

Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments

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Abstract. Behavioral response studies provide significant insights into the nature, magnitude, and consequences of changes in animal behavior in response to some external stimulus. Controlled exposure experiments (CEEs) to study behavioral response have faced challenges in quantifying the importance of and interaction among individual variability, exposure conditions, and environmental covariates. To investigate these complex parameters relative to blue whale behavior and how it may change as a function of certain sounds, we deployed multi-sensor acoustic tags and conducted CEEs using simulated mid-frequency active sonar (MFAS) and pseudo-random noise (PRN) stimuli, while collecting synoptic, quantitative prey measures. In contrast to previous approaches that lacked such prey data, our integrated approach explained substantially more variance in blue whale dive behavioral responses to mid-frequency sounds ($r^2 = 0.725$ vs. 0.14 previously). Results demonstrate that deep-feeding whales respond more clearly and strongly to CEEs than those in other behavioral states, but this was only evident with the increased explanatory power provided by incorporating prey density and distribution as contextual covariates. Including contextual variables increases the ability to characterize behavioral variability and empirically strengthens previous findings that deep-feeding blue whales respond significantly to mid-frequency sound exposure. However, our results are only based on a single behavioral state with a limited sample size, and this analytical framework should be applied broadly across behavioral states. The increased capability to describe and account for individual response variability by including environmental variables, such as prey, that drive foraging behavior underscores the importance of integrating these and other relevant contextual parameters in experimental designs. Our results suggest the need to measure and account for the ecological dynamics of predator–prey interactions when studying the effects of anthropogenic disturbance in feeding animals.

Key words: behavioral response; controlled exposure experiment; disturbance; foraging behavior; prey; whales.

INTRODUCTION

Behavioral response studies have provided significant insights into the nature, magnitude, and consequences of changes in animal behavior across a broad range of taxonomic groups. Many studies have been performed in controlled settings with sound playback experiments either in the laboratory or over relatively short ranges in the field on terrestrial animals, notably birds (Emlen 1972) and mammals (Owren and Rendall 2001). Research has been conducted on captive marine mammals, specifically small odontocetes (Kastelein et al. 2006), but the

generalization of results to free-ranging animals for any application in the context of regulatory assessments is limited by the vastly different behavioral contexts. Due in part to the logistical constraints associated with working on highly mobile animals in the open ocean, in situ experiments using controlled sound exposures with wild marine mammals have been limited. Recent controlled exposure experiments (CEEs) with various sound types (Miller et al. 2009, Tyack et al. 2011, Southall et al. 2012, Goldbogen et al. 2013) have assumed a dose–response function based on received sound level in their design and execution. However, these kinds of studies face challenges in quantifying the functional roles of and interactions among individual variability, exposure conditions, and environmental covariates in measured behavior. Increasingly, researchers have demonstrated

Manuscript received 4 May 2015; revised 30 October 2015; accepted 5 November 2015; final version received 30 November 2015. Corresponding Editor: T. E. Essington.

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that the behavioral responses of marine mammals can be context-dependent and non-linear with regard to simple exposure metrics such as received level (Ellison et al. 2012, Goldbogen et al. 2013).

Both basic biological and applied conservation questions have motivated these studies of behavior and the effects of noise on marine mammals. Sound is critically important in the life history of all marine mammal species and understanding its utility in social interactions, reproduction, foraging, navigation, and predator detection has been essential in describing their basic behavior. Because of this central importance of sound to marine mammals, the introduction of noise from a myriad of human sources into a naturally noisy ocean has both potential and realized negative effects in a variety of species (see Southall et al. 2007). Specifically, both acute, and in some cases, mortal effects of military sonar (e.g., D'Amico et al. 2009) have been observed. Additionally, broader temporal and spatial scale sub-lethal effects, such as physiological stress responses to elevated ocean noise (Rolland et al. 2012) and auditory masking of communication signals by ship noise (Hatch et al. 2012), have been documented.

Substantial research has provided direct data on the nature and scope of potential effects to inform management practices. Studies applying experimental methods, such as the present study, have sought to address specific applied questions, including how sonar exposure affects behavior in different behavioral contexts. Response data from such studies provide insights into the nature and context specificity of responses (e.g., Goldbogen et al. 2013). However, as questions have evolved beyond simply identifying responses to interpreting both the ecological context of responses and their consequences in terms of foraging, reproduction, and survival, more sophisticated and novel methods, such as the direct measurement of ecological context within response studies, are plainly needed.

There are a myriad of logistical challenges in conducting CEEs with marine mammals in the wild. These animals are largely absent from conventional visual observation, spending up to 95% of their lives underwater and out of view (Hoelzel 2009). Passive acoustic monitoring of animals producing social sounds (calling) has provided some insights into general patterns of marine mammal distribution and behavior (Stafford et al. 2001, Mellinger et al. 2007, DiMarzio et al. 2008). Advances in the miniaturization of electronics have aided in the development of multi-sensor recording tags (Johnson and Tyack 2003) that measure different aspects of the underwater behavior of individual cetaceans (e.g., diving, feeding, vocalizing) in high resolution concurrently with measurements of sound exposure. These types of tags have significantly increased our knowledge of cetacean behavior (Witteveen et al. 2008, Hazen et al. 2009, Goldbogen et al. 2012, Simon et al. 2012, Friedlaender et al. 2013) and their responses to anthropogenic sound over the past few decades (Nowacek et al. 2004, Tyack et al. 2011, McKenna et al. 2012, Southall et al. 2012).

