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Citation: The Journal of the Acoustical Society of America **141**, 900 (2017); doi: 10.1121/1.4976084
View online: https://doi.org/10.1121/1.4976084
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Short first click intervals in echolocation trains of three species of deep diving odontocetes

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(Received 10 September 2016; revised 22 December 2016; accepted 17 January 2017; published online 17 February 2017)

All odontocetes produce echolocation clicks as part of their vocal repertoire. In this paper the authors analysed inter-click-intervals in recordings from suction cup tags with a focus on the first inter-click interval of each click train. The authors refer to shorter first inter-click intervals as short first intervals (SFIs). The authors found that the context of SFI occurrence varies across three deep-diving species. In Blainville's beaked whales, 87% of click trains that were preceded by a terminal buzz started with SFIs. In Cuvier's beaked whales, only sub-adult animals produced notable amounts of SFIs. In contrast, sperm whales were much more likely to produce SFIs on the first click train of a dive. While the physiological and/or behavioural reasons for SFI click production are unknown, species differences in their production could provide a window into the evolution of odontocete echolocation. © *2017 Acoustical Society of America*.

[http://dx.doi.org/10.1121/1.4976084]

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I. INTRODUCTION

Echolocation, the production of click sounds to generate echoes off features in the environment, is a critical part of odontocete sensory biology. Echolocation clicks vary across species in duration, frequency content, and temporal production pattern (Roch *et al.*, 2011; Soldevilla *et al.*, 2008). Early work on echolocation inter-click-intervals (ICIs) in bats and dolphins often found that the focal animal waited until it heard the echo from a target before making the next click (Griffin, 1958; Morozov *et al.*, 1972). In this case the ICI may correlate with distance to the target. More recent work has shown that shallow water echolocators use their acoustic gaze by adjusting their ICIs to glean a sharp picture of both near and possible further targets (Wisniewska *et al.*, 2012). However, there are situations in which some species maintain stable ICIs as they approach targets. For example, some bats produce echolocation clicks with stable ICIs ("sonar strobe groups") as the distance to the target decreases (Moss *et al.*, 2011). Whether they alter ICIs during the search phase or not, many echolocators transition from relatively long ICIs during search for prey to shorter ICIs as they attempt to capture prey at short ranges (e.g., Blainville's beaked whales, *Mesoplodon densirostris*, and sperm whales, *Physeter macrocephalus*, Miller *et al.*, 2004). Beaked whales usually echolocate at depth, typically within ~100 m of the sea floor (median 127 m; Arranz *et al.*, 2011), with echoes detected from targets in the water column from up to 20 m away (Arranz *et al.*, 2011). While searching for prey at depth, some beaked whales produce stable ICIs corresponding to distances well beyond the prey, often even beyond the seafloor. This pattern of long ICIs at the start of click trains leading to shorter click intervals on approach to a target is not always followed when echolocators use clicks for communication. For example, during aggressive behaviours, harbour porpoise (*Phocoena phocoena*) and Hector's dolphins (*Cephalorhynchus hectori*) may produce sounds starting with very short ICIs (Clausen *et al.*, 2010; Dawson, 1991). Sperm whales produce rhythmic series of clicks called codas for communication (Schulz *et al.*, 2008; Watkins and Schevill, 1977). These codas may start with short ICIs, followed by longer ones (Rendell and Whitehead, 2003).

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

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In this study we focus on describing cases in three deep-diving odontocetes where a click train used for echolocation starts with a short first interval (SFI) followed by longer ICIs. There are multiple potential hypotheses for SFI production. Assuming that the ICI corresponds to the maximum range of echolocation leads to the hypothesis that SFIs may represent short-range inspection at the start of echolocation. This would mean a different use of short ICIs than has been described when multiple short ICIs are produced, sometimes referred to as "packets" of clicks. Packets can contain two or more clicks and have been described as being produced by both beluga whales (*Delphinapterus leucas*; Turl and Penner, 1989) and bottlenose dolphins as range to the target increases (Finneran, 2013; Ivanov, 2004). Packets of clicks with short ICIs followed by ICIs longer than the round trip travel time to long range targets are thought to allow for "multi-echo processing" without sacrificing range ambiguity due to the long interval between packets.

