

# Foraging Behavior and Disruption in Blue, Fin, and Humpback Whales in Relation to Sonar Exposure: The Challenges of Generalizing Responsiveness in Species with High Individual Variability

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## Abstract

Behavioral response studies (BRSs) are an important approach for quantifying responses of marine mammals to naval sonar exposure. Controlled exposure experiments (CEEs) are BRSs based on a formal experimental design. Impact assessment often requires prediction of the likelihood that an individual of any species present in an area will respond to a given dose of sonar. Empirical data exist for only a few species, and species are often grouped to enable estimation of responsiveness for unstudied species. In this study, data for three taxonomically close species were combined to quantitatively determine whether they could be grouped in terms of responsiveness. We focused on foraging responses of blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and humpback (*Megaptera novaeangliae*) whales in relation to sonar exposure. These species are lunge filter feeders, and the number of lunges within each phase of a CEE was used to test for changes in foraging in response to exposure. Humpback whales, which were exposed to the highest sound levels, were found to be more responsive during and after sonar exposure when compared with blue and fin whales. The lunge rates of blue and fin whales throughout the sonar exposures remained similar to baseline and no sonar control levels. The greatest challenge is the ability to generalize responsiveness in species for which responses at the individual level are probably rare and subtle. Moreover, the interpretation of these species' similarities and individual differences in responsiveness is problematic given the contextual differences between each CEE. As

in previous studies, our results reinforce the need for BRSs to incorporate environmental data collection that is relevant to the behavioral state of study animals.

**Key Words:** baleen whales, behavioral response study, generalized estimating equations, lunge feeding, naval sonar, species pooling

## Introduction

Behavioral response studies (BRSs) have been used to understand and quantify the relationship between potential anthropogenic disturbances such as sound, and responses of marine mammals (Harris et al., 2018). Lethal stranding events of beaked whales associated with naval sonar exercises (Balcomb & Claridge, 2001; Cox et al., 2006) prompted studies aimed at improving our understanding of the link between sonar exposure and behavioral or physiological changes that may lead to stranding. Though stranding events were one of the initial motivators of these studies, concern has grown in relation to sublethal behavioral effects that could accumulate such as disruption of feeding (Miller et al., 2009). Feeding disruption in response to sonar may have severe energetic consequences for individual whales if they are repeatedly exposed. Alteration of such important life functions could have the potential to impact the health of individual animals and ultimately affect vital rates (National Research Council [NRC], 2005; New et al., 2014; Farmer et al., 2018).

Controlled exposure experiments (CEEs) represent one approach that has been used to investigate

the short-term responses of cetaceans to sonar stimuli and a range of control stimuli (Southall et al., 2016; Harris et al., 2018). CEEs are BRSs that have an experimental design component and use a suite of data collection methods to quantify the behavior of the study animal before, during, and after exposure to specific doses of a stressor. These studies are logistically difficult and expensive to undertake and, therefore, sample sizes tend to be small for most studied species. However, for the purposes of impact assessment, there is generally a requirement to be able to predict the probability that an individual of any marine mammal species present in the area will respond to a given dose of sonar and the manner in which it will respond. The probability and type of response may vary depending upon the specific context in which the sonar dose is received by the whale (Ellison et al., 2012).

In lieu of empirical data, species have often been grouped, or pooled, to allow behavioral responsiveness to be predicted for, as yet, unstudied species (e.g., Finneran, 2016). The most commonly used approach whereby species are classified according to functional hearing groups that reflect specific frequency bands (Southall et al., 2007; Finneran & Jenkins, 2012; Finneran, 2016) does not appear to be appropriate for assessing behavioral responses to sonar (Harris et al., 2018). There is, therefore, a need to investigate other biologically relevant mechanisms for grouping species. Southall et al. (2016) suggested that factors such as social structure, susceptibility to predation risk, and life history parameters be examined to determine whether generalized models of functional behavioral sensitivity can be developed, perhaps based on species groups or behavioral states (e.g., feeding vs travelling). One example

where generalization seems viable is for beaked whales. Despite four beaked whale species being studied in different locations by different research groups, individuals responded in similar manners and responded at relatively low received levels compared to other cetaceans studied to date (Southall et al., 2016).

Herein, we combine data across three different Balaenopteridae whales (Mysticeti) from two different BRS projects (3S and SOCAL-BRS) to determine whether we can justifiably group these taxonomically close species in terms of responsiveness. We focus on foraging behavior and disruption, due to the potential for effect on vital rates, in blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and humpback (*Megaptera novaeangliae*) whales in relation to sonar exposure. Combining data from different project teams represents a challenge due to some fundamental differences in field methodology as well as the geographical location where each species was studied (Table 1). However, Kvasdheim et al. (2017) combined data from CEEs conducted by the 3S and SOCAL-BRS projects on minke whales (*Balaenoptera acutorostrata*) to assess responsiveness of this difficult-to-study species ( $n = 2$  for each study). The authors noted that combining data in this way can produce useful outputs when analytical approaches are consistent. It allowed them to conclude that minke whale responses to sonar exposure were similar (i.e., avoidance response but no dive response) across studies, while differences in response threshold were evident. Unfortunately, no data on lunging behavior were available for minke whales from either study, so they could not be included in the across-species comparison here.

**Table 1.** Summary of the exposure and contextual variables for each species, including cumulative sound exposure level (SEL<sub>cum</sub> [dB re 1  $\mu$ Pa<sup>2</sup>s]) statistics recorded for each species

Species	Blue whale ( <i>Balaenoptera musculus</i> )	Fin whale ( <i>Balaenoptera physalus</i> )	Humpback whale ( <i>Megaptera novaeangliae</i> )
Research project	SOCAL-BRS	SOCAL-BRS	3S
Location	Southern California	Southern California	Northern Norway
Signal frequency	3-4 kHz	3-4 kHz	1-2 kHz
Exposure duration	30 min	30 min	5 or 10 min
Vessel behavior during exposure	Stationary	Stationary	Vessel pass
Number of exposure sessions per tagged whale/group	1	1	1-3
Minimum SEL <sub>cum</sub> (dB re 1 $\mu$ Pa <sup>2</sup> s)	132	113	169
Median SEL <sub>cum</sub> (dB re 1 $\mu$ Pa <sup>2</sup> s)	158	155	178
Maximum SEL <sub>cum</sub> (dB re 1 $\mu$ Pa <sup>2</sup> s)	171	178	184

Most CEE studies have utilized acoustic and motion sensor tags (e.g., DTAG; Johnson & Tyack, 2003) to continuously monitor the behavior of whales before, during, and after exposure to different experimental treatments. These tags are non-invasively attached to focal whales by suction cups and collect data for usually 12 to 18 h before the suction cup releases and the tag is recovered. The data streams, and derivations thereof, can then be used to analyse a number of different behaviors. For example, previous publications have considered responses such as avoidance (Tyack et al., 2011; Antunes et al., 2014; Miller et al., 2014, 2015; Wensveen et al., 2017), change in vocal behavior (Stimpert et al., 2014), change in dive behavior (Tyack et al., 2011; DeRuiter et al., 2013; Wensveen et al., 2015), and change in foraging behavior (Miller et al., 2009; Goldbogen et al., 2014; Stimpert et al., 2014; Isojunno et al., 2016; Sivle et al., 2016).

