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# Acoustic characteristics and context of buzzes and rasps produced by northern bottlenose whales (*Hyperoodon ampullatus*)

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## ABSTRACT

Deep-diving northern bottlenose whales (*Hyperoodon ampullatus*) rely on sound for orientation, foraging and communication. While their regular echolocation clicks have been described, characterisations of other click types are limited. Here we quantify acoustic and behavioural differences between two types of rapid click trains: buzzes and rasps. Sound and movement data were collected from 15 animal-attached DTag deployments around Jan Mayen Island (Norway) from 2013–2016. Buzzes and rasps were manually identified, and random forest analyses revealed a classification accuracy of 93.7% ( $n = 129$  respectively). Rasps occurred more often near the surface whereas buzzes were primarily emitted at depth during foraging dives, had shorter inter-click-intervals ( $U = 263$ ,  $p < 0.001$ ), longer durations ( $U = 14413$ ,  $p < 0.001$ ), and coincided with increased movement more often than rasps ( $U = 10384$ ,  $p < 0.001$ ). On-axis clicks from nearby whales showed further differences in duration and frequency content between individual buzz and rasp clicks. Our findings demonstrate that buzzes and rasps are acoustically and contextually distinct, with buzzes associated with foraging and rasps with communication. These differences will allow identification of buzzes and rasps and inference of behaviour and habitat use in passive acoustic data, enhancing research on this cryptic beaked whale.

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## 1. Introduction

Cetaceans, particularly odontocetes, rely heavily on sound for communication, orientation and foraging due to limited visibility in the marine environment. Understanding a species' acoustic repertoire and functional use of different sound types can thus provide insight into behaviour and habitat use (Johnson et al. 2006; Simon et al. 2010; Aguilar de Soto et al. 2012). Odontocetes sense their environment using echolocation clicks, which

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are transient sounds up to a few hundred microseconds in duration (Madsen and Surlykke 2014). The characteristics of these clicks differ between species and can thus be used to acoustically distinguish them (Roch et al. 2011; Baumann-Pickering et al. 2013). In beaked whales for instance, regular echolocation clicks have a frequency upsweep (Zimmer et al. 2005) which is species-specific and, in combination with differences in frequency range, allows for species identification (Baumann-Pickering et al. 2013).

Besides regular echolocation clicks, odontocetes produce a variety of click based sound types associated either with foraging (Johnson et al. 2004; Miller et al. 2004), or communication (Watkins and Schevill 1977; Aguilar de Soto et al. 2012). In the foraging context, the production of clicks at a regular inter-click-interval (ICI) constitutes the search phase (Johnson et al. 2006), whereas terminal buzzes are produced in the final stage of prey capture attempts (Miller et al. 2004; Johnson et al. 2006). Buzzes are a type of rapid click train with short ICI, i.e. a fast click emission rate, allowing the animal to obtain a high-resolution update of its surroundings and aiding in the capture of agile and potentially evasive prey (Madsen and Surlykke 2014; Vance et al. 2021). The role of buzzes in prey capture is further supported by their correlation with short-term increases in movement activity (Johnson et al. 2004; Miller et al. 2004).

Some odontocetes have been reported to produce another type of rapid click train, often termed rasps (e.g. Blainville's beaked whales (*Mesoplodon densirostris*) (Aguilar de Soto et al. 2012; short-finned pilot whales (*Globicephala macrorhynchus*) (Marrero Pérez et al. 2017): or burst pulses (Risso's dolphins' (*Grampus griseus*) Arranz et al. 2016); which are hypothesised to serve a communication function. Compared to buzzes, rasps are emitted at a lower click rate, are typically shorter in duration, produced at shallower depths and not clearly associated with increased movement (Aguilar de Soto et al. 2012). Taken together, these differences in characteristics, timing and behavioural context of rasps compared to buzzes led to the conclusion that rasps are not associated with foraging, but more likely function in communication and group coordination (Aguilar de Soto et al. 2012; Arranz et al. 2016; Marrero Pérez et al. 2017). In Blainville's beaked whales, Aguilar de Soto et al. (2012) further found differences in click characteristics between the two types of rapid click trains. While rasp clicks showed the species' typical frequency-upsweep, buzz clicks were not frequency-modulated and were shorter in duration (Johnson et al. 2006; Aguilar de Soto et al. 2012).

Northern bottlenose whales (*Hyperoodon ampullatus*) are a member of the beaked whale family inhabiting temperate, sub-arctic and arctic waters of the North Atlantic (Gray and Flower 1882; Whitehead and Hooker 2013). Their offshore distribution (Benjaminsen 1972; Wimmer and Whitehead 2004) appears to be driven by the distribution of their main prey, squid of the genus *Gonatus* (Bjørke 2001; Hooker et al. 2001), which they search for during foraging dives regularly reaching depths between 800–1800 m (Hooker and Baird 1999; Siegal 2020). The production of regular echolocation clicks, which are species-specific frequency upsweep pulses between 15–75 kHz (Wahlberg et al. 2011; Clarke et al. 2019), is almost constant during deep foraging dives (Hooker and Whitehead 2002), and buzzes are primarily produced during these deeper dives (Miller et al. 2015; Siegal et al. 2022). Interestingly, clicks with slightly different characteristics, hypothesised to function in communication, have also been recorded at

the surface (Hooker and Whitehead 2002; Moors-Murphy 2015), which contrasts with other members of the beaked whale family which remain silent in the upper 170–400 m of the water column for acoustic crypsis (Johnson et al. 2004; Aguilar de Soto et al. 2012). Northern bottlenose whales are larger in size than most other beaked whales (MacLeod 2006) and therefore may face a lower predation pressure reducing their need to remain silent near the surface to avoid acoustic detection. The only larger species are of the genus *Berardius*, but their acoustic behaviour is poorly known (*Berardius arnuxii*: Barlow et al. 2021; Rogers and Brown 1999; *Berardius bairdii*: DeAngelis et al. 2023; Stimpert et al. 2014).

The characteristics of northern bottlenose whales' regular echolocation clicks have been reported in detail (Hooker and Whitehead 2002; Wahlberg et al. 2011; Martin and Moors-Murphy 2013; Clarke et al. 2019), whereas buzzes have only been described by Wahlberg et al. (2011) based on 469 clicks from two buzzes. As reported for other beaked whales (Johnson et al. 2006; Visser et al. 2022), the buzz clicks of northern bottlenose whales did not have a frequency upsweep pattern and were shorter in duration compared to regular clicks (Wahlberg et al. 2011). Moreover, rasp production has been mentioned for northern bottlenose whales (Wensveen et al. 2019; Haas et al. 2024) but a systematic description of their characteristics and functionality is still lacking for the species. The social behaviour of northern bottlenose whales and their association in loose fission-fusion groups of primarily 3–4 animals (Gowans et al. 2001; Miller et al. 2015) suggest that the species would benefit from producing communication signals.

Animal-attached sound and movement recording tags for cetaceans – such as DTags – allow for short-term (typically, a few hours) data collection at high resolution (Johnson and Tyack 2003). The simultaneous collection of acoustic, movement and dive data through different sensors enables reconstruction of the animals' sound production and associated behaviour, wherefrom sound type functionality can be inferred (Johnson et al. 2009). This knowledge can then be utilised to infer behaviour from other, solely acoustic data streams. Tagging beaked whales is a highly skilled, cost- and time-intensive procedure, thus, acoustic data collection alone is often more feasible to conduct over wide spatial and temporal scales. For instance, bottom-moored hydrophones can be deployed for months or years at a time and allow for long-term data collection in areas that might otherwise be difficult to reach (Zimmer et al. 2008). Applying knowledge derived from short-term, high-resolution multivariate data to such long-term, lower-resolution univariate data can provide insight into the animals' behaviour and habitat use on a longer time scale and at population level, relevant for informing conservation measures.

Here we quantify differences between northern bottlenose whale buzzes and rasps using acoustic, dive and movement parameters derived from animal-attached DTags and show how these sound types can also be reliably classified based on variables obtainable from passive acoustic monitoring (PAM) alone. We further describe the acoustic properties of individual clicks contained in these rapid click trains and investigate the hypothesis that rasps constitute communication signals by inferring sound type context from movement behaviour, temporal patterns in sound production, and acoustic presence of conspecifics.

## 2. Methods

### 2.1 Data collection

Data were collected each June between 2013–2016 in the waters around Jan Mayen Island (Norway, 70.983°N 8.533°W) as part of international research projects studying body condition and the effects of naval sonar on cetacean behaviour (Miller et al. 2015, 2016; Wensveen et al. 2019). In total, 15 suction cup attached sound and movement-recording DTags (Johnson and Tyack 2003) were deployed (Table 1) using either a long carbon fibre pole, or the ARTS (Aerial Rocket Tag System) pneumatic launching system (Kleivane et al. 2022). In 2013, tagging was performed from a fibreglass workboat deployed off the 55 m long research vessel H.U. Sverdrup II. In subsequent years, tags were deployed off the sailing vessels Prolific (23 m, 2014) or Donna Wood (32 m, 2015–2016). The deployed DTags were equipped with a pressure sensor, three-axis accelerometer, and three-axis magnetometer, each of which sampled data at 50 Hz. Together these sensors allow the reconstruction of the tagged whales' dive and fine-scale movements in the water column. The tag deployed in 2013 had one hydrophone sampling audio at 96 kHz, while all other tags had two hydrophones sampling at 192 kHz or 240 kHz (Table 1).

