Quantifying injury to common bottlenose dolphins from the *Deepwater Horizon* oil spill using an age-, sex- and class-structured population model

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ABSTRACT: Field studies documented increased mortality, adverse health effects, and reproductive failure in common bottlenose dolphins *Tursiops truncatus* following the *Deepwater Horizon* (DWH) oil spill. In order to determine the appropriate type and amount of restoration needed to compensate for losses, the overall extent of injuries to dolphins had to be quantified. Simply counting dead individuals does not consider long-term impacts to populations, such as the loss of future reproductive potential from mortality of females, or the chronic health effects that continue to compromise survival long after acute effects subside. Therefore, we constructed a sex- and age-structured model of population growth and included additional class structure to represent dolphins exposed and unexposed to DWH oil. The model was applied for multiple stocks to predict injured population trajectories using estimates of post-spill survival and reproductive rates. Injured trajectories were compared to baseline trajectories that were expected had the DWH incident not occurred. Two principal measures of injury were computed: (1) lost cetacean years (LCY); the difference between baseline and injured population size, summed over the modeled time period, and (2) time to recovery; the number of years for the stock to recover to within 95% of baseline. For the dolphin stock in Barataria Bay, Louisiana, the estimated LCY was substantial: 30 347 LCY (95% CI: 11 511 to 89 746). Estimated time to recovery was 39 yr (95% CI: 24 to 80). Similar recovery timelines were predicted for stocks in the Mississippi River Delta, Mississippi Sound, Mobile Bay and the Northern Coastal Stock.

KEY WORDS: Population model · Monte Carlo analysis · Survival · Density dependence · Bayesian model · *Deepwater Horizon* · Impact assessment · Cetacean

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INTRODUCTION

Field studies conducted to assess injury to nearshore common bottlenose dolphins *Tursiops truncatus* following the *Deepwater Horizon* (DWH) oil spill demonstrated poor health (Schwacke et al. 2014), reproductive failure (Lane et al. 2015, Kellar et al. 2017, this Theme Section), and increased mortality that contributed to the largest and longest lasting cetacean Unusual Mortality Event (UME) on record in the northern Gulf of Mexico (Litz et al. 2014). Adverse health effects documented in live dolphins after the spill included lung disease, poor body condition, and an impaired stress response indicative of injury to the adrenal pathway and consistent with adrenal insufficiency (Schwacke et al. 2014). There was a significant increase in the number of dolphin strandings spatially and temporally associated with the spill (Venn-Watson et al. 2015b), and a high prevalence of adrenal and lung lesions in dolphin carcasses recovered within the spill footprint (Venn-Watson et al. 2015a). Longitudinal photo-identification studies followed pregnant females to document birth outcome and showed the rate of reproductive failures was over 2-fold higher for stocks exposed to DWH oil than would be expected based on unexposed reference populations (Lane et al. 2015, Kellar et al. 2017). The official ending of the UME on 31 July 2014, and follow-up assessments of live dolphins 3 and 4 yr post-spill suggest that the health of nearshore dolphins has improved (Smith et al. 2017, this Theme Section). However, the prevalence of moderate to severe lung disease and impaired stress response continues to be higher than expected (as of summer 2014; see Smith et al. 2017), indicating there are lingering health effects for the dolphin cohorts exposed to DWH oil that will likely continue to affect survival. Likewise, the rate of reproductive failure remained elevated through spring 2015 when the final Natural Resource Damage Assessment (NRDA) bottlenose dolphin surveys were conducted (Kellar et al. 2017).

Under the US Oil Pollution Act (15 CFR [Code of Federal Regulations] § 990.10), the NRDA process not only assesses the nature of injuries to natural resources following an oil release, but also quantifies the extent of injuries to determine the appropriate type and amount of restoration needed to compensate for losses. Dolphins are long-lived, slow maturing species with low reproductive rates, and the loss of reproductive adults, whether through direct mortality or impaired reproduction, can have a significant impact on a population. A count of dead individuals does not fully describe the potential long-term impact to the population because it does not consider the resultant loss of future reproductive potential, nor the sublethal but chronic health effects that continue to compromise survival and reproductive success long after the acute effects have subsided. In contrast, a model of population dynamics can provide a more appropriate quantification because such models can integrate the various factors that influence long-term survival and reproduction to predict a post-spill population trajectory over time. The post-spill population trajectory can then be compared with baseline — that is, the population trajectory that was expected if the DWH incident had not occurred. Comparison of the 2 population trajectories provides for a holistic quantification of injury that considers the long-term impacts to the population expected to result from the combination of individual losses, future reproductive losses, and lingering chronic disease.

Modeling the population dynamics following an event such as the DWH oil spill requires insight into the processes that will drive the population's recovery. The dynamics by which a depleted bottlenose dolphin population may recover and eventually return to baseline condition are not known, but it is believed that population growth for cetaceans is at least partially controlled by density-dependent (DD) factors (Fowler 1984). Therefore, a population perturbed by an acute event that significantly reduces its numbers is likely to exhibit changes in one or more vital rates (e.g. increased reproduction or increased survival), resulting in an accelerated growth rate that will then slow as the population increases. Elasticity analyses of matrix population models in odontocetes have suggested that non-calf survival could have the greatest influence on population growth (Brault & Caswell 1993), yet field studies have shown variability in reproductive rates over time and across stocks or pods, while non-calf survival rates remain relatively constant (Wells & Scott 1990, Brault & Caswell 1993, Manlik et al. 2016). Other empirical data provide evidence for DD growth in at least 9 species of cetaceans: 8 of these showed evidence of DD birth rate, 5 showed evidence of DD age at first reproduction, and only 1 (*Orcinus orca*) showed evidence for DD juvenile or adult survival (Fowler 1984). However, it should be noted that due to the logistical difficulty of observing births for cetaceans, and the fact that the highest risk of mortality occurs during the neonatal period (Stolen & Barlow 2003, Mann & Watson-Capps 2005), estimates of fecundity or birth rate likely integrate early calf (neonatal) survival rate to some degree. Nonetheless, relationships among prey abundance, body condition, and fecundity (which may

include some aspect of calf survival) have been documented for cetaceans (Ward et al. 2009, Williams et al. 2013, Meyer-Gutbrod et al. 2015), suggesting a process by which DD responses in fecundity could occur. Specifically in bottlenose dolphins, shorter birth intervals were noted in a population from the US Atlantic coast following a significant depletion from a morbillivirus outbreak (Thayer 2008), and increases in calf/group ratios were documented in the years following a major hurricane in the northern Gulf of Mexico, presumably in response to increased prey availability following fishery closures or potential calf losses during the hurricane (Miller et al. 2010). This suggests that, while theoretically non-calf survival could have the greatest influence on population dynamics, biologically it is more likely that environmental or resource fluctuations influence fecundity rates, which in turn drive changes in population dynamics. It makes sense that reproductive responses would be most sensitive to resource availability and/or other environmental stressors, as pregnancy imposes increased metabolic costs and the embryonic, fetal, and neonatal stages are sensitive life periods that have been shown to be at particularly high risk under increased stress (Braastad 1998, Winneke 2011, Bellinger 2013, Shero et al. 2015).

While there is evidence that DD fecundity occurs, the functional relationship between population size and fecundity rate has not been well defined for bottlenose dolphins. It is believed that for cetaceans in general, DD responses occur close to carrying capacity and often involve birth rate (Fowler 1981, 1984). Only limited empirical data have been reported for a dolphin species, but support the hypothesis that reproductive rates do not substantially decrease until a population reaches a relatively high fraction of its equilibrium abundance (Smith 1984).

Here, we describe a population modeling framework with a DD fecundity function that drives recovery following losses associated with the DWH oil spill in order to quantify the expected long-term population impacts on *T. truncatus* stocks. For simplicity, we present an application of the model for a single stock (Barataria Bay Estuarine System Stock; see Vollmer & Rosel [2013] for a review of Gulf of Mexico dolphin stock structure), although the same population modeling framework was used for the 2 coastal *T. truncatus* stocks and 3 other Bay, Sound and Estuary (BSE) stocks for which DWH-associated excess mortality was determined. Model results for Mississippi River Delta, Mississippi Sound, and Mobile Bay BSE Stocks, and the Western and Northern Coastal Stocks are reported in the *Deepwater Horizon* Final Program-

matic Damage Assessment and Restoration Plan (DWH NRDA Trustees 2016).

