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ARTICLE

Effects of a scientific echo sounder on the behavior of short-finned pilot whales (*Globicephala macrorhynchus*)

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Abstract: Active echo sounding devices are often employed for commercial or scientific purposes in the foraging habitats of marine mammals. We conducted an experiment off Cape Hatteras, North Carolina, USA, to assess whether the behavior of short-finned pilot whales (*Globicephala macrorhynchus*) changed when exposed to an EK60 scientific echo sounder. We attached digital acoustic recording tags (DTAGs) to nine individuals, five of which were exposed. A hidden Markov model to characterize diving states with and without exposure provided no evidence for a change in foraging behavior. However, generalized estimating equations to model changes in heading variance over the entire tag record under all experimental conditions showed a consistent increase in heading variance during exposure over all values of depth and pitch. This suggests that regardless of behavioral state, the whales changed their heading more frequently when the echo sounder was active. This response could represent increased vigilance in which whales maintained awareness of echo sounder location by increasing their heading variance and provides the first quantitative analysis on reactions of cetaceans to a scientific echo sounder.

Résumé : Des échosondeurs actifs sont souvent utilisés à des fins commerciales ou scientifiques dans les habitats d'approvisionnement de mammifères marins. Nous avons mené une expérience au large du cap Hatteras (Caroline du Nord, États-Unis) pour déterminer si l'exposition de globicéphales tropicaux (*Globicephala macrorhynchus*) à un échosondeur scientifique EK60 entraînait une modification de leur comportement. Nous avons fixé des étiquettes acoustiques numériques (DTAGs) à neuf individus, dont cinq ont été exposés. Un modèle de Markov caché pour caractériser les états de plongée avec et sans exposition n'a révélé aucun indice de modification du comportement d'approvisionnement. Cependant, des équations d'estimation généralisées utilisées pour modéliser les changements de la variance du cap pour l'ensemble des enregistrements et dans toutes les conditions expérimentales ont fait ressortir une augmentation uniforme de la variance du cap durant l'exposition, pour toutes les valeurs de profondeur et d'inclinaison. Cela donne à penser que, peu importe l'état comportemental, les globicéphales modifiaient leur cap plus fréquemment quand l'échosondeur était en marche. Cette réaction pourrait refléter une vigilance accrue permettant aux globicéphales de rester au fait de l'emplacement de l'échosondeur en augmentant la variance de leur cap. Il s'agit de la première analyse quantitative des réactions de cétacés à un échosondeur scientifique. [Traduit par la Rédaction]

Introduction

Increasing levels of anthropogenic noise in the marine environment represent a major challenge to many marine mammal populations (Tyack 2008; Wright et al. 2007; Williams et al. 2015). In many areas, active echo sounding devices are used in commercial fisheries, sea floor mapping, hydrography, and navigation, often in the foraging habitats of marine mammals. Such devices are also used to map habitats, measure the movements and behavior of marine mammals underwater (e.g., Benoit-Bird et al. 2009; Doksæter et al. 2009; Williamson et al. 2016), and measure prey densities of marine mammals themselves (Hazen et al. 2011). We know very little about the potential effects of such signals on the behavior of marine mammals, but the use of any system that may inadvertently cause a behavioral reaction by the species of interest is obviously undesirable.

Echo sounders actively transmit pulses of sound in single or multi-acoustic beams directed vertically downwards, with source and half power point beam angles ranging from 5° to 15° (Simmonds and MacLennan 2005). Frequencies range from 12 to several hundred kiloHertz, which is within the hearing ranges of many species of marine mammals (Lurton and DeRuiter 2011; Nowacek et al. 2007; Southall et al. 2007). Source levels are typically high and range from 210 to 240 dB re 1 μPa @ 1 m (Lurton and DeRuiter 2011). Lurton and DeRuiter (2011) reviewed the potential risks to auditory systems of marine mammals by echo sounders. They concluded that while echo sounders transmit high sound pressure levels, their narrow beam limits the potential for direct auditory damage to marine mammals. However, some recent studies have suggested a range of behavioral responses of marine mammals to echo sounders, from avoidance to changes in vocal behavior, despite the fact that peak frequencies of the devices may lie above the hearing ranges of the species tested (Deng et al. 2014; Hastie et al. 2014; Richardson et al. 1995). For example, a high-power 12 kHz multibeam echo sounder was deemed to be the most plausible and likely behavioral trigger for a mass stranding of melon-headed whales (*Peponocephala electra*) in Madagascar (Southall et al. 2013). Echo sounders have been used to actively study movement and behavior in marine mammals (Benoit-Bird

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and Au 2003*a*; Hazen et al. 2011; Nøttestad et al. 2002; Similä 1997) and as potential technology for monitoring movements of marine mammals around a tidal turbine development (Hastie 2012). To date, however, no experiments have been conducted to explicitly test for potential effects of echo sounders on the behavior of wild cetaceans.

Short-finned pilot whales (*Globicephala macrorhynchus*) are deep-diving and highly social toothed whales that occur frequently along the shelf break near Cape Hatteras, North Carolina, USA, during spring, summer, and fall (Best et al. 2012; Roberts et al. 2016). We have been conducting a long-term study of these pilot whales using a variety of research approaches, including photo-identification, satellite-linked telemetry, and the use of short-term archival tags. There is limited information on the hearing ability of short-finned pilot whales, with data only from stranded and captive animals (Schlundt et al. 2011; Greenhow et al. 2014). These studies report a hearing range between 10 and 120 kHz, with greatest sensitivity around 40 kHz, and peak sensitivity at lower frequencies than some other odontocetes (Schlundt et al. 2011; Greenhow et al. 2014).

The pilot whales we study off Cape Hatteras exhibit deep foraging dives classified by the presence of vocal behavior (click trains and buzzes) similar to that seen in other pilot whale populations (Soto et al. 2008; Jensen et al. 2011) and analogous to that used during foraging by other deep-diving odontocetes (e.g., beaked and sperm whales; Johnson et al. 2004; Miller et al. 2004). Temporal clustering, or bouts, of dives has been suggested for both short-finned and long-finned (*Globicephala melas*) pilot whales, with periods of shallow, nonforaging dives followed by bouts of deep diving (Soto et al. 2008; Sivle et al. 2012; Visser et al. 2014). Cape Hatteras is a foraging area for short-finned pilot whales and also an important ground for both commercial and recreational fisheries, including pelagic longlines, midwater trawls, and charter troll vessels, all of which use echo sounders. Disruption of foraging behavior, or area avoidance, as a consequence of ensonification by powerful source-level sounds from echo sounders could affect foraging efficiency and have fitness consequences at both individual and population levels.

No comparable studies of effects of echo sounders exist, but previous studies of the effects of military tactical sonars on pilot whales failed to document overt avoidance responses (BRS 2008; Miller et al. 2012), such as those seen in beaked whales (DeRuiter et al. 2013; Stimpert et al. 2014; Tyack et al. 2011), but did show changes in heading variance, indicative of avoidance in long-finned pilot whales (Miller et al. 2012). These less overt responses to sound exposure may also have important consequences if they occur as a result of chronic or isolated exposure (Tyack 2008). In the absence of a dramatic flight response, other measurable changes in behavior, such as changing behavioral state or kinematic changes in pitch or heading that could indicate a subtle avoidance or vigilance response, may be difficult to detect by visual observation.

In the present study we used an experimental approach to assess potential changes in short-finned pilot whale behavior during exposure to a scientific EK60 echo sounder. We first used hidden Markov models (HMMs) to determine whether exposure changed foraging behavior. We then assessed changes in heading variance of each exposed individual over an entire tag record to measure avoidance or changes in vigilance during the exposure period. We used data from noninvasive digital acoustic recording tags (DTAGs), attached via suction cups (Johnson and Tyack 2003), to collect data while whales were exposed to signals of the echo sounder. We employed a randomized treatment and control paradigm following a baseline observation period. Exposure was designed to mimic actual echo sounder deployment, and the diving and acoustic behavior of the whales was recorded during all phases of the experiment.

Methods

Data collection

Our study was conducted off Cape Hatteras, North Carolina, USA, over 8 days in May and June 2011. Data collection was conducted from a variety of small rigid-hull inflatable vessels (all less than 10 m), during daylight hours and in variable sea states (Beaufort 0–4). In total 11 pilot whales were equipped with DTAGs (Johnson and Tyack, 2003) using a carbon fiber pole to attach the tag to the dorsal surface or fin of the whale. Ten individuals were tagged with version 2 DTAGs and one with a version 3 DTAG (Table 1). The DTAG is a multisensor archival tag, attached via suction cups that records the following: audio with 16-bit resolution at a sampling rate of 96–192 kHz; pressure at 50 Hz; and orientation of the whale from triaxial accelerometers and magnetometers at 50 Hz (Johnson and Tyack 2003). The tags were programmed to release after a predetermined period, if they had not already detached from the animal, and were located using a VHF radio transmitter embedded in the tag.