Rorqual baleen whales are lunge filter feeders. The whale accelerates forward before opening its mouth to engulf its prey, thereby transferring momentum to the engulfed water while increasing overall drag, leading to deceleration of the body (Simon et al., 2012; Goldbogen et al., 2017). Detectors have been developed that pinpoint signatures in the acoustic and movement time-series data to indicate a lunge feeding event (Simon et al., 2012; Allen et al., 2016). The number of lunges within the different experimental phases of CEE studies can then be examined to test for changes in lunge feeding rate. Using this foraging metric, Sivle et al. (2016) demonstrated that humpback whales significantly reduced foraging effort during sonar exposure, with a greater than 60% reduction in lunge rate during exposure compared to pre-exposure. In the same CEEs, humpback whales in a non-feeding state exhibited stronger avoidance responses to the sonar exposure, with lower avoidance response thresholds, than humpback whales in a feeding state (Wensveen, 2016; Wensveen et al., 2017). Similarly, Goldbogen et al. (2013b) provided evidence that foraging efficiency of blue whales was reduced during experimental exposure to sonar, particularly when animals were deep feeding. DeRuiter et al. (2017) incorporated the same data into a much larger dataset and found that blue whales had a greater probability of ceasing deep feeding during sonar exposure compared with baseline periods and were less likely to initiate deep feeding behavior during exposure.

Herein, the number of lunges conducted by an animal within a set time interval was used as the response variable in a statistical model. We combined data from all three species in the analysis to determine whether there was a significant difference between species in the level of foraging

disruption exhibited during sonar exposure and no sonar control exposure.

## Methods

Data were collected under the auspices of two long-term projects: (1) the 3S project (Miller et al., 2011; Kvadsheim et al., 2015) and (2) the SOCAL-BRS project (Southall et al., 2012). We used data on humpback whales from the 3S project, and data on blue and fin whales from the SOCAL-BRS. Full details of the field locations, methods, and experimental protocols for the 3S and SOCAL-BRS projects can be found in Southall et al. (2012) and Kvadsheim et al. (2015), respectively. A summary of the main differences that are relevant here can be found in Table 1.

### *Experimental Methodology*

All individuals studied across both projects had a DTAG (Johnson & Tyack, 2003) attached prior to any experimental trial. Tagging operations were performed from a small boat, which was then used for visual observations of the tagged individual and associated animals. In some instances, multiple individuals were tagged simultaneously and exposed to the same experimental trial. We refer to these individuals as being within a whale group as they cannot be treated independently in analysis. Following a specified post-tagging period, data were collected on baseline behavior before the experimental trials were conducted. We focused here on baseline trials, trials that involved exposure to a sequence of sonar signals, and no sonar control trials for which all aspects of the trial were identical to the sonar trials except there was no sonar transmission. Humpback whales were exposed to a no sonar control for 10 min followed by two 10-min exposures to 1 to 2 kHz sonar signals, except for two whales for which the second sonar signal lasted for 5 min (Table 1). Each trial was separated by, on average, 1.5 h. Blue and fin whales were exposed to one treatment for a target duration of 30 min—either a 3 to 4 kHz sonar signal or a no sonar control (Table 1).

The DTAG was programmed to detach from the whale after about 15 h, after which it was retrieved and the data processed. The DTAG recorded sound, depth, three-dimensional (3-D) acceleration, and 3-D magnetometer data, allowing a detailed reconstruction of whale behavior. For all whales, the acoustic time-series data were analyzed to identify the characteristic signature of a lunge, which includes a period of increased flow noise lasting several seconds followed by a rapid decrease in flow noise. The exact time, or zero-time, of a lunge was associated with the peak in flow noise (Goldbogen et al., 2006; Simon et al.,

2012; Allen et al., 2016). These timestamps were used to count the lunges for each time period.

#### Tag Data Processing

**Humpback Whales**—Lunges were identified using a “lunge detector” algorithm, programmed in *MATLAB* and described by Sivle et al. (2016), which was based on the method of Simon et al. (2012). The detection algorithm identified potential lunges based on peaks in the low-pass filtered acoustic noise (< 500 Hz) that were followed by a drop of, at least, 12 dB within 5 s. This 5-s analysis window was shortened if the whale reached the surface to exclude drops resulting from the tag being in air. The noise peaks were periods where the noise exceeded the 90th percentile of the flow noise samples from the same tag record when the animal was deeper than 5 m. Each lunge detected automatically was checked manually by visual inspection of detailed plots of time-series data, including the roll, heading, and “jerk” signal (i.e., the norm of the rate of change in tri-axial acceleration), for the period around the potential lunge. Suggested lunges were discarded in a few cases for which the judgement was still uncertain after listening to the sound clip and inspecting its spectrogram.

**Blue Whales**—Blue whale lunges were identified through examination of the animal’s pitch, roll, heading, jerk, and forward speed where it could be derived (Johnson & Tyack, 2003; Goldbogen et al., 2006). As there are a variety of kinematic signatures associated with lunging and a variety of lunge types (Goldbogen et al., 2013a; Kot et al., 2014), lunging was primarily identified by a sustained (several seconds) acceleration followed by a rapid (1 to 4 s) deceleration. As speed was derived from an exponential relationship between orientation corrected depth rate and the amplitude of flow noise (Goldbogen et al., 2006), care was taken to ensure that peaks in speed were not associated with noise from the tag entering and leaving the water, animal calling behavior, or other similar acoustic events. The lunge was verified by looking for kinematic motion consistent with lunging, including an increase in overall acceleration (as indicated by the jerk signal), and most commonly involving lateral or inverted rolling behavior accompanied by a vertical pitch orientation and a change in depth. The exact time of the lunge for blue whales is consistent with the opening of the mouth for a lunge (Cade et al., 2016). While lunges were initially detected automatically by looking for peaks in speed, all data were examined manually through graphical examination to verify the feeding event.

**Fin Whales**—Fin whale lunges were identified using the “automated detector” described by Allen et al. (2016), which is based on three variables:

(1) jerk, (2) flow noise (calculated in the 66 to 94 Hz band), and (3) roll. The distinct combination of these variables, including a peak and then drop in flow noise (drop of 15 dB in deep water; 10 dB in shallow water) and jerk (top 22% in deep water; top 16% in shallow water), as well as a roll greater than 20°, were used to identify both surface and deep lunges. Peaks due to the tag breaking the surface were excluded by removing all jerk peaks within 4 s of each other as surfacing events occur at a much faster rate than lunge feeding. As the data used in this analysis were also used to train the detection algorithm, each potential lunge detected in the tag data was inspected manually and either confirmed as a real lunge or rejected to minimise false positives.

#### Sound Exposure Levels

It was expected that the different experimental protocols used for each species would result in different levels of sound exposure, which may have an influence on the extent of foraging disruption. Therefore, in addition to lunge detection, the acoustic time-series from the DTAG was used to determine the sound levels received by each whale during each sonar exposure event. As the exposure durations differed across studies (5, 10, or 30 min), we chose to use the cumulative sound exposure level ( $SEL_{cum}$ ) to provide an indication of the total amount of sound received by each individual during each treatment. For a sonar exposure event,  $SEL_{cum}$  (expressed in decibels [dBs]) is a measure of the cumulative sum of squared pressures of each sonar pulse and is calculated using the following equation:

$$SEL_{cum} = 10 \log_{10} \frac{\sum_{n=1}^N \int_0^T p_n^2 dt}{p_{ref}^2 t_{ref}}$$

where  $p_n$  is the acoustic pressure for sonar pulse  $n$  of duration  $T$ ,  $N$  is the total number of sonar pulses during the exposure interval ( $N > 1$ ),  $p_{ref}$  is the standard reference pressure (which in water is one micropascal: 1  $\mu$ Pa), and  $t_{ref} = 1$  s (Miller et al., 2014).

