Population consequences of disturbance by offshore oil and gas activity for endangered sperm whales (*Physeter macrocephalus*)

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Keywords: Behavioral disturbance, acoustic, bioenergetics, demographic, foraging

individual resilience following disturbance events. Given our focus on a limited suite of threats and need for field verification of these modeled impacts, precautionary management application of our results is recommended for this endangered species.

Introduction

Sperm whales (*Physeter macrocephalus*) face contemporary threats associated with aggregate exposure to underwater noise and cumulative risks from multiple stressors including pollution, ship strikes, fisheries interactions, oil spills, and noise pollution ([NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board 2017). There seems to be a ubiquitous response in odontocetes to reduce/cease foraging in response to vessel disturbance (Senigaglia et al. 2016; Wisniewska et al. 2018), but short-term adverse behavioral responses by cetaceans to acoustic disturbance can vary greatly, even within the same species (Nowacek et al. 2004; Southall et al. 2007). The level of disturbance is influenced largely by the context in which the stimulus is received, including the origin and level of the sound, and the physical and behavioral state of the animal (Ellison et al. 2012; Gomez et al. 2016; Williams et al. 2014). Observed cetacean behavioral responses include avoidance (Malme et al. 1983; Stone and Tasker 2006); possible displacement (Bryant et al. 1984; Castellote et al. 2012); changes in dive behavior (Richardson et al. 1986), and changes in vocalization frequency and amplitude (Commission 2007; Holt et al. 2009; Watkins 1986). In response to seismic surveys and naval sonar, sperm whales have demonstrated avoidance, changes in locomotion/orientation, changes in dive profiles, cessation of foraging, cessation of resting, and changes in vocal behavior (Isojunno et al. 2016; Jochens et al. 2006; Miller et al. 2012; Miller et al. 2009b; Sivle et al. 2012a).

Deep-diving marine mammals have a substantial requirement for efficient foraging dives, as they must access two vital but spatially-separated resources: air at the surface and food at depth (Kramer 1988). Sperm whales forage in deep-water habitats often containing multiple, depth-segregated prey layers (Fais et al. 2015). Their primary means of locating prey is echolocation (Miller et al. 2004a). This complex acoustic information-gathering allows sperm whales to efficiently locate and access prey resources in a dark, patchy, three-dimensional (3-D) environment (Fais et al. 2015). It is possible that anthropogenic sound could reduce sensory volume (Lima and Zollner 1996), increase search effort required to locate resources (Zollner and Lima 1999), interfere with auditory processing (Fais et al. 2015), and reduce foraging efficiency (Isojunno et al. 2016; Miller et al. 2009b; Sivle et al. 2012b).

Sperm whales are listed as ‘endangered’ under the Endangered Species Act (ESA), and the northern Gulf of Mexico (NGM) stock is listed as a ‘strategic stock’ under the Marine Mammal Protection Act (MMPA), primarily due to the impacts of historical commercial whaling upon the population (Townsend 1935; United States Federal Register 2013). The MMPA defines a stock as an interbreeding group in a common spatial arrangement (United States Federal Register 2013). The NGM sperm whale stock consists of approximately 2,128 (CV=0.08) individuals that are widely distributed year-round across continental slope and oceanic habitats (Roberts et al. 2016). NOAA estimates that the Deepwater Horizon (DWH) oil spill in 2010 exposed 16.1% of the sperm whale population to high concentrations of oil at the surface (Dias et al. 2017). NGM sperm whales were also likely exposed to sub-surface oil, high concentrations of volatile gases that could be inhaled at the surface, and response activities including increased vessel operations, dispersant applications, and oil burns (Dias et al. 2017; Schwacke et al. 2017). In addition, NGM sperm whales are exposed to high levels of anthropogenic noises related to seismic surveys for hydrocarbon deposits in the seabed (**Fig. 1**). The Bureau of Ocean Energy Management (BOEM) anticipates over 4 million line km of seismic surveys in the NGM over the next ten years ([BOEM] Bureau of Ocean Energy Management 2017).

Linking immediate behavioral responses to changes in health or vital rates in a population may be subject to a number of aggregate or synergistic variables. The PCoD (Population Consequences of Disturbance) theoretical framework was developed to evaluate how changes in behavior caused by disturbance may result in population-level effects by impacting functions such as reproduction and foraging, essential to survival ([NRC] National Research Council: Ocean Studies Board 2005). PCoD models require linking the changes in an individual's behavior or physiology as a result of disturbance with health, vital rates, and ultimately population dynamics ([NRC] National Research Council: Ocean Studies Board 2005; King et al. 2015). The transfer functions that estimate the population consequences of disturbance have been determined through matrix models (Caswell 2001), expert elicitation (Martin et al. 2012), stochastic dynamic programming (Mangel and Clark 1988), and bioenergetics modeling (New et al. 2013). The PCoMS (Population Consequences of Multiple Stressors) framework extends the PCoD approach to assess the cumulative risk of exposure to multiple stressors ([NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board 2017).

In this study, we develop a probabilistic framework for quantitatively assessing the cumulative impacts of oil and sound exposure and apply this to NGM sperm whales using a combination of bioenergetic (Farmer et al. 2018) and stage-structured population models (Schwacke et al. 2017). We link reductions in survival rates and reproductive potential associated with oil exposure to reductions in foraging efficiency as a result of acoustic disturbance under differing scenarios of geological and geophysical (G&G) survey activities. We use bootstrapping and multiple model scenarios to encompass uncertainty and highlight knowledge gaps. In addition to informing the future management of G&G survey activities in the NGM ([BOEM] Bureau of Ocean Energy Management 2017), this approach provides a flexible bioenergetics-based PCoD framework that could be adapted for other species and regions.

Methods

Our modeling approach integrates a number of approaches including: (i) acoustic modeling to estimate sound propagation from various G&G survey methods; (ii) animal movement simulations to estimate exposure through three-dimensional sound fields; (iii) dose-response functions to estimate the probability of behavioral disturbance; (iv) a bioenergetic transfer function to relate behavioral responses to physiological effects and translate those physiological effects to changes in individual vital rates; (v) spatial models to determine probability of survey activity near individual whales, proposed mitigation closure effectiveness, and proportion of the population exposed to oil from the DWH spill; and (vi) a demographic model that evaluates stock level consequences of mortalities and reproductive impacts associated with oil exposure and behavioral response to G&G survey activity (**Fig. 2**).

Acoustic Propagation Modeling

Source levels and directivity of airgun arrays were predicted with JASCO's Airgun Array Source Model (AASM; (Austin 2010)). Underwater sound propagation (i.e., transmission loss) was modeled with JASCO's Marine Operations Noise Model (MONM) for a variety of G&G sound sources (**Table S1**). The MONM computes received per-pulse sound exposure levels (SEL) for directional sources at specified depths using the U.S. Naval Research Laboratory's Range-dependent Acoustic Model (RAM) modified to account for an elastic seabed (Zhang and Tindle 1995) for frequencies < 2 kHz and a BELLHOP Gaussian beam ray-trace propagation model (Porter and Liu 1994) for frequencies > 2 kHz. Broadband conversions from sound exposure level (SEL) to root-mean square sound pressure levels (SPL) (L_p, dB re 1 μPa) were calculated using a sliding 100 ms integration window developed from a subset of modeling sites modeled using a full-wave RAM parabolic equation model (FWRAM).

A nominal conversion difference of +10 dB from SEL to SPL was applied across receiver positions for short-duration single airgun and geotechnical source types under the assumption that the shortest temporal integration time of the mammalian ear is 100 ms (MacGillivray et al. 2014; Plomp and Bouman 1959). Conversion values for the larger airgun array source were determined from FWRAM simulations. FWRAM was run along 16 evenly-spaced azimuths to examine the effect of source directivity and direction-specific bathymetric variation. Conversion factors were assigned to MONM sites based on the closest full-waveform model source location and the nearest azimuthal direction, using bilinear interpolation over receiver range and depth.

The size and shape of acoustic footprints from seismic surveys in the NGM are predominantly influenced by water depth and seabed slope. For modeling purposes, the NGM was divided into three main bathymetric areas: Shelf (100-200 m depth), Slope (200-2000 m depth), and Deep (>2000 m depth). Due to depth restrictions on their distribution (Roberts et al. 2016), sperm whales were modeled in the three Slope zones and the Deep zone (i.e., Zones 4-7 in **Fig. 1**). Because the ensonified area would extend beyond the survey zone, simulations of whale behavioral disturbance were modeled to 50 km from the survey limits (red boxes, **Fig. 1**). At 50 km range, M-weighted received levels drop to 120 dB re 1 μPa SPL or lower, roughly the lower limit of the dose-response functions used for behavioral disturbance. High-resolution geophysical (HRG) surveys were modeled near the center of these large area survey boxes (green boxes, **Fig. 1**; **Table S1**). Variability in acoustic source energy propagation due to source, range from source, azimuth from source, and receiver depth was modeled at 30 sites (yellow stars, **Fig. 1**). Water depths throughout the modeled area were derived from the National Geophysical Data Center's 3-arcsecond resolution (~80-90 m) U.S. Coastal Relief Model ([NCEI] National Centers for Environmental Information 2017). Silt sediment was assumed in the Slope zone, and clay sediment was assumed in the Deep zone. Sound speed profiles varied by season, with winter profiles providing the longest propagation estimates due to a surface duct caused by upward refraction in the top 50-75 m. The winter profile was applied to January-March. A summer profile based on August and September measurements was applied to the rest of the year as there were no significant differences between Apr-Dec profiles (GDEM V 3.0; (Carnes 2009; Teague et al. 1990)). Three-dimensional sound fields for all sources (**Table S1**) were modeled for the different survey zones and seasons. The acoustic modeling process is discussed in greater detail in Zeddies (2015).

Animal Movement Modeling

The sounds animals receive in the environment are partly dependent on the location of the sound source relative to the animal. Sperm whale movements were simulated with the Marine Mammal Movement and Behavior (3MB) model (Houser and Cross 2014) parameterized as shown in **Table S2**. Avoidance was not modeled, as this behavior has not been documented in sperm whales exposed to seismic surveys (Miller et al. 2009b; Rankin and Evans 1998; Winsor et al. 2017). Individual simulated animals (animats) accumulated an exposure history as the simulation progressed (**Fig. 3**). As the locations of actual animals within a sound field are unknown, we applied repeated random sampling (Monte Carlo) to provide a heuristic approach to determine the probability of exposure. Animat densities were set as high as practical to allow reasonable computation time, and results were scaled to real-world animal densities using a habitat-based cetacean density model ((Roberts et al. 2016); **Fig. 1**).

Behavioral Disturbance

A sliding window was used to calculate SPL for a series of fixed window lengths (100 ms) within seismic survey pulses (MacGillivray et al. 2014; Plomp and Bouman 1959). The maximum value of SPL over all time window positions was taken to represent the SPL of the pulse. We evaluated disturbance in simulated animals using four different thresholds: (1) a knife-edged threshold of 160 dB SPL re 1 μPa to assess behavioral effects (“160 dB”: ([NMFS] National Marine Fisheries Service 1995, 2000)); (2) a probabilistic step function (“Stepfn”: (Wood et al. 2012)) that models incremental increases in disturbance responses as the level of noise exposure increases (i.e., a 10% probability of response at 140 dB SPL re 1 μPa, 50% probability of response at 160 dB SPL re 1 μPa, and 90% probability of response at 180 dB SPL re 1 μPa); and (3-4) two additional probabilistic dose-response functions (‘*sensu* Nowacek et al. (2015)’ versions A and B). In *sensu* Nowacek et al. (2015) version A, 10% of individuals are disturbed at 111 dB SPL, based on the lowest exposure level reported by Miller et al. (2009b). In version B, 10% of individuals are disturbed at 120 dB SPL, based on the minimum exposure level leading to severe behavioral disturbance reported by Miller et al. (2012). For both *sensu* Nowacek et al. (2015) dose-response functions, 50% of individuals are disturbed at 140 dB [following the guidance of Nowacek et al. (2015)], and 90% at 180 dB SPL [following Wood et al. (2012)]. The 160 dB threshold criteria metric was unweighted. Sounds are less likely to disturb animals at frequencies the animal cannot hear well. To adjust for less-audible frequencies, Type I weighting (Southall et al. 2007) was applied to the SPL sound fields used for the Stepfn and *sensu* Nowacek et al. (2015) dose-response functions.

Accumulated time above threshold is a product of the duration and frequency of exposure. Sperm whale movement data output from 3MB and pre-computed acoustic fields output by AASM, MONM, and FWRAM were combined in the JASCO Exposure Modeling System (JEMS; (Zeddies 2015)). JEMS provided time histories of received levels and slant ranges (the three-dimensional distance between the animat and the source) for all animats. These data were used to generate time series of acoustic exposure on a per animat basis (**Fig. 3**). Due to computational limitations, animat movements within acoustic fields were simulated for seven days. Between 3874-9023 animats were simulated within each zone. The duration of exposure (min) per animat, was tracked using a sliding window approach. The length of sliding windows was 24 h, advanced by 4 h, resulting in up to 37 exposure estimates per animat. Because we used a probabilistic approach to determine whether the animat would be in the survey area on a given day (see below), animats were not tracked once they moved outside the survey area. We summarized the number of animats (mean and SD across 37 24-h samples) exposed above threshold for different exposure durations for each survey, zone, and season. Exposure duration time steps ranged from one shot (0.33 min for large seismic surveys, 0.17 min for high-resolution sources) to a full day of shots (i.e., 1440 min).

Survey Effort Projections and Likelihood of Exposure

Projections of survey effort were developed in terms of annual estimates of the length of line-miles that would likely be surveyed based on historical trends and consultations with industry for each year, survey type, and zone (**Fig. 1**, ([BOEM] Bureau of Ocean Energy

Management 2017)). Projected line-miles were converted to survey days (**Table S3**) based on the vessel speeds for each survey (**Table S1**) and were parsed evenly across months (i.e., ~25% in ‘winter’ sound speed conditions and ~75% in ‘spring/summer/fall’ sound speed conditions).

Ten year projections of daily duration of exposure above threshold (160 dB and Stepfn) for simulated individuals were generated using a bootstrapping approach. Daily random draws modeled disturbance-minutes (D) for individual whales in a zone for each survey as follows:

$$\text{if } \underbrace{S\left(\frac{Days_{survey}}{365}\right)}_{\substack{P(survey\ in\\ zone\ that\ day)}} \times \underbrace{\frac{\left(1 - Area_{homerange}\right)}{Area_{zone}}}_{\substack{P(animat\\ in\ zone)}} \times \underbrace{\frac{Area_{survey}}{Area_{zone}}}_{\substack{P(survey\ in\\ range\ of\ animat)}} \times \underbrace{\left(1 - C_{zone}\right)}_{\substack{P(no\ mitigation\\ closure)}}$$

$$\times \underbrace{\left(1 - P(detection) \times \frac{Area_{shutdown}}{Area_{survey}}\right)}_{\substack{P(no\ shutdown\ due\ to\ animat\\ detected\ within\ 500\ m)}} \geq rand(0,1)$$

$$\text{then } D_{zone} = \underbrace{t\left(SPL > Threshold_{zone,survey,season}\right)}_{\substack{duration\ of\ animat\\ exposure\ to\ survey}}$$

$$\text{else } D_{zone} = 0$$

where *S* is the percentage of days in the season (i.e., Jan 1-Mar 31: 25%, Apr 1-Dec 31: 75%). In this approach, there is an initial hurdle that must be cleared each day for each animat, survey, and zone to determine the likelihood that the animat was exposed at all. If exposed, the duration of exposure is randomly drawn from the raw distribution of observed animat exposure durations (*t*) for that survey-zone combination (**Fig. 4**). This bootstrapping approach encapsulates the uncertainty in the probability of a survey taking place, the probability of a survey taking place next to an animat, the probability of the animat being within the zone, the probability of the animat being detected within a 500 m radius of the survey (requiring a mandatory shutdown), and the probability of an animat being exposed to sounds above the disturbance threshold in a single step across all surveys within a zone. Survey area ($Area_{survey}$) is the simulated area from JEMS for behavioral disturbance evaluation (**Table S1**). The odds of a survey taking place on a given day are based on projections (**Table S3**), incorporating bootstrapped uncertainty of ±25%. Sex-specific home ranges ($Area_{homerange}$) were based on mean kernel density estimator (KDE) home ranges reported for sperm whales tracked in the NGM (Jochens et al. 2006). Because the likelihood of being in the zone was determined on a daily basis as a scalar function without spatial weighting for the probability associated with being at different distances from the home range center, the 50% KDE was used to represent "core" home range (Powell 2000). Shutdown areas ($Area_{shutdown}$) were a 500 m circle around the survey, based on current BOEM regulations. Visual detection probability within 500 m was assumed to be 87% (CV=9%;(Barlow and Sexton 1996) (Barlow and Taylor 2005)). As sperm whale animat exposures were only modeled in regions with water depths exceeding 1000 m, only regions with water depths greater than 1000 m were considered when computing zone areas ($Area_{zone}$). Mitigation effectiveness (discussed below) was incorporated through the term C_{zone}.

Although this approach loses some of the site-specificity and spatiotemporal autocorrelation that would be captured by longer simulations, projections suggest survey duration at the individual level is mostly unknown, especially in regards to when individual exposure would begin and end ([BOEM] Bureau of Ocean Energy Management 2017; Zeddies 2015). Sensitivity runs comparing 7-day to 30-day simulations indicated that 24 h probabilities of exposure scale much more appropriately than the time-series of exposures (Zeddies 2015), providing greater credibility to the realism of these results. If an individual sperm whale was exposed to multiple surveys on a single day, the duration of exposure from the surveys was summed. This approach carries the implicit assumption that exposures to multiple surveys are not simultaneous, which is supported by regulatory and practical requirements for spacing of acoustic surveys.

Physiological Effects of Disturbance

Each 24 h day, on average, sperm whales in the NGM spend 72%±32.7% of their time in foraging dive cycles, consisting of 45 min dives to 644 m depth followed by 9 min surface intervals (Watwood et al. 2006). During a dive cycle, whales spend 53%±5% of their time actively encountering prey at mean depths between 467-643 m (Watwood et al. 2006). Truncated normal distributions were used to stochastically model the percent of time spent in the foraging dive cycle ($t_{divecycle}^{\%}$), minutes underwater per dive ($t_{underwater}^{dive}$), minutes at the surface per dive ($t_{surface}^{dive}$). Total daily time underwater ($t_{underwater}^{d}$) was expressed as:

$$t_{underwater}^{d} = (24 \times 60) \times t_{divecycle}^{\%} \times \frac{t_{underwater}^{dive}}{\left(t_{underwater}^{dive} + t_{surface}^{dive}\right)}$$

The sample distribution for $t_{underwater}^{d}$ is shown in **Fig. 4B**.

