Spatio-temporal variation in click production rates of beaked whales: implications for passive acoustic density estimation

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24 Passive acoustic monitoring has become an increasingly prevalent tool for estimating density of

25 marine mammals, such as beaked whales, which vocalize often but are difficult to survey

26 visually. Counts of acoustic cues (e.g., vocalizations), when corrected for detection probability,

27 can be translated into animal density estimates by applying an individual cue production rate

28 multiplier. It is essential to understand variation in these rates to avoid biased estimates. The

29 most direct way to measure cue production rate is with animal-mounted acoustic recorders. We

30 utilized data from sound recording tags deployed on Blainville's (*Mesoplodon densirostris*, 19

31 deployments) and Cuvier's (*Ziphius cavirostris*, 16 deployments) beaked whales, in two

32 locations per species, to explore spatial and temporal variation in click production rates. We did

33 not detect spatial or temporal variation within the average click production rate of Blainville's

34 beaked whales when calculated over dive cycles (including silent periods between dives);

35 however, spatial variation was detected when averaged only over vocal periods. Cuvier's beaked

36 whales exhibited significant spatial and temporal variation in click production rates within vocal

37 periods and when silent periods were included. This evidence of variation emphasizes the need

38 to utilize appropriate cue production rates when estimating density from passive acoustic data.

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43 PACs numbers: 43.30.Sf, 43.80.Ka

I. INTRODUCTION

Robust monitoring of the size or density of wild animal populations over time is a prerequisite for making informed management or mitigation decisions: e.g., to prioritize conservation for populations in decline, or for protecting areas with high densities of individuals. It can be challenging to estimate density for marine mammals, particularly for deep diving and oceanic species inhabiting offshore waters. Visual surveys of such species can result in estimates with high uncertainty: brief surfacing intervals and small visual detection ranges limit sample size, and spatial coverage is limited by the high costs of ship-based studies (Barlow, 1999). Passive acoustic monitoring (PAM) allows for the detection of sounds naturally produced by vocalizing animals and provides an alternative means to estimate density (Marques *et al.*, 2013). Acoustic surveys can be more cost-effective than visual surveys because PAM is less limited by sea-state, requires less human presence, and can be carried out during both day and night. In the marine environment, acoustic data can be collected by towed or fixed hydrophones (Marques *et al.*, 2013) and, most recently, by sound recorders on autonomous vehicles (Klinck *et al.*, 2012; Baumgartner *et al.*, 2013). PAM-based density estimates have been calculated for a range of cetacean species (e.g., Marques *et al.*, 2009; Marques *et al.*, 2011; Martin *et al.*, 2013, Fais *et al.*, 2016), and the method is also becoming increasingly prevalent in terrestrial ecology, most notably for songbirds (Efford *et al.*, 2009), but also for other taxa including amphibians (Stevenson *et al.*, 2015) and primates (Heinicke *et al.*, 2015).

Acoustic detections from a line transect survey can be used to estimate distances to vocal animals based on target motion analysis and the angle of arrival of their vocalizations received by the recording system (Barlow *et al.*, 2013). These distances can then be used within standard

67 methods, such as distance sampling, to estimate animal density (Buckland *et al*., 2001).

68 However, when such data are not available, often PAM frameworks rely on cue-counting density

69 estimation approaches, which require counts of cues (e.g., individual vocalizations) attributed to

70 the study species (Buckland, 2006) and the corresponding cue production rate. The number of

71 cues detected, when corrected for detection probability within the area and timescale monitored,

72 gives the overall cue density (number of cues per unit area and time) for a recording time

73 window. Cue density can then be translated into an estimate of animal density by applying an

74 individual cue production rate multiplier (average number of vocalizations per animal per unit

75 time) (Buckland *et al*., 2001). Unfortunately, due to the cost and difficulty of collecting such

76 data, accurate estimates of cue production rates are unavailable for many cetacean species, while

77 those that have been calculated are often derived from small sample sizes from specific times

78 and locations. For example, Martin *et al*. (2013) presented a preliminary 'boing' production rate

79 for minke whales (*Balaenoptera acutorostrata*) based on passively collected data from an

80 acoustic focal follow of a single tracked animal. Cue production rate multipliers obtained from

81 acoustic focal follows using recorders in the habitat of the animals (see also Matthews *et al*.,

82 2001) are useful, but not ideal, due to periods of silence between calls that can lead to focal

83 animals being lost, or calls being missed or mis-attributed.

84

85 Animal-mounted sound recording tags offer one of the few reliable methods to sample individual

86 cue production rates in a natural environment (Johnson *et al*., 2009). Continuous recordings of

87 sound and movement made by these tags also enable estimation of vocal production rates as a

88 function of behavior. It should be noted, however, that the relatively short recording time

89 (typically <1 day) of these devices could result in biased estimates of cue production rate if

90   animals are more accessible for tagging in certain behavioral states or locations. Moreover, it is

91   vital to be able to reliably distinguish sounds produced by a tagged animal from those made by

92   conspecifics in order to achieve an accurate cue production rate estimate, free from false

93   positives; however this is not always straightforward, especially in social species (Pérez *et al*.,

94   2016; Arranz *et al.*, 2016; Johnson *et al*., 2009).

95

96   Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales produce

97   broadband echolocation clicks during deep foraging dives at regular intervals of 0.2-0.6 seconds

98   (Johnson *et al*., 2006; Madsen *et al*., 2005). In both species, the regular clicks are interspersed

99   with fast click trains, known as buzzes, indicating attempts to capture prey, and occasional

100 pauses (Johnson *et al*., 2004). Beaked whales perform long silent periods of shallow diving

101 between deep foraging dives (Tyack *et al*., 2006a) and, as a consequence, their overall vocal duty

102 cycles are low: 28% for Cuvier's and 17-19% for Blainville's (Barlow *et al.,* 2013; Arranz *et al.*,

103 2011). The long silent periods mean that obtaining acoustic cue production rates solely from

104 periods when animals are vocally active (hereafter referred to as vocal periods) would lead to

105 significant underestimation of animal density (Marques *et al.*, 2009). As such, cue rates for use

106 as multipliers in long-term passively collected acoustic density estimates for beaked whales must

107 include both naturally silent and vocal periods (Marques *et al.*, 2009). As discussed, acoustic

108 focal follows are ineffective when focal animals conduct long periods of silence and are easily

109 lost, therefore, acoustic tags provide the most effective method to estimate cue production rates

110 of beaked whales.

111

112   An optimal cue for passive acoustic density estimation is a discrete unit that is produced at a rate

113   that is largely independent of external covariates, particularly density, and can be reliably

114   identified, detected and classified (Marques *et al*., 2013). Sound-recording tags mounted on

115   beaked whales are able to provide reliable click production rates specific to individuals because

116   clicks produced by the tagged animal contain low frequency energy that is absent in far-field

117   clicks from conspecifics (Johnson *et al*., 2009). Moreover, the clicks can be detected at ranges of

118   several kilometers in quiet conditions (Ward *et al*., 2008) and have a distinctive frequency

119   modulation, when observed close to the acoustic axis, that distinguishes them from clicks of

120   other toothed whales (Johnson *et al*., 2006), making them a suitable cue for detection and

121   classification within a passive acoustic framework. Previous cue-based density estimates have

122   been made from acoustic data for Cuvier's and Blainville's beaked whales (Moretti *et* al., 2006;

123   Marques *et al*., 2009; Moretti *et al*., 2010, Kusel *et* al., 2011; Hildebrand *et* al., 2015). Moretti *et*

124   *al*. (2006) estimated animal density without using individually-specific cue production rates,

125   while the other studies applied cue rates obtained from limited numbers of acoustic tag

126   deployments, or from previous estimates in the literature.