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

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

II. METHODS

Recordings of sperm whales, Blainville's, and Cuvier's beaked whales were obtained using suction cup-attached acoustic DTags (Johnson and Tyack, 2003). Four Blainville's beaked whales, three adult females and an adult male, were tagged in the Tongue of the Ocean off Andros Island in the Bahamas in 2006 and 2007. Three of the groups consisted of two adult females and an adult male (2007), and the other group of two mothers and their large juveniles (2006). Two Cuvier's beaked whales, a sub-adult of undetermined sex and a probable adult female, were tagged in the Ligurian Sea, Italy in 2003, and an adult male and sub-adult male were tagged there in 2004 (Tyack *et al.*, 2006). Finally, an adult male sperm whale was tagged in the Ligurian Sea in 2002, and another adult male, two adult females, and an individual that was presumed an adult female were tagged in the Gulf of Mexico between 2001 and 2003 (Miller *et al.*, 2004). For all stereo tags, the channel with the best signal-to-noise ratio (SNR) was chosen for this analysis.

Click production has been well characterised in all three species studied here (Goold and Jones, 1995; Miller *et al.*, 2004; Johnson *et al.*, 2004; Madsen *et al.*, 2005). During the foraging phase of dives, production of clicks usually follows a regular pattern that begins with a search phase during which clicks are produced with ICIs of 0.3–2.0 s depending on species (sperm whales 0.5–2.0 s, Miller *et al.*, 2004; beaked whales 0.3–0.4 s, Johnson *et al.*, 2004). This phase can end either with a pause, or a terminal buzz with click intervals in the range 0.01–0.2 s, again depending on species (sperm whales 0.2 s descending to 0.02 s, Miller *et al.*, 2004; beaked whales ~0.01 s, Johnson *et al.*, 2004), followed by a pause. For this study, click trains were defined as bouts of clicks separated by a non-clicking period at least twice as long as the ICI between the search phase clicks in the train. Trains were identified from spectrogram visualisations of the acoustic records in Adobe Audition CS6 (4096 point fast Fourier transform with a 75% overlap and Hamming window), and saved to separate files, one file per click train. Buzzes, where ICIs dropped to the figures outlined above for each species, were not included in these click trains. For each tag, click trains were noted wherever found, irrespective of dive phase. The first dive post tagging in sperm whales is typically shorter than subsequent dives (Miller *et al.*, 2009), and as the tagging response may also involve vocalisation alterations, the first dive greater than 200 m following a tag deployment for all species was discarded from this analysis. Click trains were determined to be produced by the tagged animals in all cases as they have higher received levels in general throughout the duration of the tag, as well as tag flow noise at low frequencies (Johnson *et al.*, 2009), which would not be the case if the trains were produced by a conspecific. During the manual selection of click trains, the presence of a buzz before and/or after the click train, and the time the click train commenced were noted.

Each click train file was then reviewed in MATLAB R2014a (8.3.0.532) (The Math Works$^{\text{TM}}$, Inc., Natick, MA), using the spectrogram function. Scripts were used to detect the first 25 clicks from each wav file using a bandpass Hanning filter to concentrate on frequencies between 5 and 10 kHz, where clicks recorded from the tagged whale contained substantial energy. Through trial and error, a limit was set for the minimum time between adjacent clicks to prevent intense echoes from being erroneously detected as separate clicks (75 ms for Blainville's beaked whales, and 110 ms for sperm whales and Cuvier's beaked whales). If the visual representation of the click train in MATLAB did not correctly identify every click in the click train due to poor SNR, that entire click train was removed from the dataset. There were no indications of patterns in these rejections sufficient to create any bias in the remaining dataset used for analysis. For sperm whales, because only click trains >25 clicks were used in the analysis, codas made during the descent before regular clicking began were by default not included.

