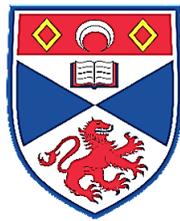


# **Rhythmically repeated patterns of pulsed vocalizations in wild narwhals (*Monodon monoceros*)**

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I hereby certify that this dissertation, which is approximately 10,400 words in length, has been composed by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a degree. This project was conducted by me at the University of St Andrews from September 2017 to August 2018 towards fulfilment of the requirements of the University of St Andrews for the degree of Master of Science in Marine Mammal Science under the supervision of Dr. Luke Rendell and Dr. Marianne Marcoux.

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## Table of Contents

<b>Abstract</b> .....	v
<b>Acknowledgements</b> .....	vi
<b>Introduction</b> .....	1
Characterizing Sequences in Vocal Repertoires .....	1
Vocal Sequences in Marine Mammals .....	2
Vocalizations in Narwhals .....	3
Objectives .....	4
<b>Materials and Methods</b> .....	4
Study System and Data Collection .....	4
Sound Auditing and Initial Call Selection .....	5
Two Types of Patterns: Pre-Classification of Paired Patterns and Burst-Pulse Series .....	6
Demonstrating Stereotyped Organization of Units .....	7
Multiple-observer classification of paired patterns .....	7
Discriminant function analysis of paired patterns .....	8
Extracting the temporal structure of burst-pulse series .....	9
Levenshtein distance analysis of burst-pulse series .....	9
Inferring Patterns of Production across Individuals .....	10
Discriminating between sequences and call exchanges .....	10
Exclusion of patterns produced by non-focal individuals .....	10
Modeling Contextual Usage .....	11
Sequence use as a function of behaviour .....	11
Repetition as a function of noise .....	12
Ethical Statement .....	13
<b>Results</b> .....	13
General Features .....	13
Summary of Identified Patterns .....	15
Paired patterns .....	15
Burst-pulse series .....	15
Demonstration of Stereotyped Organization of Units .....	16
Classification reveals repetition and multi-unit associations in paired patterns .....	16

Levenshtein distance model reveals repetition in sequences of burst-pulse series.....	19
Patterns of Production across Individuals .....	19
Indications that patterns were produced by a single individual .....	19
Tag-specific variation in paired patterns and burst-pulse series .....	20
Contextual Use of Sequences .....	20
<b>Discussion</b> .....	23
Characterization of the Structure of Narwhal Vocal Sequences .....	23
Sequences of paired patterns.....	23
Sequences of burst-pulse series.....	24
Sequences across Individuals .....	25
Discriminating between individually produced sequences and call exchanges.....	25
Evaluating evidence for individual-specific sequences .....	26
Relationships between sequence use and behaviour.....	27
Use of repetition and temporal signals in relation to environmental constraints.....	27
Limitations.....	29
Suggestions for Future Research.....	29
Conclusions .....	30
<b>References</b> .....	30
<b>Appendices</b> .....	40
Appendix I – Templates of Paired Patterns Used in Visual Classification Task .....	40
Appendix II – Custom Scripts Used in Analysis.....	42
Conversion of burst-pulse series recordings into binary representations .....	42
Discriminant function analysis of paired calls .....	43
Script to model repetition of burst-pulse series using Levenshtein distance .....	43
Script to model relationships between sequence usage and acoustic context .....	45

## Abstract

Sequences of vocalizations are indicative of communicative complexity. However, relative to birds and terrestrial mammals, the extent to which marine mammals use vocal sequences is not well understood. I provide the first investigation into vocal sequences in narwhals (*Monodon monoceros*), a gregarious Arctic cetacean.

Eight female narwhals were fitted with animal-borne recording devices, resulting in one of the largest datasets of narwhal acoustic behaviour to date. I used a combination of visual and quantitative classification procedures to rigorously demonstrate stereotyped organizational properties of subjectively defined sequence types. Next, acoustic characteristics were used to generate coarse inferences regarding patterns of sequence use across individuals. Finally, I used generalized linear models (GLMs) to assess the behavioural and acoustic contexts under which sequences were produced.

I identified two types of sequences: “paired” patterns, consisting of combinations of two stereotyped click-based calls, the pair of which were often repeated in rapid succession. While these calls were rare, I found multiple subtypes that were predominantly associated with recordings from specific tags. I secondly identified “burst pulse series”, temporally stereotyped sets of short burst-pulses which themselves were combined into repetitive vocalization events. I found few links between sequence use and behaviour, though burst-pulse series were more likely to be produced in periods when other vocalizations were heard, suggesting possible use in social contexts.

These findings extend the set of odontocetes which are known to use sequences of vocalizations. Both sequence types show rhythmic repetition of lower-level patterns, suggestive of hierarchical organizational principles. Furthermore, paired patterns constitute the first evidence of multi-unit sequences in the family *Monodontidae*. I propose that further inquiry into vocal sequences in narwhals and other understudied marine mammals is warranted.

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## Introduction

### Characterizing Sequences in Vocal Repertoires

Simple observation and characterization are crucial first steps towards understanding animal behaviour (Tinbergen 1963). This is especially true of vocal communication, where characterizing the repertoire of signals that an animal uses is a pre-requisite for further inquiry into their production, function, ontogeny, and evolution. The characterization of vocal repertoires has provided insights into diverse aspects of organismal biology, including sensory capacities (Lammers et al., 2004) behavioural state (Henderson et al., 2011), population divisions (Saulitis et al., 2005), and culture (Rendell and Whitehead 2001).

The characterization of a vocal repertoire also allows for the identification of structural patterns such as sequences, broadly defined as signals that are produced together under a non-random organizational framework (Kershenbaum et al., 2016). They are typically produced by a single animal, but can also be produced by multiple individuals, as in the overlapping song sequences of great tits (*Parus major*; Krebs et al., 1981). Sequences can be composed of repetitions of the same unit, or combinations of different units, where the individual units may be shortened or “compressed” as a function of sequence length (Collier et al., 2017; Gustison et al., 2016; Kershenbaum et al., 2016). Repetitive sequences are common, but draw special interest as the costs of repeating a signal in rapid succession are presumably outweighed by the increased transmission likelihood or the ability to convey additional information in the number of repetitions. Here I adopt Zwamborn and Whitehead’s (2017b) distinction between repeated and *rhythmically* repeated vocalizations, the latter referring to signals repeated in rapid succession.

Without direct attention to sequences, the complexity and functions of vocal repertoires may be underestimated (Collier et al., 2017; Kershenbaum et al., 2012; Luis et al., 2018). For many species, vocal production capacities are largely inherited, resulting in a limited range of producible sounds (Podos 1996). However, the combinatorial organization of sounds into sequences can convey more information than single sounds produced in isolation. As such, constraints on vocal production are hypothesized to be an evolutionary driver for the use of sequences of vocalizations. For example, the use of structured combinations of distinct call types is thought to be a means to overcome vocal limitations in Campbell’s monkeys (*Cercopithecus campbelli*; Ouattara et al.,

2009). While possible relationships between the use of multi-unit sequences and the evolution of human language are *not* resolved (Kershenbaum et al., 2014; Ouattara et al., 2009; Scott-Phillips et al., 2014), it is agreed that sequences are indicators of communicative complexity (Suzuki 2006). Even when individual units do not appear to correspond to combined meaning, the “developmental stress hypothesis” states that the complexity of a sequence (e.g. birdsong) can serve as an otherwise arbitrary indicator of mate quality (Nowicki and Searcy 2004).

### **Vocal Sequences in Marine Mammals**

Marine mammals show a high degree of complexity in vocal communication. Bottlenose dolphins are the only non-human species for which vocal production learning, functional reference, signal innovation, and the capacity for syntax have all been demonstrated (Herman 2006; Janik 2013). In contrast to the numerous and structurally complex sequences described in songbirds, terrestrial mammals and mysticetes (Payne and McVay 1971; McDonald et al., 2006; Berwick et al., 2011), there are comparatively few findings of sequences or proto-syntactic structure in the vocal repertoires of wild odontocetes. Non-random transitions between calls of different types have been identified in short-finned pilot whales (*Globicephala macrorhynchus*; Sayigh et al., 2013), killer whales (*Orca orcinus*; Saulitis et al., 2005), and bottlenose dolphins (*Tursiops sp.*; Ferrer-i-Cancho and McCowan, 2012). More specifically, bottlenose dolphins are also known to produce feeding-associated bray sequences composed of repeated pulsed units, as well as “mutli-looped” sequences of signature whistles (Janik 2000; Luis et al., 2018; Esch et al., 2009). Perhaps the most complex sequences identified in odontocetes are the temporally stereotyped click codas of sperm whales (*Physeter microcephalus*). However, beyond these species, the extent to which other odontocetes organize vocalizations into sequences remains poorly understood (Janik 2009).

Technology has traditionally been a limiting factor in the study of marine mammal communication (Lammers and Oswald 2015, pp. 125). Unlike other taxa, most marine mammal behaviour occurs underwater, and vocalizations are often produced at frequencies beyond the range of human hearing (Mann 2000). This has resulted in biases for the study of accessible species (i.e. coastal), or species that are readily kept in captivity (e.g. bottlenose dolphins). It is possible, then, that the apparent lack of structured sequences in odontocete vocal production is an artefact of methodological limitations. Alternatively, flexible vocal production mechanisms linked with

capacities for vocal imitation in odontocetes could make use of sequences unnecessary (Abramson et al., 2018). Fortunately, advancements in the engineering of animal-borne remote sensing technologies are providing novel insights into the behaviour and sounds produced by a variety of hard-to-study animals, odontocetes included (Johnson et al., 2009; Merrill and Mech 2003; Ropert-Coudert and Wilson 2005). The application of these technologies to less-studied odontocetes is necessary to extend the current findings of vocal sequences in this taxon.

### **Vocalizations in Narwhals**

Narwhals (*Monodon monoceros*) are one species whose study stands to benefit from the advent of animal-borne recording devices. Narwhals are gregarious cetaceans endemic to Arctic seas, most easily distinguishable by a long tusk formed by an overgrown left incisor in most males (Heide-Jørgensen 2009). Narwhals typically travel in small, sex-segregated pods of approximately 4 individuals which regularly coalesce into very large herds (Marcoux et al., 2009). This and other evidence has prompted some to suggest that they have a “fission-fusion” social structure similar to that of bottlenose dolphins (Watt et al., 2015), though it is unknown if herds are stable groupings, or the result of externally driven aggregations. In winter, the narwhal’s environment is characterized by heavy ice-cover and complete darkness, making acoustic signals important for spatial awareness and communication: narwhals are known to produce a range of presumably communicative signals, typically classified as “pulsed calls”, composed of clicks with short inter-click intervals, “tonal calls” or whistles, and “mixed calls”, which include overlaid pulsed and tonal components (Marcoux et al., 2012; Stafford et al., 2012). While possible sequences of burst pulses have been detected in narwhals (Marianne Marcoux, Department of Fisheries and Oceans, personal communication), they have yet to be described or analyzed, making the narwhal an excellent study system for further inquiry into possible sequences of vocalizations.

Narwhals inhabit unique acoustic environments, where mid- to high-frequency signals propagate long distances under ice (15-30 kHz), and reverberations are ubiquitous (Au and Hastings 2008a; Miller et al., 1995). This makes them a valuable ecological outgroup for understanding the evolution of acoustic communication in marine mammals. Additionally, relative to the other extant member of the *Monodontidae* family, the beluga whale (*Delphinapterus leucas*), the function and complexity of narwhal communication remains understudied (Morisaka et al., 2012; Morisaka et al., 2013).

## **Objectives**

In the summer of 2017, the “Ecosystem Approach to Tremblay Sound” research project of the Canadian Department of Fisheries and Oceans used animal-borne tags to collect one of the largest sets of recordings of narwhals (*Monodon monoceros*) to date. Initial exploration of a subset of recordings revealed the presence of two types of possible sequences, the former consisting of stereotyped “paired” patterns of pulsed calls, and the latter consisting of sets of short burst-pulses, hereafter termed “burst-pulse series”.

