Characterization and comparison of echolocation clicks of white-beaked dolphins
(*Lagenorhynchus albirostris*) off the Northumberland coast, UK

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ABSTRACT

Odontocetes produce ultrasonic clicks for navigation and foraging. These are commonly categorized as regular or buzz clicks based on the inter-click interval. Buzz clicks are linked to foraging behaviors and may be subdivided into slow buzz clicks for prey chase, and regular buzz clicks for prey capture. This study recorded these three click types produced by white-beaked dolphins (*Lagenorhynchus albirostris*) off the Northumberland coast, UK. Acoustic parameters, (including duration, centroid frequency, and root-mean-squared bandwidth) were calculated and compared across the three click types. The results showed that the regular clicks had shorter durations and higher frequencies than both the buzz click types. The regular buzz clicks had longer durations, lower frequencies, and narrower bandwidths than the slow buzz clicks. Additionally, regardless of click type, about 30% of the clicks had high-frequency (200-250 kHz) secondary peaks and > 90% of the clicks displayed spectral peak and notch patterns between 20 and 80 kHz. These findings are useful for future quantitative assessment of the echolocation

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performance of white-beaked dolphins in the wild. The patterns of spectral peaks and notches identified may facilitate for acoustic identification of this species.

1 I. INTRODUCTION

2 Odontocetes (toothed whales) generally produce two functional categories of ultrasonic
3 pulses, echolocation clicks and burst pulses, which are used in repeated patterns to produce
4 echolocation click trains and burst pulse trains, respectively (Au, 1993; Richardson *et al.*, 1995).
5 Based on the behavioral contexts and inter click interval (ICI), the echolocation click trains can
6 be further categorized as regular click trains and buzz click trains (Griffin *et al.*, 1960; Miller *et al.*,
7 1995; Johnson *et al.*, 2006; Madsen and Surlykke, 2013). The former are series of clicks with large
8 ICIs (i.e., generally defined as those > 10 ms) mainly used for navigation and detection in the
9 environment (Lammers *et al.*, 2004; Madsen and Wahlberg, 2007). The latter are click trains
10 ending with ICIs ≤ 10 ms used to locate and track prey during foraging and feeding events
11 (Lammers *et al.*, 2004; Ridgway *et al.*, 2015; Martin *et al.*, 2018). In contrast, burst pulse trains
12 associated with social communication are a discrete, isolated series of clicks with high repetition
13 rates (ICIs ≤ 10 ms), such that they appear tonal (Au, 1993; Simard *et al.*, 2008).

14 Odontocetes continuously produce different types of pulsed sounds, which offer a suitable
15 acoustic indicator for determining presence and behavior of individuals (Richardson *et al.*, 1995;
16 Temple *et al.*, 2016). Characterization of clicks can facilitate the acoustic identification of species
17 and is critical for future passive acoustic monitoring and research efforts (Wahlberg *et al.*, 2011;
18 Usman *et al.*, 2020). Comparison of click train types used in different behavioral contexts may

improve the understanding of the functional adaptations made by different echolocating species and give further insight into the drivers of acoustic behavior (Madsen and Surlykke, 2013). Additionally, baseline knowledge of odontocete sound signals is particularly useful for any future studies that will assess potential impacts of anthropogenic noise on the acoustic behavior of odontocetes (Faulkner *et al.*, 2018).

To improve echolocation performance in various contexts (e.g., navigation, target identification, prey chase and capture), odontocetes may actively control some click parameters such as duration, spectral content, directionality, and amplitude (Brumm and Slabbekoorn, 2005; Madsen *et al.*, 2005). For example, narwhals (*Monodon monoceros*) capture prey using buzz clicks that have longer durations and lower frequencies than regular clicks (Miller *et al.*, 1995). Some common bottlenose (*Tursiops truncatus*) (Wisniewska *et al.*, 2014; Luís *et al.*, 2016) and Commerson's (*Cephalorhynchus commersonii*) (Reyes *et al.*, 2015) dolphins' buzz clicks have shorter durations, lower frequencies and lower output levels than regular clicks. Blainville's beaked whales (*Mesoplodon densirostris*) use long-duration, narrow-bandwidth and frequency-modulated clicks during the search phase and the initial approach to prey, and switch to short-duration, broad-bandwidth and non-frequency-modulated buzz clicks during the final stage of prey capture (Johnson *et al.*, 2006). Acoustic differences between regular and buzz clicks vary among odontocete species, possibly reflecting different foraging strategies, prey preference, and habitat properties (e.g., bottom topography, water depth, and clutter condition) (Richardson *et al.*, 1995).