#### Analysis

The aim of the statistical analysis was to model lunge rates across all whales to determine whether there were differences in average lunge rate between species and between intervals of the experimental trials (baseline, pre-, during, post-treatment). The data from all individual whales were combined into one dataset for analysis, but in some cases, individuals were labeled as being within the same whale

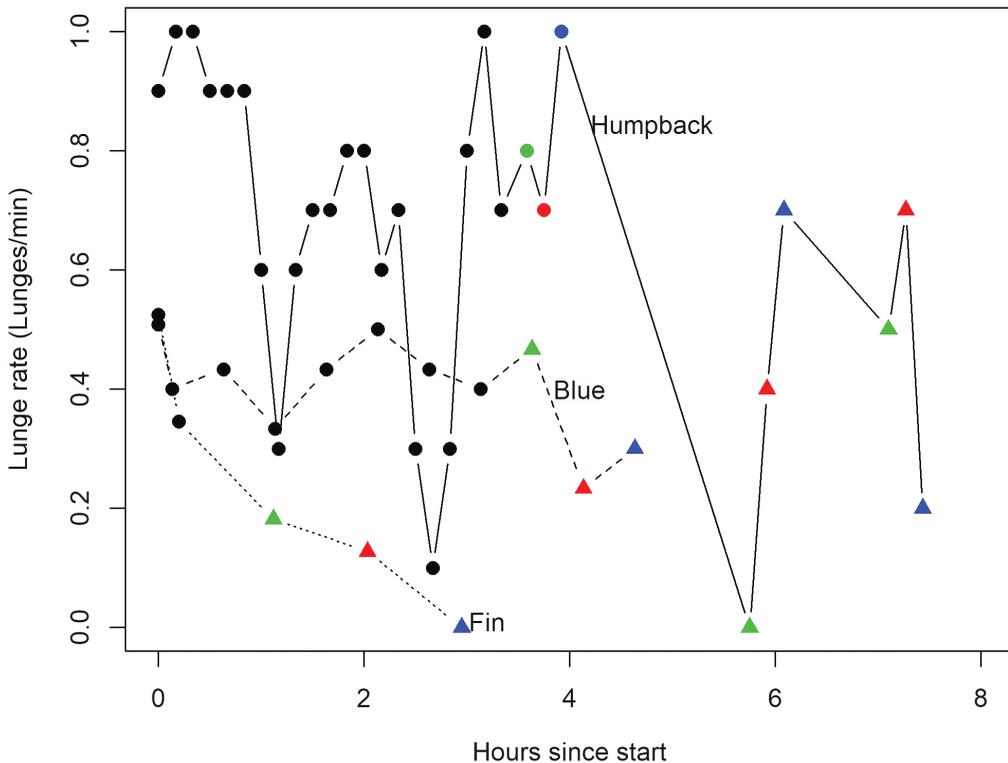
group because they were tagged simultaneously. We cannot treat these individuals as being independent as the responsiveness of one individual may have influenced the responsiveness of others in the group. We accounted for this within the model structure.

For each whale, the data recorded on the tag were divided into baseline and experimental periods. Only baseline data were available for some whales because the tag fell off before the experiments could begin. In addition, baseline data were included for those whales exposed to non-sonar signals such as pseudo-random noise. The experimental period for each tag record was divided into pre-exposure, during exposure, and post-exposure intervals; the length of each interval was determined by the length of the exposure interval for a given experiment (i.e., 5, 10, or 30 min). The baseline period was divided into intervals of the same length. For example, for a whale exposed to a treatment for 30 min, there may be several baseline periods of 30 min (since the whale was usually observed for at least 1 h post-tagging and before

any experimental treatment), a pre-treatment period of 30 min, and a during treatment period of 30 min, followed by a 30-min post-treatment period. The treatment, or signal, associated with each interval was characterized as “none” during the baseline period and as either “sonar” or “no sonar control” for the experimental period (including the pre- and post-exposure intervals). For each baseline and exposure interval, the number of lunges were counted; examples of data for three individual whales are shown in Figure 1.

Since the lunge rates in each interval were likely to be correlated for each whale group of one or more tagged individuals, generalized estimating equations (GEEs) were used as they provided a convenient way to account for correlation within a blocking unit (Hardin & Hilbe, 2012). All analyses were conducted in *R*, Version 3.3 (R Core Team, 2016), using the package ‘geepack’ (Højsgaard et al., 2006).

The response variable was the number of lunges in the interval. To account for different lengths of



**Figure 1.** Examples of the lunge rate (number of lunges per min) over time (hours) for three whales (blue whale [bw11\_210b], fin whale [bp13\_193a], and humpback whale [mn12\_178a]), showing the baseline (black dots), no sonar control treatment (coloured dots), and sonar treatment (coloured triangles). The phases are pre-exposure (green), during exposure (red), and post-exposure (blue).

intervals between individual exposures, “interval duration” (5, 10, or 30 min) was fitted as an offset term in the model. The “number of lunges” was modeled as a Poisson distribution, and “whale group” was used as a blocking unit with an independent correlation structure. Tagged whales may have been accompanied by non-tagged whales, but information on non-tagged animals was not included. The inclusion of “whale group” as a blocking unit allowed us to account for the non-independence of tagged whales exposed to the same stimulus. In most cases, whale group only included one individual whale as the deployment of multiple tags per experimental trial was relatively rare, but there were a few cases where multiple animals in the same group were tagged (see “Results”). We assumed temporal correlation within each whale group, and so intervals were ordered by time. The explanatory variables considered were four factor variables: (1) species (with levels blue, fin, and humpback), (2) signal (none, sonar, or no sonar control), (3) phase (baseline, pre-, during, and post-), and (4) exposure order (0, 1, 2, and 3 where 0 refers to the baseline phase). The variables “signal” and “phase” were partially confounded, and so these were combined to create a new factor, called *signal-phase*, with seven levels. One complicating factor in combining data from different studies was that the source strength of the sonar signals and the duration of exposures were markedly different across studies, leading to different cumulative levels of exposure (Table 1). Therefore, “SEL<sub>cum</sub>” for each exposure session was considered as a potential covariate and included as a continuous variable: for all intervals, except during exposure to sonar, SEL<sub>cum</sub> was set to 0 to ensure this variable had no effect outside of the during phase. (This does not imply a dose of 0 dB re 1  $\mu\text{Pa}^2\text{s}$ .)

Model selection was performed using analysis of variance (sequential Wald statistic). Predicted lunge rates were obtained for each level of the covariates retained in the selected model. We chose to predict over an interval of 15 min for all species to allow direct comparison since experimental trials were either 5, 10, or 30 min in duration. A parametric bootstrap was used to obtain approximate 95% confidence intervals (CIs) for each level. A new set of model coefficients were generated from a multivariate random normal distribution, with mean equal to the fitted model coefficients and variance obtained from the model covariance matrix. Predicted values were obtained using these new model coefficients; this process was repeated 5,000 times, and the 2.5 and 97.5 percentiles of the bootstrap-predicted values formed the 95% confidence limits for each predicted value.

Following Sivle et al. (2016), the output from the bootstraps was used to make comparisons

between specific factor-level combinations of interest. The mean difference between bootstrap-predicted values was used to estimate the difference in lunge rate between factor levels. Three sets of comparisons were made: (1) between phases within species (30 comparisons), (2) changes between signal-phase combinations within species (18 comparisons), and (3) differences between species for baseline and change in phase (15 comparisons). To ensure that the error rate was 95% over all comparisons within a set, each individual CI within a set was adjusted using the Bonferroni correction such that each individual CI had the significance level  $(1 - \frac{\alpha}{m})$  where  $m$  was the number of comparisons within a set and  $\alpha$  was the probability of incorrectly rejecting a Null hypothesis ( $\alpha = 0.05$ ). The required lower and upper percentiles for the differences of interest across all bootstraps formed the adjusted CI for these mean differences. The CIs were used to identify significant changes in lunge rate between factor levels: if both the upper and lower confidence limits for the differences were either positive or negative, we concluded that there was a significant change in lunge rate between factor levels; a CI containing 0 indicated no significant difference between factor levels.

