Estimating gray whale abundance from shore-based counts using a multilevel Bayesian model

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ABSTRACT

Counts of southbound migrating whales off California form the basis of abundance estimation for the eastern North Pacific stock of gray whales (*Eschrichtius robustus*). Previous assessments (1967-2007) have estimated detection probability (p) from the detection-non detection of pods by two independent observers. However, tracking distinct pods in the field can be difficult for single observers; resulting in biased estimates of pod sizes that needed correcting, and matching observations of the same pod by both observers involved key assumptions. Due to these limitations, a new observation approach has been adopted wherein a paired team of observers work together and use a computerized mapping application to better track and enumerate distinct pods and tally the number of whales passing during watch periods. This approach has produced consistent counts over four recently monitored migrations (2006/7, 2007/8, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method. To evaluate p and estimate abundance in these four years, we compared counts from two independent stations of paired observers operating simultaneously using a hierarchical Bayesian "*N*-mixture" model to simultaneously estimate p and abundance without the challenge of matching pods between stations. The overall average detectability p_o= 0.80 (95% Highest Posterior Density Intervals [HPDI] =0.75-0.85), which varied with observation conditions, observer effects and changes in whale abundance during the migration. Abundance changes were described using Bayesian model selection between a parametric model for a Normally distributed common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend. The summed estimates of migration abundance ranged from 17,820 (95% HPDI = 16,150-19,920) in 2007/8 to 21,210 (95% HPDI = 19,420-23,230) in 2009/10, consistent with previous estimates and indicative of a stable population.

INTRODUCTION

Counts of southbound migrating whales at Granite Canyon, California, form the basis of abundance estimation for the eastern North Pacific stock of gray whales (*Eschrichtius robustus*). In 23 years, between 1967 and 2007, counts of the number of observed pods have been rescaled for pods undetected during watch periods, pods passing outside watch periods, and night travel rate (Buckland *et al*., 1993; Laake *et al*., 1994; Buckland and Breiwick, 2002; Hobbs *et al*., 2004; Rugh *et al*., 2005; Laake *et al*., 2012). Notably, these previous assessments have estimated detection probability (p) from the detection-non detection of pods by independent observers using an analytical mark-recapture approach. However, tracking distinct pods in the field was difficult for a single observer using just hand-recorded entries onto a paper data form. As a result, matching observations of the same pod by both observers involved key (and untestable) assumptions, and limited observations of a given pod required corrections for bias in pod size estimation (Laake *et al*., 2012).

Due to these limitations, a new observation approach has been adopted wherein a paired team of observers work together and use a computerized mapping application to help better track distinct pods and tally the number of whales passing during watch periods. This approach enables more repeated observations of each pod, leading to larger (and presumably less biased) estimates of pod size (Durban *et al*., 2010), and has produced consistent counts over four recently monitored migrations (2006/7, 2007/8, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method (Durban *et al*., 2011). To evaluate p for this new approach, here we compared watch period counts from two independent stations of paired observers operating simultaneously during two of the four years (2009/10 and 2010/11), using a hierarchical Bayesian "*N*-mixture" model (Royle, 2004) to simultaneously estimate the probability of detection and abundance in all four years, without the challenge of matching pods between stations.

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METHODS

Data Samples

Counts of gray whales were conducted from shore-based watch stations at Granite Canyon, California, during the 2006/7, 2007/8, 2009/10 and 2010/11 southbound migrations (Table 1). Counts were made by rotating teams of observer pairs using naked eye aided by 7x50 binoculars; the primary observer in the pair kept continual visual watch while the secondary observer served as a data recorder but also kept watch and assisted with tracking already identified pods whenever possible. Each observer had one 90 min shift as primary observer, followed by a second 90 min shift as secondary observer, and then a 90 min break. Sightings were entered into a real-time data logging PC program, which had a mapping screen to help track repeated sightings of the same pod. The map projected the likely movement tracks (and error ellipses) of the pods using predicted swimming speeds (1.44 - 1.95 ms^{-1}), allowing re-sightings and new sightings to be queried. Up to six 1.5-hour watch periods were used to cover daylight hours from 07:30 to 16:30, during which the observers recorded passing whales and environmental conditions, specifically visibility (subjectively categorized from 1 to 6 for excellent to useless) and sea state (Beaufort scale). To control for weather conditions and for consistency with previous abundance estimations, we only used counts during watch periods with acceptable weather conditions throughout their entire duration, specifically visibility code <5 (excellent to fair) and Beaufort Scale <5.

