

Short first click intervals in echolocation trains of three species of deep diving odontocetes

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22 Abstract (200 words)

23

24 All odontocetes produce echolocation clicks as part of their vocal repertoire. In this paper
25 we analysed inter-click-intervals in recordings from suction cup tags with a focus on the
26 first inter-click interval of each click train. We refer to shorter first inter-click intervals as
27 short first intervals (SFIs). We found that the context of SFI occurrence varies across three
28 deep-diving species. In Blainville's beaked whales, 87% of click trains that were preceded
29 by a terminal buzz started with SFIs. In Cuvier's beaked whales, only sub-adult animals
30 produced notable amounts of SFIs. In contrast, sperm whales were much more likely to
31 produce SFIs on the first click train of a dive. While the physiological and/or behavioural
32 reasons for SFI click production are unknown, species differences in their production could
33 provide a window into the evolution of odontocete echolocation.

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42 I. INTRODUCTION

43 Echolocation, the production of click sounds to generate echoes off features in the
44 environment, is a critical part of odontocete sensory biology. Echolocation clicks vary
45 across species in duration, frequency content and temporal production pattern (Roch et al.,
46 2011; Soldevilla et al., 2008). Early work on echolocation inter-click-intervals (ICIs) in bats
47 and dolphins often found that the focal animal waited until it heard the echo from a target
48 before making the next click (Griffin, 1958; Morozov et al., 1972). In this case the ICI may
49 correlate with distance to the target. More recent work has shown that shallow water
50 echolocators use their acoustic gaze by adjusting their ICIs to glean a sharp picture of both
51 near and possible further targets (Wisniewska et al., 2012). However, there are situations in
52 which some species maintain stable ICIs as they approach targets. For example, some bats
53 produce echolocation clicks with stable ICIs (“sonar strobe groups”) as the distance to the
54 target decreases (Moss et al., 2011). Whether they alter ICI during the search phase or not,
55 many echolocators transition from relatively long ICIs during search for prey to shorter ICIs
56 as they attempt to capture prey at short ranges (e.g. Blainville’s beaked whales, *Mesoplodon*
57 *densirostris*, and sperm whales, *Physeter macrocephalus*, Miller et al., 2004). Beaked
58 whales usually echolocate at depth, typically within ~100m of the sea floor (median 127m;
59 Arranz et al., 2011), with echoes detected from targets in the water column from up to 20m
60 away (Arranz et al., 2011). While searching for prey at depth, some beaked whales produce
61 stable ICIs corresponding to distances well beyond the prey, often even beyond the seafloor.
62 This pattern of long ICIs at the start of click trains leading to shorter click intervals on
63 approach to a target is not always followed when echolocators use clicks for
64 communication. For example, during aggressive behaviours, harbour porpoise (*Phocoena*

65 *phocoena*) and Hector's dolphins (*Cephalorhynchus hectori*) may produce sounds starting
66 with very short ICIs (Clausen et al., 2010; Dawson, 1991). Sperm whales produce rhythmic
67 series of clicks called codas for communication (Schulz et al., 2008; Watkins & Schevill,
68 1977). These codas may start with short ICIs, followed by longer ones (Rendell &
69 Whitehead, 2003).

70

71 Short click intervals have been described in other odontocetes without conclusions about
72 their function. They were described as "doublets" in killer whales (*Orcinus orca*) as early as
73 1979 (Steiner et al., 1979). These doublets were often the only clicks in a train and differed
74 between each other in frequency content (Steiner et al., 1979). Hawaiian spinner dolphins
75 (*Stenella longirostris*) produce doublets that have a relatively narrowband frequency
76 structure compared to their usual clicks (Lammers and Au, 2002). Additionally, Cholewiak
77 et al., (2013) refer to clicks with shorter ICIs as "double clicks" within click trains produced
78 by Sowerby's beaked whales (*Mesoplodon bidens*), and suggest they may not be used for
79 foraging purposes. Finally, Hooker and Whitehead (2002) noted the ubiquitous nature of
80 double clicks in field recordings of northern bottlenose whales, although they considered the
81 second click likely to be an echo from the environment, rather than having been produced
82 by the whale. Here we used sound-and-movement-recording tags (DTags) that allow true
83 clicks to be distinguished from echoes.

84

85 In this study we focus on describing cases in three deep-diving odontocetes where a click
86 train used for echolocation starts with a short first interval (SFI) followed by longer ICIs.
87 There are multiple potential hypotheses for SFI production. Assuming that the ICI

88 corresponds to the maximum range of echolocation leads to the hypothesis that SFIs may
89 represent short-range inspection at the start of echolocation. This would mean a different
90 use of short ICIs than has been described when multiple short ICIs are produced, sometimes
91 referred to as ‘packets’ of clicks. Packets can contain two or more clicks and have been
92 described being produced by both beluga whales (*Delphinapterus leucas*. Turl and Penner,
93 1989) and bottlenose dolphins as range to the target increases (Finneran, 2013; Ivanov,
94 2004). Packets of clicks with short ICIs followed by ICIs longer than the round trip travel
95 time to long range targets are thought to allow for ‘multi-echo processing’ without
96 sacrificing range ambiguity due to the long interval between packets.

97

98 Another hypothesis is that the pneumatic sound production apparatus may produce SFIs as
99 an artefact of developing the appropriate muscular tensions and air pressure for long-range
100 echolocation. The physiology of pneumatic sound production presents special challenges for
101 deep diving cetacean species. The mechanism not only requires gas, but also has to function
102 in hydrostatic pressures of tens to hundreds of atmospheres experienced at depths of
103 hundreds or thousands of metres. All odontocetes except sperm whales have two pairs of
104 phonic lips, and produce echolocation clicks by pressurizing air in the nasal passages until
105 the pressure is greater than the muscular tension of the phonic lips, causing the lips to
106 briefly part allowing air to escape, generating a click (Cranford, 1998; Ridgway et al.,
107 1980). It has also been noted that serous fluid is emitted between the phonic lips during
108 click production by bottlenose dolphins (*Tursiops truncatus*) (Cranford et al., 2011),
109 suggesting that having the surface of the lip coated in a fluid may be required to produce
110 normal clicks (Thode et al., 2016). We still do not fully understand the mechanics of click

111 production in odontocetes, and it is possible that these systems sometimes need to adjust
112 pneumatic pressure and fluid and tension of the lips at the start of click production. During
113 such preparation, multiple pulses might be emitted instead of just one, for example.

