1 **Effects of a scientific echo sounder on the behavior of short-finned pilot**

2 **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 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 (HMM) to characterize diving states with and without exposure provided no evidence for a change in foraging behavior. However, Generalized Estimating Equations (GEE's), 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.

Introduction

Increasing levels of anthropogenic noise in the marine environment represent a significant 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 5-15° (Simmonds and MacLennan 2005). Frequencies range from 12 to several hundred kHz, 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 1µPa @ 1m (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 multi-beam 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-Baird and Au

75   2003a; Hazen et al. 2011; Nottestad et al. 2002; Similä 1997) and as potential technology for

76   monitoring movements of marine mammals around a tidal turbine development (Hastie 2012). To

77   date, however, no experiments have been conducted to explicitly test for potential effects of echo

78   sounders on the behavior of wild cetaceans.

79

80   Short-finned pilot whales (*Globicephala macrorhynchus*) are deep-diving and highly social toothed

81   whales that occur frequently along the shelf break near Cape Hatteras, North Carolina, USA during

82   spring, summer and fall (Best et al. 2012; Roberts et al. 2016). We have been conducting a long-term

83   study of these pilot whales using a variety of research approaches, including photo-identification,

84   satellite-linked telemetry and the use of short-term archival tags. There is limited information on the

85   hearing ability of short –finned pilot whales, with data only from stranded and captive animals

86   (Schlundt et al. 2011, Greenhow et al. 2014). These studies report a hearing range between 10-120

87   kHz, with greatest sensitivity around 40kHz, and peak sensitivity at lower frequencies than some

88   other odontocetes (Schlundt et al. 2011, Greenhow et al. 2014).

89

90   The pilot whales we study off Cape Hatteras exhibit deep foraging dives classified by the presence of

91   vocal behavior (click trains and buzzes) similar to that seen in other pilot whale populations (Soto et

92   al. 2008; Jensen et al. 2011) and analogous to that used during foraging by other deep diving

93   odontocetes, e.g. beaked and sperm whales (Johnson et al. 2004; Miller et al. 2004). Temporal

94   clustering, or bouts, of dives has been suggested for both short and long-finned (*G. melas*) pilot

95   whales, with periods of shallow, non-foraging dives followed by bouts of deep diving (Soto et al.

96   2008; Sivle et al. 2012; Visser et al. 2014). Cape Hatteras is a foraging area for short-finned pilot

97   whales and also an important ground for both commercial and recreational fisheries, including

98   pelagic longlines, mid-water trawls and charter troll vessels, all of which use echo sounders.

99   Disruption of foraging behavior, or area avoidance, as a consequence of ensonification by powerful

100   source level sounds from echo sounders could affect foraging efficiency and have fitness

101   consequences at both individual and population levels.

102

103   No comparable studies of effects of echo sounders exist, but previous studies of the effects of

104   military tactical sonars on pilot whales failed to document overt avoidance responses (BRS 2008;

105   Miller et al. 2012), such as those seen in beaked whales (DeRuiter et al. 2013; Stimpert et al. 2014;

106   Tyack et al. 2011), but did show changes in heading variance, indicative of avoidance in long-finned

107   pilot whales (Miller et al. 2012). These less overt responses to sound exposure may also have

108   important consequences, if they occur as a result of chronic or isolated exposure (Tyack 2008). In the

109   absence of a dramatic flight response, other measurable changes in behavior, such as changing

110   behavioral state or kinematic changes in pitch or heading that could indicate a subtle avoidance or

111   vigilance response, may be difficult to detect by visual observation.

112

113   In the present study we used an experimental approach to assess potential changes in short-finned

114   pilot whale behavior during exposure to a scientific EK60 echo sounder. We first used hidden

115   Markov models (HMM) to determine whether exposure changed foraging behavior. We then

116   assessed changes in heading variance of each exposed individual over an entire tag record to

117   measure avoidance or changes in vigilance during the exposure period. We used data from non-

118   invasive digital acoustic recording tags (DTAGs), attached via suction cups (Johnson and Tyack 2003)

119   to collect data whilst whales were exposed to signals of the echo sounder. We employed a

120   randomized treatment and control paradigm following a baseline observation period. Exposure was

121   designed to mimic actual echo sounder deployment and the diving and acoustic behavior of the

122   whales was recorded during all phases of the experiment.

