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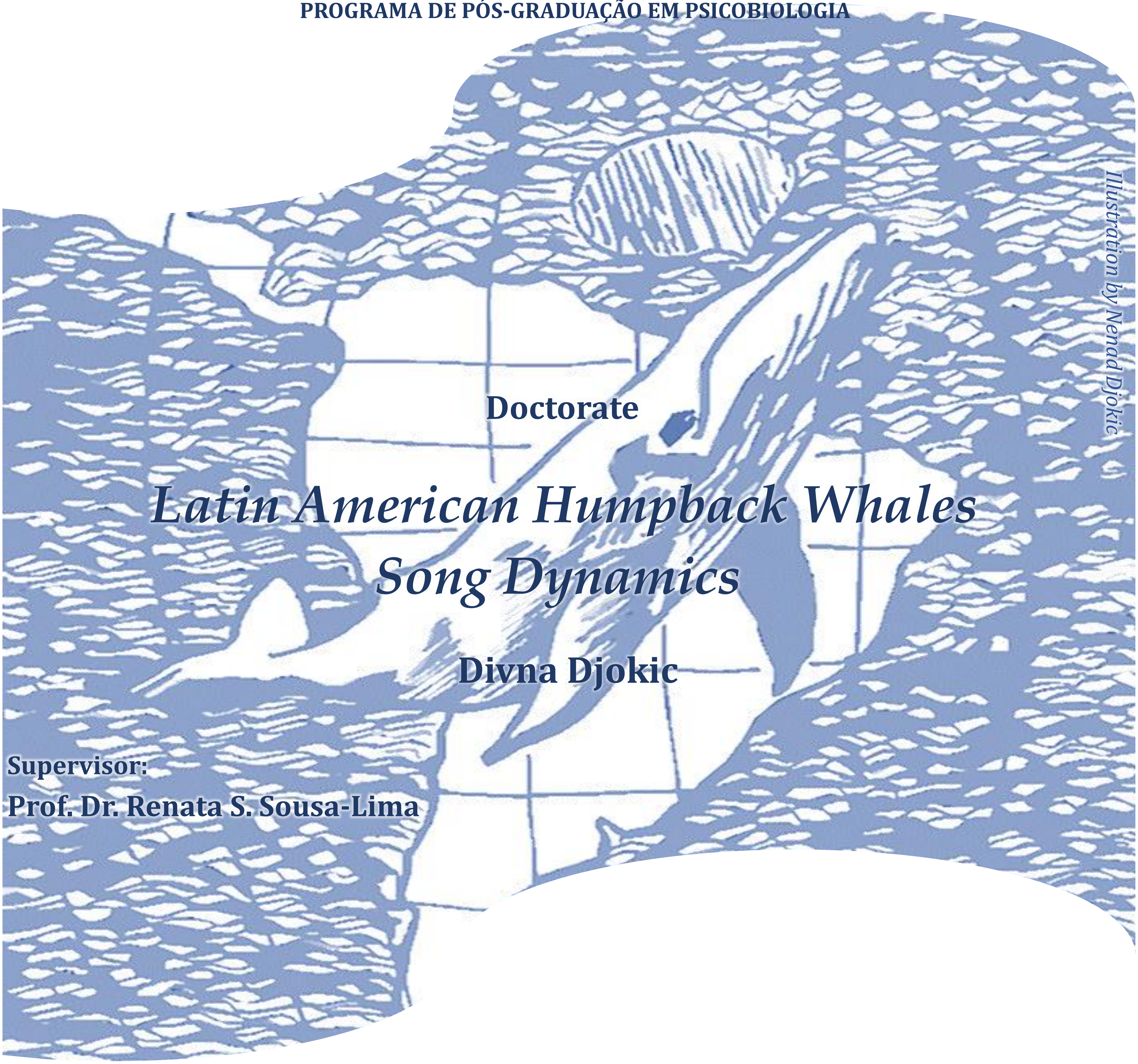

Illustration by Nenad Djokic

Doctorate

Latin American Humpback Whales Song Dynamics

Divna Djokic

Supervisor:
Prof. Dr. Renata S. Sousa-Lima

Natal, RN, Brazil
2021

DIVNA DJOKIC

DINÂMICA DO CANTO DAS BALEIAS JUBARTES DA AMÉRICA LATINA

Tese apresentada ao Programa de Pós-graduação em Psicobiologia, da Universidade Federal do Rio Grande do Norte, como requisito parcial à obtenção do título de Doutor em Psicobiologia.

Orientadora: Profa. Dr(a). Renata S. Sousa-Lima

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Observação: Em razão da pandemia por COVID-19, a defesa foi integralmente realizada por videoconferência, através da plataforma Google Meet

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To start in an official tone, I would like to thank the country of Brazil for accepting me and giving me a chance and means to work in the area I love, and to meet this beautiful country, its rich culture, and lovely people. Several in particular:

As days in Natal last very short, year-round (at least day-light wise), the time of my Ph.D. seemed much shorter than 4 years, as documents say. Yet, many lovely people managed to squeeze in and make the whole experience so pleasant, productive, and unforgettable.

I would like to start this long list with Luane Stamatto Ferreira, who was the first one to welcome me to Natal, and reassure me that everything is going to be great, even after coming for the first time all alone to a foreign country, and this continent. It was a great start, after meeting Luane and her family, I had no doubts. Next to mention would definitely need to be Jaque and Vini, who were definitely responsible for me actually reaching UFRN. And that is just, to begin with. Jaque was so patient with me diving into Brazilian bureaucracy, Lates and Sigaa, and all those forms on a language I thought I knew, but, oh boy, was I foolish. Jaque was my safety belt that dragged me to the other side of a form flood, and to the entrance of UFRN. And how we met, it's one hilarious story. Everything started in 2010 when I went to Portugal as an exchange student for a year. Over there I lived in a dorm while attending classes of Biology. One of the people in those classes were Vini and Jaque, in those days long gone, just random two people that I happen to know. We had some fun time together, but years went by, and it all faded away to a 'memories" drawer. Fast forward to 2016, I ran into this UFRN place, which I knew nothing about. Social networks have their bright sides, and one of them is allowing staying in contact with people far, far away. That's how it crossed my mind to ask one of the Brazilian friends I met in Portugal on Facebook if they know anything about this university, so far away from my every-day reality.

- Olá Felipe! How are you? Hey, do you know anything about UFRN? I found some nice lab there, so wanted to know if it is a cool place?
- Olá Divna! Yea, I have heard of it, hear it is a nice place. Hey, do you remember Vini and Jaque? You should ask her, I think Jaque was there for a while, probably she knows more than me.

This story ends up in a way that it was 5 years later, Jaque remembered me, and more than being at some point at UFRN, she was doing her Master here and just about planning to apply for a Ph.D., and more than UFRN, she was on the same department, just one corridor away from our LaB!

The bottom line is that, after the cosmos rearranging all the stars like this just so I can jump on them to cross the Ocean, I really had no doubts this is the place I should be.

And at this LaB, I met a bunch of lovely, very generous, and supportive people, Marcos, Lara, Luane (again), Leo, Eli, Isabel, Luana, Samara, Manu, Belinha, Cibele, who were my reliable source of information for when I was lost and struggling to understand (anything), full of understanding and always ready to share a smile. Three of my colleagues I need to thank additionally, Leo, who was the best right hand a Ph.D. student can ask for, selflessly working side-by-sad on my project (hopefully getting "infected" by whale song forever!), Vito, who appeared from nowhere, and gave his precious advice on polishing my writing, putting his sharp eye to pre-reading the chapters, paying attention to the smallest details, and thus, giving them an extra value, for which I am so grateful! And Ignacio, who was of immense help when the statistics kicked in and freaked me out!

I would also like to thank all the lovely staff of UFRN for their support and patience, without which I would not get this far, for sure!

On the other side, my safety –belt were people I shared my house with, and in a package, of course, lots of free time, beach-days, beers, and late-night talks. People, that "looked through my finger" as we say in Serbian, for not washing the dishes or cleaning the garden when it was my turn, instead I was stuck in front of the computer, listening to whales. One great love to Mate, Csilla, Felipe, Franzi, Leo, Terceiro, Dardo and so many more nice people I met on the way, that built a little bit of themselves in this big chunk of my life. Super special thanks to Sebas, who jumped in when it was the most critical, when I was on the break of my nerves, and feeling very lost. And for being the first person who set with me and listened to all the ideas and how I was planning to prosecute them, and actually criticized them and helped me fill the gaps and solve the problems I didn't even know I had. What every biologist in the world needs is a badass-code-running-genius friend. I had Sebas!

There is a funny saying in Serbian "Speak Serbian so the whole world can understand you", which has its base on the long history of Serbians moving around the world for different reasons. The fact is, we are such a tiny country, but so many Serbs everywhere! Almost defying the laws of physics (as being opposed is indeed Serbian favorite hobby). To prove this point, I have to mention Maja and Igor, and their family, as Serbians that I had no hope of finding in such a small, hidden place like Natal. Yet, I did, and I am very

happy it happened that way, they took me through all the saudades for my country, the language, the food! Fun fact- they were not the only Serbs living in Natal, as I discovered!

Not all the people I met on the way were physically here with me. Some of them I had a chance to see just a few times, yet their endowment was priceless. First on the list are definitely Franck and Julie, who had a crucial influence on my thesis, beyond helping with the data process, but morally and pedagogically, that helped me through rough patches. It was a great feeling to be heard and considered as equal in the opinions of two such great scientists!

Next in line are all of my collaborators, most of whom I had the luck to meet in person, and that was a great honor. They are a great example of selfless collaboration in science, a bright example, and something I am especially proud of! I like to believe that that is the world we are leaving for the future generation, where information and science will be accessible to everyone and where we will be supporting each other's curiosity and science. An extra asterisk next to 4 names: Laura, Esteban, Javier, who I have to thank for the enthusiasm that just spilled on me, from every email we shared, and Aldo to be the first to support my idea and offer his data.

All the way back to Serbia, there is a lovely bunch always holding my back, ready to make up for a lost time (or whatever is there to make up for), tap my shoulder, or slap me on my face, whatever is suitable for the situation. Love you all for high-quality discussions, late-night theory untangling, great and inspiriting ideas, or just pure laughter and fun. And by the lovely bunch, I think of people I basically know my whole conscious life: Nevena (who become more than a friend in the past year, and who's creative input seems essential for my scientific communication), Ivana, Iva, Jovana, Maja, Milica, Tijana, Lea, Tamara, Andrea, Marina, Ika, Bar, Šarac, Cesa.

I also feel eternal gratitude for having teta Ljilja and čika Mihailo in my life, while growing up, for learning the life can take you in any direction, just point your finger. They were the inchoate sparkle of my idea that the world is an open playground, and that anyone can get to anywhere, in any sense, as long as you wish for it strong enough. This lovely duo was my support through this whole journey of mine, without the slightest shred of doubt.

The Serbian language is much more similar to Portugues than English when it comes to family relationship depiction and member naming, so I'll be missing few words here to mention my family overlooking me all the way from Canada, who I get to see not so often, for every time is a blast. Maybe not physically, but I have them in my life, and it was nothing but a dash of love and support.

Coming back to Brazil, a big thanks to Milton Marcondes from IBJ for the support knowledge, and great chit-chats we had about whales, and for the inspiration! Also, Bernardo, who saved a whole season ☺ Namely in 2019 I went to Caravels to record whales, but the season was very rainy. We managed to go out to the sea just on a few occasions, with very few recordings made. And then Bernardo jumped to the rescue- he said, “Divna, we are going tomorrow to get you some awesome recordings”, and that is was happened. Bernardo is the captain of the ship that the Abrolhos field trips are usually made by. More than that, Bernardo accepted me into his home with his family and made me feel like it was indeed my home. I will always carry him and his family in loving memory, these kinds of experiences bring back faith into humanity.

A great moment to thank this country altogether, for embracing me as their own, Brasileira Potiguar. Brazil became my other home, a place where I feel welcomed and familiar. Like a secret I got to know, and cherish so preciously. I could not think of a better place I could spend the last 4 years, with all the goods and the bads, I looked at it all like it was my own. And it was a hell of a journey.

After this, I would like to start the “serious” section. First, I would like to thank Renata Sousa- Lima, my supervisor, for her support and freedom. Initially, for taking chances of welcoming an unknown Serbian girl to her lab, and having faith in my ideas and a way of thinking. It was just beyond the wildest dreams to be able to work in the area I had so much enthusiasm for, and with such a liberty of expressing ideas and testing them, finding my own ways and learning how to be independent, and to stay on track. Thank you for this privilege to work on something I love.

Talking about Love, it is the reason I did not die of forgetting to eat. Or having something to eat in the house, to start with. Of course, I am talking about the love of my life, who fought for that position with humpback whales, fair and square, and won. These years he had a serious chance to prove his love, that is for sure! The home is where you are, to cite himself.

Should not forget to thank the whole Nedeljkovic family for selflessly letting Marko go to an unknown place for crazy reasons, and being just pure support from start to end, for both of us! It meant a lot.

In the end, there is hardly words I can find to properly describe and mention everything I think and feel, but to put it simply, the biggest “Thank you” goes to my family, who always supported me selflessly, with no skepticism and doubt: mom Višnja and dad Nenad, my big sister Aleksandra and her family, husband Ivan and the little stars that made our skies brighter, kiddos Miona and Jakša, and a key member of the gang, our dogo Azra. A crucial figure in my life while growing up was my uncle čika Peđa, who was just a walking support, without any critical thinking, just pure support. And what more a chile could ask for. And we have to give my family some serious credit, as I was no simple child, but a land-locked city child who

wanted to study whales. Sometimes at night, I am awake thinking what was in their head believing it was a good choice to support me in this crazy journey. But I am really grateful they did. Sadly, my grandparents are not around anymore to see this, I am sure they would be very proud, as even they thought it was an awesome idea I wanted to study wild animals they never had a chance to see, as long as it made me happy. And a first Ph.D. in the family! :D I would also have to thank my parents for raising me as a healthy and a happy person, strong and independent, but curious and fireless. They were the best examples to learn these qualities from!

The past year brought lots of challenges for everyone, hopefully with not many consequences for the future, but even so, next to everything, I will have at in a bright memory, as it was the year I materialized my big dream of starting to learn whaleish!

It takes a village to raise a child. It takes a serious crowed to do a Ph.D.

p.s. I could not not mentioning Gandalf, a white cat, who helped me struggle through boredom and anxiety of Corona quarantine, with his cuteness and playfulness, and a stray dog named Cveta (by me), who stuck around just for friendship, a great one.

Thank you Natal for your endless sun!

FINAL WORDS

By contributing to understanding a bit more of the basic mechanisms of song transformation in humpback whales, we can expect progress in our knowledge of their biology, ecology, and social interactions. We know so little about them, that we cannot even claim that humpback whales are indeed open-end learners or not (they might actually have a limited amount of songs/sounds they can produce, but it is rather large to fit into few decades in which research monitoring their song has been conducted (PAYNE; MCVAY, 1971)). Thus, only after hitting the benchmark of understanding the basic mechanisms of song evolution, we can allow ourselves to make solid hypotheses and predictions based on the substantial knowledge we have at our disposal today. As suggested by Hauser and colleagues referring to human language, "Understanding the evolution of language requires evidence regarding origins and processes that led to change" (HAUSER et al., 2014). They further add, "… the richness of ideas (for explanations) is accompanied by a poverty of evidence, with essentially no explanation of how and why (human) linguistic computations and representations evolved". There is incomparably more investment into research done in human language than there is for animal vocal communication or humpback whales. There is a long way ahead of us, still, one step at a time can take us far.

The initial great challenge of this study was data collection. The original project proposal was to compare only two locations off each side of South American, plus some locations on the feeding ground, and look for any evidence of acoustical contacts of stocks A and G, hypothesizing the potential contact is happening on the feeding ground. In the process, the project developed into a long list of collaborators, a network, of researchers willing to share their recordings, interested in learning more about the song of humpback whales breeding in their countries. The list of collaborators is longer than the list of authors because several datasets we were just not able to be used this time, for various reasons, explained in detail in the dataset section of each chapter. The initial idea of breeding-feeding song comparison had to be put on hold, but other groups that we are collaborating with showed interest in looking into these questions.

An invaluable part of this project is the network of Latin American collaborators, which in it holds very important virtues of good scientific practice - knowledge and resources sharing, while diminishing the effort, *e.g.* data recycling, and in this way, help our environment, in addition to introducing less stress to the animals. Although the sample size used in the study corresponds to the number of resources available for individual researchers and institutions working in this part of the world, it sends a very strong message that even with little resource, good research is possible- where there is a will, there is a way. Spending almost the entire first year of this research in networking and signing MOUs paid off, not only resulting in this thesis but building a collaboration network- an exemplar of an optimal project environment, selfless and supportive, with a potential to grow, which was galvanized by the first LAMLA (Listening to Aquatic Mammals in Latin America) workshop in 2016.

Going deeper into the theory of humpback whale songs, I found caveats that I could not find the answers to. These dilemmas were the main inspiration of this work while trying to find ways to explain them to myself. Finally, novel methodologies, or old, but rearranged ones, emerged, with the help of collaborators, that offered some answers I found more commonsensical. These provided solid conclusions to our main research question- are the two South American stocks "talking"?

As you will be able to read in the next pages, we discovered they indeed do talk, moreover, this interaction is more exciting than we initially believed. For example, it was a great privilege to be able to hear those song revolutions evolving in front of our ears, and even witness a gem like the "unpatterned theme" being used, so rare and precious. Even though they did make our lives a bit more complicated, these peculiarities of the song dynamics offered a special insight, giving us a feeling of complete work, as if we managed to grasp a whole lot of the humpback whales' vocal culture dynamics in this study. Although, this is hopefully just the beginning of a systematic acoustic monitoring effort of humpback whales off South America, so necessary and important.

One cannot escape the language-culture-intelligence ethos of researching songs of humpback whales. Although mostly looking in frequency values, tables, and figures, the philosophical questions linger over the work, keeping you awake at night. The unescapable game-like feeling, always trying to solve some one-of-a-kind puzzle. I think this particular feeling is what keeps the enthusiasm about this subject alive in people, even after 50 years of work on it. I am no exception, as, while finishing my thesis, I am filled with questions still unanswered, and with plans about how to approach those.

Although dealing solo with most dilemmas is particularly challenging, mother of prosperity are necessity and difficulty, thus, I am grateful for the process and happy with the results that I managed to grasp and present in this thesis.

Finally, I would like to thank my supervisor prof. Renata, who gave me the opportunity to discover the depths of this research question and follow my instincts while looking for a way out.

PREFACE

There is a Serbian poet, named Mika Antić, who said he never wrote the first poem. He only wrote his second one, he says, as the first he presented as his, when he was 8 years old, was from another poet he found in a book he really liked.

This reminded me of humpback whales, we might never discover who sang the first song. Nonetheless, we can enjoy in the ones succeeding, trying to understand the composer and all the skills he gained in those thousands of years of unflagging practice.

I am contemplating on how this world would look like, if we were to be more like humpback whales - if we would solve all of our disagreements by singing, learning from each other, by embracing differences. By blending these differences into one, unique melody where all voices would be heard, that would be understood by everyone, and which main sense and the task would be love.

Ponestalo mi u životu soli
Život mi beše previše sladak
Reših da odem do molisejruša
I pozajmim malo od one plave

Uđoh na barku da zagrabim malo
i umesto do Salinasa
Ili bar do Ria Formoze
Stigosmo mi na drugu stranu

Na domak tom velikom prazniku
Neke nemani, divovi dubina
Ni crni ni beli
šapnuše mi zagonetku

Zagonetku kao pesmu

I tom su me pesmom,
Ni krikom, ni cvrkutom
Kao sirene iz Odiseje
Začarali

I kao pred sfingom
Bez moći da trepnem
Poklonih se pred tom zagonetkom
Da je nikada ne rešim

A ipak mi đavo nije dao mira
Htela sam da čujem vesti iz dubina
Htela sam da znam

Fiquei sem sal na minha vida
Minha vida foi doce demais
Eu decidi visitar um moliceiro
E emprestar um pouco daquele azul

Eu entrei no barco para pegar um pouco
E em vez de salinas,
Ou pelo menos até a Ria Formosa,
Chegamos ao outro lado

Pertinho daquele grande feriado
Alguns monstros, gigantes da profundidade
Nem preto nem branco,
Eles sussurraram uma enigma para mim

Uma enigma, como uma canção

E com essa música,
Sem gritos, sem chilrear
Como as sereias da Odisséia
Eles me encantaram

E como na frente de uma esfinge
Sem a capacidade de piscar
Eu me curvei diante daquele enigma
Sabendo que nunca iria resolvê-lo

E ainda assim, o diabo não me deu paz
Eu queria ouvir as novidades das profundezas
Eu queria saber

D. Dj.

GLOSSARY

Dataset

Breeding stock- a group composed of specific individual whales that always breed on a designated area, defined by IWC

BSA- South-West Atlantic breeding stock (Brazil)

BSG- South-East Pacific breeding stock

CA- Central America breeding stock

Seasonal dataset- recordings from a specific location in a particular season

General dataset- the overall recordings assembly used in this study

Methodology

Unit Classification Key- classification key used to determine the unit type, based on 5 characteristics

Key code- 5-digit code determining the unit type, obtained by the Unit Classification Key

General unit dictionary- a list containing names and 5- digit codes of all unit types found in the research

Seasonal unit dictionary- a list of all unit types used by a breeding stock in a season

Unit string- a string of units, represented by their names or codes, as they appear in the recording

Plots

Recurrence plot- matrix figures, used to visualize the periodicities of a system, the time series, where the elements of the matrix correspond to the times of the repetitiveness (of that system)

Levenshtein distance- the minimum number of insertions, deletions or substitutions necessary to turn one string of elements into the other

Levenshtein Similarity Index- Levenshtein distance calculation, normalized by the length of the longest string

Levenshtein matrix- auto- correlated recurrence plot, constructed based on the Levenshtein distance

Extract- 5-unit long string, extracted from the main string (which contains all the units of the entire recording), used to calculate the Levenshtein distance, by comparing it to the main string, for building the matrix

Key distance- distance calculated based on the number of the identical values of the (5-digit) key codes of two unit types that are being compared. It is further applied to the entire unit string, and all the unit types in it

Key matrix- auto- correlated recurrence plot, constructed based on the Key distance

Cross-correlation matrix- matrix comparing Key matrices of two different recordings

Light, dark, and mixed matrix- 3 types of cross-correlation matrix, determined by the prevailing color in it. Light-colored ones are demonstrating the high similarity of recordings building it, as in contrast to the dark ones. Mixed matrices are showing partially similar recordings

Density matrix- matrix built of the arithmetic means of each of the cross-correlation matrices together

Jaccard Similarity Index- value determined by the set of overlapping units divided by the sum of all unique unit types of the two seasonal dictionaries that are being compared

Song bearing- graph representing songs relatedness to each other in a given season (song “behavior”)

Exhaustion curve- a plot of cumulative unique song units detected as a function of time

Complexity score- values determining the song variability, grouped by the song hierarchy level they are describing

Versatility Index- number of unit types divided by the total number of units sung per song (unit diversity of an individual’s songs)

RESUMO

Machos de baleia jubarte são conhecidos pelos seus cantos complexos. As modulações desses cantos podem ser graduais, chamadas de evolução, ou rápidas — revoluções. Apesar dessa versatilidade, todos os machos da mesma área de reprodução adotam o mesmo tipo de canto, durante um determinado período reprodutivo. As regras que determinam essas modulações não são bem conhecidas. Um mecanismo possível gerador de tais mudanças no canto pode ser o intercâmbio dos componentes do canto na área de alimentação, onde populações distintas podem se encontrar, e potencialmente interagir. Outra possibilidade pode ser a visita de um indivíduo de outra população, durante a época da reprodução. Uma terceira opção em potencial seria uma deriva unidirecional do canto (até agora observada na Oceania, onde um único tipo do canto viaja de uma população a outra em anos subsequentes). Apesar de ter dados limitados sobre o nível de interação das populações distintas dos dois oceanos da América Latina, provenientes de análises genéticas e de foto identificação, nós hipotetizamos que esse tipo de contato é detectável através da natureza e construção do canto. Para determinar qual desses mecanismos mencionados anteriormente melhor explica a mudança do canto em populações distintas de baleias jubartes na América Latina, nós montamos uma base dos dados de 1718 minutos de gravações ao longo de 4 temporadas reprodutivas consecutivas (2016-2019), em 8 localidades diferentes em áreas reprodutivas na América Central e do Sul. A metodologia aplicada neste trabalho é dividida em métodos novos, construídos a partir deste estudo (uma chave para a classificação das unidades do canto e gráficos para visualização de padrões recorrentes a partir da distância de Levenshtein), métodos existentes mas não aplicados nesta área de pesquisa (ìndice de similaridade de Jaccard usado para comparar diferenças entre as unidades dos cantos) e métodos já bem estabelecidos empregados na pesquisa sobre o canto da baleia jubarte (Índice de similaridade de Levenshtein e ranqueamento de complexidade do canto). Mesmo que nem todos os resultados obtidos pela nossa pesquisa estejam de acordo com a literatura contemporânea, todos os nossos métodos concordam sobre a conclusão que as populações das baleias jubartes na América Latina, explorados nesse estudo, mantem contato acústico, que é variável em intensidade e tipo, e que esse contato (dessas ou de outras populações), é, provavelmente, um fator determinante das mudanças permanentes que observamos nos cantos das baleias jubartes.

Palavras-chave: *Megaptera novaeangliae*, baleia jubarte, canto, evolução, América Latina, BSA, BSG

ABSTRACT

Male humpback whales are known for their intricate singing. The changes of these songs can be gradual, called evolution, or rapid — revolutions. Despite this versatility, all males from the same breeding ground adopt the same type of the song during a given breeding period. The rules that determine these changes are not well known. A possible mechanism for generating such changes in singing may be the interchange of song components in the feeding area, where distinct stocks can meet, and potentially interact. Another possibility could be the visit of an individual from another stock during the breeding season. A third potential option would be a unidirectional song drift (so far observed in Oceania, where a single song type travels from one population to another in subsequent years). Despite having limited data on the level of interaction of distinct stocks from the two oceans of Latin America, from genetic analysis and photo identification, I hypothesize that this type of contact is detectable through the type and composition of the songs. To determine which of these aforementioned mechanisms best explains song change in distinct stock of humpback whales in Latin America, I assembled a database of 1718 minutes of recordings over 4 consecutive breeding seasons (2016-2019) in 8 different locations in breeding areas in Central and South America. The methodology applied in this work is divided into new methods, built for this study (a key for classification of song units and matrices for visualization of recurrent patterns in humpback whale song, based on the Levenshtein distance), existing methods, previously not applied in this area of research (Jaccard similarity index used to compare differences between song unit repertoires) and well-established methods applied in humpback whale song research (Levenshtein's similarity index and complexity scores for song units). Even though not all the results obtained by our research are in agreement with the contemporary literature, all our methods agree on the conclusion that the stocks of humpback whales in Latin America, explored in this study, maintain acoustic contact, which is variable in intensity and type, and that this contact (from these or other stocks) is probably a determining factor for the never-ending changes we see in humpback whale songs.

Key words: *Megaptera novaeangliae,* humpback whale, song, evolution, Latin America, BSA, BSG

INTRODUCTION

1 ABSTRACT

Male humpback whales are known for their complex advertisement songs. Modulations of these songs can be gradual, called evolution, or fast-song revolution. Despite this versatility, all males from the same breeding area conform to the same song type within a breeding season. Rules under which these gradual or rapid changes occur are poorly understood. One possible mechanism of song change is through exchanges of song components in feeding grounds, where distinct breeding populations could potentially interact, at least acoustically. Another possibility is an off-road visit of a member of a neighboring stock in the breeding ground. A third proposed mechanism is unidirectional song drift (reported in stocks of Oceania, where a single song type flows from one stock to the next in consecutive years). Although there is limited evidence of stocks on both sides off the South American continent are in contact based on the data of different nature (Genetic, Photo ID), here I hypothesize that such contact is potentially detectable in the content of their songs. To determine which of these previously mentioned mechanisms best explains song change in Latin American humpback whales, I have assembled a database of 1718 minutes of recordings from four consecutive breeding seasons (2016-2019) at 8 different locations of breeding areas in Central and South America. In Chapter I, I test the prediction that a unit dictionary, a simple and unbiased method, is reliable in showing the level of acoustic contact among different populations. These dictionary overlaps between different seasonal datasets (a given location in a season) were explored using Jaccard Similarity Index. In Chapter II I focused on the structure of the song and its elements, with the same aim of decoding the level of the song hierarchy which can depict the change of the song, where it can be quantified and compared. As in the third chapter, it deals with the exploration of novel methodologies for visualizing the structure of the songs and extracting its larger elements, while using the sequence of the smallest ones (units) as a base. For this purpose, I tested two methods: a newly developed Key method, describing unit types by a 5-digit code based on their characteristics, and the well-tested Levenshtein distance calculation. Both methods were proven capable of constructing the visual representation (a recurrence plot) of the song structure, hierarchically organized, agreeing with our current understanding of the humpback whale song. However, these visual representations, constructed by both methods, showed a high level of variability with each song repetition, which was not emphasized in previous studies. These methods also showed reliability in distinguishing between similar and very different content in songs. Moreover, these recurrence plots – matrices- also showed only partially similar matrices, thus several types of song structures – a syntax?- reemerging across the diverse dataset. Finally, I compared Complexity scores, Levenshtein, and Jaccard Similarity Indices to tell when a song revolution or evolution took place. However, our results do not

completely agree with the contemporary literature, coming from Australia, which shows a direct connection between song complexity and its stage of evolution. All of our methods agree in concluding that the Latin American humpback whale stocks explored in this study are in acoustic contact, which varies in intensity and type, and that this contact (of these or other stocks) is most likely a driver of the ever-changing nature of the humpback whale song.

2 HUMPBACK WHALES

The humpback whale (*Megaptera novaeangliae*, Borowski, 1781) is a marine mammal belonging to the *Balaenopteridae* family (CLAPHAM; MEAD, 1999). It is a Mysticete, meaning it has baleens instead of teeth and, next to other distinctions, vocalizes in low frequencies (PAYNE; GUINEE, 1983). Humpback whales are recognizable for their specific colorations on the fluke which helps individual identification of animals. In this species, females are slightly larger than males (males grow to be 13-14 m long, while females are around 15-16m in length) (CLAPHAM; MEAD, 1999), while other differences, like the shape and position of reproductive organs, are not easily observed. In this sense, next to biopsy, individual gender is usually distinguished by the presence or absence of a calf in their narrow surrounding (CRAIG et al., 2003).

The species is also famous for its complex aerial behaviors, including leaping, breaching, and tail slapping (BETTRIDGE et al., 2015). As the purpose of these behaviors is not clearly known, it is believed they mediate social interactions. The complete social structure of humpback whales is not well understood. However, we are aware of whales aggregating on breeding grounds, as well as in the feeding areas (to facilitate catching the prey), meanwhile mostly traveling from one area to the other in small, kin-unrelated loose groups (VALSECCHI et al., 2002). Humpback whales across the globe practice this annual migration from feeding to breeding grounds, which are happening in different seasons. Namely, breeding areas are located in low latitudes, where they would spend the winter, after which they travel to feeding areas in the higher latitudes in summertime (CLAPHAM; MEAD, 1999; VANG, 2002). This is the rule for almost all humpback whale breeding stocks (except the one located in the Arabian Sea) (MIKHALEV, 1997). As a cosmopolitan species, humpback whales can be found in all oceans. Yet, throughout their lifetime, the same animal breeds and feeds in the same 2 areas in the ocean, showing marked site fidelity (BAKER et al., 1990; MARTIN et al., 1984), although there are exceptions (FÉLIX et al., 2020). Because of this side fidelity to their breeding areas, the International Whaling Commission (IWC) divided the world population of humpback whales into 14 distinguishable breeding stocks, where half of this number is located in each of the hemispheres of our planet (IWC, 1998; Figure 1).

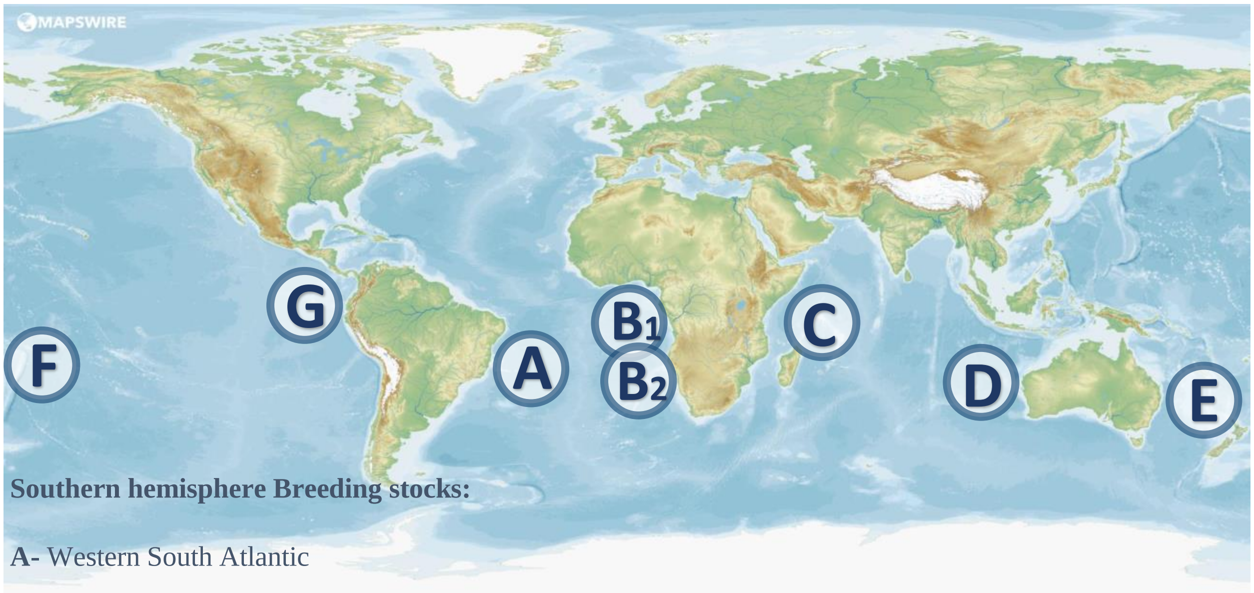

Figure 1. World map with Southern Hemisphere breeding stocks of Humpback whales labeled by letters (IWC, 1998).

3 LATIN AMERICA BREEDING STOCKS

South America hosts two breeding stocks from the Southern Hemisphere, Breeding stock A (hereinafter BSA), and breeding stock G (hereinafter BSG) (IWC, 1998). In more detail, BSA occurs along the Brazilian coast with the breeding area concentrated around the Abrolhos Bank, in the West South Atlantic Ocean (16° to 19° 30' S) (MARTINS et al., 2013). Whales of BSG appear in the area of the southern Pacific Ocean, specifically the coast of Costa Rica, Panama, Colombia, Ecuador, and Peru (4° S- 11° 16' N)(ACEVEDO et al., 2017), even all the way up to Nicaragua, as suggested by one photo-ID case (DE WEERDT; RAMOS; CHEESEMAN, 2020).

BSA and BSG breeding areas are physically separated by the continent (Fig. 2), while their feeding grounds lay in relative proximity: BSA occupies waters around South Georgia and the South Sandwich Islands (54° 31' S, 37° 24' W)(ENGEL; MARTIN, 2009; ZERBINI; ANDRIOLO; HEIDE-JØRGENSEN, 2006), while

BSG feeds partially in the southern coasts of Chile (Corcovado gulf, 43° S, 74° W) (ACEVEDO et al., 2013; GIBBONS; CAPELLA; VALLADARES, 2003; HUCKE-GAETE et al., 2013), and partially in the wide-area around the Magellan straight, all the way to the Orkney island (65° S, 63° W- 60° 54' S, 46°, 40' W)(DALLA ROSA et al., 2012).

In Central America, the breeding habitat of BSG whales is also used by the Central American breeding stock (hereinafter CA)(BETTRIDGE et al., 2015). Although CA is a northern hemisphere stock, BSG has a range all the way to 11° S, passing the equator, so that is a potential to exchange individuals from these two stocks (CHERESKIN et al., 2019; RASMUSSEN, 2006). Nonetheless, these two stocks are temporally segregated, as BSG, like all Southern Hemisphere stocks, breed during the austral winter and spring (June-November), while the Northern hemisphere stocks, where Central American breeding stocks also belongs, breed during the Austral summer and fall (December- April) (CALAMBOKIDIS et al., 2000; CLAPHAM; MEAD, 1999; DAWBIN, 1966; RASMUSSEN, et al., 2007; RASMUSSEN; CALAMBOKIDIS; STEIGER, 2011; VANG, 2002;). Yet, a recently reported case of Nicaragua humpback whales spotted in the BSG feeding ground suggests the interaction between neighboring stock occurs (DE WEERDT; RAMOS; CHEESEMAN, 2020).

Figure 2. The map of South America with labels of breeding and feeding grounds of two of its stocks of humpback whales, BSA (yellow) and BSG (violet), with hypothetical migration routes. (pins- breeding grounds, circles-feeding grounds)
Map, ®Google maps. Accessed 26/09/2020

Nonetheless, we can be very certain of the existence of breeding stocks *per se*, as the connectivity of certain whales to their breeding and feeding areas (site fidelity) is well documented using different methodologies, like satellite tracking (ACEVEDO et al., 2017; FÉLIX; GUZMÁN, 2014; ZERBINI; ANDRIOLO; HEIDE-JØRGENSEN, 2006), photo identification (STEVICK et al., 2004, 2006;) and genetics (CYPRIANO-SOUZA et al., 2010; FÉLIX et al., 2020; FÉLIX; BOTERO-ACOSTA, 2012). These methodologies also provide evidence about the level of connectivity between neighboring stocks, as on several occasions, some whales have been reported visiting areas out of their regular yearly route (DARLING et al., 2019; FORESTELL; URBÁN R., 2007; GARRIGUE et al., 2002; GARRIGUE; BAKER; CONSTANTINE, 2007; KAUFMAN et al., 2011; SALDEN et al., 1999; STEEL et al., 2018, FÉLIX et al., 2020). By now, four cases of inter-ocean traveling humpback whale have been reported: (1) a male tracked between Indian and the South Atlantic Ocean (genetic sample) (POMILLA; ROSENBAUM, 2005); (2) BSA female spotted in the waters off Madagascar (thus, she traveled from Southern Atlantic to the Western Indian Ocean, recognized by her natural tail markings, photo- ID) (STEVICK et al., 2011), (3) another female spotted In the Eastern South Pacific Ocean and afterward in the Eastern South Atlantic (photo- ID)(STEVICK et al., 2013), and the most recent one, (4) reporting a whale sighted in Peru- South Pacific, and Brazil coast of South Atlantic (FÉLIX et al., 2020). In addition, there are several unpublished accounts of individuals from BSA, found by the Happywhale platform, encountered in BSG feeding grounds (Milton Marcondes and Renata Sousa-Lima, personal communication, Cheeseman & Southerland, unpub. data)

Studying humpback whales breeding in Latin America is of great interest to the scientific community, as most of these stocks are rapidly recuperating after being notoriously hunted in the whaling era. Therefore, at this point in time, we have a chance to monitor whales returning of their uninterrupted pre-whaling behavior ecology, a priceless investigation position that should be wisely taken advantage of (BRADLEY; STERN, 2008).

The existence of inter-ocean humpback whale mixing is likely underestimated. How often does such exchange occur? Does it involve mostly males or females, or both? If males are involved, the consequences of these exchanges are likely recorded in their song structure. Therefore, acoustics has a great potential for assessing inter- stock mixing, *i.e.*, humpback whale song-based stock identification (ZERBINI et al., 2014). This subject is of the main interest of this thesis, analyzing its potential and applying adequate methodologies.

4 HUMPBACK WHALE SONG

Underwater, the sound is a reliable mode of communication because it travels fast and has low attenuation, traveling further underwater than any other type of wave (BRADLEY; STERN, 2008), allowing animals to communicate over long distances. In addition, the evolutionary history of whales indicates selection for low-frequency sounds, which also enables long-distance communication. The degree to which whales respond to this selection is, in the case of baleen whales, restricted by their body size (MAY-COLLADO; AGNARSSON; WARTZOK, 2007). Taking into account the size of oceans humpback whales live in, having a signal that can cover big areas seems advantageous. Humpback whales, like all other Mysticetes (baleen whales), do vocalize in low frequency, still in broadband tones. Their vocalizations are highly variable in frequency and usually occupy the range between 100 and 4,000 Hertz (DUNLOP, 2018; TYACK; CLARK, 2000). However, in a recent paper, researchers reported hearing humpback vocalizations in a frequency around 40 Hertz (DARLING, 2015), while certain higher frequency units of the humpback whale vocalization can have harmonics as high as 24kHz (AU et al., 2006). These findings further stress how little we still know about humpback whale vocalization capacities.

