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## Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales?

COLE C. MONNAHAN,<sup>1</sup> Quantitative Ecology and Resource Management, Box 352182, University of Washington, Seattle, Washington 98195, U.S.A.; TREVOR A. BRANCH and ANDRÉ E. PUNT, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195, U.S.A.

### ABSTRACT

Blue whales were targeted in the North Pacific from 1905–1971 and are listed as endangered by the IUCN. Despite decades without whaling, abundance estimates for eastern North Pacific (ENP) blue whales (*Balaenoptera musculus*) suggest little evidence for a recent increase. One possible reason is fatal strikes by large ships, which have affected populations of other cetaceans and resulted in mitigation. We used a population dynamics model to assess the trends and status of ENP blue whales, and the effects of ship strikes. We estimate the population likely never dropped below 460 individuals, and is at 97% of carrying capacity (95% interval 62%–99%). These results suggest density dependence, not ship strikes, is the key reason for the observed lack of increase. We also estimate future strikes will likely have a minimal impact; for example, an 11-fold increase in vessels would lead to a 50% chance the long-term population would be considered depleted. Although we estimate ship strike mitigation would have minimal impacts on population trends and status, current levels of ship strikes are likely above legal limits set by the U.S. The recovery of ENP blue whales from whaling demonstrates the ability of blue whale populations to rebuild under careful management.

Key words: blue whale, *Balaenoptera musculus*, ship strikes, recovery, eastern North Pacific, Santa Barbara Channel, status.

Blue whales (*Balaenoptera musculus*) are distributed throughout the world's oceans. From the early 1900s to the 1970s they were targeted by commercial whaling operations, and this depleted Antarctic blue whales (Branch *et al.* 2004) and likely other populations. The species as a whole is listed as endangered by the IUCN (Reilly *et al.* 2008). In the North Pacific, 9,773 blue whales were caught from 1905 to 1971 (Monnahan *et al.* 2014), and the population in the eastern North Pacific is considered a “depleted” and “strategic” population under the U.S. Marine Mammal Protection Act (MMPA; Carretta *et al.* 2012).

Although the International Whaling Commission (IWC) has formally considered only one population of blue whales in the North Pacific (Donovan 1991), there is

<sup>1</sup>Corresponding author (e-mail: colemonnahan@gmail.com).

evidence for a more complex population structure. Two populations in particular have been proposed: the eastern (ENP) and western (WNP) North Pacific blue whale populations, although some authors (Reeves *et al.* 1998) have speculated that up to five populations exist.

The main evidence for separate ENP and WNP populations is the difference in acoustic calls between whales found in the eastern and western North Pacific (Stafford *et al.* 2001) and significant differences in length between whales in the eastern and western North Pacific (Gilpatrick and Perryman 2008). The distinctiveness of the ENP population comes from demonstrated links among the eastern Tropical Pacific, Gulf of California, and Gulf of Alaska from satellite tags and photographic identifications (Mate *et al.* 1999, Calambokidis *et al.* 2009a, Bailey *et al.* 2010) and genetic links between blue whales in the Gulf of California and the west coast of the United States (Costa-Urrutia *et al.* 2013), although no genetic analyses have been performed on blue whales in other regions. Taken together, these studies provide evidence that a single population occupies the entire eastern North Pacific. While there is substantial evidence for the ENP population, the focus of our study, the population structure of the central and western North Pacific is less clear.

A series of abundance estimates for the ENP population from 1993–2008 (Calambokidis and Barlow 2004; Calambokidis *et al.* 2007, 2009b) show no clear increase in abundance, despite commercial whaling ending in 1971. One hypothesis for the observed pattern is density dependence, while another is continued sources of anthropogenic mortality that may be hindering the growth of the population.

The only known source of anthropogenic mortality to ENP blue whales is fatal collisions between whales and vessels (“ship strikes”; Carretta *et al.* 2012), although other sources, such as noise and chemical pollution, and fishery interactions may also impact them, and in a synergistic way. The most risky area for blue whales is the Santa Barbara Channel, where shipping lanes intersect with common feeding areas, leading to an average of 1.8 blue whale strikes reported per year in 2005–2010 (Redfern *et al.* 2013). In addition, two ship strike deaths were recorded off Washington State during 1980–2005 (Douglas *et al.* 2008).

These are all the known blue whale ship strikes recorded on the west coast of the United States during this period. However, these documented values likely underestimate actual ship strikes, because struck whales may go unreported or misidentified for a variety of reasons, or remain undetected since blue whale carcasses initially sink (Cassoff *et al.* 2011). For instance, a collision may only cause internal damage and go unrecognized as a ship strike, or the carcass could sink before being identified or noticed (Laist *et al.* 2001). A study on North Atlantic right whales (*Eubalaena glacialis*) estimated a 17% carcass detection rate (Kraus *et al.* 2005), and Redfern *et al.* (2013) applied this rate to Santa Barbara Channel blue whale ship strikes to estimate 10.6 blue whales struck per year, without adjusting for other sources of mortality (*e.g.*, Vanderlaan *et al.* 2009). Although the magnitude of ship strikes is uncertain, it is likely above the legal “Potential Biological Removal” (PBR) level of 3.1 whales per year (Carretta *et al.* 2012, Redfern *et al.* 2013). This has led to speculation that ship strikes may be limiting the growth of the ENP population and calls for further research into potential approaches for mitigation (Berman-Kowalewski *et al.* 2010, Redfern *et al.* 2013).