Using this dataset, I aimed to provide the first characterization of patterns of vocalizations in narwhals. First, I sought to rigorously demonstrate that these patterns are produced according to stereotyped organizational principles, satisfying the definition of sequences. Without localization using multiple simultaneous recording devices, it remains challenging to attribute specific vocalizations to specific individuals, even when instrumented – for example, an animal swimming alongside a tagged individual might have its vocal production apparatus closer to the tag hydrophone than does the tagged individual itself (Sayigh et al., 2013). Thus apparent sequences could also be the result of call exchanges between individuals, leading to misinterpretation of the sequential structure of a vocal repertoire (Kershenbaum et al., 2014). For this reason, I secondly investigated frequency and amplitude characteristics of these patterns to provide coarse inferences regarding whether they were produced by single individuals. This also allowed me to identify tag-specific differences in call patterns, which could be indicative of individual or group-specific vocalizations. Lastly, I used generalized linear models (GLMs) to investigate the acoustic context of production of paired calls and burst-pulse series.

## **Materials and Methods**

### **Study System and Data Collection**

Narwhals were temporarily captured and fitted with acoustic recording tags (Acousonde™ Model 3B) in Tremblay Sound, Nunavut (72° 28' 49.5588" N, 80° 54' 18.2592" W) as part of the ongoing “Ecosystem Approach to Tremblay” project. Tagging occurred between July 15<sup>th</sup> and September 15<sup>th</sup>, 2017.

Narwhals were simultaneously fitted with “backpack” tags secured with pins through the dorsal ridge, providing satellite location and dive data. Portions of skin and blubber extracted during the pin insertion process were used as biopsy samples for genetic and fatty acid analyses. Acoustic tags were attached just adjacent to the dorsal ridge (port side) by suction cup, allowing them to detach after several days and float to the surface for recovery. These tags were programmed to alternate every 30 minutes between low-frequency (LF) and high-power (HP) channels, with maximum sampling rates of 25.8 kHz and 232.3 kHz respectively. The HP channel included a 22 dB anti-alias filter at 100 kHz, still allowing for high quality representations of the primary bandwidth of narwhal clicks (20-70 kHz; Marcoux et al., 2012; Koblitz et al., 2016). The recording sensitivity of Acousonde 3B tags is directional, due to acoustic shadowing from the floatation apparatus, resulting in slightly reduced estimated amplitudes between 240°-290°. Two tags (NW08, NW09) were programmed with an additional 20 dB gain, which was subtracted to match the relative amplitudes of other tags prior to acoustic analyses.

### **Sound Auditing and Initial Call Selection**

Sound files of the HP channel were visually and aurally audited in 15-second viewing frames in Raven Pro 1.3 (2007). Spectrograms were calculated with Fast Fourier Transformation (FFT) length 4096, 50% window overlap, Hann window, and maximum display frequency of 80 kHz. No acoustic filters were applied prior to auditing. The purpose of this audit was to index the locations of calls, surfacing sounds, and feeding-related buzzes to provide a preliminary assessment of the contents of the recordings and to compile an index of vocalizations for further analysis.

This initial audit informed the design of a simple pre-classification procedure, where calls with sufficient signal-to-noise ratio (SNR) to be visually and aurally discernable were annotated and extracted. In assessing discernibility, some, but not excessive, overlap by surfacing noise, clicks, or other vocalizations was permitted (Kaplan et al., 2014). Initial call classes included vocalizations broadly classified as “tonal/whistles”, “pulsed”, “mixed”, “patterned”, and “burst-pulse series”. Echolocation trains and buzzes were readily distinguishable from other vocalizations by differences in click rate (Lammers et al., 2004; Arranz et al., 2016), and were typified by clicks at relatively low inter-click intervals (approx. 200 milliseconds) speeding up into very high repetition rates with inter-click intervals of around 3ms, matching the characteristics of narwhal buzzes described in

other studies (Rasmussen et al., 2015; Blackwell et al., 2018). All extracted vocalizations were checked for saturation of the recording device (i.e. clipping).

To assess possible effects of tagging on vocal behaviour, I noted the time since tag attachment until the first vocalization was recorded, as well as the time until the first buzzes occurred. Given my interest in identifying repeated call types, some of which are produced in isolation contexts (Janik and Slater 1997), I included all recordings from the point of release onwards for these analyses.

I was unable to make any assumptions regarding social affiliations between individuals. Furthermore, while all recordings used in this analysis came from tags attached to female narwhals, my inability to fully discriminate between focal and non-focal vocalizations meant that I made no assumptions regarding the sex of animals contributing calls to analysis.

### **Two Types of Patterns: Pre-Classification of Paired Patterns and Burst-Pulse Series**

Given that patterns of pulsed vocalizations have not yet been described in narwhals, I had to invent bespoke definitions of sequence types. This included the identification of “units”, a key step in the characterization of vocal sequences. I identified units according to separation by silent gaps, the most common method when concurrent observations of behaviour or knowledge of sound-production mechanisms are unavailable (Kershenbaum et al., 2016; Fitch 2012). Quantitative analyses comparing categorization procedures using different fundamental “units” were beyond the scope of this analysis (e.g. Shapiro et al., 2011).

First, I defined *paired* patterns as two stereotyped, pulsed (i.e. click-based) units that co-occur in the same order within a short time interval (< 2 seconds), the pair of which is repeated at least 3 times within 30 seconds (e.g. “A-B – A-B – A-B”). Time and repetition thresholds were informed by exploratory analyses as well as the timing of rhythmically repeated vocalizations in other odontocetes (Janik et al., 2013; Riesch et al., 2006; Zwamborn and Whitehead, 2017b). Second, I noticed series of short pulsed vocalizations. These have not been thoroughly described in narwhals, though they may be similar to the “chitter” described by Stafford et al., (2012). These patterns were characterized by series of burst pulses with much shorter durations than the paired patterns. Sub-units greater than 0.5 seconds apart were assumed to belong to separate series. For the purposes of this analysis, I took each series to be the fundamental unit, meaning that I examined

stereotyped organization between burst-pulse series. I limited my analysis to sequences of at least 3 burst-pulse series, each produced within 10 seconds of the next.

## **Demonstrating Stereotyped Organization of Units**

### ***Multiple-observer classification of paired patterns***

Visual classification has been shown to be an effective method for the classification for vocal sequences, and for marine mammal vocalizations in particular (Janik and Sayigh 2013; Kershenbaum et al., 2016). I devised a classification task with multiple independent observers to confirm that paired patterns were stereotyped and repeated, and to assess the presence of distinct “types” of pairs. While spectrographic visualizations of pulsed signals are highly contingent on FFT and time dimensions used, differences in click rate (the expected form of stereotypy) should be consistently distinguishable so long as spectrogram parameters are kept constant.

One randomly selected pair from each of the paired pattern sequences as I defined them served as a template (shown in Fig. A1; Appendix I). I then printed 100 patterns of pulsed calls to be matched to these templates. This number of patterns was chosen as a balance between including adequate variation to assess patterns across tags, while not being overly cumbersome, which could result in reduced classification performance (Rendell and Whitehead 2003). These included the remaining paired patterns from the original sequences, as well as possible pair-like patterns identified elsewhere in the classification procedure, but which were not rhythmically repeated. Given the propensity of narwhals to aggregate in groups where many (and often overlapping) vocalizations are heard, this test sample was likely to include pulsed calls that were produced close together in time, i.e. “null” patterns.

Six participants matched call patterns to one of 10 possible templates, or indicated that no match was found. Participants had varying degrees of expertise in bioacoustics (range 1-20 years), though none had previous experience classifying narwhal vocalizations. Participants were instructed to ignore any background noise or differences in frequency range for the classification task. Index numbers for calls were randomized prior to the task.

Inter-observer agreement was measured using Fleiss’ Kappa statistic. Kappa statistics assess the correlation between classifiers, accounting for the null probability of agreement by chance. Possible values for Fleiss’ Kappa statistic range between -1 (complete disagreement) to +1

(complete agreement). We calculated an overall Kappa statistic as well as paired call-type-specific measures of Kappa interobserver reliability to assess whether classifiers could reliably distinguish between patterns, as an index of stereotypy. To provide an unbiased assessment of the distribution of paired patterns across time and tags, I labelled each extracted pattern according to the class matched by the majority of raters, if at least 4/6 agreed on the same template.

### ***Discriminant function analysis of paired patterns***

It is plausible that animals produce vocalizations with silent gaps that are perceived as single calls. Further support for the interpretation that the paired patterns are composed of distinct units would come from their divisibility, i.e. if sub-units were ever produced alone (Marler 1977).

I performed an initial classification of any vocalizations that appeared to match the units of paired patterns, but that were produced alone. To verify that these lone pulsed calls did correspond to units of the respective patterns, I used a discriminant function analysis (DFA) to classify the first units of all stereotyped patterns (as classified in the independent observer task), but also included the additional “lone units” that I had identified. Duration (s), and both starting and ending pulse repetition rate (PRR, measured in Hz) were chosen as predictors, and were visually assessed for normality and homogeneity of variance (HH Package; Heiberger 2018). Prior to the estimation of click profiles, calls were filtered using a Butterworth 4-pole bandpass filter bounded by user-defined low and high-frequency limits, as in Marcoux et al. (2012). This helped to ensure the most accurate possible measures of pulse rate and avoided the inadvertent counting of overlapping clicks produced by other nearby animals. Clicks of paired pattern units were located using the “findpeaks” function from the Signal Processing Toolbox in Matlab (R2017b). Measures of mean peak prominence and duration between peaks were manually calibrated to provide the most accurate fit for each call. Starting and ending PRR were then calculated from the initial and final fourths of the unit, respectively. I chose these predictors for the DFA given the expectation that change in PRR was the dominant distinguishing feature used in the classification task (Luis et al., 2016). Only pattern subtypes with 4 or more exemplars were used, so that the number of predictors in the DFA did not exceed the smallest number of exemplars.

Successful identification of lone units would allow me to test “Menzerath’s law of linguistics”, which predicts that divisible units should have shorter durations when produced as part of longer sequences (Gustison et al., 2016). I used two-sample t-tests to determine whether lone units had shorter durations when used in full “paired” calls compared to when produced alone.

### ***Extracting the temporal structure of burst-pulse series***

I devised a method to extract the temporal organization of sub-units in burst-pulse series. Similarity among temporally stereotyped vocalizations may be more effectively compared using quantitative measures rather than human judgements, especially with large datasets (Rendell and Whitehead 2003). I used a custom Matlab (R2017b) script to plot spectrograms of each burst-pulse series and manually demarcate the start- and end-times of each individual sub-unit. These data were transformed in a binary string that represented, with one value per recording sample, the precise timing of the burst-pulse series. This was expected to capture a more precise metric of similarity than number of sub-units, or total series duration, for example. For computing ease, these binary representations were then down-sampled by including every 500<sup>th</sup> value, resulting in a temporal resolution of 465 values/second. No filters were applied to these calls, and all series were plotted with identical spectrogram parameters as used in the auditing process.

### ***Levenshtein distance analysis of burst-pulse series***

Levenshtein distance (LD) is the minimum number of insertions, deletions, substitutions, or transitions to transform one string into another. For example, the LD between “A-B-C-D” and “A-B-E-C” is 2. LD has been effectively applied to sequences as diverse as DNA, language (Petroni and Serva 2010), and humpback song (Garland et al., 2012; Kershenbaum and Garland 2015). To test for repetition in sequences of burst-pulse series, I calculated LD for *observed transitions*, defined as adjacently produced burst-pulse series from originally identified sequences. I also calculated LD values between an equal number of *random comparisons*, which were pairwise comparisons of the same burst-pulse series re-shuffled in random order. These random comparisons were calculated within samples from each tag to accommodate for any individual-specific differences in burst-pulse series, which could bias subsequent estimates of repetition. Repetition would be demonstrated by lower LD (i.e. higher similarity) values for observed vs. random transitions. The use of LD based on fine-grain binary strings should allow for any stereotyped associations between sub-units to be included in similarity measurements, without human supervision.

I fitted a generalized linear model with Poisson family and log-link to compare Levenshtein distances between observed and random transitions according to the following questions:

$$\overline{LD} = \exp(\beta_0 + \phi_{Random}\beta_1) \quad LD \sim \text{Poisson}(\overline{LD})$$

where  $LD$  represents actual measures of Levenshtein distance and  $\overline{LD}$  represents expected measures of Levenshtein distance.  $\beta_0$  is the model intercept, representing mean Levenshtein distance for observed transitions between burst-pulse series.  $\phi_{Random}$  is an indicator assuming a value of 1 for randomly generated comparisons, meaning that  $\beta_1$  is a contrast representing the difference between LD measures of random comparisons relative to observed transitions. I also fit an identical model with quasi-Poisson family to check for overdispersion in the response variable. Only recordings with more than one sequence of burst-pulse series were included.

