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REVIEW

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Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context

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Abstract

1. Marine mammals may be negatively affected by anthropogenic noise. Behavioural response studies (BRS) aim to establish a relationship between noise exposure conditions (dose) from a potential stressor and associated behavioural responses of animals. A recent series of BRS have focused on the effects of naval sonar sounds on cetaceans. Here, we review the current state of understanding of naval sonar impact on marine mammals and highlight knowledge gaps and future research priorities.

2. Many marine mammal species exhibit responses to naval sonar sounds. However, responses vary between and within individuals and populations, highlighting the importance of exposure context in modulating dose–response relationships.

3. There is increasing support from both terrestrial and marine systems for the risk-disturbance hypothesis as an explanation for underlying response processes. This proposes that sonar sounds may be perceived by animals as a threat, evoking a response shaped by the underlying species-specific risk of predation and anti-predator strategy. An understanding of responses within both the dose–response and risk-disturbance frameworks may enhance our ability to predict responsiveness for unstudied species and populations.

4. Many observed behavioural responses are energetically costly, but the way that these responses may lead to long-term individual and population-level impacts is poorly understood.

5. *Synthesis and applications.* Behavioural response studies have greatly improved our understanding of the potential effects of naval sonar on marine mammals. Despite data gaps, we believe a dose-response approach within a risk-disturbance framework will enhance our ability to predict responsiveness for unstudied species and populations. We advocate for (1) regulatory frameworks to utilize peer-reviewed research findings when making predictions of impact, (2) regulatory frameworks to

account for the inherent uncertainty in predictions of impact and (3) investment in monitoring programmes that are both directed by recent research and offer opportunities for validation of predictions at the individual and population level.

1 | INTRODUCTION

Stimulus–response studies have a long history in behaviour research (e.g. Hopp, Owren, & Evans, 1998; McGregor, 1992), but more recently have become an important approach in applied ecology for quantifying the behavioural response of animals to human-induced disturbance (Shannon et al., 2015). Many examples from terrestrial and marine environments demonstrate relationships between some measure of disturbance and the probability and/or severity of response. With respect to marine mammals, these studies are often called behavioural response studies (BRS).

In recent years, much of the research within the marine environment related to behavioural response has focused on marine mammals, in particular cetaceans and their potential vulnerability to disturbance by naval sonar (e.g. Baird, Martin, Webster, & Southall, 2014; Henderson et al., 2014; Houser, Yeates, Crocker, Martin, & Finneran, 2012; McCarthy et al., 2011; Miller et al., 2012; Moretti et al., 2014; Sivle et al., 2015; Southall, Nowacek, Miller, & Tyack, 2016; Tyack et al., 2011). Other disturbance stimuli have received attention, including shipping (e.g. Aguilar Soto et al., 2006; Lusseau, Bain, Williams, & Smith, 2009), seismic prospecting (e.g. Miller et al., 2009; Richardson, Greene, Malme, & Thompson, 1995) and the installation of offshore renewable energy technologies (e.g. pile driving, Hastie et al., 2015; Tougaard, Henriksen, & Miller, 2009). BRS research in relation to naval sonar was originally developed to study responses of baleen whales to low frequency sonar (Miller, Biassoni, Samuels, & Tyack, 2000), but more recent research has been motivated by atypical mass-stranding events, especially of beaked whales, some of which appear to have been caused by naval sonar activities (D'Amico et al., 2009).

The need to document relationships between sonar activities and behavioural or physiological changes is largely driven by legislation and regulation. For example, U.S. federal agencies are required to estimate the probability of noise-related auditory and behavioural impacts to individual marine mammals and evaluate the potential effects of these impacts on populations under the Marine Mammal Protection Act and, for some species, the Endangered Species Act. European Member States are required to monitor, and perhaps limit, levels of anthropogenic noise in European waters to recover or maintain Good Environmental Status (Dolman & Jasny, 2015). These regulatory processes often require predictions of sub-lethal consequences of disturbance at both the individual and population level. As a result, noise producers, including navies, have invested in research programmes intended to inform environmental compliance efforts and impact analyses.