In the Gulf of Mexico, controlled exposure experiments (CEE) conducted with eight tagged sperm whales over a series of 30-min intervals during pre-exposure, ramp-up, and full-array airgun firing suggested reduced foraging behavior (Miller et al. 2009b). The most closely approached whale (1.4-5.7 km), exposed to sound levels of at least 111-147 dB SPL re 1 μPa, did not forage during exposure. This unusually long (265 min) resting bout persisted throughout pre-exposure, ramp-up, and full-array conditions, and ceased 4 min after the final airgun pulse

(Miller et al. 2009b). In addition to this observed potential delay to foraging during exposure (Miller et al. 2008; Miller et al. 2009b), Bayesian analysis suggested a 20% decrease in foraging activity was more likely than no change in foraging activity for the seven foraging whales that were exposed to lower levels of sound (Jochens et al. 2006). In CEE off Norway, naval sonar exposures at received levels ranging from 120-169 SPL_{max} re 1 μPa led to foraging disturbance, including alteration or cessation of the production of foraging sounds (i.e., regular clicks and buzzes) and changes in the dive profile (Isojunno et al. 2016). Cessation of foraging did not extend much beyond the duration of the exposure (Isojunno et al. 2016; Miller et al. 2012).

A foraging effects model was developed to account for potential reductions in foraging efficiency anticipated for a given duration of exposure above threshold levels. For each year, zone, and life stage, the dive behavior of 1000 individuals were simulated on a daily basis. Foraging efficiency (f_d) was bounded between 0-100% and was expressed as the percentage of dive time during which the whale was exposed to sounds above threshold (i.e., 160 dB or Stepfn):

$$f_d = \frac{\varphi\left(t^{d}_{underwater} - \sum_{survey=2D}^{AUV} t\big(SPL > Threshold_{zone,survey,d}\big) \times t^{\%}_{divecycle} \times \frac{t^{dive}_{underwater}}{\left(t^{dive}_{underwater} + t^{dive}_{surface}\right)}\right)}{t^{d}_{underwater}}$$

where φ is a foraging impact scalar. This approach assumes that whales lose foraging opportunities during the minutes of a foraging dive when they are exposed to sound above threshold, but foraging efficiency is not impacted when they are not actively diving or receiving sounds below threshold, and they do not abort dives due to sound exposure. For example, if a whale spends 864 min a day underwater (i.e., 72% of its day in the dive cycle and 83% of the dive cycle underwater) and is exposed for 100 min above threshold on that day, its foraging efficiency would be 93% at φ=100% (i.e., 60 min lost foraging opportunity).

A bioenergetic model (Farmer et al. 2018) was developed in R (R Development Core Team 2013). The model incorporated growth, a reproductive cycle, and transitions to different life stages and sub-stages (Chiquet et al. 2013; Lockyer 1981). Bootstrapping incorporated individual variability in body condition (Farmer et al. 2018). Changes in whale body mass and associated energy reserve levels were tracked on a daily basis (**Fig. S1**). During days with undisturbed foraging, whales grew and replenished depleted reserves (Farmer et al. 2018).

During days with disturbed foraging, simulated whales compensated for caloric deficits using carbohydrate reserves, if available (Farmer et al. 2018). Remaining caloric deficits were offset through energy mobilized from lipid and protein reserves in the blubber, muscle, and viscera. If total energy reserves were insufficient to cover the caloric deficit, individuals reached terminal starvation, along with any associated fetus or calf. At terminal starvation, protein stores are greatly depleted, lipid utilization falls, circulating ketones decline, and cardiac tissue and other organs are compromised (Castellini and Rea 1992). It is unlikely that sperm whales in the wild could recover from terminal starvation. Additionally, pregnant or lactating adult females could prioritize their own survival and abort their fetus or abandon their calf if their energy stores hit critical levels (Farmer et al. 2018; New et al. 2013). Following New et al. (2013), critical levels were specified as a uniform distribution between 10^4 kcal and two times the daily energy expenditure (e.g., field metabolic rate, FMR). Relative body condition (RBC) was tracked as the ratio of body reserve energy ($tE_d^{disturbed}$) to expected body reserve energy with undisturbed foraging conditions ($tE_d^{undisturbed}$):

$$RBC = 1 - \left(tE_d^{undisturbed} - tE_d^{disturbed}\right)/tE_d^{undisturbed}$$

Bioenergetic impacts of simulated exposures to seismic survey noise and associated reductions in foraging efficiency were modeled for 10 years. Effects of foraging disturbance were tracked by year and zone as: (i) individuals reaching terminal starvation by life stage, (ii) fetal abortions, and (iii) reductions in RBC by life stage. Simulated individuals reaching terminal starvation were scaled to the real-world NGM stock using bootstrapped predictions of abundance by zone (Roberts et al. 2016). Six model scenarios were evaluated to explore the sensitivity of model outcomes to assumptions about the resilience of individual whales to disturbance (**Table 1**). To evaluate the effects of uncertainty in the foraging impact of behavioral disturbance above threshold, model scenarios were developed with φ set at 100% (Miller et al. 2009b) and with φ uniformly distributed between 20% and 100% (Jochens et al. 2006; Miller et al. 2009b). Model scenarios considered non-optimized (i.e., 'somatic' growth) and partially optimized replacement, where reserves were replaced at random rates ranging between 'somatic' and optimal (i.e., reserves perfectly replaced in proportion to prior losses). Model scenarios were also developed to evaluate the effects of a whale demonstrating a 'hunger response' (McDonald et al. 2017) on days of undisturbed foraging that would increase consumption and corresponding daily growth rate up to three-fold.

Mitigation Effectiveness

The mitigation effectiveness of proposed closures in the Central Planning Area (CPA), Eastern Planning Area (EPA), and Tortugas Area (TA) was evaluated (([BOEM] Bureau of

Ocean Energy Management 2017); **Fig. 1**). Spatial overlap between activities and stock were used to model the reduced risk of exposure (Farmer et al. 2016). Closure effectiveness (C_{zone}) was computed as ratio between the stock abundance within the closed area in the zone relative to the stock abundance in the entire zone (Roberts et al. 2016):

$$C_{zone} = \frac{\sum \bar{N}_{zone}^{closed}}{\sum \bar{N}_{zone}^{total}}$$

The inverse of C_{zone} was incorporated as a multiplier in the probability of exposure equation described above (**Table S4**). Three mitigation impact scenarios were modeled: (1) No areas closed, (2) EPA and TA closed, and (3) CPA, EPA, and TA closed.

<u>Oil Exposure and Cumulative Effects</u>

The cumulative stock impact of reduced survivorship due to oil exposure and noise disturbance were estimated using a stage-structured matrix population model (Caswell 2001; Chiquet et al. 2013). The model was parameterized following (Chiquet et al. 2013), and divided the life-cycle of female animals into five stages: dependent calf, juvenile, reproductively mature, mother with calf, and “post-breeding” female. The duration of the “mother with calf” and “post-breeding” interval combine to determine the inter-birth interval which was set at four years. The model also included a male compartment consisting of calves, immature individuals, and mature individuals (**Fig. S2**). Model runs incorporating impacts from the Deepwater Horizon (DWH) oil spill (Schwacke et al. 2017) included a second cohort of animals that were exposed to DWH oil (**Fig. S2**). In these “Spill” runs, the exposed cohort experienced both reduced survivorship and reduced reproductive success compared to the unexposed cohort. The exposed cohort also contributed “unexposed” calves to the population; the potential effects of contaminant transfer *in utero* and through milk were not considered.

Uncertainty in the population trajectory was estimated by resampling from a uniform distribution between the “worst case” and “best case” stage-specific survival rates presented in Chiquet et al. (2013). The “Baseline” (pre-disturbance and pre-DWH) stage-specific survival rates are shown in **Table S5**. For males, an additional loss term was included in the adult survival rate to account for emigration of males which results in the 72:28 female to male sex ratio observed in the NGM population (Engelhaupt et al. 2009). In “Spill” model runs, a 12% decrease in annual survival rate associated with exposure to DWH oil was included for 2011-2014, and this reduced survivorship decreased linearly over a 10 year period (2015-2025). The exposed cohort also included a 45.5% reduction in calf-production followed by a linear decline in this effect over a 15 year period. These inputs were based upon analyses of the responses of bottlenose dolphin populations to oil exposure (Schwacke et al. 2017). The initial population size was 2,138 (CV = 0.09) sperm whales (Roberts et al. 2016), and resampling from a normal distribution was used to incorporate uncertainty in initial population size into model projections. The size of the exposed cohort was calculated based upon the zone specific population size and the area of each zone that overlapped with the DWH oil exposure polygon (**Fig. S3**, (Roberts et al. 2016; Schwacke et al. 2017)). The resulting exposed cohort was 16.5% of the total initial population for the “Spill” model.

Additional mortality estimated from disturbance scenarios was subtracted from “Spill” model stock survival rates to explore the additional impact of disturbance on population growth rates and trends (e.g., “Spill+Disturbance”). As the NGM sperm whale population has experienced disturbance due to G&G surveys since 1968, terminal values for additional mortality due to disturbance from ten-year simulations were used for demographic model projections. Uncertainty in disturbance effects and sperm whale population distribution was included in these simulations by resampling from a normal distribution using the uncertainty estimated from the disturbance model. For demographic projections, terminal starvation was treated as a proxy for mortality. Annual mortality due to behavioral disturbance was calculated based on projections of the percentage of simulated individuals reaching terminal starvation in each zone scaled to the real-world estimated abundance of sperm whales in each zone (Roberts et al. 2016), across 1000 bootstrapped runs for 1000 individuals of each life stage in each zone. Demographic models were run for an undisturbed "Baseline" stock, a "Spill" impacted stock, and a "Spill+Disturbance" impacted stock for each of the six scenarios shown in **Table 1**.

Results

As modeled, individual effects of acoustic disturbance accrued over time under all scenarios (**Table 1**). Scenarios 1-3 predicted some sperm whales would reach terminal starvation (**Fig. 5**). Under Scenario 1 with a 160 dB dose-response function, 4.4±2.1% (mean±SE) of the population was predicted to reach terminal starvation by 2025, with mature females and calves accounting for the vast majority of the affected individuals (**Fig. 5**). Additionally, up to 11% of fetuses carried by females in Zone 5 were predicted to be aborted. Under the Stepfn dose-response function, by 2025, 0.3±0.2% of the stock was predicted to reach terminal starvation; all individuals reaching terminal starvation were calves and mature females (**Fig. 5**). Few fetal abortions (<1%) were predicted. Uncertainty in total effects was high, with CVs of 0.48 and 0.67 for the 160 dB and Stepfn dose-response functions, respectively. Under the Stepfn dose-response function, no sperm whales were projected to reach terminal starvation and no fetal abortions were predicted for Scenarios 2-6 (**Fig. 5**). Both *sensu* Nowacek et al. (2015) dose-response functions predicted terminal starvation for all mature females and associated calves in Zone 5 for Scenarios 1-3 (**Table S6**). As mature females and calves are still observed in Zone 5 despite decades of G&G surveys, the *sensu* Nowacek et al. (2015) dose-response functions appear overly precautionary.

Relative body condition (RBC) expressed the percentage of available reserves for a disturbed individual whale relative to an undisturbed whale with identical characteristics. The greatest effects on RBC were observed for sexually-mature females, with up to 85% reductions in mean RBC predicted in ten years under the 160 dB dose-response function (**Fig. S4**). Anthropogenic disturbance was projected to have the greatest effects on whale fitness in Zone 5, followed by Zone 6 (**Fig. 1**, **Fig. S4**). Significant (>5%) declines in relative body condition (RBC) were estimated for Scenarios 1-5 under the 160 dB dose-response function and for Scenarios 1-3 under the Stepfn dose-response function (**Fig. 5**, **Fig. S4**).

Under all scenarios, the proposed EPA and TA closures provided little to no significant reduction in predicted percentage of the population reaching terminal starvation. The proposed CPA closure nearly eliminated the risk of simulated individuals reaching terminal starvation due to its coverage of a large proportion of the sperm whale stock (**Fig. 1**).

Demographic stock projections under “Baseline” conditions suggested the sperm whale population would decrease through time even in the absence of the impacts from oil exposure or from continued behavioral disturbance; however, there was substantial uncertainty in both initial stock size and stock trajectory (**Fig. 6**). Although there was uncertainty in the magnitude of the decline, all “Spill” model runs suggested a decline due to mortalities and reproductive failure associated with oil exposure, with a mean reduction in stock size of 26% by 2025 (**Fig. 6**).

Projected changes in stock size varied substantially across “Spill+Disturbance” model runs, depending on disturbance threshold and individual resilience scenario. Substantial additional stock declines were estimated under model Scenarios 1-2 using the 160 dB threshold, with a stock decline under “Spill+Disturbance” Scenario 1 that was approximately 25% greater than “Spill” alone (**Fig. 6**). Slight stock declines were estimated under model Scenario 3 using the 160 dB threshold. Additional mortality predicted under these runs could be partially mitigated by the closure of the CPA. Using the Stepfn threshold, a slight additional decline was predicted under “Spill+Disturbance” Scenario 1 runs relative to “Spill” runs (**Fig. 6**). The Stepfn threshold runs did not predict any significant additional stock declines for “Spill+Disturbance” Scenarios 2-6.

Discussion

All scenarios in our PCoD modeling approach predicted that exposure to very large oil spills will result in significant stock declines for NGM sperm whales, and some scenarios incorporating additional noise effects predict significantly larger stock declines. Oil exposure from the DWH spill was projected to cause substantial short-term mortalities and protracted declines in reproductive success. Frequent, relatively high levels of acoustic disturbance were projected for NGM sperm whales, especially in Zone 5 where the stock, DWH oil, and projected seismic activity have the highest overlap (**Fig. 1**). Modeling individuals through time indicated substantial risk of reduced body condition, some level of fetal abortions, and individuals potentially reaching terminal starvation associated with acoustic disturbance. The substantial variability in projected effects under model Scenarios 1-6 (**Table 1**, **Fig. 5**) clearly illustrated the role of individual resilience when determining population-level consequences of acoustic disturbance. It is unclear whether whales can optimize the replacement of reserves (Farmer et al. 2018) or increase the amount of time spent foraging relative to other activities when prey availability or foraging efficiency is reduced (Boyd 1999; Crocker et al. 2006; McDonald et al. 2017). Sperm whales spend, on average, approximately three-quarters of their day in the foraging dive cycle (Watwood et al. 2006). As such, the levels of compensatory foraging assumed for Scenarios 4-6 (**Table 1**) might be unrealistic due to limits on food intake associated with constraints on prey acquisition and processing (Rosen et al. 2007).

The projected consequences of acoustic disturbance were heavily dependent upon the assumed dose-response function (see **Fig. 5**, **Table S6**). There are two major differences between the 160 dB and Stepfn thresholds: (1) the weighting function applied and (2) the probabilistic dose-response relationship. The Type I weighting applied to the Stepfn reduces the level of the received sound field for low frequency sources such as airguns relative to the unweighted 160 dB threshold. Additionally, although the Stepfn incorporates 10% of individuals disturbed between 140-160 dB SPL, it only includes 50% of the individuals exposed between 160-180 dB SPL. The appropriate lower bound and location of the 50% midpoint varies in applications of dose-response curves for marine mammal behavioral disturbance. Severe behavioral responses have been reported for sperm whales exposed to sonar at received levels as low as 120 dB SPL (Miller et al. 2012). Using data from controlled exposure experiments (CEE), the U.S. Navy has developed behavioral response functions with a 50% midpoint of 165 dB SPL ([USN] United States Department of the Navy 2017). Midpoints in dose response curves from other published CEE with odontocetes exposed to sonar have ranged from 140-172 dB SPL (Antunes et al. 2014; Houser et al. 2013; Miller et al. 2014; Moretti et al. 2014). For seismic surveys, a probabilistic function with a 50% midpoint at ~140 dB SPL has been recommended over the 160 dB threshold (Nowacek et al. 2015) . The positioning of the midpoint is critical to the level of disturbance that is estimated. In the only CEE conducted with seismic airguns in the Gulf of Mexico, all exposed whales exhibited minor to complete foraging disruption under maximum Type I weighted sound pressure levels of at least 135-147 dB SPL, with the most closely approached whale demonstrating what appeared to be the strongest response (Miller et al. 2009b). Additionally, CEE have suggested sperm whale behavioral disturbance may occur at sound exposure levels well below the minimum disturbance thresholds modeled by the 160 dB and Stepfn dose-response functions, and reduction or cessation of foraging during exposure is a likely response (Isojunno et al. 2016; Miller et al. 2009b).

We conducted sensitivity runs using dose-response functions (*sensu* Nowacek et al. (2015)) with substantially lower thresholds for the possible onset of behavioral disturbance. As parameterized, these dose-response functions more closely matched the limited data from CEE in the region (Miller et al. 2009b); however, as modeled, a high proportion of the stock demonstrated behavioral responses to common levels of exposure in Zone 5, with inadequate respites from exposure to replenish depleted reserves. Both *sensu* Nowacek et al. (2015) dose-response functions predicted up to a quarter of the NGM sperm whale stock would reach terminal starvation by 2025, including terminal starvation of all mature females in Zone 5 for Scenarios 1-3 (**Table S6**), with massive (>80%) declines in RBC predicted across all scenarios. Under the least precautionary *sensu* Nowacek et al. (2015) version B Scenario 6, RBC for females in Zone 5 was predicted to be 12.6±18.2% that of an undisturbed female. Sperm whales in Zone 5 have been exposed to similar levels of activity for decades and reproductive females are still prevalent in the area (Engelhaupt et al. 2009). Given this discrepancy between predictions and observations, either sperm whales must be substantially more resilient than modeled by Farmer et al. (2018) and our Scenarios 1-6, or our *sensu* Nowacek et al. (2015) dose-response functions are overly precautionary. The substantial variability in simulated outcomes across dose-response functions further emphasizes the need for more definitive CEE in the region coupled with *in situ* measurement of RBC or a meaningful proxy.

Exploring the effects of disturbance using multiple dose-response functions accounts for some of the uncertainty regarding the actual threshold for behavioral disturbance, which is often context-specific and seldom measured across multiple metrics of exposure (Southall et al. 2007). We also attempted to account for context in that behavioral disturbance only impacted vital rates when whales were engaged in foraging dives. Observations of behavioral responses are difficult to mathematically relate to received sound levels, partially due to inconsistencies in accounting for hearing thresholds across studies (Gomez et al. 2016; Southall et al. 2016). Additionally, more severe behavioral responses are not consistently associated with higher received sound levels (Gomez et al. 2016). Research permits have not allowed for CEE of sperm whales to reach the modeled thresholds of 160 dB for behavioral disturbance. CEE involving seismic surveys are limited and inconclusive, but suggest some sperm whales may cease or decrease foraging activity during exposures below 160 dB (Jochens et al. 2006; Miller et al. 2009b). Decreased foraging activity during exposure can result in substantial reductions in body condition, but at lower risk of terminal starvation compared to when there is complete cessation of foraging and consequently a greater energetic deficit (see **Fig. 5**).