## **Inferring Patterns of Production across Individuals**

### ***Discriminating between sequences and call exchanges***

A lack of overlap between repeated signals has been used to support inferences that a sequence is produced by a single individual (Luis et al., 2018; Sayigh et al., 2013; Zwamborn and Whitehead 2017b). However, some species produce call exchanges with highly precise and stereotyped timing (Mann et al., 2006; Pika et al., 2018), meaning that non-overlapping sequences of vocalizations can also result from exchanges between multiple individuals (Miller et al., 2004). To assess whether sequences of vocalizations are produced by a single animal or represent exchanges between multiple animals, I examined not only overlap, but also variation in amplitude and frequency spectra of pulsed vocalizations produced in sequences, with the expectation that the exceptionally directional clicks of narwhals should not be consistently recorded with the same acoustic characteristics from multiple individuals (Koblitz et al., 2016).

### ***Exclusion of patterns produced by non-focal individuals***

It is hypothesized that clicks recorded from suction-cup-tagged beaked whales (*Ziphiidae sp.*) include additional low-frequency components conducted through the body (Johnson et al., 2006; Johnson et al., 2009; Zimmer et al., 2005). This hypothesis was recently extended to clicks recorded from narwhals tagged with similar Acousonde<sup>TM</sup> tags used in this study (Blackwell et al., 2018). To improve my ability to make inferences regarding the individual-specificity of call types, I examined and discriminated click based on frequency characteristics.

A threshold for “unusual” lower-frequency was devised from examination of previous reports of narwhal click frequency ranges. Estimates of the peak frequency of narwhal clicks using standard hydrophones include 19 kHz (Miller et al., 1995), 12-20 kHz (Marcoux et al., 2012).

Others have reported that narwhals produce clicks at variable frequency ranges, the lowest having a peak frequency of 3.5-5 kHz and no energy below 3 kHz (Figure 2a in Stafford et al., 2012). In contrast, recordings of tagged narwhals contain clicks with substantial energy below frequencies ever described using standard hydrophones recording in the far field (Shapiro 2006; Blackwell et al., 2018). As such, pulsed patterns with clearly visible energy below 3 kHz were identified as “possibly focal”.

On *average*, clicks produced by non-focal individuals should have lower amplitudes than those plausibly produced by the tagged animal, acknowledging that non-focal vocalizations may sometimes produce higher received levels, given the potential for on-axis transmission (Johnson et al., 2009). I used a two-sample t-test to test the prediction that pulsed vocalizations with visible low-frequency energy (<3 kHz) should have greater RMS amplitudes, using the first unit of each paired pattern. A significant difference would provide further support for the hypothesis that click-based sounds lacking energy below 3 kHz are produced by non-focal whales. Units were filtered with a 3 kHz high-pass filter to remove the confounding effects of the low-frequency energy itself influencing amplitude. However, it is suggested that high-amplitude pulsed vocalizations produced by nearby, non-focal individuals can also result in additional low-frequency energy on a tag recording (Blackwell et al., 2018). As in-depth consideration of the conduction and propagation of low-frequency energy was beyond the scope of this analysis, I conservatively assumed that this discrimination process should allow for an increased ability to relate sequences of calls to specific individuals.

Tag-specificity of paired patterns was assessed by simple qualitative analysis of the distribution of paired pattern types across tags, with and without the “possibly focal” distinction. As a simple measure of tag-specificity for burst-pulse series, I examined and plotted the distributions of the number of sub-units per burst-pulse series, grouped by tag. I also used two-sample t-tests to determine if burst-pulse series from different tags had significantly different numbers of sub-units.

## **Modeling Contextual Usage**

### ***Sequence use as a function of behaviour***

I fit simple models to explore the context and possible function of these stereotyped patterns of vocalizations. In the 60 seconds preceding and following a sequence of pulsed calls, I noted the number of other calls, as well as the presence of surfacing events and buzzes. Vocalization counts

were  $\log_{10}$  transformed, given positive skew, and the expectation that a logarithmic representation would be a biologically appropriate measure of vocal activity. These predictors were measured separately for paired patterns and burst-pulse series. I supplemented these records with an additional 60 pseudo-absences, consisting of randomly selected 60-second periods drawn from the same tags where the sequence types in question were identified. I also did not select pseudo-absences prior to the first vocalizations identified on a tag recording or after presumed tag detachment. Models were fit according to the following equations:

$$\overline{C} = \frac{\exp(\beta_0 + \beta_1 v + \phi_S \beta_2 + \phi_B \beta_3)}{1 + \exp(\beta_0 + \beta_1 v + \phi_S \beta_2 + \phi_B \beta_3)} \quad C \sim \text{Binomial}(\overline{C})$$

where  $C$  represents the probability of a sequence occurring and  $\overline{C}$  represents expected probabilities.  $\beta_0$  is the model intercept, representing the probability of a given recording sample being preceded by a pattern of pulsed vocalizations.  $\beta_1$  represents the effect of the number of other vocalizations ( $v$ ),  $\beta_2$  represents the difference in model intercept when surfacing sounds were detected, and  $\beta_3$  represents the difference in model intercept when buzzes were detected. This model structure was applied separately to patterns of pulsed calls and burst-pulse series, and for each, according to the 60 seconds preceding a call (context models), and the 60 seconds following a call (subsequent action model). These four models were also fitted using GLMs with quasi-Binomial families to check for overdispersion.

### ***Repetition as a function of noise***

To investigate whether the number of rhythmic repetitions in a sequence is driven by ambient noise levels to increase redundancy and so improve signal detection (Brumm and Slater 2006), I fit generalized linear models with Poisson family and log-link relating the number of rhythmic repetitions of a call pattern to noise in the 5 seconds preceding the initiation of the pattern according to the following equations:

$$\overline{R} = \exp(\beta_0 + \beta_1 n) \quad R \sim \text{Poisson}(\overline{R})$$

where  $R$  represents actual number of pattern repeats and  $\overline{R}$  represents expected number of repeats.  $\beta_0$  is the model intercept, and  $\beta_1$  is the slope of the regression of repeats on noise.  $n$  refers to RMS

amplitude (dB re 1  $\mu$ Pa) noise in the 5 seconds preceding the initiation of a call pattern, or sequence of call patterns. I found that RMS noise levels for the preceding 1, 5, and 10 seconds were highly correlated, suggesting that resulting effect estimates would not be unduly influenced by this threshold.

Diagnostic plots were used to validate the use of all models prior to consideration of estimated parameters. All statistical analyses were done in R 3.4.2 (R Core Team 2017).

## **Ethical Statement**

Narwhals are too skittish to be tagged from boats like some other marine mammals, and have never been successfully kept in captivity, making net-based capture and tagging an important tool in their study (Gonzalez 2001; Blackwell et al., 2018). However, this procedure almost certainly induces stress in the animal, and complications could plausibly lead to serious injury or death. These risks were mitigated by maintaining constant visual observations of the deployed net, and hauling in the net in bad weather or when ice obfuscated its view. Handling times were kept to a minimum and any animals showing a stress response, e.g. thrashing while restrained, were released immediately.

Fieldwork was approved under a DFO Animal Use Protocol, and a License to Fish for Scientific Purposes, allowing the live-capture and instrumentation of narwhals. All procedures are in accordance with the Guidelines of the Canadian Council on Animal Care. No unexpected injuries or mortalities occurred in this study. The use of this dataset was approved by the St Andrews Animal Welfare and Ethics Committee on February 14, 2018 (attached).

## **Results**

### **General Features**

Eight female narwhals were tagged with acoustic devices. From the high-power channel of the resulting recordings, I identified 3,261 calls, including tonal calls, pulsed calls, mixed calls, and plausible patterns of pulsed calls (Table 1). Most tags (7/8) detached from the narwhal prior to maximum recording duration, resulting in varying recording lengths per tag (Table 1). Periods of multiple high-amplitude, overlapping vocalizations at rates of up to 3 calls/second were identified

on 4/8 tags, and were presumed to be the result of narwhals aggregating into larger herds. Consistent with other studies, pulsed vocalizations outnumbered whistles (Stafford et al., 2012; Miller et al., 1995), though I did note several periods when many overlapping whistles were produced, as described by Ford and Fisher (1978).

**Table 1.**—Details of female *Monodon monoceros* fitted with Acousonde™ acoustic tags in Tremblay Sound, Nunavut. Extracted vocalizations do not include vocalizations rendered indiscernible by the presence of multiple simultaneous vocalizations. Here, “Pattern” refers to any plausible stereotyped patterns of pulsed calls as well as series of burst pulses. No buzzes were detected on the recording from NW14.

Narwhal ID	Deployment date	Recording Length (HP)	Capture Duration (mins)	Time to Vocalize (minutes)		Calls Detected			
				Call	Buzz	Tonal	Pulsed	Mixed	Pattern
NW08	Aug 13,	41 hours	37	56	33	15	110	0	199
NW09	Aug 16,	16 hours	36	41	213	2	17	0	0
NW11 <sup>C</sup>	Aug 30,	4 hours	39	30	187	4	36	1	23
NW12 <sup>C</sup>	Sept 02,	4 hours	27	44	855	408	696	240	583
NW14	Sept 03,	12 hours	18	9	N/A	45	91	8	46
NW18 <sup>C</sup>	Sept 11,	11 hours	31	67	875	12	99	5	10
NW19 <sup>T</sup>	Sept 11,	8 hours	35	15	225	23	41	0	5
NW20 <sup>T</sup>	Sept 11,	16 hours	35	9	1053	13	119	27	32

<sup>C</sup> Associated with calf

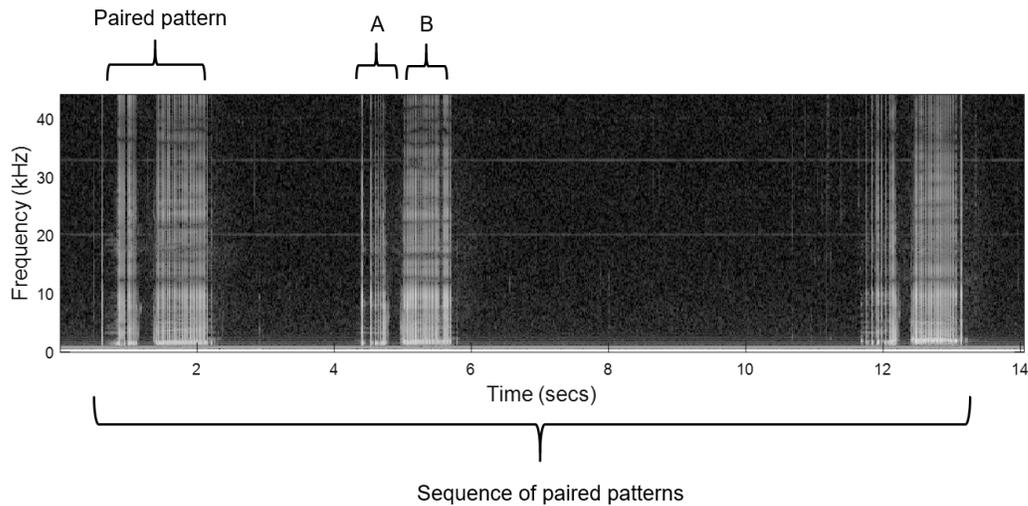
<sup>T</sup> Captured together

Contrary to suggestions in the literature that narwhals tend not to feed in the summertime (Stafford et al., 2012), buzzes indicative of prey capture attempts were identified on all but one tag (7/8; Table 1). Buzzes tended to occur in series, with a short gap after the terminal buzz, and occurred at very high frequencies on some recordings (up to 11 buzzes/minute). Periodic high-amplitude noise associated with surfacing events was detected on all tags. Clipping, where received levels exceed the dynamic range of the recording system, was only detected on recordings from tags programmed with additional gain (NW08, NW09), but was generally associated with surfacing events and not vocalizations. Narwhals did not appear to withhold from vocalizing immediately after tagging, as have been found in other studies. Even when sampling 50% of possible recordings (only the HP channel), I found that narwhals used buzzes comparatively soon after tagging ( $8.2 \pm 7.0$  [SD] hours; Table 1) compared to  $22.7 \pm 11.4$  hours (Blackwell et al., 2018).

