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Progression in humpback whale song structure and complexity on a subarctic feeding ground in Northern Norway

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Cover image: Spectrographic view of a humpback whale song (a phrase) recorded by LoVe Ocean Observatory, Norway, in March 2018 (background) with a humpback whale illustration by S.C. Martin (overlay).

Preface

This thesis has been written as a manuscript for submission to the journal *Frontiers in Marine Science*, where parts on Humpback whale song occurrence were published recently (see Martin et al. [2021]. Humpback Whale (*Megaptera novaeangliae*) Song on a Subarctic Feeding Ground). Therefore, this manuscript has been prepared according to the journal's guidelines. For better visualisation of the data, the figures and their captions were held together.

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Abstract

Male humpback whales (*Megaptera novaeangliae*) sing structurally complex songs traditionally associated with low latitude breeding grounds. This vocal behaviour is increasingly reported outside these areas. All singers in a given population sing the same version of a song that is constantly evolving with modifications on different levels within the song structure. This study provides the first detailed analysis of humpback whale songs recorded on a subarctic feeding ground in Northern Norway. Passive acoustic data from the Lofoten-Vesterålen Ocean Observatory were collected using bottom-moored underwater hydrophone and included the months January – June 2018 and December 2018 – January 2019. Two measures of the song structure were examined: (1) sequence similarities using the Levenshtein distance and (2) song complexity. More than 440 hours of recordings spread over 199 days were inspected for humpback whale song occurrence using a semi-automated approach. Overall, 750 hours of humpback whale singing activity was detected spanning 79 days between December and April. The first singing activity was detected beginning of January 2018, followed by a peak in February and was heard until mid-April. No song was found during the summer months and was detected again in December 2018, continuing over January 2019. Song structure analyses resulted in a total of 18 distinct themes; 11 themes in 2018 and 7 themes in 2019. The themes clustered into two song types, one for each year, suggesting an event of rapid song progression. As all sampled animals were singing the same version of the song within each year, this might indicate that the singers are either from the same breeding population or that song conformation was performed before the study period. Song complexity increased as songs evolved over the months in 2018 and decreased drastically between the years 2018 and 2019. The results confirm that humpback whale song can be heard over multiple months and years in Northern Norway. Finally, this study identified song progression on a shared subarctic feeding ground, indicating potential song exchange between the North Atlantic humpback whale populations already before reaching their breeding grounds. Tracing changes in whale song will help to uncover the drivers underlying this vocal display and contribute to the understanding of animal culture and its evolution.

Keywords: passive acoustics, PAM, singing, *Megaptera novaeangliae*, North Atlantic

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1 Introduction

Communicative behaviour among animals has been studied extensively for numerous taxa such as birds, bees, primates, and cetaceans (Laland and Janik, 2006; Tomecek, 2009; Whiten et al., 2017). Animal communication is very diverse in its forms and mechanisms (Bradbury and Vehrencamp, 2011) and can be divided into four types of signals: visual, auditory, tactile, or chemical (Deverell, 2003; Forrester, 2008). Within the auditory modalities, one way to send information is through vocalisation (sounds produced through respiratory system). Vocal communication serves many key functions including species identification, reproductive status and/or mate attraction, territorial defence, predator alert or conveying location of food source (Deverell, 2003; Tomecek, 2009). A broad range of animals communicate by means of vocal sound production and in various species males are known to perform specific vocalisations during mating rituals, such as singing in many avian species (Kroodsma, 2004). Singing behaviour and the production of complex songs is rare among mammals. Such vocal behaviour has only been documented for a few mammalian species, including bats (Chiroptera; Bradbury and Emmons, 1974; Davidson and Wilkinson, 2004), gibbons (Hylobatidae; Mitani, 1988; Cowlshaw, 1992), mice (Baiomyine; Holy and Guo, 2005; Miller and Engstrom, 2007), and cetacean species (Cetacea; Payne and McVay, 1971; Stafford et al., 2001, 2018; Delarue et al., 2009). Within cetaceans, this vocal display appears to be restricted to baleen whales and ranges in complexity from a few repetitive sound types produced by fin whales (*Balaenoptera physalus*; Delarue et al., 2009) and blue whales (*Balaenoptera musculus*; Stafford et al., 2001) to more complex songs of bowhead (*Balaena mysticetus*; Stafford et al., 2018) and humpback whales (*Megaptera novaeangliae*; Payne and McVay, 1971). When features of a behaviour such as vocalisations are socially learned through conspecifics, it represents a form of vocal learning also called cultural transmission (Slater, 1986). This process whereby cultural traits are passed on between individuals has also been documented for many cetacean species, both toothed and baleen whales. For example, killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) use group-specific vocalisations which are maintained through cultural transmission (Rendell and Whitehead, 2003; Deecke et al., 2010). In general, it seems that baleen whales use vocal learning in song displays that are involved in sexual selection, whereas toothed whales use learned signals in individual recognition and maintaining social relationships (Janik, 2014).

The rich acoustic display by humpback whales is well-known and typically divided into two categories: ‘singing’ (Payne and McVay, 1971) and ‘social sounds’ or ‘non-song’ (Payne, 1978; Silber, 1986). These vocalisation types typically range from 20 Hz up to 24 kHz including harmonics (Frankel, 2009), with fundamental frequency signals greater than 10 kHz (Cerchio et al., 2001). Humpback whale songs are rhythmic with a highly repetitive pattern (Payne and McVay, 1971), whereas social sounds lack this complex structure and are discrete sounds that vary through time and include surface generated signals such as breaching (Dunlop et al., 2007). While social sounds are produced by both males and females (Silber, 1986), only humpback whale males have been observed to sing (Payne and McVay, 1971; Cerchio et al., 2001; Cholewiak, 2008; Smith et al., 2008). Singing behaviour by male humpback whales is considered to play a role in sexual selection, although its specific function as a signal is still debated (Herman, 2016). Several behavioural studies support an inter- and intrasexual purpose such as to attract a mate and/or facilitate male to male interactions (e.g., Darling and Bérubé, 2001; Darling et al., 2006; Cholewiak, 2008; Smith et al., 2008), indicating that song may be a multi-message display (Murray et al., 2018). Additionally, variation in sound types within the song has been suggested to have a communicative function in terms of conveying information about individual identity (Hafner et al., 1979) or it may reveal a singer’s reproductive fitness to other whales (e.g., Chu, 1988; Payne, 2000; Parsons et al., 2008; Herman, 2016).

The humpback whale song has a complex structure due to a nested hierarchy with multiple levels of acoustically distinct ‘units’ arranged into ‘phrases’ which form a ‘theme’ (Payne and McVay, 1971; Cholewiak et al., 2013). The song of male humpback whales is a well-studied behaviour and passed among individuals by cultural transmission (Guinee et al., 1983; Payne and Guinee, 1983; Payne and Payne, 1985; Noad et al., 2000; Cerchio et al., 2001; Garland et al., 2011). Cavalli-Sforza and Feldman (1981) distinguished between three broad categories of cultural transmission in humans: vertical (directly from parent to offspring), obliquely (from parents and additional individuals from previous generations to offspring), and horizontal (among unrelated individuals of the same generational cohort). In humpback whales, song has been recognised to undergo horizontal transmission which appears to play an important role in maintaining song homogeneity (Rendell and Whitehead, 2001). Populations within the same ocean basin display a high degree of song sharing (Payne and Guinee, 1983; Helweg et al., 1990, 1998; Cerchio et al., 2001). For example, song of Pacific humpback whales has been documented to be horizontally transmitted in an eastward manner from eastern Australia to French Polynesia (Garland et al., 2011, 2013b; Schulze, 2021). Although all males

within a population typically conform to the same version of the song at any given time with some inter-individual variation, the song undergoes constant progressive change within and between years (Payne and McVay, 1971; Frumhoff, 1983; Payne et al., 1983; Payne and Payne, 1985), a process referred to as ‘cultural evolution’ (Winn and Winn, 1978; Payne et al., 1983; Payne and Payne, 1985; Cato, 1991; Noad et al., 2000). By modifying spectral and temporal features of song elements (units, phrases, and themes), individual whales create a gradually evolving song structure that all males within a population maintain by incorporating changes as they occur (Payne and McVay, 1971; Guinee et al., 1983; Payne et al., 1983). When an existing song is rapidly and completely replaced by a novel version (i.e., the songs do not share any themes or phrases), typically introduced from neighbouring a population, is a process described as ‘song revolution’ (Noad et al., 2000; Garland et al., 2011; Allen et al., 2018). A recent study by Allen et al. (2018) has revealed a pattern in which humpback songs increased in complexity as they evolved through progressive changes but became more simplified following events of song revolution. The authors suggested that more complex songs favour individuality as found in songbirds. With songs becoming more complex, e.g., longer by containing more units, they also become more unique in order to stand out (Noad, 2002).

It has been proposed that song transfer between male humpback whales happens when individuals are in acoustic contact along the migratory cycle i.e., when different breeding populations geographically overlap on a shared feeding ground (Payne and Guinee, 1983). Humpbacks typically undertake extensive annual migrations (ca. 10,000 km) between high latitude feeding grounds and low latitude breeding areas (Dawbin, 1966), representing a cultural tradition of this species (Baker et al., 1990). Traditional feeding grounds in the north-east Atlantic, stretch from subarctic waters of Iceland, Jan Mayen, Greenland, and Northern Norway to the Barents Sea (Stevick et al., 2006). Although the conformity to the migratory behaviour has been widely accepted, it appears to vary by individuals (Magnúsdóttir and Lim, 2019). Some studies proposed humpbacks to overwinter on feeding grounds (Van Opzeeland et al., 2013; Magnúsdóttir et al., 2015) and have shown that the sex, age, reproductive status of an individual and the location of a feeding ground can affect the timing of migration (Craig et al., 2003; Stevick et al., 2003). Telemetry and photo-ID studies have demonstrated that Norwegian fjords represent an important stopover in the southbound migration for humpback whales (Kettmer et al., 2019; Ramm, 2020). This migration route and feeding ground off Norway’s coast has shown to be shared with an interchange of different humpback breeding populations from Cape Verde (Africa) and the West Indies (America; Bérubé et al., 2004; Stevick et al.,

2016, 2018; Whaletrack UiT, 2018; Wenzel et al., 2020). With humpback whale singing traditionally been associated with low latitude breeding grounds, high-latitude song was considered relatively uncommon, but is increasingly reported outside the breeding season and areas, in both the southern and northern hemisphere (e.g., Garland et al., 2013a; Gridley et al., 2018; Ryan et al., 2019). In the North Atlantic, humpback song was detected on multiple high and mid-latitude feeding grounds during all seasons (Mattila et al., 1987; Clark and Clapham, 2004; Vu et al., 2012; Magnúsdóttir et al., 2014). Furthermore, humpback whale song in north-east Iceland has been identified to exhibit gradual progression over three winter seasons (Magnúsdóttir and Lim, 2019). Acoustic data recently collected by glider off Northern Norway's coast has shown extensive humpback whale vocal activity in this area during the winter months (Aniceto et al., 2020). Telemetry studies from Barents Sea and Northern Norway have demonstrated that some humpback whales pass through Icelandic waters during their migration (Whaletrack UiT, 2018; L. Kettmer, person. comm., January 22, 2021), enabling possible song exchange and cultural transmission between humpback whale populations within the North Atlantic.

The aim of this study was to (1) identify humpback whale song occurrence in Northern Norway, (2) qualitatively describe the song structure, and (3) compare songs, their contents, and complexity quantitatively over a temporal scale. This work will give an important contribution to our understanding of the features of the Norwegian humpback whale song and help to elucidate the importance of feeding grounds for song exchange at high latitudes within the North Atlantic. Furthermore, quantifying song changes and complexity in humpback whales can provide essential insights into song dynamics and aid our understanding of the vocal and social learning capacity in this species.

2 Materials and Methods

2.1 Study area and data collection

The Lofoten-Vesterålen (LoVe) Ocean Observatory is a cabled network located in an ecological hotspot about 20 km offshore forming a westward transect over a shelf-slope area (**Figure 1**). Node 1 (N68°54', E14°23', 257 m depth) includes an instrument platform which holds a hydrophone (Ocean Sonics SB35 ETH, 10 Hz–64 kHz) that continuously records biologically generated sounds and underwater noise within the area (Godø et al., 2014). The present study is based on the analysis of passive acoustic data collected from Node 1 between January 2018 and January 2019. Audio files were retrieved using the LoVe Ocean archive (Equinor and IMR, 2020), where continuous recordings are stored as adjacent 10-minute files with occasional gaps due to technical maintenance. The available data was processed using a combination of automated and manual methods.

2.2 Semi-automated song detection

To identify humpback whale vocal activity in the continuous recordings, long-term spectral averages (LTSAs) were generated using PamGuard (version 2.01.04 beta) for every month with available data. LTSAs visualise acoustic activity in recordings of extended periods of time and provide an efficient method to evaluate large acoustic data sets, visualising acoustic activity across a wide range of frequencies (Wiggins and Hildebrand, 2007). With every LTSA, PamGuard's Whistle and Moan detector (WMD) was simultaneously applied in order to detect humpback whale vocalisations (Gillespie et al., 2009, 2013). The following parameters were used: frequencies of 120–15,000 Hz, fast Fourier transform (FFT) size 4096, 50% overlap, Hann Window, detection threshold 8dB, remaining parameters as default. Running both an LTSA and WMD reduced the likelihood of false positives and false negatives by manually assessing those, while identifying humpback whale vocal occurrence (see **Figure A1** in Appendix A). Areas identified by the LTSA and WMD were manually examined using spectrographic views in Raven Pro 1.6 (Yang Center for Conservation Bioacoustics, 2019; FFT size 8092, Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap). These detections were thoroughly inspected by means of visual and auditory perceptual characteristics, determining the start and end time of vocalisations along with vocal categories (song or non-song), and the quality of the recording between excellent (1), good (2), medium

(2-3) and bad (4). The latter was assessed manually; the signal-to-noise ratio (SNR) was not used as recording quality can change within a song cycle and it is impractical to quantify the SNR for all units/sounds (Hawkey, 2020), which can range up to 400 units per song (Suzuki et al., 2006). Whenever an overall excellent song file showed parts of lower quality within a song, the noise reduction effect (12dB, sensitivity 6, frequency smoothing bands 3) in Audacity (version 2.4.2) was used. Song occurrence was classified using all files containing song, regardless of quality, and was used to calculate the percentage of files per day containing singing activity. A song was defined by a rhythmic context of units with a consistent pattern and randomly occurring sounds were considered non-song (Dunlop et al., 2008). Additionally, the number of chorusing singers was estimated by means of overlapping song elements (units and phrases) as applied by previous studies (Payne and Payne, 1985; Magnúsdóttir et al., 2015; Magnúsdóttir and Lim, 2019).

2.3 Sequence transcription

Data containing high-quality song, i.e., category 1 and 2, were transcribed for sequences of song elements (**Figure 2**), following the hierarchical structure first described by Payne and McVay (1971). A ‘unit’ is defined as the shortest basic element, a continuous sound to the human ear if played at normal speed. Some units can be divided into ‘subunits’, composed of a series of short pulses that are not distinguishable at real speed (Payne and McVay, 1971; Cholewiak et al., 2013). Every visually and aurally distinguishable sound (i.e., units and subunits) was transcribed for all songs included in the analysis. Units and subunits were labelled with a number and a name based on their acoustic characteristics including the slope and duration (e.g., short ascending moan, abbreviated ‘8-sam’) as in previous studies (Dunlop et al., 2007; Garland et al., 2017). A sequence of one or more units were grouped into a ‘subphrase’ and multiple subphrases formed a ‘phrase’ (Payne and McVay, 1971). One or more phrases repeated in succession were assigned to a ‘theme’. Phrase repetitions within a theme usually have similar subphrase types in common. A combination of distinct themes joined in a predictable sequence then makes up a ‘song’, which is then again repeated multiple times as ‘song cycles’ to form a ‘song session’ (Payne and McVay, 1971; Cholewiak et al., 2013).

The delineation of phrases, and hence themes, can be highly subjective, as emphasized by several studies (e.g., Cholewiak et al., 2013; Mercado, 2021). Therefore, the guidelines for

delineating and measuring phrases suggested by Cholewiak and colleagues were adopted in this study (see: Cholewiak et al. [2013] for a guideline description). Successive phrases within a theme are “inexact replicas” (Payne and McVay, 1971) and may change in the number of units, as well as spectral and/or temporal characteristics of units. Therefore, a small amount of variation was permitted in (sub-) units used within phrases. Phrases were considered as part of the same theme when acoustically similar units (e.g., ‘short ascending moan’ and ‘wail moan’) occurred in the same position in the phrase (Helweg et al., 1998; Garland et al., 2012). On some occasions, so-called ‘transitional phrases’ were sung between themes, which are combinations of units or subphrases of the two adjacent themes (Payne and Payne, 1985). This could either be combined subphrases or units combining characteristics of some units in the two adjacent themes (Frumhoff, 1983; Cholewiak et al., 2013). In the present study, transitional phrases were delineated as such and excluded from the analysis. Themes and associated phrases found during song transcription were labelled with numbers and new versions included letters (e.g., 2a) as used in previous humpback whale song studies (Garland et al., 2013b, 2015, 2017; Owen et al., 2019).