White-beaked dolphins (*Lagenorhynchus albirostris*) are medium-sized delphinids (adult body length 240-310 cm) that inhabit temperate and subpolar waters of the North Atlantic Ocean,

mainly on the continental shelf (water depth < 200 m) (Galatius and Kinze, 2016). The species is typically observed in small groups (< 10), however larger aggregations have been reported across their range (Galatius and Kinze, 2016). The white-beaked dolphin is listed as Least Concern in the IUCN Red List in view of its wide distribution and relatively large global abundance (Kiszka and Braulik, 2018). However, the population in the North Sea and the adjacent Atlantic European waters has been proposed as a Priority Species (Grouped Plan for Dolphins) in the UK Biodiversity Action Plan and is protected under the EU's Habitats Directive (92/43/22C), where it is listed in the Annex IV as "in need of strict protection" (Parsons *et al.*, 2010; Calderan *et al.*, 2013). A visual health assessment of white-beaked dolphins off the Northumberland coast, UK, identified high incidence of skin disease and trauma across identified individuals, highlighting a potential conservation concern for the species (Van Bressem *et al.*, 2018).

Several studies have documented the acoustic behavior of white-beaked dolphins (Rasmussen and Miller, 2002; Rasmussen *et al.*, 2002; Rasmussen *et al.*, 2004; Rasmussen *et al.*, 2006; Nachtigall *et al.*, 2008; Simard *et al.*, 2008; Mooney *et al.*, 2009; Calderan *et al.*, 2013; Rasmussen *et al.*, 2013; Rasmussen *et al.*, 2016). The acoustic characteristics of the pulsed sounds produced by white-beaked dolphins have been described in Faxaflói Bay, Iceland (Rasmussen and Miller, 2002), the west coast of Scotland and the North Sea (Calderan *et al.*, 2013), and burst-pulses have been described off the south coast of Nova Scotia, Canada (Simard *et al.*, 2008). Icelandic white-beaked dolphins' clicks resembled those of common bottlenose dolphins, but further analyses revealed that some clicks contained two frequency peaks, and the second peak occurred in the a higher frequency band (200-250 kHz) (Rasmussen and Miller, 2002). Calderan *et al.* (2013) investigated

the low frequency (< 80 kHz) characteristics of white-beaked dolphins' clicks, and showed that these exhibited spectral banding patterns, where individual clicks had distinct spectral peaks and notches between 20 and 80 kHz. Simard *et al.* (2008) described that the burst pulses of white-beaked dolphins had lower frequencies and bandwidths compared to their echolocation clicks, although such differences may be in part due to the low acoustic sampling rate used. Currently, a comprehensive analysis comparing regular and buzz click trains and burst pulse trains of white-beaked dolphins is lacking.

This study recorded underwater sounds from free-ranging white-beaked dolphins off the Northumberland coast, UK, where the species are regularly encountered between June and October (Van Bresseem *et al.*, 2018). The aims were to investigate spectral-temporal parameter differences across different click types, and to determine whether a high-frequency secondary peak frequency and spectral banding patterns were present in individual clicks.