### 2.2 Tag data processing

All 15 tag deployments were manually audited, marking times of regular echolocation click production, buzzes and rasps, using the DTag Toolbox (Johnson 2014) in MATLAB

**Table 1.** Overview of tag deployments on northern bottlenose whales. Individual IDs stem from the HYPMO project photo-id catalogue, and age/sex classes were determined as adult or juvenile females (F) through genetic analyses of biopsy samples, or adult females or juveniles of unidentified sex (FJ) based on photo-id data. Further information provided are acoustic sampling rate, duration of the analysed data, group size at the time of tagging, the number of buzzes and rasps produced by the tagged (focal) whale or nearby non-focal conspecifics, and the number of focal buzzes and rasps of five tags which were selected for detailed (section 2.2.1) and random forest analyses (section 2.3).

Tag ID	Individual ID	Age/sex class	Sampling rate (kHz)	Duration (hh:mm)	Group size	Focal buzzes	Non-focal buzzes	Focal rasps	Non-focal rasps	Buzzes/rasps analysed in detail
ha13_176a	–	–	96	10:20*	6	153	593	26	152	–
ha14_165a	–	–	192	09:16	2	181	10	3	5	–
ha14_166a	5113	F	192	12:09	3	133	122	6	33	–
ha14_174a	0060	F	192	05:46	3	69	153	23	38	23/23
ha14_174b	5304	–	192	09:15	1	127	216	27	73	24/24
ha14_175a	0065	FJ	192	12:00	3–4	189	320	33	37	26/26
ha15_171a	5112	–	192	03:46*	7–8	87	105	6	38	–
ha15_173a	0335	–	192	08:55	7–10	229	747	7	24	–
ha15_173b	0234	FJ	240	01:12	3	20	119	3	7	–
ha15_174a	0120	–	192	11:34	4	104	259	7	7	–
ha15_174b	0346	FJ	240	12:57	4+	278	1413	31	40	26/26
ha15_179b	5061	FJ	240	05:03*	4	151	73	6	0	–
ha16_169a	0161	F	240	05:47	8	108	546	68	62	30/30
ha16_170a	5302	F	240	05:10*	4	122	298	11	13	–
ha16_173a	0201	F	240	11:44	10	93	70	1	1	–

\*For four tags previously analysed as part of sonar playback studies (Miller et al. 2015; Wensveen et al. 2019), durations provided are for the pre-exposure baseline data collection periods only.

Version 9.12.0 R2022a and older (The MathWorks Inc 2022). All audits were conducted by trained analysts including author CEH who also verified all buzz and rasp assignments. Sounds were categorised based on the acoustic data by listening to the sounds and by visual examination of spectrogram (Hamming window, 50% overlap 512 FFT) and amplitude envelope plots. Regular clicks were identified based upon their known time-frequency characteristics (Wahlberg et al. 2011; Clarke et al. 2019). Buzzes were defined as rapid click trains with fast click emission rate, i.e. short ICIs (Wahlberg et al. 2011), and a decreased click intensity compared to regular clicks (Miller et al. 2004; Johnson et al. 2006). Rasps were defined as rapid click trains resembling buzzes though emitted at a slower click rate than buzzes and sounding like the ‘caressing of a comb’. Click trains were ascribed to have been produced by the tagged whale, or a nearby whale, based on low frequency content in the clicks. Focal clicks produced by the tagged whale contain sound energy below 15 kHz which is transmitted through the body to the attached tag and absent in clicks recorded from nearby conspecifics (Zimmer et al. 2005; Johnson et al. 2006).

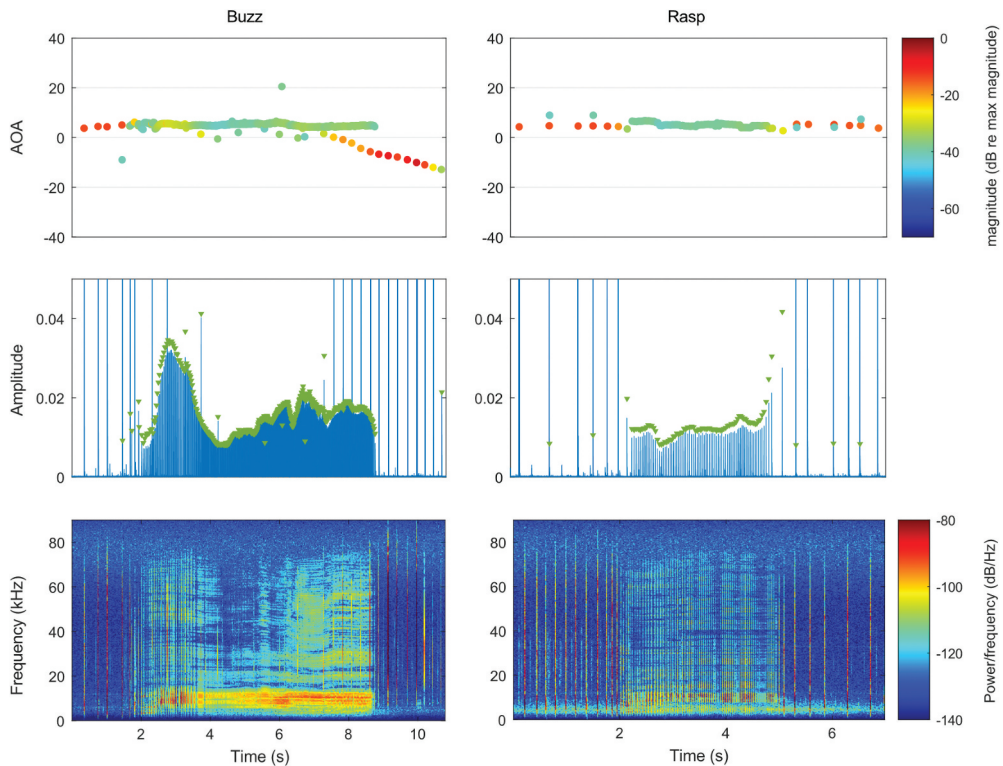
Pressure data were converted into depth, and we defined a dive as starting when the tagged whale first went deeper than 10 m, and ending when it returned to a depth shallower than 10 m. For each buzz and rasp the depth at its onset was extracted and we also calculated depth as a percentage of the dive’s maximum depth for a selection of the data (section 2.2.1). For visual inspection of acoustic behaviour throughout the tag record, dive profiles were plotted for all 15 tag deployments as depth over time with periods of regular echolocation clicking, as well as focal and non-focal buzzes and rasps indicated in the dive profiles.

### 2.2.1 Detailed analysis of a selection of buzzes and rasps

To quantify differences between buzzes and rasps, five stereo DTag deployments that each contained a minimum of 20 focal rasps were analysed in more detail (Table 1). This ensured a representative sample of rasps for each individual and roughly similar sample sizes. Audited rapid click trains and regular click sequences attributed to the tagged whale were bandpass filtered with a 5–70 kHz passband and individual clicks were analysed using a supervised energy detector (function *findclicks* in the MATLAB DTag toolbox). Customised interactive plots of the rapid click trains including 2 seconds before and after the audited click train edges were used to identify individual clicks produced by the tagged whale inside the buzz or rasp based on presence of low frequency content, and temporal patterns in click angle of arrivals (AOA) at the two hydrophones and click received level (RL). The AOA of focal clicks, i.e. clicks produced by the tagged whale, should remain constant over time but can show slight variations corresponding to the whales’ movement and placement of the tag on the whale. For clicks from nearby (non-focal) whales, the AOAs are expected to change more rapidly and drastically in accordance with the focal and non-focal whales’ movement relative to one another (Johnson et al. 2006). Ten-second control windows containing focal regular echolocation clicks were examined to obtain a mean AOA as baseline reference for the tagged whale. Buzzes and rasps with click AOAs within  $\pm 15^\circ$  of their baseline AOA were considered produced by the tagged whale as the maximum observed AOA range inside the control window was  $30^\circ$ , which was comparable with other species (Arranz et al. 2016; Marrero Pérez et al. 2017). Similar to the AOA, the RL of focal clicks within a click sequence should vary little

with time, whereas the RL of non-focal clicks will vary with the whale's orientation towards the tag (Zimmer et al. 2005). Hence, stability in RL was used as another indicator for attributing click trains to the tagged whale.

Inspection of click AOAs and RLs together with a waveform and spectrogram display (Figure 1) typically allowed for reliable attribution of clicks to the tagged whale. Nevertheless, in some instances, audited buzzes or rasps were excluded from the analysis due to: (1) uncertainty which animal was producing the sound, (2) mislabelled click train type (e.g. ICI above threshold), (3) missing values for subsequent analyses (e.g. in accelerometer data), (4) overlap with non-focal clicking that could not be disentangled with certainty, or (5) low signal-to-noise ratio. Audited buzzes and rasps of all five tag records were analysed in a randomised order, starting with rasps and matching the number of considered buzzes to that of available rasps. For deployment ha16\_169a only the first 30 rasps that fulfilled the quality criteria were included in subsequent analyses, due to the high number of audited rasps in that tag record.



