Sveučilište u Zagrebu
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Analysis of humpback whale song from the Eastern Caribbean

Diplomski rad

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TEMELJNA DOKUMENTACIJSKA KARTICA

Sveučilište u Zagrebu
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ANALIZA PJESME GRBAVOG KITA S ISTOČNIH KARIBA

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Mužjaci grbavih kitova proizvode hijerarhijski strukturirane i kompleksne pjesme. Ove pjesme su naučene i konstantno se mijenjaju kroz evolucijske i revolucijske procese vodoravnog prijenosa kulture. Populacije iz istog oceana pokazuju sličnosti u svojim pjesmama, dok geografski odvojene populacije imaju potpuno različite pjesme. Iako su detaljne analize varijacija unutar pjesama istih i različitih jedinki rijetke, prijeko su potrebne za razumijevanje kako individulno učenje pjesama utječe na kulturne promjene na razini populacija, koje se proučavaju od 1970-ih godina. U ovom istraživanju analizirane su pjesme grbavih kitova iz sjevernog Atlantika i južnog Pacifika. Za klasifikaciju jedinica pjesme je testirana automatizirana metoda, ali, budući da se pokazala nezadovoljavajućom, podjela pjesmi se oslanjala na ljudsku procjenu. Pjesme su podijeljene na jedinice, fraze i teme, koje su onda uspoređene metodom Levenshteinove udaljenosti. Rezultati su pokazali da pjesme iz sjevernog Atlantika dijele značajan dio materijala, ali da pjesma iz Australije ne pokazuje nikakve sličnosti na razini fraza i tema s pjesmama iz sjevernog Atlantika. Ovaj rad pruža dokaze o vodoravnom prijenosu pjesama grbavih kitova unutar istog oceana, koji se ne događa između geografski udaljenih područja.

(34 stranica, 11 slika, 9 tablica, 49 literaturnih navoda, jezik izvornika: engleski)

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ANALYSIS OF HUMPBACK WHALE SONG FROM THE EASTERN CARIBBEAN

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Male humpback whales produce hierarchically structured and complex songs. These songs are learned, and are constantly changing at both evolutionary and revolutionary tempos through horizontal cultural transmission processes. Populations within the same ocean basin share similarities in their song displays, whereas geographically distinct populations have completely different songs. However, fine-scale analyses of variation in song production within and between individuals are sparse, but essential for understanding the details of how individual song learning can produce the population level cultural changes that have been observed since the 1970s. In this study, songs of humpback whales from the North Atlantic and South Pacific Ocean were analysed. An automated method for song unit classification was tested, against classification by a human observer, and the latter proved more effective. All songs were divided into unit, phrase and theme sequences which were then compared using the Levenshtein distance metric. The results showed that songs from North Atlantic shared a significant portion of their material, and that the Australian song had no similarity at phrase and theme level with any of the North Atlantic songs. This study provides evidence of horizontal cultural transmission of humpback whale songs within the same ocean basin that does not occur with a wider geographical separation.

(34 pages, 11 figures, 9 tables, 49 references, original in: English)

Thesis deposited in the Central Biological Library

Key words: whale song, cultural transmission, vocal communication, Levenshtein distance

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Contents

Introduction

There are many different ways in which animals communicate, but few can compete with humpback whales (*Megaptera novaeangliae*) when it comes to the complexity of their vocal displays. Humpback whales can produce a variety of sounds that range from 'social sounds' that both males and females generate (Winn *et al*. 1979, Tyack 1983, Dunlop *et al*. 2007), to complex and highly structured songs (Payne & McVay 1971, Winn & Winn 1978, Payne *et al*. 1983) which are sung just by males (Darling *et al*. 1983, Glockner 1983).

Humpbacks belong to the baleen whales, or mysticetes, which have baleen instead of teeth, and two blowholes, opposed to tothed whales which have just one. They can grow up to 16 m and weigh more than 40 tons, but the average length for females is 13 m, and for males 12.5 m. Both females and males reach sexual maturity between the ages of 5 and 10, although males don't start breeding until later. Females give birth every two to three years to a single calf, which they nurse for a year. Humpback whales have a cosmopolitan distribution. Except the Arabian Sea population that remains there for the entire year, humpbacks from all around the world undertake long seasonal migrations from high latitude summer feeding grounds to low latitude winter feeding grounds. There are an estimated 35 – 40 000 humpbacks in the Northern Hemisphere and about 50 000 in the Southern hemisphere (Clapham 2013).

In 1971, Payne and McVay established the terminology for hierarchical structure of a humpback whale song, and the same classification of song elements has been used ever since. The smallest element of a song is a unit and it is defined as 'the shortest sound that is continuous to our ears when heard in real time' (Payne & McVay 1971). A repeated sequence of units comprises a phrase, several phrases make up a theme and a few themes constitute a song. Male humpbacks often cyclically repeat their songs during bouts of production, each repetition is referred to as a song cycle, and one or more song cycles make up a song session. These sessions can last for hours; Winn & Winn (1978) reported one whale singing continuously for 22 h. Although there is clearly some consistency in the song structure, there is quite a bit of variability both within- and between- individual whale songs.

Humpbacks from around the world have the same repertoire of units they can produce, but the order in which they are arranged varies in different areas (Payne and Guinee 1983). All individuals within a breeding population sing a similar version of the song, and populations from the same ocean basin share similarities in their song displays, but geographically distinct populations have completely different songs (Winn *et al.* 1981, Payne & Guinee 1983, Payne *et al*. 1983, Helweg *et al*. 1998, Cerchio *et al*. 2001, Darling & Sousa-Lima 2005).

A number of studies have described changes in songs across populations (Winn *et al.* 1981, Guinee *et al*. 1983, Payne *et al.* 1983, Payne & Guinee 1983, Helweg *et al.* 1998, Cerchio *et al.* 2001), but variation within the same population has also been documented. Some songs of the individual whales were so different from the 'norm' of the particular temporal and spatial region that Frumhoff (1983) termed them 'aberrant'.

Male humpbacks sing predominantly on the winter breeding grounds (Payne & McVay 1971, Winn & Winn 1978) and on the migration routes between breeding and summer feeding grounds (Payne & McVay 1971, Clapham & Mattila 1990), but they are also heard singing on their feeding grounds (Mattila *et al*. 1987, McSweeney *et al.* 1989, Clark & Clapham 2004).

Since it appears that only males sing, sexual selection is a leading hypothesis for the evolution of humpback song. However, while different hypotheses have been proposed about the role of singing in the humpback whale mating system, it is still unclear whether the primary function is of inter- or intra- sexual nature. Some researchers suggest that the songs have a role in female attraction (Tyack 1981, Clapham 1996, Smith *et al*. 2008), while others believe that its purpose is largely related to male – male interactions (Darling *et al*. 2006, Cholewiak 2008). Song may of course function in both ways.

Researchers noticed early on that songs slowly evolve from one form to another (Guinee *et al*. 1983, Payne *et al*. 1983, Payne & Payne 1985), but later research has also revealed that one populations' song can be completely replaced by a song from the other population within a period of just two years, which was referred to as 'cultural revolution' (Noad *et al.* 2000). This was initially reported as occurring just once in the Eastern Australia breeding population (Noad *et al.* 2000), but it has since been shown to be a regular occurrence in populations all across the South Pacific, which appear to regularly discard their own song completely and instead take up the song of a neighbouring population *in toto* (Garland *et al.* 2011). Both entire songs and song changes are rapidly spread across the populations via vocal learning through a process of horizontal (i.e. largely within-generation) cultural transmission (Rendell & Whitehead 2001, Eriksen *et al.* 2005, Garland *et al.* 2011).

Payne and Guinne (1983) proposed three potential paths for exchanging songs between different populations. The first one was that it might happen inbetween breeding seasons on common migration routes and/or feeding grounds, for which Garland *et al.* recently (2013) provided evidence. The second possibility was that individuals might go to more than one breeding ground within the same season, and the third one was that individuals go to different breeding grounds in subsequent winters. However, these last two possibilities are unlikely, because we now know that humpbacks show strong maternally determined fidelity to breeding grounds (Clapham *et al.* 1993, Palsbøll *et al.* 1995, Stevick *et al*. 2006).

Analysing the songs of humpbacks involves one of the most fundamental issues in studying animal behaviour, the categorisation of behavioural patterns (Janik 1999). In bioacoustics, the problem of delineating appropriate categories for sounds is perennial, whether talking about sperm whale codas (Rendell & Whitehead 2003), signature whistles in dolphins or killer whale calls (Deecke & Janik 2006). Because the same problem exists with delineation of humpback whale song (Cholewiak *et al*. 2013), there have been several attempts to develop automated methods for classifying song elements in the last decade (Maeda *et al.* 2000, Suzuki *et al*. 2006, Green *et al*. 2010, Pace *et al.* 2010, Garland *et al.* 2012). Recently, Cholewiak *et al*. (2013) carried out an extensive review of current classification issues in which they acknowledge that 'no system has yet been demonstrated which compares with the pattern recognition skills of the human brain' and propose a set of guidelines for consistent delineation of songs.

I analysed three song recordings from different locations: two from the North Atlantic (Caribbean Island of Dominica and Georges Bank) and one from the Southwest Pacific (off of Peregian Beach, Queensland). The Antillean Island chain (which includes Dominica) is a known breeding area for humpbacks and Georges Bank is one of their North Atlantic feeding grounds (Kennedy *et al.* 2014). Humpback whales from Southwest Pacific migrate along the eastern coast of Australia, so they pass Peregian beach twice every year while migrating between their feeding and breeding grounds (Cato 1991, Noad & Cato 2001).

Aims

The aims of this study were to:

1. Conduct a detailed analysis of the song recorded near the Caribbean Island of Dominica using both manual and automated method for unit classification
2. Decide which method for classifying units is to be used for the other songs
3. Delineate songs into unit, phrase and theme sequences
4. Estimate how many song units are shared within and between populations
5. Explain how different sequences are distributed across songs
6. Compare the structure of all songs at unit, phrase and theme level using the Levenshtein distance method
7. Characterise individual variation in song production (how similar are the songs from the same song session of the same whale)
8. Examine how much variance is there between different whales' song repertoires, both within the same ocean basin and between different oceans

Hypothesis

The hypothesis was, according to the current literature on humpback song, that songs from the North Atlantic should share some similarities between themselves, but very few with the Australian song (with the possibility of sharing some parts of the unit repertoire).

Materials and methods

Recordings of songs

The first song was recorded on 9th of May 2012 at 14:11:48 using a towed 2-element hydrophone array based on Benthos AQ-4 elements (Schulz *et al.* 2011) deployed from a 14 m sailboat near the Caribbean Island of Dominica (15° N, -61° W) (Figure 1). The recording was made on a laptop PC using a Fireface 400 sound card and Pamguard software with a sampling rate of 96000 Hz.