II. METHODS

A. Data collection

Underwater acoustic recordings of white-beaked dolphins were conducted in the coastal waters of Northumberland off the North East of England, UK (Fig. 1), during daylight hours from 12 August to 20 October, 2015 (four encounters) and on the 26 July and 8 August, 2019 (two encounters). Water depths where acoustic recordings were made varied between 30 and 110 m; the bottom substrate was sand and basalt in all cases. All recordings were obtained in calm seas (Beaufort scale < 3) when dolphins were within a visually estimated 30 m range of a rigid inflatable outboard powered boat. For each encounter, group size and surface group behaviors

(travelling, resting, or foraging) were collected concurrently with acoustic recordings (Stensland and Berggren, 2007). Due to white-beaked dolphins typically showing attractive responsive movement to the survey vessel (Palka and Hammond, 2001), undisturbed group behavior was difficult to observe. However, presence or absence of surface behavior associated with foraging was recorded for each group sighting. Foraging behavior was determined by rapid energetic surfacing, frequent direction changes, fish chases, and dolphins making deeper (peduncle and tail-out dives) and longer dives (Stensland and Berggren, 2007).

FIG. 1. Map of study area. Black dots represent the sound recording locations (recording date and water depth were labeled above) for white-beaked dolphins off the Northumberland coast (black box in the inset map), UK.

Underwater sounds were recorded using a single self-contained recording system, SoundTrap 300HF (Ocean Instruments, New Zealand; sampling rate: 576 kHz, sensitivity: -171 dB re 1 V/ μ Pa and flat frequency response: 0.4-150 kHz $\pm$ 3 dB). The SoundTrap contains an inner anti-

aliasing filter at 150 kHz, leading to a -6 dB roll-off per additional octave in frequency. The SoundTrap was deployed at 5 m below the sea surface, connected to a small weight and a surface buoy to reduce movement. A 25 m floating line connected the buoy to the boat and was used to retrieve the equipment. To minimize potential effect on dolphin behavior and acoustic masking, the engine and all sound generating equipment on the boat were switched off during recordings.

B. Acoustic analysis

Audio recordings were first visually and aurally scanned using Adobe Audition (version 3.0, Adobe System Inc. CA) in both time and frequency domains, with Hann windows of 1024 points and 50% overlap, to manually identify the click trains in each recording. The recordings were digitally filtered using a 10-pole Butterworth high-pass filter with a pass-band of 19 kHz to minimize the influence of whistles and low-frequency ambient noise (Au, 1993). Only click trains with at least five clear individual clicks, which should have distinct sinusoidal wave-shape and no overlap with refraction or reflection signals and other click trains, were manually selected for further analyses. To minimize pseudo-replication, selected click trains had an interval of at least two minutes between them. Additionally, to show the acoustic context of dolphin recordings, root-mean-squared (rms) sound pressure levels (SPLs) and power spectral densities (PSDs) of ambient noise between 19 and 288 kHz were averaged over 30 separate 10 s intervals randomly selected between dolphin sounds from each recording day.

The ICIs of each click train were calculated as the time between the amplitude maximum, derived from the signal envelope, of adjacent clicks. According to ICI values, click trains were assigned to two types: regular click trains [Fig. 2 (a) and Mm.1] or buzz click trains [Fig. 2 (b) and

117 Mm.2]. A buzz click train was defined as a click train including at least one ≤ 10 ms ICI; trains
118 not meeting this criterion were defined as regular click trains. All buzz click trains selected for
119 further analyses corresponded to encounters where dolphin surface behavior indicated that they
120 were engaged in foraging activities. Buzz click trains were further sub-divided into slow and
121 regular buzz trains [Fig. 2 (b)] (Griffin *et al.*, 1960; Johnson *et al.*, 2006), thought to be used by
122 dolphins during chasing and capturing prey phases, respectively. Slow buzz trains generally
123 preceded regular buzz trains in the time series. In a buzz click train, slow buzz trains had one or
124 more ICI > 10 ms, while regular buzz trains had all ICIs ≤ 10 ms. The start of a regular buzz
125 train was defined as when the first ≤ 10 ms ICI was recorded and the end was defined as the
126 point at which the ICI increased above 10 ms or the buzz click train ended (Martin *et al.*, 2018).
127 In addition, burst pulse trains were identified as isolated fast pulse trains with all ICI ≤ 10 ms
128 [Fig. 2 (c) and Mm.3].