With song sessions usually sung in a continuous bout (Winn and Winn, 1978) with arbitrary choice of a starting theme (Cholewiak et al., 2013), determining the start and end of song cycles can be difficult. Following the definition by Frumhoff (1983), a song is a theme sequence that consists of not less than three themes which are repeated in the same order at least twice. In the present study, a song was defined as a complete cycle of themes with no repetition of a theme (Payne and Payne, 1985). Consider the following example of a theme sequence where the hyphen stands for a short break and thus marking the start and end of a song cycle:

...134-1234-12345-1234-123...

The order of themes throughout all song sessions included in the analyses were invariant, meaning that e.g., theme 1 was always followed by theme 2. And although some themes were dropped in some song cycles, the starting theme in the example above consistently appears to be theme 1. Thus, a song cycle in the present study was not delineated based on a complete rendition of all themes but by the consistency of breaks followed by a specific theme. Different types of themes have been described in the literature: ‘static’, ‘shifting’, and ‘unpatterned’ (Payne and Payne, 1985). The authors described static themes to be composed of a sequence of nearly identical phrases. A theme that shows progressive changes over multiple phrase

repetitions is called a shifting theme whereas unpatterned themes are identified by an inconsistent number of units without a clear structure of phrase repetitions, resulting in a single, long phrase (Payne and Payne, 1985; Cholewiak et al., 2013). To allow for comparability across a temporal scale, a consistent number of songs per month with available data were transcribed for sequences of units, phrases, and themes. A total of 15 song sessions with 3 song cycles each were used for song analysis, resulting in 45 song cycles between January 2018 and January 2019 (**Table 1**).

2.4 Validation of classification consistency

To validate the consistency of the qualitative unit classification, a random forest analysis was carried out (Warren et al., 2020). Random forest is a machine learning algorithm that consists of an ensemble of decision trees from a randomly selected subset of data and an effective tool in prediction (Breiman, 2001). This quantitative test assesses the manual classification of humpback whale units as outlined by Allen et al. (2017) and Garland et al. (2017). All units of each present phrase type labelled during song transcription were measured for various acoustic parameters following Dunlop et al. (2007) and Garland et al. (2017). Additionally, units that solely occurred in transitional phrases or only once within the entire dataset were also measured at least once. Using Raven Pro (version 1.6; Center for Conservation Bioacoustics, 2019) with a FFT size of 8092, Hann-window frequency resolution of 5.69 Hz and a 70% overlap, the following parameters were calculated per unit: duration, high and low frequency, bandwidth, frequency range, start and end frequency, peak frequency, and number of inflections (see **Table A1** in Appendix A for parameter descriptions). The random forest analysis was conducted in R (version 4.0.4; R Core Team, 2021) using the ‘randomForest’ function (Liaw and Wiener, 2002). The assigned unit name was used as the dependent variable (mtry=1, ntrees=1000) and the random forest model then classified each unit based on the measured parameters. This resulted in a confusion matrix, representing the number of times where the predicted label matches the true label i.e., when a unit was classified correctly or was mislabelled. The model also outputs an out-of-bag (OOB) error rate, measuring the prediction error, and indicating the overall level of agreement between the classifications.

2.5 Analysis of sequence similarities

The stereotyped structure of humpback whale song with its nested hierarchy of units, phrases, and themes allows for a quantitative measure using common sequence analysis metrics. The Levenshtein distance (LD) is a robust and powerful edit distance technique that provides information of similarities between vocal sequences (Levenshtein, 1966). This method has previously been applied to investigate humpback whale song evolution through time and/or among populations (e.g., Garland et al., 2012). Following the definition by Kohonen (1985), the LD calculates the minimum number of changes (substitutions, insertions, or deletions) needed in order to convert one string into another, and is described by:

$$LD(a,b) = \min \{ s + i + d \}$$

where sequence (b) is obtained from sequence (a) by the minimum number of substitutions (s), insertions (i), and deletions (d). For example, consider the two sequences:

Sequence A: a b c d e f

Sequence B: a c d e f g h

The LD between sequence A and sequence B is three, since there are at least three changes required to turn sequence A into sequence B: one deletion of 'b', and two insertions, one 'g' and one 'h'.

There are two types of LD analyses: weighted and unweighted (Kohonen, 1985). The example above represents the unweighted LD where each change equals one regardless of the type of transition (any substitution, insertion, or deletion = 1). The weighted LD alters the relative penalties (e.g., weights scaled between 0 and 1) of the changes based on the acoustic feature similarity between pairs (e.g., of units). This study computed unweighted distances and did not explore the use of weighted LD, as for small data sets such as for whale song, the simple, unweighted LD method has been suggested to be more appropriate (Tougaard and Eriksen, 2006).

To ensure direct comparability of sequences, the LD score needed to be standardised to allow for multiple pairwise comparisons. This was done by dividing the result of the LD by the

length of the longest sequence, resulting in the Levenshtein Distance Similarity Index (LSI) at a set level (Helweg et al., 1998; Eriksen et al., 2005; Tougaard and Eriksen, 2006; Garland et al., 2012, 2013b, 2015). Thus, the LSI was computed as follows:

$$\mathbf{LSI}(a, b) = 1 - \text{LD}(a, b) / \max(\text{len}(a), \text{len}(b))$$

where the LD of sequence (a) and sequence (b) is divided by the sequence with the maximum length (len). The LSI then produces a matrix with similarity scores (between 0 and 1), representing proportions of similarity between any pair of sequences (0=no similarity, 1=complete similarity). To allow for evaluation of song sequence progression throughout the study period, a representative string, also called a set median (SM), was calculated. The SM is the sequence with the smallest summed LD to all other sequences within a set, and consequently the one with the highest overall similarity to all other sequences. Comparisons of sequences were carried out on two levels of song hierarchy, with similarities analysed between:

- (1) songs, where the string was a sequence of themes
- (2) themes, where the string was comprised of units (phrase)

Song-level analysis enables the identification of different song types within the same area and between periods, whereas fine-scale similarities within and between each song can only be detected using the theme-level, represented by different phrase types. Phrase-based analyses have been described to be most appropriate within humpback whale song, with the duration of phrases being one of the most stable features within the hierarchical structure of the song (Frumhoff, 1983; Payne et al., 1983; Cerchio et al., 2001; Cholewiak et al., 2013). Therefore, themes were represented by a SM which was made up by one phrase and not the entire sequence of all phrase repetitions within a theme (Payne and McVay, 1971). The LSI was also used to assess the qualitative assignments of phrases to a theme and calculated between every phrase (i.e., sequence of units) across the entire dataset, regardless of recording period. Comparisons of songs were carried out by condensing the data using set medians per song session to evaluate and display song progression over time. All distance analyses were calculated in R (version 4.0.4; R Core Team, 2021) using the package ‘leven’ (a custom written code, available at <http://github.com/ellengarland/leven>, by Garland and Lilley [2020]). Similarities between songs and themes were calculated by comparing all median strings to another using the ‘compare_songs’ function. Additionally, the results of all LSI similarity matrices were

hierarchically clustered to visualise connections among sequences in dendrograms using the functions ‘hclust’, ‘pvclust’ and ‘pvrect’ (Suzuki and Shimodaira, 2006). The appropriate clustering method for the data was determined by comparing the cophenetic correlation coefficient (CCC) between dendrograms with average and single linkage (value >0.8 is considered high; Sokal and Rohlf, 1962). In order to assess the stability of the resulting clusters from the similarity matrix, each matrix was also bootstrapped (1000 times) using multi-scale resampling which generated approximately unbiased (AU) values and normal bootstrap probabilities (BP; Garland et al., 2017; Rekdahl et al., 2018). Tree structures were considered stable and strongly supported by the data with $AU > 0.95$ and $BP > 0.70$ (Suzuki and Shimodaira, 2006; Garland et al., 2012), whereas lower values indicate variability in their division. Applying the described methods above allows to evaluate the song progression on both upper (song) and lower (theme) levels within the nested humpback whale song structure.

2.6 Song complexity analysis

The complexity of all transcribed songs was assessed using scores generated on the song-level (sequence of units) as previously performed by Allen et al. (2018), based on Boogert et al. (2008) and Templeton et al. (2014). The content of song complexity comprised the entire sequence of units, irrespective of phrases and themes, where three variables were used per song cycle: number of units, number of unit types, and the duration of each cycle. To represent the data of the multiple dimensions within the song, a principal component analysis (PCA) was computed using the function ‘princomp’ in R (version 4.0.4; R Core Team, 2021) including all variables for each level. A PCA allows to summarise the information content of large datasets and consequently to increase the interpretability, while preserving as much information as possible (Jolliffe, 2002). The first principal component scores (PC1) were used as the measure of song complexity, representing relative rather than absolute values giving an indication whether a song is simple or complex in relation to another. Factor loadings were investigated to determine correlations between each variable and the respective principal component. To allow the PC1 scores to represent a measure of complexity, all variables must follow the same direction (i.e., all positive or all negative).

3 Results

3.1 Singing activity

The song occurrence analysis included a total of more than 4400 hours of recordings spread over 199 days between January – June 2018 and December 2018 – January 2019 (**Table 2**). Overall, 750 hours with humpback whale singing activity was revealed by the semi-automated song detection, spanning 39% of all recording days in winter and spring between December and April (**Table 2; Figure 3**). The first humpback whale song was detected on the 3rd of January 2018, the month with the lowest singing activity in 2018. On 12 out of 29 recording days (41%) humpbacks were singing for a total of 38 of 682 hours (6%) with recordings. In February, humpback whale singing activity peaked with song detected on 15 out of 16 days with recordings, spanning 253 hours, representing 66% of all recording hours (253/384 hours). Song occurrence then decreased over March and April, with humpbacks singing for a total of 224 hours (32%) and 172 hours (27%), respectively. No song was found in May or June and no acoustic data was recorded by the hydrophone Node 1 from mid-June up to mid-December. With data collection starting again on the 10th of December, more humpback whale song was detected, which continued until the end of January 2019 with no more data added to the analysis. December resulted in a total of 22 hours of song, spanning 5 days, presenting the month with the lowest activity throughout the study period. Although January 2019 showed a slight increase in humpback singing activity (41 hours) compared to December 2018, song was only detected on 6% (41/644 hours) of all recording hours, similarly to January and December 2018.

On several occasions between February and April, singing activity lasted for more than 22 hours within one day, whereas one recording day in April multiple whales were singing for 24 hours and even beyond. In total, 131 song sessions were identified throughout the study period, with highest numbers of more than 30 sessions found in February and March (**Table 2**). Due to the continuous nature of the acoustic data, it was possible to identify full song sessions (including start and end time). Throughout all months with detected singing activity, a total of 35 complete song sessions were identified. Low numbers of full song sessions were most likely a result of poor-quality recordings (whales out of range or due to anthropogenic noise) and/or too few data to determine precise start and end times in a meaningful measure. The durations of identified complete song sessions ranged from 13 minutes in January 2019 to >13 hours (815

minutes) in April 2018. Throughout 79 days of detected humpback song, multiple whales were found singing in a chorus, with peaks of more than four individuals singing at the same time. Solo singers were generally found to predominate throughout the study period (65%) whereas multiple singers were detected during 35% of all song sessions. Similar ratios were found for full song sessions, with 63% sung by single whales and 37% chorusing.

3.2 Theme structure and similarity

Songs recorded on the subarctic feeding ground in Norway displayed the typical hierarchical structure of different themes composed of phrase repetitions reported for humpback whales. The transcription of the 45 high-quality song recordings (see **Table 1**) resulted in a total of 41 distinct unit types. The performed random forest analysis for all identified units measured across the dataset resulted in an OOB error rate of 11.08%, and consequently, 88.92% of all unit types were classified in the same way as by the human classifier. This high level of agreement confirms that the labelling of units was robust and repeatable across the dataset. During song transcription, a total of 1204 phrases were identified, with the shortest and longest phrases comprised of 2 and 46 units, respectively. All identified phrases were manually assigned to 18 different phrase types, which represent 18 distinct themes for the defined study period. Within-set comparisons of all phrases assigned to the same theme regardless of recording period resulted in high similarities (>50 %), verifying assignments of phrases to themes (**Table B1** in Appendix B). Transitional phrases were found on 72 occasions, making up 6% of all found phrases, and were due to their structure connecting two adjacent themes not considered a phrase type. Songs between January and April 2018 resulted in 11 different themes, whereas in January 2019 songs 7 distinct themes were identified (**Table 3**).

Three themes (theme 3a, 5a and 5b) were only observed in one song session each and, therefore, termed rare or uncommon theme types. Theme 1, composed of low-frequency units (ranging ~100-300 Hz), was identified as a shifting theme with units evolving from one form to another with each successive phrase sung (**Figure 4**). Theme 3 and 3a also showed a shifting pattern, with each phrase repetition, the last low-frequency unit (<50 Hz) was repeated more frequently (**Figure 5**). Theme 7, only occurring in 2019 song, showed a somewhat different shifting pattern. With each successive phrase, the last low-frequency (<100 Hz) pulsed unit increased in repetitions, however, in some song cycles this increase was followed by a decrease

in these unit-repetitions over the course of all phrases comprising theme 7 (**Figure B1** in Appendix B). Theme 2 was classified as a static theme due to a very consistent unit order (in a similar position) within each phrase repetition. However, this theme presented gradual change over 2-3 months, with units changing in slope, frequency and/or duration, resulting in different variants of the phrase type. Although these variants were first sung in an inconsistent and interchangeable manner within a song cycle, over time, their structure became consistently different to its origin. Thus, new themes were classified as theme 2a and 2b in March and April 2018, respectively (**Figure 6**). The LSI showed that all three themes overlap in similarities of 46-65% (**Table B2** in Appendix B) and form a stable cluster (**Figure 7**). The CCC for the average-linkage dendrogram of phrase to theme comparison was 0.91, indicating a good representation of the structure within the data despite some branches not reaching AU or BP significance. Consequently, theme 2 was identified as an evolving theme, progressively changing to theme 2a and 2b. The fundamental frequencies of these three theme versions stayed within the low- to mid-frequency range of ~100-800 Hz throughout the modifications.

More themes appeared to evolve across the study period of 2018 and 2019. The pulsed low-frequency units of the first subphrase in theme 6 consistently changed from a sound with one inflection point to two sounds, one with ascending and the other with descending slope. This consistent modification resulted in a new phrase type, representing theme 6a by end of February 2018. By the following year 2019, the high-frequency units of the second subphrase have changed from a high frequency of about 3.5-5 kHz to a mid- frequency range of about 1 kHz, resulting in the phrase type 6b, representing the theme of the same label (**Figure 8**). Similarities based on the LSI revealed that the change between theme 6 to 6a was greater (22% similarity) than between theme 6a to 6b (75% similarity; **Table B2** in Appendix B). Therefore, theme 6 grouped into a separate cluster from theme 6a and 6b which clustered together due to their higher similarity (**Figure 7**). Other themes evolved by a consistent insertion of units instead of modifying existing ones. Theme 4 progressively changed to theme 4a between January and February 2018 by inserting an extra sub-unit into each phrase. The added sub-unit was of high frequency at about 3-4 kHz, following a mid-frequency sub-unit at approximately 1-1.2 kHz (**Figure 9**). The LSI resulted in two separate stable clusters of themes 4 and 4a, however, connected by a branch higher up in the dendrogram, confirming that some degree of similarity exists (36%) as one originated from the other (**Figure 7**; **Table B2** in Appendix B). Theme 5, mostly composed of one long phrase, seemed to be sung in a consistent manner throughout 2018 but showed changes in several units in 2019 songs. With modifications being

consistent throughout all three measured song cycles within each session, the phrase types and consequently themes were labelled 5a and 5b. Changes from theme 5 to 5a occurred on the subphrase level with the final unit (representing a subphrase) being changed in frequency, slope, and duration, whereas theme 5b is characterised by additional high-frequency units at about 1.1-1.4 kHz (**Figure 10**). These modifications were consistent throughout all three transcribed song cycles per session, however, they only occurred during one song session each. The LSI resulted in a high degree of similarity between theme variants 5 and its variant 5a (69%, **Table B2** in Appendix B), and they consequently formed one cluster (**Figure 7**). Although the variant theme 5b only shared $\leq 36\%$ similarity to theme 5 and 5a, it also clustered with these two phrase types due to its lineage. Theme 8, only present in 2019 songs, consists of low frequency signals between 50-300 Hz and comprises a minimum of one and a maximum of two phrase repetitions (**Figure B2** in Appendix B). This theme was followed exclusively by theme 9 (**Table B3** in Appendix B) which is composed of low- to mid-frequency units (~ 150 -850 Hz) and has relatively fixed unit structure similar to theme 2 and its evolved variants (**Figure B3** in Appendix B). Both theme 8 and 9 presented low similarities to all other themes within all transcribed songs ($\leq 20\%$) and therefore clustered as two separate groups (**Figure 7**; **Table B2** in Appendix B).

