Contributed Paper

Chilean Blue Whales as a Case Study to Illustrate Methods to Estimate Abundance and Evaluate Conservation Status of Rare Species

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Abstract: *Often abundance of rare species cannot be estimated with conventional design-based methods, so we illustrate with a population of blue whales (*Balaenoptera musculus*) a spatial model-based method to estimate abundance. We analyzed data from line-transect surveys of blue whales off the coast of Chile, where the population was hunted to low levels. Field protocols allowed deviation from planned track lines to collect identification photographs and tissue samples for genetic analyses, which resulted in an ad hoc sampling design with increased effort in areas of higher densities. Thus, we used spatial modeling methods to estimate abundance. Spatial models are increasingly being used to analyze data from surveys of marine, aquatic, and terrestrial species, but estimation of uncertainty from such models is often problematic. We developed a new, broadly applicable variance estimator that showed there were likely 303 whales (95% CI 176–625) in the study area. The survey did not span the whales' entire range, so this is a minimum estimate. We estimated current minimum abundance relative to pre-exploitation abundance (i.e., status) with a population dynamics model that incorporated our minimum abundance estimate, likely population growth rates from a meta-analysis of rates of increase in large baleen whales, and two alternative assumptions about historic catches. From this model, we estimated that the population was at a minimum of 9.5% (95% CI 4.9–18.0%) of pre-exploitation levels in 1998 under one catch assumption and 7.2% (CI 3.7–13.7%) of pre-exploitation levels under the other. Thus, although Chilean blue whales are probably still at a small fraction of pre-exploitation abundance, even these minimum abundance estimates demonstrate that their status is better than that of Antarctic blue whales, which are still <1% of pre-exploitation population size. We anticipate our methods will be broadly applicable in aquatic and terrestrial surveys for rarely encountered species, especially when the surveys are intended to maximize encounter rates and estimate abundance.*

Keywords: abundance, *Balaenoptera musculus*, distance sampling, line transect, rare, spatial model, variance

Ballenas Azules Chilenas como Caso de Estudio para Ilustrar Métodos para Estimas la Abundancia y Evaluar el Estatus de Conservación de Especies Raras

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Resumen: *La abundancia de especies raras a menudo no puede ser estimada mediante métodos convencionales basados en diseño, así que ilustramos—con una población de ballena azul (*Balaenoptera musculus*)—un método basado en modelo espacial para estimar la abundancia. Analizamos datos muestreo en transectos lineales cerca de la costa de Chile, donde la población fue llevada a niveles bajos por la cacería. Los protocolos de campo permitieron el desvío de las líneas trazadas para la colección de fotografías de identificación y muestras de tejidos para análisis genéticos, lo que resultó un diseño de muestreo ad hoc con incremento de esfuerzo en áreas con densidades mayores. Por lo tanto, utilizamos métodos de modelaje espacial para estimar la abundancia. Los modelos espaciales son usados cada vez más para analizar datos de muestreos de especies marinas, dulceacuícolas y terrestres, pero la estimación de la incertidumbre de tales modelos a menudo es problemática. Desarrollamos un estimador de varianza nuevo y de aplicación general que mostró que por lo menos había 303 ballenas (95% IC 176–625) en la población. Estimamos la abundancia relativa mínima en relación con la abundancia anterior a la explotación (i.e., estatus) con un modelo de dinámica poblacional que incorporó nuestra abundancia mínima estimada, las tasas de crecimiento poblacional probables derivadas del meta-análisis de las tasas de incremento de ballenas barbadas, y dos supuestos alternativos sobre capturas históricas. De este modelo, estimamos que, en 1998, la población estaba en un mínimo de 9.5% (95% CI 4.9–18.0%) respecto a niveles previos a la explotación bajo un supuesto de captura y 7.2% (IC 3.7–13.7%) respecto al otro. Por lo tanto, las ballenas azules chilenas probablemente están en una pequeña fracción de la abundancia previa a la explotación, estas estimaciones de abundancia mínima demuestran que su estatus es mejor que el de ballenas azules en la Antártica, que aun están <1% del tamaño de la población previa a la explotación. Anticipamos que nuestros métodos serán ampliamente aplicables en muestreos acuáticos y terrestres de especies raras, especialmente cuando los objetivos del muestreo están diseñados para maximizar las tasas de encuentro y estimar la abundancia.*

Palabras Clave: abundancia, *Balaenoptera musculus*, modelo espacial, muestreo a distancia, transecto lineal, raro, varianza

Introduction

Estimating the abundance of rare species (i.e., small population size), elusive animals, and animals that are abundant overall but occur over vast areas at low densities is a perennially difficult problem (Thompson 2004). Many endangered taxa fall into this category. For example, one criterion used by the International Union for Conservation of Nature (IUCN) to define endangered taxa is a population estimated to number "fewer than 250 mature individuals" (IUCN 2001). When few animals are available to be sampled, it becomes difficult to collect enough data to reliably estimate population parameters. This difficulty can occur with both mark-recapture estimates and line-transect surveys, which are part of the distance-sampling family of methods commonly used to estimate abundance of marine and terrestrial animals (Buckland et al. 2001). If there are too few sightings to reliably estimate the width of the rectangular area searched along a transect (hereafter, the effective strip width), then abundance cannot be estimated. Low overall encounter rates can be ameliorated if information on animal distribution is available from telemetry studies, catch records, data from preliminary surveys, or local knowledge. Such information can be incorporated into the design of line-transect surveys (Thomas et al. 2007) to ensure sufficient sighting effort is allocated to high-density areas to increase the number of sightings sufficiently to allow estimation of the effective strip width (Williams & Thomas 2009). It may also be necessary to maximize the number of encounters for other reasons, such as to collect tissue samples or identify individuals for long-term mark-recapture studies. Nevertheless, for species with poorly known or unpredictable distributions, it may be impossible to devise in advance a survey design within a given budget that will ensure enough encounters. Instead, it may be necessary to adjust the design during the survey to increase encounters. The problem with this ad hoc approach is that such adjustments invalidate some of the assumptions of standard line-transect analyses and require the development of more sophisticated methods of abundance estimation. Nevertheless, the high cost of shipboard surveys means it is desirable to generate even rough abundance estimates from surveys that would, more ideally, be thought of as reconnaissance or pilot surveys.