We quantified SFIs by normalizing the ICIs in each click train to the median ICI for the entire train, thereby expressing each ICI as a proportion of the median ICI; this value for the first ICI thus gave a measure we termed "prop_ICI." Very low values of this measure indicate the presence of a SFI while values >1 imply a longer first interval than the median of the rest of the train. We did not, however, establish *a priori* a threshold for defining an SFI, but adopted instead an approach of using the prop_ICI measure to analyse these intervals as a continuous response and examining the properties that emerged from the analysis. An example of a click train with an SFI for each species is shown in Fig. 1. Generalized linear mixed and regular models were fitted for each species with a normally distributed error structure, prop_ICI as the response variable, and a set of eight predictor variables using R software version 3.0.3 (R Core Team, 2015) and the lme4 package (Bates *et al.*, 2012). The unit of analysis was a single click train and the value of prop_ICI for the first interval in the train was modeled as a function of:

- [indiv] This identified the individual whale that was tagged (data from multiple deployments on the same individual were not used) and was a random factor in mixed models to account for autocorrelation in click production within individuals.
- [sex] Sex was represented as a numerical variable that could take one of three values: −0.5 for females, 0 for unknown sex, and +0.5 for males. This coding means that only animals of known sex could affect the coefficient estimation.
- [age] Age was a categorical variable separated into subadults "As," unknown age "Av," and adults "Az."
- [time_into_dive] The time in seconds between the first click train of the dive and the current train. This could indicate whether SFI production is related to time from the start of clicking in each dive.
- [depth] Depth in metres (as measured by the tag) at the time each click train started, to test whether SFIs are related to hydrostatic pressure. A positive coefficient would represent an increase in the proportion of ICI of the first two clicks as depth increases, therefore a less pronounced SFI.
- [buzz_b4] Whether there was a buzz before the click train (Y/N factor), which may show some correlation between SFI production and prey capture attempts.
- [buzz_after] Whether there was a buzz after the click train (Y/N factor).
- [first_train_of_dive] Whether this click train was the first click train of the dive (Y/N factor). Note that not all "first trains" were included in the analysis, if there was poor SNR for example, they were removed.

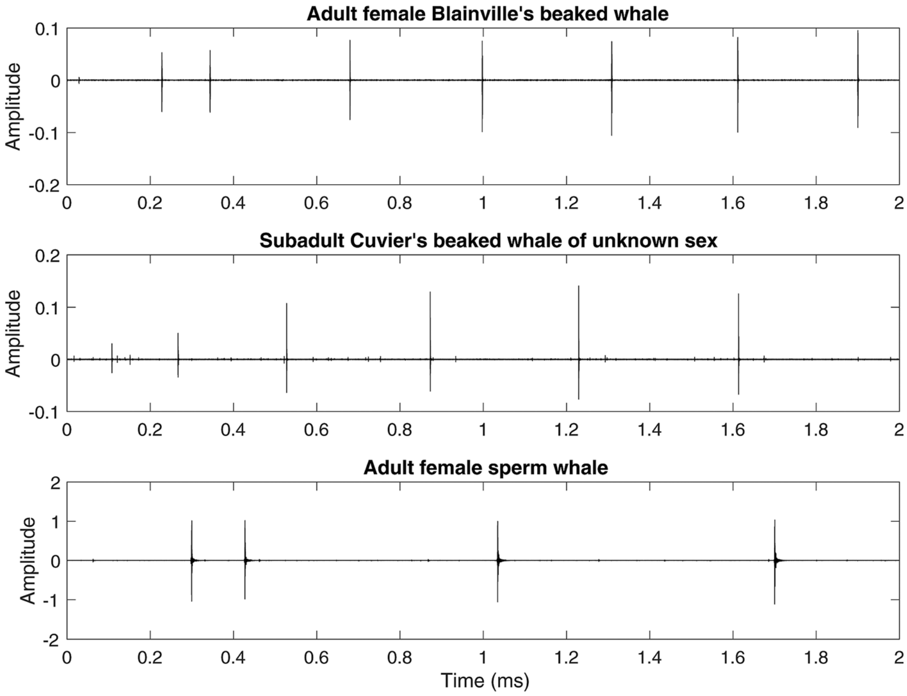

FIG. 1. A waveform of a click train with a SFI for an adult female Blainville's beaked whale, an unknown sub-adult Cuvier's beaked whale, and an adult female sperm whale.

