistics for modern whaling in Southern Africa, 1908-1930. Rep Int Whal. Commn. **44**:467-485
- Best PB, Sekiguchi K, Findlay KP. (1995) A suspended migration of humpback whales (*Megaptera novaeangliae*) on the west coast of South Africa. *Marine Ecology Progress Series*, **118**, 1-12.
- Brown, M. R., Corkeron, P. J., Hale, P. T., Schultz, K. W., & Bryden, M. M. 1995. Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London B*, **259**, 229-234.
- Budker P (1952) Quelques considerations sur la campagne baleiniere 1951 au Cap Lopez (Gabon). *Mammalia*, **14**, 54-58.
- Budker P, Collignon J (1952) Trois campagnes balenieres au Gabon: 1949-1950-1951. *Bulletin de l'Institut d'etudes Centrafricaines*, **3**, 75-100.
- Carvalho, I., Loo, J., Collins, T., Rosenbaum, H.C. (2007). First genetic comparisons between humpback whales (*Megaptera novaeangliae*) from São Tomé and Príncipe and Gabon.
- Carvalho, I., Loo, J., Pomilla, C., Leslie, M., Collins, T., Barendse, J., Best, P.B., Rosenbaum, H.C. (2010). Temporal patterns of population structure of humpback whales on the west coast of Africa (B Stock). Paper SC/62/SH8
- Cerchio S, Gabriele C, Norris T, Herman LM (1998) Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. *Marine Ecology Progress Series* **175**: 13-22.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. *Biometrics* **45**:427-438.
- Chao, A., Lee, SM., Jeng, SL. (1992). Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* **48**:201-216.
- Clapham, P. J. 1996. The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review*, **26**, 27-49.
- Clapham PJ, Palsbøll PJ (1997) Molecular analysis of paternity shows promiscuous mating in female humpback whales. *Proceedings of the Royal Society of London - series B*, **264**, 95-98.
- Collins, T., Cerchio, S., Pomilla, C., Loo, J., Carvalho, I., Ngousson, S. and Rosenbaum, H.C. 2008. Revised estimates for humpback whale breeding stock B1: Gabon. IWC document SC/60/SH28.
- Dawbin W.H. (1966) The seasonal migratory cycle of humpback whales. Pp. 145-171. In K.S. Norris (ed.) *Whales, Dolphins and Porpoises*. University of California Press, Berkeley, CA. 789pp.
- Félix, F. 2004. Assessment of the level of surface activity in humpback whales during the breeding season. *Latin American Journal of Aquatic Mammals*, **3**, 25-36.
- Findlay K.P. (2000) A Review of humpback whale catches by modern whaling operations in the Southern Hemisphere. *Memoirs of the Queensland Museum* **47**, (2):411-420. Brisbane.
- Gambell R (1976) World whale stocks. *Mammal Review*, **6**, 41-53.
- Hammond, PS (1986) Estimating the size of naturally marked whale populations using capture-recapture techniques. Report to the International Whaling Commission, Spec Issue No **8**: 253-282.
- Hammond, PS (1990). Heterogeneity in the Gulf of Maine? Estimating humpback whale population sizes when capture probabilities are not equal. Report to the International Whaling Commission, Spec Issue No **12**: 135-139.
- Hammond PS, Mizroch SA, Donovan GP. (1990). Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Cambridge, Special Issue 12.

