Abundance of humpback whales on the Abrolhos Bank wintering ground, Brazil

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ABSTRACT

Abundance estimates are presented for the humpback whales wintering off Brazil which 'visit' a surveyed area off Abrolhos Bank and display fluke-exposing behaviour. The study is based on photo-identification data collected between 1996 and 2000. Chapman-corrected Petersen estimates for all pairs of data result in estimates from 1,948 individuals up to 3,001 with coefficients of variation around 0.25. A more elaborate closed population multiple-recapture maximum-likelihood estimate is 2,393 with 95% profile-likelihood confidence interval (CI=1,924, 3,060). Replacing the closed-population assumption with a population allowed to grow (or decrease) according to some constant rate over the study period, the maximum-likelihood estimate of population size for the year 2000 becomes 3,871 (CI=2,795, 5,542) associated to an estimated annual growth rate of 31% over the study period and in the surveyed area. Although the inclusion of the growth rate results in a less restrictive assumption about population size, it is unclear at this time how to interpret it since the population around the Abrolhos Bank is some (unknown) fraction of whales wintering off Brazil. Alternatively, a fit of Whitehead's model allowing for emigration and re-immigration gives an estimate of about 3,000 whales (CI=2,500, 3,650).

KEYWORDS: ABUNDANCE ESTIMATE; ATLANTIC OCEAN; BREEDING GROUND; HUMPBACK WHALE; PHOTO-ID; SOUTH AMERICA

INTRODUCTION

The use of a catalogue of photo-identified whales and mark-recapture models to estimate cetacean abundance is well known (e.g. see review Hammond *et al.*, 1990) particularly for humpback whales (e.g. Katona and Beard, 1990; Smith *et al.*, 1999).

Although over 200 humpback whales have been individually identified in the Southern Hemisphere, relatively few studies have attempted to use the information to estimate abundance by capture-recapture models (Baker, 1995). The International Whaling Commission's Scientific Committee began a major assessment of the status of Southern Hemisphere humpback whales in 2000 (IWC, 2001). Humpback whales wintering off the Brazilian coast are considered part of the western South Atlantic breeding stock (breeding stock 'A') but there are no estimates for the total abundance of that breeding stock or any information on recent trends (e.g. see summary in IWC, 2004).

The humpback whales found on the breeding ground of Abrolhos Bank (off the southernmost coast of Bahia state, Brazil) have been studied since 1988. Work on obtaining population estimates based on the photo-identification of individual animals began in 1995. A photographic catalogue of 982 individually identified whales assembled over 11 years of surveys in the area provides the most complete record of sightings of humpback whales off the Brazilian coast. Preliminary assessment of the population abundance for 1996 using within-year resightings in a continuous time non-parametric closed population model (Bethlem, 1998) resulted in a confidence interval of 237, 1,519. An empirical-Bayes approach applied to within-year resightings in 1995 resulted in a 90% credibility interval of 1,379, 1,887 (Kinas and Bethlem, 1998). On the Abrolhos Bank the distribution of this population has also been studied in relation to bathymetry, proximity to land and water turbidity (Martins *et al.*, 2001; Freitas *et al.*, 2001). Recent aerial surveys over the whole of Abrolhos Bank (including areas never surveyed before) provide complementary information about habitat use patterns, distribution and abundance (Andriolo *et al.*, 2002).

This analysis is based on photo-identification data collected over the five years 1996-2000 and provides abundance estimates of the fraction of humpback whales wintering off Brazil which 'visit' the surveyed area off Abrolhos Bank and display fluke-exposing behaviour.

