

Estimating humpback whale abundance using hierarchical distance sampling



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ABSTRACT

We developed a Bayesian distance sampling analysis using a hierarchically structured model parameterization to estimate humpback whale abundance in the Southwest Atlantic Ocean (Breeding Stock A). We included covariates that affect detection (altitude and sighting cue) and occurrence probability (year and distance from shore). Population sizes for 2008, 2011 and 2015 were estimated to be 7,689 (P.I.95% = 6585–8931), 8652 (P.I.95% = 7696–9682), and 12,123 (P.I.95% = 10,811–13,531), respectively. The results indicate an aggregation of humpback whales in an intermediate distance from shoreline, an increasing in density from 2008 to 2011 and a substantial overlap between posterior distributions of density for 2011 and 2015, which suggests a stabilization of population growth over the last year. Our parameterization provided a clear view of observational and ecological processes and illustrates that the Bayesian hierarchical line transect approach provides a flexible tool to account for and evaluate various sources of uncertainty.

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1. Introduction

Abundance and density are the most important demographic measures of a population (Liebhold and Gurevitch, 2002; MacKenzie et al., 2006) and are essential information for population assessments, viability analyses, and evaluations of management procedures (Barlow et al., 1995; Carretta et al., 2009; Wade, 1998). Although important, one common difficulty in abundance studies is accounting for negative bias due to undetected individuals because sampling procedures do not guarantee a perfect detection in most cases (Dorazio et al., 2006; Royle and Dorazio, 2008).

In some cases, it can be reasonable to consider sampling variability and imperfect detection to be constant across spatial or temporal units. However, this option is rarely feasible. Sampling protocols and statistical inference should allow an explicit and formal representation of data using constituent models of observations and underlying ecological or state processes (e.g. Moore and Barlow, 2011; Royle et al., 2004; Royle and Dorazio, 2008; Thomson et al., 2008; Link and Barker, 2010). The state process models vary in

underlying ecological phenomena, which are the primary object of inference. This process is manifest in a state variable, which is typically unobservable. In contrast, the observation process contains a probabilistic description of mechanisms that produce data. This structure is described as a hierarchical or state-space model (Royle and Dorazio, 2008).

The humpback whale (*Megaptera novaeangliae*) is a migratory species, moving seasonally between summer feeding grounds at high latitudes and winter breeding grounds at low latitudes (Dawbin, 1956; Mackintosh, 1965). The International Whaling Commission (IWC) recognizes seven humpback whale migratory breeding grounds in the Southern Hemisphere (IWC, 1998). The population of interest in this study is Breeding Stock A, which feeds east of the Scotia Sea, around South Georgia and the South Sandwich Islands, and breeds in the Southwest Atlantic Ocean along the coast of Brazil (Engel et al., 2008; Engel and Martin, 2009; Stevick et al., 2006; Zerbini et al., 2006).

The earliest quantitative studies of humpback whale populations used data from commercial catches, where it was possible to obtain relative measures of abundance (Clapham, 2000). The development of individual identification techniques based on the recognition of ventral fluke patterns (Katona and Whitehead, 1981) or, more recently, genotyping (Palsbøll et al., 1997) have enabled the application of mark-capture methods to this species (Hammond

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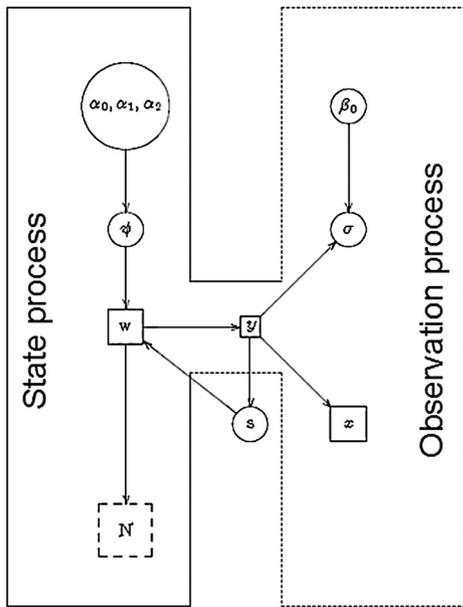


Fig. 1. Conceptual diagram of the hierarchical line transect sampling model highlighting the state and observation process.

et al., 1990). These methods are extremely useful if individual recapture probabilities are high. However, they do not perform as well if the rates of recapture are low, which can be a consequence of animals occupying relatively large areas, as is presently the case with some humpback whale populations. One of the most widely used techniques for quantifying cetacean abundance is line transect sampling. This method is suggested for widely distributed populations because it is less susceptible to failures of assumptions than are mark-recapture methods (Buckland et al., 2001, 2004).

A long period of exploitation by whaling (which ended in 1972) caused large population declines in the Southern Hemisphere humpback whale populations (Berzin, 2008; Clapham et al., 2005; Walsh, 1999; Yablokov, 1994). The majority of these populations have exhibited signs of recovery over the past decades (Bannister and Hedley, 2001; Clapham et al., 1999; Findlay et al., 1994, 2011; Flórez-González, 1991; Paterson et al., 1994; Paterson and Paterson, 1989), including Breeding Stock A (Ward et al., 2011).

The first abundance estimation for Breeding Stock A was conducted in 1995 using mark-recapture methods (Kinas et al., 1998). Since then, estimates of abundance from empirical data and assessment modelling have suggested that this population has been increasing (Andriolo et al., 2010; Freitas et al., 2004; Ward et al., 2011; Zerbinì et al., 2011). Some of these estimates (e.g. Ward et al., 2011) are similar to those obtained through modelling of known life-history parameters from populations in various ocean basins (e.g. mean rate of increase of 7.3% year⁻¹ for one of the approaches used by Zerbinì et al., 2010). Even if Breeding Stock A is growing at a rate that is approaching its maximum, some concerns remain because of the high uncertainty (evidenced through wide Bayesian probability intervals and frequentist confidence intervals) associated with the abundance estimates, which preclude precise estimates of some demographic parameters, such as the population growth rate.