114

115 Despite these numerous reports of short ICIs, to our knowledge SFIs have not been
116 systematically analysed across multiple odontocete species. Here we present a comparative
117 analysis of SFI click production from DTags attached to Blainville's beaked whales,
118 Cuvier's beaked whales (*Ziphius cavirostris*) and sperm whales, three odontocetes that
119 forage at depth. If SFIs are produced consistently across these species, and only at depth, it
120 could support a hypothesis that they are produced consistently as a result of vocalising
121 under pressure at depth. However if their production is not consistent across these species, it
122 might suggest a behavioural variation in production consistent with a form of
123 communication. Alternatively, there may be a need for short-range inspection in different
124 contexts for the different species, or there may be constraints that lead to SFI click
125 production operating differently in the different species resulting from variations in sound
126 production anatomy and physiology. Understanding these variations in click structure,
127 timing and occurrence is important to gain a proper picture of the sensory biology of
128 odontocetes.

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131 II. METHODS

132 Recordings of sperm whales, Blainville's and Cuvier's beaked whales were obtained using
133 suction cup-attached acoustic DTags (Johnson and Tyack, 2003). Four Blainville's beaked

134 whales, three adult females and an adult male, were tagged in the Tongue of the Ocean off
135 Andros Island in the Bahamas in 2006 and 2007. Three of the groups consisted of two adult
136 females and an adult male (2007), and the other group of two mothers and their large
137 juveniles (2006). Two Cuvier's beaked whales, a subadult of undetermined sex and a
138 probable adult female, were tagged in the Ligurian Sea, Italy in 2003, and an adult male and
139 subadult male were tagged there in 2004 (Tyack et al., 2006). Finally, an adult male sperm
140 whale was tagged in the Ligurian Sea in 2002, and another adult male, two adult females
141 and an individual that was presumed an adult female were tagged in the Gulf of Mexico
142 between 2001 and 2003 (Miller, 2004). For all stereo tags, the channel with the best signal-
143 to-noise ratio (SNR) was chosen for this analysis.

144

145 Click production has been well characterised in all three species studied here (Goold &
146 Jones, 1995; Miller et al., 2004; Johnson, et al., 2004; Madsen, et al., 2005). During the
147 foraging phase of dives, production of clicks usually follows a regular pattern that begins
148 with a search phase during which clicks are produced with ICIs of 0.3-2.0s depending on
149 species (sperm whales 0.5-2.0s, Miller et al. 2004; beaked whales 0.3-0.4s, Johnson et al.
150 2004). This phase can end either with a pause, or a terminal buzz with click intervals in the
151 range 0.01-0.2s, again depending on species (sperm whales 0.2s descending to 0.02s, Miller
152 et al. 2004; beaked whales ~0.01s, Johnson et al. 2004), followed by a pause. For this study,
153 click trains were defined as bouts of clicks separated by a non-clicking period at least twice
154 as long as the ICI between the search phase clicks in the train. Trains were identified from
155 spectrogram visualisations of the acoustic records in Adobe Audition CS6 (4096 point FFT
156 with a 75% overlap and Hamming window), and saved to separate files, one file per click

157 train. Buzzes, where ICIs dropped to the figures outlined above for each species, were not
158 included in these click trains. For each tag, click trains were noted wherever found,
159 irrespective of dive phase. The first dive post tagging in sperm whales is typically shorter
160 than subsequent dives (Miller et al., 2009), and as the tagging response may also involve
161 vocalisation alterations, the first dive greater than 200m following a tag deployment for all
162 species was discarded from this analysis. Click trains were determined to be produced by
163 the tagged animals in all cases as they have higher received levels in general throughout the
164 duration of the tag, as well as tag flow noise at low frequencies (Johnson et al., 2009),
165 which would not be the case if the trains were produced by a conspecific. During the manual
166 selection of click trains, the presence of a buzz before and or after the click train, and the
167 time the click train commenced were noted.

168

169 Each click train file was then reviewed in Matlab R2014a (8.3.0.532), using the spectrogram
170 function. Scripts were used to detect the first 25 clicks from each wav file using a band pass
171 Hanning filter to concentrate on frequencies between 5 and 10 kHz, where clicks recorded
172 from the tagged whale contained substantial energy. Through trial and error, a limit was set
173 for the minimum time between adjacent clicks to prevent intense echoes from being
174 erroneously detected as separate clicks (75 ms for Blainville's beaked whales, and 110 ms
175 for sperm whales and Cuvier's beaked whales). If the visual representation of the click train
176 in Matlab did not correctly identify every click in the click train due to poor SNR, that
177 entire click train was removed from the dataset. There were no indications of patterns in
178 these rejections sufficient to create any bias in the remaining dataset used for analysis. For

179 sperm whales, because only click trains > 25 clicks were used in the analysis, codas made
180 during the descent before regular clicking began were by default not included.

181

182 We quantified SFIs by normalizing the ICIs in each click train to the median ICI for the
183 entire train, thereby expressing each ICI as a proportion of the median ICI; this value for the
184 first ICI thus gave a measure we termed “propICI”. Very low values of this measure
185 indicate the presence of a SFI while values >1 imply a longer first interval than the median
186 of the rest of the train. We did not however establish *a priori* a threshold for defining an
187 SFI, but adopted instead an approach of using the “propICI” measure to analyse these
188 intervals as a continuous response and examining the properties that emerged from the
189 analysis. An example of a click train with an SFI for each species is shown in Fig. 1.