The second song was recorded in Georges Bank (40° N, -69° W) (Figure 1) on 17th of April 2012 at 12:45:00 using Marine Autonomous Recording Units (Calupca *et al.* 2000) with sampling rate of 5000 Hz. The relatively low sampling rate for this recording meant that only frequencies up to 2500 Hz were registered.

The third song was recorded on 9th of September 2012 at 7:37:32 with an Acousonde 3A recorder (Sousa-Lima *et al.* 2013) deployed off of Peregian Beach, Queensland (-26° N, 153° E) (Figure 1). The sample rate was set to 27330 Hz, but an anti-aliasing filter was used that restricted the maximum frequency to 9292 Hz, so again the high frequencies were cut off.

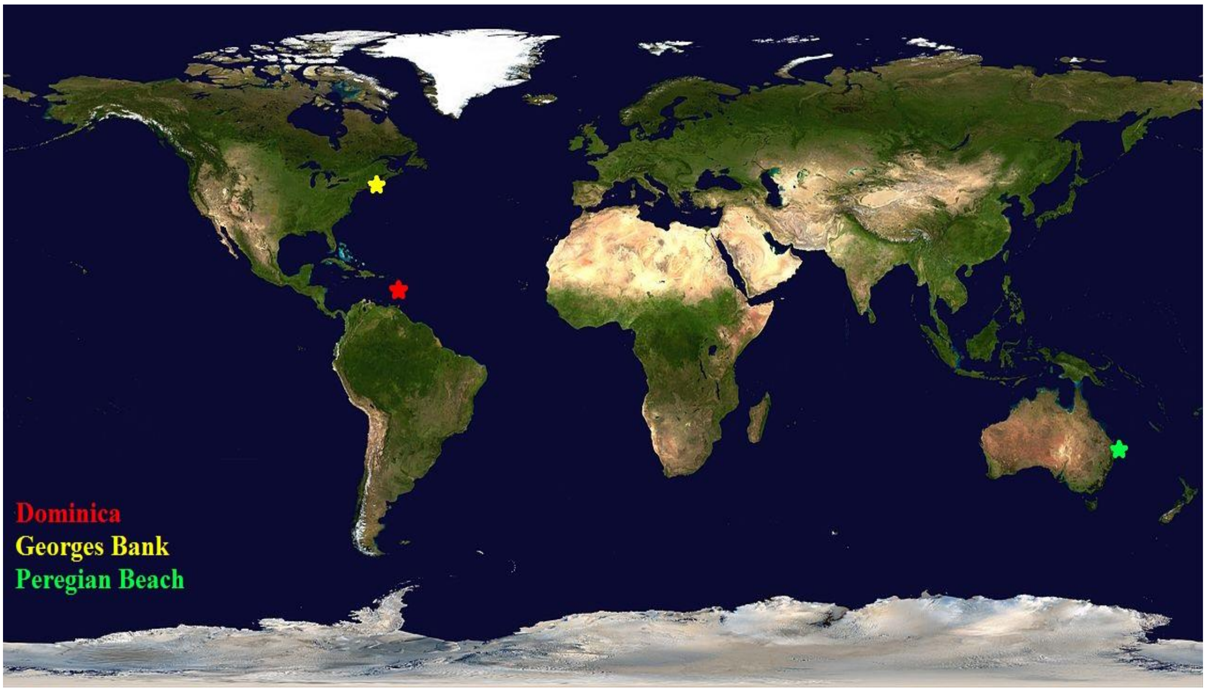

Figure 1: Locations of the recording sites

Acoustic analysis

Regardless of the quality of recordings (which varied considerably in both sampling rates and signal-to-noise ratios), all songs were viewed as spectrograms in Adobe Audition 3.0, calculated using a Blackmann–Harris window and Fast Fourier Transform (FTT) size of 1024. The songs were split into themes, phrases and units based on their visual and aural characteristics, taking into account the highly structured hierarchy of the song and the position of song elements in the song. The delineation of songs can be very challenging and subjective, so guidelines presented by Cholewiak *et al.* (2013) were followed.

Classification of units

The first song was divided into units using markers in Adobe Audition 3.0 (Figure 2). Units were classified into types and units of the same type were copied into the same file. Every file was imported separately in Raven Pro 1.3 for further analysis.

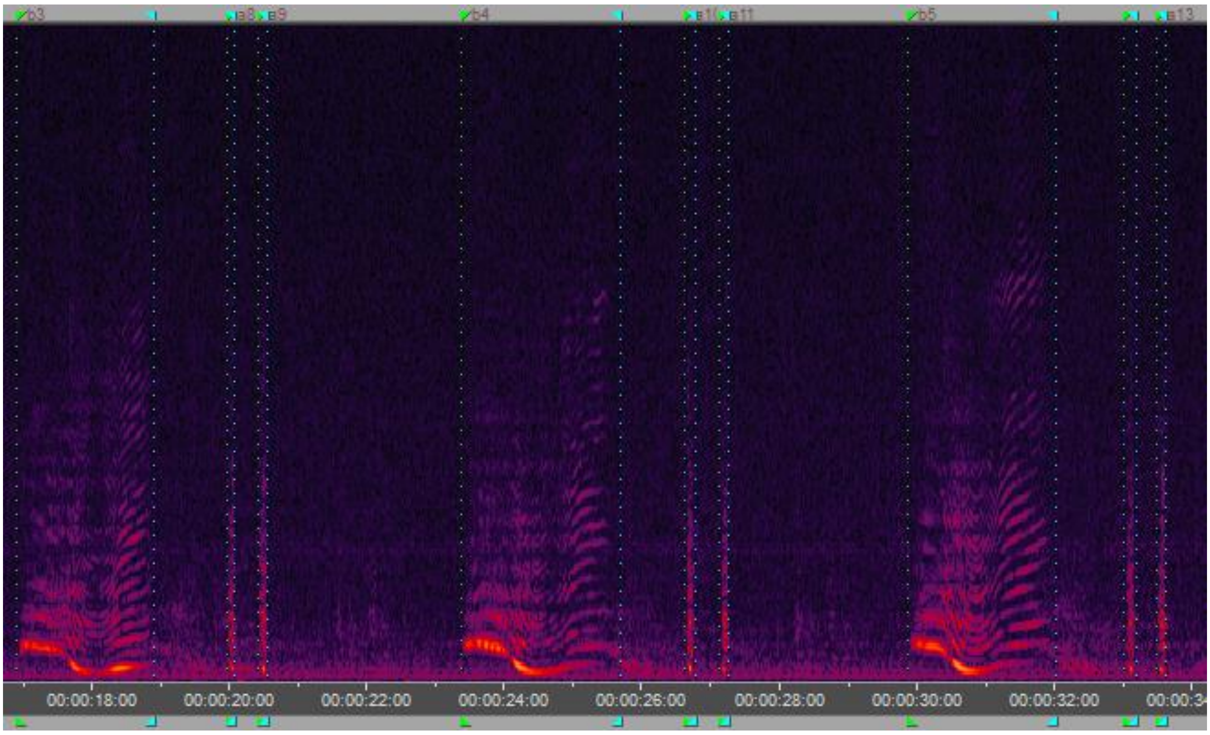

Figure 2: Example of unit markers in Adobe Audition 3.0

Spectrograms of units were produced in Raven Pro 1.3 using a Hamming window and FFT size of 8192. Measurements were made using range selections (Figure 3). By default, Raven performs four measures that define the edges of selections in spectrogram view – begin time, end time, low frequency and high frequency. In addition to these default measures, maximum frequency (the frequency at which maximum power occurs within the selection), delta frequency (the difference between the upper and lower frequency limits of the selection) and delta time (the difference between begin and end time for the selection) were also calculated, as well as robust signal measurements (measurements that do not vary much with changing the selection borders). The robust measurements included: center frequency (the frequency that divides the selection into two frequency intervals of equal energy), first quartile frequency (the frequency that divides the selection into two frequency intervals containing 25% and 75% of the energy in the selection), third quartile frequency (the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection) and inter-quartile range bandwidth (the difference between the first and the third quartile frequency).

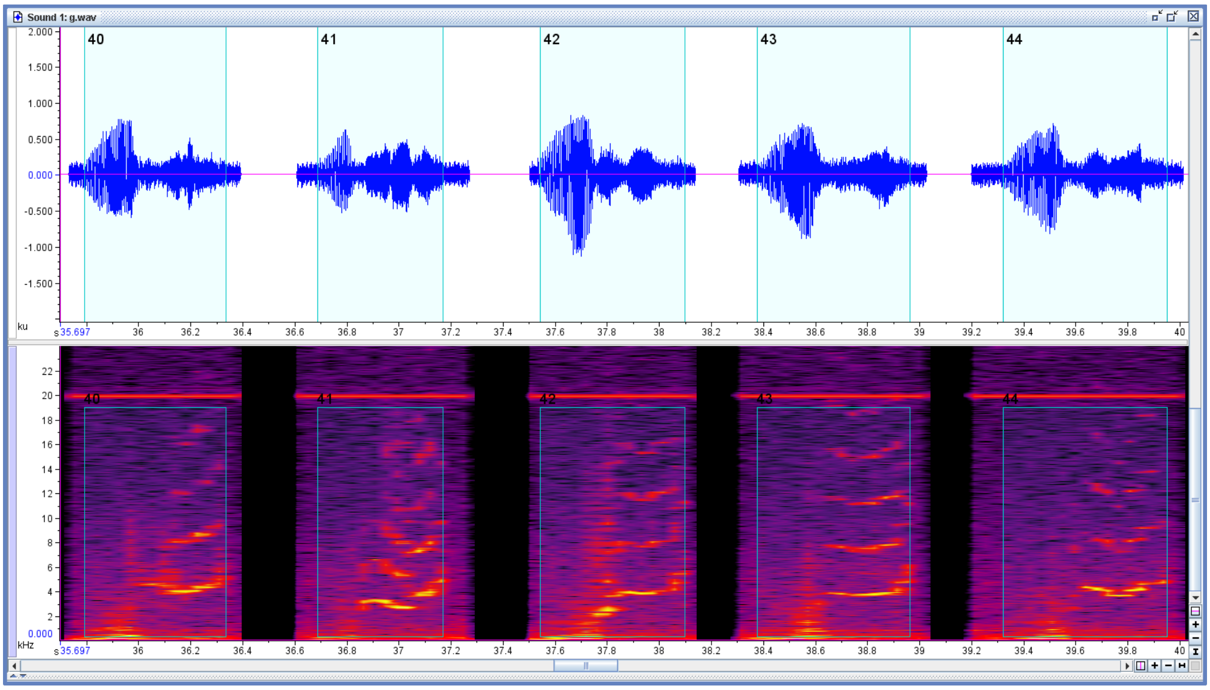

Figure 3: Example of range selections in Raven Pro 1.3

In order to test if the measurements taken in Raven Pro 1.3 could explain the human classification of units, a principal component analysis (PCA) was conducted in Matlab R2013b. It turned out that the principal components were not enough to explain all the variation within the unit types, as will be shown in the results. The decision was made to retain the original classification and use only a human classifier for the rest of the songs.