Given the importance of current abundance estimates and the development of techniques that include habitat-specific explanatory variables over density (e.g. Hedley and Buckland, 2004), the goal of this study was to estimate the size of Breeding Stock A off the Brazilian coast using line transect sampling within a Bayesian statistical framework. A hierarchical modelling approach (Royle and Dorazio, 2008) was developed that incorporates covariates that have the potential to affect detection probability (altitude and sighting cue) and humpback whale occurrence (year and distance from shore) (Fig. 1). The detection probability and abundance of

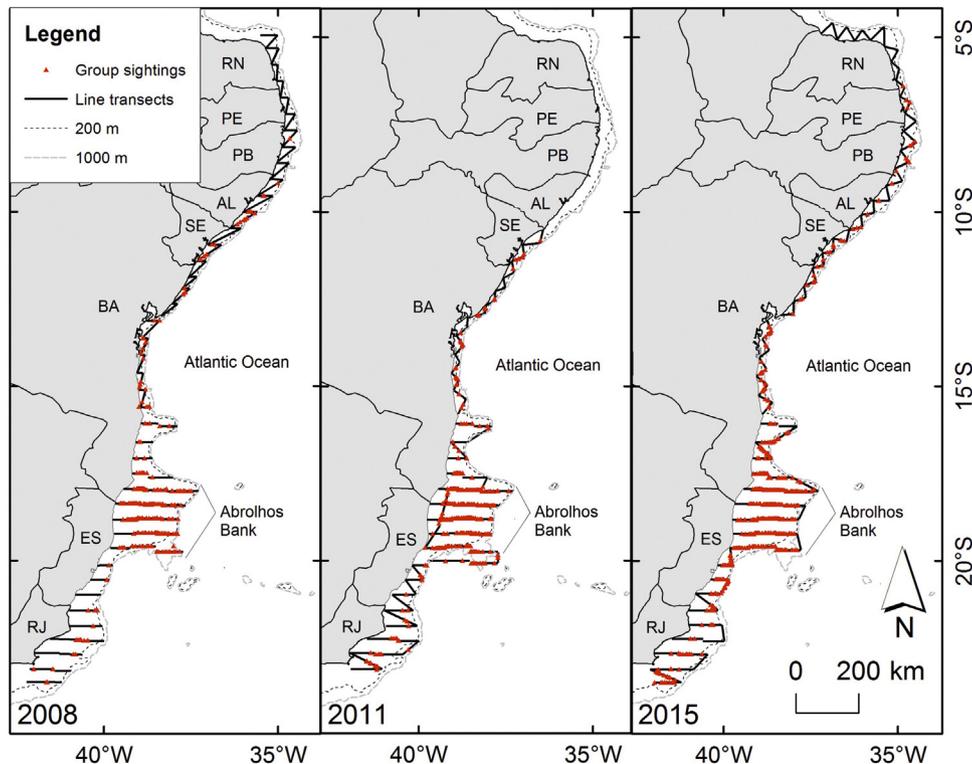


Fig. 2. Locations of sightings of humpback whale groups (red) and transect lines (black) along the Brazilian breeding ground for 2008, 2011 and 2015. The isobaths of 200 m and 1,000 m are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

humpback whales were estimated and compared with frequentist estimates. Finally, a simulation study was used to validate our approach.

2. Methods

2.1. Survey

Three systematic sighting surveys were performed between August and September of 2008, 2011 and 2015, during the peak of humpback whale abundance in the breeding season off the Brazilian coast (Martins et al., 2001; Morete et al., 2003). A high-wing aircraft (Aerocommander) equipped with bubble windows was used to survey the study area from the State of Rio Grande do Norte (4°34' S) to Rio de Janeiro (23°12' S) in 2008 and 2015. In 2011, due to funding constraints, the survey was performed from the State of Sergipe (10°8' S) to Rio de Janeiro (Fig. 2). Parallel transect lines were designed to sample the survey area from the coast until the 500 m isobath. To maximize the sampling effort, in the northern area (from Abrolhos Bank), transects were designed in a zigzag shape due to the narrow shelf. Aircraft flew during favourable weather conditions at an altitude of 1,000 ft (304.80 m) in 2008 and 500 ft (152.40 m) in 2011 and 2015 at an airspeed of 110 knots (56.59 ms⁻¹).

Observations were conducted by two observers located at the right and left bubble windows of the aircraft. For each sighting, the declination angle from the aircraft to the group of whales was measured by a hand-held clinometer whenever a group passed abeam. The geographic position of the sighting was recorded, along with the group size and sighting cue type. Sighting cue was grouped into four categories that consider similar humpback behaviours: (i) blow: animals blowing; (ii) aerial behaviour: breaching; (iii) surface: flipper and tail slapping, lobtailing and the dorsal or ventral part of the animal's body on the surface; and (iv) submerged: submerged animals.

2.2. Hierarchical Bayesian line transect model

Perpendicular distances were calculated using basic trigonometric rules from the aircraft altitude and the declination angle to the sighting. All angles measured between 3° and 0° (distances beyond 3000 m) were later discarded because of measurement inaccuracy.