MATERIALS AND METHODS

Overview

The modeling framework (Fig. 1) incorporated a sex- and age-structured model of population growth, with additional class structure to represent dolphins exposed and unexposed to DWH oil. Baseline fecundity rate for unexposed females was estimated from the literature, while baseline age-specific survival rates for unexposed males and females were estimated using data derived from dolphin stocks not overlapping geographically or temporally with the spill. The estimated fecundity and survival parameter values were consistently applied for each of the population models for BSE and coastal *Tursiops truncatus* stocks. Initial population size, as well as reduction factors for fecundity and survival rate associated with spill-related effects (i.e. for the exposed class) were stock-specific, and for Barataria Bay were parameterized using estimates from a post-spill longitudinal mark-recapture study (McDonald et al. 2017, this Theme Section).

A single run of the model involved sampling from the distribution of each input parameter (see below), deterministically projecting the population state for 150 yr under a baseline scenario to predict what the trajectory would have been if the DWH spill had not happened, paired with a trajectory for the same number of years assuming reduced survival and reduced fecundity in dolphins that were present in the population at the time of the spill (injured scenario). The 2 trajectories for each run were then compared to evaluate the population loss and the length of time required for the injured population trajectory to approach the baseline population trajectory. Three specific injury metrics were estimated (Fig. 1): (1) lost cetacean years (LCY), the difference between the baseline and injured population sizes, summed over the entire modeled time period (150 yr); (2) years to recovery (YTR), the number of years required before the injured population trajectory reaches 95% of the baseline population trajectory; and (3) maximum proportional decrease (MPD), the difference between the 2 population trajectories when the injured trajectory is at its lowest point, divided by the baseline.

A Monte Carlo approach, similar to that described by Caswell et al. (1998), was used to quantify uncertainty on the injury metrics given uncertainty in
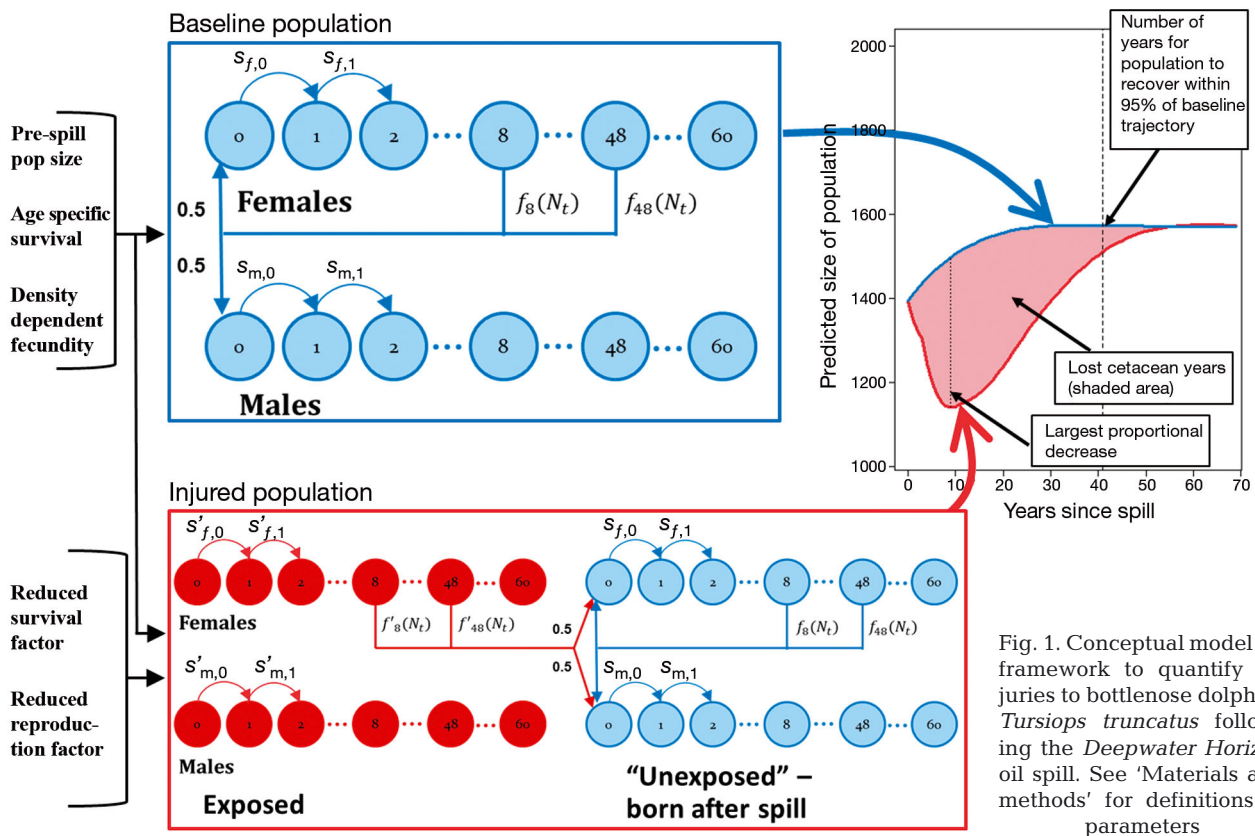
Fig. 1. Conceptual model for framework to quantify injuries to bottlenose dolphins *Tursiops truncatus* following the *Deepwater Horizon* oil spill. See 'Materials and methods' for definitions of parameters

model inputs. Each input parameter was described by a distribution, reflecting uncertainty in its value. For each simulation run, random values were drawn from these distributions. A total of 10 000 simulations were performed, producing distributions for each of the model outputs. Further details for model components and estimation of input parameter distributions are outlined in the sections that follow.

Sex-, age- and class-structured population model

It was assumed that all dolphins in the BSEs where oiling occurred were exposed to the oil, and that there would be some modified survival and fecundity rate for a period of time following the spill for these exposed dolphins. It was further assumed that as new dolphins were born, they would form an emerging cohort having baseline (unaffected) survival and fecundity rates. A matrix population model (Caswell 2001) was implemented with separate classes to represent the exposed and unexposed cohorts. Additional class structure was included to represent male and female dolphins. The collective population was therefore represented by 4 classes: exposed males,

exposed females, unexposed males, and unexposed females, each with different fecundity and age-specific survival rates (Fig. 1). Maximum age for both males and females was 60, with survival rate at age 60 assumed to be zero. Immediately following the DWH spill ($t = 0$), all individuals in the Barataria Bay stock were considered exposed with no members in the unexposed classes.

The number of individual females and males in the unexposed class at age $x(x = 0,…,60)$ is given by $n_{f,x}$ and $n_{m,x}$, respectively, and in the exposed class by $n'_{f,x}$ and $n'_{m,x}$. Survival rate for unexposed females and males at age x are given by $s_{f,x}$ and $s_{m,x}$, respectively, and for exposed females and males by $s'_{f,x}$ and $s'_{m,x}$. All offspring are contributed to the unexposed class with DD fecundity rates for the 2 classes given by $f_x(N_t)$ and $f'_x(N_t)$ where the total number of individuals in the system,

$$N_t = \sum_{x=0}^{60} n_{f,x} + \sum_{x=0}^{60} n_{m,x} + \sum_{x=0}^{60} n'_{f,x} + \sum_{x=0}^{60} n'_{m,x}$$