Similar as songs in 2018, starting themes in 2019 were comprised of high-frequency signals. Theme 10 was assigned the starting theme for most transcribed 2019 songs and composed of several high-frequency units in the first subphrase (~ 1 -1.5 kHz), followed by a low-frequency unit descending from about 250 Hz (**Figure B4** in Appendix B). Additionally, theme 4, 6 and 5b appeared highly variable. Units on the subphrase level were repeated without any clear pattern, repeating different units at irregular intervals within the first subphrase (e.g., **Figure 10C**). While most themes mainly consisted of ≥ 2 phrase repetitions, theme 5 and 10 consisted of only one long phrase, with one exception where theme 5 was composed of two phrases. The general trend of phrase repetitions throughout all transcribed songs was highly variable, with the shortest themes composed of one phrase (theme 5 and 10), and the longest themes of 23 phrase repetitions (theme 2b, 3, and 7). All transcribed songs of all sessions in both years seem to conform to the respective order and patterns of themes. Generally, songs started with themes that included high frequency units (themes 4, 4a, 10, 5, 5a, and 5b), followed by a theme which gradually lowered in frequency (theme 1 and 8). This then transitioned into a theme with a mix of high and low frequency units (theme 2, 2a, 2b and 9) which was mostly followed by lower frequency themes (theme 3, 3a, and 7), ending the song

cycle with a theme including low pulse repetitions paired with high frequency units (theme 6, 6a, and 6b). When chorusing whales were detected, the singers usually conformed to the same song pattern (themes and their order), although singing somewhat offset.

3.3 Song similarity and complexity

Comparisons on the song-level (sequence of themes) between the years 2018 and 2019 presented a change in the content and composition of themes as well as song length (**Figure B5** in Appendix B). Overall, the data showed some variation in the number of themes composing a song, ranging between 4-6 themes and with a mean of 5.4 (SD=0.61) themes per song cycle. The average number of themes in each song cycle in 2018 was 5.56 (SD=0.5), ranging between 5-6 distinct themes. Songs in 2019 appeared shorter, presenting a decrease in number of themes, with a mean of 4.9 (SD=0.74), ranging between 4-6 themes per song cycle. Starting themes in 2018 were mostly assigned to 4 and 4a (35/36=97%), with one exception where one song cycle in January started with theme 5, and terminal themes were exclusively theme 6 and 6a. The 2019 songs mostly started with theme 10 (6/9=67%), whereas the three song cycles of the last measured song session started with theme 5b. Terminal themes in 2019 were exclusively assigned to theme 6b in all songs despite varying number of themes per cycle. The order of themes appeared to follow a predictable order in all months of both years with some themes being dropped occasionally. Specifically, the theme sequence 1, 2, 3, 6 and evolved variants of those themes appeared to be consistently sung in all 2018 songs (**Table B3** in Appendix B).

Based on the changes on the theme level, the LSI on the song-level revealed a high degree of similarities across songs of 2018 and 2019, resulting in two stable clusters (**Figure 11**). The resulting dendrogram based on the LSI indicated a very good representation of the data with a CCC of 0.98. Within the cluster of 2018 songs it becomes apparent that the branches split into two groups, distinguishing between songs of January to mid-February (sessions 18_1 – 18_5) and end of February to end of April 2018 (18_6-18_12), reflecting the gradual song progression over the months within the same year. Although the LSI using the set median song of each session (**Table B4** in Appendix B) showed that songs were highly similar to another within each month (>73%), the LSI of each song cycle revealed that song became progressively less similar throughout the study period. Over the course of February 2018, songs showed a decrease in similarity to down to 50% compared to the first songs measured in January 2018. By April,

songs were only 33% similar to January (18_1). By January 2019 (19_13-19_15), no songs shared any similarity to the ones transcribed in 2018 based on the song-level (sequence of themes).

The results of the complexity analysis displayed similar temporal changes in theme and song contents; songs presented an overall increase in complexity as they evolved over the months in 2018 and decreased drastically between April 2018 and January 2019 (**Figure 12**). Songs between January and April 2018 increased in length as time progressed, containing a higher number of units, unit types, and longer duration. By the following year, songs were considerably shorter, resulting in a decrease of complexity in January 2019 compared to April 2018. The longest song contained 417 units found in April 2018 whereas the shortest was composed of 94 units in January 2019. The PC1 score of the PCA showed a high importance of component 1, with a cumulative proportion of 0.96, indicating that a large amount of the variance is explained by PC1 that was used to represent the song complexity. All three variables included in the PCA showed to contribute equally (loading scores=0.57-0.58).

4 Discussion

The present study provides the first report of humpback whale song on a subarctic feeding ground in Northern Norway. The results show that singing can be heard over several months and over adjacent years, demonstrating that it is most likely a persistent event within this area. This adds to the growing evidence that singing behaviour is not confined to breeding areas at low latitudes (e.g., Vu et al., 2012; Magnúsdóttir et al., 2014). The observed songs comprised multiple themes which presented a gradual change in song structure within 2018 and an abrupt change in the following year of 2019. The complexity of songs seemed to follow this pattern; songs became more complex throughout 2018 and presented a sudden decrease in complexity between April 2018 and January 2019.

4.1 Humpback whale song occurrence

The technique of manual song identification using visual inspections of spectrograms is very subjective based on human experience (Au et al., 2006). Song detection outcomes by human classifiers can vary greatly, while automated methods provide more objectivity and standardisation. However, with signals that are too varied or complex this approach only works to a very limited extent and classifying animal vocalisations manually usually produces accurate outcomes (Janik, 1999). Following guidelines, such as proposed by Cholewiak et al. (2013), while manually examining data, facilitates the identification of humpback whale songs as well as comparisons across different studies. In addition, these guidelines suggested by Cholewiak and colleagues (2013) aid the consistency in classification of song elements to describe the structure of humpback whale song, which is crucial to prevent misclassification within the same, as well as across other data sets. The combined method of manual and automated detection as described in this study appears to be a convenient and reliable approach in whale song detection as recently proposed by Erbs et al. (2021).

Humpback whales are known to use the Norwegian Sea as a migration corridor between their high latitude feeding areas and low latitude breeding grounds where they generally arrive sometime between February and May (Stevick et al., 2003, 2016; Kettner et al., 2019; Wenzel et al., 2020). However, since 2010, the wintering ground of the Norwegian Spring Spawning herring has been located in offshore and coastal waters between 69°N and 73°N (Huse et al.,

2010; Norges Sildesalgslag, 2010). This large mass of wintering herring represents an important food source for migrating animals, and humpback whales have been reported being present in these areas off Norway's coast from June into February (Jourdain and Vongraven, 2017; Kettner et al., 2019; Leonard and Øien, 2020; Ramm, 2020). While visual studies have not reported humpback whale presence in Norwegian waters after February (Broms et al., 2015; Ramm, 2020), the present study revealed high song occurrence until the end of April, further supported by acoustic detections made by Aniceto et al. (2020). Additionally, sporadic observations of humpback whales in Norwegian waters have been reported on social media channels during spring months (March-May) across multiple years (Hvaler i nord, 2021). This, paired with the acoustic detections from the current study and by Aniceto et al. (2020), suggests that humpback whales remain in Norwegian waters almost year-round. Ultimately, this indicates either that humpbacks may remain in foraging areas for periods when higher energetic reserves are required (Aniceto et al., 2020) or that these animals start to migrate with a delay as proposed by Vu et al. (2012). However, Stevick et al. (2003) demonstrated that male humpback whales arrive earlier at their breeding sites than females. In addition, pregnant females have been documented to depart last from feeding areas and arrive last at breeding sites (Dawbin, 1966), whereas some females were documented to not undergo migration every year (Brown et al., 1995). It has been proposed that females may remain in feeding areas to improve their body condition due to the energetic costs of reproduction and migration (Lockyer, 1984; Brown et al., 1995). This might suggest a dominance by female humpback whales at the end of a feeding season in Norway (Ramm, 2020). The lasting singing behaviour by male humpback whales in the study area could be explained by delayed departures and/or whales that remain within the area. As already proposed by Magnúsdóttir et al. (2014), this might suggest a trade-off strategy for both sexes in humpback whales.

The observed peak in singing activity in February corroborates previous findings within the north-east Atlantic (Magnúsdóttir et al., 2014; Magnúsdóttir and Lim, 2019) and appears to correlate with the reproduction cycle of humpbacks as suggested by Magnúsdóttir and Lim (2019). The periods of ovulation in females and elevated testosterone levels in males overlaps the peak in singing activity (Nishiwaki, 1959; Clark and Clapham, 2004). Although February presented the highest song occurrence, the longest complete song sessions were recorded in March and April. On breeding grounds, the duration of song sessions has shown to be associated with the hormonal cycle in humpbacks. Tyack (1981) noted an increase in the length of song bouts in relation to decreasing female reproductive activity. This could explain the increased

duration of the full sessions identified in March and April in the data. However, a study from a North Atlantic feeding ground in the Gulf of Maine presented opposing results with no song detections in February and song occurrence peaking in November (Vu et al., 2012). The observed increase in humpback singing activity in the present study could be explained by the local abundance of whales, i.e., representing the period when most males arrive within the study area. Additionally, recent results by Ryan et al. (2019) have demonstrated that humpback whale singing activity may be influenced by variations in the ecosystem, proposing humpbacks to regulate their behaviour accordingly. Thus, the variability in singing behaviour might be a result of environmental influences and/or might be driven by the abundance of humpbacks within the study area, specifically males which are to date the only ones documented to engage in this vocal display (Winn and Winn, 1978; Baker and Herman, 1984; Darling and Bérubé, 2001; Darling et al., 2006; Herman et al., 2013). In contrast to the large number of chorusing singers on low latitude breeding grounds, singers identified in the current study were mostly single whales. Other studies at high latitude feeding grounds reported similar detections, with a predominance of solo singers (Gabriele and Frankel, 2002; Vu et al., 2012). However, in a more recent study in Icelandic waters, Magnúsdóttir and Lim (2019) detected a higher number of simultaneous singers. This suggests that singing in a chorus might be location specific and/or that the number of males present within the area might be the driver of this variation. Abundance investigations including sex ratios within Norwegian waters would also help to elucidate this pattern.

4.2 Changes in song structure

The qualitative assessment of the humpback song structure in the data resulted in a total of 41 different unit types, making up 18 distinct phrase types, and thus themes. The majority of these themes occurred regularly with only three themes being less common and theme order did not appear to be random confirming the description made by Frumhoff (1983). Seven themes showed to be static, shifting, or uncommon, based on the definitions by Payne and Payne (1985). Six of these themes occurred in 2018 which did not re-occur in the following year. The quantitative analyses using the LSI revealed a gradual change in structure within songs of 2018 followed by an abrupt change in the following year of 2019. The changes in the humpback whale song found in the present study are highly directional with no themes from 2018 returning in the song the following year (2019), indicating a rapid song progression over

two years on this subarctic feeding ground. This is largely in line with findings of previous studies investigating the song structure between seasons and/or years (e.g., Winn and Winn, 1978; Guinee et al., 1983; Payne et al., 1983; Payne and Payne, 1985; Eriksen et al., 2005; Magnúsdóttir and Lim, 2019). In Iceland, humpback whale song structure has also been documented to undergo structural changes over time (Magnúsdóttir et al., 2015). The authors reported that modifications occurred in song unit repertoire and changes or replacements of phrase types. However, in contrast to the similarities found in the present study, the overlap in song content (phrase types, i.e., themes) was greater between two winters, with half the phrases found to be either the same or sharing similar spectral features. This discrepancy could be due to the variability in the degree of change between periods, as studies have shown that in some years song progresses more rapidly than in others (Payne and Payne, 1985; Noad et al., 2000; Garland et al., 2011). In addition, the one distinct song type found per year might indicate that the sampled whales are either from the same breeding population or that song conformation was performed before the study period. Structural analyses of song recorded during one winter season in Icelandic waters by Magnúsdóttir and Lim (2019) resulted in one song type, primarily composed of static and shifting themes, corroborating the results of the present study. Areas around Iceland have been documented to represent a feeding ground and migratory passage route for North Atlantic humpbacks that are known to pass Norway (Whaletrack UiT, 2018; L. Kettemer, person. comm., January 22, 2021). Using acoustic differences in song types and their content can identify the presence of a population and provide insight into its structure and migratory movements over a large spatial scale (Garland et al., 2015).

Although the present study showed some degree of overlap on the lower level of themes with evolving variants clustering together across the years, the structure on the higher song-level appeared very different. The LSI results demonstrate a high degree of song sharing within each month, and progressive song evolution throughout the study period. While the information of connections between themes (i.e., “new” and “old” versions) is available to the human classifier, it may not be as evident in the quantitative analysis using LSI (Garland et al., 2013b). Although sequence similarities showed linkages between some themes between the years (e.g., theme 5 and 5a), songs appeared to be 0% similar between 2018 and 2019. Thus, the quantitative approach resulted in a shortcoming of identified connections through changes in song elements (units) that could only be detected by qualitative inspection. Additionally, the delineation process of humpback whale song remains highly subjective (Cholewiak et al., 2013; Mercado, 2021). Although the protocol on how to delineate and measure phrases defined by

Cholewiak et al. (2013) was followed in both the present, and the study by Magnúsdóttir et al. (2015), the acceptable level of variability within the classification procedure has a large subjective component (Mercado, 2021), making comparisons between studies difficult. An example represents the themes 5 and 6, and their evolving new phrase types throughout the study period. Although theme 6 and 6a as well as 5, 5a and 5b were delineated as separate themes due to consistent unit modifications, the LSI resulted in one cluster per theme group. Hence, the number of theme (i.e., phrase types) might vary depending on the classifier as well as method used.

Due to intra-individual variations, chosen song cycles within a session can impact sequence similarity methods, as argued by Mercado (2021). Manual, subjective classification is commonly used to analyse humpback whale song (Au et al., 2006; Dunlop et al., 2007; Garland et al., 2011), however, it adds a strong subjective component with signal classifications from spectrograms varying between observers. Therefore, the inclusion of statistical methods, such as random forest analyses to assess the consistency in unit assignments, are essential to minimize classification errors and increase the robustness of the results wherever possible. A combined qualitative and quantitative assessment as applied in the present study has previously been suggested to produce more robust results (Garland et al., 2013b). Human classifiers were found to perform as well, or even better, as various quantitative computer methods (Janik, 1999; Riesch and Deecke, 2011). Thus, a combination of manual and computer techniques ensures that important components within humpback whale song are not overlooked (Garland et al., 2013b). In this study, only the unweighted LD analyses were explored as this has been suggested to be more appropriate concerning small data sets such as for whale song (Tougaard and Eriksen, 2006). However, the application of weights could improve results as the costs of the transition between similar and dissimilar sequences becomes clearer. Therefore, further analysis including a weighted LD applied to current dataset are encouraged.

4.3 Complexity of songs

The analysis of humpback whale song complexity suggests that songs became more complex as time progressed in 2018 and while the song evolved throughout 2018, and presented a sudden decrease in complexity the following year, in January 2019, when song showed a high dissimilarity to the previous year. This trend is in line with a previous study by Allen et al.

(2018) which displayed a consistent long-term pattern with songs becoming more complex as they evolved but more simplified after a song has been completely replaced by a new version. The positive association between complexity and individuality found by Allen et al. (2018), suggests that singers become more individually unique with increased song complexity. This theory of individual whales singing more complex songs in order to stand out has previously been proposed by Noad (2002). Changes in songs have been suggested to occur when singers introduce novel material into their own songs (Noad et al., 2000; Garland et al., 2011; Cholewiak et al., 2013). A longer song is the result of an increase in song elements within the hierarchical structure (e.g., an increase in the number of phrase repetitions within one or more themes; Cholewiak et al., 2013). Previous studies describing humpback whale song structure reported a high level of variation in song duration (Fristrup et al., 2003). However, measuring song duration is informative if theme order is relatively invariant (Cholewiak et al., 2013) as the results of the song structure analysis of the present study show.

In songbirds, the vocal repertoire has shown to increase in response to female sexual selection (Kroodsma, 1976; Byers and Kroodsma, 2009). Highly complex songs might indicate a higher cognitive capacity of singing males, and thus may provide information about the quality as a mate (e.g., Boogert et al., 2008). The function of song as a metric of male fitness has also been proposed for humpback whale song. Song copying by males, while constantly incorporating changes as they occur, is believed to reveal a singer's reproductive fitness to conspecifics (Payne, 2000; Herman, 2016). Sexual selection has generally been agreed to be a driving force in humpback whale song (Payne, 2000; Parsons et al., 2008). Although its specific purpose as a signal is still debated (Herman, 2016), the peak in singing activity linked to the reproductive cycle in humpback whales indicates a function in sexual advertising (Payne and McVay, 1971). In addition, humpback whale singing behaviour has shown to be associated with mate attraction and to facilitate male to male interactions (Darling and Bérubé, 2001; Darling et al., 2006; Cholewiak, 2008; Smith et al., 2008), suggesting that song may be a multi-message display (Murray et al., 2018). It is unclear whether processes of mate selection can explain why humpback whales constantly modify their songs over time, and whether females prefer males with larger song repertoires. Relatively little is known what prompts humpback whales to modify song features such as changes in units, song durations, and/or phrase repetitions.

Given the relatively low sample size (three song cycles representing 15 individuals) and considerable variability in song complexity within and between individuals, the results of this study must be interpreted with caution. As noted by Rekdahl (2012), the included songs in the analyses might have aberrant versions or a combination of two song types as previously documented by Noad et al. (2000). Thus, there is a potential for additional variability that is not captured by the sample and might have affected the outcomes by the complexity analysis trends. It is unclear what sample size is needed to reflect specific characteristics using a small subset, and consequently, to obtain representative results for humpback whale songs.