Whenever possible, we selected a well-marked individual in a discrete group as the animal for tagging. Prior to tagging, photographs of the dorsal fins of all individuals within the group were taken for photo-identification purposes. We avoided groups containing neonates in line with conditions of our permit. After tagging, we maintained nonsystematic visual observations of the tagged animal and its group. These visual observations continued for the entire duration of tag attachment, unless the animal was lost from view. We obtained biopsy samples from five of the tagged whales (typically immediately following release of the DTAG) and determined sex (see Rosel 2003 for methods) for all these individuals (Table 1). A quantitative analysis of the effects of biopsy sampling showed no evidence of disruption of foraging behavior and only low intensity responses (Crain et al. 2014).

Six of the 11 individuals were exposed to signals from the Simrad EK60 scientific echo sounder (Table 1) using a randomized treatment and control paradigm, following a baseline observation period of at least 1 h. Four of the 11 animals were tagged, but not exposed to any form of playback or vessel approach. The single remaining animal (gm11_158a) was tagged, but was immediately lost from view. Data from this animal are not considered further in the analysis. Similarly, one of the exposed animals (gm11_150a) is not considered further due to incomplete data records on the tag. In total, five individuals were exposed to signals from the echo sounder, and four individuals were control animals.

The Simrad EK60 is a scientific echo sounder with an ES38DD split-beam transducer incorporating 88 Tonpilz elements distributed over four quadrants. It has a resonant frequency at 38 kHz and a 7-degree circular beam width. The echo sounder was located on a 12.5 m playback vessel. When active, the echo sounder used a 2 kW transmit power (giving a source level of 224 dB re 1 μPa @ 1 m) with a 2048 μs pulse width. The transducer was deployed alongside the vessel using an arm attached to the ship with the transducers deployed 1 m below the sea surface. The system was calibrated (both the output source level and the received signals) once at the end of the sampling period using a 35.1 mm tungsten carbide calibration sphere and the calibration procedure described by Foote et al. (1987).

All but one of the five exposure animals experienced all four experimental conditions (Pre, Control, Active, Post; Table 1). The first experimental condition (Pre) was a baseline period of at least 1 h following tagging, but prior to the Control or exposure (i.e., Active) condition. After this baseline period, either the Control or Active condition was conducted. The Control condition consisted of the boat driving in a configuration representative of an active echo sounding survey, with the transducer in the water, the system powered but without emitting signals. In the Active condition, the boat drove in the same pattern, with the transducer in the water and with the echo sounder powered up and emitting signals. The order of Control or Active conditions were random-

Table 1. Summary of tagging information.

Date	Tag ID	Sex	Total time (h:min:s)	Experimental condition sequence	Experimental condition time (h:min:s)	Total dives	Highest RL (dB re 1 μPa, (range, no. of samples))
27 May 2011	147a	F	04:24:13	Pre	01:39:40	7	
				Control	01:03:00	4	
				Active	01:00:00	3	119 (89–119, 39)
				Post	00:41:23	4	
28 May 2011	148a	M	03:01:49	Pre	01:23:25	5	
				Active	01:00:00	2	117 (97–117, 24)
				Control	00:38:24	0	
				Post	00:00:00	0	
29 May 2011	149b	M	04:17:49	Pre	04:17:49	7	
	149c	U	03:01:17	Pre	01:00:54	1	
				Active	01:00:00	6	119 (88–119, 590)
				Control	00:59:00	3	
				Post	00:01:23	0	
30 May 2011	150a*	U					
30 May 2011	150b	U	02:38:51	Pre	02:38:51	8	
4 June 2011	155a	U	04:27:49	Pre	01:02:02	0	
				Control	01:00:00	1	
				Active	01:00:00	1	123 (91–123, 205)
				Post	01:25:47	2	
5 June 2011	156a	U	02:56:04	Pre	02:56:04	3	
7 June 2011	158a*,†	U					
7 June 2011	158b	F	04:23:43	Pre	01:16:19	3	
				Active	00:59:43	0	125 (89–125, 155)
				Control	01:00:05	2	
				Post	01:07:36	4	
14 June 2011	165a	M	03:08:12	Pre	03:08:12	9	

Note: Tag ID is based on the Julian day, with the letter representing the sequential order in which the animal was tagged (a = first animal tagged that day, b = second). Sex was obtained from biopsy data: M = male, F = female, U = unknown (animal not biopsied). Total dives indicate the number of dives used per individual, per experimental condition, in the analysis. Highest RL is the highest received level of the echo sounder calculated from the tag during the exposure condition for that individual.

*Animals not considered in the analysis.

†Animal tagged with a version 3 DTAG.

ized, but always occurred after the Pre condition, and the observers on the follow boat were blind to the condition. Once both Control and Active conditions had been completed on a focal whale, the animal was observed (Post condition) until the time of tag release. One animal did not experience a Post condition, because the tag detached prematurely.

Data processing

Data were downloaded from the tags and pressure recordings were converted to depths, using calibration information from each tag (Johnson and Tyack 2003). Calibration of the orientation offset from tag position was also performed, and all movement data were down-sampled to 5 Hz using custom written scripts in Matlab version R2014a. Dives were defined as any submergence to a depth of 20 m or deeper (Soto et al. 2008). Any interval of data during which the whale was at a depth of 20 m or less was considered time spent at the surface. For all dives, four dive and movement parameters were calculated: Dive Duration, time between start of dive descent and end of dive ascent per dive (minutes); Heading Variance, average change in heading over the entire dive; Maximum Depth, maximum depth reached during dive (metres); Number of buzzes, the number of terminal echolocation click trains recorded during the dive. Each parameter was calculated over the period of one dive (from time at surface when dive profile began to time when animal returned to the surface). If a value could not be determined, for example if the tag detached during a dive, then a mean value from all baseline and pre-exposure dives across all animals was used. This was necessary for only four of the 75 dives (5.3%). All acoustic audits of the DTAG sound files, to determine the start time and duration of buzzes, were completed by a single experienced analyst.

For the five animals that were exposed to the experimental stimulus, the mean value for depth (metres), the variance in pitch (radians), and the median variance in circular heading (radians) were calculated for 5 min time bins across the entire tag record. Experimental condition sequence and times were taken from the field notes and synchronized with the individual dive profiles. Each 5 min time bin was allocated an experimental condition (0 = Pre, 1 = Control, 2 = Active, 3 = Post). Two binary variables were created. The first was for exposure, with Pre, Control and Post being equal to 0 and active equal to 1. The second was for boat presence with Pre and Post being equal to 0 and Active and Control being equal to 1.

Start times and durations of each echo sounder pulse were noted. Each pulse was considered one sample, and samples varied across tags (five tags; samples extracted = 451, 163, 1550, 921, 1039). Variation was due to changes in background noise from splashes at the surface or animal vocalizations, which masked the signal. Received levels were calculated at the tagged animals as RMS (root-mean-squared) levels in dB re 1 μPa, using custom written Matlab scripts. All received levels were calculated within a 1/3-octave band, (using the ANSI standard that contained the EK60 center frequency of 38 kHz), spanning 35 467–44 686 kHz and were averaged over a 200 ms sliding window. The reported level is the highest level measured during any single 200 ms window that included part of the echo ping. The script also included an algorithm to exclude energy from short, intense sounds such as whale echolocation clicks, as described in Tyack et al. (2011). Signal-to-noise ratio was determined using RMS noise levels calculated in the same way as the received levels. Noise levels were determined from 1 s sound clips that preceded each echo sounder pulse.

Where the signal-to-noise ratio was less than a critical threshold of 6 dB re 1 μPa, received levels were not calculated, because the signal was buried in the noise.

Statistical analysis

We used a multivariate hidden Markov model (HMM) as a framework for the first analysis. The model was a first-order Markov model and assumed that the distribution of the current state is determined only by the previous state (Altman 2007; Rabiner 1989; Zucchini and MacDonald 2009). The four dive and movement variables calculated from each of the 75 dives were specified as the observable series and were each assumed a distribution with state-dependent mean and variance parameters. Each dive was assigned to one of the nine individual whales in the sequential order that it occurred. Dive duration and maximum depth were assumed Gamma distributions, as they were continuous positive values. The number of buzzes was assumed a Poisson distribution to allow these data to be treated as integer counts. Heading variance was assumed a Beta distribution, as it consists of values between 0 and 1. The model was constructed based on the assumption that there were two underlying nonobservable behavioral states and that the observations were conditionally independent given the states (i.e., contemporaneous conditional independence was assumed; Zucchini and MacDonald 2009). We assumed a transition matrix where all state transitions were possible so that any hidden Markov state could be reached from any other hidden Markov state. The model was run initially using all dives from all experimental conditions. The model was then run again including exposure presence–absence as a covariate on heading variance. This was to quantify differences in dive state allocation during echo sounder exposure. We did not consider individual random effects in the models and assumed all whales shared common distribution parameters for all variables (Langrock et al. 2012) based on the assumption that all diving whales were utilizing food patches.

We fitted the models via numerical maximum likelihood estimation using the nlm optimizer in R (R Core Team 2014; see Zucchini and MacDonald 2009 for details of implementation). To improve confidence that the global maximum was found during the maximization process, 1000 initial values were specified to investigate the likelihood surface prior to maximization. This enabled only those values with the highest likelihoods to be passed to the nlm optimizer for maximization. Five hundred simulation runs of the model were completed to check for numerical stability in robustness against different initial values in the log likelihood. We applied the Viterbi algorithm (Forney 1973) to find the most likely sequence of hidden states for each animal given the likelihood of the four observed variables under the estimated state-dependent distributions and the transition probabilities between states.

