



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

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## ABSTRACT

Sperm whale (*Physeter macrocephalus*) populations are still recovering from massive population declines associated with commercial whaling operations. The species continues to face a suite of contemporary threats, including pollution, ship strikes, fisheries interactions, habitat loss and degradation, oil spills, and anthropogenic noise. The sperm whale stock in the northern Gulf of Mexico was exposed to oil from the Deepwater Horizon (DWH) oil spill and is exposed to high levels of anthropogenic noises generated by geological and geophysical (G & G) surveys for hydrocarbon deposits. Population impacts from oil and gas activities were predicted from models that incorporated two stressors: (i) oil exposure from DWH and (ii) noise from G&G surveys. Oil exposure was projected to reduce survival and reproductive success, causing a mean stock decline of 26% by 2025. Additionally, exposure to underwater noise can adversely impact whale hearing, communication, foraging efficiency, and disturb essential behaviors. Exposures to G&G survey noise were determined by simulating individual movements through three-dimensional sound fields generated by different survey methods. Behavioral disturbance was evaluated as reduced foraging opportunities under four dose-response functions. Bioenergetic models tracked the depletion of reserves in blubber, muscle, and viscera. All simulations suggested significant reductions in relative fitness of reproductive females were a likely consequence of persistent disturbances to foraging behaviors. Under a 160 dB SPL unweighted dose-response function, up to  $4.4 \pm 0.3\%$  of the stock may reach terminal starvation due to behavioral disturbance associated with future G&G surveys, leading to abortions, calf abandonment, and up to 25% greater stock declines beyond those predicted from DWH oil exposure. Uncertainty in our results emphasizes a need for further controlled exposure experiments to generate behavioral disturbance dose-response curves and detailed evaluation of 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.

## 1. 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

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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, I.W., 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 2128 (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.

## 2. Methods

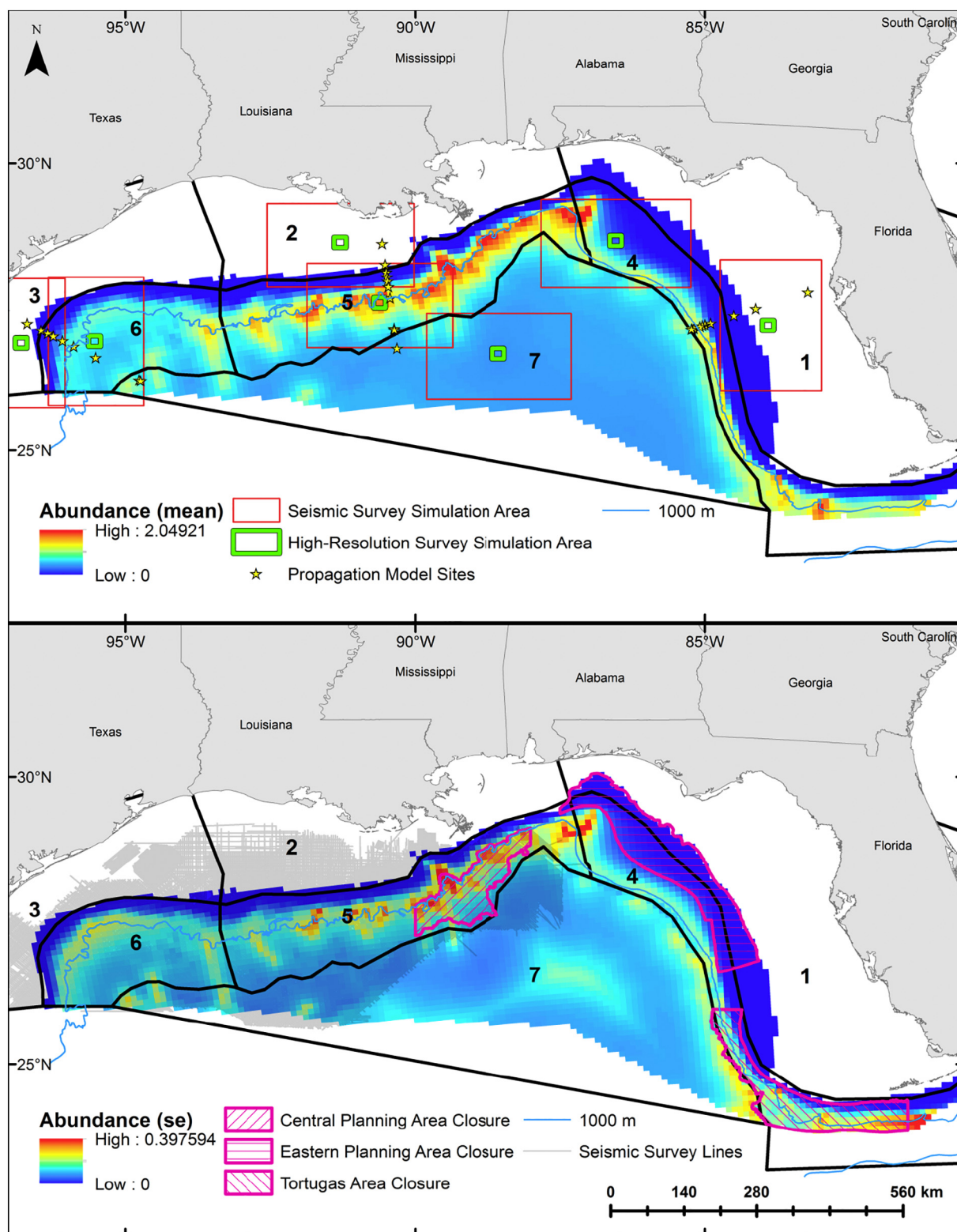
Our modeling approach integrates a number of approaches including: (i) acoustic modeling to estimate sound propagation from various G&G survey methods; (ii) animal movement simulations to estimate exposure through three-dimensional sound fields; (iii) dose-response functions to estimate the probability 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).