Blue whales are not the only cetacean species impacted by collisions with vessels, and a variety of monitoring and mitigation techniques have been proposed for other whale populations, such as onboard observers, remote sensing, passive acoustic monitoring to better detect and avoid whales, and Marine Protected Areas (Stark *et al.* 2003, Bearzi 2012). Speed restrictions and shifts in shipping lanes have been

implemented for critically endangered populations of other cetacean species, and were effective in reducing the risk of collisions for North Atlantic right whales (International Maritime Organization 2006, Vanderlaan and Taggart 2007, U.S. Federal Register 2008, Conn and Silber 2013). Voluntary speed restrictions were implemented in southern California, but have been ineffective in reducing vessel speeds (McKenna *et al.* 2012), while moving the shipping lanes in the Santa Barbara Channel would have a limited impact on the rate of blue whale and vessel interactions, because blue whales are evenly dispersed (Redfern *et al.* 2013). However, other proposed measures could reduce whale-vessel interactions in the future, and we aimed to broadly test the impact of hypothetical mitigation scenarios.

In this study we used one population dynamics model to estimate current growth with no assumptions about vessels and minimal assumptions about model structure. We used another model to estimate past, present, and future trends in abundance and status for ENP blue whales, and then test the ship-strike *vs.* density-dependence hypotheses for slowed growth. Finally, we quantified the potential impact of future ship strikes on status under different hypothetical mitigation scenarios.

## METHODS

We modeled vessel numbers, ship strikes, and the population dynamics of the ENP blue whale population from 1905 to 2050. We assumed negligible catches before 1905 because the available technology could not cope with their speed and size (Tønnessen and Johnsen 1982). The analyses were conducted within a Bayesian framework to incorporate informative biological information and assign probability distributions to parameters and derived quantities of interest.

### *Estimating Population Dynamics*

To estimate population growth over the period of published abundance estimates (1993–2008), without any assumptions about vessels, density dependence, or past dynamics, we fit a log-linear model:

$$\ln(N_y) = \ln(N_{1993}) + m(y - 1993) + \varepsilon_y \quad (1)$$

where  $N_{1993}$  is the estimated population size in the year of the first abundance estimate,  $m$  is an estimated growth rate term, and  $\varepsilon_y \sim N(0, \sigma_y^2)$  is the assumed error term. The log-linear model does not incorporate density dependence so it cannot be used to estimate population status.

To assess the past, present, and future trends in abundance, including the effect of ship strikes, we used a discrete theta-logistic model which has been presented to the IWC for other exploited cetacean populations (*e.g.*, Baker and Clapham 2004, Zerbini *et al.* 2006):

$$N_{y+1} = N_y + rN_y \left( 1 - \left( \frac{N_y}{K} \right)^\theta \right) - C_y - S_y, \quad (2)$$

where  $N_y$  is the population size in year  $y$ ,  $r$  is the intrinsic rate of growth,  $K$  is the carrying capacity parameter,  $\theta$  is a shape parameter that shifts the level of maximum

productivity,  $C_y$  is the catch, and  $S_y$  is the number of ship strikes, which are subtracted in the same way as the commercial catches, and whose estimation is detailed below.

Here we set  $\theta = 2.39$ , corresponding to maximum productivity at 60% of  $K$ , as is common practice for the IWC (e.g., Baker and Clapham 2004, Zerbini *et al.* 2006), and explored the sensitivity to this assumption (Appendix S1). We further ignored process error and assumed the population was at carrying capacity before the start of commercial exploitation (i.e.,  $N_y \leq 1905 = K$ ).

As is typical of analyses with the theta-logistic model, the nonlinear correlation between estimates of  $r$  and  $K$  led to numerical convergence issues. We therefore reparameterized Equation (2) utilizing the fact that  $MSY = rK\theta/(\theta + 1)^{1/\theta + 1}$  and setting  $K = MSY(\theta + 1)^{1/\theta + 1}/\theta r$ , so it became:

$$N_{y+1} = N_y + rN_y \left( 1 - \left( \frac{r\theta N_y}{MSY(\theta + 1)^{1/\theta + 1}} \right)^\theta \right) - C_y - S_y \quad (3)$$

Reparameterizing the model in this way is a numerical convenience and results in the same posteriors but faster convergence times.

The first set of data used to fit the population dynamics models are five abundance estimates from 1993 to 2008 (Table 1; Calambokidis and Barlow 2004; Calambokidis *et al.* 2007, 2009b). These estimates are assumed to be independent and log-normally distributed with likelihood

$$L_{\text{abundance}} = \prod_{y=1}^5 \frac{1}{N_y^{\text{obs}} \sqrt{2\pi\sigma_y^2}} \cdot \exp \left[ -\frac{\left( \ln(N_y^{\text{obs}}) - \ln(N_y) \right)^2}{2\sigma_y^2} \right], \quad (4)$$

where  $\sigma_y^2 = \ln(CV_y^2 + 1)$  is the variance on the log scale for year  $y$ ,  $N_y^{\text{obs}}$  is the observed absolute abundance and  $N_y$  is the predicted abundance from a population dynamics model (Eq. 1, 3). Line-transect estimates were also available for this population, but were excluded because they measure a variable and biased proportion of the population depending on the year (Calambokidis *et al.* 2009b).

The abundance estimates are sufficient for the log-linear model but the theta-logistic also requires catches and ship strikes. We used 1,000 catch series, estimated using Monte Carlo methods in Monnahan *et al.* (2014), to include the uncertainty in catches into this analysis. The ship strikes were modeled separately as detailed below.

Table 1. Photographic mark-recapture estimates and coefficients of variation (CV) used to fit the population dynamics and log-linear models.

Year	Estimate	CV
1993	2,000	0.20
1997	1,756	0.21
2002	1,781	0.23
2006	2,842	0.29
2008	2,497	0.18

The two models used in this study provided different information relevant to the population trends of the ENP blue whale. The log-linear model estimated recent population trends without assumptions about historical catches or ship strikes. The discrete theta-logistic model provided estimates of the carrying capacity of the population and the intrinsic rate of growth, from which past and future trends in abundance and status could be determined.