In the limit as $t \to \infty$, a stable, unexposed population emerges following a transient phase as the exposed class dies off. The system of difference equations describing the model is given by:

$$
\begin{bmatrix} n_{f,0} \\ n_{f,1} \\ \vdots \\ n_{f,60} \\ n_{m,0} \\ n_{m,1} \\ \vdots \\ n_{m,60} \\ n'_{f,0} \\ n'_{f,1} \\ \vdots \\ n'_{f,60} \\ n'_{m,0} \\ n'_{m,1} \\ \vdots \\ n'_{m,60} \end{bmatrix}_{t+1}
=
\begin{bmatrix}
\frac{f_0(N_t)}{2} & \frac{f_1(N_t)}{2} & \cdots & \frac{f_{60}(N_t)}{2} & 0 & 0 & \cdots & 0 & \frac{f'_0(N_t)}{2} & \frac{f'_1(N_t)}{2} & \cdots & \frac{f'_{60}(N_t)}{2} & 0 & 0 & \cdots & 0 \\
s_{f,0} & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\
0 & \ddots & \ddots & & & & & & & & & & & & & \\
\vdots & 0 & s_{f,59} & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\
\frac{f_0(N_t)}{2} & \frac{f_1(N_t)}{2} & \cdots & \frac{f_{60}(N_t)}{2} & 0 & 0 & 0 & 0 & \frac{f'_0(N_t)}{2} & \frac{f'_1(N_t)}{2} & \cdots & \frac{f'_{60}(N_t)}{2} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & s_{m,0} & 0 & & & & & \cdots & & & & & 0 \\
\vdots & & & & & \ddots & \ddots & \ddots & & & & & & & & \\
0 & & & & & & s_{m,59} & 0 & & & & & & & & \\
0 & & & & & & 0 & 0 & & & & & & & & \\
0 & & & & & & & & s'_{f,0} & 0 & & & & & & \\
0 & & & & & & & & & \ddots & \ddots & & & & & \\
\vdots & & & & & & & & & & s'_{f,59} & 0 & & & & \\
0 & & & & & & & & & & & 0 & 0 & & & \\
0 & & & & & & & & & & & & s'_{m,0} & 0 & & 0 \\
\vdots & & & & & & & & & & & & & \ddots & \ddots & \vdots \\
0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & s'_{m,59} & 0
\end{bmatrix}
\begin{bmatrix} n_{f,0} \\ n_{f,1} \\ \vdots \\ n_{f,60} \\ n_{m,0} \\ n_{m,1} \\ \vdots \\ n_{m,60} \\ n'_{f,0} \\ n'_{f,1} \\ \vdots \\ n'_{f,60} \\ n'_{m,0} \\ n'_{m,1} \\ \vdots \\ n'_{m,60} \end{bmatrix}_{t}
\tag{1}
$$

The population modeling framework was implemented using the R programming environment (version 3.0.3; R Core Team 2015).

Age-specific baseline mortality

To estimate age-specific mortality rates, a Siler 5-parameter competing hazard model (Siler 1979) was fit to *T. truncatus* age-at-death data collected on stranded animals from Sarasota Bay and 4 other US southeast sites (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n033p265_supp.pdf) using a Bayesian framework. The Siler functional form was selected to model age-specific mortality (1 yr intervals) due to its previous broad application to long-lived species, and particularly to cetaceans (Barlow & Boveng 1991, Stolen & Barlow 2003, Moore & Read 2008). Details of the model implementation can be found in the Supplement.

In all, data were obtained for 1035 stranded bottlenose dolphins (Table S1). Age of the stranded dolphin was determined using dentinal layer analysis as described by Hohn et al. (1989). The sex-specific survivorship function of age, $l_s(x)$, and its credible interval were estimated within a Bayesian statistical framework via the Markov Chain Monte Carlo (MCMC) algorithm. The observed data consisted of a list of dolphin strandings labeled with geographic location (g), sex (s), and age (x). Previous studies have demonstrated differing mortality rates for males and females; therefore sex was included as a factor for each of the Siler model parameters. It was assumed that mortality among the various sites is similar (i.e. the 5 Siler model parameters were not allowed to vary among sites), although it was unknown whether the stocks could be experiencing different rates of growth. Geographic location was therefore included as a factor for growth rate, r. The growth rate for the Sarasota Bay stock over the years in which the stranding data were collected was estimated as 0.018 based on a long-term photo-identification study documenting births and losses (R. S. Wells unpubl. data), and so was fixed at that value in the current analysis. The growth rates for remaining stocks are not known and therefore values were simultaneously estimated with the Siler model parameters. The full model for expected proportion of dead animals per age class, sex, and site was therefore:

$$
p_{s,g}(x) = \frac{e^{-r_g \cdot x}[l_s(x) - l_s(x+1)]}{\sum_{y=0}^{M} e^{-r_g \cdot y}[l_s(y) - l_s(y+1)]}
\tag{2}
$$

where M = 60 for the 60 one yr age classes, r_g is the growth rate for geographic location g, and

$$
l_s(x) = e^{-a_{s,1} \cdot (1 - e^{-b_{s,1} \cdot x})} \cdot e^{-a_{s,2} \cdot x} \cdot e^{a_{s,3} \cdot (1 - e^{-b_{s,3} \cdot x})}
\tag{3}
$$

following the Siler functional form (see the Supplement). Prior distributions for latent parameters $a_{s,1}$, $b_{s,1}$, $a_{s,2}$, $a_{s,3}$, and $b_{s,3}$ were assumed to be uniform over biologically relevant ranges as previously defined by Moore & Read (2008): $a_{s,1} \sim U(0.0001,3)$, $b_{s,1} \sim U(0.0001,5)$, $a_{s,2} \sim U(0.0001,1)$, $a_{s,3} \sim U(0.0001,1)$, $b_{s,3} \sim U(0.0001,1)$. Growth rate for Sarasota was fixed at 0.018. For the remaining sites, the prior distribution for growth rate was assumed to be normally distributed with hyperpriors that constrained growth rates to be within reasonable limits as previously proposed for dolphin species (Reilly & Barlow 1985, Slooten & Lad 1991, Mannocci et al. 2012): $r_g \sim$ norm (μ, τ) where $\mu \sim U(-0.10, 0.05)$, $\tau \sim$ gamma$(0.001, 0.001)$.

Posterior combinations of the 5 Siler model parameters were taken from 1000 thinned samples for each

of 4 MCMC chains (see additional method details in the Supplement), and for each sample (4000 total) the probability of surviving to age x, $l_s(x)$, for $x = 1…60$ was computed by applying the Siler function, independently for males and females. The probability of surviving from age x to age $x + 1$, s_x, was then computed as $s_x = [l_s(x + 1)]/[l_s(x)]$, providing the inputs needed for the diagonal of the transition matrix (Eq. 1). The resulting 4000 lifetables (i.e. $s_{f,x}$ and $s_{m,x}$ for $x = 0…59$) were saved, and for each execution of the population simulation a paired lifetable for males and lifetable females was randomly drawn with replacement — this procedure preserves posterior correlation between model parameters.

DWH-associated survival reduction factor

A survival reduction factor, SF_t, was calculated for each year post-spill, $t = 1,…,150$, as the ratio of the estimated survival rate (S_t) for dolphins in Barataria Bay exposed to DWH oil and a baseline annual survival rate, $S_{baseline}$:

$$SF_t = S_t/S_{baseline} \tag{4}$$

For the first 3 years post-spill ($t = 1, 2, 3$), estimated annual survival rates for Barataria Bay dolphins were available from mark-recapture analysis of photo-identification data (McDonald et al. 2017). $S_{baseline}$ was estimated based on a previously reported annual survival rate (0.951) for a BSE bottlenose dolphin stock near Charleston, SC (Speakman et al. 2010), derived using similar mark-recapture analysis of photo-identification data. A similar survival rate (0.962) was previously reported for dolphins in Sarasota Bay (Wells & Scott 1990), but the survival rate for the Charleston stock was used as baseline due to similarity of approach with the Barataria Bay survival estimates (i.e. mark-recapture analysis of photo-identification data). Beta distributions were fit to all survival rates and associated estimates of uncertainty.

Reduced survival in the exposed classes likely continued beyond the 3 yr in which the NRDA studies were conducted, but data were not available to quantify the form of this reduction. Therefore, to estimate future reduced survival (i.e. potential lingering effects), opinion was elicited from 6 veterinary experts. All 6 experts hold a Doctor of Veterinary Medicine (DVM) degree, have experience through practice and/or research with bottlenose dolphin health and physiology, and have specific knowledge of post-spill disease conditions in dolphins from involvement with the NRDA dolphin health assessment studies or from involvement in the cetacean UME investigation following the DWH spill.

The experts were asked the following question: 'Given the observed disease conditions and current evidence for changing/improving condition over time, how many years do you believe it will be before the dolphins with these conditions return to a pre-spill health state?'

Of the 6 experts, 2 indicated that they believed that the injuries to dolphins exposed to DWH oil in Barataria Bay would continue as chronic disease conditions, and that these exposed dolphins would never return to a normal (baseline) health state. The remaining 4 experts indicated that they believed the dolphins would recover to a baseline health state within 10 to 12 yr (mean = 10.7 yr). To account for the 2 of 6 experts that stated the exposed dolphins would never return to a baseline health state, population model simulations were executed with a probability of 0.33 having the survival reduction factor never improve for $t = 4…150$ (i.e. $SF_{4…150} = SF_3$). A gamma distribution for the number of years required to return to a pre-spill health state (i.e. until the reduced survival factor returns to 1.0) was fit to the remaining experts' responses. Simulations, with a probability of 0.67, were executed drawing a value for the number of years to return to pre-spill health status, YH, and fitting a linear function between the final year of an observed survival rate ($t = 3$) and YH such that ($SF_{YH…150} = 1.0$); this linear function estimated the reduced survival factor for remaining years, $t = 4…150$.