Yet, some facts about the song are well known. For example, only male humpback whales vocalize using very well structured and melodic articulations, which, because of its complexity, stereotypy and repetitiveness are considered a song (PAYNE; MCVAY, 1971). Both genders are known to vocalize (emitting sounds consider to be social and feedings sounds) (SIMAO; MOREIRA, 2005), yet only males are found to sing (DARLING; BÉRUBÉ, 2001; GLOCKNER; VENUS, 1983).

The song can be heard most intensely in the breeding area (e.g. CERCHIO et al, 2001), however, there are reports of songs in the feeding area (in different levels of complexity) (e.g. GARLAND et al., 2013; KOWARSKI et al. 2019; MAGNÚSDÓTTIR et al., 2014; VU et al., 2012), as well on the migration routes (e.g. MIKSIS-OLDS et al., 2008). All of this can be used in building the hypothesis of the song’s role in sexual selection for the species, both serving to facilitate females’ choice and to mitigate male-male interaction (HERMAN, 2017; CHOLEWIAK et al., 2018).

Humpback whale songs are very distinctive and complex. The basics of these vocalizations were first described by Payne and McVay in 1971 (PAYNE; MCVAY, 1971; WINN; WINN, 1978), and not much has changed since. These songs are hierarchically structured and a well-organized system: the song is constructed of units, phrases, and themes. Different unit types (as the smallest fragments of song organization) in different combinations form phrases, a repetition of phrases represents a theme, and a song contains several different themes sung in a sequence (PAYNE; MCVAY, 1971; WINN; WINN, 1978) (Fig. 3).

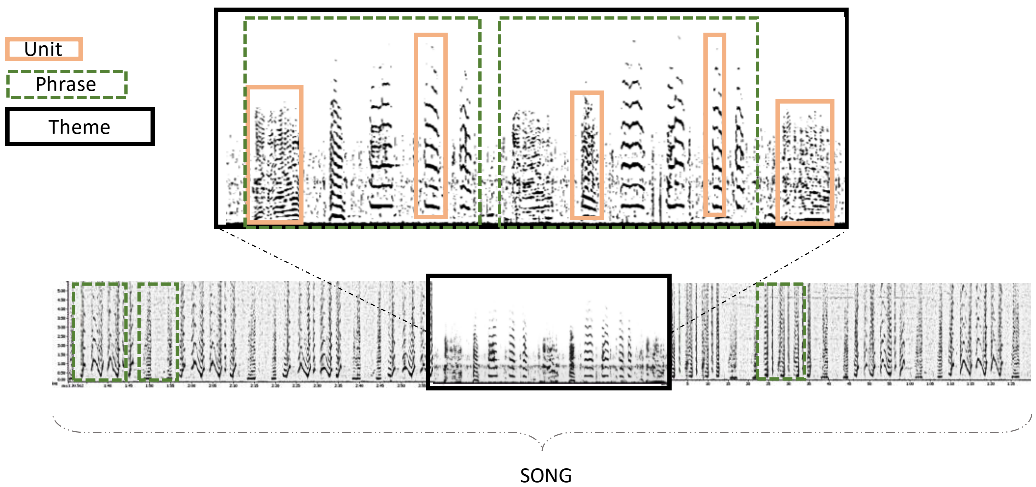

Figure 3. Graphic representation of a humpback whale song fragment, with song elements, as described by Payne and McVay, 1971, labeled with different box types: Units, phrases and themes

All male humpback whales in the world use the same system to organize their songs (PAYNE; GUINEE, 1983; WINN; WINN, 1978). More than just a system, males belonging to the same breeding stock conform to the same song type (WINN; WINN, 1978; PAYNE et al., 1983; PAYNE; GUINEE, 1983; PAYNE; PAYNE, 1985; HELWEG et al., 1998; CERCHIO et al., 2001). However, there is more to it- the song is under constant change. Sources of these changes can be further discussed, but what needs to be stressed in this context, is that, even though the song suffers constant transformation, all males from the stock conform to these changes, thus maintaining a single song type within the stock and the season (within some level of variation). This is not where humpback whales stop to fascinate us- slight changes in the song accumulate over time, which will eventually bring the change of the entire song to a different song type. This threshold usually takes a few seasons to be visible, when the song is totally changed to a different type, meanwhile changing slightly from season to season. The biggest leaps in accumulations of changes are happening in the breeding seasons, as in those periods, humpback whales sing the most (PAYNE; PAYNE, 1985). In this sense, the song changes most from one breeding season to the next. However, these changes can happen in different intensities, thus taking more or less time for a stock´s song to change its type. The moderate and steady change intensity described earlier, is known as song evolution. General mechanisms underlying these changes are described by several authors (Winn and Winn, 1978; Payne et al., 1983; Payne and Payne, 1985; Cato, 1991), indicating that changes can take place in any of the hierarchical levels of the songs- units, phrase, themes, finally bringing the overall song change. These changes include unit splitting or stretching, inclusion or exclusion of unit types, but also entire themes.

Important to understand is the difference of the source of change- namely, as Podos and Warren (2007) stress out, it is important to distinguish between memes and mechanisms, as the main basis for vocal innovation. In particular, memes are acoustic characteristics of the song that are passed on via some kind of social learning, while mechanisms describe physical predispositions for producing the sounds in question, and are inherited genetically (PODOS et al., 2004). As genetic changes in anatomy, physiology, and so on take a much larger time scale to be expressed, researchers mainly focus on memes differentiations. This is particularly useful for humpback whales, where geographical differences in the song, but also though time need to be compared and validated. There are several known scenarios under which the song, like any other phenotype, can change. One of them is drift- cultural or genetic. It is widely accepted that Cultural drift is the main source of change in humpback whale songs, as it comes from the individual singers, by making mistakes or introducing small modifications for other reasons (GARLAND et al., 2011; SLATER, 1986). It is noted, however, that the song can go through an additional type of change, that is rapid and intense, and it is known as song revolution (GARLAND et al., 2011; NOAD et al., 2000). In this case, the song does not follow a slight, steady pace of change over long periods of time, but rather changes abruptly, beyond recognition, in a matter of one or a few seasons. We can hypothesize that this type of change fits under the realm of Cultural selection, as this scenario is specified by certain (vocal) memes being favoured over others (PODOS; WARREN, 2007), for reasons still unknown.

More than cultural selection, the matter of abrupt song change is also considered a cultural revolution. When we can track the source of this new, stemmed in another stock, song, since the humpback whale song is considered a cultural trait, thus passing a song to the next stock is seen as a case of cultural revolution. (GARLAND et al., 20013; CERCHO et al., 2001; RENDELL; WHITEHEAD, 2001; NOAD et al., 2000; PAYNE and GUINEE, 1983;).

The reasoning behind this specific behavior is beyond our understanding at the time. However**,** the need for novelty is something common across the animal kingdom (MULER; WAGNET, 1991), and the pattern under which the song of humpbacks most often change seem to fit into the theory of "optimal mismatches" (PAYNE, 2000). The idea behind this is that the novel expression needs to maintain a certain level of "known" in order to seem familiar, so as not to be totally disregarded as strange, but also to incorporate new material to a certain extent, which can, for example, tell about the fitness of an expressing animal**.** Novelty is favoured in the evolution in animals, as it is a sign of fresh genes, new information, and potential new functions (morphological innovations, for example) (MAYER, 1960; NEI et al., 1975), which is directly benefiting the next generation of that population.

Humpback whale song, in a way, has a dual nature- on one hand, there is a song structure, which is universal for the species, on the other, collection of song elements, their combination, and organization within the known hierarchy is specific for every breeding stock in a season. Thus, neglecting the song's ever-changing nature, if we observe a single song of a specific stock in a single season, we can draw a parallel to the tail marking of an individual whale, used for photo identification. Similarly, using a song type sung in a particular season, we can tell which breeding stock it belongs to. Therefore, the song can be used for stock identification (HELWEG et al., 1990).

Of course, as we learned by now, humpback whales have more "tricks in their sleeves"- we briefly mentioned the possible sources of change when it comes to song evolution, but we did not discuss the origins of song revolutions. There are not many publications reporting these events (GARLAND et al., 2011; NOAD et al., 2000; GONÇALVES et al., in prep.), and base on them it seems song revolutions only occur in the Southern hemisphere. One important aspect of the Southern hemisphere humpback whales ecology that should be taken into consideration when contemplating on this observation, is that these whales show us there are stock mixing, facilitated by not having physical barriers between their feeding grounds (as almost all feed in the waters of Antarctic). A few visiting singers from a neighboring stock, brought their stock's song type, introducing it to other singers, and in the course of a couple of seasons, their song was the only one heard in the visited stock (NOAD et al., 2000).

This of course complicates the system of identifying stocks by the song they sing, yet as song revolutions are observed rarely, we can consider it more of an opportunity to measure stock exchange, than an unsolvable problem. If we hear a neighboring song or a part of it (theme, for example) during a season, we can conclude that whales of two neighboring stocks met at some point since the previous breeding season. In this sense, simply by comparing songs, we can understand if the interaction of the two stocks took place in the course of one year (HELWEG et al., 1990). A stock song identification tool can serve in better understanding the ecology of this species, their movements, and their process of conformity to novelty. This can further help us understand the elusive role of the song, as by now, it remains unknown (HERMAN et al., 2013).

As stated before, only male humpback whales sing. This brings an intuitive conclusion that song serves as the main tool for the mate attraction and courtship (BAKER; HERMAN, 1984; CERCHIO; JACOBSEN; NORRIS, 2001; CHU; HARCOURT, 1986; CLAPHAM, 1996; CLARK; CLAPHAM, 2004; FRANKEL et al., 1995; HELWEG et al., 1992; HERMAN et al., 2013; HERMAN; TAVOLGA, 1980; MEDRANO; BAKER, 1994; MOBLEY; HERMAN, 1985; TYACK, 1981; TYACK; WHITEHEAD, 1983; WINN, H.E. and WINN, 1978). Still, we have no strong evidence to confirm this. As stated in the paper by Luis Herman (2017), although it seems most probable, some other explanations for the role of the song in the humpback whale system could be territory defense, an honest signal of their fitness and hierarchical position, or some other, more out-of-the-box ideas, proposing the song is used as sonar for echolocation, similar to the ones of Odontocetes (MERCADO, 2018). Although humpback whales predominantly live as solitary animals throughout the year, in breeding grounds they do aggregate into pods of variable sizes, mostly dyads, spread throughout large sea areas. (HERMAN, 2017). These male aggregations are called “floating leks”, based on well-studied bird leks (CLAPHAM, 2000, 1996; CONNOR; READ; WRANGHAM, 2000; HERMAN; TAVOLGA, 1980; STEVICK et al., 2011). These loose aggregations consist of many males of different ages, where they gather to sing (CLAPHAM, 1996; HERMAN; TAVOLGA, 1980). In contrast to bird leks, where males compete by singing and/or dancing, it seems that in humpback whales, these leks are actually a remarkable example of cooperation (CONNOR; READ; WRANGHAM, 2000; HERMAN, 2017; HERMAN et al., 2013). Considering the vastness of the ocean, and scattered patterns of daily motions of humpback females (DARLING; JONES; NICKLIN, 2006; GUZMAN; FELIX, 2017; WEDEKIN et al., 2010), it seems very likely that males are joining forces in order to cover vocally the biggest possible area for the longest possible time. Thus, with more males singing the same song at the same time, the song propagates further, also taking a break of an individual singer does not mean a complete cessation of the overall song (FOSTER, 1983), benefiting everyone. It is believed that females are attracted to these temporary acoustic pods (DURAES et al., 2009; EMLEN; ORING, 1977; HERMAN et al., 2013; LANK; SMITH, 1992), but how they choose their mates is yet to be discovered (CHOLEWIAK et al., 2018). Cholewiak et al. (2018) additionally confirmed another leading hypothesis on the role of the humpback whale song, that song mediates male-male interactions in dyads. In this study, it was shown that male humpback whales alter their song presentation in the presence of other singers, eventually leading to the complete cessation of singing if two males come too close.

No one has witnessed the mating of humpback whales so far (HERMAN et al., 2013). Their courtship practices remain an unsolved puzzle, however, it seems that the crucial piece in it is played by their song. Going back to the uniformity of song across a breeding stock, yet its uniqueness (per stock and per season), brings us to the discussion on how and why the song "behaves" the way it does. As we cannot clearly understand its direct purpose, we can speculate its importance, as a certain effort is required in maintaining the mentioned processes (constant change, yet, uniformity; but also song sharing events between stocks). If a matter constantly changes, but one needs to be updated with every version of it, the situation requires an effort of constant updating, or simply put, learning (or copying, or both). In this particular case, vocal learning (copying) (MESOUDI; THORNTON, 2018)

5 CULTURE, LEARNING, AND GRAMMAR IN HUMPBACK WHALES

Culture in non-human animals is a matter of ongoing debate. While mostly dependent on the definition of it, culture-like elements can be found anywhere from invertebrates (DEMAY et al., 2018), all the way to defining it as a unique attribute of the human species (GALEF, 1992). However, the drift of science in the past decade strived to the realization that culture indeed is a phenomenon common for many animal species (ALLEN, 2019; APLIN, 2018; BRAKES et al., 2019; GROSS, 2017; LALAND; JANIK, 2006; PERRY, 2010). In order to cover all of its varieties, Whitehead and Rendell came up with a broad, but informative definition of culture, where it is considered to be "information or behavior—shared within a community—which is acquired from conspecifics through some form of social learning" (WHITEHEAD; RENDELL, 2015).

More than just the culture, a question of Cumulative Cultural Evolution (CCE) in the animal kingdom, brought insights into culture and cognition of other non-human animals: birds- crows and pigeons, in their behaveiour and tool use (HUNT and GRAY, 2003; SASAKI and BIRO, 2017); monkeys- macaques, chimpanzees, and baboons, in their social interaction and ecological skills (CLAIDIERE; SMITH; KIRBY; FAGOT, 2014; YAMAMOTO; HUMLE; TANAKA; 2013; SCHOFIELD; MCGREW; TAKAHASHI; HIRATA, 2018), but also in the level of vocalizations of some species of song birds (FEHER et al., 2009) and cetaceans (FILATOVA; BURDIN; HOYT, 2013). Most recent publications bring humpback whales into this picture, exactly because of the specificities of their song (ex. GARLAND; MCGREGOR, 2020).

Concerning the nature of male humpback whale vocalization and all aspects of it, it is considered that humpback whales have developed an elaborate oral culture. On one hand, this culture remains within the breeding stock, in the shape of the stock-specific song, that is most often shared only with conspecifics of the same stock, while on the other hand, in the rare occasions of song revolution, passing songs to neighboring stocks can be considered as cultural transmission (FRAGASZY; PERRY, 2004; GARLAND et al., 2017; RENDELL; WHITEHEAD, 2001; WHITEN, A., J. GOODALL, W. C. MCGREW, T. NISHIDA, V. REYNOLDSK, Y. SUGIYAMA, C. E. G. TUTIN, 1999). More than rare song revolution events, we are familiar with the existence of a song flow, from one stock to the next (GARLAND et al., 2011). This phenomenon is a part of the natural process of song dynamics, which can be considered a cultural exchange (transmission) (BAKER et al., 1990; CERCHIO; JACOBSEN; NORRIS, 2001; ERIKSEN et al., 2005; GARLAND et al., 2013). Overall, the cultural evolution of the humpback whale song is one of a kind in the natural world as we know it, because of its intensity, time, and spatial scale (GARLAND; MCGREGOR, 2020). Only several bird species have shown similar elaborate, ever-changing vocal skills, such as corn bunting (GARLAND; MCGREGOR, 2020), village indigo birds (PAYNE, 1985), great tits (HUNTER; KREBS, 1979), etc. These skills are best reflected in (sometimes only seemingly) life–long learning abilities, that shape local culture and its dynamics.

When talking about culture, we are inevitably talking about learning. Social learning can have three pathways: Vertical- when knowledge is passed down from parents to the offspring, Oblique- when the recipient is an indirect offspring, or an unrelated next-generation member, or Horizontal- when the information is shared between peers (CAVALLI-SFORZA; FELDMAN., 1981). Considering the nature of humpback whale song, it is most probable the social learning in this species occurs in all 3 levels, the first one to be the least probable, as patriarchal parental care is not observed so far, and only males sing (DARLING; BÉRUBÉ, 2001; GLOCKNER; 1983). In this way, social, or in this particular case, vocal learning, in humpback whales seems omnidirectional (shared), opposed to, for example, birds, where most often young males tend to learn songs only from neighboring males, thus an example of oblique vocal learning (ALLEN, 2019; GARLAND; MCGREGOR, 2020).

One element in vocalization binding birds and whales, otherwise relatively rare in nature, are so-called "Dialects" (FORD, 2002). In bird species they are very well studied, however, in whales, dialects are reported by now only in several species: orcas, sperm, and humpback whales. Dialect (vocal geographic variation) (CONNER, 1986) seems to be a "by-product" of physical isolation (of parts) of populations, where, together with other local adaptations (evolutions), vocal communication also diverges in different directions. Thus, in part, it goes in hand with genetic differentiations (FORD, 2002). Dialects, as such, seem to reflect the relatedness between different local populations of the same species, as more interacting ones share more of their vocal repertoire (DEECKE et al., 2000). This is well documented for the whale species earlier mentioned, where vocally distinct populations form clans. In humpbacks, however, we know that the stocks geographically close together share more of the vocal repertoire in consecutive years (PAYNE; PAYNE, 1985; GARLAND, 2013). But because of the ever-changing nature of their song, it is under debate if local differences in vocalization in humpbacks can be considered as dialects.

Ford (2002) further suggested dialects have a role “that help maintain cohesion and integrity of matrilineal groups". This is because orcas and sperm whales both are matriline-connected species. Interestingly, in humpback whales only mothercare towards the offspring is reported, however, only males sing, and as a species, they are not particularly social (as known for all mysticetes), in contrast to sperm whales and orcas. However, concerning the specificity of the dialect phenomenon including only several whale species, it is probable that cultural transmission plays a much bigger role than genetic mechanism (FORD, 2002). Ultimately, this distinction develops an overall species vocal culture.

Taking birds as a comparing subject to humpback whales make sense because of their similar vocal abilities, cultural tendencies, and is especially convenient, as birds’ vocalizations are much better studied than whales. The same goes for learning. In birds, it is believed that learning fits into 2 categories, open and closed-end learning (BEECHER; BRENOWITZ, 2005). Closed-end learners are species that would learn one or several songs within the first year of their life, thus in the developing stage, and those songs would be used for the rest of their life. Open-end learners can acquire new song types beyond the first year of life, thus species able to learn new songs beyond the most plastic years of their brain development. However, some bird species made this strict division a bit more complicated, as in the case of the great tits (*Parus major*), where scientists learned that it takes several years for some avian species to start acquiring different song types (MCGREGOR; KREBS, 1989). So, if not observed carefully, the species would seem closed-end learners, to prove differently only after a couple of years. This can also depend on the number of inspected animals, as it takes only one to prove species to be open-end learners, while it takes much more to prove the opposite (BRENOWITZ; BEECHER, 2005; NORDBY; CAMPBELL; BEECHER, 2002).

Similarly, for now, we can consider humpback whales to be open-end learners, as no records exist of the same song being used again after it was outdated (GARLAND; MCGREGOR, 2020). However, could it be just a matter of the sampling effort we have for this species? Opposite to great tits, it may turn out humpback whales are closed-end learners, just reaching the peak of learning abilities at a really late age. Moreover, there could also be differences between different breeding stocks- the same way they practice singing different songs, according to different mechanisms of song modifications (evolutions and revolutions) seem to govern their vocal culture (song revolutions is so far registered only in the Southern hemisphere)(GARLAND et al., 2011; NOAD et al., 2000; REKDAHL et al., 2018).

In this regard, beyond the existence of evolution and revolution song changes, we are not aware of the mechanisms under which these changes take place. One of the hypotheses could be that each of the breeding stocks, or maybe between hemispheres, have their own set of rules, or “grammar”. We are familiar with the rate of similarity between songs of different breeding stock somewhat depends on their physical proximity, as nicely put by Darling in his most recent publication, concluding that geographic distance (of stocks) is not a predictor, but is a factor for song similarity (DARLING et al., 2019; GARLAND; MCGREGOR, 2020). Although being unique in periodically revolving their oral culture, considering that similarity/dissimilarity of humpback whale cultures depends on physical distance, as well the mutual influence of neighboring stocks, a parallel can be drawn with human language, where similar processes are known to take place. In human language evolution, geographical proximity can be observed as an important factor in the relatedness of languages (Figure 4). More than that, there are several language families in human culture, under which several distinctive languages are gathered, but which function under a similar set of (grammatical) rules (which was the factor for grouping them in families). Language families can be geographically spread over large areas at this stage, but in the history of their development, we can see the point where there were spoken in the areas of close proximity (MUSSER et al., 2014). A similar concept is seen in the animal kingdom, in marine mammals in particular, but with the twist of active initiation to approximate vocalizations (so-called vocal contextual learning). Namely, there are reports of orcas adapting their vocalization to the ones of bottlenose dolphins with whom they were in contact in captivity (MUSSER et al., 2014). More than that, the same phenomenon is also observed in wild animals, in multispecies groups of Odontocetes (Yasmin Viana, in prep.).

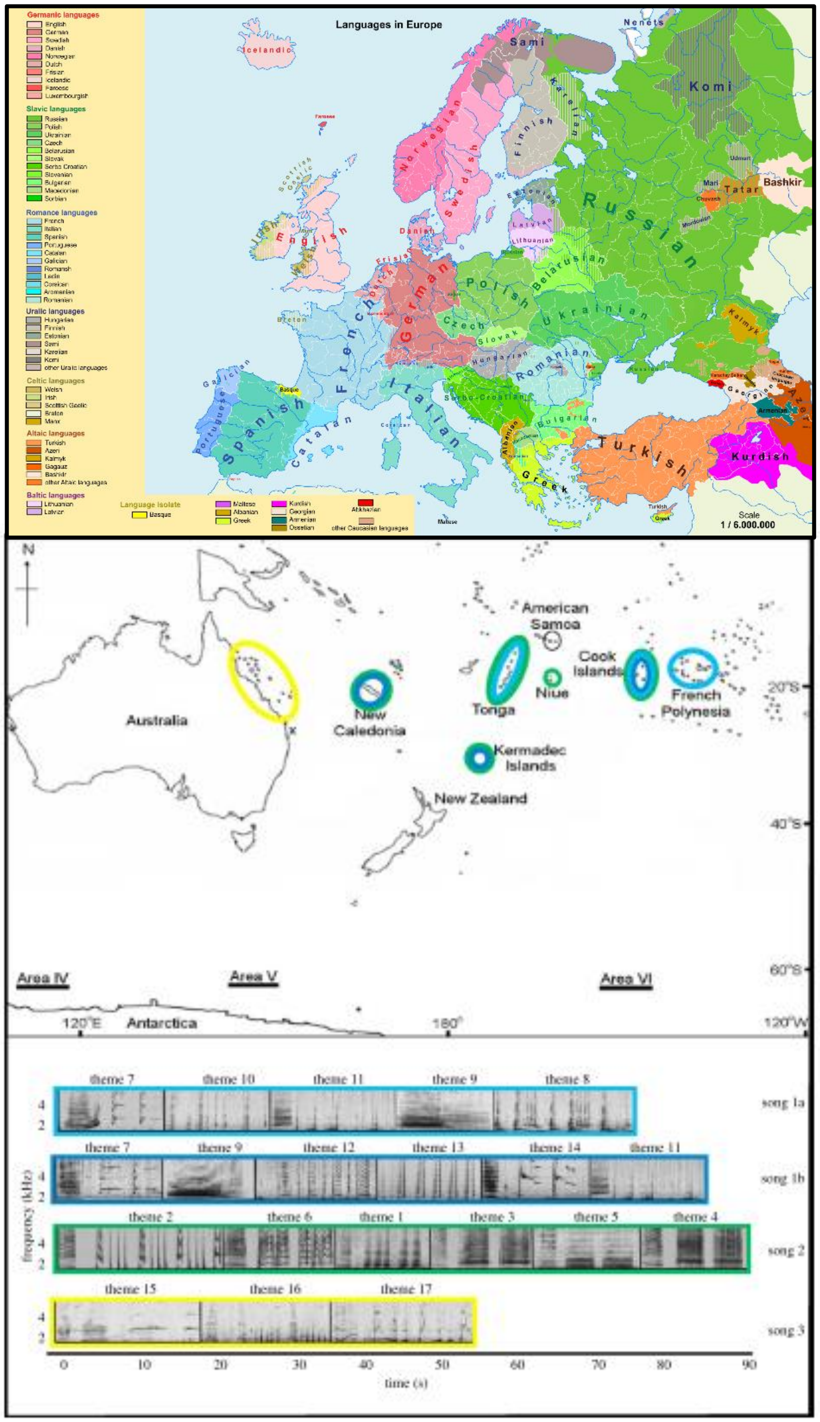

Figure 4. In the top figure, a map of Europe is presented, with different colors labeling areas where languages of the same family are spoken (Andrei Nacu at English Wikipedia, CC BY-SA 3.0 ,creativecommons.org/licenses/by-sa/3.0, via Wikimedia Commons). On the bottom, a map of the south-western Pacific is presented, showing different humpback whale song types sung in the same season, and corresponding spectrograms (retreived from Owen et al, 2019).

Similarly, songs of humpback whales sung in adjacent breeding stocks are often more alike, and *vice versa*. Although these regional (geographical) differences in humpback whale songs can be considered as dialects, the rate of song change should also be taken into consideration when applying this label. Considering the term "dialect" is borrowed from linguistics, perhaps a more precise term to use would be "geographic variation", in the case of humpback whale song, until we do find specific rules under each breeding stock changes its song differences in songs remain "random" song variations, connected to a certain region (CONNER, 1978; FORD, 2012). Dialect, on the other hand, carries an element of stability, where a language "behaves" slightly different in a particular region, compared to others, under its specific set of rules (WOLFRAM; SCHILLING., 2015). To conclude, although a bit long-fetched a concept of comparing humpback whale songs to human culture (even beyond cultural revolutions specific for the humpback whale species), the analogy between the two is an idea worth exploring (at least in this stage of our (in)experience with humpback whale song).

What seems not to be affected by geography or any other parameter whatsoever, is the organization of the humpback whale song structure (PAYNE; MCVAY, 1971). Namely, every breeding stock of humpback whales in the world uses a species-specific structure to compose their song. This phenomenon draws attention, especially taking into consideration all other, very variable aspects of their vocalization (unit types innovations, song evolutions, revolutions….). One possible explanation could be the language acquisition theory, namely, Language acquisition Device (LAD), as proposed by Chomsky (CHOMSKY, 1986). LAD would be a hypothetical tool, biologically hardwired in the brain of all individuals, that enables (humans) to acquire and reproduce language (under all complex and still not well-understood rules) with ease. This theory is interesting because it shows that every human infant can acquire any language in the first years of its life, independent of differences of its maternal language, to the one it is exposed to, with equal ease. More than this, they can innately understand grammar and syntax (MARCUS et al., 1999). This means that our brains understand some language structures and use it to learn a language, even though we are, for the most part, not consciously aware of what those are. Chomsky explains it by the theoretical existence of a "Universal Grammar", which gathers those "unfamiliar language rules", potentially governing all of the human languages.

When we think that most humpback whales stocks never get in touch, but still use the same song structure, as much as "Universal Grammar" theory couldn't be acknowledged for human languages (TOMASELLO, 2009), humpback whales seem like a very good study model for this idea. More than that, sex differences for singers and non-singing humpback whales is also a very interesting topic when it comes to brain anatomy and functionality, providing grammar acquiring and similar abilities (Renata S. Lima, personal communication). However, in the discussion on the "Faculty of Language" and language evolution, it is urged to distinguish between the language as a communication system, and the hardwired system responsible for its computation, as those two are completely different subjects, and thus, debate mixing the two cannot be of any use (HAUSER; CHOMSKY; FITCH, 2002). We are not aware of the mechanisms of whales learning the songs from peers, and more than that, mechanisms or rules under which these songs change, but it must be in a certain way, facilitating for all the males being able to learn, reproduce it, and maybe even participate in the process of song evolution. Considering the requirements needed to stay updated (keeping track of every song change and be able to reproduce it), it is hardly unlikely these processes are happening at random (CERCHIO; JACOBSEN; NORRIS, 2001). Interesting propositions on song acquisition and reproduction were tested so far in humpback whale songs, one of them to be a song partitioning to a more convenient-to-remember-parts, used in so-called "song hybridization events" (GARLAND et al., 2017). These events occur in song-type substitution periods (revolutions) when there is a "hybrid" song, constructed of parts of a new and an old song. According to Garland and colleagues, there is a specific part of the song more convenient for merging, determined by structural similarity rules.

These processes delve deep into individual song learning of male humpback whales, which is a micro-scale of song management within stocks. However, in this work, we were more interested in learning the large-scale song modulation mechanisms, and if these can help us learn more about the species, its ecology, and in more detail, about acoustically understudied Latin American breeding stocks of humpback whales.

6 THESIS OUTLINE

As BSA whales have proven cultural contact with the whales of Gabon (DARLING; SOUSA-LIMA, 2005), the main hypothesis of this thesis was that the cultural vocal contact of BSA whales is also maintained with another adjacent stock, the BSG. The aim was to closely look into this cultural exchange between the two biggest Latin American stocks, and their dynamics.

After 7 years of the first published data (STEVICK et al., 2013), only the second-ever report on a single humpback whale crossing from one of the Latin American breeding stock to the other (BSG to BSA) was published last year (FÉLIX et al., 2020), which could be a precursor for cultural exchange. In this thesis, more than animal culture in general, the main focus was on the vocal culture of humpback whales.

The scope of the first chapter was to access the interaction of two breeding stocks, focusing only on the content of their songs, namely, on their repertoire - unit dictionaries - each of the stock used in each of the 4 consecutive seasons included in this study. As humpback whale song is a highly structured system, it was of our interest to understand if the overlap in the dictionaries alone could show any important results, albeit disregarding the song structure. However, if relying only on one element, the definition of it needs to be very clear and unambiguous, as even a slight mistake or misinterpretation can lead to false results. In this manner, a unit classification key was developed, to determine units based on their 5 major acoustic characteristics. After running every unit through the key, each would get a name constructed of a random letter, a number, or the combination of two, and a unique 5-number code, expressing each of the 5 main characteristics of that particular unit. The final product of this process was the unit dictionary, which further was used as a base for calculations explored in other chapters, with each of the two units "naming" systems.

Surely, as humpback whales do maintain the system of song arrangement across their species, the hierarchy of its elements must be holding some importance. Having this in mind, I strived to develop a method that could help us unbiasedly determining the song elements within the non-stop vocalization of males (a recording), and in this way, resulting in a clearly established structural element for further comparison. Assuring it, we would be escaping misleading results by comparing vocalization elements of different types or scales. In this regard, a sequence of units described as their unique 5-number element - a unit string - representing any recording, was used to construct key matrices that would visually represent well-known song hierarchical levels. After realizing some elements are more similar than others in their composition, nicely represented by the matrix, our next goal was to compare matrices. This was done by building cross-correlation matrices, which, inevitably, touched on the question of song structure comparison and its visual representations, which helped us discover different levels of similarities between recordings, thus the songs.

However, as the methodology used in the first and second chapters is novel and still understudied, I believed it is in my best interest to compare the results gained by our new methods to some already well-established and recognized methodologies. Accordingly, I reached for a similar approach to the key-matrix system but using the Levenshtein distance calculation - a metric proven to confidently tell the similarity of different humpback whale songs (e.g. OWEN et al., 2019). The twist I gave in this chapter in using the Levenstain calculation, was that, instead of applying it to two different recordings or songs, I aimed for determining the auto-similarity within the same recording. In this way, I was once again able to see the hidden structures in the singing of humpback whales. Additionally, a system able to automatically delineate the beginning and ending unit of every song or theme within the recording was developed, and in this way, potentially helping in the future treatment of longer recordings and their elements´ determination.

In the final chapter of this thesis, the classical methodology in the humpback whale song field, namely the Levenstain Similarity Index and Complexity scores (ALLEN et al., 2018) were contrasted against our methods introduced in preceding chapters, in order to compare the results and discuss the benefits and flaws of these alternative methods, hopefully helping in choosing methodologies for future research in a broader array of possibilities than those currently available.

The thesis is wrapped up by a General conclusion section, including a short recapitulation of the methodology applied and a list of the most important findings in this research while offering theories and possible explanations for the results gained by the different methods contrasted. Finally, I offer comments targeting the main questions that need to be answered in future research, as well as how the used methods can be improved or adjusted for the field of humpback whale song research. In the figure below (Figure 5), the methodology flowchart is presented, showing the step-by-step processes taken during our research.

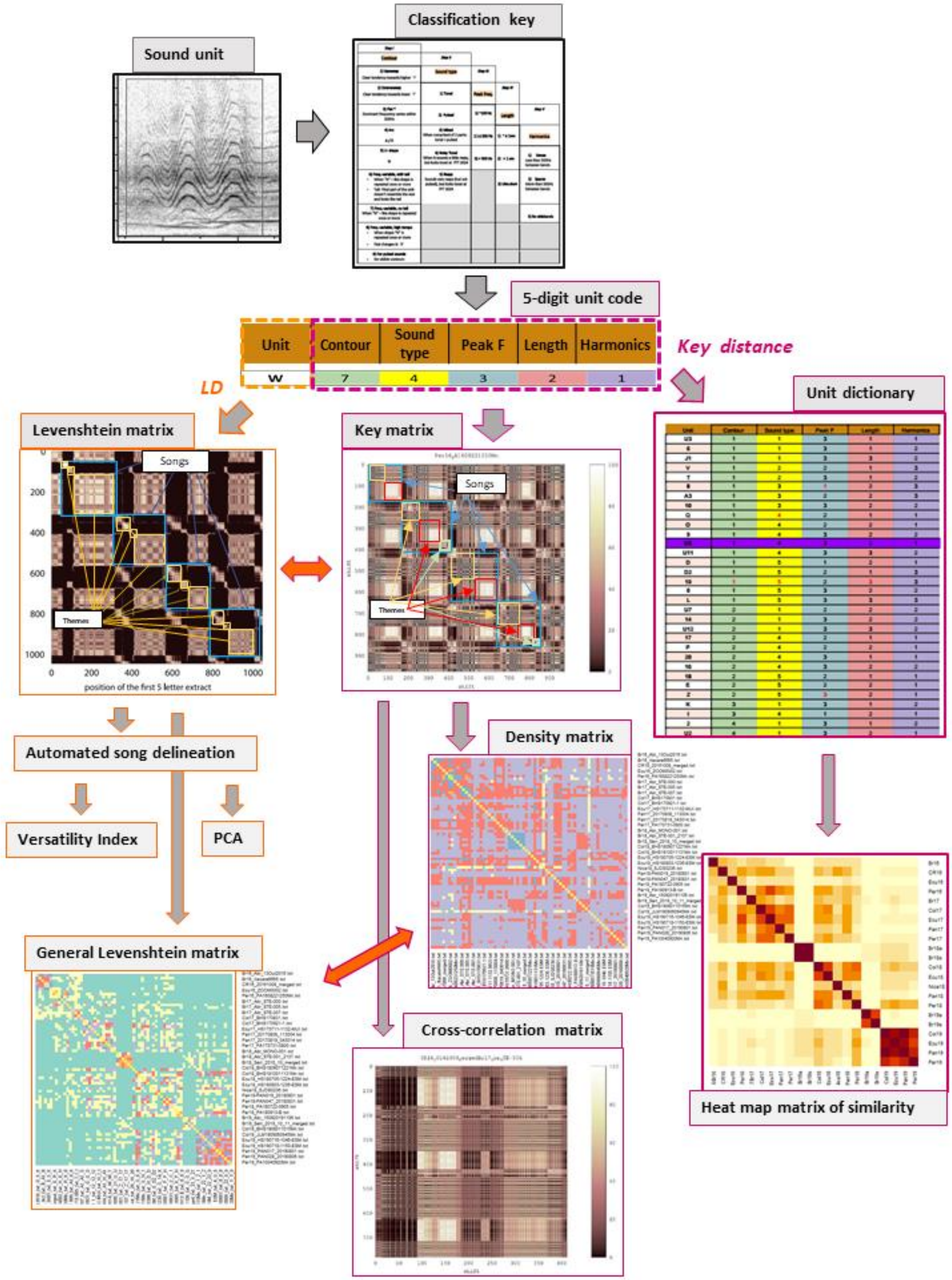

Figure 5 Thesis methodology flow-chart

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CHAPTER I

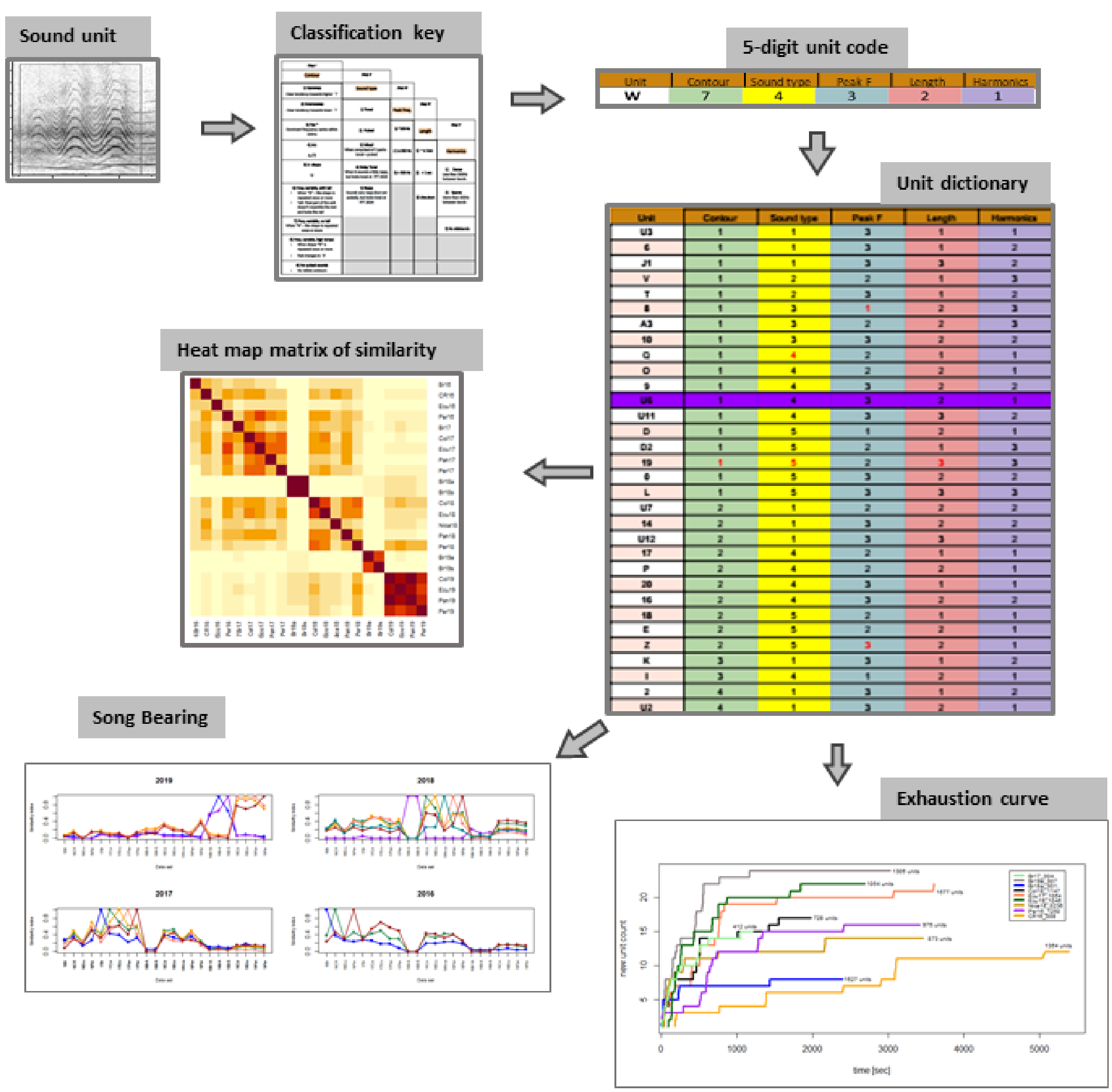
Unit dictionary* as a tool for assessing humpback whale stock interactions

** Acoustic dictionary as a representative of a whale song repertoire (Allen et al., 2017)*

Table of figures and tables

1 Abstract

Male humpback whales are famous for their stock and season-specific songs so that any overlap between the song of two different stocks can indicate some sort of interaction or contact between them. Following this premise, we assessed the song of 3 Latin American breeding stocks (A, G, and Central- American), in 4 consecutive seasons, by building a dictionary of the units each stock used in each of the seasons and compared separate dictionaries among the stocks. The song units were chosen as a level of comparison, as the simplest and least- contentious elements in the humpback whale song hierarchy. Units were classified using a custom-made classification Key, following their 5 basic features: Contour type, Tonal type, Peak Frequency, Duration, and Harmonics presence. The results show the cultural exchange between A and G breeding stocks, in several seasons, while the level of interaction varied. Additionally, the direction of song transmission between stocks also appears to change. Future research is needed to straighten our knowledge of the cultural ecology of humpback whales in Latin America.