### 2.1. Acoustic propagation modeling

Source levels and directivity of airgun arrays were predicted with JASCO's Airgun Array Source Model (AASM; (Austin et al., 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  $\mu$ Pa) 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



**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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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  $\mu$ Pa 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



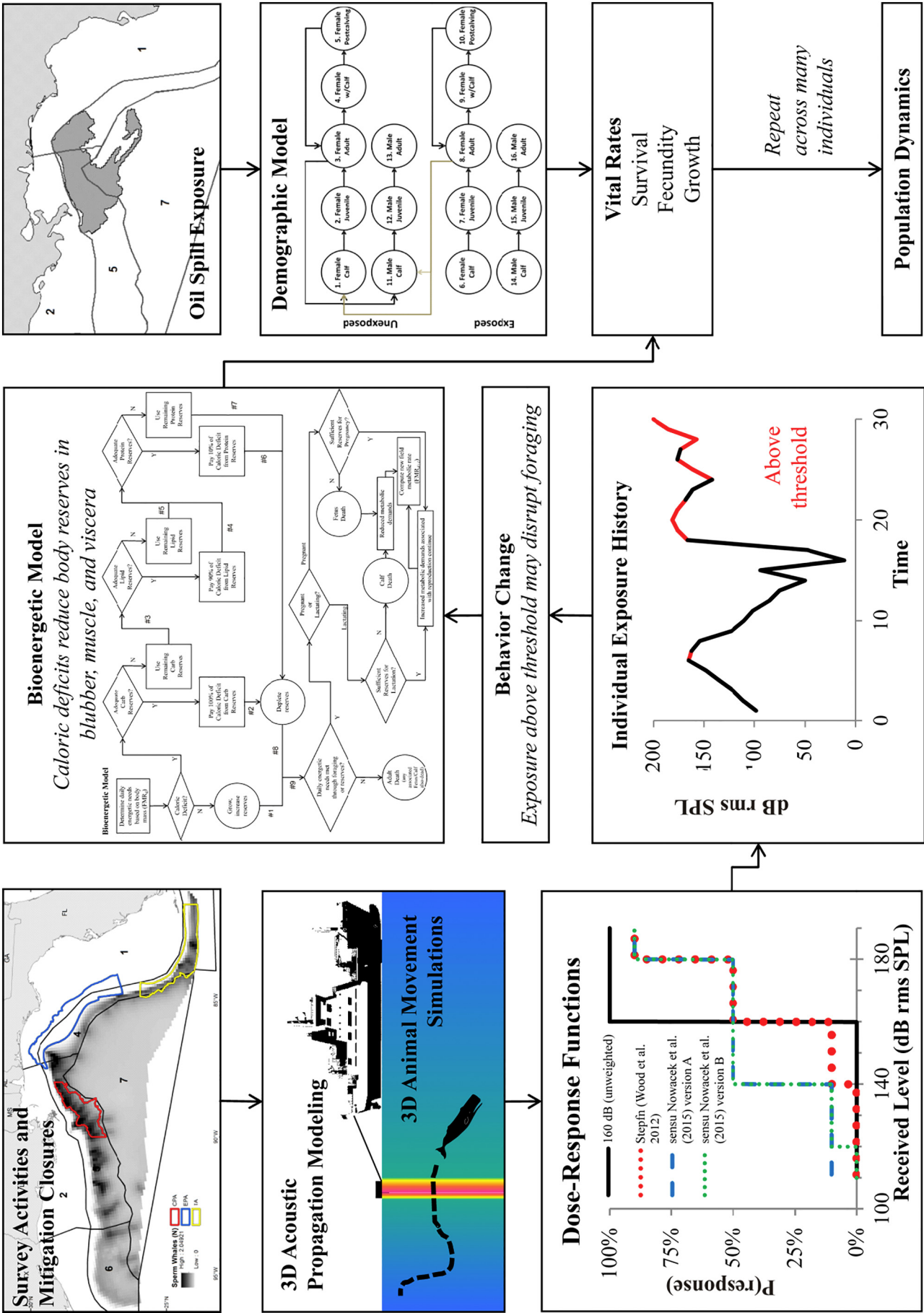


Fig. 2. Modeling process flow chart. Our modeling approach estimates the consequences of sperm whale exposure to sound in areas open to seismic survey activities by integrating (i) acoustic modeling to estimate the sound propagation from various G&G survey methods, (ii) animal movement simulations to 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 DWK spill, and (vii) a demographic model that evaluates stock level consequences of mortalities and reproductive impacts associated with both oil exposure and behavioral disturbance.

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 et al. (2015).

## 2.2. 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 (3 MB) 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).

## 2.3. 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  $\mu$ Pa 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  $\mu$ Pa, 50% probability of response at 160 dB SPL re 1  $\mu$ Pa, and 90% probability of response at 180 dB SPL re 1  $\mu$ Pa); 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 3 MB and pre-computed acoustic fields output by AASM, MONM, and FWRAM were combined in the JASCO Exposure Modeling System (JEMS; (Zeddies et al., 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 and 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).