The median variance in heading every 5 min, across all five exposure tags, was modelled using a generalized additive model (GAM) with a Gaussian error distribution and a log link function. The log link prevented the model returning negative estimates for heading variance. Two separate models were constructed with a choice of either "presence of exposure" or "boat presence" fitted as a binary factor covariate. Additionally, the covariates pitch and depth were fitted as continuous terms in each of the two models. Initially, the continuous covariates were fitted as smooth terms using B-splines, with their flexibility (selection of number and location of knots) determined using the Spatially Adaptive Local Smoothing Algorithm (SALSA; Walker et al. 2011). Fivefold cross-validation (CV) was used to select covariates for inclusion and, for the continuous covariates, whether they were best suited as linear or smooth terms. Interaction terms between depth and exposure and between pitch and exposure were also tried in both models. Variables were checked for colinearity using generalized variance inflation factors (Fox 2008), which indicated no issues with colinearity in the data set.

The data are repeated measures on individual whales, and so the temporal correlation present in model residuals was incorporated using a population-average approach: generalized estimating equations (GEEs; Liang and Zeger 1986; Prentice and Zhao 1991). GEEs require a blocking structure, which denotes blocks of data within which residuals were permitted to be correlated and between which the residuals are independent (e.g., see Pirotta et al. 2011). The blocking structure here represents 19 blocks, one for each unique combination of individual and experimental condition. Plots of the autocorrelation between residuals and within these blocks showed the blocking structure to be suitable. An independent working correlation matrix was specified, and robust standard errors were used for model inference.

The GAM–GEE analysis was carried out using R software (R Core Team 2014). Specifically, the MRSea (Scott-Hayward et al. 2014) and geepack (Yan and Fine 2004; Højsgaard et al. 2005) packages were used for model fitting.

Predictions were made for the best model for each selected continuous covariate at both levels (for exposure model sonar; sonar on or sonar off). For assessment of the relationship of a given covariate with the response, the other covariates were fixed at their mean values (depth = 71.63 m, pitch = 0.08 radians). A parametric bootstrap from the GEE model was used to calculate 95 percentile confidence intervals for each set of predictions.

Results

The tag deployments produced 32 h, 19 min, and 47 s of recording time from the nine individual whales (Table 1). Data were not distributed evenly across all four experimental conditions. Twenty hours were allocated to the Pre condition; 4 h, 40 min to the Control condition; 5 h to the Active condition, and 3 h, 16 min to the Post condition (Table 1). Visual observations were completed for all individuals considered in the analysis for the duration of the tagging period.

Received levels were calculated for all five tags. The number of samples processed per tag above the critical signal-to-noise ratio of 6dB was variable (39, 24, 590, 205, and 155; Table 1). The maximum received level across all tags ranged from 117 to 125 dB re 1 μPa (Table 1).

The HMM, including the covariate of exposure, produced a marginally better Akaike information criterion (AIC) score (714.50) than the model excluding exposure (717.59). Rerunning of both models showed stable AIC and maximum log-likelihood values and consistent state allocation of all dives. Dive allocation to state between the two models differed only by a single dive. Therefore, all but one dive had the same probability of state with and without exposure to the echo sounder. The dive that was allocated differently was a control dive (dive number 8; Fig. 1). This dive was to 188 m, lasted for 9 min, 53 s, but contained no buzzes.

The state summaries of the observed variables are shown in Table 2. Forty-eight of the dives were allocated to state 1 and 27 to state 2. The two states appear to represent the following: (1) deep dives with longer durations, the presence of buzzes, and greater variation in heading; and (2) shallow dives of short duration, no buzzes, and less variance in heading. However, analysis of each dive by variable (Fig. 1) and plots of the dive profiles (Fig. 2) show a high degree of variation within each state. Dive duration was the only variable that showed no overlap between states (Table 1). All state 1 dives had durations longer than 7 min (mean 13.2 min), but depths ranged from 30 to 805 m, and there was a range of 0 to 51 buzz events. Heading variance varied over almost the entire possible range between zero and one for state 1 dives (Table 2; Figs. 1, 2). State 2 dives had no foraging buzzes and were, on average, less than 4 min long, with maximum depths, on average, of less than 40 m (Table 2; Figs. 1, 2). Heading variance of state 2 dives covered a smaller range than state 1 dives, but was still highly variable (Table 2; Fig. 1).

Fig. 1. State allocation per dive for each of the four observed variables. Circles represents state 1, triangles represent state 2.

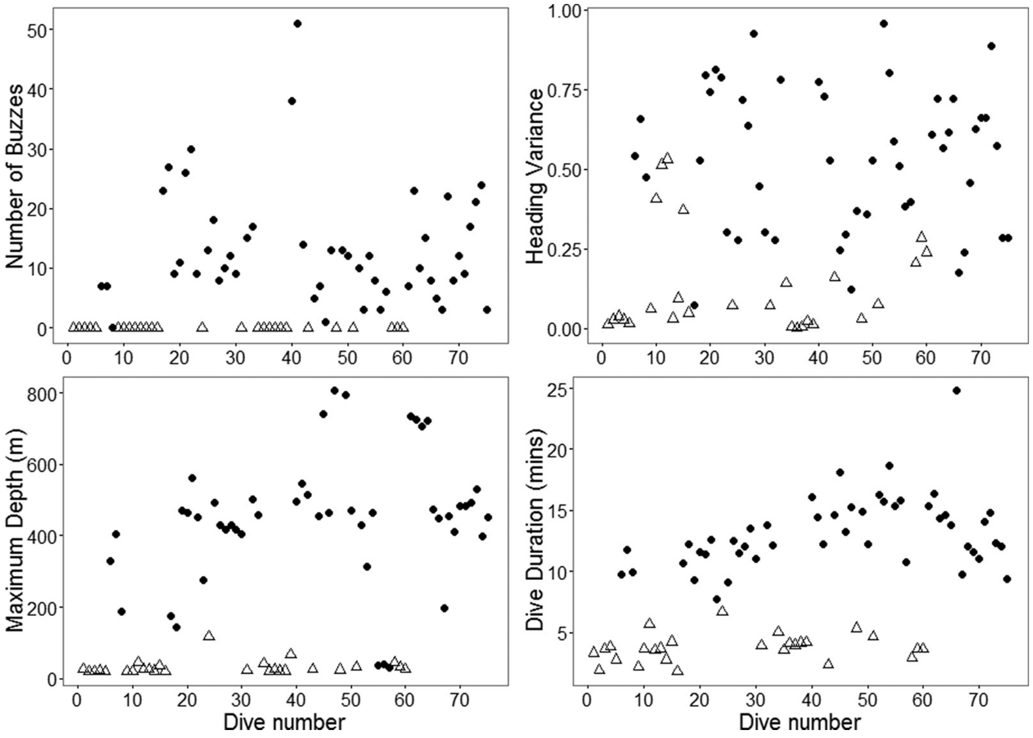


Table 2. State summaries of observed variables for each state.

State	Variable	Mean	Median	Min.	Max.
1	Dive duration (min)	13.2	12.4	7.8	24.8
	Max. depth (m)	444.5	457	30	805
	Heading variance	0.537	0.554	0.075	0.958
	No. of buzzes	13.2	10.5	0	51
2	Dive duration (mins)	3.7	3.7	1.8	6.7
	Max. depth (m)	31.9	26	20	117
	Heading variance	0.130	0.063	0.003	0.532
	No. of buzzes	0	0	0	0

Both states contained dives from all four experimental conditions: Pre, Control, Active, and Post. The Control ($n = 7$) and Active ($n = 12$) dives appeared similar in profile to many of the Pre and Post dives within each state (Fig. 2). The distribution of dives between states was not equal, suggesting that both states were not equally likely. Plots of the entire tag records for each animal showed dives of state 1 clustered together in what appear to be foraging bouts, interspersed with clusters of state 2 dives of unknown function (Fig. 3).

During the Active experimental condition, one of the exposed animals did not exhibit any diving state; two undertook state 2 shallow dives, one a deep state 1 dive, and the other a state 2 followed by a state 1 dive. No animals performed multiple state 1 deep dives during the Active condition, in contrast with all the other conditions where multiple deep state 1 dives were seen (Fig. 3). Three of the exposed animals performed the first example of a dive within a given state during the Active condition (Fig. 3). The four baseline animals exhibited primarily state 1 dives, with only seven state 2 dives recorded across all four baseline animals (Fig. 3).

State persistence and state switching was observed within and across both states (Table 3). The probability of persisting within one state was higher for both states compared with state switching. (Table 3). Mapping the most likely (Viterbi) state sequences onto the dive profiles supports the existence of bouts (i.e., state persistence), but also shows examples of animals readily switching from one state to another (Fig. 3).