4.4 Potential song exchange

With humpback whales in Norway being reported to originate from different breeding populations in Cape Verde, Africa, and the West Indies, America, (Broms et al., 2015; Whaletrack UiT, 2018; Wenzel et al., 2020), the findings indicate strong potential for acoustic interaction and opportunities for cultural transmission to occur on this shared feeding ground in Northern Norway. This is supported by the findings that all individuals appeared to constantly incorporate the progressive changes throughout the study period. Song sharing within each month was high, indicating that different humpback whale populations exchange song content already before reaching their breeding grounds. In addition, the song seemed to have progressed so rapidly that most themes were replaced by novel material over the course of one year within the study area. The variation exhibited at this temporal level suggests that the song might be completely replaced by a new version the following year. Compositions of humpback whale song in Bermuda and Hawaii were documented to have a complete turn-over within 4-5 years (Payne et al., 1983; Payne and Payne, 1985), whereas a study off eastern Australia reported a turn-over rate of a two-year period (Noad et al., 2000). Song evolutions and/or revolutions have been suggested to be a result of different factors such as the degree of exposure to new material (Darling et al., 2019). The song revolution found off eastern Australia by Noad et al. (2000) was due to an interchange of two populations, where humpbacks from eastern Australia adopted the song type from the western Australian population. However, this song revolution event to incorporate a new song into a population's repertoire might have actually taken longer than initially believed, as proposed by Rekdahl (2012). Yet, far more empirical testing, including more samples over several seasons and years, is needed to put a

hypothesis forward regarding rapid humpback whale song change on the feeding ground and migratory route in Northern Norway.

Song exchange on high latitude feeding ground might be a key driving force behind cultural transmission for humpback whale populations within the North Atlantic, as already proposed by Magnúsdóttir and Lim (2019). To elucidate the degree of song exchange between different breeding populations coming together on this shared high latitude feeding ground, detailed comparisons of song patterns across locations and multiple years are necessary. The use of passive acoustic monitoring (PAM) to collect data and comparisons of song types within the North Atlantic could identify the degree of mixing of these two populations. Song learning has been suggested to be facilitated through contact of different populations on feeding grounds or overlapping migration routes (Garland et al., 2011, 2013b; Schulze, 2021). Although the underlying drivers of humpback whale song remain elusive, a number of explanations for high latitude singing behaviour have been proposed (Clark and Clapham, 2004; Stimpert et al., 2012; Garland et al., 2013a; Herman et al., 2013; Magnúsdóttir et al., 2015), the main involving the reproduction cycle (Clark and Clapham, 2004; Vu et al., 2012; Magnúsdóttir et al., 2015) and song practicing and/or learning by males (Clark and Clapham, 2004; Herman et al., 2013). Furthermore, a study on the movement behaviour of humpback whales has suggested that these animals engage in different behavioural roles while singing (Henderson et al., 2018). This provokes further investigations of humpback whale singing in relation to foraging behaviour on high latitude feeding grounds such as in subarctic waters of Northern Norway.

5 Conclusion

This study provides a detailed account of humpback whale song occurrence on a subarctic feeding ground in Northern Norway using PAM. Norwegian waters represent a biologically important feeding and migratory area for different breeding populations of North Atlantic humpback whales. The high levels of singing activity, occupying five months in 2018, revealed longer humpback whale presence within the study area and further support the critical role of this region. Comparisons of song structure similarities and complexity indicated gradual song changes over time, suggesting a rapid song progression, with a strong potential for song exchange and opportunities for cultural transmission on this shared feeding ground. However, future studies including larger sample sizes from multiple years and locations are required before this can be determined conclusively. Establishing a common technique for the delineation of humpback whale song elements is essential for cross-comparisons between different locations. Analyses of acoustic similarities can identify different populations and determine if individuals have been in acoustic contact. Therefore, song sequence comparisons present an efficient method to examine humpback whale population structure, its migratory movements, and possible song transmission between different humpback whale populations within the North Atlantic. Further studies investigating the feeding and breeding behaviour of humpback whales and how vocalisations might relate to environmental conditions in Norwegian waters are also recommended. In the light of rapidly changing environments, long-lived species like the humpback whale are highly vulnerable and need to adapt fast. Improving our understanding of variations in humpback presence and behaviour will further aid management bodies to make informed and effective decisions regarding marine protection in Norwegian waters. The results presented here will bridge a knowledge gap on North Atlantic Humpback whale song evolution and will provide insights into potential drivers of cultural revolutions in humpbacks. In addition, this study demonstrates that PAM is an effective and cost-efficient method to collect data in an oceanic environment, and thus, reinforces the use of PAM as an essential tool to investigate humpback whale populations and their connectivity.

Tables

Table 1. Summary of all acoustic files used in song sequence analyses. File start and end refers to the recordings retrieved from the LoVe Ocean archive (Equinor and IMR, 2020).

| Year | Month | Date | File start | File end | Session start | Session end |
|------|----------|----------------|------------|----------|---------------|-------------|
| 2018 | January | 03-01 (/04-01) | 23:47 | 00:07 | 23:51 | 00:10 |
| | | 18-01 | 06:10 | 06:30 | 06:11 | 06:34 |
| | | 24-01 | 00:18 | 00:48 | 00:19 | 00:53 |
| | February | 17-02 | 12:52 | 13:12 | 12:53 | 13:16 |
| | | 20-02 | 19:03 | 19:23 | 19:05 | 19:28 |
| | | 25-02 | 00:57 | 01:27 | 01:03 | 01:25 |
| | March | 03-03 | 04:05 | 04:35 | 04:08 | 04:38 |
| | | 13-03 | 21:34 | 22:04 | 21:39 | 22:04 |
| | | 27-03 | 22:26 | 23:06 | 22:32 | 23:07 |
| | April | 03-04 | 01:24 | 02:04 | 01:34 | 02:12 |
| | | 09-04 | 10:42 | 11:12 | 10:48 | 11:37 |
| | | 22-04 | 01:38 | 02:08 | 01:40 | 02:24 |
| 2019 | January | 01-01 | 16:56 | 17:16 | 16:58 | 17:18 |
| | | 25-01 | 20:16 | 20:36 | 20:20 | 20:37 |
| | | 31-01 (/01-02) | 23:51 | 00:11 | 23:54 | 00:17 |

Table 2. Summary of recordings by the LoVe Ocean Observatory (Node 1) and detected humpback whale singing activity. Empty cells indicate no data.

| Year Month | Dates | Recordings | | Singing activity | | No. song sessions ** | No. full song sessions | Song session duration [minutes] *** | | | Max. no. chorusing singers |
|-------------------------|-----------------------|------------|-------------|------------------|------------|----------------------------|------------------------------|--|-------------|----------------------|----------------------------------|
| | | days* | hours | days | hours | | | Min | Max | Mean (SD) | |
| 2018 January | 02.-30.01 | 29 | 682 | 12 | 38 | 15 | 1 | 112 | 112 | -- | 2 |
| February | 12.-27.02 | 16 | 384 | 15 | 253 | 33 | 2 | 14 | 52 | 33 (27) | > 4 |
| March | 01.31.-03 | 31 | 707 | 20 | 224 | 35 | 12 | 31 | 789 | 245 (234) | 3 |
| April | 01.-30.04 | 30 | 638 | 12 | 172 | 17 | 7 | 17 | 815 | 200 (277) | > 4 |
| May | 01.-31.05 | 31 | 697 | | | | | | | | |
| June | 01.-07, 11.-15.06 | 12 | 270 | | | | | | | | |
| // | | | | | | | | | | | |
| December | 10.-15., 18.-31.12 | 20 | 396 | 5 | 22 | 10 | 3 | 40 | 90 | 65 (25) | 2 |
| 2019 January | 01.-11., 13.-31.01 | 30 | 644 | 15 | 41 | 21 | 10 | 13 | 362 | 84 (105) | 2 |
| Total | | 199 | 4419 | 79 | 750 | 131 | 35 | 227 | 2220 | 159 (201) | |

* The number of recording days might not represent full days (<24hours, n=41); **No. song sessions = all sessions included, also when fading in/out, with too many singers chorusing the session was considered as one; *** Average song session length of full sessions = only sessions that included start and end time.

Table 3. Theme occurrence throughout the study period (January 2018 – January 2019).

| Theme | Period | | | | | Jan-19 |
|-----------|--------|--------|--------|--------|----|--------|
| | Jan-18 | Feb-18 | Mar-18 | Apr-18 | | |
| 1 | x | x | x | x | | |
| 2 | x | x | x | | | |
| 2A | | | x | x | | |
| 2B | | | | x | | |
| 3 | x | x | x | x | | |
| 3A | x | | | | | |
| 4 | x | x | | | | |
| 4A | | x | x | x | | |
| 5 | x | x | x | x | // | |
| 5A | | | | | | x |
| 5B | | | | | | x |
| 6 | x | x | | | | |
| 6A | | x | x | x | | |
| 6B | | | | | | x |
| 7 | | | | | | x |
| 8 | | | | | | x |
| 9 | | | | | | x |
| 10 | | | | | | x |

Figures

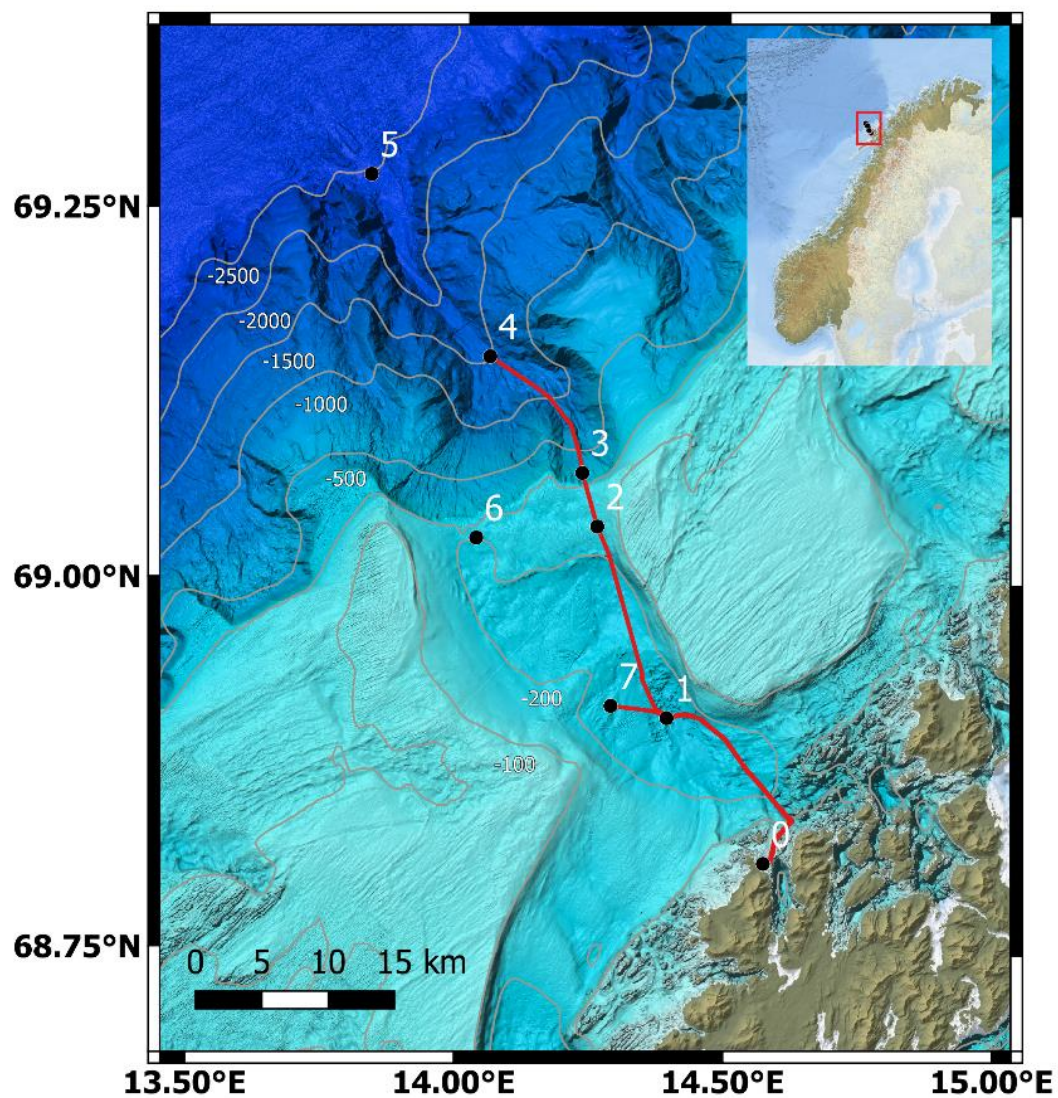


Figure 1. Map of the sampling-nodes of the LoVe Ocean Observatory, Norway. Data used in this study were collected by Node 1 (Equinor and IMR, 2020). Produced by Geir Pedersen.

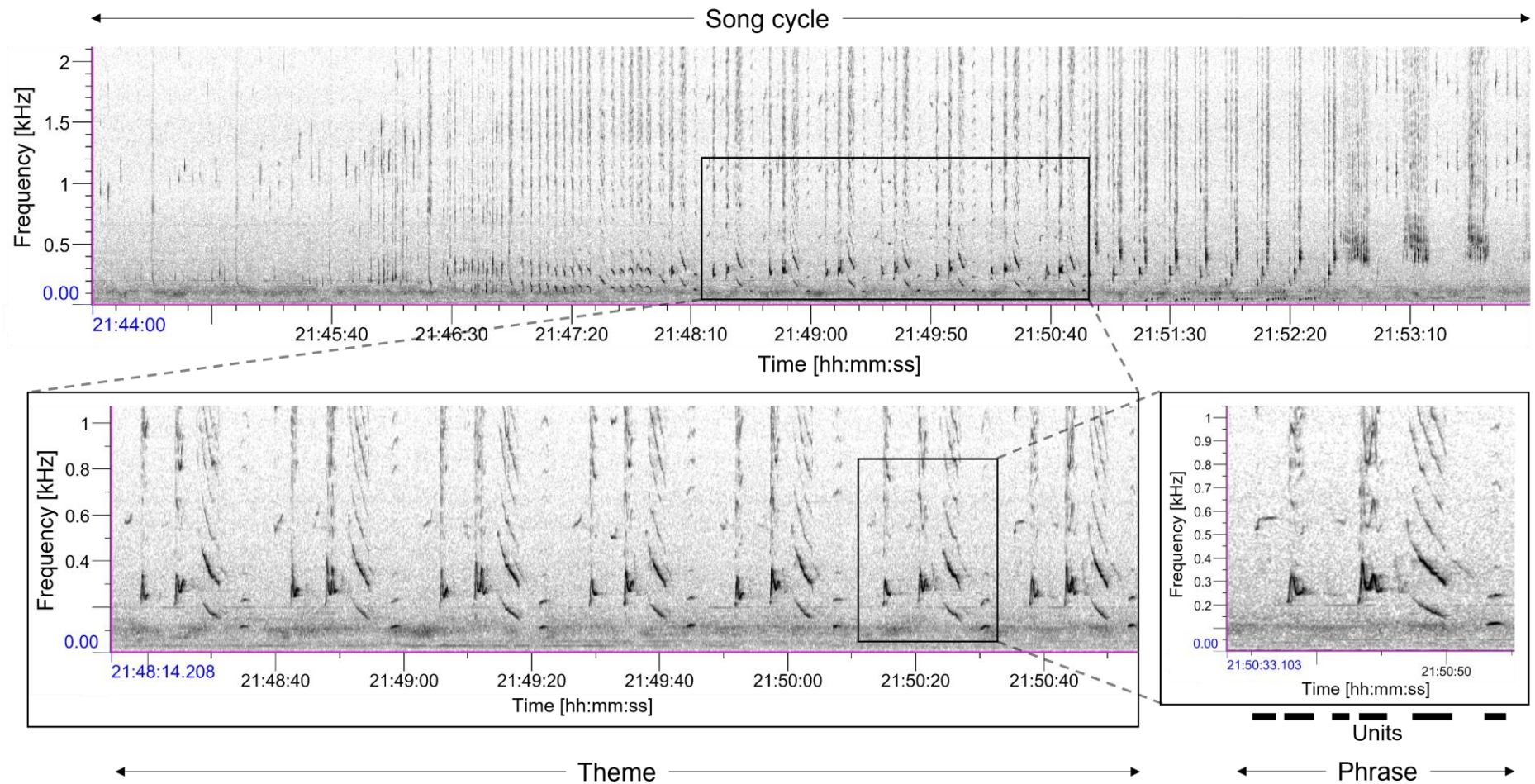


Figure 2. Spectrographic representation of humpback whale song and its structural elements (units, phrase, theme, song cycle), recorded by LoVe Ocean Observatory in March 2018. The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. The illustrated full song cycle consists of several themes. The theme example of the song cycle is composed of several phrase repeats. One phrase is composed of a repeating pattern of individual units. Time on the x-axes is given in hours:minutes:seconds.