Nearly two decades of BRS research has been funded by the worlds' navies (e.g. Miller et al., 2000; Southall et al., 2016), resulting in better understanding of potential effects of naval sonar on marine mammals. Improvements in technology, protocols and analytical techniques have led to scientific outputs of sufficient maturity to help inform regulatory decision making. However, gaps in our knowledge and the complex nature of responses have also become increasingly apparent, resulting in a need for assessment and prioritization of future research. This paper synthesizes the outcomes of the past research efforts, provides a review of the lessons learned and identifies remaining key questions. In addition, we suggest that evaluating questions of potential sonar impacts within ecological theory can help inform applied science and improve its application in management decisions.

2 | METHODOLOGICAL APPROACH AND RESEARCH QUESTIONS

Several methodological approaches have been adopted in conducting BRS on the effects of navy sonar, and some broad distinctions can be drawn. One relies on a formal experimental design and the other does not. We refer to the former as controlled exposure experiments (CEEs) and the latter as opportunistic exposure studies (Tyack, Gordon, & Thompson, 2004). CEEs determine whether exposure to potential stressors results in response, and compare responses to specific doses of exposure relative to control (non-exposure) conditions. Many experimental studies collect fine-scale measurements of behaviour to reduce the risk of missing potentially subtle responses. CEEs have been carried out with both captive and wild free-ranging animals (Figure 1). However, for logistical reasons, these experiments often rely on simulated sonar signals transmitted from scaled sound sources deployed on research vessels (as opposed to full-scale sonar on navy vessels). The difference between patterns of response under these experimental conditions vs. real-world conditions is not well known. Opportunistic exposure studies involve making observations around real-world naval activities. The observer typically has no control over the doses received by the subjects; hence, experimental protocols such as randomization into control and treatment groups are not possible. Thus, strictly, observational studies cannot demonstrate causation between exposure and reaction. They nevertheless offer the potential to collect data from many more separate exposure events and over longer time-scales than are typically involved in CEEs. Therefore, opportunistic studies are important in defining the

	Visual observations	Animal-borne loggers (short-term, high-resolution acoustic tags)	Animal-borne loggers (medium to long-term satellite tags)	Animal-borne loggers (long-term satellite tags with GPS and acoustic recorders)	Passive acoustic monitoring
Controlled exposure experiments on *captive* animals	🔭				🎧
Controlled exposure experiments on *free-ranging* animals	🔭	▬	📡		🎧
Opportunistic exposure studies on *free-ranging* animals	🔭		📡	📡 + 🎧	🎧

FIGURE 1 A matrix showing the primary data collection methods currently being used within each of the main Behavioural response studies (BRS) approaches. Populated cells indicate that the method is used within the corresponding approach. Proposed data collection methods which are actively being pursued are included in grey rather than black

relationship between exposure and specific aspects of potential response in more realistic settings once controlled experimental studies have demonstrated the connection between exposure and reaction and have defined how animals respond.

A second distinction is between the methods used for collecting data, which include visual observations, animal-borne tags and passive acoustic monitoring (Figure 1). The choice of approach is related to the question(s) being addressed, which may include the following: What is the probability that an individual will respond to sonar and, if they respond, how will they respond and how long will this response last? How do the probability and nature of the responses vary within and between individuals, species and populations, and how are they modulated by extrinsic and intrinsic factors? And what are the consequences of response at the individual and population levels? We provide a review of the current state of knowledge for each question.

2.1 | What is the probability that an individual will respond to sonar and how do they respond?

These are the fundamental questions underlying most BRS efforts. Some governments require noise producers to provide a metric, which varies across jurisdictions, of the number of individuals expected to respond to an activity and whether this level of effect could be expected to affect the future status of the population. Dose–response functions provide a framework for estimating the probability of an individual responding as a function of some metric of exposure to potential disturbance (e.g. RL, received level) (Figure 2). Quantitative uncertainty bounds around dose–response functions provide an indication of the underlying variability in responsiveness for a given dose and a measure of confidence in predictions of an individual's response

(Figure 2). The U.S. Navy has used sigmoidal dose–response functions to assess the behavioural impact of sonar on some cetacean species (but not beaked whales or harbour porpoise) (Finneran & Jenkins, 2012). However, so far the functions used have been relatively simple, based on little data, and measures of uncertainty have not been incorporated. Additionally, many jurisdictions still rely primarily on single thresholds for received exposure to determine whether an animal will respond.