We developed a hierarchical distance sampling formulation by using data augmentation (Royle and Dorazio, 2008; Link and Barker, 2010; Kéry and Royle, 2016). Data augmentation is a convenient scheme for obtaining Bayesian posterior distributions via Markov chain Monte Carlo methods (Tanner and Wong, 1987). The imputed values for the augmented data in this scheme can be viewed as a special way of using auxiliary variables to accelerate Gibbs sampling algorithms (Liu and Wu, 1999).

Let n denote the total number of groups for which x_i are the known perpendicular distances and $y_i = 1$ is the observed variable of detection for $i = 1, 2, \dots, n$. Data augmentation consists of appending $M - n$ 'observations' for some large value of M , with $x_i = \text{NA}$ defined as missing values and $y_i = 0$ indicating no detection for $i = (n + 1), \dots, M$.

For each of the M 'observations' in the augmented dataset, the auxiliary indicator variable w_i was introduced to represent the group's occurrence. We assume that w_i are independent random variables with a Bernoulli distribution, where ψ is the probability that a group from the superpopulation M is part of the effective population. It immediately follows that the total number of groups $N_g = \sum_{i=1}^M w_i$ has a Binomial distribution $N_g \sim \text{Bin}(M, \psi)$. Hence, in this formulation, estimating the expected value of N_g is equivalent

to estimating ψ . Since the variance of the binomial distribution is dependent on ψ ($\text{var}(N_g) = M\psi(1 - \psi)$) and given that the binomial converges to the Poisson ($M\psi$) as far as the number of trials (M) tend to infinity and ψ tends to 0, we tested different M values to fit the model.

Since we jointly computed the abundance in 2008, 2011 and 2015, we assigned a categorical covariate 'year' on the logit scale of ψ to address differences between abundance in those years. Geographic region has already been used in a previous analysis conducted in the Brazilian breeding ground through Distance software (Thomas et al., 2010), because the sampled area had been expanded, i.e. stratification was implemented in the design phase (see Andriolo et al., 2010 for details). In the present surveys, the samplings were continuous, and we opted to introduce a habitat covariate to account for areas that have potentially different densities. Thus, we included distance from shore (km) and its quadratic term on ψ to account for this variability as follows:

$$\log\left(\frac{\psi_{ij}}{1 + \psi_{ij}}\right) = \alpha_0[t_{ij}] + \alpha Z_{ij} \text{ for } j = 1, 2, 3,$$

where α_0 is the intercept for each year ($t = 1, 2, 3$ for 2008, 2011, 2015), α is the vector of coefficients associated with the covariate matrix Z , which contains distance from shore (d) and its quadratic term (d^2).

Another way to use a site-specific covariate like year on density is to describe abundance (N) as a Poisson random variable, and the intensity parameter as a function of covariates in a discrete space model (Kéry and Royle, 2016). In this case, the data augmentation parameter ψ is confounded with the intercept of the Poisson mean and a thinning process of the Poisson mean is then used to specify ψ (see Kéry and Royle, 2016, Chapter 9 for further details). Because we are dealing with a continuous space model, we preferred to specify the covariate model in the data augmentation parameter instead.

To add distance x as an individual covariate for $i = 1, 2, \dots, M$, we used a half-normal detection function:

$$g(x_{ij}) = \exp\left(-\frac{x_{ij}^2}{2\sigma_{ij}^2}\right).$$

We addressed possible variations on the scale parameter σ by extending the detection function to:

$$\log(\sigma_{ij}) = \beta_0[h_{ij}, c_{ij}],$$

where β_0 is a matrix that represents the coefficient of the interaction term between altitude (h) and sighting cue (c). For the covariates sighting cue and distance from shore (d), $M - n$ data were completed with 'NA' and prior distributions were assumed:

$$d_{ij} \sim N(0, 0.7)$$

$$c_{ij} \sim \text{Cat}(K, p)$$

$$p \sim \text{Dir}(K, a),$$

where $K = 1, \dots, 4$ (levels of sighting cue) and $a = a_1, \dots, a_K$.

Since transect lines were randomly placed with respect to humpback whale groups, distances were assumed to have a uniform distribution defined on some continuous interval (a, b), $x_{ij} \sim U(0, X_{max})$, where X_{max} is a given maximum at which distance measurements were truncated (3000 m in this study).

Finally, we used a shifted Poisson distribution with average group size by year ($\mu_j + 1$) or equivalently $(s_{ij} - 1) \sim \text{Pois}(\mu_j)$ to change the inference from groups (N_g) to individuals.

If we define a_j as the areas that were effectively covered by the surveys (i.e. areas in which groups had positive detection probability) and A_j as the overall study area in which the transect lines have

Table 1
Prior distributions assigned for model parameters.

Parameter	Prior
α_0	N(0, 100)
α_1	N(0, 100)
α_2	N(0, 100)
β_0	N(0, 100)
s	U(0, 10)

been placed, then the parameters of primary interest are population density D_j and size N_j , which are defined:

$$D_j = \sum_{i=1}^M \left(\frac{w_{ij} s_{ij}}{a_j} \right)$$

$$N_j = A_j D_j$$

To address the unrealistic assumption of perfect detection at distance $x = 0$ in aerial line transect surveys of cetaceans (Buckland et al., 2001), we included $g(0)$ as an uncertain, partially known parameter by simulating from N(0.67, 0.15) (Andriolo et al., 2006) at the final step of the analysis, after the estimate of N_j had been obtained. The IWC Scientific Committee had recommended the use of this $g(0)$ estimate as a correction factor for aerial survey-based abundance incorporated in the assessment of Breeding Stock A (IWC, 2010).