2 INTRODUCTION

Vocal communication is essential for the survival and reproduction of marine mammals, especially those that move along great distances. The sound propagated faster underwater than in the air, resulting in the best method for sound propagation over the vast areas at sea (ABILEAH et al., 1996; AU et al., 2006). Vocal communication can carry different quantities of information, mostly depending on the complexity of the sound signal, but also the structure it holds and rules under which it is used (sound repertoires and song syntax) (ENGESSER; TOWNSEND, 2019; MANN; HOESCHELE, 2020; MIKSIS-OLDS et al., 2008; SUZUKI; BUCK; TYACK, 2006).

Humpback whales (*Megaptera novaeangliae*) are known for their elaborate, complex, and melodic vocal expression, that because of their properties reached the status of a song. Humpback whale songs have properties that resemble human songs: they are very well structured and organized, with established patterns of repetitions. Its simplest element is named "unit", and it is highly variable in its properties. Combinations of units further comprise a "phrase" and a group of similar phrases makes up a "theme". A sequence of various themes composes a single, season-specific, and breeding stock-specific "song" (GARLAND et al., 2011; NOAD et al., 2000; PAYNE; PAYNE, 1985). It should be taken into consideration that some unit types are used in multiple combinations (within the same song or in different ones as building blocks for different phrase types). Indeed, some unit types seem universal, as they are present across the stocks (FOURNET et al., 2018). The humpback whale song structure was first described in the early 1970s by Payne and McVay (PAYNE; MCVAY, 1971), and it is in use to this day. Nowadays, it is widely accepted that vocal traits of each breeding stock of humpback whales are a matter of culture, which defines that breeding stock identity (CERCHIO; JACOBSEN; NORRIS, 2001; GARLAND et al., 2011).

Although seemingly clear, the aforementioned song dissection comes with certain caveats, which one starts encountering once deeply into the matter of humpback song classification. Most of these uncertainties are mentioned and well elaborated in the paper of Cholewiak and colleagues (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). In this paper, the authors aim to establish a roadmap for assessing humpback songs, proposing a standard classification for studying song structure, as even to this day, the vague areas of classification and element definitions are being filled arbitrarily, by personal preferences and needs of researchers. Once using different methodologies, researchers can not fully compare their results, potentially losing a great amount of information. To avoid any kind of discordance around humpback whale song classification, I would like to advocate for the use of units as the most simple, unambiguous, and well-defined element to assess the humpback whale songs.

Because of its simplicity in the organization, (most often being a one-component element) (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013), units are easy to define as an entity, while with their high variability in acoustic properties can reliably describe the song they form and be used as sentinels for determining song attributes (season, stock, etc). However, units as the main focus of describing humpback whale songs were not often used so far (MAEDA; KOIDO; TAKEMURA, 2000; SUZUKI et al., 2006; MIKSIS-OLDS et al., 2008).

Despite being a baleen whale, humpback male communication resembles more bird vocal expression than of other mammals (MERCADO; HERMAN; PACK, 2005; PARSONS; WRIGHT; GORE, 2008). In particular, because of its ever-changing nature, it is comparable to open-end learners in bird species, such as the zebra finch (*Taeniopygia guttata*). This means that, as the song is under constant change, animals need to keep up with it constantly and learn throughout their lifespan (BEECHER; BRENOWITZ, 2005; WHITEHEAD et al., 2019). Additionally, the copying mechanism should be considered when comparing humpback whale song to the ones of birds (CERCHIO; JACOBSEN; NORRIS, 2001; MERCADO; HERMAN; PACK, 2005). There are different copying mechanisms - the sound can be reproduced exactly the same as the original, or it can be reproduced with certain modifications (APLIN, 2018; PARSONS; WRIGHT; GORE, 2008). Humpback whales are thought to present the second-mentioned form of copying (MERCADO; HERMAN; PACK, 2005).

Indeed, the humpback male song is constantly changing, within and between seasons (GARLAND et al., 2011, 2012, 2015). The sources and pace of change (novelty introduction) in humpback whale song can vary, likely due to the input of individual singers (errors in copying the contemporary song) (GARLAND et al., 2013a, 2017a; MCLOUGHLIN et al., 2018). This type of change is a moderate, slow change of song, and it is called “song evolution” (GARLAND et al., 2013a, 2017; MCLOUGHLIN et al., 2018). The song can also change rapidly, suddenly, and completely, which is considered a “song revolution” (GARLAND et al., 2013b; NOAD et al., 2000). This type of change was first described by Noad and colleagues in 2000 (NOAD et al., 2000), recorded in Australian waters. It was believed that for this type of change, at the time, few immigrants from a different stock were responsible for bringing their own, significantly different song, from their original stock. Whales from the population receiving the immigrants conformed to the new song type. This change occurred in the course of four breeding seasons. Since, there are several records of the Australian song undergoing this type of change (ALLEN et al., 2018; KERSHENBAUM; GARLAND, 2015; REKDAHL et al., 2018). Based on my dataset, I recognize two types of song revolutions- a *midseason*, the one that takes place in the breeding area, while whales are most singing-active (with a hybrid version of the song), and an *instant revolution*- when the breeding season starts with a totally different song, compared to the previous one.

An important aspect of the revolution of the song (of any type) is "cultural revolution", and in this case, the researcher is aware of the source of this new song, the stock it originated in. In that scenario, it is unquestionable that the song was passed from one stock to the other (cultural pathway of this kind was so far well documented for the stocks of Australia and Oceania (GARLAND et al, 2011)). There are several explanations that researchers came up with, in order to explain this phenomenon in humpback whales- the song can be passed in the feeding/breeding grounds, or while migrating (PAYNE; GUINEE, 1983). More recent data, including observation made by Noad and colleagues (2000), where they confirmed the particular case of the song transfer, explore the potential of individual animals traveling off their usual migrating pathways, visiting stock different from their born ones (POMILA & ROSENBAUM, 2005; STEVICK et al., 2010; STEVICK et al., 2013; FELIX et al., 2020). We can hypothesize that in the cases where the visiting animals are males, they would be bringing their own song with them (as in the case of Noad et al. (2000)). Having this in mind, we can imagine how a song suddenly changes from one type to a completely different one, constructed of different themes, phrases, and unit types.

As earlier discussed, units are the most simple elements of the humpback whale song. Assuming the possibility that the number of unit types these whales use is limited, *i.e.* that humpback whales are closed-end learners, different units are modified and used in different combinations on different occasions (Renata Sousa-Lima, personal communications; DARLING; BÉRUBÉ, 2001). Thus, by comparing different songs, the unit assembly can be used as a tool for assessing interactions of different stocks (DARLING; BÉRUBÉ, 2001). Furthermore, the version of the humpback whale song (or "song type") (GARLAND et al., 2011) depends on the season and the breeding stock the singing whale belongs to, as all males of the same breeding stock are singing the same song (BAKER; HERMAN, 1984; DARLING; BÉRUBÉ, 2001; GLOCKNER; VENUS, 1983; WINN; WINN, 1978; DARLING; JONES; NICKLIN, 2006; GARLAND et al., 2013a; NOAD et al., 2000; PAYNE; PAYNE, 1985). In this way, for any given season, we can tell from which year and breeding stock the song we are listening to came from.

Each breeding stock of humpback whales in the world is singing their own particular song of that season (GARLAND et al., 2013; PAYNE; PAYNE, 1985; WINN; WINN 1978). Despite the song changing at different rates over the season, it is still maintained as the predominant song type in that particular season for that particular breeding stock (PAYNE and PAYNE, 1985). This approach likely requires a higher cognitive effort than if the song was stable over the years (recall vs. learning; synaptic plasticity) (see for example MARTIN et al., 2000). Therefore, it is reasonable to assume that learning plays an important role in the tendency of this species to constantly transform their means of vocal expression - the song.

We are unable to answer the question of how important it is for this species to keep their song under constant transformation, assumptions can be found in the literature, mostly as an expression of the ability to learn (NOWICKI; SEARCY, 2004; PARSONS; WRIGHT; GORE, 2008). Since we still know too little to make any solid assumptions, I first tried to explain the mechanisms under which this transformation takes place, describe them, and explore the methodologies suitable for making inferences about it. Additionally, I tried to understand on what level of song element complexity these interactions can be tracked, and if it can be seen even when neglecting the acclaimed nested hierarchical structure of the song. Here I hypothesize that one of the main mechanisms of the constant song evolution of humpback whales lies in the vocal interaction of neighboring stocks, even beyond the same ocean basin scale. This would be achieved by comparing the simple assembly of song units of different breeding stocks in several breeding seasons.

3 MATERIALS AND METHODS

In this chapter, the interaction between stocks A and G, both breeding in Latin America (IWC, 1998) (hereinafter referred to as BSA and BSG, respectively) was assessed. The convenience of using these two stocks, in particular, is their geographical relative position which limits where these interactions could occur. The interaction between BSA and BSG is only possible on their feeding ground, as both migrate to Antarctica waters to feed. Yet, as their migratory routes are physically separated by land, migration as an option for interaction is impossible (PAYNE; GUINEE, 1983). One alternative is the “sidetrack” visit of individual whales from a neighboring breeding stock, as reported in several studies, where individual whales would visit a stock different from the one they usually spend the breeding season with (e.g. FÉLIX, et al, 2020) (since this species shows sight fidelity) (IWC, 1998).

3.1 STUDY SITES AND DATASET

A collaborative network across Latin America was established with the purpose of gathering recordings of humpback whale songs primarily to be used in this study. To our knowledge, this is the biggest collaboration network of its kind in this part of the world.

The total dataset is composed of recordings from 4 consecutive breeding seasons, from 2016 to 2019, of two Latin American breeding stocks of humpback whales, A and G (IWC, 1998), along with the Nicaragua part of the Central American breeding stock, that migrates from the Northern hemisphere (hereinafter referred to as CA) (BETTRIDGE et al., 2015). The equipment used to obtain these recordings was diverse (detailed description of each can be found in Appendix), and the most common were manual recorders connected to the hydrophones, submerged from the vessel, or in several cases, autonomous recorders (more detail can be found in the Appendix).

Locations of data collections can be seen in Figure 1. Overall, there are 22 different locations: 19 sites are located throughout the BSG area, more specifically on the eastern South Pacific coast: Costa Rica, Panama, Colombia, Ecuador, and Peru; 2 sites are in the BSA area, on the Brazilian Atlantic coast: Abrolhos Bank (and surrounding) and Serra Grande, State of Bahia, Brazil; the last location is in Nicaragua(CA) (BETTRIDGE et al., 2015). Recordings from every location in a certain season are referred to as a "seasonal dataset", while the overall recordings assembly I used in this study is named "general dataset".

Humpback whales are present in Central America year-round (CHERESKIN et al., 2019; RASMUSSEN, 2006). Nicaragua recordings used in this study were made in April, therefore I assumed the whales recorded are not part of BSG (CA breeds from December to April; BSG breeds from June to November) (CALAMBOKIDIS et al., 2000; CHERESKIN et al., 2019; RASMUSSEN; CALAMBOKIDIS; STEIGER, 2011). CA songs were included as an outgroup to determine the possible level of interaction between the CA and South American breeding stocks. All other recordings used in the study were collected during the Austral winter and spring (from June to December). All further technical information (file format, sampling rate, sampling size, etc.) of the recordings can be found in the Appendix.

Figure 1 Dataset locations map.

Locations of 22 datasets used for this study, across 4 seasons, 2016- 2019 (year is coded in the color of the location point). The data were obtained through a collaboration network across Latin America, which was established for the purpose of this study. The dataset includes recordings of 2 breeding stocks, A and G (IWC, 1998), and 2018 recordings off Central American (Nicaragua breeding stock) (BETTRIDGE et al., 2015). Map, ®Google maps. Accessed 26/09/2020, compass oNline Web Fonts

3.2 DATA ASSESSMENT

As expected, due to the very diverse source of recordings used in this research, data quality varied. Before starting any processing, I had to make sure the data used were suitable for the analysis. The initial selection was based on the duration of the recordings, since I was looking for the ones containing at least one full song cycle (includes a complete rendition of all themes available in that season) (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). I have established that recordings at least 20 minutes long fulfill this requirement (check Exhaustion curve results section 5.2) (MIKSIS-OLDS, J. L. et al.), thus, I only used shorter recordings if there was no alternative for a specific location and year. Further, the quality of the selected recordings was inspected aurally and visually, using Raven Pro 1.5 (Center for Conservation Bioacoustics, 2014). I used the following spectrogram parameters: window type: Hann; window size: 2048 samples; time grid overlap: 50%; frequency grid spacing: 43.1 Hz. I narrowed down the dataset to the recordings containing the most clearly distinctive units (aurally and visually).

Finally, I removed recordings with less than a one-day interval whenever possible, to minimize the chance of resampling the same singer, avoiding individual idiosyncrasies. In conclusion, each seasonal dataset (location per season) has a sample size of approximately 90 minutes, which includes several short recordings or at least 2 long ones. Most humpback whale songs last on average 10 to 15 minutes (CERCHIO; JACOBSEN; NORRIS, 2001). Therefore, each sample would contain around 6 song cycles, which should be enough to give a general overview of that season’s song attributes and include most if not all unit types. Additionally, 90 minutes was the most we could use from several lower-quality datasets, thus I used it as an upper limit to homogenize effort and allow comparison among recording methods, as manual recorders render less data than autonomous recorders.

3.2.1 Exhaustion curve

The exhaustion curve is the plot of cumulative unique song unit types detected as a function of time (BALLENTINE; BADYAEV; HILL, 2003; KROODSMA, 1982; SALDÍVAR; MASSONI, 2017), and it serves to estimate a reasonable sampling time effort. To check if the duration of an estimated minimum of 20 minutes for a usable recording for this type of research question (MIKSIS-OLDS, J. L. et al.), as well as the 90 minutes of cumulative duration for each seasonal dataset, are valid thresholds, I used the 9 longest recordings of the total dataset to plot an exhaustion curve. These recordings contained more than one song cycle and covered both BSA and BSG in all four seasons, with the exception of the BSA 2016 dataset as it lacked long continuous recordings.

4 DATA PROCESSING

4.1 UNIT TRANSCRIPTION

After the initial quality inspection, I used Raven Pro 1.5 (Center for Conservation Bioacoustics, 2014) to annotate humpback whale sound units in each of the recordings. On the time axis, selection boundaries (boxes) were set around each unit as close as possible to its real-time duration. On the frequency axis, selection boundaries were set to 2 kHz, 3 kHz, or 4 kHz, depending on the unit's dominant frequency (close to 0 Hz, medium-high, or very high pitched, respectively), so the peak frequency would fit in the selection box. I chose the aforementioned values due to the diversity of the recordings of my dataset. In several cases, the recording quality was low, boats or other types of noise were present, and vocalizations of other animals could be heard. Having standardized selection boxes facilitated comparison between units, minimizing the interference of other types of sounds that could mask the acoustic properties of humpback whale sounds and interfere with precise unit types measurements.

After labeling, the units were further classified by type. For this purpose, I constructed a custom classification Key, composed of five steps, modeled on a standard polytomous classification key (table 1). Additionally, where needed, the unit context was taken into consideration (the adjacent units in the recordings) to facilitate classification. Using the Key, unit types were identified based on 5 major unit characteristics: **Contour, Tone, Peak Frequency, Duration, and Harmonics**, where each characteristic represents one key step (Table 1). Rather than assigning a specific value for each of the key steps, I defined categories or classes, allowing units to vary, as they tend to (e.g. individual singers discrepancies, substrate, depth, recording equipment, etc.) (HELWEG et al., 1998; REKDAHL et al., 2018). The number of these classes, sub-categories, vary depending on the step versatility (e.g. duration is divided into 3, while contour type class in 9 categories). Following the key, the outcome of going through all 5 steps was a 5-digit code, representing a unit type, and its characteristics. In this way, we can compare the units based on their given codes, and estimate their similarity. A schematic representation of the example use of the Key can be found in the Appendix. Based on these codes, I built a complete dictionary, containing all the unit types, and each unit was further given a name (random letter, number, or combination of the two) (Table 3). In the dictionary, the units are arranged based on their similarity (expressed by a 5-digit code). Dictionaries' overlaps between breeding stocks were further evaluated, as an indicator of two stocks' interaction and mutual cultural influence.

It is important to mention that I did not run every unit through the Key, but rather a several **representatives** of each type, initially perceived as such after visual and aural assessment of each different phrase in the song. The representative units were always picked from the middle of the theme, to avoid transitional phrases, where units are known to diverge from the standard structure of its type (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013; PAYNE; PAYNE, 1985). Once all unit types of the seasonal dataset were determined, every unit from every chosen recording of that dataset was transcribed into its type and was given a name accordingly.

Finally, I would get completely transcribed each of the **selected recordings into a string of units**, regardless of any other level of song structure, ordered based on units' appearance in the recording. Two analysts separately labeled all the units, following the key, and decided on definitive codes after reviewing each other's classification if they diverged. The string of units in this chapter was used for plotting the exhaustion curve. Additionally, it was used a base of the methods explored in other chapters

Table 1 Unit classification key

The key is organized based on the 5 major unit characteristics: *Contour type*, *Sound type*, *Peak frequency class*, *Duration class and Harmonics presence*. Fallowing the key, the analyst should choose a category per steps where the unit being classified best fits in. The final product of the Key classification is a 5-digit code, assigning a unit to a type.

Step I				
Contour type	**Step II**			
1) Upsweep The clear tendency towards higher frequency	*Tone type*	**Step III**		
2) Downsweep The clear tendency towards lower frequency	**1) Tonal**	*Peak frequency class*	**Step IV**	
3) Flat Dominant frequency varies within 100Hz	**2) Pulsed**	**1) ~100 Hz**	*Duration class*	**Step V**
4) Arc Λ / Π	**3) Mixed** When comprised of 2 parts: tonal + pulsed	**2) ≤ 500 Hz**	**1) ~ ≤ 1sec**	*Harmonics presence*
5) U- shape U	**4) Noisy Tonal** When it sounds a little raspy, but looks tonal at FFT 2024	**3) > 500 Hz**	**2) > 1sec**	**1) Dense** Less than 500Hz between bands
6) Freq.-variable, with tail • When shape "N" is repeated once or more • Tail- Final part of the unit doesn't resemble the rest and looks like a tail	**5) Raspy** Sounds very raspy (but not pulsed), but looks tonal at FFT 2024	**in the case of units with "tales", disregard the tail part when measuring pear freq.	**3) Ultrashort***	**2) Sparse** More than 500Hz between bands
7) Freq.-variable, no tail When shape "N" is repeated once or more			* When the value is notably shorter than 1 second.	**3) No sidebands**
8) Freq.-variable, high tempo • When shape "N" is repeated once or more • Fast changes in frequency				
9) For pulsed sounds No visible contours				

4.2 JACCARD SIMILARITY INDEX AND SONG BEARINGS

As the sample sizes in my dataset were quite variable, I decided to have an index as a measure of similarity to uniform the data. We found the Jaccard Coefficient also known as the Jaccard Similarity Index (JACCARD, 1901), the most convenient, simple yet effective to use. The Jaccard Similarity Index is calculated by applying the following equation:

$$J(A,B) = \frac{|A \cap B|}{|A \cup B|} = \frac{|A \cap B|}{|A| + |B| - |A \cap B|}$$

where A and B are unit dictionaries (*i.e.* datasets transcribed into unit types). The numerator is the set of overlapping units and the denominator is the sum of all unique unit types of both dictionaries. The Jaccard Index gives us the level of similarity between two dictionaries, thus the similarities between two locations in a specific season are expressed in the number of shared unit types.

The average phrase (theme) is made of about 4 different unit types, and the song type holds between 4-6 different themes (these conclusions were made based on reviewing spectrograms presented in various publications of humpback whale songs of different stocks in different years (e.g. CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013; GARLAND et al., 2013a; HELWEG et al., 1998; MURRAY et al., 2018)). Thus, any overlap larger than 4 unit types between two dictionaries implies a great possibility these units are forming a theme, thus a theme might be shared between the two songs in question and it should demonstrate a non-random significance of the song exchange. A smaller number of shared unit types suggests these units are possibly spread throughout all themes (or could be shared as "universal units" (FOURNET et al., 2018)), and so do not represent a shared behavioral trait. This difference smaller than 4 unit types should further be looked in.

Every unit type that was repeated less than 3 times in all the recordings from the dataset was excluded from the dictionary, as it was considered a mistake (typo, false identification, or a recording flaw). We calculated the Jaccard Similarity Index with a custom script written in R (R Core Team, 2020), and used the results to plot a heat map matrix, representing the similarity of each site and year across 4 breeding seasons. Additionally, we used the same results to plot Song Bearings, representing how songs relate to each other (song "behavior") in each season, throughout the general dataset.

4.2.1 Evolution vs. Revolution

We tested if the Jaccard Similarity Index is able to express the level of change in the song between evolution and revolution events, through an exact cut-off value. We calculated this value as an average value of the similarity between songs of the same location of the same breeding stock in a 2-year time (e. g. Colombia 2016 vs. Colombia 2018). All available 2-consecutive-year data were used to calculate the average index (32 pair-values). Taking the average similarity that is left after all the changes that the song goes through in the course of two years, showing the same or smaller value from one year to the next, can be regarded as a radical change, thus a revolution (the song changes in one-year time as much as it usually does in 2 years). Everything else happening in a one-year time is a moderate change and should be considered an event of evolution.

5 Results and Discussion

We labeled and transcribed 69 different recordings of various durations (anywhere from 5 to 60 minutes long) into strings of units, from eight different locations in four consecutive seasons (though not all locations are present in all four seasons). Altogether, we processed and compared 22 different seasonal datasets, each representing a location in a season (see Appendix).

5.1 Unit dictionary

As explained in detail, unit transcription was done based on the key and its 5 steps. Its final product, the 5-digit key code reflects specific unit characteristics, used to determine its type. These 5-digit codes seem to give a solid level of available variation between the units, balancing between excessive “lumping” or “splitting” among unit types. This was apparent after it is applied to every new seasonal dataset bringing new unit types, to which the key unequivocally assigned a new 5–digit code. However, some key categories are slightly subjective, thus future improvement of categories definition is needed. Nevertheless, for the purpose of this study, the categories were sufficient to result in the same unit types between two independent

transcribers. Slightly specific treatment (more inclusive categories) was given to the units belonging to the unpatterned themes, which in general, tend to vary much more than units in patterned themes.
Altogether, we identified 79 different unit types, out of which 15 belong to two similar and poorly structured themes (*i.e.* "unpatterned" themes *sensu* PAYNE; PAYNE, 1985) sang in Brazil in 2019. Unpatterned themes' units were more variable than others, thus giving an extra caveated in determining their type.
On average, each seasonal dataset has 19 different unit types with a standard deviation of 6.88 (Table 2). While Ecuador 2016, BrazilA 2018, and BrazilS 2018 have the least number of unit types per seasonal dataset, with 6, 8, and 8 respectively, Colombia 2018 and Brazil 2019 have the most unit types, 33 and 32 respectively. A seasonal unit dictionary, listing every unique unit type by its label and the total amount of unit type per season used is presented in Table 3.

Table 2 Summary statistics of the number of unit types present in each of the seasonal datasets

Median	19
St. Dev.	6.88
Max. Value	33
Min. Value	6

Table 3 Seasonal unit dictionary
Table of all unit types contained in every dataset separately, and the total number of different types used in that season

Seasonal Dataset	Unit Type	Total
Brazil 16	O 5 K G A1 B R 21 D2 Q F A2 S I	**14**
Brazil 17	A1 6 G X O I V A3 J A2 S D2 5 M N Q C E U P	**20**
BrazilA 18	16 17 18 19 20 X Y Z	**8**
BrazilS 18	16 17 18 19 20 X Y Z	**8**
BrazilA 19	U5 U4 U9 U6 U3 O Q 33 25 31 26 19 18 U 32 27 28 X2 6 U1 U2 U8 34 X 17 29 U0 U7	**27**
BrazilS 19	25 31 19 8 26 18 32 28 27 X U12 U5 33 U11 U7 U10 U2 U16 U9 U6 U13 U14 U1 U4 O Q 17 X2 U0 15 10 9	**32**
Costa Rica 16	E R K I A1 C N M B T F D2 L H G U M2	**17**
Columbia 17	H A1 V W U 21 A2 R Q F D2 M L M2 P E 12 A3 N K D I O	**23**

Columbia 18	1 2 4 6 7 8 9 10 12 22 24 A3 C D D2 E F G H I J1 K L M N O P Q R T U V Y	**33**
Columbia 19	1 2 C 0 4 G 6 22 L Y 9 Z 19 17 D 8 U 9 F 24	**19**
Ecuador 16	H E R K I A1	**6**
Ecuador 17	H I M A1 W N 21 Q L F D P 22 M2 C U D2 E K V A3 T	**22**
Ecuador 18	7 H L P R D A3 I O U Q M F K V N J1 M2 10 1 2 6 9 D2 22 A1	**26**
Ecuador 19	C G 6 4 D 8 9 24 1 2 0 22 L X 7 U Y Z 19 17 12 10 D2 5	**24**
Nicaragua 18	M 14 15 U 13 A1 C K M2 6 G O L 1 F	**15**
Panama 17	A1 H W 21 T F Q M P E 12 V L K	**14**
Panama 18	P A3 T V O N M Q F H 7 K R L A1 D2 4 D 8 2 C 1	**22**
Panama 19	6 G 4 D 8 9 U 2 C 0 1 22 L 24 D Y Z 19 17 18	**19**
Peru 16	R K E I H 22 T D F M2 M 6 A1 C W P L V 21	**19**
Peru 17	21 U W Q F D 6 M M2 E H L I A3 V K	**16**
Peru 18	K P H 7 L G R 4 D 8 U D2 A3 B T 22 9 1 2 10 6	**21**
Peru 19	Y 9 1 C 0 G 6 22 2 4 D 8 U 24 Z 5	**16**

5.2 Exhaustion curve

Observing the plotted exhaustion curve (Figure 2), we noticed that datasets usually have a sharp, continuous rise in new unit counts over time, which means that songs take a long time to get saturated with new unit types. In this sense, we propose that: *a) the song reaches its full potential (total saturation by new unit types) when the last step of the curve in the exhaustion curve graph is longer than any of the previous ones of the same recording (plateau); b) the majority of unit types are expressed when the curve is beyond its steep phase.*

Taking into consideration these proposed criteria for total saturation or the optimum recording time, two things stood out: (1) none but one of the recordings reached a stable plateau (Br19a_007); (2) the majority of the recordings ended their steep phase slightly before the 15th minute (*i.e.* 900 s).

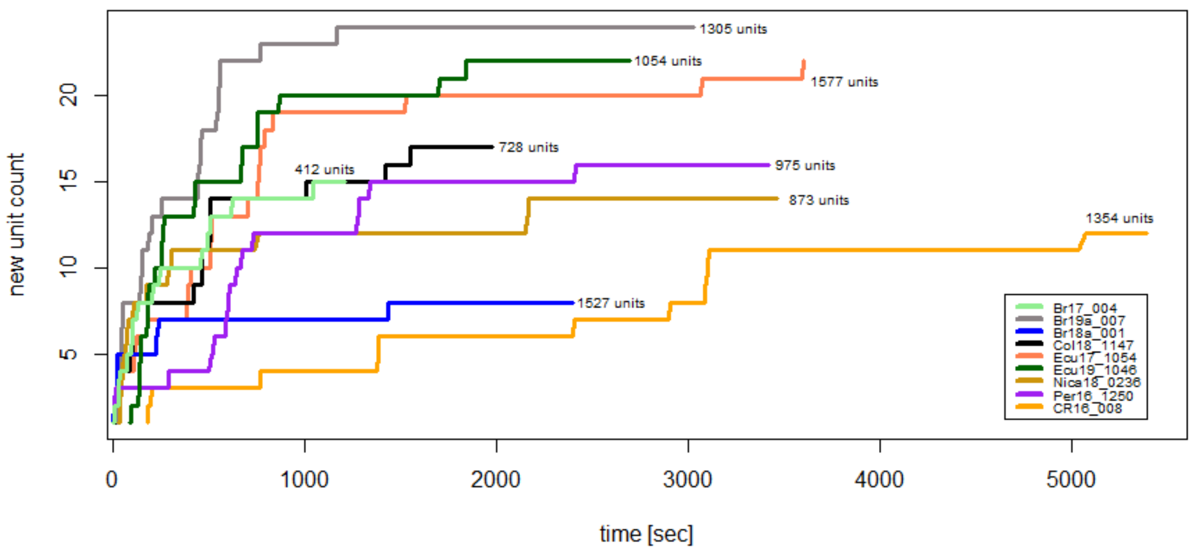


Figure 2 Exhaustion curve

Novel unit type over the time of the recording in seconds. Each color represents a different recording, which names can be seen in the legend. All recordings are of different duration and were chosen based on a minimum of 30 minutes. Next to the curve of each recording is the cumulative number of units labeled in it. The duration of the recording is apparently not related to the number of units used. Additionally, if we take the definition of the plateau as the step longer than any of the previous steps of the same recording, we can see that none of the recordings, except Brazil 2019, reached the total saturation (no novel unit types) .

5.3 Similarity Index

Figure 3 represents the Jaccard Similarity Index values in the symmetrical, heat map matrix, with ones on the diagonal. Each column/row on the matrix represents one seasonal dataset, and they are arranged by the year and in alphabetical order of recording sites. The color gradient corresponds to the Similarity Index values: from 0- lowest (white) to 1- highest (dark red) between two datasets. Jaccard Similarity Index values can be found in the Appendix. The average cut-off value of similarity between 2-year data (calculated for all 32 pairs of 2-year data, *e.g.* Peru 2017 vs. Peru 2019,) was found to be 0.16, marking a moderate change of evolution. The same or smaller values for the time span of a single year indicate a revolution of the song.

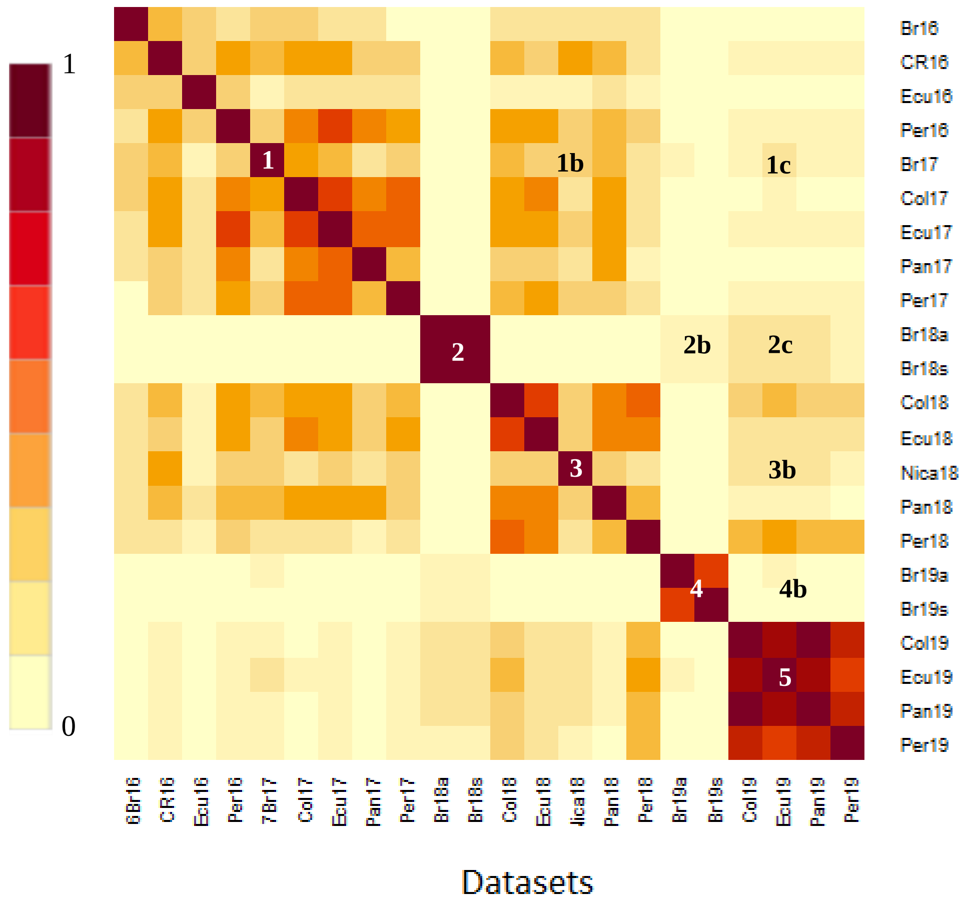


Figure 3 Similarity Index heat map

In this figure, values of Jaccard Similarity Index (JACCARD, 1901) between unit dictionaries of 22 different seasonal datasets are plotted. The heat map has ones on it diagonal, as the maximum similarity between one element and itself, and datasets are arranged by season and alphabet. The color gradient is correlated to the values of Similarity index (darker shades are closer to 1, and lighter to 0). Ordinal numbers of each patch are explained in the text below.

season and stock (Figure 3, number of patches are centralized within each patch). As datasets are arranged alphabetically and by year, this influenced the formation, number, and size of the patches. The first and biggest patch gathers seasonal datasets of two years (2016 and 2017), and two stocks (patch 1). As an example, in 2016, Costa Rica had more in common than Ecuador with the rest of its stock in that season, but it was placed further to the rest of its patch. An interesting observation from this patch is that Costa Rica is more similar to Brazil (BSA) than Ecuador, which belongs to the BSG. Additionally, for 2017, Brazil seems fairly distinct from its neighboring datasets, but it was placed in patch 1 because of its name and season. However, indeed it is somewhat similar to Ecuador and Colombia of the same season, which are highly similar to each other, as expected based on their geographical proximity. This can be observed throughout the seasons.

Patch 2 grouped **BSA 2018** songs of two locations, which are apparently very alike. On the contrary, they appear highly dissimilar to the rest of the dataset, including **BSA 2017** song. This observation suggests that a revolution (NOAD et al., 2000) took place, as the driver of this intense change of songs from one season to the next. This does not seem to be the case for **BSG 2018** song, which similarity we can observe within patch 3. This patch seems coherent, except for the Nicaragua song, and this comes as no surprise. The recordings in this location were made in April (Appendix I), these whales are known to be part of the Central America distinct population segment (BETTRIDGE et al., 2015), so there was a low chance of these whales having contact with the whales of the **BSG.** Yet, some level of dictionary overlap is shown in the similarity matrix (patch 3). This could be explained by the existence of the innate/ever-present unit types for all the humpback whales (FOURNET et al., 2018), or that several individuals of Nicaragua whales did get to learn a **BSG** song partially, and introduced it in the song of their own stock (or *vice versa*).

Similarities of **BSG 2018** song to the one of the preceding season of the same stock can be observed in patch 1b. It is worth noticing that in this patch the Panama 2018 song seems to share a lot in common with the previous year's song of its stock, similar to overlaps of Colombia and Ecuador 2018 songs to the one from Peru 2016.

Like 2018, **2019 BSA** song also appears radically changed, and this divergence is evident in patch 4. This time, the two Brazilian locations seem slightly different, yet forming an apparently distinct patch. Its correlation to the previous year can be seen in patch 2b (and to other datasets as black spaces up and down from it). The explanation of this low similarity to any other song lays in the appearance of an unpatterned theme (*sensu* PAYNE; PAYNE, 1985; CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013)**,** which seems to be specific for two Brazil locations separately. Namely, in an unpatterned theme, there is no obvious structure, nor the units are repeated in a predictable way. On the contrary, there is an astonishing number of unit types used in this particular theme (in 2 locations, 14 different unit types for the same theme) (Appendix).

On contrary, **BSG 2019** song appears very distinct and homogeneous, with the Peruvian song being the least alike (patch 5). The clarification of this distinctiveness might be found in patch 3b, where we can see that certain **2018 BSG** songs seem to have a high level of similarity to the 2019 song, specifically when compared to the rest of the locations from the patch. Here, we can hypothesize that the song sung in 2019 was a product of a revolution (much like BSA 2018) that actually started in the previous season. Another possible evidence for the revolution starting midseason is the high similarity of the Peru 2018 song to the one from 2019, as Peru is considered the exit destination from the BSG breeding area to the feeding grounds (GUZMAN; FELIX, 2017; VALDIVIA et al., 2017), the last version of that season's song can be recorded in Peru. Evidence of this phenomenon is also noticeable in the songs themselves, as these midseason changes in the song were noticeable in the field (Esteban Duque Mesa- personal communication).

Even with the high divergence of the **BSG 2019** song from the rest of the matrix (patch 5), it is interesting to note the slight overlap with the **BSA 2018** song (patch 2c). This is likely due to the acoustic interactions of these two stocks between the 2018 and 2019 breeding seasons. Other correlations to the **BSG 2019** songs can be observed in patches 1c, 3b, and 4b. Correlations of this song to the other seasons of the same stock are best observed in the separate heat map, where only BSG locations are plotted (Figure 4, left). Note that the labels on the matrices of the season 2018 are rearranged, so the differences between data are best observed. In the same figure, we can see how BSA songs throughout the seasons are clearly separated and poorly correlated with others.

In table 4, the unit dictionaries of the seasonal datasets of BSG 2017-2019 are shown, with the labeled units demonstrating direct overlaps of the dictionaries. We can see how 2018 songs from all BSG locations are assembled of a combination of units from previous and following seasons, showing how these heat maps highlight dictionaries' similarities. A similar comparison can be found in Table 5 for BSAa dictionaries for the same seasons, but with a visibly different similarity level, from season to season.

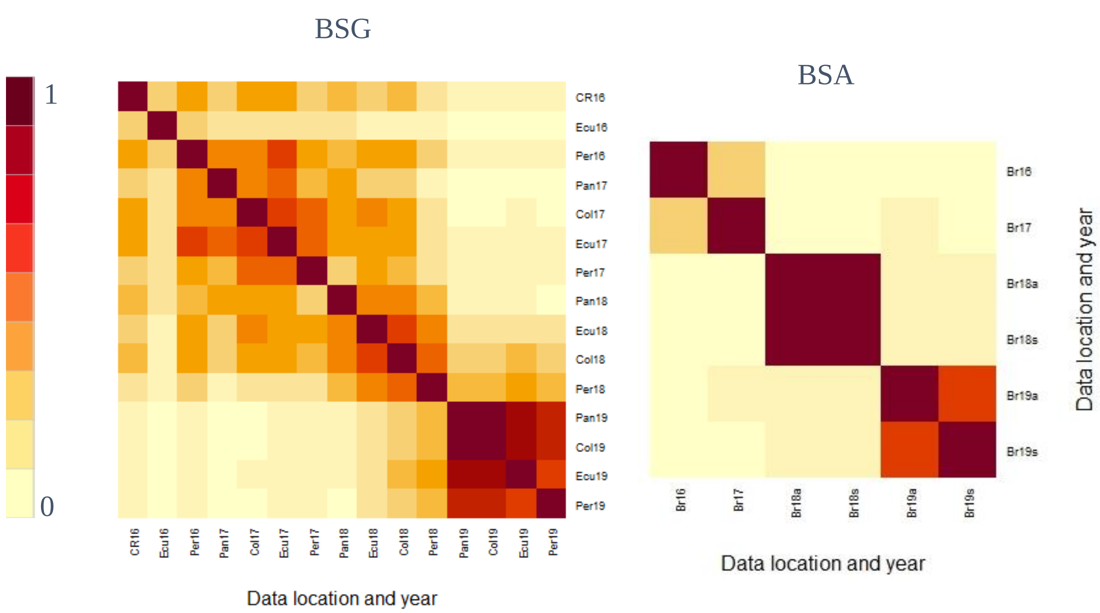


Figure 4 Similarity Index heat map- BSG and BSA

Table 4 BSG locations dictionary overlaps 2017- 2019

Colors represent the year the units are used in: blue- 2018 +2017; yellow- 2018 + 2019; green: 2018 + 2017 + 2019. In white are units specific for only that one year. We can notice the 2018 dictionary is mostly assembled of units used in 2017 or 2019.