The lack of information regarding the number, location, duration, and distribution of future seismic surveys in the NGM is a major source of uncertainty in this analysis. BOEM estimates of survey effort were generated by forward-projecting historical trends; however, industry activities are sensitive to the pricing and supply and demand for oil and gas. To account for this uncertainty, we modeled effort as ±25% of BOEM's projected levels ([BOEM] Bureau of Ocean Energy Management 2017). This analysis did not consider other sources of anthropogenic noise such as underwater sounds associated with on-lease development activities and vessel traffic noise. Thus, our impact assessment may be an underestimate of aggregate sound exposure in the Gulf of Mexico.

One of the most important contemporary questions in marine ecology is how to assess the cumulative effects of multiple stressors (Rudd 2014). Quantifying the cumulative impact of these stressors on marine stocks is essential for effectively implementing and adaptively managing anthropogenic activities (United States Congress 1969). There is a growing interest in predicting how different stressors will interact to affect individuals and populations of marine mammals; however, interaction rates are difficult to quantify ([NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board 2017). We evaluated the cumulative effects of oil exposure and behavioral disturbance associated with G&G activities, but did not quantify the interaction rate between these processes, if such an interaction exists.

Modeling a dynamic environment over a long time period is challenging and computationally intensive. We attempted to capture the uncertainty in sperm whale bioenergetics modeling through bootstrap Monte Carlo sampling. Due to data limitations and computational demands, assumptions were made that have directional bias that is difficult to quantify but easily understood (**Table 2**). The unevaluated consequences of a dynamic metabolic rate, migration, social grouping, localized variability in acoustic propagation parameters, or interactions between stressors could lead to over- or under-estimation of effects. Our modeling approach failed to account for a variety of factors that would likely result in more pessimistic stock projections, including: (i) the energetic consequences of avoidance, (ii) depensatory reproductive rates, (iii) the effects of seismic survey pulses on sperm whale prey and resulting effects on foraging sperm whales, (iv) increased sound production, (v) potential disturbances below modeled thresholds, (vi) acoustic signal masking, (vii) effects of temporary and permanent threshold shifts on foraging sperm whales, (viii) elevated stress levels, (ix) dehydration and ketosis, (x) health effects of reduced body condition, (xi) increased risk of decompression sickness due to behavioral and physiological responses to received sound; and (xii) cultural effects of individual mortalities (**Table 2**).

The majority of our PCoD model scenarios predicted significant reductions in sperm whale body condition as a consequence of anthropogenic disturbance. Oil exposure was implicated in reduced vital rates in the baseline population due to mortality and reproductive failure, but is also likely to result in reduced body condition for survivors (Carmichael et al. 2012; Schwacke et al. 2013). Oil spills may produce a pulse of polycyclic aromatic hydrocarbon exposure that may cause long-lasting lung disease, altered immune response, and disruption of the hypothalamic-pituitary-adrenal axis (Mazet et al. 2001; Mohr et al. 2008; Schwacke et al. 2013; Schwartz et al. 2004). It is unclear how disturbance and oil exposure stressors might interact (i.e., additive, antagonistic, synergistic) when they co-occur; however, interaction effects beyond those listed in **Table 2** could lead to more pessimistic conclusions regarding stock status than those we have presented. Adult female NGM sperm whales are, on average 1.5-2.0 m smaller than the global mean (Jaquet 2006) and calves may be substantially smaller at birth than the expected size of calves from whaling data (Jaquet & Gendron, unpublished data). This may be an adaptation to a unique environment (Best et al. 2017); however, it is also possible that decades of behavioral disturbance have resulted in reduced body reserves and associated stunted growth (De Onis et al. 1997). Reduced body reserves have been implicated in lower reproductive potential (Le Boeuf et al. 2000; Lockyer 1987; Miller et al. 2011; Williams et al. 2013) and reduced calf size and fitness (Christiansen et al. 2014; Christiansen et al. 2018).

Our PCoD modeling process has clarified major sources of uncertainty in the estimation of oil and G&G survey effects on the NGM sperm whale stock. We propose the following ranked list of research priorities: (i) historical context for seismic survey activity, (ii) improved dose-response functions for behavioral disturbance, (iii) estimated sperm whale hunger response levels, (iv) noise effects on sperm whale prey, (v) relative body condition estimates for NGM sperm whales, and (vi) improved population abundance estimates. NGM sperm whales are long-lived and have been exposed to some level of offshore seismic survey activities since the 1960s. Having a better sense of the level of historical survey effort would provide context for projected effort levels and inform status quo whale body condition, and potentially also help identify which model scenarios are most realistic. Model results for the 160 dB, Stepfn, and *sensu* Nowacek et al. (2015) dose-response functions were quite different. Having an activity context-specific dose-response function for sperm whales (e.g., (Harris et al. 2015)) exposed to seismic survey sound would require additional CEE similar to Miller et al. (2009a). The biggest contributor to modeled individual resilience is the ability of whales to increase consumption rates on days following a disturbance event to mitigate caloric losses (Farmer et al. 2018). Information collected in the Gulf of Mexico using a BACI (Before-After-Control-Impact) design where foraging levels before, during, and after exposure are tracked over several days across many individuals would provide the statistical power to quantify compensatory consumption rates following exposure while controlling for individual variability. Laboratory and field experiments have suggested that anthropogenic sound may indirectly affect sperm whales by altering prey abundance, behavior, and distribution (André et al. 2011; Engås et al. 1996; Slotte et al. 2004). The BACI design proposed above could be coupled with measurement of prey species concentration using trawls (Judkins et al. 2015) or echosounders (Goss et al. 2001). The effects of seismic survey noise on body condition could be informed through a comparison of buoyancy-based estimates of sperm whale body condition from D-tag data (Miller et al. 2004b) between heavily-exposed NGM whales to whales in the historically "unexposed" Tortugas Area as well as other locations across the globe, or aerial photogrammetry to assess volume changes in individual whales over the course of repeated exposures (Christiansen et al. 2018). Finally, substantial discrepancy exists in current population estimates for NGM sperm whales [i.e., 763 (CV=0.38) (Waring et al. 2016); 2,138 (CV=0.09) (Roberts et al. 2016)] and a long-term series of estimates with tight confidence limits does not exist, confounding efforts to use population estimates to infer which model scenarios might be the most realistic.

Sperm whale populations are still recovering from massive population declines associated with commercial whaling operations (Whitehead 2002). The NGM sperm whale stock is relatively small, with individual home ranges that heavily overlap with areas of current and proposed G&G survey activities (**Fig. 1**, (Jochens et al. 2006)). Medium-sized (≥159 kL) oil spills are anticipated every 2-4 years in the NGM, with large spills (≥1590 kl) every 10-16 years (Ji et al. 2017). Global spill trend analysis suggests that a DWH-sized oil spill may occur in the Gulf of Mexico every 17 years (range: 8 to 91 years; (Eckle et al. 2012)). Demographic model projections under some model scenarios predicted that declines in the sperm whale stock anticipated as a result of DWH oil exposure would be exacerbated by behavioral disturbance associated with proposed G&G surveys. These simulations suggest frequency and duration of exposure are the primary drivers for behavioral disturbance leading to population consequences (Farmer et al. 2018). Managers should consider the cumulative impacts of multiple, sublethal stressors when determining allowable harm limits (Williams et al. 2016). The CPA is the primary area of overlap between G&G activities and the sperm whale stock, and simulations indicated a partial closure of the CPA to G&G activity would nearly eliminate the risk of individuals reaching terminal starvation due to behavioral disturbance. Area-specific survey effort caps across survey methods in biologically important areas or broader-scale scale shutdown requirements (e.g., based on PAM detections or aerial surveys within several kilometers of the survey activity) could greatly limit the probability of significant adverse effects by reducing the duration and frequency of exposures in areas where the NGM stock may be most sensitive to disturbance. Unmitigated and frequent behavioral disturbance from the projected levels of G&G surveys in the future may lead to reduced body condition and possibly terminal starvation for adult whales and associated calves. Future analyses should consider the additional potential reproductive impacts of reduced female body condition or fetal abortions, which were predicted under nearly all model scenarios.

Evaluating extinction risk is a synergistic process that should consider multiple threatening processes simultaneously over the long term (Brook et al. 2008). There are numerous additional stressors associated with oil and gas activity that should be considered in future analyses, including vessel strike injury and mortality; sound exposure from oil transport, survey and support vessels; pile driving sounds associated with construction activities; marine debris ingestion and/or entanglement; and potential exposure to future oil spills and dispersants. It is critical to develop a Population Consequences of Multiple Stressors (PCOMS; ([NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board 2017)) model for cetaceans in the Gulf of Mexico to address the cumulative effects of the myriad anthropogenic threats that may have population consequences – even with imperfect parameterization, this tool would allow for a meaningful relative comparison between management alternatives.

Given our limited focus on two stressors (DWH oil exposure and aggregate noise exposure) out of a suite of threats to this endangered species, precaution in applying these results is warranted. Currently, U.S. regulations focus on the exposure limits for auditory impacts in marine mammals, but there is no final guidance on probabilistic dose-response functions required to evaluate the impacts of sound exposure for marine mammals under the regulatory requirements of the MMPA and ESA. The likelihood of population level impacts of disturbance is potentially much greater than auditory impacts due to the lower thresholds and larger areas over which disturbance may occur. The results of these simulations provide a quantitative framework that can assist marine wildlife managers to evaluate sound exposure limits for disturbance and evaluate the possible benefits of mitigation alternatives to support policy decisions for sperm whales in the NGM.

Disclaimer: The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of NOAA, BOEM, the U.S. Department of Commerce, or the U.S. Department of the Interior.

Acknowledgments: The authors would like to thank Laura Engleby, Rachel Sweeney, David Bernhart, Allison Hernandez, Benjamin Laws, Eric Patterson, D. Ann Pabst, Heather Koopman, Robin Dunkin, and Christina Lockyer for their assistance in the development of this manuscript. Special thanks to the Marine Mammal Institute of Oregon State University and International Association of Geophysical Contractors for providing the survey lines used in Figure 1. The acoustic exposure modeling portion of this work was supported by the US Department of the Interior, Bureau of Ocean Energy Management, Environmental Studies Program, Washington, DC [Contract Number M14PC00004]. Electronic versions are available upon request from the senior author through the project database.

Literature Cited

[BOEM] Bureau of Ocean Energy Management, 2017. Gulf of Mexico OCS proposed geological and geophysical activities: Western, Central, and Eastern planning areas. Final Environmental Impact Statement, ed. B.o.O.E. Management. Bureau of Ocean Energy Management, Washington, D.C.

[NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board, 2017. Approaches to understanding the cumulative effects of stressors on marine mammals. National Academies Press.

[NCEI] National Centers for Environmental Information, 2017. U.S. Coastal Relief Model, ed. NOAA-NCEI.

[NMFS] National Marine Fisheries Service, 1995. Small takes of marine mammals incidental to specified activities; offshore seismic activities in southern California: Notice of issuance of an incidental harassment authorization, pp. 53753-53760. National Oceanographic and Atmospheric Administration, Federal Register.

[NMFS] National Marine Fisheries Service, 2000. Small takes of marine mammals incidental to specified activities; Marine seismic-reflection data collection in southern California, ed. D.o. Commerce, pp. 16374-16379. National Oceanographic and Atmospheric Administration, Federal Register.

[NRC] National Research Council: Ocean Studies Board, 2005. Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. National Academies Press.

[USN] United States Department of the Navy, 2017. Final supplemental environmental impact statement/supplemental overseas environmental impact statement for surveillance towed array sensor system low frequency (SURTASS LFA) sonar, p. 723. Department of the Navy,, Arlington, Virginia.

André, M., Solé, M., Lenoir, M., Durfort, M., Quero, C., Mas, A., Lombarte, A., van der Schaar, M., López-Bejar, M., Morell, M., 2011. Low-frequency sounds induce acoustic trauma in cephalopods. Frontiers in Ecology and the Environment 9, 489-493.

Antunes, R., Kvadsheim, P.H., Lam, F.P., Tyack, P.L., Thomas, L., Wensveen, P.J., Miller, P.J., 2014. High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (Globicephala melas). Mar Pollut Bull 83, 165-180.

Austin, M., A. MacGillivray, D. Hannay, M. Zykov, 2010. Marine Acoustics (Enbridge Northern Gateway Project 2006), In Technical Data Report. ed. J.A. Sciences, Dartmouth, Nova Scotia, Canada.

Austin, M.E., MacGillivray, A.O., Chapman, N.R., 2012. Acoustic transmission loss measurements in queen charlotte Basin. Canadian Acoustics 40, 27-31.

Ball, Z.B., Barnes, R.H., Visscher, M.B., 1947. The effects of dietary caloric restriction on maturity and senescence, with particular reference to fertility and longevity. American Journal of Physiology--Legacy Content 150, 511-519.

Barlow, J., Sexton, S., 1996. The Effect of Diving and Searching Behavior on the Probablility of Detecting Track-line Groups, Go, of Long-diving Whales During Line Transect Surveys. National Marine Fisheries Service, Southwest Fisheries Center.

Barlow, J., Taylor, B.L., 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. Marine Mammal Science 21, 429-445.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395, 177-185.

Best, P.B., Tormosov, D., Brandão, A., Mikhalev, Y., 2017. Geographical variation in the body size of adult female sperm whales (Physeter macrocephalus)–an example of McNab's resource rule? Mammalia 81, 189-196.

Boyd, I., 1999. Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. Behavioral Ecology 10, 198-208.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J., 2008. Synergies among extinction drivers under global change. Trends in ecology & evolution 23, 453-460.

Bryant, P.J., Lafferty, C.M., Lafferty, S.K., 1984. Reoccupation of Laguna Guerrero Negro, Baja California, Mexico, by gray whales. The gray whale, Eschrichtius robustus, 375-387.

Buckingham, M.J., 2005. Compressional and shear wave properties of marine sediments: Comparisons between theory and data. The Journal of the Acoustical Society of America 117, 137-152.

Carder, D., Ridgway, S., 1990. Auditory brainstem response in a neonatal sperm whale, Physeter spp. The Journal of the Acoustical Society of America 88, S4-S4.

Carmichael, R.H., Graham, W.M., Aven, A., Worthy, G., Howden, S., 2012. Were multiple stressors a 'perfect storm'for northern Gulf of Mexico bottlenose dolphins (Tursiops truncatus) in 2011? PloS one 7, e41155.

Carnes, M.R., 2009. Description and Evaluation of GDEM-V 3.0. Naval Research Lab Stennis Space Center Ms Oceanography Div.

Castellini, M., Rea, L., 1992. The biochemistry of natural fasting at its limits. Cellular and Molecular Life Sciences 48, 575-582.

Castellote, M., Clark, C.W., Lammers, M.O., 2012. Acoustic and behavioural changes by fin whales (Balaenoptera physalus) in response to shipping and airgun noise. Biological Conservation 147, 115-122.

Caswell, H., 2001. Matrix population models. Wiley Online Library.

Chiquet, R.A., Ma, B., Ackleh, A.S., Pal, N., Sidorovskaia, N., 2013. Demographic analysis of sperm whales using matrix population models. Ecological modelling 248, 71-79.

Christal, J., Whitehead, H., Lettevall, E., 1998. Sperm whale social units: variation and change. Canadian Journal of Zoology 76, 1431-1440.

Christiansen, F., Víkingsson, G.A., Rasmussen, M.H., Lusseau, D., 2014. Female body condition affects foetal growth in a capital breeding mysticete. Functional Ecology 28, 579-588.

Christiansen, F., Vivier, F., Charlton, C., Ward, R., Amerson, A., Burnell, S., Bejder, L., 2018. Maternal body size and condition determine calf growth rates in southern right whales. Marine Ecology Progress Series 592, 267-281.

Commission, I.W., 2007. Report of the standing working group on environmental concerns. Journal of Cetacean Research and Management 9, 227-296.

Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales. Trends in ecology & evolution 13, 228-232.

Cranford, T.W., Krysl, P., 2015. Fin whale sound reception mechanisms: skull vibration enables low-frequency hearing. PloS one 10, e0116222.

Crocker, D.E., Costa, D.P., Le Boeuf, B.J., Webb, P.M., Houser, D.S., 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. Marine Ecology Progress Series 309, 1-10.

Crum, L.A., Mao, Y., 1996. Acoustically enhanced bubble growth at low frequencies and its implications for human diver and marine mammal safety. The Journal of the Acoustical Society of America 99, 2898-2907.

De Onis, M., Blossner, M., Organization, W.H., 1997. WHO global database on child growth and malnutrition.

Dias, L.A., Litz, J., Garrison, L., Martinez, A., Barry, K., Speakman, T., 2017. Exposure of cetaceans to petroleum products following the Deepwater Horizon oil spill in the Gulf of Mexico. Endangered Species Research 33, 119-125.

Eckle, P., Burgherr, P., Michaux, E., 2012. Risk of large oil spills: a statistical analysis in the aftermath of Deepwater Horizon. Environmental science & technology 46, 13002-13008.

Ellison, W., Southall, B., Clark, C., Frankel, A., 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conservation Biology 26, 21-28.

Engås, A., Løkkeborg, S., Ona, E., Soldal, A.V., 1996. Effects of seismic shooting on local abundance and catch rates of cod ((Gadus morhua) and haddock)(Melanogrammus aeglefinus). Canadian Journal of Fisheries and Aquatic Sciences 53, 2238-2249.

Engelhaupt, D., Hoelzel, A.R., Nicholson, C., Frantzis, A., Mesnick, S., Gero, S., Whitehead, H., Rendell, L., Miller, P., De Stefanis, R., Canadas, A., Airoldi, S., Mignucci-Giannoni, A.A., 2009. Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (Physeter macrocephalus). Mol Ecol 18, 4193-4205.

Fais, A., Soto, N.A., Johnson, M., Pérez-González, C., Miller, P., Madsen, P.T., 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. Behavioral Ecology and Sociobiology 69, 663-674.

Farmer, N.A., Gowan, T.A., Powell, J.R., Zoodsma, B.J., 2016. Evaluation of Alternatives to Winter Closure of Black Sea Bass Pot Gear: Projected Impacts on Catch and Risk of Entanglement with North Atlantic Right Whales Eubalaena glacialis. Marine and Coastal Fisheries 8, 202-221.

Farmer, N.A., Noren, D.P., Fougères, E.M., Machernis, A., Baker, K., 2018. Resilience of the endangered sperm whale (Physeter macrocephalus) to foraging disturbance in the Gulf of Mexico, USA: A bioenergetic approach. Marine Ecology Progress Series In Press.