## 2.4. 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).

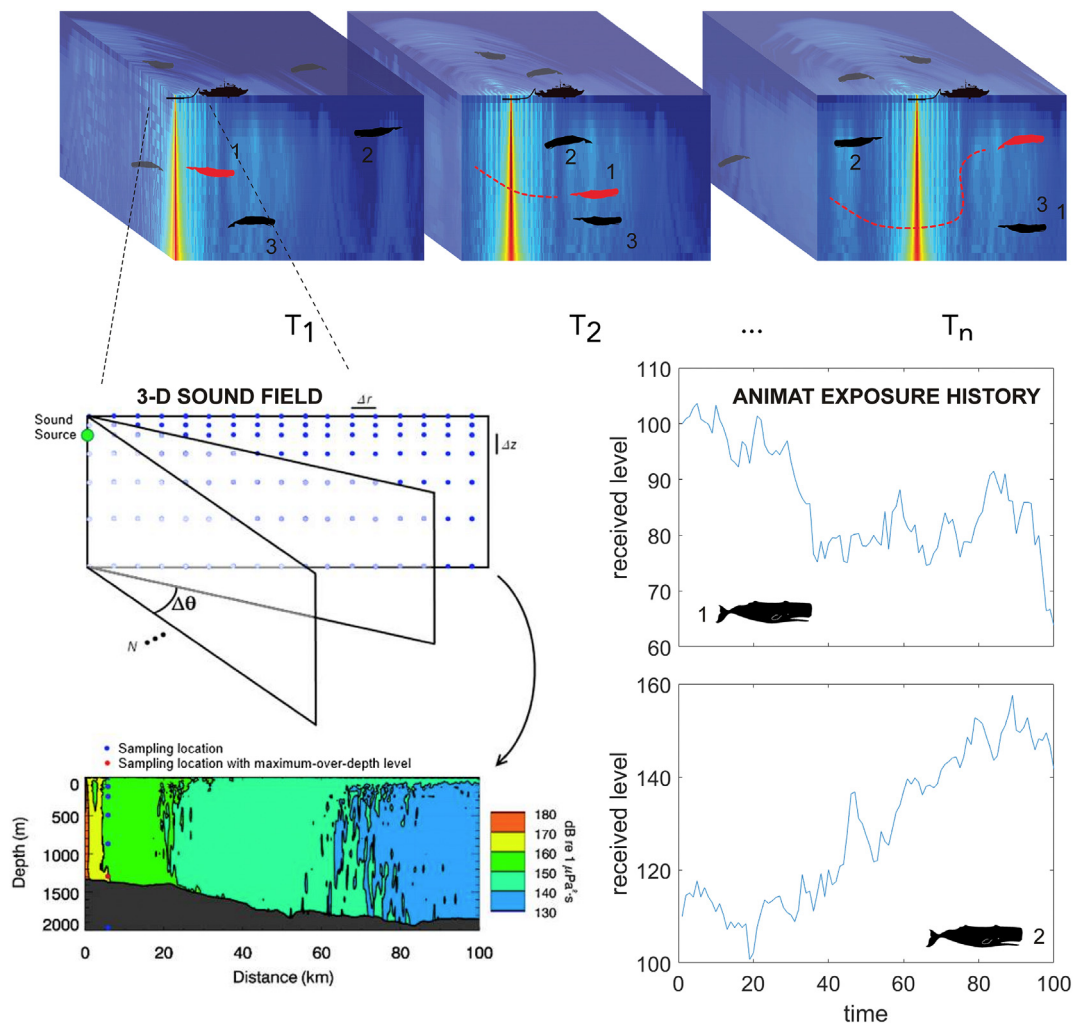
Ten year projections of daily duration of exposure above threshold (160 dB and Stepfn) for simulated individuals were generated using a bootstrapping approach. Daily random draws modeled disturbance-minutes (D) for individual whales in a zone for each survey as follows:

$$\text{if } S \left( \frac{\text{Days}_{\text{survey}}}{365} \right) \times \underbrace{\frac{(1 - \text{Area}_{\text{homerange}})}{\text{Area}_{\text{zone}}}}_{P(\text{survey in zone that day})} \times \underbrace{\frac{\text{Area}_{\text{survey}}}{\text{Area}_{\text{zone}}}}_{P(\text{animat in zone})} \times \underbrace{\frac{(1 - C_{\text{zone}})}{P(\text{survey in range of animat})}}_{P(\text{no mitigation closure})} \times \underbrace{\left( 1 - P(\text{detection}) \times \frac{\text{Area}_{\text{shutdown}}}{\text{Area}_{\text{survey}}} \right)}_{P(\text{no shutdown due to animat detected within 500 m})} \geq \text{rand}(0, 1)$$

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

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

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.



**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.

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  $\pm 25\%$ . 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 > 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 et al., 2015). Sensitivity runs comparing 7-day to 30-day