## Summary of Identified Patterns

### *Paired patterns*

I identified 8 call patterns consistent with my definition of “paired” calls (Fig. 1). I also included one pattern of two stereotyped pulsed calls with an additional small set of clicks preceding a clear pair of calls, and one pattern for which both units were linked by a tonal “bridge”. Each of these patterns appeared to be a distinct and consistent “sub-type”, and so all 10 were included as templates in the subsequent matching task.



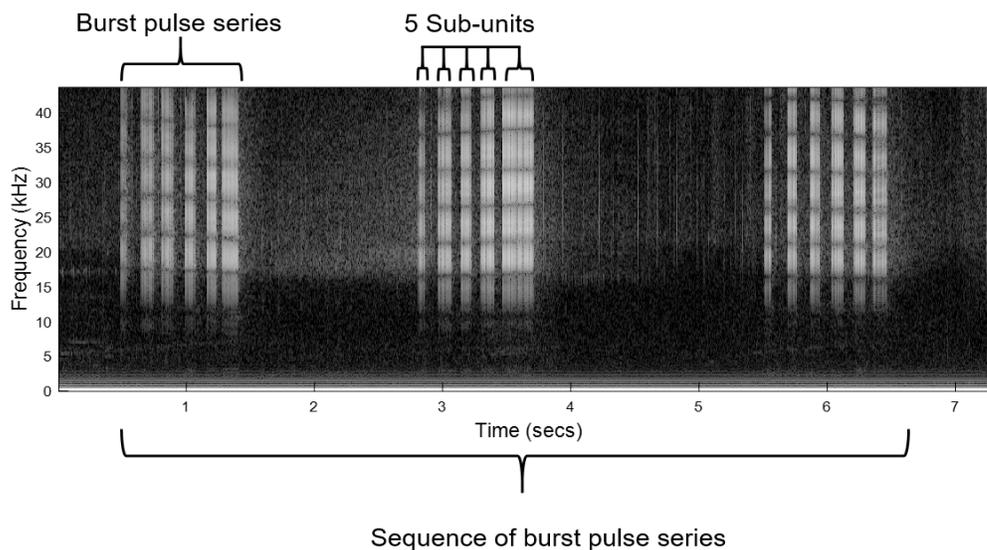
**Fig. 1**—Sample spectrogram showing definition of repeated “paired” vocalizations produced by *Monodon monoceros* (FFT length: 4096, window: Hann, overlap: 50%).

### *Burst-pulse series*

Burst-pulse series were detected on nearly all tag recordings (7/8) but were distributed unevenly. Sequences of at least three burst-pulse series with intervals of less than 10s between each (Fig. 2), were identified on fewer tag recordings (3/8), but still comprised a large portion of the burst-pulse series detected (40%). Inspection of these sequences revealed that single sub-units matching the amplitude and frequency of other burst-pulse series were produced. These, while rare, were also included in the analysis of burst-pulse series. Aural assessment at 0.1x speed confirmed that the apparent structure in the burst-pulse series were not an artefact of the spectrogram, as distinct sets of clicks interspersed with clearly defined periods of silence were obvious.

In total I isolated 36 sequences comprising varying numbers of burst-pulse series ( $n_{\text{series}}=212$ ). From these sequences I extracted 176 transitions between burst-pulse series. While I

did not quantify PRR for individual sub-units in burst-pulse series, aural assessment suggested that PRR was relatively consistent within and across burst-pulse series. Some sequences were composed of burst-pulse series with different numbers and temporal organization of sub-units. However, most patterns appeared to be broadly repetitive, with small modifications such as the addition or subtraction of a single sub-unit (Fig. 2). The length of individual sub-units in burst-pulse series often appeared to increase over the course of the call, and some (approximately 14%) of burst-pulse series were initiated by an especially short sub-unit.



**Fig. 2**—Sample spectrogram showing definition of burst-pulse series produced by *Monodon monoceros* (FFT length: 4096, window: Hann, overlap: 50 %).

## Demonstration of Stereotyped Organization of Units

### *Classification reveals repetition and multi-unit associations in paired patterns*

Six participants naïve to the original ordering and context of vocalizations consistently classified paired call patterns to provided templates, confirming that they are stereotyped, though interobserver agreement varied between call types (Table 2). These classifications matched the patterns that I initially identified as occurring in sequence, providing evidence that these are stereotyped patterns of pulsed calls that are rhythmically repeated (Fig. 3). Each of these 29 sequences was composed of a single paired call pattern only. Of these classified patterns, mean

PRR of the second unit was higher than that of the first unit for 9/10 subtypes (See Fig. A2 in Appendix I).

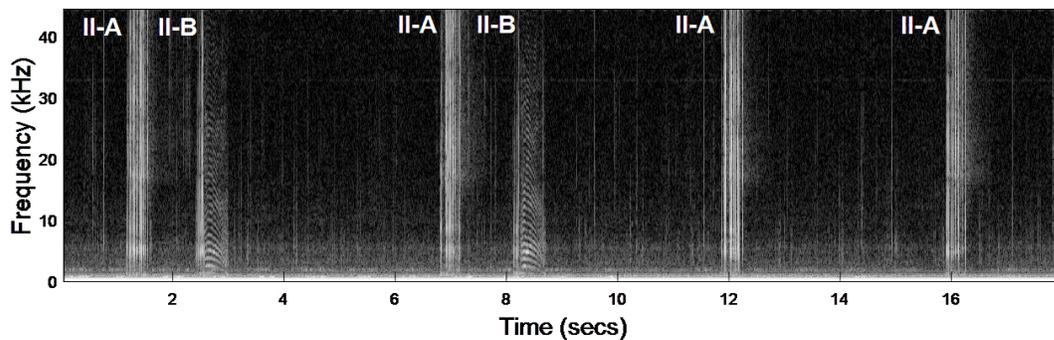
**Table 2.**—Summary statistics of Fleiss’ Kappa test applied to multiple observer classification of patterns of *Monodon monoceros* pulsed calls recorded in Tremblay Sound, Nunavut. Six independent classifiers reliably matched 100 patterns to template patterns or to a “no match” class. Reliability descriptors taken from Landis and Koch (1977). Tag specificity indicates the tags where from which each call pattern was identified, with bolded numbers designating patterns “possibly focal” calls.

Call Pattern	<i>k</i>	<i>z</i>	<i>p</i>	Reliability Descriptor	Tag Specificity ( <i>n</i> )
I	0.813	31.472	<0.001	Near-perfect	<b>NW08 (7)</b>
II	0.921	35.683	<0.001	Near-perfect	<b>NW12 (6)</b>
III	0.399	15.469	<0.001	Fair	NW12 (4)
IV	0.757	29.316	<0.001	Substantial	NW12 (4)
V	0.660	25.551	<0.001	Substantial	NW12 (7)
VI	0.492	19.060	<0.001	Moderate	<b>NW12 (1)</b> , NW14 (4)
VII	0.533	20.633	<0.001	Moderate	NW08 (3)
VIII	0.772	29.893	<0.001	Substantial	<b>NW08 (16)</b> , <b>NW11 (1)</b>
IX	0.607	23.525	<0.001	Substantial	<b>NW11 (5)</b> , NW12 (2)
X	0.373	14.439	<0.001	Fair	NW12 (2)
No match	0.321	12.447	<0.001	Fair	(All)
<b>Overall</b>					
All classes	0.584	63.4	<0.001	Substantial	

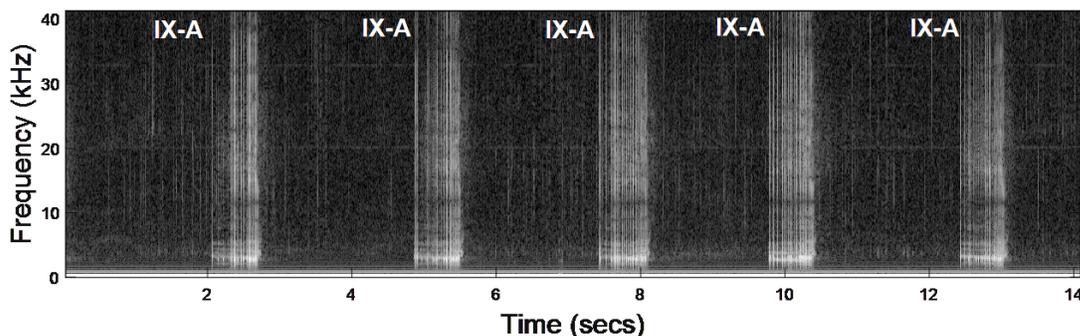
I detected possible “lone units” associated with only two subtypes (II and IX). Duration, starting PRR and ending PRR of “A” units for all classified subtypes satisfied the assumptions of linear discriminant analysis. The DFA using these parameters classified patterns with 80.6% accuracy relative to labelled call patterns in the visual matching task, when using jackknifed cross-validation (Wilk’s  $\Lambda = 0.04$ ,  $X^2 = 205.5$ ,  $DF = 21.0$ ,  $p < 0.001$ ). However, as in the matching task, classification accuracy depended on the pattern type: four classes had very high classification accuracies (I, 100%; II, 100%; IV, 100%; VIII, 94%; IX, 88.9%) and three classes were not accurately discriminated (III, 0%; V, 50%; VI, 0%). The failure of the DFA to classify some templates suggests that PRR and duration of the “A” unit alone were not predictive for these types.

Additional lone first units expected to be associated with II and IX patterns, respectively, were classified to the correct category with 100% accuracy, confirming that individual units of the stereotyped patterns are sometimes produced alone. I detected no lone “B” units for any patterns.

Lone first units were sometimes rhythmically repeated (Fig. 4), and were often produced in close proximity to full “pairs” (Fig. 3). When both units of a pattern were produced together, they were always produced in the same order, i.e. A → B (Fig. 4). Some lone units appeared to have shorter durations when produced in sequences, compared to when they were combined into full “paired” sequences, as has been described for vocal sequences in primates (Gustison et al., 2016). Statistical analysis confirmed that “A” units of sub-type IX had longer durations when produced alone than when produced in multi-unit patterns ( $\bar{\mu}_{\text{alone}} = 0.68$ ,  $\bar{\mu}_{\text{pair}} = 0.56$ ,  $t(6.2) = -4.0$ ,  $p = 0.006$ ). However, I did not detect a significant difference between unit durations for type II (type II ( $\bar{\mu}_{\text{alone}} = 0.45$ ,  $\bar{\mu}_{\text{pair}} = 0.43$ ,  $t(14.2) = -1.5$ ,  $p = 0.170$ ).



**Fig. 3**—Sample spectrogram showing a stereotyped pattern of calls (II) followed by two additional lone “A” units (FFT length: 4096, window: Hann, overlap: 50 %). Classified visually (*Kappa* statistic 0.921,  $p < 0.001$ ) and by DFA (100% classification for subtype II).



**Fig. 4**—Sample spectrogram showing lone “A” units of a stereotyped pattern of calls repeated in rapid succession (subtype IX; FFT length: 4096, window: Hann, overlap: 50%). Classified visually (*Kappa* statistic 0.607,  $p < 0.001$ ) and by DFA (88.9% classification for subtype IX).