127

128   Cue production rates can vary with context (e.g., Matthews *et al*., 2001); therefore, to avoid

129   biased density estimates, it is important that rates used as multipliers are appropriate for the time

130   and location of the passive acoustic survey. An ideal cue rate multiplier would be collected from

131   individuals selected at random from the population, concurrently with the passive acoustic

132   survey, and an optimum survey design to collect this secondary data would sample individuals

133   across the entire spatial and temporal range of the intended PAM survey. If the collection of

134   concurrent cue rate data is not possible, statistical models informed by large, reliable datasets

135 must be relied upon to predict the most appropriate cue rate. However, when using models to

136 predict cue rate, it is only reasonable to extrapolate within the range of available covariates, and

137 only when the relationships between cue rate and the main factors affecting cue rate are known.

138

139 Data from sound recording tags indicate that click production rates within the echolocation phase

140 of beaked whale foraging dives show substantial fine-scale variation, possibly tracking changing

141 prey density and body turning rates (Madsen *et al.*, 2013). It is not essential that cue production

142 is consistent over short timescales within animals, because it is the *average* cue rate that is of

143 interest and this can be obtained with high precision by sampling over a sufficiently long time

144 period. Nevertheless, consistency in the average rate between individuals is desired as it is

145 typically this value that contributes to the variance (i.e., uncertainty) of the overall average cue

146 rate. Cue production rates could, however, also vary over longer temporal scales and by location,

147 neither of which has been examined in beaked whales. Vocal period click rate is known to vary

148 at a diel scale for other toothed whale species including Risso's dolphins (*Grampus griseus*)

149 (Soldevilla *et al.*, 2010a) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*)

150 (Soldevilla *et al.*, 2010b), based on data collected by autonomous bottom-mounted hydrophones.

151 There is also evidence that groups of mostly male sperm whales (*Physeter macrocephalus*) in

152 high latitudes off New Zealand conduct longer silent periods between dives than other sperm

153 whale populations with different social structures (e.g. matrilineal groups, which are mainly

154 found in the tropics and sub-tropics (Whitehead, 2002)) suggesting that an average cue

155 production rate for this species could be spatially specific (Douglas *et al.*, 2005).

156

157 This study aims to quantify cue production rate metrics, relevant to Blainville's and Cuvier's

158 beaked whales, which are appropriate for passive acoustic density estimation. Using the most

159 comprehensive beaked whale tag dataset available, with a reasonable quantity of samples from

160 two locations for each species, this study tests for spatial and temporal differences that could

161 represent potential sources of bias when estimating cue production rate metrics for beaked

162 whales. The dataset provides the basis for models predicting click production rates for both

163 species, over the four locations and a range of temporal scales.

164

II.   METHODS

166 Suction-cup sound and movement recording tags (DTAGs, Johnson and Tyack, 2003) were

167 deployed on Cuvier's and Blainville's beaked whales at four sites (Bahamas, Canary Islands,

168 Ligurian Sea and southern California) between 2003 and 2013 (**Table I**). Blainville's beaked

169 whales were tagged in May (11 dives), June (8 dives), August (6 dives), September (12 dives)

170 and October (33 dives). Cuvier's beaked whales were tagged in June (30 dives), July (8 dives)

171 and September (10 dives). Both DTAG2s and DTAG3s were deployed, with 96, 192 or 240kHz

172 acoustic sampling of one (in 2003) or two (all other years) hydrophone channels, and 50Hz or

173 200Hz sampling of a pressure sensor and three-axis accelerometer (Tyack *et al*., 2006a). Tags

174 were deployed from small rigid-hulled inflatable boats using a 5m long hand-held pole (Johnson

175 *et al*., 2006) and remained attached for a mean of 11.7 hours, ranging from 1.9 to 24.0 hours.

176 Following detachment, the tags were collected from the sea surface *via* VHF radio detection.

177 Data were stored to flash memory in the tag and downloaded upon retrieval (Johnson and Tyack,

178 2003).

179

180   The data utilized in this study were not collected specifically for the analysis of click production

181   rate. In 2010 and 2011, the two Cuvier's beaked whales in southern California were part of a

182   controlled exposure experiment during which they were exposed to mid-frequency active (MFA)

183   sonar. The acoustic behavior of these whales was significantly altered during the exposure

184   (DeRuiter *et al*., 2013), so only the dives prior to the controlled exposure were included in this

185   analysis, hence the low final sample size for southern California (**Table I**). Moreover, incidental

186   MFA sonar was also audible in the remaining 2011 dive (DeRuiter *et al*., 2013), potentially

187   leading to bias, but as this dive was not obviously altered by the sound exposure it was included

188   in the analysis due to the low sample size.

189

190   All tagged animals were photographed for photo-ID purposes. No photo-ID matches were found

191   across tag deployments on Cuvier's beaked whales, although individuals can be difficult to

192   distinguish and the possibility of re-tagging within this species cannot be dismissed. In El Hierro,

193   three Blainville's beaked whales were tagged in multiple years; one twice, and two on three

194   occasions (Arranz *et al*., 2011). Cue rate values from each of these animals appeared to be

195   randomly distributed within the range of the other individuals, so each tag deployment was

196   treated as an independent unit.

197

198   Acoustic analyses were performed using custom tools from the DTAG toolbox (Johnson, 2014)

199   in MATLAB (The MathWorks, Inc, version R2013a). The vocal period in each dive was defined

200   as the interval from the first to the last click recorded during the dive. These clicks were

201   identified manually by inspection of spectrograms (512 sample FFT (Fast Fourier Transform)

202   with a Hamming window and 50% overlap) formed from successive 15s intervals of the sound

203   recording. Sound data during each vocal period were then passed through a supervised click

204   detector to identify likely clicks from the tagged animal. The detector first applied a bandpass

205   filter (20-60 kHz, covering the frequency range of clicks from both species) and then computed

206   the Hilbert envelope of the filtered sound. Transients above a threshold, adjusted to track the

207   average signal strength in 10 s intervals, were retained as potential clicks. For stereo DTAGs, the

208   angle-of-arrival of each transient was computed from the time difference of arrival of the signal

209   at the two hydrophones in the tag (Johnson *et al.*, 2009). Transients were plotted in a time vs

210   angle-of-arrival display, colored by received level. Trained analysts using this display ascribed

211   clicks to the tagged animal when they had a consistently high received level and came from a

212   consistent angle of arrival. For the 4 monaural tag recordings, transients were plotted in a time vs

213   received level display allowing the generally weaker and more variable clicks from other animals

214   to be readily separated from those of the tagged whale. Selected clicks were subsequently

215   reviewed by visually examining spectrograms to check for missed clicks and false positives.

216   Sounds produced by the tagged animal could be verified in spectrograms as they contained high

217   energy at low frequencies due to the placement of the tag behind the directional sound source

218   and reverberation within the body (Johnson *et al.*, 2009). The result was a vector of times at

219   which clicks were produced by the tagged animal during each dive. Clicks with inter-click

220   interval (ICI) <0.1s were omitted from the analysis to exclude buzzes (Madsen *et al.*, 2005).

221   Buzz clicks are much less likely to be detected by passive acoustic monitoring systems than

222   regular clicks due to their 10-20dB lower source level (Madsen *et al.*, 2013).