Fernández, A., Edwards, J., Rodriguez, F., De Los Monteros, A.E., Herraez, P., Castro, P., Jaber, J., Martin, V., Arbelo, M., 2005. “Gas and fat embolic syndrome” involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. Veterinary Pathology 42, 446-457.

Gomez, C., Lawson, J.W., Wright, A.J., Buren, A.D., Tollit, D., Lesage, V., 2016. A systematic review on the behavioural responses of wild marine mammals to noise: the disparity between science and policy. Canadian Journal of Zoology 94, 801-819.

Goss, C., Middleton, D., Rodhouse, P., 2001. Investigations of squid stocks using acoustic survey methods. Fisheries Research 54, 111-121.

Harris, C.M., Sadykova, D., DeRuiter, S.L., Tyack, P.L., Miller, P.J., Kvadsheim, P.H., Lam, F.-P.A., Thomas, L., 2015. Dose response severity functions for acoustic disturbance in cetaceans using recurrent event survival analysis. Ecosphere 6, 1-14.

Holt, M.M., Noren, D.P., Dunkin, R.C., Williams, T.M., 2015. Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. Journal of Experimental Biology 218, 1647-1654.

Holt, M.M., Noren, D.P., Veirs, V., Emmons, C.K., Veirs, S., 2009. Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise. The Journal of the Acoustical Society of America 125, EL27-EL32.

Hooker, S.K., Fahlman, A., Moore, M.J., De Soto, N.A., De Quiros, Y.B., Brubakk, A.O., Costa, D.P., Costidis, A.M., Dennison, S., Falke, K., 2012. Deadly diving? Physiological and behavioural management of decompression stress in diving mammals, In Proc. R. Soc. B. pp. 1041-1050. The Royal Society.

Houser, D., Howard, R., Ridgway, S., 2001. Can diving-induced tissue nitrogen supersaturation increase the chance of acoustically driven bubble growth in marine mammals? Journal of Theoretical Biology 213, 183-195.

Houser, D.S., Cross, M.J., 2014. Marine Mammal Movement and Behavior (3MB): A Component of the Effects of Sound on the Marine Environment (ESME) Distributed Model. BIOMIMETICA.

Houser, D.S., Martin, S.W., Finneran, J.J., 2013. Exposure amplitude and repetition affect bottlenose dolphin behavioral responses to simulated mid-frequency sonar signals. Journal of Experimental Marine Biology and Ecology 443, 123-133.

Isojunno, S., Curé, C., Kvadsheim, P.H., Lam, F.P.A., Tyack, P.L., Wensveen, P.J., Miller, P.J.O., 2016. Sperm whales reduce foraging effort during exposure to 1–2 kHz sonar and killer whale sounds. Ecological applications 26, 77-93.

Jaquet, N., 2006. A Simple Photogrammetric Technique to Measure Sperm Whales at Sea. Marine Mammal Science 22, 862-879.

Jaquet, N., Gendron, D., 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. Marine Biology 141, 591-601.

Ji, Z.-G., Johnson, W.R., DuFore, C.M., 2017. Oil-Spill Risk Analysis: Gulf of Mexico Outer Continental Shelf (OCS) Lease Sales, Eastern Planning Area, Central Planning Area, and Western Planning Area, 2017–2022, and Gulf-wide OCS Program, 2017–2086, ed. United States Department of the Interior. Bureau of Ocean Energy Management, Division of Environmental Sciences, Sterling, VA.

Jochens, A., Biggs, D., Engelhaupt, D., Gordon, J., Jaquet, N., Johnson, M., Leben, R., Mate, B., Miller, P., Ortega-Ortiz, J., 2006. Sperm Whale Seismic Study in the Gulf of Mexico. Summary Report: 2002-2004. United States Department of the Interior. Minerals Management Service. Gulf of Mexico OCS Region.

Judkins, H., Arbuckle, S., Vecchione, M., Garrison, L., Martinez, A., 2015. Cephalopods in the potential prey field of sperm whales (Physeter macrocephalus)(Cetacea: Physeteridae) in the northern Gulf of Mexico. Journal of natural history 49, 1267-1280.

Kawakami, T., 1980. A review of sperm whale food. Sci. Rep. Whales Res. Inst 32, 199-218.

King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L., Harwood, J., Kurle, C., 2015. An interim framework for assessing the population consequences of disturbance. Methods in Ecology and Evolution 6, 1150-1158.

Kramer, D.L., 1988. The behavioral ecology of air breathing by aquatic animals. Canadian Journal of Zoology 66, 89-94.

Kvadsheim, P.H., Miller, P.J., Tyack, P.L., Sivle, L.L., Lam, F.-P.A., Fahlman, A., 2012. Estimated tissue and blood N2 levels and risk of in vivo bubble formation in deep-, intermediate-and shallow diving toothed whales during exposure to naval sonar. Frontiers in physiology 3, 125.

Le Boeuf, B., Crocker, D.E., Costa, D.P., Blackwell, S.B., Webb, P.M., Houser, D.S., 2000. Foraging ecology of northern elephant seals. Ecological monographs 70, 353-382.

Lima, S.L., Zollner, P.A., 1996. Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers. Behavioral Ecology and Sociobiology 38, 355-363.

Lockyer, C., 1981. Estimates of growth and energy budget for the sperm whale, Physeter catodon. FAO Fisheries Series (FAO).

Lockyer, C., 1987. The relationship between body fat, food resource and reproductive energy costs in North Atlantic fin whales (Balaenoptera physalus), In Symposia of the Zoological Society of London. pp. 343-361.

MacGillivray, A.O., Racca, R., Li, Z., 2014. Marine mammal audibility of selected shallow-water survey sources. The Journal of the Acoustical Society of America 135, EL35-EL40.

Madsen, P.T., Johnson, M., Miller, P.J.O., Aguilar Soto, N., Lynch, J., Tyack, P., 2006. Quantitative measures of air-gun pulses recorded on sperm whales (Physeter macrocephalus) using acoustic tags during controlled exposure experiments. The Journal of the Acoustical Society of America 120, 2366-2379.

Malme, C., Miles, P., Clark, C., Tyack, P., Bird, J., 1983. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. BBN Report 5366, Bolt Beranek & Newman Inc., Cambridge, Mass., for US Minerals Management Service, Anchorage, Alaska. NTIS PB86-174174. Report from Bolt Beranek and Newman Inc. for US Minerals Management Service, Anchorage, AK.

Mangel, M., Clark, C.W., 1988. Dynamic modeling in behavioral ecology. Princeton University Press.

Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., LOW-CHOY, S., McBride, M., Mengersen, K., 2012. Eliciting expert knowledge in conservation science. Conservation Biology 26, 29-38.

Matthews, L.H., 1938. The sperm whale, Physeter catodon. University Press.

Matthews, M.-N.R., MacGillivray, A.O., 2013. Modelled and measured sound levels from a seismic survey in the Canadian Beaufort Sea. The Journal of the Acoustical Society of America 133, 3398-3398.

Mazet, J.A., Gardner, I.A., Jessup, D.A., Lowenstine, L.J., 2001. Effects of petroleum on mink applied as a model for reproductive success in sea otters. Journal of wildlife diseases 37, 686-692.

Mazzariol, S., Di Guardo, G., Petrella, A., Marsili, L., Fossi, C.M., Leonzio, C., Zizzo, N., Vizzini, S., Gaspari, S., Pavan, G., 2011. Sometimes sperm whales (Physeter macrocephalus) cannot find their way back to the high seas: a multidisciplinary study on a mass stranding. PloS one 6, e19417.

McCauley, R., Fewtrell, J., Duncan, A., Jenner, C., Jenner, M., Penrose, J., Prince, R., Adhitya, A., Murdoch, J., McCabe, K., 2000. Marine seismic surveys—a study of environmental implications. The APPEA Journal 40, 692-708.

McDonald, E.M., Morano, J.L., DeAngelis, A.I., Rice, A.N., 2017. Building time-budgets from bioacoustic signals to measure population-level changes in behavior: a case study with sperm whales in the Gulf of Mexico. Ecological Indicators 72, 360-364.

Miller, C.A., Reeb, D., Best, P.B., Knowlton, A.R., Brown, M.W., Moore, M.J., 2011. Blubber thickness in right whales Eubalaena glacialis and Eubalaena australis related with reproduction, life history status and prey abundance. Marine Ecology Progress Series 438, 267-283.

Miller, P.J., Antunes, R.N., Wensveen, P.J., Samarra, F.I., Catarina Alves, A., Tyack, P.L., Kvadsheim, P.H., Kleivane, L., Lam, F.-P.A., Ainslie, M.A., 2014. Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. The Journal of the Acoustical Society of America 135, 975-993.

Miller, P.J., Aoki, K., Rendell, L.E., Amano, M., 2008. Stereotypical resting behavior of the sperm whale. Current biology 18, R21-R23.

Miller, P.J., Johnson, M., Madsen, P.T., Biassoni, N., Quero, M., Tyack, P., 2009a. Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico. Deep Sea Research Part I: Oceanographic Research Papers 56, 1168-1181.

Miller, P.J., Johnson, M.P., Tyack, P.L., 2004a. Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. Proceedings of the Royal Society of London B: Biological Sciences 271, 2239-2247.

Miller, P.J., Johnson, M.P., Tyack, P.L., Terray, E.A., 2004b. Swimming gaits, passive drag and buoyancy of diving sperm whales Physeter macrocephalus. Journal of Experimental Biology 207, 1953-1967.

Miller, P.J., Kvadsheim, P.H., Lam, F.-P.A., Wensveen, P.J., Antunes, R., Alves, A.C., Visser, F., Kleivane, L., Tyack, P.L., Sivle, L.D., 2012. The severity of behavioral changes observed during experimental exposures of killer (Orcinus orca), long-finned pilot (Globicephala melas), and sperm (Physeter macrocephalus) whales to naval sonar. Aquatic Mammals 38, 362.

Miller, P.J.O., Johnson, M.P., Madsen, P.T., Biassoni, N., Quero, M., Tyack, P.L., 2009b. Using at-sea experiments to study the effects of airguns on the foraging behavior of sperm whales in the Gulf of Mexico. Deep Sea Research Part I: Oceanographic Research Papers 56, 1168-1181.

Mohr, F., Lasley, B., Bursian, S., 2008. Chronic oral exposure to bunker C fuel oil causes adrenal insufficiency in ranch mink (Mustela vison). Archives of environmental contamination and toxicology 54, 337-347.

Moretti, D., Thomas, L., Marques, T., Harwood, J., Dilley, A., Neales, B., Shaffer, J., McCarthy, E., New, L., Jarvis, S., Morrissey, R., 2014. A risk function for behavioral disruption of Blainville's beaked whales (Mesoplodon densirostris) from mid-frequency active sonar. PloS one 9, e85064.

New, L.F., Moretti, D.J., Hooker, S.K., Costa, D.P., Simmons, S.E., 2013. Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). PloS one 8, e68725.

Noren, D.P., Holt, M.M., Dunkin, R.C., Williams, T.M., 2017. Echolocation is cheap for some mammals: Dolphins conserve oxygen while producing high-intensity clicks. Journal of Experimental Marine Biology and Ecology 495, 103-109.

Nowacek, D.P., Clark, C.W., Mann, D., Miller, P.J.O., Rosenbaum, H.C., Golden, J.S., Jasny, M., Kraska, J., Southall, B.L., 2015. Marine seismic surveys and ocean noise: time for coordinated and prudent planning. Frontiers in Ecology and the Environment 13, 378-386.

Nowacek, D.P., Johnson, M.P., Tyack, P.L., 2004. North Atlantic right whales (Eubalaena glacialis) ignore ships but respond to alerting stimuli. Proceedings of the Royal Society of London B: Biological Sciences 271, 227-231.

Parks, S.E., Clark, C.W., Tyack, P.L., 2007. Short-and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. The Journal of the Acoustical Society of America 122, 3725-3731.

Plomp, R., Bouman, M., 1959. Relation between hearing threshold and duration for tone pulses. The Journal of the Acoustical Society of America 31, 749-758.

Porter, M.B., Liu, Y.-C., 1994. Finite-element ray tracing. Theoretical and computational acoustics 2, 947-956.

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. Research techniques in animal ecology: controversies and consequences 1, 476.

R Development Core Team, 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rankin, S., Evans, W.E., 1998. Effect of low-frequency seismic exploration signals on the cetaceans of the Gulf of Mexico. The Journal of the Acoustical Society of America 103, 2908-2908.

Rea, L.D., Costa, D.P., 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (Mirounga angustirostris). Physiological zoology 65, 97-111.

Richardson, W.J., Greene Jr, C.R., Malme, C.I., Thomson, D.H., 2013. Marine mammals and noise. Academic press.

Richardson, W.J., Würsig, B., Greene Jr, C.R., 1986. Reactions of bowhead whales, B alaenamysticetus, to seismic exploration in the Canadian Beaufort Sea. The Journal of the Acoustical Society of America 79, 1117-1128.

Richter, C., Gordon, J., Jaquet, N., Würsig, B., 2008. Social structure of sperm whales in the northern Gulf of Mexico. Gulf Mex. Sci 26, 118-123.

Roberts, J.J., Best, B.D., Mannocci, L., Fujioka, E., Halpin, P.N., Palka, D.L., Garrison, L.P., Mullin, K.D., Cole, T.V., Khan, C.B., McLellan, W.A., Pabst, D.A., Lockhart, G.G., 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Sci Rep 6, 22615.

Rolland, R.M., Parks, S.E., Hunt, K.E., Castellote, M., Corkeron, P.J., Nowacek, D.P., Wasser, S.K., Kraus, S.D., 2012. Evidence that ship noise increases stress in right whales. Proceedings of the Royal Society of London B: Biological Sciences 279, 2363-2368.

Romano, T., Keogh, M., Kelly, C., Feng, P., Berk, L., Schlundt, C., Carder, D., Finneran, J., 2004. Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. Canadian Journal of Fisheries and Aquatic Sciences 61, 1124-1134.

Rosen, D.A., Winship, A.J., Hoopes, L.A., 2007. Thermal and digestive constraints to foraging behaviour in marine mammals. Philos Trans R Soc Lond B Biol Sci 362, 2151-2168.

Rudd, M.A., 2014. Scientists' perspectives on global ocean research priorities. Frontiers in Marine Science 1, 36.

Schulz, T.M., Whitehead, H., Gero, S., Rendell, L., 2011. Individual vocal production in a sperm whale (Physeter macrocephalus) social unit. Marine Mammal Science 27, 149-166.

Schwacke, L.H., Smith, C.R., Townsend, F.I., Wells, R.S., Hart, L.B., Balmer, B.C., Collier, T.K., De Guise, S., Fry, M.M., Guillette Jr, L.J., 2013. Health of common bottlenose dolphins (Tursiops truncatus) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. Environmental science & technology 48, 93-103.

Schwacke, L.H., Thomas, L., Wells, R.S., McFee, W.E., Hohn, A.A., Mullin, K.D., Zolman, E.S., Quigley, B.M., Rowles, T.K., Schwacke, J.H., 2017. Quantifying injury to common bottlenose dolphins from the Deepwater Horizon oil spill using an age-, sex-and class-structured population model. Endangered Species Research 33, 265-279.

Schwartz, J.A., Aldridge, B.M., Stott, J.L., Mohr, F.C., 2004. Immunophenotypic and functional effects of bunker C fuel oil on the immune system of American mink (Mustela vison). Veterinary immunology and immunopathology 101, 179-190.

Scrimshaw, N.S., Taylor, C.E., Gordon, J.E., Organization, W.H., 1968. Interactions of nutrition and infection.

Senigaglia, V., Christiansen, F., Bejder, L., Gendron, D., Lundquist, D., Noren, D.P., Schaffar, A., Smith, J.C., Williams, R., Martinez, E., Stockin, K., Lusseau, D., 2016. Meta-analyses of whale-watching impact studies: comparisons of cetacean responses to disturbance. Marine Ecology Progress Series 542, 251-263.

Sharp, S.M., Knoll, J.S., Moore, M.J., Moore, K.M., Harry, C.T., Hoppe, J.M., Niemeyer, M.E., Robinson, I., Rose, K.S., Brian Sharp, W., Rotstein, D., 2014. Hematological, biochemical, and morphological parameters as prognostic indicators for stranded common dolphins (Delphinus delphis)from Cape Cod, Massachusetts, U.S.A. Marine Mammal Science 30, 864-887.

Sivle, L.D., Kvadsheim, P.H., Fahlman, A., Lam, F., Tyack, P.L., Miller, P.J., 2012a. Changes in dive behavior during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. Frontiers in physiology 3.

Sivle, L.D., Kvadsheim, P.H., Fahlman, A., Lam, F.P., Tyack, P.L., Miller, P.J., 2012b. Changes in dive behavior during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. Front Physiol 3, 400.

Slotte, A., Hansen, K., Dalen, J., Ona, E., 2004. Acoustic mapping of pelagic fish distribution and abundance in relation to a seismic shooting area off the Norwegian west coast. Fisheries Research 67, 143-150.

Southall, B.L., Bowles, A.E., Ellison, W.T., Finneran, J.J., Gentry, R.L., Greene Jr, C.R., Kastak, D., Ketten, D.R., Miller, J.H., Nachtigall, P.E., 2007. Criteria for behavioral disturbance. Aquatic Mammals 33, 446.

Southall, B.L., Nowacek, D.P., Miller, P.J.O., Tyack, P.L., 2016. Experimental field studies to measure behavioral responses of cetaceans to sonar. Endangered Species Research 31, 293-315.

Stone, C.J., Tasker, M.L., 2006. The effects of seismic airguns on cetaceans in UK waters. Journal of Cetacean Research and Management 8, 255.

Teague, W.J., Carron, M.J., Hogan, P.J., 1990. A comparison between the Generalized Digital Environmental Model and Levitus climatologies. Journal of Geophysical Research: Oceans 95, 7167-7183.

Thomas, J.A., Kastelein, R.A., Awbrey, F.T., 1990. Behavior and blood catecholamines of captive belugas during playbacks of noise from an oil drilling platform. Zoo Biology 9, 393-402.

Townsend, C.H., 1935. The distribution of certain whales as shown by logbook records of American whaleships. New York Zoological Society.

United States Congress, 1969. National Environmental Policy Act of 1969. Public Law 91, 1-5.

United States Federal Register, 2013. Endangered and Threatened Wildlife; Notice of 12-Month Finding on a Petition To List the Sperm Whale (Physeter macrocephalus), ed. N.O.a.A.A.N. National Marine Fisheries Service (NMFS), Commerce, pp. 68032-68037. National Oceanic and Atmospheric Administration, United States of America.