**Figure 1.** Representative examples of a buzz (left) and rasp (right) produced by the tagged whale, showing (top) the clicks' angle of arrivals (AOAs) in degrees, (middle) positive click amplitudes in arbitrary linear units, with green triangles indicating clicks detected by the supervised energy detector, and (bottom) spectrogram (Hamming window, 50% overlap, 1024 FFT) of the rapid click sequence. The buzz is preceded by regular echolocation clicks and followed by a pause in focal clicking, and overlaps with a click train of a nearby (non-focal) whale with quickly changing AOAs from  $10^{\circ}$  to  $-20^{\circ}$ . The focal rasp is preceded and followed by regular echolocation clicks of the focal whale, and few non-focal clicks are detected at lower magnitude.

For each buzz and rasp retained in this detailed analysis, we calculated its duration and ICIs. ICI was defined as the time difference between two consecutive clicks, where the time cue of each click was extracted at the maximum magnitude within a Hilbert transform envelope. To account for missed click detections, ICI values larger than 1.5 times the previous ICI were replaced with the mean of the three preceding ICIs. Buzzes and rasps were defined as starting and ending, respectively, when the ICI dropped below and rose above 100 ms, as ICIs of beaked whales' regular echolocation clicks typically remain above this threshold (Johnson et al. 2006; Wahlberg et al. 2011; Clarke et al. 2019). Duration was then calculated as the time difference between the first and last click within this ICI threshold. To obtain a measure of change in ICI within the rapid click train over time, we computed the ICI slope over time as the change in ICI from one click to the next, divided by the ICI. Slope measurements were then averaged to obtain a single value per rapid click train. As most buzzes or rasps showed a smooth transition from and back to regular clicking, the ICI slope was calculated for 10–90% of clicks within the buzz or rasp to eliminate the influence of relatively long ICIs around the on- and offset.

Movement and dive behaviour associated with buzzes and rasps were analysed by examining acceleration jerk and depth at sound production as actual depth and depth relative to the dive's maximum depth. Movement at rapid click train production was calculated as the root-mean-square (RMS) jerk, i.e. the differential of 3-axis acceleration, over a 0.6 s sliding window (following Siegal 2020). For each buzz and rasp we extracted the RMS-jerk peak in a 7 s window around the click train's end, defined as 5.5 s before and 1.5 s after the end point (Siegal 2020). Similarly, we extracted the jerk peak within a 7 s control time window ending 5.5 s prior to rapid click train onset, ensuring there could be no overlap between the control and rapid click train time windows. To account for the influence of tag placement on jerk magnitude, we calculated the relative percentage of jerk increase from just before to around the rapid click train end. A negative/positive value indicates a decrease/increase in jerk, indicating a decrease/increase in movement from before to during rapid click train production. Additionally, jerk change was converted into a binary variable of overall increase versus decrease in movement.

For later investigation of behavioural aspects associated with buzz and rasp production (section 2.5), we created a binary variable of acoustic presence/absence of conspecifics during rapid click train production. We further examined the acoustic behaviour of the tagged whale in the 2-s window immediately before and after buzz or rasp production. Rapid click trains associated with foraging are expected to be preceded by regular search clicks and, at least in the case of successful prey capture, might be followed by a short pause in clicking while the animal ingests the captured prey (Miller et al. 2004; Johnson et al. 2006). Rapid click trains produced for communication are not expected to follow such a specific pattern of transitions from and to regular clicking.

Differences between buzzes and rasps in terms of acoustic presence/absence of conspecifics, regular clicking before and after rapid click train production, duration, mean ICI, ICI slope, depth, depth as percentage relative to a dive's maximum depth, percentage of jerk increase and the binary variable of jerk increase versus decrease were tested for statistical significance using a Mann-Whitney-U test on the respective variable.

### 2.3 Random forest analysis

To quantitatively separate buzzes and rasps and determine which of their features are most important for distinguishing the two types of rapid click trains, we trained random forest models on the selection of buzzes and rasps described in section 2.2.1. A random forest is an ensemble of classification trees (Breiman 2001) with each tree trained on a bootstrap sample of the data, leaving out a set of so-called out-of-bag (OOB) samples for classification performance evaluation. The trees' OOB error rates are then averaged across the random forest model as a measure of classification performance (Breiman 2001; Strobl et al. 2009). Variable importance is determined through random permutation of a predictor variable in the OOB sample and returned as percentual decrease in correct classification rate by comparing the performance on the permuted against the original sample (Breiman 2001; Strobl et al. 2009). Random forests have been successfully applied to marine mammal call repertoires (e.g. Rekdahl et al. 2013; Garland et al. 2015; Selbmann et al. 2023) and are useful for small datasets with non-independence, non-normality, and unknown correlations across predictor variables (Breiman 2001).

We constructed random forests in R (R Core Team 2023) using the *randomForest* (Liaw and Wiener 2002) and *caret* (Kuhn 2008) packages. We used six predictor variables: duration, mean ICI, ICI slope, absolute depth, depth relative to maximum dive depth, and relative increase in acceleration jerk from before to during sound production. The number of trees inside each forest was set to 1000 and two predictor variables were considered at each split, following Breiman and Cutler (2003). To ensure model stability, we constructed five random forests and calculated the mean and standard deviation (SD) of the OOB error and variable importance across models, which should yield similar results across re-runs of a stable model (Strobl et al. 2009). To evaluate potential overfitting, the data were split into training and test data. While the OOB approach already provides a built-in separation in training and test data (Breiman 2001), that split is performed at random. However, our data stems from five tags, thus five individual whales where for each of them multiple buzzes and rasps were included in the analysis. To account for potential individual differences between tagged whales, we thus constructed random forest models using four tag deployments for model training and the remaining deployment as test data and repeated this approach until each deployment once served as the test data. The same analysis was repeated using a reduced set of predictor variables that can be obtained from PAM data: duration, mean ICI, and ICI slope.

### 2.4 Characteristics of clicks within non-focal click trains

To investigate differences between the individual clicks produced during regular echolocation, buzzes and rasps, we characterised time-frequency parameters of a selection of non-focal clicks received on the DTags. For this aspect of the analysis, we only considered tag deployments with a minimum of 20 audited non-focal rasps ( $n = 9$  deployments; Table 1) and detected individual clicks with a supervised energy detector (*findclicks*, DTag toolbox). The outgoing clicks of northern bottlenose whales have a narrow beam pattern (Wahlberg et al. 2011). Consequently, the characteristics of the received clicks differ depending on the recording angle relative to the animal's acoustic axis (Møhl et al.

2003; Zimmer et al. 2005), with off-axis clicks having lower received peak-to-peak levels and generally not showing the characteristic frequency upsweep pattern. Therefore, the click with the highest amplitude within the buzz, rasp or regular clicking sequence, together with one preceding and one succeeding click, were extracted. To keep only those clicks that were presumably recorded on- or near the acoustic axis, we removed clicks that had a peak-to-peak level below 90 dB re 1 $\mu$ Pa, for buzz and rasp clicks, and 110 dB re 1 $\mu$ Pa for regular echolocation clicks. While this approach did not guarantee our sample contained exclusively on- and near-axis clicks, it represented the best approximation possible with the data at hand.

Following this initial click selection, we extracted a 5 ms long window centred around the maximum amplitude and applied a 15–95 kHz bandpass filter to enhance signal-to-noise ratio. We visually inspected the waveform, power spectral density and a Wigner-Ville time-frequency distribution plot to ensure no overlap with other sounds before reducing the analysis window to 0.5 ms and extracting duration and frequency characteristics. Each click was upsampled by a factor of 10 using a polyphase filter to increase time resolution. We then calculated each click's 95% energy duration and from its power spectral density extracted the centroid frequency, peak frequency, and –10 dB bandwidth. To assess frequency change within a click, we computed the Wigner-Ville time-frequency distribution and extracted the click's start and end frequency as the points when sound intensity first and last reached 60% of the click's maximum intensity. The difference between the end and start frequency was then calculated as a measure of frequency change over each click.

Exploratory data plots of our rasp click sample suggested that rasps contained two types of clicks that differed in duration and frequency modulation. During regular echolocation, northern bottlenose whales emit frequency-modulated clicks but switch to producing shorter and unmodulated broadband clicks inside buzzes (Wahlberg et al. 2011). As rasp clicks shared similarities with both these click types, we investigated whether the switch from longer frequency-modulated to shorter broadband clicks was correlated with the decrease in ICI, which could suggest a physical constraint of producing the longer modulated clicks at high rates. To test this hypothesis, we examined the relationships between rasp click duration, ICI to the preceding click and frequency change by calculating Pearson's correlation coefficients.

## **2.5 Behavioural aspects of buzz and rasp production**

To infer the context of buzz and rasp production, we investigated the timing of rapid click trains in relation to the animal's dive behaviour considering all 15 tag deployments (Table 1). Therefore we grouped all audited buzzes and rasps by dive phase into: (1) at or near the surface (0–50 m), (2) during descent, being between 50 m until the animal first reached 65% of the dive's maximum depth, (3) during the bottom phase, being the time spent within 65% of the dives' maximum depth, or (4) during ascent, when the animal leaves the bottom phase and before reaching 50 m depth. The 65% criterion was chosen to account for variability in depth during what visually appeared as the bottom phase of the dive (following Arranz et al. 2016). We performed a chi-squared test to evaluate potential differences between buzzes and rasps and their proportion of occurrence in each dive phase. Post-hoc analysis of the chi-square test was conducted comparing

pairwise critical values calculated for the proportions of buzzes and rasps in each dive phase with the chi-square critical value adjusted using Scheffé's method of taking the square root of the critical value to account for multiple comparisons (Goodman 1964; Franke et al. 2012). Rapid click trains associated with foraging are expected to occur primarily during the bottom phase of the dive (Johnson et al. 2004; Miller et al. 2004), sounds for group coordination would be expected primarily during descent and ascent at the start and end of acoustic foraging activity (Aguilar de Soto et al. 2012), and social sounds should predominantly occur at the surface (Hooker and Whitehead 2002; Arranz et al. 2016).

