



FEATURE ARTICLE

Population consequences of the *Deepwater Horizon* oil spill on pelagic cetaceans

Tiago A. Marques^{1,2,*}, Len Thomas¹, Cormac G. Booth³, Lance P. Garrison⁴,
Patricia E. Rosel⁵, Ryan Takeshita⁶, Keith D. Mullin⁷, Lori Schwacke⁶

¹Centre for Research into Ecological and Environmental Modeling, The Observatory, University of St Andrews, St Andrews, Fife KY16 9LZ, UK

²CEAUL–Centro de Estatística e Aplicações & Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

³SMRU Consulting, Scottish Oceans Institute, University of St Andrews, Fife KY16 8LB, UK

⁴National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida 33149, USA

⁵Marine Mammal and Sea Turtle Division, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Lafayette, Louisiana 70506, USA

⁶National Marine Mammal Foundation, San Diego, California 92106, USA

⁷National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, Mississippi 39567, USA

ABSTRACT: The *Deepwater Horizon* disaster resulted in the release of 490 000 m³ of oil into the northern Gulf of Mexico. We quantified population consequences for pelagic cetaceans, including sperm whales, beaked whales and 11 species of delphinids. We used existing spatial density models to establish pre-spill population size and distribution, and overlaid an oil footprint to estimate the proportion exposed to oil. This proportion ranged from 0.058 (Atlantic spotted dolphin, 95% CI = 0.041–0.078) to 0.377 (spinner dolphin, 95% CI = 0.217–0.555). We adapted a population dynamics model, developed for an estuarine population of bottlenose dolphins, to each pelagic species by scaling demographic parameters using literature-derived estimates of gestation duration. We used expert elicitation to translate knowledge from dedicated studies of oil effects on bottlenose dolphins to pelagic species and address how density dependence may affect reproduction. We quantified impact by comparing population trajectories under baseline and oil-impacted scenarios. The number of lost cetacean years (difference between trajectories, summed over years) ranged from 964 (short-finned pilot whale, 95% CI = 385–2291) to 32 584 (oceanic bottlenose dolphin, 95% CI = 13 377–71 967). Maximum proportional population decrease ranged from 1.3% (Atlantic spotted dolphin 95% CI = 0.5–2.3) to 8.4% (spinner dolphin 95% CI = 3.2–17.7). Estimated time to recover to 95% of baseline was >10 yr for spinner dolphin (12 yr, 95% CI = 0–21) and sperm whale (11 yr, 95% CI = 0–21), while 7 taxonomic units remained within 95% of the baseline



Striped dolphins *Stenella coeruleoalba* swimming amidst oil on the aftermath of the *Deepwater Horizon* oil spill.

Photo: NOAA

population size (time to recover, therefore, as per its definition, was 0). We investigated the sensitivity of results to alternative plausible inputs. Our methods are widely applicable for estimating population effects of stressors in the absence of direct measurements.

KEY WORDS: Environmental impact assessment · Fecundity · Gulf of Mexico · Injury quantification · Marine mammals · Natural resource damage assessment · Population dynamics model · Survival

*Corresponding author: tiago.marques@st-andrews.ac.uk

1. INTRODUCTION

The explosion and subsequent sinking of the *Deepwater Horizon* (DWH) drilling platform resulted in an estimated 490 000 m³ of crude oil being released into the northern Gulf of Mexico (GoMx) over an 87 d period (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). The resulting impacts occurred at multiple levels (Beyer et al. 2016), both abiotic (Barron 2012) and biotic, including microbes (e.g. King et al. 2015), plants (e.g. Hester et al. 2016), invertebrates (e.g. Buskey et al. 2016), vertebrates (e.g. Schwacke et al. 2014, Pasparakis et al. 2019), and humans (e.g. Shultz et al. 2015). A decade after the oil spill, research on the topic remains very active (e.g. McClain et al. 2019). Here, we focus on the population-level impacts on pelagic cetaceans in the northern GoMx (i.e. those inhabiting the shelf and oceanic zones, from 20 m water depth to the US exclusive economic zone).

Assessing impacts on populations can be complex, and evaluating the population impacts of an oil spill on cetaceans is particularly challenging (Takeshita et al. 2017). For oceanic cetaceans, for which stranding data are scarce, it is difficult to measure mortality directly (Williams et al. 2011). This difficulty is compounded when reliable information on baseline conditions is lacking, as was the case for most cetacean populations in the GoMx.

There are 57 stocks of cetaceans in the northern GoMx: 32 stocks inhabiting the bays, sounds and estuaries (BSEs) from Florida Bay to the Texas–Mexico border, 3 stocks inhabiting nearshore coastal waters from land out to 20 m depth, 2 stocks inhabiting waters of the continental shelf (20–200 m depth) and 20 stocks inhabiting oceanic waters ≥ 200 m deep (Hayes et al. 2021). While information on distribution and estimates of abundance were available for oceanic stocks just prior to the spill (Mullin & Fulling 2004, Maze-Foley & Mullin 2007), recent abundance estimates were not available for shelf and coastal stocks or for most of the BSE stocks. In addition, estimates of demographic parameters for GoMx cetacean populations were lacking, with the notable exception of the bottlenose dolphin *Tursiops truncatus*; henceforth Ttru) (e.g. Barratclough et al. 2019). This limited baseline data and resultant inability to directly measure potential post-spill population decline or change in demographic rates complicated the quantification of impacts of the DWH spill on these populations.

Model-based options offer an alternative for estimating population-level changes. The model we propose builds on the framework developed by Schwacke

et al. (2017, 2021) to quantify the DWH injury to estuarine populations of Ttru. In that framework, numerical simulation from an underlying assumed population dynamics model was used to compare population trajectories under baseline conditions and under oil-spill conditions to compute a set of injury metrics. Schwacke et al. (2017, 2021) applied the framework to Ttru in Barataria Bay, Louisiana, a population that was strongly impacted and for which a suite of targeted field studies were undertaken to provide information about adverse health effects and changes to demographic parameters. Here, we build on that work to estimate the impacts of DWH on pelagic stocks. We incorporate information about animal density over space, combining it with information on the oil footprint to obtain the exposed proportion of the population. Survival and fecundity rates are scaled from Ttru based on gestation duration (GD), and we use expert elicitation (EE) to fill in gaps in knowledge about density dependence and effects of oil exposure on these rates. We present estimates of population injury and undertake sensitivity and uncertainty analyses for input parameters. Our approach could be useful under other scenarios and for other wildlife populations to evaluate impacts of anthropogenic stressors when population changes cannot readily be observed directly.

2. METHODS

In addition to the methods presented here, further details are provided in the Supplements (Supplements S1–S8, with S1 being a master document, at www.int-res.com/articles/suppl/m714p001_supp/). In addition, 'live' versions of these documents together with all code and data required to reproduce the results are available at <https://github.com/TiagoAMarques/CARMMHApapersSI>.