223

224 A dive cycle was defined as the time between the start of a dive containing a vocal period and

225 the start of the next dive containing a vocal period (sensu Tyack *et al.*, 2006a and Arranz *et al.*,

226 2011) (**Figure 1**).
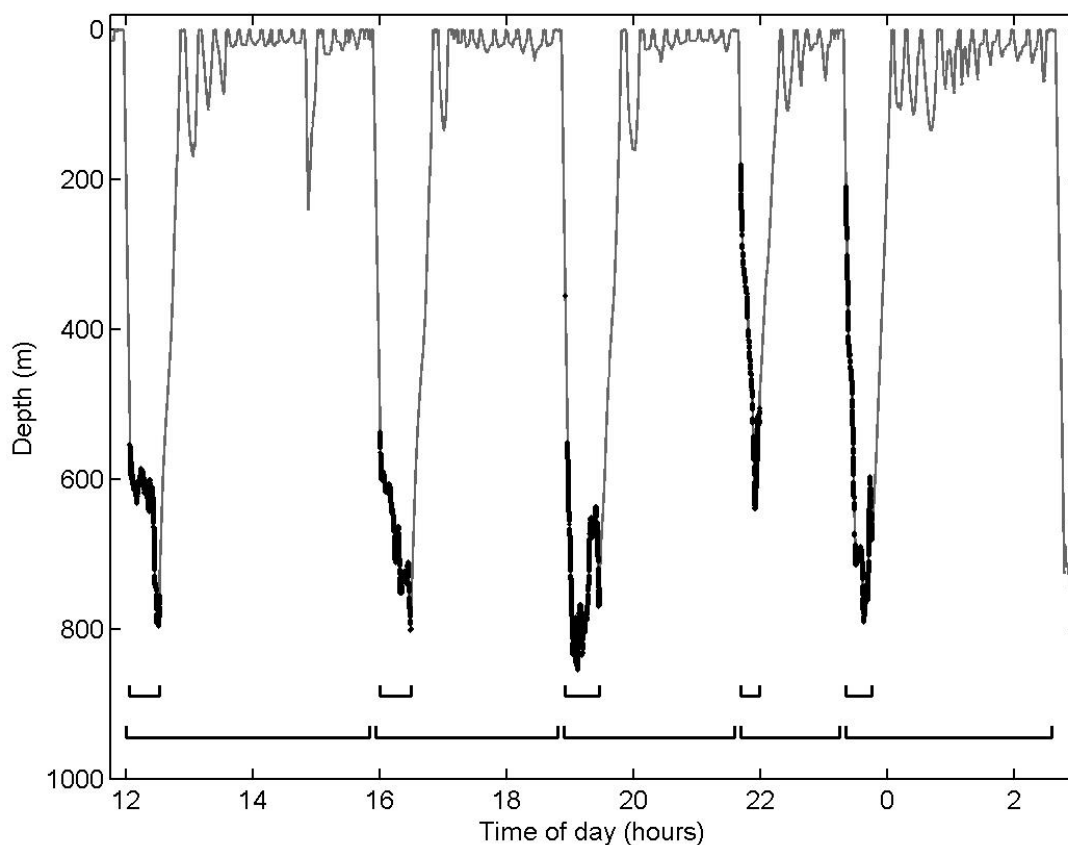
227

228 **FIGURE 1**: Example dive profile of a Blainville's beaked whale tagged in the waters adjacent to

229 El Hierro, Canary Islands. Bold sections indicate the presence of foraging clicks. Shorter, upper

230 markers delineate vocal periods, while lower, longer markers indicate the lengths of individual

231 dive cycles. The final dive featured tag detachment and was not analyzed.

232

233 Two click rate metrics were calculated within each dive cycle: (i) the vocal period click

234 production rate, i.e., the number of clicks in a vocal period divided by the vocal period length (in

235 seconds), and (ii) the dive cycle click production rate, i.e., the number of clicks in a vocal period

236 divided by the length of the dive cycle containing this period (in seconds). The sample size of

237 these two metrics differed (**Table I**): in some tag records, the final dive cycle was incomplete

238 due to tag detachment; the final dive cycle length could not be calculated for these records.

239 However, if the final dive contained a complete vocal period the first metric could be calculated.

240

241 Although Cuvier's and Blainville's beaked whales are reported rarely to produce sounds outside

242 of deep foraging dives (Tyack *et al*., 2006b; Aguilar de Soto *et al*., 2012), all dives exceeding

243 approximately four body lengths in depth (24m for Cuvier's and 20m for Blainville's) were

244 checked for clicking within 30 seconds before and after their maximum depth. The depth limits

245 were selected graphically from dive profiles to exclude frequent short submersions between

246 respirations which contained confounding surface water noise. 97.5% of dives with maximum

247 depth exceeding 400m contained a vocal period, therefore this threshold was used to define a

248 deep foraging dive. Three dives exceeding 400m were silent, and fives dives with maximum

249 depths shallower than 400m also contained clicking. The impact of these eight anomalous dives

250 on the results will be discussed. Long pauses (of more than a minute) within clicking are rare

251 during deep foraging dives (Tyack *et al*., 2006b), thus all vocal periods were expected to be

252 identifiable by the presence of clicks within the one minute defined analysis window. Deep dives

253 without clicks in the 30-second windows either side of maximum depth were checked throughout

254 their entire duration for unusual vocal activity before being deemed silent.

255

256 To investigate spatial and temporal variation in click production rates, and to identify covariates

257 that explained most of the variation present, statistical models were fitted to each of the four

258 click data sets (i.e., two click production rates per species). Clicking rate was not modelled

259 directly, instead, 'total number of clicks' was chosen as a Poisson distributed response variable

260 (with a log link function) and an offset, either 'length of vocal period (seconds)' or 'length of

261 dive cycle (seconds)', was included in the model as appropriate. The model outputs, once

262 converted to the response scale, were thus click production rates per second. Runs tests revealed

263 the presence of weak autocorrelation within model residuals due to longitudinal sampling, i.e.,

264 multiple observations of the same animal over time. Generalized Estimating Equations (GEEs)

265 were therefore used in R (version 3.3.1; package 'geepack', version 1.2-0 (Højsgaard *et al*.,

266 2006)), with 'Tag ID' specified as the clustering factor, ordered by dive index. An

267 'independence' correlation matrix and robust standard errors were used in light of only weak

268 autocorrelation in click rates between successive dives within individuals (Overall and

269 Tonidandel, 2004; Højsgaard *et al*., 2006) (see Quick *et al*. (2016) for a similar approach). GEEs

270 are appropriate for data containing a large number of clusters (tag deployments) with relatively

271 few observations (dives or dive cycles) per cluster (Bailey *et al*., 2013).

272

273 Potential covariates of interest were identified *a priori* and checked for collinearity by computing

274 correlograms. Although the DTAG dataset analyzed here is the most comprehensive to date for

275 these two beaked whale species, sample sizes were not large (**Table 1**). Each species was tagged

276 in one location per year, resulting in 'location' and 'year' being confounded. As the dataset

277 contained two years with a Cuvier's sample size of one dive, 'location' was included as an

278 explanatory covariate rather than 'year' in order to generate models using the greatest possible

279 sample sizes per category. Confounding also occurred within the Blainville's beaked whale data

280 with respect to 'location' and 'month'; El Hierro fieldwork was conducted during May, June and

281　October while the Bahamas were sampled in August, September and October. 'Month' was

282　therefore excluded as a covariate within the Blainville's beaked whale models. Initial

283　explanatory covariates were therefore: location as a factor covariate; month, also as a factor

284　(Cuvier's only); a binary covariate for whether the dive was the first dive post tag-attachment in

285　order to account for any short-term tagging effects; and time of day of the dive (as a factor

286　covariate comprising six values: night (sun angle below -10° from the horizon), dawn (-10° to

287　+10° sun angle), morning, midday (11am-1pm), afternoon and dusk (+10° to -10° sun angle)).

288　The time of day of the dives breaks down to: morning (5 Blainville's dives); midday (13

289　Blainville's, 3 Cuvier's dives); afternoon (19 Blainville's, 17 Cuvier's dives); dusk (7

290　Blainville's, 11 Cuvier's dives); and night (26 Blainville's, 17 Cuvier's dives). These variables

291　were all entered into the models as main effects; due to the relatively small sample sizes, no

292　interaction terms were fitted.