Many of the CEEs conducted to date have focused on toothed whales, and particularly beaked whales, given the fact that numerous mass stranding mortality events in these species have been associated with military mid-frequency active sonar (MFAS; D'Amico et al. 2009). However, a few of these events have included baleen whales and, despite the fact that these species primarily produce quite low-frequency sounds, they are very likely able to hear within the range (1–10 kHz) of many of these active sonar systems (Southall et al. 2007).

Because of the fact that many baleen whale species are threatened or endangered, and there have been some documented negative impacts of sonar on some marine mammals in certain conditions, there is increasing interest in direct measurements of their behavior and responses to anthropogenic sound, specifically active military sonar. One of the unique characteristics of all cetaceans, and specifically baleen whales (*Balaenoptera*), is their enormous body size. Baleen whales have evolved the ability to feed in bulk on aggregations of small-bodied organisms, which has, in turn, allowed for the evolution of massive body size and large overall energetic demands (Goldbogen et al. 2010, Pyenson et al. 2012). Many species satisfy their energetic demands during only a portion of the year when foraging is their primary activity. However, bulk-filter feeding is strongly dependent on high-density prey for energetically efficient foraging (Goldbogen et al. 2007). Consequently, large baleen whales are principally dependent on high quality (dense) prey (Friedlaender et al. 2009, Hazen et al. 2015) in order to satisfy their substantial energetic demands during an abbreviated summer foraging season. There has been considerable research on these requirements and how they are met, but relatively few assessments of the potential consequences of sub-lethal human disturbance that could affect foraging duration and efficiency.

Goldbogen et al. (2013) quantified behavioral responses of blue whales (*Balaenoptera musculus*) to simulated MFAS and pseudo-random noise (PRN) using CEEs off southern California. A complex multivariate analysis was used that included a broad suite of variables ranging from surface and dive behavior to animal kinematics. Significant changes in behavior were measured during sound exposure for both sound types. However, there was considerable variability in the nature and magnitude of response evident within individual whales. Responses were largely dependent on the behavioral state of the whale when the sound exposure began, with the greatest changes observed when whales were deep feeding rather than feeding at the surface or in a non-feeding behavioral state. While Goldbogen et al. (2013) examined some contextual covariates (e.g., number of boats in the area), the most robust model in their analysis only explained a relatively small proportion of changes in dive behavior during CEEs ($r^2 = 0.14$). Much of the remaining variability in blue whale dive behavioral response was likely related to contextual environmental features that had a

relatively larger influence on whale behavior than sound exposure yet were not included in the statistical models. The lack of quantitative measures of prey during CEEs was noted as a significant limitation of this study, as it is for nearly all studies of the behavioral response of feeding animals. Direct measurements of factors influencing foraging could provide context for interpreting changes in behavior coincident with an external stimulus such as noise exposure.

In order to more completely describe the complex nature of behavioral responses of blue whales, we conducted additional CEEs with simulated MFAS and PRN stimuli (described in Southall et al. 2012, Goldbogen et al. 2013), while collecting quantitative measures of prey before and after noise exposure. The objective was to evaluate previous results regarding deep-feeding blue whale dive response to acoustic playbacks while explicitly accounting for variability in the prey environment. The inclusion of relevant prey metrics as a contextual covariate was expected to substantially improve our ability to understand the variability and potential energetic consequences of behavioral responses. Given that current management approaches to acoustic disturbance have been based on either simple exposure thresholds or dose–response functions based purely on received sound level, quantifying the role of individual variability and environmental covariates in determining response probability is critical to improving the management of these ecologically important and federally protected species.

METHODS

We conducted CEEs in coastal and offshore waters throughout the Southern California Bight in conjunction with the Southern California Behavioral Response Study (SOCAL-BRS), during the summers of 2011–13 (Southall et al. 2012, Goldbogen et al. 2013). Acoustic prey surveys were conducted in close spatial and temporal overlap with blue whales outfitted with multi-sensor acoustic recording archival suction cup tags (DTAGs; Johnson and Tyack 2003) between 30 and 60 min preceding and following CEEs (Table 1). Tags were deployed using a

6-m long carbon fiber pole from a 6.3 m Zodiac RHIB (Zodiac Milpro, Paris, France) following established protocols to minimize disturbance to the whales when approaching them. DTAGs contain tri-axial accelerometers and magnetometers, as well as pressure and temperature sensors and hydrophones. Sensors sample at either 50 or 200 Hz (but are down-sampled to 5 Hz in post-processing), and sound is recorded continuously at either 64 or 200 kHz depending on the specific tag deployed.

We used previously described methods (Friedlaender et al. 2013) to analyze sensor and acoustic data to identify individual feeding lunges and describe different behavioral states (e.g. feeding, traveling, socializing/calling). Feeding lunges are determined through an iterative process of assessing changes in the absolute values of the accelerometer signals (Goldbogen et al. 2012, Simon et al. 2012,), changes in speed derived from its correlation with flow noise on the tag’s acoustic recordings (Goldbogen et al. 2007, Ware et al. 2011, Friedlaender et al. 2013), and expert examination of the whale’s kinematic movement patterns in Trackplot (a customized software program for visualizing multi-sensor tag data; Ware et al. 2014). Whale positions were tracked by the tagging boat typically once during each surface series with the aid of calibrated compass-bearing laser range finders. During foraging behavior, the number, time, location, and depth of each individual feeding lunge was determined for our analysis.