Table 1: The number of whales recorded during the southbound gray whale surveys from 2006/7 to 2010/2011. Data are the total counts, hours and distinct days for watches during acceptable observation conditions.

Migration	North Station			South Station		
	Dates	Whales	Hours (days)	Dates	Whales	Hours (days)
2006/7	02 Jan–03 Feb	2691	204 (34)	-	-	-
2007/8	02 Jan–09 Feb	2079	202.5 (34)	-	-	-
2009/10	30 Dec–19 Feb	2034	246 (43)	11 Jan-06 Feb	1551	105 (20)
2010/11	03 Jan–18 Feb	2885	265 (45)	10 Jan-04 Feb	1754	141 (24)

Estimating Detection Probability

We used the "*N*-mixture" approach (Royle, 2004) to simultaneously estimate detection probability p_{ijt} and abundance N_{jt} for each watch period j in each year t, based on the total aggregated counts n_{ijt} of passing whales recorded by each of $i = 1:2$ watch stations in each period. The observed counts n_{ijt} were modeled as a binomial outcome conditional on the unknown true number of whales passing N_{jt} and the detection probability p_{ijt} with hierarchical models assumed to describe variability in both N and p (e.g. Chelgren et al. 2011). The power to estimate detectability was achieved by comparing gray whale counts from two independent stations of paired observers operating simultaneously during two years (2009/10 and 2010/11) from watch stations that were positioned 35m apart at the same elevation (22.5m) above sea level. In 2009/10 counts were compared from the two watch stations operating simultaneously during 70 1.5-hour watch periods with acceptable weather conditions, covering 20 different days of the migration; in 2010/11 simultaneous counts were available from 94 watch periods over 24 different days (Table 1). However, we could also extrapolate detectability for all monitored watch periods in each of the four years based on the fitted model for detectability. In order to accomplish this, the counts for the south watch station were treated as zero-inflated binomial outcomes, with the binomial probability specified as a function $u_{ijt} p_{ijt}$ where $u = 1$ or 0 to indicate whether or not count data were actually collected from that station, thus ensuring that structural zero counts from periods without a second watch did not contribute to the likelihood for estimation of p or N.

Consistent with Laake *et al.* (2012), the model for detectability incorporated fixed effects β for visibility (VS) and Beaufort Scale (BF), as well as random effects associated with each observer o in 1:OB observers. We selected for the inclusion of these effects using Bayesian model selection with stochastic binary indicator variables g to switch

each of the three possible effects either in or out of the model depending on their relevance to the observed data (Kuo and Mallick, 1998):

$$\text{logit } (p_{ijt}) = \text{logit}(p_{o}) + g^{bf}\beta^{bf}\,\text{BF}_{jt} + g^{v}\beta^{vs}\,\text{VS}_{jt} + g^{ob}\beta^{ob}_{ijt=o}$$

where p_{o} is the overall average detection probability, assigned a Uniform(0,1) prior distribution, and logit(p_{o}) = ln($p_{o}/1-p_{o}$). Centered around this overall average, each of the fixed effects β^{bf} and β^{bf} was assigned a Normal distribution with mean zero and standard deviation 10 to allow non-zero effects to emerge. The random effect for each observer $\beta^{ob}_{o=1:n.obs}$ was drawn from a Normal distribution with mean zero and standard deviation σ^{ob}~Uniform(0,10). Each of the binary indicator variables, g, was assigned a Bernoulli(0.5) distribution to specify equal probability of inclusion or not of the effect in the model.