2017				2018			2019			
Colombia	**Ecuador**	**Panama**	**Peru**	**Colombia**	**Ecuador**	**Panama**	**Colombia**	**Ecuador**	**Panama**	**Peru**
12	21	12	6	1	1	1	0	0	0	0
21	22	21	21	2	2	2	1	1	1	1
A1	A1	A1	A3	4	6	4	2	2	2	2
A2	A3	E	D	6	7	7	4	4	4	4
A3	C	F	E	7	9	8	6	5	6	5
D	D	H	F	8	10	A1	8	6	8	6
D2	D2	K	H	9	22	A3	9	7	9	8
E	E	L	I	10	A1	C	17	8	17	9
F	F	M	K	12	A3	D	19	9	18	22
H	H	P	L	22	D	D2	22	10	19	24
I	I	Q	M	24	D2	F	24	12	22	C
K	K	T	M2	A3	F	H	C	17	24	D
L	L	V	Q	C	H	K	D	19	C	G
M	M	W	U	D	I	L	F	22	D	U
M2	M2		V	D2	J1	M	G	24	G	Y
N	N		W	E	K	N	L	C	L	Z
O	P			F	L	O	U	D	U	
P	Q			G	M	P	Y	D2	Y	
Q	T			H	M2	Q	Z	G	Z	
R	U			I	N	R		L		
U	V			J1	O	T		U		
V	W			K	P	V		X		
W				L	Q			Y		
				M	R			Z		
				N	U					
				O	V					

Table 5 BSAa unit dictionary overlaps 2017-2019

Colors represent the year the units are used in: yellow- 2018 + 2019; green: (2018 +) 2017 + 2019. In white are units specific for only that year. We can notice the 2018 dictionary is mostly assembled of specific unit types (revolution), but also interesting is the 2016 units reappearance in 2019. If compare to BSG dictionary overlaps (Table 3), in Abrolhos they are very much different from one season to the next

Brazil- Abrolhos (BSAa)		
2017	**2018**	**2019**
5	16	6
6	17	17
A1	18	18
A2	19	19
A3	20	25
C	X	26
D2	Y	27
E	Z	28
G		31
I		32
J		33
M		34
N		O
O		Q
P		U
Q		U0
S		U1
U		U2
V		U3
X		U4
		U5
		U6
		U7
		U8
		U9
		X
		X2

5.4 SONG BEARING

Song Bearing graphs used the Jaccard Index values as well, to show how seasonal dataset unit dictionaries relate to others in each season, throughout the whole general dataset (Figure 5). Figure 5 shows that songs of the same season (and especially from the same breeding stock) present similar bearings. Although the index values varied, the tendencies are the same within each stock, with the exception of the 2018 season (the year of the revolution). If we observe the bearing graphs of seasons 2016 and 2017, some overlap in bearing patterns are visible: These coinciding trajectories start at the axis label of the year 2018 (a marked decrease in similarity) onwards, which suggests the same degree of similarity between the unit dictionaries from 2016 and 2017 to the ones from 2018 and 2019. In 2019, the unit content of the songs within each stock are so alike that their bearings almost coincide. Nonetheless, when comparing 2019 bearings to the ones from the previous year, not much in common is found, which possibly reveals extensive gradual evolution, which progressed continuously throughout the breeding season.

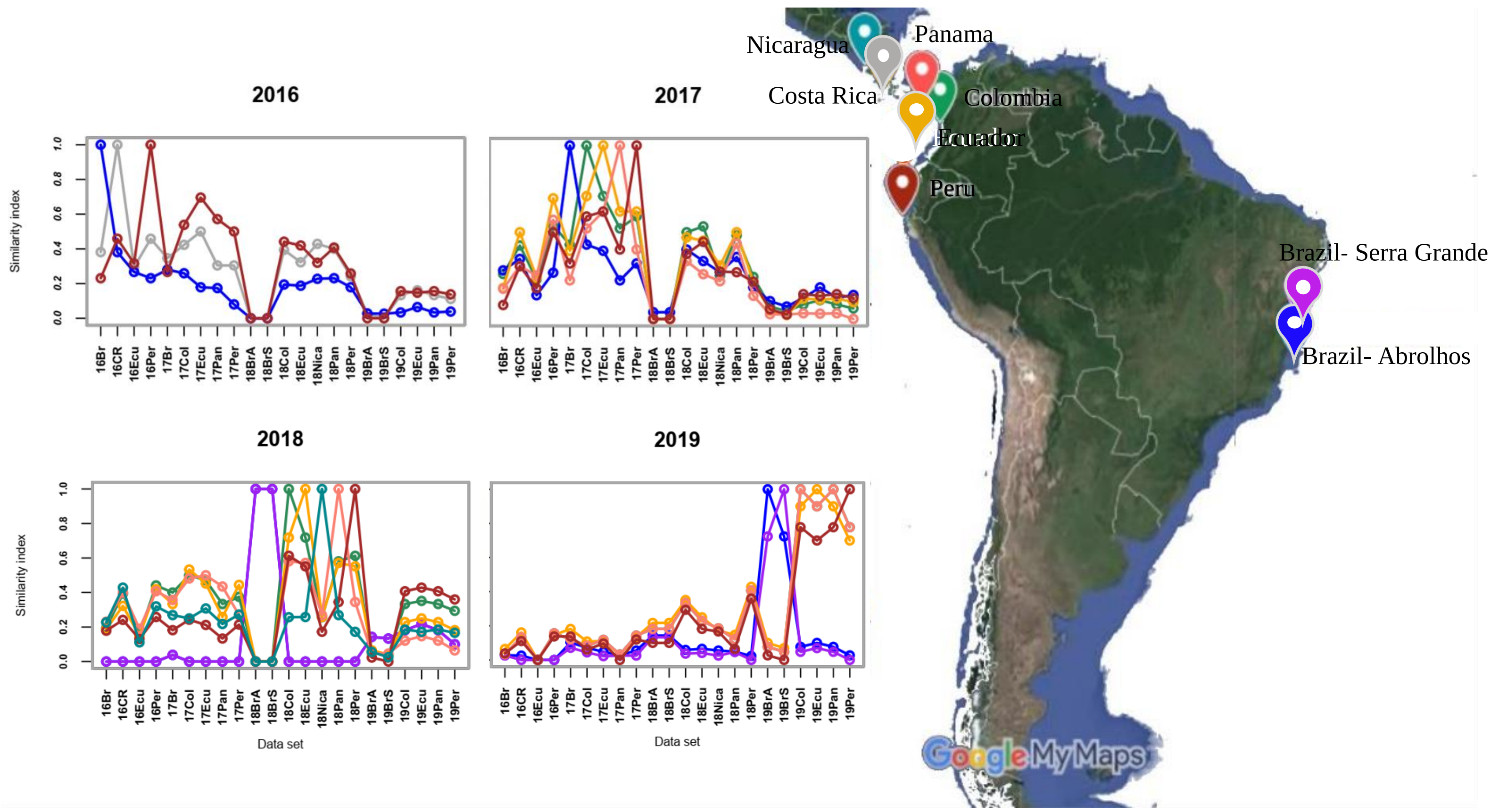


Figure 5 Song Bearing graph

Unit dictionaries combined by year are plotted against all 22 seasonal datasets, arranged by season. The values plotted are the Jaccard Similarity Index. Line colors represent datasets, which locations are shown on the map.

Map, ®Google maps. Accessed 26/09/2020

5.5 GENERAL DISCUSSION

Here, we presented for the first time evidence of song sharing among 3 breeding stocks around Latin America (Stock A, G, and Central American PDS), throughout 4 consecutive seasons.

Previous genetic and photo-ID studies suggest BSA and BSG do get into contact, in different intensities, depending on the season, supporting our results (ALBERTSON et al., 2015; CYPRIANO-SOUZA et al., 2016; DALLA ROSSA et al., 2018). Furthermore, the genetic analysis also suggests most of the inter-stock mixing is male-driven (CYPRIANO-SOUZA et al., 2016), which works in favor of song sharing and song evolution as males are the ones singing. Additional evidence comes from individual animals transiting between two stocks: (1) a male tracked between Indian and the South Atlantic Ocean (genetic sample) (POMILA & ROSENBAUM, 2005), (2) BSA female spotted in the waters off Madagascar (thus, she traveled from Southern Atlantic to the western Indian Ocean) (STEVICK et al., 2010), (3) another female spotted in the eastern South Pacific Ocean and afterward in western South Atlantic Ocean. (STEVICK et al., 2013) and the most recent one, (4) reporting the same individual sighted in Peru - South Pacific, and Brazil - South Atlantic coasts (FELIX et al., 2020). Our results tell the same story: breeding stocks A and G are in contact, yet this interaction is not constant, nor predictable. This brings us to song evolution mechanics and its unpredictable nature, with different intensities of change over a variable time frame, as already proposed for other breeding stocks (REKDAHL et al., 2018; GARLAND et al., 2011).

The humpback whale song modulation mechanism works in two modes: revolution and evolution. Even though general descriptions of these two terms are available in the literature (GARLAND et al., 2012; NOAD et al., 2000; REKDAHL et al., 2018), we were unable to track their exact definition, as researchers use them to describe both the type and the rate of change (thus making them metric-specific). In this study, we used unit dictionary similarities to track song changes and potential vocal exchange rates among stocks of humpback whales that can interact on limited occasions (feeding grounds). As a community interested in humpback whale culture, we need a more general definition of revolution and evolution, applicable even when researchers measure different parameters. Hence, we propose a definition for this term: a song revolution occurs when the parameter of interest changes entirely from one season to another, and the new values are adopted by all sampled individuals from the same area. On the contrary, when evolution is the main mechanism of change, the values of interest are changing gradually, with no obvious jumps or drops.

We recognize two types of revolutions. One appears as the breeding season progresses, possibly initiated by visitors from a different stock introducing a new song (NOAD et al., 2000) and happens when the singing whales are most vocally active (VU et al., 2012). This type of change we call a midseason revolution, and it contains a hybrid version of the song. Alternatively, the breeding season can start with a completely new song. Most likely, this happens when members of different stocks encounter on the feeding grounds or migratory routes, consequently, the entire stock acquires a new song type and starts the following season with it. This is called an instant revolution and is what we encountered in our data. Other scenarios are equally possible, for example, that the revolution started in the preceding season, but the data collection we used failed to "catch" the emerging new song (as implied in the Results section about BSG 2019 song).

Metric for determining a Song Revolution:

Allen and colleagues (ALLEN et al., 2018), measured song evolution using theme order, which seems to influence the determination of similarity between songs, on top of determining the value of 0% similarity as a sentinel for revolution. In our study considering the unit dictionary similarity matrix, we are unable to find 0% similarity to consider it a revolution, since unit types can be recycled, but in a different context, or can be stable over generations when considered a "call type" (FOURNET et al., 2018). Thus, the probability of 0% similarity between the unit content of two songs is small.

Although the revolution of the unit dictionary similarity metric cannot be 0%, it is likely to be below 16% (or Jaccard's Similarity Index value < 0.16). Thus, when the Jaccard Similarity Index between unit dictionaries from one year to the next show values less than an average index calculated between every other year, that song should be considered as a product of a song revolution. On the contrary, all other changes, showing greater values from one year to the next, can be considered as song evolutions.

Yet, if we stick to the mentioned exact values, the song of Brazil 2019 should also be considered a revolution (Jaccard's Similarity Index between it and BSA 2018 song is 0.13-0.14). However, due to the extremely large dictionary size and the "unpatterned" theme included in the BGA 2019 repertoire, we intend to process the 2020 season song before making any further conclusions (additional argument against the 2019 season for BSA being a revolution is that it contradicts the literature, implying the song evolution includes song simplification, where in our data set it peaked in unit type content. This will further be explored in chapter IV, where the calculation of Complexity indexes will be presented (ALLEN et al., 2018). Overall, we can conclude that the Jaccard Similarity applied to the stock seasonal dictionaries is a good index for assessing the intensity of song change and indicate if it is a revolution or an evolution.

Using a bearing graph to determine the dynamics of song evolution:

The bearing graph gave a different perspective of the similarity calculated through Jaccard's Index. The song-bearing graphs gave us a more detailed impression of the song evolution through time and space (Figure 5). In those graphs, we saw how songs changed over the breeding grounds, and how each location compares to the others in all 4 seasons: in most cases, the songs evolved in a predictable and stable way. For example, we perceived a general pattern for the 2016 song. It is particularly interesting how similar the Brazilian and Peruvian songs were to Costa Rica's, yet between themselves (Brazil and Peru), their similarity was low. It was also the case for the 2017 season: the BSA song was different from all BSG locations, still, it followed a bearing pattern. In 2018, the Brazilian song distinctiveness clearly stood out, and we observed some elements of its dictionary used by both BSA and BSG in the following season.

Our Bearing graph results (Figure 4) suggest almost an equal level of similarity of BSG 2018 songs to both, previous and succeeding years. We believe this is related to the midseason revolution that occurred in that season. Essentially, the 2018 BSG song is composed partially of the 2017 song and partially of the 2019 BSG song (Table 4). Going back to the raw data, we found whales singing the old song, the new song, and a hybrid version, almost at the same time, and this sort of phenomenon has been described in other populations (GARLAND et. al., 2017b). This is evident in the exceptionally large unit dictionary of Colombian song (33 unit types). Still, looking at the values of the Jaccard Similarity Index, we cannot tell so directly if the revolution did occur, as the similarity between two BSG songs of two seasons does not indicate abrupt change, typical for a song revolution (i.e. a value < 0.16). This is plausibly due to the midseason revolution type, so in this case, it is probably better to compare the similarity between the songs 2-seasons apart. However, we should not disregard the Figure 4 gradual transition from the 2018 to 2019 song.

One last intriguing piece of information lies at the very beginning of the 2016 graph and the Brazilian 2016 song. When we compared the similarity between locations to this song, with their geographic position, we observed a gradient, with the similarity decreasing from north to south, in the 2016 and 2017 seasons separately. Could be a pure coincidence, yet, it is a precise overlap of 6 locations on the map (Panama 2017 has equal value to Ecuador 2017, thus does not "fit" in the geographic pattern). Therefore, we believe this gives a small clue on song evolution mechanisms, explaining that the song evolves as the breeding season progresses, thus being less and less similar to the one of the preceding season (PAYNE; PAYNE, 1985).

<u>Clues about the mechanics of song evolution from an exhaustion curve:</u>

The exhaustion curve gave us an insight into a song-changing mechanism on the smallest possible scale, and that is the cumulative unique song unit types detected as a function of time (Figure 2). In this graph, we can see that whales rarely, if ever, repeat the song identically (i.e. use the same exact set of units), but rather they always add a new unit type to the song. The song change seems a never-ending process, but on a much smaller scale than previously believed. Of course, although exciting, these results should be interpreted with caution due to the limited sample size (9 recordings in the assessment) and the danger of over-splitting by the analysts.

The exhaustion curve also showed that, for the purpose of acoustic analysis, the minimum sampling effort for humpback whale song is 15 minutes, which coincides with previous recommendations (CERCHIO; JACOBSEN; NORRIS, 2001; CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). As expected, it indicated that longer recordings raise the probability of recording more unit types, yet we cannot tell with certainty how long the sampling time must be to capture all available units, as almost no recordings reached a plateau.

<u>Different rates of song change:</u>

We like to further discuss the processes that led to this different song change rate. We proposed it is partially driven by variable acoustic interactions between stocks (next to the potentially intra-individual change introduction, as implied by the exhaustion curve, although most of the unit types are used up after a certain period of time, the full saturation is never reached, suggesting sporadic novel unit type introduction throughout the singing process by each individual singer). To explore in detail the song change mechanism, we arranged the units in the general unit dictionary by their 5-digit code, as it holds potential for quantifying differences between datasets (analyzing if two datasets differ significantly, or their differences lie in similar unit types).

In Figure 3, the Jaccard Similarity Index values clearly demonstrate how the song changed over time: uniformly across the same breeding stock, and in most cases, different from the evolution of the adjacent stock's song. Yet, there are cases where some level of acoustic connection between stocks exists (e.g. BSA 2017 and BSG 2018, Figure 3, patch 1b/ BSA 2018 and BSG 2019, patch 2c). Indeed, going back to the raw data, we found a complete BSA 2018 theme on the Pacific coast in the following season (figure 14, chapter II), not only suggesting cultural interaction between these two stocks but also providing evidence that songs in humpback whale culture can flow westward. This finding contradicts the literature, which suggests song travels eastwards (GARLAND et al., 2011).

Song evolution is evident within BSG, as similarity was high for consecutive years and it weakened over time, something expected when song change is gradual and progressive (Figure 4, left). As for BSA, song development appears more hectic as the song changed greatly over seasons, namely the 2018 dictionary shared elements with none of the previous ones, but there was a slight overlap with BSG 2019 (Figure 4, right). This pronounced specificity of the BSA 2018 song, compared with the Pacific song is one of our major findings, as it represents a case of a song revolution. Song revolutions are known only in Southern hemisphere populations (ALLEN et al., 2018; GARLAND et al., 2011, 2013a; NOAD et al., 2000), yet, this is the first case reported in the Atlantic Ocean. Still, it seems that the same rules apply in both the South

Atlantic and South Pacific Oceans (ALLEN et al., 2018). The revolution significantly reduced the unit dictionary size (i.e. song complexity), as we observed a drop from 20 to 8 types used per year (GONÇALVES et al., in prep.).

Following our previously proposed definition, we describe the BSA 2018 song as an instant revolution, since the whales showed up on the breeding ground with a very different song type, compared to the previous year. The origin of this song type is unknown. Even though we know that our sample size is far from ideal and additional recordings from that area are needed to shed some light on this phenomenon, we believe there are three possible explanations for it: one possibility is that the song came from Africa's west coast (DARLING; SOUSA-LIMA, 2005); another option is the acoustic interaction with different stock members on the feeding ground; alternatively, the revolution could actually started in the previous season (as described in NOAD et al., 2000), but we simply did not detect it in our recordings.

For both stocks, the 2019 songs are slightly similar to the previous season. This is especially true to Peru 2018 (Figure 3, patch 3c). There is evidence of whales from BSG in the breeding season first being seen in the Panama coast (VALDIVIA et al., 2017) and later on descending towards Peru as the season progresses (GUZMAN; FELIX, 2017) that could account for that result. This is one possible explanation for the direction of song evolution, as Peru's song is most similar to the next season's and least similar to other BSG songs from the current season. As whales intensively decrease singing activity towards the end of the breeding season, the rate of song evolution does as well (PAYNE; PAYNE, 1985). Nonetheless, evidence from previous work in Brazil shows the number of singers tend to increase as the season progresses, although the rate of song change has not been evaluated (SOUSA-LIMA et al., 2018). Thus, even though the rate of song evolution might not always decrease towards the end of the breeding season, Peru's song can be seen as a preview of BSG next season's songs.

6 CONCLUSION

Although 4 consecutive seasons are not the optimum time-frame for studies about humpback whale song evolution, this work did bring further insights into mechanisms driving the general fluctuating nature of the humpback whale song, reporting gradual and continuous song evolutions, next to one instant revolution, and a midseason revolution, during the study period. Additionally, an unpatterned theme was a part of the 2019 BSA song. Therefore, we had a very rich insight into mechanisms driving the general fluctuating nature of the humpback whale song. Yet, the opportunity to observe the most common and simple mechanisms, like the simple evolution, was rare.

Intense song change was recorded before in the region of Oceania, yet this is the first record of song revolution in Atlantic waters. As for BSG, based on genetic and other studies, we know they are in stable contact with the Eastern Australian breeding stock (e.g. GARRIGUE et al., 2012), thus it makes sense that a similar level of change should be present. On the other hand, as in Australian breeding stock and Oceania, and further over the Pacific to BSG, the song travels eastwards. In my dataset, we found a single case of a theme being passed in the other direction. However, we need to conduct more studies and collect more data in order to say this westward transmission is a rule for Latin America. Thus, it is of immense importance that the acoustic monitoring of BSG and BSA becomes systematic, as our short study gave a glance at how much more there is to learn about these vocal animals and the mechanisms of their communication.

Our general conclusion is that BSA and BSG do interact culturally and that intensity and mechanisms of this synergy vary from season to season reflected on the song evolutionary paths of each breeding stock. Additionally, we would like to stress the significance of our collaborative network that supplied this study with acoustic data. These types of international cooperation between research institutions and individuals are of great importance, as they are promoting and facilitating science while being a bright example of collaboration in research, and data recycling.

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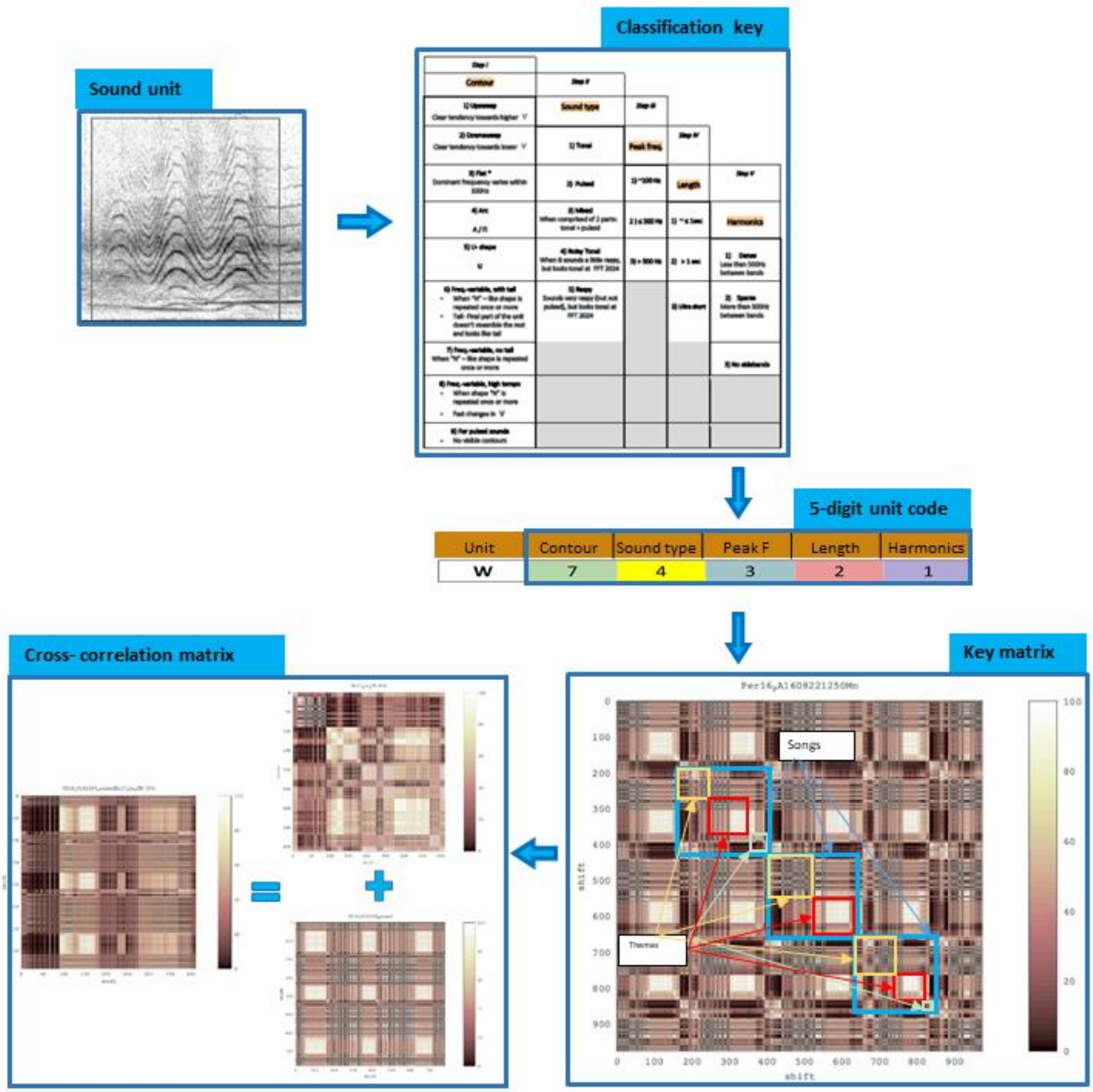
CHAPTER II

Comparison of the song structure and composition of different stocks of humpback whales

Table of figures and tables

1 ABSTRACT

Units of humpback whale song recordings were run through a classification key for determining their type. After determination, and forming a string on units, expressed by their 5-digit key code, a Key matrix was formed. It was built by calculating the auto-distance of the string, counting the number of overlapping values of the two 5-digid codes in comparison. After the visualization of the recording as a recurrence plot - the Key matrix - we noticed song repetitions within it, with differentiation of theme types, based on their visual structure. Comparison between two Key matrices was performed by building Cross-correlation matrices, which can tell how similar the two recordings are, based on its general shade, but also to track the unique similarities, showed by white-shaded patches.



2 INTRODUCTION

Exploring new ways to assess animal interactions is a challenge, especially when such interactions induce cultural change (GARLAND et al., 2013a; NOAD et al., 2000; OWEN et al., 2019). Acoustics can be considered a fantastic tool to determine these interactions, with all of its unexplored potentials, and it is especially useful for animals with highly elaborated oral culture, like humpback whales (PAYNE, 2000). Monitoring sounds is a generally noninvasive technique (with the exception of some types of DTAGS (JOHNSON and TYACK, 2003)), and allows us to explore the natural behaviors of animals. Yet, humpback whales are hard to track since they occupy great areas in all oceans, however, acoustics can help us work around that. More than tracking, we can use acoustics to assess stock interactions by comparing the level of connectivity, through the similarity of their songs (PAYNE; GUINEE, 1983). These species-specific humpback male songs are known to have a nested stable structure and to be repetitive (PAYNE; MCVAY, 1971). Nonetheless, to build a solid and unambiguous methodology, original observations should be zealously revisited.

Humpback whales are a cosmopolitan species, practicing seasonal migrations from breeding to feeding grounds and back, with exceptional fidelity to their seasonal habitat (CYPRIANO-SOUZA et al., 2017). Predominantly while on their breeding ground, males tend to partake in singing their species-specific melodic songs, which are likewise stock-specific (PAYNE, 2000; PAYNE; GUINEE, 1983). More than being steadily sung only in a particular breeding ground, these songs gravitate towards constant change and spread-out, from one season to the next, on different magnitude and pace (GARLAND et al., 2013a, 2015; NOAD et al., 2000; OWEN et al., 2019). We are only able to track these changes by relying on the distinct structure of humpback whale song, which we are aware of for the past 50 years (PAYNE; MCVAY, 1971). By exploiting it we are able not only to compare songs of the same breeding stock from one season to the next but also songs of different breeding stocks throughout the years. A song is a structured, well-defined, and repetitive system: the unit is its simplest element, units compose phrases, and several phrases combine into themes, which, when repeated in a predictable pattern, are called a song (PAYNE; MCVAY, 1971).

This song structure is common for the entire species, however, the song type, that follows a different pace of change from one season to the next, is specific for each of the breeding stocks, in every season (PAYNE; GUINEE, 1983). There are several specificities regarding song similarity we are aware of- (1) geographically more close stocks usually have similar songs (PAYNE; PAYNE, 1985); (2) revolutionized songs most probably stemmed in a neighboring stock (NOAD et al., 2000); (3) songs of the same stock from the years close together are more similar, and from the seasons further apart are more dissimilar (PAYNE; PAYNE, 1985). Based on these "rules", we can noninvasively assess the possible interactions of different breeding stocks, since the song, thus, can be used as a stock indicator (HELWEG et al., 1990).

Even so, as the song structure definition seems clear and objective, in practice, humpback whale song researchers need to deal with several open-ended interpretations of these rules while inevitably imposing human bias in filling these gaps. One of the main questions is defining the beginning and ending point of the song. Another issue is the general idea that themes are the exact copy of themselves in each repetition. In our experience, the structure is rarely as clear, and easy to define. As my data set was composed of 3 different breeding stocks, over 4 seasons (not all stocks in all seasons) (Breeding stock A, Breeding stock G, and Central American DP, hereinafter called BSA, BSG, and CA, respectively) (BETTRIDGE et al., 2015;- IWC, 1998), I had a chance to encounter different peculiarities of the ever-changing nature of humpback whale song, and more than that, track the change that might be unpredictable in its form and intensity.

Aiming for a more unbiased, straightforward, and repeatable way to assess the structures of the song, I focused on avoiding human input in setting boundaries for each of the structure categories and build a robust method that avoids pre-described structure demands. For this purpose, a custom script was written to computationally explore the recordings of humpback whale song, by starting from its simplest and least controversial building blocks - units. Objectively quantifying and visualizing the structure of humpback whale song would improve significantly the field, as so far slight variations between song elements were rather overlooked.

The subject I wanted to explore with these novel methods was the level of interaction between Latin American humpback whale breeding stocks, estimated through the similarities of their songs, over several breeding seasons. Moreover, while monitoring the song evolution of the same stock through different seasons, we can also try to understand a bit more about the mechanisms under which these song changes occur. I explored the potential of visual representations of song components to claim similarities of different songs in different seasons, as unit types on their own can progress within the same song repetition (GREEN; PACK, 2011; MERCADO, 2018; SCHNEIDER; MERCADO, 2018). This is something impossible to track just by comparing unit dictionaries (see Chapter I).

3 MATERIALS AND METHODS

3.1 DATA COLLECTION

A collaborative network across Latin America was established with the purpose of gathering recordings of humpback whale songs primarily to be used in this study. To our knowledge, this is the biggest collaboration network of its kind in this part of the world.

The total dataset is composed of recordings from 4 consecutive breeding seasons, from 2016 to 2019, of two Latin American breeding stocks of humpback whales, along with the Nicaragua part of the Central American breeding stock, that migrates from the Northern hemisphere (BSA, BSG, and CA) (BETTRIDGE et al., 2015; IWC, 1998). The equipment used to obtain these recordings was diverse (detailed description of each can be found in Appendix), and the most common were manual recorders connected to the hydrophones, submerged from the vessel, or in several cases, autonomous recorders.

Locations of data collections can be seen in Figure 1. Overall, there are 22 different locations: 19 sites are located throughout the BSG area, more specifically on the South Pacific coast: Costa Rica, Panama, Colombia, Ecuador, and Peru (FELIX and HASSE, 2001; PACHECO et al., 2009; GUZMAN el al., 2015; CHERESKIN et al., 2019; WEERDT; RAMOS; CHEESEMAN, 2020), 2 sites are in the BSA area, on the Brazilian Atlantic coast: Abrolhos Bank and Serra Grande, State of Bahia, Brazil (BETTRIDGE et al., 2015; IWC, 1998). The final location is on the humpback whales breeding ground in Nicaragua (BETTRIDGE et al., 2015). Recordings from every location in a certain season are referred to as a “seasonal dataset”, while the overall recordings assembly we used in this study is named “general dataset”.

Humpback whales are present in Central America year-round (CHERESKIN et al., 2019). Nicaragua recordings used in this study were made in April, therefore we assumed the recorded whales are not part of BSG as CA breeds from December to April and BSG breeds from June to September (CALAMBOKIDIS et al., 2000; CHERESKIN et al., 2019; RASMUSSEN; CALAMBOKIDIS; STEIGER, 2011; STEIGER, G. H. et al., 1991). They were included as an outgroup, a blind test, and to determine the possible level of the interaction between the CA and the South American breeding stocks. All other recordings used in the study were collected during the Austral winter and spring (from June to December). All further technical information (file format, sampling rate, sampling size, etc.) of the recordings can be found in the Appendix.

Figure 1 Dataset location map

Locations of 22 datasets used for this study, across 4 seasons, 2016- 2019 (year is coded in the color of the location point). The data were obtained through a collaboration network across Latin America, which was established for the purpose of this study. The dataset includes recordings of 2 breeding stocks, A and G (IWC, 1998), and 2018 recordings off Central American (Nicaragua breeding stock) (BETTRIDGE et al., 2015). Map, ®Google maps. Accessed 26/09/2020

3.2 DATA ASSESSMENT

As expected, due to the very diverse source of recordings used in this research, data quality varied. First, I had to make sure the data used were suitable for the analysis. The initial selection was based on the duration of the recordings since I was looking for the ones that are containing at least one full song cycle *(i.e.*, includes a complete rendition of all themes available in that season)(CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). I have established that recordings with at least 20 minutes long fulfill this requirement, thus, I only used shorter recordings if there was no alternative for a specific location and year (check Chapter I, section 5.3).

Second, I inspected the quality of the selected recordings, aurally and visually, using Raven Pro 1.5 (CENTER FOR CONSERVATION BIOACOUSTICS, 2014). I used the following spectrogram parameters- window type: Hann; window size: 2048 samples; time grid overlap: 50%; frequency grid spacing: 43.1 Hz. We narrowed down the dataset to the recordings containing the most clearly distinctive units.

Finally, I removed recordings with less than a one-day interval whenever possible, to minimize the chance of resampling the same singer, which could influence the analysis with its idiosyncrasies. In the end, each seasonal dataset had a sample size of approximately 90 minutes, which included several short recordings or at least 2 long ones. Most humpback whale songs last on average 10 to 15 minutes (CERCHIO; JACOBSEN; NORRIS, 2001). Therefore, each sample would contain around 6 song cycles, which should be enough to give a general overview of that season's song attributes and include most unit types. Additionally, 90 minutes was the most we could use from several lower-quality datasets, thus we used it as an upper limit to homogenize effort and allow comparison among recording methods, as manual recorders render less data than autonomous recorders.

3.3 Data Processing

3.3.1 Unit transcription and recording strings

After the initial quality inspection, I used Raven Pro 1.5 (CENTER FOR CONSERVATION BIOACOUSTICS, 2014) to label humpback whale sound units in each of the recordings. On the time axis, selection boundaries (boxes) were set around each unit as close as possible to its real-time duration. On the frequency axis, selection boundaries were set to 2 kHz, 3 kHz, or 4 kHz, depending on the unit's dominant frequency (close to 0 Hz, medium-high, or very high pitched, respectively), so the peak frequency would fit in the selection box. I chose these values due to the diversity of the recordings of my dataset: in several cases, the recording quality was low, boats or other types of noise were present, and vocalizations of other animals could be heard. Having standardized selection boxes facilitated comparison between units, minimizing the interference of other types of sounds that could mask the acoustic properties of humpback whale sounds and interfere with precise unit types measurements.

After labeling, the units were further classified by type. For this purpose, I constructed a custom classification Key, composed of 5 steps, modeled on a standard polytomous classification key (table 1). Additionally, the unit's context was taken into consideration where needed (*i.e.*, the adjacent units in the recordings), to facilitate classification. Using the Key, unit types were identified based on 5 major unit characteristics: **Contour, Tone, Peak Frequency, Duration, and Harmonics**, where each characteristic represents one Key step. Rather than assigning a specific value for each of the Key steps, I defined categories or classes, allowing units to vary, as they tend to (e.g., individual singers discrepancies, substrate, depth, recording equipment, etc.) (HELWEG et al., 1990; REKDAHL et al., 2018a). Following the key, the outcome of going through all 5 steps was a 5-digit code, representing a unit type.

Based on these codes, I built a complete dictionary, containing all unit types, and each unit was further given a name, as previously explained (random letter, number, or combination of the two; see Chapter I, paragraph 4.1). In the dictionary, the units are arranged based on their similarity (expressed by a 5-digit code). An example of the Key can be found in Table 1, in the first chapter.

It is important to mention that I did not run every unit through the Key, but rather several representatives of each type initially perceived as such after visual and aural assessment of each different phrase in the song. The representative units were always picked from the middle of the theme, to avoid transitional phrases, where units are known to diverge from the standard structure of its type (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013; FOURNET et al., 2018).

The final step included a transcription of each of the **selected recordings into a string of units**, regardless of any other level of song structure, just based on their appearance in the recording. Two analysts separately labeled all the units, following the Key, and decided on definitive codes after reviewing each other's classification when they diverged.

3.4 KEY MATRIX- RECURRENCE PLOTS

The strings of units served as a base for building a Key Matrix for every recording. These matrices were constructed for exploration of structures hidden in the song recordings, thus a custom-written code was applied to every recording string in the general dataset. The script was written using Octave (EATON, JW, BATEMAN, D. and HAUBERG, 2009). A code was set to construct a Key Matrix, which is by its nature a Recurrence plot or a distance matrix (MALIGE et al., 2020). The 5–digit codes describing a unit type were used to calculate the distance between every unit within the recording, and in this way, represent the similarity of different parts of the same recording. Thus, the base on which each Key matrix was constructed were the strings of units, translated into 5-digit codes. The string was compared to itself, comparing unit by unit, and counting how many, out of maximum 5 levels the two unit types in question have in common. This calculation will tell us the distance. Once the single unit was run down the entire string, the second unit from the string would undergo the same process, and so on. The final product of this calculation is the Key matrix, which visually represents the entire recording containing all the hierarchical structures known to exist in every song. Using this approach, we are able to track various song repetitions within a single recording. More than the start and endpoint of the songs, we are also able to detect the themes within the songs (MALIGE et al., 2020).

3.4.1 Recurrence plots

Recurrence plots are used to visualize and analyze, at a global level, long series of states of a system (see definition by (ECKMANN; KAMPHORS; RUELL, 1987; RAVIGNANI; NORTON, 2017) in the case of a general dynamical system). This tool and its graphical representation have been used in several scientific topics: first in medicine (ZBILUT et al., 1991), and then in astronomy, neuroscience, mechanics, geology, climate changes (see review by MARWAN et al., 2007). This tool has been recently proposed to study structures in animal movements or communication (PAULUS; MÜLLER; KLAPURI, 2010). It was used in acoustics - monitoring of air guns (MIRALLES et al., 2015), and bioacoustics - shrimps sound production (HEE-WAI et al. 2013). A closer application to our problem of analyzing humpback whale songs has been to visualize structures of a music extract (FOOTE, 1999) or to cut it automatically as in Foote (2000) or PAULUS et al. (PAULUS; MÜLLER; KLAPURI, 2010). It has recently been used to study the rhythm of humpback whale sound production (SCHNEIDER; MERCADO, 2018), without focusing on the spectral content of the sounds (MALIGE et al., 2020).

The Octave (EATON, BATEMAN, and HAUBERG, 2009) code was written to build the Key matrix work in the following way: each recording is transcribed as a string of N units, represented by 5-digit codes of each of its units (see section 3.3). Further, the distance between each pair of units of the same recording was calculated, running the first unit down the entire string, after which it would switch to the second unit of the string, and so on. As previously mentioned, every unit is presented by a 5-digit code, thus, each step would count 5 digits, in the matrices represented as “shifts”. The distance between two units is computed by counting the number of their identical parameters (digits within 5-digit code): how many, out of 5 digits, two units have in common. Two units that have no parameters in common will have 0% similarity; two units that have all the same parameters will have 100% similarity. Therefore, coefficient 0 means maximum distance and minimal correlation, and *vice-versa*. The resulting matrix is a square, symmetrical matrix, with ones on its diagonal (maximal correlation between one element and itself) - the Key Matrix recurrence plots.

Once we got the final Key matrices for every recording, I was able to recognize the structures within it. For longer recordings, several song renditions were visible, and within them, higher hierarchical song structures, predominantly themes. Once I confirmed the mentioned structures are indeed themes, by going back to the raw data, the next step was to use these structures for comparison across the total dataset, thus, among all the recordings.

3.5 CROSS-CORRELATION MATRIX

A cross-correlation matrix was constructed to compare different recordings and visualize structural similarities or dissimilarities between them. It was built the same way as the Key matrix, the difference being the cross-correlation matrix uses strings **of two different recordings** as input data. Therefore, the cross-correlation matrix is not symmetrical.

The cross-correlation matrix was calculated for each pair of recordings in the total dataset. Thus, unlike the Key matrix, the cross-correlation matrix shows no structure in the recordings *per se*, but it is rather tracking similarities in the structures of two different recordings it is composed of. In the legend, we can read the level of similarity within the matrix, corresponding to the color gradient (the smaller the distance, the lighter the color, thus higher the similarity).

The matrix is interpreted by reading the "shifts", marked on the axis, explaining the length of the string of particular recordings- of how many units those recordings are composed of (Figure 2). In the matrix title, we can read the name of two recordings used to build that particular matrix. The name of the first recording appears on the y-axis, while the second will be found on the x-axis. Values on the axis of the matrix represent a unit ordinal number, which tells its position in the string. This number was initially retrieved from the selection table generated in Raven Pro 1.5

4 RESULTS

4.1 KEY MATRIX- RECURRENCE PLOTS RELIABILITY

The Key matrix was successfully built for all 69 recordings contained in our total dataset. The Key Matrix indeed proved as a good method for visualizing structures hidden in humpback whale male vocalizations (Figure 2), corresponding to the song hierarchy described in the scientific literature (PAYNE; MCVAY, 1971).