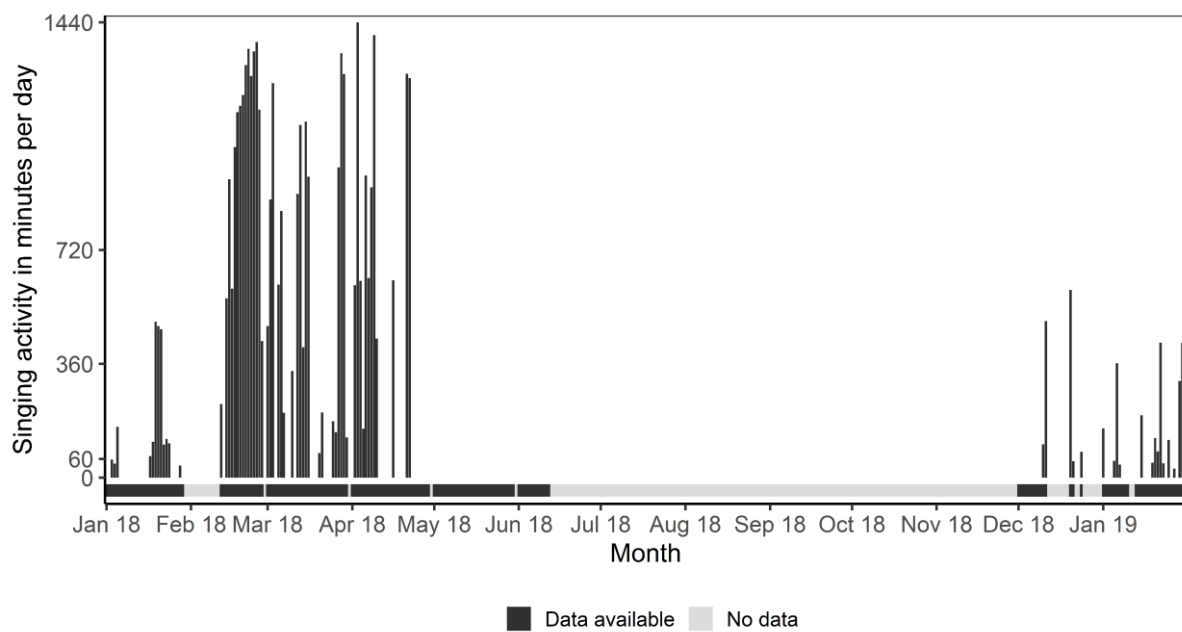


Figure 3. Humpback whale singing activity recorded by LoVe Ocean Observatory in Northern Norway throughout the study period January 2018 – January 2019. The horizontal bar at the bottom indicates data availability. Reprinted with permission from Martin et al. 2021 (Copyright 2021, *Frontiers in Marine Science*).

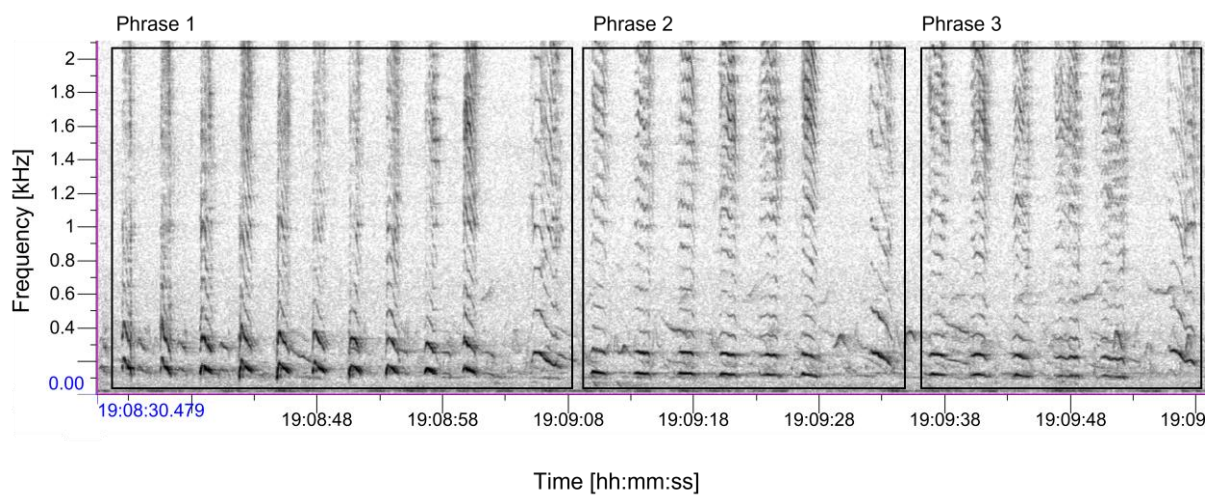


Figure 4. Spectrographic representation of the shifting theme 1, composed of three phrase repetitions of which each phrase comprises two unit types with varying number of units. The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

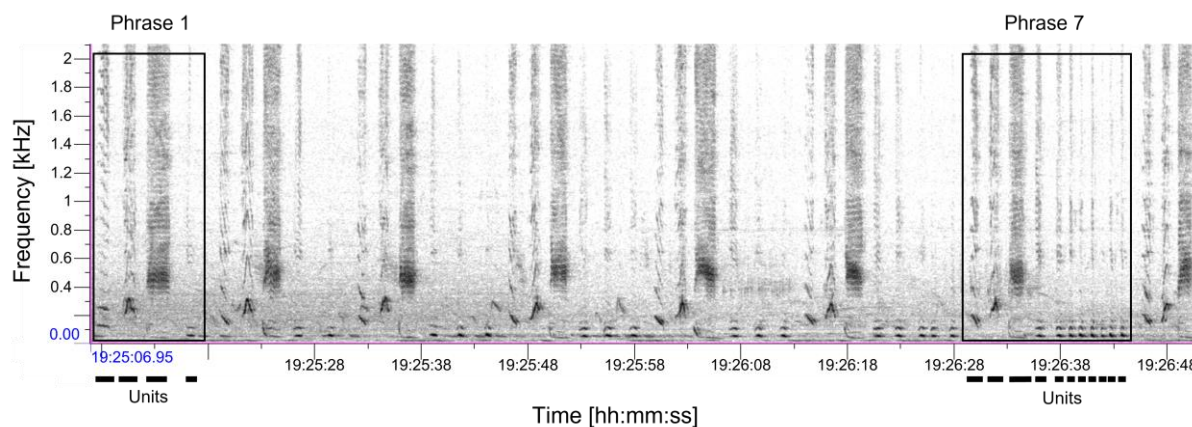


Figure 6. Spectrographic representation of the shifting theme 3 composed of seven phrase repetitions; the last unit within each phrase increases in repetition with each successive phrase, with phrase 1 being composed of four units (last unit being sung once) and phrase 7 being composed of 11 units (last unit being repeated eight times), see black bars indicating units underneath each respective phrase. The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

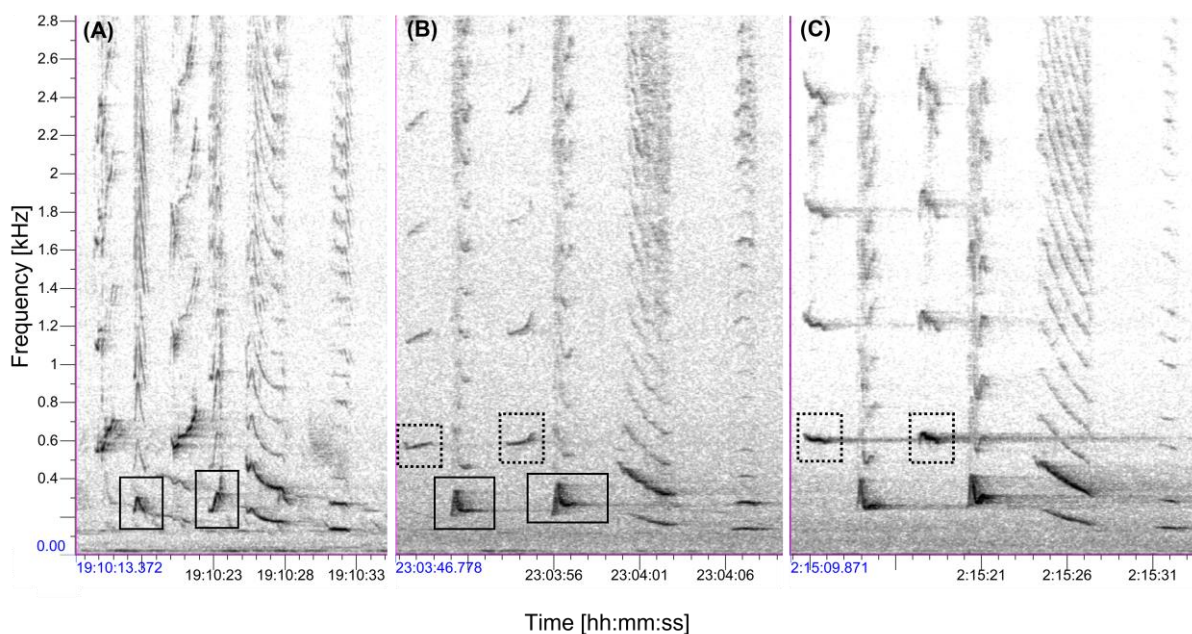


Figure 5. Spectrograms of an evolving phrase type representing an evolving theme in 2018. Phrase type 2 (A) changed to 2a (B) and 2a changed to 2b (C). Changes in units over time are indicated by rectangles: solid=phrase type 2 to 2a; dotted=phrase type 2a to 2b. The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

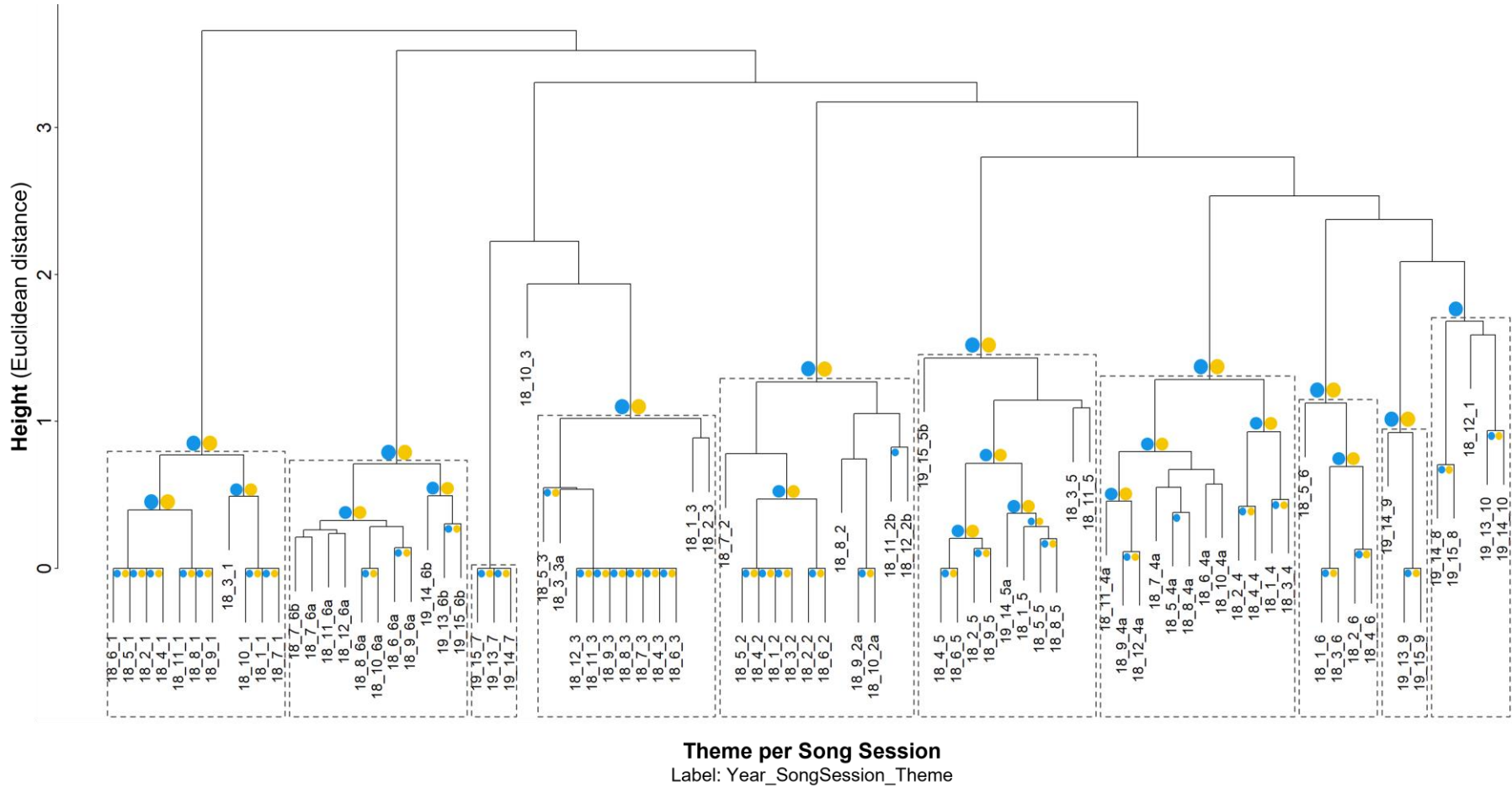


Figure 7. Dendrogram of bootstrapped (1000) LSI of average-linkage hierarchical clustered set medians per theme (most representative phrase) per song session. The Cophenetic Correlation Coefficient (CCC)=0.91, indicating a good representation of the structure within the data. Multiscale bootstrap resampling is represented by dots: blue (left) indicates AU > 95% and yellow (right) indicates normal BP > 70%. Lower values (no dots) indicate variability in their division whereas branches with high AU values represent stable divisions. Stable and highly supported clusters were marked using rectangles at the highest level.

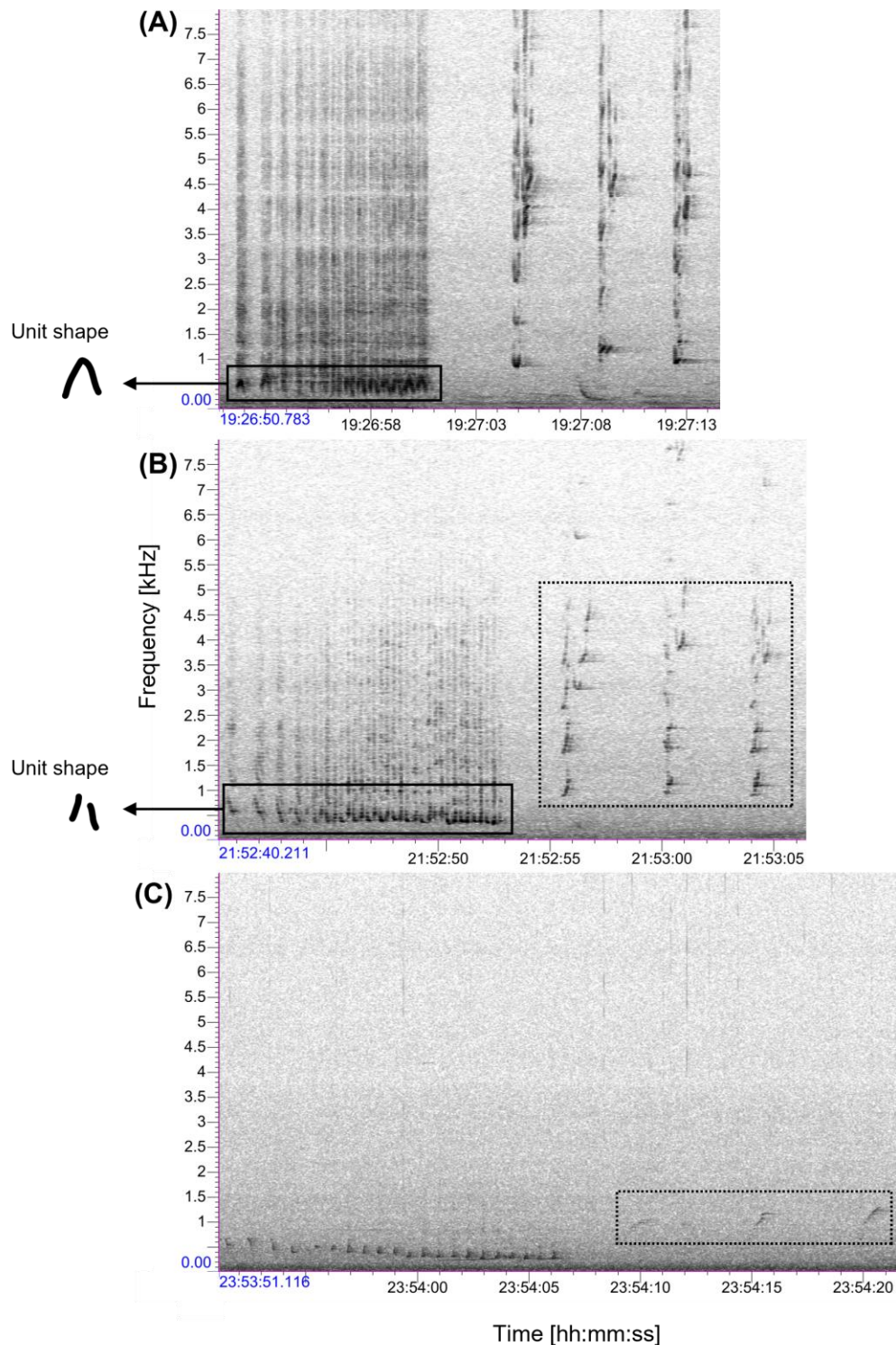


Figure 8. Spectrograms of an evolving phrase type representing an evolving theme. Phrase type 6 (A) changed to 6a (B) by changing the pulsed units in the first subphrase (solid rectangles) from one sound with one inflection point to two separate sounds, one ascending and one descending (see unit shapes). Phrase type 6a then evolved to 6b (C) by changing the slope and/or frequency of units in the second subphrase (dotted rectangles). Note, no harmonics are visible in spectrogram (C) due to a decreased quality of the recording. The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axes is given in hours:minutes:seconds.