We examined data from a sightings survey of a population of blue whales (*Balaenoptera musculus*) off the coast of Chile to illustrate one solution to the problem of estimating abundance and conservation status of rare species. Here *status* means "abundance relative to pre-exploitation levels," which is a standard way of measuring depletion in natural resources and the definition used by the International Whaling Commission (IWC) to assess whale populations. Many blue whale populations were hunted to near extinction in the twentieth century, and although the species was protected internationally in the 1960s, illegal whaling continued into the 1970s (Branch et al. 2004). In the southeast Pacific blue whales were caught primarily off Chile, but some were also taken off Peru and Ecuador (Clarke et al. 1978; Ramírez 1983; Van Waerebeek et al. 1997). Hundreds were caught annually in many years from the 1910s–1960s in Chilean waters (Clarke et al. 1978; Van Waerebeek et al. 1997). Whaling off Chile, Ecuador, and Peru probably led to substantial decreases in abundance of blue whales in the southeast Pacific. This decrease was not thought to have been as severe as for other populations of blue whales, but the extent of decreases and of any subsequent recovery remained unknown (Donovan 1984). To better understand the current status of Chilean blue whales and their relation to other populations of blue whales, a research cruise was undertaken off Chile in 1997. The cruise was part of the Southern Ocean Whale and Ecosystem Research (SOWER) program of the IWC (for full details see Findlay et al. [1998]).

The primary aims of the SOWER surveys were to identify which subspecies was found in Chilean waters, maximize encounters with blue whales, collect genetic and acoustic data, photograph individuals for identification, and videotape activity for subsequent behavioral analyses. Two recognized subspecies of blue whales occur in the Southern Hemisphere: Antarctic (or true) blue whales (*B. musculus intermedia*) and pygmy blue whales (*B. m. brevicauda*). During the austral summer, nearly all Antarctic blue whales are in the Southern Ocean south of 55°S, whereas pygmy blue whales are in more northerly waters, primarily in the Indian Ocean and around Australia and New Zealand (e.g., Ichihara 1966; Branch et al. 2007*a*; Branch & Mikhalev 2008). Blue whales also occur off Chile, Peru, and Ecuador, but it was not clear at the time of the survey whether these blue whales were Antarctic blue whales, pygmy blue whales (Aguayo 1974; Van Waerebeek et al. 1997), or an undescribed subspecies (Branch et al. 2007*a*, 2007*b*, 2009). During the survey, 37 groups (45 animals) were recorded as pygmy blue whales and 2 groups were recorded to the level of subspecies (Findlay et al. 1998). Visual identification to subspecies level is unreliable, however, and genetic data indicate blue whales in the southeastern Pacific (Chilean blue whales), Indian Ocean (pygmy blue whales), and the Southern Ocean (Antarctic blue whales) form three distinct groups (Leduc et al. 2007). Therefore we considered all these sightings to be of undetermined subspecies.

Although the survey was designed primarily for discrimination of subspecies, researchers on the survey did collect line-transect data that could be used to estimate abundance provided the nonrandom placement of search effort could be addressed statistically. The survey proceeded as follows. Two vessels departed from Iquique, Chile (20°12′S 70°09′W), in December 1997. One headed to 18°30′S and began surveying southward and the other headed to 38°S and began surveying northward. The inner boundary of the survey region was defined as the 12-nautical-mile (22.2 km) territorial boundary of Chile. The outer boundary was delineated by historical catch distribution limits, the 200 nautical mile (370.4 km) exclusive economic zone and the time limits of the survey (Fig. 1).

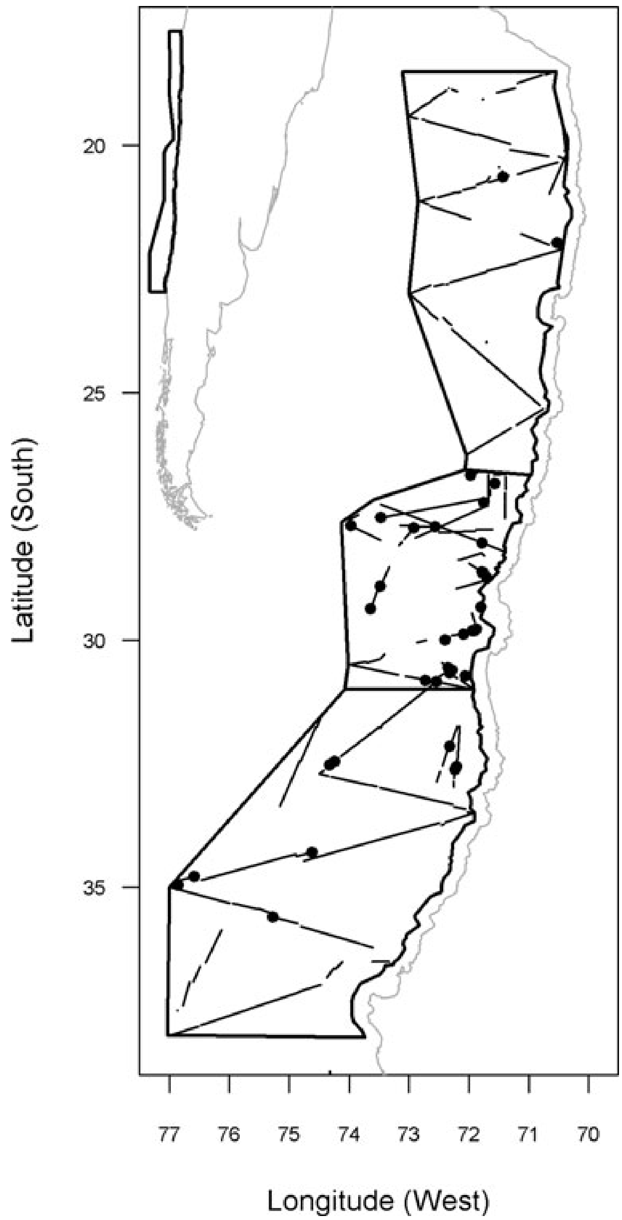

Figure 1. Sightings of blue whales (filled circles) and survey track lines (lines within the polygon) made by vessels surveying in Chilean waters (inset shows South America south of 15°S) for blue whales from December 1997 through January 1998. Polygon outline marks the boundary of the survey region.