123

124

125

Methods

Data Collection

Our study was conducted off Cape Hatteras, North Carolina, U.S.A. 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 multi-sensor archival tag, attached via suction cups that

records: audio with 16-bit resolution at a sampling rate of 96 – 192 kHz; pressure at 50 Hz; and

orientation of the whale from tri-axial 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 non-systematic 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 eleven 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

152 period of at least one hour. Four of the eleven animals were tagged, but not exposed to any form of

153 playback or vessel approach. The single remaining animal (gm11_158a) was tagged, but was

154 immediately lost from view. Data from this animal are not considered further in the analysis.

155 Similarly, one of the exposed animals (gm11_150a) is not considered further due to incomplete data

156 records on the tag. In total, five individuals were exposed to signals from the echo sounder and four

157 individuals were control animals.

158

159 The Simrad EK60 is a scientific echo sounder with an ES38DD split-beam transducer incorporating 88

160 Tonpilz elements distributed over four quadrants. It has a resonant frequency at 38 kHz and a 7

161 degree circular beam width. The echo sounder was located on a 12.5 m playback vessel. When

162 active, the echo sounder used a 2 kW transmit power with a 2048 μsec pulse width. The transducer

163 was deployed alongside the vessel using an arm attached to the ship with the transducers deployed

164 1 m below the sea surface. The system was calibrated (both the output source level and the received

165 signals) once at the end of the sampling period using a 35.1 mm tungsten carbide calibration sphere

166 and the calibration procedure described by Foote et al. (1987).

167

168 All but one of the five exposure animals experienced all four experimental conditions (Pre, Control,

169 Active, Post) (Table 1). The first experimental condition (Pre) was a baseline period of at least one

170 hour following tagging, but prior to the control or exposure condition. After this baseline period,

171 either the control or active condition was conducted. The control condition consisted of the boat

172 driving in a configuration representative of an active echo sounding survey, with the transducer in

173 the water, the system powered but without emitting signals. In the active condition, the boat drove

174 in the same pattern, with the transducer in the water and with the echo sounder powered up and

175 emitting signals. The order of control or active conditions were randomized, but always occurred

176 after the pre-condition, and the observers on the follow boat were blind to the condition. Once both

177 control and active conditions had been completed on a focal whale, the animal was observed (Post

178   condition) until the time of tag release. One animal did not experience a post condition, because the

179   tag detached prematurely.

180

Data Processing

182   Data were downloaded from the tags and pressure recordings were converted to depths, using

183   calibration information from each tag (Johnson and Tyack 2003). Calibration of the orientation offset

184   from tag position was also performed and all movement data were down-sampled to 5 Hz using

185   custom written scripts in Matlab version R2014a. Dives were defined as any submergence to a depth

186   of 20m or deeper (Soto et al. 2008). Any interval of data during which the whale was at a depth of

187   20m or less was considered time spent at the surface. For all dives, four dive and movement

188   parameters were calculated: *Dive Duration*, time between start of dive descent and end of dive

189   ascent per dive (minutes); *Heading Variance*, average change in heading over the entire dive;

190   *Maximum Depth*, maximum depth reached during dive (meters); *Number of buzzes*, the number of

191   terminal echolocation click trains recorded during the dive. Each parameter was calculated over the

192   period of one dive (from time at surface when dive profile began to time when animal returned to

193   the surface). If a value could not be determined, for example if the tag detached during a dive, then

194   a mean value from all baseline and pre exposure dives across all animals was used. This was

195   necessary for only 4 of the 75 dives (5.3%). All acoustic audits of the DTAG sound files, to determine

196   the start time and duration of buzzes, were completed by a single experienced analyst.

197

198   For the five animals that were exposed to the experimental stimulus, the mean value for depth

199   (meters), the variance in pitch (radians), and the median variance in circular heading (radians) were

200   calculated for five minute time bins across the entire tag record. A five minute time resolution was

201   chosen to match that of the focal observations. Experimental condition sequence and times were

202   taken from the field notes and synchronized with the individual dive profiles. Each five minute time

203   bin was allocated an experimental condition (0 = pre, 1= control, 2=active, 3=post). Two binary

204   variables were created. The first was for exposure, with pre, control and post being equal to zero

205   and active equal to one. The second was for boat presence with pre and post being equal to zero

206   and active and control being equal to one.

207

208   Start times and durations of each echo sounder pulse were noted. Each pulse was considered one

209   sample, and samples varied across tags (five tags; samples extracted = 451, 163, 1550, 921, 1039).