Controlled exposure experiments have been used to generate the empirical data necessary to create dose–response functions. They allow examination of short-term responses to specific, measured noise exposures, typically at high resolution and using multiple metrics, at known source-animal ranges. In captivity, it has been possible to expose multiple individuals to a range of different sound levels, with
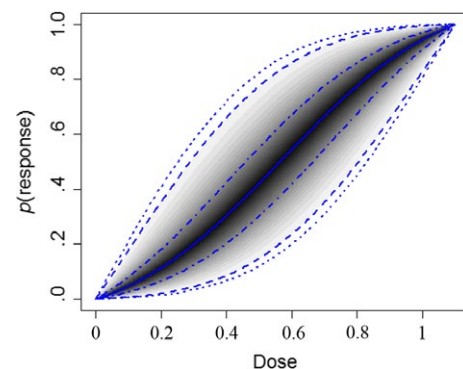
FIGURE 2 Example of a probabilistic dose–response function relating probability of behavioural response to exposure intensity (here shown on a scale of 0–1). The solid central line represents the mean, followed by 50%, 95% and 99% credible interval lines [Colour figure can be viewed at wileyonlinelibrary.com]

each individual being allocated a specific dose in each experimental trial (Houser, Martin, & Finneran, 2013a, 2013b). Several free-ranging studies have conducted dose-escalation experiments, in which the dose of sound increases over the duration of exposure (Southall et al., 2016). Captive and free-ranging CEEs have resulted in dose–response functions for California sea lions *Zalophus californianus* (Houser et al., 2013a), bottlenose dolphins *Tursiops truncatus* (Houser et al., 2013b), harbour porpoise *Phocoena phocoena* (Kastelein, Gransier, van den Hoogen, & Hoek, 2013), killer whales (Harris et al., 2015; Miller et al., 2014), long-finned pilot whales *Globicephela melas* (Antunes et al., 2014; Harris et al., 2015), sperm whales *Physeter macrocephalus* (Harris et al., 2015) and humpback whales *Megaptera novaeangliae* (Sivle et al., 2015; Wensveen, 2016), all in relation to naval sonar. Moretti et al. (2014) provide an example of a risk function for defined responses generated from real-world navy sonar sources, from an opportunistic exposure study of Blainville's beaked whales *Mesoplodon densirostris*, using passive acoustic monitoring data from bottom-mounted hydrophones on a naval testing range (see also Melcón et al., 2012). There remains an important question of how functions derived from exposure to scaled or simulated sonar relate to exposure to actual naval sonar. Through comparison of different exposure events, Kuningas, Kvadsheim, Lam, and Miller (2013) and DeRuiter et al. (2013) provide some indication that there may be differences in response to scaled or simulated sonar and actual naval sonar. The use of lower source levels for some CEEs means that a given RL would occur at much shorter ranges than the predicted distance at which full-powered operational sonars would expose animals to the same RL (Southall et al., 2016). This creates a need to test for how response varies as a function of RL and range.

Identifying dose–response relationships for different exposure metrics is useful for impact assessment; ongoing efforts are employing model selection methods to pool species objectively in terms of responsiveness, and extrapolate to unstudied species using random effects models (Harris et al., 2016). However, the relationship between sonar exposure 'intensity' and response may be modulated by other factors (e.g. species, context, experience), resulting in uncertainty in dose–response functions produced to date (Antunes et al., 2014; Harris et al., 2015; Houser et al., 2013a, 2013b; Miller et al., 2014; Sivle et al., 2015). Thus, understanding the underlying processes for response may improve predictive ability. Evidence of a more mechanistic hypothesis for response would allow broader, and more useful, predictions of responsiveness.

The way animals respond to sound relates to underlying processes. Ellison, Southall, Clark, and Frankel (2012) suggested that several processes are involved. At high exposure levels, they argue that response is likely to be predicted by the RL of sound. At lower levels, the animal will not respond until it can detect the signal, but if the signal level is detectable, then response will be influenced by behavioural context. There is clear evidence among mammals that acoustic startle responses occur when received signals have a rise-time <15 ms and exceed a sensation level (intensity above the hearing threshold) of about 90 dB (Yeomans, Li, Scott, & Frankland, 2002). Stimuli with longer rise-times and lower sensation levels are more likely to lead to

habituation (Götz & Janik, 2011). Similarly, among humans, the sensation of unpleasant loudness is associated with sensation levels of about 100 dB (Hood & Poole, 1966). At exposure levels below those that cause pain or startle, responses are more likely to depend upon contextual factors in addition to acoustic dosage, with some individuals showing severe responses at low sensation levels (e.g. Miller et al., 2012, 2014 for killer whale responses to sonar). In addition, experience will influence reactions. Processes such as habituation, sensitization or associative learning from past encounters can lead to stronger or weaker reactions than those found in a naïve animal.