METHODS

Survey area and photographic identification

The surveyed area is located off the northern portion of the Abrolhos Bank (16°40'S-19°30'S; 37°25'W-39°45'W). The region (Fig. 1) is an extension of the Brazilian continental shelf that rarely exceeds depths of 40m and reaches a maximum distance from shore of approximately 245km. The bank (average depth = *ca* 30m) is formed by coral reefs, some of them rising above the sea level in the low tide, mud and calcareous algae bottoms. Five small volcanic islands form the Abrolhos archipelago, located 30 n.miles offshore. The average annual sea surface temperature ranges from 22° to 27°C (winter from 22°-24°C) (IBAMA/FUNATURA, 1991). These features are typically associated with breeding grounds for humpback whales (Baker *et al.*, 1995; Clapham and Mead, 1999). Abrolhos Bank is considered the most important breeding and calving ground for the species in the western South Atlantic (Martins *et al.*, 2001). The whales use the area during the austral winter, between July and November each year (Siciliano, 1997).

Humpback whales were individually identified by the pigmentation patterns of the ventral flukes (Katona and Whitehead, 1981). Calf photographs were excluded from the analysis, since their fluke pigmentation patterns can change considerably in short periods of time (Carlson *et al.*,

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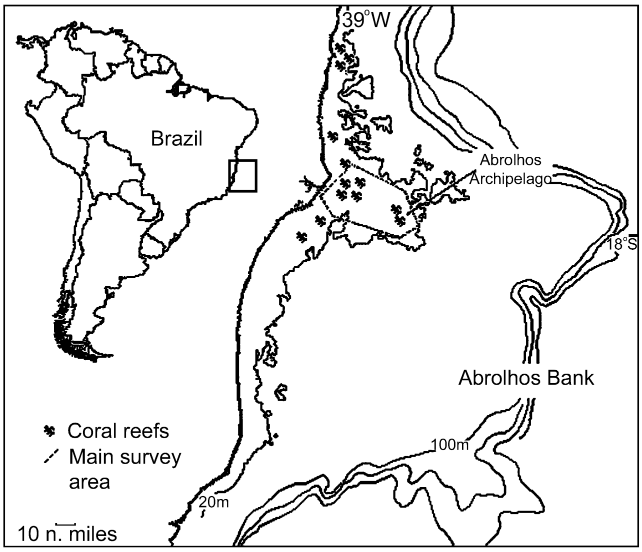

Fig. 1. Map showing Abrolhos Bank and the survey area.

1990) which would be characterised as loss of marks. Photographs were taken using Nikon 35mm power winder cameras with 200 or 300mm lenses. Colour negative and slide films (100, 200 and 400 ASA) were used.

Data analysis and statistical models

Photographs in the catalogue were selected according to image quality (focus, glare, angle) regardless of recognition pattern of the flukes (i.e. the presence of distinctive scars or pigmentation that would improve one's ability to re-identify the animal; Mizroch *et al.*, 1990). This is essential in order to decrease the recapture heterogeneity and the likelihood of flukes not being recognised on recovery (Hammond, 1986; Friday *et al.*, 2001; Stevick *et al.*, 2001). Only the quality-screened photographs were compared within and across years to determine the total number of identified whales (marks) and the number of resightings (recaptures).

Within any year, sampling without replacement was used because multiple recaptures of whales may not be independent. This will also reduce heterogeneity in capture probabilities among whales as a source of bias in abundance estimates (Seber, 1982; Otis *et al.*, 1978; Hammond, 1986; Hammond *et al.*, 1990).

Four abundance estimation models are used. First, the Chapman-modified Petersen estimator (Hammond, 1986) is applied to all pairs of consecutive seasons. The model assumes: (1) a closed population; (2) a constant probability of capture among animals; and (3) neither loss nor misclassification of marks (Seber, 1982). The estimated abundance ($\tilde{N}$) is calculated as follows:

$$\tilde{N} = \frac{(n_1+1)(n_2+2)}{m+1} - 1 \quad (1)$$

where n_i is the number of (distinct) whales photo-identified in season i (i=1, 2) and m the number of whales seen in both seasons. The estimated standard error (SE) of $\tilde{N}$ is:

$$SE = \sqrt{\frac{(n_1+1)(n_2+1)(n_1-m)(n_2-m)}{(m+1)^2(m+2)}} \quad (2)$$

Given five seasons of data, four different estimates of $\tilde{N}$ (and SE) are obtained.