2.1. Taxonomic units and population model

We investigated effects of the DWH oil spill on 15 cetacean taxonomic units (see Table 1) that inhabit pelagic and continental shelf waters of the northern GoMx (Fig. 1). The taxonomic units comprised 11 units distinguished at the species level, 2 units of Ttru distinguished by stock (continental shelf stock [Ttrs] and oceanic stock [Ttro]) and 2 species groups. The species groups combined multiple species because there was insufficient information to treat them separately: (1) a group with 3 species of beaked whales

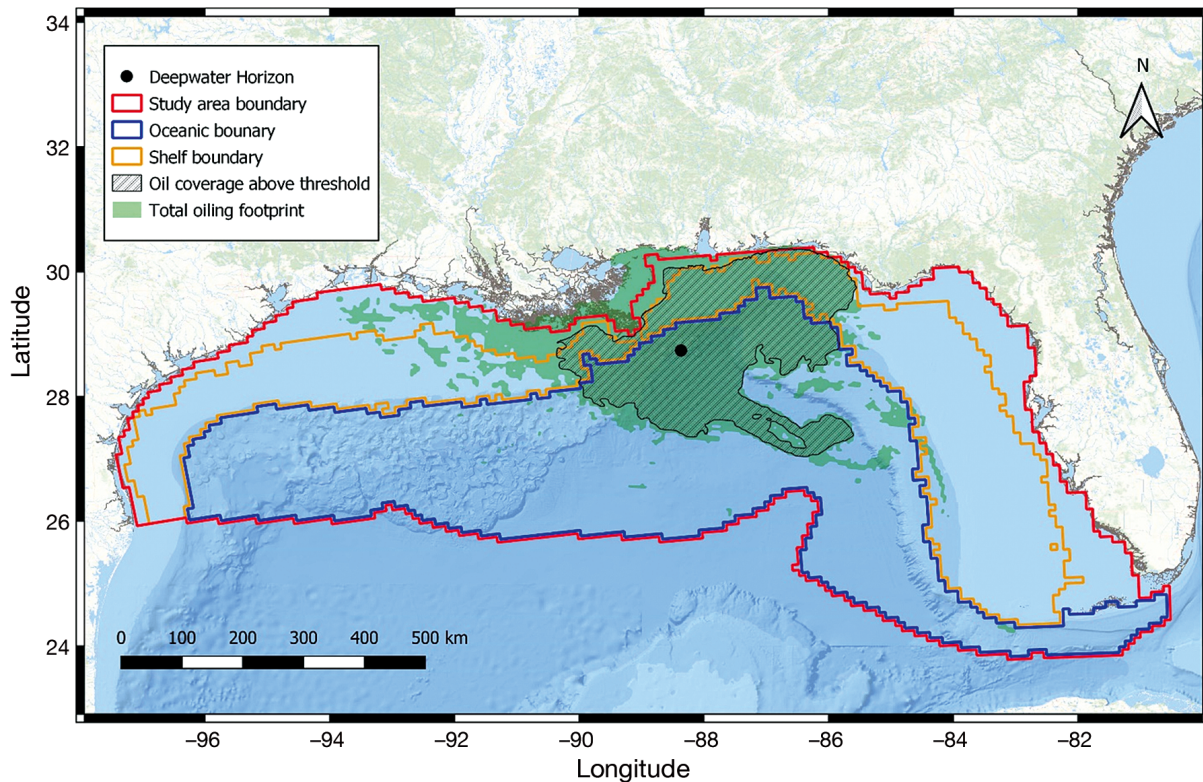


Fig. 1. Study area in US waters of the northern Gulf of Mexico. Red line: study area boundary, derived from a 10×10 km grid used to predict spatial density of the taxonomic units considered. Bottlenose dolphins were separated into shelf and oceanic stocks, with stock boundaries shown as orange and blue lines, respectively. Green shading: the footprint of oil; hatched area: oil coverage above the threshold used for determining exposure; black dot: location of the *Deepwater Horizon* wellhead

(abbreviated Bwsp), including Cuvier's beaked whale *Ziphius cavirostris*, Blainville's beaked whale *Mesoplodon densirostris* and Gervais' beaked whale *M. europaeus* and (2) a group (abbreviated Kosp) that pooled the dwarf sperm whale *Kogia sima* and pygmy sperm whale *K. breviceps*. Taxonomic units were categorized into classes as pelagic, mesopelagic or bathypelagic depending on their foraging ecology (see Table 1).

The killer whale *Orcinus orca*, false killer whale *Pseudorca crassidens* and Fraser's dolphin *Lagenodelphis hosei* were not considered in our analysis; while they are part of the GoMx ecosystem, sightings are rare and abundance estimates are highly uncertain (Hayes et al. 2021). Rice's whale *Balaenoptera ricei* was also not considered because the population size is so small that our modeling approach at the population level was unlikely to be reliable.

The modeling framework used was heavily based on that of Schwacke et al. (2017, 2021) for Ttru in Barataria Bay. We used a sex- and age-structured model of population growth for each taxonomic unit, with additional structure representing 3 exposure classes: (1) animals that were not exposed to oil; (2)

animals that were exposed but will potentially recover; and (3) animals that were exposed and will never recover. The time step for the model was 1 yr, and it incorporated both survival and reproduction impacts of exposure to oil. Each taxonomic unit was assumed to be at carrying capacity pre-spill. Fecundity was assumed to be density-dependent, hence providing a mechanism for recovery to the baseline trajectory after population size was reduced by oil-spill-related effects on demography. Populations were assumed to be closed to immigration and emigration. The model was deterministic, but the population dynamics model propagated uncertainty in its input parameters via a Monte Carlo simulation. Therefore, for each relevant input parameter, we also characterized a full distribution of plausible values to account for the uncertainty, based on either data sources or the EE workshops described below.

2.2. Expert elicitation (EE)

EE is a structured process by which expert knowledge of an uncertain quantity is captured in the form

of a probability distribution (O'Hagan 2019). We used EE to derive distributions for some model parameters where there was limited empirical information. Our methodology followed that of Booth & Thomas (2021), which was based on the Sheffield elicitation framework (Gosling 2018). We held 2 EE workshops. The first, on 13–14 January 2020, elicited parameters relating to the effect of oiling on survival and reproduction as well as the expected recovery of oiled animals. Six experts participated, drawn from the fields of marine mammal epidemiology, animal physiology and veterinary science. The second workshop, on 15–16 January 2020, elicited a parameter related to density dependence. Six (different) experts participated, with expertise in statistics and marine mammal population ecology. Both workshops elicited parameters relevant to Barataria Bay Ttru, as detailed in Schwacke et al. (2021). However, a second focus was on how to translate the knowledge obtained from the field- and desk-based studies undertaken on Barataria Bay Ttru to the pelagic taxa. Further information about the EEs is given in Supplement S2, including details about the rationale behind the assessments made regarding oil-induced reductions in survival and fecundity; more details about each parameter elicited for pelagic taxa are given in the relevant parts of subsequent sections.