Fitting Migration Curves
The *N*-mixture approach also accounted for variation in *p* relative to changes in *N* (latent watch period abundances) during the migration. So, some power to estimate detectability was achieved by assuming a model for changes in watch period abundance over the course of the migration. We adopted a Poisson distribution $N_{jt} \sim \text{Poisson}(\lambda_{jt})$ as a hierarchical prior for the distribution of abundances, and specified a model for the Poisson mean λ in terms of the number of whales passing each day (*d*), with an offset for the effort duration of each watch period, E_{jt} in decimal days (e.g. Laake *et al.,* 2012),:

$$\log(\lambda_{jt}) = \log(E_{jt}) + \text{model}_{d(j)t}$$

$$\text{model}_{dt} = z_{dt}\text{Common}_{dt} + (1-z_{dt})\,\text{Specific}_{dt}$$

Days were specified as d= 0 to D_{t}. In all four years *t* we used D_{t} = 90, where days were counted from 12:00am on 1 December, and we added an abundance of 0 whales passing for day 0 and D_{t} to anchor the fitted model when we assumed whales did not pass (following Buckland et al. 1993). Estimates from the remaining days were derived from a mixture (or compromise) of two competing models ("Common" and "Specific"; e.g. Li *et al*., 2012) describing changes in abundance across each annual migration. The model contributing each daily estimate was indicated using stochastic binary indicator variables z_{dt}, each assigned a non-informative Bernoulli(0.5) prior distribution.

For the "Common model", we assumed a typical trend in abundance throughout each annual migration (e.g. Buckland *et al*., 1993), with abundance changes assumed Normally distributed around a migration mid-point, with a Normal distribution specified as a quadratic function of days, on the log scale:

$$\text{Common}_{dt} = a_{t} + b_{t}*d_{t} + c_{t}*d_{t}^{2}$$

where the mid-point of the migration curve for each year *t* was derived by $-b_{t}/2a_{t}$. This assumed common migration curve allowed information to be "borrowed" across years when needed, specifying association across years to strengthen inference about migration curves in years with relatively sparse counts. However, we specified each of the curve parameters a_{t}, b_{t} and c_{t} to be drawn from hierarchical Normal distributions with means μ^{a}, μ^{b}, μ^{c}~ N(0, 10) and standard deviations σ^{a}, σ^{b}, σ^{c} ~Uniform(0,10); hyper-parameters that were common across years, rather than assuming that the parameters themselves were constant. This random effects formulation allowed the timing, level and extent of the Normal migration curve to vary annually around the general pattern, if supported by the data.

Although it is likely that there is a typical pattern to the migration, we acknowledged that abrupt departures may occur in any particular year. To incorporate unusual patterns, we allowed for the selection of an alternative "Specific" migration model: a semi-parametric model that estimated the time trends independently for each year (e.g. Laake *et al*., 2012). We adopted a method in which the shape of the relationship of abundance across days was determined by the data without making any prior assumptions about its form, by using penalized splines (Ruppert, 2002). Following Crainiceanu *et al*. (2005) we used a linear (on the log scale) penalized spline to describe this relationship:

$$\text{Specific}_{dt} = S_0 + S_1 * d_t + \sum_{k=1}^{K} s_k (d_t - \kappa_k)$$

Where S_0, S_1, s_1,…,s_k were regression coefficients to be estimated and $\kappa_1 < \kappa_2 < ... < \kappa_k$ were fixed knots. We used K = 15 knots; a relatively large number to ensure the desired flexibility, and let k_k be the sample quantile of d's corresponding to $k/K+1$. To avoid overfitting, we penalized the s's by assuming that the coefficients of $(d_t - \kappa_k)$ were Normally distributed random variables with mean 0 and standard deviation σ^s~Uniform(0,10). The parameters S_0, S_1 were modeled as fixed effects with Normal(0, 10) prior distributions .