### *Estimating Ship Strikes*

Past and future ship strikes were a key part of the analysis, but precise time series of these values were unavailable. We therefore estimated the annual number of fatally struck whales for each year and incorporated them into Equation (3). We assumed ship strikes were proportional to the product of the number of whales and vessels in the shipping lanes. For example, one would expect few strikes if abundance was high but vessel traffic was minimal (*e.g.*, preexploitation) or if abundance was low and vessel traffic high (*e.g.*, ship strikes depleting the population). We modeled ship strikes in each year as:

$$S_y = cN_yV_y, \quad (5)$$

where  $S_y$  is the estimated fatal ship strikes during year  $y$ ,  $N_y$  is the estimated population size from Equation (3),  $V_y$  is the estimated number of vessels (defined below), and  $c$  is an estimated parameter which scaled the estimated ship strikes.

There is substantial uncertainty about the number of ship strikes in 2013 (which we use here as data). We used 10 per year as a base case, and tested the sensitivity of this assumption by including a scenario where 35 was considered as a high case. Much higher levels are unlikely, but possible (see Appendix S1). We further assumed that observed ship strikes in 2013,  $S_{2013}^{\text{obs}}$ , were Poisson distributed with mean  $S_{2013}$  so that the likelihood was:

$$L_{\text{strikes}} = \frac{(S_{2013})^{S_{2013}^{\text{obs}}} e^{-S_{2013}}}{S_{2013}^{\text{obs}}!}, \quad (6)$$

where  $S_{2013}$  is the model estimate of the number of strikes during 2013 from Equation (5). Estimating the strikes during year  $y$  required an estimate of the number of vessels,  $V_y$ . We defined a “vessel” as a ship moving through ENP blue whale territory that was large and fast enough that a collision would be fatal. Data on the historical vessel traffic in the eastern North Pacific were unavailable, but the number of vessels worldwide larger than 100 gross tons was available from 1890 to 2003 (as used in Laist *et al.* (2001); Table 2). We assumed the worldwide vessel traffic was proportional to vessel traffic in ENP blue whale habitat, and that it followed a logistic curve:

$$V_y = V_{y-1} + r_v V_{y-1} \left( 1 - \frac{V_{y-1}}{K_v} \right), \quad (7)$$

where  $V_y$  is the predicted number of vessels during year  $y$ ,  $r_v$  is the intrinsic rate of growth of the number of vessels, and  $K_v$  is the asymptote. This model also needs a parameter to initialize the vessel trajectory. We parameterized the model with  $V_{1950}$ ,

Table 2. Historical vessel traffic. Data on vessels over 100 gross tons worldwide used in the vessel model to infer changes in vessel traffic over time.

Year	Vessels $\times 10^3$	Year	Vessels $\times 10^3$
1890	11.1	1950	30.9
1900	15.9	1960	36.3
1910	22.5	1970	52.4
1920	26.5	1980	79.8
1930	30.0	1990	78.4
1939	29.7	2003	89.9

which minimized parameter correlation, and helped to improve the numerical efficiency of the fitting process.

We assumed that errors between observed vessel numbers and model predictions were independent and normally distributed with an unknown variance parameter, so the likelihood of the vessel model was:

$$L_{\text{vessels}} = \prod_y \frac{1}{\sqrt{2\pi\sigma_v^2}} \cdot \exp \left[ -\frac{(V_y - V_y^{\text{obs}})^2}{2\sigma_v^2} \right], \quad (8)$$

where  $V_y^{\text{obs}}$  is the number of observed vessels (Table 2), and  $\sigma_v^2$  is the estimated variance.

#### *Estimating Current and Future Status*

The MMPA considers a population “depleted” if it falls below its level of “maximum net productivity” (MNPL), which in this case is at 60% of carrying capacity since  $\theta = 2.39$  was assumed in model (3). We adopted the MMPA definition and define the status of the population as “recovered” if it is above its MNPL and depleted otherwise, and where recovery is the process of becoming recovered. Thus the past, present, and future status of the population is determined by the relative abundance, *i.e.*, the abundance in a year relative to the carrying capacity:  $N_y/K$ , using Equation (3). The posterior distributions for status depended on the assumptions made in the model, particularly the choice of prior distribution for  $r$  (see Appendix S1) and the number of observed ship strikes in 2013. We therefore compared posteriors across scenarios to assess the impact each assumption had on the results of this analysis.

Estimating the future status of ENP blue whales depends on the number of ship strikes, which are influenced by the number of vessels and potential mitigation scenarios. We explored future status in two ways: a “short-term” and “long-term” approach.

The short-term approach compared status for three hypothetical mitigation strategies under vessel model projections. It was impossible to predict the exact effect of particular mitigation strategies, so we used the following mitigation scenarios to quantify the impacts of potential mitigation on future status.

*Status quo*—No measures to mitigate mortalities are implemented and the rate of strikes remain the same into the future:  $c_{\text{status quo}} = c$  for  $y > 2013$ , in Equation (5).

*Mitigation*—Some hypothetical action is taken to reduce the rate of strikes by half after 2013, so that  $c_{\text{mitigation}} = c/2$ .

*Elimination*—In this extreme case ship strikes were eliminated completely after 2013, *i.e.*,  $c_{\text{elimination}} = 0$ . This scenario provided a “best-possible” case against which to judge the relative impact of the other scenarios.

Mitigation scenarios only occurred after 2013 and thus had no impact on the fits of the model or the estimates of current status. Substantial differences between these three scenarios would suggest ship strikes are threatening the status of the population, and this risk should be minimized. This short-term approach estimated the impact of ship strikes over the next several decades using the vessel model.

The long-term approach addressed future status without making any assumptions about future vessel traffic or mitigation scenarios. Instead, we assumed a constant level of vessel traffic and estimated the equilibrium relative abundance by projecting the model forward 100 yr. This process generated a posterior distribution for the equilibrium relative abundance and was repeated over a range from 0- to 20-fold the estimated vessels in 2013. If values close to  $V_{2013}$  led to a low equilibrium relative abundance then the current level of vessel traffic would have a large impact on the future status of this population. In contrast, if blue whale abundance remained high for cases with high numbers of vessels, then the population is more resilient to ship strikes.