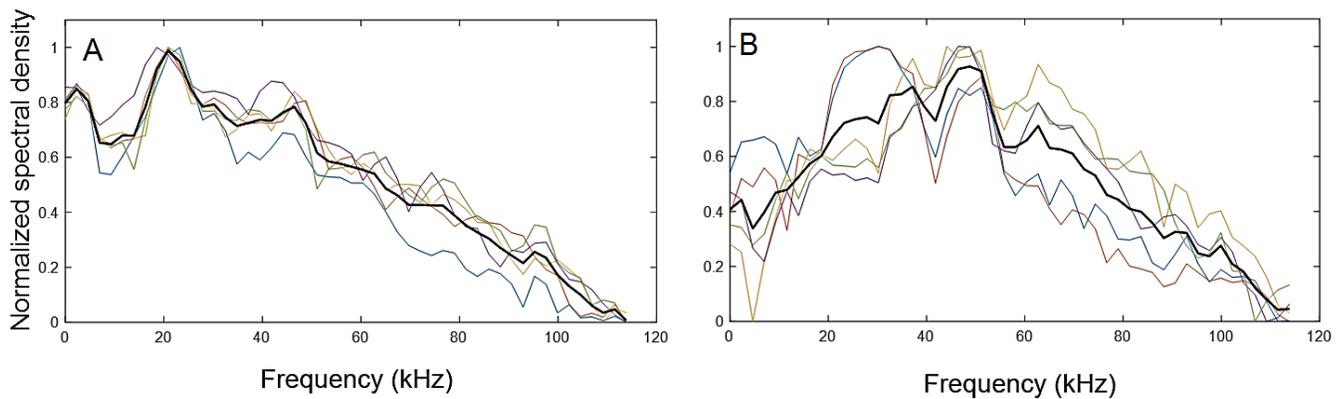
### ***Levenshtein distance model reveals repetition in sequences of burst-pulse series***

Measures of LD distance were overdispersed (dispersion parameter 104.9), so I interpreted effect coefficients calculated in the GLM with quasi-Poisson family. Pairs of burst-pulse series extracted from observed transitions were more similar (less dissimilar) than pairs from randomly generated transitions ( $-0.34 \pm 0.09$ ,  $z = -3.91$ ,  $p < 0.001$ ). This constitutes evidence of non-random structure to sequences of burst-pulse series, based on the temporal pattern of sub-units alone.

### **Patterns of Production across Individuals**

#### ***Indications that patterns were produced by a single individual***

Frequency and amplitude measures were highly consistent both between units of paired patterns and between instances of rhythmically repeated paired patterns in the same sequence. There was one exception to this rule: a sequence of sub-type VIII included one pair produced with clicks of higher frequency than others in the sequence (Fig. 5). While this matched the expected differences in frequency attributable to focal and non-focally produced clicks, this could also be the result of sequence production by a single non-focal individual who was close enough to sometimes register low-frequency energy on the tag recording (Blackwell et al., 2018). I did not identify any instances of overlapping units (i.e. “A”, “B”) of paired patterns, nor was there any overlap of repeated pairs.



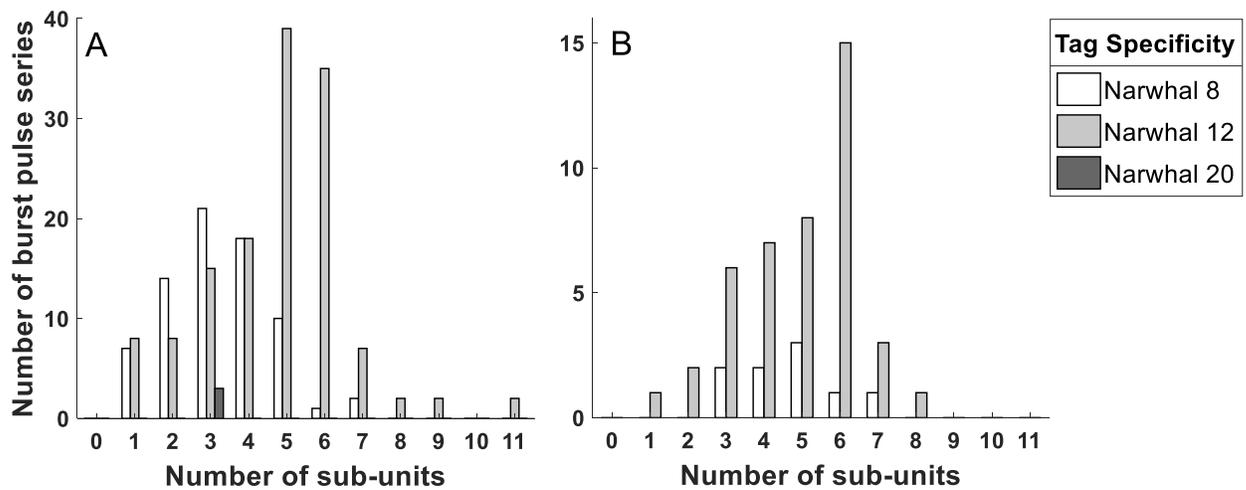
**Fig. 5**—Spectral density levels calculated of clicks extracted from “VIII” type pulsed call patterns recorded from *Monodon monoceros* (coloured lines) with (A) and without (B) substantial energy below 3 kHz, with mean spectral density shown by the thick black line.

Sequences of burst-pulse series were generally produced with consistent frequencies and amplitudes (Fig. 2), though I detected 2 sequences (5.5%) with overlapping series, suggesting that they are occasionally used in call exchanges.

***Tag-specific variation in paired patterns and burst-pulse series***

As predicted, pulsed vocalizations with energy below 3 kHz had higher RMS amplitudes ( $\mu = 156.8$ ,  $SD = 7.8$ ) than calls lacking energy below 3 kHz ( $\mu = 142.4$ ,  $SD = 8.0$ ;  $t(108) = 9.57$ ,  $p < 0.001$ ), even when energies below 3 kHz were filtered out. When excluding patterns attributable to non-focal individuals, 97% (38/39) of remaining paired calls were identified on a single recording only (Table 2). This trend was consistent over time: call subtypes I, II, VIII, and IX were found 7.2, 10.2, 38.6, and 40.7 hours apart on recordings from their respective tags, suggesting that subtypes were not an artefact of a single vocalization event.

Though sequences of burst-pulse series (as defined above) were only detected on 3 tags, and only two of these had more than one sequence, I detected tag-specific differences in burst-pulse series characteristics: series recorded from NW08 had fewer sub-units than series recorded from NW12 ( $\bar{\mu}_{NW08} = 3.29$ ,  $\bar{\mu}_{NW12} = 4.79$ ;  $t(207) = -6.1$ ,  $p < 0.001$ ; Fig. 6A).

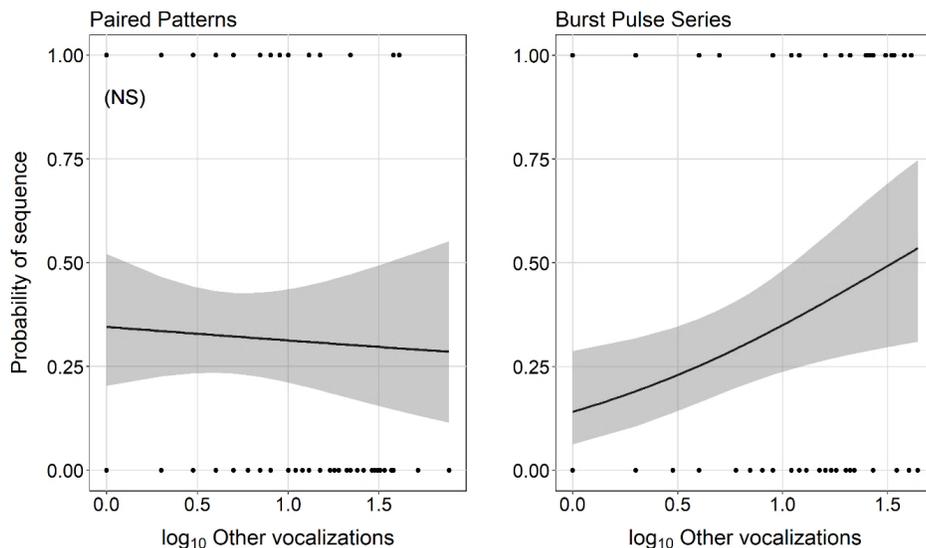


**Fig. 6**—Histograms showing distributions of number of segments per burst-pulse series recordings taken from individual *Monodon monoceros* including (A) and excluding (B) series with no click energy below 3 kHz, suggesting possible production by the tag-bearing whale (B).

## Contextual Use of Sequences

Overall, I detected few substantial relationships between the occurrence of sequences of pulsed calls and other behavioural measures. Relative to randomly selected samples, paired patterns were 58% more likely to be followed by buzzes, though this estimate was associated with very large standard error (Table 3). The models estimated varying relationships between surfacing events and sequences of pulsed calls: Paired patterns were 72% more likely to be preceded by surfacing events, whereas burst-pulse series were estimated to be 44% *less* likely to be preceded by surfacing events (Table 3; Table 4). However, both estimates were associated with high standard error and were not statistically significant. A one-unit increase in  $\log_{10}$  transformed counts of vocalizations in a 60-second recording sample corresponded to a 330% increase in the probability of the sample being followed by a burst-pulse series, suggesting they are associated with vocal exchanges generally (Table 4). In contrast, I detected no relationship between paired patterns and preceding vocalization counts (Fig. 7).

Noise did not have an appreciable effect on the number of repetitions in a rhythmically repeated sequence of either paired patterns or burst-pulse series (Table 3; Table 4). Diagnostic plotting revealed no signs of structural misspecification or overdispersion in any models.



**Fig. 7**—Marginal effects of other vocalizations preceding the occurrence of sequences of *Monodon monoceros* pulsed calls. Effects were estimated using GLMs with Binomial families.

**Table 4.**—Parameter estimates for generalized linear models (GLMs) relating occurrences of paired (n=29) and burst-pulse series (n=24) calls to the acoustic behavioural context preceding and following the call. Previous and subsequent activity models were fit with Binomial families (logit-link), and the noise models were fit with Poisson family (log-link). Behavioural context was inferred from acoustic data alone. Call occurrences were supplemented with 60 randomly selected 60-second samples to provide pseudo-absences. Data used were collected from tags attached to *Monodon monoceros* in Tremblay Sound, Nunavut.

	Estimate	SE	z	p
<b>Paired Patterns</b>				
<b>Previous Activity Model</b>				
Intercept	-0.775	0.489	-1.584	0.113
Vocalizations	-0.147	0.432	-0.341	0.733
Surfacing Events	0.545	0.518	1.053	0.293
Buzzes	-0.124	0.642	-0.193	0.847
<b>Subsequent Activity Model</b>				
Intercept	-0.885	0.453	-1.951	0.051
Vocalizations	-0.089	0.413	0.216	0.829
Surfacing Events	-0.060	0.535	-0.112	0.911
Buzzes	0.461	0.552	0.835	0.404
<b>Noise Model</b>				
Intercept	0.640	0.143	3.889	0.318
Noise level (dB RMS)	-0.004	0.021	-0.191	0.848
<b>Burst-Pulse Series</b>				
<b>Previous Activity Model</b>				
Intercept	-1.675	0.597	-2.804	0.005
Vocalizations	1.184	0.475	2.494	0.013
Surfacing Events	-0.574	0.638	-0.900	0.368
Buzzes	0.228	0.627	0.363	0.717
<b>Subsequent Activity Model</b>				
Intercept	-1.315	0.529	-2.484	0.013
Vocalizations	1.069	0.458	2.335	0.020
Surfacing Events	-0.770	0.610	-1.264	0.206
Buzzes	-0.704	0.662	-1.064	0.288
<b>Noise Model</b>				
Intercept	0.782	0.866	0.903	0.367
Noise level (dB RMS)	-0.025	0.03	-0.821	0.412

## Discussion

Together, my results show that wild narwhals use at least two broad types of vocal sequences, subsumed under the description of rhythmically repeated patterns of pulsed calls. Paired patterns appear to be composed of distinct units which are combined into strictly ordered sequences, providing parallels to well-described structures of vocal sequences in avian and mammalian species. Burst-pulse series, which appear to have been ignored in previous analyses of narwhal vocalizations, were shown to be combined into structured “sequences of series”. The finding that subtypes of paired patterns and characteristics of burst-pulse series varied between tags opens the possibility that these sequences support individual or group recognition, as has been suggested for other narwhal vocalization (Shapiro 2006). The use of vocal sequences in less-studied marine mammals may be more common than the current paucity of findings suggests, and is expected to be a rich area for further inquiry.

### **Characterization of the Structure of Vocal Sequences in Narwhals**

#### ***Sequences of paired patterns***

The visual classification task confirmed that narwhals produced multiple subtypes of stereotyped, rhythmically repeated “paired patterns”. Consensus between the visual classification task and the DFA for most subtypes suggests that they are readily distinguishable. Strikingly, I found that 9/10 paired pattern subtypes had “B” units with higher mean PRR than first units. The finding that the first units of two subtypes were also produced alone provides further support for the interpretation of these as combinations of calls, rather than single calls with silent gaps. I am unable to conclude with certainty that other subtypes are also composed of divisible units, as I did not identify any candidate cases. However, this may have largely been an artefact of the rarity of certain subtypes, as the two patterns for which I identified lone units were relatively common (Table 1).