293

294　Backwards selection, using marginal ANOVA, from the four (two species with two response

295　variables each) initial full models was used to determine which covariates were significant (i.e.,

296　$p \leq 0.05$) and therefore retained in the final models (Zuur *et al*., 2009). Model fit was checked by

297　examining plots of fitted values against observed values, and calculating concordance correlation

298　values (Lin, 1989; Scott-Hayward *et al*., 2013).

299

III.　RESULTS

301　A total of 118 vocal periods and 106 dive cycles from 35 tag deployments were analyzed from

302　the four study sites (**Table I**). The overall pattern of vocal behavior was similar to that reported

303　by Tyack *et al*. (2006a) for a subset of the same data: deep foraging dives, each containing a

304 vocal period of regular clicking, were interspersed with shallower, silent dives. Three deep dives

305 (maximum depth >400m) were silent: one Cuvier's dive, and two dives by the same Blainville's

306 beaked whale. These three dives were all steep V-shaped dives with no significant bottom phase,

307 occurred directly after deep dives with vocal periods, and were less than half the duration of deep

308 dives with vocal periods.

309

310 The vast majority of shallow dives (<400m) were silent, however five of 157 Cuvier's dives with

311 maximum depth between 24m and 400m were not silent. The five shallow dives with clicks

312 occurred during four different tag deployments in Liguria. The number of clicks recorded in each

313 vocal shallow dive ranged from 39 to 219 and clicking persisted for between 180 and 336s.

314 These clicks accounted for approximately 0.45% of the total click production of Cuvier's beaked

315 whales recorded here. As these clicks occurred outside of our definition of vocal periods they

316 were not added to the vocal period click count totals. However, in order to incorporate these

317 additional data, three of these click counts were included in the total counts for their enveloping

318 dive cycles, while the remaining two vocal shallow dives occurred before the first deep dive and

319 corresponding dive cycle in their respective records and so were excluded. All Blainville's dives

320 with maximum depth less than 400m were silent.

321

322 The total number of clicks produced during a vocal period ranged from 1001 (during the shortest

323 vocal period of 8mins 46s) to 7558 (during the longest vocal period of 46 mins 18s) for

324 Blainville's beaked whales, and 1387 (during the second shortest vocal period; the shortest vocal

325 period was 23mins 35s and contained 2428 clicks) to 6097 (during the longest vocal period of 54

326 mins 41s) for Cuvier's beaked whales. A comparison of diving and vocal parameters between the

327 two species and in the four locations (results provided in order for Bahamas and El Hierro in the

328 case of Blainville´s, and for Liguria and southern California for Cuvier´s) indicated that Cuvier's

329 beaked whales clicked at a slower rate (1.67 clicks/sec ± 0.16 and 1.46 clicks/sec ± 0.14) during

330 vocal periods than Blainville's (2.59 clicks/sec ± 0.15 and 2.38 clicks/sec ± 0.06), and tended to

331 perform longer vocal periods (35.2 mins ± 5.7 and 35.1 mins ± 9.1, compared to 29.9 mins ± 5.8

332 and 24.5 mins ± 2.3) (**Figure 2; Table II**). Values given are mean values with standard

333 deviations weighted by the number of dives in the enveloping tag record. Furthermore, the dive

334 cycle lengths of Cuvier's beaked whales in Liguria (133.0 mins ± 29.8), which represent 90% of

335 the data for this species, were shorter than those of Blainville's beaked whales (181.0 mins ±

336 53.2 and 145.0 mins ± 31.0), resulting in similar average dive cycle click rates for the two

337 species (0.50 clicks/sec ± 0.06, compared to 0.50 clicks/sec ± 0.11 and 0.43 clicks/sec ± 0.14)

338 (**Figure 3; Table II**). In comparison, the five Cuvier's tagged in southern California performed

339 substantially longer dive cycles (228.0 mins ± 47.4), resulting in an average dive cycle click rate

340 (0.24 clicks/sec ± 0.08) approximately half that of Blainville's, and of the Cuvier's tagged in

341 Liguria (**Figure 3; Table II**). Note that this result should be treated with caution due to the small

342 sample size and potentially confounding MFA sonar exposure. In all cases, between-individual

343 variation was higher in dive cycle click production rates than vocal period click production rates

344 (**Coefficients of variation, Table II**).

345

346
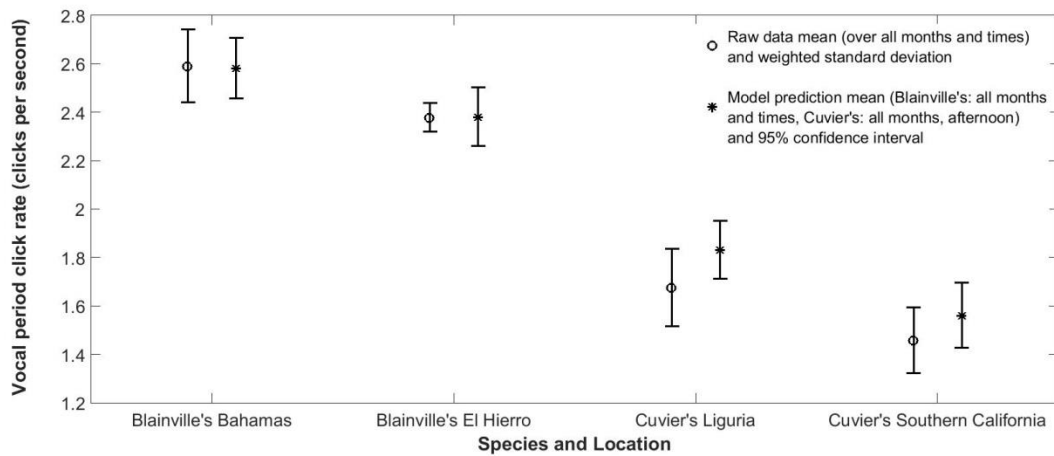
FIGURE 2: Raw and modelled vocal period click production rates (with weighted standard deviation and 95% confidence interval respectively) for both species, and both locations per species. Due to factor covariates in the Cuvier's model, the modelled predictions are appropriate for any of the modelled months, but are only relevant for afternoons.

351
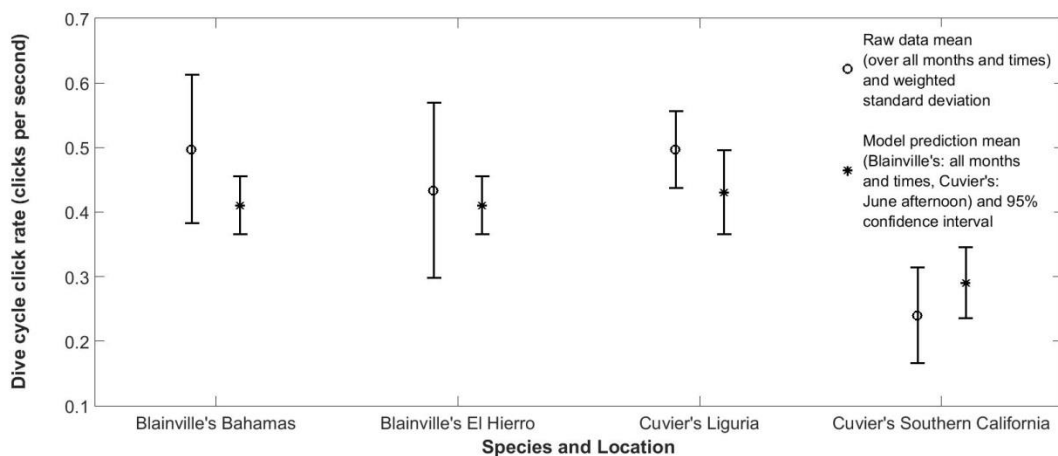
FIGURE 3: Raw and modelled dive cycle click production rates (with weighted standard deviation and 95% confidence interval respectively) for both species, and both locations per

354 species. Due to factor covariates in the Cuvier's model, the modelled predictions are only

355 relevant for June afternoons.