A second model estimates the population size N by using all data simultaneously in a multiple-recapture model. Changes to previously listed assumptions are as follows: (1) population is closed to recruitment and immigration but death and emigration are allowed if they affect marked and unmarked animals equally (Gazey and Staley, 1986); (2) the probability of capture at any given season is equal to the proportion of marked whales in the population at the time. This corresponds to a M_t-type model (Otis *et al.*, 1978), constrained to a non-decreasing sequence of capture probabilities.

Since sampling without replacement is used, the hypergeometric model applies. Therefore, the likelihood function is:

$$L(N) = \prod_{i=2}^{s} \frac{\binom{M_i}{m_i}\binom{N-M_i}{n_i-m_i}}{\binom{N}{n_i}} \quad (3)$$

where s is the number of seasons, n_i the number of whales identified in season i, m_i the number of whales identified in season i that had already been 'marked' in some previous season and M_i the total number of (distinct) whales that have been marked before the i-th season. Notice that $M_{s+1}=M_s + n_s - m_s$ is the total number of distinct whales identified during the study and determines a lower bound for N provided there were neither deaths nor emigration among marked whales during the study period.

A third model drops the assumption of population closeness and replaces it with: (i') an open population with constant growth rate. The population size N_i in any given year i, is related to the population size N_{i-1} in a previous year by:

$$N_i = N_{i-1}e^r \quad (4)$$

Parameter r indicates the population growth rate over the period. Although r can be positive, zero or negative – indicating a growing, constant or declining population, respectively – it is assumed to be constant over the study period. The value e^r denotes the annual rate of change in population size.

For convenience $N=N_s$ is defined as the population size in the wintering season of year 2000. Hence, by rearranging equation (4), population sizes for all previous years can be defined as a function of N:

$$N_i = N \cdot e^{-(s-i)r} \quad (4a)$$

for seasons i=1, ..., s-1. The likelihood function for model 3 is an extension of equation (3) resulting in:

$$L(N,r) = \prod_{i=2}^{s} \frac{\binom{M_i}{m_i}\binom{N_i-M_i}{n_i-m_i}}{\binom{N_i}{n_i}} \quad (5)$$

subject to the restrictions $N_i \geq M_{i+1}$ for i=1 to s and with N_i given by equation (4a).

Finally, the fourth model was taken from Whitehead (1990) and includes the possibility for animals to emigrate and later re-immigrate into the study area. The emigration and re-immigration rates (λ and μ, respectively) are estimated together with population size N. The overall population is assumed to be reasonably constant over the period.

For all models except the first, the maximum-likelihood estimates are calculated by evaluating the likelihood functions for a large number of points and determining its maximum on the grid. Confidence interval or two-dimensional confidence regions were determined through the method of profile likelihood (Buckland *et al.*, 1993). If $R(N)=L(N)/L(\hat{N})$ and $R(N.r)=L(N,r)/L(\hat{N}, \hat{r})$ denote the relative likelihood functions for equations (3) and (5) respectively, and if R_n is the normal approximation of R, then $-2\log(R_n)$ has a chi-square distribution with p degrees of freedom (where p is the number of parameters in the model). Let $\chi^2(\alpha)$ be the 100(1-α) percentile of a chi-square distribution with p degrees of freedom. The collection of points that satisfy $-2\log(R) \leq \chi^2(\alpha)$ will be used to build the 100(1-α)% profile likelihood confidence set. For p=1, the smallest and the largest values in the selected collection define the confidence interval. For p=2, a scatter plot of the selected points defines the approximate shape of the joint confidence region. Marginal confidence intervals can be obtained as before. Similar criteria were used to analyse estimates obtained with Whitehead's model.