The presence or absence of conspecifics during focal buzz and rasp production can further shed light on potential communicative functions and was examined acoustically for a selection of the data (section 2.2.1). Furthermore, we investigated potential co-occurrence of focal and non-focal buzzes versus rasps to test for a potential direct communication function, i.e. a rapid click train eliciting an immediate acoustic reaction from a conspecific as documented in social interactions of Risso's dolphins (Arranz et al. 2016). Additionally, a great temporal overlap of foraging associated click trains could indicate synchronised group foraging behaviour as reported for other beaked whales (Aguilar de Soto et al. 2020), which might require coordination through acoustic communication (Aguilar de Soto et al. 2012). Therefore, within each dive we calculated the time interval between two consecutive rapid click trains of the same type produced by the focal and a non-focal whale (focal – non-focal interval). Moreover, the time interval between the same type of focal rapid click train (focal – focal interval) produced within the same dive was calculated to investigate potential production of buzzes or rasps in bouts. Differences in focal – non-focal and focal – focal time intervals between buzzes and rasps were statistically investigated calculating Mann-Whitney U tests.

Finally, we tested whether rasps function in communicating prey availability to conspecifics by testing for a correlation between the number of buzzes and rasps produced within a dive cycle, i.e. a dive and subsequent surface period. Previous studies have used buzzes as a proxy for foraging due to their function in prey capture attempts (Johnson et al. 2004; Miller et al. 2004). If the function of rasps were to communicate prey availability to conspecifics, we would expect a positive correlation between the number of buzzes and rasps produced within a dive cycle.

### 3. Results

#### 3.1 Detailed characteristics of buzzes and rasps

The five tag deployments analysed in detail had a total duration of 45 hours and 45 minutes, during which 771 buzzes and 182 rasps were manually audited and attributed to the tagged whales (Table 1). Of these, 129 rasps fulfilled the quality criteria to be included in the detailed (section 2.2.1) and random forest (section 2.3) analyses. To obtain a balanced sample of audited buzzes and rasps, a random selection of the same number of buzzes was included.

Differences between buzzes and rasps were evaluated using Mann-Whitney U tests which revealed that buzzes had shorter ICIs (mean  $11.7 \pm 3.5$  ms SD) compared to rasps (mean  $32.9 \pm 11.4$  ms SD;  $U = 263$ ,  $p < 0.001$ ). Rasps had shorter durations (mean  $2.58 \pm$

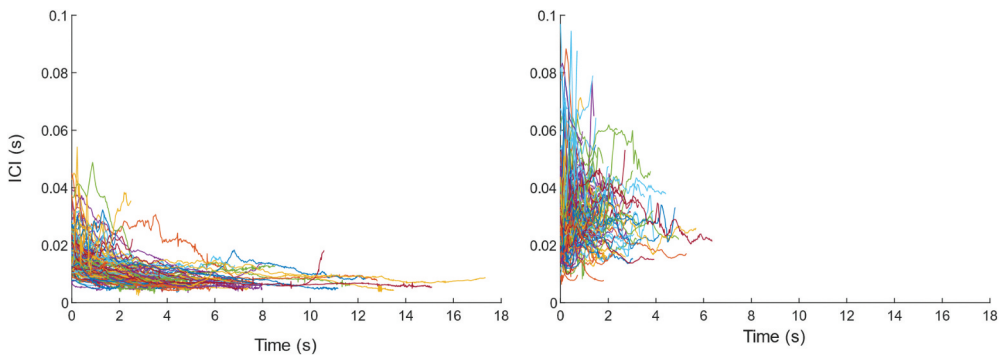
1.59 s SD) than buzzes (mean  $6.89 \pm 4.22$  s SD;  $U = 14413$ ,  $p < 0.001$ ), with more variation in rasp ICI slope (Table 2;  $U = 4272$ ,  $p < 0.001$ ) whereas buzz ICIs showed a consistent decrease over time until reaching a plateau around 10 ms (Figure 2).

The increase in jerk (calculated from the tag accelerometer data) from before to the end of a click train showed a mean increase in jerk for both types of rapid click trains, but was  $9.7 \times$  higher ( $U = 13590$ ,  $p < 0.001$ ) for buzzes (mean  $915 \pm 1357\%$  SD) than rasps (mean  $94 \pm 431\%$  SD; Table 2). When considering jerk change as a binary variable of overall increase versus decrease, significantly more buzzes (83%) than rasps (42%) were associated with an increase in movement ( $U = 10384$ ,  $p < 0.001$ ; Table 4). The depths at

**Table 2.** Characteristics of northern bottlenose whale buzzes ( $n = 129$ ) and rasps ( $n = 129$ ), and the importance of these variables for correct classification in two random forest models using data from five tag deployments. The full model used the six presented variables as predictors, whereas the passive acoustic monitoring (PAM) model only used three predictor variables obtainable from PAM data, being mean inter-click-interval (ICI), duration and ICI slope. Variable importance is given as the percent decrease in the random forest's correct classification rate when the respective variable was randomly permuted (Breiman 2001). Thus, higher values indicate greater variable importance for correct classification.

	Buzzes mean $\pm$ SD (range)	Rasps mean $\pm$ SD (range)	Percentual decrease of correct classification rate [%]	
			Full model mean ( $\pm$ SD)	PAM model mean ( $\pm$ SD)
Mean ICI [ms]	$11.7 \pm 3.5$ (6.7–27.5)	$32.9 \pm 11.4$ (12.2–70.6)	$85.76 (\pm 3.05)$	$163.95 (\pm 3.06)$
Duration [s]	$6.89 \pm 4.22$ (1.19–23.72)	$2.58 \pm 1.59$ (0.29–8.63)	$30.55 (\pm 1.08)$	$33.79 (\pm 0.42)$
ICI slope	$-0.0013 \pm 0.0026$ (-0.0111–0.019)	$0.0082 \pm 0.0236$ (-0.0378–0.1571)	$25.69 (\pm 0.45)$	$27.57 (\pm 0.54)$
Jerk increase [%]	$914.71 \pm 1356.6$ (-87.72–10,061.71)	$94.08 \pm 431.23$ (-92.73–3587.78)	$21.36 (\pm 0.39)$	-
Depth [m]	$430 \pm 201$ (60–913)	$326 \pm 176$ (5–805)	$13.27 (\pm 0.44)$	-
Depth [% rel. to max depth]	$74.81 \pm 3.85$ (23.15–99.63)	$70.04 \pm 14.11$ (0* – 99.45)	$6.44 (\pm 1.08)$	-

\*0% depth relative to the maximum dive depth indicates sound types produced at the surface (0–10 m depth) and thus not part of a dive



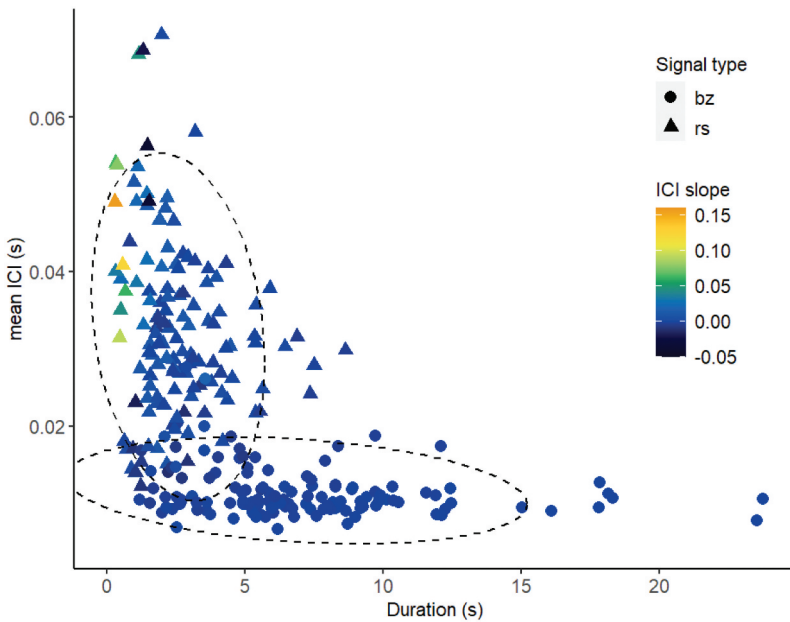
**Figure 2.** Progression of inter-click-interval (ICI) over time for (left) buzzes and (right) rasps. The first and last 10% of clicks contained within each click train were omitted to eliminate high ICIs during transitions from or to regular clicking.

which buzzes and rasps were produced showed substantial overlap and variability, nevertheless differed significantly ( $U = 10797$ ,  $p < 0.001$ ) with buzz production on average approximately 100 m deeper than rasps. The depth at rapid click train production relative to the maximum depth of a dive spanned from the surface to the bottom of the dive for rasps (0–99%) whereas buzz production occurred significantly deeper within dives (23–100%;  $U = 10760$ ,  $p < 0.001$ ).