2.3. Parametrizing the model

2.3.1. Initial population size and proportion exposed

We estimated the abundance of each taxonomic unit at the time of the oil spill by using the spatial density surface models for cetaceans in the GoMx created by Roberts et al. (2016). These models were based on analysis of shipboard and aerial line transect survey data collected between 1992 and 2014 during all months of the year, but more frequently in spring and summer. Estimates accounted for missed detections within the surveyed transects using line transect analysis methods including a correction for animals missed on the trackline. Outputs of the line transect analysis were used as inputs to a generalized additive model (see Roberts et al. 2016 for details). Roberts et al. (2016) fitted a variety of models; we used the final selected climatological model for each taxonomic unit. Climatological models were based on a suite of candidate time-invariant spatial covariates (such as depth, slope and distance to coast) and 8 d dynamic spatial covariates (such as sea surface temperature, distance to geostrophic eddy and chloro-

phyll *a* concentration). The dynamic covariates were averages over a 30 yr time window for a given 8 d of the year period (e.g. 1–8 January). Given the absence of known patterns of seasonal movement for any of the taxonomic units, we estimated abundance for each of the 46 eight-day periods and took the mean as our overall estimate of baseline abundance. All estimates were made on a 10 × 10 km grid and were clipped to include grid cells with centers inside the stock boundaries for each taxonomic unit (shown in Supplement S3). We used a posterior simulation procedure to quantify uncertainty on the estimates of total abundance for each taxonomic unit: we simulated 10 000 sets of model coefficients from their posterior distribution using a Metropolis Hastings sampler (as implemented in the 'gam.mh' function in the 'mgcv' package in R) and thinned by a factor of 10 to yield 1000 replicate sets. Each of these was used to produce a new density surface on the 10 × 10 km grid for each of the 46 eight-day periods. These were in turn used to estimate, at each iteration, abundance within the stock boundary and within the oil polygon (details of which are given below), leading to a corresponding proportion of the population exposed. Average values were taken over the 46 time periods. The induced link between the outputs across simulation iterations ensured that we preserved the possible correlation between the number of animals in the stock and the number of animals exposed to oil. In a small number of cases, the resampling produced abundance estimates that were unrealistically high (greater than the estimated abundance plus 5 times the estimated standard deviation). These were discarded to avoid distorting the results. This happened at most 1–2 times per taxonomic unit (median and mode 0). Further details are given in Supplement S3.

To characterize the spatial extent of oil exposure in offshore waters, we used data on surface oil coverage and thickness from MacDonald et al. (2015). We assumed that survival and reproductive effects in pelagic cetaceans were restricted to areas where the cumulative amount of DWH surface oil was greater than or equal to that in Barataria Bay. MacDonald et al. (2015) summarized daily (24 April–3 August 2010) oil percent coverage within 5 × 5 km spatial cells in 2 classes: sheen (~1 µm thick) and 'thick' oil emulsions (average thickness ~70 µm). Based on the percent coverage and oil thickness classes, we calculated the average cumulative oil volume per 5 × 5 km cell to be 38.5 m³ over the course of the spill within the waters of Barataria Bay and the adjacent coastal waters out to the 20 m isobath. Oceanic (bottom depth > 200 m) spatial cells where the cumulative oil volume exceeded this

metric were used to create a spatial polygon characterizing the oiling footprint, using ArcGIS (ArcGIS Desktop v.10.5, ESRI) (Fig. 1). The resulting polygon covered an area of approximately 61 820 km². Note that the ‘thick’ oil class was not observed in Barataria Bay, and cells near the wellhead exceeded the cumulative volume metric by 2 to 3 orders of magnitude.

2.3.2. Population dynamics

In the absence of the oil spill, we would not expect any difference between the population dynamics before and after April 2010 for any of the taxonomic units. Here, we describe what was known and assumed for demographic parameters related to both survival and fecundity prior to the oil spill. As noted above, lacking better information, we assumed that all stocks were at carrying capacity (i.e. with constant population size) prior to the oil spill and would have remained so under the no-spill scenario.

A commonly used model to describe age-specific survival is the Siler model (Siler 1979). Schwacke et al. (2017) provided a description of the Siler model and how it was fitted to Ttru strandings data within a Bayesian statistical framework to estimate age- and sex-specific survival. We used 4000 samples from the posterior distribution of the model parameters obtained by Schwacke et al. (2017) as inputs for sex- and age-specific survival in our simulations. Point estimates for these sex- and age-specific survival estimates were presented in Schwacke et al. (2017, their Table S1). Corresponding age-specific survival curves for Ttru and corresponding credible intervals are given here in Supplement S5. We assumed that the results from the Siler model were applicable to Ttrs and Ttro stocks. For the other taxonomic units, information to estimate the parameters of the Siler model was lacking. Therefore, we scaled the model parameterized with Ttru data for the remaining taxonomic units. Using demographic parameters from one species to support inferences for other species has been discussed by several authors (e.g. Barlow & Boveng 1991, Eakin 1994, Caswell et al. 1998). The scaling is typically performed by considering a parameter that links the 2 life histories. Here, we opted to use GD (see Section 4 for justification): the scaling factor for the Siler model was, therefore, the GD for Ttru divided by the GD for each of the other taxonomic units. This means that the same shape is maintained for survival, but the survival function is stretched or compressed to adjust to a rescaled maximum age (com-

pared to Ttru), which was increased or decreased given the scaling factor for each taxonomic unit. The GD used for Ttru was 375 d, and for the other taxonomic units it ranged from 483 d for sperm whales to 327 d for spinner dolphins, leading to scaling factors of 0.776 and 1.15 for sperm whales and spinner dolphins, respectively (see Table 1 and Supplement S4 for justification and references for values used). Given the lack of information to quantify the precision in GD, we ignored any uncertainty in this scaling factor. Nonetheless, we propagated the uncertainty from the original Siler model to the corresponding Siler model for the different taxonomic units by applying the scaling factor to realizations from the posterior of the original Ttru Siler model parameters.