The songs from the second and the third recording were viewed as spectrograms in Adobe Audition 3.0 and each unit was given a descriptive name (e. g., moan, groan, squeak, whoop) to make the process of unit recognition faster. Descriptive names were then replaced with coded names (e. g., a, b, c, d). There were seven unit types that occurred in more than one song, so the same names were used for the units of the same type, regardless of which song they came from. Spectrograms of all the unit types are presented in Appendix I and all song sequences represented by unit codes are shown in Appendix II.

Classification of phrases and themes

The classification of phrases and themes was especially challenging because there were many ways in which they could be delineated. However, as many authors (Frumhoff 1983, Payne *et al.* 1983, Cerchio *et al*. 2001) agreed that phrase duration is one of the most stable characteristics of the humpback whale song, duration was the main criterion used for the phrase interpretation. Phrases were measured from the beginning of one to the beginning of another (subsequent) phrase, as suggested by Cholewiak *et al*. (2013). Figure 4 shows two different phrase types, both lasting for 14 seconds.

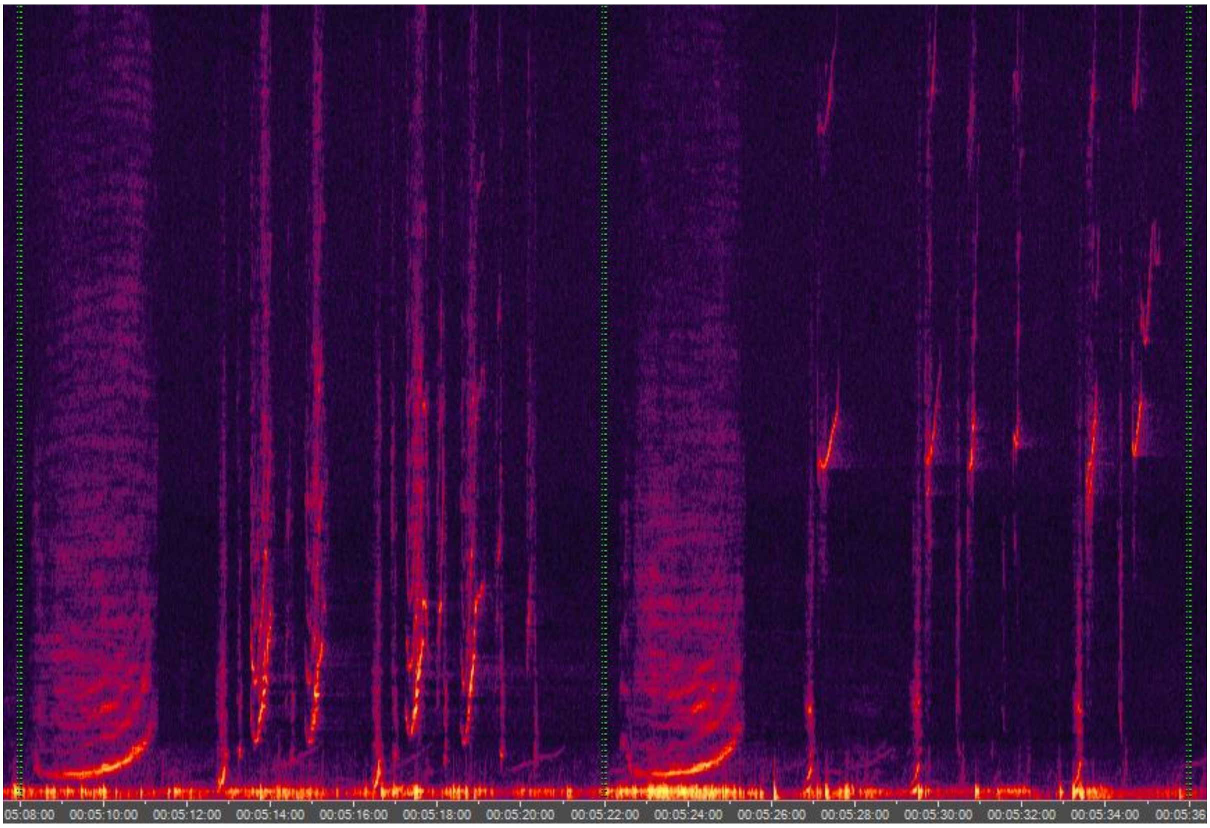

Figure 4: Duration of phrases

Because the number of phrases in themes can be extremely variable, the duration of themes is not a reliable feature, therefore decisions about theme delineation depended only on theme structure. Figure 5 shows the end of one and the beginning of the other theme.

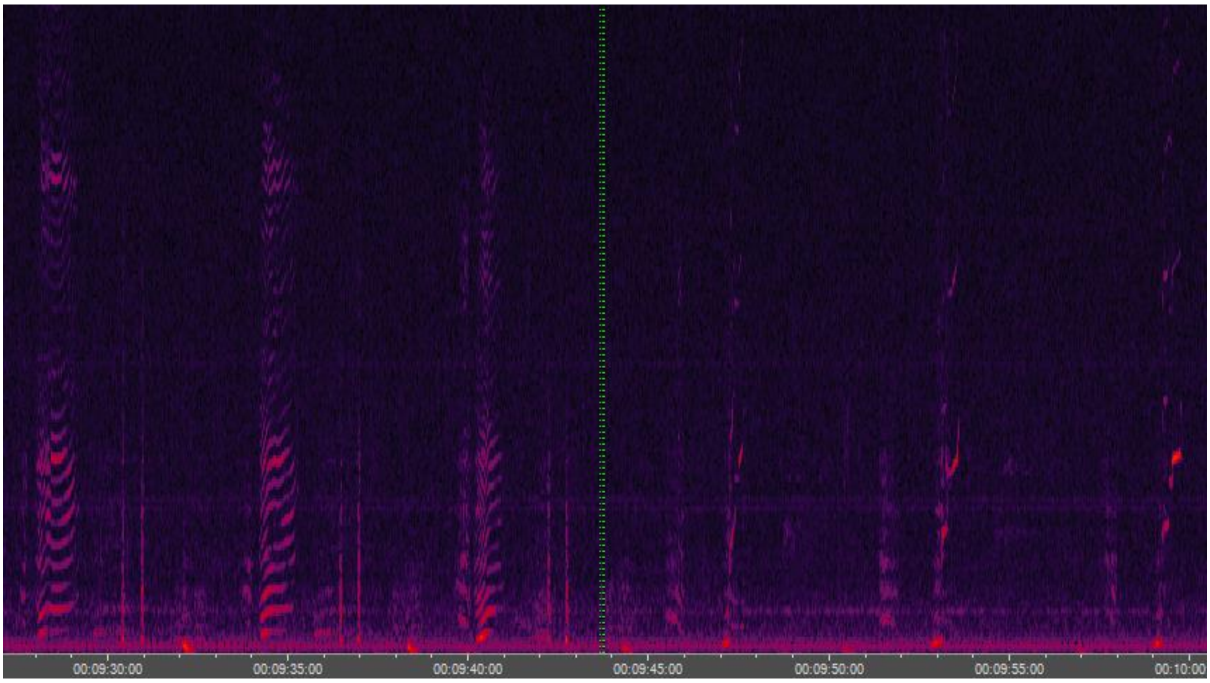

Figure 5: The switch from one theme to another

Song classification

The Eastern Caribbean recording captured only one complete song cycle, so the analysis included just one song from that area which was named ‘song 1’. The recording from Georges Bank included six full songs from the same song session and all of them were analysed. They were given names that started with the number two followed by consecutive letters (e.g., 2a, 2b, 2c). The Australian recording contained part of a song session which included three songs. Because the first one was not recorded from the beginning and the recording stopped before the end of the third one, just the second song (named ‘song 3’) was included in the analysis.

The ‘splitting’ and ‘lumping’ issue

The biggest challenge in delineating songs was to decide how similar two elements of a song have to be to be treated as of the same type, or how different should they be to be assigned different names. In the extreme case, ‘splitter’ approach would be the one in which a new type is assigned every time there is even a small difference, and ‘lumper’ would be if everything that is remotely similar was grouped together.

In songs 1 and 2 some units evolved throughout the song and changed slowly from one type to another, so the problem was to decide at which point in the song the unit changed enough to allocate a new name. The Australian recording was much easier to deal with regarding the unit classification, because the units did not alter during the entire song. For the songs 1 and 2 I tried to decide on something in-between the two approaches, so I allowed some degree of variation in frequency and duration of units, but was very rigorous about the position of units within phrases.

The ‘splitting’ and ‘lumping’ issue was also present when classifying phrases and themes. They also changed throughout the songs; for example, the same unit could be repeated a few more times in subsequent phrases of the same type, or the number of phrase repetitions within themes of the same type could also vary; sometimes one unit stopped appearing, or a new one was introduced, without changing the overall pattern of the song. These examples are shown from a ‘lumper’ perspective; a ‘splitter’ would name all of them different types. Example of theme classification using two different approaches is shown in Figure 6.