### 3.2 Random forest analysis

The random forest model trained on five tag deployments and using six predictor variables was stable as it produced similar results across runs with a mean OOB error of 6.1% ( $\pm 0.4\%$ ). The most important variable for correct classification was mean ICI, followed by duration and ICI slope, whereas increase in jerk ranked fourth and the two measures of depth at sound production were of lower importance (Table 2). The random forest models created with four training tag deployments and one test data deployment had a mean OOB error of 6.2% ( $\pm 1.6\%$ ) and a mean classification accuracy of 93.7% ( $\pm 3.8\%$ ) on the set aside test data.

For the model trained on five tag deployments using just three predictor variables which would be obtainable from PAM data, the mean OOB error was 5.7% ( $\pm 0.3\%$ ), showing that ICI characteristics and duration are sufficient for separating buzzes and rasps (Figure 3). As for the six-variable model, mean ICI was the most important predictor variable, followed by duration and ICI slope (Table 2). Inspection of potential



**Figure 3.** Separation of audited northern bottlenose whale buzzes and rasps based on the three most important predictor variables in the random forest analysis, duration and mean ICI, with differences in ICI slope indicated through colour coding. The dashed line ellipses represent the 85% density distribution of the two respective types of rapid click trains.

model overfitting revealed mean OOB error rates of 5.7% ( $\pm 1.6\%$ ) for the training models using data of four tag deployments, and a mean classification accuracy of 94.3% ( $\pm 2.7\%$ ) on the test data.

### 3.3 Characteristics of clicks within non-focal click trains

For analysing time-frequency characteristics of individual clicks, we identified a total of 32 regular echolocation clicks from 20 click sequences, 22 buzz clicks from 10 different buzzes, and 33 rasp clicks from 17 rasps produced by nearby conspecifics as received on- or near the acoustic axis. Clicks differed in duration and frequency characteristics, with regular echolocation clicks being the longest (mean  $234 \pm 32 \mu\text{s}$  SD), and buzz clicks the shortest (mean  $70 \pm 22 \mu\text{s}$  SD; Table 3). Rasp clicks had more variable durations (mean  $132 \pm 60 \mu\text{s}$  SD) which, on average, fell between regular and buzz click durations. Regular echolocation and rasp clicks

**Table 3.** Characteristics (mean  $\pm$  SD) of northern bottlenose whale regular echolocation, buzz and rasp clicks. The 95% energy duration was calculated in a 0.5 ms time window, and centroid frequency, peak frequency and  $-10$  dB bandwidth were extracted from the power spectral density computed over the 95% energy duration. Start and end frequency were extracted from a Wigner-ville time-frequency distribution at the first and last point where sound intensity was within 60% of the click's maximum intensity. Frequency change was calculated as end frequency minus start frequency, thus upsweeps have positive values.

Parameter	Regular clicks	Buzz clicks	Rasp clicks
Sample size	32	22	33
95% energy duration [ $\mu\text{s}$ ]	$234 \pm 32$	$70 \pm 22$	$132 \pm 60$
Centroid frequency [kHz]	$35.8 \pm 4.9$	$47.1 \pm 7.0$	$36.1 \pm 8.6$
Peak frequency [kHz]	$33.6 \pm 4.6$	$45.9 \pm 10.8$	$36.2 \pm 11.6$
$-10$ dB bandwidth [kHz]	$22.8 \pm 5.8$	$50.7 \pm 17.6$	$31.9 \pm 16.1$
Start frequency [kHz]	$29.6 \pm 3.8$	$44.2 \pm 5.2$	$33.8 \pm 5.9$
End frequency [kHz]	$44.9 \pm 8.1$	$48.6 \pm 8.2$	$37.9 \pm 11.3$
Frequency change [kHz]	$+15.4 \pm 5.1$	$+4.4 \pm 7.1$	$+4.1 \pm 7.3$

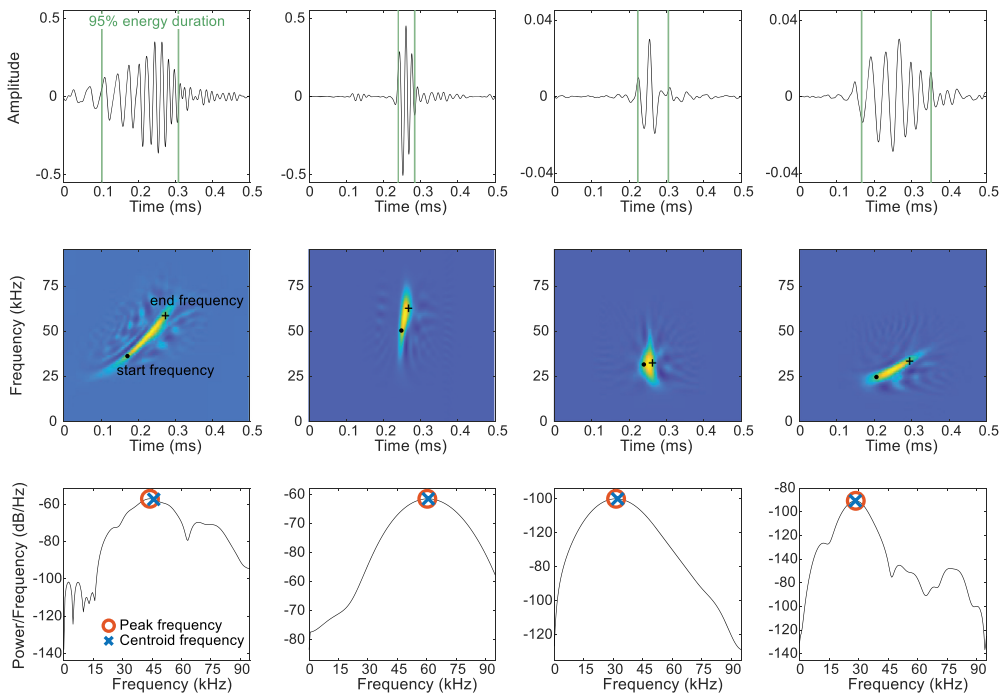
**Table 4.** Behaviour and context associated with northern bottlenose whale buzzes and rasps. Acoustic presence of conspecifics, regular echolocation clicks before and after rapid click train production, and presence of jerk increase are given as percentages for buzzes and rasps ( $n = 129$  each). For  $n = 1922$  buzzes and  $n = 253$  rasps, the percentage of these occurring in each of the four defined phases of a dive is given. Intervals (provided as median and range) describe the time passed between two consecutive rapid click trains of the same type, within the same dive, produced by the tagged whale (focal – focal;  $n = 144$  for rasps and  $n = 1754$  for buzzes) or the tagged and nearby whales (focal – non-focal;  $n = 200$  for rasps and  $n = 1752$  for buzzes).

	Buzz	Rasp	p-value
Conspecific presence [%]	85.27	76.74	0.08
Regular clicking before [%]	96.12	90.70	0.08
Regular clicking after [%]	54.26	72.09	0.003*
Jerk increase [%]	83.23	41.95	<0.001*
Surface [%]	0.10	13.83	<0.05*
Descent [%]	18.57	18.97	>0.05
Bottom [%]	74.40	54.55	<0.05*
Ascent [%]	6.92	12.65	>0.05
Focal – focal interval [mm:ss]	00:41 (00:01–10:08)	01:29 (00:03–26:01)	<0.001*
Focal – non-focal interval [mm:ss]	00:24 (00:00–26:30)	02:41 (00:01–20:09)	<0.001*

\*Level of significance  $\alpha = 0.05$ .

had similar mean peak ( $33.6 \pm 4.6$  kHz SD and  $36.2 \pm 11.6$  kHz SD respectively) and centroid frequencies ( $35.8 \pm 4.9$  kHz SD and  $36.1 \pm 8.6$  kHz SD respectively), whereas buzz clicks were higher in frequency (mean  $45.9 \pm 10.8$  kHz SD peak and  $47.1 \pm 7.0$  kHz SD centroid frequency) and more broadband (Table 3). The average frequency change from start to end was highest in regular echolocation clicks (mean  $15.4 \pm 5.1$  kHz SD), and comparable between buzz and rasp clicks (mean  $4.4 \pm 7.1$  kHz SD and  $4.1 \pm 7.3$  kHz SD respectively), though buzz clicks averaged higher start ( $44.2 \pm 5.2$  kHz SD) and end frequencies ( $48.6 \pm 8.2$  kHz SD) than regular echolocation (mean  $29.6 \pm 3.8$  kHz SD to  $44.9 \pm 8.1$  kHz SD start to end) and rasp clicks (mean  $33.8 \pm 5.9$  kHz SD to  $37.9 \pm 11.3$  kHz SD start to end; Table 3). Only regular echolocation clicks consistently contained a frequency upsweep (Table 3; Figure 4).

Our sample of rasp clicks appeared to consist of two different types of clicks that were either longer and frequency-modulated, similar to regular echolocation clicks, or shorter and more broadband like buzz clicks though emitted at lower frequencies (see examples in Figure 4). We thus investigated whether these differences in rasp click durations were correlated with ICI but only found



**Figure 4.** Time-frequency characteristics of a representative example of a regular echolocation click (left column), buzz (column second from the left) and two types of rasp clicks (two right-hand side columns). (top) Waveform with green solid lines indicating the 95% energy duration. (middle) Wigner-Ville time-frequency distribution plot with the colours corresponding to relative sound intensity on a linear scale from minimum to maximum intensity. The marked start and end frequency were extracted from the Wigner-Ville distribution at the first and last point where sound intensity was within 60% of the click's maximum intensity. (bottom) Power spectral density (Hamming window, 4096 FFT) with peak and centroid frequency marked.

a weak correlation which was not significant (Pearson's correlation,  $\rho(31) = 0.14$ ,  $p = 0.44$ ,  $n = 33$ ).