We followed Schwacke et al. (2017, 2022) in assuming that density dependence operates in the population by decreasing annual fecundity as population size increases according to a generalized Beverton-Holt function. This required the definition of 3 different parameters: (1) maximum fecundity rate (F_{\max}); (2) nominal fecundity rate (F_{nom}); and (3) a density-dependent shape parameter (ρ). Following Schwacke et al. (2017, 2022), the first 2 were modeled as beta-PERT (i.e. 4 parameter beta) distributions and the latter as a Gamma distribution. The beta-PERT parameter values used for Ttru F_{\max} were min.: 0.33, mode: 0.34, max.: 0.41 and ρ : 4.0; for F_{nom} , values were min.: 0.13, mode: 0.24, max.: 0.34 and ρ : 4.0. To allow for taxon-specific differences in fecundity and because it is expected that longer-lived animals will also have wider inter-birth intervals (and hence lower fecundity), we scaled the obtained F_{\max} realization by multiplying it by GD, akin to what was described above for survival. Hence, the F_{\max} for an animal with a longer GD than Ttru would be decreased, and vice versa. As recommended by experts in the EE, we used the same distribution for the density dependence parameter ρ as for Ttru in Schwacke et al. (2022): a shifted gamma (to ensure a minimum value for ρ of 2.5) with shape: 6.34 and scale: 1.17. This resulted in a mean value for ρ of 9.93 with a variance of 8.71. Two additional fecundity-related parameters were required and adapted from Schwacke et al. (2022): the baseline reproductive success rate and the age at sexual maturity. Both parameters were scaled for the different taxonomic units based on GD as described above.

The assumption of the populations being at carrying capacity was enforced by solving for the value of F_{nom} that would lead to a stable population, given all the other parameters.

2.3.3. Effects of oil exposure

Experts in the EE considered that the effects on fecundity would, in general, align with the effects on survival. For an exposed animal, its survival and fecundity will be reduced by a given amount following the oil spill. How we obtain that reduction factor for survival and fecundity is described in the next 2 subsections. Whether and how animals recover to baseline levels is described in additional detail after that. The reduction factor (range: 1 to 0) is the quantity required to multiply the baseline value by to obtain a post-oil value: a reduction factor of 1 would mean no reduction.

Schwacke et al. (2022) obtained the following survival reduction (SR) factor for Ttru: $SR_{Ttru} = 0.868$ (95% CI = 0.737–0.964). Based on this, for all other taxonomic units, we elicited expert knowledge, using a shifted scaled beta distribution, to obtain a distribution for the effect of oil on SR, separately for each of 3 foraging classes: pelagic, mesopelagic and bathypelagic.

The impact on fecundity was assumed to be quantified via a reduction in the reproductive success rate. Given that reliable information was only available for BSE Ttru, we used this information to evaluate the relative fecundity to SR ratio, and then, based on the SR for each taxonomic unit, estimated a scaled fecundity reduction (FR). For BSE Ttru, based on Kellar et al. (2017) and following Schwacke et al. (2022), a point estimate for the reproductive success rate before and after the oil spill was 0.65 and 0.19, respectively. This leads to an FR factor of $FR_{Ttru} = 1 - 0.19 / 0.65 = 0.708$. For the taxonomic units considered in this paper, the reduction in fecundity with respect to the reduction in survival was assumed to be proportional to that observed for Ttru, represented here by FR_{Ttru} / SR_{Ttru} . Therefore, the reduction in fecundity for a taxonomic unit, s (FR_s), was given by:

$$FR_s = SR_s \times FR_{Ttru} / SR_{Ttru} = SR_s \times 0.708 / 0.868 \quad (1)$$

where SR_s represents the effect in SR for the taxonomic unit s obtained in the EE. Note that Equation (1) is shown with point estimates only for illustration purposes. For each iteration, we used the sampled values for the fecundity reduction in Ttru and for the reduction in survival both for Ttru and for the taxonomic unit under consideration.

A fundamental aspect of the oil impact is how exposed animals recover over time. Following Schwacke et al. (2022), we defined 2 types of exposed animals: (1) those that never recover from the initial impact, and hence remain with reduced levels of survival and fecundity until they die; and (2) those that do

recover to baseline levels of survival and fecundity. For the proportion of the population that recover, survival and F_{max} were assumed to increase linearly from their impacted level to the baseline level over a number of years equal to the expected lifetime of an animal alive at the time of the spill. The expected lifetime was around 15 yr for Ttru based on estimates of expected lifetime obtained by analysis of the Ttru population projection matrix (see Schwacke et al. 2022 for details of this calculation); for all other taxonomic units, it was derived using the same method. The proportion of the animals exposed to oil that recover to baseline survival and fecundity levels was elicited from the EE experts for Ttru and assumed to be the same across all other taxonomic units.

2.4. Implementation and evaluation of the model

The simulations and model evaluation were implemented in R version 4.2.0 (R Core Team 2023).

To evaluate injury, we simulated the population for each taxonomic unit under 2 scenarios: baseline (no oil spill) and with the oil spill. Simulations were started from the date of the oil spill (April 2010) and projected forward for 75 yr, with a time resolution of 1 yr. The model was run separately for each of the 15 taxonomic units considered. For each of 4000 iterations, a set of random samples from the distributions of all the parameters described above were generated, and the 2 scenarios were run. Care was taken to preserve the correlation across parameter values—for example, each scenario would be run using population sizes and proportions exposed induced by the same realization of the density surface model, and the distributions for the parameters of the Siler model would be from the same draw from the posterior distribution.

The 3 injury metrics used by Schwacke et al. (2017, 2022) were calculated for each iteration: (1) lost cetacean years (LCY), the difference between the baseline and exposed population sizes, summed over the entire modeled time period; (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 at that time.

The size of the injury metrics was expected to vary among taxonomic units. To better understand the sources of this variation, we undertook a regression analysis of the mean value of each injury metric (response variable) as a function of the mean value of

the input parameters (explanatory variables), using taxonomic unit as the sample unit. After a preliminary exploratory analysis, it was clear that only a few inputs were able to explain the injury metrics. We considered an exhaustive search over all the possible models associated with each potential input in this reduced set of inputs, selecting the most parsimonious model based on minimum Akaike information criterion values for interpretation. Details of this analysis are presented in Supplement S6.

Accounting for uncertainty sources in population dynamics models is fundamental (see, e.g. Zylstra & Zipkin 2021). For each taxonomic unit, we evaluated how uncertainty on each input parameter affected the injury metrics. For each parameter within a taxonomic unit, we sampled 500 random deviates from the input distribution and ran the model, holding all other parameters at their mean nominal value. Such uncertainty analysis can inform which variables are causing the greatest uncertainty in the injury metrics; however, uncertainty comes from 2 confounded sources: variability in the input variable and sensitivity of the injury metric to variation in the input variable. To isolate the latter, we also conducted an elasticity analysis to evaluate proportional change in each injury metric resulting from a 1% increase in each input variable (i.e. mean value $\pm 0.5\%$) while holding all other variables at nominal values.