The survival rates for the exposed classes for age x and year t were then estimated as:

$$s'_{f,x}(t) = SF_t \cdot s_{f,x} \tag{5}$$

and

$$s'_{m,x}(t) = SF_t \cdot s_{m,x} \tag{6}$$

where $s_{f,x}$ and $s_{m,x}$ are the survival rates for the unexposed females and males, respectively, at age x determined from the computed lifetables.

Density-dependent fecundity

To model DD fecundity, we chose a generalization of the Beverton-Holt function with an additional parameter that provides flexibility for the representation of a range of DD relationships (Shepherd 1982, Thomas & Harwood 2005). We recomputed the equation to derive a functional form that re-

quired no specific assumption of carrying capacity, but estimated fecundity for the population size at time $t(N_t)$ using an assumed maximum achievable fecundity rate (F_{max}), estimates of fecundity and population size at a particular point in time ($F_{nominal}$ and $N_{nominal}$, respectively), and an additional parameter (ρ) that controls the shape of the density dependent function and how quickly the fecundity rate will change:

$$f(N_t) = F_{max}/[1 + (\beta \cdot N_t)^\rho] \quad (7)$$

where

$$\beta = 1/N_{nominal} \cdot [(F_{max} - F_{nominal})/F_{nominal}]^{(1/\rho)} \quad (8)$$

With this function, fecundity is at a maximum (i.e. F_{max}) when $N_t = 0$ and decreases with increasing population size, with the rate of reduction being controlled by β and ρ. Higher ρ values produce DD curves that remain relatively constant around F_{max}) but then decline sharply (Fig. 2), at which point the population quickly reaches an effective carrying capacity, as would be expected for a long-lived mammal with low reproductive rate (Fowler 1981). In contrast, low values for ρ produce DD relationships that begin to decline even at lower population levels but change at a slower rate, a form of DD that might be expected for short-lived species with high reproductive rates (Fowler 1981). Note that if
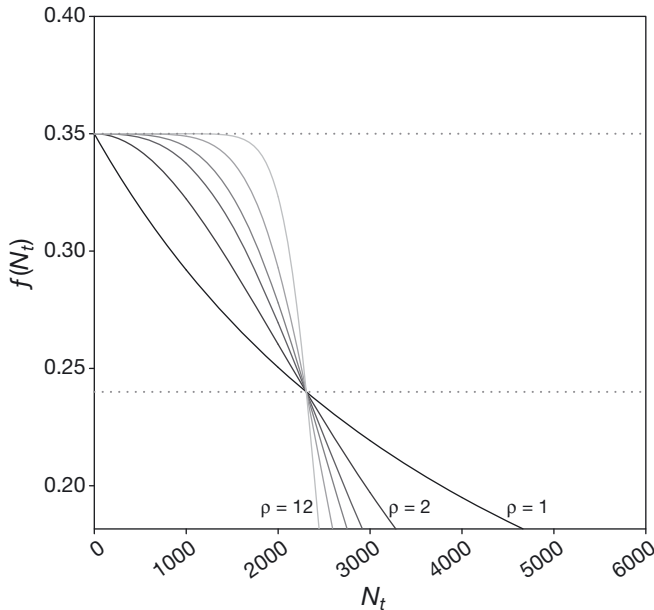

Fig. 2. Fecundity rate, $f(N_t)$, as a function of bottlenose dolphin *Tursiops truncatus* population size, N_t. Solid curves demonstrate the generalized Beverton-Holt function with $N_{nominal} = 2306$, $F_{nominal} = 0.24$, and $F_{max} = 0.34$, and varying values of the shape parameter, $\rho = 1, 2, 3, 4, 6,$ and 12. Dotted horizontal gray lines indicate F_{max} and $F_{nominal}$ values

F_{max}, $F_{nominal}$ and $N_{nominal}$ are held constant, then smaller values of ρ lead to larger equilibrium population size, and equivalent changes at smaller versus larger values of ρ (e.g. 1 to 3 versus 6 to 12) produce more substantial changes to the shape of DD (Fig. 2).

Thomas & Harwood (2005) used the generalized Beverton-Holt function in a Bayesian state space model to examine both DD fecundity and DD pup survival in gray seals *Halichoerus grypus*. Smith (1984) fit a similar functional form for reproductive rate in spinner dolphins *Stenella longirostris* and estimated a comparable shape, although the analysis was based on only 3 sampling points and intervals of uncertainty were not estimated. DD responses occur close to carrying capacity in both cetaceans and pinnipeds; responses have been observed as a change in birth rate (which may reflect both fecundity and neonatal survival due to the difficult of observing births) for cetaceans while DD pup survival is more frequently seen in pinnipeds (Fowler 1981, 1984, SCOS 2014). To represent the uncertainty in the shape of the DD fecundity function, we used a gamma distribution covering a range of possible values (Table 1) roughly based on the posterior distribution for ρ for DD pup survival in gray seals (SCOS 2014).

Distributions representing the knowledge and associated uncertainty with respect to the remaining parameter values for the DD fecundity function were derived from existing literature, and discussion among a group of subject matter experts (authors R. S. Wells, A. A. Hohn, and L. H. Schwacke). Selection of values from the literature focused, where possible, on reproductive studies from other BSE bottlenose dolphin populations as these would be most similar to the northern Gulf of Mexico BSE stocks being modeled. Distributions used are given in Table 1 and described below.

$N_{nominal}$ was assumed to be the pre-spill population size, and the abundance estimate and associated uncertainty reported by McDonald et al. (2017) were used to parameterize a normal distribution from which a value of $N_{nominal}$ was drawn for each population simulation. A corresponding estimate of pre-spill fecundity was not available; therefore, a distribution for likely $F_{nominal}$ values was derived using a range of fecundity rates that have been reported for similar BSE bottlenose dolphin stocks. A special case of the beta distribution (beta-PERT) (Vose 2000) was parameterized with a minimum, mode, and maximum value for $N_{nominal}$ with scale parameter $\lambda = 4$, producing a reasonably symmetric distribution. The mode

Table 1. Input parameters and uncertainty distributions for the population model

Parameter	Description	Point estimate (nominal value)	Distribution	Distribution parameters	Source(s)
N_0 (also $N_{nominal}$)	Initial population size; also nominal population size	2306	Normal	Mean = 2306, SD = 169.81	McDonald et al. (2017)
Density dependent fecundity function					
F_{max}	Maximum fecundity rate	0.34	Beta-PERT	Min. = 0.33, Mode = 0.34 Max. = 0.41, Shape = 4.0	Myrick et al. (1986), Kasuya et al. (1997), Thayer (2008)
$F_{nominal}$	Nominal fecundity rate	0.24	Beta-PERT	Min. = 0.13, Mode = 0.24 Max. = 0.34, Shape = 4.0	Thayer (2008), R. S. Wells (unpubl. data)
ρ	Shape parameter for density dependent fecundity function	6	Gamma	Shape = 6.4, Scale = 1.0	SCOS (2014)
Factors for reductions in survival					
$S_{baseline}$	Baseline survival rate	0.951	Beta	$a = 75.8$, $b = 4.85$	Speakman et al. (2010)
S_1	Survival rate for 1st year post-spill	0.846	Beta	$a = 126$, $b = 22.8$	McDonald et al. (2017)
S_2	Survival rate for 2nd year postspill	0.827	Beta	$a = 343$, $b = 71.6$	McDonald et al. (2017)
S_3	Survival rate for 3rd year post-spill	0.804	Beta	$a = 262$, $b = 63.8$	McDonald et al. (2017)
YH	Number of years to return to pre-spill health status	10.7	Gamma	Shape = 163, Scale = 0.066	Expert opinion, panel of 6 marine mammal veterinarians
Factors for reductions in reproductive success					
$R_{baseline}$	Baseline reproductive success rate	0.65	Binomial	N = 34, p = 0.65	Kellar et al. (2017)
R_1	Reproductive success rate for 1st year post-spill	0.19	Binomial	N = 26, p = 0.19	Kellar et al. (2017)
R_2	Reproductive success rate for 2nd year post-spill	0.19	Binomial	N = 26, p = 0.19	Kellar et al. (2017)
R_3	Reproductive success rate for 3rd year post-spill	0.19	Binomial	N = 26, p = 0.19	Kellar et al. (2017)
YR	Number of years to return to pre-spill reproductive state	17.3	Gamma	Shape = 6.49, Scale = 2.67	Expert opinion, panel of 6 marine mammal veterinarians

(most likely value) for $F_{nominal}$ was derived from the mean birth interval (4.14 yr) estimated for bottlenose dolphins having successful calves in Sarasota Bay (R. S. Wells unpubl. data). The minimum value for $F_{nominal}$ was based on the maximum birth interval (8 yr) observed for Sarasota Bay bottlenose dolphins (R. S. Wells unpubl. data). To our knowledge, the shortest mean birth interval reported for a bottlenose dolphin stock is 2.9 yr, estimated for bottlenose dolphins along the coast of North Carolina (Thayer 2008), and this was used as the basis for the maximum $F_{nominal}$ value.