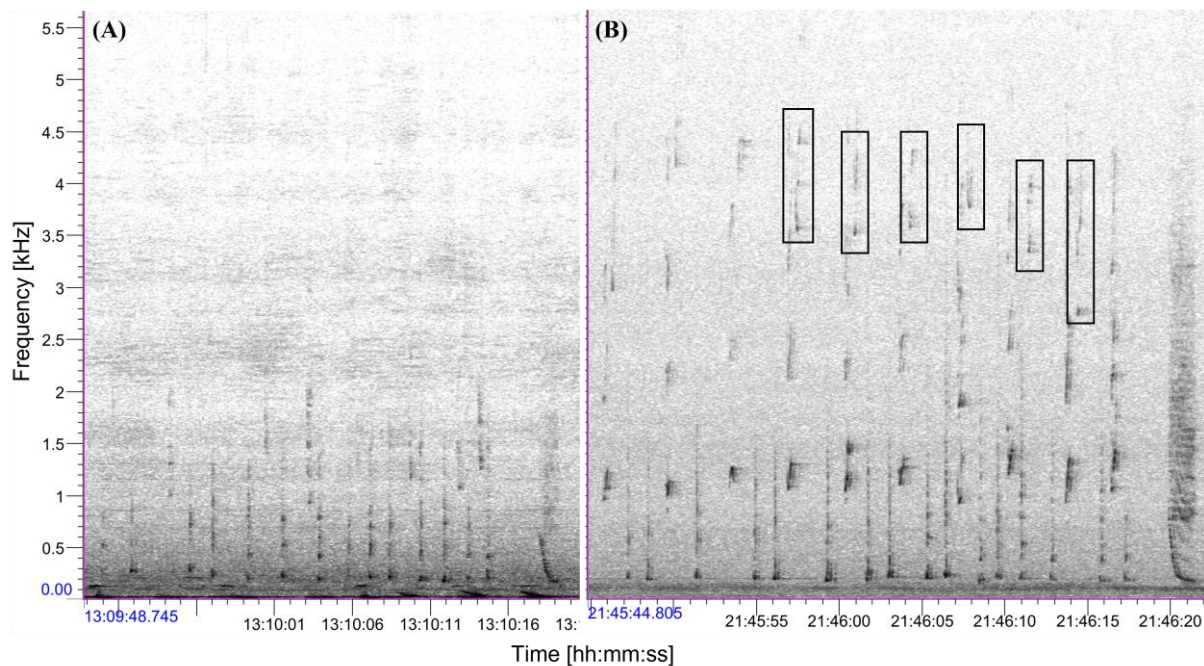


Figure 9. Spectrograms of an evolving phrase type representing an evolving theme. Phrase type 4 (A) changed to 4a (B) by inserting an additional unit (rectangles) at a high frequency ($\geq 3\text{kHz}$). The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

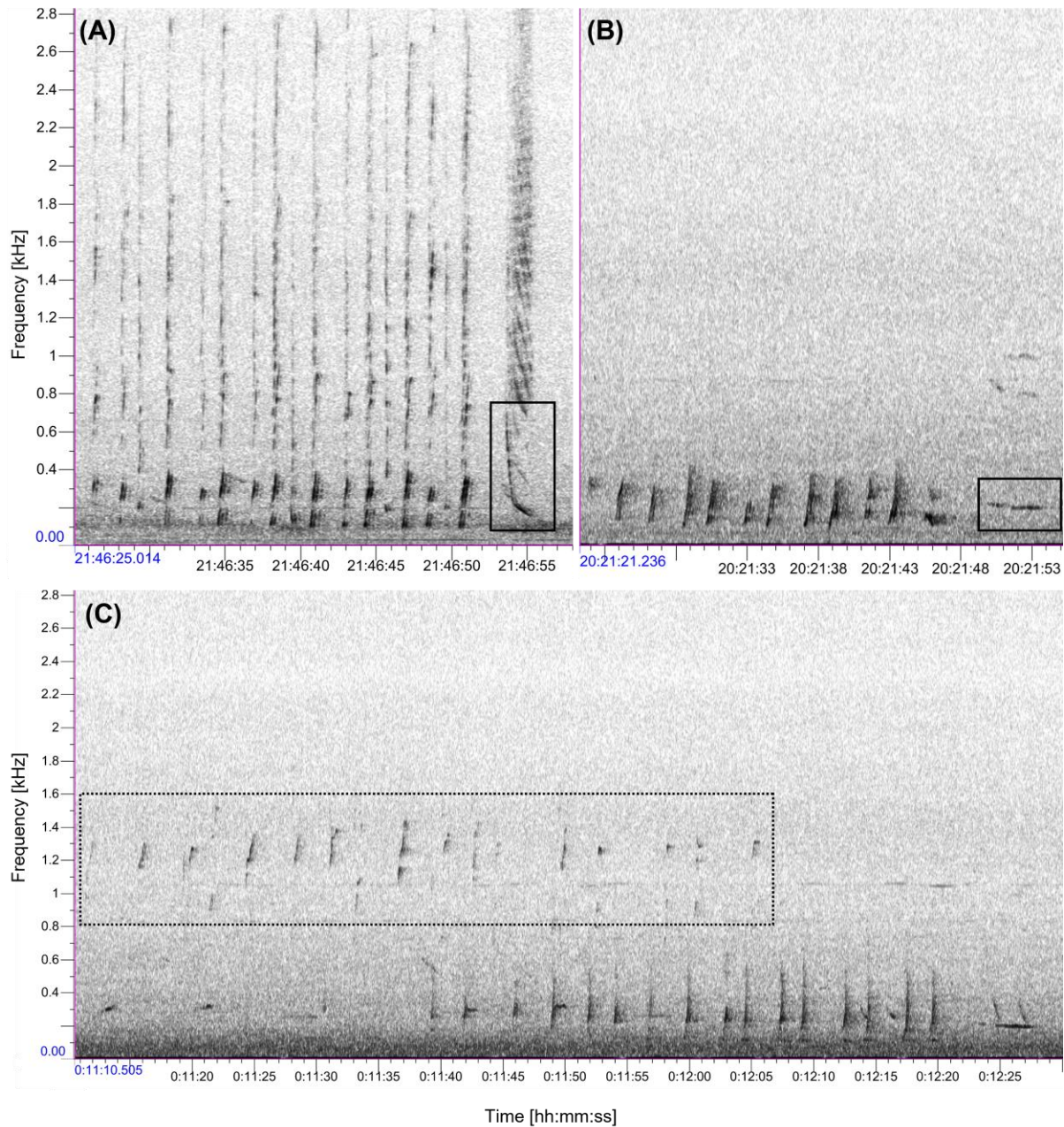


Figure 10. Spectrograms of a changing phrase type representing a theme. From phrase type 5 occurring in 2018 songs (A) to phrase type 5a (B) and 5b (C) in 2019 songs. Changes from phrase type 5 to 5a are indicated in solid rectangles and from phrase type 5a to 5b in dotted rectangles (added units at high frequencies ≥ 900 Hz). The spectrograms were produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axes is given in hours:minutes:seconds.

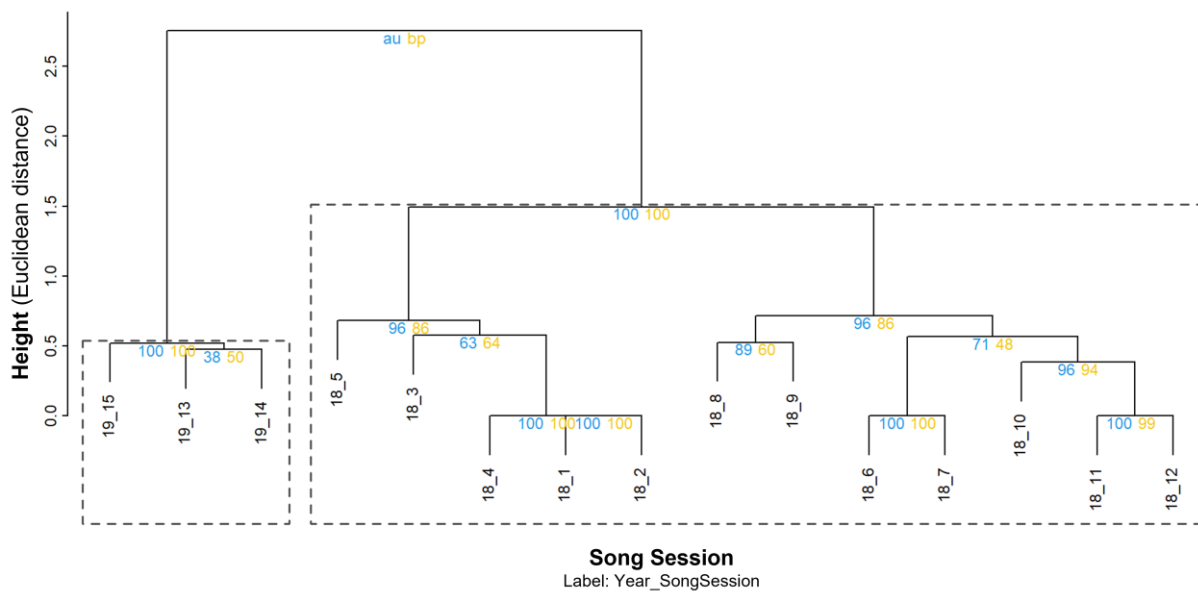


Figure 12. Dendrogram of bootstrapped (1000) LSI of average-linkage hierarchical clustered set medians per song cycle (sequence of themes). The Cophenetic Correlation Coefficient (CCC)=0.98, indicating a good representation of the structure within the data. Numbers represent multiscale bootstrap resampling (AU, blue left) and normal bootstrap probability (BP, yellow right) which is considered significant if AU $p > 95\%$ and BP $p > 70\%$. Lower values indicate variability in their division whereas branches with high AU values represent stable divisions. Stable and highly supported clusters were marked using dashed rectangles at the highest level.

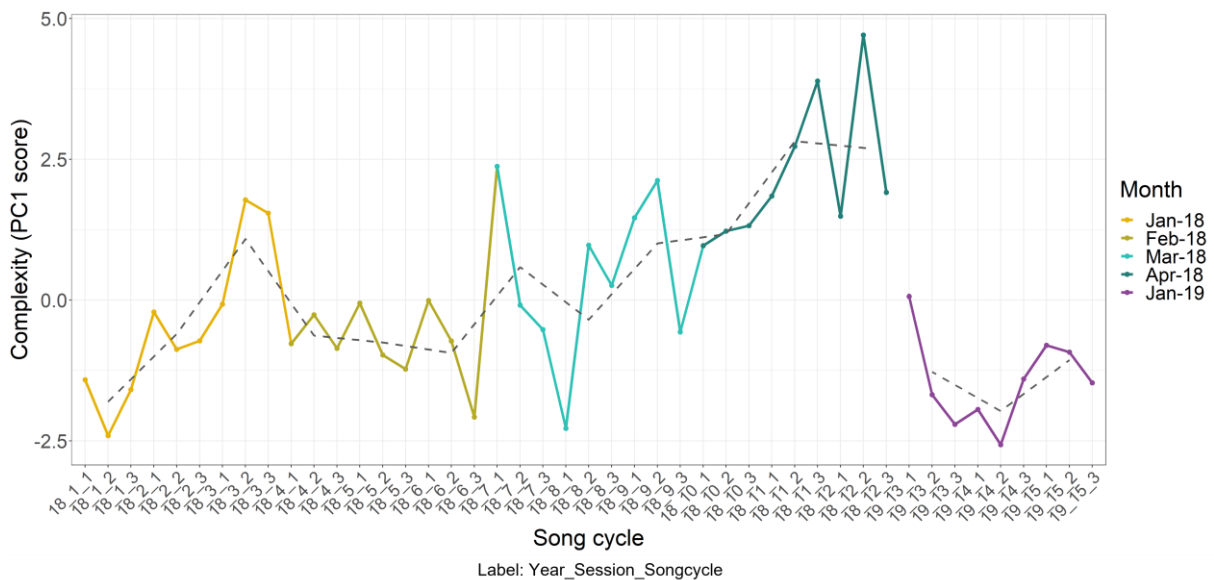


Figure 11. Song complexity over the study period January 2018 – January 2019. Three song cycles were measured per song session i.e., per individual. The grey dashed line gives the average PC1 score per session to display a more overall trend in the data. The split in lines indicates lack of songs and/or data (July – November).