Estimating Migration Abundance

The multi-level model was fit using Markov Chain Monte Carlo (MCMC) sampling using the WinBUGS software (Lunn *et al.,* 2000). Inference was based on 15,000 repeated draws from the posterior distribution of each model parameter conditional on the observed data, following MCMC convergence over 5000 iterations determined from three independent chains begun from over-dispersed starting values (Brooks and Gelman, 1998). This sampling approach allowed uncertainty to be propagated across levels of the model. Notably, estimates of parameter values across MCMC iterations were used to estimate the probability of inclusion of covariate effects in the model for detectability, given by the posterior probability p(g=1) of each indicator variable g. Similarly using between-model moves indicated by z_{dt} , the posterior probability of conforming to the common trend model was calculated, and inference about abundance on each day was based on a weighted compromise between the competing models.

The total number of whales passing during each migration was estimated by summing the expected value from the model-averaged number of whales passing each day from time 0 to D_t (e.g. Laake *et al*., 2012). These estimates were then rescaled to account for the differential passage rate at night (Perryman *et al*., 1999), based on the 9-hour day multiplicative correction factor of Rugh *et al*. (2005). Specifically, we applied a constant nighttime correction factor that was assumed to be a Normally distributed fixed effect with mean of 1.0875 and standard deviation of 0.037.

RESULTS

The overall average detectability p_o=0.80 (95% Highest Posterior Density Intervals [HPDI] =0.75-0.85), which was modified by observation conditions and observer effects (Table 1). The posterior distribution for the effect of sea state, measured using the Beaufort scale β^{bf}, largely overlapped with zero and there was therefore low support for including this effect in the model with p(g^{bf}=1)= 0.004. In contrast, there was a relatively strong negative effect of visibility on detectability (higher visibility code=lower visibility=lower detectability), with the entire distribution for β^{vs} falling below zero [p(g^{vs}=1)=1]. There was also support for inclusion of observer effects [p(g^{bs}=1)=1], with both positive and negative effects reflecting relatively high and low counts by different observers. A total of 35 different observers were used over 4 years between North and South stations; 15/35 counted in multiple years (2 years = 7, 3 years =4, 4 years=4). The Posterior medians for observers' effects ranged from -0.59 to 0.80, but only five observer effects (all positive) had posterior distributions that did not include zero, and the majority of observer effects overlapped significantly with zero.

Table 2: Parameters of models for detectability, *p*. All estimates are presented as the 0.025,0.50, 0.975 highest density probability intervals of the posterior probability distribution, plus the probability of inclusion in a model (if tested), given by the posterior probability p(*g*=1) of each indicator variable *g*. Observers are arbitrarily numbered, differently for each year.