Structurally similar combinations of vocalizations are found in other taxa, and have been linked to communicative complexity. For example, meerkats produce similar “di-drrr” calls composed of two units, the pair of which are rhythmically repeated. These are interpreted as evidence for hierarchical communication, a central aspect of zebra finch (*Taeniopygia guttata*) song or human language (Collier et al., 2017). Putty-nosed monkeys (*Cercopithecus nictitans*) produce “pwoy” and “hack” calls which are regularly combined into ordered sequences but are also

sometimes produced alone. Playback experiments have demonstrated that the ordering of these calls conveys distinct meaning, and is considered a rare example of syntax in a wild organism (Arnold and Zuberbühler 2008; Kershenbaum et al., 2016; Marler 1977). The finding that “B” units of paired calls were only ever found following “A” units may even suggest that narwhals use simple, “finite-state” grammars to construct sequences, which are well-documented in primate and avian taxa (Berwick et al., 2011; Fitch and Hauser 2009; Shettleworth 2010). While strict, “A-B” grammars are fundamentally different from the recursive grammatical structures that support human language (Berwick et al., 2011; Fitch and Hauser 2009), simple combined signals can convey a large amount of information (Bradbury and Vehrencamp 1998, pp. 395). Granted, it is possible (though seemingly unlikely) that I failed to identify lone “B” units in the call selection process.

Lastly, Type II “A” units were produced with shorter durations when combined into sequences, providing *preliminary* evidence of Menzerath’s law in narwhal communication. This could simply be driven by physiological constraints on sound production, but could also indicate the principle of “compression”, whereby sequences are scaled down in duration to allow more efficient signalling (Gustison et al., 2016). The small sample size of these calls makes it impossible to make firm conclusions. Nevertheless, further investigation into this trend is warranted, especially given that gelada monkeys (*Theropithecus gelada*) and humans are the only species for which this phenomenon has been demonstrated (Gustison et al, 2016).

### ***Sequences of burst-pulse series***

While burst-pulse series show high variability in structure (e.g. in number of sub-units; Fig. 6), I found that narwhals combine these series into repetitive sequences. Similar series are known to be produced by northern right whale dolphins (*Lissodelphis borealis*; Rankin et al., 2007), dusky dolphins (*Lagenorhynchus obscurus*; Vaughn-Hirshorn et al., 2012), and pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Henderson et al., 2011), though there are non-trivial differences between species. For example, the “burst pulse sequences” produced by dusky dolphins rarely had more than 2 sub-units, and the “patterned burst pulses” in northern right whale dolphins are the only other series that are rhythmically repeated. Similar to these northern right whale series and the click “codas” of sperm whales, the burst-pulse series of narwhals show slight deviations from perfect stereotypy (e.g. Fig. 4. in Rankin et al., 2007; Antunes et al., 2016). This variation could be an artefact of imperfect repetition or may be structured ornamentations with possible function (Zwamborn and Whitehead, 2017a). As with the paired calls, rhythmically repeated burst-

pulse series do appear to show simple hierarchical organization, as “sequences of sequences” (Berwick et al., 2011).

Note, however, that temporal series of vocalizations are not necessarily communicative. Burst pulse series bear some resemblance to the “click packets” first described in a captive beluga, which are used for long-distance echolocation (Finneran et al., 2013; Turl and Penner 1989; Au and Hastings 2008b; Ridgway et al., 2018) The burst-pulse series produced by narwhals appear distinct from these “click packets” though, in terms of number of clicks and higher-level repetition (i.e. of series). Furthermore, I noticed plausible click packets in the narwhal recordings similar to those identified in other studies (e.g. Figure 3a in Rankin et al., 2015). In any case, the finding that series of burst pulses can be used in echolocation suggests that the burst-pulse series I describe in narwhals may serve echolocation functions, perhaps in addition to being communicative (e.g. Götz et al., 2006).

## **Sequences across Individuals**

### ***Discriminating between individually produced sequences and call exchanges***

I am unable to rule out the possibility that sequences were sometimes produced by multiple individuals in coordinated call exchanges, which has important implications for the interpretation of communicative complexity (as discussed above). However, several findings were inconsistent with this explanation: First, the exceptional directionality of narwhal clicks makes it unlikely that multiple individuals would be able to consistently produce clicks resulting in near-identical frequency ranges on an animal-attached tag (Kobliz et al., 2016). One would expect, at least occasionally, to detect differences in amplitude between units, which was never found for paired patterns. Second, overlap between burst-pulse series was very rare, and never identified in paired patterns, supporting the interpretation that they were produced by a single individual (Sayigh et al., 2013). If these sequences were the result of call exchanges, they would require a surprising (though possible) degree of temporal synchrony, akin to duetting or even “turn taking”, given the highly stereotyped inter-unit intervals between units (Pika et al., 2018). As such, the most parsimonious interpretation is that paired patterns were produced by single individuals. The same can be concluded for burst-pulse series, though the detection of some cases of overlap suggests that they may also be produced in call exchanges.

Converging lines of evidence suggest that pulsed calls with energy below 3 kHz were attributable to the focal individual or possibly a very nearby individual. An alternative explanation for differences in both frequency and amplitude range of distinct call types could be crypsis from predators. In the presence of predators with high auditory acuity (e.g. killer whales), narwhals might benefit from shifting their signals outside of their predators' optimal hearing range (approximately 20 kHz; Szymanski et al., 1999). However, calls with and without low-frequency components were consistently detected at short intervals, inconsistent with a context-specific change in behaviour. I conclude that the discrimination of clicks based on low-frequency energy increased the resolution at which I was able to consider the individual-specificity of vocal sequences.

### ***Evaluating evidence for individual-specific sequences***

A distinguishing feature of the paired patterns is that there are multiple subtypes under a seemingly similar organizational structure. Furthermore, these subtypes were almost exclusively recorded from single individuals' tags, especially when excluding vocalizations attributable to non-focal animals. The identification of subtypes within a class of vocalizations associated with specific tag recordings has been taken as preliminary evidence for individual-specific vocalizations in other odontocetes. For example, Quick et al., 2018 showed that 4 of 23 recordings of tagged pilot whales included a predominant mixed call, evidence for individual specificity. I similarly noticed tag-specificity in the "paired patterns" subtypes of narwhals, which were re-produced on the same tags up to 40 hours apart. This provides strong evidence that subtypes were *predominantly* produced by a single individual (King et al., 2013).

However, three considerations make me hesitant to suggest that paired patterns are "signature sequences". First, tonal calls are typically used for long-distance communication (Lammers et al., 2006; Panova et al., 2013; but see Thomsen et al., 2002), a feature which allows signature whistles to facilitate reunions between separated individuals (Janik and Slater 1998). The high-PRR second units of paired patterns could be sufficient as directional cues, as in stereotyped calls of killer whales (Miller 2002). However, narwhals do produce mixed calls (Shapiro 2006), often in bouts (personal observation), which seem more fitting candidates for signature vocalizations. Second, a signature vocalization is likely to be the predominant signal in an individual's repertoire (Cook et al., 2004), which was not true of paired patterns. Third, for species with large vocal repertoires, a sufficiently small sample size of recorded calls can be expected to result in "tag-specific" differences, even if repertoire composition were identical across individuals.

For these reasons, I suggest that caution be taken in the interpretation of the individual-specificity of these calls.

It is puzzling that burst-pulse series recorded from two different individuals had different and continuous (i.e. not obviously incomplete or under-sampled) distributions of numbers of sub-unit. Nevertheless, these patterns seem even less likely to be stereotyped signals disclosing individual identity, given the wide range of numbers of sub-units used (Fig. 6).

## **Contextual Usage of Sequences**

### ***Relationships between sequence use and behaviour***

Linking acoustic signals to behaviour can provide insights into their function (Papale et al., 2017). Burst-pulse series were more likely to be produced in contexts of high vocal activity. This suggests that they are used in social contexts, or at least contexts when animals aggregate into loquacious groups. I did not detect a similar effect for paired patterns, supporting anecdotal observations that these calls were often produced in very quiet periods, when no other vocalizations could be heard. The finding that paired patterns are not related to subsequent feeding events or surfacing sounds (King and Janik 2015), suggests that they are not functionally similar to the “bray sequences” of bottlenose dolphins (Janik 2000; King and Janik 2015).

Combining my findings with finer-grain behavioural data (using depth recorders, accelerometers, visual observations etc.) might reveal further associations between context and sequence use. For example, call sequences could be used for contact and recognition between mothers and calves (Smolker et al., 1999), like the “type A” pulsed vocalizations of belugas (Vergara et al., 2010). Female narwhals give birth in mid-summer (Furgal and Laing 2012; Heide-Jørgensen 2009), and paired patterns were recorded on all tags attached to narwhals observed with calves during capture (Table 1). Alternative modeling strategies like time-series modeling or power analyses to explore effects at different temporal scales (e.g. Leblond et al., 2017) would also offer a more comprehensive test of these relationships. However, stereotyped call sequences with specific functions can also be used in a variety of contexts (Janik 2009; Templeton et al., 2005).

### ***Use of repetition and temporal signals in relation to environmental constraints***

Both sequence types identified in narwhals are characterized by rhythmic repetition. While the energetic cost of vocalizing underwater may not be a significant limitation for odontocetes (Jensen

et al., 2012), the risks of eavesdropping by killer whales is probably important for narwhals (Deecke et al., 2002; Breed et al., 2017; Furgal and Laing 2012; Laidre et al., 2006), making the *ad libitum* use of vocalizations maladaptive. Important signals may be repeated to increase the likelihood of successful transmission though, especially in noisy or dense environments (Brumm and Slater 2006; Ey and Fisher 2008). For example, links between noise and signal redundancy have been identified in blue whales (Miller et al., 2000) and killer whales (Foote et al., 2004). Vergara et al., (2010) proposes that the reverb-prone icy environs inhabited by *Monodontidae* may require especially unambiguous signal types, such as mixed calls, or calls that are rhythmically repeated.

In a similar vein, I investigated whether narwhals modify signal repetition in response to noise. Contrary to predictions though, I detected no effect of noise on the rhythmic repetition rates of paired patterns, nor of burst-pulse series. However, this negative result does not rule out the possibility that narwhals use rhythmic repetition to increase signal transmission. Narwhals may not modify repeat number according to short-term differences in noise or perhaps this result was influenced by frequencies outside of the hearing range of narwhals: applying an M-weighting filter for “high-frequency cetaceans” to noise sample prior to RMS calculation might reveal otherwise confounded effects (Southall et al., 2007).

Alternatively, this result may suggest that repetition is sustained until a response is achieved in a target individual, or that the number of repetitions itself encodes specific information (Payne and Pagel 1997; Janik and Sayigh 2013; Sloan and Hare 2004). For example, the number of “dee” units in call sequences of black-capped chickadees is inversely proportional to the size of an encroaching predator (Templeton et al., 2005). Encoding specific information in temporally stereotyped, broadband signals is consistent with the optimization of signal transmission: the temporal features of a signal degrade slightly less than other acoustic properties over long distances (Bradbury and Vehrencamp 1998, pp. 129). This reasoning is proposed for the encoding of information in the temporal stereotypy of white-eyelid mangabeys (*Cercocebus sp.*; Waser 1982, pp. 134), sperm whale codas (Gero et al., 2016), and forest-dwelling chingolo sparrows (*Zonotrichia capensis*; Bradbury and Vehrencamp 1998, pp. 136). Furthermore, the risks of eavesdropping by killer whales could impose constraints on the range of safely producible vocalizations for small odontocetes (Morisaka and Connor 2007), which could make the ability to convey information in the temporal organization of “safer” vocalization types advantageous. Links between predation and sequence use are well-described in other taxa, but, to my knowledge, have

not been identified for marine mammals (Blumstein 1999; Darwin 1874, pp. 103).