### 3.4 Behavioural aspects of buzz and rasp production

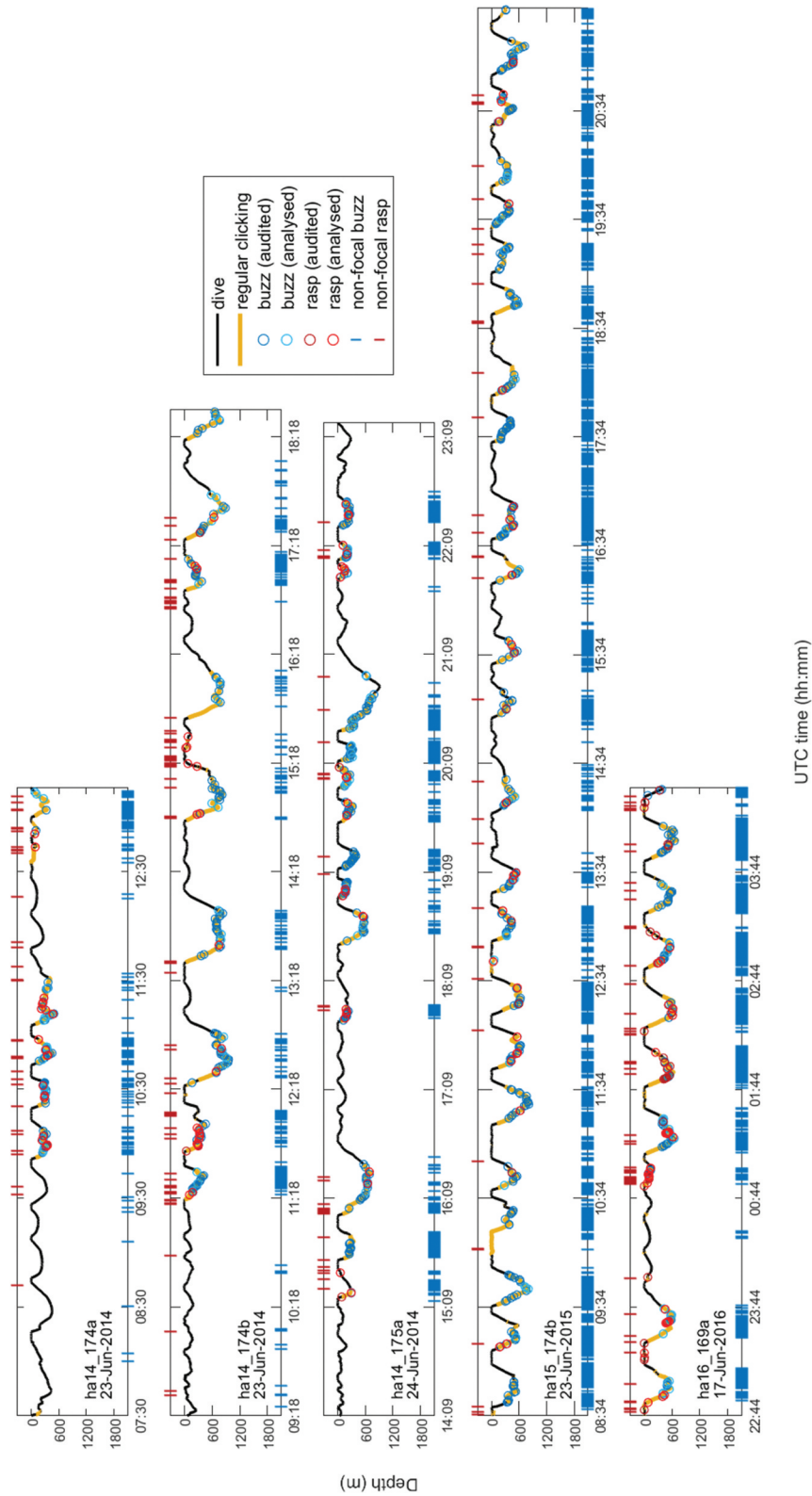
The focal buzzes and rasps analysed in detail ( $n = 129$  respectively, see [section 2.2.1](#) and [Table 1](#)) were examined for acoustic presence of conspecifics, and the tagged whale's own echolocation behaviour two seconds before and after rapid click train production. Acoustic presence of conspecifics was similarly high for both types of rapid click train (Mann-Whitney U test,  $U = 9030$ ,  $p = 0.08$ ) as conspecifics were detected during or within 2 s of 85% of focal buzzes and 77% of focal rasps ([Table 4](#)). Most buzzes (96%) and rasps (91%) were preceded by regular echolocation clicks ( $U = 8772$ ,  $p = 0.08$ ) but significantly fewer buzzes (54%) than rasps (72%) were followed by them ( $U = 6837$ ,  $p = 0.003$ ).

Investigation of buzz and rasp timing throughout the dive cycle was conducted for all 15 tag deployments and we found a significant relationship between proportions of buzzes and rasps in the four dive phases (chi-square test,  $\chi^2(3, 2175) = 269.66$ ,  $p < 0.001$ ). For  $\alpha = 0.05$  and  $df = 3$ , the chi-square critical value is 7.815 which we adjusted using Scheffé's method using the square root of the chi-square critical value, resulting in  $z = \pm 2.80$  for post-hoc pairwise comparison of multiple groups. The significance of the chi-square test was driven by the higher proportion of rasps at the surface ( $z = 6.32 > 2.8$ ) and greater proportion of buzzes produced during the bottom phase ( $z = 6.04 > 2.8$ ) of a dive ([Table 4](#)). Neither descent ( $z = 0.15 < 2.8$ ) nor ascent ( $z = 2.64 < 2.8$ ) showed significant differences in proportions of buzzes and rasps produced during these phases of a dive. We did not find any correlation between the number of buzzes and rasps produced within a dive and subsequent surface period (Spearman Rank correlation,  $\rho = -0.09$ ,  $p = 0.25$ ,  $n = 180$ ).

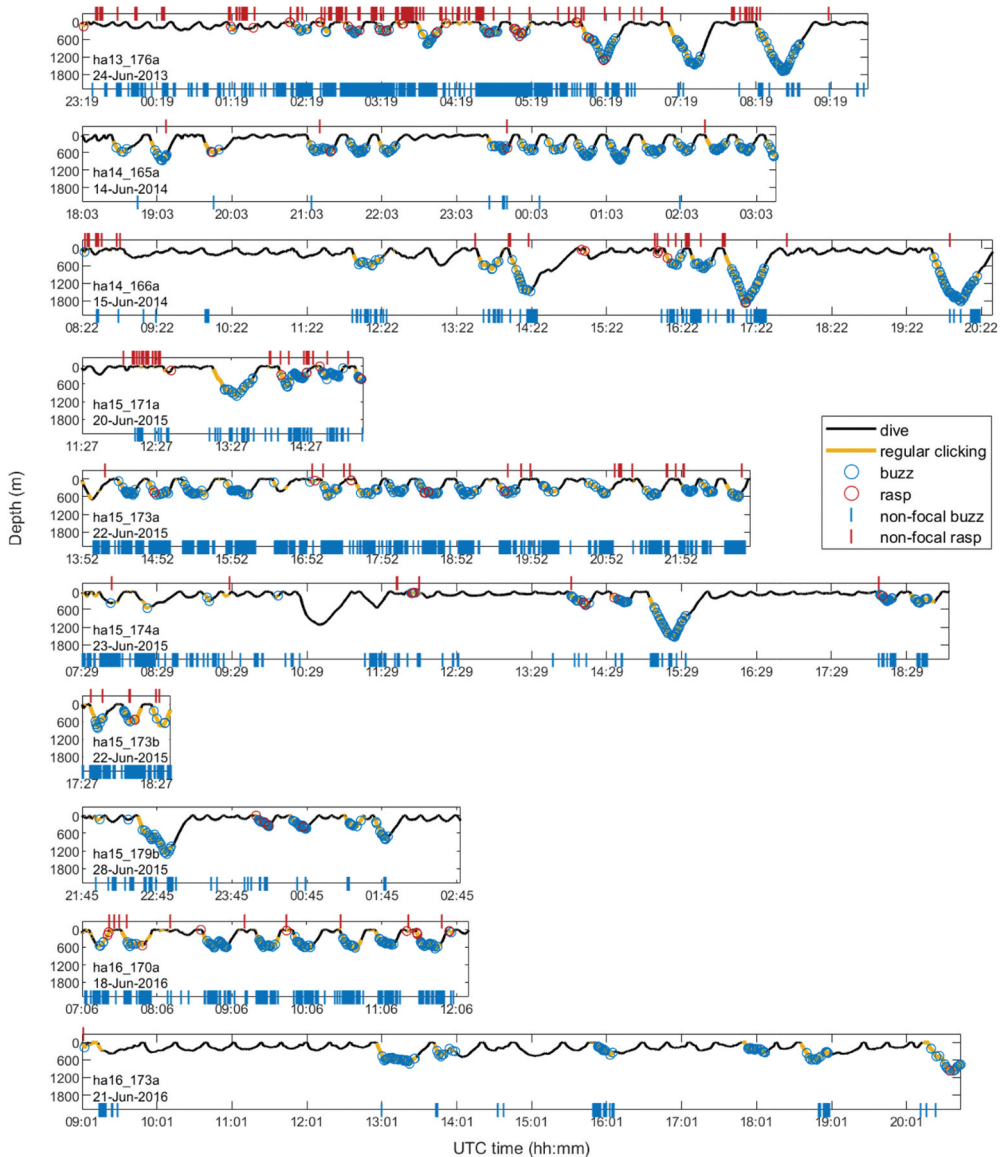
While focal rasps may occur as single instances, the production of rasps in bouts, i.e. discrete periods with increased rates, appeared common from the dive profiles ([Figures 5–6](#)). However, the interval between two consecutive focal rapid click trains of the same type, produced within the same dive, was significantly longer for rasps (median = 1.48 min,  $n = 144$ ) than for buzzes (median = 0.68 min,  $n = 1754$ ; [Table 4](#); Mann-Whitney U test,  $U = 101169$ ,  $p < 0.001$ ). Similarly, the intervals between focal and non-focal rasps (median = 2.68 min,  $n = 200$ ) were significantly longer than the intervals between focal and non-focal buzzes (median = 0.36 min,  $n = 1752$ ;  $U = 84644$ ,  $p < 0.001$ ).