Therefore the full model was defined as

$$\begin{aligned}\text{propICI}_{ti} = {} & (\beta_0 + b_{0i}) + \beta_1(\text{sex } i) + \beta_2(\text{age } i) \\ & + \beta_3(\text{time\_into\_dive } t) + \beta_4(\text{depth } t) \\ & + \beta_5(\text{buzz\_b4 } t) + \beta_6(\text{buzz\_after } t) \\ & + \beta_7(\text{first\_train\_of\_dive } t) + \varepsilon_{ti},\end{aligned}$$

where propICI_{ti} represents click train t, produced by individual i, b_{0i} is independent Normal(0, σ_b^2), errors ε_{ti} are independent Normal(0, σ_e^2), and b_{0i} are independent of the errors ε_{tij}.

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

III. RESULTS

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

TABLE I. Dataset. (AF = adult female; AM = adult male; SM = sub-adult male; SU = sub-adult 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	

A. Blainville's beaked whale

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

B. Cuvier's beaked whale

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

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

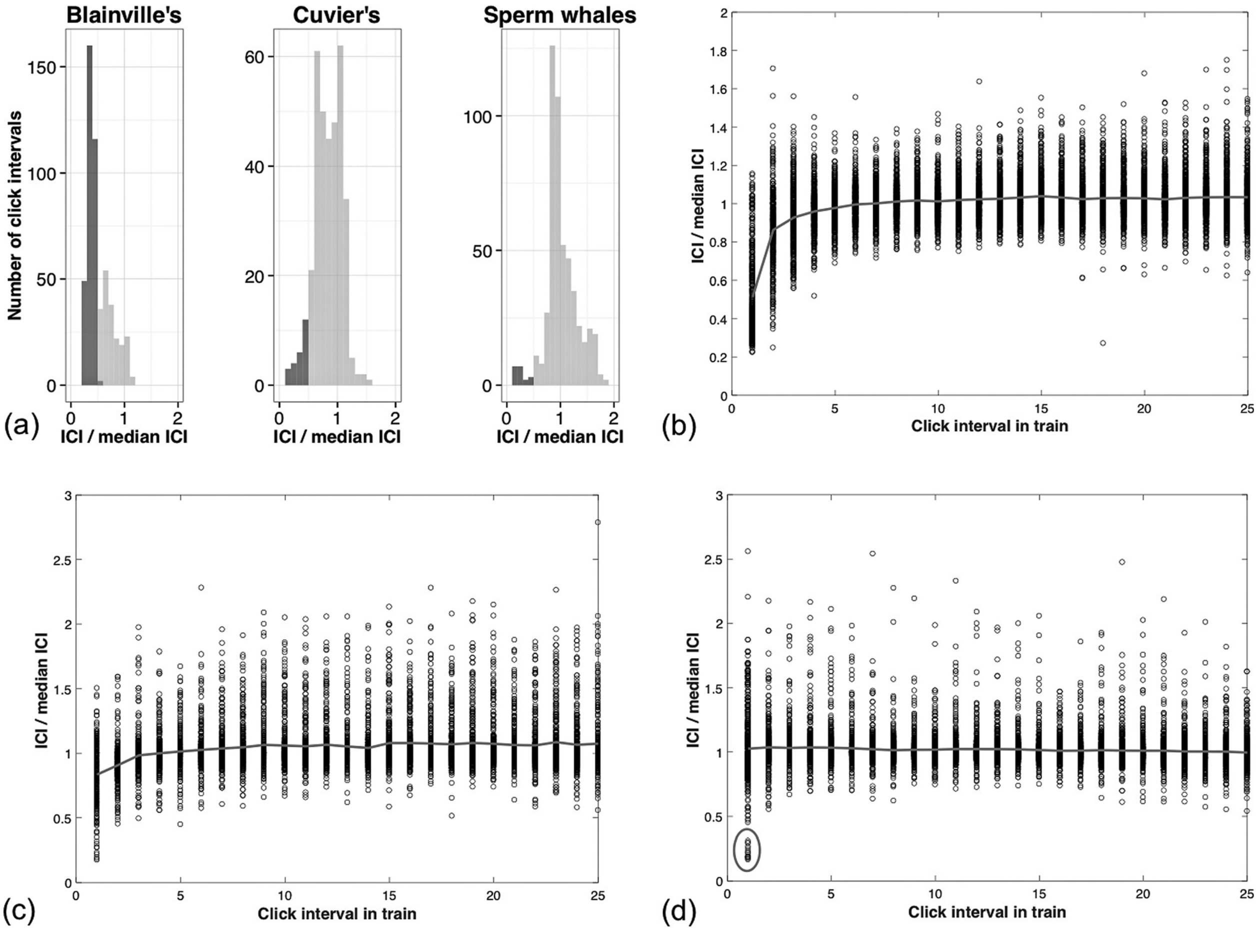

FIG. 2. (a) Plots for Blainville's beaked whales, Cuvier's beaked whales, and sperm whales, showing the number of click intervals <0.5 (in darker shading), and ≥0.5 of the proportion of the median ICI for the entire click train. (b) Click intervals expressed as a proportion of the median ICI for all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

Because the estimated random effects from individuals showed some differences, we plotted each individual's first click intervals (Fig. 4). The distribution of first ICIs expressed as a proportion of the median ICI was centered on 1 for both adults, implying little or no occurrence of SFIs. This was in contrast to the sub-adults whose