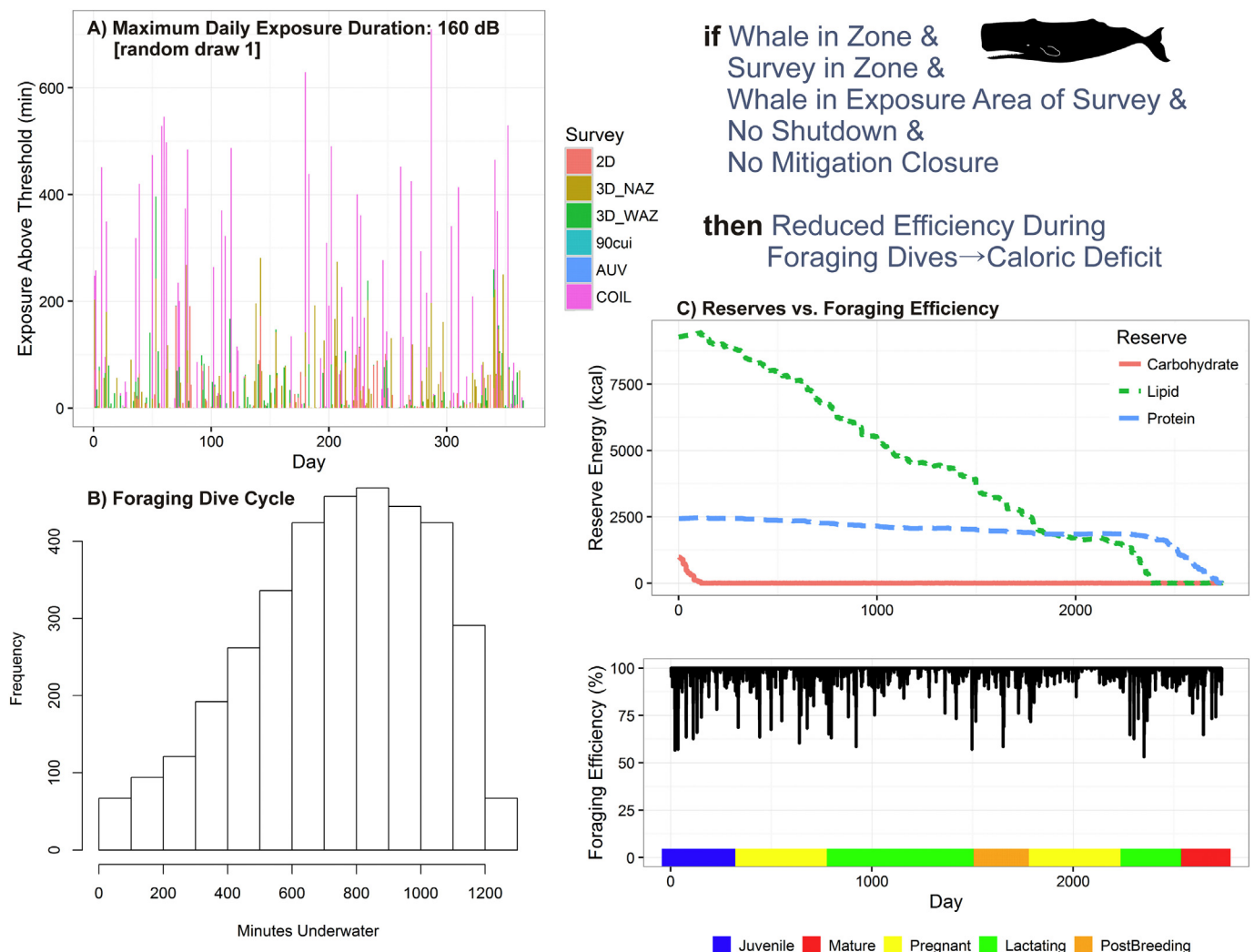
simulations indicated that 24 h probabilities of exposure scale much more appropriately than the time-series of exposures (Zeddies et al., 2015), providing greater credibility to the realism of these results. If an individual sperm whale was exposed to multiple surveys on a single day, the duration of 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.

## 2.5. Physiological effects of disturbance

Each 24 h day, on average, sperm whales in the NGM spend  $72\% \pm 32.7\%$  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  $53\% \pm 5\%$  of their time actively encountering prey at mean depths between 467 and 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:

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





**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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The sample distribution for  $t_{\text{underwater}}^d$  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  $\mu$ Pa, 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

levels ranging from 120 to 169 SPL<sub>max</sub> re 1  $\mu$ Pa 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 and 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):

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

foraging whales that were exposed to lower levels of sound (Jochens et al., 2006). In CEE off Norway, naval sonar exposures at received

where  $\varphi$  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  $\phi = 100\%$  (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 ( $tE_d^{undisturbed}$ ):

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

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  $\phi$  set at 100% (Miller et al., 2009b) and with  $\phi$  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.

## 2.6. 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):

$$C_{zone} = \frac{\sum N_{zone}^{closed}}{\sum N_{zone}^{total}}$$

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.

## 2.7. Oil exposure and cumulative effects

The cumulative stock impact of reduced survivorship due to oil exposure and noise disturbance was 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

**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)	1.5 ×
5	U (20–100%)	U (somatic-optimal)	1.5 ×
6	U (20–100%)	U (somatic-optimal)	3 ×



exposure (Schwacke et al., 2017). The initial population size was 2138 (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.

### 3. 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,  $4.4 \pm 2.1\%$  (mean  $\pm$  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,  $0.3 \pm 0.2\%$  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,