Prior to the survey, little was known about whale distribution in the area, so a series of systematic track lines was planned throughout the survey area. To maximize whale encounters, track-line design was ad hoc and track lines were not followed rigidly if aggregations of whales were found. Thus, these data were not collected systematically and do not lend themselves to conventional line-transect analysis (e.g., Buckland et al. 2001). This pragmatic approach—start by finding the animals—is a common first stage in pilot studies of rare or poorly studied animals (McArdle 1990; Barlow et al. 1997; Evans & Hammond 2004). We implemented a model-based method appropriate for use when certain departures from standard line-transect designs occur and applied this method to our data to estimate the abundance of Chilean blue whales within the surveyed region. We devised a new method of estimating variance from the model-based method, allowing uncertainty in the estimation of effective strip width (as would also have been estimated by a conventional line-transect analysis) to be explicitly accounted for when estimating abundance with the spatial model. We also developed a simple population model that incorporated all available information, including these abundance estimates and historical catches, to estimate the minimum current status of the population relative to pre-exploitation levels.

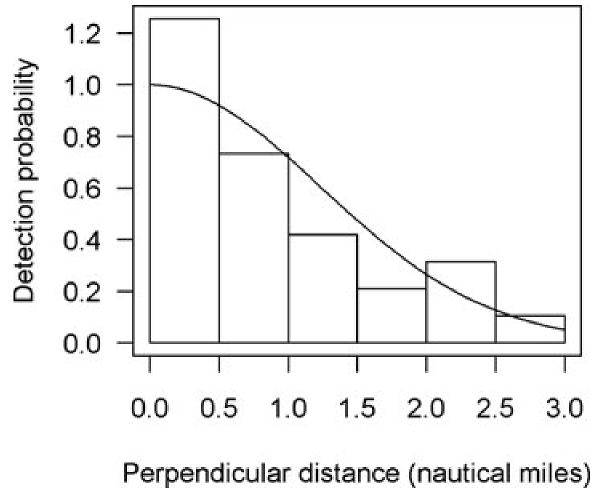

Figure 2. Blue whale detection function showing histogram of perpendicular distance data for the original sightings and the fitted detection probability (line) predicted by the half-normal model. The detection function assumes certain detection of blue whales on the track line and models the decreasing probability of observing whales as perpendicular distance increases.

Methods

Abundance Estimates

The count method we used (Hedley et al. 1999; Hedley & Buckland 2004; Williams et al. 2006) involves two separate statistical models. The first model fitted a detection function to the perpendicular sighting distances, as in a conventional distance-sampling analysis, to estimate the effective strip width. In addition to perpendicular distance, other variables that may affect detectability (e.g., adverse sea conditions) may be incorporated in this model component (Marques & Buckland 2003). Following subdivision of the track lines into segments of approximately equal length, the second model—the spatial density component of the model—was then fitted. The number of whales seen in each segment was described by a generalized additive model (e.g., Wood 2006) with a spatial smoother and an offset term provided by the effective area of each segment (i.e., the product of its effective strip width and its length).

Twenty-six sightings of pygmy blue whales (30 animals total) were available to model the detection function. We binned the perpendicular-distance data into intervals of 0.93 km (0.5 nautical miles) and fitted a half-normal detection function to these binned data (Buckland et al. 2001) (Fig. 2). Because of the small number of sightings, we did not consider more-complex detection functions that incorporate additional detectability covariates. We estimated detection probability ($\hat{p}$) for each of the sightings within a truncation distance of 5.6 km (3 nautical miles) with functions written in *R* (R Development Core Team 2008).

For the spatial model, we divided the track lines into segments of approximately 37 km (20 nautical miles). Not all sightings used in the Distance model were available for the spatial model; 2 of the 26 were outside the survey area. One sighting occurred the instant observers began searching, which meant the search effort immediately stopped and the associated segment length was zero. This left 23 sightings for spatial modeling. Given that the spatial coverage was reasonable overall, albeit locally patchy, this was sufficient for fitting the model and estimating an overall abundance. With such a small number of sightings, however, we could not draw conclusions about spatial distribution within the area—this would require many more sightings than the number required to estimate abundance.

The counts per segment showed some evidence of overdispersion when a Poisson distribution was assumed in the GAM. We addressed this overdispersion by assuming the number of whales seen in each segment followed a Tweedie rather than Poisson distribution, and we assumed residual autocorrelation was negligible. Tweedie distributions offer a single-model approach to dealing with zero-inflated count data and are readily handled within a GAM framework. They are the subset of exponential-family distributions for which variance (of the response, Y) is proportional to some power (θ) of its mean (i.e., $\mathrm{var}[Y] = \varphi E[Y]^{\theta}$ for some scale parameter φ); thus, Gaussian, Poisson, and gamma distributions are special cases, with θ being 0, 1, and 2, respectively (Joergensen 1987). Noninteger values of θ are both statistically valid and practically useful. Formal maximum-likelihood estimation of θ is possible, but difficult to compute (e.g., Candy 2004). In our experience, choosing θ through graphical inspection of residual plots for different θ is often adequate because overall results are usually not very sensitive to θ. For these data, $\theta = 1.1$ yielded reasonable fits.