210   Variation was due to changes in background noise from splashes at the surface or animal

211   vocalizations, which masked the signal. Received Levels (RL) were calculated at the tagged animals as

212   RMS (root-mean-squared) levels in dB re 1 µPa, using custom written Matlab scripts. All received

213   levels were calculated within a 1/3-octave band, (using the ANSI standard that contained the EK60

214   center frequency of 38 kHz); spanning 35,467-44,686 kHz and were averaged over a 200 msec sliding

215   window. The reported level is the highest level measured during any single 200 msec window that

216   included part of the echo ping. The script also included an algorithm to exclude energy from short,

217   intense sounds such as whale echolocation clicks as described in Tyack et al. (2011). Signal-to-Noise

218   Ratio (SNR) was determined using RMS noise levels calculated in the same way as the received

219   levels. Noise levels were determined from 1-second sound clips that preceded each echo sounder

220   pulse by 2 sec. Where the signal to noise ratio was less than a critical threshold of 6 dB re 1 µPa,

221   received levels were not calculated, because the signal was buried in the noise.

222

223   **Statistical Analysis**

224   We used a multivariate hidden Markov model (HMM) as a framework for the first analysis. The model

225   was a first order Markov model and assumed that the distribution of the current state is determined

226   only by the previous state (Altman 2007; Rabiner 1989; Zucchini and MacDonald 2009). The four dive

227   and movement variables calculated from each of the 75 dives were specified as the observable series

228   and were each assumed a distribution with state-dependent mean and variance parameters. Each

229   dive was assigned to one of the nine individual whales in the sequential order that it occurred. Dive

230   duration and maximum depth were assumed Gamma distributions as they were continuous positive

231   values. The number of buzzes was assumed a Poisson distribution to allow these data to be treated as

232   integer counts. Heading variance was assumed a Beta distribution as it consists of values between

233   zero and one. The model was constructed based on the assumption that there were two underlying

234   non-observable behavioral states and that the observations were conditionally independent given the

235   states, i.e., contemporaneous conditional independence was assumed (Zucchini and MacDonald

236   2009). We assumed a transition matrix where all state transitions were possible so that any hidden

237   Markov state could be reached from any other hidden Markov state. The model was run initially using

238   all dives from all experimental conditions. The model was then run again including exposure

239   presence/absence as a covariate on heading variance. This was to quantify differences in dive state

240   allocation during echo sounder exposure. We did not consider individual random effects in the

241   models, and assumed all whales shared common distribution parameters for all variables (Langrock

242   et al. 2012) based on the assumption that all diving whales were utilizing food patches.

243

244   We fitted the models via numerical maximum likelihood estimation using the nlm optimizer in R (R

245   Core Development Team 2014; see Zucchini and MacDonald 2009, for details of implementation). To

246   improve confidence that the global maximum was found during the maximization process, 1000 initial

247   values were specified to investigate the likelihood surface prior to maximization. This enabled only

248   those values with the highest likelihoods to be passed to the nlm optimizer for maximization. Five

249   hundred simulation runs of the model were completed to check for numerical stability in robustness

250   against different initial values in the log likelihood. We applied the Viterbi algorithm (Forney 1973) to

251   find the most likely sequence of hidden states, for each animal, given the likelihood of the four

252   observed variables under the estimated state-dependent distributions and the transition probabilities

253   between states.

254

255   The median variance in heading every five minutes, across all five exposure tags, was modelled using

256   a GAM with a Gaussian error distribution and a log link function. The log link prevented the model

257   returning negative estimates for heading variance. Two separate models were constructed with a

258   choice of either 'Presence of exposure' or 'boat presence' fitted as a binary factor covariate.

259   Additionally, the covariates pitch and depth were fitted as continuous terms in each of the two

260   models. Initially, the continuous covariates were fitted as smooth terms using B-splines, with their

261   flexibility (selection of number and location of knots) determined using the Spatially Adaptive Local

262   Smoothing Algorithm (SALSA, Walker et al. 2011). Five-fold Cross Validation (CV) was used to select

263   covariates for inclusion and, for the continuous covariates, whether they were best suited as linear or

264   smooth terms. Interaction terms between depth and exposure and pitch and exposure were also tried

265   in both models. Variables were checked for co-linearity using Generalized Variance Inflation Factors

266   (GVIF, Fox 2008), which indicated no issues with co-linearity in the dataset.

267

268   The data are repeated measures on individual whales and so the temporal correlation present in

269   model residuals was incorporated, using a population-average approach, Generalized Estimating

270   Equations (GEEs) (Liang and Zeger 1986; Prentice and Zhao 1991). GEEs require a blocking structure,

271   which denotes blocks of data within which residuals were permitted to be correlated and between

272   which the residuals are independent (e.g. see Pirotta et al. 2011) The blocking structure here

273   represents nineteen blocks, one for each unique combination of individual and experimental

274   condition. Plots of the autocorrelation between residuals and within these blocks showed the blocking

275   structure to be suitable. An independent working correlation matrix was specified and robust standard

276   errors were used for model inference.