129 Mm. 1. Example of regular click train produced by white-beaked dolphins off the
130 Northumberland coast, UK.

131 Mm. 2. Example of buzz click train produced by white-beaked dolphins off the
132 Northumberland coast, UK.

133 Mm. 3. Example of burst pulse train produced by white-beaked dolphins off the
134 Northumberland coast, UK.

FIG. 2. (Color online) Examples of waveforms (upper panels) and spectrograms (bottom panels) showing representative (a) regular click train, (b) buzz click train, and (c) burst pulse train produced by white-beaked dolphins off the Northumberland coast, UK. The buzz click train was sub-divided into two types: slow and regular buzz clicks based on click inter-interval.

Spectrograms settings: Hann window, FFT size = 1024, overlap = 50 %.

Given that only a single hydrophone was used during the field recordings, it was not possible to determine whether a click was recorded on the acoustic axis of the dolphin sonar beam (Rasmussen *et al.*, 2004). To address this, the click with the highest amplitude was identified and selected from each click train and subsequently analyzed following the methods for on-axis clicks (Madsen and Wahlberg, 2007; Martin *et al.*, 2018). The selected pulsed sounds were labeled as either regular click, slow buzz click, regular buzz click, or burst pulse, based on its original sound signal.

Three acoustic parameters, i.e., duration, centroid frequency, and rms bandwidth, were extracted from each selected individual click according to methods for measuring on-axis click parameters (Au, 1993; Madsen and Wahlberg, 2007). A 32-point rectangular window around the

peak of the amplitude envelop was used to analyze all selected clicks to minimize the influence of reflections and ambient noise when estimating the click parameters. The waveform of each click was interpolated with a factor of 10 to give a better time resolution. To allow comparison with previous research (Rasmussen and Miller, 2002), the duration was defined as the time period containing 87.5% of the energy of the signal (Madsen and Wahlberg, 2007). The power spectrum of each click was calculated as the squared Fast Fourier Transform (FFT) of a 32-point window centered on the peak envelope. The power spectrum was then normalized between 0 and 1, and interpolated with a factor of 100, resulting in a linearly interpolated spectral resolution of 180 Hz. The centroid frequency (defined as the frequency separating the spectrum into equal energy halves on a linear scale) and rms bandwidth (defined as the standard deviation of a linear spectrum around centroid frequency) were determined from this power spectrum (Zimmer, 2011). Peak frequency and -3 or -10 dB bandwidth were not considered in the present analyses as they are not stable parameters for broadband clicks when compared to centroid frequency and rms bandwidth (Kinsler *et al.*, 1999).

The characteristics of high-frequency secondary peak (HFSP) and spectral banding pattern (SBP) were visually examined in the spectra of each individual click. The HFSP was defined as when the click spectrum had at least one distinct peak over 200 kHz with a spectral magnitude of more than half of the primary peak (Fig. 3) (Rasmussen and Miller, 2002). The SBP was defined by the click spectrum having at least two peaks and two notches between 20 kHz and 80 kHz, and the difference of relative power levels between the peak (or notch) and notch (or peak) immediately following was > 2 dB (Fig. 3) (Soldevilla *et al.*, 2008; Calderan *et al.*, 2013). Given that

the SBP mainly occurred at the ring-down stage of the click pulse (Soldevilla *et al.*, 2008), a relatively long 512-point (~ 0.89 ms) window centered on the peak of the amplitude envelop was used for calculation of the click spectra. To achieve a better spectral resolution, the FFT size was set as 512 and the interpolated factor as 10. The presence or absence of HFSP (or SBP) in an individual click was denoted as 1 or 0, respectively.

FIG. 3. (Color online) Normalized spectrum (left panel) and spectrogram (right panel) of echolocation click example for white-beaked dolphins off the Northumberland coast, UK, showing two acoustic characteristics: secondary peak over 200 kHz (HFSP, black dot) and spectral banding pattern (SBP, black rectangle) between 20 kHz and 80 kHz. Spectrum is constructed from a 512-point Hann window around the peak of the envelope and interpolated with a factor 10. Spectrogram settings: Hann window, FFT size = 1024, overlap = 50 %.