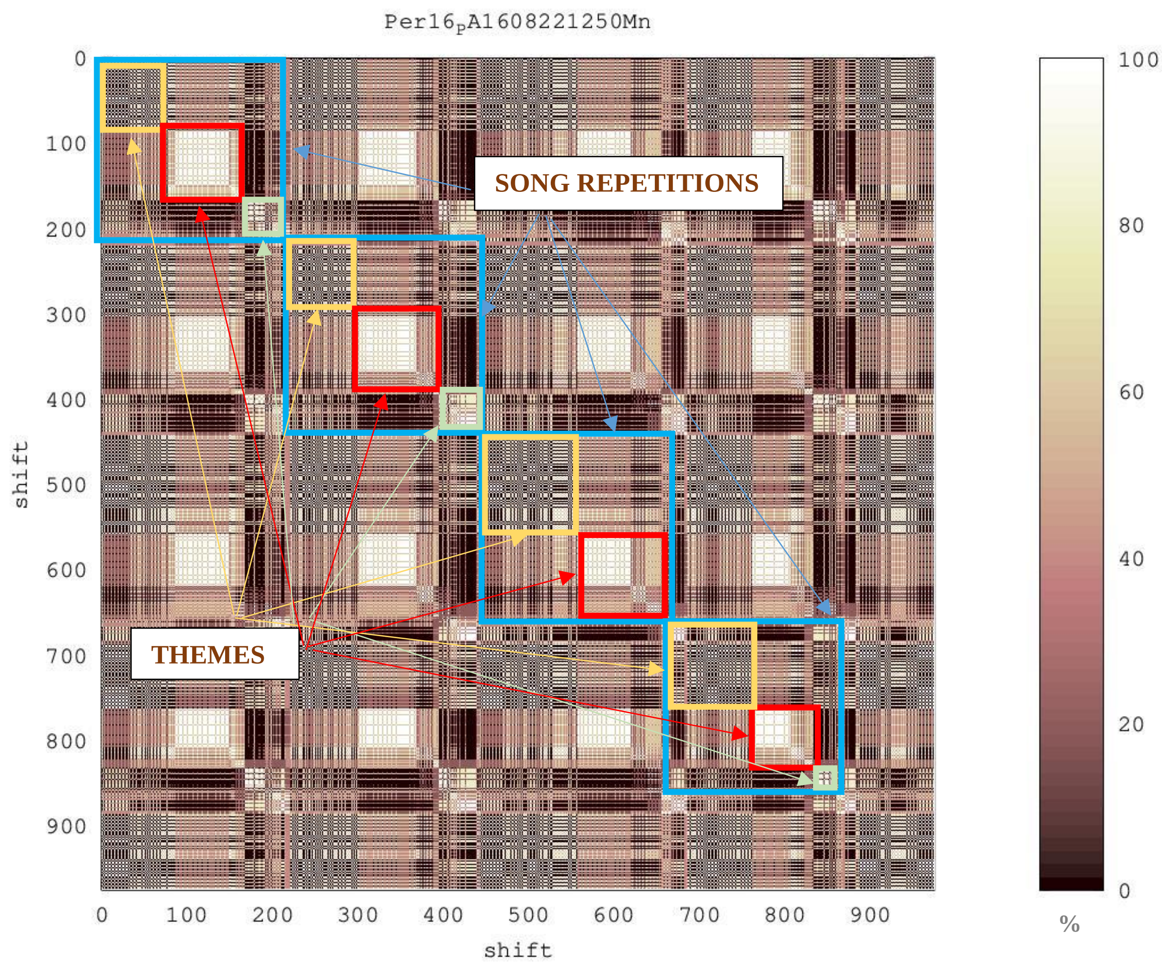


Figure 2 The Key matrix

Key matrix (recurrence plot) of humpback whale song of Peru 2016 recording, where both sides of the matrix represent the size of the recording in units (shifts). The side bar represents the auto-correlation level (similarity) of the string and its elements, coordinated within the matrix with respect to color shade (lighter the color, higher the similarity, smaller the distance). In this 57 min. long recording, the matrix registered 4 full song repetitions (blue squares), each containing 2 to 3 different themes (yellow, red and green squares). Interestingly, each of the structures seems to slightly defer in every repetition (in size or structure).

For most of the recordings (63), the Key-matrix was a reliable way to manually delineate the start and the end of every song repetition within the recording: only for ten per cent (6) of the recordings the matrix was not clear enough to define the boundaries between recording elements, as recurrent structures were not evident and explicit (Figure 3). For the matrices where songs were identifiable, its first and last unit, as well as the beginning and ending unit of each theme contained in each song rendition, it was easy to find and delineate these elements out of the whole recording (Figure 4).

The matrices would show their full capacity for longer recordings only, where there was at least one full song noted. The shorter recordings could be used, but only when consulting the longer one of the same seasonal datasets, to make sure the shorter recordings contain at least one full theme (or several of them) (Figure 5).

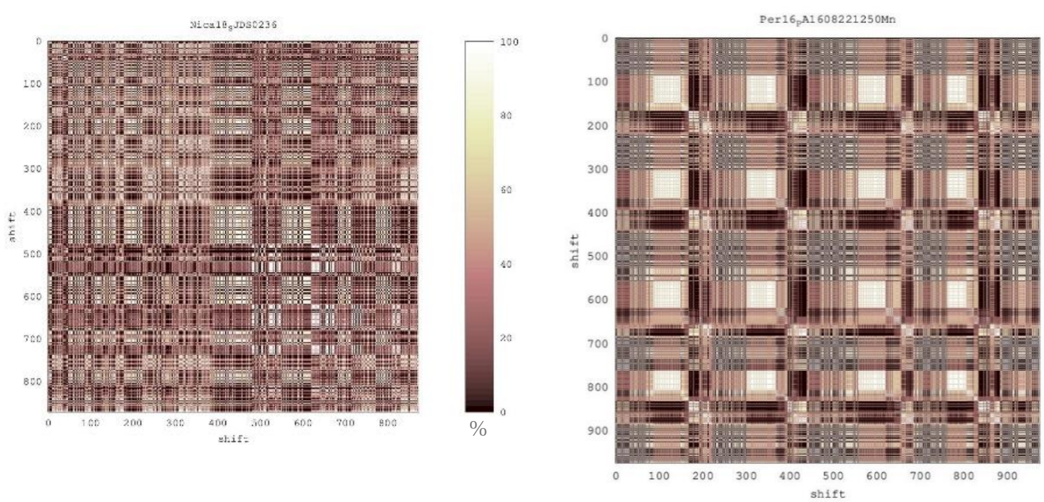
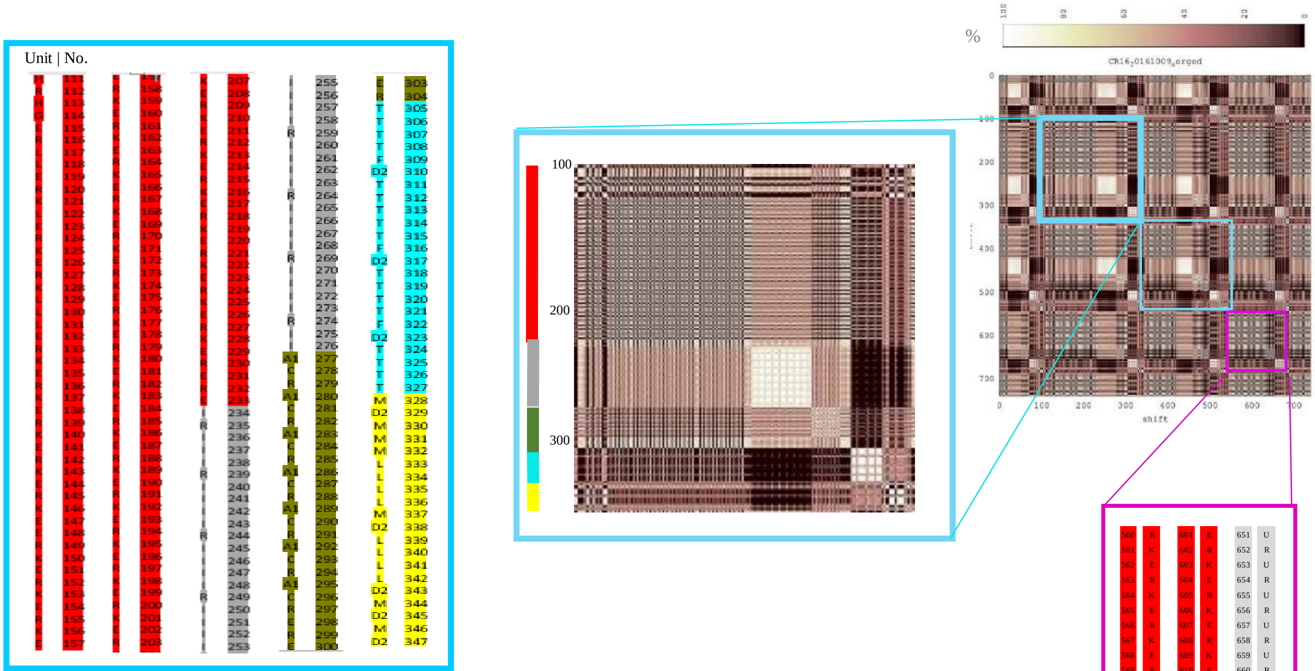


Figure 3 Different quality Key matrices

Examples of key matrices of humpback whale song units. On the left, a Nicaragua 2018 recording lacking clear boundaries between elements and with unstable repetition pattern. On the right, a Peru 2016 recording with clear boundaries and repetition structure, visible by bare eye.



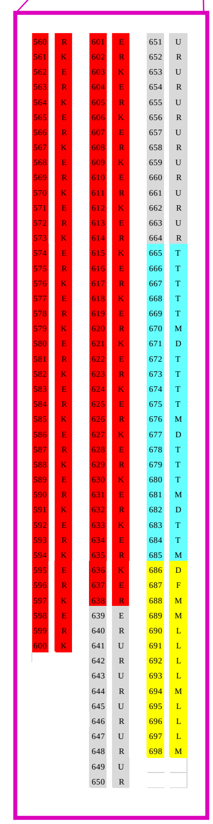


Figure 4 Theme delineation within one song, shown by the Key matrix

Theme delineation within a Key matrix of humpback whale song units in a Costa Rica 2016 recording. A full song repetition is highlighted in blue (right); each theme in the song is represented by a colored bar, as suggested by the matrix song cut-out (center); each unit in the theme is represented in a table by its alphanumeric code and its ordinal number in the matrix Y axis (left). Note the unit repetition within themes: R, K, E and L (red); I and R (gray); A1, C and R (green); T, F and D2 (blue); M, D2, L (yellow). Lastly, the purple song repetition is different from the blue, as it is missing one theme (green), moreover, its "gray" theme is slightly different by its unit content.

4.2 SONG COMPARISONS ACROSS TIME AND SPACE

Once I confirmed the method is reliable, I realized song repetitions are not always the same as previously believed. In the "Origins of music" (PAYNE, 2000), Katherine Payne reported the number of phrase repetitions varies with each display, but the researchers would neglect it when defining a theme. This was firstly noted by herself and Roger Payne in 1985 (PAYNE; PAYNE, 1985).

In Figure 5 we can see how the same song on the same recording varies in size (number of units).

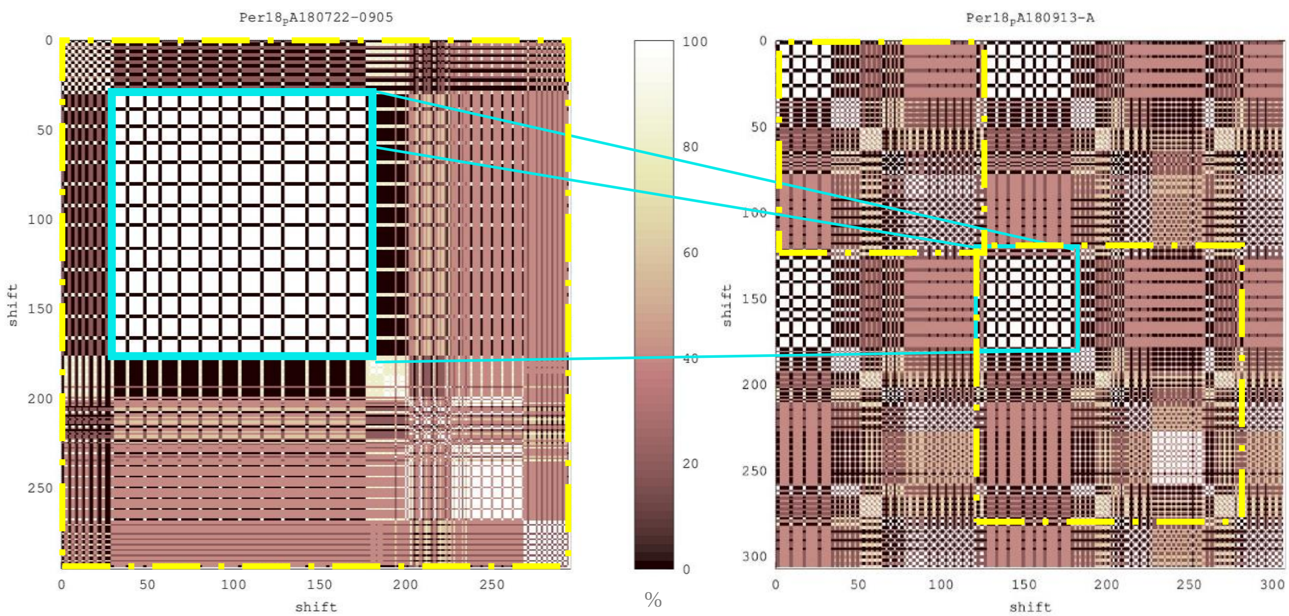


Figure 5 Similar-size size matrices of the same seasonal dataset showing different-size structures

Comparison of two key matrices of humpback whale song units of two different Peru 2018 recordings, similar in lengths (~300 units). On the right, the recording with two song repetitions highlighted in yellow, and a theme from it highlighted in blue with approximately 50 units. On the left, a matrix with only one song highlighted in yellow (the entire recording) and a theme highlighted in blue with approximately 150 units. Note that, despite the length difference, both themes are remarkably similar to each other.

Additionally, in figure 4, we can see the same song aspect, next to its variation in the theme composition and their order (blue and purple square), *i.e.*, certain themes can be omitted from time to time in some song renditions (ALLEN, 2019; GARLAND et al., 2015, 2017a; PAYNE; MCVAY, 1971; PAYNE; PAYNE, 1985; REKDAHL et al., 2018). In my datasets, song renditions are rarely identical. Although this seems to be the rule, previous literature assumed a fixed order of themes and songs considered stereotyped (ALLEN et al., 2018; GARLAND et al., 2017b; NOAD et al., 2000).

The recognition of similar patterns across seasonal datasets was another important result of the identification of the recording structures (Figure 6). The composition of different themes can be characterized by the color pattern in the matrix (thus, the unit organization within it). In this way, similar patterns can be observed across the dataset, which was a cue for developing the method that could directly represent the similarity of patterns between two recordings. This was accomplished by building cross-correlation matrices of every pair of strings of the 69 recordings in my dataset.

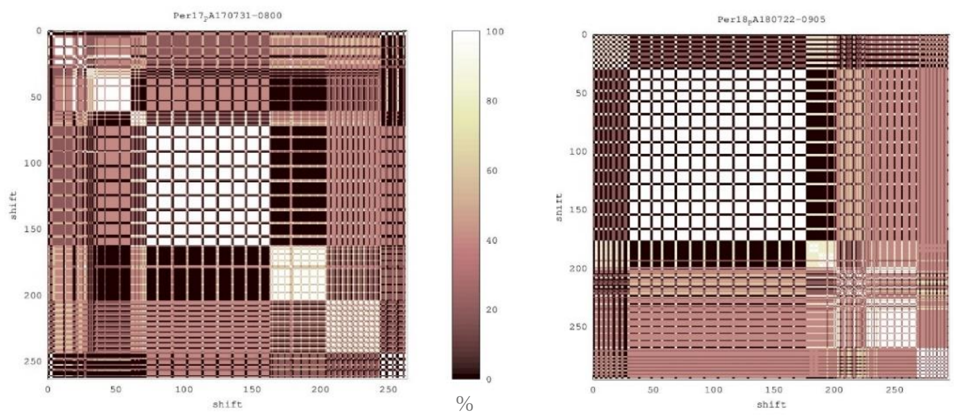


Figure 6 Different recordings exhibiting the same structure

Comparison of two key matrices of humpback whale song units, similar in size, both from Peru, recorded in two different seasons, 2017 and 2018 (left and right, respectively). Note that both have a similar structure (a theme): a black-and-white grid with black lower and right boundaries and a beige square on the lower-right corner, but different in scale. This was a cue for further exploring this occurrence.

Further, as expected, matrices of different recordings of the same season and location (Figure 6), and often the entire breeding ground, are very similar (Figure 7). The similarity can be tracked even between different seasons of the same stock, as long as no intense change took place in the song, *i.e.*, a “song revolution” (NOAD, 2000). If it did, this change is clearly visible in the matrix (Figure 8). The composition of the matrix, its structure, and the visual repetitiveness of patterns depend on the song, in the way that songs with larger unit repertoires usually have more structured visual representations and are less repetitive. Accordingly, less of the structured repetitions can “fit” in the same recording time compared to more simple songs, composed of fewer units.

The duration of the song depends on the season and the song type. In my dataset, the simplest song repetitions last only a few minutes, where the most extreme case is the Brazil 2018 song, which lasted 3 minutes, and had 8 unit types altogether. In one specific case of this season, one whale used only 5 unit types, to sing a sequence of 1071 units, or 26 minutes (Figure 8). In others, the song is much more complex, and themes are often repeated in an unpredictable way. Thus, we cannot always be sure if we have on record all available themes, in addition to complications of telling the song structure out of a very long recording matrix.

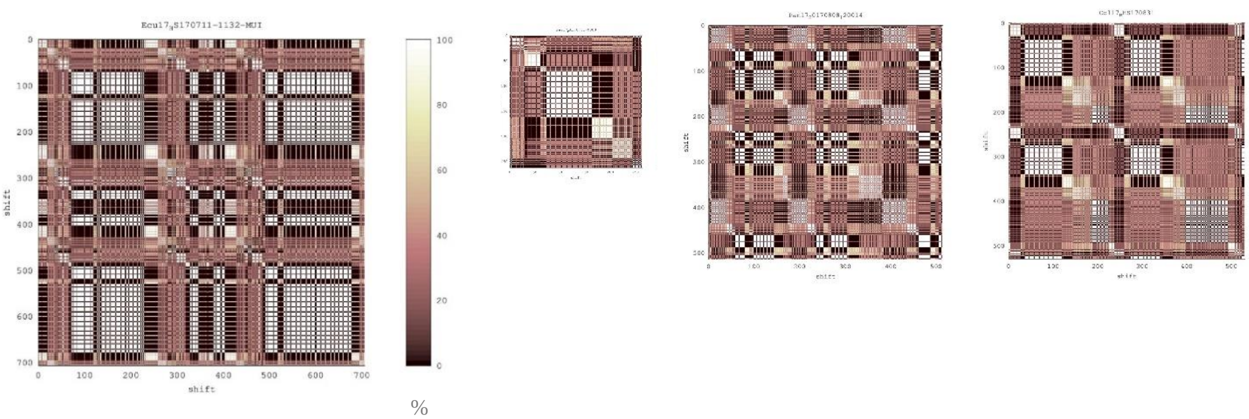


Figure 7 Breeding stock G 2017 song

Comparison of four key matrices of humpback whale song units of four different locations of BSG 2018 recordings: Ecuador, Peru, Panama and Colombia (from left to right, respectively). Note their similarity despite the difference in length (matrices are at the same scale).

4.2.1 Song revolutions

As mentioned earlier, if the song changes at a moderate pace, the matrices are highly similar among locations within a stock and from one season to the next on the same breeding stock. This is the most common way of song progression and is known as “song evolution”. On the other hand, when songs are changed completely, which is the main characteristics of a song revolution (NOAD et al., 2000), this change can be visible in the matrix, as everything about the song changes: the number of unit types used, resulting in a different structure of the themes and their duration (ALLEN et al., 2018). Altogether, the visual representation of the revolved song – the matrix – is highly distinctive from the previous year (Figure 8).

The year 2018 apparently was a year of song revolution for both stocks (Figures 8 and 9). Yet, the revolution developed in a different mode in two stocks, BSA and BSG (this was discussed thoroughly in Chapter I). BSA whales started the season with a brand-new song (see Figure 8).

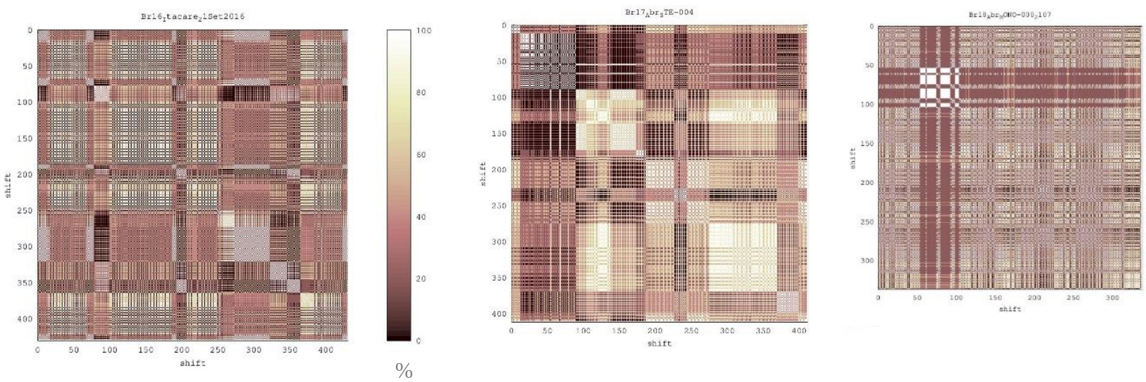


Figure 8 Brazil 2016, 2017 and 2018 song matrices

Comparison of three similar size key matrices of humpback whale song units of Brazil recordings in three different seasons, 2016, 2017 and 2018 (left to right, respectively). Note how different the lest one is by its structure (2018), compared to other two, indicating a song revolution. Matrices are to scale.

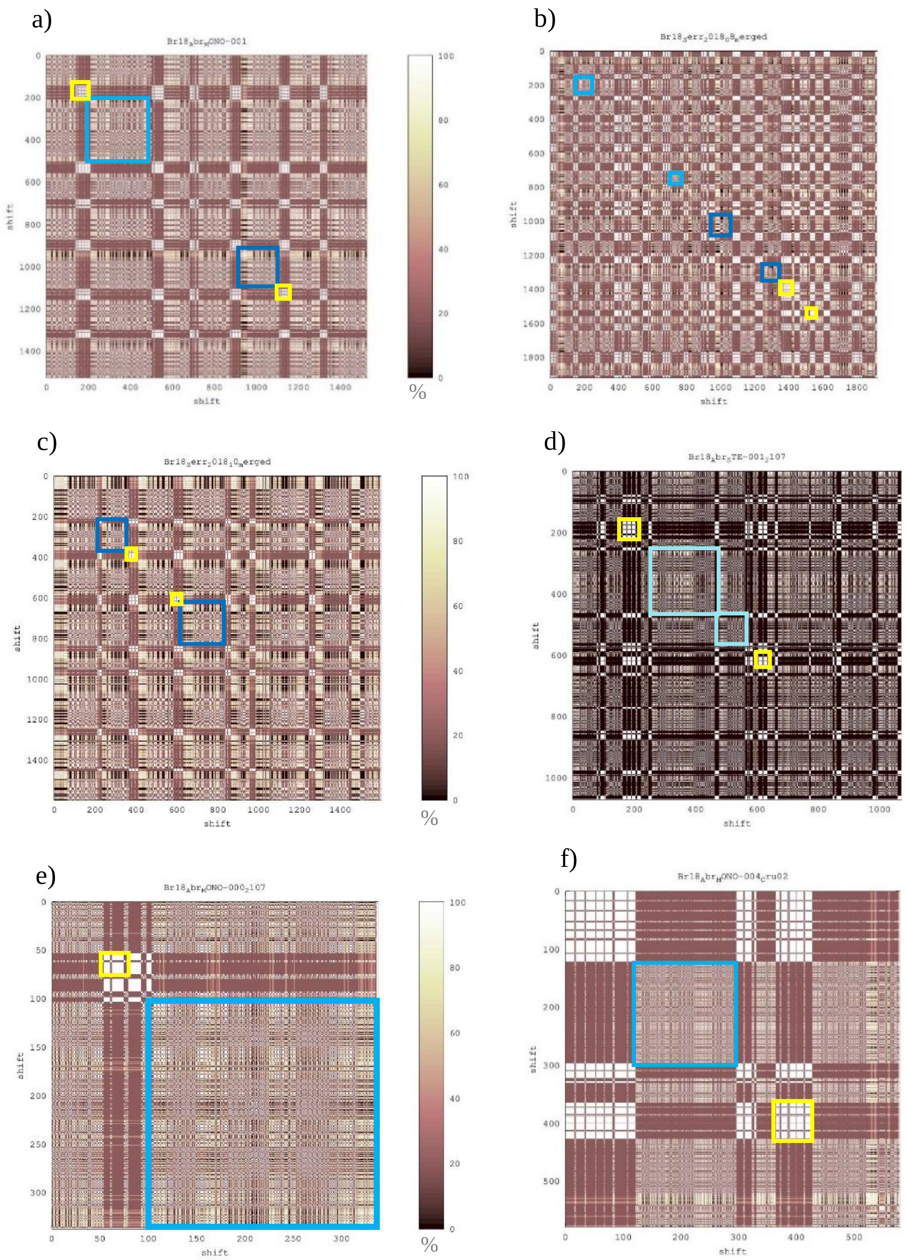


Figure 9 Brazil 2018 revolutionary song Key matrix

Comparison of six Key matrices of humpback whale song recordings of Brazil 2018. Matrices b) and c) are from Serra Grande, the rest are from Abrolhos. The simplified, revolutionary song was composed of only eight different unit types, forming two themes (highlighted in blue and yellow). Based on these matrices, we concluded that there were two slightly different versions of the same theme (highlighted in different shades of blue): note the darker elements on the theme (highlighted in dark blue on matrices a), b) and c)). Finally, note how distinct matrix d) is: this particular recording had a whale singing only 5 different unit types, thus variation was limited (*i.e.*, more of the darker shades present). The matrices are not to scale.

For BSG whales, the season started with a song very similar to the previous one. However, around midseason, several whales could be heard singing a new song type, while some were singing a hybrid type (the mix of the new and the old song type) (Esteban Duque Mesa, personal communication). This phenomenon is also noticeable in the Key matrix of each of the song types from the Colombia 2018 dataset (Figure 10) (Please find more details in the appendix).

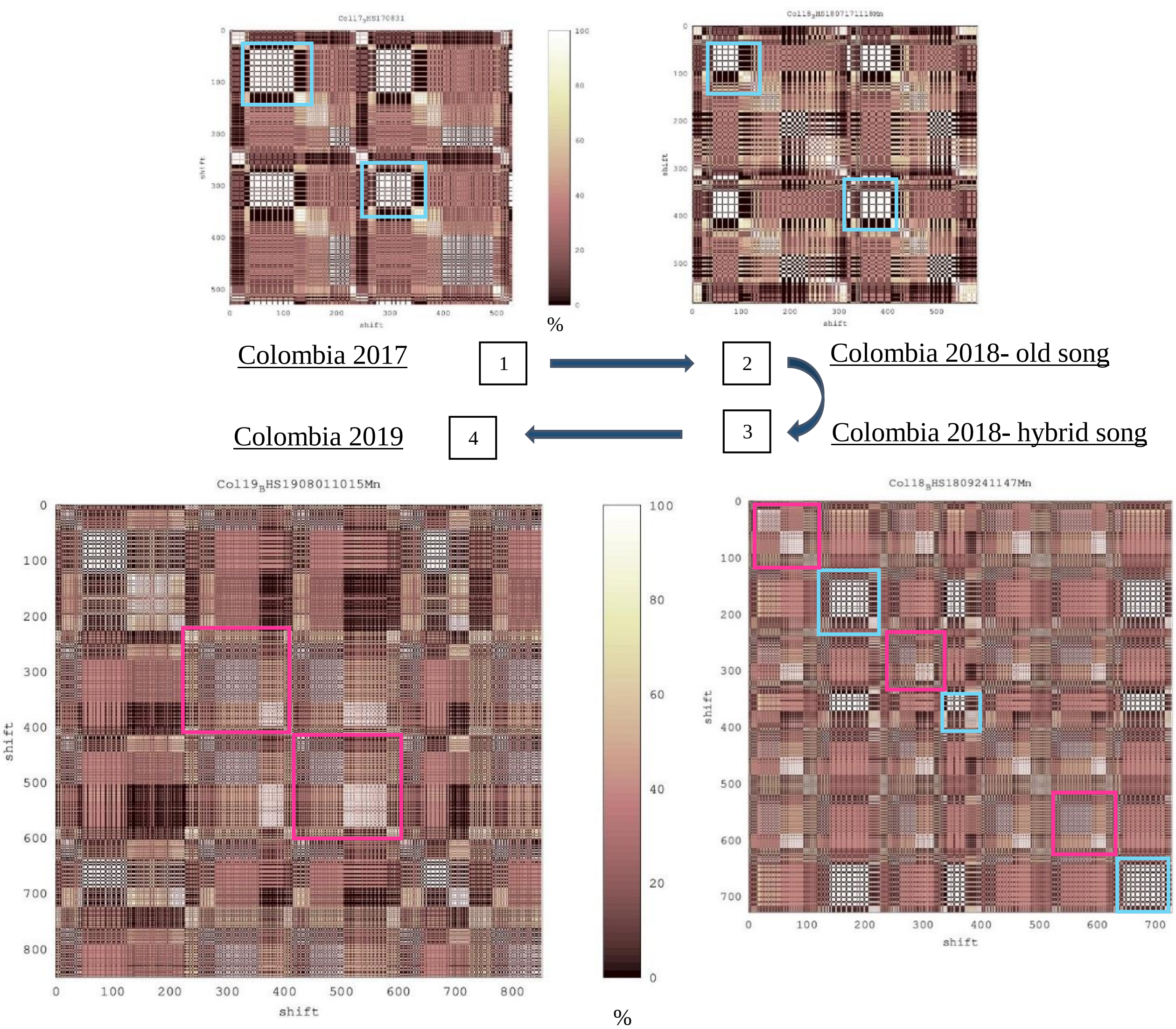
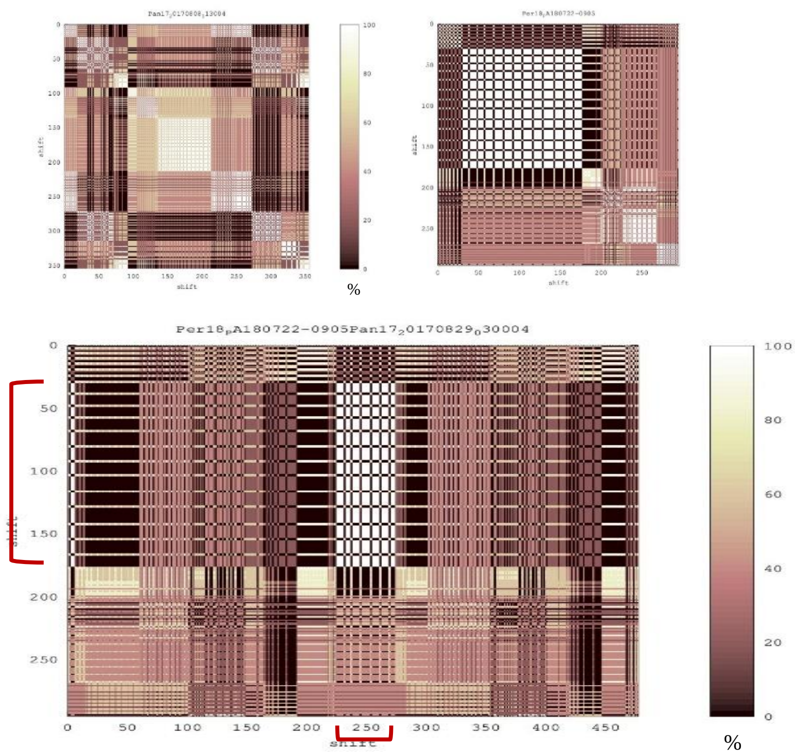


Figure 10 Key matrix of Colombian song in 3 season: 2017-2019

Key matrices representing the song from the coast off Colombia in 3 consecutive seasons (2017-2019). The song of 2018 is represented by 2 matrices different in structure- one (top right) represents a Colombian song with which that season started, very much alike the song of the previous season (2017- top left). The second 2018 recording (bottom right) is what we believe to be a case of a hybrid song, where some elements from both matrices, 2018 and 2019 songs (bottom left) can be noticed (represented by blue and pink squares). This graph represents the direction of the song evolution, with an extra step in-between -the hybrid song, because of which this can also be considered a revolution (flow-chart in the middle).

4.3 TRACKING SONG SIMILARITIES

The cross-correlation matrix was designed to highlight the evident repetition of certain levels of unit organization patterns across the dataset. Thus, a matrix constructed by each pair of the recordings contained in my dataset was calculated, resulting in 2346 cross-correlation matrices. As explained in the methodology section, the shade of the color represents the similarity level of the structures (lighter area, higher the similarity, and *vice-versa*). As this is not a symmetrical matrix, in most cases we are not able to see the actual song structures as they appear. Rather, we should use the visible patches as a guide for the positions the recordings where to find the overlaps of the structures (the position of the song structure can be read from the matrix axis, and further found in the Raven selection table, under the ordinal number of the unit of our interest) (Figure 11).



Recording Pan17_20170829_030004 unit string:
[1]E H L L L E E H E E E H E E 12 H 12 12 12 H 12 12 12 12 H 12 12 12 12 H 12 12 12 12 H 12 12 12 12
[40]H 12 12 12 12 H 12 12 12 12 H 12 12 12 12 H 12 12 12 12 H A1 A1 V H A1 A1 V H A1 A1 V H A1
[80]A1 V H A1 A1 V H A1 A1 H A1 A1 V H A1 A1 V H A1 A1 V H A1 A1 H A1 A1 W W T T 21 T W 21
[120]W 21 W 21 W 21 T T T W T T T W W 21 T T W T T 21 T T W W T T 21 T T W W T T T 21 T T W
[160]21 Q Q Q Q Q Q Q Q M T Q Q Q Q M M M F M F F M M F F F M F F F F F F M F F F F F F F F M
[200]P H P P H P P H P P H P P H P P H P P H P P H P P M E M E M E H L L L L L L E H L L L L E H L
[240]L L L L L E H L L L L L L E H L L L L L LE H L L L L L L E H L L L L E E H E E E H E E 12 12 H
[280]12 12 12 12 H 12 12 12 12 H 12 12 12 12 H A1 A1 H A1 A1 H A1 A1 V H A1 A1 V H A1 A1 V H A1
[320]A1 V H A1 A1 V H A1 A1 V H A1 A1 V H A1 A1 V H A1 A1 V H A1 A1 V H A1 A1 H A1 A1 V W
[360]21 21 T T W 21 W W 21 W W 21 W 21 W 21 W 21 W 21 W W 21 T T W 21 T T 21 T T W W T T 21
[400]T T W 21 T T 21 T W 21 Q Q Q Q Q Q Q Q Q M Q Q Q Q Q Q M Q M M F M M F M M F F F F M F
[440]F F F F F F M F F F F F F M P H P P H P P H P P H P P H P P H P P M K E M K E M K E M E

Recording Per18_PA180722 0905 unit string:
[1]K P H 7 K P H 7 K P H 7 K P H 7 K K P H 7 K K P H K K K P H L L L L L L L P H L L L L L L L L P
[40]H L L L L L L L P H L L L L L L L L L P H L L L L L L L L L L P H L L L L L L L L L L P H L L L
[80]L L L L L L P H L L L L L L L L L L L P H L L L L L L L L L L P H L L L L L L L L L L L L P H L L
[120]L L L L L L L L P H L L L L L L L L L L P H L L L L L L L L L P P H G G G H G G G H R R R H R
[160]R 4 R H R R R D H D 8 D U D2 D2 H D U D2 8 D2 D2 U H D U D2 8 D2 D2 4 H D2 4 D 8 D D H D
[200]4 D 8 D D H D D D D D H D D D D D H D D D D D H D D D D D H D D D D D H A3 A3 B A3 A3
[240]A3 A3 B A3 A3 B A3 A3 B A3 A3 B A3 A3 B A3 A3 B A3 A3 T B

Figure 11 Key matrices vs. their Cross- correlation matrix

Cross-correlation between two key matrices of humpback whale songs from two different locations and seasons. On the top left, a key matrix from Panama 2017; on the top right, a key matrix from Peru 2018; on the bottom, the cross-correlation matrix of these two recordings. Note the central white block on the cross-correlation matrix indicating highly correlated parts. By using the ordinal number of units, it is possible to identify the common sequence (highlighted in red). Matrices are not to scale.

Depending on the overall shade of the color prevailing in the matrix, we can recognize 3 different types of cross-correlation matrices: light, dark, and mixed (Figure 12). In this way, we can tell which pair of recordings are more similar, and which are very different. Light matrices would show overall similar recordings, structure-vise (unit types with the similar 5-digit codes organized in a similar pattern), or in unit composition (same unit types used in the same pattern). Dark matrices result from recordings made far-apart, in time or space, whose songs are often noticeably different (in pattern and unit types). It is interesting to concentrate attention where mixed matrices (overall dark matrices with specific light-colored patches) which some unexpected overlap, in a small portion of otherwise very different recordings, these features would be hard to find comparing unit dictionaries (Chapter I), or using a simpler method of comparison (Figure 11).

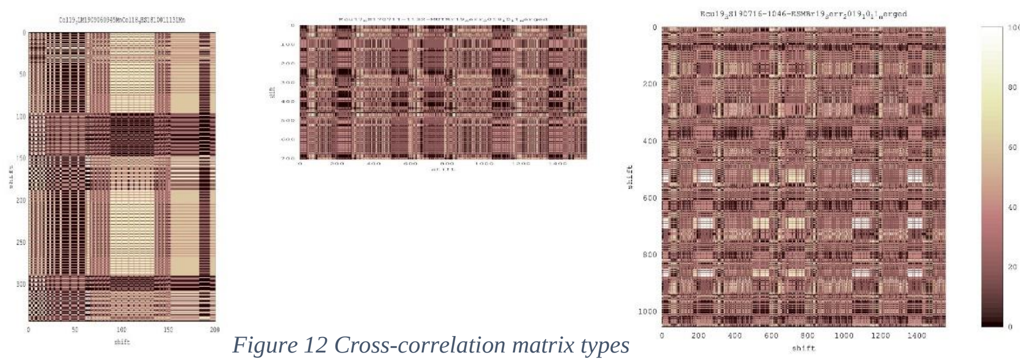


Figure 12 Cross-correlation matrix types

Comparison of three cross-correlation matrices of humpback whale song units. Note how lighter and darker patches appear in each matrix, indicating highly and poorly correlated structures, respectively. The matrices are not to scale

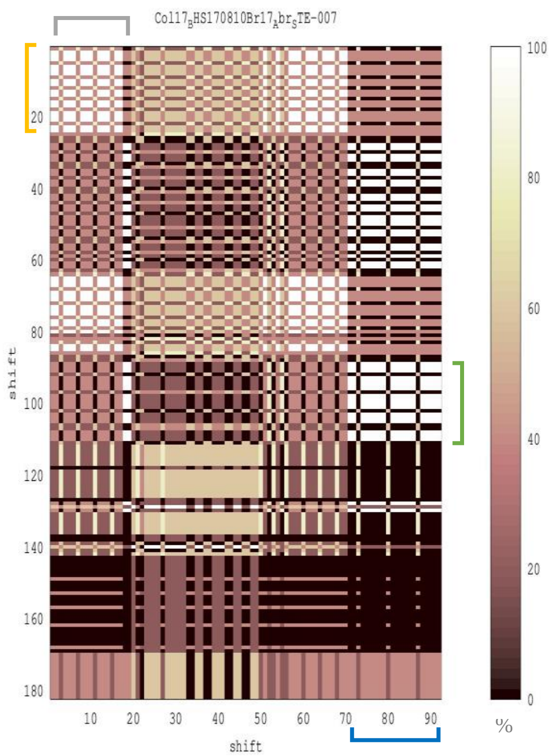
It is important to mention the sensitivity of this method, which would determine the cross-correlation matrix type in the first place -whether it will recognize just a similar pattern of different unit types (structure, that could also be understood as syntax), or the same pattern constructed of the same unit types. Namely, the cross-correlation matrix will also show white-colored patches for the areas that, when going back to the string of units, have not a single unit in common. What it tracks though is the phrase structure, *i.e.*, the unit organization pattern. Often, units in these similar patches have 5-digit codes that differ slightly. Thus, although it is not composed of the same unit types (composition) or pattern repetition between two recordings (structure), the method reveals information about how similar the units are among themselves and see it as highly similar (structure and composition) (Figure 10). In particular, the method highlights as similar patches of the matrix were also similar, not only the same units are shown, organized in a particular pattern. Yet, as we discovered it on the way, the most reliable and notable findings were the ones colored in whiter shades. Two interesting examples of this observation have been found in two song sequences of the recordings from Brazil and Colombia in the 2017 season (Br17_Abr_STE-007 and Col17_BHS170810). The similarity was found in two parts of the song, one composed of units “O U U U 2 U U”, in Colombian song, and of units “W U U U 21 U U” from Brazil. The other was composed of “H A1 A1 H” in Colombia, and “O A1 A1 A1 O” in Brazil (Figure 13). Other examples are shown in Figures 14 and 16.