277

278   The GAM-GEE analysis was carried out using R software (R Core Development Team 2014).

279   Specifically, the MRSea (Scott-Hayward et al. 2014) and geepack (Yan and Fine 2004; Højsgaard et al.

280   2005) packages were used for model fitting.

281

282 Predictions were made for the best model for each selected continuous covariate at both levels (for

283 exposure model sonar; sonar on or sonar off). For assessment of the relationship of a given covariate

284 with the response, the other covariates were fixed at their mean values (depth = 71.63, pitch = 0.08).

285 A parametric bootstrap from the GEE model was used to calculate 95 percentile confidence intervals

286 for each set of predictions.

287

288 **Results**

289 The tag deployments produced 32 hours 19 minutes and 47 seconds of recording time from the 9

290 individual whales (Table 1). Data were not distributed evenly across all four experimental conditions.

291 Twenty hours were allocated to the pre-condition; four hours and 40 minutes to the control

292 condition; five hours to the active condition and three hours 16 minutes to the post condition (Table

293 1). Focal follows were completed for all individuals considered in the analysis for the duration of the

294 tagging period.

295

296 Received levels were calculated for all five tags. The number of samples processed per tag, above

297 the critical signal to noise ratio of 6dB was variable, (39, 24, 590, 205 and 155) (Table 1). The

298 maximum received level across all tags ranged from 117-125 dB re 1μPa (Table 1).

299

300 The hidden Markov model, including the covariate of exposure, produced a marginally better AIC

301 (714.50) score than the model excluding exposure (717.59). Re-running of both models showed

302 stable AIC and maximum log-likelihood values and consistent state allocation of all dives. Dive

303 allocation to state between the two models differed only by a single dive. Therefore all but one dive

304 had the same probability of state with and without exposure to the echo sounder. The dive that was

305 allocated differently was a control dive (dive number 8, Fig. 1). This dive was to 188m, lasted for 9

306 minutes 53 seconds, but contained no buzzes.

307

308   The state summaries of the observed variables are shown in Table 2. Forty-eight of the dives were

309   allocated to state 1 and twenty-seven to state 2. The two states appear to represent: (1) deep dives

310   with longer durations, the presence of buzzes and greater variation in heading; and (2) shallow dives

311   of short duration, with no buzzes and less variance in heading. However, analysis of each dive by

312   variable (Fig. 1) and plots of the dive profiles (Fig. 2) show a high degree of variation within each

313   state. Dive duration was the only variable that showed no overlap between states (Table 1). All state

314   1 dives had durations longer than 7 minutes (mean 13.2 minutes) but depths ranged from 30-805m

315   and there were from 0 to 51 buzz events. Heading variance varied over almost the entire possible

316   range between zero and one for state 1 dives (Table 2 and Figs. 1, 2). State 2 dives had no foraging

317   buzzes and were, on average, less than 4 minutes long, with maximum depths, on average, of less

318   than 40m (Table 2 and Figs. 1, 2). Heading variance of state 2 dives covered a smaller range than

319   state 1 dives, but was still highly variable (Table 2, Fig. 1).

320

321   Both states contained dives from all four experimental conditions: pre, control, active and post. The

322   control (n = 7) and active (n = 12) dives appeared similar in profile to many of the pre and post dives

323   within each state (Fig. 2). The distribution of dives between states was not equal, suggesting that

324   both states were not equally likely. Plots of the entire tag records for each animal showed dives of

325   state 1 clustered together in what appear to be foraging bouts, interspersed with clusters of state 2

326   dives of unknown function (Fig. 3).

327

328   During the active experimental condition, one of the exposed animals did not exhibit any diving

329   state; two undertook state 2 shallow dives, one a deep state 1 dive and the other a state 2 followed

330   by a state 1 dive. No animals performed multiple state 1 deep dives during the active condition, in

331   contrast to all the other conditions where multiple deep state 1 dives were seen (Fig. 3). Three of the

332   exposed animals performed the first example of a dive within a given state during the active

333   condition (Fig. 3). The four baseline animals exhibited primarily state 1 dives, with only seven state 2

334   dives recorded across all four baseline animals (Fig. 3).

335

336   State persistence and state switching was observed within and across both states (Table 3). The

337   probability of persisting within one state was higher for both states compared to state switching.

338   (Table 3). Mapping the most likely (Viterbi) state sequences onto the dive profiles supports the

339   existence of bouts, i.e. state persistence, but also shows examples of animals readily switching from

340   one state to another (Fig. 3).