A well-supported theoretical framework for understanding behavioural response is the risk-disturbance hypothesis, which essentially postulates that animals perceive and respond to human disturbance as a potential form of predation risk (Frid & Dill, 2002). The nature of the response is mediated by trade-offs between the benefit of avoiding perceived risk and the cost of disrupting other fitness-enhancing activities such as feeding, parental care or mating (Frid & Dill, 2002). Thus, if marine mammals respond to an acoustic stimulus as a potential predation threat, the response should reflect a species-specific strategy and be mediated by trade-offs specific to the focal individual and its social group, if one is present. The risk-disturbance framework provides predictions for research, and, if supported by data, could allow prediction of responsiveness in unstudied species, based on their risk of being predated upon and their anti-predator strategies. Such generalizations "would shorten the path towards effective mitigation measures that do not over-regulate human activities" (Frid & Dill, 2002).

The risk-disturbance hypothesis has motivated research into how individuals respond (fight, flight or social defence) to predator sounds, compared with responses to sonar. This has involved experimental playbacks of killer whale calls (alongside various control stimuli) to free-ranging individuals. In most species studied, individuals responded to active sonar sounds in a manner similar to their responses to the calls of predators (e.g. Curé et al., 2016; Isojunno et al., 2016; Tyack et al., 2011). However, there is evidence to suggest that most individuals perceive sonar as a lesser threat than killer whale sounds, as the responses to killer whale playbacks have been stronger and more consistent than responses to sonar (e.g. Curé et al., 2016; Isojunno et al., 2016; Miller et al., 2012; Sivle et al., 2015; Tyack et al., 2011). There is direct evidence of this from comparisons of responses made by individuals exposed to both sonar and killer whale playbacks for sperm whales (Curé et al., 2016; Isojunno et al., 2016), humpback whales (Curé et al., 2015) and Blainville's beaked whale (Tyack et al., 2011), all of which are at risk of predation by killer whales. An exception are long-finned pilot whales, which exhibit attraction to killer whale sounds (Curé et al., 2012), perhaps as part of a defensive mobbing strategy, while avoiding sonar sounds at high RLs (Antunes et al., 2014; Visser et al., 2016). Here, the avoidance of high exposure levels may involve a different response than their social defence against predation. An interesting anomalous species is the killer whale itself, which has been found to be more sensitive than other species to sonar (Harris et al., 2015; Miller et al., 2014) despite having a low predation risk. However, the risk function for killer whales was strongly

influenced by one group of killer whales in the sample that responded at very low levels (Miller et al., 2014). Further research will be needed to show what is representative for killer whales in general.

2.2 | How do the probability and nature of the responses vary within and between individuals, species and populations, and how are they modulated by extrinsic and intrinsic factors?

All studies conducted thus far have demonstrated high levels of intra- and inter-individual variation in responsiveness and response severity. It is not only important to recognize this uncertainty but also desirable to understand its drivers at the individual, species and population levels. Many extrinsic and intrinsic factors may influence an individual's propensity to respond, via their contribution to the cost-benefit decision an individual makes when faced with a threat.

Baseline data provide insight into the underlying behavioural states of undisturbed animals, the importance of such states, and variation within and among individuals, species and populations. Past studies have focused on characterizing baseline diving (e.g. Tyack, Johnson, Soto, Sturlese, & Madsen, 2006), foraging (e.g. Moretti et al., 2010, 2014; Samarra & Miller, 2015; Visser et al., 2014) and vocal behaviour (e.g. Goldbogen et al., 2014; Sayigh, Quick, Hastie, & Tyack, 2013; Stimpert et al., 2015). This improved understanding of baseline behaviour aids interpretation of data collected during sound exposures (Samarra & Miller, 2016; Tyack et al., 2011). There is still a need for more baseline data to be collected over longer time periods across a greater range of species. Ongoing sonar activity can compromise collection of such data in some localities; it is important to ensure that behaviour characterized as baseline does not include incidental periods of exposure.