An additional beta-PERT distribution was parameterized to represent likely maximum fecundity rates and was derived using reproductive rates reported for recently exploited or depleted dolphin populations. The mode for F_{max} was based on the

mean birth interval estimated by Thayer (2008). The population for which the estimate was made had recently experienced significant mortality due to a morbillivirus outbreak, potentially depleting the population by as much as 50% (Scott et al. 1988), and following the morbillivirus die-off, the stock continued to be impacted by incidental fishery-related mortality (reviewed by Thayer 2008). The lower and upper limits for F_{max} were based on pregnancy rates reported for spotted dolphins *Stenella attenuata* impacted by the tuna fishery in the eastern tropical Pacific in the 1970s (Myrick et al. 1986), and exploited bottlenose dolphin populations off the coast of Japan (Kasuya et al. 1997), respectively.

Fecundity was assumed to be 0 for animals less than 8 yr of age and greater than 48 yr of age based

on observations in Sarasota Bay, where by age 8, 40% of female dolphins have given birth to their first calf and the oldest observed female to give birth was 48 yr (R. S. Wells unpubl. data). The simplifying assumption was made that fecundity does not vary within the reproductive range, i.e. $f_8(N_t) = f_9(N_t) = \ldots f_{48}(N_t)$.

DWH-associated fecundity reduction factor

A reduced reproductive success factor, RF_t, was calculated as:

$$RF_t = R_t/R_{baseline} \quad (9)$$

where R_t is reproductive success rate in year t for dolphins exposed to DWH oil, and $R_{baseline}$ is a baseline reproductive success rate expected for dolphins not exposed to oil. Values for R_t and $R_{baseline}$ were derived from estimates reported by Kellar et al. (2017) for dolphins within the DWH oil footprint, and reference sites where dolphins were not exposed to DWH oil, respectively. Reproductive success estimates for dolphins within the DWH oil footprint were pooled across the 3 yr and across studies in Barataria Bay and Mississippi Sound due to the limited number of observations. The pooled estimate was applied for R_t, $t = 1, 2, 3$ consistent with the application of the survival reduction factors.

As with the survival reduction factor, reduced reproductive success beyond the first 3 yr post-spill was estimated based on elicitation of expert opinion. The same 6 experts were asked the following question: 'Given the observed disease conditions and current evidence for changing/improving condition over time, how many years do you believe it will be before the female dolphins with these conditions return to a pre-spill reproductive state?'

The experts indicated that they believed it would take between 9 and 25 yr (mean = 17.3 yr) for the female dolphins to return to a pre-spill reproductive state. A gamma distribution for the number of years required to return to a pre-spill reproductive state was fit to the experts' responses. For each population model simulation, a value for the number of years to return to pre-spill reproductive state, YR, was drawn and a linear function was fit between $t = 3$ and YR such that ($RF_{YR\ldots150} = 1.0$); this linear function estimated the reduced reproductive success factor for remaining years, $t = 4,\ldots, 150$.

The fecundity for the exposed class for year t was then estimated as:

$$f'(N_t) = RF_t \times f(N_t) \quad (10)$$

Sensitivity analysis

The relative influence of each model input parameter (Table 1) on each of the estimated output metrics (LCY, YTR, and MPD) was evaluated by sampling one input variable at a time, drawing randomly from that input variable's distribution, while holding all other input variables at their nominal value. The 95th percentiles for each output metric obtained by sampling from each input metric distribution were calculated and compared to examine relative changes in output metric range.

RESULTS

Age-specific baseline mortality

Age-specific survival curves indicated higher survival rates for females compared to males (Fig. S1, Tables S2 & S3 in the Supplement at www.int-res. com/articles/suppl/n033p265_supp.pdf), particularly in the youngest and oldest age classes. Similar sex differences in survival have been previously reported (Wells & Scott 1990, Stolen & Barlow 2003). The median of the posterior distribution for population growth rates (μ) was 0.021 (95% CI: −0.026 to 0.047), with median values for Charleston SC, Indian River Lagoon, FL, Mississippi Sound, MS, and Texas of 0.023 (0.005−0.040), 0.028 (0.008−0.049), 0.027 (0.004−0.050), and 0.011 (−0.009 to 0.031), respectively. Additional model results can be found in the Supplement.

Estimation of injury

The population model predicted a sharp decline for the Barataria Bay population in the decade following the DWH spill (Fig. 3), dropping to a low of 1246 (95% CI: 810.3−1786) dolphins 9 yr post-spill. In contrast, had the spill not occurred, the model predicted initial slow growth for the population, reaching an equilibrium size of approximately 2600 dolphins within 20 yr. Comparing the 2 trajectories over time indicated 30347 (11511−89746) LCY due to the DWH oil spill and 39 (24−80) YTR. The MPD was predicted to be 0.51 (0.32−0.72) of the baseline population size.

Examining growth rates (Fig. 4), an initial −0.135 (−0.052 to −0.210) decline was predicted following the spill, but the growth rate was predicted to then steadily increase and become positive in the ninth
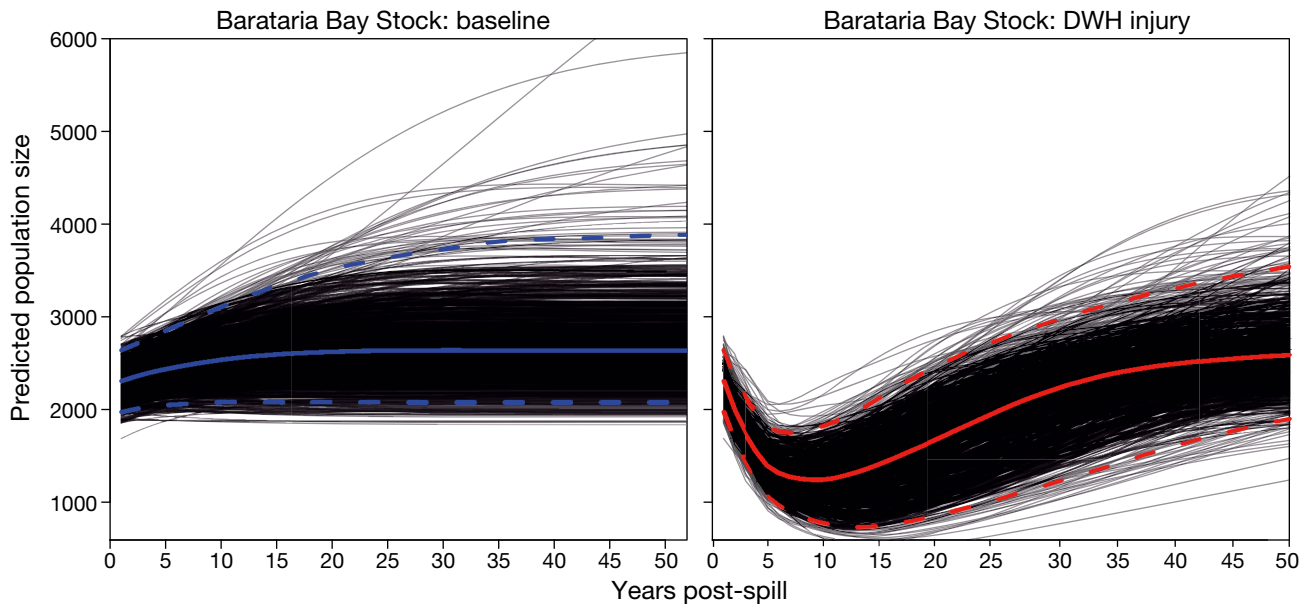
Fig. 3. Simulated population trajectories for Barataria Bay bottlenose dolphin *Tursiops truncatus* stock under baseline conditions (left), and with *Deepwater Horizon* (DWH) injury (right). Each black line represents the result from 1 simulated trajectory; trajectories were thinned by a factor of 10 for graphing. Solid and dashed blue/red lines represent median and 95th percentiles for trajectories

year post-spill, reaching a maximum growth rate of 0.034 in year 16 post-spill. In contrast, under the control scenario the population would have begun with a 0.018 (−0.006 to 0.037) growth rate in 2010, with that growth rate slowing to less than 0.010 within 5 yr.