## Results

There were data on 97 whales in total: 63 blue whales (in 42 groups), 19 fin whales (in 14 groups), and 15 humpback whales (in 13 groups) (Table 2). SEL<sub>cum</sub> was missing for one blue whale exposed to sonar, and so the during and post-treatment intervals were excluded for this whale. Nearly 331 h of data were available, with 76 h recorded during experiments, and 255 h of baseline data (Table 3), with 4,721 identified lunges.

The distribution of lunge rates (for each interval) indicated that the lunge rates for humpback whales were higher, and more variable, than for the other species (Figure 2). There was a difference in SEL<sub>cum</sub> during sonar exposures for each species: humpback whales received a higher SEL<sub>cum</sub> (with a median value of 178 dB re 1  $\mu\text{Pa}^2\text{s}$ ) than blue whales (158 dB re 1  $\mu\text{Pa}^2\text{s}$ ) or fin whales (155 dB re 1  $\mu\text{Pa}^2\text{s}$ ) (Table 1; Figure 2).

### Analysis Results

The selected model included terms for species, signal-phase, and their interaction. Exposure order and SEL<sub>cum</sub> were not retained in the final model. The interaction term between species and signal-phase indicated a significant effect of signal-phase on lunge rate, but this effect differed across species. As it can be hard to interpret model outputs when an interaction term is included, we used the bootstrap predictions of the number of

**Table 2.** The number of whales receiving each treatment

Species	Received treatment (Exposure order)	Number of whales
Blue	Baseline (0)	33
	Baseline (0), No sonar control (1)	6
	Baseline (0), Sonar (1)	24
Fin	Baseline (0)	6
	Baseline (0), No sonar control (1)	4
	Baseline (0), Sonar (1)	9
Humpback	Baseline (0)	2
	Baseline (0), No sonar control (1)	1
	Baseline (0), No sonar control (1), Sonar (2), Sonar (3)	12

**Table 3.** Total number of hours in each signal and phase by species

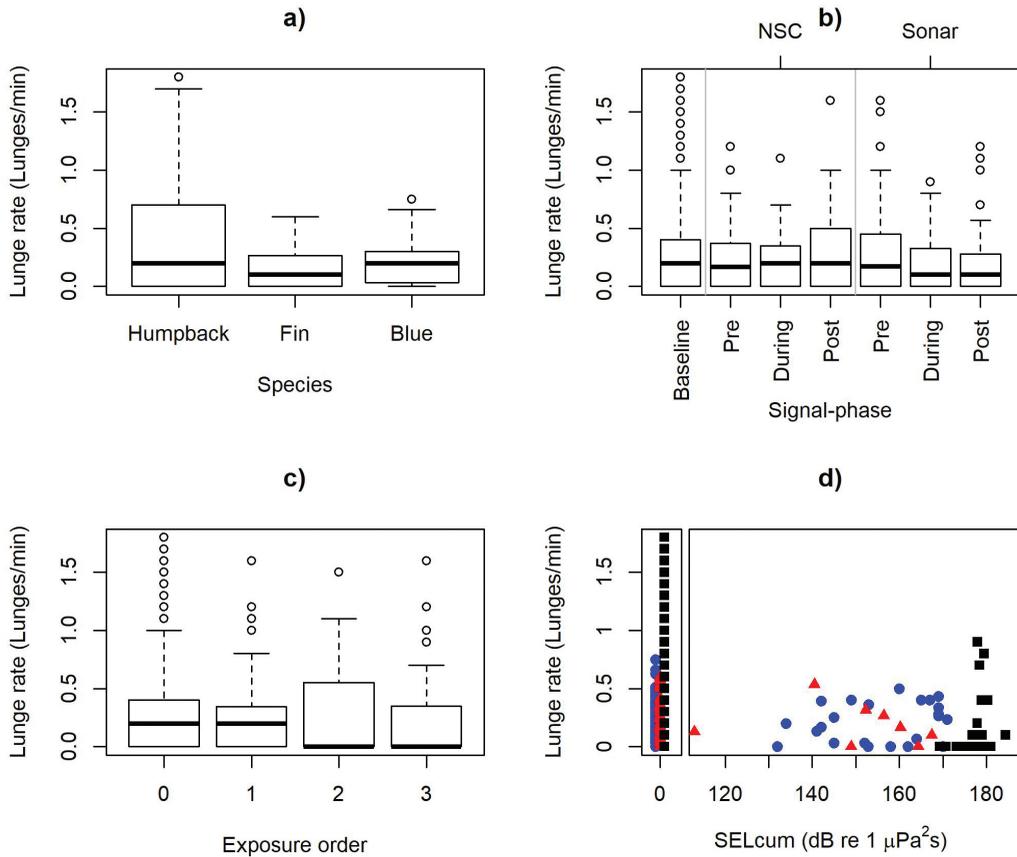
Signal	Phase	Blue	Fin	Humpback	Total
None	Baseline	151.7	33.8	69.0	254.5
No sonar control	Pre-exposure	2.7	2.0	2.2	6.9
	During exposure	2.7	2.0	2.2	6.9
	Post-exposure	2.0	2.0	2.2	6.2
	Total	7.4	6.0	6.6	20.0
Sonar	Pre-exposure	11.2	4.5	3.8	19.5
	During exposure	10.8	4.2	3.8	18.9
	Post-exposure	9.8	4.2	3.8	17.8
	Total	31.8	12.9	11.4	56.2
Total		190.9	52.7	87.0	330.7

lunge rates from the selected model to quantify the differences between signal-phase combinations within and between species. This analysis indicated that lunge rates during each phase of the no sonar control exposures were not significantly different from baseline lunge rates for any species (95% CI) (Figure 3; Table 4). However, the lunge rate for fin whales in the during phase of the no sonar control trial was significantly higher than pre no sonar control (Table 4). A similar change was not evident in the sonar exposure phases for fin whales. There was no evidence of significant differences in lunge rates in any of the signal-phase categories for blue whales, indicating no response to either the no sonar control exposures nor the sonar exposures (Figure 3; Table 4). For humpback whales, the lunge rate was significantly lower in both the during and post-phases of the sonar exposure compared with the pre-phase (Figure 3; Table 4).

When we compared the differences between two sets of phases (e.g., comparing the change in lunge rate between baseline and sonar pre with the change between sonar pre and sonar during),

we found no significant effect of exposure on humpback whales (Table 5). For fin whales, there was further evidence of a significant difference between the pre- and during phases of the no sonar control exposure as the change between these phases was greater than the change between the baseline phase and the no sonar control pre-phase (Table 5; Figure 3).

When comparing species, we found no significant difference between blue and fin whales in terms of baseline lunge rates nor in terms of change in lunge rates between signal-phases, implying no difference in responsiveness (Figure 3; Table 6). Humpback whales significantly differed from both blue and fin whales in terms of both their baseline lunge rate and the change in lunge rate between pre- and during exposure (Figure 3; Table 6). In addition, humpback whales significantly differed from blue whales with respect to the change in lunge rate between pre- and post-phases (Figure 3; Table 6). In both cases, the humpback whale lunge rate decreased between phases, whereas there was little change evident for blue and fin whales (Figure 3).