Captive studies, with a high degree of control over extrinsic factors, have demonstrated the impact on responsiveness from intrinsic factors, such as species, sex and age (e.g. Houser et al., 2013a, 2013b). In addition, inter-species variation in responsiveness has become evident with the increasing number of species studied (e.g. Harris et al., 2015; Miller et al., 2012; Sivle et al., 2015). Some of these differences may be driven by evolutionary forces such as predation risk, while others may be due to experience and the cost-benefit trade-off associated with responding. The picture is further complicated because responsiveness is shaped both by the "personality" of an individual animal (e.g. aggressive vs. non-aggressive) and its behavioural plasticity under changing environmental conditions (Dingemanse, Kazem, Réale, & Wright, 2010).

The role of extrinsic factors is difficult to determine because the context of each study on free-ranging animals is different, both in terms of the behaviour of subjects and also the exposure itself. This can result in a large array of varying, and often interacting, contextual variables (Ellison et al., 2012). However, understanding the role of both behavioural and exposure context is a critical component of future research efforts (Harris & Thomas, 2015) and incorporating context into behavioural response impact assessments can decrease uncertainty (Ellison et al., 2012; Harris & Thomas, 2015; Southall

et al., 2007). Many contextual variables are likely to affect the probability of response, including the behavioural and motivational state of the animal, the nature and novelty of the sound, and the sound source spatial configuration relative to the receiving animal (Ellison et al., 2012). For instance, recent studies suggested that a beaked whale's probability of response to sonar may be influenced by its distance from the source (DeRuiter et al., 2013; Moretti et al., 2014). This is consistent with response probability being shaped by anti-predator behaviour and implies that source-whale range may be a key contextual variable. Other studies indicated the importance of behavioural state in relation to foraging: Goldbogen et al. (2013) and Harris et al. (2015) both found that behavioural state (deep feeding, shallow feeding or non-feeding in blue whales—Goldbogen et al., 2013; feeding or non-feeding in killer whales, long-finned pilot whales and sperm whales—Harris et al., 2015) affected the responsiveness of individuals to exposure.

Initial BRS sample sizes were generally too small to incorporate the influence of contextual variables in analysis (e.g. Tyack et al., 2011). However, there are now sufficiently large sample sizes for some species to investigate quantitatively how context may influence responsiveness (e.g. Goldbogen et al., 2013). Behavioural context has generally been described in terms of states such as foraging, travelling, resting and socializing. In some analyses the categorization of states and examination of transitions between states in the presence and absence of exposure has been the goal (e.g. DeRuiter et al., 2017; Isojunno et al., 2016), while others have qualitatively categorized behavioural states and used them as model covariates in dose–response models (e.g. Harris et al., 2015; Miller et al., 2014), or examined responses associated with specific behavioural states (Curé et al., 2015; Sivle et al., 2016; Stimpert et al., 2014). More recently there have been attempts to map prey fields to better understand the motivational state of animals within the foraging context (Hazen, Friedlaender, & Goldbogen, 2015; Hazen, Nowacek, St Laurent, Halpin, & Moretti, 2011), and to understand how responses may be mediated by the presence of prey patches (Friedlaender et al., 2016; see also Kuningas et al., 2013). Friedlaender et al. (2016) reported that including prey data to account for variation in foraging explained substantially more variance in blue whale responses to sonar.

Numerous CEEs have demonstrated the role of exposure context, as individuals and species vary their responses to sonar signals with different characteristics. These include frequency (Isojunno et al., 2016; Kastelein, Schop, Gransier, Steen, & Jennings, 2014; Miller et al., 2012), source level (Houser et al., 2013a, 2013b) repeated exposures (Sivle et al., 2016; Wensveen, 2016) and whale-source range (DeRuiter et al., 2013 although distant exposures were not under experimental control and did not reach the same maximum RLs). Most analysis efforts have included only one or two variables relating to exposure context, primarily frequency and RL, but the afore-mentioned studies suggest that more aspects of exposure context, particularly whale-source range and exposure history, should be considered. Understanding the range over which animals respond to sonar is particularly important when evaluating the extent of the animals' habitat that is affected.