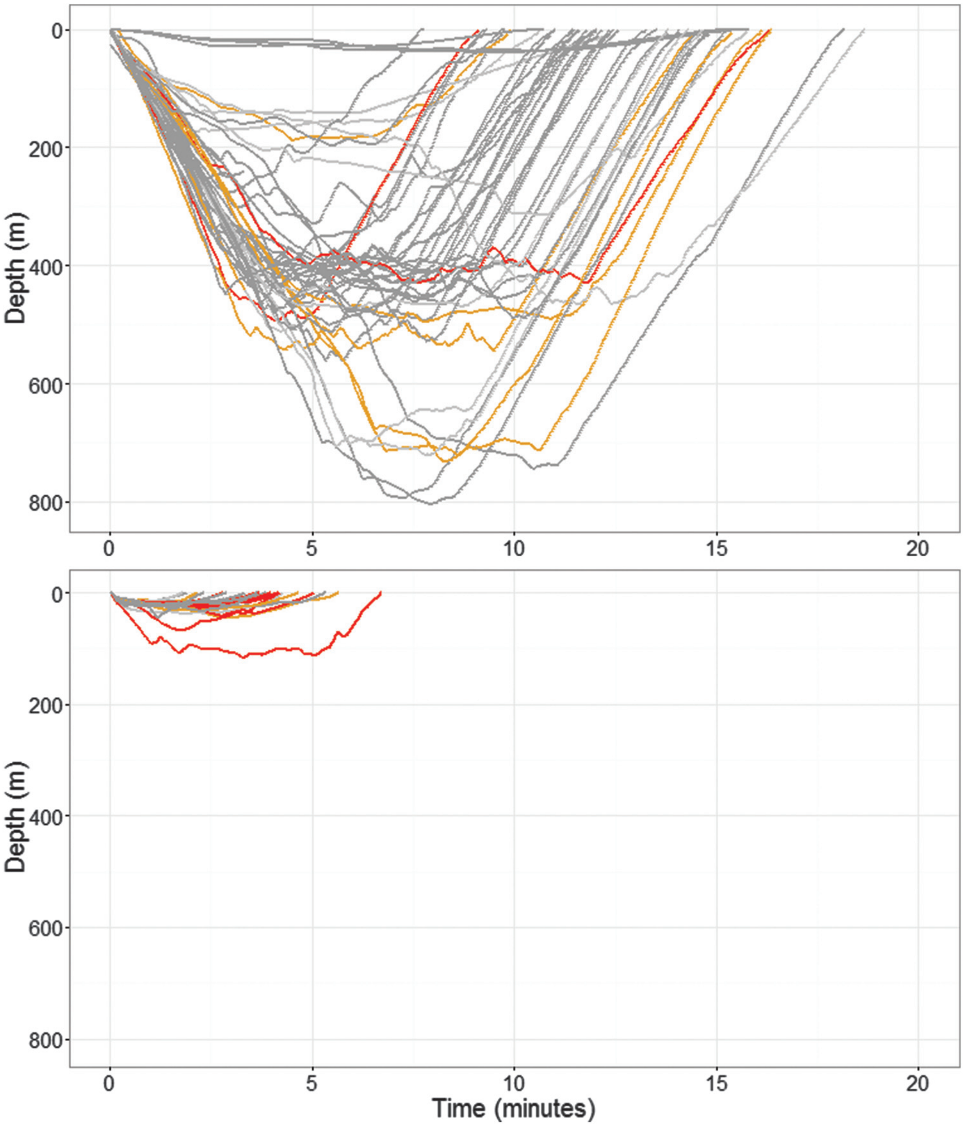
The GEE model containing exposure as a binary factor had a marginally better fivefold CV score (0.02218) than the model containing boat presence as a binary factor (0.02278). Even though we had an unbalanced design, with more data in the nonexposed than exposed condition, the assumption of constant error variance holds for this model. This exposure model contained depth as a linear variable (df = 1) and pitch as a smooth term (df = 3). Positive relationships were seen between heading variance and all covariates (Table 4). The ANOVA results (sequential Wald test) for pitch and depth show a highly significant relationship ($p < 0.0001$). The parameter estimates for depth and pitch were positive, so as depth and pitch increased so did the heading variance (Fig. 4). Depth increased linearly, but the relationship for pitch showed a sharp increase in heading variance for pitch < 0.1 and a shallower increase thereafter (Fig. 4). Exposure also showed a positive relationship, suggesting that heading variance increased during periods of exposure to the echo sounder ($p = 0.069$; Table 4; Fig. 5). While the exposure covariate is not significant at the 5% level, it is only marginally not so, and the CV score indicated a better fit with exposure retained.

Discussion

The goal of our study was to test for behavioral responses of short-finned pilot whales during exposure to a scientific echo sounder. We looked first for changes in diving state that could indicate a change in foraging behavior and then for changes in heading variance that could suggest a general avoidance response. We did not observe an overt response to the echo sounder or a change to foraging behavior of tagged whales, but the whales increased heading variance when exposed to signals from the echo sounder.

The HMM identified two states across multiple whales and all four experimental conditions. Our predictions of state are based on the multivariate distributions of four observed variables. Three of these variables, dive duration, maximum depth, and number of

Fig. 2. Dive profiles, for all dives from all individuals, per state. Top panel: state 1, bottom panel: state 2. Colours represent experimental condition. Dark grey dives are during Pre condition; gold dives are during Control condition; red dives are during Active condition; and light grey dives are during Post condition. Note the presence of dives from the Control (gold lines) and Active condition (red lines) in both states.



buzzes, have been considered in previous studies as good descriptors of pilot whale diving behavior (Soto et al. 2008; Jensen et al. 2011; Alves et al. 2013). Most prior studies have relied on depth to classify shallow nonforaging and deep foraging behavior in pilot whales (e.g., Alves et al. 2013; Baird et al. 2002; Soto et al. 2008). Variability in heading was included to look for differences in linearity of movement within dives that might indicate directed movement. The HMM allowed us to classify diving behavior more objectively using several relevant variables, while accounting for the autocorrelation in the time series data, but a considerable amount of variation remained among dives of the same state, particularly within state 1.

All exposed individuals and two baseline animals showed diving behavior consistent with both state 1 and state 2 dives. The remaining two baseline animals only showed dives consistent with state 1.

During the Active exposure condition, not all whales were engaged in the same behavior. Dive profiles show that one whale remained in surface waters (<20 m) and did not engage in any form of diving. Two whales exhibited shallow state 2 dives interspaced with surface time. One whale performed a single state 1 foraging dive and then remained in surface waters, and the last whale exhibited a single state 2 shallow dive and a single state 1 deep dive interspaced with surface time. Such combinations of behavior were not only seen during the Active exposure condition. Periods of surface time, state 2 shallow dives interspaced with surface time, single deep state 1 dives, and state 2 shallow dives followed by state 1 deep dives were all seen in the baseline animals or during the Pre condition.

Several previous studies have described the existence of two diving states, deep foraging and shallow nonforaging, in pilot whales (Soto et al. 2008; Jensen et al. 2011), but our recent study of short-finned pilot whale diving behavior off Cape Hatteras suggests that diving behavior is more complex than a simple dichotomy of deep foraging and shallow nonforaging diving states. Furthermore, it appears that individual whales are able to adapt their diving strategy on a dive by dive basis (N. Quick, S. Isojunno, D. Sadykova, M. Bowers, D. Nowacek, and A. Read, unpublished data). This behavioral plasticity enables pilot whales to successfully exploit patches of mobile aquatic prey, but also leads to large natural variation in diving behavior. Our data show that while some dives are shallow (<50 m) and some are deep (>600 m), many

Fig. 3. Dive profile data with the probability of state mapped onto the dives. Blue lines indicate highest probability of being in state 1, pink lines indicate highest probability of being in state 2. Grey lines indicate data classified as surface and not used in the model, and black asterisks indicate individual foraging buzzes. Exposed animals are shown in bottom five panels; red blocks indicate Active condition, gold blocks indicate Control condition. (Note different *x* axis range). [Colour online.]