356

357 As anticipated from the raw data (summarized in **Table II**), the models predicted that the vocal

358 period click production rate of Blainville's beaked whales (averaging 2.38 to 2.58 clicks/sec) is

359 approximately twice that of Cuvier's beaked whales (with averages ranging from 1.27 to 1.83

360 clicks/sec) (**Figure 2; Table III**). However, the dive cycle click rates are very similar between

361 the two species (with averages ranging from 0.29 to 0.52 clicks/sec), excepting the limited data

362 from southern Californian Cuvier's beaked whales (which ranged from 0.18 to 0.35 clicks/sec)

363 (**Figure 3; Table III**). Both the dive cycle and the vocal period click rates for the southern

364 California Cuvier's are notably lower than for the Ligurian whales. While the southern California

365 Cuvier's data from 2011 appears anomalous within the dataset, its removal does not lead to any

366 significant changes in the results due to the small sample size from California. Effect sizes and

367 standard errors were produced on the link scale, and converted to the response scale by

368 exponentiation of the effect size, and via the Delta method for the standard errors (Oehlert,

369 1992).

370

371 Concordance correlation values indicated that the vocal period click production rates were

372 modelled well (Blainville's 0.97, Cuvier's 0.80), while the dive cycle rate models resulted in

373 adequate fits (Blainville's 0.27, Cuvier's 0.35). For both species, location was retained in the

374 GEE models for click rate averaged over vocal period. This suggests that spatial differences in

375 click rate are present within each species, however it must be reiterated that the confound

376 between the location and year covariates means that this could also, or instead, reflect annual

377 differences in vocal period click rate. When the click rates were averaged over dive cycles,

378 location was retained only within the Cuvier's beaked whale model, implying that on a dive

379 cycle scale, Blainville's beaked whale click rates are not spatially (or annually) specific.

380

381 No further explanatory covariates were retained for either of the two Blainville's click

382 production rate models. For Cuvier's beaked whales, time of day was retained in both vocal

383 period and dive cycle click rate models, with month additionally retained in the dive cycle click

384 rate model. There was no evidence for a significant effect of tagging (comparing the first dive

385 post-tagging to later dives) within click production rates for either species.

386

387 Within the entire data set for both species, no dives were recorded during dawn and only five

388 dives were recorded during the morning. This gap occurred because most tags were attached

389 during late morning or afternoon and detached before the following morning. The Cuvier's

390 beaked whale that carried a tag for 24 hours was part of a controlled exposure experiment, and

391 only data from before the experiment were retained. All morning dives were performed by

392 Blainville's beaked whales; hence the lack of dawn or morning estimates for both of the Cuvier's

393 click rates (**Table III**).

394

395 It was not possible to test directly for long-term temporal effects (i.e., year) due to the small

396 sample sizes within some years and confounding with location; however, exploratory plots

397 indicated the presence of some inter-annual variation within locations in the vocal period and

398 dive cycle click rates of both beaked whale species (**Figure 4**).

19
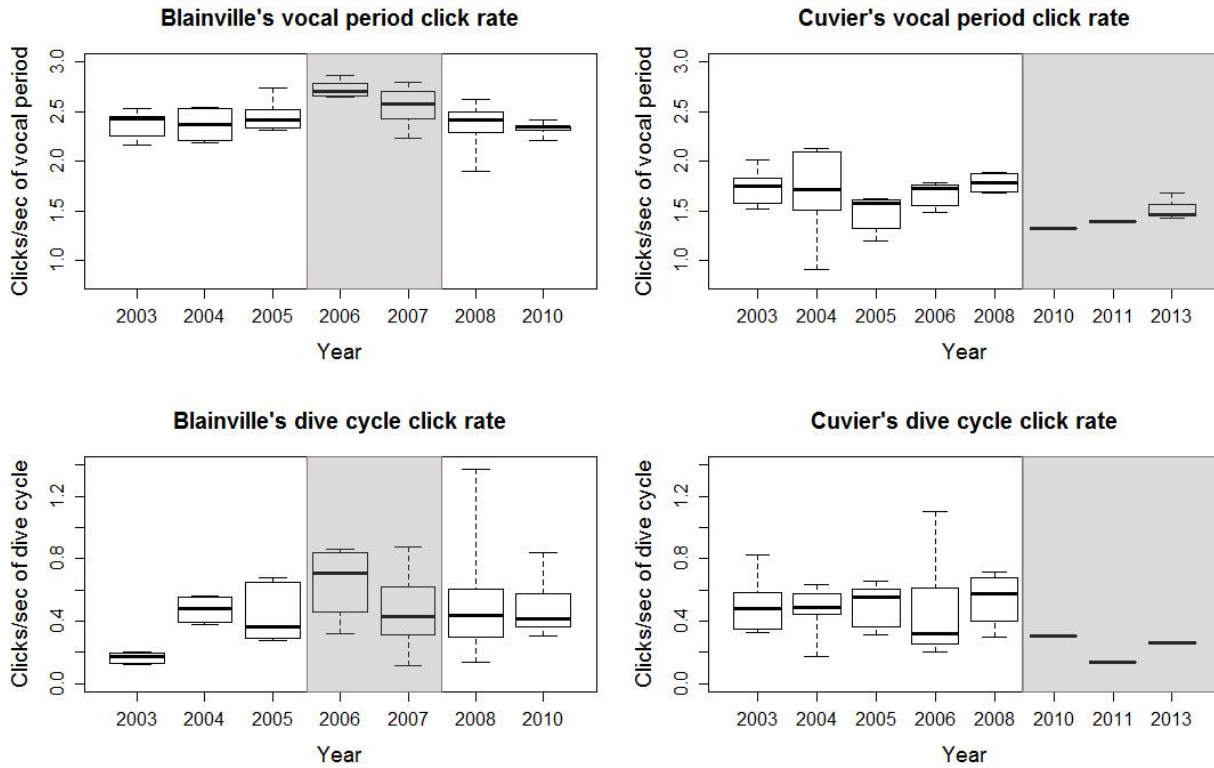
FIGURE 4: Inter-annual variation in vocal period and dive cycle click production rates for Blainville's (left) and Cuvier's (right) beaked whales. Box plots consist of median, interquartile range and maximum/minimum extremes. In the Blainville's data, boxes in white areas represent animals tagged in El Hierro and boxes in grey areas (2006 and 2007) indicate tags deployed in the Bahamas. In the Cuvier's plots, boxes in the white area represent Liguria, and boxes in the grey area (2010, 2011 and 2013) are southern California deployments. See Table I for respective sample sizes. Y axes scales differ between vocal period plots (upper) and dive cycle plots (lower).

IV.   DISCUSSION

Acoustic surveys provide a powerful tool to study the occurrence of marine mammals, and may be the most effective way of assessing populations with low probability of visual detection, such as beaked whales (Barlow *et al.*, 2013). In a cue-counting density estimation framework, individual whales cannot be distinguished and the number of whales is solely estimated from the number of cues detected. The increasing use of moored hydrophones to study whale occurrence and distribution (Marques *et al.*, 2013) emphasizes the need to obtain good quality data on relevant cue production rates to improve the accuracy of cetacean density estimates from acoustic point samples.