Once a tag was deployed, we conducted pre-exposure prey mapping surveys covering the area in and around the tagged whale surfacing positions (being tracked by the tagging vessel) lasting for 30–75 min. This was followed by a 30-min pre-exposure baseline period (no sound transmissions), a typically 30-min series of sound transmissions, a 30-min post-exposure (no sound transmissions) period, and a second post-exposure 30–75-min prey mapping period. During the entire experimental period (including prey mapping before and after sound exposure experiments), the focal whale’s position was tracked from the tag boat. Both MFAS and PRN signals were used in CEEs with signal type included as a

TABLE 1. Tagged blue whales, CEE type, and details of the timing of prey mapping before and after playback; all times are local.

Date	ID	CEE type	Time tag on	Prey mapping before	CEE time	Prey mapping after	Focal timing (before)	Focal timing (after)
29 Jul 2011	bw11_210b	MFAS	1117	1228–1334	1525–1555	1614–1710	1228–1334	1614–1710
30 Jul 2011	bw11_211a	PRN	0910	0914–1055	1108–1126	1135–1246	0914–1055	1135–1246
8 Jan 2011	bw11_213b	MFAS	0832	1020–1139	1246–1316	1330–1500	1020–1139	1330–1500
8 Feb 2011	bw11_214b	PRN	0902	0734–0940	1120–1150	1246–1422	0901–0940	1246–1422
8 Jun 2011	bw11_218b	PRN	1644	1622–1658	1739–1802	1842–1905	1622–1650	1842–1905
8 Sep 2011	bw11_221a	PRN	1150	1242–1342	1459–1529	1608–1653	...	1612–1653
18 Oct 2011	bw12_292a	PRN	1000	1111–1220	1334–1404	...	1111–1220	...
26 Jul 2011	bw13_207a	CON	1544	1555–1649	1744–1814	1859–1925	1555–1649	1859–1925
2 Aug 2011	bw13_214b	CON	1015	1153–1300	1353–1420	1438–1536	1153–1300	1438–1536

categorical variable in the final analytical models (as in Goldbogen et al. 2013). We also examined two CEEs designed as no-sound controls where the sound source was lowered in the water for 30 min during a mock exposure period with the source vessel maintaining position as typical during CEEs but with no MFAS or PRN transmissions. Results from no-sound controls are described relative to those from MFAS and PRN exposures in comparative bar plots to contextualize response, but were not used in the final GAMMs due to limited sample size.

Prey species (krill, presumed to be *Euphausia pacifica* and *Thysanoessa spinifera*) were measured using two SIMRAD EK-60 echo sounders (SIMRAD, Horten, Norway) with 38 kHz and 120 kHz frequencies in close spatial proximity to tagged whales (<1 km). By using two frequencies, the differential scattering of sound allows a coarse approach to differentiate acoustically identified schools (e.g., fish with swim bladders vs. zooplankton). In addition to the relatively narrow beam pattern of these sound sources, active acoustic sources at these high frequencies are almost certainly well above the presumed hearing range of baleen whales (Mooney et al. 2012). We deployed a towfish 1–2 m below the surface at speeds between 2–5 kn surveying in either a clover-leaf or zig-zag sampling protocol based on the movements of focal individuals (Hazen et al. 2009). When the whale was feeding within a relatively stationary location, the boat would pass within 200 meters of the tagged whale and then survey out to 1 km before turning back to obtain multiple measures of prey patch characteristics with a series of passes. When the whale was feeding while moving in a directed manner, the sampling strategy was a zig-zag pattern following the whale's track, which measured patches that were targeted by the whale. Echosounders were calibrated using 23-mm copper and 38.1-mm tungsten-carbide spheres of known target strength (Demer et al. 1999). Acoustic data were collected with pulse widths of 512 and 256 ms for the 38 and 120 kHz echosounders, respectively, and were processed using 10 × 250 m vertical and horizontal bins and acoustically detected schools (SHAPES algorithm, -75 dB threshold, 5-m linking distance; Coetzee 2000) in Echoview 5 (Echoview, Hobart, Tasmania, Australia). Given the strong response of marine predators to patch size and density (Croll et al. 2005, Hazen et al. 2009, Benoit-Bird et al. 2013), we used patches as the metric of prey density in subsequent analyses.

We compared school linear density (sv) between the 120 kHz and 38 kHz data to ensure schools were consistent with krill-scattering properties (Watkins and Brierley 2002, Simmonds and MacLennan 2005). For each krill patch, we measured prey patch density, prey patch height, mean prey patch depth, and bottom depth. Because we could not measure prey during sound exposure, we examined dive/foraging behavior before and after playback to test for behavioral changes that were not explained by changes in bottom depth or prey

patch metrics. In all but one deployment, prey was mapped within 2 km of the initial animal location. Because of the near-field of acoustic transducers, we were unable to measure prey shallower than 5 m (Simmonds and MacLennan 2005). With the additional knowledge from Goldbogen et al. (2013) that deep feeding is the behavioral state in which blue whales are most likely to respond to CEEs, we limited our analysis to those whales feeding >50 meters deep.