190 Generalized linear mixed and regular models were fitted for each species with a normally
191 distributed error structure, propICI as the response variable, and a set of eight predictor
192 variables using R software version 3.0.3 (R Core Team, 2015) and the lme4 package (Bates
193 et al., 2012). The unit of analysis was a single click train and the value of propICI for the
194 first interval in the train was modelled as a function of:

195

- 196 • [indiv] This identified the individual whale that was tagged (data from multiple
197 deployments on the same individual were not used) and was a random factor in
198 mixed models to account for autocorrelation in click production within individuals.
- 199 • [sex] Sex was represented as a numerical variable that could take one of three values:
200 -0.5 for females, 0 for unknown sex, and +0.5 for males. This coding means that only
201 animals of known sex could affect the coefficient estimation.

- 202 • [age] Age was a categorical variable separated into subadults ‘As’, unknown age
 203 ‘Av’, and adults ‘Az’.
- 204 • [time_into_dive] The time in seconds between the first click train of the dive and the
 205 current train. This could indicate whether SFI production is related to time from the
 206 start of clicking in each dive.
- 207 • [depth] Depth in metres (as measured by the tag) at the time each click train started,
 208 to test whether SFIs are related to hydrostatic pressure. A positive coefficient would
 209 represent an increase in the proportion of ICI of the first two clicks as depth
 210 increases, therefore a less pronounced SFI.
- 211 • [buzz_b4] Whether there was a buzz before the click train (Y/N factor), which may
 212 show some correlation between SFI production and prey capture attempts.
- 213 • [buzz_after] Whether there was a buzz after the click train (Y/N factor).
- 214 • [first_train_of_dive] Whether this click train was the first click train of the dive (Y/N
 215 factor). Note that not all ‘first trains’ were included in the analysis, if there was poor
 216 SNR for example, they were removed.

217
 218 Therefore the full model was defined as,

$$219
 220 \text{propICI}_{ti} = (\beta_0 + b_{0i}) + \beta_1(\text{sex } i) + \beta_2(\text{age } i) + \beta_3(\text{time_into_dive } t) + \beta_4(\text{depth } t) + \beta_5(\text{buzz_b4 } t) \\
 221 + \beta_6(\text{buzz_after } t) + \beta_7(\text{first_train_of_dive } t) + \varepsilon_{ti},$$

222
 223 where propICI_{ti} represents click train t , produced by individual i , b_{0i} is independent $\text{Normal}(0, \sigma^2_b)$, errors ε_{ti} are independent $\text{Normal}(0, \sigma^2_e)$, and b_{0i} are independent of the errors ε_{tij} .

225

226 For each species, we first determined whether a mixed model was necessary to account for
227 correlations within individuals by comparing Akaike Information Criterion (AIC) values for
228 otherwise full models with and without the random effect, and visualising the random effect
229 structure with the ‘ranef’ function within the lme4 package. Then AIC was used to select the
230 best fixed effect structure (Burnham and Anderson, 2002), or which structures to average
231 over, if more than one was within three AIC units of the best, across models with the same
232 random effects (or lack thereof if the previous procedure indicated they were not needed).
233 The ‘dredge’ function from the MuMIn package (Barton, 2014) was used to first identify the
234 top models, and summed Akaike weights were used to estimate the relative importance of
235 variables within the fitted fixed effect structures or lack thereof (Burnham and Anderson,
236 2002).

237

238

239 III. RESULTS

240 From a total of 2773 click trains manually extracted, 1399 click trains from 13 individual
241 whales were used in the final analysis (Table I). The excluded trains were either fewer than
242 25 clicks long, or had poor SNR resulting in the potential for missed click detections in a
243 click train, which would strongly affect any ICI measurement.

244

245 IIIa. Blainville’s beaked whale

246 The tagged Blainville’s beaked whales often produced two clicks at the start of a click train
247 with a considerably shorter ICI than the median of the ICI for the entire click train

248 (propICI was less than 0.5 in 63% of analysed trains, and less than 0.9 in 91% of trains;
249 Fig. 2a), and then proceeded to a regular ICI for the remainder of the click train almost
250 immediately, with very little ‘ramp-up’ of ICI (Fig. 2b). The estimated random effects
251 (produced by including the individual animal [indiv] as a random effect in the model)
252 showed little variation across individuals, and a model including them had higher AIC (-
253 422.7 compared to -424.6), therefore we removed it. The best model included all parameters
254 except age, as all Blainville’s beaked whales in this study were adults. The first click
255 intervals in Blainville’s beaked whales trains were smaller when the previous train ended in
256 a buzz (buzzes occurred before 67% of the analysed click trains, and 86% of those trains
257 began with a propICI < 0.5) and the further the animal was into the dive (Table II).
258 However the frequency of SFIs did not increase linearly with the depth of the animal, as
259 presumably they were concentrated around the best foraging depth due to their high
260 correlation with buzzes (Fig. 3).

261

262 IIIb. Cuvier’s beaked whale

263 The Cuvier’s beaked whales also tended to produce a smaller ICI at the start of click trains
264 than the median ICI of the remaining clicks in each train (Fig. 2c). The first clicks started,
265 on average at 0.8 of the click train median ICI, and approached the median values over the
266 next two or three intervals, so the distinctiveness of the first interval (and hence SFI effect)
267 was not as pronounced. Instead the intervals show more of a ‘ramp-up’ pattern than the
268 Blainville’s beaked whales, where the difference between the first and second ICIs tended to
269 be larger.

270

271 The estimated random effects from the mixed effects model for Cuvier's beaked whales
272 with all predictor variables showed no overlap, and the AIC of the full model with random
273 effects was 13.4 units lower than the full model without. Therefore in this case the random
274 effect of individual whale was retained in the model. Important variables, those whose
275 summed Akaike weights tended towards 1 (Burnham and Anderson, 2002), included all
276 those that were important in the Blainville's beaked whale analysis, as well as whether or
277 not the click train was the first train of the dive (Fig. 3; Table II). The distribution of
278 propICI with respect to depth (Fig. 3) and time into the dive showed a cluster of clicks at
279 depths > 1500 m, and correspondingly longer times into the dive. This cluster represents
280 click trains from the single adult male, hence the model results might be sensitive to the
281 presence of this particular individual and should therefore be treated with caution. Cuvier's
282 beaked whales produce clicks with a first ICI much lower than the median of the entire click
283 train at depths between approximately 300 and 1000 m and, although Cuvier's beaked
284 whales regularly dive to and forage at greater depths than Blainville's beaked whales
285 (Schorr et al., 2014), the latter produced their SFIs deeper, coinciding more with their
286 foraging depths.