Col17_BHS170810

No.	Unit
1	H
2	A1
3	A1
4	A1
5	H
6	A1
7	A1
8	A1
9	H
10	A1
11	A1
12	H
13	A1
14	A1
15	H
16	A1
17	A1
18	H
19	A1
20	A1
21	A1
22	H
23	A1
24	A1

Br17AbrSTE-007

No.	Unit
1	A1
2	A1
3	O
4	A1
5	A1
6	A1
7	O
8	A1
9	A1
10	A1
11	O
12	A1
13	A1
14	A1
15	O
16	A1
17	A1



Br17AbrSTE-007

No.	Unit
71	U
72	U
73	O
74	U
75	U
76	U
77	U
78	U
79	U
80	O
82	U
83	U
84	U
85	U
86	U
87	U
88	O
89	U
90	U

Col17_BHS170810

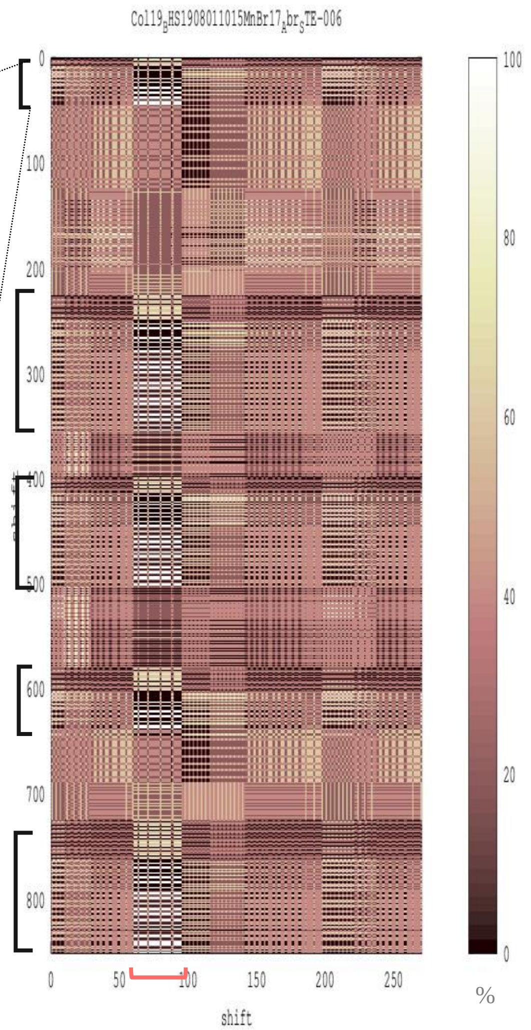
No.	Unit
85	A1
86	A1
87	V
88	W
89	21
90	U
91	U
92	U
93	W
94	U
95	U
96	U
97	U
98	21
99	U
100	U
101	U
102	U
103	W
104	U
105	U
106	U
107	21
108	21
109	U
110	U
111	U
85	A1
86	A1
87	V
88	W
89	21
90	U
91	U
92	U
93	W
94	U
95	U
96	U
97	U
98	21
99	U
100	U
101	U
102	U
103	W
104	U
105	U
106	U
107	21
108	21

Figure 13 Cross-correlation light matrix- similarity in structure

Cross-correlation between two Key matrices of humpback whale song units, Colombia 2017 and Brazil 2017. The two differently composed white patches on the matrix indicate highly correlated parts of the songs, and one of each is presented as a unit sequence highlighted in green vs. blue and yellow vs. gray, on each side of the matrix.

19Col_BHS1908011015Mn

Ordinal no.	Unit type
10	**4**
11	**G**
12	**6**
13	**G**
14	**4**
15	**G**
16	**6**
17	**G**
18	**4**
19	**G**
20	**6**
21	**G**
22	**4**
23	**G**
24	**6**
25	**G**
26	**4**
27	**G**
28	6
29	**6**
30	**G**
31	**4**
32	**G**
33	**6**
34	**6**
35	**G**
36	**4**
37	**G**
38	**6**
39	**6**
39	**6**



Unit dictionary

Unit type	Contour type	Sound type	Peak ν	Duration category	Harmonics presence
6	1	1	3	1	2
O	1	4	2	2	1
G	7	4	2	2	1
4	9	2	2	2	3

Br17AbrSTE-006

Ordinal no.	Unit type
60	**O**
61	**6**
62	**6**
63	**6**
64	**O**
65	**6**
66	**6**
67	**6**
68	**6**
69	**6**
70	**6**
71	**O**
72	**6**
73	**6**
74	**6**
75	**6**
76	**6**
77	**6**
78	**6**
79	**6**
80	**O**
81	**6**
82	**6**
83	**6**
84	**6**
85	**6**
86	**6**
87	**6**
88	**I**
89	**O**
90	**6**
91	**6**
92	**6**
93	**6**
94	**6**
95	**6**
95	**6**

Figure 14 Cross- correlation matrix showing oblique overlap in the structure

Cross-correlation between two key matrices of humpback whale song units, Colombia 2019 and Brazil 2017. Note the unit sequences highlighted in black and red on each side of the matrix. The white patches on the matrix indicate highly correlated parts, however the sequences don't match. This is explained by the similarity between the 5-digit code of unit types O and G, on the bottom table, where in blue is marked the only non-overlapping category between the two units.

By closely examining the mixed-type matrices, we can see certain types of structures appear across the dataset (same structure, different composition). An example for this is the syntax “R-I-I-I-I-R” (Peru16), also shown as “ O-I-I-I-O” (Brazil 17); “M-L-L-L-L-M” (Panama 17) presented as similar to “I-H-L-L-L-L-L-L-L-L-L-I-H” (Ecuador 16) and “R-H-L-L-L-L-L-L-L-L-L-L-R-H” (Ecuador 18); as in the next shade of white, the syntax would show like this “Z-17-X-X-X-X-X-X-X-X-X-X-X-X-Z-17” (Brazil 18). Note the code of each of these unit types presented in Table 2:

Table 1 5-digit codes of units constructing similar syntaxes

Comparison of different unit types with similar characteristics. Colors highlight same classes within a parameter, and units with similar colored cells are considered more correlated.

Unit type	Contour type	Sound type	Peak v class	Length class	Harmonics presence
R	6	4	2	2	1
I	3	4	1	2	1
O	1	4	2	2	1
M	6	1	2	2	2
L	1	5	3	3	3
H	8	4	2	2	1
Z	2	5	3	2	1
17	2	4	2	1	1
X	4	3	3	1	3

From this table, we can understand why the matrix showed the same structures (syntax) composed of different unit types (but with very similar 5-digit codes) as highly similar song fragments. (Figure 10).

Yet, in certain cases, mixed-type matrices indeed reliably show the overlap in structure as well in the composition of song fragments, even themes. The most exciting finding of a mixed-type cross-correlation matrix was the sequence of the revolutionary 2018 BSA song found in the BSG song of the following season, shown in the figure below (Figure 15) (Please find more details in the appendix).

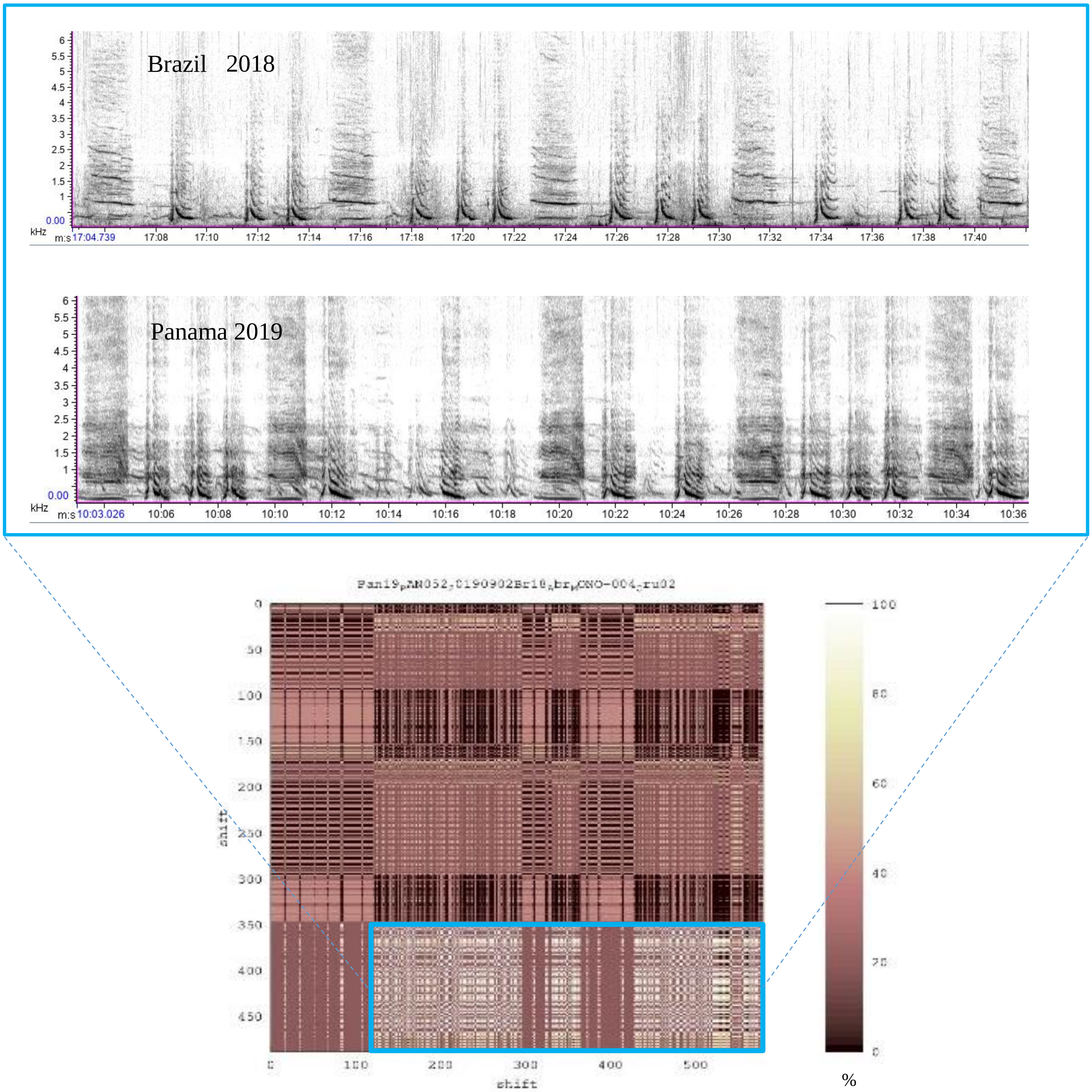


Figure 15 Cross- correlation matrix discovered a theme-sharing event

Cross-correlation between two key matrices of humpback whale song, Panama 2019 and Brazil 2018. Note the white block on the cross-correlation matrix indicating highly correlated parts and the corresponding the spectrogram, highlighted in blue. Spectrogram is produced in Rave Pro 1.5

5 DISCUSSION

5.1 THE KEY MATRIX

Having a key to classify humpback whale song unit types is a step towards unifying the study methodology, as this subject is still in its beginnings. For now, each research group is mostly working under their own protocols, however, it would be in everyone's best interest to build a common strategy so the data can be comparable, with no need for repetitions. In this sense, the 5-digit classification code used in our study proved useful in building the recurrence plots, unveiling the structure we already knew existed in the humpback whale male vocalization. Furthermore, determining that structure with an unsupervised method such as ours assures that human bias is greatly reduced while revealing two of its highest hierarchical levels: songs and themes.

Nonetheless, this task is not always straightforward. The main reasons for it lay in blurred boundaries between the structures in some of the matrices or the absence of a clear repetitive pattern within the recording. This probably means that the song is constantly changing throughout the recording, even beyond its basic characteristic- repetitiveness, and the evolution mechanisms we are familiar with, described by the classic understandings of the song. In our data, commonly, within the same recording, a song often seems to change a bit in every repetition: predominantly in length, as in the number of phrase repetitions (PAYNE and PAYNE, 1985), but also theme order, as themes are not always repeated in a predictable, stable order. This was already suggested by some earlier publications (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). Despite rare examples of structureless matrices (songs) (Figure 2), most often the song structure was clearly visible and distinguishable in a matrix, yet, with theme order and length (quantity-wise) highly variable and unstable. This brings the question of the importance of these characteristics in the determination of a humpback whale song. As variable as it seems, should we be putting all of our focus on theme order when determining a song? In light of this evidence, we should reconsider the definition of the humpback whale song. Maybe the most realistic way to determine it would be *as a collection of themes that are sung in a particular season*. A similar concept was already proposed by Darling and colleagues (DARLING et al., 2019), where ”song cycle” is defined as one sequence of all the phrases a singer is currently using, before repeating.

However, we can consider the existence of “ordered” and “unordered” (which Frumhoff (FRUMHOFF, 1983) named “aberrant”) theme singing in a different light- as actually having a purpose. Namely, there are plenty of examples in the literature that the breeding stocks sing songs with themes in the exact order, deviating very slightly, if at all (FRUMHOFF, 1983; GARLAND et al., 2013a, 2013b; PAYNE; GUINEE, 1983; PAYNE; PAYNE, 1985). We also know from our data that BSA whales, depending on the season, tend to switch from theme order-specific song (e.g., in the year 2000, Chapter III) to more chaotic ones (e.g., 2016-2019, Chapter II). Could it be that the stereotypy of the song depends on the season, or the song type itself (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013; ERIKSEN et al., 2005; HELWEG et al., 1990)? One possible explanation for this phenomenon could be the existence of songs with a different purpose. Could be that the ordered or unordered (aberrant) theme singing actually serves different purposes (GAHR, 2018). Namely, in 1980, Sossinka and Boher (SOSSINKA; BOHNER, 1980) reported the existence of 2 types of songs in zebra finches, very similar in composition, but different in structure, where one is aimed at females, being more stereotyped, somewhat longer, and the syllables are presented faster (GAHR, 2018), and the other serving different, not clearly defined purposes (*i.e.*, defending territory). Could it be that the song of male humpback whales can transmit different information, serve a different purpose, dependent on its structure (theme order), similar to Zebra finches’ songs? (Figure 15).

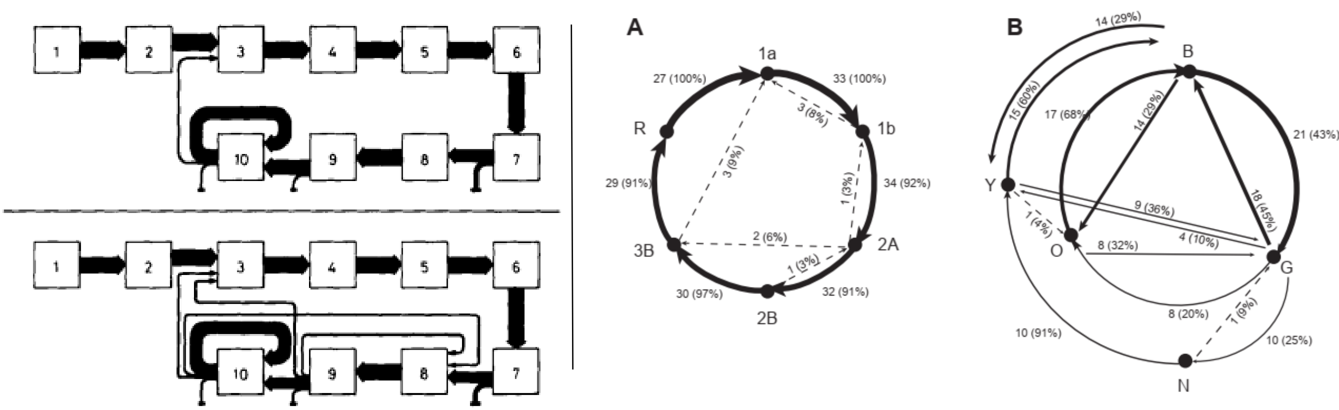


Figure 16 Song element sequence order in birds and humpback whales

Schematics of the male zebra finch and male humpback whale songs. On the left, the flowcharts of the zebra finch songs: the female-directed (top) and the undirected one (bottom) (retrieved from (SOSSINKA; BOHNER, 1980)). On the right, the transition diagrams showing the order of multiple humpback whale songs: A) “ordered” song, Hawaii, 1991, B) “unordered” song, Mexico, 2004. Retrieved from CHOLEWIAK et al., 2013.

The structure of the song varies from year to year. Depending on the season and its song type, a song can be very simple (as in the case of Brazil 2018 song) or highly complex, with extensive unit repertoire (found in Colombia 2019 song, for example) (Chapter I). These characteristics will further influence the song length and composition. Additionally, song organization can depend on the phrase repetitions, thus theme length, but also their order. Having very short recordings (shorter than 15-20 min.) reduces the possibility of grasping the whole song repetition, accordingly, we cannot tell whether we are able to see all available themes. Thus, in the interest of properly using the method of recurrence plots for visualizing humpback whale's song structures, it is very important to have several recordings of different durations in the same dataset, to be able to tell with certainty what is the song, what are the themes, and how many of them there are in that particular season.

Song structure, as explained in the methodology section, is visible on the diagonal of the matrix. The matrix "background", thus further from the diagonal, can tell us about the correlations of different structures within the song. The way the background is presented can influence our understanding of the main song structure, the diagonal, and how we interpret the boundaries of it. The main precursor of the composition of the "background" is the method of building the matrix, namely, the distance by which the matrix elements are distinguished. In my case, based on the 5-digit Key-code for every unit, the distance is in the order of 5, as a maximum. As being a relatively small value, it does not give a lot of space for variation. In this sense, the "background" in some matrixes is shown in a lot of detail with little contrast between different elements. This gives the impression of an overcrowded figure, which further impedes the determination and delineation of target elements. This can be given as the main "flaw" of this method. However, this characteristic can be taken as an advantage, if our goal is to look into more detail of song elements.

Key matrix methodology allows visualizing the structures of themes, and in that way, tracking them throughout the recordings. For example, it allowed us to observe that theme order is something much more variable than we previously thought. When looking between different matrices, detailed visual representation help to observe that some structures are present across the dataset (Figure 5). Examples of structural similarity (syntax) showing song structures composed of several short, high-pitch units in between one longer, low-pitch unit at the beginning and the end of the theme, are fairly common across the dataset. This opens up new questions of the "grammar" of the humpback whale song, or the rules they might follow in constructing the songs, and while using different unit types, they might be organizing them in the same way under these rules. Something similar was proposed decades ago by Katherine Payne (PAYNE, 2000), where she talked about "rhymelike" phrases in the song, that could facilitate the whales memorizing all the novelties accumulating fast. These rhymes were present in the adjacent themes, by phrases that had similar beginning and ending parts. Although apparently different, could both of these strategies serve humpback whales as facilitators in memorizing such elaborate and evolving acoustic behavior? Are there more of these kinds of rules under which humpback whales "compose" their ever-changing songs, that we missed registering so far?

5.2 CROSS-CORRELATION MATRIX

As understanding song dynamics between different breeding grounds, as well across time within the same one, is the main goal of this research, having a method to compare the recordings was our priority. The cross-correlation matrix system enables visualizing the similarities and differences of different recordings. Using this method, we are able to understand the relations between songs of different stocks, and between seasons.

The greatest example of the performance of the cross-correlation methodology is the theme of Brazil 2018 revolutionized song tracked in BSG 2019 song (Figure 14).

Yet, not all findings were this clear. Namely, we need to go back to the unit dictionary and how the recurrence plot is constructed, to unveil this problem. The distance between units was calculated by counting the number of 5-digit code digits the two units are sharing. Thus, only the fully white area in the cross-correlation matrix, as the minimum distance, would show the exact same units in the exact same repetition between two recordings. Anything less required further inspection. The matrix would read any two units similar if they have 3 or more digits from their code equal. In this way, the matrix rather displays an overlap in the syntax, than its content (the exact same units organized in a particular way). The exploration of solving this caveat is presented in Chapter III. Once the syntax overlap is observed, we can go back to the unit dictionary and check its content. Indeed, in most cases, the syntax shown as similar would not only have very similar structures but would be comprised of related units (5-digit code-wise). At this point, we can discuss the sensitivity of the method, as it is obviously influencing the output of similarity estimation between, sometimes, not so similar structures. No weighing system was applied when it comes to the key classification system, designating sound categories as more important than others (Contour type, Tonal type, Peak Frequency, Duration, and Harmonics presence), nor in building key or cross-correlation matrices (valuing some types of similarities between units more than others, and vice-versa). The choice was made base on my principal focus on avoiding human bias in the methodology since human perception is unlike the perception of humpback whales. However, including a weighing system in building matrices is, indeed, a subject worth exploring, as it could be a way of tuning the over-sensitivity of this method, so it better distinguishes between the structure and composition of song elements, thus be more precise. Should be beard in mind the element of bias that could be introduced on the way.

The future methodology should be developed further towards the quantification of similarity between songs, or even tracking the change of the song within the same breeding stock, perhaps leaning on the Levenshtein method (LEVENSHTEIN, 1965), as previously shown suitable (GARLAND et al., 2012, 2017a; TOUGAARD; ERIKSEN, 2005). I fairly reached this goal with the cross-correlation matrix system, however, in it, the sense of similarity between different songs still lays in the domain of visual. Although the human ability to visually track structures and repetitions is powerful, for large sets of data (like in this research- 2346 cross-correlation matrices) this becomes overwhelming to process, bringing a high probability to overlook important information. Thus, a method suitable for bigger datasets is needed, for more efficient and automated larger-scale comparisons, desirably able to compare more samples at once, thus quantifying similarity levels. As for a detailed look into the song similarities in the structure level, but also composition, the cross-correlation method performed very well, allowing us to understand the overlaps and differences, in a very straightforward way, avoiding human bias in interpretations of results. More importantly, it is the first method, to the best of my knowledge, that exactly pin-points highly similar/different song elements of any two longer recordings, guiding us where to look for elements worthy of additional investigation. For example, the already mentioned Brazil 2018 theme found in the BSG of the following season, maybe can tell us something more about the way humpback whales learn and construct their song. Why only one theme was passed on? Why only that particular theme? This theme is possibly holding answers to some of the main questions of humpback whale song evolution.

5.3 HOW DO SONGS CHANGE?

This newly designed methodology helps us detect patterns of humpback whale song, in a very visual and detailed way, consequently helping in tracking and understanding the change incorporated in an ever-present song evolution. What I learned from the result gained by this method, is that the song is changing primarily within each of its repetitions, in different ways (phrase repetitions, theme order, and so on). Secondly, it varies with every singer. Further, I was able to track the rapid, intense changes in the song (revolutions) by having very different matrices, from one year to the next (or within the same season) for the same breeding stock. Consequently, I tracked hybrid songs, peculiar events of the song revolution caught in the process, where we can see elements of the old and the new song within the same recording.

More than finding these peculiar recordings, we can now see how and where the two, old and new, songs merge, or how one becomes the other. So, by identifying the smallest elements, the units, through the matrix we can see “a bigger picture”, the general overview of the song structure and composition. More importantly, the matrix helps us understand what the song actually is, unbiasedly delineating where it starts and finishes, together with the elements (themes) it is composed of. Having a way to see the overall song structure, several song renditions contained in one recording, we can further analyze the overlaps or differences between different recordings on various scales. In this way, we are free to explore options of song evolution beyond generally excepted song structure descriptions. However, the method did bring us back to the classic song organization concept (PAYNE; MCVAY, 1971), confirming once more it is a very solid criterion, as in the aforementioned Brazil 2018 theme. Additionally, some very interesting findings, like in the case of the syntax similarity (Table 2), were found in the level of phrases (*sensu* unit type reports from DARLING et al., 2019; DARLING; SOUSA-LIMA, 2005; GARLAND et al., 2017b; REKDAHL et al., 2018a).

However, this discussion brings new reasons to re-validate the overall concept of the term “song”, as well as the song evolution and revolution concept. What should be done in the cases when unit types change, but the syntax, the composition of a phrase, or a theme remains the same (different unit types composed in the same pattern)? And if these units are replaced by a totally different unit type, or by a related type, should we weigh the song modification differently? Which of these song modifications should be considered a revolution, and which just an evolution? Our method can help in solving this dilemma, by future inspection of the types of changes governing the humpback song modification.

5.4 CULTURAL EXCHANGE OF LATIN AMERICA BREEDING STOCKS

All of our results indicate that Latin American humpback whale breeding stocks have direct contact, its intensity varying from season to season. Additionally, the effect of this contact can also vary in its influence (passing a single theme, or potentially bringing the entire song revolution). Although the exact moment of cultural interaction remains a mystery, we can now tell that it is one of the forces that drives the constant song change of Latin American humpback whale stocks. Next to it, as mentioned earlier, a song usually slightly defers with each of its repetitions, and this is a fertile ground for song moderations and, in a long run, overall song change. However, we cannot discuss this matter in more detail, due to our small recordings sample, and thus, differences in songs between the beginning and end of the same season, for example, will stay out of the scope of this discussion. What we could see in these datasets, though, is that the songs of the same breeding stock, except in the case of revolutions, have highly similar matrices, even between different locations, as noticeable in the case of Colombia and Ecuador 2017 songs – their composition was so similar, that even in the cross-correlation matrix of the two, the same structure was visible (Figure 17).

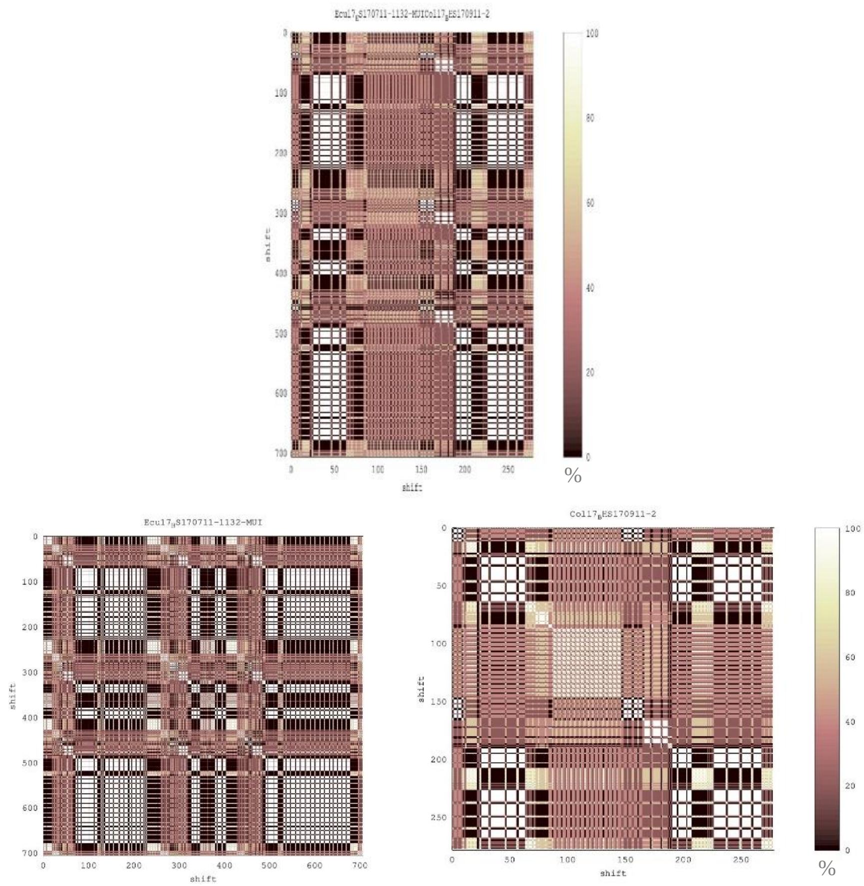


Figure 17 Example of a cross-correlation matrix showing song structure

Cross-correlation between two key matrices of humpback whale song units from two different locations on the same season. On the top, the cross-correlation matrix between Ecuador 2017 and Colombia 2017; on the bottom left- a key matrix from Ecuador 2017; on the bottom right- a key matrix from Colombia 2017. Note the song structures of these two recordings, taken in different locations of the same season of BSG: They are so distinctive and similar that it is visible even in the cross-correlation matrix (a rare occurrence).

6 CONCLUSION

Unit classification key, further used to build the Key matrix, as a base for Cross-correlation matrices proved a useful tool for assessing the humpback whale song, as well for tracking song evolution and revolution, and in this way, qualitatively evaluate the cultural exchange of different stocks based on the similarities of their songs. Accordingly, we can learn much more much faster about the song exchange, and whether certain syntaxes are present across the breeding stocks (echoing examples reported for the unit types) as innate, or as a product of close acoustic contact of animals. In addition, with long-term studies, we can track the change of song of proximate breeding stocks in parallel and understand the level of contact they are maintaining (IWC, 1998). In this way, our method can assist in further understanding the ecology of this species. Long-term monitoring of breeding stocks' song status and further comparisons can reveal movements, interaction, and conformity levels of the species, possibly stock-dependent.

However, caveats of this methodology include encountering several matrices not clearly structured, in addition to significant, time-costly, manual input in running the analysis. Further development is needed, precisely for defining vocalization structures clearly, but also for automating the process, as manual work is very time-consuming, thus not optimal for large datasets and long-term research. Additionally, finding a way to quantify the similarity between recordings is needed, for clear, unbiased, and fast comparisons, that could further be used in numerous studies.

Finally, as the main conclusion based on the assessment of the songs of Latin American breeding stocks, I can report that the cultural exchange in this region is present and strong.

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CHAPTER III

Use of recurrence plots for identification and extraction of patterns in humpback whale song recordings

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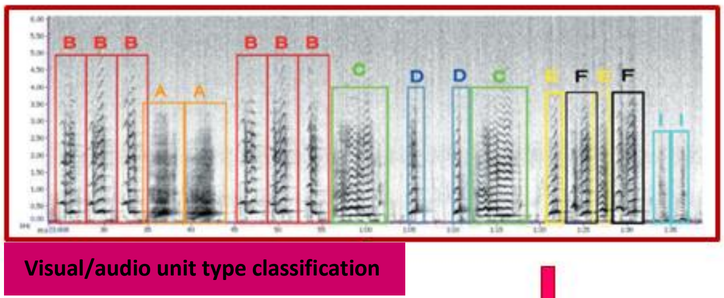
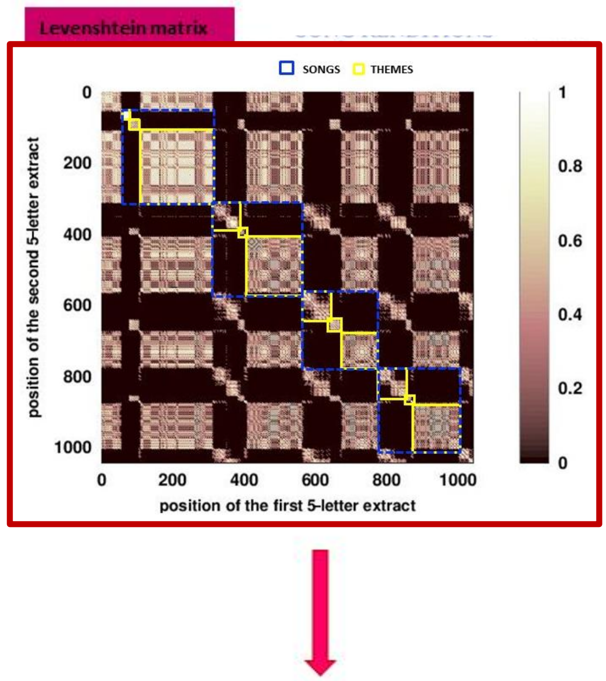
Original available in the Appendix

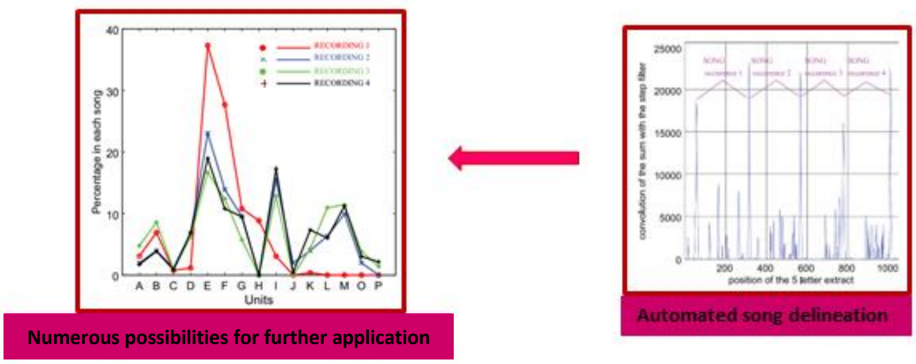
Table of figures and tables

ABSTRACT



Humpback whale song is comprised of well-structured distinct levels of organization: combinations of sounds, repetition of combinations, and a sequence of repetitions, which have no clear silent intervals. This continuous sound output can be hard to delimit, rather, it could be interpreted as a long series of states of a system. Recurrence plots are graphical representations of such series of states and have been used to describe animal behavior previously. Here, we aim to apply this tool to visualize and recognize structures traditionally used in inferences about behavior (songs and themes) in the series of units manually extracted from recordings of humpback whales. Data from the Abrolhos bank, Brazil were subjected to these analyses. Our analytical tool has proven efficient in identifying themes and songs from continuous recordings, avoiding some of the human perception bias and caveats. Furthermore, our song extraction is robust to errors coming from both manual and automated transcriptions, constructing a level of description largely independent of the first stage of analysis.





1 INTRODUCTION

Songs usually describe sequences of sounds organized in a certain structure. Complex strings or sequences of sounds have evolved in many taxa (KERSHENBAUM et al. 2014) and animals may sing with varying degrees of complexity. Depending on the research question, one may or may not consider the adjacent acoustic context in which such songs or sound sequences are delivered, *i.e.*, some are separated by silent intervals, while others are not. These long and continuous complex sequences of sounds impose the added challenge of limiting when one biological meaningful sequence ends, and another begins. The humpback whale male song is an example of such an animal acoustic output structure which is very hard to characterize due to the issues just described.

1.1 STRUCTURE OF HUMPBACK WHALES SONGS

Schreiber (1952) was the first to describe sounds recorded in the ocean by the U. S. Navy in 1951 which were later attributed to humpback whales, *Megaptera novaeangliae* (SCHEVILL and WATKINS 1962). Nonetheless, the complex structure of the humpback whale acoustic display - the song - was noticed almost a decade later by Katy and Roger Payne in 1969 and formally published by Payne and McVay (1971). Three decades after that, genetic confirmation (DARLING and BRUB 2001) supported the behavioral and morphological evidence that only males sing (DARLING, 1983; GLOCKNER, 1983). According to Payne and McVay's description, singing males emit sound units that are arranged in phrases that are repeated to form a theme. Themes are sung in a fixed order which is a song and a song session is the continued rendition of the song. Constant changes in the song throughout the singing season called song evolution characterize the dynamic of singing activity in humpback whales (PAYNE et al. 1983). This hierarchical song structure that cycles in a fixed order was revised by Cholewiak et al. (2013) to incorporate multi-level variation in song structure and to address some caveats with the original structure and order proposition. Fundamental differences between bird song literature that inspired Payne and McVay (1971), such as the lack of silences between-song renditions hindered the acknowledgment that boxing humpback whale song into static artificial hierarchical levels was potentially misleading inferences (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). Especially complicated is to arbitrarily define limits of songs and themes that would vary depending on who was describing it. Methodology on humpback whale song elements identification (and extraction) is still advancing, as consensus on the best protocols is not yet established. As the song and its elements vary in length and order (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013), it is challenging to manually identify them (and their limits) without subjectivity. Automating the process of song structure recognition would significantly reduce frequent human bias. As a mean of going a step closer to this goal of automation, I propose a method based on the "unit" level of vocalization. Unit is the best-defined element of the humpback whale song and can be described as "the shortest sound entity recognized by the human ear, separated from other sounds by a short period of silence" (PAYNE and MCVAY 1971).

Even though classifying units can be a tricky process since there is some versatility in the renditions of the same unit, yet as an entity, the unit remains the most unambiguous element of the humpback whale song hierarchy. In order to reliably define patterns of higher hierarchical level - themes and songs, as assemblies of units, I propose a new method to remove some of the human influence in defining the start and endpoints of songs. This is done by adopting a semi-automated protocol to detect, analyze, or extract the aforementioned features from transcribed unit label strings.

1.2 RECURRENCE PLOTS

Recurrence plots are used to visualize and analyze, at a global level, long series of states of a system (see definition by Eckmann et al. (1987) in the case of a general dynamical system). This tool and its graphical representation have been used in several scientific topics: first in medicine in Zbilut et al. (1990) and then in astronomy, neuroscience, mechanics, geology, climate changes (see review by Marwan et al. (2007)). This tool has recently been proposed to study structures in animal movements or communication in Ravignani and Norton (2017). It was used in acoustics - monitoring of air guns (MIRALLES et al. 2015), and bioacoustics - shrimps sound production (HEE-WAI et al. 2013). A closer application to our problem of analyzing humpback whale songs has been to visualize structures of a music extract (FOOTE, 1999) or to cut it automatically as in Foote (2000) or Paulus et al. (2010). It has recently been used to study the rhythm of humpback whale sound production in Schneider and Mercado-III (2018), without focusing on the spectral content of the sounds. The main topic of this paper is to apply this tool to visualize and recognize the main structures (songs and themes) in unit series of humpback whales. This method was applied to data taken in the Abrolhos Archipelago, off the northeastern coast of Brazil (see section 2.1). These recordings were manually transcribed into a string of units named as letters (see section 2.2). This input was further used to compute a matrix of distances, based on the Levenshtein distance, as done in recurrence plots (see section 3). A method for the automatic extraction of songs in the series of units is proposed (see section 4) and tested on our data set in the final section 5.

2 DATA COLLECTION

Data was collected in the Abrolhos Archipelago, located off the Northeastern coast of Brazil (17oS and 38oW) where humpback whales come during the austral winter and spring, and which is considered the main calving grounds for the species in the western South Atlantic Ocean (MARTINS et al.,2001; ANDRIOLO et al.,2006). During 2000 and 2001 research cruises, groups of humpback whales were sighted and monitored for acoustic an activity using one HTI 90 min hydrophone connected to a portable DAT Sony TCD D-10 (sampling rate of 48 kHz). Vocalizing males were then identified and located by monitoring the amplitude decrease of an individual's sounds as it surfaced to breathe. Silent approaches to these focal singers were performed using a small zodiac with an improvised sail. Songs were collected from the zodiac at distances that varied from 100-500m to the focal male while its behavioral activity was continuously registered. Several recordings were made but only the best quality ones were used in our analyses. Selected recordings made in September of the year 2000 (made by Renata Sousa-Lima) generated 3 high-quality audio files (recordings #1,2,3) lasting respectively 58 minutes, 1 hour 37 minutes, and 2 hours and 7 minutes. In September of 2001, the two selected audio files (recordings #4 and # 5) were respectively 26 minutes and 1 hour and 38 minutes long. Another study of song sessions in the same place in 2000 will serve as a comparison for the data we present (ARRAUT and VIELLIARD, 2004).

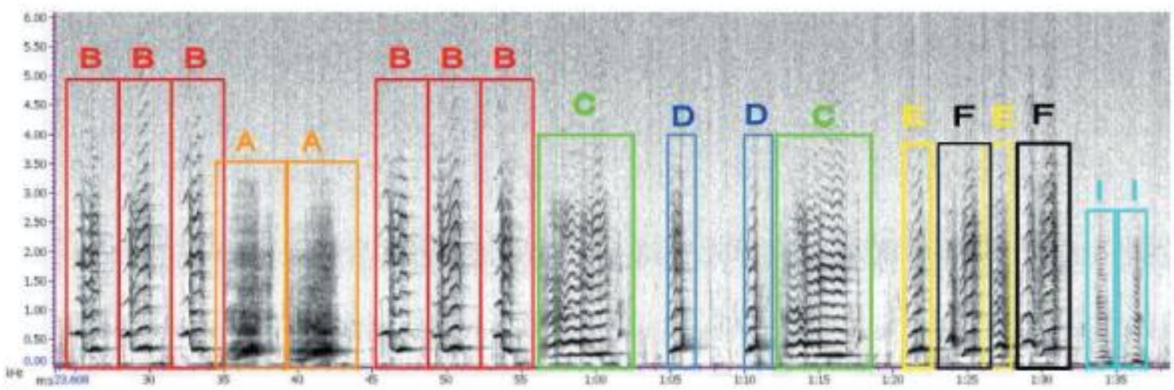


Figure 1. Time (min:sec) / frequency (kHz) representation of an extract of recording #3 (from Abrolhos Archipelago 2000, recorded by Renata Sousa-Lima), 1024 point FFTs, Hann window, 43.1 Hz resolution, and 50% overlap. Unit transcription into letters is signaled above the boxes.