341

342   The GEE model containing exposure as a binary factor had a marginally better 5-fold CV score

343   (0.02218) than the model containing boat presence as a binary factor (0.02278). Even though we

344   had an unbalanced design, with more data in the non-exposed than exposed condition, the

345   assumption of constant error variance holds for this model. This exposure model contained depth as

346   a linear variable (d.f. =1) and pitch as a smooth term (d.f. =3). Positive relationships were seen

347   between heading variance and all covariates (Table 4). The ANOVA results (sequential Wald test) for

348   pitch and depth show a highly significant relationship ($p = <0.0001$). The parameter estimates for

349   depth and pitch were positive, so as depth and pitch increased so did the heading variance (Fig. 5).

350   Depth increased linearly, but the relationship for pitch showed a sharp increase in heading variance

351   for pitch <0.1 and a shallower increase thereafter (Fig. 4). Exposure also showed a positive

352   relationship, suggesting that heading variance increased during periods of exposure to the echo

353   sounder ($p = 0.069$) (Table 4 and Fig. 5). Whilst the exposure covariate is not significant at the 5%

354   level it is only marginally not so, and the CV score indicated a better fit with exposure retained.

355

356   **Discussion**

357   The goal of our study was to test for behavioral responses of short-finned pilot whales during

358   exposure to a scientific echo sounder. We looked first for changes in diving state that could indicate

359   a change in foraging behavior and then for changes in heading variance that could suggest a general

360   avoidance response. We did not observe an overt response to the echo sounder or a change to

361   foraging behavior of tagged whales, but the whales increased heading variance when exposed to

362   signals from the echo sounder.

363

364   The HMM identified two states across multiple whales and all four experimental conditions. Our

365   predictions of state are based on the multivariate distributions of four observed variables. Three of

366   these variables, dive duration, maximum depth and number of buzzes, have been considered in

367   previous studies as good descriptors of pilot whale diving behavior (Soto et al. 2008; Jensen et al.

368   2011; Alves et al. 2013). Most prior studies have relied on depth to classify shallow non-foraging and

369   deep foraging behavior in pilot whales (e.g. Alves et al. 2013; Baird et al. 2002; Soto et al. 2008).

370   Variability in heading was included to look for differences in linearity of movement within dives that

371   might indicate directed movement. The HMM allowed us to classify diving behavior more objectively

372   using several relevant variables, whilst accounting for the autocorrelation in the time series data, but

373   a considerable amount of variation remained among dives of the same state, particularly within

374   state 1.

375

376   All exposed individuals and two baseline animals showed diving behavior consistent with both state

377   1 and state 2 dives. The remaining two baseline animals only showed dives consistent with state 1.

378   During the active exposure condition, not all whales were engaged in the same behavior. Dive

379   profiles show that one whale remained in surface waters (<20m) and did not engage in any form of

380   diving. Two whales exhibited shallow state 2 dives interspaced with surface time. One whale

381   performed a single state 1 foraging dive and then remained at the surface waters, and the last whale

382   exhibited a single state 2 shallow dive and a single state 1 deep dive interspaced with surface time.

383   Such combinations of behavior were not only seen during the exposure condition. Periods of surface

384   time, state 2 shallow dives interspaced with surface time, single deep state 1 dives, and state 2

385   shallow dives followed by state 1 deep dives were all seen in the baseline animals or during the pre-

386   condition.

387

388   Several previous studies have described the existence of two diving states, deep foraging and

389   shallow non-foraging, in pilot whales (Soto et al. 2008; Jensen et al. 2011), but our recent study of

390   short-finned pilot whale diving behavior off Cape Hatteras suggests that diving behavior is more

391   complex than a simple dichotomy of deep foraging and shallow non-foraging diving states.

392   Furthermore, it appears that individual whales are able to adapt their diving strategy on a dive by

393   dive basis (Quick et al. In review). This behavioral plasticity enables pilot whales to successfully

394   exploit patches of mobile aquatic prey, but also leads to large natural variation in diving behavior.