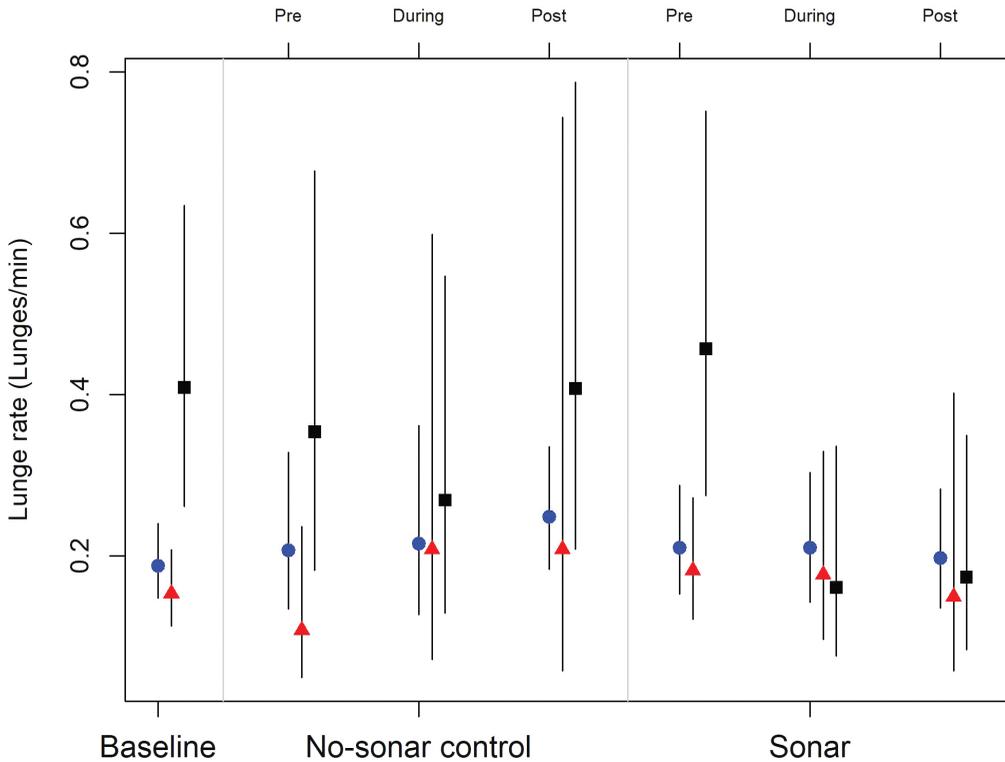
**Figure 2.** Distribution of the lunge rate (number of lunges per min) for each level of each covariate. The thick black lines on the box plots indicate the median, and the dots indicate outliers. In (b), NSC refers to no sonar control. In (d), the  $\text{SEL}_{\text{cum}}$  (dB re 1  $\mu\text{Pa}^2\text{s}$ ) values at 0 have been offset slightly to distinguish the different species: blue whales (blue dot), fin whales (red triangle), and humpback whales (black square). Zero represents a baseline dose for all phases except for during sonar exposure; it does not imply a dose of 0 dB re 1  $\mu\text{Pa}^2\text{s}$ .

## Discussion

The availability of BRS data collected using comparable CEE methodologies and technologies within and across species has provided opportunities to examine the potential for data pooling (Southall et al., 2016; Kvasdheim et al., 2017). One objective of combining data across species is to allow generalizations to be made regarding behavioral responsiveness of species groups or species' responsiveness within behavioral states. Herein, we focused on lunging behavior in three rorqual baleen whale species. As more data become available from these efforts, there will undoubtedly be opportunities to apply a similar approach to, for example, feeding buzz rates in odontocetes.

The statistical analysis indicated that blue and fin whales had similar baseline lunge rates, which

differed from the baseline lunge rate (and level of variability) of humpback whales. There are a number of possible explanations for this. It could be a result of the basic physiology of the different species as the duration of lunges (accelerating and engulfing the water) and the filter phase (time in between lunges to filter the water out of the mouth) are substantially different between humpback and blue or fin whales due to the relative size of the engulfment apparatus and time it takes to filter feed (for more, see Goldbogen et al., 2012). It may also be related to local prey density, distribution, depth, and quality (Hazen et al., 2015; Friedlaender et al., 2016). All three species feed on krill, but humpbacks in the same region as the 3S project have also been found to feed on other zooplankton, such as amphipods, and small fish, such as capelin and herring (Skern-Mauritzen et al., 2011;



**Figure 3.** Predicted lunge rate (number of lunges per min) from the selected model by signal type and phase for blue whales (blue dot), fin whales (red triangle), and humpback whales (black square). Lines indicate approximate 95% confidence intervals (CIs).

Nøttestad et al., 2014). Studies on herring in this region have shown no behavioral response to sonar signals (Sivle et al., 2012), suggesting that sonar-induced changes in herring distribution are unlikely to be the cause of any changes in humpback whale feeding activity observed in this study (Sivle et al., 2016). Alternatively, the species differences could be related to some other aspect of the study locality. Blue and fin whales were both studied in waters off southern California, while humpback whales were studied in northern Norway.

There was no evidence of a change in lunge behavior from baseline as a result of the no sonar control exposures, nor was there evidence of a change in lunge behavior in the pre-phase of the sonar exposures compared to baseline for any species. However, within the no sonar control exposures, there was an increase in fin whale lunge rate between the pre- and during phases. This appears to be due, in part, to a slightly reduced lunge rate in the pre-phase of the no sonar control exposures, although this reduction was not significantly different from baseline (Figure 3). The changes in

lunge rate between pre- and during, and pre- and post-phases for the no sonar control exposures were not significantly different from the analogous changes for the sonar exposures (Table 5). Overall, the results for the no sonar control exposures and the pre-sonar exposure phase provided reassurance that the effects of research activity and research vessel proximity were not the reason for any changes from the sonar exposures. Exclusion of a research vessel effect is important because it is well known that prey—for example, small fish—can avoid approaching vessels (e.g., De Robertis & Handegard, 2013).

In terms of the sonar exposures, there was no evidence to suggest that blue or fin whales responded to the sonar by changing overall lunge rate during or post-exposure. The lunge rates for both species remained similar to baseline and no sonar control levels throughout the sonar exposures. In addition, there were no differences between these two species in their responsiveness and no indication that changes in lunge rate between experimental phases differed between

**Table 4.** Predicted differences in lunge rate (lunges per min) between phases (Phase 1 – Phase 2) *within* species. Significant differences (as defined by the CIs) are indicated by \* in the right-hand column.

Phase 1	Phase 2	Species	Bootstrap mean difference	Lower percentile	Upper percentile	* indicates a difference at the adjusted confidence level
No sonar control pre	Baseline	Blue	0.0237	-0.119	0.251	
		Fin	-0.0375	-0.178	0.236	
		Humpback	-0.0462	-0.263	0.297	
No sonar control during	Baseline	Blue	0.0327	-0.122	0.322	
		Fin	0.0864	-0.154	0.968	
		Humpback	-0.1317	-0.418	0.284	
No sonar control post	Baseline	Blue	0.0621	-0.081	0.208	
		Fin	0.1032	-0.167	1.422	
		Humpback	0.0115	-0.211	0.430	
Sonar pre	Baseline	Blue	0.0235	-0.080	0.156	
		Fin	0.0312	-0.098	0.202	
		Humpback	0.0521	-0.367	0.600	
Sonar during	Baseline	Blue	0.0243	-0.099	0.185	
		Fin	0.0306	-0.134	0.314	
		Humpback	-0.2460	-0.675	0.126	
Sonar post	Baseline	Blue	0.0112	-0.112	0.166	
		Fin	0.0135	-0.169	0.535	
		Humpback	-0.2333	-0.669	0.208	
No sonar control during	No sonar control pre	Blue	0.0090	-0.301	0.369	
		Fin	0.1239	0.006	0.745	*
		Humpback	-0.0856	-0.428	0.241	
No sonar control post	No sonar control pre	Blue	0.0384	-0.165	0.193	
		Fin	0.1407	-0.005	1.206	
		Humpback	0.0577	-0.258	0.446	
Sonar during	Sonar pre	Blue	0.0008	-0.114	0.136	
		Fin	-0.0006	-0.069	0.162	
		Humpback	-0.2981	-0.760	-0.029	*
Sonar post	Sonar pre	Blue	-0.0123	-0.136	0.112	
		Fin	-0.0177	-0.136	0.390	
		Humpback	-0.2854	-0.711	-0.049	*