We ran the model under four scenarios: two priors for  $r$  and two levels of observed ships strikes in 2013. Details of model fitting and Bayesian diagnostics can be found in Appendix S1.

## RESULTS

### *Population Dynamics*

We estimated a growth rate of  $m = 0.02/\text{yr}$  (interval<sup>2</sup>  $-0.011$ – $0.052$ ) using the log-linear model, corresponding to a probability of positive growth of 0.9. Thus, there is evidence that the population increased in size from 1993 to 2008.

For the theta-logistic model, results are shown for  $\theta = 2.39$  since current status was robust to the value of  $\theta$  used (Fig. S1). For the base case (*i.e.*, uninformative  $r$  prior and  $S_{2013}^{\text{obs}} = 10$ ) the prewhaling abundance,  $K$ , was 2,210 (interval 1,823–3,721). Estimates of  $K$  changed little with the informative  $r$  prior and different levels of  $S_{2013}^{\text{obs}}$  (Table 3). The choice of prior for influenced the posterior distribution for  $r$  substantially (Fig. 1A, B), indicating there was little information about this parameter in the data. In contrast, the informative prior for  $r$  had a much smaller effect of decreasing the upper tail of the posterior for  $K$  (Fig. 1D). This suggests that the results for estimates for carrying capacity are robust across the assumptions explored in this analysis.

### *Ship Strikes*

The vessel model for the base case predicted that vessel traffic grew under an intrinsic rate of  $r_v = 0.022/\text{yr}$  (interval 0.017–0.148). The asymptotic number of vessels was estimated to be  $K_v = 283$  thousands of vessels over 100 metric tons (interval 112–489), with the broad interval resulting because the data contained little information about this parameter (*i.e.*, there is little evidence for the rate of increase in vessel traffic dropping). The future projections of the vessels are uncertain, ranging from

<sup>2</sup>This and all subsequent intervals are 95% Bayesian credible intervals.

Table 3. Estimated intrinsic rate of increase ( $r$ ), carrying capacity ( $K$ ), 2013 abundance, and 2013 abundance relative to carrying capacity. Results are shown for a uniform prior for  $r$ , and an informative prior from a meta-analysis, as well as assumed ship strikes in 2013 ( $S_{2013}^{obs}$ ) of either 10 or 35. The base case scenario is indicated in bold.

$r$ Prior	$\Sigma_{2013}^{obs}$	$r$	Median (2.5%–97.5%)				2013 absolute abundance	2013 relative abundance
			$K$					
Uniform	10	0.083 (0.017–0.113)	2,210 (1,823–3,721)				2,138 (1,774–2,584)	0.97 (0.62–0.99)
Uniform	35	0.081 (0.020–0.113)	2,349 (1,931–4,262)				2,102 (1,744–2,532)	0.91 (0.49–0.95)
Informative	10	0.098 (0.063–0.112)	2,152 (1,797–2,593)				2,104 (1,752–2,536)	0.98 (0.96–0.99)
Informative	35	0.098 (0.062–0.112)	2,257 (1,897–2,702)				2,083 (1,728–2,510)	0.93 (0.87–0.95)



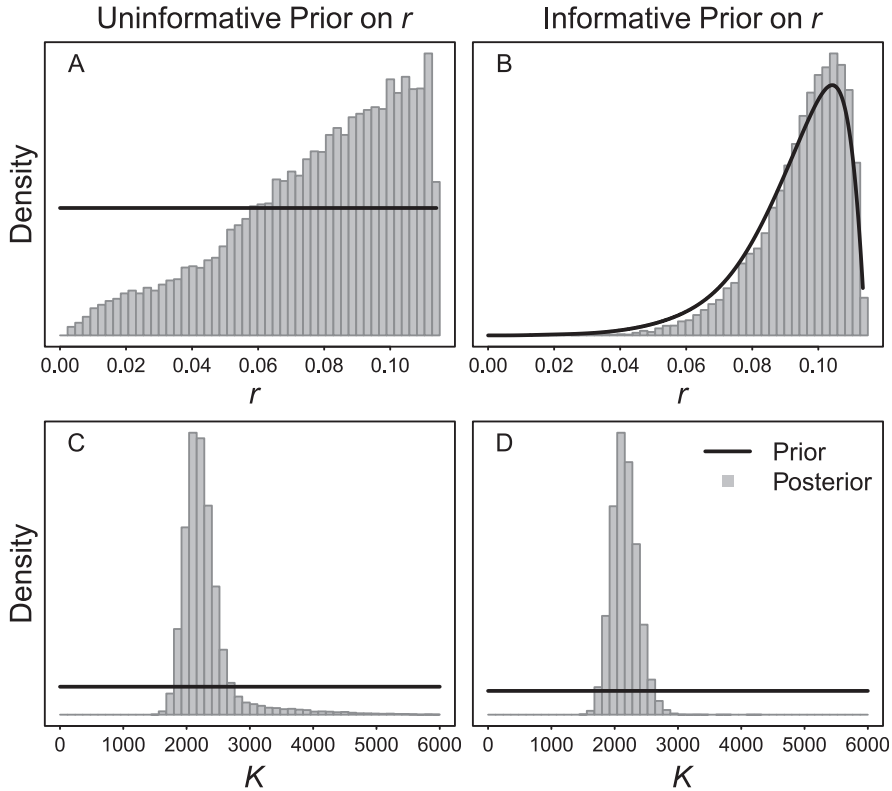


Figure 1. Prior and marginal posterior probability distributions for the parameters of the theta-logistic population dynamics model for  $S_{2013}^{\text{obs}} = 10$  and both priors for  $r$  (columns).

leveling out within the next 10 yr to continuing to grow at an almost exponential rate (Fig. 2). Assumptions regarding priors for  $r$  and the value of  $S_{2013}^{\text{obs}}$  had virtually no effect on the vessel model fits because the population model was essentially independent of the historical ship strikes within the plausible range (Fig. S2).