3. RESULTS

The abundance, proportion of the population exposed and corresponding precisions for each taxonomic unit considered are shown in Table 1. Initial population sizes were highly variable across taxonomic units, ranging from just over 2000 animals for Risso's dolphin *Grampus griseus*, pygmy killer whale *Feresa attenuata* and *Kogia* spp. (note this comprises 2 species pooled together) to over 80 000 individuals for pantropical spotted dolphin *Stenella attenuata*. Likewise, the proportion of animals exposed to oil also varied markedly, from 5.7% for Atlantic spotted dolphin *S. frontalis* to 38% for spinner dolphin *S. longirostris*. Using sperm whale as an example, we illustrate the input parameters of the model in Fig. 2, showing the animals' spatial density, the distribution of population sizes and the corresponding proportion exposed for each iteration and age-specific survival by sex.

The EE results for the mean SR for each of the 3 foraging classes for animals exposed to oil were 0.88 (SD: 0.04), 0.86 (0.05), and 0.84 (0.06) for bathypelagic divers, mesopelagic divers and pelagic dolphins, re-

spectively. While SR was thought to be largest for bathypelagic divers, followed by mesopelagic divers and pelagic dolphins, all 3 distributions indicate considerable overlap in these assessments (Fig. 3).

The elicited distribution for the proportion of animals that will recover, assumed to be the same for the taxonomic units considered, was a shifted scaled beta distribution with a mean of 0.166 (95% CI = 0.014–0.411), showing a low value but with considerable uncertainty associated with the upper range of the distribution (Fig. 4).

The estimated injury metrics (LCY, YTR and MPD) for each taxonomic unit are shown in Table 1. The taxonomic units with the highest estimated LCY were Ttrs and pantropical spotted dolphin, with over 30 000 yr, followed by spinner dolphin, Ttro and Atlantic spotted dolphin (all over 10 000 yr; CIs given in Table 1). These large values of LCY were mostly induced by the large population sizes (see also below). In terms of MPD, reported as percentages, there was less variation between taxonomic units, with values ranging from 8.4% (95% CI = 3.3–17.7) for spinner dolphin to under 2% for Clymene dolphin and Atlantic spotted dolphin. Finally, for YTR, average population size was reduced by more than 5% for only 6 taxonomic units; thus, only for those was mean YTR greater than 0 (since 'recovery' was taken to be within 5% of the baseline trajectory). YTR was highest for spinner dolphin (12, 95% CI = 0–21) and sperm whale (11, 95% CI = 0–21).

Our analysis of the main drivers of injury metrics across taxonomic units showed that the main determinants of the magnitude of LCY were initial population size, accounting for 87.7% of the total variance, and proportion of animals exposed, accounting for an additional 4.94%. The main determinants of YTR were the proportion exposed and GD, accounting for 73.89 and 11.13% of the variance explained, respectively. For MPD, the main determinants were proportion exposed, GD and SR, corresponding to 91.19, 6.1 and 2.14% of variance explained. Further details are given in Supplement S6.

The uncertainty analysis revealed that, in general, uncertainty in the results was mostly driven by uncertainty in the density-dependence parameter, baseline age-specific survival, SR factor and proportion exposed. As expected, uncertainty in initial population size only had a strong effect on LCY. In terms of elasticity, the parameters that had a higher influence on results by percent change were the baseline age-specific survival, SR and proportion exposed. Further details are given in Supplement S7. Note that for taxonomic units for which the estimated injury metrics were small, it was difficult to evaluate which param-

Table 1. Inputs and results from a simulation study of the effect of the *Deepwater Horizon* oil spill on pelagic cetaceans, divided into 15 taxonomic units. Rows are sorted by 4 letter taxonomic unit abbreviation. Input columns are foraging ecology (B: bathypelagic; M: mesopelagic; P: pelagic), assumed gestation duration (d), estimated abundance within the study area and proportion exposed to oil over a threshold level. Uncertainty in initial abundance and proportion exposed is given as [coefficient of variation] and (95% confidence interval). Results columns show values and (95% confidence intervals) of 3 injury metrics: LDY: lost cetacean years; YTR: years to recovery; and MPD: maximum proportional decrease

Taxonomic unit	Abbreviation	Inputs				Results		
		Foraging ecology	Gestation duration	Baseline abundance	Proportion exposed	LCY	MPD	YTR
Beaked whales	Bwsp	B	342	3098 [23.2] (2236–4323)	0.14 [18.5] (0.093–0.191)	1207 (445–2899)	3.7 (1.4–7)	0 (0–11)
Pygmy killer whale <i>Feresa attenuata</i>	Fatt	M	424	2152 [31.1] (1137–3762)	0.145 [5.9] (0.128–0.161)	1122 (437, 2809)	4.2 (1.9–6.6)	0 (0–13)
Risso's dolphin <i>Grampus griseus</i>	Ggri	M	418	2065 [18.7] (1378–2910)	0.12 [19.3] (0.077–0.165)	2264 (978–5049)	5.6 (2.6–9.5)	8 (0–18)
Short-finned pilot whale <i>Globicephala macrorhynchus</i>	Gmac	M	453	3063 [10.6] (2489–3759)	0.197 [11.9] (0.154–0.248)	964 (385, 2291)	3.4 (1.5–6.2)	0 (0–12)
Kogia spp.	Kosp	M	348	2322 [18.1] (1650–3288)	0.197 [9.7] (0.166–0.24)	1294 (519–3112)	5.1 (2.3–8.5)	5 (0–14)
Melon-headed whale <i>Peponocephala electra</i>	Pele	B	383	5784 [25.5] (3483–9074)	0.152 [4.8] (0.138–0.166)	2761 (1081–6767)	4.1 (1.9–6.6)	0 (0–12)
Sperm whale <i>Physeter macrocephalus</i>	Pmac	B	483	2561 [9.5] (2117–3094)	0.191 [6.4] (0.168–0.216)	2356 (996–5240)	6.3 (2.7–10.2)	11 (0–21)
Pantropical spotted dolphin <i>Stenella attenuata</i>	Satt	P	345	81233 [5.5] (72954–90464)	0.155 [4.2] (0.142–0.168)	31372 (12884–67606)	3.4 (1.6–5.6)	0 (0–9)
Rough-toothed dolphin <i>Steno bredanensis</i>	Sbre	M	376	4867 [19.0] (3271–6804)	0.148 [2.2] (0.14–0.152)	2232 (901–5207)	4 (1.8–6.3)	0 (0–11)
Clymene dolphin <i>Stenella clymene</i>	Scly	P	346	9065 [14.1] (6873–11826)	0.082 [18.6] (0.054–0.113)	1726 (664–4067)	1.7 (0.7–3.3)	0 (0–0)
Striped dolphin <i>Stenella coeruleoalba</i>	Scoe	P	365	5011 [16.5] (3579–6751)	0.247 [16.0] (0.174–0.323)	3387 (1369–7897)	5.7 (2.5–10.4)	8 (0–17)
Atlantic spotted dolphin <i>Stenella frontalis</i>	Sfro	P	365	48688 [13.7] (37527–62825)	0.058 [16.4] (0.041–0.078)	6961 (2722–15509)	1.3 (0.5–2.3)	0 (0–0)
Spinner dolphin <i>Stenella longirostris</i>	Slon	P	327	16501 [27.9] (9589–27477)	0.377 [22.5] (0.217–0.555)	15255 (5302–44903)	8.4 (3.3–17.7)	12 (0–21)
Bottlenose dolphin <i>Tursiops truncatus</i> (oceanic)	Ttro	M	375	15791 [7.6] (13705–18445)	0.206 [7.8] (0.173–0.239)	10537 (4597–23220)	5.6 (2.5–9.1)	8 (0–16)
Bottlenose dolphin <i>Tursiops truncatus</i> (shelf)	Ttrs	P	375	64897 [6.6] (56992–73804)	0.177 [5.4] (0.159–0.195)	32584 (13377–71967)	4.2 (1.9–6.8)	0 (0–13)

eters most influence the results: it is hard to attribute an effect to a cause when the effect is small.