RESULTS

The data collected during the years 1996 to 2000 (after selection for photographic quality) were compared between seasons to obtain information on recaptures (Table 1). The survey effort (in number of searching hours per year) has been stable over the study period (Table 2).

Pairwise abundance estimates for the Abrolhos Bank using the Chapman-modified Petersen estimates resulted in a population size between 1,848 (for 1996-1997) and 3,001 (for 1998-1999) with CV ranging from 0.246 (1997-1998) to 0.310 (1996-1997) (Table 3).

Table 1

Number of humpback whales identified at Abrolhos Bank in different seasons (years) and re-identifications for pairwise comparisons between seasons.

Year	No. identified [newly]	Re-identification year			
		1997	1998	1999	2000
1996	101 [101]	7	15	7	6
1997	143 [136]	*	12	13	6
1998	216 [193]	*	*	11	11
1999	164 [137]	*	*	*	12
2000	218 [188]	*	*	*	*

Table 2

Vessel effort in hours per month for surveys between 1996-2000.

Year	Jul.	Aug.	Sept.	Oct.	Nov.	Total
1996	70.25	98.91	83.16	70.91	81.58	404.81
1997	106.75	138.83	80.41	96.5	105.08	527.57
1998	101.25	128	115.6	64.38	37.66	446.89
1999	82.58	83.08	72.33	107.91	64.83	410.73
2000	73.58	122.16	95.16	81.83	102.5	475.23

Table 3

Chapman-modified Petersen pairwise abundance estimates, standard errors and 95% confidence intervals (all numbers were rounded to nearest integer).

Pair of seasons	*N*	*SE*	95% CI
1996 – 1997	1,848	573	725-2,971
1997 – 1998	2,414	595	1,247-3,581
1998 – 1999	3,001	777	1,478-4,524
1999 – 2000	2,791	693	1,433-4,150

The abundance estimate obtained with the multiple-recapture, closed population model 2, for the period from 1996 to 2000 (s=5) resulted in the maximum-likelihood estimate of 2,393 whales. The relative likelihood function (Fig. 2) is used to define the 95% confidence interval given in Table 4. The multiple-recapture, open population, two-parameter model 3, estimates a population size of 3,871 whales for the 2000 winter season and a growth rate r=0.267 over the period 1996 to 2000. The approximate 95% confidence region of the maximum-likelihood estimate for (N, r) is delimited by the plotted points which represent a projection of $R(N,r) \geq \exp(\chi^2/2)$ onto the N x r space (Fig. 3). This interval displays a marked positive correlation between these parameters. It also makes clear why the marginal confidence interval (Table 4) is so wide. Although the estimate of r is not precise, ranging (marginally) from 0.028 to 0.400, it clearly suggests a growing population (r>0).

Whitehead's three-parameter model (N,λ,μ), was fitted to a three-dimensional grid of 8,100 points ranging from 1,000 to 5,000 for N and between 0 and 1 for λ and μ. A likelihood ratio test showed that the hypothesis μ=0 is not rejected ($\chi^2_{(1)}$=0.045; p=0.832); a second likelihood ratio test to check if λ=0 (given that μ=0) is not rejected either ($\chi^2_{(1)}$=1.34; p=0.247). With both rates set to zero, Whitehead's model reduces to the Schnabel model of a closed population being randomly sampled. The maximum-likelihood estimate of N resulted in 3,000 whales (Table 4).

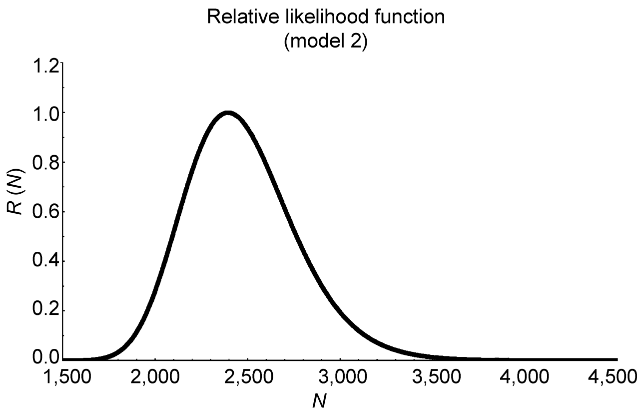

Fig. 2. Relative likelihood function for population size N of humpback whales at Abrolhos Bank according to assumption of a constant population size (model 2).