We applied a common statistical framework, as used in Goldbogen et al. (2013), so that results would be directly comparable across studies. This consisted of a combination of principal component analyses (PCAs) to reduce the dimensionality of whale dive metrics and generalized additive mixed models (GAMMs) to assess the effect of CEEs on a subset of previously selected categorical and continuous behavioral metrics for blue whales (sensu Goldbogen et al. 2013). The PCA was run using the `prcomp` function in the `stats` package (v3.1.2) and the GAMM using the `mgcv` package (v1.8-7) in R (v3.1.2). Individual behavioral metrics used include dive time, maximum dive depth, post-dive surface time, descent time, ascent time, bottom time, and number of breaths between dives. Behavioral metrics were quantified with no knowledge (blind) of playback timing or type of treatment on a dive-by-dive basis and subsequently were categorized as either before or after sound exposure. Whale responses were defined as a significant change in dive behavior from before to after the sound exposure. Explanatory variables were checked for normality and GAMMs with individual whale as a random variable were fitted using the first PCA eigenvector as the response variable with an identity link function (Eq. 1). In addition, GAMMs were subsequently fit using a single explanatory variable as a response of the first eigenvector (Eq. 2). Then the GAMMs were iteratively fit using the same single explanatory variable removed from the best-fit model (Eq. 3; Table 2). This process allows for an estimate of the variance in whale behavior accounted for by each variable independently and then for each variable, taking into account the other modeled variables. This approach provides a quantitative means to evaluate the importance of each explanatory variable in the model individually as well as when removed from the full model.

$$PCA_{dive} \sim f(\text{before/afterplayback} + \text{distancetosource} + s(\text{krilldensity}(Sv)) + s(\text{schooldepth}) + s(\text{bottomdepth}) + s(\text{patchheight})) \quad (1)$$

$$PCA_{dive} \sim f(\text{variable}_i) \quad (2)$$

$$PCA_{dive} \sim f(\text{fullmodel} - \text{variable}_i) \quad (3)$$

In order to examine behavioral response in the presence and absence of prey, both individual whale dive response and change in prey depth (comparing the mean

TABLE 2. GAMM summary statistics for best fit model with variables from PCA dive axis 1 as a function of prey behavior and CEE playback state.

Variable	df	F statistic	P value
Intercept	-1.50751	-5.291	<0.001
Before–after	0.78035	3.772	<0.001
Distance from source	0.0712	1.04	0.301
s(Sv_mean)	9.47E-01	0	<0.001
s(Height_mean)	9.13E-01	3.501	<0.001
s(Depth_mean)	1.02E+00	17.595	<0.001
s(BotDep)	9.82E-01	9.848	<0.001

Note: Bold values represent significant variables.

depth of patches before and after sound exposure for significant differences) were examined across all whale dives. Individual dive metrics were compared before and after each playback type (MFAS, PRN, Control). In addition, prey patch depths were plotted before and after exposure periods, not to examine potential causality, but instead to consider scenarios where a whale may have targeted a different patch or where prey patches may have vertically migrated over the ~1.5 h lapse in mapping prey. Prey patch depth was divided by the dive metrics (dive axis 1) to create a non-dimensional comparison ratio illustrating potential whale response across all dives taking into account any change in prey patch depths. For example, an observed change in dive behavior from before to after a playback that coincides with a change in prey patch depth may be misinterpreted as a response to playback if prey had not been measured. Such dimensional analysis approaches have been used previously to simplify complex ecological problems (Schneider 2009). In this case, raw units were retained rather than normalizing to non-dimensional quantities given that comparisons are relative within before and after states. This offers ease of interpretation and results in a comparison ratio of prey patch depth (m)/axis 1 dive metric.

RESULTS

Prey data were collected before and after CEEs for nine tagged blue whales in August–September of 2011–13 (Table 1), a dataset unique from previous CEE analyses (Goldbogen et al. 2013). PCAs fit using the selected suite of metrics defining dive behavior resulted in 81% of the variance loading on dive-axis 1 with all dive variables loading in the same direction (eigenvalues of -0.24 to -0.47 ; Figs. 1 and 2). Dive axis 2 explained 8.7% of the variance and included dive time and maximum dive depth loading positively (0.319 and 0.634), while surface time and number of breaths loaded negatively (-0.489 and -0.324). These behavioral states represent long dives with short recovery or short dives with long recovery. The loadings on axis 1 are similar to those obtained by Goldbogen et al. (2013), specifically that dive variables

(dive time, surface time, number of breaths, dive depth, number of lunges) increase in the same direction such that longer dives occur coincidentally with deeper dive depths, longer surface time, and increased number of breaths. A strong relationship between dive depth and dive axis 1 is apparent when plotting dive depths greater (blue) and less (red) than the mean (171 m) against dive axis 1 (x -axis) and 2 (y -axis; Fig. 2).

The full GAMM examining blue whale dive behavioral response resulted in both a significant before–after effect and significant differences in dive behavior relative to prey patch depth, prey patch height, prey patch density, and bottom depth. This indicates that the behavior of all foraging whales was significantly correlated with multiple factors, including sound exposure, bottom depth, and changes in the distribution of prey. Only by accounting for both exposure and prey conditions into the statistical models is it possible to identify these simultaneous and interacting forces affecting whale behavior. Dive-axis 1 increased (shallower, shorter dives) as a function of prey patch height, and decreased (longer, deeper dives) with bottom depth, prey patch depth, prey patch density, and prey patch height (Fig. 3, Table 2). Single parameter GAMM results illustrated that only prey patch depth and bottom depth had significant explanatory power for changes in blue whale dive behavior when considered independent of other variables (R^2 single; Table 3).