## 4. Discussion

Our results confirmed that northern bottlenose whale buzzes and rasps constitute two distinct types of rapid click train that could be quantitatively separated based on multiple predictor variables. However, neither buzzes nor rasps were fully stereotyped but instead had some overlap in their characteristics ([Figure 3](#)). The random forest analysis showed a high agreement between manual and automatic (unsupervised) rapid click train classification and revealed ICI characteristics and duration as most important for correct classification. In fact, the random forest models with mean ICI, ICI slope and duration showed similar OOB error rates



**Figure 5.** Dive profiles of the five tagged whales that were included in the random forest analysis, with tag ID and date at tagging indicated inside each subplot. Buzzes and rasps produced by the tagged whale are plotted onto the dive profile, and non-focal sound types produced by nearby whales are indicated above (rasps) and below (buzzes) the respective echolocation clicks produced by the tagged whale are indicated in yellow.



**Figure 6.** Dive profiles of 5 out of 10 tagged whales that were not included in the random forest analysis. Figure layout is the same as Figure 5, except that there is no differentiation between audited and analysed buzzes.

and classification accuracies as the full model which also included increase in jerk as a movement measure and depth at sound production. Buzzes and rasps showed the clearest separation by mean ICI (Figure 3), supporting the use of ICI as a criterion during manual auditing for which rasps were defined as resembling buzzes though emitted at a slower click rate. The differences in ICI characteristics were also apparent when looking at how ICI changed over time within the click

trains (Figure 2). Rasps did not show a consistent pattern, whereas the ICI of buzzes initially decreased before remaining constant at around 10 ms.

#### 4.1 Proposed function of buzzes

Buzzes of odontocetes, as well as echolocating bats, function in the terminal phase of prey capture for which the short ICI of buzzes allow for rapid updates on the position and movement of evasive prey (Madsen and Surlykke 2014; Vance et al. 2021). The function of northern bottlenose whale buzzes in active prey capture was supported by the animals' behaviour associated with buzz production, as 82% of buzzes coincided with an increase in jerk movement. The whales further showed a transition from regular search clicks into terminal buzzes of which 46% were followed by a pause in clicking, indicating prey ingestion as reported for other odontocetes (Miller et al. 2004; Johnson et al. 2006). Across all 15 tag records, buzzes were recorded primarily at depth and particularly during the bottom phase (74%) rather than at or near the surface (0.1%; Figures 5–6), which is in line with the foraging behaviour reported for this and other deep-diving odontocetes (Hooker and Baird 1999; Johnson et al. 2004; Miller et al. 2004).

The depth distribution of buzz production correlates with the vertical distribution of northern bottlenose whale's preferred squid prey (Bjørke 2001). In the western North Atlantic, northern bottlenose whales regularly forage near the seafloor at depths beyond 800 m (Hooker and Baird 1999) whereas in our study area in the eastern North Atlantic, acoustic foraging behaviour has also been detected in dives to intermediate depths between 200–600 m (Miller et al. 2015). The great range in depth at buzz production could thus be a result of the animals performing foraging dives to variable depths and producing buzzes in descent, bottom phase, and ascent. This expansion of acoustic foraging behaviour into descent and ascent together with the short time interval of approximately 41 seconds between the production of two focal buzzes could be indicative of high prey availability in the study area around Jan Mayen.

The time interval between focal and non-focal buzzes was similarly low (Table 4) and conspecifics were acoustically present during over 85% of analysed focal buzzes. This temporal overlap of focal and non-focal buzzes was particularly evident in some tag records (Figures 5–6, e.g. ha16\_169a) and could be explained as coordination of acoustic foraging. Aguilar de Soto et al. (2020) found that Blainville's and goose-beaked whales (*Ziphius cavirostris*) were highly coordinated in their vocal activity during dives, meaning that they started and ceased clicking at nearly the same time during deep foraging dives. Efforts of simultaneous tagging of multiple animals within one group further revealed that in the Canary Islands these species foraged apart at depth, yet within an audible range of one another, and reunited to ascent and surface together (Aguilar de Soto et al. 2020; Alcázar-Treviño et al. 2021). The synchrony of foraging dives taken together with these species remaining silent in surface waters has been interpreted as predator avoidance strategy by minimising the time when the animals are acoustically detectable by predators (Aguilar de Soto et al. 2020). While we found high co-occurrence of northern bottlenose whale foraging buzzes suggesting synchronised diving behaviour, we also recorded sequences of echolocation clicks and rasps in surface waters contradicting the acoustic crypsis for predator avoidance hypothesis. Given the larger body size of

northern bottlenose whales, the species may face lower predation risk compared to smaller beaked whale species and therefore do not need to remain silent in surface waters.

#### 4.2 Proposed function of rasps

Rasps differed from buzzes in their spectral, temporal and contextual characteristics. While buzzes were clearly associated with foraging, we found that rasps were unlikely to function in prey capture as they had longer ICIs, were significantly less often (42% of rasps vs 83% of buzzes) associated with an increase in movement and more often (72% of rasps vs 54% of buzzes) followed by regular echolocation clicks. The differences in ICI between buzzes and rasps could, however, be an artefact due to differences in ICI being used as a distinguishing criterium in the manual auditing process. If rasps were indeed misclassified or attempted buzzes that got cut short due to the prey capture attempt being unsuccessful, we would have expected no difference in timing of buzzes and rasps regarding the dive cycle. However, we recorded a significantly higher proportion of rasps at the surface (14% of recorded rasps opposed to 0.1% of buzzes), countering the foraging hypothesis, and instead suggesting a communication function. Northern bottlenose whale clicks previously recorded by Hooker and Whitehead (2002) during socialising behaviours at the surface showed highly variable ICIs which were shorter than those for regular echolocation click trains (Hooker and Whitehead 2002; Wahlberg et al. 2011; Clarke et al. 2019; Haas et al. 2024), but instead largely resemble the mean ICIs of rasps that we report here.

We investigated whether rasp production is linked to social interactions through the timing of focal and non-focal rasps relative to one another. Risso's dolphins were found to produce rasp-like communication sounds, termed burst pulses, primarily in surface waters (Arranz et al. 2016) and during the reunion of dispersed animals (Neves 2013). The production of a burst pulse by a tagged Risso's dolphin and a nearby conspecific was only separated by a few seconds (Arranz et al. 2016) suggesting a direct communication function of these sounds with a burst pulse eliciting an immediate acoustic response. In our study, the dive profiles of bottlenose whales that produced high numbers of rasps (Figure 5) indicated a similar, yet not consistent, temporal overlap of focal and non-focal rasps. Calculation of time intervals between focal and non-focal rasps, however, contradicted the direct communication hypothesis as these intervals averaged over 2.6 minutes, despite conspecifics being acoustically present during most (77%) of the rasps analysed in detail.

Depending on the context in which a sound is produced, the behavioural response elicited by it might not necessarily be of acoustic nature. For instance, captive harbour porpoises (*Phocoena phocoena*) were found to produce communicative high repetition rate, i.e. rapid, click trains whilst orientated towards another individual, which elicited a flight response in the receiving conspecific and were thus categorised as aggressive (Clausen et al. 2011). Comparably, echolocating Mexican free-tailed bats (*Tadarida brasiliensis*) were found to produce buzz-like sounds when defending food resources and chasing away conspecifics (Schwartz et al. 2007). However, these aggressive sounds, described for both Mexican free-tailed bats and harbour porpoises, had shorter ICIs compared to the respective species' foraging buzzes (Schwartz et al. 2007; Clausen et al. 2011), being contrary to the longer ICIs in bottlenose whale rasps opposed to buzzes.

Thus, if rasps were to function in similar aggressive interactions or resource defence, we would have expected to record more on-axis non-focal rasps at higher click rates than buzzes.