The estimated annual historical ship strikes were a product of the estimated abundance and vessels. As expected, the assumption about  $S_{2013}^{\text{obs}}$  directly influences the estimated trajectory of historical strikes (Fig. 3). For the base case there was a total of 534 strikes (interval 269–053) from 1905 to 2013, and 1,790 (interval 1,181 to 2,650) if  $S_{2013}^{\text{obs}} = 35$ . The prior on  $r$  had little impact on the estimated numbers of strikes (results not shown). The estimate of the total number of whales caught by commercial whalers over the same period was 2,963 (interval 2,460–3,389; Monna-han *et al.* 2014), so ship strikes were less than catches, but still substantial, particularly for the  $S_{2013}^{\text{obs}} = 35$  strikes case.

#### Current and Future Status

We estimated a 0.978 probability the population is recovered in 2013, under the base case and using the MMPA definition of recovered that the population is greater than 0.6K. This high probability of recovery held across all scenarios explored here

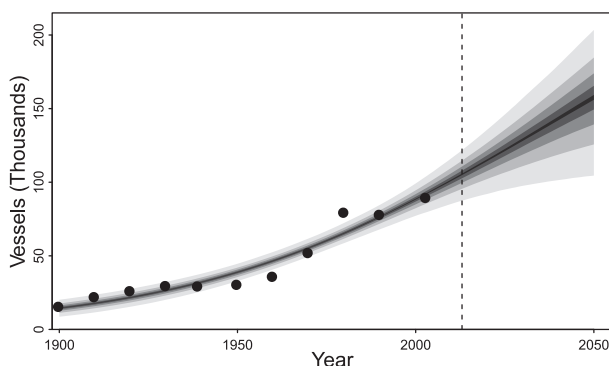


Figure 2. Results of the vessel model. The points are data from worldwide statistics for vessels over 100 gross tons from Lloyd's of London, as used in Laist *et al.* (2001). Model trajectories are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles.

(Fig. 4), as well as a much wider range of current ship strikes (Fig. S3). The trajectory of relative abundance over time suggests that the population was lowest in 1931 and has been increasing ever since, except for a short period in the late 1960s due to Soviet whaling (Fig. 5). Absolute abundance at the minimum point was 951 (interval 460–1,730) whales, corresponding to 42% (interval 23%–60%) of its original levels. Median catches were at their highest in the years immediately before this low point (339 and 275 in 1928–1929; Monnahan *et al.* 2014; Fig. 6).

The short-term approach for quantifying future status used three mitigation scenarios. Under the status quo scenario (*i.e.*, no mitigation) the strikes continue to increase and the median population begins a slight decline (Fig. 7A–C). The decline in abundance is noticeably slower for the mitigation case where the strikes after 2013 were cut in half (Fig. 7D–F). However, compared to the case with no future strikes there is little qualitative difference among the three cases (Fig. 7B, E, H). These patterns hold across all scenarios explored (results not shown).

The long-term approach found that an 11-fold increase in the current number of vessels would lead to an approximately 50% chance that the equilibrium population would be below its maximum level of productivity and thus depleted (Fig. 8). Using our vessel model and base case, we found the median ratio of number of vessels in 2050 to 2013 (*i.e.*, the multiplier in 2050) to be about 1.5 (Fig. 8), suggesting an 11-fold increase is not imminent.

## DISCUSSION

Our analysis suggests that while current levels of ship strikes are likely above legal limits, they do not immediately threaten the status of the ENP blue whale. This conclusion is based on the log-linear model which suggested the population has likely increased since 1993 (despite ship strikes), and from the theta-logistic model, which found this growth has slowed due to density dependence, not ship strikes. However, we have demonstrated an increasing impact to the population as vessel traffic increases and ship strikes become more common. Mitigation approaches will become