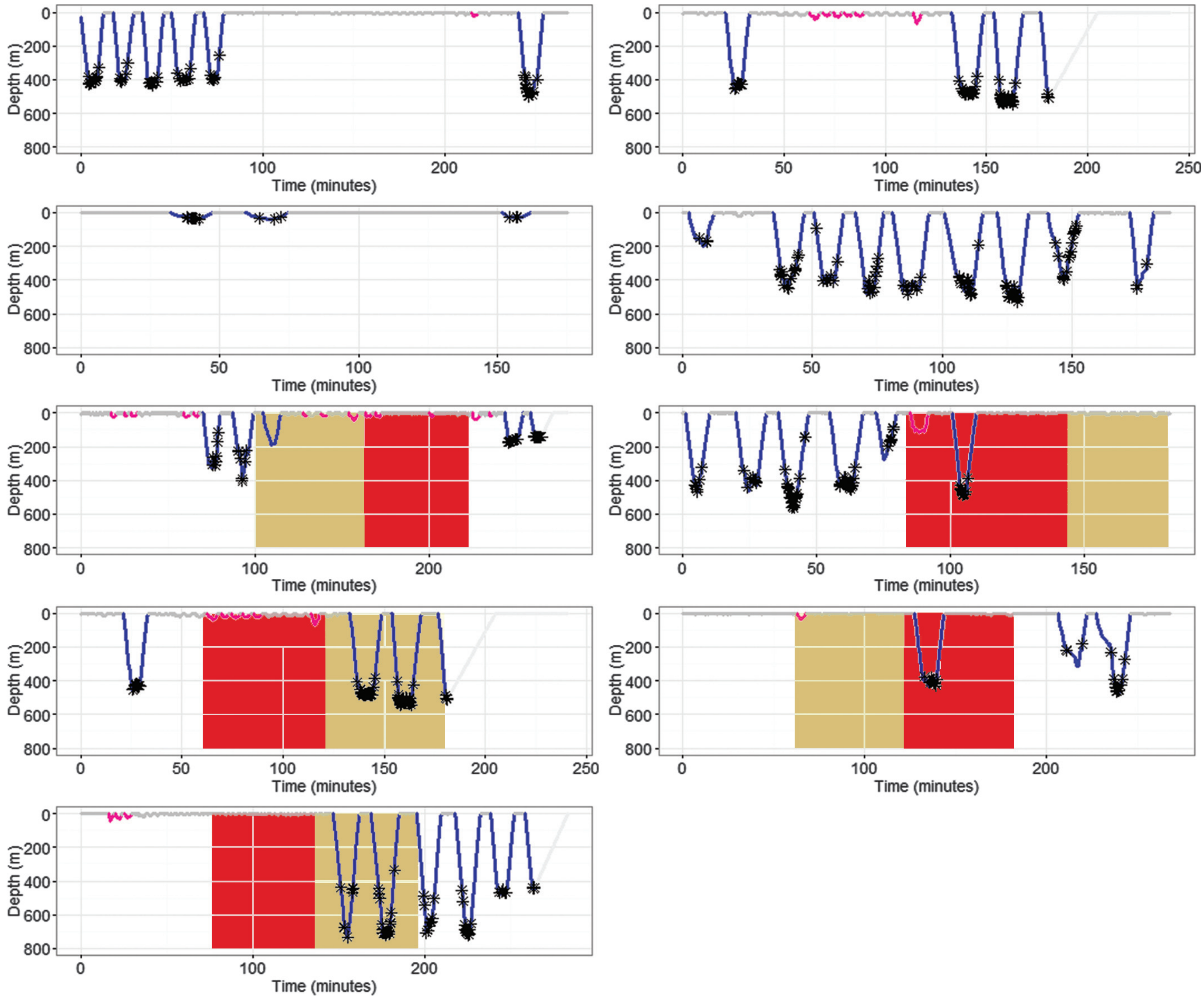


Table 3. Transition probabilities for both states and number of dives within each state.

	State 1	State 2	No. of dives
State 1	0.67	0.33	48
State 2	0.13	0.87	27

Table 4. Model outputs from the best model.

Variable	Estimate	Robust SE	*p*
Intercept	−3.9685	0.40819	
Exposure (as factor)	0.22101	0.09166	0.069
Pitch (as smooth)	2.56755	0.46698	<0.0001
	2.94062	0.40499	
	3.41632	0.45511	
Depth	0.00167	0.00017	<0.0001

Note: Parameter estimates and standard errors (SE) are on the scale of the link function (log). The test *p* values are from a sequential Wald test (GEE-based ANOVA; H_0: covariate coefficient(s) = 0); *p* values were not used in model selection.

occur at intermediate depths, and the number of buzzes per dive is highly variable. The aim of our HMM analysis was to assess changes to foraging behavior. We interpret state 1 as a foraging state and state 2 as a nonforaging state, but the observed variation in state 1 suggests it may also contain examples of failed and (or) nonforaging dives. We have no means to assess success during prey capture, and the variation seen in state 1 dives could be due to a range of factors, including foraging efficiency, the environment, and social behavior. Short-finned pilot whales off Cape Hatteras exploit a wide range of food types, with a predominance of oceanic deepwater squid (Mintzer et al. 2008). Their diving ability enables them to exploit a range of habitats, suggesting that prey selection and abundance could be driving the variation we observed within state 1. The local environment may also be driving the variation. Our experiment took place in an area with steep bathymetric gradients (Savidge and Bane 2001), and perhaps the foraging depth of some whales was driven by bottom topography.

Fig. 4. The predicted heading variance and 95 percentile confidence intervals for depth (top panel) and pitch (bottom panel), with the echo sounder on (blue) and off (black). The mean depth = 71.63 m for the top plot; and mean pitch = 0.08 radians for the bottom. [Colour online.]

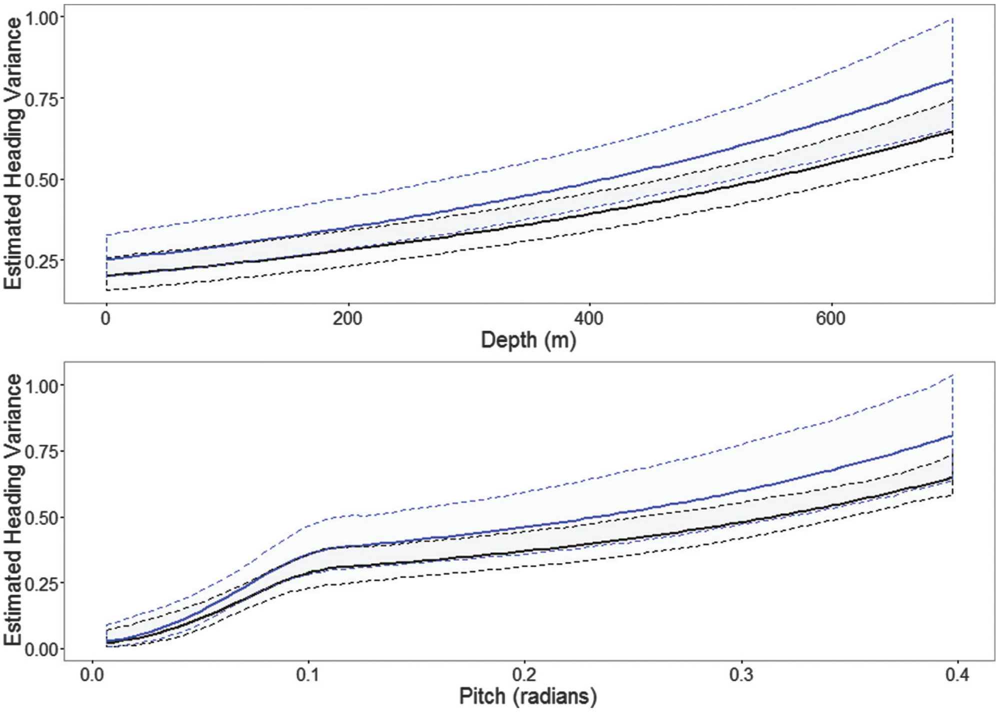
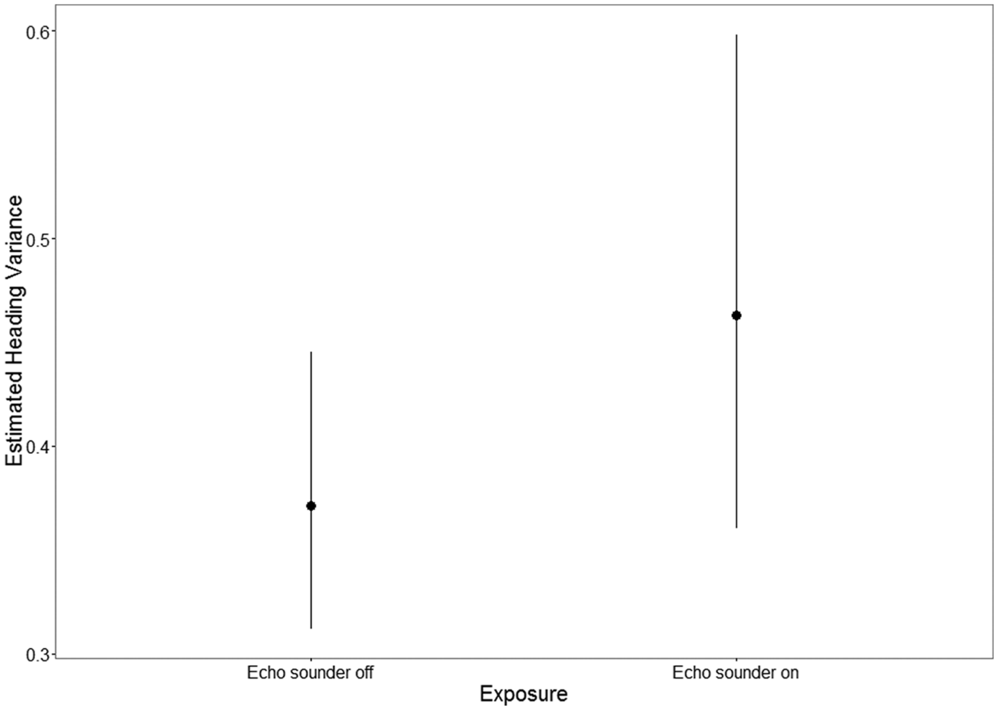


Fig. 5. The predicted heading variance and 95 percentile confidence intervals with the echo sounder on and off (mean depth = 71.63 m, mean pitch = 0.08 radians).



Some of this variation may also be explained by social behavior. Pilot whales are highly social animals, which live in long-term stable groups (Amos et al. 1993) and perform highly synchronous behavior (Senigaglia and Whitehead 2012). Long-finned pilot whales from the same social group coordinate their foraging behavior (Visser et al. 2014), and the need for social cohesion may dictate diving behavior.