Within the Bayesian framework, flat priors were assigned to all parameters (Table 1), and posterior distributions were obtained through Markov chain Monte Carlo methods (MCMC) by using JAGS in combination with R software (Kellner, 2015). The MCMC algorithm was implemented with 3 chains of 400,000 samples each, burn-in of 200,000 and thinning of 200, resulting in a posterior sample of 3,000 values. Diagnostics to verify any indications of lack of convergence of the Markov chains were run through the *coda* package (Plummer et al., 2006). The R code is available in Appendix A.

We compared our results with standard line transect estimates (Buckland et al., 2001). Multiple covariate distance sampling (MCDS) (Buckland et al., 2004; Marques and Buckland, 2003) was used to fit distance data by year along with the sighting cue covariate and a stratified estimate. We used the default analysis, which estimates variance empirically and uses the size-bias regression method to estimate group size. We also selected a multiplier to account for $g(0)$ as recommended by IWC (2010). We then examined the frequentist point estimate in comparison with the Bayesian posterior mean, frequentist confidence interval in comparison with the Bayesian probability interval, and coefficient of variation (CV) of both frequentist and Bayesian analyses. We defined a CV for the Bayesian analysis using the posterior mean and standard deviation of N . Hence, Bayesian CVs have a different meaning as they do not relate to the frequentist sampling distribution of estimates.

2.3. Simulation study

We performed a small simulation study to evaluate the precision of humpback whale parameters estimated through the hierarchical line transect model.

This study was performed for two years with different survey altitudes (denoted by 1 and 2) by establishing a superpopulation $M = 1,500$. Numeric covariates on ψ were simulated through N(0, 1) (such as the standardized covariate distance from shore in the humpback whale dataset), whereas factor covariates on σ were simulated as a categorical distribution with three levels and dif-

Table 2

Posterior summary (mean, median and standard deviation) of parameters α_0 , α_1 and α_2 regarding the influence of the covariates year, distance from shore and quadratic term on occurrence probability (ψ); $\beta_0[h, c]$ regarding the influence of the interaction term between altitude ($h = 1$: 1000 ft, $h = 2$: 500 ft) and sighting cue ($c = 1$: blow, $c = 2$: aerial behaviour, $c = 3$: submerged, $c = 4$: surface) on scale parameter (σ); and s regarding mean group size.

Parameter	Mean	Median	SD
α_0 [2008]	-2.528	-2.528	0.088
α_0 [2011]	-2.228	-2.229	0.068
α_0 [2015]	-1.999	-1.999	0.065
α_1	0.006	0.006	0.031
α_2	-0.167	-0.166	0.022
β_0 [1, 1]	-0.504	-0.519	0.129
β_0 [1, 2]	-0.515	-0.670	1.28
β_0 [1, 3]	-1.563	-1.568	0.127
β_0 [1, 4]	-1.005	-1.007	0.073
β_0 [2, 1]	-0.413	-0.420	0.091
β_0 [2, 2]	7.647	6.763	5.176
β_0 [2, 3]	-1.781	-1.783	0.087
β_0 [2, 4]	-0.871	-0.872	0.047
s [2008]	1.600	1.599	0.045
s [2011]	1.557	1.556	0.037
s [2015]	1.587	1.585	0.034

ferent replacement probabilities of 0.5, 0.3 and 0.2. Perpendicular distances were also simulated from U(0, 1).

The parameters α_0 [1] = 0.5, α_0 [2] = 0.7, $\alpha_1 = 0$, and $\alpha_2 = -0.3$ and β_0 [1, 1] = -0.5, β_0 [1, 2] = -1, β_0 [1, 3] = -1.5, β_0 [2, 1] = -0.7, β_0 [2, 2] = -1.2 and β_0 [2, 3] = -1.6 were fixed to derive the latent parameters ψ and σ through linear regressions on the logit and logarithmic scales, respectively.

After adjusting the perpendicular distances using the half-normal function, we obtained the detected groups y_1 and y_2 as a binomial trial of the true population sizes of groups $N_{g1} = 837$ and $N_{g2} = 897$ and the detection probabilities. Note that the number of detected groups ($n_1 = 444$ and $n_2 = 394$) is obtained as $\sum_{i=1}^M y_i$. Group sizes were simulated through a shifted Poisson distribution with mean $s_1 = s_2 = 1.5$. We then obtained the population size of individuals as $N_i = \sum_{i=1}^{N_g} s_i$ which resulted in $N_1 = 1250$ and $N_2 = 1366$.

The parameters were estimated using the same line transect model developed above. Different values for M were also tested until the N_g variance reached stabilization. Finally, the estimated parameters were compared with the true parameter values in terms of the mean and 95% probability interval of posterior distributions.

3. Results

3.1. Humpback whale abundance

A total of 325, 445 and 607 groups of humpback whales were observed in 2008, 2011 and 2015, respectively, in an inference area of 130,546.2 km² for 2011 and 174,154.9 km² for 2008 and 2015. The group sizes ranged from 1 to 8. We used a superpopulation M with an upper bound of 9,000 groups (without incorporating A/a to save computation time), which was considered to exceed any realistic number of groups within the effectively covered area a and enough to provide a Poisson approximation.

A posterior summary of the parameters related to occurrence probability and perpendicular distances is presented in Table 2. There was a significant effect of distance from shore and its quadratic term (posterior of parameters did not cover zero), wherein the occurrence probability peaks were found in 72, 86 and 65 km for 2008, 2011 and 2015, respectively (Fig. 3). The occurrence probability ψ significantly increased across the years (Table 2).