The reduced models indicated that the effects of CEEs on animal behavior (before/after exposure) resulted in an additional 4.5% of variance explained when other terms were included. This demonstrates that sound exposure–related changes in dive behavior were significant in our sample only when ecological covariates were included.

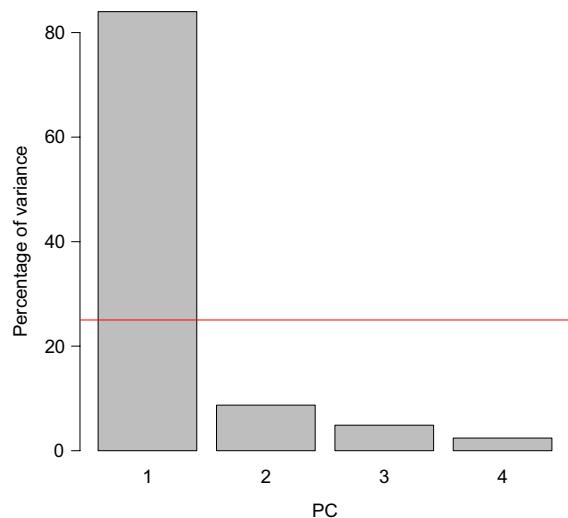


FIG. 1. PCA results from dive metrics for use in prey-mediated response analysis. The red line represents the 25% variance explained threshold where all PCs would measure if loadings were equal among four axes. Only axis 1 falls above that threshold.

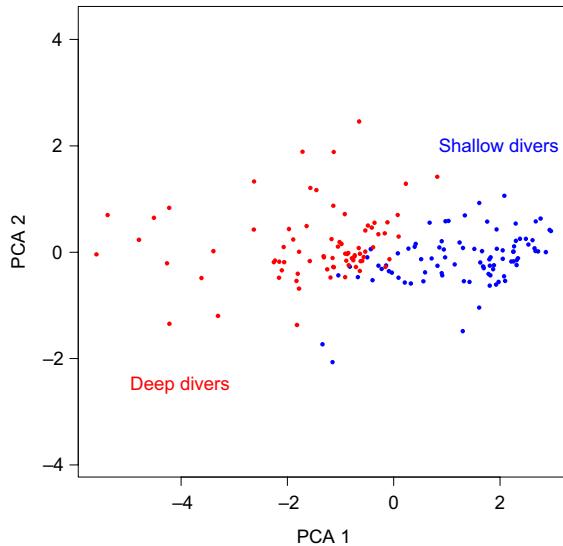


FIG. 2. Scatterplot of PCA scores for PCA axis 1 vs. PCA axis 2, colored by whale dive depth. Blue whales diving deeper (red) and shallower (blue) than the mean depth across all whales are colored to highlight the importance of axis 1 in the differentiation among dive depths.

The fully parameterized GAMM results demonstrated that environmental covariates including bottom depth, prey patch height, and prey patch depth provide significantly more variability explained by dive axis 1 than CEE

effects alone ($r^2 = 0.725$ compared to 0.000; Fig. 1, Table 3). Relative to the similar PCA-GAMM dive model results without prey from Goldbogen et al. (2013), the incorporation of prey metrics and bottom depth together provide a fivefold increase in the variance explained by models of blue whale deep-feeding behavior before and after CEEs ($r^2 = 0.14$ vs. 0.725).

The behavioral responses of blue whales as an integrated measure of behavior relative to the dive metrics identified from PCA dive-axis 1 are shown in Fig. 4a for each CEE condition (Goldbogen et al. 2013). Based on this analysis, which uses the data from this study independent of prey metrics, there is an apparent change in behavior from MFAS exposures (with large error estimates), little difference from PRN (small error), and an apparent difference during the silent control sequences (small error). However, the incorporation of prey metrics (specifically patch depth as the metric that independently has a significant effect on whale behavior in the model) with the same CEE exposure and response data results in very different conclusions. We created non-dimensional ratios of prey depth and scaled dive response (axis 1) that allow for comparison between observed changes in blue whale dive behavior and changes in the prey environment. Significantly different comparison ratios were identified for both sound exposure types, while the comparison ratio before and after control periods remained insignificant (Fig. 4c). These results indicate that behavioral differences resulting during CEEs with transmissions are