Our HMM analysis imposed a number of restrictive assumptions, including that the parameter set was common to all individuals. This assumes that all tagged individuals, regardless of sex, age, body condition, and social group, all act in the same way. Studies of the effects of sonar exposure on blue whales (*Balaenoptera musculus*) have shown that their responses can vary depending, among other things, on behavioral state (Goldbogen et al. 2013). All of our pilot whales were at the surface at the onset of the Active condition, but not all had been in an identical behavioral state prior to exposure. We also do not know the sex and age class of all our exposed animals, so we could not include these covariates to explore heterogeneity across individuals. We could have assumed that each individual had its own set of parameters or considered a number of possible outcomes of discrete random effects to account for potential heterogeneity across individuals based on hierarchical modelling (partial pooling) (Langrock et al. 2012), but we assumed that all foraging individuals would dive to forage on a deep foraging patch, and increasing the number of states or including random effects was not possible because of the size of our data set.

Time activity budgets for short-finned pilot whales off Cape Hatteras (N. Quick, S. Isojunno, D. Sadykova, M. Bowers, D. Nowacek, and A. Read, unpublished data) suggests that individuals engage in bouts of behavior and rarely behave in a sequentially random fashion (Karniski et al. 2015). This is further supported by the higher probability of state persistence than state transitions observed in this study. Our aim was to assess changes in diving behavior that may indicate effects on foraging, but we only recorded two deep state 1 dives during the Active exposure condition. We looked at effect of exposure as a covariate on heading variance to test for any potential avoidance response through increases in the linearity of travel. Including exposure produced a difference in state allocation of one Control condition dive to state 1 from state 2. This dive fell between the two states, as it was deeper than all other state 2 dives but contained no buzzes. In general, variation in heading was greater during the deeper state 1 dives, but including exposure as a covariate on heading variance showed no evidence of increased linearity of heading during dives in the Active exposure condition compared with any of the other experimental conditions.

The two deep foraging dives and 10 shallow dives that occurred during exposure clustered with similar dives from the baseline animals and Pre condition, even when received level was included as a covariate. This suggests that foraging behavior during the two deep state 1 dives was not different to that during Pre condition or baseline and that, for these two examples, exposure to the echo sounder did not change the foraging behavior of these short-finned pilot whales.

The results from our GAM–GEE analysis showed that while not highly significant ($p = 0.069$), there was a consistent increase in heading variance during exposure to the echo sounder over all values of depth and pitch. Interactions between depth and exposure and between pitch and exposure neither improved the CV score nor had significant p values. This suggests that regardless of behavioral state, the whales changed their heading more frequently while the echo sounder was active. Changes in heading variance, indicative of avoidance, have been seen in studies of the effects of tactical sonars on cetaceans (Miller et al. 2014; Tyack et al. 2011) and, specifically, in long-finned pilot whales (Miller et al. 2012). Other cetacean species have been documented to show changes in movement and heading in response to boats, including bottlenose dolphins (*Tursiops truncatus*; Nowacek et al. 2001) and killer whales (*Orcinus orca*; Williams et al. 2002). We discounted the model that included boat presence, rather than exposure, based on CV scores, indicating that echo sounder status was a better predictor of response than the presence of the boat. The echo sounder was within audible range for the pilot whales (Schlundt et al. 2011; Greenhow et al. 2014), and the received levels ranged from 117 to 125 dB re 1 μPa.

A previous study on long-finned pilot whales predicted a higher probability of response to received levels of tactical sonars greater than 165 dB re 1 μPa (Antunes et al. 2014) and suggested that pilot whales may have higher avoidance response thresholds than some other cetaceans. Due to the characteristics of echo sounding devices (small beam angles and downward-directed beams; Simmonds and MacLennan 2005) and results from previous studies that have assessed the effects of military sonar on pilot whales, (BRS 2008; Miller et al. 2012), we did not predict that the pilot whales we studied would flee from the sound source. However, studies have documented less overt reactions, such as changes in movement and vocal behavior (Alves et al. 2014; Miller et al. 2012; Rendell and Gordon 1999), in response to some sonars. In fact, our GEE analysis suggested an overall increase in heading variance during exposure to the EK60 signals. This change in heading was not a directed avoidance response away from the echo sounder and was likely a vigilance response, with animals maintaining awareness of the location of the echo sounder through increased changes in heading variance. Vigilance can be defined as individual alertness of the environment for substantial events that may impact survival and is seen in many group-living animals (e.g., Lima 1995; Lima and Dill 1990). Scanning the environment for threats constitutes vigilance behavior within an antipredator strategy and aids predator detection (Bednekoff and Lima 1998). Although perhaps unlikely, pilot whales may consider the echo sounder a predation threat and respond to its signals. Killer whale echolocation signals overlap in frequency (Barrett-Lennard et al. 1996) with that of the EK60, and despite clear differences, killer whale signals and the EK60 signals do show some level of acoustic similarity. Maintaining an awareness of the echo sounder source location may have allowed the whales to maintain social cohesion within their social groups and (or) to enable flight behavior if signals from the echo sounder passed a critical threshold. Our surface visual observations of their behavior did not indicate any dramatic response, such as fast travel away from the source. We also did not visually record any unusual behaviors or changes in heading, suggesting the changes we observed from the tag data were subtle. Studies with captive dolphins have shown that individuals are able to sustain high levels of auditory vigilance for extended periods of time (Ridgway et al. 2006) and during states of parturition (Hill et al. 2008). This suggests that vigilance behavior in wild cetaceans may be commonplace when required by behavioral or social drivers.

A number of studies have used the EK60 scientific echo sounder to measure the movements and behavior of marine mammals underwater and make prey field measurements (e.g., Benoit-Bird and Au 2003*b*; Benoit-Bird et al. 2009; Doksæter et al. 2009; Williamson et al. 2016). These studies acknowledge a lack of empirical data on potential behavioral responses of marine mammals and accept the possibility that marine mammals may be attracted or repulsed by the echo sounder.

We did not observe cessation of biologically important behavior such as feeding during our study, and we did not try to directly measure the movements and behavior of the pilot whales themselves. The subtly of the responses may preclude detection by the sonar system itself, but the possibility of a behavioral response should be considered in future studies using this system for behavioral research on marine mammals.

The assumption of independent errors does not apply to our data set because we collected multiple data points from each whale and conducted multiple treatments per individual. We accounted for this autocorrelation by using GEEs (Liang and Zeger 1986) and blocking our data according to the structure of the treatments. We also randomly allocated the treatment order for the exposed animals. Due to the small number of exposed animals, we cannot prove that the two treatments, Control and Active, were independent of each other, and our sample size is too small to statistically test the animals that received the same treatment order separately. However, we did attempt to retain the structure within our data, through blocking by the unique combination of individual and treatment. It is possible, however, that the reactions of the animals during the second treatment were influenced by the first treatment. Further experimentation would be needed to answer this question completely. No visual observations noted any adverse reaction by the pilot whales during the experiment, so the responses we documented from the tags were too subtle to be observed by surface visual monitoring alone. This is an important consideration for studies designed to look for subtle responses.

Our study is the first attempt to quantify the behavioral response of deep-diving odontocetes to a scientific echo sounder. We showed that short-finned pilot whales do respond to signals from a scientific echo sounder, but this response is subtle, and perhaps akin to an increase in vigilance, and would be impossible to discern from visual observations. The increase in heading variance during exposure was not overt enough for animals to stop foraging or to flee the area. However, the sample size of exposed dives was small, and we do not have complete contextual information for all animals. Contextual variables can strongly affect the response of marine mammals to sound stimuli (Ellison et al. 2012), but our limited sample size precluded their inclusion in the present analysis. Interpretation of these results to infer biological significance is challenging, and we do not know whether these subtle changes in heading variance held any cost to individuals or if continual exposure to echo sounders might create a change in behavior at any measurable level. However, these observations provide the first data on reactions of deep diving odontocetes to a scientific echo sounder and provide a starting point for analysis of baseline diving behavior in short-finned pilot whales.

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References

Altman, R. 2007. Mixed hidden Markov models: an extension of the hidden Markov model to the longitudinal data setting. J. Am. Stat. Assoc. **102**(477): 201–210. doi:10.1198/016214506000001086.

Alves, A.C., Antunes, R., Bird, A., Tyack, P.L., Miller, P.J.O., Lam, F.P.A., and Kvadsheim, P.H. 2014. Vocal matching of naval sonar signals by long-finned pilot whales (*Globicephala melas*). Mar. Mammal Sci. **30**(3): 1248–1257. doi:10.1111/mms.12099.

Alves, F., Dinis, A., Ribeiro, C., Nicolau, C., Kaufmann, M., Fortuna, C.M., and Freitas, L. 2013. Daytime dive characteristics from six short-finned pilot whales *Globicephala macrorhynchus* off Madeira Island. Arquipelago Life Mar. Sci. **31**: 1–8.

Amos, B., Schlotterer, C., and Tautz, D. 1993. Social structure of pilot whales revealed by analytical DNA profiling. Science, **260**(5108): 670–672. doi:10.1126/science.8480176. PMID:8480176.