The transition from a population with all members belonging to an exposed class to a population dominated by unexposed members, i.e. a population with >50% of its members belonging to an unexposed class, is predicted to take approximately 7 yr (Fig. 5, top). The continued low survival of the exposed cohort, which included the only reproductive adults in the years immediately following the spill, results in a low point for population abundance around year 9. This will also create a dearth of new births until approximately 11 or 12 yr post-spill, when a significant number of females from the unexposed class reach reproductive age and can contribute new members (Fig. 5b). The lack of births from approximately year 7 to 11 creates a hollow cohort that propagates as a diagonal across the age structure over time (Fig. 5b).

Sensitivity analysis

Of the 10 input parameters examined, the 2 that prompted the largest change in the injury metrics LCY and YTR were ρ (the shape parameter for the

DD fecundity function), and YH (the number of years expected for exposed dolphins to return to baseline health status) (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/n033p265_suppl.pdf). Sampling from the input distribution for ρ resulted in a 1.5-fold increase in LCY at the 97.5th percentile,
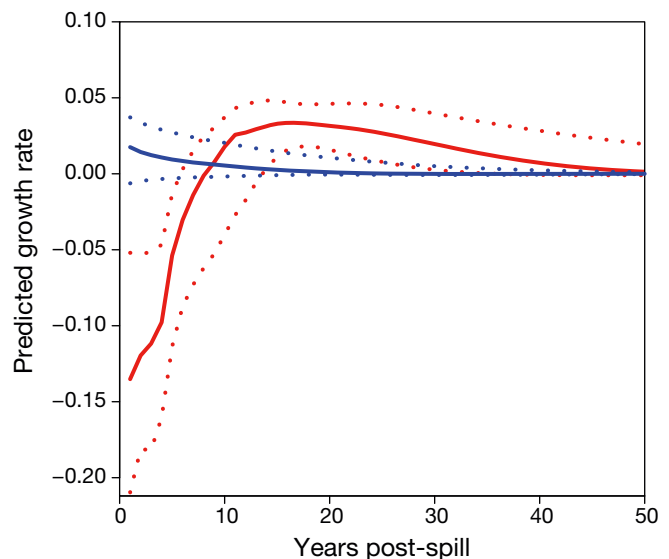

Fig. 4. Instantaneous bottlenose dolphin *Tursiops truncatus* population growth rates over time for baseline scenario and with *Deepwater Horizon* (DWH) injury. Solid red line: median for DWH injured scenario; solid blue line: median for baseline scenario; dotted lines: 95th percentiles
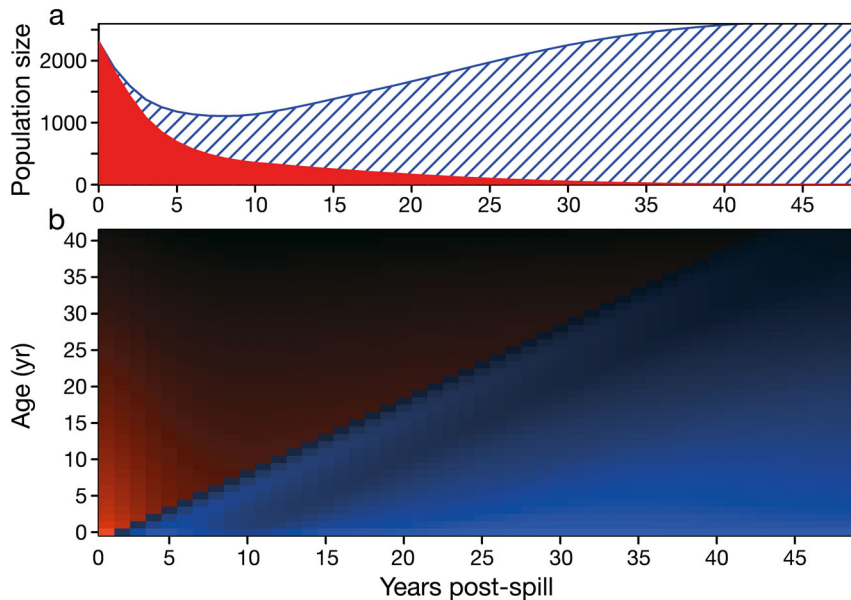
Fig. 5. (a) Population size and (b) age distribution for Barataria Bay bottlenose dolphins *Tursiops truncatus* over time under the *Deepwater Horizon* (DWH) injured scenario. In (a) solid red: exposed class; blue hatched: unexposed class. In (b) brighter colors represent age classes with greater number of members, red represents exposed class and blue represents unexposed class

although the majority of the resulting distribution of LCY values represented less than a 33% increase (75th percentile = 33%). MPD, which describes a more short-term impact on the population, was also strongly influence by ρ and YH, but $S_{baseline}$ had the greatest effect.

DISCUSSION

Under the US Oil Pollution Act, the objective of restoration is to recover the resource back to the state that it would have been had the spill not occurred (15 CFR § 990.10). Fully evaluating the loss and needed restoration for bottlenose dolphins following the DWH spill required not only examination of the immediate post-spill population status, but also prediction of the recovery transient relative to the population trajectory that would have been expected had the spill not occurred. The multi-class structured model with DD fecundity we present allows for analysis of the transient population dynamics, making assumptions regarding the likely recovery process using estimates of post-spill survival and reproductive success rates, as well as available knowledge and observations of fecundity patterns from other previously studied dolphin populations. The model's estimation of LCY provides a holistic metric of injury that represents all of the years of life lost, including

years lost due to premature mortality as well as the resultant loss of reproductive output.

The examination of post-spill population trajectories produced by our model demonstrates the significant impact of the DWH spill on Gulf of Mexico bottlenose dolphin populations. Here, we presented results for the Barataria Bay population, for which we estimate it will take nearly 4 decades for recovery to baseline. As noted in the 'Introduction', the same modeling framework was applied to 5 other stocks for which DWH-associated excess mortality was determined, including BSE populations in the Mississippi River Delta, Mississippi Sound, and Mobile Bay, as well as the Northern and Western Coastal Stocks. Similar times to recovery (range: 31 to 52 yr) were estimated in these stocks (see Table 4.9-10 in DWH NRDA Trustees 2016) with the exception of the Western Coastal Stock. The proportion of the Western Coastal Stock assigned to the exposed class was based on an overlay of DWH surface oiling with the stock's distribution estimated from aerial surveys, and the overlap was determined to be limited. Only 23% of the overall Western Coastal Stock was initially assigned to the exposed cohort, compared to 82% for the Northern Coastal Stock and 100% for each of the BSE stocks, resulting in a smaller injury.

For the Barataria Bay population, the model predicts that it will take 7 yr for an unexposed cohort to emerge through new births, and as this occurs, a younger, presumably more resilient cohort will become dominant (Fig. 5) such that positive population growth can be achieved. However, this scenario is premised on the assumption that new births contribute to an unexposed class, and that the unexposed class into which new births feed truly is physiologically unaffected by the DWH spill. In actuality, effects on offspring later in life following *in utero* exposure and even transgenerational effects have been reported for petroleum-associated compounds (Jurisicova et al. 2007, Mohamed et al. 2010, Perera & Herbstman 2011), and we cannot rule out the possibility of greater susceptibility to disease or reproductive impairment in the offspring of exposed individuals. Such effects were not included in our current model due to lack of available information to estimate factors for reduced reproduction or survival for

subsequent generations. Other ecological impacts of the DWH spill in Barataria Bay and other BSE habitats within the northern Gulf of Mexico (DWH NRDA Trustees 2016) were also not considered by the model, and there is certainly potential that injuries to other ecosystem components will ultimately influence dolphin vital rates, of both exposed and unexposed cohorts, into the future.