395   Our data show that whilst some dives are shallow (less than 50m) and some are deep (greater than

396   600m) many occur at intermediate depths and the number of buzzes per dive is highly variable. The

397   aim of our HMM analysis was to assess changes to foraging behavior. We interpret state 1 as a

398   foraging state and state 2 as a non-foraging state, but the observed variation in state 1 suggests it

399   may also contain examples of failed and/or non-foraging dives. We have no means to assess success

400   during prey capture, and the variation seen in state 1 dives could be due to a range of factors

401   including foraging efficiency, the environment and social behavior. Short-finned pilot whales off

402   Cape Hatteras exploit a wide range of food types, with a predominance of oceanic deep water squid

403   (Mintzer et al. 2008). Their diving ability enables them to exploit a range of habitats, suggesting that

404   prey selection and abundance could be driving the variation we observed within state 1. The local

405   environment may also be driving the variation. Our experiment took place in an area with steep

406   bathymetric gradients (Savidge and Bane 2001) and perhaps the foraging depth of some whales was

407   driven by bottom topography. Some of this variation may also be explained by social behavior. Pilot

408   whales are highly social animals, which live in long-term stable groups (Amos et al. 1993) and

409   perform highly synchronous behavior (Senigaglia and Whitehead 2012). Long-finned pilot whales

410   from the same social group coordinate their foraging behavior (Visser et al. 2014) and the need for

411   social cohesion may dictate diving behavior.

412

413   Our HMM analysis imposed a number of restrictive assumptions, including that the parameter set

414   was common to all individuals. This assumes that all tagged individuals, regardless of sex, age, body

415   condition, and social group, all act in the same way. Studies of the effects of sonar exposure on blue

416   whales (*Balaenoptera musculus*) have shown that their responses can vary depending, amongst

417   other things, on behavioral state (Goldbogen et al. 2013). All of our pilot whales were at the surface

418   at the onset of the active condition, but not all had been in an identical behavioral state prior to

419   exposure. We also do not know the sex and age class of all our exposed animals, so we could not

420   include these covariates to explore heterogeneity across individuals. We could have assumed that

421   each individual had its own set of parameters or considered a number of possible outcomes of

422   discrete random effects to account for potential heterogeneity across individuals based on

423   hierarchical modelling (partial pooling) (Langrock et al. 2012), but we assumed that all foraging

424   individuals would dive to forage on a deep foraging patch, and increasing the number of states or

425   including random effects was not possible because of the size of our data set.

426

427   Time activity budgets for short-finned pilot whales, off Cape Hatteras (Quick et al. In review)

428   suggests that individuals engage in bouts of behavior and rarely behave in a sequentially random

429   fashion (Karniski et al. 2015). This is further supported by the higher probability of state persistence

430   than state transitions observed in this study. Our aim was to assess changes in diving behavior that

431   may indicate effects on foraging, but we only recorded two, deep state 1 dives during the exposure

432   condition. We looked at effect of exposure as a covariate on heading variance to test for any

433   potential avoidance response through increases in the linearity of travel. Including exposure

434   produced a difference in state allocation of one control condition dive to state 1 from state 2. This

435   dive fell between the two states as it was deeper than all other state 2 dives but contained no

436 buzzes. In general, variation in heading was greater during the deeper state 1 dives, but including

437 exposure as a covariate on heading variance showed no evidence of increased linearity of heading

438 during dives in the exposure condition compared to any of the other experimental conditions.

439

440 The two deep foraging dives and ten shallow dive that occurred during exposure clustered with

441 similar dives from the baseline animals and pre-exposure condition, even when received level was

442 included as a covariate. This suggests that foraging behavior during the two deep state 1 dives was

443 not different to that during pre-exposure or baseline and that, for these two examples, exposure to

444 the echo sounder did not change the foraging behavior of these short-finned pilot whales.

445

446 The results from our GAM - GEE analysis showed that whilst not highly significant ($p=0.069$), there

447 was a consistent increase in heading variance during exposure to the echo sounder over all values of

448 depth and pitch. Interactions between depth and exposure and pitch and exposure neither improved

449 the CV score nor had significant p-values. This suggests that, regardless of behavioral state, the

450 whales changed their heading more frequently while the echo sounder was active. Changes in

451 heading variance, indicative of avoidance, have been seen in studies of the effects of tactical sonars

452 on cetaceans (Miller et al. 2014; Tyack et al. 2011) and, specifically, in long-finned pilot whales

453 (Miller et al. 2012). Other cetacean species have been documented to show changes in movement

454 and heading in response to boats, including bottlenose dolphins (Nowacek et al. 2001), and killer

455 whales (Williams et al. 2002). We discounted the model that included boat presence, rather than

456 exposure, based on CV scores, indicating that echo sounder status was a better predictor of

457 response than the presence of the boat. The echo sounder was within audible range for the pilot

458 whales (Schlundt et al. 2011, Greenhow et al. 2014) and the received levels ranged from 117-125 dB

459 re 1μPa.