The ICI determination, sound signal selection, acoustic parameter calculation, and examination of HFSP and SBP were all implemented using custom-written code (Yang *et al.*, 2020) in MATLAB (version R2016a, MathWorks, Natick, MA).

C. Statistical analysis

Continuous variables (including duration, centroid frequency, and rms bandwidth) were tested for normality within groups graphically and by a Kolmogorov-Smirnov (> 50 samples) or Shapiro-Wilks (≤ 50 samples) test, and for homogeneity of variances between groups by a Levene's test. These data were reported as medians with 5th-95th percentile ranges, as some groups did not meet normality assumptions. The number and proportion of clicks which contained a HFSP or SPB were calculated for each of the three click types (i.e., regular clicks, slow buzz clicks, and regular buzz clicks) and for the burst pulses. A series of generalized linear models (GLMs) were used to compare the three acoustic parameters and the presence of the HFSP and SPB, between regular clicks and slow or regular buzz clicks (independent variables). Given that slow and regular buzz clicks occurred in the same click trains, and thus were not independent, comparisons between these two buzz click types (independent variables) were made using generalized linear mixed models (GLMMs) with the click train identity set as a random effect variable. The distribution family for the continuous variables used in each GLM and GLMM was selected for the most reasonable approximation of the parameter distribution. In instances where more than one distribution family was considered reasonable, the best fitting model was selected using the model AIC (Akaike information criterion) (Akaike, 1981). When comparing the presence of HFSP and SPB among click trains the binomial family was selected.

205 Statistical comparison was not performed for burst pulse data due to the small sample size,
206 however the median signal parameter values with 5th-95th percentile range were reported. All
207 statistical analyses were conducted using R statistical software (version 4.0.0) (R Core Team,
208 2020). Statistical significance was set at a threshold of 0.05.

209 **III. RESULTS**

210 A total of 162 regular clicks, 34 slow buzz clicks, 34 regular buzz clicks, and two burst pulses
211 were extracted from the original sound recordings of white-beaked dolphins off the
212 Northumberland coast, UK. Table I provides information on recording time, location, water
213 depth, group size, and behaviors during the different encounters. The rms SPLs of ambient noise
214 between 19 and 288 kHz across different encounters were significantly different (Kruskal-Wallis
215 test, $\chi^2 = 58.2$, $p < 0.05$, Dunn's post hoc test); and their median PSDs varied with encounters
216 (Fig. SI and SII). However, the median rms SPLs were around 103 dB re 1 μ Pa and the
217 differences between these encounters were not above 2 dB, and the spectral energy distributions
218 had a similar tendency (increase followed by decrease). For further information on the ambient
219 noise, see Electronic Supporting Information¹ (Fig. SI and SII).

220 The descriptive statistics of the duration, centroid frequency, rms bandwidth, and the number
221 and proportion of clicks which contained a HFSP or SBP for the three click types and burst
222 pulses are shown in Table II. The results of the statistical comparisons among the three click
223 types are presented in Table III. Further details of the statistical models provided in Electronic
224 Supporting Information (Table SI).

225 TABLE I. Summary of data used in pulsed sound analysis of white-beaked dolphins off the
226 Northumberland coast, UK. Recording date, start time with sound file length (in parentheses),
227 locations, water depths, group sizes, behaviors (if behavior indicative of foraging was observed),
228 and numbers of click/pulse trains are presented for each recording.