Waring, G., Josephson, E., Maze-Foley, K., Rosel, P., 2016. US Atlantic and Gulf of Mexico. MarineMammal Stock Assessments–2015. NOAA Technical Memorandum NMFS-NE 238.

Watkins, W.A., 1986. Whale reactions to human activities in Cape Cod waters. Marine Mammal Science 2, 251-262.

Watwood, S.L., Miller, P.J., Johnson, M., Madsen, P.T., Tyack, P.L., 2006. Deep-diving foraging behaviour of sperm whales (Physeter macrocephalus). J Anim Ecol 75, 814-825.

Webb, P.M., Costa, D.P., Le Boeuf, B.J., Andrews, R.D., 1998. Heart rate and oxygen consumption of northern elephant seals during diving in the laboratory. Physiological zoology 71, 116-126.

Weilgart, L.S., 2007a. A brief review of known effects of noise on marine mammals. International Journal of Comparative Psychology 20.

Weilgart, L.S., 2007b. The impacts of anthropogenic ocean noise on cetaceans and implications for management. Canadian Journal of Zoology 85, 1091-1116.

Whitehead, H., 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral Ecology and Sociobiology 38, 237-244.

Whitehead, H., 2002. Estimates of the current global population size and historical trajectory for sperm whales. Marine Ecology Progress Series 242, 295-304.

Whitehead, H., Rendell, L., 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology 73, 190-196.

Williams, R., Erbe, C., Ashe, E., Beerman, A., Smith, J., 2014. Severity of killer whale behavioral responses to ship noise: A dose–response study. Marine pollution bulletin 79, 254-260.

Williams, R., Thomas, L., Ashe, E., Clark, C.W., Hammond, P.S., 2016. Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: A case-study approach using two whale populations. Marine Policy 70, 58-64.

Williams, R., Vikingsson, G.A., Gislason, A., Lockyer, C., New, L., Thomas, L., Hammond, P.S., 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 Journal of Marine Science 70, 1273-1280.

Williams, T.M., Kendall, T.L., Richter, B.P., Ribeiro-French, C.R., John, J.S., Odell, K.L., Losch, B.A., Feuerbach, D.A., Stamper, M.A., 2017. Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. Journal of Experimental Biology 220, 1135-1145.

Winsor, M.H., Irvine, L.M., Mate, B.R., 2017. Analysis of the Spatial Distribution of Satellite-Tagged Sperm Whales (Physeter macrocephalus) in Close Proximity to Seismic Surveys in the Gulf of Mexico. Aquatic Mammals 43, 439-446.

Wisniewska, D.M., Johnson, M., Teilmann, J., Siebert, U., Galatius, A., Dietz, R., Madsen, P.T., 2018. High rates of vessel noise disrupt foraging in wild harbour porpoises (Phocoena phocoena). Proc. R. Soc. B 285, 20172314.

Wood, J., Southall, B., Tollit, D., 2012. PG&E offshore 3-D Seismic Survey Project EIR–Marine Mammal Technical Draft Report. SMRU Ltd.

Zeddies, D.G., M. Zykov, H. Yurk, T. Deveau, L. Bailey, I. Gaboury, R. Racca, D. Hannay, S. Carr, 2015. Acoustic Propagation and Marine Mammal Exposure Modeling of Geological and Geophysical Sources in the Gulf of Mexico: 2016–2025 Annual Acoustic Exposure Estimates for Marine Mammals, In Technical report by JASCO Applied Sciences for Bureau of Ocean Energy Management (BOEM). Dartmouth, Nova Scotia, Canada.

Zhang, Z., Tindle, C., 1995. Improved equivalent fluid approximations for a low shear speed ocean bottom. The Journal of the Acoustical Society of America 98, 3391-3396.

Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. Ecology 80, 1019-1030.

Table 1. Different model scenarios for individual resilience. *Foraging Impact*: assumed reduction in foraging efficiency during times of exposure above thresholds (160 dB, Stepfn); *Replacement of Lost Reserves*: assumed individual ability to optimally allocate new growth to previously lost reserves proportional to their loss; *Hunger Response*: assumed individual ability to increase consumption to replenish lost reserves and grow on days of undisturbed foraging. Note: "U" denotes a uniform distribution between lower and upper bounds listed. Model scenarios organized from most to least precautionary assumptions regarding individual resilience to foraging disruption. Individuals were assumed to begin simulations in "perfect" body condition.

Scenario	**Foraging Impact**	**Replacement of Reserves**	**Hunger Response**
1	100%	Somatic	None
2	U(20-100%)	Somatic	None
3	100%	U(Somatic-Optimal)	None
4	100%	U(Somatic-Optimal)	1.5X
5	U(20-100%)	U(Somatic-Optimal)	1.5X
6	U(20-100%)	U(Somatic-Optimal)	3X

Table 2. Processes that were not considered in modeling efforts, their likely directional impact on the Gulf of Mexico sperm whale stock (↑: positive, ↕: unclear, ↓: negative), associated discussion and references.

Not Considered	Impact	Discussion
Dynamic metabolic rate	↑	• Extreme fasting leads to metabolic depression (Castellini and Rea 1992; Rea and Costa 1992) • Unclear if functional adaptation for a whale that must dive to acquire food (Watwood et al. 2006) • Metabolic rate decreases during diving in marine mammals (Webb et al. 1998)
Long-distance Movements and Migration	↕	• Sperm whales do not appear to make seasonal migrations in the Gulf of Mexico (Waring et al. 2016) • Could result in slight short-term changes in density and also modify individual exposure histories • Unlikely that competitive displacement would be common in areas during anthropogenic disturbance events

Not Considered	Impact	Discussion
Grouping	↕	• Sperm whales may form temporary or permanent social groups (Christal et al. 1998) • May serve a social function (e.g., “all-mothering”) and/or facilitate exploitation of patchy food resources (Connor et al. 1998; Jaquet and Gendron 2002; Whitehead 1996) • Groups in the Gulf of Mexico consist primarily of females, calves, and sub-adult males; mature males occasionally return to the area to breed (Richter et al. 2008) • Grouping proportionally decreases the likelihood of exposure but increases the effect when an exposure occurs (Zeddies 2015) • Sensitivity runs suggest grouping effects the distribution of exposure estimates but not the mean (Zeddies 2015)
Hydrodynamic Variability in Sound Propagation	↕	• Level of received sound at depth impacted by 1) changes in the average sound velocity profile as the surface layer temperature changes, 2) the presence or absence of local bathymetric features (Buckingham 2005), and 3) variability in measured bathymetry • Sensitivity runs suggest low levels (<4 dB) of uncertainty associated with hydrodynamic variability in sound propagation (Austin et al. 2012; Matthews and MacGillivray 2013; Zeddies 2015)
Interaction of Stressors	↕	• Multiple stressors can cause additive, antagonistic, or synergistic direct or indirect effects on individual condition through an interaction web ([NAS] National Academies of Sciences Engineering and Medicine: Ocean Studies Board 2017)

Not Considered	Impact	Discussion
Avoidance	↕/↓	• Whales may temporarily avoid or move away from an ensonified area (Richardson et al. 2013; Stone and Tasker 2006) • May reduce sound exposure and associated reductions in foraging; however, costs the animal energy associated with movement (Williams et al. 2017) and potentially reduces foraging opportunities and access to important habitats (Bejder et al. 2009; Jochens et al. 2006) • CEE and analyses of satellite tracks of sperm whales exposed to seismic surveys have not documented avoidance behaviors (Miller et al. 2009b; Rankin and Evans 1998; Winsor et al. 2017) • Avoidance is challenging in a multipath propagation environment; to reduce their sound exposure, sperm whales might move closer to the array or change depth, which could reduce received levels in the short-term but extend overall exposure time and accumulated SEL (Madsen et al. 2006)
Depensatory Reproductive Rates	↕/↓	• Female mammals are less fertile when their diets are restricted (Ball et al. 1947; Miller et al. 2011) • Lower calf production→ fewer calves and females at terminal starvation, but also reduced stock size

Not Considered	**Impact**	**Discussion**
Noise Impacts on Prey	↕/↓	• Disturbance events may disrupt the availability of prey resources (André et al. 2011; Engås et al. 1996; McCauley et al. 2000; Slotte et al. 2004) • Anthropogenic sound may alter prey abundance, behavior, and distribution (Engås et al. 1996; Slotte et al. 2004) • Squid are an extremely important food source for sperm whales (Kawakami 1980; Matthews 1938) and may avoid (McCauley et al. 2000) or be killed by relatively low levels of low-frequency sound (André et al. 2011)
Increased Sound Production	↓	• Changes in call amplitude increase metabolic costs (Holt et al. 2015; Holt et al. 2009; Noren et al. 2017)

Not Considered	Impact	Discussion
Disturbance Below Threshold	↓	• Disturbance is often context-specific and seldom measured across multiple metrics of exposure (Southall et al. 2007) • More severe consistent behavioral responses are not consistently associated with higher received sound levels (Gomez et al. 2016) • Responses have been observed to sound levels well below the established thresholds (e.g., starting at approximately 110 dB re 1 μPa), and lack of response has been observed at sound levels above the thresholds (Gomez et al. 2016) • Sperm whale hearing range is based on audiogram from one neonate (Carder and Ridgway 1990); skeletal transmission of energy may indicate superior hearing than modeled, especially given the fused ear bone of sperm whales (Cranford and Krysl 2015)
Signal Masking	↓	• Decreases the range over which an animal can communicate, locate and suckle calf, detect predators, find food, or increase metabolic costs by forcing the animal to increase call amplitude and repetition (Holt et al. 2009; Jochens et al. 2006; McDonald et al. 2017; Parks et al. 2007; Schulz et al. 2011) • Amount of time spent foraging relative to other activities increases when prey availability or foraging efficiency is reduced (Boyd 1999; Crocker et al. 2006; McDonald et al. 2017)

Not Considered	Impact	Discussion
TTS/PTS	↓	• Intense sounds can physically damage an animal's auditory system, resulting in temporary or permanent threshold shifts (PTS or TTS; (Weilgart 2007b)) • There is a high potential for TTS and repeated exposures that could lead to PTS associated with continued G&G activities in the Gulf of Mexico (Zeddies 2015) • TTS and PTS could lead to reductions in foraging efficiency, reproductive potential, social cohesion, and ability to detect predators (Weilgart 2007a)
Elevated Stress Levels	↓	• Exposure to sound can lead to elevated stress levels (Rolland et al. 2012; Romano et al. 2004; Thomas et al. 1990) • Elevated stress levels can reduce the immune system's ability to fight infection (Romano et al. 2004)
Dehydration or Ketosis	↓	• Fasting health impacts include dehydration and ketosis associated with the catabolism of energy stores (Castellini and Rea 1992) • May have neurotoxic and immunotoxic effects (Castellini and Rea 1992) • Implicated in marine mammal strandings (Mazzariol et al. 2011; Sharp et al. 2014)
Increased Risk of Disease	↓	• Stress and malnutrition reduce immune system function (Romano et al. 2004; Scrimshaw et al. 1968)

Not Considered	Impact	Discussion
Decompression Sickness	↓	• High-intensity, low-frequency sounds could lead to gas bubble formation in body tissue through rectified diffusion (Crum and Mao 1996) • Acoustic activation of bubble nuclei at depth can theoretically cause bubbles to grow rapidly by the degree of supersaturation and the animal's continued exposure to sounds (Houser et al. 2001) • As a deep-diving species, sperm whales may be particularly vulnerable to bubble growth and associated tissue damage and blood vessel obstruction (Fernández et al. 2005; Kvadsheim et al. 2012) • When exposed to unanticipated threats, whales may forgo nitrogen load management, increasing their risk of decompression sickness (Hooker et al. 2012)
Cultural Impact	↓	• Information regarding how to best respond to environmental fluctuation may be held within social groups by older individuals and transferred culturally between generations within social units such as clans (Jochens et al. 2006) • Many lines of evidence (e.g., unique codas, unique individuals based on photo-id, limited long-distance movements, distinct genetic signatures, smaller average size) suggest sperm whales in the northern Gulf of Mexico are somewhat isolated from global sperm whale populations (Jochens et al. 2006) • The loss of individuals may represent a greater impact for a sperm whale group than can be easily captured by a simple demographic model (Jochens et al. 2006; Whitehead and Rendell 2004)

Figure Captions

Fig. 1. *Study area.* Predicted mean (top) and standard error (bottom) sperm whale abundance in Gulf of Mexico (Roberts et al. 2016) relative to modeled survey effort zones (black). Behavioral disturbance simulation areas for large seismic surveys (red) and high-resolution sources (green) also shown. Yellow stars denote sites for calculation of acoustic propagation loss grids as functions of source, range from the source, azimuth from the source, and receiver depth. Bottom figure shows proposed mitigation closure areas and seismic survey tracks 2002-2007.

Fig. 2. *Modeling process flow chart.* Our modeling approach estimates the consequences of sperm whale exposure to sound in areas open to seismic survey activities by integrating (i) acoustic modeling to estimate the sound propagation from various G&G survey methods, (ii) animal movement simulations to estimate exposure through three-dimensional sound fields, (iii) dose-response functions to estimate the associated level of behavioral response based on individual exposure histories, (iv) a bioenergetic transfer function to relate behavioral responses to physiological effects and translate those physiological effects to changes in individual vital rates, (vi) a spatial overlap model to determine oil exposure associated with the DWH spill, and (vii) a demographic model that evaluates stock level consequences of mortalities and reproductive impacts associated with both oil exposure and behavioral disturbance.

Fig. 3. *Exposure modeling*. Schematic describing general approach to exposure modeling. Simulated sperm whales moved within behavioral disturbance simulation areas containing modeled three-dimensional sound fields for various geological and geophysical surveys, with time of exposure (minutes above threshold) recorded for each individual. Graphics © JASCO Applied Sciences, used with permission.

Fig. 4. *Individual impacts of exposure*. Schematic of computations of individual consequences of exposure above threshold. Probabilistic model considers likelihood of individual being within range of active survey, with random draws determining A) maximum daily exposure duration across geological and geophysical surveys and B) minutes underwater during foraging dive cycle. Reduced foraging effectiveness during exposure leads to C) depletion of carbohydrate (red), protein (green), and lipid (blue) reserves (top) relative to foraging efficiency (black) and life stage (bottom). Note this sperm whale mother abandoned her second calf due to low energy reserves, reverting to mature female rather than post-breeding.

Fig. 5. *Consequences of disturbance*. Percent stock reaching terminal starvation across 1000 bootstrapped runs for each life stage across all zones and relative body condition in terminal year relative to undisturbed individuals for females in Zone 5 (mean ± SE). Outputs presented for different model scenarios for individual reduction in foraging efficiency during exposures above threshold (160 dB, Stepfn), ability to optimize replacement of lost reserves, and ability to increase consumption to support increased growth on days of undisturbed foraging (see **Table 1**).

Fig. 6. *Stock impacts: Scenario 1.* Demographic model estimates under Model Scenario 1 of baseline total population size relative to behavioral disturbance for 160 dB (top) and Stepfn (bottom) criteria. Impacts under three mitigation scenarios: Base, Eastern Planning Area and Tortugas Area closures (EPA+TA), and Eastern Planning Area, Tortugas Area, and Central

Planning Area closures (EPA+TA+CPA) are shown. The ‘baseline’ population trajectory (no anthropogenic mortality) is indicated by solid black line. The mean ‘spill’ population trajectory, incorporating the impacts of DWH oil exposure, is indicated by the solid blue line. The 95% confidence limits are indicated by dashed lines. The mean and 95% confidence bands for the ‘spill+disturbance’ population trajectory, incorporating the additional impacts of seismic survey acoustic disturbance, are indicated with solid red lines and gray shading.

Fig. S1. *Bioenergetic model*. A decision tree representing a daily time step in the model simulations for the energy budget of an individual sperm whale. Individuals with acoustic disturbance forage at less than 100% efficiency and have to repay their caloric debt from body energy reserves. How much energy is needed (FMR: field metabolic rate) and how body reserves are apportioned between blubber, muscle, and viscera depends on the whale’s reproductive status and total body mass. Squares represent computations, diamonds represent decision points, and circles represent possible outcomes. Model adapted from (Farmer et al. 2018).

Fig. S2. *Life-cycle*. Life-cycle graph for the “DWH” stage-structured model. Arrows indicate possible transitions between stages with reproduction indicated by arrows connecting Female adults (Stage 3) to calves (Stages 1 and 6). Calves are produced at a 50:50 sex ratio. Model stages are separated into an “unexposed” cohort and an “exposed” cohort. The “exposed” cohort represents the proportion of the population that was estimated to overlap with DWH surface oil at sufficient levels to cause additional mortality and reproductive effects (see (Schwacke et al. 2017)). The exposed cohort produces unexposed calves and thus dies out over time. For males, an additional loss term was included in the adult survival rate to account for emigration of males which results in the 72:28 female to male sex ratio observed in the NGM population (Engelhaupt et al. 2009).

Fig. S3. *DWH Oil Exposure*. JASCO zones used to estimate acoustic disturbance impacts and polygon representing the extent of DWH surface oil exposure.

Fig. S4. *Relative body condition: Scenario 3.* Mean (solid line) and 95% confidence intervals (dotted lines) for available reserve energy of simulated mature whales exposed to behavioral disturbance under 160 dB (top) and Stepfn (bottom) criteria relative to undisturbed whales of identical characteristics, by zone (4: red, 5: green, 6: blue, 7: purple).