species. It should be noted that single-species analysis on these species has detected responses to sonar on finer time-scales and when more consideration was given to environmental covariates (Goldbogen et al., 2013b). At the resolution of the analysis conducted here, with the restriction of only including covariates available for all species, subtle or fine-scale responses may be masked. For example, if a whale exhibited cessation of feeding in one or a few dives but resumed feeding shortly after, the overall lunge rate for that time period relative to the overall mean would not be very different. This would result in a response that may not be detectable from natural variation in

feeding rates. This type of brief, low-to-moderate severity response has been documented for these same individuals in another study (Southall et al., 2019). Additionally, Goldbogen et al. (2013b), Friedlaender et al. (2016), and Southall et al. (2019) have all noted the importance of contextual covariates for understanding blue whale responsiveness. For example, Southall et al. (2019) found that around half of deep feeding individuals responded to sonar, while no shallow feeding animals responded. In this study, for which we combined all individuals in one analysis, it is likely that the responses of a few have been masked by the lack of response of most.

**Table 5.** Predicted differences in the *change* in lunge rates (lunges per min) between signal-phase combinations (Change 1 – Change 2) *within* species. Significant differences (as defined by the CIs) are indicated by \* in the right-hand column.

Change 1	Change 2	Species	Bootstrap mean difference	Lower percentile	Upper percentile	* indicates a difference at the adjusted confidence level
Baseline/ no sonar control pre	No sonar control pre/during	Blue	-0.0147	-0.523	0.394	
		Fin	0.1614	0.082	0.475	*
		Humpback	-0.0394	-0.624	0.330	
Baseline/ no sonar control pre	No sonar control pre/post	Blue	0.0147	-0.400	0.247	
		Fin	0.1782	0.071	0.906	*
		Humpback	0.1039	-0.460	0.569	
Baseline/ sonar pre	Sonar pre/during	Blue	-0.0227	-0.223	0.127	
		Fin	-0.0318	-0.175	0.097	
		Humpback	-0.3502	-1.275	0.142	
Baseline/ sonar pre	Sonar pre/post	Blue	-0.0358	-0.250	0.118	
		Fin	-0.0490	-0.218	0.268	
		Humpback	-0.3375	-1.238	0.136	
No sonar control pre/ during	Sonar pre/during	Blue	-0.0082	-0.335	0.299	
		Fin	-0.1245	-0.704	0.079	
		Humpback	-0.2125	-0.745	0.179	
No sonar control pre/post	Sonar pre/post	Blue	-0.0507	-0.241	0.165	
		Fin	-0.1585	-1.134	0.289	
		Humpback	-0.3431	-0.893	0.008	

Humpback whales did, however, exhibit a clear reduction in lunge rates in response to the sonar exposure. The model predicted a significant decrease in lunge rate during and post-sonar exposure compared to pre-sonar exposure; however, the change in lunge rate between sonar exposure phases was not found to be significantly different from the changes in lunge rate between no sonar control phases. Similarly, the change in lunge rate between baseline and sonar pre was not significantly different from the change between sonar pre and sonar during (also for sonar pre and sonar post). Therefore, despite the clear result when directly comparing one phase with another, when we compare changes between sets of phases, the results indicate that the responses to sonar may be within the baseline levels of variability. The high variability in lunge rate across all phases is likely being driven by contextual variables not accounted for here. These results generally support previous analysis by Sivle et al. (2016), who demonstrated a greater response of humpback whales to the first exposure compared to the second exposure through inclusion of an exposure order covariate. Here, exposure order was not selected, and data across all exposures were combined, precluding inclusion of this order effect and the detection of a significant change for the first exposure event.

Regardless, when comparing the responsiveness of humpback whales with blue and fin whales, we can conclude that the humpback whales showed a greater degree of foraging disruption both during and up to 15 min after sonar exposure.

The greatest challenge is the interpretation of these species similarities (blue and fin) and differences (humpback) in responsiveness. Humpback whales may have been more responsive simply because they were exposed to much higher sound levels, perhaps in combination with the source moving directly towards them in the 3S experiments (which agrees with Kvadsheim et al., 2017, for minke whales). The minimum  $SEL_{cum}$ , accumulated over the exposure interval, was higher across humpback whales than the maximum  $SEL_{cum}$  experienced by any fin whale and only 2 dB lower than the maximum  $SEL_{cum}$  for any blue whale. Therefore, one could speculate that the exposures on blue and fin whales did not reach the response threshold for most individuals. The covariate  $SEL_{cum}$  was included at the model fitting stage; however, it was not found to be significant. This may partly be due to the difficulty of including a sound metric relating to sonar for the during phases, when all other phases are allocated a 0, or because it is somewhat confounded with species.

**Table 6.** Predicted differences in lunge rate (lunges per min) *between* species for each phase (baseline) or change in phase (no sonar control and sonar exposures). Significant differences (as defined by the CIs) are indicated by \* in the right-hand column.

Species 1	Species 2	Phase	Bootstrap mean difference	Lower percentile	Upper percentile	* indicates a difference at the adjusted confidence level		
Blue	Fin	Baseline	0.0351	-0.064	0.132			
		No sonar control pre/during	0.1149	-0.233	0.702			
		No sonar control pre/post	0.1023	-0.146	1.069			
		Sonar pre/during	-0.0014	-0.143	0.181			
		Sonar pre/post	-0.0054	-0.179	0.377			
		Baseline	-0.2288	-0.608	-0.002	*		
Blue	Humpback	No sonar control pre/during	-0.0945	-0.507	0.299			
		No sonar control pre/post	0.0193	-0.289	0.425			
		Sonar pre/during	-0.2989	-0.708	-0.017	*		
		Sonar pre/post	-0.2731	-0.635	-0.017	*		
		Fin	Humpback	Baseline	-0.2638	-0.661	-0.036	*
				No sonar control pre/during	-0.2095	-0.760	0.105	
No sonar control pre/post	-0.0830			-1.054	0.318			
Sonar pre/during	-0.2975			-0.725	-0.035	*		
		Sonar pre/post	-0.2677	-0.522	0.006			

One of the major limitations of this case study was that we had two species from one locality studied by one project team and one species from a very different locality studied by a different project team. The fact that the species that showed the clearest effect of sonar exposure on lunge rates was the one from the different location studied by the different project team immediately makes it difficult to conclude whether the differences are due to species, location, timing in the year, or project. However, we note the similarities in the response found for beaked whale species (Southall et al., 2016) and minke whales (Kvadsheim et al., 2017) from these two projects. Factors that may contribute to location-level differences include the reason for presence in location (e.g., feeding, travelling, and breeding), sex and age distribution of animals present in location (including presence of calves), exposure to predators, prey availability and quality, and previous levels of sonar exposure at each location. Differences that may result from decisions made by project teams include the exposure parameters such as signal strength (source level), signal type, duration of exposure, number of exposures, distance to whale during exposure, and the use of a moving vs drifting source (Table 1). Differences in

the detailed context of the sonar exposures could be a critical factor leading to greater responses in humpback whales. For example, the 3S project conducted their studies on humpback whales in waters north of Norway where there is very little sonar activity, whereas the SOCAL project conducted their blue and fin whale studies in southern California in and around an active naval testing range; the 3S project used a towed sonar source that approached the tagged whale, while the drifting source in the SOCAL study did not move in any directed fashion towards the tagged whale; and the 3S project exposed humpback whales to 1 to 2 kHz signals for 10 min, while the SOCAL project exposed blue and fin whales to 3 to 4 kHz signals for 30 min. Kvadsheim et al. (2017) concluded that these factors may have led to the observed differences in response threshold for the minke whales across the studies but that the overall type of response was similar.