- Hammond PS. 1990. Capturing whales on film: estimating cetacean population parameters from individual recognition data. *Mammal Review* **20**: 17–22.
- Lambertsen RH (1987) A biopsy system for large whales and its use for cytogenetics. *Journal of Mammalogy*, **68**, 443–445.
- Lutjeharms, I. & Ansorge J (2007). The Cetacean Environment off Southern Africa. In *Whales and Dolphins of the Southern African Subregion* pp: 5–13. Peter. B. Best. Cambridge University Press
- Lass, H.U., M. Schmidt, V. Mohrholz, and G. Nausch, 2000: Hydrographic and current measurements in the area of the Angola-Benguela front. *Journal of Physical Oceanography*, **30**, 2589–2609
- Mattila et al (1998)
- Matthews LH (1938) The humpback whale, *Megaptera nodosa*. *Discovery Reports*, 17, 7–92.
- Olsen Ø (1914) Hvaler og hvalfangst i Sydafrika. *Bergens Museums Aarbok 1914–15*, **5**, 1–56.
- Otis DL, Burnham KP, White GC, Anderson R (1978) Statistical inference for capture data closed animal populations. *Wildlife Monographs* **62**: 1–135.
- Palsbøll PJ, Allen J, Bérubé M, et al. (1997) Genetic tagging of humpback whales. *Nature*, **388**, 767–769.
- Park S (2001) MS Toolkit: Excel add-in tool package for microsatellite data. Genetics Department, Trinity College, Dublin.
- Peakall, R., and Smouse, P. E. (2006) GENALEX 6: Genetic Analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288–295.
- Pomilla C., Best P.B., Findlay K.P., Collins, T., Engel. M., Minton, G., Ersts, P., Barendse, J., Kotze, P.G.H., Razafindrakoto, Y., Ngouesso, S., Meyer, M., Thornton, M. and Rosenbaum, H. 2006. Population structure and sex-biased gene flow in humpback whales from Wintering Regions A, B, C, and X based on nuclear microsatellite variation. SC/A06/HW38 presented to the IWC Scientific Committee Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales. April 2006, Hobart, Australia (unpublished).
- Pomilla and Rosenbaum (2006). Estimates of relatedness in groups of humpback whales (*Megaptera novaeangliae*) on two wintering grounds of the southern hemisphere. *Molecular Ecology*, **15**, 2541–255
- Pompanon, F., Bonin, A., Bellemain, E., Taberlet, P. (2005). Genotyping errors: causes, consequences and solutions. *Nature Reviews Genetics* **6**: 847–856.
- Rosenbaum H.C., Pomilla C.C., Leslie M.C., Mendez, M.C., Best P.B., Collins, T., Engel. M., Ersts, P., Findlay K.P., Bonato, S., Kotze, P.G.H., Meyer, M., Minton, G., Barendse, J., Thornton, M., Razafindrakoto, Y., and Ngouesso, S. 2006. MtDNA diversity and population structure of humpback whales from their wintering areas in the Indian and south Atlantic Ocean (Breeding regions A, B, C and X). IWC Scientific Committee Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales. presented to the IWC Scientific Committee Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales. April 2006, Hobart, Australia (unpublished)..
- 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. 425–433. In: Natural History of the Gamba Complex. Alonso, A. and Campbell, P. (eds). Smithsonian Press, Washington D.C.
- 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.
- Rosenbaum HC, Pomilla CC, Mendez MC, Leslie M, Best P, Findlay K, Minton G, Ersts P, Collins T, Engel M, Bonatto S, Kotze D, Meyer M, Barendse J, Thornton M, Razafindrakoto Y, Ngouesso S, Vely M, Kiszka J (2009) Population Structure of Humpback Whales from Their Breeding Grounds in the South Atlantic and Indian Oceans. *PLoS ONE* **4**, e7318.
- Sambrook J, Fritsch EF, Maniatis T (1989) *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.
- Stevick, P., Palsbøll, P.J., Smith, T.D., Bravington, M.V., Hammond, P.S. (2001). Errors in identification using natural markings: rates, sources, and effects on capture–recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* **58**: 1861–1870
- Strindberg, S., Ersts, P., Collins, T., Sounguet, G.P., Rosenbaum, H.C. (in press). Line Transect Estimates of humpback whale abundance and distribution on their wintering grounds in the coastal waters of Gabon (In Press)

- Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whale ships. *Zoologica* 19:1-50
- Van Waerebeek K, Tchiboza S, Montcho J, Nobime G, Sohounhoue P, Dossou C (2001) The Bight of Benin, a North Atlantic breeding ground of the Southern Hemisphere humpback whale population, likely related to Gabon and Angola substocks. Paper SC/53/IA21 presented to the Scientific Committee of the IWC, (unpublished).
- Van Waerebeek K. (2003) A newly discovered stock of humpback whales in the northern Gulf of Guinea. CMS Bulletin 18, 6–7
- Van Waerebeek K., Ofori-Danson P.K. and Debrah J. (2009) The cetaceans of Ghana: a validated faunal checklist. *West African Journal of Applied Ecology* 15, 61–90
- Waits W.L. and Leberg, P.L (2000). Biases associated with population estimation using molecular tagging. *Animal Conservation* 3: 191-199
- Waits W.L, Luikart G, Taberlet P (2001) Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology*, 10, 249-256.
- Walsh P, Fay JM, Gulick S, Sounguet GP (2000) Humpback whale activity near Cap Lopez, Gabon. *Journal of Cetacean Research and Management*, 2, 63-67.
- White, G. C., and K. P. Burnham. 1999. Program MARK(v5.1): survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120-138.

Iguela	2001	2002	2003	2004	2005
Yearly Effort					
Start Date	7/30/2001	7/14/2002	8/4/2003	8/8/2004	7/10/2005
End Date	9/15/2001	9/12/2002	10/6/2003	10/5/2004	9/26/2005
Duration	47	60	63	58	69
Within-Year Recaptures – Photos - unfiltered sample					
Individuals	180	203	186	180	150
Recaptured Individuals	5	0	7	6	2
Recapture Rate	2.78%	0.00%	3.76%	3.35%	1.33%
Within-Year Recapture Intervals (days) – unfiltered sample					
Mean	5.40	-	6.57	8.33	3.00
Median	6	-	4	9	5
Min	1	-	1	3	5
Max	10	-	27	15	5

Table 1. Within year effort and sighting characteristics by year.

Mayumba	2005	2006
Yearly Effort		
Start Date	8/17/2005	8/5/2006
End Date	10/2/2005	9/18/2006
Duration	46	44
Within-Year Recaptures – Photos - unfiltered sample		
Individuals	107	211
Recaptured Individuals	2	5
Recapture Rate	1.87%	2.37%
Within-Year Recapture Intervals (days) – unfiltered sample		
Mean	1.00	7.00
Median	1	3
Min	1	1
Max	1	15

Table 2. Within year effort and sighting characteristics by year.

		July				August				September				October			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
2001	<i>Iguela</i>																
2002	<i>Iguela</i>																
	<i>Gamba</i>																
2003	<i>Iguela</i>																
2004	<i>Iguela</i>																
2005	<i>Iguela*</i>																
	<i>Mayumba</i>																
2006	<i>Mayumba</i>																

Table 3. Data availability across all sites, 2001-2006

*Although sampling occurred over a wide time span, effort quality was reduced. Constraints on boat use limited boat time, and correspondingly limited work to near shore areas. This is at odds with the sampling pattern for previous years (long days offshore)

Fluke Photo - ID dataset**Fluke Photo – ID Dataset – Total Sample from all sites (2000-2006)**

n	2000	2001	2002	2003	2004	2005	2006
	24	111	233	161	142	221	214

m	2000	2001	2002	2003	2004	2005	2006
2000	X	0	1	0	0	0	0
2001		x	5	6	5	2	1
2002			x	12	2	4	5
2003				x	8	2	1
2004					x	4	2
2005						x	9
2006							x

Table 4a**Fluke Photo – ID Dataset - Iguela Only (2001-2005)**

n	2001	2002	2003	2004	2005
	111	143	161	140	123

m	2001	2002	2003	2004	2005
2001	x	4	6	5	1
2002		X	6	6	1
2003			x	8	1
2004				x	2
2005					X

Table 4b**Fluke Photo – ID Dataset - Mayumba Only (2005-2006)**

n	2005	2006
	96	186

m	2005	2006
2005	x	6
2006		X

Table 4c

Genotypic dataset**Genotypes - Total Sample (All sites, 2000-2006)**

N	2000	2001	2002	2003	2004	2005	2006
samples	90	181	299	331	239	332	224
Individuals	82	155	257	274	215	304	209
Resamples	8	26	42	57	24	28	15
Resample rate	8.9%	14.4%	14.0%	17.2%	10.0%	8.4%	6.7%