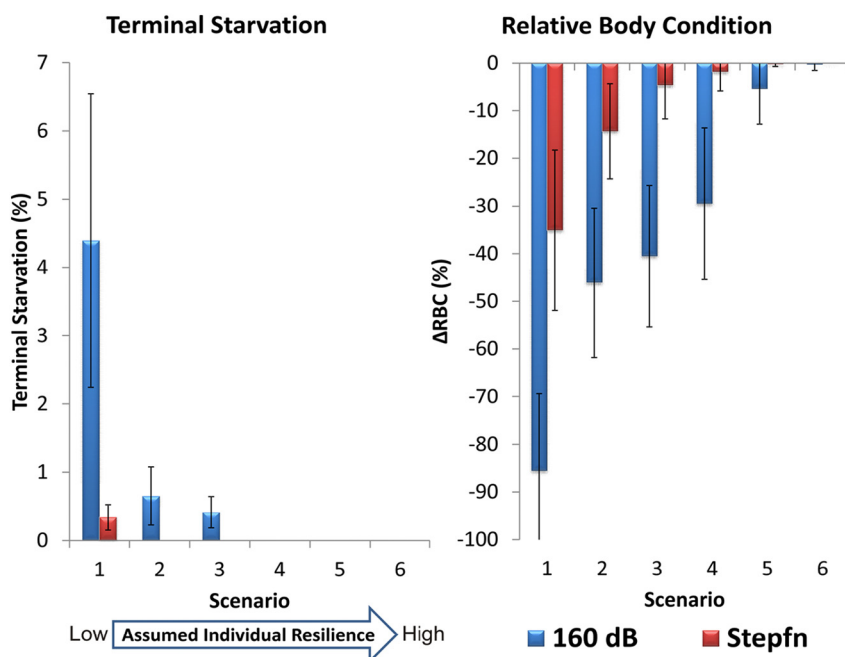
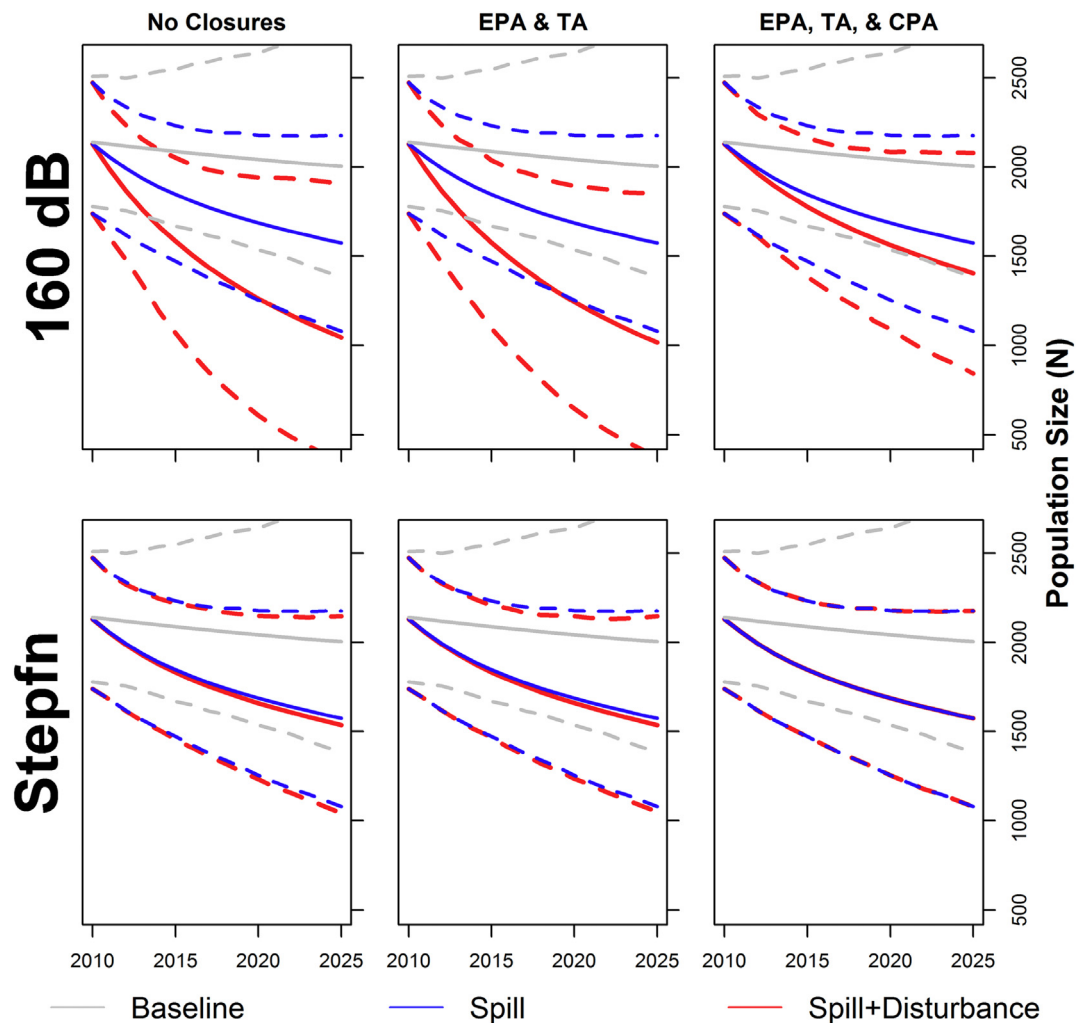


Fig. 5. Consequences of disturbance. Percent stock reaching terminal starvation across 1000 bootstrapped runs for each life stage across all zones and relative body condition in terminal year relative to undisturbed individuals for females in Zone 5 (mean  $\pm$  SE). Outputs presented for different 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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.