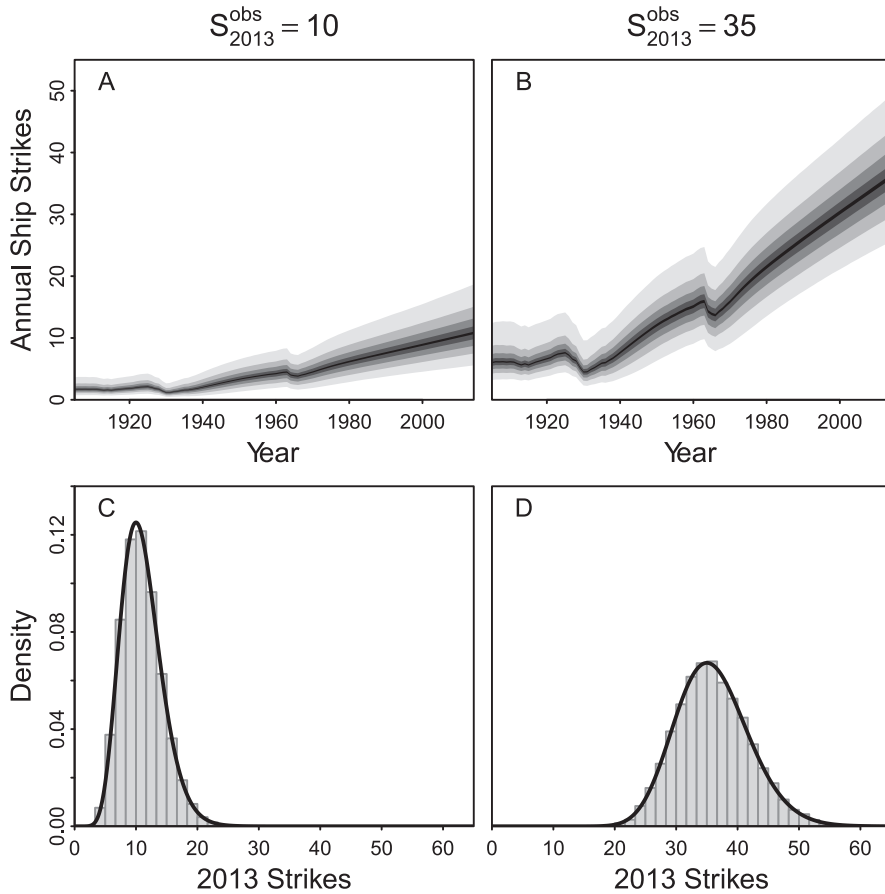


Figure 3. Results of the ship strike model. Predicted ship strikes for the uninformative prior for  $r$  and observed ship strikes in 2013 as 10 or 35. Annual trajectories (panels A and B) are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles. Panels C and D show the posterior distributions of strikes in 2013 (histogram) as well as the Poisson likelihood (line).

increasingly necessary if the rate of ship strikes increases faster than predicted, the current level of ship strikes is much higher than the scenarios used here, or other sources of anthropogenic disturbance or mortality increase. Continued monitoring of ship strikes and population abundance will provide crucial information about the health and status of ENP blue whales.

Ship strikes are currently a major concern for other endangered cetacean populations (e.g., Kraus *et al.* 2005), and we argue incorporating them into population assessments is a critical step for quantifying and exploring the impact of potential mitigation strategies. Furthermore, it may be important to consider the impacts on population status of multiple species, not just the absolute number of ship strikes, when a mitigation scenario increases strikes for one population and decreases them for another, as is the case in the Santa Barbara Channel for fin (*Balaenoptera physalus*)

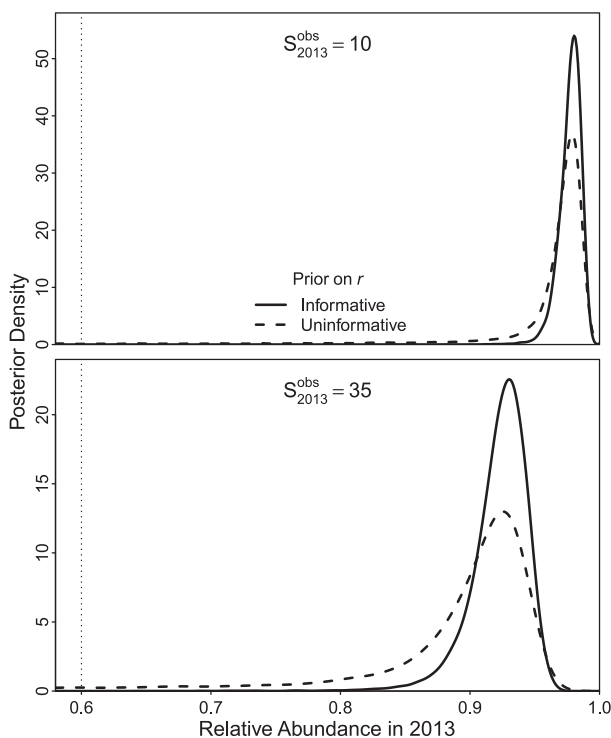


Figure 4. Posterior densities for the abundance relative to carrying capacity in 2013 for  $S_{2013}^{obs} = 10$  (top) and  $S_{2013}^{obs} = 35$  (bottom) and the two priors for  $r$ . The vertical line at 0.6 denotes the level below which the population is considered depleted.

and humpback (*Megaptera novaeangliae*) whales (Redfern *et al.* 2013). Although we have shown the ENP blue whale population is not threatened, the current level of ship strikes is likely above the PBR and hence the legal limits set in the MMPA. Our focus here was on population trends and status, but there are a variety of legal and moral reasons to minimize ship strikes as much as possible.

Where possible, we have incorporated uncertainty into our analysis (*e.g.*, historical catches, past and future trends in vessels, and the estimates of abundance) and explored cases to test the sensitivity of our results (*e.g.*, Bayesian priors, value for  $\theta$ , and current levels of ship strikes). Our findings, that there is no immediate threat to the population, held across all scenarios tested here, and even when we used the uninformative prior on the rate of increase and assumed higher than likely levels of current strikes (Fig. S3). However, we highlight some further assumptions and caveats that may influence our results and conclusions.

We used the mark-recapture abundance estimates exclusively for both population dynamics models and implicitly assumed they were reliable. Some confidence in this assumption is provided by the fact that line-transect estimates show a similar absolute abundance, although their contrasting downward trend is likely caused by an expanding distribution, rather than an actual population decline (Calambokidis *et al.* 2009b). The trend in mark-recapture estimates is also consistent using different samples and model types (Calambokidis *et al.* 2009b).

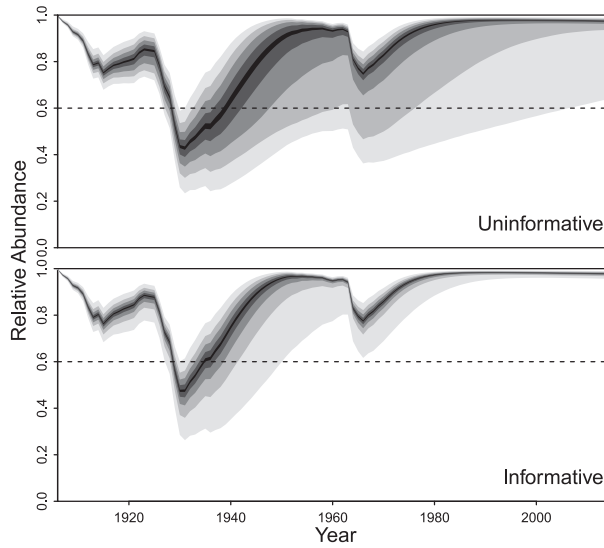


Figure 5. Trajectories for Abundance relative to carrying capacity for  $S_{2013}^{\text{obs}} = 10$  and both priors for  $r$ . Model trajectories are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles. The horizontal lines at 0.6 denote the level below which the population is considered depleted.