click trains began with an ICI of approximately 0.6 of the median of the ICIs in the rest of the click train. However, the summed Akaike weights did not highlight age as an important factor (Table II). This is explained by noting that younger animals dived to shallower depths (Fig. 5). The effect size from the model shows the proportion of ICI of the first two clicks increases by 0.37 over the depth range (300 to 1000 m) of a dive, and this may explain the apparent association between age and SFI production in Cuvier's beaked whales if adult Cuvier's beaked whales produce fewer SFIs because they are diving deeper. While the analysis suggests depth is the more powerful predictor, because age class and dive depth

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	5.735×10^{-3}	2.503×10^{-2}
Depth	1.00	1.609×10^{-4}	5.389×10^{-5}	1.00	5.249×10^{-4}	5.894×10^{-5}	0.82	1.272×10^{-4}	6.042×10^{-5}
Time into dive	1.00	-2.982×10^{-5}	1.224×10^{-5}	1.00	3.677×10^{-5}	1.309×10^{-5}	0.50	-1.143×10^{-5}	8.005×10^{-6}
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	-1.143×10^{-5}	8.005×10^{-6}
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			

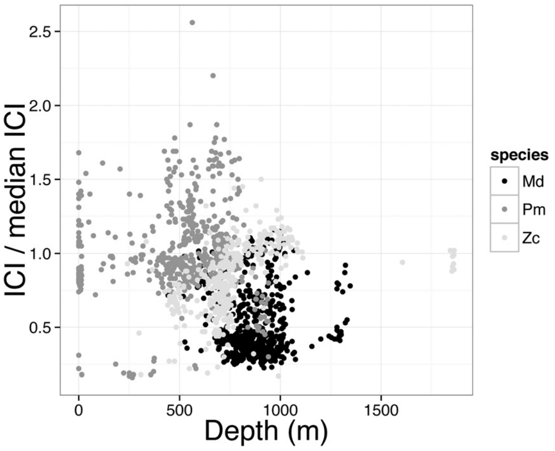

FIG. 3. The depth of each click train, taken at the time of the first click of the click train, for all three species, plotted against the ICI of the first two clicks in the click train (expressed as a proportion of the median ICI for the entire train).

are confounded in this dataset, definitive interpretation is challenging without additional data.

C. Sperm whale

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

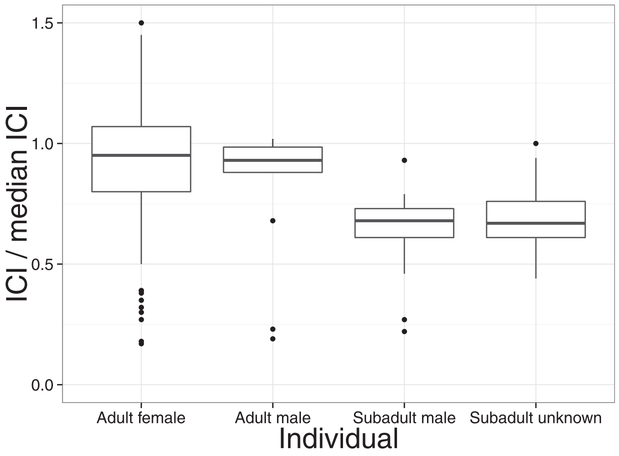

FIG. 4. The proportion of the ICI of the first two clicks in all click trains for two adult and two sub-adult Cuvier's beaked whales.