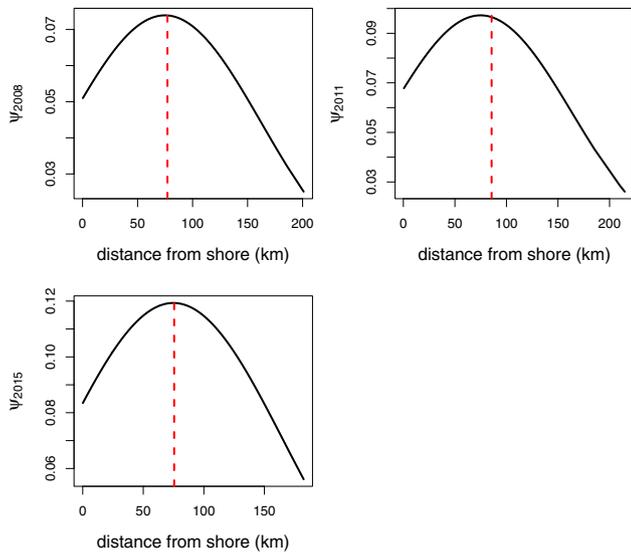


Fig. 3. Occurrence probabilities ψ as a function of distance from shore for 2008, 2011 and 2015. Thin red lines indicate the density peak related to distance from shore. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

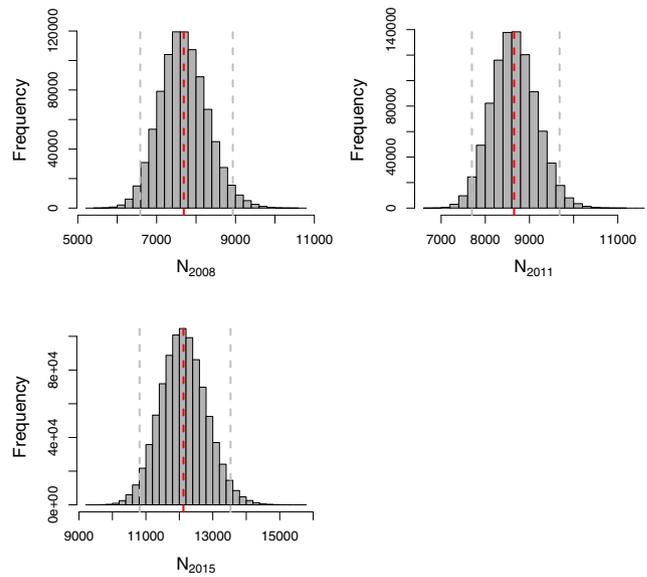


Fig. 5. Humpback whale abundance estimates for 2008, 2011 and 2015. Histograms represent the full posterior distributions; thin red lines indicate the posterior mean; thin grey lines indicate the 95% probability interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

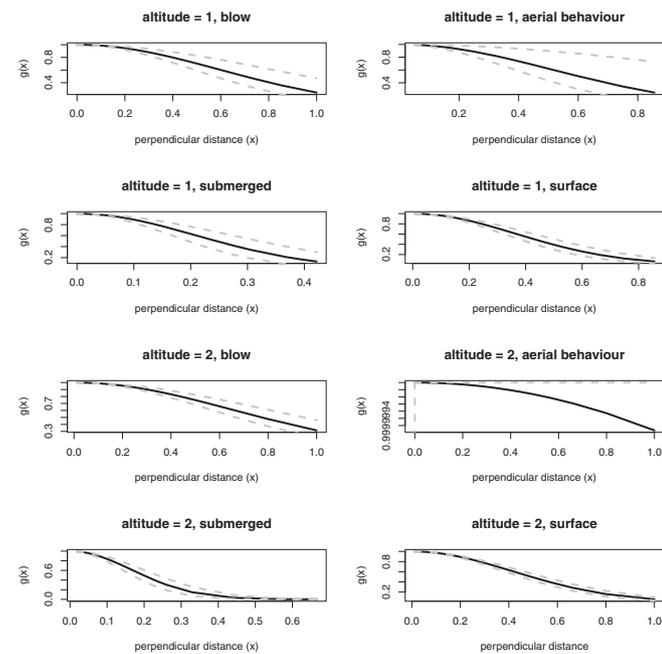


Fig. 4. Half-normal detection functions fitted to perpendicular distances with effects of altitude and sighting cue effect (blow, submerged, surface and aerial behaviour). Black lines indicate the posterior median; thin grey lines indicate the 95% probability interval. Altitude = 1 corresponds to 500 ft (2011 and 2015); altitude = 2 corresponds to 1,000 ft (2008).

Regarding the half-normal function fitted to distances, for the altitude of 1,000 ft (2008), all sighting cues produced a decrease in σ (Table 2). For the altitude of 500 ft (2011 and 2015), the same pattern was observed except for the sighting cue aerial behaviour, which had a strong positive mean effect on σ but with a large associated uncertainty (Table 2 and Fig. 4). The mean group sizes ranged from 1.558 to 1.601 and were not different across years (Table 2).

The population size estimates had an increasing pattern from 2008 to 2015 (Fig. 5), as did the density estimates (Table 3). Considering the smallest area surveyed (2011), the mean annual rate of increase was 5.21% ($SD=0.747$), which represents an

Table 3

Summary of posterior distribution of the hierarchical line transect model by year: mean, coefficient of variation (%) and 95% probability interval. N is abundance; D is density.

Year	N	D	CV	P.I.95%	Area (km ²)
2008	7689	0.044	7.78	6585–8931	174,154.9
2011	8652	0.066	5.87	7696–9682	130,546.2
2015	12,123	0.07	5.71	10,811–13,531	174,154.9

Table 4

Summary of parameters (point estimate, coefficient of variation and 95% confidence interval) estimated through the multivariate distance sampling using sighting cue effect and post-stratification. $E(s)$ is expected group size; N is abundance; D is density.