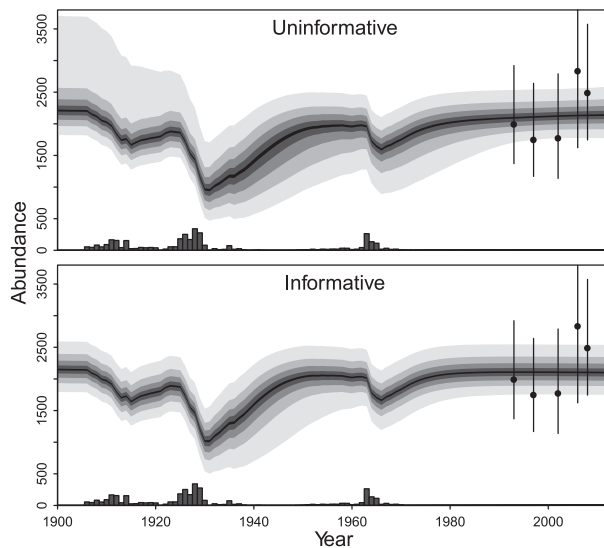


Figure 6. Absolute abundance, the abundance estimates and anthropogenic mortalities for  $S_{2013}^{\text{obs}} = 10$  and the two priors for  $r$ . The rectangles at the bottom denote total estimated mortalities (median catches + median strikes) for each year. The five abundance estimates (points) are shown with their 95% confidence intervals (bars). Model trajectories are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles.

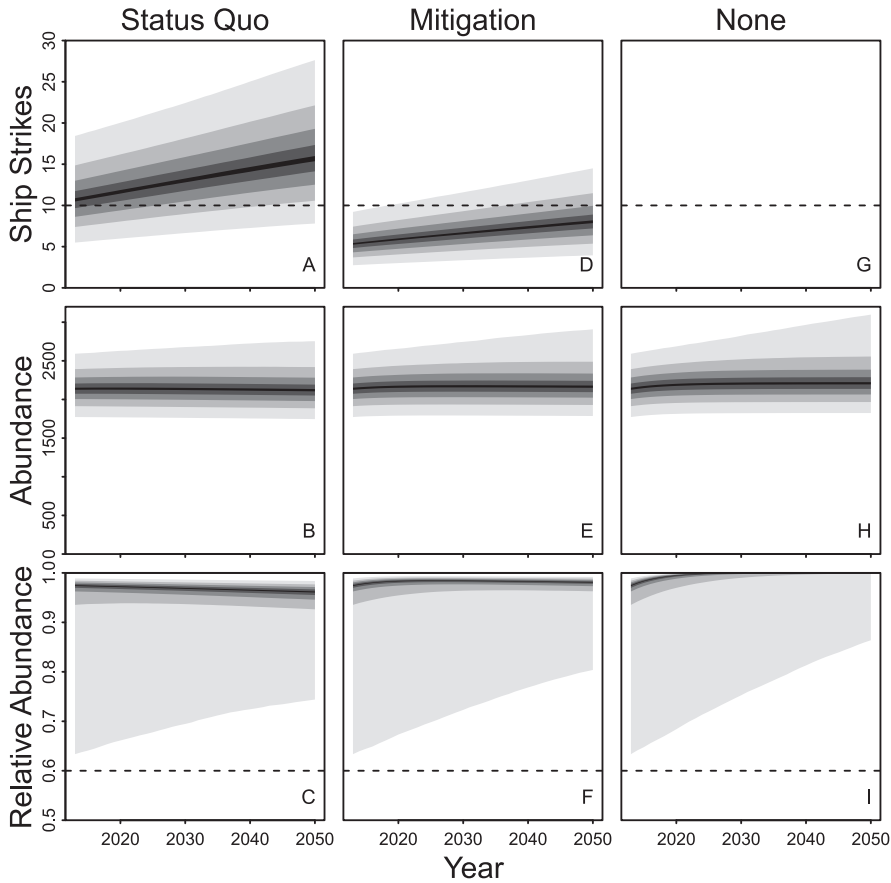


Figure 7. Results of the short-term approach to future status. Future ship strikes, abundances, and abundances relative to carrying capacity for  $S_{2013}^{obs} = 10$  are shown for three mitigation cases (columns). Model trajectories are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles. “Status quo” means no additional mitigation, “mitigation” refers to halving the ship strikes after 2013, and “none” is a complete elimination of future ship strikes. The horizontal lines at 0.6 denote the level below which the population is considered depleted.

There is also substantial uncertainty about the past and future number of vessels and ship strikes. Our vessel model included uncertainty and predicted similar future trends as another model based on growth in Gross Domestic Product and its relationship with maritime trade and vessels (Eyring *et al.* 2005). The results were also robust to different levels of ship strikes (10 *vs.* 35 in 2013; also see Fig. S3), suggesting errors in predicted ship strikes, whether *via* errors in predicted vessels or observed ship strikes, are unlikely to impact our conclusions.