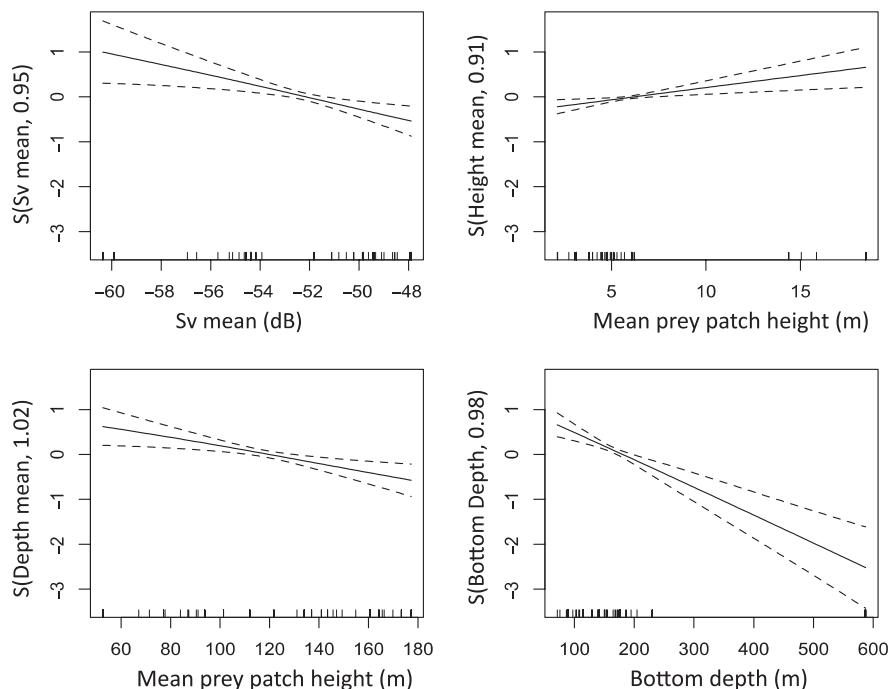


FIG. 3. GAMM partial plots with response (change in dive axis 1) on the y-axis as a function of each additive predictor on the x-axis. The GAMM models simplified to linear responses in the best fit model shown here (degrees of freedom included on the y-axis). Rug plots are included to show the spread of data for each variable: sv_mean a measure of prey density, height_mean as the height of the school, depth_mean as the depth of the center of the school, and BotDep the depth of the seafloor.

TABLE 3. GAMM summary from model selection process with full model, individual variable model, and full – 1 model and their effect on overall model variance explained.

Variable	R^2 full	R^2 single	R^2 reduced	R^2 deviance
Before–after	0.725	0	0.681	0.044
Distance from source	0.725	0	0.725	0.000
s(Sv_mean)	0.725	0	0.512	0.213
s(Height_mean)	0.725	0	0.659	0.066
s(Depth_mean)	0.725	0.225	0.612	0.113
s(BotDep)	0.725	0.328	0.121	0.604
		Dive axis 1 ~ f(all)	Dive axis 1 ~ f(var)	Dive axis 1 ~ f(all-var)

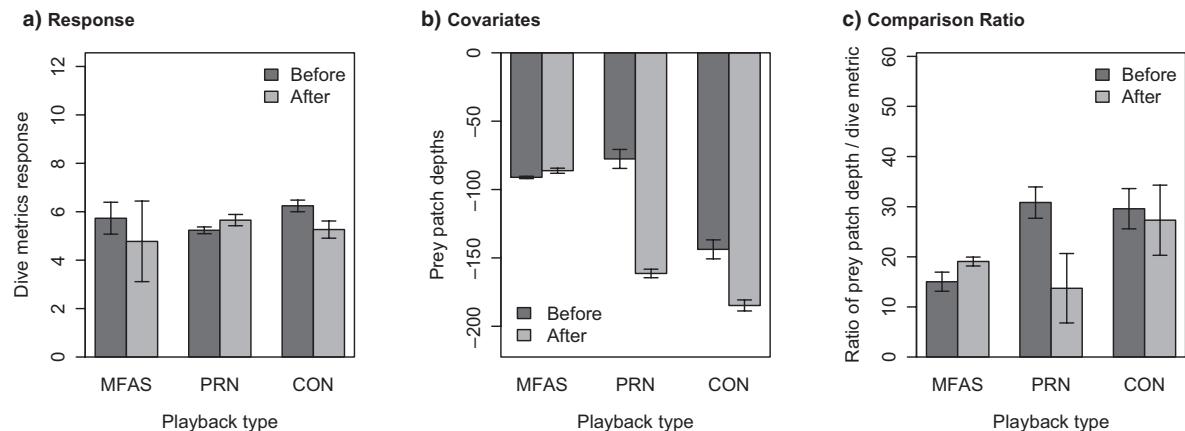


FIG. 4. Plots of before/after playback changes for response variables, a single explanatory variable, and combined comparison ratio for mid-frequency sonar (MFAS), pseudorandom noise (PRN), and control (CON). Standard error is shown with whiskers. (a) Change in dive axis 1 (y -axis) before and after playback shows ambiguity in response across playback types. (b) Change in prey patch depth before and after playback included as a covariate (situations where whale switched prey patches) rather than a response. (c) Ratio of scaled prey patch depth to dive response identifying when animal dive behavior changed taking into account prey patch depth.

the result of an interaction between sound exposure and environmental covariates, whereas changes in control dives were solely responses to changes in the distribution and behavior of prey. Relative differences in the comparison ratios for both sound types demonstrate that when explicitly accounting for prey, responses of foraging blue whales were relatively stronger for PRN than for MFAS (Goldbogen et al. 2013).

DISCUSSION

The results of this study underscore the need to quantify the ecological dynamics of predator–prey interactions when studying the effects of anthropogenic disturbance on feeding animals. Without these contextual variables, the ability to fully describe any behavioral response of animals resulting from noise exposure may be limited. While these observations are both intuitive and evident in terrestrial systems (Owren and Rendall 2001), they have often been overlooked or insufficiently measured in studying the ecology and behavior of marine mammals (Ellison et al. 2012). Our study demonstrates that without the ability to

adequately characterize and quantitatively account for the ecological context, including prey distribution and availability, interpreting potential changes in the behavior of feeding whales can be difficult or, worse, misleading. In fact, for the current study, with a smaller sample size than Goldbogen et al. (2013), it would not have possible to accurately identify the effects of sound exposures on dive behavior without understanding parameters related to the environment (bottom depth and prey distribution).