#### 4. 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 and 160 dB SPL, it only includes 50% of the individuals exposed between 160 and 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 to 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  $12.6 \pm 18.2\%$  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  $\pm 25\%$  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) compensatory 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



**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	↑	<ul style="list-style-type: none"> <li>● Extreme fasting leads to metabolic depression (Castellini and Rea, 1992; Rea and Costa, 1992)</li> <li>● Unclear if functional adaptation for a whale that must dive to acquire food (Watwood et al., 2006)</li> <li>● Metabolic rate decreases during diving in marine mammals (Webb et al., 1998)</li> </ul>
Long-distance movements and migration	‡	<ul style="list-style-type: none"> <li>● Sperm whales do not appear to make seasonal migrations in the Gulf of Mexico (Waring et al., 2016)</li> <li>● Could result in slight short-term changes in density and also modify individual exposure histories</li> <li>● Unlikely that competitive displacement would be common in areas during anthropogenic disturbance events</li> </ul>
Grouping	‡	<ul style="list-style-type: none"> <li>● Sperm whales may form temporary or permanent social groups (Christal et al., 1998)</li> <li>● 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)</li> <li>● 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)</li> <li>● Grouping proportionally decreases the likelihood of exposure but increases the effect when an exposure occurs (Zeddies et al., 2015)</li> <li>● Sensitivity runs suggest grouping effects the distribution of exposure estimates but not the mean (Zeddies et al., 2015)</li> </ul>
Hydrodynamic variability in sound propagation	‡	<ul style="list-style-type: none"> <li>● 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</li> <li>● Sensitivity runs suggest low levels (&lt; 4 dB) of uncertainty associated with hydrodynamic variability in sound propagation (Austin et al., 2012; Matthews and MacGillivray, 2013; Zeddies et al., 2015)</li> </ul>
Interaction of stressors	‡	<ul style="list-style-type: none"> <li>● 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)</li> </ul>
Avoidance	‡/↓	<ul style="list-style-type: none"> <li>● Whales may temporarily avoid or move away from an ensonified area (Richardson et al., 2013; Stone and Tasker, 2006)</li> <li>● 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)</li> <li>● 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)</li> <li>● 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)</li> </ul>
Depensatory reproductive rates	‡/↓	<ul style="list-style-type: none"> <li>● Female mammals are less fertile when their diets are restricted (Ball et al., 1947; Miller et al., 2011)</li> <li>● Lower calf production→ fewer calves and females at terminal starvation, but also reduced stock size</li> </ul>
Noise impacts on prey	‡/↓	<ul style="list-style-type: none"> <li>● 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)</li> <li>● Anthropogenic sound may alter prey abundance, behavior, and distribution (Engås et al., 1996; Slotte et al., 2004)</li> <li>● 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)</li> <li>● Changes in call amplitude increase metabolic costs (Holt et al., 2015; Holt et al., 2009; Noren et al., 2017)</li> <li>● Disturbance is often context-specific and seldom measured across multiple metrics of exposure (Southall et al., 2007)</li> <li>● More severe consistent behavioral responses are not consistently associated with higher received sound levels (Gomez et al., 2016)</li> <li>● 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)</li> <li>● 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)</li> </ul>
Signal masking	↓	<ul style="list-style-type: none"> <li>● 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)</li> <li>● 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)</li> </ul>
TTS/PTS	↓	<ul style="list-style-type: none"> <li>● Intense sounds can physically damage an animal's auditory system, resulting in temporary or permanent threshold shifts (PTS or TTS; (Weilgart, 2007b))</li> <li>● There is a high potential for TTS and repeated exposures that could lead to PTS associated with continued G&amp;G activities in the Gulf of Mexico (Zeddies et al., 2015)</li> <li>● TTS and PTS could lead to reductions in foraging efficiency, reproductive potential, social cohesion, and ability to detect predators (Weilgart, 2007a)</li> </ul>
Elevated stress levels	↓	<ul style="list-style-type: none"> <li>● Exposure to sound can lead to elevated stress levels (Rolland et al., 2012; Romano et al., 2004; Thomas et al., 1990)</li> <li>● Elevated stress levels can reduce the immune system's ability to fight infection (Romano et al., 2004)</li> </ul>
Dehydration or ketosis	↓	<ul style="list-style-type: none"> <li>● Fasting health impacts include dehydration and ketosis associated with the catabolism of energy stores (Castellini and Rea, 1992)</li> <li>● May have neurotoxic and immunotoxic effects (Castellini and Rea, 1992)</li> <li>● Implicated in marine mammal strandings (Mazzariol et al., 2011; Sharp et al., 2014)</li> </ul>
Increased risk of disease	↓	<ul style="list-style-type: none"> <li>● Stress and malnutrition reduce immune system function (Romano et al., 2004; Scrimshaw et al., 1968)</li> </ul>

(continued on next page)

Table 2 (continued)

Not considered	Impact	Discussion
Decompression sickness	↓	<ul style="list-style-type: none"> <li>• High-intensity, low-frequency sounds could lead to gas bubble formation in body tissue through rectified diffusion (Crum and Mao, 1996)</li> <li>• 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)</li> <li>• 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)</li> <li>• When exposed to unanticipated threats, whales may forgo nitrogen load management, increasing their risk of decompression sickness (Hooker et al., 2012)</li> </ul>
Cultural impact	↓	<ul style="list-style-type: none"> <li>• 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)</li> <li>• 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)</li> <li>• 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)</li> </ul>

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); 2138 (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 ( $\geq 159$  kL) oil spills are anticipated every 2–4 years in the NGM, with large spills ( $\geq 1590$  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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.09.006>.