While it is possible that humpback whales are, in general, more sensitive to disturbance from sonar than blue or fin whales, we cannot make such a conclusion given the many differing exposure and contextual variables. One possibility would be to account for some of the contextual variability by only including individuals within

particular contexts—for example, deep diving blue whales—or ensuring that the received levels, particularly at the higher end, are comparable. Thus, we cannot conclude categorically that blue and fin whales should be pooled in terms of foraging response and that humpback whales be treated separately because we cannot disentangle the reason for the different levels of responsiveness. What we can do, however, is stimulate discussion and highlight factors that should be considered in the design of future studies to maximise opportunities for the pooling of data across projects, locations, and species. If we had one species in common between the two locations and/or projects, then we may have been able to begin teasing apart some of the complexity. We recommend that future studies consider previous efforts and available data at the experimental design stage. This will include full and open collaboration and communication to ensure compatibility of data and to minimise confounding factors in any analysis.

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### Literature Cited

- Allen, A. N., Goldbogen, J. A., Friedlaender, A. S., & Calambokidis, J. (2016). Development of an automated method of detecting stereotyped feeding events in multi-sensor data from tagged orca whales. *Ecology and Evolution*, 6(20), 7522-7535. <https://doi.org/10.1002/ece3.2386>
- Antunes, R., Kvaldsheim, P. H., Lam, F-P. A., Tyack, P. L., Thomas, L., Wensveen, P. J., & Miller, P. J. O. (2014). High response thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). *Marine Pollution Bulletin*, 83(1), 165-180. <https://doi.org/10.1016/j.marpolbul.2014.03.056>
- Balcomb, K. C., & Claridge, D. E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science*, 5, 2-12.
- Cade, D. E., Friedlaender, A. S., Calambokidis, J., & Goldbogen, J. A. (2016). Kinematic diversity in orca whale feeding mechanisms. *Current Biology*, 26(19), 2617-2624. <https://doi.org/10.1016/j.cub.2016.07.037>
- Cox, T. M., Ragen, T. J., Read, A. J., Vos, E., Baird, R., Balcomb, K., . . . Benner, L. (2006). Understanding the impacts of acoustic sound on beaked whales. *Journal of Cetacean Research and Management*, 7, 177-187.
- De Robertis, A., & Handegard, N. O. (2013). Fish avoidance of research vessels and the efficiency of noise-reduced vessels: A review. *ICES Journal of Marine Science*, 70, 34-45. <https://doi.org/10.1093/icesjms/fss155>
- DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., & Southall, B. L. (2017). A multivariate mixed hidden Markov model for blue whale behaviour and responses to sound exposure. *Annals of Applied Statistics*, 11, 362-392. <https://doi.org/10.1214/16-AOAS1008>
- DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M. X., Sadykova, D., Falcone, E. A., . . . Thomas, L. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, 9, 20130223. <https://doi.org/10.1098/rsbl.2013.0223>
- Ellison, W. T., Southall, B. L., Clark, C. W., & Frankel, A. S. (2012). A new context-based approach to assess marine mammal behavioral responses to anthropogenic sound. *Conservation Biology*, 26, 21-28. <https://doi.org/10.1111/j.1523-1739.2011.01803.x>
- 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*, 589, 241-261. <https://doi.org/10.3354/meps12457>
- Finneran, J. J. (2016). Auditory weighting functions and TTS/PTS exposure functions for marine mammals exposed to underwater noise. In *Technical guidance for assessing the effects of anthropogenic sound on marine mammal hearing: Underwater acoustic thresholds for onset of permanent and temporary threshold shifts* (NOAA Technical Memorandum NMFS-OPR-55, pp. 38-110). Washington, DC: U.S. Department of Commerce, National Oceanic and Atmospheric Administration.
- Finneran, J. J., & Jenkins, A. K. (2012). *Criteria and thresholds for U.S. Navy acoustic and explosives effects analysis* (Technical Report). San Diego, CA: Space and Naval Warfare Systems Center Pacific. <https://doi.org/10.21236/ADA561707>
- Friedlaender, A. S., Hazen, E. L., Goldbogen, J. A., Stimpert, A. K., Calambokidis, J., & Southall, B. L. (2016). Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications*, 26, 1075-1085. <https://doi.org/10.1002/15-0783>

- Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., & Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology*, 209, 1231-1244. <https://doi.org/10.1242/jeb.02135>
- Goldbogen, J. A., Cade, D., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., & Werth, A. J. (2017). How baleen whales feed: The biomechanics of engulfment and filtration. *Annual Review of Marine Science*, 9, 367-386. <https://doi.org/10.1146/annurev-marine-122414-033905>
- Goldbogen, J. A., Calambokidis, J., Croll, D. A., McKenna, M. F., Oleson, E., Potvin, J., . . . Tershy, B. R. (2012). Scaling of lunge feeding performance in rorqual whales: Mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Functional Ecology*, 26, 216-226. <https://doi.org/10.1111/j.1365-2435.2011.01905.x>
- Goldbogen, J. A., Calambokidis, J., Friedlaender, A. S., Francis, J., DeRuiter, S. L., Stimpert, A. K., . . . Southall, B. (2013a). Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge-feeding blue whales. *Biology Letters*, 9, 20120986. <https://doi.org/10.1098/rsbl.2012.0986>
- Goldbogen, J. A., Southall, B. L., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Hazen, E. L., . . . Kyburg, C. (2013b). Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences*, 280(1765), 20130657. <https://doi.org/10.1098/rspb.2013.0657>
- Goldbogen, J. A., Stimpert, A. K., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Schorr, G. S., . . . Southall, B. L. (2014). Using accelerometers to determine the calling behavior of tagged baleen whales. *Journal of Experimental Biology*, 14, 2449-2455. <https://doi.org/10.1242/jeb.103259>
- Hardin, J. W., & Hilbe, J. M. (2012). *Generalized estimating equations*. London: Chapman and Hall/CRC. <https://doi.org/10.1201/b13880>
- Harris, C. M., Thomas, L., Falcone, E., Hildebrand, J., Houser, D., Kvadsheim, P., . . . Janik, V. M. (2018). Marine mammals and sonar: Dose-response studies, the risk-disturbance hypothesis and the role of exposure context. *Journal of Applied Ecology*, 55(1), 396-404. <https://doi.org/10.1111/1365-2664.12955>
- Hazen, E. L., Friedlaender, A. S., & Goldbogen, J. A. (2015). Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science Advances*, 1(9), e1500469. <https://doi.org/10.1126/sciadv.1500469>
- Højsgaard, S., Halekoh, U., & Yan, J. (2006). The R package geepack for generalized estimating equations. *Journal of Statistical Software*, 15(2), 1-11. <https://doi.org/10.18637/jss.v015.i02>
- Isojunno, S., Curé, C., Kvadsheim, P. H., Lam, F-P. A., Tyack, P. L., Wensveen, P. J., & Miller, P. J. O. (2016). Sperm whales reduce foraging effort during exposure to 1-2 kHz sonar and killer whale sounds. *Ecological Applications*, 26(1), 77-93. <https://doi.org/10.1890/15-0040>
- Johnson, M., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, 28, 3-12. <https://doi.org/10.1109/JOE.2002.808212>
- Kot, B. W., Sears, R., Zbinden, D., Borda, E., & Gordon, M. S. (2014). Rorqual whale (*Balaenopteridae*) surface lunge-feeding behaviors: Standardized classification, repertoire diversity and evolutionary analyses. *Marine Mammal Science*, 30, 1335-1357. <https://doi.org/10.1111/mms.12115>
- Kvadsheim, P. H., DeRuiter, S., Sivle, L. D., Goldbogen, J., Roland-Hansen, R., Miller, P. J. O., . . . Southall, B. (2017). Avoidance responses of minke whales to 1-4 kHz naval sonar. *Marine Pollution Bulletin*, 121, 60-68. <https://doi.org/10.1016/j.marpolbul.2017.05.037>
- Kvadsheim, P. H., Lam, F-P., Miller, P., Sivle, L. D., Wensveen, P., Roos, M., . . . Dekeling, R. (2015). *The 3S2 experiments – Studying the behavioral effects of naval sonar on northern bottlenose whales, humpback whales and minke whales* (FFI-Rapport 2015/01001). Retrieved from [www.ffi.no/no/Rapporter/15-01001.pdf](http://www.ffi.no/no/Rapporter/15-01001.pdf)
- Miller, P. J. O., Johnson, M. P., Madsen, P. T., Biassoni, N., Quero, M., & Tyack, P. L. (2009). Using at-sea experiments to study the effects of airguns on the foraging behaviour of sperm whales in the Gulf of Mexico. *Deep-Sea Research I*, 56, 1168-1181. <https://doi.org/10.1016/j.dsr.2009.02.008>
- Miller, P. J., Antunes, R., Alves, A. C., Kvadsheim, P. H., Kleivane, L., Nordlund, N., . . . Tyack, P. L. (2011). *The 3S experiments: Studying the behavioural effects of naval sonar on killer whales (Orcinus orca), sperm whales (Physeter macrocephalus), and long-finned pilot whales (Globicephala melas) in Norwegian waters* (Scottish Oceans Institute Technical Report SOI-2011-001). Retrieved from <http://soi.st-andrews.ac.uk/documents/424.pdf>
- Miller, P. J. O., Antunes, R. N., Wensveen, P. J., Samarra, F. I. P., Alves, A. C., Tyack, P. L., . . . Thomas, L. (2014). Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *The Journal of the Acoustical Society of America*, 135, 975-993. <https://doi.org/10.1121/1.4861346>
- Miller, P. J. O., Kvadsheim, P. H., Lam, F-P. A., Tyack, P. L., Curé, C., DeRuiter, S. L., . . . Hooker, S. K. (2015). Northern bottlenose whales are highly sensitive to noise disturbance. *Royal Society Open Science*, 2, 140484. <https://doi.org/10.1098/rsos.140484>
- National Research Council (NRC). (2005). *Marine mammal populations and ocean noise: Determining when noise causes biologically significant effects*. Washington, DC: National Academies Press.
- New, L. F., Clark, J. S., Costa, D. P., Fleishman, E., Hindell, M. A., Klanjscek, T., . . . Harwood, J. (2014). Using short-term measures of behaviour to estimate long-term fitness