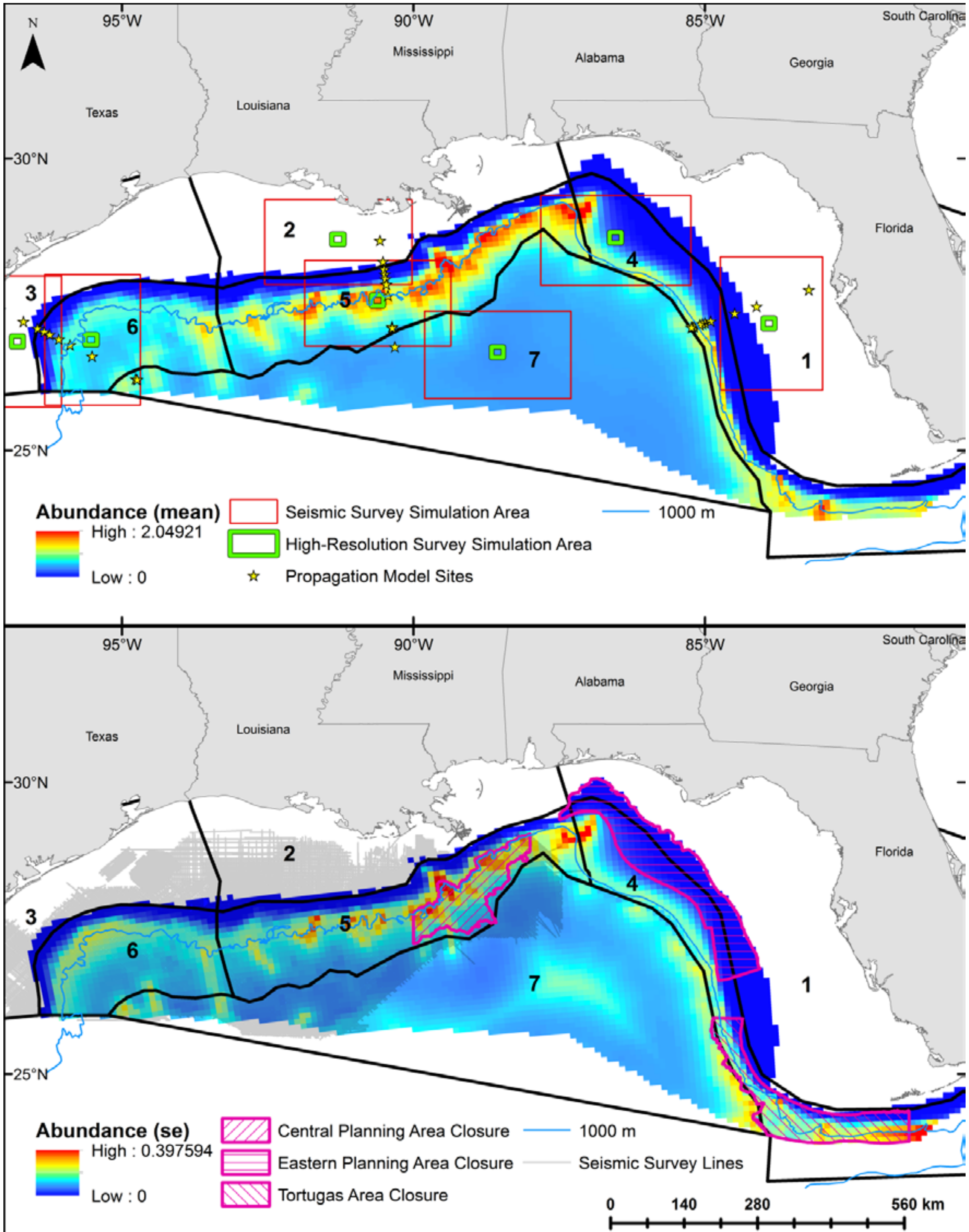
N
95°W
90°W
85°W
30°N
25°N
Texas
Louisiana
Mississippi
Alabama
Georgia
South Carolina
Florida
1
2
3
4
5
6
7
Abundance (mean)
High : 2.04921
Low : 0
Seismic Survey Simulation Area
High-Resolution Survey Simulation Area
Propagation Model Sites
1000 m
Abundance (se)
High : 0.397594
Low : 0
Central Planning Area Closure
Eastern Planning Area Closure
Tortugas Area Closure
1000 m
Seismic Survey Lines
0
140
280
560 km

Fig. 1. *Study area.* Predicted mean (top) and standard error (bottom) sperm whale abundance in Gulf of Mexico (Roberts et al. 2016) relative to modeled survey effort zones (black). Top panel shows behavioral disturbance simulation areas for large seismic surveys (large thin rectangles) and high-resolution sources (small thick rectangles) also shown. Stars denote sites for calculation of acoustic propagation loss grids as functions of source, range from the source, azimuth from the source, and receiver depth. Bottom panel shows proposed mitigation closure areas and seismic survey tracks 2002-2007.

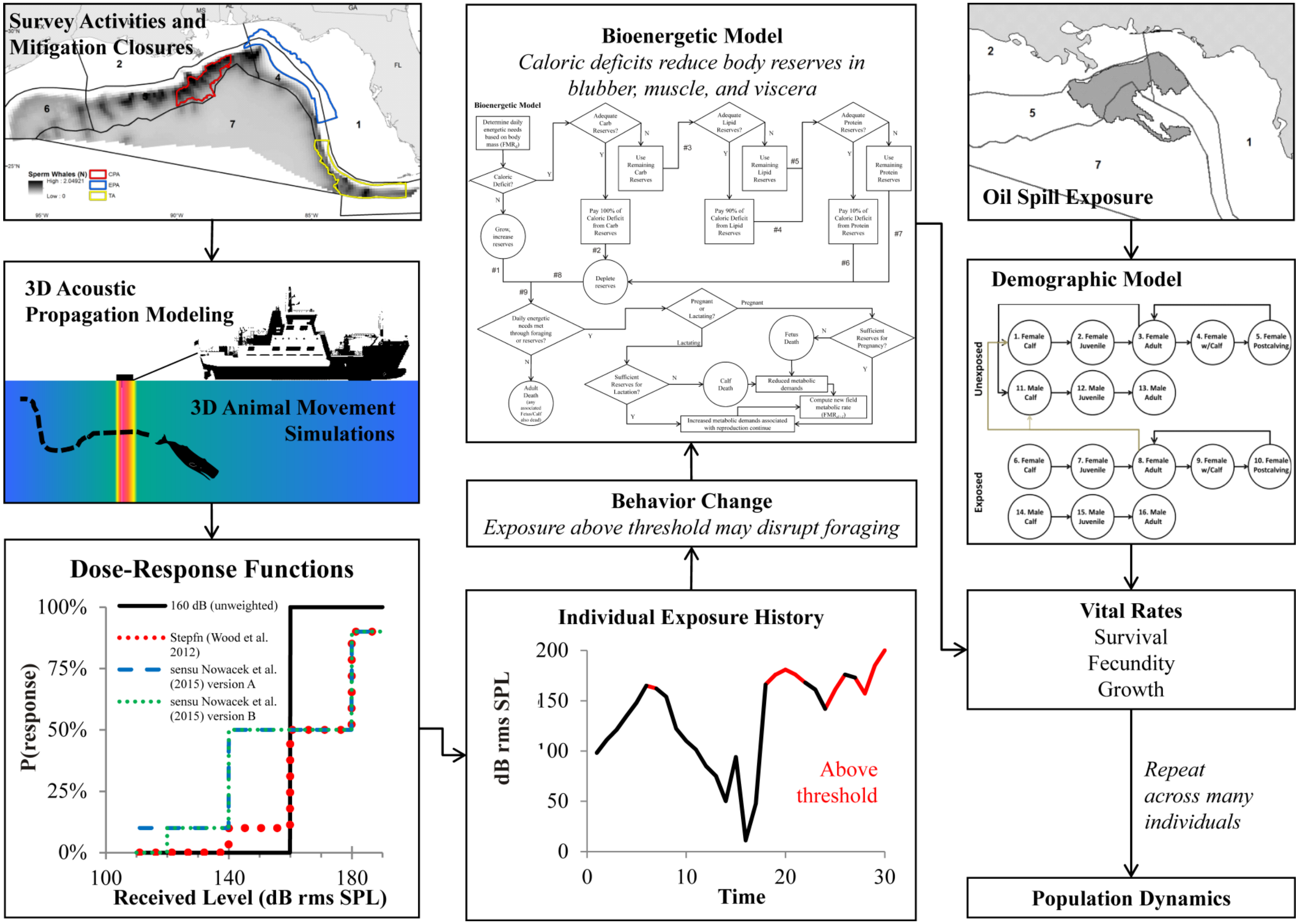
Survey Activities and Mitigation Closures
MS
AL
GA
FL
30°N
25°N
95°W
90°W
85°W
1
2
4
6
7
Sperm Whales (N)
High : 2.04921
Low : 0
CPA
EPA
TA
3D Acoustic Propagation Modeling
3D Animal Movement Simulations
Dose-Response Functions
100%
75%
50%
25%
0%
P(response)
100
140
180
Received Level (dB rms SPL)
160 dB (unweighted)
Stepfn (Wood et al. 2012)
sensu Nowacek et al. (2015) version A
sensu Nowacek et al. (2015) version B
Bioenergetic Model
Caloric deficits reduce body reserves in blubber, muscle, and viscera
Bioenergetic Model
Determine daily energetic needs based on body mass (FMR$_d$)
Caloric Deficit?
Y
N
Grow, increase reserves
Adequate Carb Reserves?
Use Remaining Carb Reserves
Pay 100% of Caloric Deficit from Carb Reserves
Adequate Lipid Reserves?
Use Remaining Lipid Reserves
Pay 90% of Caloric Deficit from Lipid Reserves
Adequate Protein Reserves?
Use Remaining Protein Reserves
Pay 10% of Caloric Deficit from Protein Reserves
#1
#2
#3
#4
#5
#6
#7
#8
#9
Deplete reserves
Daily energetic needs met through foraging or reserves?
Adult Death (any associated Fetus/Calf also dead)
Pregnant or Lactating?
Pregnant
Lactating
Sufficient Reserves for Pregnancy?
Fetus Death
Sufficient Reserves for Lactation?
Calf Death
Reduced metabolic demands
Compute new field metabolic rate (FMR$_{d+1}$)
Increased metabolic demands associated with reproduction continue
Behavior Change
Exposure above threshold may disrupt foraging
Individual Exposure History
dB rms SPL
200
150
100
50
0
10
20
30
Time
Above threshold
Oil Spill Exposure
1
2
5
7
Demographic Model
Unexposed
Exposed
1. Female Calf
2. Female Juvenile
3. Female Adult
4. Female w/Calf
5. Female Postcalving
6. Female Calf
7. Female Juvenile
8. Female Adult
9. Female w/Calf
10. Female Postcalving
11. Male Calf
12. Male Juvenile
13. Male Adult
14. Male Calf
15. Male Juvenile
16. Male Adult
Vital Rates
Survival
Fecundity
Growth
Repeat across many individuals
Population Dynamics

Figure 2. *Modeling process flow chart.* Our modeling approach estimates the consequences of sperm whale exposure to sound in areas open to seismic survey activities by integrating (i) acoustic modeling to estimate the sound propagation from various G&G survey methods, (ii) animal movement simulations to estimate exposure through three-dimensional sound fields, (iii) dose-response functions to estimate the associated level of behavioral response based on individual exposure histories, (iv) a bioenergetic transfer function to relate behavorial responses to physiological effects and translate those physiological effects to changes in individual vital rates, (vi) a spatial overlap model to determine oil exposure associated with the DWH spill, and (vii) a demographic model that evaluates stock level consequences of mortalities and reproductive impacts associated with both oil exposure and behavioral disturbance

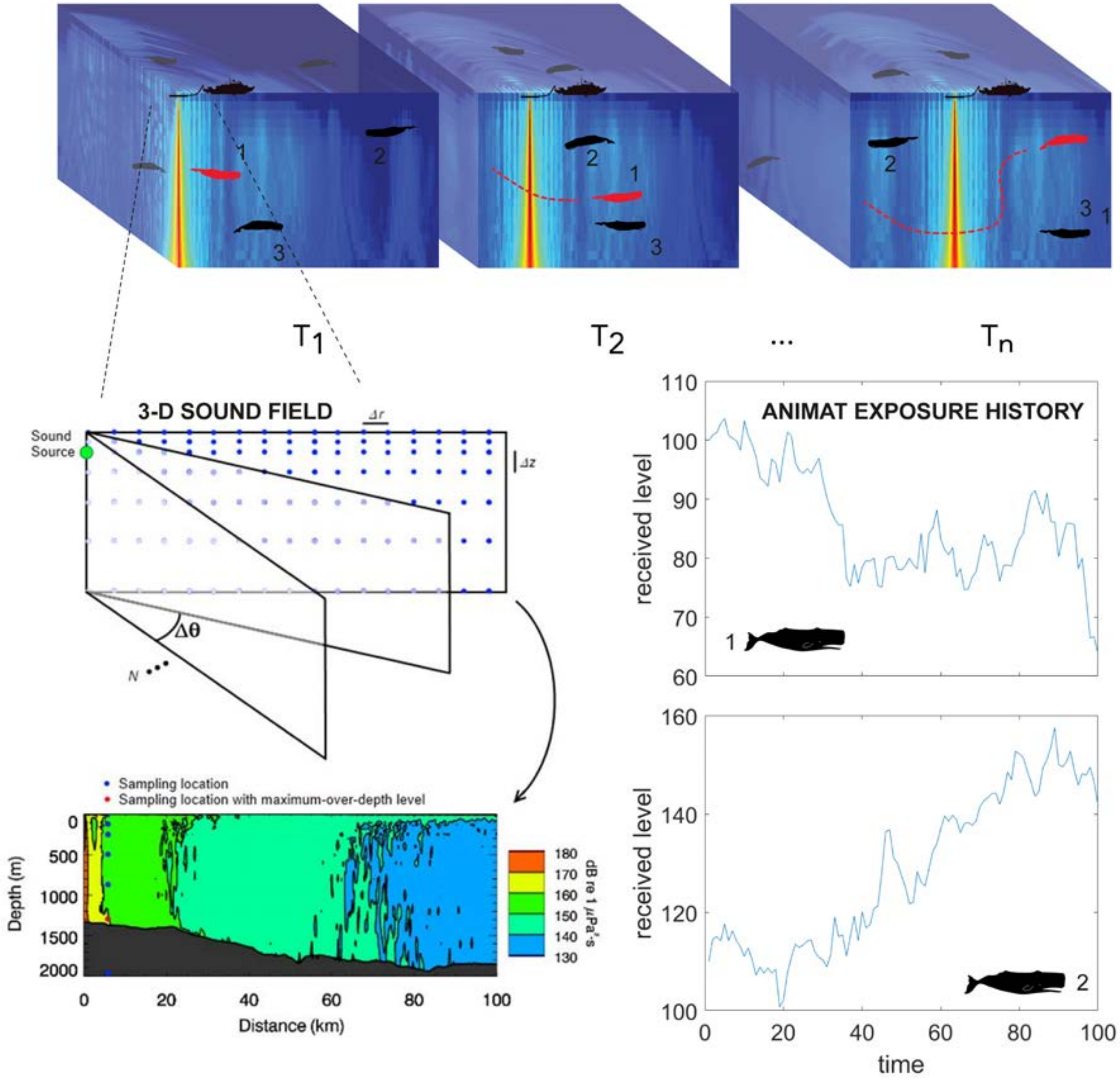
1
2
3
2
1
3
2
3
1
T1
T2
...
Tn
3-D SOUND FIELD
Δr
Δz
Sound Source
Δθ
N
Sampling location
Sampling location with maximum-over-depth level
Depth (m)
0
500
1000
1500
2000
0
20
40
60
80
100
Distance (km)
180
170
160
150
140
130
dB re 1 μPa²·s
ANIMAT EXPOSURE HISTORY
received level
110
100
90
80
70
60
1
received level
160
140
120
100
2
0
20
40
60
80
100
time

Fig. 3. *Exposure modeling*. Schematic describing general approach to exposure modeling. Simulated sperm whales moved within behavioral disturbance simulation areas containing modeled three-dimensional sound fields for various geological and geophysical surveys, with time of exposure (minutes above threshold) recorded for each individual. Graphics © JASCO Applied Sciences, used with permission.

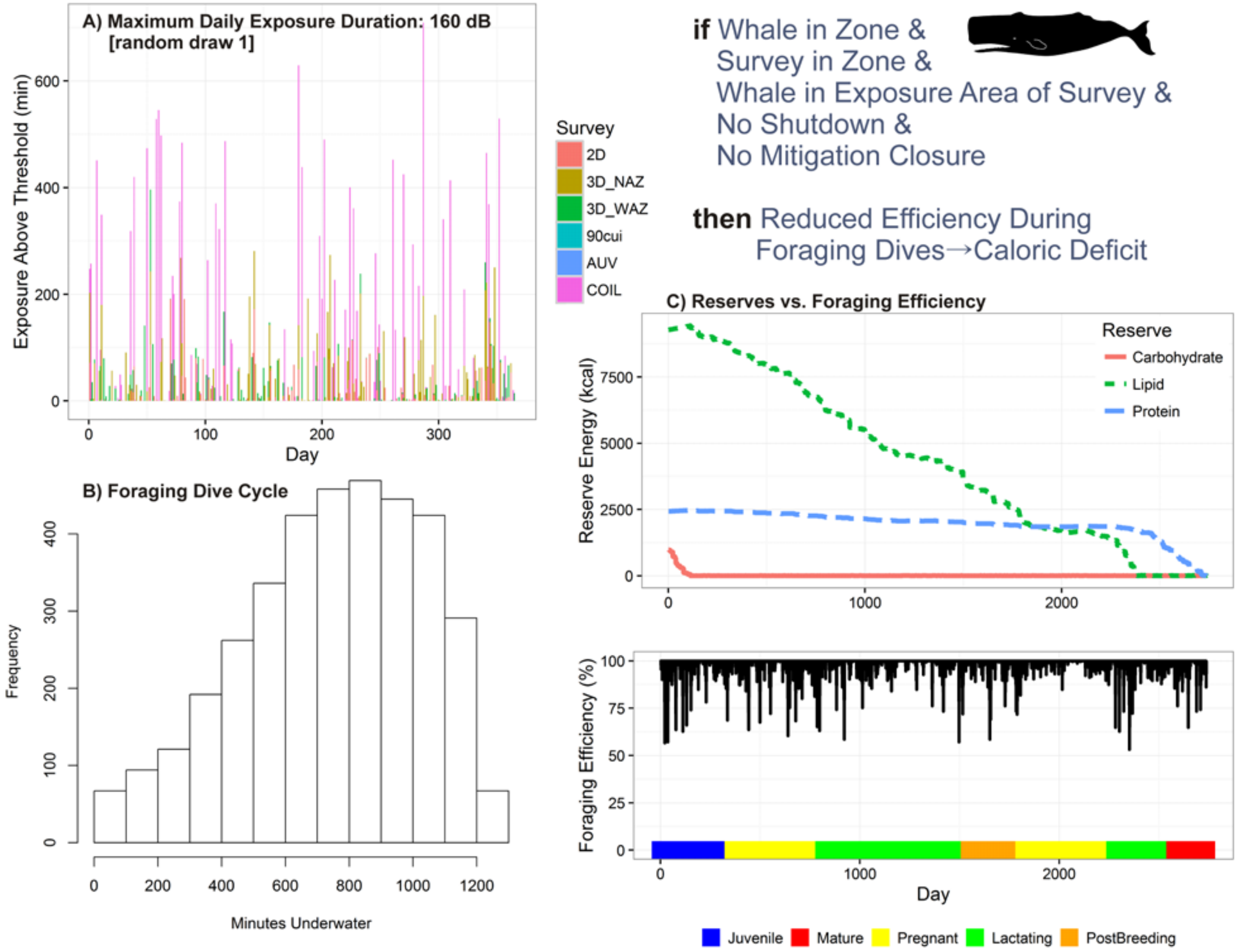

Fig. 4. *Individual impacts of exposure*. Schematic of computations of individual consequences of exposure above threshold. Probabilistic model considers likelihood of individual being within range of active survey, with random draws determining A) maximum daily exposure duration across geological and geophysical surveys and B) minutes underwater during foraging dive cycle.