460

461   A previous study on long-finned pilot whales predicted a higher probability of response to received

462   levels of tactical sonars greater than 165 dB re 1µPa (Antunes et al. 2014) and suggested that pilot

463   whales may have higher avoidance response thresholds than some other cetaceans. Due to the

464   characteristics of echo sounding devices (small beam angles and downward directed beams

465   (Simmonds and MacLennan 2005)), and results from previous studies that have assessed the effects

466   of military sonar on pilot whales, (BRS 2008; Miller et al. 2012), we did not predict that the pilot

467   whales we studied would flee from the sound source. However, studies have documented less overt

468   reactions, such as changes in movement and vocal behavior (Alves et al. 2014; Miller et al. 2012;

469   Rendell and Gordon 1999), in response to some sonars. In fact, our GEE analysis suggested an overall

470   increase in heading variance during exposure to the EK60 signals. This change in heading was not a

471   directed avoidance response away from the echo sounder, and was likely a vigilance response, with

472   animals maintaining awareness of the location of the echo sounder through increased changes in

473   heading variance. Vigilance can be defined as individual alertness of the environment for significant

474   events that may impact survival, and is seen in many group living animals (e.g. Lima 1995; Lima and

475   Dill 1990). Scanning the environment for threats constitutes vigilance behavior within an anti-

476   predator strategy and aids predator detection (Bednekoff and Lima 1998). Although perhaps

477   unlikely, pilot whales may consider the echo sounder a predation threat, and respond to its signals.

478   Killer whale echolocation signals overlap in frequency (Barrett-Lennard et al. 1996) with that of the

479   EK60 and despite clear differences, killer whale signals and the EK60 signals do show some level of

480   acoustic similarity. Maintaining an awareness of the echo sounder source location may have allowed

481   the whales to maintain social cohesion within their social groups and/or to enable flight behavior if

482   signals from the echo sounder passed a critical threshold. Our surface visual observations of their

483   behavior did not indicate any dramatic response, such as fast travel away from the source. We also

484   did not visually record any unusual behaviors or changes in heading, suggesting the changes we

485   observed from the tag data were subtle. Studies with captive dolphins have shown that individuals

486   are able to sustain high levels of auditory vigilance for extended periods of time (Ridgeway et al.

487   2006), and during states of parturition (Hill et al. 2008). This suggests that vigilance behavior in wild

488   cetaceans may be commonplace when required by behavioral or social drivers.

489

490   A number of studies have used the EK60 scientific echo sounder to measure the movements and

491   behavior of marine mammals underwater and make prey field measurements (e.g. Benoit-Baird and

492   Au 2003b; Benoit-Bird et al. 2009b, Doksæter et al. 2009, Williamson et al. 2016). These studies

493   acknowledge a lack of empirical data on potential behavioral responses of marine mammals and

494   accept the possibility that marine mammals may be attracted or repulsed by the echo sounder.

495   We did not observe cessation of biologically important behavior such as feeding during our study

496   and we did not try to directly measure the movements and behavior of the pilot whales themselves.

497   The subtly of the responses may preclude detection by the sonar system itself, but the possibility of

498   a behavioral response should be considered in future studies using this system for behavioral

499   research of marine mammals.

500

501   The assumption of independent errors does not apply to our dataset because we collected multiple

502   data points from each whale and conducted multiple treatments per individual. We accounted for

503   this autocorrelation by using Generalized Estimating Equations (Liang and Zeger 1986) and blocking

504   our data according to the structure of the treatments. We also randomly allocated the treatment

505   order for the exposed animals. Due to the small number of exposed animals, we cannot prove that

506   the two treatments, control and active, were independent of each other and our sample size is too

507   small to statistically test the animals that received the same treatment order separately. However,

508   we did attempt to retain the structure within our data, through blocking by the unique combination

509   of individual and treatment. It is possible, however, that the reactions of the animals during the

510   second treatment were influenced by the first treatment. Further experimentation would be needed

511   to answer this question completely. No visual observations noted any adverse reaction by the pilot

512   whales during the experiment, so the responses we documented from the tags were too subtle to be

513   observed by surface visual monitoring alone. This is an important consideration for studies designed

514   to look for subtle responses.

515

516   Our study is the first attempt to quantify the behavioral response of deep-diving odontocetes to a

517   scientific echo sounder. We showed that short-finned pilot whales do respond to signals from a

518   scientific echo sounder but this response is subtle, and perhaps akin to an increase in vigilance, and

519   would be impossible to discern from visual observations. The increase in heading variance during

520   exposure was not overt enough for animals to stop foraging or to flee the area. However, the sample

521   size of exposed dives was small, and we do not have complete contextual information for all

522   animals. Contextual variables can strongly affect the response of marine mammals to sound stimuli

523   (Ellison et al. 2012), but our limited sample size precluded their inclusion in the present analysis.