With a logarithmic link function, the resultant spatial model may be written

$$E(n_i) = \exp\left[\log\left(2l_i w \hat{p}\right) + s(\text{lat}_i, \text{lon}_i)\right], \qquad (1)$$

where $E(n_i)$ is the expected number of whales in the ith segment; l_i is the length of segment i; w is the perpendicular truncation distance; $\hat{p}$ is the estimated probability of detection of a blue whale pod; lat_i and lon_i denote the midpoint of the ith segment; and s is a smooth function. We used the soap-film smooth (Wood et al. 2008) because we have found it is less prone than other types of smoothers to make extreme predictions near the edges of the survey region. For abundance estimation, we used the spatial model to predict densities at points within a grid across the survey area and hence estimate abundance.

Estimating the Variance of an Abundance Estimate

Variance in spatial models of abundance is often estimated by resampling, in particular through the use of parametric, nonparametric, or moving-block bootstraps (e.g., as in the software Distance, version 6.0; Thomas et al. 2010). In practice these bootstrapping techniques frequently yield unstable and biased results when models are smoothed, especially in cases such as ours in which survey design precludes easy identification of an independent resampling unit (Hedley et al. 1999; Williams et al. 2006). By using a soap-film smoother, we partially addressed the problems that can occur when bootstrapping because this smoother is much less prone to make extreme predictions near the edges of the survey. Nevertheless, bootstrapping spatial models is intrinsically problematic regardless of which type of smoother is used. Wood (2006) proposes an alternative Bayesian approach that is simple to implement and appears not to suffer from the bias often associated with the bootstrapping approaches. We adopted this method, which requires estimation of a prediction matrix and simulation of replicate parameter sets from the posterior distribution of the estimated parameters of the spatial model.

Spatial models, such as the one we used, include variability that comes from estimating the parameters of the detection function. This variability appears via the offset in the linear predictor because log(effective area) is based on at least one estimated parameter (the effective area of each segment is the product of twice its length and the estimated strip half-width [$\hat{\mu}$]). Hedley and Buckland (2004) suggest the delta method (Seber 1982) can be used to combine this component of the variance with the variance from estimation of the spatial component. Although pragmatic, this solution is somewhat ad hoc and rests on an assumption of no correlation between effective strip width and animal density. We propose instead an integrated method for systematically propagating the uncertainty through the two modeling stages.

We denoted the parameters used to estimate the detection function as $g\ (y;\ \pi)$ (and hence effective area, a) by $\hat{\pi}_y$ (where y is perpendicular distance). In considering the ith segment of effort, we assumed n_i whales were seen and the mean location of the segment was (lat_i, lon_i). Using a spatial smooth $s\ (\cdot)$ to describe spatial abundance, we wrote the logarithm of the expected number of whales in the segment as

$$\begin{aligned}\log[E(n_i)] &= \log(a_i) + s(\text{lat}_i, \text{lon}_i)\\ &= \log(2l_i w) + \log[p_i(\pi)] + s(\text{lat}_i, \text{lon}_i)\\ &= \log(2l_i w) + \log[p_i(\pi + \gamma)] + X_i\beta, \qquad (2)\end{aligned}$$

where γ is $(\pi - \hat{\pi}_y)$ and $\boldsymbol{X}$ is the design matrix associated with the smoother. Because the first derivative of a function $f(x)$ may be approximated by $[f(x+\delta) - f(x)] \cdot \delta^{-1}$ for $\delta << x$, the above expression for the model may be written

$$\log[E(n_i)] \approx \log(2l_i w) + \left[\frac{d \log p_i}{d\pi}\right]_{\pi=\hat{\pi}_y} + X_i\beta, \qquad (3)$$

assuming that the detection function parameter estimates $(\hat{\pi}_y)$ are fairly close to the unknown true values. The $[\frac{d\log p_i}{d\pi}] \cdot \gamma$ and $X_i\beta$ have identical shape (i.e., they are both matrices dotted with vectors). The matrix of first derivatives may be thought of as another design matrix and γ as a vector of unknown parameters. The distributional properties of both γ and β are known and are given by $\gamma \sim N(0, -H_\pi^{-1})$ and $\beta \sim N(0, \theta \mathbf{S}^{-1})$, where H_π is the Hessian from maximizing the likelihood of the detection function from the line-transect data, $\boldsymbol{S}$ is the penalty matrix associated with the smoother, and θ is the smoothing parameter vector (to be estimated). Thus, γ and β operate similarly; the only difference is that the smoothing parameter, or penalty, for γ is fixed in advance (it equals one), whereas for β, the smoothing parameter (vector) needs to be estimated. Thus, the spatial model comprised a smooth of location, an offset representing log(effective area), and a random-effect term (the matrix of first derivatives from estimation of the detection function) with precision determined by the supplied Hessian matrix.

Within the *R* package mgcv (Wood 2008), it is possible to fit such a model with the paraPen argument to gam to specify the first derivative term. Nevertheless, additional customized *R* code was necessary to fit the model described above. This code was needed because the scale parameter in the spatial model was unknown (because we assumed a Tweedie distribution for the response) and because the smoothing parameters in gam were defined relative to the scale parameter. To force gam into use of the fixed penalty we required, we implemented a numerical routine to optimize the gam fit over the scale parameter, adjusting the smoothing parameter for γ in each iteration so that its absolute value would always be one.

Population Model

We developed a population model to find lower bounds on the past and current abundance of Chilean blue whales. The model incorporated our minimum abundance estimate, known catches, and likely population growth rates for large whales. We assumed that likely population growth rate came from a normal distribution with a mean of 6.20% (SD 2.90) obtained from a meta-analysis of maximum intrinsic growth rates of large cetacean species recovering from exploitation (Punt & Allison 2010). We further bounded population growth rates between 0% and 11.8%; the upper bound corresponded to the maximum estimated population growth rate for humpback whales (*Megaptera novaeangliae*) (Zerbini et al. 2010). We developed two alternative catch series (C. Allison, personal communication). The first catch series included only catches taken from boats returning their catches to Chilean land stations for processing (hereafter Chilean catch assumption), and the second catch series included all regional catches, including catches from pelagic whalers (whales processed on board) that were categorizedas "Chile," "Peru," and "Chile/Peru/Ecuador" (hereafter southeastern Pacific catch assumption). We assumed catches of unspecified species in Chilean waters (in years 1908–1911, 1913, 1927, 1934–1935; total 1229 whales) included 31.5% blue whales—the average over 1912–1926 (Van Waerebeek et al. 1997).