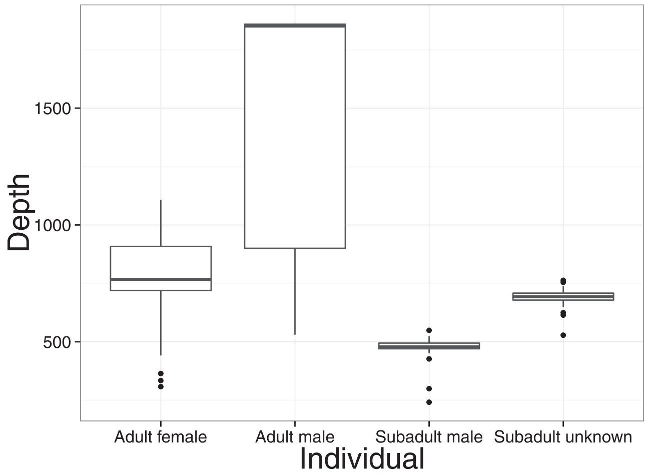

FIG. 5. The depths in meters of all click trains for two adult and two sub-adult Cuvier's beaked whales.

Assigning the animal with tag Sw03_156a as an adult female (most likely since it was sighted in a group) showed moderate variability between individuals, and because removing the random effect variable raised the AIC by just over 2 units, it was retained. As all animals were presumed to be adults, age class was not included in the model, resulting in three variables with relatively high importance (Table II). The presence of a buzz after the click train increased the first ICI, while males had relatively smaller first ICIs and, as in Blainville's beaked whales, there were fewer SFIs with increasing depth (Fig. 3). The single largest effect however was a more pronounced SFI on the first click train of each dive (Fig. 6).

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

IV. DISCUSSION

Our results show strong yet diverse patterns across the three species studied. Blainville's beaked whales produced more SFIs on the majority of their click trains compared to

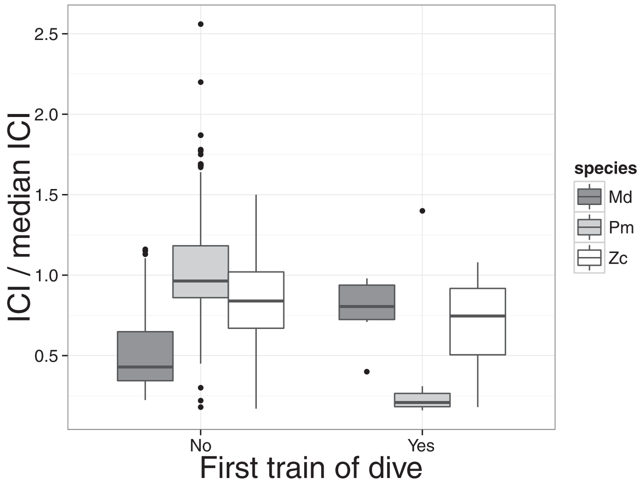

FIG. 6. Distributions of the first ICI in a click train (expressed as a proportion of the median ICI for the entire train) for trains that were and were not the first click train of a dive, for all species (Md = Blainville's beaked whales; Pm = sperm whales; Zc = Cuvier's beaked whales).