SPLITTING	
song	**themes**
1	1Aa-1Ab-1B-1Ca-1Cb-1Da-1Db-1Ea-2A-2B-2C-2D-3-4
2a	5Aa-5Ba-5Bb-5Bc-1Fa-1Cc-1Ga-1Ha
2b	5Ab-5Ac-5Ad-5Ae-5Af-5Ac-5Bb-5Bd-1Fb-1Fc-1Fd-1Fd-1Fe-1Ff-1Cd-1Gb-1Hb
2c	5Ac-5Ac-5Af-5Be-5Bf-5Bg-1Fg-1Fd-1Fb-1Fh-1Cd-1Ce-1Ce-1Gc-1Hc
2d	5Ac-5Ac-5Ag-5Ac-5Bh-5Be-5Bj-5Bc-1Fi-1Fc-1Fj-1Ff-1Fk-1Fj-1Cf-1Ce-1Dc-1Dd-1De-1Eb-1Hd
2e	5Af-5Ah-5Ac-5Ca-5Cb-5Cc-5Cd-5Ce-5Cf-5Bc-5Bk-1Fb-1Fl-1Ff-1Fj-1Fm-1Cg-1Ch-1Gd-1He
2f	5Cg-5Ch-5Ci-5Ai-5Ab-5Bl-5Bm-5Be-5Bn-5Bc-1Fi-1Ff-1Fn-1Fm-1Fm-1Ci-1Ce-1Ec-1Hf
3	6-7-8-9-10-11
LUMPING	
song	**themes**
1	1-1-1-1-1-1-1-1-2-2-2-2-3-4
2a	5-5-5-5-1-1-1-1
2b	5-5-5-5-5-5-5-5-1-1-1-1-1-1-1-1-1
2c	5-5-5-5-5-5-1-1-1-1-1-1-1-1-1
2d	5-5-5-5-5-5-5-5-1-1-1-1-1-1-1-1-1-1-1-1-1
2e	5-5-5-5-5-5-5-5-5-5-5-1-1-1-1-1-1-1-1-1
2f	5-5-5-5-5-5-5-5-5-5-1-1-1-1-1-1-1-1-1
3	6-7-8-9-10-11

Figure 6: 'Splitting' and 'lumping' of theme strings

Transcription of names

The sequences (or strings) of phrases were named with simple combinations of letters and numbers (e.g., A1a, A1b, B1a, B1b). Similar transcription was carried out for themes, but the combinations of characters used were different (e.g., 1Aa, 1Ab) in order to make it more transparent.

For example, the song 1 can be represented by a theme string:

1Aa-1Ab-1B-1Ca-1Cb-1Da-1Db-1Ea-2A-2B-2C-2D-3-4;

and theme 1Aa can be represented by sequence of phrases:

A1a-A1a-A1a-A1a-A1a-A1b-A1c-A1c-A2-B.

As with the units, the same phrases and themes (regardless of which song they came from) were given the same names.

They were then converted into coded names which were later used in the Levenshtein distance analysis. Coding was done so that the same letters and numbers could be used just within the same phrase type, because the results of the analysis were incorrect if just different combinations of the same characters were used. Table 1 contains all the original and corresponding coded names of themes and phrases. Similar colours were used for similar themes and phrases (e. g., blue for themes of type 1) and black was used for all the themes and phrases that came from the Australian song because none of them occurred in any other songs.

Table 1: Transcription of names

original names		coded names		original names		coded names	
themes	phrases	themes	phrases	themes	phrases	themes	phrases
1Aa	A1a	1Aa	A1a	2A	Ib	2II	IIw̄
1Ab	A1b	1Ab	A1b	2B	Ic	2JJ	IIç
1B	A1c	1Bs	A1c	2C	Ja	2KK	JJғ
1Ca	A1d	1Cc	A1d	2D	Jb	2LL	JJƼ
1Cb	A2	1Cd	A22	3	Jc	333	JJȝ
1Cc	A3a	1Ce	A3e	4	Ka	444	KKҧ
1Cd	A3b	1Cf	A3f	5Aa	Kb	5Mτ	KKɷ
1Ce	A3c	1Cg	A3g	5Ab	La	5Mυ	LLç
1Cf	A3d	1Ch	A3h	5Ac	Lb	5Mφ	LLɏ
1Cg	A3e	1Ci	A3i	5Ad	Lc	5Mχ	LLӄ
1Ch	A3f	1Cj	A3j	5Ae	UNP	5Mψ	UNP
1Ci	A3g	1Ck	A3k	5Af		5Mω	
1Da	A4a	1Dl	A4l	5Ag		5Mб	
1Db	A4b	1Dm	A4m	5Ah		5Mв	
1Dc	A5	1Dn	A55	5Ai		5Mг	
1Dd	A6a	1Do	A6n	5Ba		5Nд	
1De	A6b	1Dp	A6o	5Bb		5Nж	
1Ea	A6c	1Eq	A6p	5Bc		5Nз	
1Eb	A6d	1Er	A6q	5Bd		5Nи	
1Ec	A6e	1Es	A6r	5Be		5Nй	
1Fa	A6f	1Ft	A6s	5Bf		5Nл	
1Fb	B	1Fu	BBB	5Bg		5Nм	
1Fc	C1	1Fv	CCt	5Bh		5Nн	
1Fd	C2	1Fw	CCu	5Bi		5Nп	
1Fe	C3	1Fx	CCv	5Bj		5Nц	
1Ff	C4	1Fy	CCw	5Bk		5Nч	
1Fg	C5	1Fz	CCx	5Bl		5Nш	
1Fh	C6	1Fα	CCy	5Bm		5Nщ	
1Fi	C7	1Fβ	CCz	5Bn		5Nъ	
1Fj	D	1Fγ	DDD	5Ca		5Oь	
1Fk	Ea	1Fδ	EEќ	5Cb		5Oэ	
1Fl	Eb	1Fε	EEѝ	5Cc		5Oю	
1Fm	F1a	1Fζ	FꙌў	5Cd		5Oя	
1Fn	F1b	1Fη	FꙌџ	5Ce		5Oђ	
1Ga	F2a	1Gθ	FѤw	5Cf		5Oє	
1Gb	F2b	1Gι	FѤѣ	5Cg		5Oљ	
1Gc	F3a	1Gκ	FѦѩ	5Ch		5Oњ	
1Gd	F3b	1Gλ	FѦѫ	5Ci		5Oћ	
1Ha	F3c	1Hμ	FѦѭ	6		666	
1Hb	G	1Hξ	GGG	7		777	
1Hc	Ha	1Hπ	HHǯ	8		888	
1Hd	Hb	1Hρ	HHө	9		999	
1He	Hc	1Hς	HHọ	10		£££	
1Hf	Ia	1Hσ	IIῶ	11		$$$	

Levenshtein distance analysis

All the coded unit, phrase and theme strings were imported into Matlab R2013b, and using custom written code the unweighted Levenshtein distance analysis (LD) was undertaken. LD is a method that calculates the minimum number of insertions (i), deletions (d) and substitutions (s) needed for one string (str1) to convert into another (str2):

LD (str1, str2) = min (i+d+s)

The method used was the unweighted LD that doesn't differentiate between insertions, deletions and substitutions; all of them have the same value of 1, thus assuming that all types of change hold equal significance. Because the longer sequences produced bigger LD scores, the distance was normalised by the length of the longest string:

LD_{norm} (str1, str2) = min (i+d+s) / max [length (str1), (str2)]

Every theme string was compared to all of the other theme strings from all songs. The same analysis was conducted for all the phrase and unit strings. We used average – linkage cluster analysis which produced the agglomerative hierarchical cluster trees that showed how closely related are the songs at the unit, phrase and theme level.

Because there is no agreement about which approach for delineating songs is better ('splitter' or 'lumper'), Levenshtein distance analysis was carried out for both.

Results

Principal component analysis (PCA)

The four unit measurements entered into the PCA were: center frequency, delta time, first quartile frequency and third quartile frequency. The first two principal components explained 87% of the variability in the data. In Table 2 columns represent principal components, rows represent unit variables and the cell values are the loading coefficients. The first principal component (PC1) is mostly loaded on frequency measurements, and the second principal component (PC2) is almost completely loaded on duration.

The results shown in Figure 7 suggested that the features other than these measurements have to be taken into account when classifying units. Different colours represent different unit types. Even though some of the units (e. g., unit 'a') were clearly separated from the others, most of the unit types were overlapping with the others (e. g., unit 'd' and unit 'f'). The automated PCA lacked the ability to recognize one very important aspect of the song structure, and that is the position of units in the song. Because of that, the original classification by a human observer was maintained.

Table 2: Principal component loading coefficients

PC1, PC2, PC3, PC4: principal components

	PC1	PC2	PC3	PC4
center frequency	0.6101	-0.0372	-0.0417	0.7904
delta time	0.0303	0.9834	0.176	0.0322
first quartile frequency	0.5561	-0.1325	0.7176	-0.3977
third quartile frequency	0.5636	0.1182	-0.6725	-0.4649

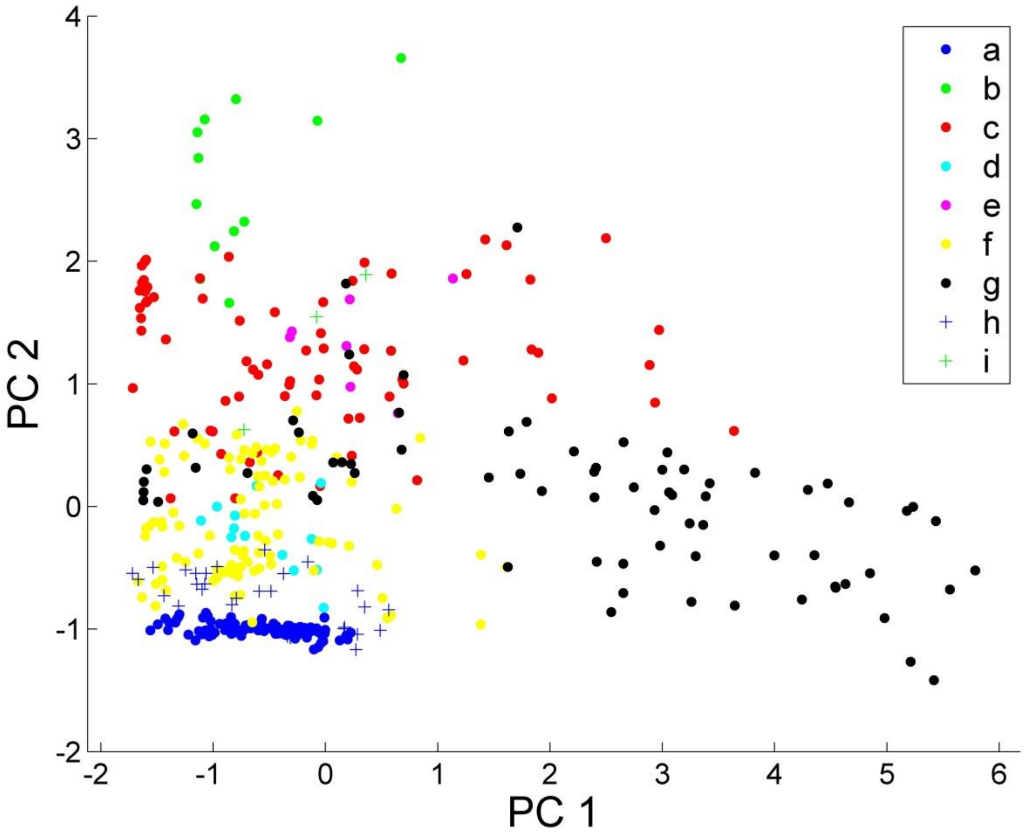

Figure 7: The results of the principal component analysis

PC1: 1st principal component, PC2: 2nd principal component

a, b, c, d, e, f, g, h, i: unit types

The structure of songs

All songs were divided into themes, phrases and units. Table 3 shows how many different types of themes, phrases and units there were in each song. Songs from Georges Bank had the smallest variation at all levels, so they were clearly the least complex of all songs.