	2006/07	2007/08	2009/10	2010/11
Detection model				
p_o	0.75, **0.80**, 0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85
β^{bf} [p(g^{bf}=1)]	-19.34, **-0.003**, 19.98 [0.004]	-19.34, **-0.003**, 19.98 [0.004]	-19.34, **-0.003**, 19.98 [0.004]	-19.34, **-0.003**, 19.98 [0.004]
β^{vs} [p(g^{vs}=1)]	-0.38, **-0.30**, -0.20 [1]	-0.38, **-0.30**, -0.20 [1]	-0.38, **-0.30**, -0.20 [1]	-0.38, **-0.30**, -0.20 [1]
σ^{ob} [p(g^{bs}=1)]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]
Observer 1	-0.36, **0.02**, 0.49	0.03, **0.37**, 0.81	-0.42,**-0.24**, 0.06	-0.13, **0.08**, 0.30
Observer 2	0.03, **0.37**, 0.81	-0.78, **-0.03**, 0.70	-0.09, **0.30**, 0.81	-0.36, **0.02**, 0.46
Observer 3	-0.24, **-0.07**, 0.11	-0.24, **-0.07**, 0.11	0.03, **0.37**, 0.81	-0.42, **-0.24**, 0.06
Observer 4	-0.42, **-0.01**, 0.49	-0.42, **-0.24**, 0.06	-0.13, **0.08**, 0.30	-0.25, **0.01**, 0.29
Observer 5	-0.04, **0.14**, 0.35	-0.13, **0.08**, 0.30	-0.24, **-0.07**, 0.11	0.16, **0.43**, 0.73
Observer 6	0.06, **0.42**, 0.83	-0.04, **0.14**, 0.35	-0.27, **-0.06**, 0.18	-0.04, **0.14**, 0.35
Observer 7	-0.17, **0.11**, 0.46	-0.18, **0.19**, 0.61	-0.04, **0.14**, 0.35	-0.50, **-0.13**, 0.26
Observer 8	-0.39, **-0.16**, 0.07	-0.17, **0.11**, 0.46	0.12, **0.33**, 0.59	-0.39, **-0.16**, 0.07
Observer 9	0.12, **0.33**, 0.59	0.12, **0.33**, 0.59	-0.25, **0.01**, 0.29	-0.09, **0.23**, 0.60
Observer 10	-	-0.39, **-0.16**, 0.07	-0.08, 0.26, 0.64	-0.27, **-0.06**, 0.18
Observer 11	-	-	-0.71, **-0.43**, 0.13	0.31, **0.80**, 1.46
Observer 12	-	-	-0.66, **-0.37**, 0.07	-0.54, **-0.29**, 0.04
Observer 13	-	-	-0.42, **0.00**, 0.49	-0.75, **-0.22**, 0.33
Observer 14	-	-	-0.63, **-0.13**, 0.40	0.12, **0.33**, 0.59
Observer 15	-	-	0.31, 0.**80**, 1.46	-0.73, **-0.29**, 0.14
Observer 16	-	-	-0.18, 0.19, 0.61	-0.18, **0.19**, 0.61
Observer 17	-	-	0.16, **0.43**,0.72	-0.70, **0.02**, 0.76
Observer 18	-	-	-0.39, **-0.16**, 0.07	-0.63, **-0.13**, 0.40
Observer 19	-	-	-0.22, **0.22**, 0.72	-0.83, **-0.59**, 0.36
Observer 20	-	-	-0.28, **0.14**, 0.59	-0.24, **-0.07**, 0.11
Observer 21	-	-	-0.18, **0.28**, 0.83	-0.21, **0.11**, 0.47
Observer 22	-	-	-	-1.05, **-0.49**, 0.06

Detectability also varied with changes in whale abundance during the migration, as shown by the extent of extrapolation from the daily summed counts (effort adjusted) to the estimated daily abundances (Figure 1). Detectability declined with increasing abundance, with a greater proportion of whales estimated to be missed as more whales passed during busy watch periods. In general, changes in abundance during the migrations were adequately described by a Normal curve over time, but there was greater uncertainty in the tails of the distribution resulting from generally sparse coverage. The Normal trend was useful for comparing migration timing: the median of the curve midpoints was 53.5 days since December 01 (23-24th of January), ranging between 49 and 57 days. However, there were some notable deviations from the Normal trend, with estimates from the year-specific non-parametric trend model being favored for some days in each of the four years. In particular, there was a high probability in favor of the Specific model [p(*z*=0)>0.75] on 9 days in 2006/7, 9 days in 2007/8, 16 days in 2009/10 and 11 days in 2010/11, representing key departures from the Normal migration trend. The summed (model-averaged) estimates of migration abundance ranged from a posterior median of 17,820 (95% HPDI = 16,150-19,920) in 2007/8 to 21,210 (95% HPDI = 19,420-23,230) in 2009/10, consistent with previous estimates (Figure 2). These new estimates were also relatively precise with coefficients of variation (CV = Posterior Standard Deviation /