Reduced foraging effectiveness during exposure leads to C) depletion of carbohydrate (red), protein (green), and lipid (blue) reserves (top) relative to foraging efficiency (black) and life stage (bottom). Note this simulated sperm whale mother abandoned her second calf due to low energy reserves, reverting to mature female rather than post-breeding.

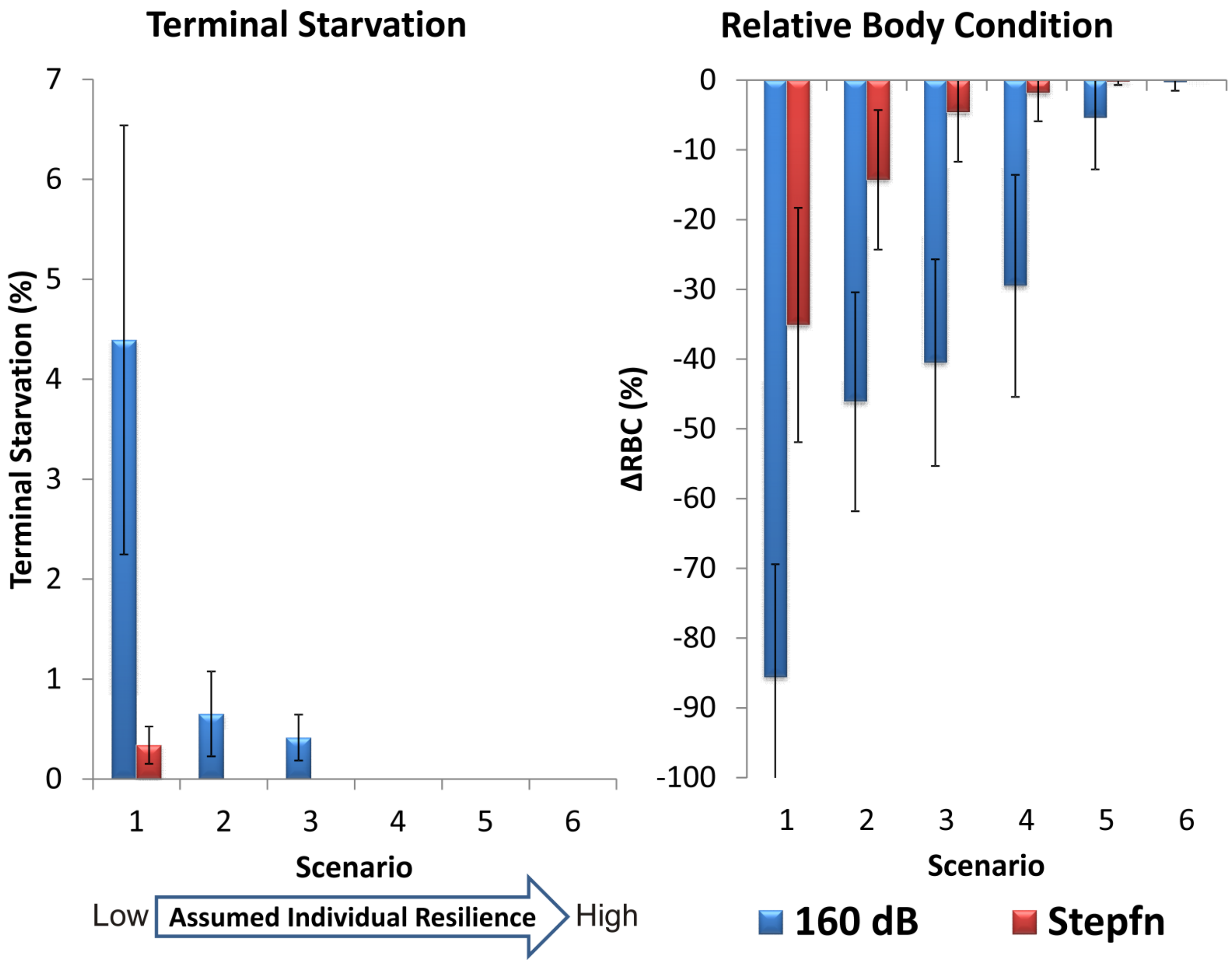

Fig. 5. *Consequences of disturbance*. Percent stock reaching terminal starvation across 1000 bootstrapped runs for each life stage across all zones and relative body condition in terminal year relative to undisturbed individuals for females in Zone 5 (mean ± SE).

Outputs presented for six different model scenarios for individual reduction in foraging efficiency during exposures above threshold (160 dB, Stepfn), ability to optimize replacement of lost reserves, and ability to increase consumption to support increased growth on days of undisturbed foraging (see **Table 1**).

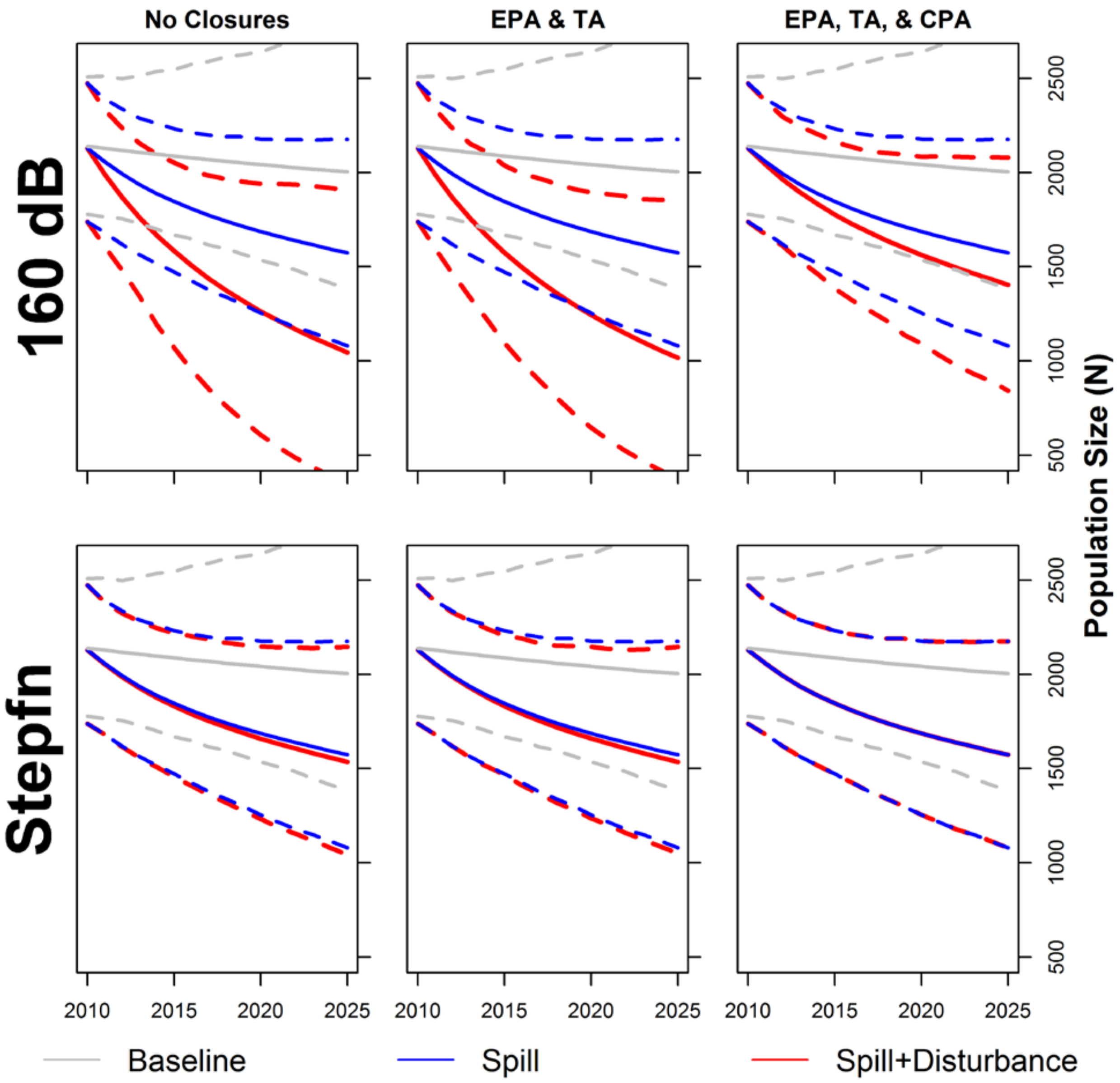

Fig. 6. *Population impacts: Scenario 1. Stock impacts: Scenario 1.* Model Scenario 1 demographic model mean (solid lines) and 95% confidence limit (dashed lines) population trajectories for 'Baseline' (gray; no anthropogenic mortality), 'Spill' (blue; incorporating the impacts of DWH oil exposure), and 'Spill+Disturbance' (red; incorporating the additional impacts of behavioral disturbance under 160 dB and Stepfn criteria). Impacts are shown for

three mitigation scenarios: (i) No closures, (ii) Eastern Planning Area and Tortugas Area closures (EPA & TA), and (iii) Eastern Planning Area, Tortugas Area, and Central Planning Area closures (EPA, TA, & CPA).

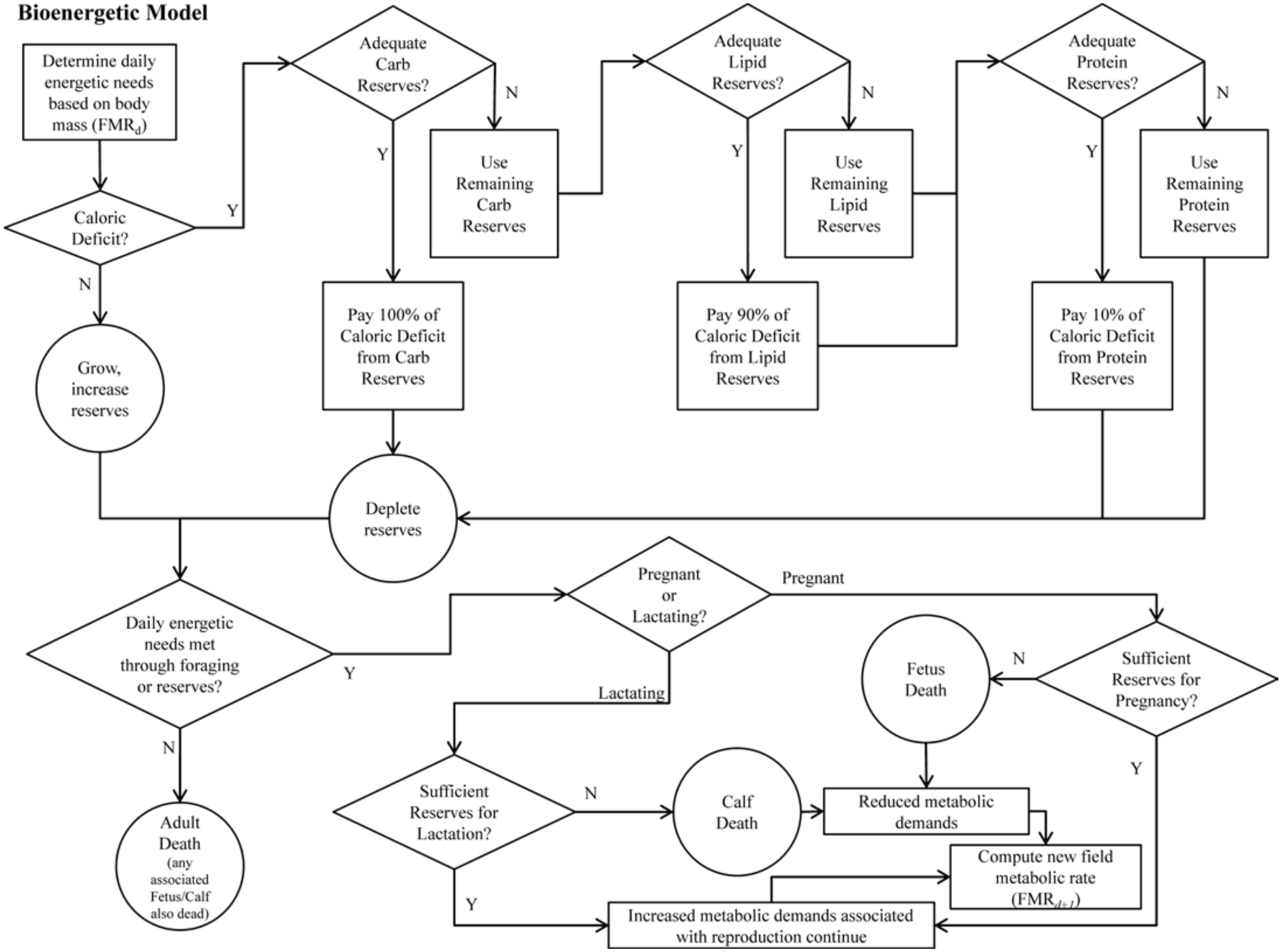

Fig. S1. *Bioenergetic model*. A decision tree representing one time step (a day) in the model simulations for the energy budget of an individual sperm whale. Individuals with acoustic disturbance forage at less than 100% efficiency and have to repay their caloric debt from body energy reserves. How much energy is needed (FMR: field metabolic rate) and how body reserves are apportioned between blubber, muscle, and viscera depends on the whale's reproductive status and total body mass. Squares represent computations, diamonds represent decision points, and circles represent possible outcomes. Model adapted from (Farmer et al. 2018).

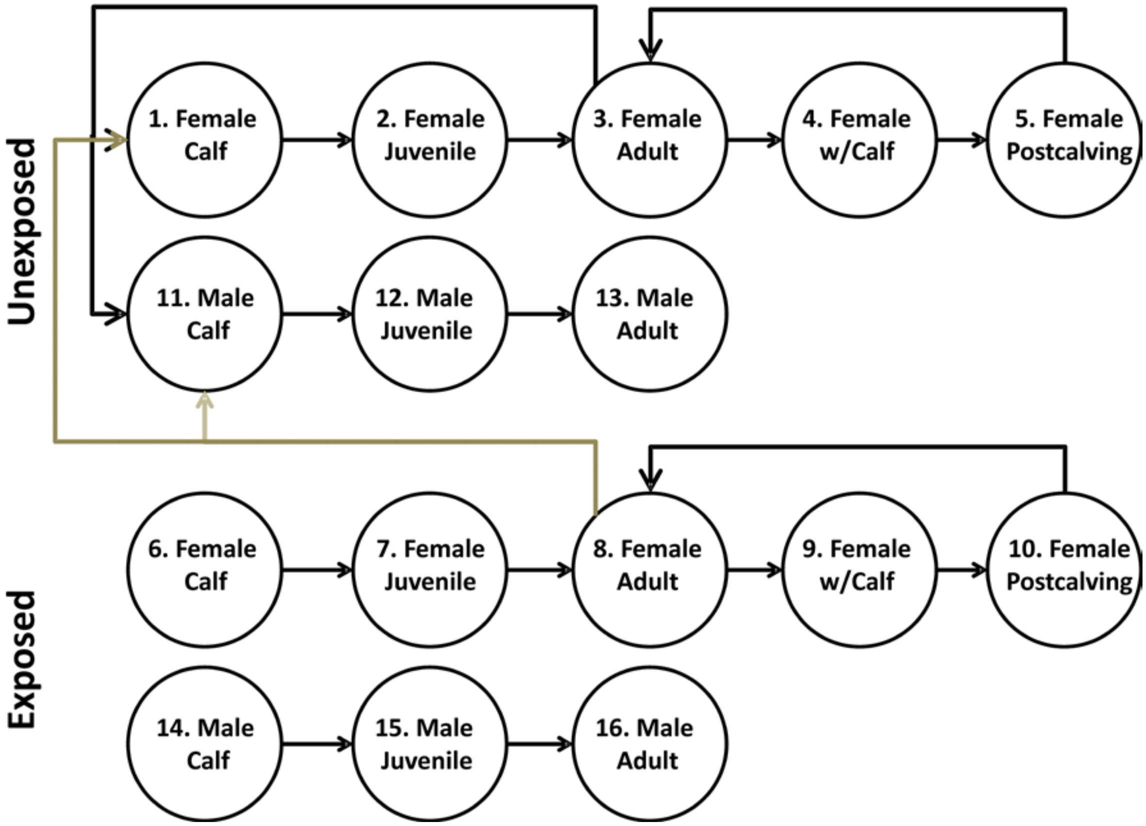

Fig. S2. *Life-cycle*. Life-cycle graph for the “DWH” stage-structured model. Arrows indicate possible transitions between stages with reproduction indicated by arrows connecting Female adults (Stage 3) to calves (Stages 1 and 6). Calves are produced at a 50:50 sex ratio. Model stages are separated into an “unexposed” cohort and an “exposed” cohort. The “exposed” cohort represents the proportion of the population that was estimated to overlap with DWH surface oil at sufficient levels to cause additional mortality and reproductive effects (see (Schwacke et al. 2017)). The exposed cohort produces unexposed calves and thus dies out over time. For males, an additional loss term was included in the adult survival rate to account for emigration of males which results in the 72:28 female to male sex ratio observed in the NGM population (Engelhaupt et al. 2009).