Our findings concur with and empirically strengthen the results presented by Goldbogen et al. (2013) that deep-feeding blue whales show significant behavioral responses to CEEs with both MFAS and PRN. Specifically, with the set of explanatory dive metrics and prey included in our analysis, we measured a fivefold increase ($r^2 = 0.14$ vs. 0.725) in the variance explained in our models of changes in blue whale dive behavior before and after CEEs. As in Goldbogen et al. (2013), a suite of synoptic variables measured in high resolution are useful to characterize diving behavior change as a function of sound exposure across individuals within a common and controlled experimental condition. These results

demonstrate that behavioral changes in deep-feeding blue whales result from a complex interaction of ecological, biological, and environmental variables, including factors affecting prey distribution, individual whale variability, and the presence of an external acoustic disturbance. Studies measuring a limited set of behavioral and environmental covariates with coarse resolution are likely limited in their ability to detect the type and probability of behavioral response. Furthermore, we added full experimental control sequences (entire experimental sequences with no controlled sound exposure), and by comparing behavior in these contexts and accounting for characteristics of the prey environment, found no indication of behavioral changes from the deployment and mock transmissions from a silent sound source. Further, as suggested by Goldbogen et al. (2013), our results demonstrate that blue whales in some contexts respond to simulated MFAS exposures from scaled sources, as well as, and perhaps even more strongly, to PRN. We emphasize that our sample size is still relatively small and that future studies should include a greater number of playbacks across a broader set of behavioral states and ecological contexts. Blue whales in the areas off southern California where these studies occurred are regularly exposed to real MFAS from recurring Navy training and testing operations, but PRN is generally unlike any other typical sound in their environment. The relative novelty of these mid-frequency sounds is likely an additional contextual factor in the probability of response, interacting with other parameters such as proximity, animal behavioral state, and the clearly important ecological covariates examined here. Recognizing the importance of these contextual factors, notably experiential factors, caution should be drawn in directly extending these results to areas with less regular MFAS exposure or to potentially more vulnerable sex and age classes (e.g., young calves) than those tested here. While neither our study nor Goldbogen et al. (2013) was designed to analyze specific changes at certain exposure levels within individuals, ongoing analyses including data from individual animals in both studies indicate that when responses do occur, they include relatively short-term cessation of feeding and minor changes in diving and orientation. Similar caution should be drawn in extrapolating results to larger temporal and spatial scales given the limited understanding of how these results relate to those from longer exposures to louder but more distant sources, including operational MFAS sources that may result in similar received levels but have quite different exposure contexts.

The dramatic improvement in our ability to explain variability in both foraging behavior and the response of whales to sound by including noise exposure variables and the ecological variables driving foraging behavior (prey) underscores the importance of measuring these parameters and applying them in field experiments. Put more directly, CEEs investigating potential changes in foraging behavior that lack accurate measures of prey

distribution and density may lack explanatory power with which to draw conclusions or may even result in misleading interpretation of observed behavior. Where these kinds of relevant environmental covariates are not directly incorporated, even the inclusion of basic physical parameters, such as bathymetry when examining changes in blue whale dive depths, may provide additional insight into sources of variability beyond those used in many CEEs (almost exclusively received level). Our study design was limited in that we could only measure prey distribution and density before and after noise exposure not during, minimizing the use of prey measurements within individual whale response analyses. Thus, if the distribution and behavior of prey changed from and then returned to pre-exposure conditions over this period of time or space we would have no way to measure this and could resultantly misinterpret changes in whale behavior. We believe this is unlikely to have occurred in our data given the scales over which our sequential measurements before and after CEEs were conducted (e.g., <2 hours and generally within 2 km of one another) relative to the typical time/space scales over which prey patch changes are likely occur. However, subsequent studies may consider simultaneous acquisition of prey data with sound exposures during CEEs, provided that measures are taken to ensure that this does not introduce potentially confounding contextual factors as well.

The results presented here have both specific implications for assessing noise impacts on an endangered marine mammal and making informed conservation decisions, as well as advancing a more comprehensive understanding of the effects of noise on animals in the ocean generally. While blue whale responses appear to (1) differ among individuals, (2) be relatively subtle, and (3) rather quickly abate following responses to sound exposure, multiple studies have now demonstrated significant changes in foraging behavior resulting from CEEs using simulated MFAS and PRN signals (Goldbogen et al. 2013, this study). As evident here, the ability to quantify differences in foraging in relation to bottom depth and prey patch metrics amplifies and enhances the power to draw clear conclusions about behavioral changes. Consequently, we have a greater ability to understand the behavior of feeding whales and how it may change in relation to both ecological factors and noise exposure. The combined evidence demonstrates (1) a strong behavioral state dependence (deep feeding) of response (Goldbogen et al. 2013), (2) high individual variability in response (Goldbogen et al. 2013), and (3) the clear importance of understanding prey dynamics in understanding baseline behavior and potential changes resulting from sound exposure. These all support the conclusion that blue whale responses to human noise, much like our own reactions to sound, depend critically on a suite of contextual aspects of exposure (see Ellison et al. 2012). Given the clear context dependence of blue whale response to CEEs demonstrated by Goldbogen et al. (2013) and expanded upon

here by integrating direct measurements of the key covariate of prey, we suggest that a conventional dose–response approach of assessing exposure purely as a function of received sound level may be insufficient and potentially misleading for baleen whales. Despite the increase in our ability to understand responses to CEEs in blue whales through this recent work, there are certainly additional contextual variables (e.g., relative proximity of animals and sound sources, environmental factors affecting sound propagation conditions) that may also have substantial influence on the magnitude of behavioral responses and should be considered.