Posterior Median) ranging from 0.04 to 0.06 (median= 0.05), but nonetheless the 95% HDPI's of all four estimates overlapped.
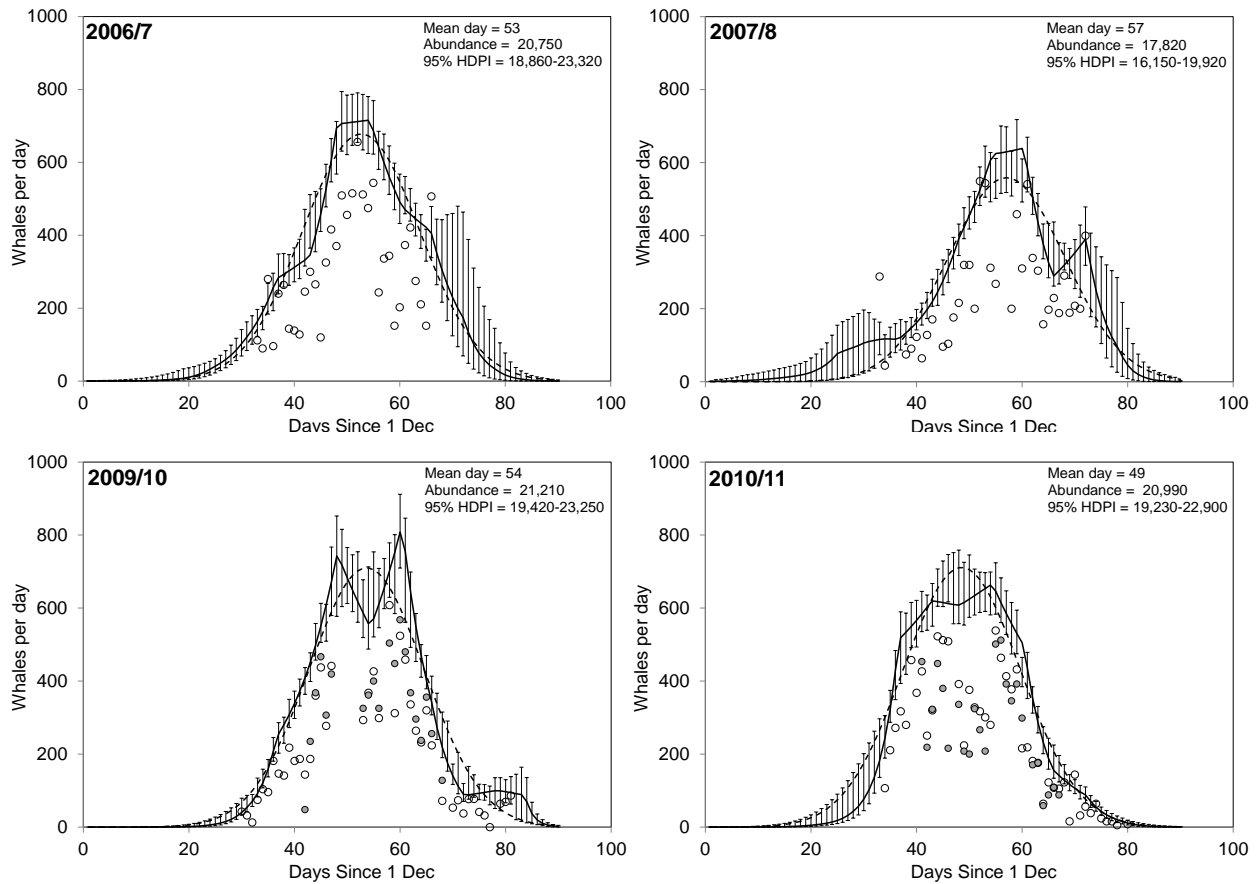
Figure 1. Observed whale passage rates expressed as total counts per day/ proportion of day observed (circles) and fitted migrations models (lines) for the four southbound gray whale migration counts from 2006/7 to 2010/11. Solid circles represent counts from a second watch station, when operating. The broken line represents a hierarchical Normal model for migration and the solid line represents a semi-parametric model of penalized