M	2000	2001	2002	2003	2004	2005	2006
2000	x	1	1	4	2	3	0
2001		x	6	8	6	3	2
2002			x	7	6	6	4
2003				X	8	7	1
2004					x	11	3
2005						x	11
2006							X

Table 6a**Genotypes – Iguela Only (2001-2005)**

n	2001	2002	2003	2004	2005
	155	167	274	215	138

m	2001	2002	2003	2004	2005
2001	x	4	8	6	0
2002		x	5	2	6
2003			x	8	3
2004				x	4
2005					x

Table 6b**Genotypes – Mayumba Only (2005-2006)**

n	2005	2006
	169	209

m	2005	2006
2005	x	11
2006		x

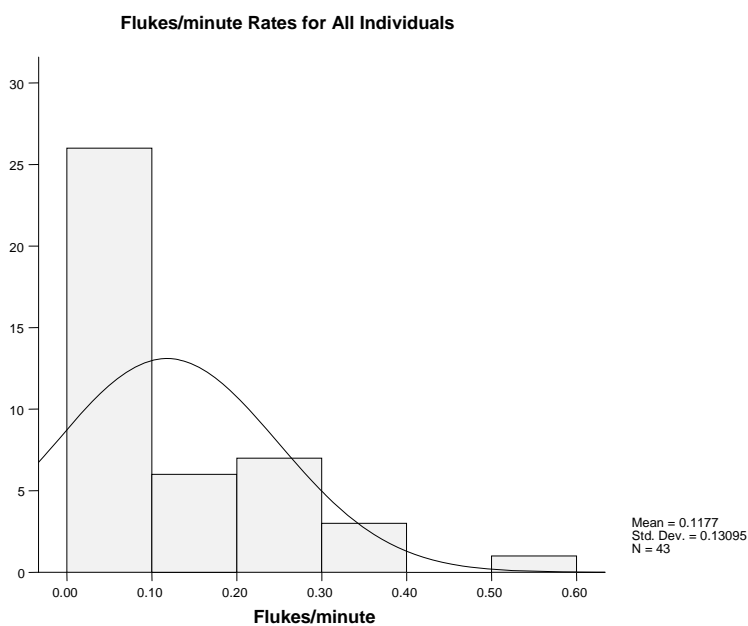
Table 6c

Chapman's Modified Petersen Estimator – Iguela Only (2001 – 2005)

Years	Photo-IDs			
	N	SE	CV	95% CI
2001-2002	3225	1265	0.39	± 2479
2002-2003	3332	1124	0.34	± 2203
2003-2004	2537	668	0.28	± 1310
2004-2005	5827	2848	0.28	± 5582
Schnabel (Mt)				
2001-05	4672	1072	0.23	± 2571

Table 7**Chapman's Modified Petersen Estimator – Mayumba Only**

Years	Photo-IDs			
	N	SE	CV	95% CI
2005-2006	2590	866	0.33	±1697

Table 8**Figure 3. Fluke rates (flukes/min) for individuals observed in Mayumba, Gabon**

Gabon – MARK Flukes

Iguela and Mayumba - 2001-2003 vs 2004-2006

Table 9

Weighted average of all models for two non overlapping datasets (2001-2003, 2004-2005)
based on AIC_c weights (Iguela 2005 excluded)

Dataset	Model	N	SE	CV	LCI	UCI
2001-2003	Weighted Average	4204	1128.73	0.27	1992.28	6416.90
2004-2006 (no Iguela '05)	Weighted Average	6303	2038.38	0.32	2308.45	10298.89
	ROI	0.145				
<i>Weighted</i>						
2004-2006 (with Iguela 2005)	<i>Average</i>	7595.92	1961.97	0.26	3750.46	11441.38

Gabon - Iguela - 2001-2003

Table 10

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-3880.3007	0.0000	0.8686	1.0000	5	27.5159
{Mo}	-3876.5233	3.7774	0.1314	0.1513	2	37.3159
	Weight	N	SE	CV	LCI	UCI
{Mt}	0.8686	4314	801.27	0.19	3040.80	6235.31
{Mo}	0.1314	4338	806.01	0.19	3056.80	6270.20