## **Limitations**

First, a major challenge in the initial curation of vocal sequences is that decisions regarding the definition of sequence “types” and subsequently, “units” are subjective. While the visual identification of temporally structured sequence types in marine mammal vocalizations is common (Henderson et al., 2011; Luis et al., 2018; McDonald et al. 2006; 2018; Rankin et al., 2007; Riesch et al., 2008; Vaughn-Hirshorn et al., 2012; Zwamborn and Whitehead 2017), my analysis leaves open the possibility that the sequences I have identified fit into a gradient of other patterns of pulsed calls. Unfortunately, quantitative discrimination of these classes is unlikely to be much more informative, as humans and animals alike are able to perceive categories in continuously varying distributions (Baugh et al., 2008; Caves et al., 2018). The best demonstration that paired patterns and burst-pulse series constitute meaningful and separate classes would be further differentiation in contextual usage (as in Fig. 7), more refined methods to attribute vocalizations to individuals, and playback experiments in the field (Fischer et al., 2013).

Second, live-capture and tagging procedures can lead to abnormal physiological and behavioural responses in narwhals upon release, such as abstaining from using clicks or buzzes (Williams et al., 2017; Blackwell et al., 2018). We did not detect effects of the same magnitude: one individual in this study even produced buzzes within 30 minutes of release. This could have been the result of comparatively shorter capture durations, or perhaps the whales tagged in this study had faster access to high-quality feeding areas (Blackwell et al., 2018). Regardless, the possible effect of tagging remains an important caveat in this research. As in other studies recording odontocetes with animal-borne acoustic devices, we found that vocalizations were unevenly distributed across tags (Kaplan et al., 2014), a finding which may have been influenced by heterogeneous effects of tagging for different narwhals. For tags with short total recording durations, diurnal variation in vocalization rates could also have been a contributing factor (Blackwell et al., 2018).

## **Suggestions for Future Research**

Further inquiry into the function and prevalence of these sequences seems warranted. For example, if paired patterns are conclusively demonstrated to contain group- or individual-specific signals,

they could be exploited in spatially explicit mark-recapture studies to provide improved acoustically-derived estimates of abundance (Marques et al., 2013; Marcoux et al., 2011). Furthermore, while I have demonstrated that burst-pulse series are produced in repetitive sequences, this does not preclude the presence of non-random transitions between distinct “types” of burst-pulse series. Clustering algorithms could be applied with LD to determine whether burst-pulse series can reliably be grouped into types (Garland et al., 2012). Determining whether similar patterns of vocalizations are used by the East Greenland narwhal population, which has been separated from this study population for approximately 10,000 years (Blackwell et al., 2018) could lead to insights regarding the genetic, ecological, and/or cultural development of narwhal communication (Garland et al., 2011; Janik 2000; May-Collado and Wartzok 2008; Rendell and Whitehead 2001). Finally, future work should seek to identify possible differences in vocal behaviour between male and female narwhals, which exhibit clear morphological dimorphisms. It is likely that the sounds analyzed in this study are more representative of female vocal behaviour, especially given that pods of narwhals are often sex-segregated (Marcoux 2009; Furgal and Laing 2012).

## **Conclusions**

I conclude that narwhals produce at least two types of vocal sequences. The paired patterns appear to be one of few ordered, multi-unit sequences in odontocetes, and to my knowledge, the first in the *Monodontidae*. The demonstration of costly repetition in successive burst-pulse series suggests that they are important enough signals to warrant the costs associated with redundant signaling, though their specific function remains a mystery. Together, my findings provide a small contribution to the understanding of the vocal behaviour of narwhals, and to the phylogenetic distribution of vocal sequence production. It may be that vocal sequences in marine mammals are more common than the current literature suggests. My hope is that future inquiry will elucidate the function(s) of these sequences in narwhals, and continue to widen the set of species in which vocal sequences are identified, ultimately supporting comparative studies to better understand evolution of vocal communication.

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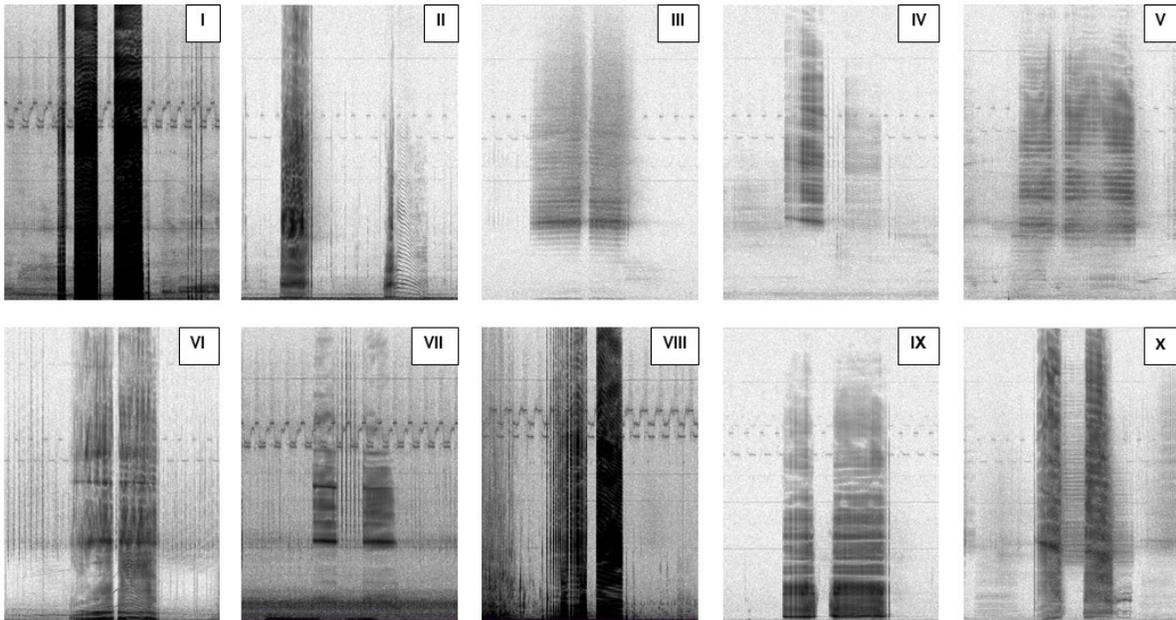
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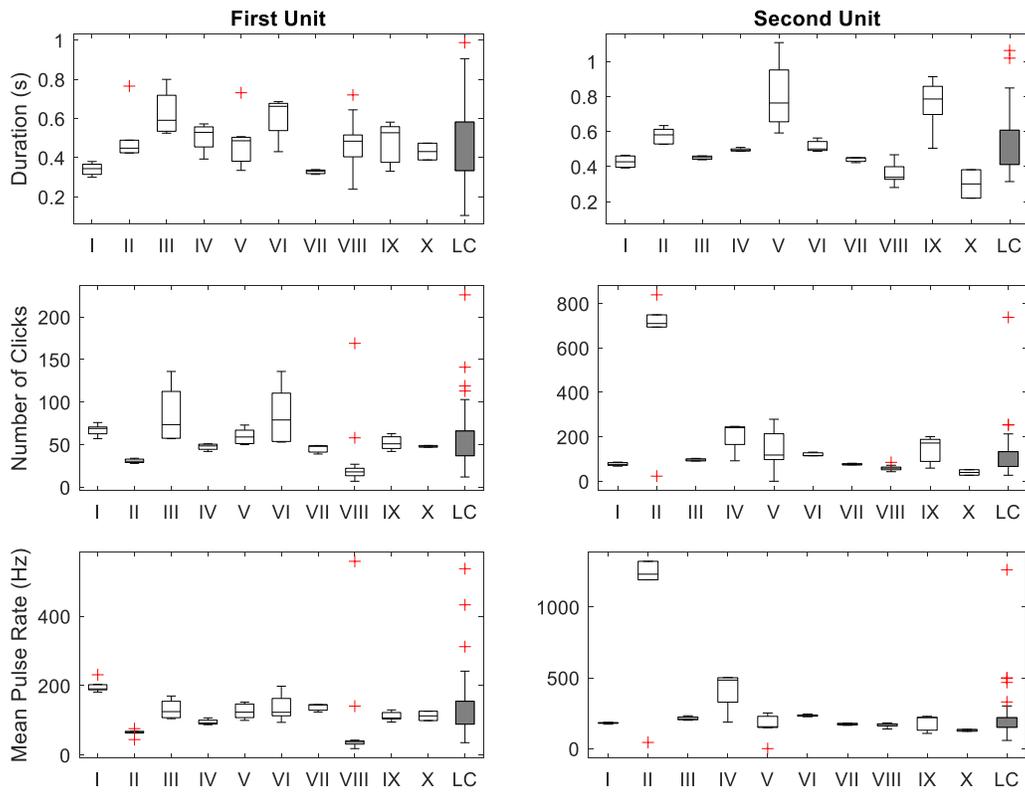
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## Appendices

### Appendix I – Templates of Paired Patterns Used in Visual Classification Task



**Fig. A1**--Templates of patterns of pulsed calls used in visual classification task. Vocalization patterns were recorded using animal-borne hydrophones attached to female *Monodon monoceros* in Tremblay Sound, Nunavut between August 3<sup>rd</sup> and September 11<sup>th</sup>, 2017. All templates are shown with identically calculated spectrograms shown with 80 kHz maximum frequency and 3s duration (FFT length: 4096, window: Hann, overlap: 50%).



**Fig. A2**—Distributions of measured characteristics of stereotyped patterns of pulsed calls produced by *Monodon monoceros* in Tremblay Sound, Nunavut. LC refers to “low-consensus” and includes call patterns that were not classified into a given template, or that were consistently classified as not matching available templates.

## Appendix II – Custom Scripts Used in Analysis

### *Conversion of burst-pulse series recordings into binary representations (Matlab R2017b)*

```
%% Script to transform recordings of burst-pulse series to binary representations
% Author: Sam Walmsley
% July 21, 2018

% starting here, segData is a Struct object where each item has data for a
% single burst-pulse series, including the original sequence ID from which
% it was extracted in the call selection process
for i = (1:size(segData,2)) % loop through selected calls
    segData(i).binaryString = zeros(1,size(segData(i).Call,1)) % pre-allocate 0's
    matching length of call
    spectrogram(segData(i).Call,hanning(1024),903,4096,Fs,'yaxis') % plot call
    g = ginput() % select out segments
    g = g(:,1)
    if g(1)<5 % indicates spectrogram is in seconds
        g = g*Fs
    elseif g(1)>=5 % indicates spectrogram is in milliseconds
        g = g*Fs/1000
    end
    for j = (1:size(g,1)) % loop through manually identified segment boundaries
        if (mod(j,2) ~= 0) % check if number from ginput is odd (indicates start of "on"
portion of segment")
            seg_start = round(g(j));
            seg_end = round(g(j+1));
            segData(i).binaryString(seg_start:seg_end) = 1; % ignore warnings
        end
    end
end
end
% downsample binary strings and make sure them all start on first '1' value
for i = (1:size(segData,2)) % loop through selected calls
    segData(i).DS_binarystring = downsample(segData(i).binaryString,500)
    segData(i).numSegments = sum(diff(segData(i).binaryString)>0); % save number of sub-
units
    call_start = find(diff(segData(i).DS_binarystring)>0,1,'first')+1 % new starting
point (want to trim off outer '0' edges)
    call_end = find(diff(segData(i).DS_binarystring)<0,1,'last') % new ending point
    segData(i).tidyString = segData(i).DS_binarystring(call_start:call_end) % trim off
edges that you don't need
end
% create new array where each row is a binary string of a burst pulse
% series (in order)
blank_array = NaN(length(segData),1300); % maximum length of downsampled calls
for i = (1:size(segData,2))
    for j = 1:length(segData(i).tidyString); % length of fixed up binary strings
        blank_array(i,j) = segData(i).tidyString(j); % each row will be a string
    end
end
end
% VISUAL CHECK: scan plots of all burst-pulse series binary reps.
for i = (1:size(segData,2))
    plotBS = segData(i).tidyString;
    x_series = 1:size(plotBS,2);
    bar(plotBS,'FaceColor',[0.25, 0.25, 0.25],'BarWidth', 1)
    hold on
    bar(-1*plotBS,'FaceColor',[0.25, 0.25, 0.25],'BarWidth', 1)
    ylim([-2 2])
    ax = gca
    ax.Visible = 'off'
    ginput()
```

```

    clf
end
% Export table of downsampled BPS representations for LD modeling in R
my_table = array2table(blank_array)
csvwrite('tableCSV.csv',blank_array)