splines; the abundance estimate for each day (95% highest posterior density interval shown by vertical lines) is a model averaged compromise between the migration models, and these were summed to estimate the overall abundance for the migrations.
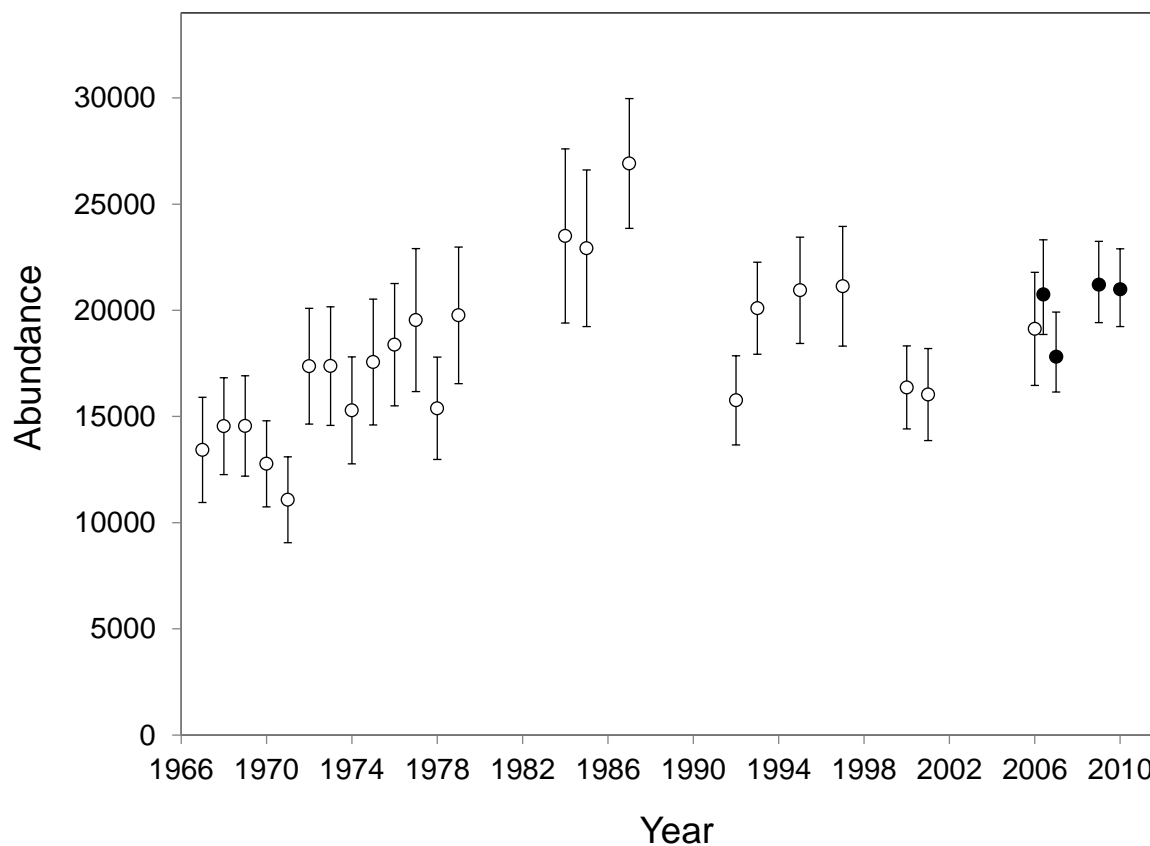
Figure 2: Gray whale abundance estimates for each of 23 southbound migrations with an end year between 1967 and 2007 (open squares, with 95% confidence intervals; from Laake *et al.,* 2012) together with the four recent migrations reported here (closed squares, with 95% highest posterior density intervals).