We applied the standard population dynamics model used by the IWC for large baleen whales, which is a generalized logistic model with $z = 2.39$, thus ensuring that maximum sustainable catch (yield) occurs at 60% of pre-exploitation abundance. The model has two free parameters: r, the intrinsic (or maximum) growth rate obtained from the meta-analysis, and K, the pre-exploitation abundance (or carrying capacity). Under this formulation, K must be estimated to ensure the modeled abundance in 1997 equals the abundance estimate:

$$N_{1905}=K \quad \text{and} \quad N_{t+1} = N_t + rN_t\left(1-\left(\frac{N_t}{K}\right)^z\right) - C_t, \quad (4)$$

where N_t is abundance and C_t is the catch in year t.

This assessment used a Monte Carlo procedure. First, we generated a single population size N_{1997} from the abundance distribution, and generated a single rate of increase r from the rate-of-increase distribution. We then found the corresponding value of K that resulted in a model-predicted abundance equal to N_{1997} in 1997. This procedure was repeated to produce 10,000 abundance trajectories, from which median and 95% probability intervals could be obtained for abundance over time.

Results

Distribution and Abundance Estimates

Most sightings of blue whales were in the central part of the survey area, between about 26 and 33°S, although blue whales were sighted farther north and farther south (Fig. 1). The linear distance traveled by the survey vessel was 8354 km, within an area of 546,900 km^2. The selected detection function was a half-normal function with a truncation distance of 5.6 km (3 nautical miles) (Fig. 2), which yielded an estimated effective strip half-width of 2.8 km (1.5 nautical miles). Thus, the area effectively searched covered about 8.5% of the study area. The model-based estimate of whale abundance in the survey area (Fig. 3), excluding areas covered during transit legs, was 303 (95% CI 176–625).

Preliminary Population Model

Total catches were 4288 from Chile alone and 5782 from the southeastern Pacific. The southeastern Pacific estimate is similar to a previous estimate of 5878 (Van Waerebeek et al. 1997). Except for a gap during World War II (1939–1944), catches levels were consistent from the 1910s to the 1960s (Fig. 4).

Minimum population trajectories from the logistic model (Fig. 4) showed that abundance declined consistently from pre-exploitation abundance (K) of 2000–6200 between the early 1900s and 1940, stabilized or increased during World War II, and then declined greatly in the 1950s and 1960s, at which point whaling ended and the population stabilized or increased from the 1970s to the present. When we assumed our minimum abundance estimate applied to the entire population, the population was at a minimum of 5–18% of pre-exploitation levels in 1997–1998 under the Chilean catch assumption and at 4–14% of pre-exploitation levels under the southeastern Pacific catch assumption (Fig. 5). These sample trajectories represent minimum abundances because the 1997–1998 abundance estimate referred to only a portion of the total population.

Discussion

Our abundance estimate and population trajectories for Chilean blue whales allowed us to compare their current status with the status of Antarctic blue whales. Although the survey covered much of the blue whale habitat within Chilean waters, we know the survey did not cover the full geographic extent of the population. Consequently, our

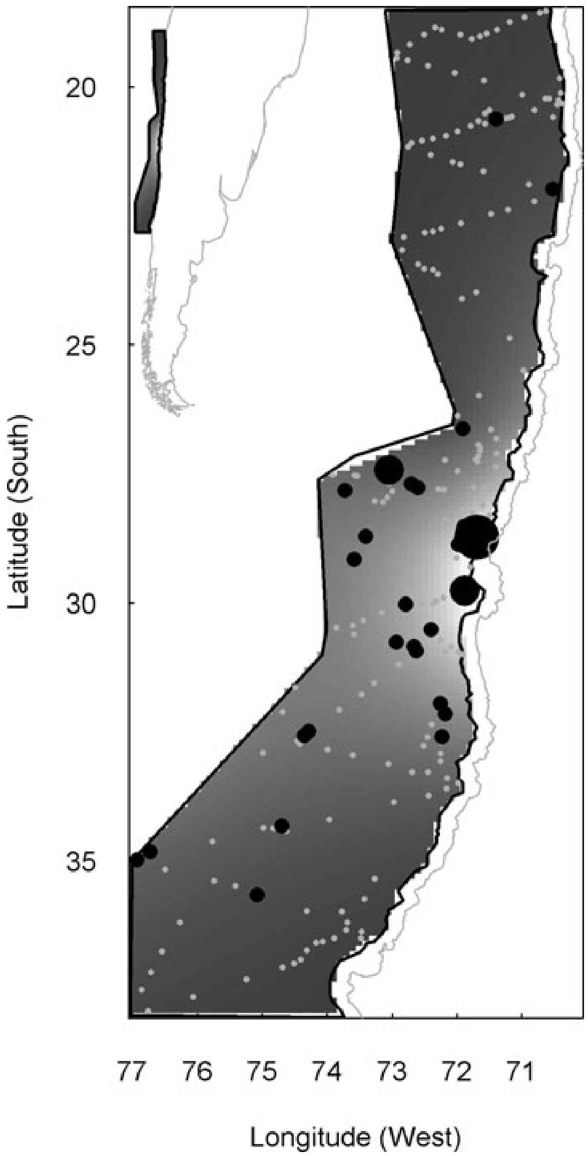

Figure 3. Predicted density surface from the spatial model of blue whale density in the survey region (small gray circles, survey effort by segment; filled black circles, whale sightings [scaled by pod size = 1–3]; light gray shading, highest densities).

results place only a lower limit on the current abundance of the population (303, 95% CI 176–625).