4. DISCUSSION

Our models indicated that the magnitude of population injury from the DWH oil spill varied across cetacean species and taxonomic units, with the greatest impact on spinner and striped dolphins, sperm whales, Ttro, and Kosp, all of which had estimated decreases of over 5% of the stock at their maximum decline point. The larger decreases were driven by the relatively high proportions of the taxonomic units estimated to be within the oil spill footprint: spinner and striped dolphins (0.377 and 0.247, respectively),

sperm whales (0.191), Ttro (0.206), and Kosp (0.197). Conversely, estimated decreases were lowest for Atlantic spotted and Clymene dolphins, for which only a small proportion of the taxonomic units (0.058 and 0.082, respectively) were exposed.

We found that other model inputs related to density dependence, baseline age-specific survival, and oil-associated SR were also sensitive parameters based on elasticity analysis, and that uncertainty in their values influenced the degree of uncertainty in model outputs. However, the average values of these input parameters were similar across the various taxonomic groups. Mean SR factor from the EE ranged only between 0.84 and 0.88 (Fig. 3). Baseline survival and density dependence factors were scaled based on GD, with scaling factors at the extremes being

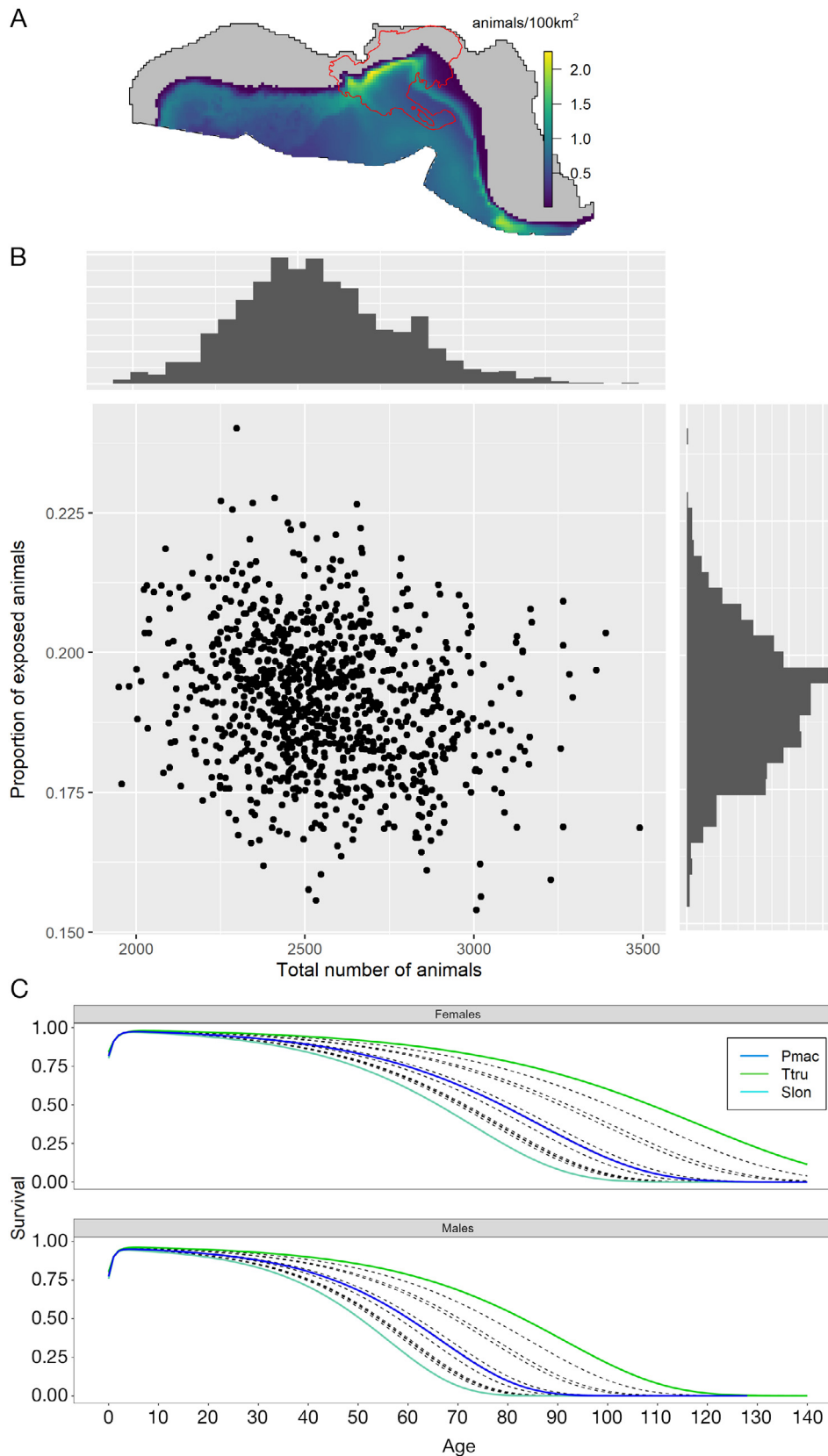


Fig. 2. Example of model inputs for sperm whale, showing (A) animal density over space (animals 100 km⁻²); (B) simulated values of initial population size (x-axis) and proportion of the population exposed to oil (y-axis), with marginal histograms showing the distribution of these 2 inputs; and (C) age-specific survival for males and females for all taxonomic units shown as black dashed lines, with the sperm whale (Pmac; highest survival) highlighted in solid color line. For comparison bottlenose dolphin (Ttru; the baseline) and spinner dolphin (Slon; lowest survival) are also highlighted in solid color lines