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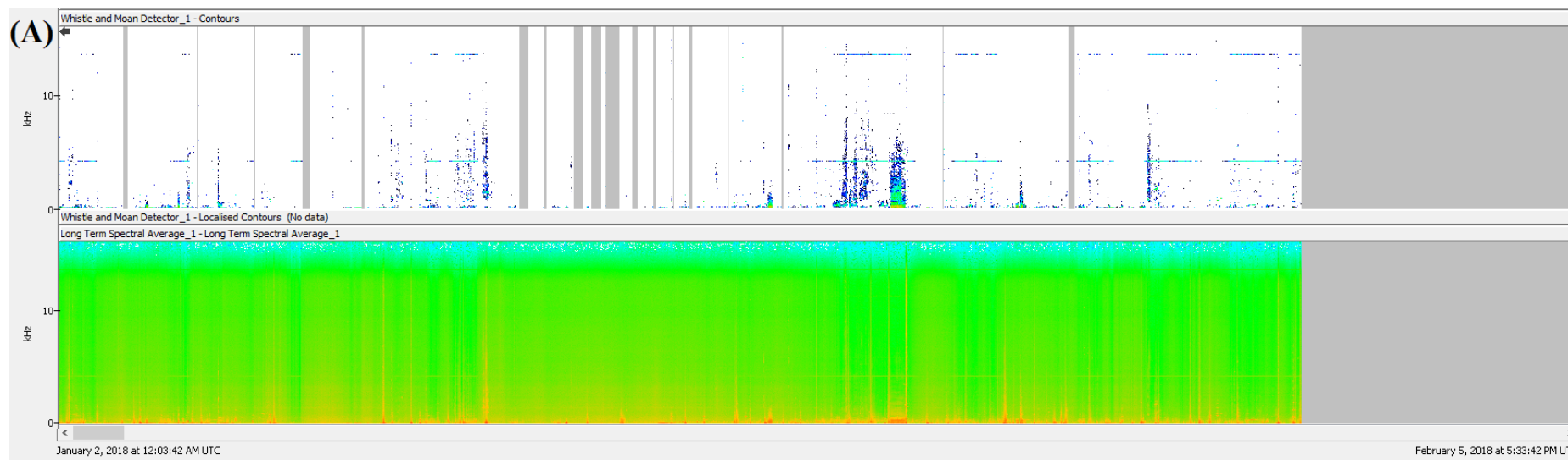
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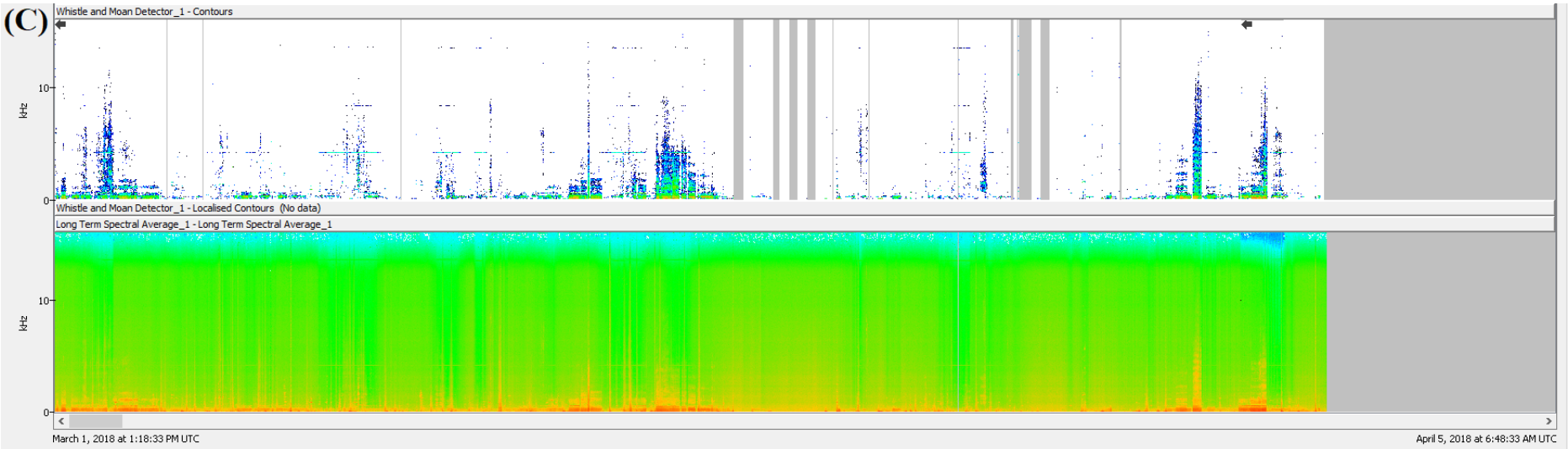
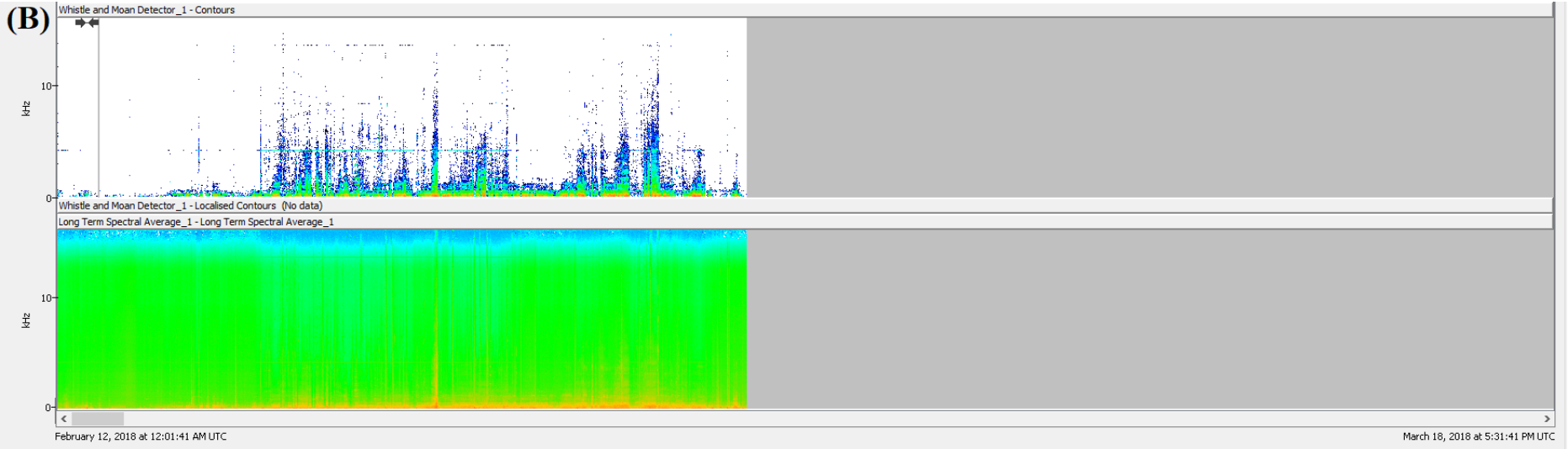
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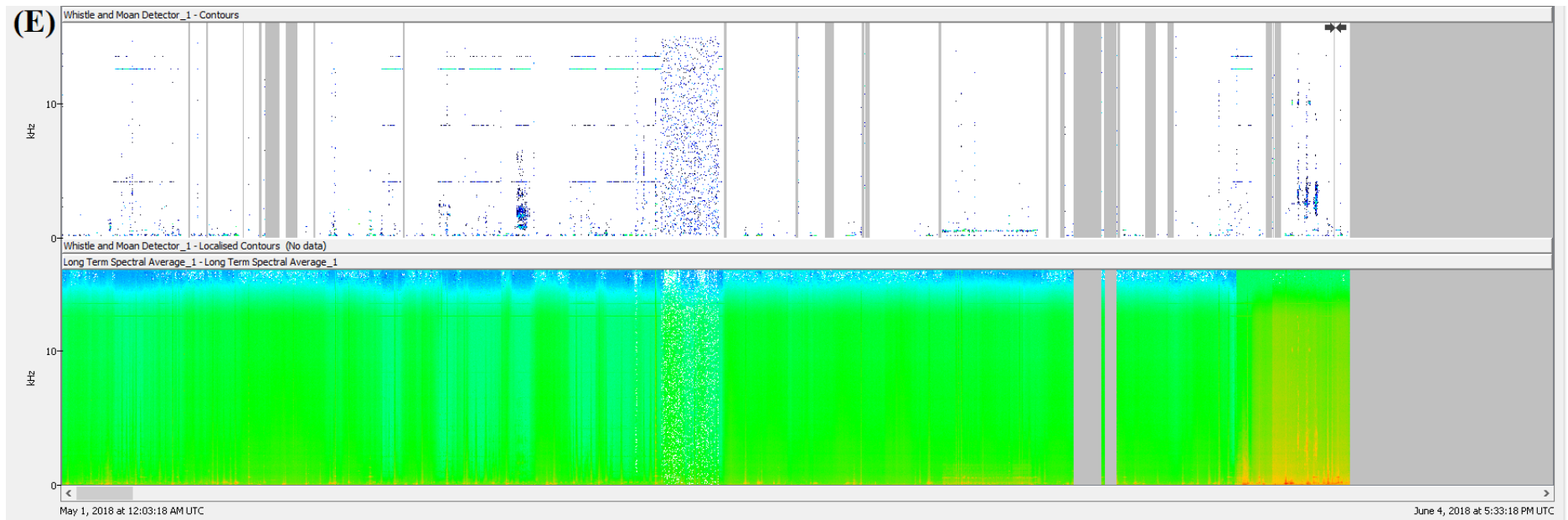
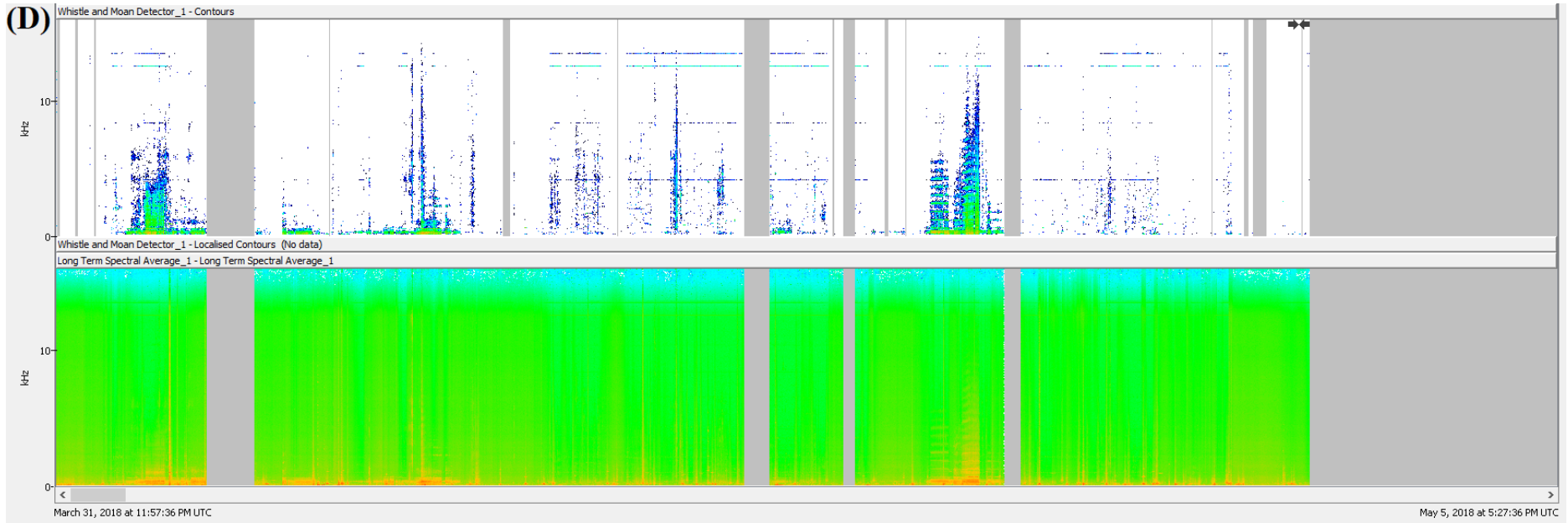
Appendices

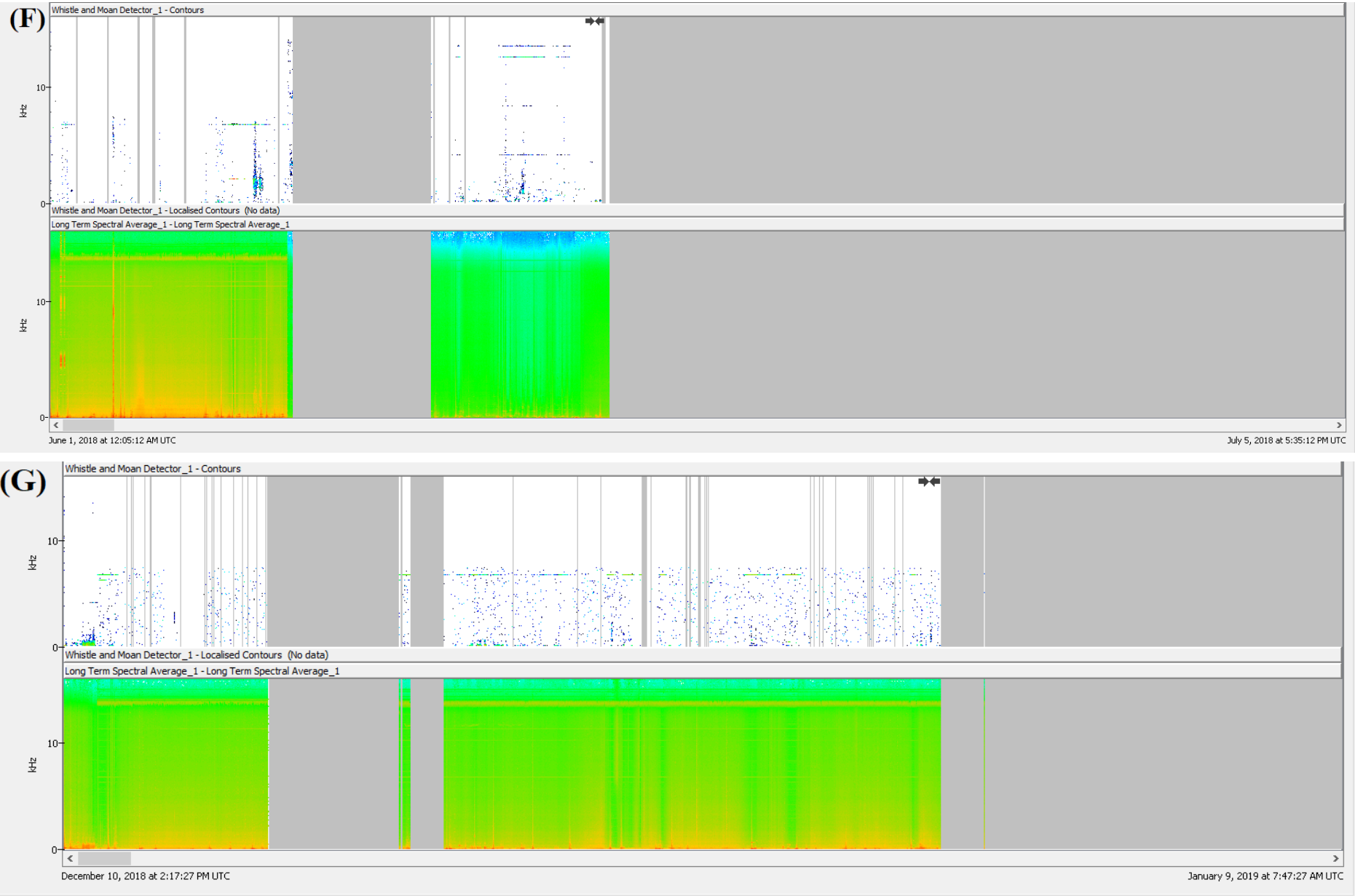
Appendix A

Outputs by PamGuard's LTSA and WMD for each month throughout the study period January 2018 – January 2019.









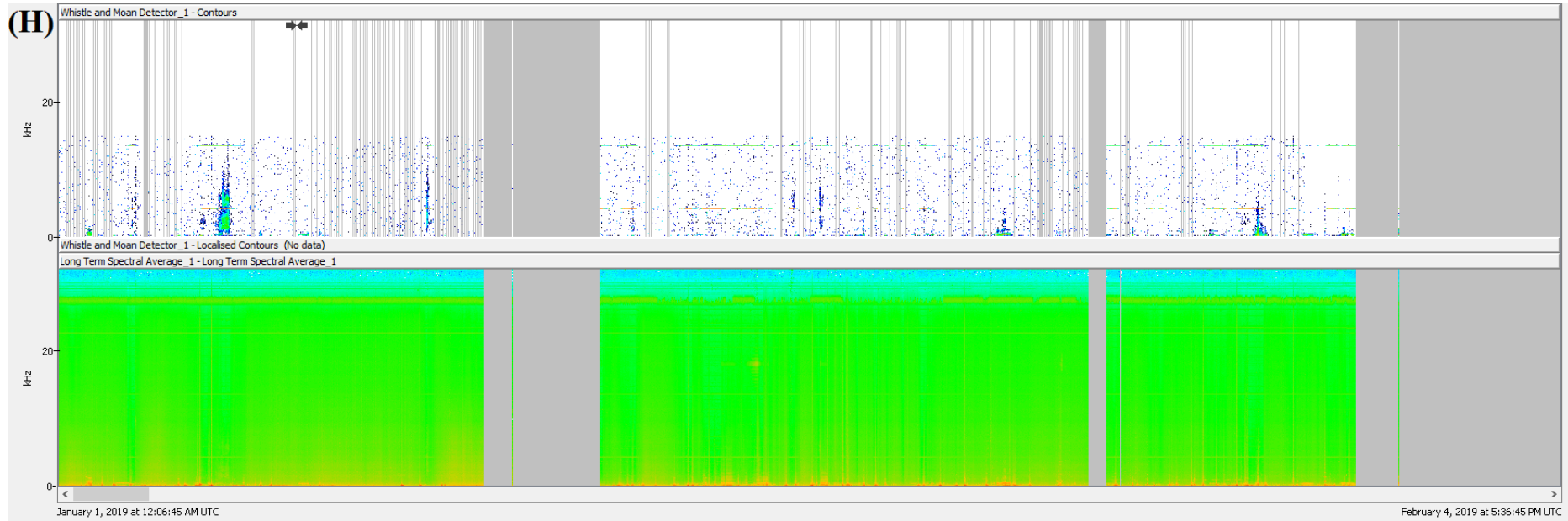


Figure A1. Output by PamGuard’s LTSA and Whistle and Moan Detector (WMD) of data from 2018: January (A), February (B), March (C), April (D), May (E), June (F), December (G), and 2019: January (H). Vocal activity within the set frequency is indicated by blue-green areas/dots in the WMD (top) and red-yellow areas in the LTSA (bottom). Parameters used as follows: frequencies of 120– 15,000 Hz, fast Fourier transform (FFT) size 4096, sample rate 32,000 Hz, frequency resolution 7.81 Hz, remaining parameters as default. Note, missing (grey) areas in the WMD are due to software issues, whereas missing areas in the LTSA are due to missing data.

Table A1. Parameter description of all variables used in the random forest analysis.

| Acoustic parameter | Description |
|-----------------------|--------------------------------|
| Duration (s) | Vocalisation length |
| High frequency (Hz) | Maximum frequency |
| Low frequency (Hz) | Minimum frequency |
| Bandwidth (Hz) | High – Low frequency |
| Frequency range (Hz) | High / Low frequency |
| Start frequency (Hz) | Start frequency |
| End frequency (Hz) | End frequency |
| Frequency trend (Hz) | Start / End frequency |
| Peak frequency (Hz) | Frequency of the spectral peak |
| Number of inflections | Number of reversals in slope |

Appendix B

Table B1. Summary of all identified themes and the number phrases across the defined study period. Set medians as unit sequences (=phrase) representing each identified theme across the entire dataset, regardless of recording period. Within-set similarity reveals the average similarity of all phrase sequences within the same theme (0=no similarity, 1=complete similarity).

| Theme | No. of phrases | Period | Set median (unit sequence) | Within-set similarity |
|-----------|----------------|--------|---|-----------------------|
| 1 | 42 | Jan-18 | 4-sm, 4-sm, 4-sm, 4-sm, 4-sm, 5-dmm | 0.74 |
| | 32 | Feb-18 | | |
| | 25 | Mar-18 | | |
| | 44 | Apr-18 | | |
| 2 | 36 | Jan-18 | 19-awl, 6-wamo, 19-awl, 6-wamo, 7-dgr, 4-sm | 0.67 |
| | 35 | Feb-18 | | |
| | 43 | Mar-18 | | |
| 2a | 31 | Mar-18 | 19-awl, 14-mofe, 19-awl, 14-mofe, 7-dgr, 4-sm | 0.83 |
| | 38 | Apr-18 | | |
| 2b | 85 | Apr-18 | 27-dwl, 14-mofe, 27-dwl, 14-mofe, 7-dgr, 4-sm | 0.82 |

Table B2. LSI matrix showing averaged similarities between the set medians of all phrase types representing a theme calculated per song session.