Table 3: Number of theme, phrase and unit types

song	location	No. theme types	No. phrase types	No. unit types
1	Dominica	4	6	9
2a	Georges Bank	2	4	7
2b	Georges Bank	2	4	7
2c	Georges Bank	2	4	7
2d	Georges Bank	2	4	7
2e	Georges Bank	2	4	7
2f	Georges Bank	2	4	7
3	Peregian Beach	6	6	12

Songs from Georges Bank shared a substantial proportion of their elements with the song from Dominica. One out of two themes present in the songs from Georges Bank also appeared in the Dominica song. The other theme was specific to Georges Bank (Table 4). The same pattern could be observed with phrases and units. Three out of four phrase types and six out of seven unit types from Georges Bank were present in Dominica song (Table 5 and Table 6). Other types of themes, phrases and units that were not seen in songs from Georges Bank were unique to Dominica song, except one unit type that was also present in the Australian song.

The Australian song shared no similarities with the songs from North Atlantic at the level of themes and phrases (Table 4 and Table 5). However, there was some similarity at the unit level. Unit type 'g' showed up in both Australian and Dominica song, and unit type 'f' was present in all songs (Table 6). The examples of unit 'f' from all three locations are represented in Figure 8.

Table 4: Theme types

theme	song 1	song 2a	song 2b	song 2c	song 2d	song 2e	song 2f	song 3
1	yes	yes	yes	yes	yes	yes	yes	no
2	yes	no	no	no	no	no	no	no
3	yes	no	no	no	no	no	no	no
4	yes	no	no	no	no	no	no	no
5	no	yes	yes	yes	yes	yes	yes	no
6	no	no	no	no	no	no	no	yes
7	no	no	no	no	no	no	no	yes
8	no	no	no	no	no	no	no	yes
9	no	no	no	no	no	no	no	yes
10	no	no	no	no	no	no	no	yes
11	no	no	no	no	no	no	no	yes

Table 5: Phrase types

phrase	song 1	song 2a	song 2b	song 2c	song 2d	song 2e	song 2f	song 3
A	yes	yes	yes	yes	yes	yes	yes	no
B	yes	yes	yes	yes	yes	yes	yes	no
C	yes	no	no	no	no	no	no	no
D	yes	yes	yes	yes	yes	yes	yes	no
E	yes	no	no	no	no	no	no	no
F	no	yes	yes	yes	yes	yes	yes	no
G	no	no	no	no	no	no	no	yes
H	no	no	no	no	no	no	no	yes
I	no	no	no	no	no	no	no	yes
J	no	no	no	no	no	no	no	yes
K	no	no	no	no	no	no	no	yes
L	no	no	no	no	no	no	no	yes

Table 6: Unit types

unit	song 1	song 2a	song 2b	song 2c	song 2d	song 2e	song 2f	song 3
a	yes	yes	yes	yes	yes	yes	yes	no
b	yes	yes	yes	yes	yes	yes	yes	no
c	yes	yes	yes	yes	yes	yes	yes	no
d	yes	no	no	no	no	no	no	no
e	yes	yes	yes	yes	yes	yes	yes	no
f	yes	yes	yes	yes	yes	yes	yes	yes
g	yes	no	no	no	no	no	no	yes
h	yes	no	no	no	no	no	no	no
i	yes	yes	yes	yes	yes	yes	yes	no
j	no	yes	yes	yes	yes	yes	yes	no
k	no	no	no	no	no	no	no	yes
l	no	no	no	no	no	no	no	yes
m	no	no	no	no	no	no	no	yes
n	no	no	no	no	no	no	no	yes
o	no	no	no	no	no	no	no	yes
p	no	no	no	no	no	no	no	yes
q	no	no	no	no	no	no	no	yes
r	no	no	no	no	no	no	no	yes
s	no	no	no	no	no	no	no	yes
t	no	no	no	no	no	no	no	yes

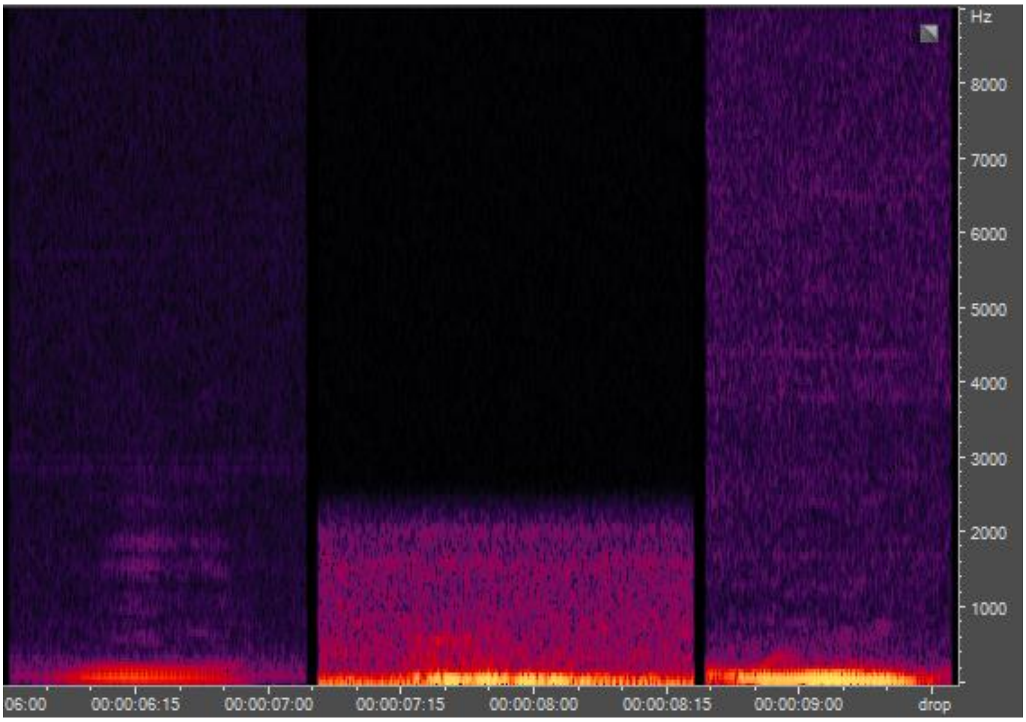

Figure 8: Unit ‘f’ from the song 1, song 2 and song 3

Levenshtein distance analysis

Presented below are the results of the Levenshtein distance analysis. The value of 0 stands for the same strings; whereas the value of 1 means that the strings are completely different.

Table 7 and Figure 9 present the results of the LD analysis for the unit strings. LD values are shown in Table 7. Songs '2' were the most similar within themselves, which was expected because they all came from the same song session. Song '1' was the closest one to the songs '2', and the song '3' was the most distant one of all. It had the highest LD values compared to songs 1 and 2, but they were still not 1 because the Australian song did share some units with the other songs.

Table 7: Distances between unit strings

UNITS

	Song 1	Song 2a	Song 2b	Song 2c	Song 2d	Song 2e	Song 2f	Song 3
Song 1	0	0.774752	0.673267	0.690594	0.665842	0.678218	0.648515	0.876238
Song 2a	0.774752	0	0.462617	0.418367	0.528	0.5	0.531746	0.935484
Song 2b	0.673267	0.462617	0	0.214953	0.264	0.323009	0.313492	0.945161
Song 2c	0.690594	0.418367	0.214953	0	0.28	0.389381	0.357143	0.932258
Song 2d	0.665842	0.528	0.264	0.28	0	0.4	0.384921	0.945161
Song 2e	0.678218	0.5	0.323009	0.389381	0.4	0	0.261905	0.987097
Song 2f	0.648515	0.531746	0.313492	0.357143	0.384921	0.261905	0	0.993548
Song 3	0.876238	0.935484	0.945161	0.932258	0.945161	0.987097	0.993548	0

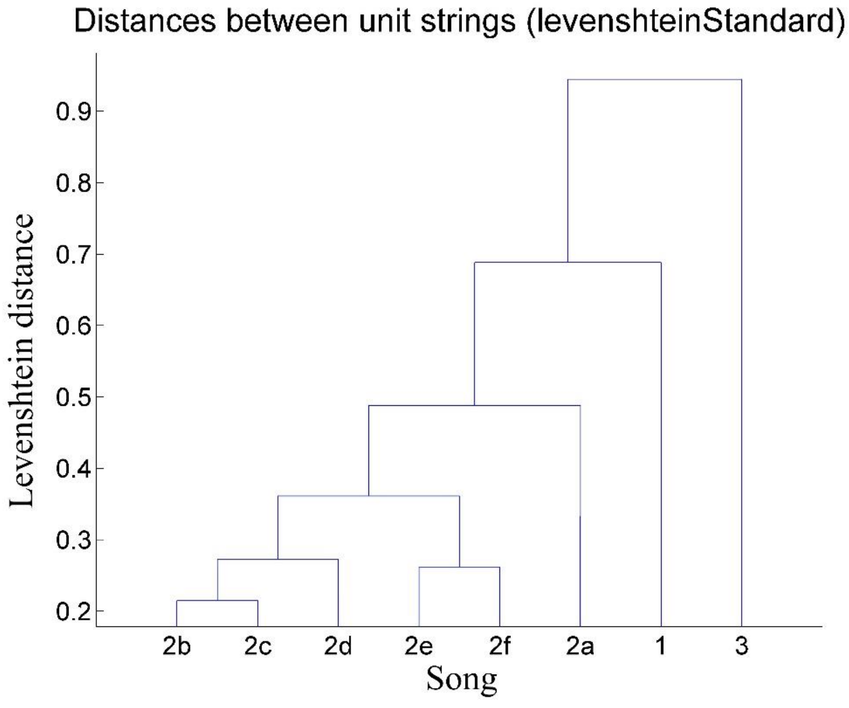

Figure 9: Distances between unit strings

The results of the LD analysis for phrase strings are shown in Table 7 and Figure 9. Because of the 'splitting' and 'lumping' issue, both approaches to phrase delineation were used. The LD values from the 'lumper' analysis were smaller than the 'splitter' values, but the overall pattern was the same. There was a substantial variation within the songs from Georges Bank, even though they came from the same song session of the same individual. The songs from Georges Bank shared some similarities with the Dominica song. All of the Australian song LD scores equalled 1, which means it was completely different from any other song.