2.1 SOUND UNIT TRANSCRIPTION

Classifying units into specific types is a complex problem since there is a large versatility in the acoustical properties of a single unit (JANIK, 1999). Several issues can be encountered: firstly, there is a seemingly infinite number of different unit types used by whales, in an ever-changing song. Secondly, even the units belonging to the same type may vary to a certain level throughout the same song, in the recordings of different singers, and depending on the quality of the dataset. Thus, a different final product of classification can arise from the same dataset due to differences in the methods used to determine the units. The final number of different unit types in different studies varies greatly, from twelve to more than one hundred (PINES, 2018). The challenge to group the units by type (as similar or different), opens the debate on what is the acceptable level of variation within the same unit type. In order to overcome this difficulty, I used the context *i.e.* the position of the unit in the song (or more commonly in the phrases within each theme), defined by the arrangement of adjacent units (GREEN et al., 2011). The context has proven as a good way to help determine the unit type (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). For this work, all recordings were inspected by hand. Spectrograms were created using 1024 point FFTs, Hann window, 43.1 Hz resolution, and 50% overlap

(created by software Raven pro 1.5 - Cornell Lab of Ornithology, Ithaca, NY, Program, 2014), and subjected to aural and visual inspection by two trained analysts. Each analyst separately inspected and labeled the whole dataset. This procedure is a common protocol adopted by humpback whale song researchers (PAYNE and MCVAY, 1971, DARLING ET al., 2019). Our protocol for unit classification also takes context into consideration, *i.e.* the position where the unit is placed, so that other hierarchical levels of the organization can help define how much variation is allowed in a single unit type. Note that even when studies carry on unit annotation using computational methods, the results are usually validated using manual classification (PACE et al., 2010; GARLAND et al, 2013; ALLEN et al., 2017). The labeling was done by attributing an alphabet letter to every unit type, based on its distinctiveness from other units (DARLING et al. 2019). Analysts considered visually and auditory perceptual characteristics for classification such as unit tonal or pulsed quality, its pitch content and frequency modulation pattern, its duration, and its placement within phrases (context). Each time the specific unit would arise in the recording, it was labeled in Raven, according to its type, minding its context (adjacent units). The final product of every separate recording would be a list of N consecutive letters, the way the units appeared in that specific humpback whale vocalization (see Figure 1 and supplementary material #1). This list of letters (units) – *the string*- will, in the later steps of the method, serve as an input for computing recurrence plots (section 3). Finally, an inexperienced analyst, using another software (Audacity, using an 8192 points FFT, Hanning window, 99% overlap) independently transcribed part of recording #3 into a series of units as a comparison with the first transcription and a check on the robustness of our method (see section 5.2).

3 THE LEVENSHTEIN DISTANCE RECURRENCE PLOTS

3.1 DEFINITION OF THE LEVENSHTEIN DISTANCE RECURRENCE PLOT OF ORDER N

To visualize the structures contained in a recording, a distance matrix was computed in OCTAVE (EATON et al. 2009) in the following way- each recording is transcribed as a string of N letters representing sound units (see section 2.2). Further was needed to define the extract i as an n-letter extract beginning with the unit number i. The length of the extracts n is taken much smaller than the total length of the string N. The Levenshtein distances dij = Levenshtein distance (extracti, extractj) between all pairs of n-letters extracts are computed.

The Levenshtein distance between two strings is the minimum number of insertions, deletions, and substitutions necessary to transform one string into the other (LEVENSHTEIN, 1965). Note that the other types of distance matrix could be achieved by choosing other distances between two strings of letters: Jaro-Winkler, Damerau-Levenshtein, or Hamming distances for example. For convenience, a correlation index was defined by :

$$c_{ij} = \frac{n - d_{ij}}{n}$$

Thus, the coefficients of the matrix satisfy $c_{ij} \in [0; 1]$. The coefficient 0 means maximum Levenshtein distance and thus minimal correlation. The coefficient 1 means zero Levenshtein distance and thus a maximal correlation. The resulting matrix (c_{ij}) is a square matrix of size N - n + 1 ≃ N, symmetrical, and has ones on its diagonal (maximal correlation between one element and itself). As an example, Figure 2 shows the graphical representation of this Levenshtein distance matrix of recording #2 (a total of N =1260 units), with 5-letters extracts (n=5). The result is a recurrence plot of a dynamical system (as defined in ECKMANN et al., 1987) in which a state is a vector of n letters. This special recurrence plot was named the Levenshtein distance recurrence plot (matrix) of an order n (LD matrix). To recapitulate, the LD matrix shows a visual representation of the structure of the entire recording, constructed by calculating the Levenshtein distance between the string of units of the entire recording and itself, but "sliced" into n (5-unit) long comparison steps.

The value of n is chosen by the analyst. In my data, the visual information is basically the same when n varies (see Figure 3). For low values of n, there are a few levels of Grey. For high values of n, the resulting Figure is more blurred (see Figure 3), and the computation of Levenshtein distance is rather time-consuming (the time of computation of the distance between two strings of n letters is proportional to n^2 (WAGNER and FISCHER 1974)). The computation of the LD matrix for n = 17 and N = 800 in Figure 3, takes around one hour in a domestic computer. The parameter n can be adapted depending on the use of the LD matrix: visual analysis, extraction of structures, etc.

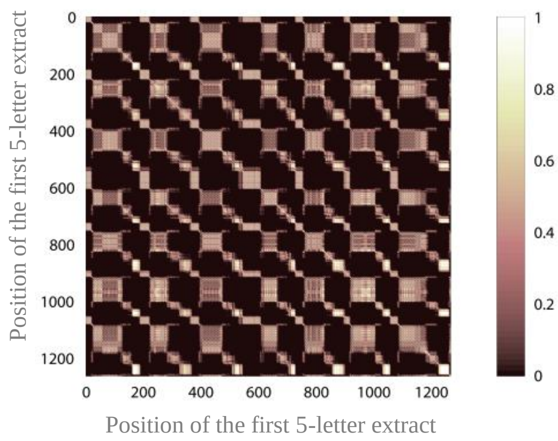


Figure 2 *Example of a Levenshtein distance recurrence plot (5 letter extracts) created form recording number #2 from Abrolhos Archipelago (2000). The number of units of this recording is* N ¼ *1260. The coefficients of the matrix denote correlation between 5 letter extracts (0 is no correlation, 1 is maximal correlation)*

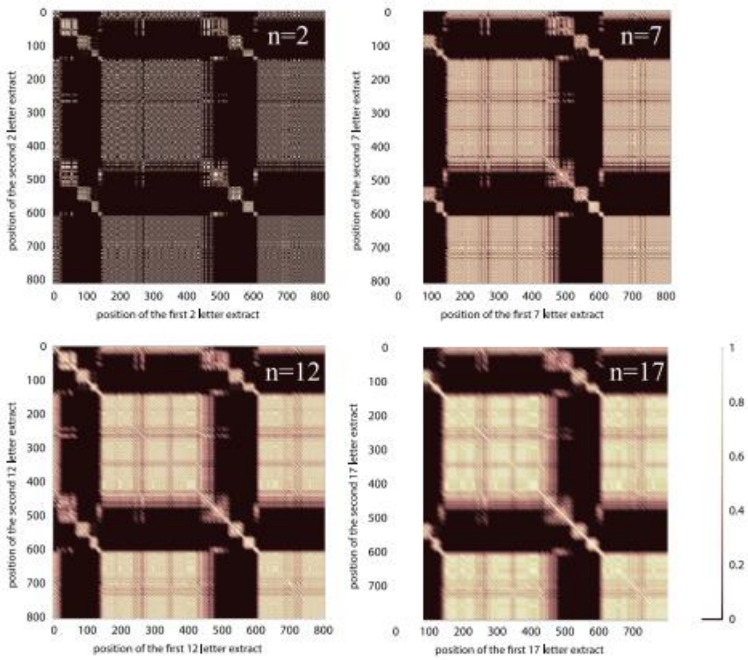


Figure 3 Recording #5 (from Abrolhos Archipelago 2001): Levenshtein distances recurrence plots for different values of the length *n* of the extract (2, 7, 12 and 17)

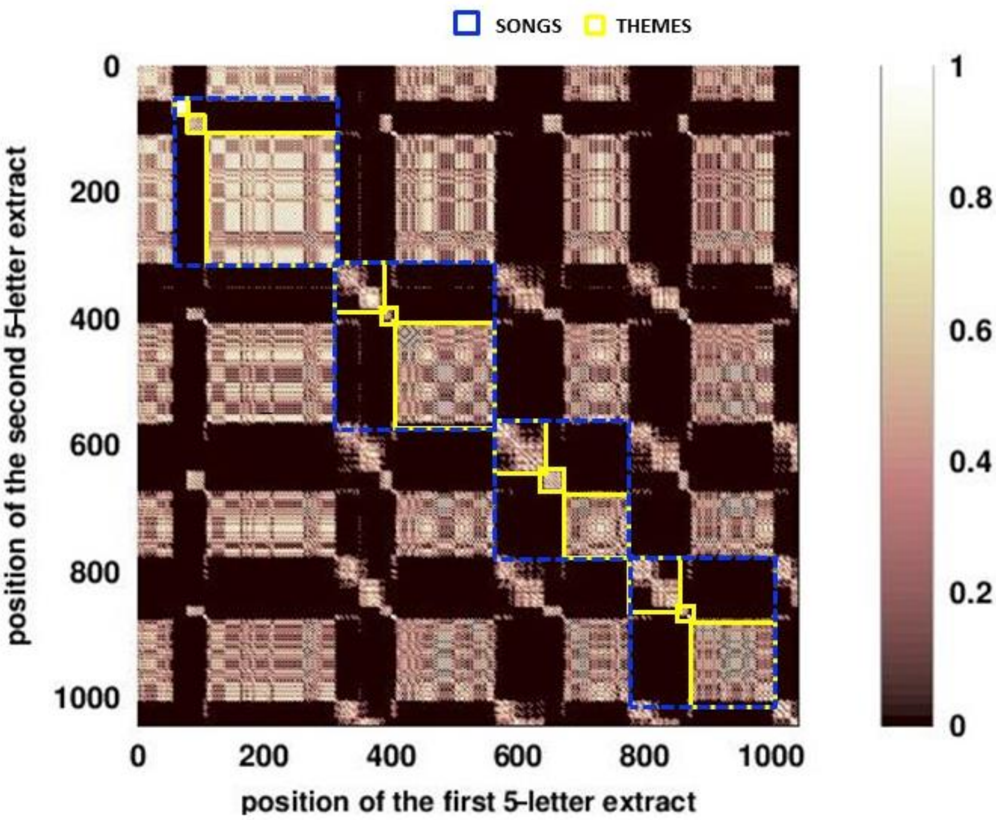


Figure 4 Recording #1 from Abrolhos archipelago, 2000: Levenshtein distances recurrence plot commented (n=5). The main structures of humpback whale sound production appear: songs in blue, themes in yellow

3.2 VISUAL IDENTIFICATION OF MAIN STRUCTURES IN THE RECURRENCE

Figures 2, 3, and 4 show obvious structures in the recording. On the diagonal of the matrix, squares represent auto-similar structures. Rectangles out of the diagonal show whether these structures correlate with each other. The high contrast of this representation is due to the sparsity of the input representation (letters), added to the efficiency of the distance operator.

Figure 4 annotates two different scales of structures found in all recordings of this study. First, a periodically reproduced global pattern can be seen (the “period” can be seen in the horizontal or vertical regularly spaced correlations of parts of the recording). Thus a song is defined as the largest repeated structure that can be found in a recurrence plot. The song is repeated with a high level of similarity, apparent in the non-zero correlation with other songs. This structure is obvious in our representation, it is also in accordance with the general literature on humpback whale bioacoustics (PAYNE and MCVAY, 1971; MERCADO-III et al.,2003; CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013).

A second scale of the structure is visible in the LD matrix: each song is itself composed of several auto-similar parts or ’squares’ (Figure 4). These parts are not repeated within a song (square 1 does not correlate with others within the same song). A theme is defined as the string of units corresponding to a “square”, or self-similar part of a song. With this definition, I am consistent with the general literature on humpback whales (MERCADO-III et al. 2003, PAYNE et al. 1985) which states that a theme is a repetition of similar phrases composed of similar sound units. Nevertheless, it is difficult to see a distinct visual signature of phrases in the recurrence plot. Anyway, the separation of themes in squares could help a humpback whale song analyst to identify phrases in each series of units corresponding to a square.

4 AUTOMATION OF THE EXTRACTION OF SONGS

Based on the computation of the distance recurrence plots, a routine that separates songs in a fully automatic way was written. The song was defined as a structure that is repeated with a good amount of similarity, with the largest possible scale in our recording. The approximate size (in the number of units) of a song can be estimated by a 2-dimensional FFT of the Levenshtein distance recurrence plot of order n (see Figure 5, left). Then, the following algorithm for song extraction is proposed:

(1) Compute the Levenshtein distance recurrence plot for a given value of n

(2) Perform a 2D Fast Fourier transform of the matrix considered as an image. A peak at a frequency-inverse to the mean length of the song can be seen (Figure 5, left). The abscissa of this peak is then measured to obtain an order of magnitude of the lengths of the songs.

(3) Read the first line of the Levenshtein distance recurrence plot and select the columns with non-zero correlation. Sum all these columns to improve the signal-to-noise ratio. The resulting column is represented in Figure 5, center.

(4) Find sudden increases or upward steps in the resulting column using convolution with a step filter (Figure 5, right). Keep only the steps compatible with the average song size predicted by the 2D Fourier transform. Here, the margin of acceptability is defined at one-third of the average size given by FFT analysis.

(5) Extract the units transcribed from the recording between two upward steps: this is a song (Figure 6).

5 Results: song extraction

5.1 Extraction of songs in a series of units from Abrolhos Archipelago in 2000/2001

The algorithm presented in the previous section was applied to the five recordings of this study. Visually, the same features corresponding to our definition of songs and themes appear in each Levenshtein distance recurrence plot. Recording #4 is too short and does not present a complete song, consequently, our routine did not extract any song.

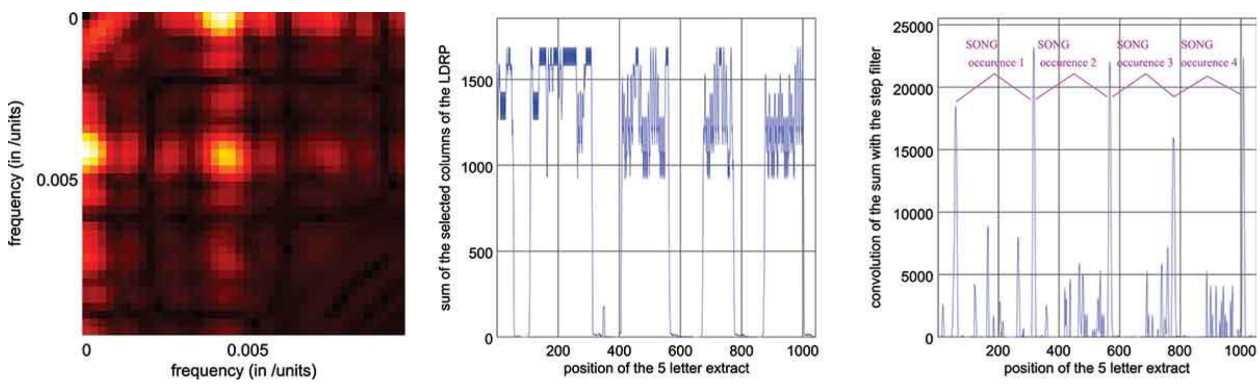


Figure 5 Steps in the extraction of the songs. Left: Step 2 of the algorithm, extract of the 2D fast Fourier transform of the Levenshtein distance matrix (for n=5, recording #1). A peak is visible at a frequency of about 0.045 units (which means a scale of 200 to 250 units of the recording) center: Step 3 of the algorithm, the horizontal sum of selected columns of the recording 1,n =5. Right: Step 4 of the algorithm, each peak shows the transition between two songs.

In all the other recordings, the extraction of songs was achieved successfully. In recording #5, only one song is present. I compared the extraction of songs carried out by the routine, based on the Levenshtein distance recurrence plot, and songs delineated by a human expert. A comparison was performed for recording #3. The analyst followed the instructions described in Cholewiak et al. (2013), and the choice for the beginning point of the first song was the first complete theme (composed of the same type of units). The extraction of the songs is equivalent to both methods, manual and automated. The only difference sits in a few transitional units (less than 5 units per song). It is interesting to note that recurrence plots can show transitional phrases, which are combinations of units from the previous theme with ones from the next theme the male sings (FRUMHOFF, 1983; PAYNE et al. 1983; CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). Transitional phrases appear in our recurrence plots as blurry areas around self-similar ”squares”, representing the themes. It is particularly clear in Figure 6 (right), where three squares corresponding to themes number 1, 2, and 3 inter-penetrate each other. On the contrary, the transition between themes in Figure 6 (left) is quite abrupt: the squares are well separated.

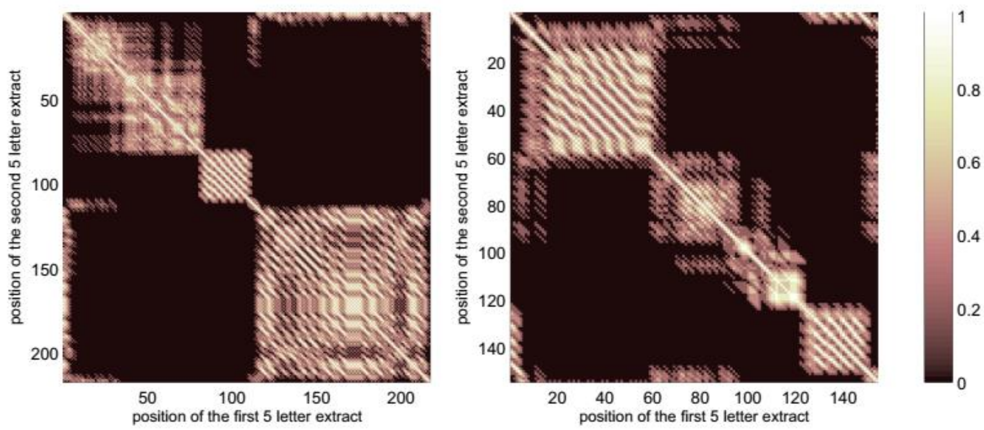


Figure 6 Two songs, automatically extracted. Left*:* Recording #1 from Abrolhos archipelago, 2000: third song automatically extracted from Figure 4. In order to see clearly the song, the frame of the figure is chosen a bit larger for representation. Right*:* recording #2 from Abrolhos archipelago, 2000: zoom on the third song occurrence in the Levenshtein distance recurrence plot of Figure 2. Different types of transition between themes appear

Once the songs are extracted, the automatic measurement of the song's parameters is easily done. As an example, one can automatically compute songs’ length, repertoire (set of different unit types - or letters - used in the song), and the pertinence of units (% of the occurrence of a particular unit type in a song occurrence compared to the length of this song). These results are presented in Table 1 and Figure 7.

Table 1 : Mean and standard deviation of the songs' length for recordings #1,2,3 and 5

Recording	Year	No. of songs	Mean length (in units)	Standard dev. (in units)
#1	2000	4	238	22
#2	2000	6	177	25
#3	2000	8	301	72
#5	2001	1	438	none

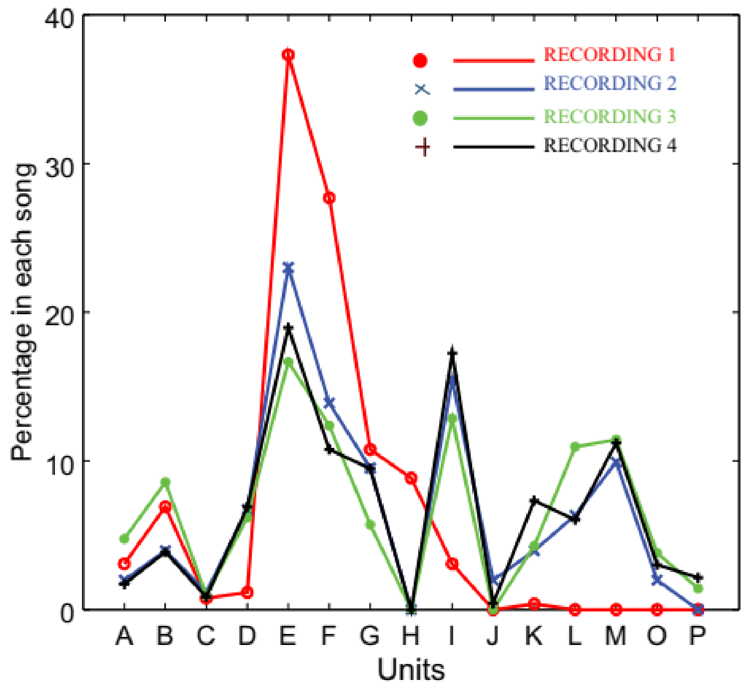


Figure 7 Percentage of each unit type in the four song occurrences of recording #1 from Abrolhos archipelago, 2000 (colors are red, blue, green and black for song occurrences 1,2,3,4 respectively). The first occurrence of the song in the recording (see Figure 4), in red in this figure is quite different from the other occurrences in term of its unit types content, due to the boat noise that prevented an accurate identification of several units.

Figure 7 gives the percentage of each unit in the song occurrence of recording #1. The first occurrence of the song, in red (or circles), is quite different from the other songs. Indeed, during the first song occurrence, a series of units are masked by boat noise and were labeled with a special letter (H) in place of a whole theme containing the letters J, K, L, M, O, P. It can be seen in the Levenshtein distance recurrence plot where the first theme of the first rendition of the song does not correlate with any of the themes of other renditions (Figure 4). However, the recurrence plot still enabled us to extract the song structure accurately. The results of Table 1, where the mean length of all the songs analyzed is 255, compares well with the results of Arraut and Vielliard (2004), working with the same data but with manual analysis, where the mean song length is around 250-300 units.

5.2 Robustness of the extraction method

In order to test the robustness of our method of songs extraction, first needed to be checked that the extraction is not dependent on the order n of the Levenshtein distance recurrence plot, the LD matrix. For each recording (#1 to #3) the number of songs extracted was the same for n going from 4 to 10. Further, to check that the extraction is not heavily dependent on the unit transcription. For recording #3, an inexperienced analyst transcribed part of it in a string of units. Even though the confirmed analysts transcribed 1614 units and the inexperienced one 1855, the recurrence plots have the same appearance (Figure 8).

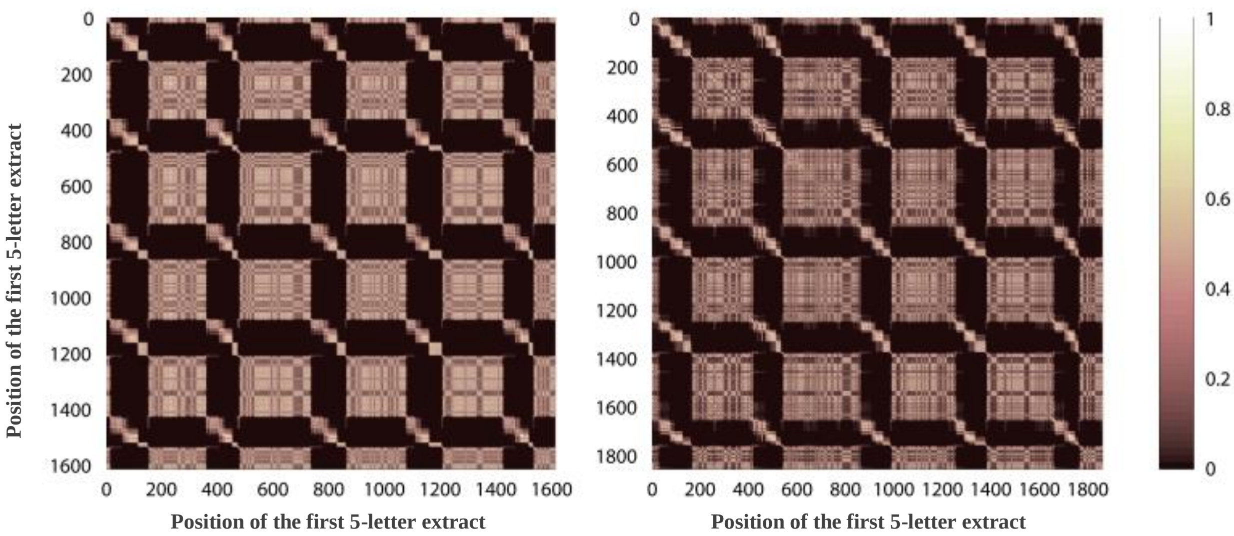


Figure 8 Recurrence plots of part of the recording #3 from the Abrolhos archipelago, 2000, with n= 5. Left: transcription into units by confirmed analysts, Right: transcription into units by an inexperienced analyst

The automatic extraction of the song was then performed on these two strings of units and it gave similar results: four songs are extracted in each case. The ratio r_u of the length of the song extracted from the series of units produced by the confirmed analysts and the length of the song extracted from the series of units produced by the inexperienced analyst (measured in unit) is very stable for each song extracted ($r_u = 0.86 \pm 0.006$. It was also checked that the determination of the start and end of an automatically extracted song is consistent between the human transcriptions (with a ratio between songs' duration (measured in seconds) of $r_t = 1.01 \pm 0.04$ between the two human analysts). Thus, our method of song extraction is remarkably robust to differences in unit labeling due to the subjectivity or lack of training of the analyst. In addition, I checked the robustness of our method to accidental errors in units transcription, not considering whether this was done automatically or manually. The extraction routine was applied to the strings of units of recording #1 and #2, gradually and randomly changing a percentage of these units (replacing it randomly with a unit from the same recording). For each percentage of error, the test was repeated 20 times and the number of extracted songs was noted. The result is visible in Figure 9 where, for each percentage of errors in unit identification, the average number of extracted songs is plotted, along with the error bar corresponding to the variation across the 20 draws. We see that for less than 5% of randomly changed units, the results are very coherent with the original recording. Even as the rate of error grows, the number of extracted songs stays close to the nominal one (1 song of difference for up to 20% of errors).

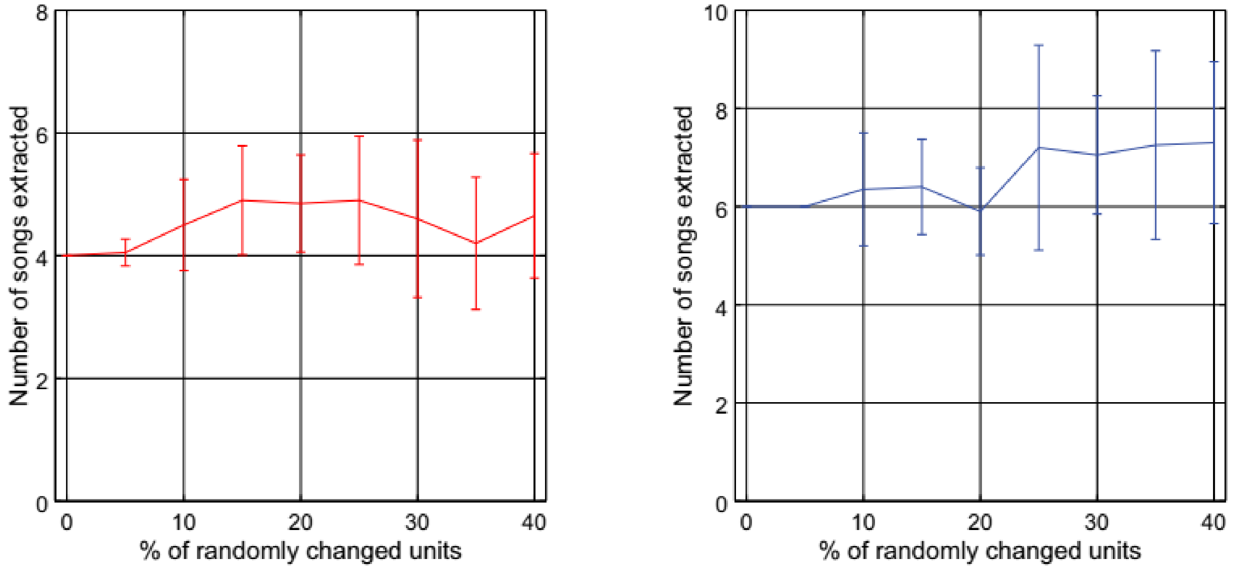


Figure 9 Number of songs correctly found in the function of the percentage of randomly changed units. The test is done on 20 random tries and the error bar quantifies the distribution of the results over the 20 tries. Left: Recording 1 from the Abrolhos archipelago, 2000, right: recording #2 from the Abrolhos archipelago, 2000.

Lastly, the extraction routine was applied to strings of units of recording #1 where we gradually and randomly removed a percentage of these units. In this case, until 40% of units were removed, the routine extracts the correct number of songs for more than 90% of the tries. Therefore, this extraction method is robust to missing units during the transcription, for example when the signal to noise ratio of the vocalizations of the humpback whale is low. However, this was done for randomly chosen units and does not account for systematic errors (such as would happen if one type of unit only would be lost in the noise, which is not an improbable case).

6 DISCUSSION

6.1 USE OF RECURRENCE PLOTS

Recurrence plots are a very visual way of representing the sequence of units, allowing immediate global identification of the structures of the highly organized vocalization emitted by male humpback whales, presented in the preceding sections. It helps with getting a qualitative view of their variability (in size and song element order) as well as the type of transition (abrupt versus gradual change) between these structures. It could be used as a valuable tool for every highly structured type of sound emission by animals and seems particularly well fitted to study the ever-changing structures of humpback whale songs. This tool allows us to methodologically access the humpback whale song in its natural, unaltered form, and in this way get the most authentic observations. Finally, we can overcome the established manner of overlooking the small-scale variabilities of the songs (PAYNE, 2000), which can actually give us valuable information about the mechanisms of song evolution and construction in a long run (how the song varies with every repetition, and between different singers), and use this knowledge to reconsider classical methodologies in the field (e.g. “Kohonen median” (KOHONEN, 1985)).

Recurrence plots can also be used for automatic unsupervised selection of different structure levels in the recording translated as a series of units. Primarily, the question of the definition of the song, its beginning, and ending was troubling researchers since they first discovered the overall structure of it (PAYNE; MCVAY, 1971). Several publications since have tried to shed a light on this problem (FRUMHOFF, 1983; WIN; WIN, 1978; PAYNE; PAYNE, 1985), some offering a framework with definitions and criteria on how to determine the song and its internal elements, discussing further all the artifacts that each of the possibilities brings (FRUMHOFF, 1983; CHOLEWIAK et al., 2013). Finally, depending on the delineation protocol and song definition one would choose, the overall results would vary between researchers (CHOLEWIAK et al., 2013). This would inevitably bring disagreement in comparison and the inability for the accumulation of information that would be confidential. Another important issue that is closely connected to song delineations is the smaller-scale element transcriptions. Whether we are using themes, phrases, or units, there are several approaches to undertake. Consequently, the final result will most definitely deviate. In this paper, the first step toward leaving the least room for deviation was taken by looking at the units, as the smallest and least biased song elements. Further, the method was also tested for error resilience in the unit transcription. The results of the previous section indicate that this method of extraction is quite robust to errors during manual or automatic transcription of the sound units into a string of letters. The quantification of errors detected for unit classification systems in studies such as Dunlop et al. (2007), Ou et al. (2013), or Rekdahl et al. (2018) is usually from 10% to 20%, which compares well with the percentage of errors that still enables us to automatically extract songs. The use of a recurrence plot to extract songs is still a work in progress but these results are encouraging. Even in the situation of different criteria for unit labeling in different recordings, the song session structure will probably still be visible. This is an additional benefit of the proposed recurrence plot methodology, as it undermines differences in unit labeling among studies.

The plot gives a representation of each recording, rather independent of the string it was calculated on. In this way, the recurrence plots provide standardized limits of patterns in the recordings that can be further explored and compared. Ultimately, this method offers standardization of the song delineation criteria, which would further help to solidify the comparison between different datasets and research groups.

This automated song extraction is the first step for many more studies regarding song analysis, and comparison between songs. The automated extraction of other structures (such as themes) could be performed based on this tool but is not as straightforward as songs extraction. Some of the difficulties of theme extractions are a blurred or imprecise transition between themes, unclear definition of a theme, and very short or evanescent themes. Thus any method of automated theme extraction would probably be rather *ad hoc*, which is the reason why we did not perform it on our limited set of data. Finally, a matrix comparing two series of units extracted from two different recordings can be computed which shows the similarity between two recordings in terms of song rendition. This type of analysis could enable people to compare quickly two-song bouts distant in time or space.

6.2 Large scale automatic treatment of humpback whales' recordings

This study is a step towards the automatic treatment of large-scale recordings. Automatic tools to transcribe sounds into letters such as the one developed in Dunlop et al. (2007), Glotin et al. (2008), Rickwood and Taylor (2008), Pace et al. (2012), Ou et al. (2013), Razik et al. (2015), Bartcus et al. (2015) or Rekdahl et al. (2018) could be used beforehand. Then our method could be applied to the extract, to classify and compare songs and their features, along with other approaches to visualize the structures of humpback whale songs. Finally, analyzing humpback whale song structures with recurrence plots would be difficult in the case of a recording where many singers are vocalizing together. In this case, the separation of these singers is a challenge that has to be addressed.

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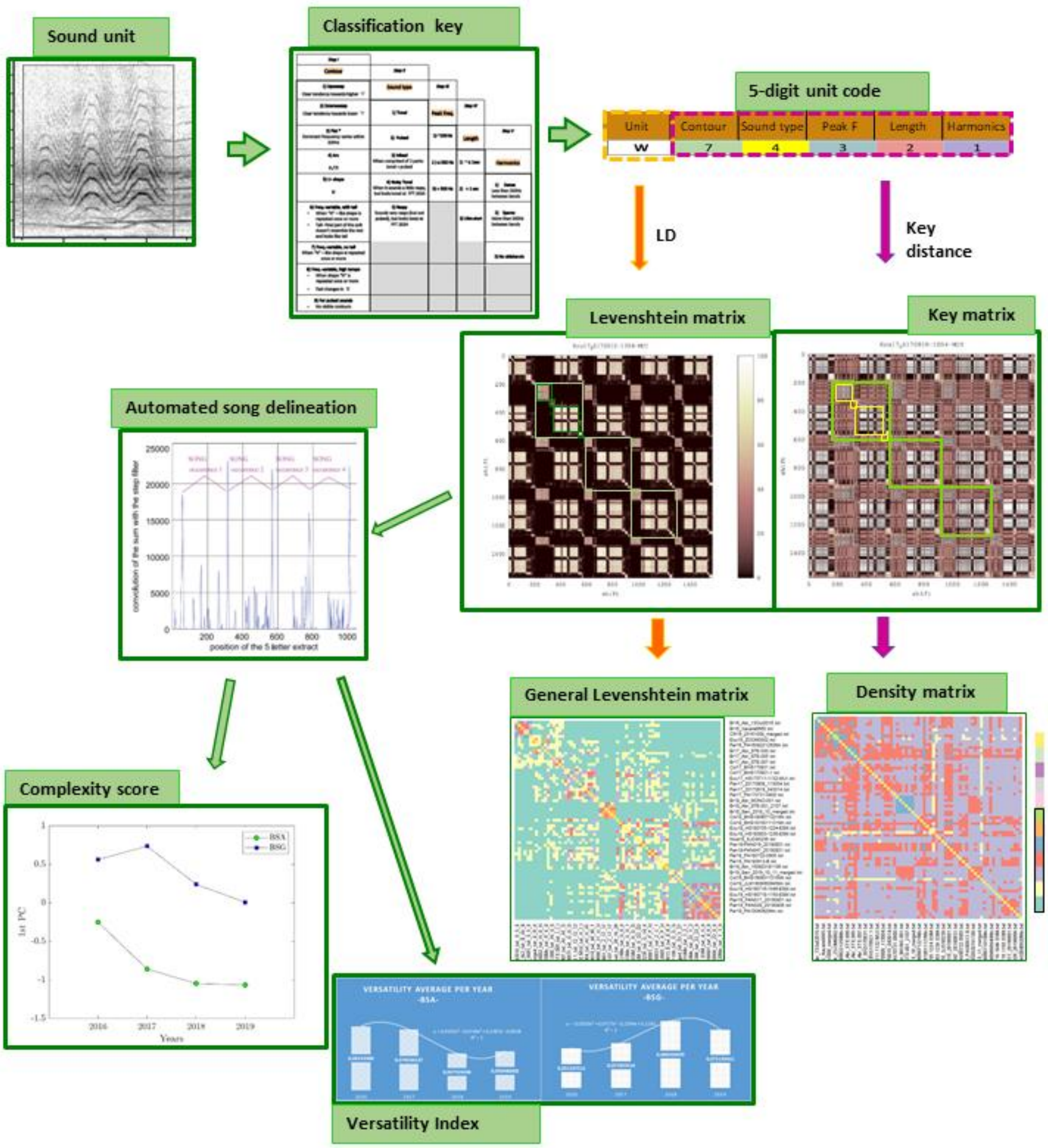
CHAPTER IV

Comparison of methodologies for the assessment of humpback whale song dynamics

Table of figures

1 ABSTRACT

In this chapter, we compared different methods for assessing humpback whale song dynamics, in particular, the Key and the Levenshtein methods. After classifying units using the Key, the strings of units were used to build: 1) the Key matrix, based on units' 5-digit codes and 2) the Levenshtein matrix, based only on the unit name. Pros and cons of these distance calculation methods (Key code or LD) were contrasted. Additionally, Key matrices were used for building a cross-correlation matrix. The Density plot was built to demonstrate the correlations across the dataset. The same was done for the Levenshtein distance matrix approach. Afterwards, the Levenshtein matrix was used to automatically extract songs from recordings, and a song complexity score was built on results of a PCA. The complexity scores were plotted against the years, explaining the song dynamics in each of the stocks.



2 INTRODUCTION

From the first publication describing humpback whale song structure (PAYNE and MCVAY, 1971), intense researchers' input in trials of determining, detecting, and describing this species' vocalizations resulted in the development of a vast range of different methodologies (ALLEN, 2019; CAZAU; ADAM, 2016; CERCHIO; JACOBSEN; NORRIS, 2001; DARLING et al., 2019; DARLING; SOUSA-LIMA, 2005; ERIKSEN et al., 2005; GREEN et al., 2011; MAGNÚSDÓTTIR et al., 2015; MALIGE et al., 2020; MERCADO; HERMAN; PACK, 2005; MURRAY; ANTUNES; DUNLOP, 2017; OÑA; GARLAND; DENKINGER, 2017; WINN, H.E., and WINN, 1978). Consequently, different pieces of information were extracted using different methodologies, and that is how we learned much about the humpback whale's song structure, but also organization and its dynamics, in the last 50 years. We learned that songs are stock-specific (PAYNE; GUINEE, 1983; WINN, H.E. and WINN, 1978), thus they can help us in determining the interaction between different stocks. Moreover, we found proof that the humpback whale song represents unique vocal cultures, pushing further the idea of animal culture in general (BRAKES et al., 2019; NOAD et al., 2000; WHITEHEAD, 2009). Nevertheless, we are still learning how and when the song changes (ALLEN et al., 2018; HAWKEY, JAMES SEYMOUR, ELWEN et al., 2020; KOWARSKI et al., 2019).

Multiple methodologies are being used in this field of research, which in turn hinders diverse results, conclusions, and finally, even contradicting information (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). This confusion mostly originates from metric-dependent results. A good example of this caveat is the definition of a song revolution in humpback whales. This phenomenon has been described using specific metrics and methods, *i.e.*, each study that has determined a song revolution describes it based on a specific metric, measured in a certain way, showing changes above a certain value (ALLEN, 2019, ALLEN et al 2018; GARLAND et al., 2011, 2013a, 2017a; NOAD et al., 2000). This approach is surely problematic if we take into consideration the diversity of methods in use, specifically the options for looking into different levels of male vocalizations hierarchy- units, phrases, themes, songs, etc. The absence of a consensus of the best hierarchical level to use adds to the complexity of this issue. In addition, the optimal time span in which the level of change is considered also seems to vary (compare for example Allen et al. (2018) to Noad et al. (2000)). Inasmuch, there is no clear definition of the revolution phenomenon. All of this makes it very hard to initially specify the occurrence of song revolutions, also surly to compare the same phenomenon with other studies described in the literature.