The modeling framework incorporated sampling from distributions that represent uncertainty in input values, allowing for the propagation of uncertainty to provide probabilistic estimates for the injury metrics and determine the contribution of the various input parameters to uncertainty in the metrics. Not surprisingly, the greatest changes in estimated injury metrics were observed in relation to input parameters ρ (shape of density dependence) and YH (number of years for the population to return to pre-spill health status) (Fig. S2 in the Supplement), which predict recovery processes that are not yet fully understood for cetaceans. The value of ρ ultimately determines the magnitude of difference between achievable growth rates under injured versus baseline scenarios, as well as equilibrium size (i.e. carrying capacity) of the populations when other DD fecundity parameters are held constant (Fig. S3 in the Supplement at www.int-res.com/articles/suppl/n033p265_supp.pdf). In scenarios with lower values of ρ, it takes longer for the injured trajectory to catch up with the baseline trajectory, and thus can significantly increase the number of LCYs. In addition, a relatively broad distribution for potential values of ρ was incorporated, reflecting the uncertainty in the underlying processes that drive DD fecundity. Similarly, YH had a strong influence relative to other input parameters on LCY. Estimated based on expert opinion, this parameter could be refined by collecting additional data on the health of exposed dolphins as time elapses and exposed dolphins potentially recover. Continued monitoring to document pregnancy rates and calving success would also help to confirm or refine model predictions, e.g. improve estimates of ρ, and in general advance understanding of population recovery processes for cetaceans following a catastrophic event.

Our model incorporated DD fecundity, but other reproductive processes, such as age at first reproduction, could also change in response to reduced population size. Shift in age at first reproduction has been suggested as a DD response for some cetaceans (Fowler 1984, Eberhardt 2002), although it has not been as frequently documented. While we did not incorporate in our model a DD decrease in age of first reproduction in response to reduced population size, we anticipate that the effect on the population trajectory would have been very similar to the increase in fecundity we did include: both lead to increased births. It is unknown whether DD fecundity and DD age at first reproduction would act independently, or whether one DD response might dampen the magnitude of the other. Without understanding the potential covariance of the two and assuming independence, adding DD age at first reproduction into our model would likely result in unrealistic population growth rates. Our incorporation of DD fecundity alone resulted in population growth rates of up to 3.4 % yr^{-1} (Fig. 4), which approach the theoretical maximum population growth rate (4 %) that has been proposed for bottlenose dolphins based on life history characteristics (Barlow et al. 1995, Wade 1998). The 3.4 % rate is also well above growth rates that have been observed or modeled for other *Tursiops truncatus* populations, i.e. 1.8 and 0.5 % for Sarasota Bay, and Shark Bay, Australia, respectively (Manlik et al. 2016, R. S. Wells unpubl. data), and well above the growth rates estimated from our Bayesian framework using age-at-death data for the 4 baseline BSE sites (range 1.1 to 2.8 %).

There is evidence that odontocete populations exploited by fisheries or depleted by a catastrophic event can be slow to recover and often do not meet theoretical expectations for their recovery transient. Two populations of killer whales suffered losses of 33 and 41 % in the year following the *Exxon Valdez* oil spill, and 16 yr post-spill, recovery of both populations has been unexpectedly slow (Matkin et al. 2008). One resident population has increased, but at an average rate of only 1.6 % yr^{-1}, significantly less than the average rate of 3.2 % yr^{-1} for other resident killer whale populations unaffected by the spill (Matkin et al. 2008). The other smaller, transient population is still in decline and now listed as depleted under the Marine Mammal Protection Act. The loss of reproductive age females following the spill clearly contributed to the population's decline, but persistent pollutant exposure (Ylitalo et al. 2001), decline of a primary prey source (Hoef & Frost 2003), and disruption of social groups (Matkin et al. 2008, Wade et al. 2012) may also be contributing factors. Populations of spotted and spinner dolphins (*Stenella attenuata attenuata* and *S. longirostris orientalis*), depleted as the result of tuna fishery bycatch in the eastern tropical Pacific, also demonstrated slower than expected rates of recovery (Gerrodette & Forcada 2005), with median population growth estimates of only 1.7 and 1.5 % yr^{-1}, respectively (Wade

et al. 2007). Potential reasons for their lack of recovery include long-term ecosystem changes and continued harassment by the tuna fishery (Gerrodette & Forcada 2005). Interactions with the fishery likely elevate stress levels and increase energetic demands, as well as separating social groups including mother/calf pairs, leading to orphaned calves that likely do not survive (Noren & Edwards 2007, Wade et al. 2012). It has been suggested that, in general, odontocete populations may be less resilient to exploitation compared to mysticete populations, partially due to older age at first reproduction and longer calving intervals, but also potentially related to social and behavioral factors (Wade et al. 2012). Social relationships may be even more important for small, resident inshore bottlenose dolphin populations such as the Barataria Bay stock. Female dolphins in Sarasota Bay that rear calves in larger, more stable groups exhibit greater reproductive success (Wells 2000, 2003). Group living likely provides increased protection for calves, and opportunities for socialization, learning, and allomaternal care. Older, more experienced mothers also have greater reproductive success. Such factors are poorly understood and difficult to observe and measure, and as such were not incorporated into our model. However, the potential influence of ecosystem, social, and behavioral factors should not be overlooked, and as restoration projects are planned and considered for BSE and coastal areas as part of the DWH Gulf of Mexico Restoration Plan, the probable impact of these factors should be considered.

In fact, numerous restoration approaches are being considered for the Gulf of Mexico following the DWH spill, and although not necessarily targeted for marine mammals, many proposed approaches have significant potential to positively or negatively influence the recovery of many stocks. For example, river diversions within and outside of the Mississippi River are being considered to restore wetlands and nearshore habitat (DWH NRDA Trustees 2016), and could significantly alter salinity patterns and fish communities. The potential negative impacts of such projects on nearshore dolphin stocks, many of which exhibit a high degree of site fidelity within specific bays or sounds, are unknown and must be carefully considered, monitored, and evaluated throughout the process. Adaptive management will be critical for such efforts, and this will require monitoring of not only abundance and distribution as mandated under the Marine Mammal Protection Act, but also of more sensitive indicators of population status such as disease prevalence, body condition, reproduction, and survival rates.

LITERATURE CITED

Barlow J, Boveng P (1991) Modeling age-specific mortality of marine mammal populations. Mar Mamm Sci 7: 50−65

Barlow J, Swartz S, Eagle T, Wade P (1995) US marine mammal stock assessments: guidelines for preparation, background, and a summary of the 1995 assessments. NOAA Tech Memo NMFS-OPR-95-6. NOAA, NMFS, and US Department of Commerce, Washington, DC

Bellinger DC (2013) Prenatal exposures to environmental chemicals and children's neurodevelopment: an update. Saf Health Work 4:1−11

Braastad BO (1998) Effects of prenatal stress on behaviour of offspring of laboratory and farmed mammals. Appl Anim Behav Sci 61:159−180

Brault S, Caswell H (1993) Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74:1444−1454

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland, MA

Caswell H, Brault S, Read A, Smith T (1998) Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecol Appl 8:1226−1238

DWH NRDA Trustees (*Deepwater Horizon* Natural Resource Damage Assessment Trustees) (2016) *Deepwater Horizon* oil spill: final programmatic damage assessment and restoration plan (PDARP) and final programmatic environmental impact statement (PEIS). www.gulfspill-restoration.noaa.gov/restoration-planning/gulf-plan

Eberhardt L (2002) A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841−2854

Fowler C (1981) Density dependence as related to life history strategy. Ecology 62:602−610

Fowler C (1984) Density dependence in cetacean populations. In: Perrin W, Brownell R, DeMaster D (eds) Reproduction of whales, dolphins and porpoises. Rep Int Whal Comm Spec Issue 6:373−379

Gerrodette T, Forcada J (2005) Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. Mar Ecol Prog Ser 291:1−21

Hoef JV, Frost K (2003) A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. Environ Ecol Stat 10:201−219