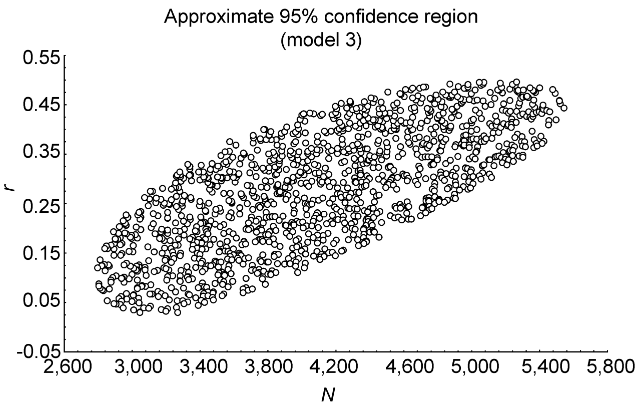

Fig. 3. Scatter plot representing the approximate 95% profile likelihood confidence region of the maximum-likelihood estimate for (N,r) in model 3. (Includes all pairs (N,r) with $-2\log R(N,r) \leq 5.9915$).

Table 4

Maximum-likelihood abundance estimates for three population models: the closed population hypergeometric model (HG); an open population hypergeometric model with constant intrinsic growth rate *r* (HG+*r*) and Whitehead's model allowing for emigration and re-immigration. Years 1996-2000.

Model	*N*	95% CI
HG (model 2)	2,393	1,924-3,060 [b]
HG + *r* (model 3)	3,871[a]	2,795-5,542 [b]
Whitehead	3,000	2,500-3,650[b]

[a]Maximum-likelihood estimate for year 2000. [b]Profile likelihood confidence intervals.

DISCUSSION

All models considered in this analysis assume that the probability of photo-identifying a whale is constant within a season. As it stands, this assumption is hardly ever satisfied for at least three reasons.

First, the behaviour of adequately exposing the tail to facilitate a photographic record will depend on sex, age and group composition (Perkins *et al.*, 1984; Hammond, 1990; Friday *et al.*, 2001). For instance, animals which execute the 'tail up' behaviour (consisting of tail exposition for minutes, even hours – Morete *et al.*, 2003) will have an increased probability of being photo-identified, while other groups like resting mothers and calves rarely expose the tail in fluke-up dives. The effect of this variability could only be reduced by some kind of stratification into sub-groups of similar behaviour (Hammond, 1986). However, the information needed to stratify properly is not available and sample sizes within strata will be small.

Second, the surveyed region represents only a fraction of the home range for the whales using the Abrolhos Bank wintering ground. Photographic data collected opportunistically in 1997 and 1999 and during vessel surveys in 2000 off Salvador (approximately 550km north of the Abrolhos Archipelago) resulted in 15 photo-identified individuals. Three matches of whales previously sighted on the Abrolhos Bank were found among them, indicating that Abrolhos' humpbacks use other areas off Brazil as well. This suggests that in different cruises different animals might be available for marking. Furthermore, within-season resightings might not be independent as a given whale can stay in the region for the period of the cruise and be sighted more than once. The heterogeneity in photo-identification probability induced by both phenomena will be reduced if the whole season is taken as a single (without replacement) sampling event. Finally, by considering all photo-identifications over the whole season without replacement, effectively means we have been using a yearly 'mean probability of capture' for each whale and we would therefore expect lower variability.

Third, whales with significant tail pigmentation patterns are easier to photo-identify than animals with poor recognition quality patterns, although this problem is greatly reduced by first selecting only high quality photographs (Hammond, 1986; Friday *et al.*, 2001; Stevick *et al.*, 2001).