Table 7: Distances between phrase strings

PHRASES

SPLITTER	Song 1	Song 2a	Song 2b	Song 2c	Song 2d	Song 2e	Song 2f	Song 3
Song 1	0	0.85977	0.806897	0.786207	0.783908	0.848276	0.848276	1
Song 2a	0.85977	0	0.537954	0.501792	0.556604	0.545455	0.564815	1
Song 2b	0.806897	0.537954	0	0.264026	0.292453	0.339934	0.32716	1
Song 2c	0.786207	0.501792	0.264026	0	0.320755	0.393939	0.361111	1
Song 2d	0.783908	0.556604	0.292453	0.320755	0	0.380503	0.373457	1
Song 2e	0.848276	0.545455	0.339934	0.393939	0.380503	0	0.287037	1
Song 2f	0.848276	0.564815	0.32716	0.361111	0.373457	0.287037	0	1
Song 3	1	1	1	1	1	1	1	0

LUMPER	Song 1	Song 2a	Song 2b	Song 2c	Song 2d	Song 2e	Song 2f	Song 3
Song 1	0	0.767123	0.650685	0.616438	0.671233	0.726027	0.732877	1
Song 2a	0.767123	0	0.49505	0.451613	0.518868	0.484848	0.527778	1
Song 2b	0.650685	0.49505	0	0.108911	0.103774	0.217822	0.157407	1
Song 2c	0.616438	0.451613	0.108911	0	0.141509	0.222222	0.222222	1
Song 2d	0.671233	0.518868	0.103774	0.141509	0	0.207547	0.185185	1
Song 2e	0.726027	0.484848	0.217822	0.222222	0.207547	0	0.12963	1
Song 2f	0.732877	0.527778	0.157407	0.222222	0.185185	0.12963	0	1
Song 3	1	1	1	1	1	1	1	0

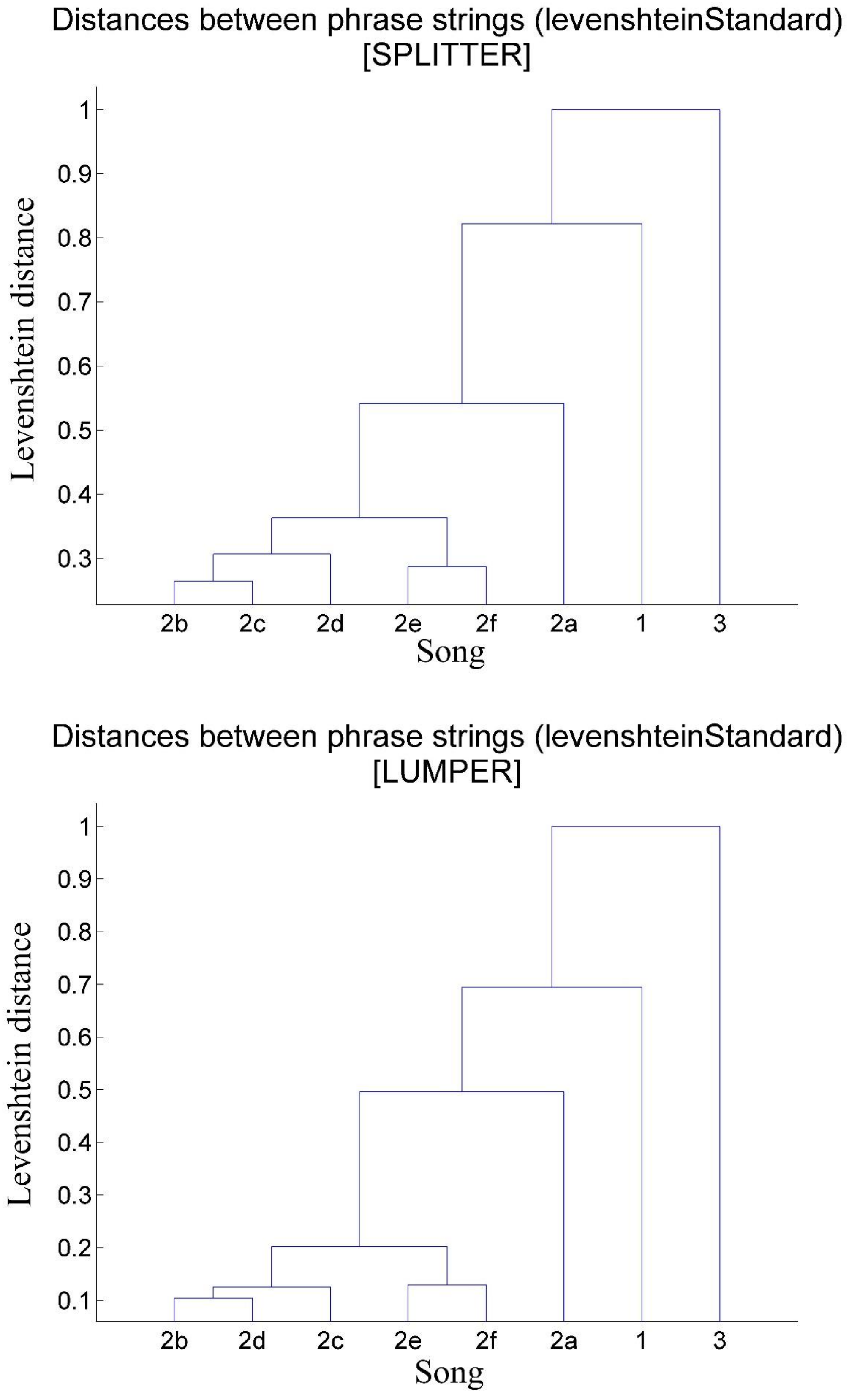

Figure 9: Distances between phrase strings

The LD values for theme strings are shown in Table 8 and Figure 10. As with the phrases, both 'splitter' and 'lumper' analysis was conducted for the theme strings. Again, the LD values from the 'splitter' analysis were higher than the ones from the 'lumper' analysis. The songs from Georges Bank varied even more within themselves at the theme than at the phrase level. The LD scores of the song '1' in comparison to songs '2' were also higher than in the analysis of phrase strings. All of the LD scores of the Australian song were still 1.

Table 8: Distances between theme strings

THEMES

SPLITTER	Song 1	Song 2a	Song 2b	Song 2c	Song 2d	Song 2e	Song 2f	Song 3
Song 1	0	0.904762	0.941176	0.933333	0.888889	0.95	0.947368	1
Song 2a	0.904762	0	0.686275	0.644444	0.746032	0.75	0.719298	1
Song 2b	0.941176	0.686275	0	0.431373	0.47619	0.483333	0.508772	1
Song 2c	0.933333	0.644444	0.431373	0	0.492063	0.533333	0.491228	1
Song 2d	0.888889	0.746032	0.47619	0.492063	0	0.603175	0.52381	1
Song 2e	0.95	0.75	0.483333	0.533333	0.603175	0	0.483333	1
Song 2f	0.947368	0.719298	0.508772	0.491228	0.52381	0.483333	0	1
Song 3	1	1	1	1	1	1	1	0

LUMPER	Song 1	Song 2a	Song 2b	Song 2c	Song 2d	Song 2e	Song 2f	Song 3
Song 1	0	0.714286	0.823529	0.8	0.666667	0.85	0.842105	1
Song 2a	0.714286	0	0.529412	0.466667	0.619048	0.6	0.578947	1
Song 2b	0.823529	0.529412	0	0.117647	0.190476	0.15	0.105263	1
Song 2c	0.8	0.466667	0.117647	0	0.285714	0.25	0.210526	1
Song 2d	0.666667	0.619048	0.190476	0.285714	0	0.190476	0.190476	1
Song 2e	0.85	0.6	0.15	0.25	0.190476	0	0.05	1
Song 2f	0.842105	0.578947	0.105263	0.210526	0.190476	0.05	0	1
Song 3	1	1	1	1	1	1	1	0

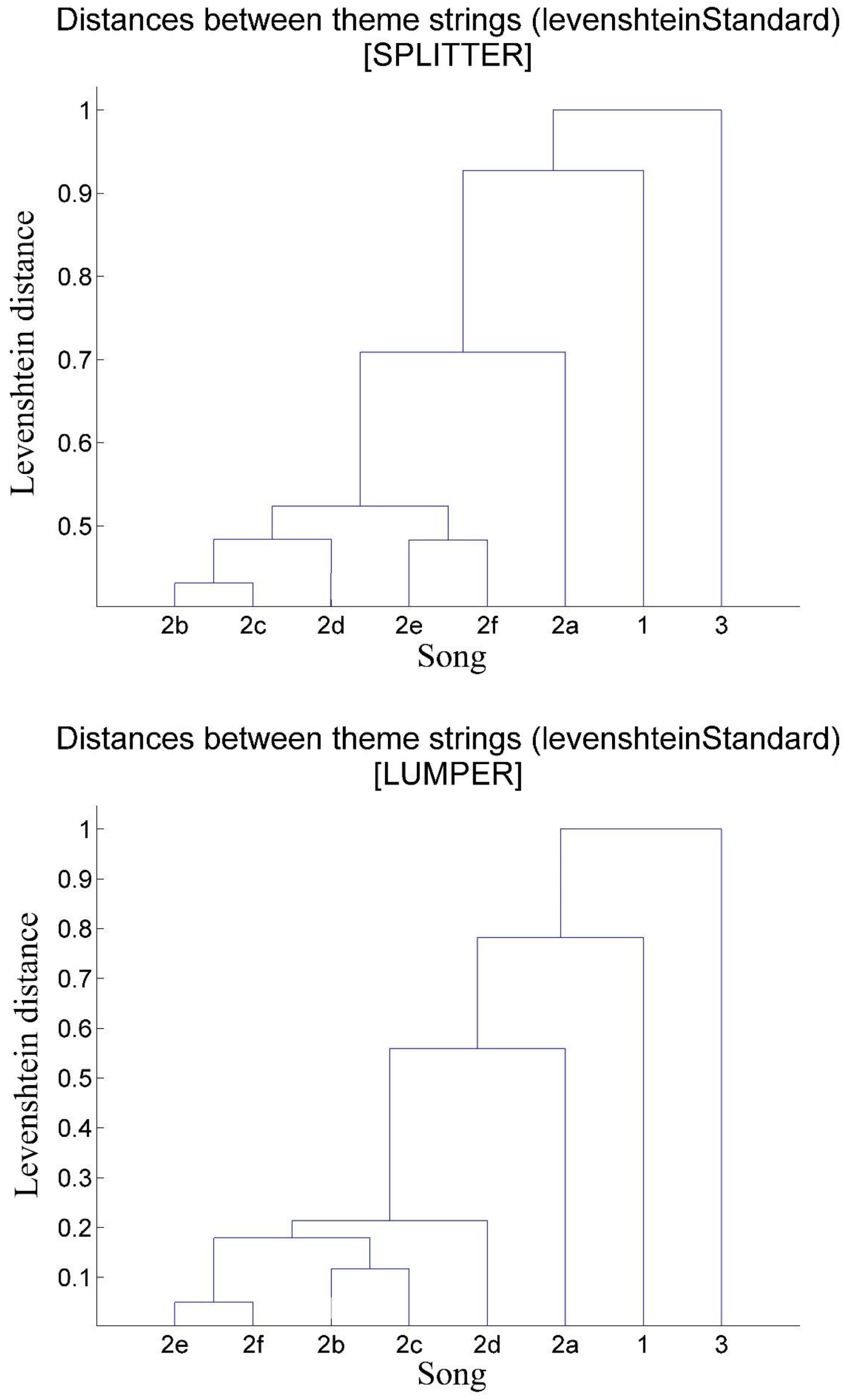

Figure 10: Distances between theme strings

Discussion

Review of the methods used

Some of the methods used proved to be better than others. Categorization of song elements was carried out both by human and computer. However, as all computer analyses relied on previous human classification, no method used was completely objective; all of them had at least some degree of subjectivity which couldn't be avoided with just one human observer.