Comparison of the current abundance of Chilean blue whales (minimum of 4–18% of pre-exploitation levels) with the current abundance of Antarctic blue whales sheds light on which subspecies of blue whale occurs off the coast of Chile. Abundance of Antarctic blue whales overall and in their austral winter whaling grounds off Saldanha Bay and Durban, South Africa, was reduced by hunting to a low of <500 individuals in the early 1970s (<0.15% of pre-exploitation abundance), and Antarctic blue whales currently number about 2000 (<1% of pre-exploitation levels) (Branch & Butterworth 2001; Branch et al. 2004; Branch 2007). If Chilean blue whales were part of the Antarctic population, one would expect similar proportional changes in abundance. Instead, our current minimum estimates were much higher (>6.8% of pre-exploitation levels). Additionally, when we examined the proportion of blue whales among catches of all species in the IWC catch database, we found that this proportion decreased by >99% off Saldanha Bay (from 36.1% in 1913–1939 to 0.1% in 1952–1967) and by 97% off Durban (from 9.8 to 0.3%), but declined 67% off Chile (from 23.5 to 7.7%). In 1952–1967 blue whale catches were <6/year off Saldanha Bay and Durban, but were 130/year off Chile. Although catch estimates are affected by factors other than abundance, these data together with the comparison in current status provide strong evidence that Chilean blue whales and Antarctic blue whales belong to separate populations and perhaps subspecies. Further support for this division comes from length frequency data (Branch et al. 2007*a*), geographic separation of populations (Branch et al. 2007*b*), population genetics (Conway 2005; LeDuc et al. 2007), and acoustic detections of individuals (McDonald et al. 2006; Buchan et al. 2010). Our abundance estimate is a minimum because the survey did not cover the inshore waters of Chile, waters farther offshore than the economic exclusive zone, or waters south of 38°S (except for the transits) and north of 18°S in Ecuador and Peru. Subsequent findings of a major feeding and nursing ground in the Chiloé–Corcovado region, south and inshore of the survey area, indicate that a large number of blue whales were probably missed by the survey (Hucke-Gaete et al. 2003; Galletti Vernazzani et al. 2006). Given these findings, the total abundance of Chilean blue whales is probably substantially greater than our survey and model estimate. Furthermore, the SOWER survey was carried out during an El Niño event, when the distribution of blue whales may have extended well inshore of our study area.

Implied Status of Southeast Pacific Blue Whales

We fitted simple generalized logistic models to the catch series to assess the status (i.e., abundance relative to pre-exploitation levels) of blue whales in the region. If it is conservatively assumed that the baseline estimate applied to the entire population, then the population was at a minimum of 5–18% of pre-exploitation levels in 1997 under the Chilean catch assumption and at a minimum of 4–14% of pre-exploitation levels under the southeastern Pacific catch assumption. Nevertheless, the real status is likely better than these results indicate. As an estimate of southeastern Pacific blue whales, our results are further biased low because blue whales are present off Peru and Ecuador at the same time of the year (Donovan 1984; Ramirez 1985), but our model-based estimate did not take distribution farther to the north into

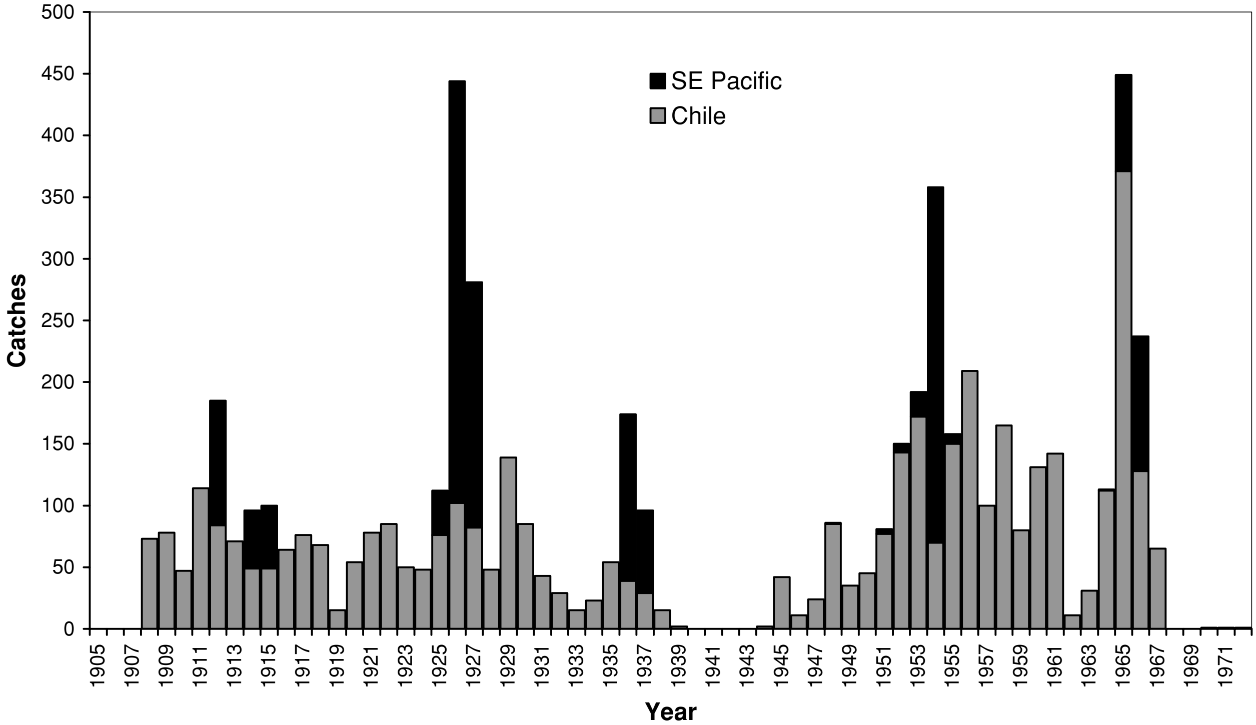

Figure 4. Historical catches of blue whales from Chilean waters (gray bars) and additional catches from broader regions within the southeastern Pacific (black bars, reported as either Peru or Chile/Ecuador/Peru).

account. It is not clear which catch series is the best to use for population modeling because the relation between the area from which catches from Chile, Peru, and Ecuador were taken and the area of the current survey remains unknown. Including Peru and Ecuador catches therefore resulted in further negative bias of the current status of the population of Chilean blue whales.