Encounter	Recording date	Start time (sound file length)	Latitude, Longitude	Water depth	Group size	Behavior indicative of foraging	Selected regular click trains	Selected buzz click trains	Selected burst pulse trains
1	19 Sep 2015	15:42 (130 min)	55° 32' N 1° 9' W	101 m	7	Yes	51	16	1
2	27 Sep 2015	15:45 (59 min)	55° 28' N 0° 59' W	99 m	11	Yes	28	4	0
3	4 Oct 2015	15:20 (127 min)	55° 30' N 1° 7' W	97 m	20	Yes	48	12	0
4	10 Oct 2015	16:59 (39 min)	55° 28' N 1° 2' W	90 m	15	Yes	16	1	1
5	26 Jul 2019	14:55 (112 min)	55° 20' N 1° 30' W	38 m	8	Yes	16	1	0
6	8 Aug 2019	13:07 (21 min)	55° 6' N 1° 23' W	36 m	3	No	3	0	0

TABLE II. Acoustic parameters of regular clicks, slow buzz clicks, regular buzz clicks, and burst pulses of white-beaked dolphins off the Northumberland coast, UK. The values are given as median with 5th and 95th percentile values (in parentheses) and n = sample size. The number and proportion (in parentheses) of clicks which contained a HFSP (high frequency secondary peak) or SBP (spectral banding pattern) for each sound type are shown in the last two rows.

	Regular click n = 162	Slow buzz click n = 34	Regular buzz click n = 34	Burst pulse n = 2
Duration (μ s)	21 (14, 31)	24 (18, 36)	29 (17, 45)	39 (34, 44)
Centroid frequency (kHz)	80 (58, 100)	69 (47, 94)	61 (41, 84)	41 (34, 48)
Root-mean-squared bandwidth (kHz)	16 (11, 22)	15 (11, 25)	14 (10, 20)	10 (9, 10)
HFSP	46 (28%)	10 (29%)	11 (32%)	1 (50%)
SBP	148 (91%)	31 (91%)	32 (94%)	2 (100%)

TABLE III. Statistical comparisons of acoustic characteristics for regular clicks, slow buzz clicks, and regular buzz clicks recorded from white-beaked dolphins off the Northumberland coast, UK. For each comparison, the absolute difference between the two medians and p value (in parenthesis) are given. * = $p < 0.05$, HFSP = high frequency secondary peak, and SBP = spectral banding pattern.

		Slow buzz click	Regular buzz click
Duration (μ s)	Regular click	3 (0.001*)	8 (<0.001*)
	Slow buzz click	-	5 (0.018*)
Centroid frequency (kHz)	Regular click	11 (<0.001*)	19 (<0.001*)
	Slow buzz click	-	8 (0.038*)
Root-mean-squared bandwidth (kHz)	Regular click	1 (0.667)	2 (0.056)
	Slow buzz click	-	1 (0.007*)

HFSP	Regular click	1% (0.905)	4% (0.644)
	Slow buzz click	-	3% (0.793)
SBP	Regular click	0% (0.973)	3% (0.596)
	Slow buzz click	-	3% (0.417)

Regular clicks displayed significantly shorter durations [21 μ s (5th-95th percentile range: 14-31)] and higher centroid frequencies [80 kHz (5th-95th percentile range: 58-100)] than the two buzz click types. The rms bandwidths [16 kHz (5th-95th percentile range: 11-22)] of regular clicks were similar to those of slow buzz clicks, but significantly wider than those of regular buzz clicks.

Regular buzz clicks had significantly longer durations [29 μ s (5th-95th percentile range 17-45)], lower centroid frequencies [61 kHz (5th-95th percentile range 41-84)] and narrower rms bandwidths [14 kHz (5th-95th percentile range 10-20)] compared to slow buzz clicks [duration: 24 μ s (5th-95th percentile range 18-36), frequency: 69 kHz [5th-95th percentile range 47-94] and bandwidth: 15 kHz [5th-95th percentile range 11-25]].

Further, no significant differences were detected in either the presence of HFSP or SBP among regular clicks, slow buzz clicks and regular buzz clicks. Regardless of click types, the percent of HFSP was relatively low ($\sim 30\%$), and the percent of SBP was high ($> 90\%$).

In addition, the duration, centroid frequency, and rms bandwidth parameters of the burst pulses were 39 μ s (5th-95th percentile range 34-44), 41 kHz (5th-95th percentile range 34-48) and 10 kHz (5th-95th percentile range 9-10), respectively. Both burst pulses included SBP but only one showed presence of HFSP in its spectrogram.