287

288 Because the estimated random effects from individuals showed some differences, we plotted
289 each individual's first click intervals (Fig. 5). The distribution of first ICIs expressed as a
290 proportion of the median ICI was centred on 1 for both adults, implying little or no
291 occurrence of SFIs. This was in contrast to the subadults whose click trains began with an
292 ICI of approximately 0.6 of the median of the ICIs in the rest of the click train. However,
293 the summed Akaike weights did not highlight age as an important factor (Table II). This is

294 explained by noting that younger animals dived to shallower depths (Fig. 6). The effect size
295 from the model shows the proportion of ICI of the first two clicks increases by 0.37 over the
296 depth range (300 m to 1000 m) of a dive, and this may explain the apparent association
297 between age and SFI production in Cuvier's beaked whales if adult Cuvier's beaked whales
298 produce fewer SFIs because they are diving deeper. While the analysis suggests depth is the
299 more powerful predictor, because age class and dive depth are confounded in this dataset,
300 definitive interpretation is challenging without additional data.

301

302 IIIc. Sperm whale

303 The mean of the first ICI across click trains for sperm whales does not indicate the regular
304 production of SFIs (propICI was less than 0.5 in 4% of analysed trains, and less than 0.9 in
305 9% of trains; Fig. 2a), however there was a bimodal distribution in the propICI value (Fig.
306 2a) with a sub-group of trains having a first interval whose proportional ICI is lower than
307 0.5 (Fig. 2d). This indicates that while sperm whales can produce initial clicks with a
308 propICI < 0.5 of the median of the rest of the click train, they only do so rarely.

309

310 Assigning the animal with tag Sw03_156a as an adult female (most likely since it was
311 sighted in a group) showed moderate variability between individuals, and because removing
312 the random effect variable raised the AIC by just over 2 units, it was retained. As all
313 animals were presumed to be adults, age class was not included in the model, resulting in
314 three variables with relatively high importance (Table II). The presence of a buzz after the
315 click train increased the first ICI, while males had relatively smaller first ICIs and, as in
316 Blainville's beaked whales, there were fewer SFIs with increasing depth (Fig. 3). The single

317 largest effect however was a more pronounced SFI on the first click train of each dive (Fig.
318 4).

319

320 Adult male sperm whales appear to produce more first clicks with smaller ICIs than adult
321 female sperm whales. However, there were prop_ICIs that were outliers for each of the
322 females that are all around 0.25 (Fig. 7). Both adult male tags only recorded data for the
323 duration of one dive, and neither animal's first click train of that dive was included.
324 However, all three adult females always produced SFIs (in this case, all propICI < 0.3) at
325 the start of their dives, where the first click train of a dive was included in the analysis.

326

327

328 IV. DISCUSSION

329 Our results show strong yet diverse patterns across the three species studied. Blainville's
330 beaked whales produced more SFIs on the majority of their click trains compared to the
331 other species in all age and sex classes analysed, especially when the previous train ended in
332 a buzz. Among Cuvier's beaked whales only subadults produced SFIs, and only
333 occasionally, whereas only sperm whales that were not adult males produced SFIs, and only
334 on the first click train of every dive.

335

336 The single variable that was highlighted as having high relative importance in the models of
337 all three species was depth. However the effect of this variable on the production of SFIs
338 was not the same across the species. Blainville's beaked whales produced SFIs at the depths
339 where they were foraging, producing them on almost every click train following a buzz.

340 Sperm whales in contrast only produced SFIs on the first train of a dive (coincident with
341 them being at relatively shallow depths). Finally Cuvier's beaked whales produced more
342 SFIs at shallower depths than Blainville's beaked whales. Therefore the production of SFIs
343 does not appear to be a result of pressure at a specific depth.

344

345 The variation in SFI production by the three species analysed here is hard to explain with
346 our poor current state of knowledge regarding the physiology and specific mechanisms of
347 click production as well as the neural mechanisms involved in echo processing. Based on a
348 simple two-way travel time argument, SFIs may be related to a need for a short range scan
349 at the start of a train, relative to the rest of the longer ICI search phase clicks in that train.
350 Finneran et al., (2014) however report that bottlenose dolphins are more likely to produce
351 packets of clicks with small click intervals as the range to a target increases, and by this
352 argument, SFIs could reflect a need for long range information only obtainable through
353 click packets. At the present time therefore, all we can say is that in either case, it is hard to
354 explain the variation we report across species, i.e. at different depths, and with different
355 frequency of occurrence, with a consistent function related to either shorter or longer range
356 inspections, although it is always possible that this functional need varies across species
357 with some factor not measured in this study.

358

359 SFIs could be a functionless by-product of pneumatic click production, which explains why
360 they are being produced at the start of a click train. It is possible that the first click in a dive
361 may be significantly different due to the phonic lips having been parted for surface
362 breathing, or a need to reconfigure the vocal tract for clicking rather than breathing, by

363 filling specific airsacs for example. If the suggestion that phonic lips require a layer of fluid
364 to function in click production stands (Cranford et al., 2011; Thode et al., 2016), SFIs may
365 relate to a lack of fluid, or may even function to introduce fluid after a period of no clicking
366 by using air pressure to blow fluid through the phonic lips, before reliable single clicking
367 can commence. Moreover, the production of SFIs may be related to the adjustment of the
368 tension of the phonic lips, coupled with re-pressuring the nasal passages after some pause,
369 i.e. a surface interval and therefore breathing, as seen in sperm whales in our results, or time
370 between click trains, as seen in both beaked whales species in our results. It is worth noting
371 that whereas sperm whales produce the same click type for search and buzz clicks, beaked
372 whales switch click types and therefore tuning the production mechanism to produce long
373 range search clicks may cause the byproduct of an SFI when the animal is retuning its
374 apparatus for search clicks following a buzz. Even if they do not function in echolocation,
375 SFIs potential role as a communicative cue to the behavioural, age and sex state of the
376 producer, however, should not be overlooked. More data from varying age/sex classes in all
377 three species, and from other species in which shorter ICIs have been noted, are required to
378 refine these hypotheses.