Unit classification

There were some difficulties regarding categorisation of units into different types. Units from the Australian song didn't change much, but units from Atlantic changed throughout the songs. Allocating different types to these evolving units was challenging and in some cases there was just no clear border at which a new unit type replaced the old one. In these cases there was no criterion but my own decision, which depended mostly on the position of units within the song. To test if automated measures can explain human classification of units, a principal component analysis was conducted. It turned out that these measurements couldn't explain all the variation between different unit types. The measurements relied on frequency and time properties of the units, but they didn't consider the position of units within the song, or finer scaled frequency structure beyond simple energy distribution. Until such automated analysis which takes the position of units into account is invented, a human classifier is needed to account for this important unit characteristic.

Delineation of phrases and themes

There is still no agreed method in the literature for delineation of phrases and themes. A review of the humpback whale song hierarchical structure and its classification issues does give some very useful instructions (Cholewiak *et al*. 2013), which were followed in this study whenever possible. Unfortunately, there were several situations for which these guidelines were not applicable, especially when it came to phrase delineation. For example, Cholewiak *et al*. (2013) recommends that 'phrases should be delineated in a way that minimizes the occurrence of an incomplete phrase at the end of a sequence of similar phrases', but in the Dominica song these 'hanging' phrases could not be avoided; whichever way you divide the song, there would still be a 'hanging' phrase almost at the end of every theme. The biggest difficulty I encountered was phrases that appeared to be 'transitional' (phrases that combine units from two subsequent phrases). They contained units from two phrases which were not consecutive. In these cases, a decision had to be made about when to name a new phrase type, and it was based on a subjective interpretation. However, Cholewiak *et al*. (2013) did point out that examination of songs from multiple individuals and years is crucial for appropriately delineating phrases, so a bigger data set would probably elucidate some of the uncertainties. The same applies for themes, although they were slightly easier to deal with. Payne & McVay (1971) defined theme as sequence of similar phrases, so as Cholewiak *et al.* (2013) suggested, a new theme type was assigned every time there was a new phrase type. This means that delineation of themes heavily relied on phrase delineation.

Levenshtein distance method

Levenshtein distance analysis turned out to be an effective method for comparing humpback whale songs. The beauty of it lies in its conceptual simplicity, yet it gives a clear representation of the level of similarity between different strings, whether comparing unit, phrase or theme strings. In my opinion, it is the most appropriate method for quantifying similarity (or dissimilarity) between any given song sequences. It also proved to be a very robust qualitative measure, regardless of the approach taken ('splitting' or 'lumping'). Although the LD values were higher for the 'splitter' than for the 'lumper' analysis, the clustering showed that the overall pattern of similarity between songs was the same.

Comparison with the previous studies

Although there were a lot of difficulties regarding different approaches and methods used, and also some sub-optimal technical aspects, such as discrepancies in quality of recordings (different sampling rates and signal–to–noise ratios) and small sample size, the results were in accordance with the previous findings (Winn *et al.* 1981, Payne & Guinee 1983, Helweg *et al*. 1998, Cerchio *et al*. 2001, Darling & Sousa-Lima 2005) and they confirmed the hypothesis.

Even though two humpbacks from the North Atlantic were recorded in quite distant areas, they shared a relatively large portion of their song material. This conforms well with expectations derived from the literature (Winn *et al.* 1981, Guinee *et al*. 1983, Payne *et al.* 1983, Helweg *et al.* 1998, Cerchio *et al.* 2001) and suggests that these two individuals had to be in acoustic contact at some point. Perhaps they went to the same breeding or feeding grounds, or they might have shared a part of their migration routes. This study highlights the importance of horizontal cultural transmission for social and vocal learning in humpback whales.

On the other hand, it is quite hard to imagine a whale from Australia ever being in contact with whales from North Atlantic, so the opportunity for them to learn songs from each other is not really possible. Obtained results support this idea, and they clearly show that there is no similarity between any song sequences that come from these separated populations. There were a couple of shared unit types, but that was expected, as humpbacks do have a common repertoire of units (Payne & Guinee 1983).

The results of the Levenshtein distance analysis indicated that there was a substantial variation between songs of the same whale from Georges Bank at all levels (unit, phrase and theme), suggesting that, along with the differences between individuals, there is also a notable intra-individual variability.

Future research

Why do humpback whales sing and why and how do these songs change? The answers to these questions are still unknown, but looking at the individual level might be the way to answer them. Instead of focusing on the big changes across populations, it would be interesting to compare more songs from whales within the same population and see how much do they differ. It would be exciting to find out is there significance in variation between individual singers, both for a group of whales and individuals themselves. One way to explore the importance of individuality would be to investigate if individual male fitness increases with more diverse and complex vocal displays.

Conclusions

The overall conclusion is that humpbacks from North Atlantic share some of their song material and sequences, but, with the exception of two unit types, they have no similarities in their song displays with the whale from Australia. These results support the leading current theory of horizontal cultural transmission of humpback whale song.

Depending on the method and approach that was used, several conclusions can be drawn. If taking a 'lumping' approach and just looking at numbers of different theme, phrase and unit types, songs from the same song session seem identical, and they are similar to the other song from North Atlantic. If looking at sequences, there is a much greater variability, both between the songs of the same individual and songs from different whales. The Levenshtein distance method proved to be an excellent tool for comparing sequences. Although the overall pattern is the same, there are differences regarding the approach used. 'Splitting' gives much higher values of dissimilarity, which suggest a lot more variability, then 'lumping' approach, but these two approaches do not differ in terms of qualitative conclusions.

The principal component analysis is not able to explain all of the variation between different unit types, because it cannot take into account the position of units in the song and fine-scale frequency variation; therefore a human observer is a better choice for unit classification. It is still not perfect because, as with delineating phrases and themes, there is certainly a degree of subjectivity which can't be avoided unless a more intensive protocol with multiple observers is used.

Hopefully in the future a more comprehensive and unambiguous set of rules for song delineation will be established that could be applied even on small data sets. Also, a much better automated method for unit categorisation is needed, which would include unit position as an important variable, together with robust frequency and duration properties of units.

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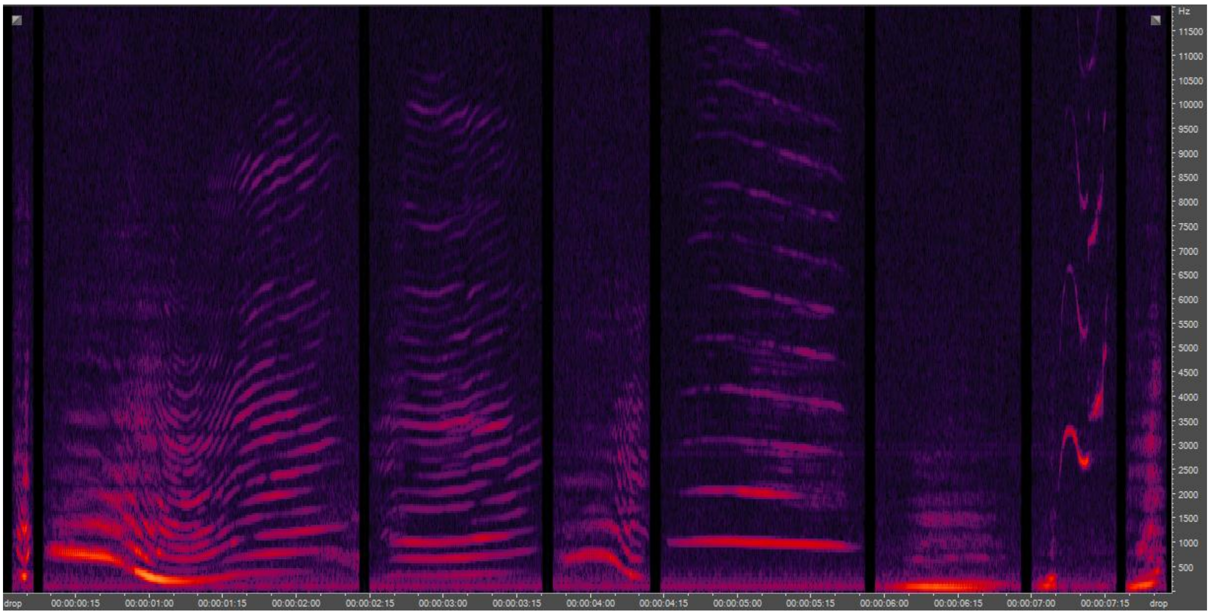
Appendices