## References

- [BOEM] Bureau of Ocean Energy Management, 2017. Gulf of Mexico OCS proposed geological and geophysical activities: western, central, and eastern planning areas. In: B.o.O.E. Management (Ed.), Final Environmental Impact Statement. 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. In: NOAA-NCEI (Ed.), U.S. Coastal Relief Model.
- [NMFS] National Marine Fisheries Service, 1995. Small takes of marine mammals incidental to specified activities. In: Offshore Seismic Activities in Southern California: Notice of Issuance of an Incidental Harassment Authorization. National Oceanographic and Atmospheric Administration, Federal Register, pp. 53753–53760.
- [NMFS] National Marine Fisheries Service, 2000. Small takes of marine mammals incidental to specified activities. In: D.o. Commerce (Ed.), Marine Seismic-reflection Data Collection in Southern California. National Oceanographic and Atmospheric Administration, Federal Register, pp. 16374–16379.
- [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. Department of the Navy, Arlington, Virginia, pp. 723.
- 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. *Front. Ecol. Environ.* 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. Zzykov, 2010. Marine acoustics (Enbridge northern gateway project 2006), In Technical Data Report. J.A. Sciences, (Dartmouth, Nova Scotia, Canada).
- Austin, M.E., MacGillivray, A.O., Chapman, N.R., 2012. Acoustic transmission loss measurements in green charlotte Basin. *Can. Acoust.* 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. *Am. J. Phys.* 150, 511–519.
- Barlow, J., Sexton, S., 1996. The Effect of Diving and Searching Behavior on the Probability 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. *Mar. Mamm. Sci.* 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. *Mar. Ecol. Prog. Ser.* 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. *Behav. Ecol.* 10, 198–208.
- Brook, B.W., Sodhi, N.S., Bradshaw, C.J., 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460.
- Bryant, P.J., Lafferty, C.M., Lafferty, S.K., 1984. Reoccupation of Laguna Guerrero Negro, Baja California, Mexico, by gray whales. In: The Gray Whale, *Eschrichtius Robustus*, pp. 375–387.
- Buckingham, M.J., 2005. Compressional and shear wave properties of marine sediments: comparisons between theory and data. *J. Acoust. Soc. Am.* 117, 137–152.
- Carder, D., Ridgway, S., 1990. Auditory brainstem response in a neonatal sperm whale, *Physeter* spp. *J. Acoust. Soc. Am.* 88, 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. *Cell. Mol. Life Sci.* 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. *Biol. Conserv.* 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. *Ecol. Model.* 248, 71–79.
- Christal, J., Whitehead, H., Lettevall, E., 1998. Sperm whale social units: variation and change. *Can. J. Zool.* 76, 1431–1440.
- Christiansen, F., Vikiingsson, G.A., Rasmussen, M.H., Lusseau, D., 2014. Female body condition affects foetal growth in a capital breeding mysticete. *Funct. Ecol.* 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. *Mar. Ecol. Prog. Ser.* 592, 267–281.
- Commission, I.W., 2007. Report of the standing working group on environmental concerns. *J. Cetacean Res. Manag.* 9, 227–296.
- Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales. *Trends Ecol. Evol.* 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. *Mar. Ecol. Prog. Ser.* 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. *J. Acoust. Soc. Am.* 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. *Endanger. Species Res.* 33, 119–125.
- Eckle, P., Burgherr, P., Michaux, E., 2012. Risk of large oil spills: a statistical analysis in the aftermath of Deepwater Horizon. *Environ. Sci. Technol.* 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. *Conserv. Biol.* 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*). *Can. J. Fish. Aquat. Sci.* 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. *Behav. Ecol. Sociobiol.* 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*. In: *Marine and Coastal Fisheries*. 8. pp. 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., Rodríguez, F., De Los Monteros, A.E., Herraiz, 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. *Vet. Pathol.* 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. *Can. J. Zool.* 94, 801–819.
- Goss, C., Middleton, D., Rodhouse, P., 2001. Investigations of squid stocks using acoustic survey methods. *Fish. Res.* 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., Veirs, V., Emmons, C.K., Veirs, S., 2009. Speaking up: killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *J. Acoust. Soc. Am.* 125, EL27–EL32.
- 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. *J. Exp. Biol.* 218, 1647–1654.
- 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. The Royal Society*, pp. 1041–1050.
- 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., Howard, R., Ridgway, S., 2001. Can diving-induced tissue nitrogen supersaturation increase the chance of acoustically driven bubble growth in marine mammals? *J. Theor. Biol.* 213, 183–195.
- 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. *J. Exp. Mar. Biol. Ecol.* 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. *Ecol. Appl.* 26, 77–93.
- Jaquet, N., 2006. A simple photogrammetric technique to measure sperm whales at sea. *Mar. Mamm. Sci.* 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. *Mar. Biol.* 141, 591–601.
- Ji, Z.-G., Johnson, W.R., Dufore, C.M., 2017. In: United States Department of the Interior (Ed.), *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*. 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. In: *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. *J. Nat. Hist.* 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., Kurlle, C., 2015. An interim framework for assessing the population consequences of disturbance. *Methods Ecol. Evol.* 6, 1150–1158.
- Kramer, D.L., 1988. The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* 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 N<sub>2</sub> levels and risk of in vivo bubble formation in deep-, intermediate- and shallow diving toothed whales during exposure to naval sonar. *Front. Physiol.* 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. *Ecol. Monogr.* 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. *Behav. Ecol. Sociobiol.* 38, 355–363.