Abundance Estimates of a Rare Species

The problems we faced are inherent in the study of rare species; therefore, the solutions we developed are transferable to other species for which it is difficult to acquire large numbers of sightings from line-transect surveys. We illustrate these analytical problems with a blue whale case study, but the analytical methods we propose can also be used to study terrestrial and marine mammals, birds, fishes, reptiles, and plants (Thomas et al. 2010). There is a great deal of advice available for dealing with zero-inflated data (reviewed in Thompson [2004] and Ellison & Agrawal [2005]). There is less statistical advice on what to do when there will never be more than a few sightings, acoustic detections, or other observations to model. In cases where there is little information on geographic distribution prior to conducting a survey, adaptive sampling (whether formal or ad hoc) may be needed to increase sample size in the field whenever animals are seen. The trade-off, however, is that analyses will be complicated when rules of systematic, randomized, or adaptive sampling are violated. The key strength of our approach is its ability to produce an estimate of abundance from data that might otherwise only be used to calculate simple encounter rates along the surveyed track lines. If there are reasons to expect that spatial patterns in distribution will be similar in the future, then the resulting density surface can be used to design future surveys. By allocating more effort to regions with higher densities and less effort to regions with lower densities, future surveys become more cost-effective because for the same amount of survey effort, estimates should be more precise (Buckland et al. 2001). Perhaps most importantly, our variance estimator is a simple way to propagate the uncertainty associated with detection-function modeling to the final abundance estimate from a spatial model and avoids the problems associated with bootstrapping spatial models.

We believe that estimating abundance and evaluating status of rare or endangered taxa requires the combined skills of both field biologists and statisticians. Biologists can draw on their understanding of their study animal to guide collection of field data that best satisfies the assumptions that need to be made in statistical models. Statisticians, in turn, can offer analytical solutions for those cases in which, despite the best of intentions, sample size will always be low. In the best possible outcome, such collaborations would make field biologists more quantitative and get statisticians into the field. Although it is important to develop field protocols and analytical methods for cases in which sample size will be small

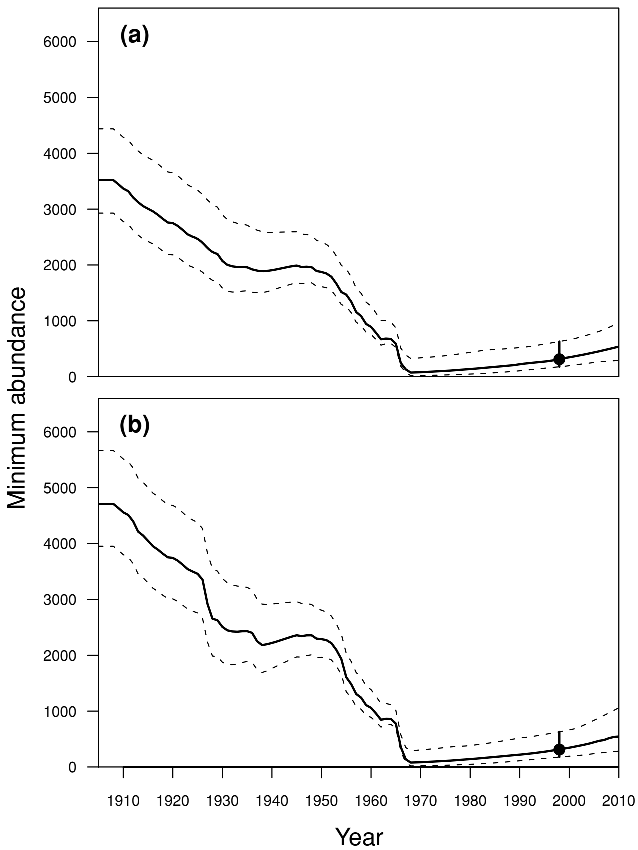

Figure 5. Projections of abundance of blue whales from logistic models fitted to the baseline survey estimate (depicted as a circle with 95% CI) with an intrinsic rate of increase (distribution of r = *6.20% [SE 2.90]) and (a) catches reported from shore stations in Chile (Chilean catch assumption) and (b) catches reported from the entire southeastern Pacific (Chile, Peru, Chile/Peru/Ecuador, i.e., southeastern Pacific catch assumption). The trajectories represent the minimum status of Chilean blue whales because the estimate applies to only a portion of the total population.*

(Jaramillo Legorreta et al. 1999), we do not offer false hope that a tentative abundance estimate generated from spatially biased samples will fit all purposes. If an application hinges on robust estimates of abundance, there is no substitute for good survey design (Thomas et al. 2007) coupled with appropriate statistical analyses, whether the methods are design based or model based. Ultimately, surveys and analyses such as the one presented here may be as much about managing expectations as they are about science.

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Literature Cited

Aguayo, L. A. 1974. Baleen whales off continental Chile. Pages 209–217 in W. E. Schevill, editor. The whale problem: a status report. Harvard University Press, Cambridge, Massachusetts.

Barlow, J., T. Gerrodette, and G. Silber. 1997. First estimates of vaquita abundance. Marine Mammal Science **13**:44–58.

Branch, T. A., and D. S. Butterworth. 2001. Estimates of abundance south of 60°S for cetacean species sighted frequently on the 1978/79 to 1997/98 IWC/IDCR-SOWER sighting surveys. Journal of Cetacean Research and Management **3**:251–270.

Branch, T. A., K. Matsuoka, and T. Miyashita. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. Marine Mammal Science **20**:726–754.

Branch, T. A. 2007. Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. Journal of Cetacean Research and Management **9**:87–96.

Branch, T. A., E. M.N. Abubaker, S. Mkango, and D. S. Butterworth. 2007*a*. Separating southern blue whale subspecies based on length frequencies of sexually mature females. Marine Mammal Science **23**:803–833.

Branch, T. A., et al. 2007*b*. Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. Mammal Review **37**:116–175.

Branch, T. A., and Y. A. Mikhalev. 2008. Regional differences in length at sexual maturity for female blue whales based on recovered Soviet whaling data. Marine Mammal Science **24**:690–703.