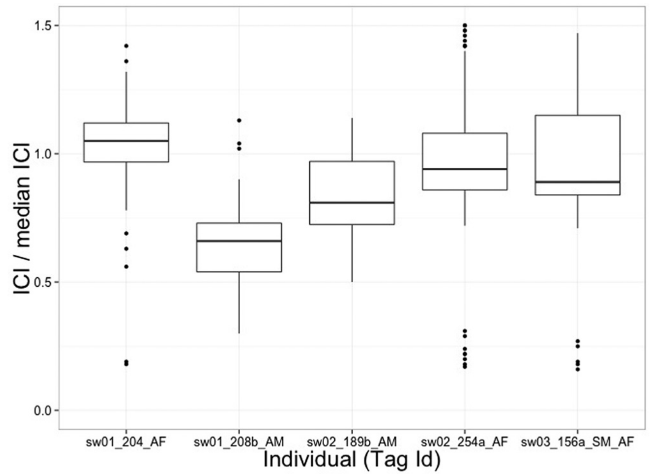

FIG. 7. The ICI (expressed as a proportion of the median ICI) of the first two clicks for the five sperm whales. (AF = adult female, AM = adult male, SM = sub-adult male).

the other species in all age and sex classes analysed, especially when the previous train ended in a buzz. Among Cuvier's beaked whales only sub-adults produced SFIs, and only occasionally, whereas only sperm whales that were not adult males produced SFIs, and only on the first click train of every dive.

The single variable that was highlighted as having high relative importance in the models of all three species was depth. However the effect of this variable on the production of SFIs was not the same across the species. Blainville's beaked whales produced SFIs at the depths where they were foraging, producing them on almost every click train following a buzz. Sperm whales in contrast only produced SFIs on the first train of a dive (coincident with them being at relatively shallow depths). Finally Cuvier's beaked whales produced more SFIs at shallower depths than Blainville's beaked whales. Therefore the production of SFIs does not appear to be a result of pressure at a specific depth.

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

SFIs could be a functionless by-product of pneumatic click production, which explains why they are being produced at the start of a click train. It is possible that the first click in a dive may be significantly different due to the phonic lips having been parted for surface breathing, or a need to reconfigure the vocal tract for clicking rather than breathing, by filling specific airsacs for example. If the suggestion that phonic lips require a layer of fluid to function in click production stands (Cranford *et al.*, 2011; Thode *et al.*, 2016), SFIs may relate to a lack of fluid, or may even function to introduce fluid after a period of no clicking by using air pressure to blow fluid through the phonic lips, before reliable single clicking can commence. Moreover, the production of SFIs may be related to the adjustment of the tension of the phonic lips, coupled with re-pressuring the nasal passages after some pause, i.e., a surface interval and therefore breathing, as seen in sperm whales in our results, or time between click trains, as seen in both beaked whales species in our results. It is worth noting that whereas sperm whales produce the same click type for search and buzz clicks, beaked whales switch click types and therefore tuning the production mechanism to produce long range search clicks may cause the by-product of an SFI when the animal is retuning its apparatus for search clicks following a buzz. Even if they do not function in echolocation, SFIs potential role as a communicative cue to the behavioural, age, and sex state of the producer, however, should not be overlooked. More data from varying age/sex classes in all three species, and from other species in which shorter ICIs have been noted, are required to refine these hypotheses.

ACKNOWLEDGMENTS

The data we report from the Bahamas was collected during "The Behavioral Response Study-2008" which was funded by the U.S. Navy Chief of Naval Operations Submarine Warfare Division (Undersea Surveillance), the U.S. Navy Environmental Readiness Division, the U.S. Office of Naval Research, the Oil and Gas Producers Joint Industry Program on Sound and Marine Life, the U.S. Department of Defence Strategic Environmental Research and Development Program (SERDP), and the U.S. National Oceanic and Atmospheric Administration (National Marine Fisheries Service, Office of Science and Technology). We thank everyone involved in the fieldwork for this study. The work in the Bahamas was conducted under permits issued to BMMRO, Bahamas research Permit No. 12 (Bahamas Marine Mammal Protection Act 2005) and Professor Ian Boyd, and under Bahamas Marine Mammal Research Organization's and Woods Hole Oceanographic Institution's Institutional Animal Care and Use Committee guidance and protocols. L.R. and P.T. were supported by the Marine Alliance for Science and Technology for Scotland (MASTS) pooling initiative and their support is gratefully acknowledged. MASTS is funded by the Scottish Funding Council (Grant Reference No. HR09011) and contributing institutions. We would also like to thank Jonathan Kemp from the School of Physics and Astronomy at the University of St. Andrews for useful discussions surrounding this manuscript, and Hilary Moors-Murphy and others who were involved in early versions of this manuscript.

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