DISCUSSION

The new counting method adopted here was intended to reduce reliance on the ability of single observers acting independently to record and track distinct whale groups. By adopting teams of paired observers working together, with the benefit of a real-time computerized tracking and visualization tool, this approach has proved successful in increasing detection probability (Durban *et al*., 2011) and also reducing variability in detections due to observer effects. Although still present, the magnitude of observer effects estimated from the new counts (Table 2) was generally not as great as those apparent with the traditional counting approach (see Laake *et al*., 2012, Table 7). Furthermore, our method for estimating detectability has departed from the mark-recapture approach of matching detections and non-detections of specific pods by independent observers. Instead we based inference on total watch period counts that were not sensitive to differential lumping and splitting of pods by observers, and avoided the assumptions required to match observed pods between pairs of observers. Instead, we have shown how tallied watch period counts from two (or more) observer pairs counting simultaneously can lead to similar inference when analyzed using the *N*-mixture approach (Royle, 2004).

This "*N*-mixture" approach has been successfully used to estimate abundance and detectability from replicate count data in cases where it has not been possible to match repeat sightings of individuals (e.g. Kery *et al*., 2005; Joseph *et al*., 2009, Chelgren *et al*., 2011). It allows models for linking detectability to key covariates, as in previous gray whale assessments (e.g. Laake *et al*., 2012), but notably also accounts for variation in *p* relative to changes in abundance during the migration. Previously, two contrasting approaches have been used to model changes in

abundance over the course of the annual gray whale migration: either by assuming a parametric model to determine the shape of the migration curve (Buckland *et al*., 1993) or by fitting a non-parametric smoother to allow the data to determine the trend in abundance over time (Laake *et al*., 2012). Here we drew on elements of both these approaches in a flexible framework using Bayesian model selection between a parametric model for a common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend.

The abundance estimates produced for 2006/7, 2007/8, 2009/10 and 2010/11 were internally consistent, consistent with previous estimates and indicative of a stable population (Figure 2). The 95% HDPI's of all four estimates overlapped, and there was substantial overlap between the 95% HDPI from the 2006/7 estimate with the 95% confidence intervals of the estimate for the same migration produced using the previous counting and estimation approach (Laake et al. 2012). Further, our estimates are very similar to the predictions of Punt and Wade (2012) based on assessment models for the full time series; their baseline model prediction for 2009/10 had 90% posterior density intervals ranging from 17,726 to 23,247; the posterior distribution for our 2009/10 estimate was centered within these intervals at 21,210 (95% HPDI = 19,420 – 23,250). It is noteworthy that the estimates produced using our approach were relatively precise with CVs ranging from 0.04 to 0.06 (median= 0.05) in contrast to CVs ranging from 0.06 to 0.09 (median = 0.08) for the 23 previous estimates.

This consistency provides a level of confidence in our approach and resultant estimates, but nonetheless there are limitations to address. Despite our flexible approach for describing abundance trends throughout the migration, precise inference about the shape of the migration curve relies on count data being collected from throughout the migration time span. During at least 3 / 4 years reported here, count data were sparse (or non-existent) during the tails of the migration, resulting in uncertainty over the shape of the abundance curve. While this uncertainty was propagated into inference about overall abundance in our Bayesian inference using MCMC sampling, the resulting imprecision will ultimately constrain power to detect between-year changes in migration patterns and abundance.

Previous work has shown that the new counting approach produces estimates of pod size that are typically larger (and presumably less biased) than the traditional counting approach (Durban *et al*., 2010), likely because the computerized tracking software facilitates more repeated observations of the same groups. In fact, we have assumed here that estimates of pod size using this observation approach are effectively unbiased and have not been rescaled to tally watch period counts. This is an assumption that remains to be tested, but suitable calibration experiments are difficult to design and implement, particularly due to the inherently subjective differences between observers in lumping and splitting whales to define groups. Similarly, although observer effects have been accommodated in the model for detectability, it is clear that too many observers (35 in total) counted too infrequently to allow precise parameterization of their relative effects on detectability in many cases. This will have resulted in further imprecision.

Although there may be field protocols that could be adapted to address these limitations within the current approach, we recommend further modernization of the observation process. Specifically, more accurate information could be gleaned from observations recorded with high-definition video files to allow subsequent review and re-review, rather than relying on instantaneous assessment by visual observers. The use of infra-red sensors would further allow for 24-hour monitoring (e.g. Perryman *et al*., 1999) and provide greater coverage of the entire migration during acceptable weather conditions; automated blow detectors (e.g. Santhaseelan *et al*., 2012) can be developed to eliminate observer effects and standardize detectability to provide counts with minimal (and quantifiable) bias. These extensions would further serve to build a more robust and automated observation model to combine with the flexible abundance model for the migration process described in this paper.

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