- Lockyer, C., 1981. Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. In: *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. *J. Acoust. Soc. Am.* 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. *J. Acoust. Soc. Am.* 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. In: *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. *Conserv. Biol.* 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. *J. Acoust. Soc. Am.* 133, 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. *J. Wildl. Dis.* 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. *APPEA J.* 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. *Ecol. Indic.* 72, 360–364.
- Miller, P.J., Johnson, M.P., Tyack, P.L., 2004a. Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. *Proc. R. Soc. Lond. B Biol. Sci.* 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*. *J. Exp. Biol.* 207, 1953–1967.
- Miller, P.J., Aoki, K., Rendell, L.E., Amano, M., 2008. Stereotypical resting behavior of the sperm whale. *Curr. Biol.* 18, R21–R23.
- Miller, P.J., Johnson, M., Madsen, P.T., Blassoni, 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 Res. I Oceanogr. Res. Pap.* 56, 1168–1181.
- Miller, P.J.O., Johnson, M.P., Madsen, P.T., Blassoni, 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 Res. I Oceanogr. Res. Pap.* 56, 1168–1181.
- 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. *Mar. Ecol. Prog. Ser.* 438, 267–283.
- 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. *Aquat. Mamm.* 38, 362.
- 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. *J. Acoust. Soc. Am.* 135, 975–993.
- Mohr, F., Lasley, B., Bursian, S., 2008. Chronic oral exposure to bunker C fuel oil causes adrenal insufficiency in ranch mink (*Mustela vison*). *Arch. Environ. Contam. Toxicol.* 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. *J. Exp. Mar. Biol. Ecol.* 495, 103–109.
- Nowacek, D.P., Johnson, M.P., Tyack, P.L., 2004. North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 227–231.
- 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. *Front. Ecol. Environ.* 13, 378–386.
- 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. *J. Acoust. Soc. Am.* 122, 3725–3731.
- Plomp, R., Bouman, M., 1959. Relation between hearing threshold and duration for tone pulses. *J. Acoust. Soc. Am.* 31, 749–758.
- Porter, M.B., Liu, Y.-C., 1994. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiol. Zool.* 65, 97–111.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: *Research Techniques in Animal Ecology: Controversies and Consequences*. 1. pp. 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. *J. Acoust. Soc. Am.* 103, 2908.
- Rea, L.D., Costa, D.P., 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiol. Zool.* 65, 97–111.
- Richardson, W.J., Würsig, B., Greene Jr., C.R., 1986. Reactions of bowhead whales, *Balaenamysticetus*, to seismic exploration in the Canadian Beaufort Sea. *J. Acoust. Soc. Am.* 79, 1117–1128.
- Richardson, W.J., Greene Jr., C.R., Malme, C.I., Thomson, D.H., 2013. *Marine Mammals and Noise*. Academic press.
- 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. *Proc. R. Soc. Lond. B Biol. Sci.* 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. *Can. J. Fish. Aquat. Sci.* 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. Ser. B Biol. Sci.* 362, 2151–2168.
- Rudd, M.A., 2014. Scientists' perspectives on global ocean research priorities. *Front. Mar. Sci.* 1, 36.
- Schulz, T.M., Whitehead, H., Gero, S., Rendell, L., 2011. Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. *Mar. Mamm. Sci.* 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., Guillelte Jr., L.J., 2013. Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. *Environ. Sci. Technol.* 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. *Endanger. Species Res.* 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*). *Vet. Immunol. Immunopathol.* 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. *Mar. Ecol. Prog. Ser.* 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. *Mar. Mamm. Sci.* 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. *Front. Physiol.* 3, 400.
- 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. *Fish. Res.* 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. *Aquat. Mamm.* 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. *Endanger. Species Res.* 31, 293–315.
- Stone, C.J., Tasker, M.L., 2006. The effects of seismic airguns on cetaceans in UK waters. *J. Cetacean Res. Manag.* 8, 255.
- Teague, W.J., Carron, M.J., Hogan, P.J., 1990. A comparison between the generalized digital environmental model and Levitus climatologies. *J. Geophys. Res. 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 Biol.* 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. In: N.O.a.A.A.N. National Marine Fisheries Service (NMFS) (Ed.), Notice of 12-month Finding on a Petition to List the Sperm Whale (*Physeter macrocephalus*). Commerce National Oceanic and Atmospheric Administration, United States of America, pp. 68032–68037.
- Waring, G., Josephson, E., Maze-Foley, K., Rosel, P., 2016. US Atlantic and Gulf of Mexico. In: *Marine Mammal Stock Assessments–2015*. NOAA Technical Memorandum NMFS-NE 238.
- Watkins, W.A., 1986. Whale reactions to human activities in Cape Cod waters. *Mar. Mamm. Sci.* 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. *Physiol. Zool.* 71, 116–126.
- Weilgart, L.S., 2007a. A brief review of known effects of noise on marine mammals. *Int. J. Comp. Psychol.* 20.
- Weilgart, L.S., 2007b. The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Can. J. Zool.* 85, 1091–1116.
- Whitehead, H., 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* 38, 237–244.
- Whitehead, H., 2002. Estimates of the current global population size and historical trajectory for sperm whales. *Mar. Ecol. Prog. Ser.* 242, 295–304.
- Whitehead, H., Rendell, L., 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *J. Anim. Ecol.* 73, 190–196.
- 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 J. Mar. Sci.* 70, 1273–1280.
- Williams, R., Erbe, C., Ashe, E., Beerman, A., Smith, J., 2014. Severity of killer whale behavioral responses to ship noise: a dose–response study. *Mar. Pollut. Bull.* 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. *Mar. Policy* 70, 58–64.
- 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. *J. Exp. Biol.* 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. *Aquat. Mamm.* 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., Zykov, M., Yurk, H., Deveau, T., Bailey, L., Gaboury, I., Racca, R., Hannay, D., Carr, S., 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. *J. Acoust. Soc. Am.* 98, 3391–3396.
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030.