Antunes, R., Kvadsheim, P.H., Lam, F.P.A., Tyack, P.L., Thomas, L., Wensveen, P.J., and Miller, P.J.O. 2014. High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). Mar. Pollut. Bull. **83**: 165–180. doi:10.1016/j.marpolbul.2014.03.056. PMID:24820645.

Baird, R.W., Borsani, J.F., Hanson, M.B., and Tyack, P.L. 2002. Diving and nighttime behavior of long-finned pilot whales in the Ligurian Sea. Mar. Ecol. Prog. Ser. **237**: 301–305. doi:10.3354/meps237301.

Barrett-Lennard, L.G., Ford, J.K.B., and Heise, K.A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim. Behav. **51**: 553–565. doi:10.1006/anbe.1996.0059.

Bednekoff, P.A., and Lima, S.L. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. TREE, **13**(7): 284–287. doi:10.1016/S0169-5347(98)01327-5. PMID:21238305.

BRS. 2008. Cruise Report, Unpublished [online]. Behavioral Response Study. Available from http://sea-inc.net/assets/pdf/brs_08_finalcruisereport.pdf.

Benoit-Bird, K.J., and Au, W. 2003*a*. Hawaiian spinner dolphins aggregate midwater food resources through cooperative foraging. J. Acoust. Soc. Am. **114**(4): 2300. doi:10.1121/1.4780872.

Benoit-Bird, K.J., and Au, W.W.L. 2003*b*. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav. Ecol. Sociobiol. **53**(6): 364–373. doi:10.1007/s00265-003-0585-4.

Benoit-Bird, K.J., Dahood, A.D., and Wursig, B. 2009. Using active acoustics to compare lunar effects on predator–prey behavior in two marine mammal species. Mar. Ecol. Prog. Ser. **395**: 119–135. doi:10.3354/meps07793.

Best, B.D., Halpin, P.N., Read, A.J., Fujioka, E., Good, C.P., LaBrecque, E.A., Schick, R.S., Roberts, J.J., Hazen, L.J., Qian, S.S., Palka, D.L., Garrison, L.P., and McClellan, W.A. 2012. Online cetacean habitat modeling system for the US east coast and Gulf of Mexico. Endanger. Species Res. **18**(1): 1–15. doi:10.3354/esr00430.

Crain, D.D., Friedlaender, A.S., Johnston, D.W., Nowacek, D.P., Roberts, B.L., Urian, K.W., Waples, D.M., and Read, A.J. 2014. A quantitative analysis of the response of short-finned pilot whales, *Globicephala macrorhynchus*, to biopsy sampling, Mar. Mammal Sci. **30**(2): 819–826. doi:10.1111/mms.12074.

Deng, Z.D., Southall, B.L., Carlson, T.J., Xu, J., Martinez, J.J., Weiland, M.A., and Ingraham, J.M. 2014. 200 kHz commercial sonar systems generate lower frequency side lobes audible to some marine mammals. PLoS ONE, **9**(4): e95315. doi:10.1371/journal.pone.0095315. PMID:24736608.

DeRuiter, S.L., Southall, B.L., Calambokidis, J., Zimmer, W.M.X., Sadykova, D., Falcone, E.A., Friedlaender, A.S., Joseph, J.E., Moretti, D., Schorr, G.S., Thomas, L., and Tyack, P.L. 2013. First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. Biol. Lett. **9**(4): 1–5. doi:10.1098/rsbl.2013.0223.

Doksæter, L., Godø, O.R., Olsen, E., Nøttestad, L., and Patel, R. 2009. Ecological studies of marine mammals using a seabed-mounted echosounder. ICES J. Mar. Sci. **66**(6): 1029–1036. doi:10.1093/icesjms/fsp130.

Ellison, W.T., Southall, B.L., Clark, C.W., and Frankel, A.S. 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. Conserv. Biol. **26**(1): 21–28. doi:10.1111/j.1523-1739.2011.01803.x. PMID:22182143.

Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. Calibration of acoustic instruments for fish density information: a practical guide. Int. Coun. Explor. Sea Coop. Res. Rep. **144**: 1–57.

Forney, G.D. 1973. The Viterbi algorithm. Proc. IEEE, **61**(3): 268–278. doi:10.1109/PROC.1973.9030.

Fox, J. 2008. Applied regression analysis and generalized linear models. Sage, Los Angeles, Calif.

Goldbogen, J.A., Southall, B.L., DeRuiter, S.L., Calambokidis, J., Friedlaender, A.S., Hazen, E.L., Falcone, E.A., Schorr, G.S., Douglas, A., Moretti, D.J., Kyburg, C., McKenna, M.F., and Tyack, P.L. 2013. Blue whales respond to simulated mid-frequency military sonar. Proc. R. Soc. B Biol. Sci. **280**(1765): 20130657. doi:10.1098/rspb.2013.0657.

Greenhow, D.R., Brodsky, M.C., Lingenfelser, R.G., and Mann, D.A. 2014. Hearing threshold measurements of five stranded short-finned pilot whales (*Globicephala macrorhynchus*). J. Acoust. Soc. Am. **135**(1): 531–536. doi:10.1121/1.4829662. PMID:24437793.

Hastie, G.D. 2012. Tracking marine mammals around marine renewable energy devices using active sonar [online]. SMRU Ltd. report URN: 12D/328 to the Department of Energy and Climate Change. September 2012 (unpublished). Available from http://tethys.pnnl.gov/sites/default/files/publications/SMRU-2013.pdf.

Hastie, G.D., Donovan, C.R., Gotz, T., and Janik, V.M. 2014. Behavioral responses by grey seals (*Halichoerus grypus*) to high frequency sonar. Mar. Pollut. Bull. **79**(1–2): 205–210. doi:10.1016/j.marpolbul.2013.12.013. PMID:24445129.

Hazen, E.L., Nowacek, D.P., St. Laurent, L., Halpin, P.N., and Moretti, D.J. 2011. The relationship among oceanography, prey fields, and beaked whale foraging habitat in the tongue of the ocean. PLoS ONE, **6**(4): e19269. doi:10.1371/journal.pone.0019269. PMID:21556355.

Hill, H.M., Carder, D.A., and Ridgway, S.H. 2008. Vigilance in female bottlenose dolphins (*Tursiops* sp.) before and after calving. J. Comp. Psychol. **21**: 35–57.

Højsgaard, S., Halekoh, U., and Yan, J. 2005. The R package geepack for generalized estimating equations. J. Stat. Softw. **15**(2): 1–11.

Jensen, F.H., Marrero, Perez, J., Johnson, M., Aguilar, Soto, N., and Madsen, P.T. 2011. Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. Proc. R. Soc. B Biol. Sci. **278**(1721): 3017–3025. doi:10.1098/rspb.2010.2604.

Johnson, M.P., and Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J. Ocean. Eng. **28**(1): 3–12. doi:10.1109/JOE.2002.808212.

Johnson, M.P., Madsen, P.T., Zimmer, W.M.X., Aguilar Soto, N., and Tyack, P.L. 2004. Beaked whales echolocate on prey. Proc. R. Soc. B Biol. Sci. **271**(S6): S383–S386. doi:10.1098/rsbl.2004.0208.

Karniski, C., Patterson, E.M., Krzyszczyk, E., Forouchirad, V., Stanton, M.A., and Mann, J. 2015. A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. Mar. Mammal Sci. **31**(3): 839–852. doi:10.1111/mms.12198.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., and Morales, J.M. 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology, **93**(11): 2336–2342. doi:10.1890/11-2241.1. PMID:23236905.

Liang, K.Y., and Zeger, S.L. 1986. Longitudinal data analysis using generalized linear models. Biometrika, **73**(1): 13–22. doi:10.1093/biomet/73.1.13.

Lima, S.L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. **49**(1): 11–20. doi:10.1016/0003-3472(95)80149-9.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**(4): 619–640. doi:10.1139/z90-092.

Lurton, X., and DeRuiter, S.L. 2011. Sound radiation of seafloor-mapping echosounders in the water column, in relation to the risks posed to marine mammals [online]. International Hydrographic Review, November 2011, pp. 7-17. Available from: https://www.iho.int/mtg_docs/IHReview/2011/IHR_Nov032011.pdf.

Miller, P.J.O., Johnson, M.P., and Tyack, P.L. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proc. R. Soc. B Biol. Sci. **271**(1554): 2239–2247. doi:10.1098/rspb.2004.2863.

Miller, P.J.O., Kvadsheim, P.H., Lam, F-P.A., Wensveen, P.J., Antunes, R., Alves, A.C., Visser, F., Kleivane, L., Tyack, P.L., and Sivle, L.D. 2012. The severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. Aquat. Mamm. **38**(4): 362–401. doi:10.1578/AM.38.4.2012.362.

Miller, P., Antunes, R.N., Wensveen, P.J., Samarra, F.I.P., Alves, A.C.D.C., Tyack, P.L., Kvadsheim, P.H., Kleivane, L., Lam, F-P.A., Ainslie, M.A., and Thomas, L. 2014. Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. J. Acoust. Soc. Am. **135**(2): 975–993. doi:10.1121/1.4861346. PMID:25234905.