Year	Parameter	Point estimate	CV (%)	95% C.I.
2008	$E(s)$	1.766	2.82	1.670–1.867
	N	10,286	28.26	5770–18,335
	D	0.064	28.26	0.036–0.115
2011	$E(s)$	1.653	2.19	1.583–1.725
	N	13,782	26.71	8026–23,664
	D	0.106	26.71	0.062–0.182
2015	$E(s)$	1.699	2.00	1.634–1.767
	N	16,690	24.94	9983–27,901
	D	0.104	24.94	0.0624–0.174

increase of 475 individuals by year ($SD=83$). However, the annual growth from 2008 to 2011 was larger than that from 2011 to 2015 ($r_{2008-2011}=11.08\%$; $r_{2011-2015}=1.173\%$). Analysing the density posterior distributions, there is almost no overlap between densities in 2011 and 2008, whereas there is a significant overlap between densities in 2011 and 2015 (Fig. 6).

The results obtained from MCDS are summarized in Table 4. The standard abundance estimates were higher than those estimated by the Bayesian hierarchical model with a difference of 2,597 for 2008, 5,130 for 2011 and 4,567 individuals for 2015 (calculated as the difference between the maximum likelihood and posterior mean estimates). The CV for the Bayesian inference was on average 76% smaller than the standard inference. The Bayesian 95% probability intervals for 2008 and 2015 are completely covered by the frequentist confidence interval (between 2.5% quantile and point

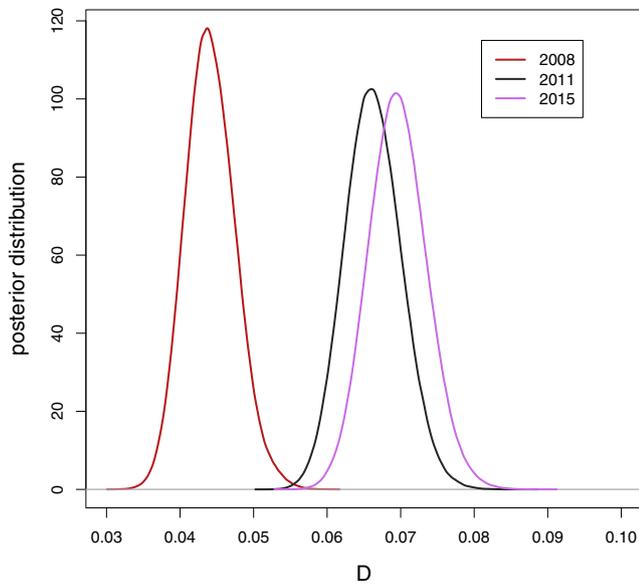


Fig. 6. Humpback whale density estimates for 2008, 2011 and 2015. Density plots represent the full posterior distributions.

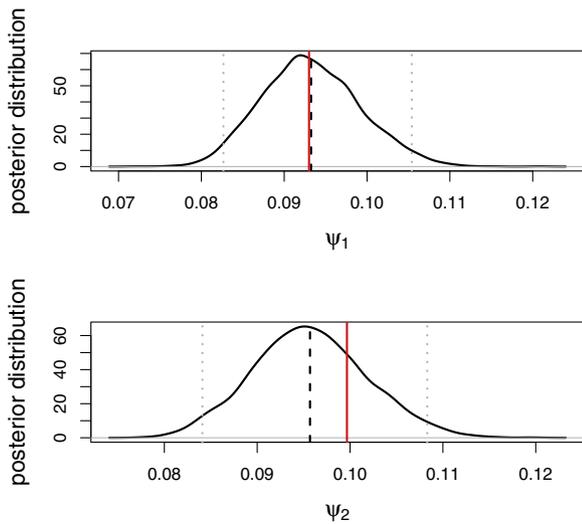


Fig. 7. Occurrence probability parameters (ψ_1 and ψ_2) estimated for the simulation study. Red lines indicate the true parameter value; thin black lines indicate the posterior mean; thin grey lines represent the 95% probability interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

estimate). For 2011, the lower quantile of the probability interval is outside the frequentist confidence interval by a small fraction.

3.2. Simulation study

The true parameter values were always covered by the 95% probability interval of posterior distributions (Figs. 7–9). Note that, since we increased the superpopulation size M to assure reliable variance estimates, the vector of parameters α were no longer correspondent to the parameters fixed in the simulation experiment. For this reason, we show the posterior distributions of ψ , which were readily obtained through $\psi = N_g/M$, instead of α .

The mean posterior distributions were quite similar to the true values for all parameters (Figs. 7–9), although there was a tendency to overestimate the true parameter values for α_0 (Fig. 7), $\beta_0[2, 1]$,

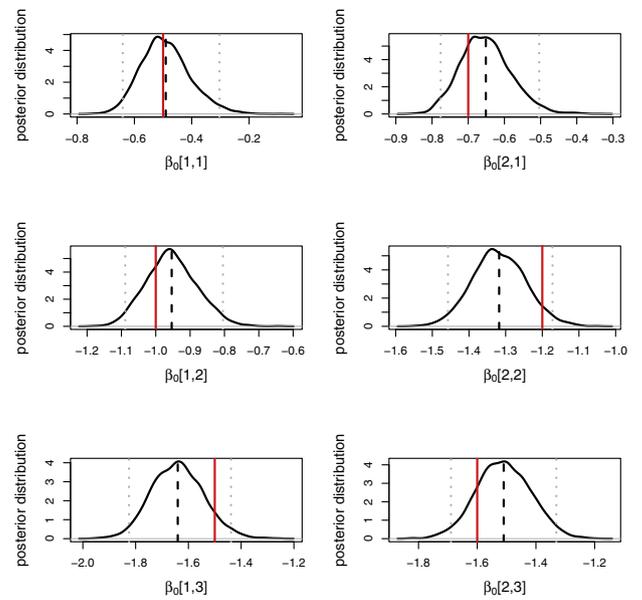


Fig. 8. Parameters regarding detection probability ($\beta_0[1, 1]$, $\beta_0[2, 1]$, $\beta_0[1, 2]$, $\beta_0[2, 2]$, $\beta_0[3, 1]$ and $\beta_0[2, 3]$). Red lines indicate the true parameter value; thin black lines indicate the posterior mean; thin grey lines represent the 95% probability interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