379

380

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513 TABLES

514 Table I. Dataset. (AF = adult female; AM = adult male; SM = subadult male; SU = subadult
 515 unknown; PF = probable adult female).

Species	Individual	Sex / Age-class	# Click trains	Location
Blainville's	Md06_296a	AF	118	Andros, Bahamas
Blainville's	Md07_245a	AF	88	Andros, Bahamas
Blainville's	Md07_248a	AF	185	Andros, Bahamas
Blainville's	Md07_248b	AM	132	Andros, Bahamas
Total Blainville's beaked whales			523	
Cuvier's	Zc04_160a	AM	15	Ligurian Sea, Italy
Cuvier's	Zc04_161a	SM	39	Ligurian Sea, Italy
Cuvier's	Zc04_179a	SU	73	Ligurian Sea, Italy
Cuvier's	Zc03_263a	PAF	231	Ligurian Sea, Italy
Total Cuvier's beaked whales			358	
Sperm whale	Sw03_156a	SM / AF	104	Gulf of Mexico
Sperm whale	Sw02_189b	AM	15	Ligurian Sea, Italy
Sperm whale	Sw01_208b	AM	25	Gulf of Mexico
Sperm whale	Sw01_204	AF	113	Gulf of Mexico
Sperm whale	Sw02_254a	AF	261	Gulf of Mexico
Total Sperm whales			518	

Table II. Click train effects on prop_ICI for the first interval in each train for Blainville's beaked whales, Cuvier's beaked whales, and sperm whales with the animal whose tag was Sw03_156a categorized as an adult female. Summed Akaike weights ($\sum \omega_i$), model averaged estimates and their standard errors for click train variables.

Species	Blainville's			Cuvier's			Sperm whales		
Variable	$\sum \omega_i$	Estimate	Std. Error	$\sum \omega_i$	Estimate	Std. Error	$\sum \omega_i$	Estimate	Std. Error
Buzz before	1.00	-0.3139	0.0162	1.00	0.0944	0.0195	0.22	5.735e-03	2.503e-02
Depth	1.00	1.609e-04	5.389e-05	1.00	5.249e-04	5.894e-05	0.82	1.272e-04	6.042e-05
Time into dive	1.00	-2.982e-05	1.224e-05	1.00	3.677e-05	1.309e-05	0.50	-1.143e-05	8.005e-06
Buzz after	0.60	0.0025	0.0152	0.46	-0.0257	0.0192	1.00	0.1063	0.0244
First train of dive	0.42	0.0801	0.0694	1.00	0.2034	0.0749	0.50	-1.143e-05	8.005e-06
Sex	0.23	0.0039	0.0184	0.61	-0.2554	0.1242	1.00	-0.3200	0.0633
Age				0.36	-0.1090	0.1239			

FIGURES

FIG. 1. A waveform of a click train with a short first interval for an adult female Blainville's beaked whale, an unknown subadult Cuvier's beaked whale, and an adult female sperm whale.