IV. DISCUSSION

This study is the first quantitative report of both regular and buzz echolocation clicks of the white-beaked dolphins off the Northumberland coast, UK. The buzz clicks had longer durations (median: slow buzz click 24 μ s, regular buzz click 29 μ s) and lower centroid frequencies (median: slow buzz click 69 kHz, regular buzz click 61 kHz) than regular clicks (median duration and centroid frequency: 21 μ s and 80 kHz). The regular buzz clicks had longer durations (median: 29 μ s), lower frequencies (median: 61 kHz), and narrower rms bandwidths (median: 14 kHz) than the slow buzz clicks (median duration, centroid frequency and rms bandwidth: 24 μ s, 69 kHz, and 15 kHz) preceding them. This indicates that white-beaked dolphins were actively adjusting the acoustic parameters for different click types. It should be noted that the sample size in this analysis is relatively small and therefore there is a risk of Type II error (i.e., significant differences between parameters exists but were not found to be different in this study). Thus, larger sample sizes would be desirable in future to improve statistical power and subsequent application. However, these results are meaningful for evaluating the echolocation performance of wild white-beaked dolphins when using different click types. When the results are applied to behavioral contexts, they may improve the understanding of the functional adaptations made by the species. Further, regardless of click type, over 90% of the clicks had spectral banding patterns, a feature which provides for potential acoustic species identification of white-beaked dolphins.

The regular clicks of white-beaked dolphins in this study had similar duration but lower frequency and bandwidth parameters compared to white-beaked dolphins in Icelandic waters (Rasmussen and Miller, 2002) (Table IV). Further, the burst pulses of white-beaked dolphins in

this study had longer duration but lower frequency and bandwidth parameters than white-beaked dolphins in Icelandic waters (Rasmussen and Miller, 2002) (Table IV); however these differences could be attributed to the small sample size from this study ($n = 2$). Similarly, the burst pulses produced by white-beaked dolphins in Canadian waters had longer duration but lower frequency and bandwidth parameters compared to Icelandic waters (Simard *et al.*, 2008). Unfortunately, due to different sampling and sound processing methodologies used, and lack of information on behavior among these studies, it is not possible to draw any robust conclusions about the potential differences among locations and their drivers.

TABLE IV. Acoustic parameter comparisons of regular clicks and burst pulses produced by the white-beaked dolphins in Faxaflói Bay, Iceland (Rasmussen and Miller, 2002)) and off the Northumberland coast, UK. Values expressed as mean and standard deviation (in parentheses) and n = sample size.

Population	Regular click			Burst pulse	
	Icelandic		UK	Icelandic	UK
Sample size	$n = 22^a$	$n = 20^a$	$n = 162^b$	$n = 100^a$	$n = 2^b$
Duration (μ s)	17 (3)	22 (3)	22 (5)	15 (3)	39 (8)
Centroid frequency (kHz)	94 (4)	98 (7)	80 (13)	85 (4)	41 (11)
Root-mean-squared bandwidth (kHz)	24 (3)	31 (5)	16 (4)	32 (2)	10 (2)

^a Individual click/pulse sounds were selected from the same click train.

^b Individual click/pulse sounds selected had the highest amplitude from each of the different trains.

The regular clicks of white-beaked dolphins were shorter and higher in frequency than both buzz click types. Similar results have also been found in narwhal echolocation clicks (Miller *et al.*, 1995). One possible explanation is that dolphins are unlikely to be focusing on a specific target when producing regular click trains (Buscaino *et al.*, 2015), which are generally produced to avoid obstacles and inspect the surrounding environment at distance (Au, 1993; Akamatsu *et al.*, 2005). High frequency regular clicks with short wavelengths are more directional compared to buzz clicks and functionally beneficial for discriminating small objects in highly cluttered waters (Richardson *et al.*, 1995).