Hohn A, Scott M, Wells R, Sweeney J, Irvine A (1989) Growth layers in teeth from free-ranging, known-age bottlenose dolphins. Mar Mamm Sci 5:315−342

Jurisicova A, Taniuchi A, Li H, Shang Y and others (2007) Maternal exposure to polycyclic aromatic hydrocarbons diminishes murine ovarian reserve via induction of Harakiri. J Clin Invest 117:3971–3978

Kasuya T, Izumisawa Y, Komyo Y, Ishino Y, Maejima Y (1997) Life history parameters of bottlenose dolphins off Japan. IBI Rep 7:71–107

Kellar NM, Speakman TR, Smith CR, Lane SM, and others (2017) Low reproductive success rates of common bottlenose dolphins *Tursiops truncatus* in the northern Gulf of Mexico following the *Deepwater Horizon* disaster (2010–2015). Endang Species Res 33:143–158

Lane SM, Smith CR, Mitchell J, Balmer BC and others (2015) Reproductive outcome and survival of common bottlenose dolphins sampled in Barataria Bay, Louisiana, USA, following the *Deepwater Horizon* oil spill. Proc R Soc B 282:20151944

Litz JA, Baran MA, Bowen-Stevens SR, Carmichael RH and others (2014) Review of historical unusual mortality events (UMEs) in the Gulf of Mexico (1990–2009): providing context for the multi-year northern Gulf of Mexico cetacean UME declared in 2010. Dis Aquat Org 112:161–175

Manlik O, McDonald J, Mann J, Raudino H and others (2016) The relative importance of reproduction and survival for the conservation of two dolphin populations. Ecol Evol 6:3496–3512

Mann J, Watson-Capps J (2005) Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp. Anim Behav 69: 899–909

Mannocci L, Dabin W, Augeraud-Veron E, Dupuy JF, Barbraud C, Ridoux V (2012) Assessing the impact of bycatch on dolphin populations: the case of the common dolphin in the eastern North Atlantic. PLOS ONE 7:e32615

Matkin CO, Saulifis EL, Ellis GM, Olesiuk P, Rice SD (2008) Ongoing population-level impacts on killer whales *Orcinus orca* following the 'Exxon Valdez' oil spill in Prince William Sound, Alaska. Mar Ecol Prog Ser 356:269–281

McDonald TL, Hornsby FE, Speakman TR, Zolman ES and others (2017) Survival, density, and abundance of common bottlenose dolphins in Barataria Bay (USA) following the *Deepwater Horizon* oil spill. Endang Species Res 33:193–209

Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. Mar Ecol Prog Ser 535:243–258

Miller LJ, Mackey AD, Hoffland T, Solangi M, Kuczaj SA (2010) Potential effects of a major hurricane on Atlantic bottlenose dolphin (*Tursiops truncatus*) reproduction in the Mississippi Sound. Mar Mamm Sci 26:707–715

Mohamed ESA, Song WH, Oh SA, Park YJ and others (2010) The transgenerational impact of benzo(a)pyrene on murine male fertility. Hum Reprod 25:2427–2433

Moore JE, Read AJ (2008) A Bayesian uncertainty analysis of cetacean demography and bycatch mortality using age-at-death data. Ecol Appl 18:1914–1931

Myrick AC, Hohn AA, Barlow J, Sloan PA (1986) Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. Fish Bull 84: 247–259

Noren SR, Edwards EF (2007) Physiological and behavioral development in delphinid calves: implications for calf separation and mortality due to tuna purse-seine sets. Mar Mamm Sci 23:15–29

Perera F, Herbstman J (2011) Prenatal environmental exposures, epigenetics, and disease. Reprod Toxicol 31: 363–373

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reilly S, Barlow J (1985) Rates of increase in dolphin population size. Fish Bull 84:527–533

Schwacke LH, Smith CR, Townsend FI, Wells RS and others (2014) Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the *Deepwater Horizon* oil spill. Environ Sci Technol 48: 93–103

SCOS (Special Committee on Seals) (2014) Scientific advice on matters related to the management of seal populations: 2014. National Environment Research Council (NERC), University of St Andrews. www.smru.st-andrews.ac.uk/research-policy/scos/

Scott GP, Burn DM, Hansen LJ (1988) The dolphin dieoff: long-term effects and recovery of the population. In: Oceans '88: a partnership of marine interests. IEEE Cat. No. 88-CH2585-8, Vol. 3:819–823

Shepherd J (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J Cons Int Explor Mer 40:67–75

Shero MR, Krotz RT, Costa DP, Avery JP, Burns JM (2015) How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? Funct Ecol 29:1278–1291

Siler W (1979) A competing risk model for animal mortality. Ecology 60:750–757

Slooten E, Lad F (1991) Population biology and conservation of Hector's dolphin. Can J Zool 69:1701–1707

Smith CR, Rowles TK, Hart LB, Townsend FI and others (2017) Slow recovery of Barataria Bay dolphin health following the *Deepwater Horizon* oil spill (2013–2014), with evidence of persistent lung disease and impaired stress response. Endang Species Res 33:127–142

Smith T (1984) Estimating the dolphin population size yielding maximum net production. In: Perrin W, Brownell R, DeMaster D (eds) Reproduction of whales, dolphins and porpoises. Rep Int Whal Comm Spec Issue 6:187–190

Speakman T, Lane S, Schwacke L, Fair P, Zolman E (2010) Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. J Cetacean Res Manag 11:153–162

Stolen MK, Barlow J (2003) A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon System, Florida, USA. Mar Mamm Sci 19:630–649

Thayer V (2008) Life history parameters and social associations of female bottlenose dolphins (*Tursiops truncatus*) off North Carolina, USA. PhD dissertation, Duke University, Durham, NC

Thomas L, Harwood J (2005) Estimates of grey seal population size 1984–2004. In: Scientific advice on matters related to the management of seal populations: 2005, Annex II. SCOS. Special Committee on Seals (SCOS) briefing paper 05/02. www.smru.st-andrews.ac.uk/research-policy/scos/

Venn-Watson S, Colegrove KM, Litz J, Kinsel M and others (2015a) Adrenal gland and lung lesions in Gulf of Mexico common bottlenose dolphins (*Tursiops truncatus*) found dead following the *Deepwater Horizon* oil spill. PLOS ONE 10:e0126538

Venn-Watson S, Garrison L, Litz J, Fougeres E and others (2015b) Demographic clusters identified within the northern Gulf of Mexico common bottlenose dolphin (*Tursiops truncates*) unusual mortality event: January 2010–June 2013. PLOS ONE 10:e0117248

Vollmer N, Rosel P (2013) A review of common bottlenose dolphins (*Tursiops truncatus truncatus*) in the northern Gulf of Mexico: population biology, potential threats, and management. Southeast Nat 12:1–43

Vose D (2000) Risk analysis, a quantitative guide, 2nd edn. John Wiley & Sons, Chichester

Wade P (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar Mamm Sci 14:1–37

Wade PR, Watters GM, Gerrodette T, Reilly SB (2007) Depletion of spotted and spinner dolphins in the eastern tropical Pacific: modeling hypotheses for their lack of recovery. Mar Ecol Prog Ser 343:1–14

Wade P, Reeves R, Mesnick S (2012) Social and behavioural factors in cetacean responses to overexploitation: Are odontocetes less 'resilient' than mysticetes? J Mar Biol 12:567276

Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. J Appl Ecol 46:632–640

Wells R (2000) Reproduction in wild bottlenose dolphins: overview of patterns observed during a long-term study. In: Duffield D, Robeck T (eds) Bottlenose reproduction workshop report. AZA Marine Mammal Taxon Advisory Group, Silver Spring, MD, p 57–74

Wells R (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA, p 32–56

Wells RS, Scott MD (1990) Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Rep Int Whal Comm Spec Issue 12:407–415

Williams R, Vikingsson GA, Gislason A, Lockyer C, New L, Thomas L, Hammond PS (2013) Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. ICES J Mar Sci 70: 1273–1280

Winneke G (2011) Developmental aspects of environmental neurotoxicology: lessons from lead and polychlorinated biphenyls. J Neurol Sci 308:9–15

Ylitalo GM, Matkin CO, Buzitis J, Krahn MM, Jones LL, Rowles T, Stein JE (2001) Influence of life-history parameters on organochlorine concentrations in free-ranging killer whales (*Orcinus orca*) from Prince William Sound, AK. Sci Total Environ 281:183–203