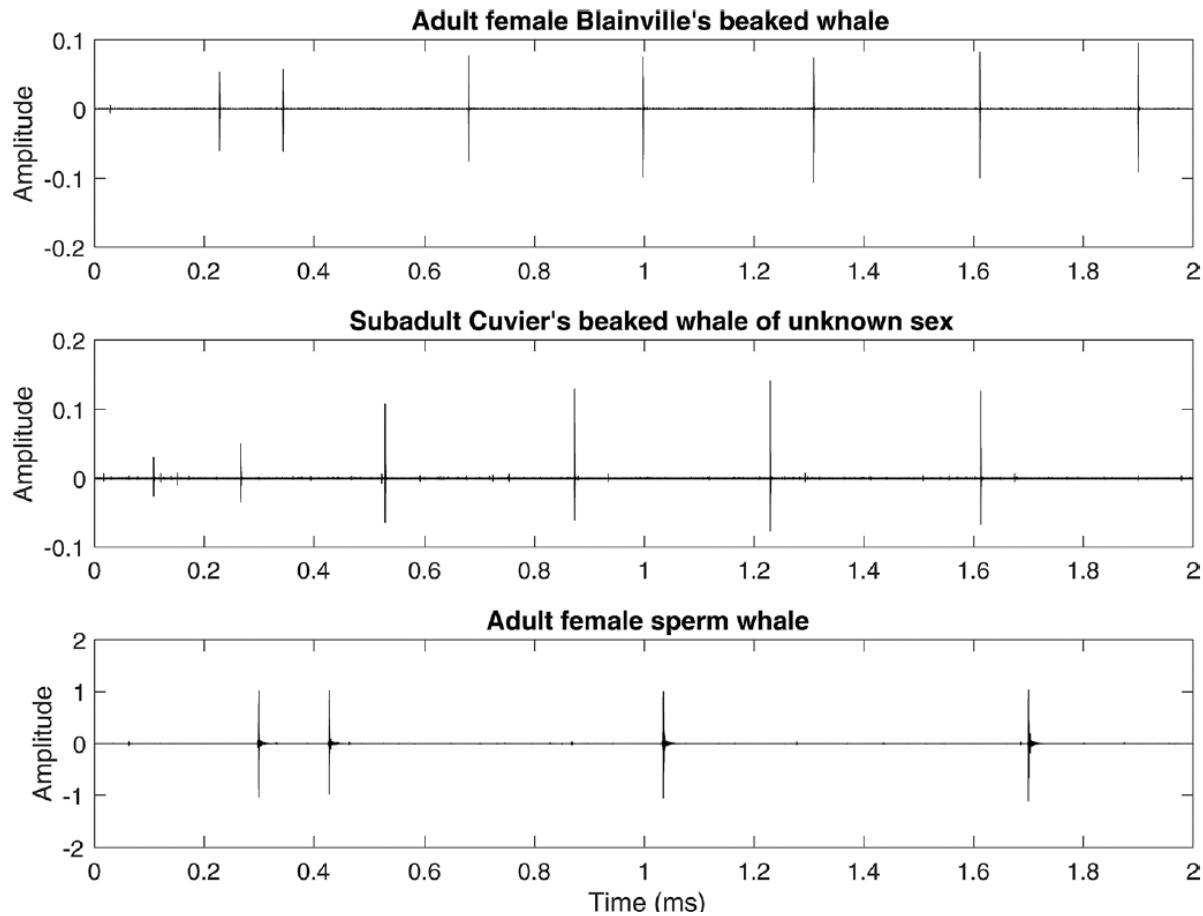


FIG. 2a Plots for Blainville's beaked whales, Cuvier's beaked whales, and sperm whales, showing the number of click intervals < 0.5 (in darker shading), and ≥ 0.5 of the proportion of the median ICI for the entire click train. (b) Click intervals expressed as a proportion of the median ICI for all analysed Blainville's beaked whale click trains. The solid grey line shows mean values for each click train interval. (c) Click intervals expressed as a proportion of the median ICI for all analysed Cuvier's beaked whale click trains. (d) Click intervals expressed as a proportion of the median ICI for all analysed sperm whale click trains.

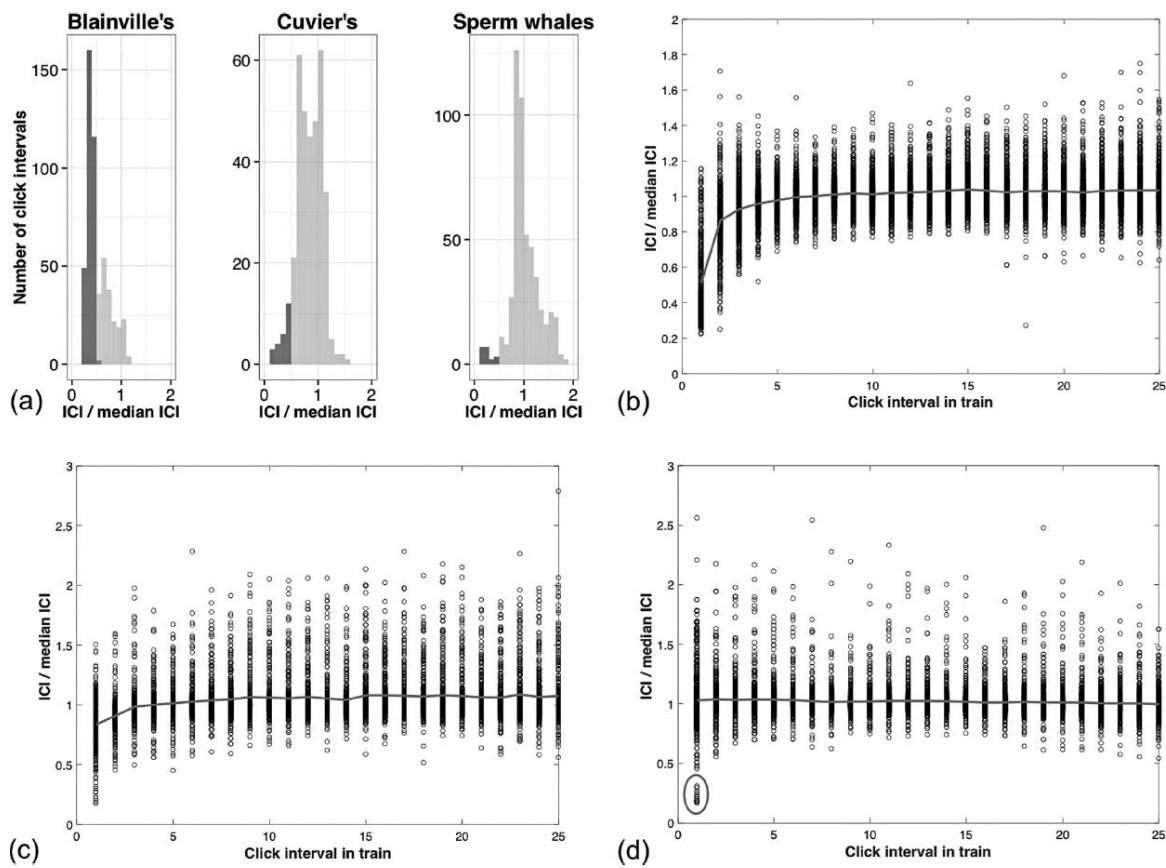


FIG. 3. The depth of each click train, taken at the time of the first click of the click train, for all three species, plotted against the ICI of the first two clicks in the click train (expressed as a proportion of the median ICI for the entire train).