Gabon - Iguela and Mayumba - 2004-2006 (Iguela 2005 included)

Table 11

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-4609.4457	0.0000	0.9999	1.0000	4	14.5202
{MO}	-4591.3336	18.1121	0.0001	0.0001	2	36.6490
	Weight	N	SE	CV	LCI	UCI
{Mt}	0.9999	7595	1961.97	0.26	4675.05	12589.47
{MO}	0.0001	7733	1998.99	0.26	4756.56	12820.06

Gabon - Iguela & Mayumba - 2004-2006 (Iguela 2005 excluded) – Table 12

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-3177.0232	0.0000	1.0000	1.0000	4	17.0367
{MO}	-3151.1634	25.8598	0.0000	0.0000	2	46.9192
{Mh}	-3151.1540	25.8692	0.0000	0.0000	4	42.9059
	Weight	N	SE	CV	LCI	UCI
{Mt}	1.0000	6303	2038.38	0.32	3460.20	11800.48
{MO}	0.0000	6525	2112.86	0.32	3576.97	12221.29

{Mh}	0.0000	8194.74	3146.36	0.38	4042.54	17097.11
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Gabon – Fluke Estimates

Iguela and Mayumba

Site separated estimates

Iguela Only 2001 – 2005

Table 12

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-4721.7213	0.0000	0.8337	1.0000	6	43.6450
{Mo}	-4718.4965	3.2248	0.1663	0.1994	2	54.8920
	Weight	N	SE	CV	LCI	UCI
{Mt}	0.8337	5957	1038.62	0.17	4279.48	8410.373
{Mo}	0.1663	5980	1043.04	0.17	4295.89	8444.34

Iguela Only 2001 – 2004

Table 13

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-3880.3007	0.0000	0.86861	1.0000	5	27.5159
{Mo}	-3876.5233	3.7774	0.13139	0.1513	2	37.3159
	Weight	N	SE	CV	LCI	UCI
{Mt}	0.86861	4314	801.27	0.19	3040.8	6235.313
{Mo}	0.13139	4338	806.01	0.19	3056.8	6270.198

Mayumba Only 2005- 2006

Table 14

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-2142.9852	0.0000	1.0000	1.0000	3	7.3612
{Mo}	-2114.4149	28.5703	0.0000	0.0000	2	37.9534
	Weight	N	SE	CV	LCI	UCI
{Mt}	1.0000	2953	1147.85	0.39	1472.6	6264.929
{Mo}	0.0000	3290	1285.79	0.39	1628.71	6993.788

Gabon - Iguela - 2001-2003 - Sex Aggregated

No mis-identifications assumed

Table 15

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-4834.5125	0.0000	1.0000	1.0000	4	11.6207
{Mo}	-4796.0524	38.4601	0.0000	0.0000	2	54.097
{Mh}	-4794.3642	40.1483	0.0000	0.0000	4	51.769

Model	Weight	N	SE	CV	LCI	UCI
{Mt}	1.0000	7051	1696.30	0.24	4484.25	11305.42
{Mo}	0.0000	7315	1762.91	0.24	4646.58	11735.08
{Mh}	0.0000	8159	2171.47	0.27	4951.19	13723.93

Gabon - Iguela and Mayumba - 2004-2006 - Sex Aggregated

No mis-identifications assumed

Table 16

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt}	-6082.6159	0.0000	0.9999	1.0000	4	13.5201
{Mo}	-6063.2910	19.3249	0.0001	0.0001	2	36.8582
{Mh}	-6060.5254	22.0905	0.0000	0.0000	4	35.6105

Model	Weight	N	SE	CV	LCI	UCI
{Mt}	0.9999	7148.67	1393.30	0.19	4943.07	10501.85
{Mo}	0.0001	7264.26	1417.16	0.20	5020.51	10674.33
{Mh}	0.0000	7714.22	1591.76	0.21	5221.27	11582.97