Blue whale populations remain endangered and their abundance in the eastern North Pacific is estimated at about 2000 animals (Calambokidis and Barlow 2004), though one recent population model has suggested this may be at carrying capacity for the current environment (Monnahan et al. 2014). Because of their massive size and long-range migration patterns, these species also have among the highest energetic demands in extant animals (Goldbogen et al. 2012). Consequently, understanding how they meet these requirements and how the ecological parameters that influence foraging behavior may interact with potential disturbance is critical to the informed management of their recovery. Blue whales respond to several kinds of mid-frequency anthropogenic sound and these responses include relatively short-term changes in foraging behavior, with associated energetic costs that need further refinement (Goldbogen et al. 2013).

While understanding the absolute energetic consequences to blue whales from disturbance-related behavioral responses remains challenging, new information suggests they may be significant in certain conditions. Hazen et al. (2015) demonstrated that blue whales optimize foraging by maximizing energy gain on deep dives targeting dense krill patches and switch to maximizing oxygen consumption (at the expense of decreased energy intake) when feeding on shallow and less dense krill patches. While Goldbogen et al. (2013) found that a proportion of blue whales in 2010 ($n = 3$) were engaged in surface feeding, all whales from 2011 to 2013 (this study) fed only on deeper prey patches. Additionally, it was recently demonstrated that when feeding on dense and deep krill patches, blue whales likely expend less energy and show significantly less maneuvering relative to when feeding on less dense and shallower prey patches (Goldbogen et al. 2015). The combined results suggest that deep feeding on dense krill patches is both behaviorally and energetically optimal and may represent periods of greatest net energy intake. If acoustic disturbance causes either a complete cessation of deep-feeding or displacement to lower density prey patches, this will decrease the energetic efficiency of individuals (Goldbogen et al. 2011). Such reductions in efficiency, if sustained over greater temporal scales, can have direct effects on reproductive efficiency and ultimately population demographics for baleen whales (Wiedenmann et al. 2011). Because deep-feeding blue whales are most likely to be

affected by sound exposure, repeated behavioral responses to military sonar could have significant cumulative impacts that have not been quantified in this study. Together these studies underscore the importance of understanding chronic species-specific sub-lethal yet consequential results of disturbance.

There has been recent progress in identifying the magnitude of disturbance to behaviors, such as feeding, required to result in measurable population consequences, both in situations where there is extensive information on population demographics and magnitude and probability of response (New et al. 2013) and where such data are more limited. Our study considers acoustic disturbance events that are intentionally shorter in duration and relatively lower in magnitude than real MFAS operations in order to identify the onset of behavioral changes in a controlled, experimental manner. Thus, the magnitude of potential population consequences from real MFAS sonar operated in complex scenarios with multiple sources or for much longer periods are not readily extrapolated directly from these scaled studies. However, our results, and those of Goldbogen et al. (2013), (1) demonstrate the nature of behavioral responses in foraging blue whales; (2) demonstrate conditions in which foraging behavior may or may not be affected; (3) provide a quantitative basis for describing the consequence of changes in terms of individual energetics; and (4) demonstrate how the ecological context of prey distribution affects response probability. The combined recent progress in basic ecology, behavior, and type and probability of behavioral response in blue whales provides key input parameters for models considering population consequences of disturbance from longer term, higher magnitude exposures from real MFAS. Further, the integration of these ecological and experimental CEE measurements allow for a fuller description of behavior relative to highly relevant contextual factors and should be considered within subsequent response studies in other marine mammal species.

The notion that prey distribution drives predator behavior is a well-established and described ecological relationship. However, understanding the interactions among environmental variables and anthropogenic disturbance within CEEs is a critical advancement and enduring need in experimental methods to describe and reduce potential anthropogenic disturbance, especially for sustained or broadly distributed activities, across a broad range of taxonomic groups.

ACKNOWLEDGMENTS

We thank the numerous institutions and individual members of the SOCAL-BRS field team, notably Stacy DeRuiter, Greg Schorr, Erin Falcone, Annie Douglas, Selene Fregosi and Todd Pusser for their efforts, as well as the crew of the R/V Truth. We thank Doug Nowacek for the use of echosounder equipment. Special thanks to Caroline Casey for her thoughtful discussions and constructive editing of the manuscript throughout. We also thank Jay Barlow (SWFSC) and the anonymous reviewers for

their comments. All research was conducted under NMFS Permit #14534, Channel Islands National Marine Sanctuary permit no. 2010-004, and multiple IACUC authorizations. Research funding for the active acoustic components of this study was provided by the U.S. Office of Naval Research (ONR) Marine Mammal Program. The overall SOCAL-BRS effort was supported in part by ONR Marine Mammal Program, but largely by the U.S. Navy's Living Marine Resources Program.

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DATA AVAILABILITY

Data associated with this paper have been deposited in the Stanford Digital Repository: <https://purl.stanford.edu/ty541py2242>