| Theme | 4 | 5 | 1 | 2 | 3 | 6 | 3a | 4a | 6a | 6b | 2a | 2b | 10 | 9 | 7 | 5a | 8 | 5b |
|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|---|------|------|----|
| 4 | 0.67 | | | | | | | | | | | | | | | | | |
| 5 | 0.06 | 0.71 | | | | | | | | | | | | | | | | |
| 1 | 0 | 0 | 0.78 | | | | | | | | | | | | | | | |
| 2 | 0 | 0 | 0.08 | 0.82 | | | | | | | | | | | | | | |
| 3 | 0 | 0 | 0 | 0.14 | 0.78 | | | | | | | | | | | | | |
| 6 | 0.06 | 0 | 0 | 0 | 0 | 0.75 | | | | | | | | | | | | |
| 3a | 0 | 0 | 0 | 0.15 | 0.72 | 0 | 1 | | | | | | | | | | | |
| 4a | 0.36 | 0.06 | 0 | 0 | 0 | 0.00 | 0 | 0.67 | | | | | | | | | | |
| 6a | 0 | 0 | 0 | 0 | 0 | 0.22 | 0 | 0.01 | 0.90 | | | | | | | | | |
| 6b | 0.01 | 0 | 0 | 0 | 0 | 0.20 | 0 | 0.00 | 0.75 | 0.81 | | | | | | | | |
| 2a | 0 | 0 | 0.08 | 0.65 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | | | | | | |
| 2b | 0 | 0 | 0.08 | 0.46 | 0.08 | 0 | 0.08 | 0 | 0 | 0 | 0.58 | 0.92 | | | | | | |
| 10 | 0 | 0 | 0.10 | 0 | 0 | 0 | 0 | 0 | 0 | 0.01 | 0 | 0 | 0.68 | | | | | |
| 9 | 0 | 0 | 0 | 0.20 | 0.05 | 0 | 0.06 | 0 | 0 | 0 | 0.15 | 0.18 | 0 | 0.87 | | | | |
| 7 | 0 | 0 | 0 | 0 | 0.29 | 0 | 0.33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | | |
| 5a | 0 | 0.69 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.08 | 0.75 | |
| 5b | 0 | 0.36 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.02 | 0 | 0 | 0.15 | 0 | 0 | 0.35 | 0.03 | 1 |

Table B3. Transcribed theme sequences of all sessions throughout the study period January 2018 – January 2019. Hyphen (--) represent the split between song cycles.

| Year | Date | Session label | Theme sequence | Set median |
|------|-------|---------------|---|---------------------|
| 2018 | 03-01 | 18_1 | 4, 5, 1, 2, 3, 6 -- 5, 1, 2, 3, 6, -- 4, 5, 1, 2, 3, 6 | 4, 5, 1, 2, 3, 6 |
| | 18-01 | 18_2 | 4, 5, 1, 2, 3, 6 -- 4, 1, 2, 3, 6 -- 4, 5, 1, 2, 3, 6 | 4, 5, 1, 2, 3, 6 |
| | 24-01 | 18_3 | 4, 1, 2, 3a, 6 -- 4, 5, 1, 2, 3a, 6 -- 4, 5, 1, 2, 3a, 6 | 4, 5, 1, 2, 3a, 6 |
| | 17-02 | 18_4 | 4, 5, 1, 2, 3, 6 -- 4, 5, 1, 2, 3, 6 -- 4, 5, 1, 2, 3, 6 | 4, 5, 1, 2, 3, 6 |
| | 20-02 | 18_5 | 4a, 5, 1, 2, 3, 6 -- 4a, 5, 1, 2, 3, 6 -- 4a, 5, 1, 2, 3, 6 | 4a, 5, 1, 2, 3, 6 |
| | 25-02 | 18_6 | 4a, 1, 2, 3, 6a -- 4a, 5, 1, 2, 3, 6a -- 4a, 1, 2, 3, 6a | 4a, 1, 2, 3, 6a |
| | 03-03 | 18_7 | 4a, 1, 2, 3, 6a -- 4a, 1, 2, 3, 6a -- 4a, 1, 2, 3, 6a | 4a, 1, 2, 3, 6a |
| | 13-03 | 18_8 | 4a, 5, 1, 2, 3, 6a -- 4a, 5, 1, 2, 3, 6a -- 4a, 5, 1, 2, 3, 6a | 4a, 5, 1, 2, 3, 6a |
| | 27-03 | 18_9 | 4a, 5, 1, 2a, 3, 6a -- 4a, 5, 1, 2a, 3, 6a -- 4a, 5, 1, 2a, 3, 6a | 4a, 5, 1, 2a, 3, 6a |
| | 03-04 | 18_10 | 4a, 1, 2a, 3, 6a -- 4a, 1, 2a, 3, 6a -- 4a, 1, 2a, 3, 6a | 4a, 1, 2a, 3, 6a |
| | 09-04 | 18_11 | 4a, 1, 2b, 3, 6a -- 4a, 1, 2b, 3, 6a -- 4a, 5, 1, 2b, 3, 6a | 4a, 1, 2b, 3, 6a |
| | 22-04 | 18_12 | 4a, 1, 2b, 3, 6a -- 4a, 1, 2b, 3, 6a -- 4a, 1, 2b, 3, 6a | 4a, 1, 2b, 3, 6a |
| 2019 | 01-01 | 19_13 | 10, 9, 7, 6b -- 10, 9, 7, 6b -- 10, 9, 7, 6b | 10, 9, 7, 6b |
| | 25-01 | 19_15 | 10, 5a, 8, 9, 7, 6b -- 10, 5a, 8, 7, 6b -- 10, 5a, 8, 9, 7, 6b | 10, 5a, 8, 9, 7, 6b |
| | 31-01 | 19_15 | 5b, 8, 9, 7, 6b -- 5b, 8, 9, 7, 6b -- 5b, 8, 9, 7, 6b | 5b, 8, 9, 7, 6b |

Table B4. LSI matrix showing similarities between set medians representing a song (sequence of themes) per song session.

| Month year | Jan18 | Jan18 | Jan18 | Feb18 | Feb18 | Feb18 | Mar18 | Mar18 | Mar18 | Apr18 | Apr18 | Apr18 | Jan19 | Jan19 | Jan19 |
|------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Session | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| Jan18_1 | 1 | | | | | | | | | | | | | | |
| Jan18_2 | 1 | 1 | | | | | | | | | | | | | |
| Jan18_3 | 0.83 | 0.83 | 1 | | | | | | | | | | | | |
| Feb18_4 | 1 | 1 | 0.83 | 1 | | | | | | | | | | | |
| Feb18_5 | 0.83 | 0.83 | 0.67 | 0.83 | 1 | | | | | | | | | | |
| Feb18_6 | 0.5 | 0.5 | 0.33 | 0.5 | 0.67 | 1 | | | | | | | | | |
| Mar18_7 | 0.5 | 0.5 | 0.33 | 0.5 | 0.67 | 1 | 1 | | | | | | | | |
| Mar18_8 | 0.67 | 0.67 | 0.5 | 0.67 | 0.83 | 0.83 | 0.83 | 1 | | | | | | | |
| Mar18_9 | 0.5 | 0.5 | 0.33 | 0.5 | 0.67 | 0.67 | 0.67 | 0.83 | 1 | | | | | | |
| Apr18_10 | 0.33 | 0.33 | 0.17 | 0.33 | 0.5 | 0.8 | 0.8 | 0.67 | 0.83 | 1 | | | | | |
| Apr18_11 | 0.33 | 0.33 | 0.17 | 0.33 | 0.5 | 0.8 | 0.8 | 0.67 | 0.67 | 0.8 | 1 | | | | |
| Apr18_12 | 0.33 | 0.33 | 0.17 | 0.33 | 0.5 | 0.8 | 0.8 | 0.67 | 0.67 | 0.8 | 1 | 1 | | | |
| Jan19_13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | |
| Jan19_14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.67 | 1 | |
| Jan19_15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.6 | 0.67 | 1 |

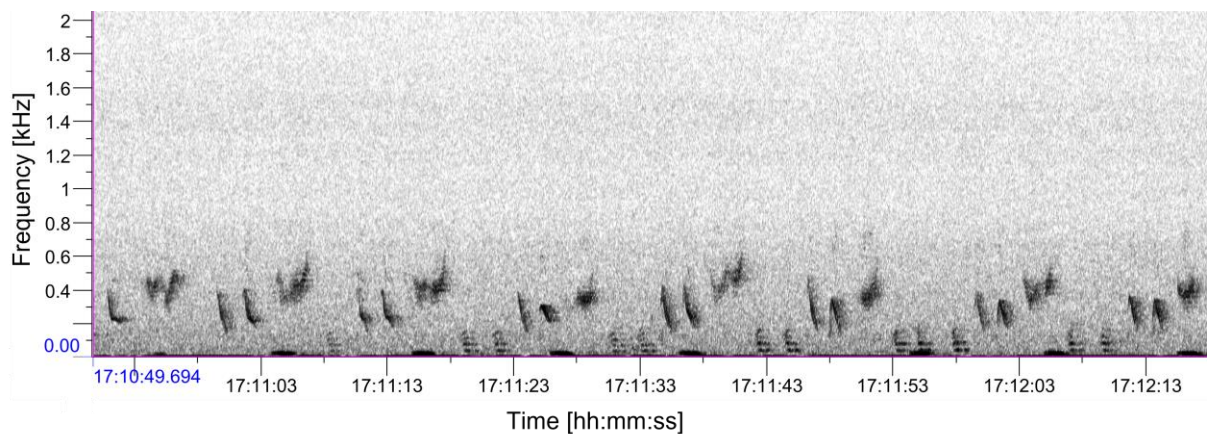


Figure B1. Spectrographic representation of theme 7 in January 2019. The spectrogram was produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

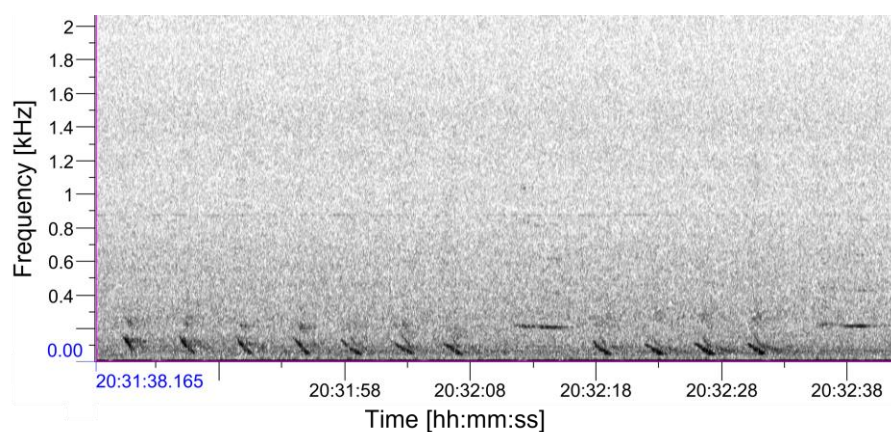


Figure B2. Spectrographic representation of theme 8 in January 2019. The spectrogram was produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

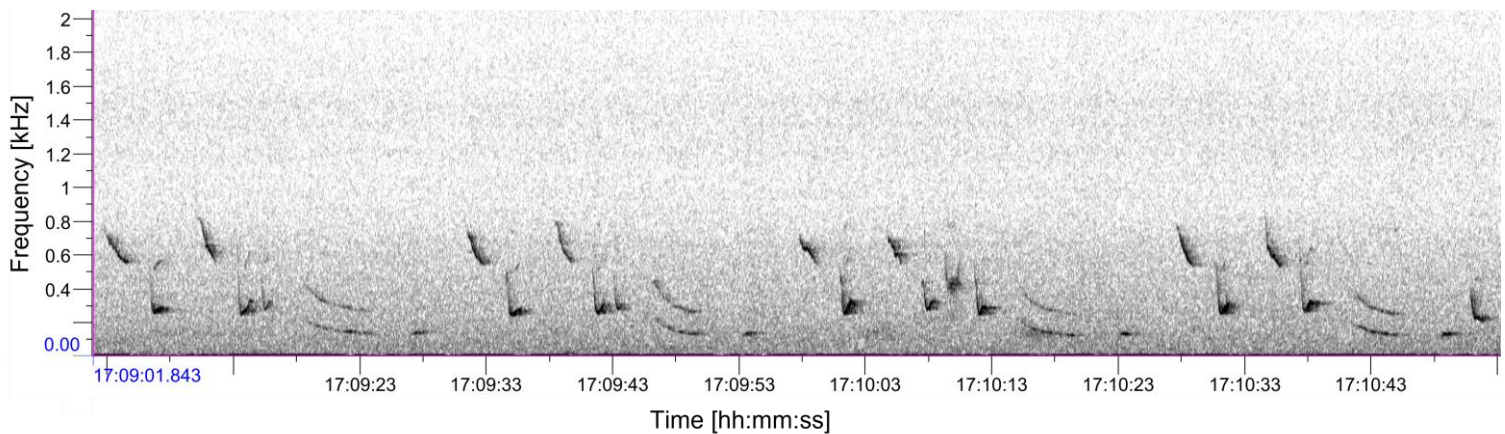


Figure B3. Spectrographic representation of theme 9 in January 2019. The spectrogram was produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

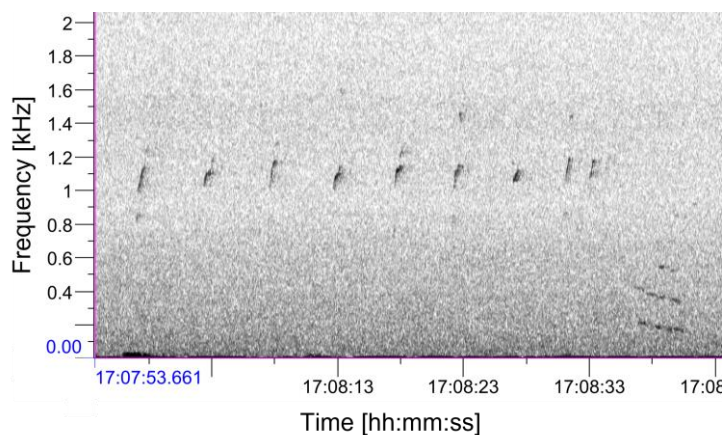


Figure B4. Spectrographic representation of phrase type and theme 10 in 2019 song. The spectrogram was produced using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

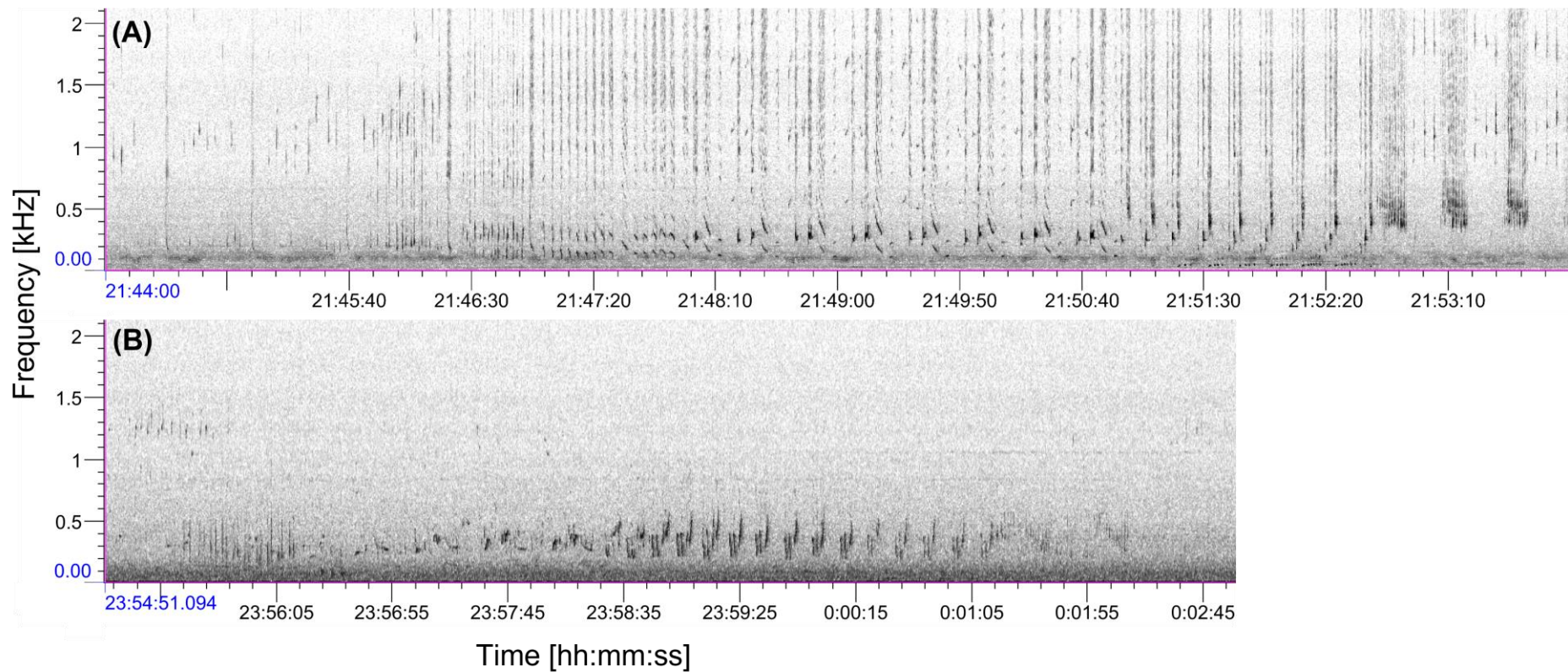


Figure B5. Spectrographic representation of an observed humpback whale song cycle in March 2018 (A) and January 2019 (B) showing changes within the hierarchical structure between years. Note, no harmonics are visible in spectrogram (C) due to a decreased quality of the recording. Spectrograms generated using fast Fourier transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Time on the x-axis is given in hours:minutes:seconds.