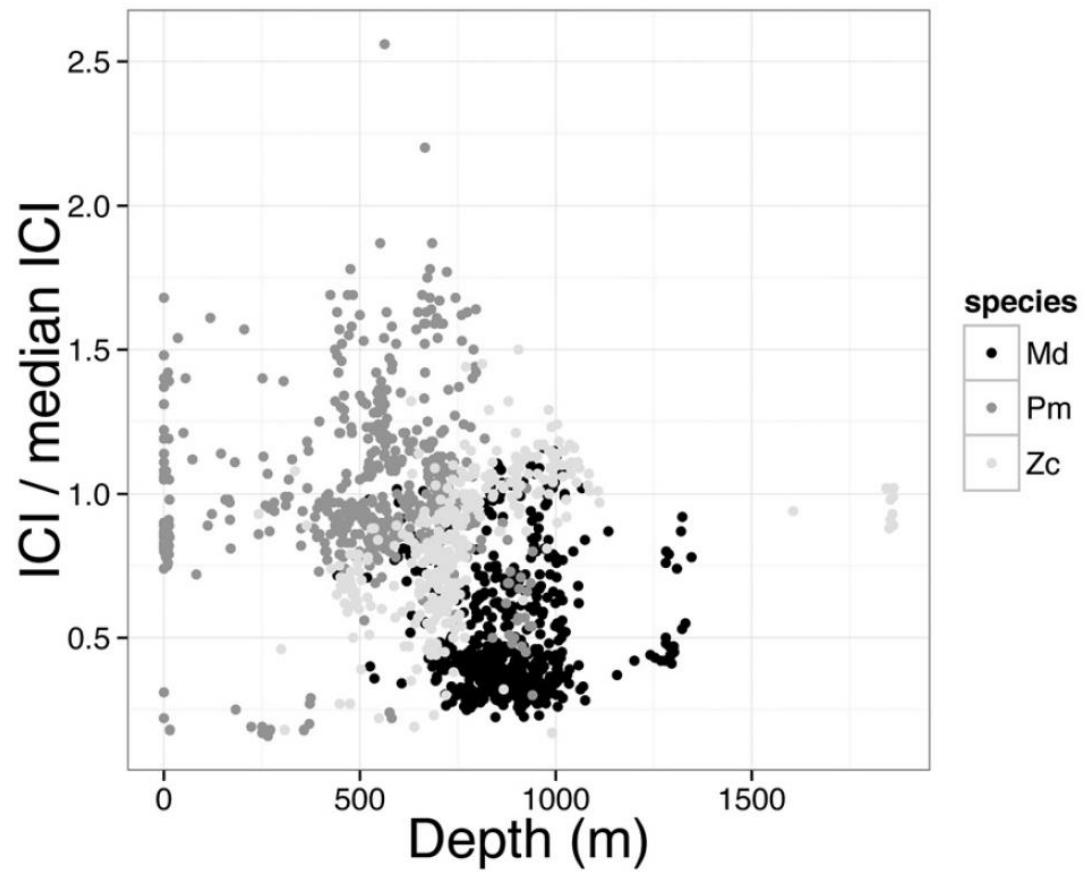


FIG. 4. Distributions of the first ICI in a click train (expressed as a proportion of the median ICI for the entire train) for trains that were and were not the first click train of a dive, for all species (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

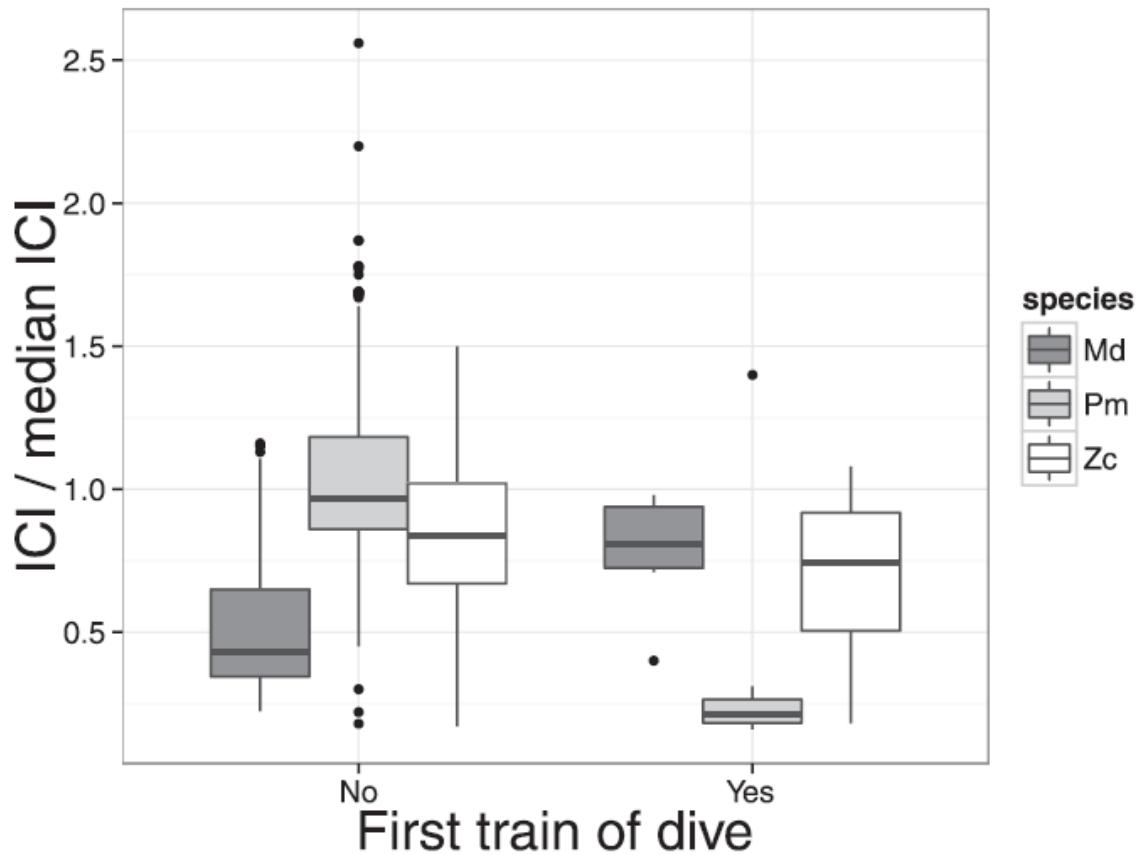


FIG. 5. The proportion of the ICI of the first two clicks in all click trains for two adult and two subadult Cuvier's beaked whales.