```

### *Discriminant function analysis of paired calls (R version 3.4.2)*

```

### Script to compute discriminant function analysis on pulsed vocalizations of monodon
monoceros
# Author: Sam Walmsley, sjfw@st-andrews.ac.uk
# August 03, 2018

# call in necessary libraries
library(irr)
library(data.table)
library(MASS)
library(rrcov)

# pull in and prepare dataframe for DFA
DFA_sheet<-data.table(read.csv("LoneUnit_DFA_Sheet.csv",header = TRUE))
DFA_sheet = DFA_sheet[!is.na(Role),,]
# scale and centre predictors
DFA_sheet[,scale_Duration:=scale(Duration,scale=TRUE,center=TRUE),]
DFA_sheet[,scale_First:=scale(First,scale=TRUE,center=TRUE),]
DFA_sheet[,scale_Fourth:=scale(Fourth,scale=TRUE,center=TRUE),]

# run DFA (with cross-validation)
firstUnit_DFA<-lda(Role~scale_Duration + scale_First +
scale_Fourth,data=DFA_sheet,CV=TRUE)
t<- table(DFA_sheet$Role, firstUnit_DFA$class)
diag(prop.table(t, 1))
# total percent correct
sum(diag(prop.table(t)))
# run Wilks test
Wilks.test(Role~scale_Duration+scale_First+scale_Fourth, data=DFA_sheet, method="c")

```

### *Script to model repetition of burst-pulse series using Levenshtein distance (R version 3.4.2)*

```

### Script to Analyze Monodon monoceros burst pulse
# Author: Sam Walmsley, sjfw@st-andrews.ac.uk
# July 21, 2018

# call necessary libraries
library(data.table)
library(irr)
library(MASS)
library(heemod)
library(markovchain)
library(stringdist)
library(R.matlab)
library(h5)

## Setup
# Bring in the data
segmentedFull <-
data.table(read.csv("SegmentedSelectionsMatchtoSegData_20180722.csv",header=TRUE)) # data
frame in same order as matlab
segmentedFull <- segmentedFull[1:212] # trim off extra rows of NA values

```

```

# Call in table of burst-pulse series (each row is a binary string representing the
temporal features of the call)
TidyStrings<-data.table(read.csv("tableCSV.csv",header = FALSE)) # ordered strings from
Matlab
# Merge binary strings from matlab extraction to dataframe
for (i in 1:nrow(segmentedFull)){
  call_string =
paste(as.character((as.numeric(TidyStrings[i,]))[is.finite((as.numeric(TidyStrings[i,]))
)],collapse = ""))
  segmentedFull[i,callString:=call_string,]
}
## Are Sequences of Burst-pulse series Repetitive (i.e. are burst-pulse series produced
in sequence more similar than random chance would suggest?)

# first, add lagged option but only within a sequence
segmentedFull[,lag_callString:=shift(callString),by="SequenceID"]

# Repeated for each individual
# generate data frame with LD values linked to "observed" and "random" transitions for
NW8
segmentedFull_8 = segmentedFull[NarwhalID=="NW08",,]
segmentedFull_8[,lag_callString:=shift(callString),by="SequenceID"]
for (i in 1:nrow(segmentedFull_8)) { # loop through and add lagged call strings to the
dataframe (for true transitions only)
  if (!is.na(segmentedFull_8[i,lag_callString,])) {
    cS = segmentedFull_8[i,callString,]
    l_cS = segmentedFull_8[i,lag_callString,]
    segmentedFull_8[i,transitionDistance:=(adist(cS,l_cS)),]
  }
}
segmentedFull_8[!is.na(lag_callString),.N,] # number of true transitions
mean(segmentedFull_8$transitionDistance,na.rm = TRUE) # mean LD of true transitions
# now make a randomly ordered segmentedFull_8 and calculate first X transitions (same
number as previous)
random_segmentedFull_8 = segmentedFull_8[sample(nrow(segmentedFull_8),
nrow(segmentedFull_8)), ]
# delete previous columns related to transition calculations
random_segmentedFull_8[, c("lag_callString","transitionDistance"):=NULL,]
random_segmentedFull_8[1:57,lag_callString:=shift(callString)] # range is 1+ number of
true transitions in ordered dataset
for (i in 1:nrow(random_segmentedFull_8)) { # loop to add (random) transition distances
  if (!is.na(random_segmentedFull_8[i,lag_callString,])) {
    cS = random_segmentedFull_8[i,callString,]
    l_cS = random_segmentedFull_8[i,lag_callString,]
    random_segmentedFull_8[i,transitionDistance:=(adist(cS,l_cS)),]
  }
}
segmentedFull_8[!is.na(lag_callString),TrueTrans:='Y',]
random_segmentedFull_8[,TrueTrans:='N']
# bind observed and random transition dataframes together
NW8_dframe<-
rbindlist(list(segmentedFull_8,random_segmentedFull_8),use.names=TRUE,fill=TRUE)
NW8_dframe[, TrueTrans:=as.factor(TrueTrans),]

# Statistical Analysis
Full_dframe<-rbindlist(list(NW8_dframe,NW12_dframe),use.names=TRUE,fill=TRUE) # create
dataframe from consitent recording dataframes
hist(Full_dframe$transitionDistance) # examine distribution of response variable
Full_model<-glm(transitionDistance~TrueTrans,data=Full_dframe,family=poisson()) # fit
Poisson model
summary(Full_model)
plot(allEffects(Full_model))

```

```
quasi_Full_model<-glm(transitionDistance~TrueTrans,data=Full_dframe,family=quasipoisson)
# fit quasipoisson model to assess overdispersion
summary(quasi_Full_model)
plot(allEffects(quasi_Full_model))
```

### *Script to model relationships between sequence usage and acoustic context (R version 3.4.2)*

```
### Script to model relationships between Monodon monoceros call sequences and acoustic
indicators of behavior
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# call required packages
library(data.table)
library(rsq)
library(MASS)

## Paired Patterns

# Model relating "Patterns of Pulsed Calls" to Previous behaviour
context<-data.table(read.csv("Context_Sheet.csv",header = TRUE))
context[, Repeat.Number:=as.numeric(as.character(Repeat.Number)),]
context[, logCalls:=log10(Calls_P60+1),] # log transforming raw vocalization counts
context_model <-
glm(Pattern~logCalls+Surfacing_P60+Buzzes_P60,data=context,family=binomial())
summary(context_model)
plot(context_model) # diagnostics
# fit a quasibinomial model to check for overdispersion
quasi_context_model <-
glm(Pattern~Calls_P60+Surfacing_P60+Buzzes_P60,data=context,family=quasibinomial())
summary(quasi_context_model)
# Model relating "Patterns of Pulsed Calls" to Subsequent behaviour
follow<-data.table(read.csv("Follow_Sheet_2.csv",header = TRUE))
follow[, Surfacing0:=as.factor(ifelse(Surfacing=="Y",1,0)),]
follow[, Pattern:=as.factor(Pattern),]
follow[, logCalls:=log10(Calls+1),]
follow_model <-
glm(Pattern~logCalls+Surfacing0+Buzzes.or.Buzz_Clicks,data=follow,family=binomial())
summary(follow_model)
plot(follow_model) # diagnostics
# fit a quasibinomial model to check for overdispersion
quasi_follow_model <-
glm(Pattern~Calls+Surfacing0+Buzzes.or.Buzz_Clicks,data=follow,family=quasibinomial())
summary(quasi_follow_model)
# Model relating "Patterns of Pulsed Calls" to Preceding noise levels
context_PatternOnly = context[Pattern=="1",]
context_PatternOnly[, Noise5DB:=20*log10(Noise5),]
noise_model <-
glm(Repeat.Number~Noise5DB,data=context_PatternOnly,family=poisson(link="log"))
summary(noise_model)
plot(noise_model) # diagnostics
Dsquared(noise_model)
# fit a quasipoisson model to check for overdispersion
quasi_noise_model <-
glm(Repeat.Number~Noise5DB,data=context_PatternOnly,family=quasipoisson)
summary(quasi_noise_model)

## Sequences of Burst-pulse series
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# Model relating "Sequences of Burst-pulse series" to Previous behaviour
segContext<-data.table(read.csv("Seg_ContextSheet.csv",header = TRUE))
segContext[,Calls:=Calls_P60,]
segContext[, Pattern:=ifelse(Pattern=="Y",1,0),]
segContext[,logCalls:=log10(Calls+1),]
seg_context_model <-
glm(Pattern~logCalls+Surfacing_P60+Buzzes_P60,data=segContext,family=binomial())
summary(seg_context_model)
plot(seg_context_model) # diagnostics
# fit a quasibinomial model to check for overdispersion
quasi_seg_context_model <-
glm(Pattern~Calls+Surfacing_P60+Buzzes_P60,data=segContext,family=quasibinomial)
summary(quasi_seg_context_model)
# Model relating "Sequences of Burst-pulse series" to Subsequent behaviour
segFollow<-data.table(read.csv("Seg_FollowSheet.csv",header = TRUE))
segFollow[,logCalls:=log10(Calls+1),]
seg_follow_model <-
glm(Pattern~logCalls+Surfacing+Buzzes.or.Buzz_Clicks,data=segFollow,family=binomial())
summary(seg_follow_model)
plot(seg_follow_model) # diagnostics
# fit a quasibinomial model to check for overdispersion
quasi_seg_follow_model <-
glm(Pattern~Calls+Surfacing+Buzzes.or.Buzz_Clicks,data=segFollow,family=quasibinomial())
summary(quasi_seg_follow_model)
# Model relating "Sequences of Burst-pulse series" to Preceding noise levels
seg_context_PatternOnly = segContext[Pattern=="Y",,]
seg_context_PatternOnly[, Noise5DB:=20*log10(Noise5),] # convert to decibel scale
seg_noise_model <-
glm(Repeat.Number~Noise5DB,data=seg_context_PatternOnly,family=poisson(link="log"))
summary(seg_noise_model)
plot(seg_follow_model) # diagnostics
# fit a quasipoisson model to check for overdispersion
quasi_seg_noise_model <-
glm(Repeat.Number~Noise5DB,data=seg_context_PatternOnly,family=quasipoisson())
summary(quasi_seg_noise_model)

```

## Supplement – Inter-unit intervals for narwhal vocal sequences

### *Paired patterns*

<b>A → B intervals (between A and B within each pair)</b>		
Type	mean interval duration (between A & B) in seconds	SD of interval duration (between A & B) in seconds
I	0.751	0.118
II	0.931	0.147
III	0.181	0.068
IV	0.390	0.126
V	0.192	0.054
VI	0.228	0.082
VII	0.453	0.058
VIII	0.294	0.110
IX	0.335	0.051
X	0.335	0.075
All types	0.403	0.254

<b>B → A intervals (between adjacent A-B pairs)</b>		
Type	mean B to A interval duration in seconds	SD of B to A interval duration in seconds
I	3.733	1.095
II	10.223	7.056
III	2.001	0.482
IV	1.834	0.147
V	10.16	5.655
VI	6.398	4.932
VII	2.524	0.443
VIII	4.195	4.046
IX	3.167	2.292
X	5.402	1.204
All types	4.843	4.236

<b>Lone A units produced in sequence</b>		
Type	mean interval duration (between A's) in seconds	SD of interval duration (between A's) in seconds
II	5.222	1.351
IX	2.611	0.367
Both types	3.264	1.351

### *Burst pulse series*

<b>Burst pulse series produced in sequence</b>		
Measurement	mean	SD
Inter-sub-unit interval (seconds)	0.105	0.047
Inter-burst-pulse-series interval (seconds)	3.579	2.564



13 March

<b>Project Title:</b>	Individual-specific vocalizations in Narwhals
<b>Researchers Name(s):</b>	Luke Rendell and Sam Walmsley
<b>Supervisor(s):</b>	Dr Luke Rendell
<b>Biology SEC Ref:</b>	SEC18006

Thank you for submitting your application which was considered by the Biology School Ethics Committee on the 13 March. The following documents were reviewed:

1. Animal Ethics Form 14/02/2018

The School of Biology Ethics Committee approves this study from an ethical point of view.

Approval is given for five years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the five year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the condition that local permits are obtained prior to the project starting, and also on the understanding that the [ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching published in Animal Behaviour, 2003, 65, 249-255, are adhered to.](#)

Yours sincerely,

Convenor of the School Ethics Committee

Ccs School Ethics Committee  
Dr Tamara Lawson (Home Office Liaison Officer)