- of southern elephant seals. *Marine Ecology Progress Series*, 496, 99-108. <https://doi.org/10.3354/meps105477>
- Nøttestad, L., Sivle, L. D., Krafft, B. A., Langård, L., Anthonypillai, V., Bernasconi, M., . . . Axelsen, B. E. (2014). Ecological aspects of fin whale and humpback whale distribution during summer in the Norwegian Sea. *Marine Ecology*, 35, 221-232. <https://doi.org/10.1111/maec.12075>
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from [www.R-project.org](http://www.R-project.org)
- Simon, M., Johnson M., & Madsen, P. T. (2012). Keeping momentum with a mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *Journal of Experimental Biology*, 215, 3786-3798. <https://doi.org/10.1242/jeb.071092>
- Sivle, L. D., Kvasdheim, P. H., Ainslie, M. A., Solow, A., Handegard, N. O., Nordlund, N., & Lam, F-P. A. (2012). Impact of naval sonar signals on Atlantic herring (*Clupea harengus*) during summer feeding. *ICES Journal of Marine Science*, 69(6), 1078-1085. <https://doi.org/10.1093/icesjms/fss080>
- Sivle, L. D., Wensveen, P. J., Kvasdheim, P., Lam, F-P. A., Visser, F., Curé, C., . . . Miller, P. (2016). Naval sonar disrupts foraging behaviour in humpback whales. *Marine Ecology Progress Series*, 562, 211-220. <https://doi.org/10.3354/meps11969>
- Skern-Mauritzen, M., Johannesen, E., Bjørge, A., & Øien, N. (2011). Baleen whale distributions and prey associations in the Barents Sea. *Marine Ecology Progress Series*, 426, 289-301. <https://doi.org/10.3354/meps09027>
- Southall, B. L., Nowacek, D. P., Miller, P. J. O., & Tyack, P. L. (2016). Experimental field studies to measure behavioral responses of cetaceans to sonar. *Endangered Species Research*, 31, 293-315. <https://doi.org/10.3354/esr00764>
- Southall, B., Moretti, D., Abraham, B., Calambokidis, J., & Tyack, P. (2012). Marine mammal behavioral response studies in southern California: Advances in technology and experimental methods. *Marine Technology Society Journal*, 46, 46-59. <https://doi.org/10.4031/MTSJ.46.4.1>
- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Jr., . . . Richardson, W. J. (2007). Marine mammal noise exposure criteria. *Aquatic Mammals*, 33(4), 411-521. <https://doi.org/10.1578/AM.33.4.2007.411>
- Southall, B. L., DeRuiter, S. L., Friedlaender, A., Stimpert, A. K., Goldbogen, J. A., Hazen, E., . . . Calambokidis, J. (2019). Behavioral responses of individual blue whales (*Balaenoptera musculus*) to mid-frequency military sonar. *Journal of Experimental Biology*, 222, 1-15. Retrieved from <https://jeb.biologists.org/content/jexbio/222/5/jeb190637.full.pdf>; <https://doi.org/10.1242/jeb.1906377>
- Stimpert, A. K., DeRuiter, S. L., Southall, B. L., Moretti, D. J., Goldbogen, J. A., Friedlaender, A., . . . Calambokidis, J. (2014). Acoustic and foraging behavior of a tagged Baird's beaked whale (*Berardius bairdii*) exposed to simulated sonar. *Scientific Reports*, 4, 7031. <https://doi.org/10.1038/srep07031>
- Tyack, P. L., Zimmer, W. M., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., . . . McCarthy, E. (2011). Beaked whales respond to simulated and actual navy sonar. *PLOS ONE*, 6, e17009. <https://doi.org/10.1371/journal.pone.0017009>
- Wensveen, P. J. (2016). *Detecting, assessing, and mitigating the effects of naval sonar on cetaceans* (PhD thesis). University of St Andrews, St Andrews, UK. Retrieved from <http://hdl.handle.net/10023/8684>
- Wensveen, P. J., von Benda-Beckmann, A. M., Ainslie, M. A., Lam, F-P. A., Kvasdheim, P. H., Tyack, P. L., & Miller, P. J. O. (2015). How effectively do horizontal and vertical response strategies of long-finned pilot whales reduce sound exposure from naval sonar? *Marine Environmental Research*, 106, 68-81. <https://doi.org/10.1016/j.marenvres.2015.02.005>
- Wensveen, P. J., Kvasdheim, P. H., Lam, F-P. A., von Benda-Beckmann, A. M., Sivle, L. D., Visser, F., . . . Miller, P. J. O. (2017). Lack of behavioural responses of humpback whales (*Megaptera novaeangliae*) indicate limited effectiveness of sonar mitigation. *Journal of Experimental Biology*, 220, 4150-4161. <https://doi.org/10.1242/jeb.161232>