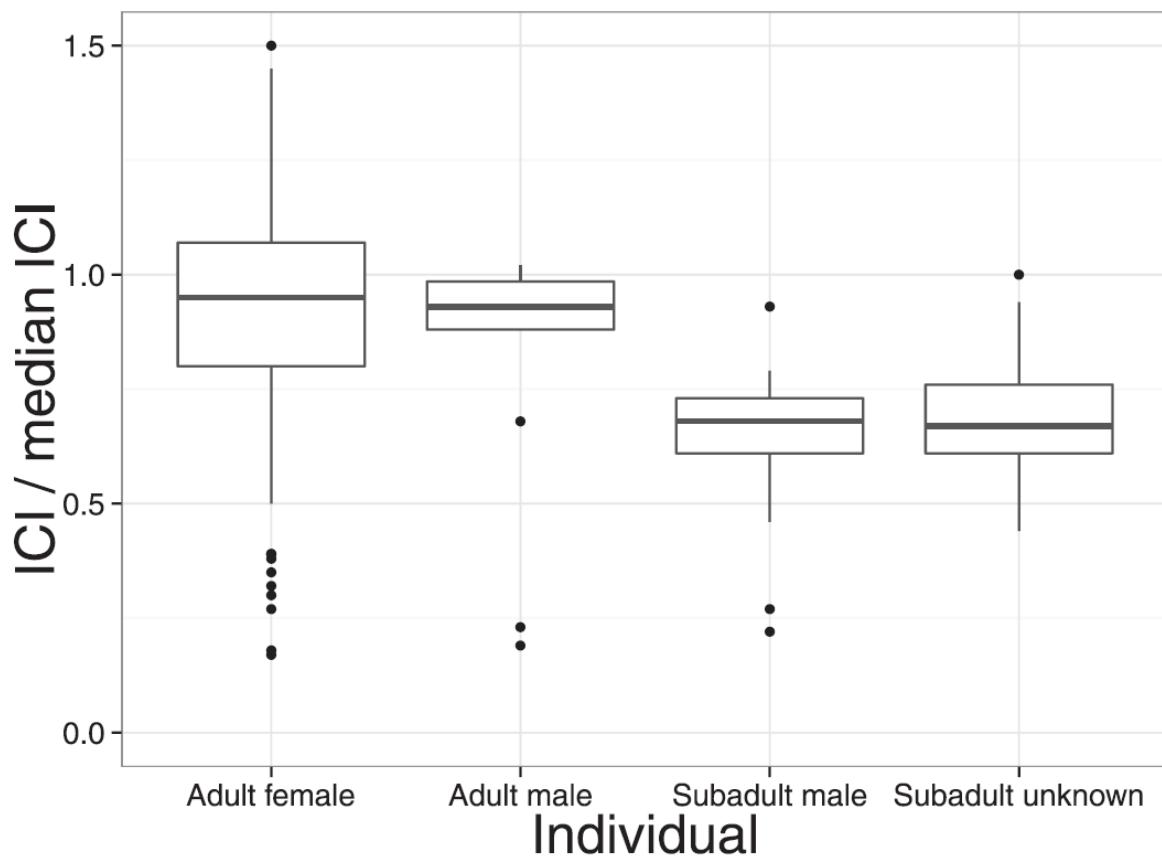


FIG. 6. The depths in meters of all click trains for two adult and two subadult Cuvier's beaked whales.

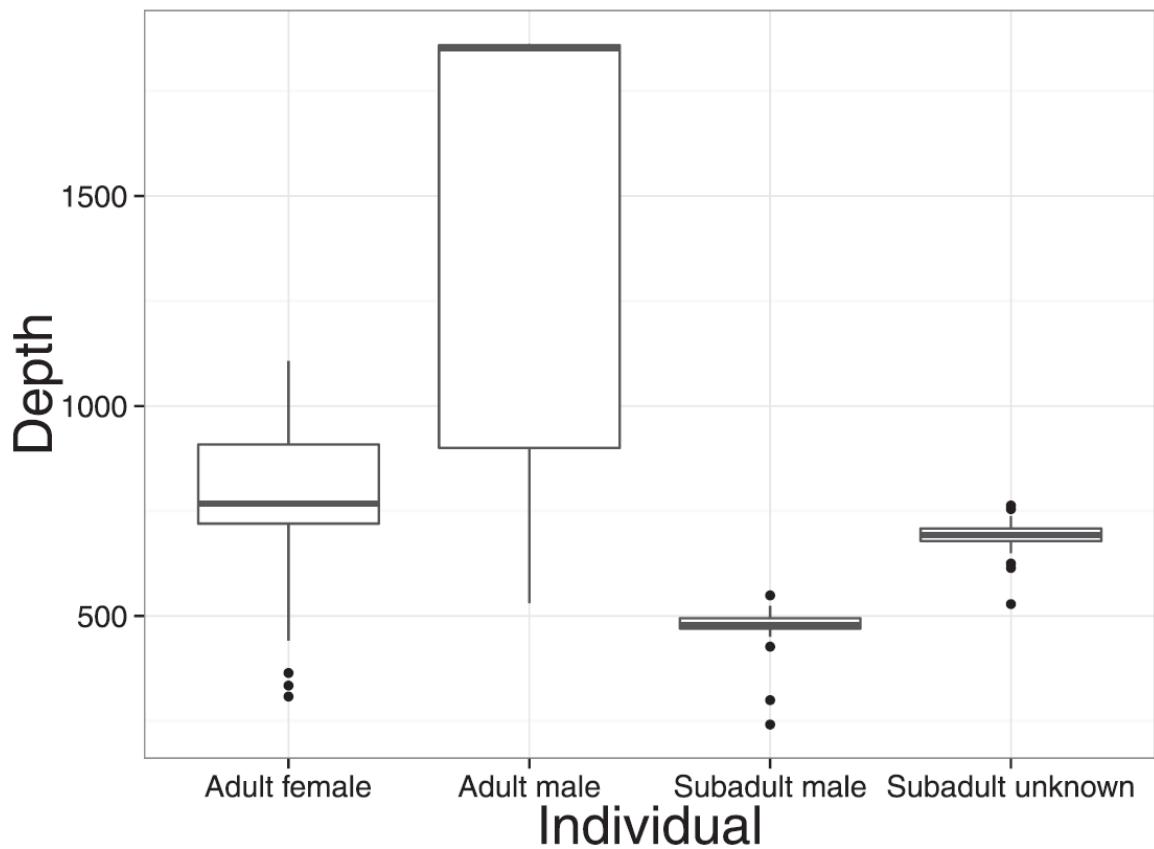


FIG. 7. The ICI (expressed as a proportion of the median ICI) of the first two clicks for the five sperm whales. (AF = adult female, AM = adult male, SM = subadult male)