Instead, our results indicated that rasps function in group coordination and contact maintenance. Rasps of Blainville's beaked whales were hypothesised to facilitate coordination of foraging dives as they were produced primarily at the start of acoustic foraging (Aguilar de Soto et al. 2012) when animals descend together and before dispersing to forage apart (Aguilar de Soto et al. 2020; Alcázar-Treviño et al. 2021). Timing of northern bottlenose whale rasps did not follow such a set pattern but their occurrence throughout foraging dives nevertheless suggests a group coordination function advertising one's position to nearby conspecifics. Whales in the vicinity of one another could, however, also intercept another whale's location from its regular echolocation clicks, thus as for other odontocetes (Aguilar de Soto et al. 2012; Arranz et al. 2016) the question remains what additional information rasps may convey.

Female sperm whales (*Physeter macrocephalus*) produce codas which are stereotyped series of clicks emitted during social interactions primarily near the surface (Watkins and Schevill 1977). The ICI patterns of these codas have been found to convey information about individual and group identity (Oliveira et al. 2016). The development of recognition mechanisms in sperm whales was likely driven by their complex social structure of long-term matrilineal social units (Richard et al. 1996). Northern bottlenose whales on the other hand form loose fission-fusion groups and females do not preferentially associate with specific individuals (Gowans et al. 2001) suggesting they would not face ecological pressure to develop individual vocal recognition. However, male bottlenose whales form more stable associations lasting up to multiple years (Gowans et al. 2001) suggesting a higher need for individual recognition in male than female bottlenose whales. Unfortunately, our sample primarily contained tag records from females or juvenile whales of unidentified sex (Table 1), thus testing this hypothesis was beyond the scope of this study. The potential for rasps to contain individual or group signature information could be a fruitful avenue for future study.

In a variety of species from birds to mammals, acoustic signals were found to serve in initiating and coordinating group movement from one foraging patch to another. For instance, meerkats (*Suricata suricatta*) produce context specific moving-calls to initiate the groups collective movement to a new foraging patch (Bousquet et al. 2011). Green woodhoopoes (*Phoeniculus purpureus*) vocalise while moving to a new foraging area to inform other group members and animate them to follow (Radford 2004). Northern bottlenose whales might use rasps in a similar way to initiate synchronised foraging dives, coordinate movements to different depth and foraging layers, or simply facilitate group cohesion throughout all dive phases. Simultaneous tagging of multiple animals within a group would be necessary to investigate this hypothesis further through analysing group dispersal and movement behaviour around rasp production.

Another foraging related hypothesis we investigated was whether rasps may communicate high prey availability and foraging success to other group members, in which case we would expect a positive correlation between the number of buzzes as foraging proxy (Johnson et al. 2004; Miller et al. 2004; Siegal et al. 2022), and the number of rasps produced within a dive and subsequent surface period. However, we did not find such

a correlation, nor a negative correlation, counter-indicating that rasps convey information about prey availability.

### 4.3 Characteristics of clicks within buzzes and rasps

The difference between buzzes and rasps becomes more apparent when looking at the individual clicks contained in these different types of rapid click trains. The peak and centroid frequencies of rasp clicks closely resembled those of regular echolocation clicks, whereas buzz clicks were higher in frequency, more broadband and shorter in duration (Table 3). Like in other beaked whales (Johnson et al. 2006; Aguilar de Soto et al. 2012), our sampled buzz clicks were non-modulated whereas regular echolocation clicks showed clear upsweeps in line with what was reported for the northern bottlenose whales' on-axis clicks (Wahlberg et al. 2011). Rasp clicks of Blainville's beaked whales were also found to contain the species-specific frequency upsweep pattern of regular echolocation clicks (Aguilar de Soto et al. 2012), however, our sample of rasp clicks identified as recorded on or near the acoustic axis showed great variability in frequency modulation. While some clicks showed an upsweep comparable to that of regular echolocation clicks, others were shorter without any frequency modulation (Figure 4).

This variability in rasp clicks led us to investigate whether northern bottlenose whales' switch from producing longer and frequency modulated clicks to shorter more broadband clicks was driven by a decrease in ICI which might constitute a potential physical constraint to emitting frequency-modulated clicks at a high rate. However, we could not find a correlation between rasp click duration and ICI to the preceding click. The more likely alternative explanation for the observed variability in rasp clicks would thus be that our sample also contained recordings too far off the acoustic axis to fully capture time-frequency characteristics (Møhl et al. 2003; Zimmer et al. 2005). Although we aimed to set conservative criteria for which clicks to analyse, with the data at hand we cannot rule out the possibility that our selection included some off-axis clicks. A different recording system with a minimum of three evenly spaced hydrophones would be necessary to more precisely infer recording angles (Madsen et al. 2004; Wahlberg et al. 2011) and reliably identify on-axis clicks.

Nevertheless, the occurrence of frequency modulated clicks within rasps, and their differences in bandwidth and lower frequency characteristics compared to buzz clicks, indicated that northern bottlenose whale buzzes and rasps were composed of different types of clicks. Attenuation of sound energy is lower for lower frequencies (Kuperman and Roux 2014) increasing their detection range, which would support the communication and group coordination function of rasps amongst dispersed animals. However, visual inspections of clicks during data processing indicated lower amplitudes of rasp clicks compared to regular echolocation, suggesting a longer detection range for the latter, though estimates of source levels would be necessary to calculate detection range differences between the click types. However, regardless of detection range, the differences in click characteristics between buzzes and rasps together with the patterning of clicks into a rasp likely conveys additional information that cannot be obtained from eavesdropping on echolocation-based foraging alone.

#### 4.4 Implications for passive acoustic monitoring

The high importance of ICI characteristics and duration for correct classification suggests that buzzes and rasps can be reliably distinguished in PAM data, potentially enabling insight into the animal's behavioural state. Inferring habitat use and behaviour through PAM data is of great interest as, compared to tagging, PAM methods decrease human-animal interactions, allow for long-term data collection on annual and seasonal patterns, and provide information on a population rather than individual level.

However, additional considerations must be made when attempting to classify buzzes and rasps in PAM data. DTags are attached to the animal allowing for reliable calculation of ICI and duration (Johnson and Tyack 2003; Johnson et al. 2009), whereas the accuracy of these measures in PAM data will depend on the animals' distance and orientation relative to the receiver (Zimmer et al. 2008; Hildebrand et al. 2015). Consequently, movement associated foraging and buzz production is prone to missed detections which could result in overestimating ICI and thus falsely classifying buzzes as rasps (Table 2). Correcting buzz ICI for missed detections can be done considering the typical slope pattern of an initial decrease in ICI before it remains at a constant low around 10 ms in the later part of the buzz (Figure 2). For rasps the correction of ICI for missed detections may not be feasible as their slope shows higher variations with ICIs changing throughout the rasp. While missed detections during the buzz or rasp would lead to an overestimation of mean ICI, missed detections at the edge would result in underestimating duration. Thus, combining information on ICI characteristics and duration will be necessary to reliably classify buzzes and rasps.

The location of the recording system within the water column can further impact detectability of different sounds. For instance, buzzes recorded with hydrophones near the surface might be more susceptible to missed detections due to the increased distance between source and receiver as northern bottlenose whales regularly forage near the seafloor (Hooker and Baird 1999; Hooker and Whitehead 2002). Accordingly, their buzzes are more likely to be detected on recording systems near the seafloor (Moors 2012), which can further be expected to yield higher signal to noise ratios (SNR) due to typically lower noise interference at depth (Zimmer et al. 2008). A quiet recording environment is crucial for buzz detection in PAM data (Jarvis et al. 2022) as buzz clicks are emitted at lower amplitudes compared to regular echolocation clicks (Miller et al. 2004; Johnson et al. 2006; Arranz et al. 2016) limiting detectability to a short range. For both, recording systems close to the surface or seafloor, surface and bottom reflections of clicks must be identified and excluded as they would otherwise falsely reduce ICIs. If a recording system with multiple receivers is used, the inspection of carefully selected on-axis clicks for time-frequency characteristics can further aid the classification of buzzes and rasps.

Alongside these considerations, the differences between northern bottlenose whales' buzzes and rasps presented in this study can be used as a guideline for classifying the two types of rapid click trains in PAM data. However, to do so, the variability within buzz and rasp characteristics (Table 2) must be carefully considered as neither buzzes nor rasps appear fully stereotyped but can overlap in ICI and duration (Figure 3). In some cases, this may well result in uncertainty about which type to assign a rapid click train to,

nevertheless, classifying these rapid click trains in PAM data can allow for a better interpretability of the animals' behaviour and habitat use across locations.

## 5. Conclusions

Our results showed that northern bottlenose whale buzzes and rasps constitute two quantitatively distinct types of rapid click trains that can be classified based on primarily ICI characteristics and duration (Figure 3). Similar to Blainville's beaked whales, buzz clicks did not show the species-specific frequency upsweep known for regular echolocation clicks, whereas at least some rasp clicks showed an upsweep pattern and generally shared more similarities in frequency characteristics with regular echolocation rather than buzz clicks. The movement associated with buzz production and their occurrence almost exclusively during the dive and primarily during the bottom phase supports the functionality of buzzes in prey capture attempts and is in line with buzz production in other odontocetes. Rasps on the other hand were produced in all phases of the dive cycle including at the surface and were not clearly associated with an increase in movement, showing that they are not associated with prey capture. Instead, our investigation of behavioural aspects associated with rasp production suggests rasps to be a separate type of rapid click train produced for communication. We propose rasps function in coordinating group movement both at the surface and during foraging dives, though further data ideally stemming from multiple tagged animals within the same group would be necessary to fully dissect the information conveyed in rasps.

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