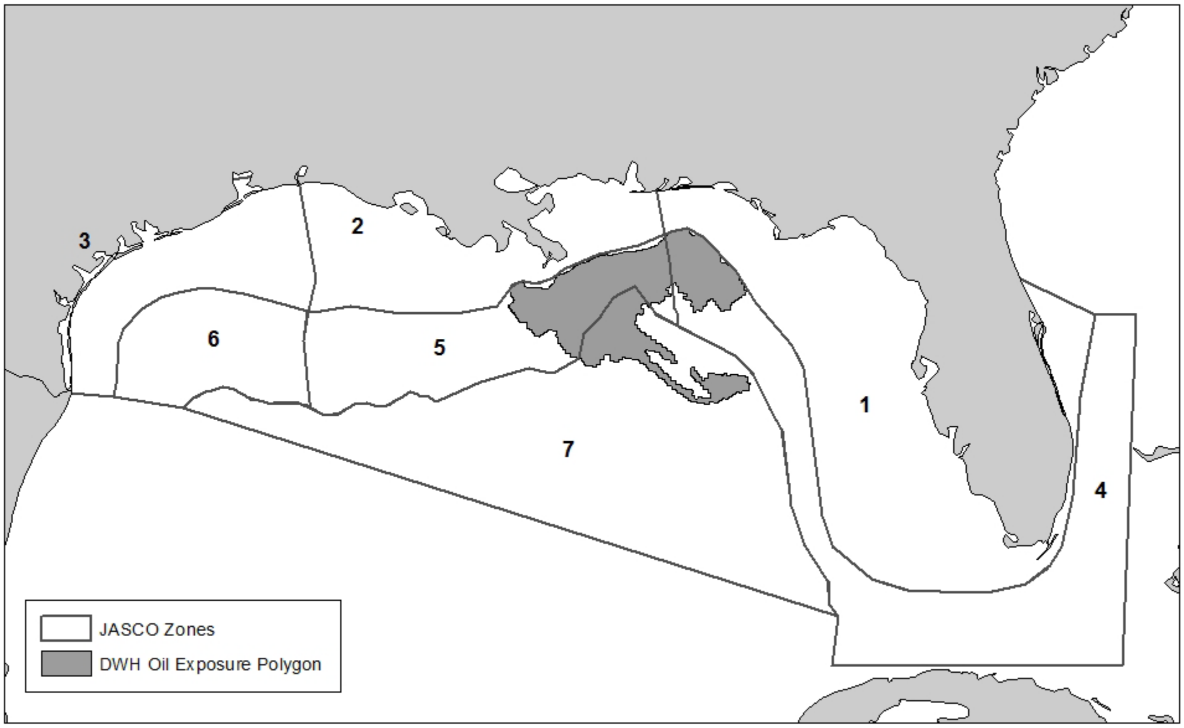

Fig. S3. *DWH Oil Exposure*. JASCO zones used to estimate acoustic disturbance impacts and polygon representing the extent of DWH surface oil exposure.

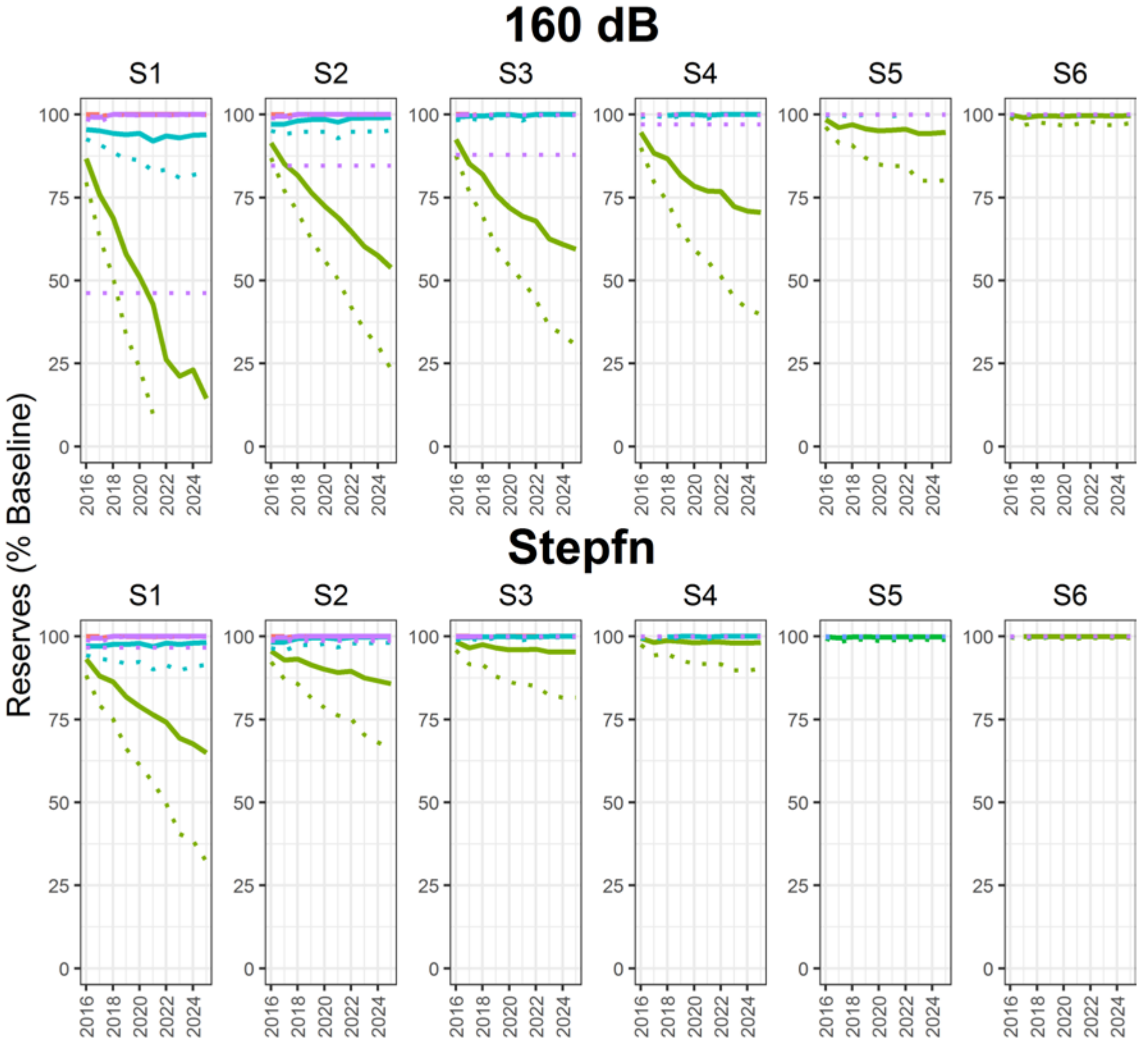

Fig. S4. *Relative body condition.* Mean (solid line) and 95% confidence intervals (dotted lines) for available reserve energy of simulated mature whales exposed to behavioral disturbance under 160 dB (top) and Stepfn (bottom) criteria relative to undisturbed whales of identical characteristics, by zone (4: red, 5: green, 6: blue, 7: purple). Outputs presented for six different model scenarios for individual reduction in foraging efficiency during exposures above threshold, ability to optimize replacement of lost reserves, and ability to increase consumption to support increased growth on days of undisturbed foraging (see **Table 1**).

Table S1. Summary of seismic surveys considered to determine sperm whale behavioral exposure. The high resolution geophysical survey (HRG) sources (90cui, Boomer, AUV) were modeled independently.

Survey	Area (km^2)	Source	Frequency	Speed (m/s)	Shot Interval (s)
2D	6960	1 x 8000 in^3	10 Hz-5 kHz (peak <200 Hz)	2.3	21.6
3D NAZ	6960	2 x 8000 in^3	10 Hz-5 kHz (peak <200 Hz)	2.5	15
3D WAZ	6960	4 x 8000 in^3	10 Hz-5 kHz (peak <200 Hz)	2.5	86.4
Coil	3364	4 x 8000 in^3	10 Hz-5 kHz (peak <200 Hz)	2.5	20
90cui	72.5	1 x 90 in^3	10 Hz-5 kHz (peak <600 Hz)	n/a	n/a
Boomer	72.5	~40 cm baffle	100 Hz-10 kHz	n/a	n/a
AUV	72.5	multibeam echosounder, side-scan sonar, sub-bottom profiler	200 kHz, 120/410 kHz, 14 kHz	n/a	n/a

2D: Two-dimensional survey, 3D NAZ: Three-dimensional narrow azimuth survey, 3D WAZ: Three-dimensional wide azimuth survey, Coil: four vessels sailing separated circular tracks, 90cui: 90 cubic inch single airgun, Boomer: omni-directional boomer plate (90cui results used as conservative substitute for Boomer), AUV: autonomous underwater vehicle with multi-source sampling system. See Zeddies et al. (2015) for more details.

Table S2. Parameterization of 3MB (Houser and Cross 2014) movement model for sperm whales.

Behavior	Variable	Value	Reference
Deep foraging dive	Travel direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.88 (0.27)	Miller et al. 2004
	Ascent rate (m/s)	Gaussian 1.3 (0.2)	Watwood et al. 2006
	Descent rate (m/s)	Gaussian 1.1 (0.2)	Watwood et al. 2006
	Average depth (m)	Gaussian 546.9 (130)	Watwood et al. 2006
	Bottom following	No	Best estimate
	Reversals	Gaussian 8.2 (4.2)	Aoki et al. 2007
	Reversal dive rate (m/s)	Gaussian 1.8 (0.5)	Aoki et al. 2007
	Time in reversal (s)	Gaussian 141 (82.7)	Amano & Yoshioka 2003, Aoki et al. 2007
	Surface interval (s)	Gaussian 486 (156)	Watwood et al. 2006
Inactive bottom time	Travel Direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.88 (0.27)	Miller et al. 2004
	Ascent rate (m/s)	Gaussian 1.13 (0.07)	Amano & Yoshioka 2003

	Descent rate (m/s)	Gaussian 1.4 (0.13)	Amano & Yoshioka 2003
	Average depth (m)	Gaussian 490 (74.6)	Amano & Yoshioka 2003
	Bottom following	No	Best estimate
	Reversals	Gaussian 1.0 (0)	Best estimate
	Reversal dive rate (m/s)	Gaussian 0.1 (0.1)	Best estimate
	Time in reversal (s)	Gaussian 1188 (174.6)	Amano & Yoshioka 2003
	Surface interval (s)	Gaussian 546 (354)	Amano & Yoshioka 2003
V dive	Travel Direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.88 (0.27)	Miller et al. 2004
	Ascent rate (m/s)	Gaussian 0.67 (0.43)	Amano & Yoshioka 2003
	Descent rate (m/s)	Gaussian 0.85 (0.05)	Amano & Yoshioka 2003
	Average depth (m)	Gaussian 282.7 (69.9)	Amano & Yoshioka 2003
	Bottom following	No	Best estimate
	Reversals	No	Best estimate
	Surface interval (s)	Gaussian 408 (114)	Amano & Yoshioka 2003
Surface inactive (head down)	Travel Direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.0 (0.0)	Best estimate

	Ascent rate (m/s)	Gaussian 0.1 (0.1)	Miller et al. 2008
	Descent rate (m/s)	Gaussian 0.1 (0.1)	Miller et al. 2008
	Average depth (m)	Gaussian 16.5 (4.9)	Miller et al. 2008
	Bottom following	No	Best estimate
	Reversals	Gaussian 1.0 (0)	Best estimate
	Reversal dive rate (m/s)	Gaussian 0.0 (0.0)	Best estimate
	Time in reversal (s)	Gaussian 804 (522)	Miller et al. 2008
	Surface interval (s)	Gaussian 462 (360)	Miller et al. 2008
	Bout duration*	T50 = 8.1, K = 0.9	Best estimate
Surface inactive (head up)	Travel Direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.0 (0.0)	Best estimate
	Ascent rate (m/s)	Gaussian 0.1 (0.1)	Miller et al. 2008
	Descent rate (m/s)	Gaussian 0.1 (0.1)	Miller et al. 2008
	Average depth (m)	Gaussian 8.6 (4.8)	Miller et al. 2008
	Bottom following	No	Best estimate
	Reversals	Gaussian 1.0 (0)	Best estimate
	Reversal dive rate (m/s)	Gaussian 0.0 (0.0)	Best estimate
	Time in reversal (s)	Gaussian 708 (552)	Miller et al. 2008
	Surface interval (s)	Gaussian 462 (360)	Miller et al. 2008
	Bout duration*	T50 = 8.1, K = 0.9	Best estimate

Surface active	Travel Direction	Correlated random walk	Best estimate
	Perturbation value	10	Best estimate
	Termination coefficient	0.2	Best estimate
	Travel rate (m/s)	Gaussian 0.88 (0.27)	Miller et al. 2004
	Ascent rate (m/s)	Gaussian 0.67 (0.43)	Amano & Yoshioka 2003
	Descent rate (m/s)	Gaussian 0.85 (0.05)	Amano & Yoshioka 2003
	Average depth (m)	Gaussian 25.0 (25.0)	Amano & Yoshioka 2003
	Bottom following	No	Best estimate
	Reversals	No	Best estimate
	Surface interval (s)	Gaussian 408 (114)	Amano & Yoshioka 2003

* Sigmoidal function: T50 is the midpoint in minutes, K is the steepness

Table S3. Projected level of effort in days (24 h) for survey types in years 2016 to 2025. 2-D seismic survey is an 8000 in^3 airgun array with 1 vessel. 3-D seismic survey is an 8000 in^3 airgun array with two vessels. The 3D WAZ seismic survey is an 8000 in^3 airgun array with four vessels. Coil seismic survey is an 8000 in^3 airgun array with four vessels. Shallow hazards 90cui seismic survey is a 90 in^3 airgun. The high resolution sources (AUV) include side-scan sonar, multibeam, and sub-bottom profiler.

Year	**Survey**	**Zone4**	**Zone5**	**Zone6**	**Zone7**
2016	2D	0.0	55.5	0.0	69.5
2016	3D NAZ	0.0	389.1	185.5	515.5
2016	3D WAZ	0.0	192.3	48.6	248.1
2016	Coil	0.0	82.4	20.8	106.3
2016	90cui	0.0	0.0	0.0	0.0
2016	Boomer	0.0	0.0	0.0	0.0
2016	AUV	0.0	25.9	9.9	34.0
2017	2D	32.9	0.0	0.0	29.6
2017	3D NAZ	0.0	389.1	99.1	502.0
2017	3D WAZ	0.0	192.3	0.0	240.5
2017	Coil	0.0	82.4	0.0	103.1
2017	90cui	0.0	0.0	0.0	0.0
2017	Boomer	0.0	0.0	0.0	0.0
2017	AUV	0.3	25.9	10.8	34.3
2018	2D	0.0	0.0	0.0	0.0
2018	3D NAZ	0.0	341.8	185.6	456.4

2018	3D WAZ	0.0	160.3	48.6	208.0
2018	Coil	0.0	68.7	20.8	89.1
2018	90cui	0.0	0.0	0.0	0.0
2018	Boomer	0.0	0.0	0.0	0.0
2018	AUV	0.5	27.1	11.7	36.2
2019	2D	65.7	27.8	0.0	94.0
2019	3D NAZ	61.3	247.3	99.1	380.0
2019	3D WAZ	21.5	96.2	0.0	139.6
2019	Coil	9.2	41.2	0.0	59.8
2019	90cui	0.0	0.0	0.0	0.0
2019	Boomer	0.0	0.0	0.0	0.0
2019	AUV	0.5	27.1	11.7	36.2
2020	2D	0.0	0.0	0.0	0.0
2020	3D NAZ	92.0	294.6	99.1	466.8
2020	3D WAZ	0.0	192.3	0.0	240.5
2020	Coil	0.0	82.4	0.0	103.1
2020	90cui	0.0	2.2	0.0	2.7
2020	Boomer	0.0	1.4	0.0	1.8
2020	AUV	0.3	25.1	12.6	33.6
2021	2D	0.0	0.0	0.0	0.0
2021	3D NAZ	92.0	247.3	185.6	421.1
2021	3D WAZ	0.0	160.3	48.6	208.0
2021	Coil	0.0	68.7	20.8	89.1

2021	90cui	0.0	0.0	0.0	0.0
2021	Boomer	0.0	0.0	0.0	0.0
2021	AUV	0.5	30.1	12.6	40.1
2022	2D	32.9	27.8	0.0	64.4
2022	3D NAZ	61.3	247.3	99.1	380.0
2022	3D WAZ	21.5	160.3	0.0	219.8
2022	Coil	9.2	68.7	0.0	94.2
2022	90cui	0.0	0.0	0.0	0.0
2022	Boomer	0.0	0.0	0.0	0.0
2022	AUV	0.8	32.4	13.3	43.3
2023	2D	11.0	9.3	0.0	21.5
2023	3D NAZ	61.3	247.3	99.1	380.0
2023	3D WAZ	0.0	128.2	0.0	160.3
2023	Coil	0.0	54.9	0.0	68.7
2023	90cui	0.0	0.0	0.0	0.0
2023	Boomer	0.0	0.0	0.0	0.0
2023	AUV	1.1	34.7	13.3	46.5
2024	2D	0.0	0.0	0.0	0.0
2024	3D NAZ	61.3	200.0	99.1	320.9
2024	3D WAZ	0.0	192.3	0.0	240.5
2024	Coil	0.0	82.4	0.0	103.1
2024	90cui	0.0	0.0	0.0	0.0
2024	Boomer	0.0	0.0	0.0	0.0

2024	AUV	1.1	34.7	13.5	46.5
2025	2D	5.5	0.0	0.0	4.9
2025	3D NAZ	61.3	200.0	99.1	320.9
2025	3D WAZ	0.0	160.3	0.0	200.4
2025	Coil	0.0	68.7	0.0	85.9
2025	90cui	0.0	0.0	0.0	0.0
2025	Boomer	0.0	0.0	0.0	0.0
2025	AUV	1.1	37.0	13.5	49.4

Table S4. Mean sperm whale abundance (N) within proposed mitigation closure areas, by zone, relative to total mean abundance (N) in the modeled zone (Roberts et al. 2016).

Proposed Mitigation Closure	**Zone**	**N in Closure**	**N in Zone**	**% Coverage**
Eastern Planning Area Closure	4	3.55	357.59	1%
	5	0.24	662.20	0%
Tortugas Area Closure	4	162.57	357.59	45%
	7	6.66	847.15	1%
Central Planning Area Closure*	5	188.16	662.20	28%

Table S5. Stage-specific survival rates and stable age distribution for the "base" demographic model. In both models, the inter-birth interval was 4 years with a 2 year weaning period. The calf interval is 2 years duration, and maturity is reached at age 9. The DWH model used the same initial stage specific survival rates with the exposed cohort accounting for 16.5% of the total population.

Stage	**Base Survival Rate**	**Initial proportion of population**
1. Female Calf	0.9070 (0.8841-0.9850)	0.0593
2. Female Juvenile	0.9424 (0.8841-0.9850)	0.1449
3. Female Adult	0.9777 (0.9390-0.9800)	0.2522
4. Female w/ Calf	0.9777 (0.9390-0.9800)	0.1243
5. Female Postcalving	0.9777 (0.9390-0.9800)	0.1166
6. Male Calf	0.9070 (0.8841-0.9850)	0.0592
7. Male Juvenile	0.9424 (0.8841-0.9850)	0.1449
8. Male Adult	0.8500 (0.7395-0.8526)	0.0984

Table S6. Maximum annual percentage of the NGM sperm whale stock projected to reach terminal starvation over 10 years of projected G&G survey acoustic exposure under the '*sensu* Nowacek et al. (2015)' model runs A (10% @ 111, 50% @ 140, 90% @ 180 dB SPL) and B (10% @ 120, 50% @ 140, 90% @ 180 dB SPL).

Scenario	**A**	**B**
1	25.8±2.6	22.4±2.0
2	20.5±1.9	13.1±2.5
3	20.4±1.7	16.2±2.6
4	12.5±2.5	12.8±2.5
5	7.3±2.5	7.6±2.7
6	5.1±2.2	5.3±2.4