For our main analysis of historical and future trends, we used the theta-logistic model because the paucity of available data precluded a more complicated model. This model does have many explicit and implicit assumptions that merit discussion. We incorporated an informative biological prior for  $r$  which indicated the intrinsic

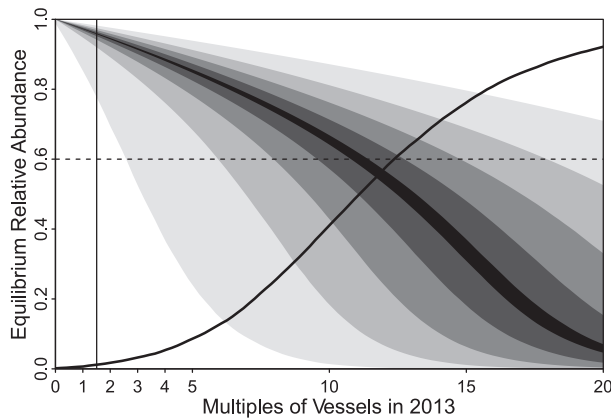


Figure 8. Results for the long-term approach to future status. Equilibrium abundance relative to carrying capacity is shown for  $S_{2013}^{bs} = 10$  and a range of multipliers of current levels of vessels. The model was projected forward 100 yr for each posterior sample under a constant multiplier ( $x$ -axis value). Model trajectories are shown as filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles. The probability that the population is depleted (*i.e.*, below 60% of  $K$ ) is shown as a curved line. The solid vertical line denotes the median ratio of vessels in 2050 to 2013, *i.e.*, the multiplier in 2050 estimated by our vessel model.

growth rate is likely above 0.04, the default value for  $r$  assumed when PBR is calculated for cetacean populations (see, *e.g.*, Carretta *et al.* 2012), and as large as 0.114 (Appendix S1; Fig. 1B). The data supported a larger value (Fig. 1A), but the model may have favored recovery by allowing for higher productivity than biologically possible for this population. However, the conclusions regarding status hold for  $r > 0.03$  and suggest a depleted status only for  $r < 0.02$  (Fig. S4)—indicating our results hold unless the productivity of this population is much lower than expected based on other populations (Appendix S1; International Whaling Commission 2013).

Following convention, we assumed carrying capacity was constant across the time period modeled and that the population was at carrying capacity at the start of whaling in 1905. If the carrying capacity has changed substantially, particularly due to anthropogenic factors, it is not clear how our results and conclusions would change.

Compared to the current abundance (about 2,200) there were relatively few catches (about 3,500) spread over seven decades and these ceased four decades ago. As such, it is not surprising the model estimates a recovered population. Given that the population recovered from commercial whaling, it is also not surprising that ship strikes (at an annual rate much lower than whaling) are not an immediate threat. Thus it is unlikely that alternative models would lead to qualitatively different conclusions than found here. Uncertainty in catches was explicitly included in our analysis, but had minimal impact on the status (Fig. S5), suggesting that our results are also robust to missing catches.

Our analysis also assumes that there is a single eastern North Pacific blue whale population, as supported by genetics, morphology, acoustics, satellite tags, and photographic mark-recapture (Gilpatrick and Perryman 2008, Calambokidis *et al.* 2009a, Bailey *et al.* 2010, Costa-Urrutia *et al.* 2013). A more complicated population structure in the eastern North Pacific is possible and would require

revisiting this assessment if the ENP is not a single population that encompasses the geographic range used to estimate ENP catches in Monnahan *et al.* (2014).

We estimate that despite seven decades of commercial whaling, ENP blue whales have recovered and are in no immediate threat from ship strikes. This conclusion conflicts with the depleted and strategic designation under the MMPA for ENP blue whales (Carretta *et al.* 2012). The Antarctic population had abundance relative to carrying capacity of 0.7% in 1996 (Branch *et al.* 2004) and the Chilean population at least 7.2% (Williams *et al.* 2011), while the status of other populations of blue whales is unclear. Thus the ENP population is the only population of blue whales shown to have recovered from whaling, and we have demonstrated that an exploited population of blue whales can recover given appropriate conservation measures and time.

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#### SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12157/supinfo>.

*Appendix S1.* Sensitivity analyses to  $\theta$  and ship strike levels, and further details of Bayesian priors and model fitting.

*Figure S1.* Sensitivity of results to the assumption that  $\theta = 2.39$ . Violin plots show the distribution of abundance relative to carrying capacity in 2013 for  $\theta = 1, 2.39$ , and 18.17 across two scenarios for the prior for  $r$  (columns) and observed ship strikes in 2013 (rows). The horizontal line at 0.6 denotes the level below which the population is considered depleted.

*Figure S2.* Joint posterior distributions for the base case. Lower triangle of matrix shows pairwise parameter scatterplots, the diagonal shows the priors (black lines) and marginal posteriors (gray histogram), and the upper triangle denotes the empirical pairwise parameter correlations, whose magnitude is proportional to the size of text. The priors for  $\sigma_v$  and  $c$  are so broad they lie nearly on the  $x$ -axis and are difficult to see.

*Figure S3.* Impact of the number of strikes assumed for 2013,  $S_{2013}^{\text{obs}}$ , on relative abundance for 2013 and 2050 (using the vessel model under no mitigation). Filled gray areas representing the 0.95, 0.75, 0.5, 0.25, and 0.05 posterior percentiles are shown. The probability of being classified as depleted (*i.e.*, below 60% of  $K$ ) is shown as the solid black line.

*Figure S4.* Relationship between  $r$  and abundance relative to carrying capacity in 2013. Posterior draws for the base case are shown as points. The horizontal line at 0.6 denotes the level below which the population is considered depleted, and the vertical line at 0.04 indicates the default net productivity rate (equivalent to  $r$ ) used for cetaceans (Marine Mammal Protection Act; Carretta *et al.* 2012).

*Figure S5.* Relationship between total catches and base case abundance relative to carrying capacity in 2013. Points are shown for the base case for each of the 1,000 catch series and the median relative abundance (filled squares) and 5th percentile (circles). A linear model fit is shown for both sets of points: median (solid line;  $R^2 < 0.01$ ;  $P$ -value of slope = 0.68) and 5th percentile (dashed line;  $R^2 = 0.01$ ;  $P$ -value of slope  $< 0.001$ ). The horizontal line at 0.6 denotes the level below which the population is considered depleted.

*Table S1.* Summary of ship strike scenarios used to define the plausible range for  $S_{2013}^{\text{obs}}$ .