A. Cue production rate multipliers for passive acoustic density estimation

A cue-based method to estimate animal density from passive acoustic detections, requires a reliable cue production rate multiplier. Acoustic recording tags offer a practical solution to sample the acoustic behavior of marine mammals in a natural environment providing precise cue production rates from individual animals which are difficult to obtain by other means (Johnson and Tyack, 2003). When tags are deployed at random, concurrent with a passive acoustic survey, tag data can be used to calculate an average population cue rate multiplier that is directly relevant to the survey. However, this is typically not possible and it is often necessary to rely on measurements taken at other times and places. In such cases, it is essential to understand the cue production behavior of the study species, and its variability with context, to establish a reliable cue production multiplier. A large dataset from tag deployments over a range of times, locations and external covariates, allows the development of statistical models for the prediction of cue

433   rate within the range of modelled covariates. Here, GEEs were used to model click production

434   rates of Blainville's and Cuvier's beaked whales, and these models demonstrated that spatial and

435   temporal variation can be present in cue production rates with the potential to bias animal density

436   estimates that do not use specific multipliers.

437

438   Cue rates can be quantified in multiple ways and the most appropriate measure for density

439   estimation depends on the acoustic behavior of the species and the monitoring duration of the

440   passive acoustic survey (Marques *et al*., 2013). For species that produce sound in bouts, such as

441   beaked whales, silent periods must be included in cue rate quantification to avoid

442   underestimation of density. Given their stereotyped diving behavior, dive cycle click rate is

443   therefore the correct metric for acoustic density estimation of beaked whales, as it integrates

444   vocal output over complete behavioral cycles. Vocal period click production rates were

445   presented here for comparison and to help interpret variability in the dive cycle rates.

446

447   **B. Spatio-temporal variation in beaked whale click production rates**

448   For Blainville's beaked whales, significant variation was present within vocal period click rate,

449   although the confounding between location and year in this dataset meant that spatial variation

450   could not be distinguished explicitly from inter-annual variation. In contrast, the dive cycle click

451   production rate of Blainville's beaked whales, which is directly relevant as a multiplier for

452   density estimation using PAM, was not found to vary significantly over time or space. This lack

453   of statistical significance should not be interpreted as confirmation of lack of biological

454   significance. Although the estimated click rates were very similar between sites, they were

455   enveloped by wide confidence intervals, giving an indication that the rates could potentially

456   vary, but the variation may not be significantly detectable. A larger sample size would provide

457   greater confidence.

458

459   The modelled click production rates of Cuvier's beaked whales indicated the presence of

460   significant variation at both vocal period and dive cycle scales. Diel and monthly differences of

461   up to 40% were apparent within both Cuvier's cue production rate metrics, and differences of up

462   to 15 and 30% in click production rate were detected between locations for vocal period and dive

463   cycle click rates respectively. The small sample size in southern California and the confound

464   between location and year in the data lead to some uncertainty, but, irrespective of the cause of

465   variation, its presence indicates that cue rate multipliers for Cuvier's beaked whales should be as

466   specific to the PAM survey as possible in order to estimate animal density reliably.

467

468   Temporal variation in Cuvier's click rates occurred at a range of scales. At the finest scale, both

469   vocal period and dive cycle click rates varied with time of day. Deep diving marine mammals,

470   such as beaked whales, target prey near the seafloor (benthic boundary layer) or vertically

471   stratified prey layers that undergo diel migrations through the water column (Benoit-Bird *et al*.,

472   2001; Arranz *et al*., 2011). Beaked whales may change foraging strategy or target different prey

473   species (affecting vocal period rate), or forage at different depths (thus altering transit and

474   recovery time, and therefore dive cycle click rate) depending on the time of day. Baird *et al*.

475   (2008) previously noted diel changes in diving activity of Cuvier's beaked whales, but not in the

476   rate of deep foraging dives, although the sample size was not large enough to test for statistical

477   significance. Arranz *et al*. (2011) noted diel variation in the depth at which Blainville's beaked

478   whales started clicking in deep foraging dives, but no diel change was detected in the depth

479   distribution of clicking time. Here, we found no evidence for diel variation in either of the two

480   click production rates for Blainville's beaked whales.

481

482   Cuvier's dive cycle click rate also varied significantly between months, with the fastest rates

483   predicted during June. Month was not a significant covariate to explain variation in Cuvier's

484   vocal period click rate, however, implying that the inter-month differences reflect changes in the

485   length of silent periods between dives. Variation in target prey or seasonal behaviors, such as

486   mating or nursing calves, may drive these changes in diving behavior. The data for Californian

487   Cuvier's beaked whales was particularly limited in its temporal range, however the modelling

488   approach utilized here allowed for specific predictions for click production rates based on

489   features of the Ligurian Cuvier's beaked whale data. It should be reiterated that extrapolation is

490   only recommended within the range of available covariates.

491

492   While it was not possible explicitly to distinguish spatial variation from inter-annual variation,

493   spatial differences in cue production rate should not be surprising for allopatric populations. Both

494   the physical environment and its prey resources vary spatially, which can lead to differences in

495   foraging behavior; for example, variation in depth of foraging (often a function of bathymetry)

496   may affect the time available for echolocation-based foraging (due to increased transport time

497   from surface to foraging depth), which may in turn affect the duration of vocal periods.

498   Allopatric populations may also target different prey types with different detection ranges, which

499   would be reflected in inter-click intervals of echolocation-based foraging. Spatial separation may

500   also enable differences to manifest in physiology as well as behavior; populations with naturally

501 larger individuals may click at a different rate due to physiological constraints (Fitch and Hauser,

502 1995).

503

504 Exploratory plots (**Figure 4**) aimed at distinguishing between spatial and inter-annual differences

505 indicated possible variation in click rate between years within locations, perhaps reflecting

506 changes in prey between years, or wider contextual changes, such as El Niño events: 2002/3,

507 2004/5, 2006/7 and 2009/10 were El Niño years, while 2007/8 and 2010/11 were La Niña years

508 (NOAA Climate Prediction Center, 2015).

509

510 External variables, such as anthropogenic sound, can also directly influence the diving behavior

511 and vocal output of odontocetes (Weilgart, 2007; Sivle *et al*., 2012). Marine mammals living in

512 industrialized ocean regions may experience anthropogenic noise pollution that can alter both

513 their vocal output and our probability of detecting their sounds (Weilgart, 2007; Aguilar de Soto

514 *et al*., 2006; Ward *et al*., 2011). Here, both species, in all four locations, experienced varying

515 levels of anthropogenic noise. Sounds from 50kHz fish finders were frequently audible in

516 Blainville's data from El Hierro, while Cuvier's beaked whales in the Ligurian Sea were exposed

517 to high levels of ship traffic, which may affect vocal and dive behavior (Aguilar de Soto *et al.*,

518 2006). Although dives conducted during controlled sonar exposures were removed from the

519 Californian Cuvier's data, low levels of incidental navy sonar occurred within the southern

520 Californian tag record from 2011 (DeRuiter *et al*., 2013). Cuvier's beaked whales have been

521 reported to increase the interval between foraging dives in response to sonar (DeRuiter et al.

522 2013), so the increased dive cycle duration observed in the southern California data could have

523 been a result of these sonar exposures. The Blainville's beaked whales tagged around the

524   Bahamas were within an active naval range and were likely subject to sounds from naval sources

525   (Moretti *et al*., 2014). These whales had a higher vocal period click production rate than

526   Blainville´s from the Canary Islands, which may be explained as an adaptation to different prey

527   (Johnson *et al*., 2008). Here we assumed that site-specific anthropogenic sound sources were

528   absorbed within the 'location' covariate, but further work should investigate the relationship

529   between each type of anthropogenic activity and click production rate

530

531   Marques *et al*. (2009) calculated a cue production rate for Blainville's beaked whales from

532   acoustic tag data from five whales tagged in the Tongue of the Ocean, Bahamas in 2005 (a sub-

533   sample of the dataset for the current study). The study calculated a dive cycle click production

534   rate of 0.407 clicks/sec, with a standard error of 0.04 and CV of 9.8%. This estimate is almost

535   identical to the average Blainville's dive cycle click production rate modelled in this study.