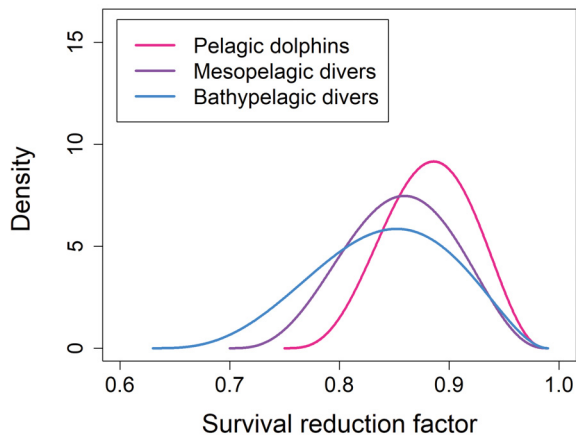


Fig. 3. Distributions obtained from the expert elicitation exercise for the reduction in survival for each foraging ecology group considered

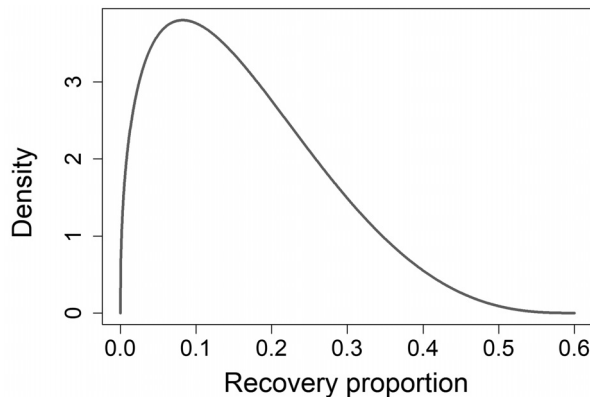


Fig. 4. Expert elicited distribution for the proportion of animals exposed to oil that recover to survival baseline levels within their lifetime

0.77 (sperm whale) and 1.15 (spinner dolphin). In fact, the MPD for sperm whales (0.063) was higher than for other dolphin or *Kogia* spp. (0.051–0.057) that had similar proportions of their stocks exposed. Besides the noted sperm whale and spinner dolphin extremes, other taxonomic groups had a scaling factor within the range of 0.83–1.10. Therefore, while the model outputs were relatively sensitive to these parameters, the input values were not variable enough to create a substantial difference in the estimate of effects among the taxonomic units.

The declines estimated here for pelagic cetaceans are not as large as those estimated by Schwacke et al. (2022) for the population of Ttru in Baratara Bay (MPD: 0.45, 95% CI = 0.14–0.74), nor are the recovery times as long (YTR: 35, 95% CI = 18–67). This is because, as noted above, only a fraction of each pelagic taxonomic unit was estimated to have been exposed to the oil footprint. Nevertheless, we esti-

mate that some individuals were lost in all taxa considered, and that for some taxa, the population may take over 2 decades to recover (upper 95% CI on YTR is 21 for spinner dolphins and sperm whales). The loss of individuals is important for cetaceans, which are protected in the USA under the Marine Mammal Protection Act (MMPA; 16 U.S.C. §1361 et seq.), as well as for all taxa when evaluating injury under natural resource damage assessments. Further, the consequences for the broader GoMx ecosystem may be more important, as the loss of many high trophic predators, even if it represents a relatively small proportion of a given stock, could cascade through the ecosystem (Baum & Worm 2009). For example, the maximum decrease for pantropical spotted dolphins was only 3.4% of the stock, but due to the size of the stock (81 233 individuals), this represents a large loss of individuals. Such a loss is best represented by the LCY metric, which quantifies the number of individuals per year that will not be in the population (or ecosystem) but would have been had the oil spill not occurred. In this respect, the greatest losses were from shelf Ttru and pantropical spotted dolphins, with 32 584 and 31 372 LCY, respectively. In both cases, the high LCY was driven by the large abundance of the stock.

Our modeling framework demonstrates a practical approach for evaluating the impacts of a large-scale environmental event in the face of limited knowledge about population demographics, toxicological dose–response or directly quantifiable exposures. An obvious measurable impact would be an increase in mortality determined from the number of carcasses washing ashore. This is often how ecological effects were previously quantified for non-cetacean species (e.g. see Haney et al. 2014, for an example with birds). However, observed casualties immediately following the event are likely a severe underestimation of true deaths, particularly for pelagic species for which carcasses are extremely unlikely to make it to shore (Williams et al. 2011). Measures from carcass counts also fail to consider the chronic effects that affect survival and reproduction over time. Potentially much longer-lasting and far-reaching impacts at a population level are those less visible because acute mortality immediately following the event is difficult to quantify and, even if it could be measured, it would not include the individuals suffering chronic effects that manifest as reduced survival and reproduction over years to come. Our model addresses these issues.

Our model also addresses limitations in knowledge of demographic parameters for offshore cetaceans, which are difficult to observe and study, by scaling pa-

parameters from a well-studied inshore cetacean species, Ttru. Schwacke et al. (2022) developed a robust population dynamics model for Ttru and it is reasonable to assume that GoMx cetacean species have similar age-specific survival patterns (e.g. Barlow & Boveng 1991). While different parameters including longevity, mean age at death and age at first reproduction have been previously considered for scaling demographic parameters (e.g. Barlow & Boveng 1991, Eakin 1994, Caswell et al. 1998), we chose to use GD. GD is a quantity available for all the species and is less likely to vary across different populations of the same species, providing higher confidence in the transferability of the information available. We found that the GD had only a small influence on YTR and MPD across taxonomic units. Using other scaling factors would lead to different results and essentially would contribute as unquantified variability in our results. This underreported variance conditional on analysis choices is a feature that is pervasive in ecological models and more often ignored than discussed (although see Stanton-Geddes et al. 2014 and Silberzahn et al. 2018).

Limited information was available with respect to GD for some stocks. Therefore, we were not able to incorporate uncertainty in the stock-specific GD estimates. However, for the reasons given above, we do not believe that this uncertainty would substantially affect the injury metrics.

We assume that the rescaled survival function is an adequate model for what would be the survival of the corresponding species. While untested, that seems a plausible assumption. In particular, we assumed that the results from the Siler model were applicable to any Ttru stock in the GoMx; here, both the Ttrs and Ttro stocks. However, it is hard to know to what extent this holds. There are indications that there could be multiple species of *Tursiops* in the western North Atlantic and GoMx (Kingston & Rosel 2004, Moura et al. 2020, Costa et al. 2022), which would then mean that these could also potentially have different demographics. The data used to fit the Siler model come from stranded animals (see details in Schwacke et al. 2017), from which age at death was derived. We would expect that an offshore animal is less likely to be included in a sample of stranded animals than an animal from a coastal or BSE stock (Williams et al. 2011, Carretta et al. 2016). Therefore, if differences in survival exist between nearshore coastal and oceanic populations of Ttru, the results of our model are more likely to reflect inshore than oceanic stocks. Nonetheless, if in the future a better data set to directly parametrize a survival model is obtained for the Ttro stocks, our results for them could be readily revised.