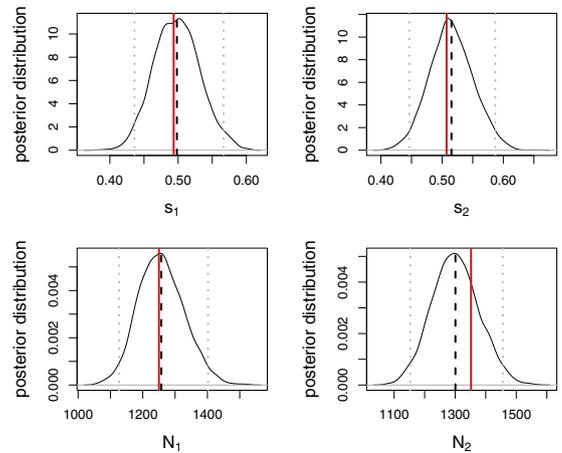


Fig. 9. Parameters regarding group size (s_1 and s_2) and abundance (N_1 and N_2) estimated for the simulation study. Red lines indicate the true parameter value; thin black lines indicate the posterior mean; thin grey lines represent the 95% probability interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$\beta_0[1, 2]$ and $\beta_0[2, 3]$ (Fig. 8) and underestimate for $\beta_0[2, 2]$, $\beta_0[1, 3]$ (Fig. 8) and N_2 (Fig. 9).

4. Discussion

4.1. Modelling issues

We developed an extension of the hierarchical line transect model proposed by Royle et al. (2004), in which a Bayesian formulation using data augmentation was given by Royle and Dorazio (2008) and Link and Barker (2010). First, we extended the analysis in a temporal scale (three years), which allowed the estimation of abundance across years by pooling distance data. Second, we inserted covariates with potential to adjust for occurrence probability at the level of observational units.

To improve precision and reduce the bias of estimates, line transect samplings are generally analysed using stratification, computing abundance independently by geographic regions (strata) (Buckland et al., 2001). Andriolo et al. (2010) defined five blocks (i.e. strata) at the design step of the aerial surveys from 2002 to 2004, and this was further expanded to eight blocks for 2005. The abundances in each block were computed independently and pooled to obtain total population sizes. From 2008 onward, we no longer performed design stratification in the aerial surveys. Rather, the transects were continuously travelled depending on weather and logistical conditions. Thus, post-stratification (i.e. stratification of data after collection) is a possibility since encounter rate can differ in space (Wedekin et al., 2008). Post-stratification is straightforward to implement in a hierarchical setting by introducing a categorical individual covariate that assigns each detection (group) to a stratum (see Kéry and Royle, 2016 chapter 9 for an example).

Including habitat-specific variables in distance sampling data is of interest in many studies. For example, Hedley and Buckland (2004) fitted spatial models (linear and additive models) to line transect data. A Bayesian approach for spatial inference on density from line transect survey data was developed by Niemi and Fernández (2010), in which density was described as an inhomogeneous Poisson process whose intensity function incorporates covariate effects and spatial smoothing of residual variation. In both studies and in this work, the assumption of transects randomly placed in relation to groups (or individuals) can be relaxed since we were able to link covariate effects to variation on density. Thus, this approach might be used with data arising from sources other than designed-based surveys, for instance, opportunistic data. The hierarchical Bayesian line transect model could be extended depending on the purpose of the study. For example, it is possible to insert other detection and ecological covariates on ψ and σ by specifying prior distribution on covariates; using other detection functions (Oedekoven et al., 2014); and adding dual observer data to estimate perception bias related to detection on the trackline (Conn et al., 2012; Guilherme-Silveira and Kinas, 2016). Although these types of models are conceptually straightforward to implement and to interpret, their disadvantage is the high demand for computational time due to the data augmentation scheme, which can hinder analyses of large datasets with many covariates. This may be overcome by using a reversible jump algorithm (rjMCMC), which is useful when the dimensionality of the parameter space is unknown (Link and Barker, 2010; Conn et al., 2012; Oedekoven et al., 2014).

Our simulation study provides evidence that the hierarchical model is accurate. The estimated 95% probability intervals always included the true parameter values, but deviations from the posterior mean to the true parameter values were identified. However, we do not believe that these relatively small differences are a problem that might prevent any further inference. However, a more complete simulation study is advised in helping to clarify in which situations the Bayesian hierarchical line transect model using data augmentation might fail.