2.3 | What are the consequences of responding at the individual and population level?

It is critically important to understand the ways in which responses may result in long-term impacts to individuals and populations. One early conceptual model for linking behavioural changes associated with disturbance with life functions, vital rates and population effects was developed by the National Research Council (2005). Research following this "Population Consequences of Disturbance (PCoD)" model has developed it into a formal mathematical structure, which has been applied to several case studies (e.g. New, Moretti, Hooker, Costa, & Simmons, 2013; New et al., 2014). These case studies pick up where BRS leave off, by quantifying the potential chronic effects of behavioural responses on individual health, and ultimately on population dynamics (e.g. Christiansen & Lusseau, 2015). These models require many input parameters and, for most species, there are insufficient data for parameterization. The data need of such models is a priority for future research; sensitivity analyses can help determine which inputs are most influential on the outputs of interest (e.g. population size and trend). Also required are new approaches to better understand the linkages of the PCoD model: how response to disturbance affects the long-term health of individuals and populations through impacts on life functions and vital rates. Here, we discuss in more detail how outputs from BRS can inform some of these linkages.

Qualitative scoring of the severity of behavioural responses has been used to specify the probability that specific responses could lead to biologically significant effects (Miller et al., 2012; Sivle et al., 2015; Southall et al., 2007). Outputs based on qualitative scoring reflect one interpretation of the experiment outcome (Miller et al., 2012), and although there is potential for bias (some behavioural changes scored as responses may not have been in response to the exposure), inter-observer comparisons can mitigate this. Some changes in behaviour have the potential to impact an individual's health (including condition), but the biological consequences, and the potential aggregate and cumulative impact of repeated disturbance are poorly understood (National Academies of Sciences, Engineering, and Medicine, 2016). One approach to better understand the importance of these responses is to view them in the context of a biologically meaningful currency such as a time-energy budget. State-based time-series models are being used to analyse data from CEEs, providing insight into behavioural changes, such as foraging disruption, horizontal avoidance, increased travel speed or the alteration of dive parameters, which may impact an individual's energy budget (e.g. DeRuiter et al., 2017; Isojunno et al., 2016). The experimental data being used in these analyses are fine-scale, which increases the ability to detect subtle and, often complex, responses. For example, Isojunno et al. (2016) developed a behavioural state transition model for sperm whales and established that, when exposed to low frequency active sonar (LFAS, 1–2 kHz), sperm whales changed from foraging to non-foraging behaviour and the model was used to estimate the duration of this disruption. A shift away from foraging, with no change in overall locomotion activity, suggested a net effect on energy balance during and immediately following sonar exposure (Isojunno et al., 2016). As

in this example, such changes in time and energy budgets can be used in models that extrapolate short-term effects to long-term effects (Christiansen, Rasmussen, & Lusseau, 2013).

A combination of opportunistic and experimental BRS research has allowed estimation of the scale of foraging disruption in Blainville's beaked whales in response to naval sonar exercises (McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011). These studies demonstrated that groups of Blainville's beaked whales, resident on a naval range, ceased foraging and moved out of the range during sonar exercises (McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011). The animals took up to 3 days to return and resume foraging activity (Moretti et al., 2010; Tyack et al., 2011). For this species, total caloric intake is directly related to the number of foraging dives, which occur at a known rate. Therefore, under a worst-case scenario that assumes no foraging off the range, a simple energetics model could be used to translate lost dives into an estimate of total energy loss. Similar foraging disruption has been observed in other beaked whales (Cuvier's beaked whales *Ziphius cavirostris*; DeRuiter et al., 2013); Baird's beaked whale *Berardius bairdii* (Stimpert et al., 2014); northern bottlenose whale *Hyperoodon ampullatus* (Miller et al., 2015), as well as humpback whales (Sivle et al., 2016), blue whales (Goldbogen et al., 2013) and sperm whales (Isojunno et al., 2016). For seasonal feeders such as blue whales that rely on dense prey aggregations, the energetic consequences of foraging disruption during periods of high prey availability can be significant (Goldbogen et al., 2013).