Mintzer, V.J., Gannon, D.P., Barros, N.B., and Read, A.J. 2008. Stomach contents of mass-stranded short-finned pilot whales (*Globicephala macrorhynchus*) from North Carolina. Mar. Mammal Sci. **24**(2): 290–302. doi:10.1111/j.1748-7692.2008.00189.x.

Nøttestad, L., Ferno, A., Mackinson, S., Pitcher, T., and Misund, O.A. 2002. How whales influence herring school dynamics in a cold-front area of the Norwegian Sea. ICES J. Mar. Sci. **59**(2): 393–400. doi:10.1006/jmsc.2001.1172.

Nowacek, D.P., Thorne, L.H., Johnston, D.W., and Tyack, P.L. 2007. Responses of cetaceans to anthropogenic noise. Mammal Rev. **37**(2): 81–115. doi:10.1111/j.1365-2907.2007.00104.x.

Nowacek, S.M., Wells, R.S., and Solow, A.R. 2001. Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Mar. Mammal Sci. **17**(4): 673–688. doi:10.1111/j.1748-7692.2001.tb01292.x.

Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., and Rendell, L. 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Mar. Ecol. Prog. Ser. **436**: 257–272. doi:10.3354/meps09236.

Prentice, R.L., and Zhao, L.P. 1991. Estimating equations for parameters in means and covariances of multivariate discrete and continuous responses. Biometrics, **47**(3): 825–839. doi:10.2307/2532642. PMID:1742441.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabiner, L.R. 1989. A tutorial on hidden Markov models and selected applications in speech recognition. Proc. IEEE, **77**(2): 257–285. doi:10.1109/5.18626.

Rendell, L.E., and Gordon, J.C.D. 1999. Vocal response of long-finned pilot whales (*Globicephala melas*) to military sonar in the Ligurian Sea. Mar. Mammal Sci. **15**(1): 198–204. doi:10.1111/j.1748-7692.1999.tb00790.x.

Richardson, W.J., Greene, C.R.J., Malme, C.I., and Thomson, D.H. 1995. Marine mammals and noise. Academic Press Inc., San Diego, Calif.

Ridgway, S.H., Carder, D., Finneran, J., Keough, M., Kamolnick, T., Todd, M., and Goldblatt, A. 2006. Dolphin continuous auditory vigilance for five days. J. Exp. Biol. **209**: 3621–3628. doi:10.1242/jeb.02405. PMID:16943502.

Roberts, J.J., Best, B.D., Mannocci, L., Fujioka, E., Halpin, P.N., Palka, D.L., Garrison, L.P., Mullin, K.D., Cole, T.V.N., Khan, C.B., McLellan, W.A., Pabst, D.A., and Lockhart, G.G. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Sci. Rep. **6**: 22615. PMID:26936335.

Rosel, P.E. 2003. PCR-based sex determination in odontocete cetaceans. Conserv. Genet. **4**: 647–649. doi:10.1023/A:1025666212967.

Savidge, D.K., and Bane, J.M., Jr. 2001. Wind and Gulf Stream influences on along-shelf transport and off-shelf export at Cape Hatteras, North Carolina. J. Geophys. Res. **106**(C6): 11505–11527. doi:10.1029/2000JC000574.

Schlundt, C.E., Dear, R.L., Houser, D.S., Bowles, A.E., Reidarson, T., and Finneran, J.J. 2011. Auditory evoked potentials in two short-finned pilot whales (*Globicephala macrorhynchus*). J. Acoust. Soc. Am. **129**(2): 1111–1116. doi:10.1121/1.3531875. PMID:21361467.

Scott-Hayward, L., Oedekoven, C., Mackenzie, M., Walker, C.G., and Rexstad, E. 2014. Using the MRSea Package (v0.1.2) Statistical Modelling of bird and cetacean distributions in offshore renewables development areas [online]. Centre for Research into Ecological and Environmental Modelling (CREEM) at the University of St. Andrews, performed under contract for Marine Scotland (SB9(CR/2012/05)). Unpublished. Available from http://creem2.st-andrews.ac.uk/software/.

Senigaglia, V., and Whitehead, H. 2012. Synchronous breathing by pilot whales. Mar. Mammal Sci. **28**(1): 213–219. doi:10.1111/j.1748-7692.2011.00465.x.

Similä, T. 1997. Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. Aquat. Mamm. **23**(3): 119–126.

Simmonds, J., and MacLennan, D. 2005. Fisheries acoustics — theory and practice. 2nd ed. Blackwell Science, Oxford.

Sivle, L.D., Kvadsheim, P.H., Fahlman, A., Lam, F.P., Tyack, P.L., and Miller, P. 2012. Changes in dive behaviour during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. Front. Physiol. **3**: 400. doi:10.3389/fphys.2012.00400. PMID:23087648.

Soto, N.A., Johnson, M.P., Madsen, P.T., Diaz, F., Dominguez, I., Brito, A., and Tyack, P. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands) J. Anim. Ecol. **77**(5): 936–947. doi:10.1111/j.1365-2656.2008.01393.x.

Southall, B.L., Bowles, A.E., Ellison, W.T., Finneran, J.J., Gentry, R.L., Greene, C.R., Kastak, D., Ketten, D.R., Miller, J.H., Nachtigall, P.E., Richardson, W.J., Thomas, J.A., and Tyack, P.L. 2007. Marine mammal noise exposure criteria: initial scientific recommendations. Aquat. Mamm. **33**(4): 411–509. doi:10.1578/AM.33.4.2007.411.

Southall, B.L., Rowles, T., Gulland, F., Baird, R.W., and Jepson, P.D. 2013. Final report of the Independent Scientific Review Panel investigating potential contributing factors to a 2008 mass stranding of melon-headed whales (*Peponocephala electra*) in Antsohihy, Madagascar [online]. Available from http://www.cascadiaresearch.org/Hawaii/Madagascar_ISRP_Final_report.pdf.

Stimpert, A.K., DeRuiter, S., Moretti, D., Friedlaender, A.S., Schorr, G., Falcone, E., Goldbogen, J., Calambokidis, J., and Southall, B. 2014. Acoustic and foraging behavior of a tagged Baird's beaked whale (*Berardius bairdii*) exposed to simulated sonar. Sci. Rep. **4**: 7031. doi:10.1038/srep07031. PMID:25391309.

Tyack, P. 2008. Implications for marine mammals of large-scale changes in the marine acoustic environment. J. Mammal. **89**(3): 549–558. doi:10.1644/07-MAMM-S-307R.1.

Tyack, P.L., Zimmer, W.M.X., Moretti, D., Southall, B.L., Claridge, D.E., Durban, J.W., Clark, C.W., D'Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E., Morrissey, R., Ward, J., and Boyd, I.L. 2011. Beaked whales respond to simulated and actual navy sonar. PLoS ONE, **6**(3): e17009. doi:10.1371/journal.pone.0017009. PMID:21423729.

Visser, F., Miller, P.J.O., Antunes, R.N., Oudejans, M.G., Mackenzie, M.L., Aoki, K., Lam, F.-P.A., Kvadsheim, P.H., Huisman, J., and Tyack, P.L. 2014. The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). Behaviour, **151**(10): 1453–1477. doi:10.1163/1568539X-00003195.

Walker, C., Mackenzie, M., Donovan, C., O'Sullivan, M. 2011. SALSA — a Spatially Adaptive Local Smoothing Algorithm. J. Stat. Comput. Sim. **81**(2): 179–191. doi:10.1080/00949650903229041.

Williams, R.M., Trites, A.W., and Bain, D.E. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching: opportunistic observations and experimental approaches. J. Zool. (Lond.), **256**(2): 255–270. doi:10.1017/S0952836902000298.

Williams, R., Wright, A.J., Ashe, E., Blight, L.K., Bruintjes, R., Canessa, R., Clark, C.W., Cullis-Suzuki, S., Dakin, D.T., Erbe, C., Hammond, P.S., Merchant, N.D., O'Hara, P.D., Purser, J., Radford, A.N., Simpson, S.D., Thomas, L., and Wale, M.A. 2015. Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. Ocean Coast. Manage. **115**: 17–24. doi:10.1016/j.ocecoaman.2015.05.021.

Williamson, B.J., Blondel, P., Armstrong, E., Bell, P.S., Hall, C.B., Waggitt, J.J., and Scott, B. 2016. A self-contained subsea platform for acoustic monitoring of the environment around marine renewable energy devices — field deployments at wave and tidal energy sites in Orkney, Scotland. IEEE J. Ocean. Eng. **41**(1): 67–81. doi:10.1109/JOE.2015.2410851.

Wright, A.J., Soto, N., Baldwin, A.L., Bateson, M., Beale, C.M., Clark, C., Deak, T., Edwards, E.F., Fernández, A., Godinho, A., Hatch, L., Kakuschke, A., Lusseau, D., Martineau, D., Romero, L.M., Weilgart, L., Wintle, B., Notarbartolo, di, Sciara, G., and Martin, V. 2007. Are marine mammals stressed by anthropogenic noise? J. Comp. Psychol. **20**: 274–316.

Yan, J., and Fine, J.P. 2004. Estimating equations for association structures. Stat. Med. **23**(6): 859–880. doi:10.1002/sim.1650. PMID:15027075.

Zucchini, W., and MacDonald, I.L. 2009. Hidden Markov models for time series: an introduction using R. Chapman & Hall, London.