524   Interpretation of these results to infer biological significance is challenging, and we do not know

525   whether these subtle changes in heading variance held any cost to individuals or if continual

526   exposure to echo sounders might create a change in behavior at any measurable level. However,

527   these observations provide the first data on reactions of deep diving odontocetes to a scientific echo

528   sounder and provide a starting point for analysis of baseline diving behavior in short-finned pilot

529   whales.

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869   **Table 1**: Summary of tagging information. Tag ID is based on the Julian day with the letter

870   representing the sequential order in which the animal was tagged (a= first animal tagged that day, b

871   = second), * indicates animal tagged with a version 3 DTAG. ^ indicates animals not considered in the

872   analysis. Sex was obtained from biopsy data, M= male, F=female, U= unknown (animal not biopsied).

873   Total dives indicates the number of dives used per individual, per experimental condition, in the

874   analysis. Highest RL is the highest Received Level of the echo sounder calculated from the tag during

875   the exposure condition for that individual.

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Date	Tag ID	Sex	Total time (hh:mm:ss)	Experimental condition sequence	Experimental condition time (hh:mm:ss)	Total dives	Highest RL (dB re 1 µPa,(range, #of samples))
27-May-11	147a	F	04:24:13	Pre	01:39:40	7	
				Control	01:03:00	4	
				Exposure	01:00:00	3	119 (89-119, 39)
				Post	00:41:23	4	
28-May-11	148a	M	03:01:49	Pre	01:23:25	5	
				Exposure	01:00:00	2	117 (97-117, 24)
				Control	00:38:24	0	
				Post	00:00:00	0	
29-May-11	149b	M	04:17:49	Pre	04:17:49	7	
	149c	U	03:01:17	Pre	01:00:54	1	
				Exposure	01:00:00	6	119 (88-119, 590)
				Control	00:59:00	3	
				Post	00:01:23	0	

Date	ID		Total	Phase	Time	Count	
30-May-11	150a^	U					
30 May-11	150b	U	02:38:51	Pre	02:38:51	8	
4-June-11	155a	U	04:27:49	Pre	01:02:02	0	
				Control	01:00:00	1	
				Exposure	01:00:00	1	123 (91-123, 205)
				Post	01:25:47	2	
5-June-11	156a	U	02:56:04	Pre	02:56:04	3	
7-June-11	158a*^	U					
7-June-11	158b	F	04:23:43	Pre	01:16:19	3	
				Exposure	00:59:43	0	125 (89-125, 155)
				Control	01:00:05	2	
				Post	01:07:36	4	
14-June-11	165a	M	03:08:12	Pre	03:08:12	9	

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888 **Table 2**: State summaries of observed variables for each state

State	Variable	Mean	Median	Min	Max
1	Dive Duration (mins)	13.2	12.4	7.8	24.8
1	Max Depth (m)	444.5	457	30	805
1	Heading Variance	0.537	0.554	0.075	0.958
1	Number of Buzzes	13.2	10.5	0	51
2	Dive Duration (mins)	3.7	3.7	1.8	6.7
2	Max Depth (m)	31.9	26	20	117
2	Heading Variance	0.130	0.063	0.003	0.532
2	Number of Buzzes	0	0	0	0

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901 **Table 3:** Transition probabilities for both states and number of dives within each state

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	State 1	State 2	Number of dives
State 1	0.67	0.33	48
State 2	0.13	0.87	27

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923 **Table 4:** Model outputs from the best model. Parameter estimates and standard errors are on the

924 scale of the link function (log). The test p-values are from a sequential Wald test (GEE-based

925 ANOVA; H_0: covariate coefficient(s) = 0). P-values were not used in model selection.

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Variable	Estimate	Robust Standard Error	p-value
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

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Figure Legends

Fig. 1: State allocation per dive for each of the four observed variables. Circles represents state 1, triangles represent state2.

Fig. 2: Dive profiles, for all dives from all individuals, per state. Top panel state 1, bottom panel state 2. Colors represent experimental condition. Dark grey are dives 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 exposure condition (red lines) in both states.

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 indicates highest probability of being in State 2. Grey indicates data classified as surface and not used in the model and black asterisk indicate individual foraging buzzes. Exposed animals shown in top five panels, red block indicates active condition, gold block indicates control condition. (Note different x axis range).

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 for the top plot and mean pitch = 0.08 for the bottom.

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