536   Moretti *et al*. (2010) utilized the click rate value from Marques *et al*. (2009) for density

537   estimation from a 2008 passive acoustic survey in the same location. The lack of significant

538   temporal variation in Blainville's dive cycle click rates observed in this study corroborates the

539   density estimate calculated by Moretti *et al*. (2010).

540

541   Hildebrand *et al*. (2015) calculated dive cycle click production rates for Cuvier's beaked whales

542   across three locations within the Gulf of Mexico by taking the mean proportion of a dive cycle

543   spent clicking and multiplying by the inverse of the average ICI. This method resulted in dive

544   cycle click production rates of 0.45-0.49 clicks/sec (with CV of 0.09 for each value) across the

545   three sites. While these values lie within the range calculated here for this species in the Ligurian

546   Sea, they are greater than any dive cycle click production rate value calculated for southern

547   Californian Cuvier's, supporting the conclusion that click production rates used for density

548   estimation should ideally be spatially and temporally relevant.

549

550   **C. Caveats and limitations**

551   Beaked whales often surface and dive in groups (Aguilar de Soto *et al*., 2012) and, like all

552   echolocating animals, have the potential to eavesdrop on the vocalizations produced by

553   conspecifics (Dechmann *et al*., 2009). As such, the acoustic footprint of a group of foraging

554   beaked whales may not increase linearly with group size (Tyack *et al*., 2006b). However, beaked

555   whales apparently produce very few social sounds (Aguilar de Soto *et al*., 2012) and foraging

556   theory suggests that density dependence in an individually-obligated foraging sound should be

557   low (Pyke, 1984). Therefore, the rates calculated here ought not to be strongly influenced by

558   group size.

559

560   The short attachment period of suction-cup tags means that there is potential for a significant

561   proportion of the data collected to be biased if the instrumented animal responds to the

562   attachment. To test for this, the models included a covariate for first dive after tagging; its lack of

563   inclusion in the final models implied that first dives were not significantly unusual, suggesting

564   the lack of a strong tagging effect, although the limited sample size means that some effect

565   cannot be ruled out. Similarly, Tyack *et al*. (2006a) did not detect tagging responses in a subset

566   of the same data (N=8). Conversely, Barlow *et al*. (2013) removed all first dive cycles from a

567   dataset that included some of the data here (both species, N=27) due to significantly longer inter-

568   dive intervals immediately subsequent to tagging. Hildebrand *et al*. (2015) also removed first

569   dives from Cuvier's beaked whale tag data (the same Ligurian dataset used here) due to a

570 reduced number of click-positive-seconds. Neither of these effects were detected in the click

571 production rates presented here, however, implying that the effects were not detectable in this

572 larger dataset, or were not directly reflected in click rate.

573

574 Here, the raw data informing the models indicated that a greater level of between-individual

575 variation was present within dive cycle click rates compared to vocal period click rates, implying

576 that the length of a dive cycle is not simply proportional to the length of the encompassed vocal

577 period. This resulted in a better model fit for the vocal period model than for the dive cycle

578 model for both species, suggesting that the variation in dive cycle click production rate was not

579 fully explained by the covariates included in the models. As such, any differences that were

580 present, but within the range of natural variation of the data, may not have been detected for this

581 metric. The backwards selection framework using p-values from the GEE was an adequate

582 model selection method to demonstrate that significant spatiotemporal variability was present in

583 the cue production rate estimates, which was the main aim of our study. However, model

584 selection is a broad and active area of research and other approaches could have been

585 implemented. K-fold cross validation is one such criterion-based method (as opposed to using

586 hypothesis testing) that is particularly good at testing a model's predictive capabilities, as

587 demonstrated by Quick *et al*. (2016).

588

589 It is possible that the tagged beaked whales are not representative of the wider populations from

590 which they were sampled. If certain animals, with particular vocal patterns, are more available

591 for tagging, then the click rates calculated will be biased. Extreme bias could occur if highly

592 vocal animals were found via PAM and then tagged. Animals in this study were found relatively

593 close to shore where they were accessible for tagging from small boats and may, in some cases,

594 belong to resident populations (Claridge, 2013; Falcone *et al*., 2009). As a result, the data may

595 not reflect the vocal behavior of animals in off-shore areas. Both beaked whale species are

596 broadly distributed and can be found associated with a variety of bathymetric features including

597 submarine canyons, seamounts, and abyssal plains (Lanfredi *et al.*, 2016). Although vocal

598 production may well be linked with environmental features, there are significant practical and

599 economic difficulties in sampling animals from these offshore domains.

600

601 The short periods of clicking observed in a small number of shallow Cuvier's dives reveal that

602 vocal output by beaked whales is not exclusive to deep dives. The purpose of the clicks produced

603 at shallow depth is not clear, but we included the counts of shallow clicks within the dive cycle

604 click rates, despite their rarity. These clicks inherently added to the vocal activity of the Cuvier's

605 beaked whales and would be essentially indistinguishable from regular clicks when detected by

606 passive acoustic survey hydrophones (unlike buzz clicks which can be differentiated by their ICI

607 and reduced source level).

608

609 Despite using the most comprehensive beaked whale tag dataset available, confidence in the

610 results of this study is limited by the small sample size. Had a larger data set been available,

611 interaction terms could have been added to the models in order to assess whether the populations

612 displayed independent, and different, responses to each covariate considered (e.g. Soldevilla *et*

613 *al*., 2010b). However, the small sample size and confounded location and year covariates meant

614 that it would not have been feasible to study interactions with this data set. On a global scale,

615 tagging is a rare event: tags are only deployed in good weather conditions, in certain locations

616 and, so far, only on a limited number of species. However, as more tagging data become

617 available, statistical models, such as those used in this study, will be better able to explore

618 variation in click production rate over space and time. If such models are robust with strong

619 predictive power, then it may be possible to predict location-specific and time-specific cue rates

620 for study areas where tagging is not possible. Predictive models can also inform which time

621 periods are most effective for estimating density: e.g., what time of day, or which month of the

622 year, might yield least variation. Given this, efforts to collate and model tagging studies are

623 particularly valuable.

624

625 **D. Collecting click production rates: tags and other techniques**

626 Acoustic tag deployments result in reliable individual-oriented data from which cue production

627 rates can be calculated, and, just as importantly, are able to quantify silent intervals when

628 animals will be undetected by a PAM survey. The latter point is particularly pertinent when

629 estimating density of baleen whales, some of which seldom vocalize (e.g. Martin *et al*., 2013).

630 Unlike the stereotyped duty cycles of beaked whales, short term acoustic tags mounted on baleen

631 whales have revealed significant, variable periods of silence. Indeed, Parks *et al*. (2011) noted

632 that 28 of 46 North Atlantic right whales produced no sound during tag deployments with

633 average duration of 4.5 hours. In comparison, the recording durations in the present study were

634 sufficiently long in all cases to include at least one vocal cycle.

635

636 Although the limited attachment time of suction cup tags on cetaceans restrict the durations over

637 which individual behavior can be observed with these devices, it is also important to consider the

638 effects of different sampling and sub-sampling routines when collecting cue rates. A large

639   number of short samples on many individuals (as is the case here with many short-term tag

640   deployments) captures variation more reliably than one long term recording from a single animal

641   (Thomisch *et al*., 2015). Furthermore, using a large dataset of real click counts from continuous

642   sampling over entire dive cycles allows for accurate representation of the distributions of the

643   metrics, ensuring models are robust.