Even though we considered $g(0) < 1$ regarding availability bias in our analysis, the population size estimated here may be biased downwards. A preliminary analysis indicates that the average group size is underestimated by approximately 17.5% (P.I.95% = 13.9–21.1%) in aerial surveys when compared to vessel surveys, suggesting that once a correction factor for this problem is included, the estimated abundance should increase. Another negative bias that we are not taking into account is perception bias, which corresponds to the fraction of groups missed by observers for a series of reasons, including fatigue, poor sighting conditions, inexperience, and so forth (Marsh and Sinclair, 1989). In high density areas, the perception bias might increase as many available groups can be missed due to the small time frame resulting from the aircraft speed. Concerned with this type of bias, we are cur-

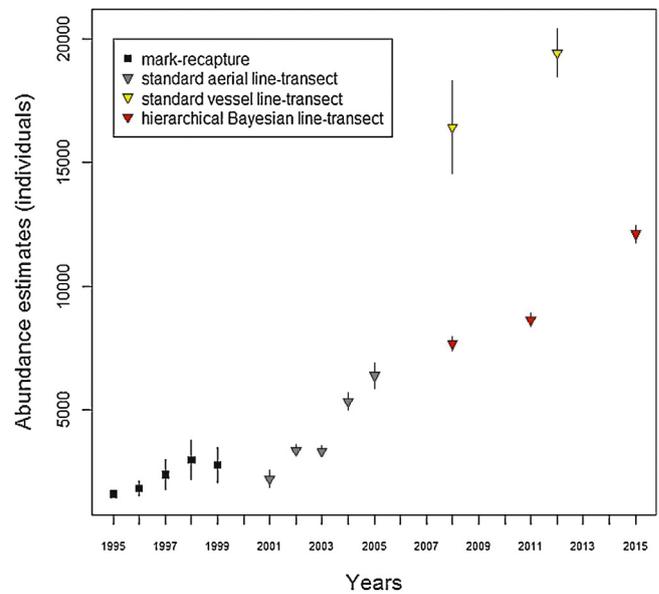


Fig. 10. Abundance estimates with respective intervals based on CVs from 1995 to 2015. Dark grey squares indicate estimates derived from mark-recapture analyses (Kinas et al., 1998; Freitas et al., 2004); light grey triangles indicate estimates derived from standard aerial line transect sampling analyses (Andriolo et al., 2006, 2010); yellow triangles indicate estimates derived from standard vessel line transect sampling analyses (Bortolotto et al., 2016); red triangles indicate estimates derived from the hierarchical line transect sampling model. Estimate from Zerbini et al. (2004) were not included due to its small fraction of Breeding Stock A surveyed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rently developing hierarchical line transect models using a double observer configuration. These two biases might explain the difference between aerial and vessel surveys as was pointed out by Bortolotto et al. (2016). For instance, in 2008 a frequentist analysis using ship survey data estimated 16,410 whales (CV = 0.228) (Bortolotto et al., 2016) while the corresponding aerial survey frequentist estimation was 10,286 (CV = 0.283) and the Bayesian estimation was 7,689 (CV = 0.078). On the other hand, although bias regarding double counting is likely small in line transect sampling, it becomes a potential problem if animals often are double counted in the same sampling unit. It may lead to overestimation of encounter rates and abundance. Observers onboard a vessel at an average speed of 17 km h⁻¹ (Bortolotto et al., 2016) have the potential to count the same group more than once in high density areas, and an evaluation of the dimension of this bias should be a topic of future research.

4.2. Ecological implications

The results of Andriolo et al. (2010) pointed to block D, corresponding to the centre of the Abrolhos Bank, as having the highest density from 2002 to 2005. Our result indicates that density peaks occur in intermediate distances from shore (65–86 km), which agrees with Andriolo et al. (2010) and Martins et al. (2001). Our study proposed the introduction of a habitat covariate into the line transect sampling analysis, which leads to a clear picture of how humpback whales use their breeding habitat on the Brazilian coast. This approach is also important for evaluating whether and how concentration areas change across years. This not only improves our understanding of the ecology of the species but should also lead to more effective conservation measures.

The present results, obtained three years after the last available estimate from aerial platform (Andriolo et al., 2010), indicated that the population consistently grew until 2011 (Fig. 10). However,

when analysing the posterior distributions estimate for humpback density (Fig. 6), the overlap between densities in 2011 and 2015 suggests a decrease in the rate of growth and might be evidence that the population is moving towards stabilization. To elucidate whether the population is stabilizing and reaching its carrying capacity, prospective surveys should be carried out and a proper evaluation should be drawn.

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Appendix A.

The code below implements the hierarchical Bayesian line transect model used to estimate humpback whale abundance through JAGS. The variables are as follows:

- x: perpendicular distances measured to each animal or group detected
- gs: observed group size
- t (year), d (distance from shore), h (altitude) and c (cue): covariates

Model in JAGS syntax

```
model{
# Likelihood:
for(i in 1:M){M=superpopulation size
for(j in 1:J){J=years
w[i,j] ~ dbern(psi[i,j])
logit(psi[i,j]) <- alfa0[t[i,j]] + alfa1*d[i,j] + alfa2*d[i,j]*d[i,j]
d[i,j] ~ dnorm(0, 0.7)
x[i,j] ~ dunif(0,1)
np[i,j] <- -(x[i,j] * x[i,j]) / (2 * sigma2[i,j])
sigma2[i,j] <- sigma[i,j] * sigma[i,j]
log(sigma[i,j]) <- beta0[h[i,j] * c[i,j]]
c[i,j] ~ dcat(x[])
p[i,j] <- exp(np[i,j])
mu[i,j] <- w[i,j] * p[i,j]
y[i,j] ~ dbern(mu[i,j])
gs[i,j] ~ dpois(g[j])
wgs[i,j] <- w[i,j] * (gs[i,j] + 1)
}j
}i
N2008 <- sum(wgs[1:M,1])
N2011 <- sum(wgs[1:M,2])
N2015 <- sum(wgs[1:M,3])
}
#
```

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