The Chapman-corrected Petersen abundance estimates calculated for all possible combinations of seasons were included to provide a direct comparison to similar results presented elsewhere for other wintering seasons for humpbacks (Baker *et al.*, 1992; Rosenbaum *et al.*, 2000). Calculated coefficients of variation are reasonable (around 0.25), and abundance estimates suggest an increasing time trend.

More precise abundance estimates are obtained when simultaneously using all data as part of a multiple-recapture experiment. This was possible to achieve with models 2 to 4. In closed population model 2, the associated 95% profile-likelihood confidence interval (1,924-3,060) does not cover the Petersen estimates for 1996-97. Calculating the identification frequencies of individual whales across the five years and confronting them with expected frequencies calculated for a zero-truncated Poisson distribution (Caughley, 1977) resulted in a significant departure ($\chi^2_{[1]}$=76.445, *p*=0.0111) between both sequences (Table 5). According to Caughley, this difference could be caused by heterogeneity in captures or by changes in population size. The consequences of each of these two possibilities are examined below.

To check for the effect of heterogeneity, the data were fitted with program CAPTURE (Otis *et al.*, 1978). The model selection index and resulting estimates are summarised in Table 6. The inclusion of heterogeneity only (model M_h) causes the estimate of *N* to be low. The most realistic model from a biological standpoint (model M_{th}) results in estimates which are closest to those obtained by open model 3 (model HG+r in Table 4).

Table 5

Observed and expected frequencies of observation for 755 humpback whales photo-identified between 1996 and 2000 ($\chi^2_{[1]}$ = 76.445; *p* = 0.0111).

	Identification frequency (seasons)				
	1	2	3	4	5
Observed	681	63	9	2	0
Expected[a]	674.2	74.9	5.5	0.3	0.0

[a]Calculated from the zero-truncated Poisson distribution.

Table 6

Model selection and maximum-likelihood abundance estimates obtained with program CAPTURE. Years 1996 to 2000.

Model (index)	M_h (1.0)	M_{th} (0.83)	M_0 (0.74)	M_t (0.01)
N	2,040	4,107	2,770	3,031
95% CI	(1,921; 2,171)	(3,196; 5,358)	(2,509; 3,874)	(2,536; 3,688)

Alternatively, if we assume that we have dealt with heterogeneity by considering sampling without replacement, we can focus attention on the second possible cause: the population growth over the period. Model 2 was modified in order to include a second parameter, the growth rate *r*. By giving up some precision in the estimate of population size, some insight was gained into the rate of population change between 1996 and 2000. The analysis suggests an annual growth rate of about 31% (e^r=1.31) over the period – biologically implausible. The interpretation of *r* is difficult, however, until a better understanding of the whale distribution in the area is available. Since the surveyed area is only a fraction of the wintering ground off Brazil, the estimated population growth rate might include some change in behaviour pattern in favour of this sub-area without any substantial change in population size in area A. However, regardless of the interpretation of *r*, we believe that its inclusion in model 3, allows for a better estimate of population size in year 2000.

The positive correlation observed in the 95% profile-likelihood confidence region for (*N*, *r*) reveals an important aspect of the uncertainty in estimating the parameters of model 3. The interval allows for relatively small population sizes associated to small growth rates or alternatively large growth rates and associated large population size in year 2000. However, the location of the confidence region away from r=0 suggests that the number of whales using Abrolhos during the reproductive season has been growing between 1996 and 2000.

Finally, the use of Whitehead's model allowed us to explore the possibility of measuring emigration and re-immigration rates to the Abrolhos Bank over the years. The statistical tests suggest that these rates are negligible and the fitted model (Table 4) reduces to a closed population model M_t. In fact, a comparison with the estimate obtained in CAPTURE (Table 6) confirms this. The small observed differences are caused by rounding errors due to a somewhat coarse grid.

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