Not all individual effects will manifest themselves at the population level, but there is clearly a potential for long-term effects of chronic exposure on population dynamics (McCarthy et al., 2011). A longitudinal study compared a subpopulation of beaked whales resident on a naval range with another in a similar, but more pristine environment. Claridge (2013) used photo-identification methods and molecular genetics to estimate the size and composition of two subpopulations of Blainville's beaked whales in the Bahamas over a 10-year period. She found a lower average annual abundance and a lower calf:female ratio on the naval range, suggesting lower recruitment, which may be the result of lower rates of fecundity or calf survival (Claridge, 2013). It is possible these differences in population demographics are associated with the frequent use of navy sonars on the range, but the sample size is just one pair of populations and other factors could also be at play. Comparative studies with multiple independent pairs of populations in areas with different levels of disturbance will allow us to better understand population-level consequences.

3 | DISCUSSION AND CONCLUDING REMARKS

Noise-producing activities in the ocean are likely to increase further to meet growing demands for energy, food and trade (Frisk, 2012), and naval sonar will continue to be relevant to national security as submarines become quieter and more accurate long-range weapon systems are developed. Alongside this, there will be calls for greater regulation, management and mitigation of sound-producing activities (Dolman &

Jasny, 2015). To this end, recent advances in our understanding of why and how animals respond to sonar must be incorporated into the impact assessment process. However, we have little, if any, data for most species, and many uncertainties remain as to how the data collected can be translated to real-world scenarios. Ultimately, we do not yet have the data to underpin the link between behavioural response and population consequences. Therefore, we recommend that this area of research be expanded, and encompass more species, larger spatial and temporal scales, and a greater range of geographical regions.

The first step is to develop a better framework for generalizing responsiveness within and across species, so that the response of unstudied species may be estimated. The current approach used in the United States, in which species are classified into functional hearing groups (Finneran, 2016; Finneran & Jenkins, 2012; Southall et al., 2007), does not appear to be appropriate for assessing the behavioural impacts of sonar based on the small number of species studied thus far. For example, in the class of mid-frequency cetaceans (hearing range 150 Hz–160 kHz, as defined by Finneran & Jenkins, 2012), pilot whales appear to be relatively tolerant, whereas sperm whales and killer whales show increasing levels of response and beaked whales are the most responsive (e.g. Antunes et al., 2014; Harris et al., 2015; Miller et al., 2014, 2015; Tyack et al., 2011). Therefore, we suggest two alternative options for grouping species—either a multi-species dose–response analysis with an objective method for grouping species according to responsiveness, or using the risk-disturbance hypothesis and our understanding of predation risk and anti-predator strategies. Both approaches will rely on meta-analysis across species, locations and contexts to determine when and where it may be possible to group species and where they should be treated separately.

The next step will be the adoption of probabilistic dose–response functions, with associated uncertainty, for each species group to replace the deterministic functions currently used for some species (e.g. Finneran & Jenkins, 2012). Context-specific dose–response functions, with separate functions for different behavioural states, could reduce uncertainty in predicted behavioural effects. Such an approach would require increased understanding of these contexts, of behavioural states and transitions between states. A more workable solution may be to derive dose–response relationships for settings where operations are planned, where it may be reasonable to assume similar distributions of context.

We advocate using research outputs in developing mitigation and monitoring protocols, particularly those that allow validation of predictions. Outputs of BRS include predictions of responsiveness and the role of both behavioural and exposure context in determining response severity. We now need to determine the relationship between predictions generated under experimental conditions and opportunistic exposure studies to aid the prediction of how animals will respond to real naval exercises. Opportunistic exposure studies, utilizing passive acoustic monitoring methods, for example, are key components of long-term monitoring studies (e.g. Henderson et al., 2014; Martin, Martin, Matsuyama, & Henderson, 2015; McCarthy et al., 2011; Moretti et al., 2014). Data from these monitoring studies should be used to detect behavioural responses and to test expectations and predictions of experimental studies (Moretti et al., 2014). In general, the emphasis in BRS research is shifting towards combining experimental and opportunistic exposure studies to first define responses experimentally and then to collect data over more relevant spatial and temporal scales, and finally to link short-term behavioural response to long-term fitness consequences of repeated exposure. Overall, BRS research has greatly enhanced our understanding of the potential effects of human disturbance on marine mammals, but significant knowledge gaps remain and this field of scientific study is still at an early stage of development.

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AUTHORS' CONTRIBUTIONS

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DATA ACCESSIBILITY

Data have not been archived because this article does not contain data.

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