The modeling approach can be tailored to other taxonomic levels, provided the required data at the required scale can be obtained. For example, Ttru are known to have a marked social structure with a fission–fusion system (e.g. Connor et al. 2000). Within the considered taxonomic units, there could be smaller groups of animals that might be interesting to consider as units for analysis (e.g. Speakman et al. 2022). This level of structure has been ignored in our modeling approach but could potentially be incorporated where the appropriate data for each group are available. The analysis by Thomas et al. (2022) to evaluate the impact of a proposed land restoration project on the Ttru in Baratara Bay is a good example.

Despite recent evidence for decreased fecundity with age in cetaceans (e.g. for older females in Indo-Pacific Ttru; Karniski et al. 2018), we assumed no fecundity senescence. Our approach is extendable to deal with age-specific fecundity. That would require information currently lacking for most species. The effect on population trajectory is likely to be negligible because older, potentially senescent, animals make up a very small proportion of the adult population.

Our results are conditional on the inputs considered. While we used what we believe is the best information available at this time, the approach is modular and hence the results can be re-run, including new values or distributions for any of the considered components. Changes in some inputs should lead to proportional changes in some injury metric(s), and the between-taxa and sensitivity analyses allow us to understand what the impact might be. As an example, if new estimates of baseline population size were obtained, one could readily re-run the simulations with these new inputs; if one increased or decreased the initial population size of a given taxonomic unit, keeping everything else the same, we would expect a proportional increase or decrease in the LCY, while MPD and YTR should remain largely unaffected. As another example, we assumed that the populations were at carrying capacity before the oil spill. If a population were below carrying capacity and all other aspects of the scenario were the same, we would expect YTR and LCY to be smaller because the population would recover faster (under density dependence models, populations farther away from carrying capacity grow faster than those closer to it). However, MPD would be similar because this metric is dominated by the size of the initial injury rather than the ensuing recovery process.

The population projection under the no-oil scenario assumes no change to the environment, and so the population remains at carrying capacity. The

projection under the oil-spill scenario assumes that the proportion of the population within the oil footprint is affected in the same way that Barataria Bay Ttru were affected (with some adjustments for species differences). Hence, if there were lurking environmental variables that changed in Barataria Bay, they will affect the estimation here. However, we believe that oil pollution was the dominant factor driving the survival and fecundity changes documented in the Barataria Bay Ttru population after the DWH oil spill, and hence that this will be the dominant factor driving the changes we present in this paper. If additional environmental changes were to be included in the assessment, their effect would have first to be estimated under both no-spill and oil-spill scenarios, and then they could be included in the population model.

Given that we are estimating the injury due to the impact of the oil, a key aspect that directly impacts the results was, perhaps not surprisingly, the proportion of the population exposed to oil. This was evident from the fact that the proportion exposed was the only input parameter that explained significant variation in the mean value of all 3 injury metrics across taxonomic units, and also from the results of the sensitivity analysis, both for the uncertainty component and the elasticity component. Here, we considered the oil footprint present in Fig. 1 as defining the area of impact. In reality, surface oil varied through time in its composition and concentration (Berenshtein et al. 2020, Bracco et al. 2020). The animals themselves were also mobile, although there was evidence that cetaceans did not move to actively avoid surface oil (e.g. Aichinger Dias et al. 2017). Therefore, animals may have moved into and out of varying concentrations of oil, resulting in a larger proportion of the population being affected for a shorter time. Modeling this would require including stock-specific models for animal movement and for the cumulative consequences of short- and long-term exposure to oil at a range of concentrations, all of which are essentially unknown. Our model is a simplification based on available information, and further research is required to determine how the inclusion of finer scale exposure information may influence the estimates of impact. Similarly, we assumed no seasonal movement of populations and used an annual average density surface to estimate the number of animals exposed. While there is no definitive evidence of seasonal movement, there is, for example, evidence for seasonal fluctuations in passive acoustic detections of sperm whales at sites along the continental shelf (Morano et al. 2020). If definitive information about

seasonal movements were available, it could be incorporated into the model by using a seasonal density surface or adding an animal movement component.

Our model only considered direct toxic effects from oil and did not consider indirect effects that could have manifested through changes in the ecosystem, including declining or changing composition of cetacean prey. This could include feedback from the environment on any of the parameters. As an example, Ainsworth et al. (2018), looking at DWH impacts on fish, considered a model that combined ocean physics, chemistry and biology. In addition, reduced numbers of some pelagic cetaceans, near the top of the food chain, could, in turn, affect prey numbers (e.g. Baum & Worm 2009). Evidence exists that there may have been significant changes in the trophic structure in the GoMx as a consequence of the oil spill (e.g. Woodstock et al. 2021). More complex models are required to deal explicitly with such indirect effects and with environmental stochasticity. Methods for assessing the effect of multiple stressors is currently an active research topic (e.g. Tyack et al. 2022).

Another source of uncertainty is the assumption that adverse health effects were limited to pelagic cetaceans in areas with surface oiling greater than or equal to that in Barataria Bay. Spatiotemporal trends in oil weathering, aerial dispersant applications and surface conditions (e.g. wind, waves and rain) would affect both the composition and concentration of oil components available for cetacean inhalation and aspiration, and in turn the resulting toxic effects to each animal (Takeshita et al. 2017). In the estuarine environment, oil may accumulate within the closed system, and the composition and toxicity of the deposited oil changes over time as it decomposes. In contrast, in oceanic waters, the initial exposure was much higher (based upon estimated surface volume), oil was fresher and perhaps contained more volatile components, and oil that never reached the surface was not detected but would be part of the exposure for deep-diving animals. Again, more complex models are required to integrate environmental stochasticity and dose-specific toxicity from different types of oil exposures. However, given the inability to directly measure the effects of oil exposure in oceanic cetaceans, using the proxy of exposure impacts in Barataria Bay based on a comparable metric of oil exposure seems to be the most justified approach.

Although over a decade has passed since the DWH spill, there are few empirical data to support or refute our model's projected changes for these offshore populations, which are inherently difficult to study. Lim-

ited line transect surveys have been conducted to produce updated abundance estimates for some stocks (see Supplement S8), but the large uncertainty in the abundance estimates produced by these surveys means that only large deviations from the projected estimates from our simulations could be detected. Nonetheless, for a few species of dolphin, notably Risso's, Clymene, striped and spinner dolphins, it seems as though we may have underestimated the impact of the oil spill.

The approach presented, building on a population dynamics model informed by available literature and expert knowledge via the EE workshops, is readily transposed to other stocks, species and locations, provided the required information to parametrize the model is available, can be scaled from other related species or can be elicited. Our approach is designed for scenarios where baseline data are missing but severe anthropogenic impacts on natural populations need to be promptly evaluated. By laying a framework for injury quantification under such a scenario, and by discussing its implications and limitations, we hope that our work will help when that time comes.

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