Gabon - Genotypic Estimates

Gabon - Iguela - 2001-2003 - Sex Aggregated Table 17

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt} a=0.9285}	-4834.6431	0.0000	0.3419	1.0000	4	11.4901
{Mt} a=0.9409}	-4834.6198	0.0233	0.3379	0.9884	4	11.5133
{Mt} a=1.0}	-4834.5125	0.1306	0.3203	0.9368	4	11.6207
{Mo} a=1.0}	-4796.0524	38.5907	0.0000	0.0000	2	54.0970
{Mo} a=0.9409}	-4795.7476	38.8955	0.0000	0.0000	2	54.4018
{Mo} a=0.9285}	-4795.6781	38.9650	0.0000	0.0000	2	54.4712
{Mh2} a=1.0}	-4794.3642	40.2789	0.0000	0.0000	4	51.7690
{Mh2} a=0.9409}	-4793.9725	40.6706	0.0000	0.0000	4	52.1607
{Mh2} a=0.9285}	-4793.8844	40.7587	0.0000	0.0000	4	52.2488

Model	Weight	N	SE	CV	LCI	UCI
{Mt} a=0.9285}	0.3419	6096	1463.10	0.24	3834.26	9694.45
{Mt} a=0.9409}	0.3379	6257	1502.31	0.24	3934.41	9951.76
{Mt} a=1.0}	0.3203	7051	1696.31	0.24	4429.43	11224.39
{Mo} a=1.0}	0.0000	7315	1762.91	0.24	4591.76	11654.03
{Mo} a=0.9409}	0.0000	6574	1581.57	0.24	4130.52	10465.82
{Mo} a=0.9285}	0.0000	6424	1544.76	0.24	4036.86	10224.60
{Mh2} a=1.0}	0.0000	8160	2190.52	0.27	4865.75	13684.65
{Mh2} a=0.9409}	0.0000	7325	1906.70	0.26	4435.18	12099.76
{Mh2} a=0.9285}	0.0000	7156	1868.40	0.26	4326.31	11838.05

Gabon - Iguela and Mayumba - 2004-2006 - Sex Aggregated (Iguela 2005 Included)

Table 18

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt} a=0.9285}	-6082.7407	0.0000	0.3415	1.0000	4	13.3952
{Mt} a=0.9409}	-6082.7185	0.0222	0.3377	0.9890	4	13.4174
{Mt} a=1.0}	-6082.6159	0.1248	0.3208	0.9395	4	13.5201
{Mo} a=0.9285}	-6063.4336	19.3071	0.0000	0.0001	2	36.7157
{Mo} a=0.9409}	-6063.4086	19.3321	0.0000	0.0001	2	36.7406
{Mo} a=1.000}	-6063.2910	19.4497	0.0000	0.0001	2	36.8582
{Mh2} a=0.9285}	-6060.5432	22.1975	0.0000	0.0000	4	35.5928
{Mh2} a=0.9409}	-6060.5403	22.2004	0.0000	0.0000	4	35.5956
{Mh2} a=1.0}	-6060.5254	22.2153	0.0000	0.0000	4	35.6105

Model	Weight	N	SE	CV	LCI	UCI
{Mt} a=0.9285}	0.3415	6187	1201.63	0.19	4243.43	9021.68
{Mt} a=0.9409}	0.3377	6349	1233.85	0.19	4353.30	9259.80
{Mt} a=1.0}	0.3208	7148	1393.30	0.19	4896.28	10437.29
{Mo} a=0.9285}	0.0000	6285	1221.75	0.19	4309.60	9168.01
{Mo} a=0.9409}	0.0000	6450	1254.59	0.19	4421.25	9410.35
{Mo} a=1.0}	0.0000	6258	1216.24	0.19	4290.83	9127.30
{Mh2} a=0.9285}	0.0000	6661	1386.46	0.21	4449.13	9973.76
{Mh2} a=0.9409}	0.0000	6631	1381.89	0.21	4427.25	9933.85
{Mh2} a=1.0}	0.0000	7714	1599.25	0.21	5160.43	11532.12