Buzz click trains produced by white-beaked dolphins in this study consisted of the slow buzz clicks followed by regular buzz clicks. The slow buzz clicks are thought to be used during searching and chasing of prey, and their higher frequencies and wider bandwidths may be helpful to enhance details about the prey, such as location, size, shape, and species (Møhl and Andersen, 1973; Richardson *et al.*, 1995). For the regular buzz clicks, the narrower bandwidth and lower frequency parameters increase the transmission range and reduce the directionality of clicks (Au, 1993; Starkhammar *et al.*, 2019), which may be critical in ensuring that prey remains within the acoustic field of view to avoid prey escaping. Consequently, echolocating dolphins would be expected to benefit from adjusting the acoustic parameters during different phases of foraging.

Sound levels were not directly compared among click types as the distance between the echolocating dolphins and the hydrophone could not be estimated with confidence and hence transmission loss could not be accounted for. Given that the water depth at some of recording locations is about 100 m and most clicks had no conspicuous bottom-reflection signals, it was

314 not robust to use the “one hydrophone method” to locate the echolocating dolphins (Aubauer *et*
315 *al.*, 2000). Some other odontocete species (e.g., Blainville’s beaked whales) in the wild actively
316 lower the sound levels in their regular buzz clicks after slow buzz clicks (Johnson *et al.*, 2006). For
317 these species, clicks with lower source levels also have decreased bandwidth and centroid
318 frequency (Au *et al.*, 1995). If this is also the case in white-beaked dolphins, it could explain why
319 the regular buzz clicks displayed narrower bandwidth and lower frequency. Further, it is
320 noteworthy that the odontocetes’ foraging behavior can be affected by group size, water depth,
321 and other ecological factors, and the animals may adjust their click parameters to increase their
322 foraging success (Torres and Read, 2009). Although the data used in this study were collected in
323 different locations with different water depths (TABLE I), the sample size was not sufficient to
324 include these factors in the statistical models. Future studies should be conducted to explore
325 potential influences of these factors on the acoustic parameters of different click types.

326 Regardless of the click type, about 30% of the clicks had a secondary peak over 200 kHz,
327 similar to what was found in Icelandic white-beaked dolphins (Rasmussen and Miller, 2002),
328 indicating that the presence of the peak over 200 kHz is not related to behavior and click type
329 used. In other words, the result does not provide evidence that the high-frequency secondary
330 peak is used for foraging buzzes specifically.

331 Nachtigall *et al.* (2008) measured the hearing of the white-beaked dolphin in Faxaflói Bay,
332 Iceland and found that the species could hear frequencies up to 181 kHz but showed no
333 response to signals at 215 kHz. If this apparent hearing threshold was applied to our study area,
334 the component over 200 kHz in the clicks would be non-functional. Given that the fast

attenuation of frequencies above 200 kHz, echoes produced from this higher portion of the spectrum would only convey information from targets at very short distances (Reyes *et al.*, 2015).

Clicks with spectral banding patterns have been described for white-sided (*Lagenorhynchus obliquidens*) and Risso's (*Grampus griseus*) dolphins, which may be explained by morphological characteristics of the head (Soldevilla *et al.*, 2008). As with the population off the west coast of Scotland and the North Sea (Calderan *et al.*, 2013), the clicks of white-beaked dolphins in this study (also the North Sea) had spectral banding patterns, which was present in > 90% of all clicks regardless of click type. This result indicates that white-beaked dolphin could be acoustically distinguished from other co-occurring species (Galatius and Kinze, 2016), such as common bottlenose dolphins, which do not show evidence of spectral banding (Soldevilla *et al.*, 2008). Thus, this finding has the potential to facilitate for effective acoustic identification of white-beaked dolphins and future species-specific acoustic monitoring in areas where others species co-occur.

In conclusion, this study provides new quantitative information on white-beaked dolphin echolocation click sounds that facilitate development of species-specific algorithms for acoustic monitoring of the species. Regardless of click type, about 30% of the recorded clicks had a secondary peak over 200 kHz and > 90% of the clicks included spectral banding patterns. The importance and functions of these features will be the focus of future research efforts to improve the understanding of this relatively poorly investigated species.

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¹ See supplementary material at [URL will be inserted by AIP] for details of statistical models (Table SI) and further information on ambient noise (Fig. SI and SII).

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