Branch, T. A., Y. A. Mikhalev, and H. Kato. 2009. Separating pygmy and Antarctic blue whales using long-forgotten ovarian data. Marine Mammal Science **25**:833–854.

Buchan, S. J., L. E. Rendell, and R. Hucke-Gaete. 2010. Preliminary recordings of blue whale (*Balaenoptera musculus*) vocalizations in the Gulf of Corcovado, northern Patagonia, Chile. Marine Mammal Science **26**:451–459.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Estimating abundance of biological populations. Oxford University Press, New York.

Candy, S. G. 2004. Modelling catch and effort data using generalised linear models, the Tweedie distribution, random vessel effects and random stratum-by-year effects. CCAMLR Science **11**: 59–80.

Clarke, C., A. Aguayo, and S. Basulto. 1978. Whale observation and whale marking off the coast of Chile in 1964. The Scientific Reports of the Whales Research Institute, Tokyo **30**:117–177.

Conway, C. A. 2005. Global population structure of blue whales, *Balaenoptera musculus ssp.*, based on nuclear genetic variation. PhD dissertation. University of California, Davis.

Donovan, G. P. 1984. Blue whales off Peru, December 1982, with special reference to pygmy blue whales. Reports of the International Whaling Commission **34:**473–476.

Ellison, A. M., and A. A. Agrawal. 2005. The statistics of rarity. Ecology **86:**1079–1080.

Evans, P. G.H., and P. S. Hammond. 2004. Monitoring cetaceans in European waters. Mammal Review **34:**131–156.

Findlay, K., et al. 1998. 1997/1998 IWC-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) blue whale cruise, Chile. Paper SC/50/Rep2. International Whaling Commission, Cambridge, United Kingdom.

Galletti Vernazzani, B., C. Carlson, E. Cabrera, and R. L. Brownell Jr. 2006. Blue, sei and humpback whale sightings during 2006 field season in northwestern Isla de Chiloe, Chile. Paper SC/58/SH17. International Whaling Commission, Cambridge, United Kingdom.

Hedley, S. L., S. T. Buckland, D. L. Borchers. 1999. Spatial modelling from line transect data. Journal of Cetacean Research and Management **1:**255–264.

Hedley, S. L., and S. T. Buckland. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological and Environmental Statistics **9:**181–199.

Hucke-Gaete, R., L. P. Osman, C. A. Moreno, K. P. Findlay, and D. K. Ljungblad. 2003. Discovery of a blue whale feeding and nursing ground in southern Chile. Biology Letters **271:**S170–S173.

Ichihara, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. Pages 79–111 in K. S. Norris, editor. Whales, dolphins, and porpoises. University of California Press, Berkeley.

IUCN (International Union for Conservation of Nature). 2001. IUCN Red List categories and criteria: version 3.1. Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.

Jaramillo Legorreta, A. M., L. Rojas Bracho, and T. Gerrodette. 1999. A new abundance estimate for vaquitas: first step for recovery. Marine Mammal Science **15**: 957–973.

Joergensen, B. 1987. Exponential dispersion models. Journal of the Royal Statistical Society B **49:**127–162.

LeDuc, R. G., A. E. Dizon, M. Goto, L. A. Pastene, H. Kato, S., Nishiwaki, C. A. LeDuc, and R. L. Brownell. 2007. Patterns of genetic variation in Southern Hemisphere blue whales and the use of assignment test to detect mixing on the feeding grounds. Journal of Cetacean Research and Management **9:**73–80.

Marques, F. F. C., and S. T. Buckland. 2003. Incorporating covariates into standard line transect analyses. Biometrics **59:**924–935.

McArdle, B. H. 1990. When are rare species not there? Oikos **57:**276–277.

McDonald, M. A., J. A. Hildebrand, and S. L. Mesnick. 2006. Biogeographic characterization of blue whale song worldwide: using song to identify populations. Journal of Cetacean Research and Management **8:**55–65.

Punt, A. E., and C. Allison. 2010. Appendix 2. Revised outcomes from the Bayesian meta-analysis, Annex D: report of the sub-committee on the revised management procedure. Journal of Cetacean Research and Management **11**(Suppl. 2):129–130.

Ramírez, P. 1983. Capturas y observaciones de la ballena azul *Balaenoptera musculus*, L., en Paita-Perú 1961–1966 y 1975–1982. Revista de la Comisión Permanente del Pacífico Sur **13:**97–102.

Ramirez, P. A. 1985. Peru. Progress report on cetacean research, October–December 1983. Reports of the International Whaling Commission **35:**176–177.

Seber, G. A.F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Edward Arnold, London.

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

Thomas, L., R. Williams, and D. Sandilands. 2007. Designing line transect surveys for complex survey regions. Journal of Cetacean Research and Management **9:**1–13.

Thompson, W. L., editor. 2004. Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters. Island Press, Washington, D. C.

Van Waerebeek, K., L. A. Pastene, J. Alfaro-Shigueto, J. L. Brito, and D. Mora-Pinto. 1997. The status of the blue whale *Balaenoptera musculus* off the west coast of South America. Paper SC/49/SH9. International Whaling Commission, Cambridge, United Kingdom.

Williams, R., and L. Thomas. 2009. Cost-effective abundance estimation of rare animals: testing performance of small-boat surveys for killer whales in British Columbia. Biological Conservation **142:**1542–1547.

Williams, R., S. Hedley, and P. S. Hammond. 2006. Modelling distribution and abundance of Antarctic baleen whales using ships of opportunity. Ecology and Society **11**: http://ecologyandsociety.org/vol11/iss1/art1/

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall-CRC, Boca Raton, Florida.

Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society B **70:**495–518.

Wood, S. N., M. V. Bravington, and S. L. Hedley. 2008. Soap film smoothing. Journal of the Royal Statistical Society B **70:**931–955.

Zerbini, A. N., P. J. Clapham, and P. R. Wade. 2010. Assessing plausible rates of population growth in humpback whales from life-history data. Marine Biology **157:**1432–1793.