Gabon - Genotypic Estimates

Gabon - Iguela - 2001-2003 - Male only

Table 19

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt} a=1.0}	-2983.4081	0.0000	0.3346	1.0000	4	9.0406
{Mt} a=0.9409}	-2983.3982	0.0099	0.3329	0.9951	4	9.0505
{Mt} a=0.9285}	-2983.3959	0.0122	0.3325	0.9939	4	9.0527
{Mo} a=1.0}	-2944.0673	39.3408	0.0000	0.0000	2	52.4051
{Mo} a=0.9409}	-2943.7417	39.6664	0.0000	0.0000	2	52.7307
{Mo} a=0.9285}	-2943.6685	39.7396	0.0000	0.0000	2	52.8039
{Mh2} a=1.0}	-2940.0435	43.3646	0.0000	0.0000	4	52.4051
{Mh2} a=0.9409}	-2939.7179	43.6902	0.0000	0.0000	4	52.7307
{Mh2} a=0.9285}	-2939.6447	43.7634	0.0000	0.0000	4	52.8039

Model	Weight	N	SE	CV	LCI	UCI
{Mt} a=1.0}	0.3346	4274	1181.31	0.28	2511.17	7274.26
{Mt} a=0.9409}	0.3329	3793	1046.15	0.28	2231.41	6449.03
{Mt} a=0.9285}	0.3325	3696	1018.83	0.28	2174.81	6282.19
{Mo} a=1.0}	0.0000	4516	1252.04	0.28	2649.75	7698.83
{Mo} a=0.9409}	0.0000	4061	1123.50	0.28	2384.91	6915.12
{Mo} a=0.9285}	0.0000	3968	1097.41	0.28	2331.13	6756.05
{Mh2} a=1.0}	0.0000	4516	1252.04	0.28	2649.75	7698.83
{Mh2} a=0.9409}	0.0000	4061	1123.49	0.28	2384.91	6915.11
{Mh2} a=0.9285}	0.0000	3968	1097.41	0.28	2331.14	6756.04

Gabon - Iguela and Mayumba - 2004-2006 - Male Only

Table 20

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Mt} a=0.9285}	-3435.4988	0.0000	0.3024	1.0000	4	11.6091
{Mt} a=0.9409}	-3435.4782	0.0206	0.2993	0.9898	4	11.6298
{Mt} a=1.0}	-3435.3821	0.1167	0.2853	0.9433	4	11.7259
{Mo} a=0.9285}	-3430.8894	4.6094	0.0302	0.0998	2	20.2394
{Mo} a=0.9409}	-3430.8545	4.6443	0.0297	0.0981	2	20.2744
{Mo} a=1.0}	-3430.6931	4.8057	0.0274	0.0905	2	20.4357
{Mh2} a=0.9285}	-3428.4009	7.0979	0.0087	0.0288	4	18.7070
{Mh2} a=0.9409}	-3428.3896	7.1092	0.0087	0.0286	4	18.7183
{Mh2} a=1.0}	-3428.3376	7.1612	0.0084	0.0279	4	18.7703

Model	Weight	N	SE	CV	LCI	UCI
{Mt} a=0.9285}	0.3024	3567	818.79	0.23	2288.09	5561.82
{Mt} a=0.9409}	0.2993	3660	840.68	0.23	2346.79	5708.15
{Mt} a=1.0}	0.2853	4118	948.99	0.23	2636.82	6431.72
{Mo} a=0.9285}	0.0302	3592	824.87	0.23	2303.61	5601.71
{Mo} a=0.9409}	0.0297	3686	847.28	0.23	2363.57	5751.38
{Mo} a=1.0}	0.0274	4155	958.29	0.23	2660.33	6492.50
{Mh2} a=0.9285}	0.0087	3931	977.59	0.25	2432.73	6354.23
{Mh2} a=0.9409}	0.0087	4037	1003.12	0.25	2498.81	6522.58
{Mh2} a=1.0}	0.0084	4560	1138.28	0.25	2816.59	7383.46

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