644

645   As previously mentioned, it is also possible to obtain cue production rates through

646   methodologies other than acoustic tags. Acoustic focal follows allow individual vocalizing

647   animals to be tracked through time and space, resulting in a vocal record similar to that from a

648   short-term acoustic tag. However, such acoustic tracking may involve complex beamforming

649   arrays to maximize range and accuracy (Miller and Tyack, 1998; Von Benda-Beckman *et al*.,

650   2010) as well as frequent movement of recording vessels with the attendant risk of modulating

651   behavior. Moreover, this approach is virtually impossible with animals occurring in large groups,

652   or those that are silent for long periods.

653

654   Understanding the vocal behavior of a study species, and the contexts in which a sound cue may

655   be produced, generates possibilities to infer cue rate from other data sources (e.g., Barlow *et al*.,

656   2013). Acoustic tags are ultimately limited by storage capacity; thus they are typically deployed

657   with short-term, non-invasive attachments such as suction-cups. Although longer duration sound

658   recording tags are being developed (Moore *et al*., 2012), most long term tags currently sample

659   movement and depth rather than sound. These time-depth recorders (TDRs) are usually mounted

660   to cetaceans with trans-dermal pins (Andrews *et al*., 2008) and so may have a greater potential

661   for harm than suction cups, but collect long-term movement data from which dive-linked vocal

662   activity can potentially be inferred. For species such as beaked whales with strongly stereotyped

663   vocal behavior, dive durations and inter-dive intervals can be extracted from TDR data and

664   entered into statistical models constructed from acoustic tag data to predict the number of clicks

665   the animals were likely to have produced during these dives, and therefore provide rough

666   estimates of click rates. Although there are dangers in such an approach, it may enable the

667   collection of a much larger sample size than is possible using acoustic tags (e.g., Barlow *et al*.,

668   2013).

669

670   **E. Conclusion**

671   This research provided a case-study of vocal cue production rates from Blainville's and Cuvier's

672   beaked whales, collected in two sites for each species by acoustic-recording tags, to test for

673   spatial and temporal variability. Cue rates were found to vary significantly by location and over

674   time for Cuvier´s beaked whales, and spatial differences were also detected on a vocal period

675   scale for Blainville´s beaked whales, highlighting the importance of using relevant cue

676   production rates as multipliers within a passive acoustic density estimation framework to reduce

677   bias.

678

679   Barlow *et* al. (2013) recommended beaked whales as an ideal species for acoustic density

680   estimation due to the stereotyped nature of their echolocation clicks. This study provides

681   evidence to suggest that even cue rates of species well suited to PAM and acoustic density

682   estimation can vary significantly in relation to a range of explanatory covariates. When densities

683   are estimated from cue counts, cue production rate multipliers should be collected concurrently

684   with the passive acoustic survey from which density will be estimated, and animal-mounted

685   telemetry has proven to be a viable method for collecting this auxiliary data (Marques *et al.*,

686   2013). When it is not possible to collect such data concurrently, a large dataset of acoustic tag

687   records, from a variety of times and locations, can be used to inform a model to predict cue rate

688   multipliers. Click production rate multipliers, collected separately from the PAM survey from

689   which density will be estimated, should be applied with caution, with potential biases recognized

690   and reported.

691

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911 **TABLES**

912 TABLE I: Overview of the tag deployments (by species, location and year) and total number of

913 vocal periods and dive cycles analyzed in this study. Tag detachment after to the end of a vocal

914 period meant that the total number of complete dive cycles is sometimes lower than the number

915 of vocal periods for the same tag deployment.

916 [see following page]

Species	Location	Year	Tag deployments	Vocal periods	Dive cycles
Cuvier's beaked whale (*Ziphius cavirostris*)	Ligurian Sea, Mediterranean	2003	2	8	6
		2004	5	18	15
		2005	2	8	7
		2006	2	5	5
		2008	1	4	4
		Total	**12**	**43**	**37**
	Southern California	2010	1	1	1
		2011	1	1	1
		2013	2	3	2
		Total	**4**	**5**	**4**
Blainville's beaked whale (*Mesoplodon densirostris*)	El Hierro, Canary Islands	2003	2	7	6
		2004	1	4	4
		2005	4	11	10
		2008	5	17	15
		2010	2	9	8
		Total	**14**	**48**	**43**
	Bahamas	2006	1	4	4
		2007	4	18	18
		Total	**5**	**22**	**22**

917

918

919   TABLE II: Acoustic and dive metrics for Blainville's and Cuvier's beaked whales, in two

920   locations per species. Standard deviations, weighted by the number of dive units recorded by

921   each tag, are given in parentheses. Coefficients of variation were calculated from standard

922   deviation divided by the mean for each deployment, both weighted by the number of dives in

923   each tag record. Sample sizes are given in Table I.

924   [see following page]

925

Parameter	Blainville's beaked whales		Cuvier's beaked whales	
	Bahamas	El Hierro	Liguria	Southern California
Mean number of clicks during a vocal period	4628 (913)	3500 (333)	3523 (586)	3046 (717)
Mean vocal period duration (mins)	29.9 (5.8)	24.5 (2.3)	35.2 (5.7)	35.1 (9.1)
Mean dive cycle duration (mins)	181.0 (53.2)	145.0 (31.0)	133.0 (29.8)	228.0 (47.4)
Mean vocal period click rate (clicks/sec)	2.59 (0.15)	2.38 (0.06)	1.67 (0.16)	1.46 (0.14)
Between-tag coefficient of variation in vocal period click rate	5.80%	2.51%	9.59%	9.31%
Mean dive cycle click rate (clicks/sec)	0.50 (0.11)	0.43 (0.14)	0.50 (0.06)	0.24 (0.07)
Between-tag coefficient of variation in dive cycle click rate	23.14%	31.28%	11.98%	30.83%

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928   TABLE III: Modelled click production rates. Different combinations of factor covariates alter

929   the predicted click rates, hence the ranges given below. 95% confidence intervals are given in

930   parentheses.

931   [see following page]

Blainville's beaked whale click production rates (clicks/second)		
	Bahamas	**El Hierro**
Vocal period	2.58 (2.46-2.71)	2.38 (2.26-2.50)
Dive cycle	0.41 (0.37-0.46)	
Cuvier's beaked whale click production rates (clicks/second)		
	Ligurian Sea	**Southern California**
Vocal period	Afternoon: 1.83 (1.71-1.95) Dusk: 1.49 (1.26-1.75) Midday: 1.67 (1.50-1.81) Night: 1.64 (1.52-1.78)	Afternoon: 1.56 (1.43-1.70) Dusk: 1.27 (1.07-1.49) Midday: 1.42 (1.28-1.54) Night: 1.40 (1.29-1.51)
Dive cycle	June afternoon: 0.43 (0.37–0.50) June dusk: 0.52 (0.38-0.72) June midday: 0.31 (0.24-0.41) June night: 0.52 (0.40-0.68) July afternoon: 0.36 (0.32-0.41) July dusk: 0.44 (0.32-0.61) July midday: 0.26 (0.19-0.35) July night: 0.44 (0.34-0.57) September afternoon: 0.40 (0.37-0.43) September dusk: 0.48 (0.35-0.66) September midday: 0.29 (0.22-0.38) September night: 0.48 (0.37-0.63)	June afternoon: 0.29 (0.24–0.35) June dusk: 0.35 (0.26-0.48) June midday: 0.21 (0.16-0.28) June night: 0.35 (0.27-0.46) July afternoon: 0.24 (0.21-0.28) July dusk: 0.30 (0.22-0.41) July midday: 0.18 (0.13-0.23) July night: 0.29 (0.23-0.38) September afternoon: 0.27 (0.25-0.29) September dusk: 0.32 (0.24-0.45) September midday: 0.19 (0.15-0.25) September night: 0.32 (0.25-0.42)

932