Appendix I: Unit types

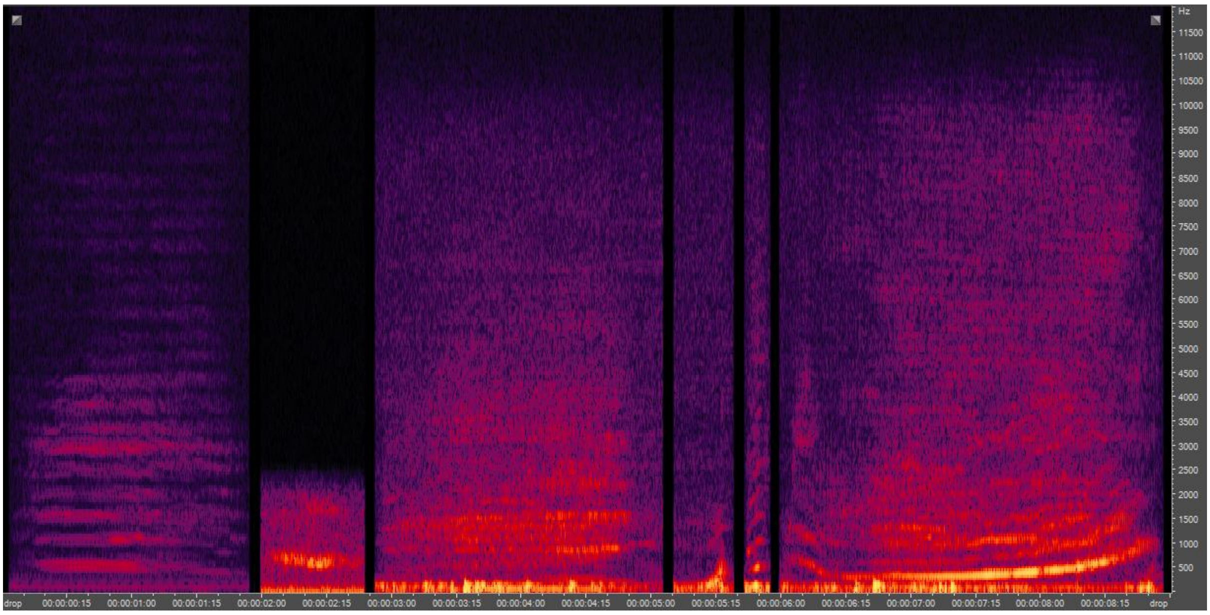
Appendix II: Song sequences represented by unit codes

Appendix I

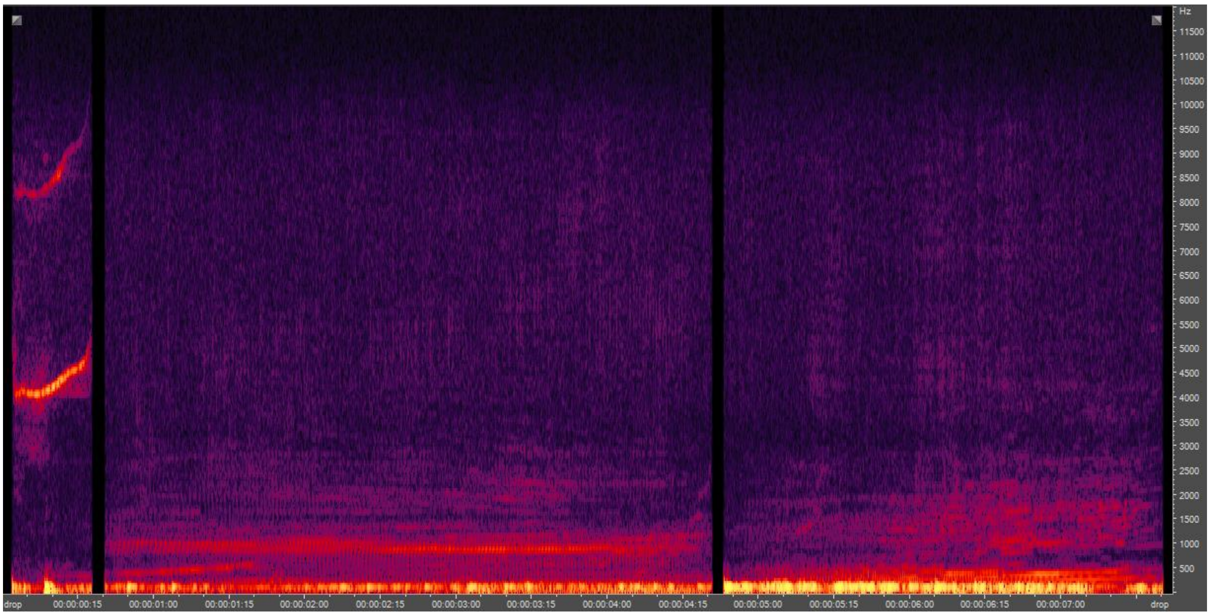
Unit types



a **b** **c** **d** **e** **f** **g** **h**



i **j** **k** **l** **m** **n**


Hz
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11000
10500
10000
9500
9000
8500
8000
7500
7000
6500
6000
5500
5000
4500
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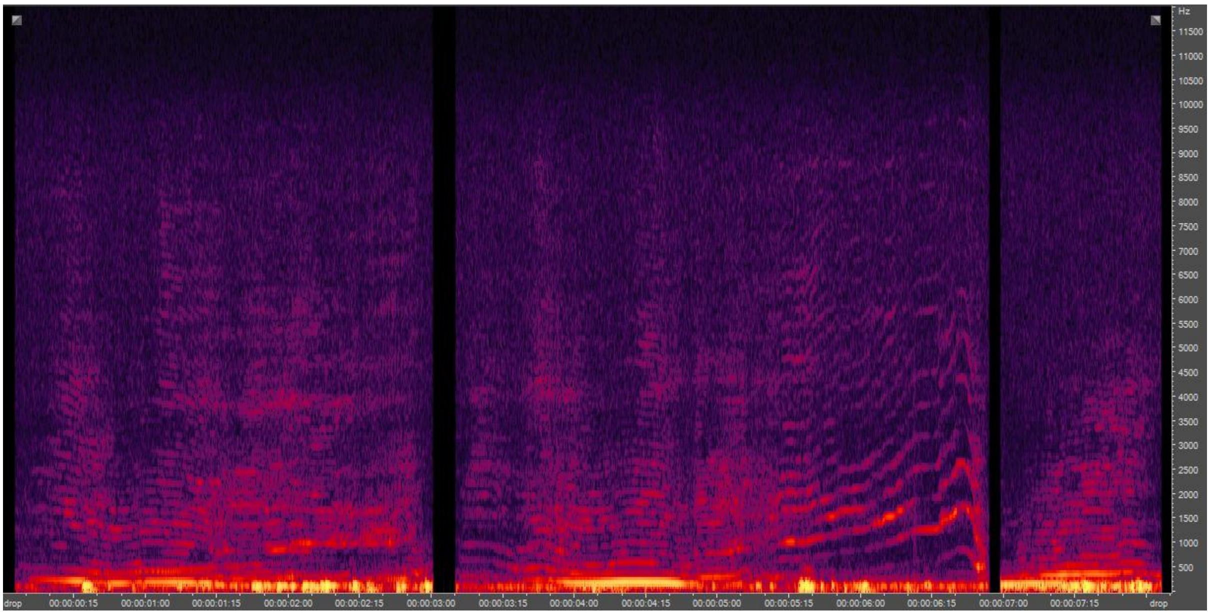
3000
2500
2000
1500
1000
500
drop
00:00:00:15
00:00:01:00
00:00:01:15
00:00:02:00
00:00:02:15
00:00:03:00
00:00:03:15
00:00:04:00
00:00:04:15
00:00:05:00
00:00:05:15
00:00:06:00
00:00:06:15
00:00:07:00
drop

o **p** **q**


Hz
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11000
10500
10000
9500
9000
8500
8000
7500
7000
6500
6000
5500
5000
4500
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2500
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00:00:02:00
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00:00:04:00
00:00:04:15
00:00:05:00
00:00:05:15
00:00:06:00
00:00:06:15
00:00:07:00
00:00:07:15
drop

r **s** **t**

Appendix II

Song sequences represented by unit codes

Song 1:

'baabaabaabaabaacaadcaadcaabedcaadcaadcaadcaaabecaacaafcaafcaafcaafcaafcaafcaafcafcaf
cfcfcefcfcfcfcfcfcefcfcfcfcfcfcfcfcfcfcfcfcfcfcfcfcfcfcfcefcaafdcaafbaafbaafbaafbaafbaafdc
aafcaafcaafcaafcaafcaafcaafcaafcaafcaafcefcaafcaafcaafcaafcaafcaafcefdcaafcaafcaafdcaafdg
fdgfdgfgfgfgfgfgfgfgfgfgfggggggggggggghghghfhghfgghfghfghfggfghfghfgfgfghfghfghfghfg
hfghfghfghfghfghhfghhgighhgaghhghggggghggggggggigggcgcgci'

Song 2a:

'cccccccccijccjccjccijccccjccijcjcjcifcfbfbfcfifbfbfbfbfbfbfbafbefbfbfbfbaafbaafbaafbaaafbafba
fbafafafafaafaafaafaafaaafai'

Song 2b:

'cccccccicccccccicccciccccciccccccciccccccijccccjccijccjcjccifcfcfifcfbfcfifbfbfcfifbfbfcfifbfbf
cfcfifbfcfcfifbfbfbfbfbfbfbefbfbfbfbfbafbfbfbafbaafbaafbaafbaafbafbafafaafafaafafaafaafaaaf
afaafaafafaafaaafaafaafaaafai'

Song 2c:

'cccccciccccccicccccccijcccccijccjccccijcjcjcjcifcfbfbifbfbfcfifcfcfifbfbfbfifbfbfbfbfbfbfbefbf
bfbfbefbfbfbfbefbfbfbafbaafbaafbaafbaafbaafbafbafafaafafaafafaafafaafafafafafafafaafaaafafa
aafaafaafci'

Song 2d:

'ccccccicccccciccccccicccccciccjccccijcccccijcccjcijcjcjcifcfcfbifcfbfcfifbfbfbifbfcfcfifcfbfifb fbfbifbfbfbfbfefbfbfbfbefbfbafbaafbaafbefbaafbaaaafbaafbaaaafbefbaafbaafbaafbaaafbaaafba aaafbefbaaafbaafbaaafbaafbaaafbafbafaafafaafafaafaafaafafaaaafaaaai'

Song 2e:

'cccccccicccccicccccciccccccaaccccciaaccccccccciaacccccccciaacccaaccccciaacaaccccciaaccccccijc jcjcijcccifcfcfifbfcfifbfcfcfifbfbfbifcfcfcfifcfbfbfbefbfbfbfbfbefbfbfbaafbaafbaafbaafbaafbaaf baaafbaafbafbafaafafafafafaafafaafafaafacafaci'

Song 2f:

'ccccccaacccaacciccaacccaaccaacciaaccaacccccciccccccccccciccccccccijcjccccijccccjcijcccccij cccjcjcijcjcjcifcfcfbifbfcfcfifcfcfbfifcfcfcfifcfcfcfifcfcfbfbfbefbfbfbfbefbafbaafbaafbaafbaaaf baafbaafbaafbaaafbafbaaafbafafafaafafaafafaafaafafaafafaafafaafafaci'

Song 3:

'kllflfklll mmmmllmmmmmllmmmmmmllmmmmmllmmmgllmgmgllmgmgmgnlmgglmgmglmgmgnl mgglmgmglmgmgnlglmgmglmgmgmmnlmglmgmglmgmgnlolooooonlolooooonlolooooonlolooo onlolooonlolopppnoopppqqmqrstmtrstmtrstmtrstmtrstmtrstmtrstmtr'