In the previous chapters of this thesis, I have described novel methodologies that had a goal to objectively describe the structure of the humpback whale song, as well as to identify similarities and differences among songs from different locations and seasons. Generally speaking, these methods are divided into two groups- one defines structures in the song (Key matrix), and the other determines song changes (Cross-correlation matrix and Unit dictionary comparisons).

In this chapter, I am exploring comparisons of the aforementioned methodologies to determine how the songs of stocks of Latin America evolve. In doing so, I compare these new methods to those already established (ALLEN et al., 2018; GARLAND et al., 2017a), to contrast changes among songs from different locations and seasons. The Levenshtein distance calculation (matrix)(LEVENSHTEIN, 1962) will be used similarly to the Key matrix, built on the different levels of song hierarchy and data organization, to explore the potential of an alternative approach to the classical way of Levenshtein calculation application (e.g. HELWEG et al. 1998, GARLAND et al., 2013) method. Finally, a Versatility index (JARVI, 1983) and an adapted version of complexity scores (ALLEN et al., 2018) will also be calculated for my dataset, in order to explore the best ways to describe song dynamics. By comparing the results from all these analyses, I aimed to determine the advantages and disadvantages of these different methods. Aiming to achieve this, songs, themes (both identified from recurrence plots), and units were the focus of our cross-method comparison.

3 MATERIALS AND METHODS

The methodologies compared in this chapter are divided into two approaches: song pattern extraction from recurrence plots and exploration of metrics of song dynamics.

3.1 DATA COLLECTION

A collaborative network across Latin America was established with the purpose of gathering recordings of humpback whale songs primarily to be used in this study. To our knowledge, this is the biggest collaboration network of its kind in this part of the world.

The total dataset is composed of recordings from 4 consecutive breeding seasons, from 2016 to 2019, of two Latin American breeding stocks of humpback whales (BSA and BSG) (IWC, 1998). The equipment used to obtain these recordings was diverse (detailed description of each can be found in Appendix), and the most common were manual recorders connected to the hydrophones, submerged from the vessel, or in several cases, autonomous recorders.

Locations of data collections can be seen in Figure 1. Overall, there are 21 different locations: 19 sites are located throughout the BSG area, more specifically on the South Pacific coast: Costa Rica, Panama, Colombia, Ecuador, and Peru (FELIX and HASSE, 2001; PACHECO et al., 2009; GUZMAN el al., 2015; CHERESKIN et al., 2019; WEERDT; RAMOS; CHEESEMAN, 2020) and 2 sites are in the BSA area, on the Brazilian Atlantic coast: Abrolhos Bank and Serra Grande, State of Bahia, Brazil (IWC, 1998).

Recordings from every location in a certain season are referred to as a "seasonal dataset", while the overall recordings assembly we used in this study is named "general dataset".

All recordings used in the study were collected during the Austral winter and spring (from June to December). All further technical information (file format, sampling rate, sampling size, etc.) of the recordings can be found in the Appendix.

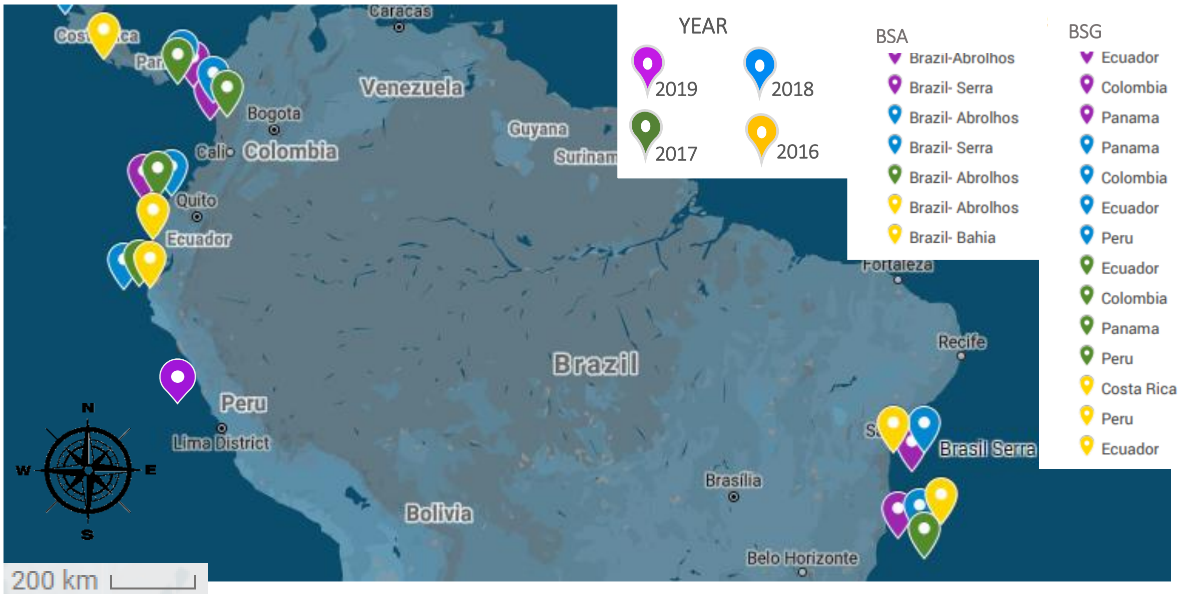


Figure 1 Dataset location map

Locations of 22 datasets used for this study, across 4 seasons, 2016- 2019 (year is coded in the color of the location point). The data were obtained through a collaboration network across Latin America, which was established for the purpose of this study. The dataset includes recordings of 2 breeding stocks, A and G (IWC, 1998), and 2018 recordings off Central American (Nicaragua breeding stock) (BETTRIDGE et al., 2015). Map, ®Google maps. Accessed 26/09/2020

3.2 Data assessment

As expected, due to the very diverse source of recordings used in this research, data quality varied. First, I had to make sure the data used were suitable for the analysis. The initial selection was based on the duration of the recordings since I was looking for the ones that are containing at least one full song cycle *(i.e.*, includes a complete rendition of all themes available in that season)(CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013). I have established that recordings with at least 20 minutes long fulfill this requirement, thus, I only used shorter recordings if there was no alternative for a specific location and year (check Chapter I, section 5.3).

Second, I inspected the quality of the selected recordings, aurally and visually, using Raven Pro 1.5 (CENTER FOR CONSERVATION BIOACOUSTICS, 2014). I used the following spectrogram parameters- window type: Hann; window size: 2048 samples; time grid overlap: 50%; frequency grid spacing: 43.1 Hz. We narrowed down the dataset to the recordings containing the most clearly distinctive units.

Finally, I removed recordings with less than a one-day interval whenever possible, to minimize the chance of resampling the same singer, which could influence the analysis with its idiosyncrasies. In the end, each seasonal dataset had a sample size of approximately 90 minutes, which included several short recordings or at least 2 long ones. Most humpback whale songs last on average 10 to 15 minutes (CERCHIO; JACOBSEN; NORRIS, 2001). Therefore, each sample would contain around 6 song cycles, which should be enough to give a general overview of that season's song attributes and include most unit types. Additionally, 90 minutes was the most we could use from several lower-quality datasets, thus we used it as an upper limit to homogenize effort and allow comparison among recording methods, as manual recorders render less data than autonomous recorders.

3.3 RECURRENCE PLOTS METHODS

Considering the repetitive structure of the song of humpback whales - different unit types as building blocks for phrases, organized in different themes, which repetitions further assemble a song - the recurrence plots approach can adequately demonstrate the nested nature of it. Recurrence plots are matrix figures, used to visualize the periodicities of a system, the time series, where the elements of the matrix correspond to the times of the repetitiveness (of that system) (MARWAN et al., 2007). We have used two different approaches to build the recurrence plots from humpback whale song recordings. In both cases, the matrix was built based on a string of predefined elements (song units). The main differences between the two approaches are the unit labeling method and the distance calculation between them. These differences also modify how the matrices will be constructed. Depending on the approach, the matrices are expected to show different levels of detail of the structure of the vocalization recordings.

It is important to mention that, except for the unit transcription, songs were not treated or modified in any way. Thus, the original appearance of the song, its structure, and the order of its elements was not manipulated, nor any weighting system was applied. Compared to some prior studies, which used the hypothetical order of elements to represent a specific seasons' song, for example, "Kohonen median" (KOHONEN, 1985)**,** used to estimate the best song representative (ALLEN et al., 2018; ERIKSEN et al., 2005; GARLAND et al., 2013a), our study includes data which is represented in the same way it is recorded, as we believe it is the best way to convey the real nature of humpback whale song.

3.3.1 Key matrix

The strings of units served as a base for building a Key Matrix for every recording. These matrices were constructed for exploration of structures hidden in the song recordings, thus a custom-written code was applied to every recording string in the general dataset. The script was written using Octave (EATON, JW, BATEMAN, D. and HAUBERG, 2009). A code was set to construct a Key Matrix, which is by its nature a Recurrence plot or a distance matrix (MALIGE et al., 2020). The 5–digit codes describing a unit type were used to calculate the distance between every unit within the recording, and in this way, represent the similarity of different parts of the same recording. Thus, the base on which each Key matrix was constructed were the strings of units, translated into 5-digit codes. The string was compared to itself, comparing unit by unit, and counting how many, out of maximum 5 levels the two unit types in question have in common. This calculation will tell us the distance. Once the single unit was run down the entire string, the second unit from the string would undergo the same process, and so on. The final product of this calculation is the Key matrix, which visually represents the entire recording containing all the hierarchical structures known to exist in every song. Using this approach, we are able to track various song repetitions within a single recording. More than the start and endpoint of the songs, we are also able to detect the themes within the songs (MALIGE et al., 2020).

3.4 METHOD FOR COMPARING THE RECORDINGS

3.4.1 Levenshtein distance

Levenshtein distance calculation (LEVENSHTEIN, 1962), is an established method in the field of animal vocalization in general (ALLEN et al., 2018; ERIKSEN et al., 2005; GARLAND et al., 2011, 2013a), as well as in other fields of biology (BERGER; WATERMAN; YU, 2020), although it was initially proposed by a soviet linguist Nikolai Levenshtein. This method's basic function is to quantify the similarity between any two strings of elements. It does so by calculating the minimum number of steps in order to turn one string of elements into the other. The steps are represented by tree operations: insertions, deletions, and substitutions of the elements. Rather than following the structure, Levenshtein focuses on the sequence of the elements in the string.

In this particular case, next to regular LD calculation applied on a string of units of humpback whale songs (details of the LD calculations are explained in Chapter III, section 3.1; for the unit labeling method, check Chapter I, section 4.1), we also used a slightly modified version of it. This calculation version is called Levenshtein Similarity Index (LSI) (HELWEG et al., 1998; ERIKSEN et al., 2005; GARLAND et al., 2012, 2013), and it normalizes the LD value by the longest string of the comparison, using the following equation:

$$\mathrm{LSI}\ (\mathrm{a,b}) = \frac{1 - \mathrm{LD}\ (\mathrm{a,b})}{\max(\ \mathrm{len}(\mathrm{a}), \mathrm{len}(\mathrm{b}))}$$

For both approaches, one whole recording of a humpback whale song represents the string. The data string is assembled of song units named by a random letter, number, or combination of two.

Here, I used LD in two different perspectives: (1) to construct an auto-similar recurrence plot, built on the values of a string of units compared to itself, and calculating LD between the elements of that one recording (LD matrix, Chapter III); (2) to set up the LD calculation in a standard way, thus calculating the similarity between two (or more) different strings (recordings), in the similar fashion of many of the Ellen Garland's papers, thus using LSI (e.g. GARLAND et al., 2011, 2013b, 2017b)**.**

LD matrices (for a single recording) were obtained through Octave custom-written code (as explained in Chapter III). To build the recurrence plot, it is necessary to choose a scale of comparison, by using extracts of the recording that will be compared (see Chapter III, section 3.1). The extract represents a short string of several units in a row (a piece of the entire recordings string), based on which the LD will be calculated. In Chapter III, I explored the possibility of the size of the extract (how many units in a row will be taken as a sample) influencing the result, and it was concluded that it does not have an impact on the structure of the LD matrix, but merely on the sharpness of the recurrence plot (the LD matrix) (Chapter III, Figure 3). Leaning on the output of the "computation time vs. matrix sharpness" (Chapter III, Figure 3), the maximum distance between the elements was decided to be five (5).

As for LSI matrices, a custom-written code in R using *Leven* package (GARLAND et al., 2017b) was applied to calculate the values and build a heat map, visualizing similarities between recordings grouped per seasonal datasets (location per year), opposed to the LD matrices whose task was to explore the internal structure of the song. The LSI calculation was applied to all recordings contained in the general dataset. As recordings were transcribed into unit types and were represented as a string of units in the order they appear in the song, there was no need to include themes in the calculation, thus the theme section of the string was skipped (when the Leven package was applied). The LSI was applied with no cost matrix, thus there was no weighting system in use. Values gained in this way were further used to build a heat map, with no clustering. This heat map represents data organized as they appear in the raw data table- arranged by year and geographical distance. The start point was the assumption that every recording represents a separate singer, due to our sampling strategy (see Chapter I).

3.4.2 Density matrix

To build the Key matrix for the whole general dataset, *i.e.*, the Density matrix, I used the individual cross-correlation matrices for every pair of recordings previously constructed (see Chapter II, section 3.5). Every point of the Density matrix represents the density of the cross-correlation matrix between 2 recordings. This density indicates the average value, the arithmetic mean of the matrix - the sum of all its values divided by the number of values. The values obtained describe the general tendency of each cross-correlation matrix (similarity of the two recordings).

$$\text{Cross-correlation density} = \frac{\sum_{n=1}^{k} x_n}{k}$$

k- number of points in each cross-correlation matrix; n = the value of each point;

X- cross-correlation matrix points, Xn = value of the n point of the matrix

These calculations were computed in the Octave open source programming language (custom-written script). The values obtained were further used to build the heat map in the same manner as done for the LSI matrix, in addition to multiplying the whole dataset results by 100, as the cross-correlation matrix values are expressed in percentages. The data are represented in the same way as for the LSI matrix.

3.4.3 Key vs Levenshtein recurrence plots

There are two main differences between the Key and the Levenshtein recurrence plots (matrix) approaches: (1) the unit labeling system, where for naming the unit types for the Key matrix method, we used a unit classification key, which gives a 5-digit code name for every unit type and in the Levenshtein based approach, where the unit types were randomly given a name composed of an alpha-numeric code (*i.e.*, letter, number, or the combination of two); and (2) The difference in distance calculation is based on the unit names. In particular, while for the Key matrix, the distance was the simple number of overlapping values within the 5-digit codes of units in question (how many, out of 5 digits in their codes, are the same), for building the Levenshtein matrices, we used the Levenshtein distance equation (LD). For the LD matrix, the maximum distance between the elements was decided to be 5 (Chapter III, Figure 3). To recapitulate, the same variable, the maximum distance, in the Key matrix is also 5 (due to the unit code assembled of 5 digits, thus 5 possibilities for the difference).

3.5 SONG DYNAMICS EXPLORATION

3.5.1 Seasonal song complexity and versatility

While focusing on determining the dynamics of the song of Latin America in 4 consecutive seasons, I encountered inconsistency in defining the main mechanisms of this behavioral evolution system - the song revolution and evolution. The main problem was identified to be the metric-related definition of these phenomena. Therefore, I tried to explore the methodology used by other researchers, and apply it in a simpler and replicable way, thus using song elements in their simplest form, and the ones most unbiased to determine: units, themes, and songs extracted from recurrence plots (MALIGE et al. 2020). The phrase level of the song hierarchy was omitted, as, well put by Cholewiak et al**.** (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013) “delineation of phrases may be difficult and ambiguous”, with which, from a personal experience, I agree. I tried to avoid all possible pitfalls by applying a clear and sensible methodological approach. Using these elements (units, themes, and songs), I calculated the Versatility index and applied a Principal component analysis to generate the Complexity scores. The idea was to explore the variables which hold the potential to describe the aspects of the song in a robust and repeatable way. This approach theoretically could help us to determine the mechanisms of song dynamics (revolution and evolution) in my dataset, identifying if and when these events took place.

3.5.2 Versatility Index

Jarvї (JARVI, 1983) defines Versatility as a repertoire size. It is a simple mathematical expression that has been adjusted to humpback whale songs. Such adjustment is done by calculating the number of unit types per song, divided by the total number of units sung in that same song (thus a song that repeats few unit types will have a low versatility). Additionally, I calculated the average versatility per breeding stock per year. The versatility index, to the best of my knowledge, has not been assessed in humpback whale songs,

but I advocate for its future use because it is a simple metric and yet holds the potential to clearly express the level of structure of the current song (its variability). This information can perhaps be taken as an index of the song evolution or revolution, as suggested by Allen and colleagues (ALLEN et al., 2018)**-** these authors concluded that "cultural revolutions reduce complexity in the songs of humpback whales", *i.e.,* revolutions imply simplification of the song structure. Here we had a goal to test if this simple metric, the Versatility index, can result in similar conclusions.

3.5.3 Principal component analysis for complexity scores

Principal component analysis (PCA) previously showed as an adequate multivariate statistical method to estimate which of the given parameters contribute the most to the variance between songs' quality, in humpback whales, as well as the songs of birds (ALLEN, 2019; BOOGERT; GIRALDEAU; LEFEBVRE, 2008; MAEDA; KOIDO; TAKEMURA, 2000; TEMPLETON; LALAND; BOOGERT, 2014)**,** and other animal vocalizations (CLARK, 1982; MARTINDALE, 1980; SPARLING, 1978). It does so by reducing dimensions -a large number of variables to only a few- focusing on the ones that explain the most variation/highest relative importance (SPARLING 1978).

The choice for variables that will be analyzed by the statistical approach of the PCA, was based on measures of song complexity (BOOGERT; GIRALDEAU; LEFEBVRE, 2008), as suggested by Allen et al. (ALLEN et al., 2018). That methodology was adjusted to my dataset, based on the variables I used to define the unit types following the Classification key (Chapter I, section 4.1). Thus, some measures of song complexity were not used, such as duration, in order to avoid any variable that could influence the results in an undesirable way, by being dependent on the external factors, *i.e.*, recording quality, which can affect the duration estimation. Some other modified measures of complexity, phrase level-based ones, were also excluded, due to the ambiguity in their delineation (CHOLEWIAK et al. 2013). The final adjusted methodology in our work consisted of four following variables, organized in two hierarchical levels: (a) song-level: number of unit types and number of themes per song and; (b) theme-level: average number of units and average number of unit types per theme.

I assumed that every recording represents an individual singer, due to our sampling strategy (see Chapter I, section 3.2). It is important to mention that, for this work, the recordings were automatically cut into songs (MALIGE et al., 2020). For each automatically cut song within each recording, I manually counted the number of themes that a specific song contains, based on its recurrence plot. All further analyses involving themes were carried out based on these counts. Unit-based variables were calculated considering the output of the R or Octave scripts (dividing for example the number of units in the song by the manually counted number of themes contained in that song (based on its recurrence plot), to get the average number of units contained per theme in that song).

From here, I randomly picked one song per recording, to ensure data independence. All 4 variables of 53 chosen songs were used to run a PCA. I initially normalized the data, by using the logarithm to the base of 2 of the raw values, because of the great diversity in values and data range, due to the different-scale variables used. Based on the PC1 and PC2, a Linear discriminant analysis (LDA) was applied to estimate the boundary that represents a linear separation of the analysed data in 2-dimensional space (PC1 vs. PC2). Finally, data centroids per seasonal dataset were estimated in the same 2-D space (PC1 vs. PC2).

The values of the PC1 of these centroids were plotted against the years of data sampling (*sensu* ALLEN et al., 2018) in order to estimate if these alternative song metrics (Complexity scores) are able to show a clear pattern of change in song complexity, corresponding to the events of song evolutions/revolutions.

As earlier discussed, determining events of song revolutions/evolutions seems to be quite a challenge. Different estimations of this phenomenon bring different interpretations of the data. Because of this situation, I tried to establish a solid and reproducible way to tell the difference between these phenomena. One option is offered in Allen et al. (2018), estimating that the song is revolutionized if its similarity to the song of the previous season, measured by Levenshtein distance, is equal to 0%. We argued why this could not be the case at the unit level, thus while using Jaccard Similarity Index (see Chapter I), and this is why our cut-off value is estimated to be **0.16**. Thus, if the song differs from the one of the previous season > 0.16, I considered it as an end-product of a song revolution (Chapter I, section 4.2.1).

When talking about Levenshtein calculation, I also tried to simplify the methodology offered by Allen et al. (2018). In this paper, the authors applied various statistical approaches, adjusted for every hierarchical level of the humpback song, in order to find a "set median", which sequences will further be used to estimate if the revolution or the evolution took place between a two-season period. The set median is an element with the highest LSI score, highest similarity to all the other elements of the same hierarchical level, within its dataset. Additionally, penalty costs that valued different types of changes in the song differently were applied. Finally, if the difference between the two compared songs was equal to 0%, it was considered that a revolution occurred. Otherwise, the period in question should be considered as an evolution.

In our cases, no penalty cost was applied. The Levenshtein Similarity Index was calculated for every pair of song unit strings (initially delineated out of the whole recording by the Octave script). In this way, all other hierarchical levels were left out. The recording "representative" of every seasonal dataset was estimated as the recording with the highest score compared to all the other recordings of its dataset (the one that is most similar to all the others). Every breeding stock had one representative per season, and these particular recordings were further used as a comparison point in order to estimate the events of the song revolution/evolution, from one year to the next. Representative recordings were strictly compared for the same stock for the adjacent seasons. It is important to explain here the process of determining the cut-off values, done the same way for the Jaccard Similarity Index - it was estimated how much the song (recordings) changes in a two-year time (*i.e.* 2016 vs. 2018), and this was taken as a cut-off value (all recordings from all locations of the same breeding stock, two years apart). The logic behind taking this value is that if the song changes from one season to the next as much as it usually does in 2-year time, that change can be considered a radical change, thus a revolution (the cut-off value, calculated as an average of the 325 values, is **0.04,** for the Levenshtein Similarity Index.).

In order to tell if the revolution took place or the season's song was a product of simple evolution, each seasonal dataset had a representative recording (chosen according to the highest similarity criteria as earlier explained). From every season and breeding stock, these particular recordings' LSI scores were compared, in a meaningful way (the same breeding stock's representative to the one of its previous season). If the value comparing the two was <0.04, the song was considered to be the product of a revolution.

4 RESULTS

4.1 RECORDING-BASED METHODS: LEVENSHTEIN AND THE KEY MATRIX

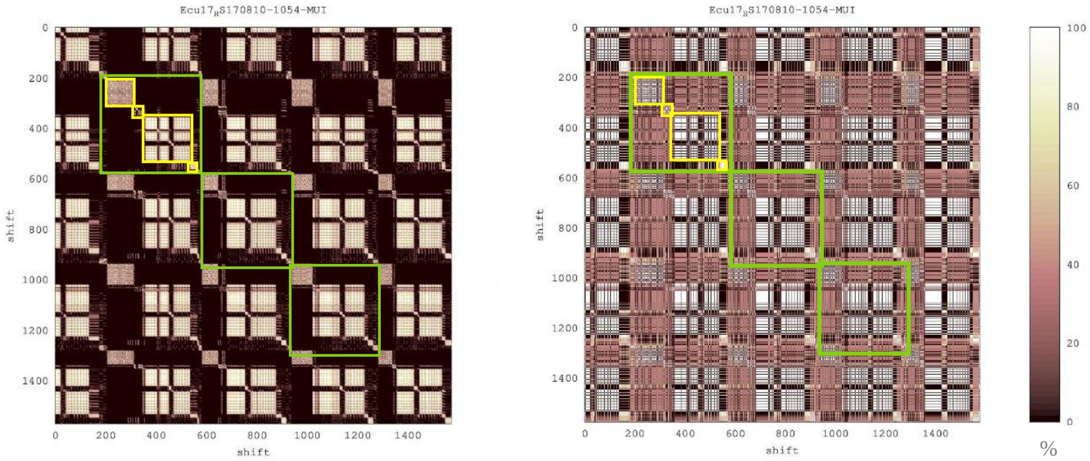
The formula used to calculate the distances as well as the technique of calculating the distance influence the results. Namely, for the Key-code approach, 5 digits represent a song unit, and as the calculation was performed comparing unit by unit, steps would include a different set of 5 digits every time. As for the LD, the calculation was applied by a pair of 5 units at any one time (the main string and the extract), but the set will be 100% changed every 6th step, as the 5-unit long sample would move by one position every time the LD would be applied. We can see these very different values for the two different distance calculations (Key distance and LD), although they are both presented in the same unit (% of the overlap), and the same scale (Figure 1).

It is important to repeat here that in both matrix types, we can distinguish songs and themes. However, looking at the recurrence plots of the two approaches (Key and LD matrix), we can see how the different values of their maximum distances influence the visual appearance of the song structure (Figure 1). Simply put, within the Key matrix, the recording is auto-compared at a unit level: hence the high sharpness of the image. With the Levenshtein matrix, on the other hand, the recording is auto-compared at an extract-level (we compare two extracts, 5 units long) - it is like having a 5-letter low-pass filtering: all the variations more "sharp" than 5-letters are blurred out. We saw in Chapter II how this detailed, unit-level representation of the Key matrix can be used as an advantage to discriminate the theme types, as their structure can be seen as a composition of different patterns. However, this property also can be a caveat when it comes to defining limits between themes (or songs), *i.e.*, because of very detailed background, the key matrix sometimes gives a false impression of 2 different themes merged into a single one (Figure 2). This happens most likely because

two themes are assembled of similar unit types, based on their 5-digit key codes, but organized in a different pattern (phrase level variation).

This problem is not present in the Levenshtein matrices, where we can clearly see the song structures and limits, against a much-contrasted background (Figure 2). Such clear element delimitation is an important advantage of this method, as borders are very well defined and clear and this is a common difficulty in processing song recordings from humpback whales. However, the problem that persists are the blurred areas between elements, but usually on a very small scale, only a few-units-long patches (See Figures 3 and 4). These blurred areas are assigned to the transitional phrases, a "… combination of units from two different phrase types (PAYN; PAYNE, 1985), usually an entire subphrase from the previous and subsequent themes" (CHOLEWIAK; SOUSA-LIMA; CERCHIO, 2013) (Figure 3) (Please find more details in the appendix). In several cases, we discovered that those areas were not transitional phrases under the definition proposed by Payne and Payne (PAYN; PAYNE, 1985)**.** Instead, these blurred areas sometimes differ from the transitional phrases by not being assembled of a subphrase from the previous and subsequent themes, but basically of any two or more subphrases found in the song. You can observe this by the unit content of these "blurred areas" (Figure 4).

a) Matrices: Levenshtein and the Key



b) Unit strings

Levenshtein code

1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
A	6	6	6	6	G	A	6	X	X	G	A	X	X	X	X	G	A	X	X	X	X	G	A	X

Key 5-digid code

1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**11**	**22**	**23**	**24**	**25**
5	1	1	1	1	4	5	1	3	3	4	5	3	3	3	3	4	5	3	3	3	3	4	5	3
2	1	1	1	1	2	2	1	1	1	2	2	1	1	1	1	2	2	1	1	1	1	2	2	1
2	3	3	3	3	2	2	3	3	3	2	2	3	3	3	3	2	2	3	3	3	3	2	2	3
3	2	2	2	2	1	3	2	3	3	1	3	3	3	3	3	1	3	3	3	3	3	1	3	3
9	1	1	1	1	7	9	1	4	4	7	9	4	4	4	4	7	9	4	4	4	4	7	9	4

c) Distance calculation

Key distance (%)

100	0	0	0	0	40	100	00	20	20	40	100	20	20	20	20	40	100	20	20	20	20	40	100	20

Levenshtein distance (%)

100	60	40	40	20	20	40	0	0	0	0	20	0	0	0	0	0	20	0	0	0	0	00	20	100

Figure 1 Levenshten vs. Key method

Recording *Br17_Abr_STE-000*. In the upper part of the figure a) on the left, the Levenshtein and on the right, the Key matrix of the same recording are shown. In both matrices, 3 consecutive songs are labeled in greed squares. Within the first song, 4 themes are labeled yellow; b) Fist 25 units of the recording are show labeled by their name (used for the Levenshtein matrix), and their 5- digit code (Key matrix), first row are the units' ordinal numbers. Equally colored columns represent the same units in both tables (e.g. blue is the first unit of the recording); c) Values of the first 25 pixels of the matrix, obtained by the different methods for calculating distances of the same unit strings

Name	Key code					No.
R	4	2	2	1	6	75
R	4	2	2	1	6	76
H	4	2	2	1	8	77
R	4	2	2	1	6	78
R	4	2	2	1	6	79
R	4	2	2	1	6	80
H	4	2	2	1	8	81
R	4	2	2	1	6	82
R	4	2	2	1	6	83
R	4	2	2	1	6	84
H	4	2	2	1	8	85
R	4	2	2	1	6	86
R	4	2	2	1	6	87
G	5	1	2	3	1	88
G	5	1	2	3	1	89
H	4	2	2	1	8	90
R	4	2	2	1	6	91
R	4	2	2	1	6	92
G	5	1	2	3	1	93
G	5	1	2	3	1	94
G	5	1	2	3	1	95
P	4	2	2	1	2	96
D2	3	2	2	3	1	97
D2	3	2	2	3	1	98
P	4	2	2	1	2	99
D	3	2	2	3	1	100
D	3	2	2	3	1	101

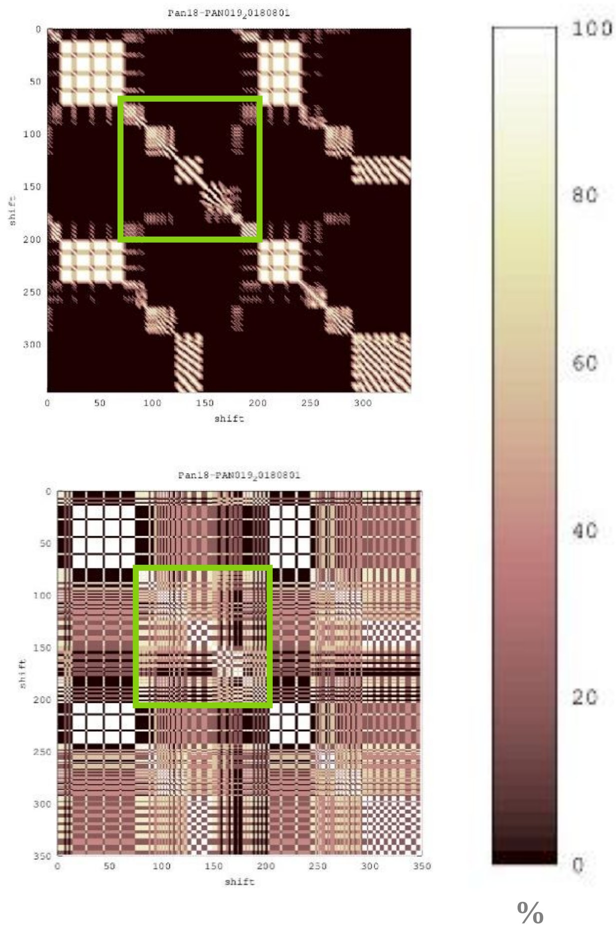


Figure 2 Differences in representations: Levenshtein vs. Key matrix

Recording *Pan18-PAN019_20180801*. On the right, two matrices (up Levenshtein; down- Key) of the same recording are showing the same song structures, labeled by the green square. In the table, the unit string of the same recording part as labeled in the matrix is shown, with the comparative overview of the units' name and their 5-digit key codes, also the ordinal numbers in the string, shown in the last column. In the matrices we can notice difference in the presentation of the song structure. We can see that the codes of the units in use are similar, which could be the reason for a blurred representation of the structure by the Key matrix.

No.	Unit
260	T
261	T
262	T
263	T
264	Q
265	O
266	O
267	Q
268	Q
269	T
270	T
271	T
272	T
273	Q
287	F
288	Q
289	Q
290	Q
291	Q
292	Q
293	J1
294	F
295	F
296	F
297	Q
298	Q
299	Q
300	F
301	Q
302	F
303	F
304	F
305	M
306	F
307	F
308	M
309	F
310	F
311	F
312	F
313	F
314	M
315	F
316	F
317	L
318	L
319	L
320	L
321	L
322	L
323	L
324	F
325	H
326	E
327	E
328	H
329	E
330	E
331	H
332	E
333	E

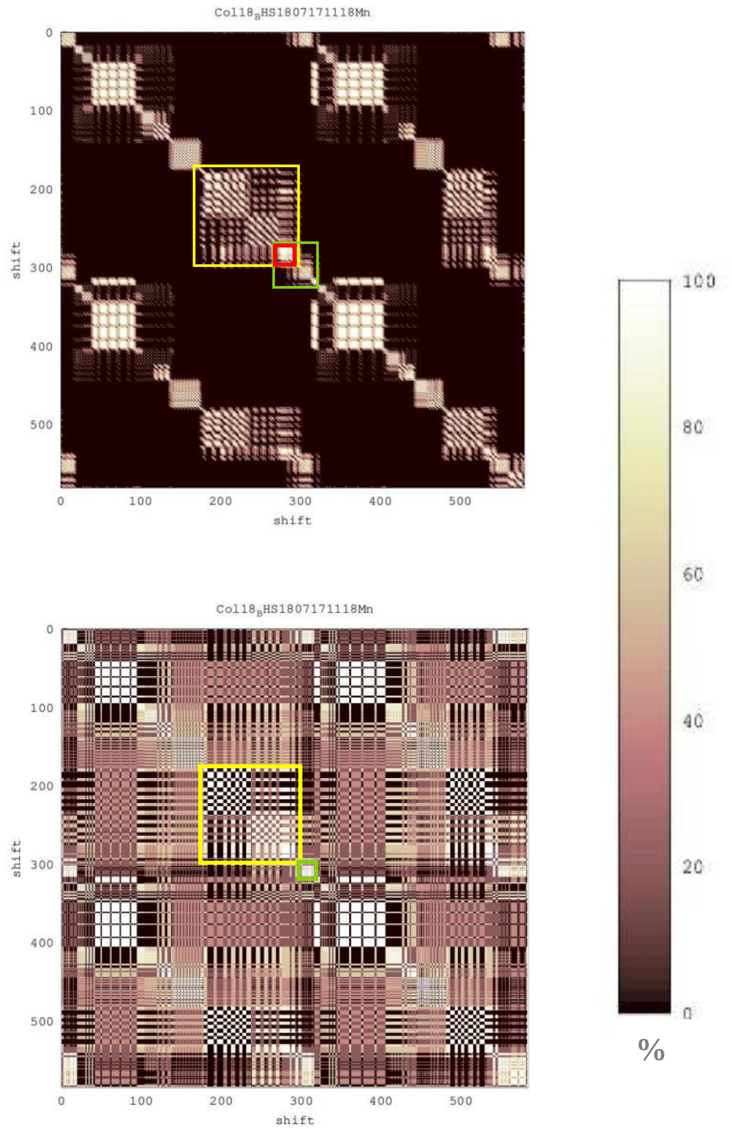


Figure 3 No-transitional phrase traverse

Recording *Col18_BHS1807171118Mn.* Two matrices of the same recording (up-Levenshtein; down- Key). Two same structures are labeled in both matrices, within the yellow and the green square. However, in the Levenshtein matrix, we can notice a small red square, which represents a traverse between the two separate themes. This structure is not visible in the Key matrix. In contrast to Figure 3, this traverse seems not to correspond to the general definition of a transitional phrase by Payne and Payne, 1985. Namely, on the left, we can see a piece of the unit string corresponding the area marked in the Levenshtein matrix. Here, observing the unit types in use in the traverse area, we can see they are different from the ones in the preceding and the following theme.

No.	Unit
149	G
150	6
151	G
152	4
153	G
154	6
155	G
156	4
157	G
158	6
159	G
160	4
161	G
162	6
163	6
164	6
165	G
166	G
167	6
168	6
169	6
170	G
171	G
172	6
173	6
174	G
175	G
176	6
177	6
178	6
179	22
180	22
181	6
182	6
183	6
184	22
185	22
186	6
187	6
188	6
189	22
190	22

191	9
192	22
193	9
194	22
195	22
196	9
197	22
198	22
199	9
200	22
201	22
201	22

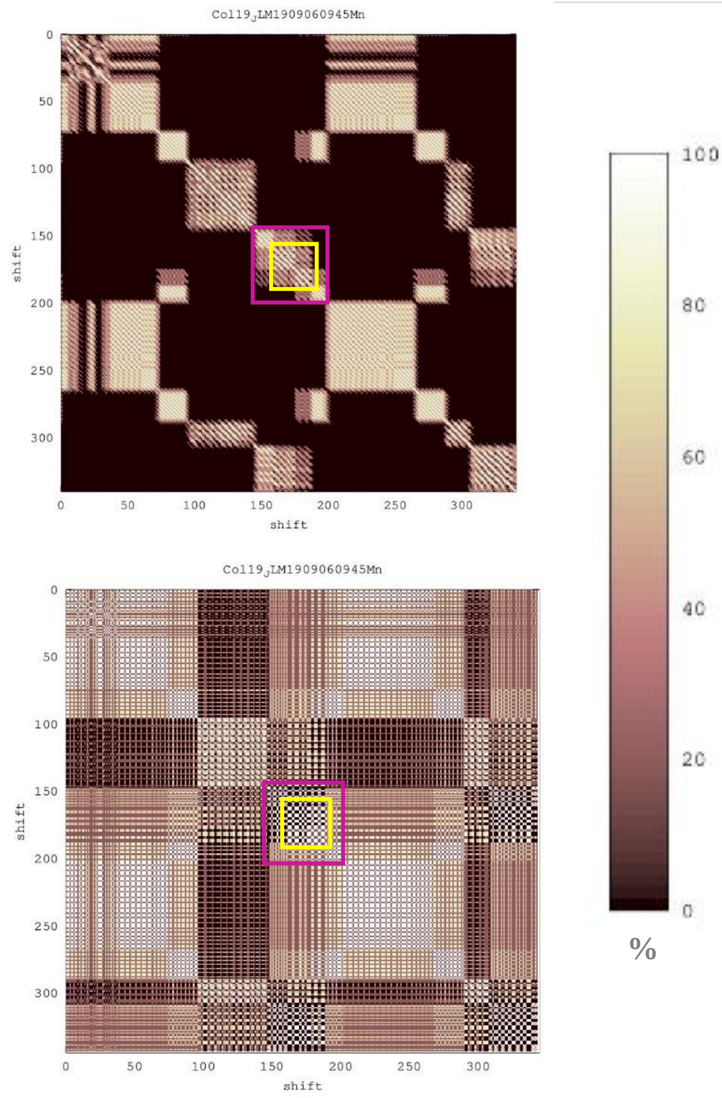


Figure 4 Transitional phrase traverse

Recording *Col19_JLM1909060945Mn.* Two matrices of the same recording (up-Levenshtein; down- Key). In both, pink square labels what is supposed to be a transition phrase structure (in yellow) and the area around it. We can notice that this traverse structure between two themes is not very well defined in the Key matrix. On the contrary, Levenshtein-based matrix nicely demonstrates the blurred area, where inside the yellow square, we can observe the overlap of two themes. If we take a look at the table on the right, where we can find a piece of the unit string, corresponding to the area marked by pink in the matrix (and in yellow, labeled extra), we can conclude based on the unit types appearing in the traverse structure, that it corresponds to the definition of the transitional phrase, by Payne and Payne, 1985.

4.2 GENERAL DATASET COMPARISON: DENSITY MATRIX VS. LEVENSHTEIN SIMILARITY INDEX MATRIX

To compare the entire dataset and get a more general conclusion of the song dynamics of the two South American breeding stocks of humpback whales throughout 4 breeding seasons, I had two analytical approaches: using a standard Levenshtein distance calculation (LEVENSHTEIN, 1962), and the Key approach, in more detail, the cross-correlation. In both cases, the calculations are applied to all 69 recordings contained in the general dataset, and the results are presented as a symmetrical heat matrix with no clustering, built with a custom-written script in R.

As expected, based on the comparison between Key and LD individual matrices, we can see much more contrast in the general Levenshtein calculation (LSI- Levenshtein Similarity Index) (Figure 5). The reason is the wider range of values (than in the Key matrices) describing the distance between recordings (distance expressed in more detail), where in LD methodology - we can notice that the minimum similarity (0) is prevalent, as this method takes into consideration the sequence of elements. The LD method performed better than expected, taking into consideration that the sequences of elements (units) were rather long, and more than that, they were not strictly confined (as it is the usual case when using this method, in other studies for example (ERIKSEN et al., 2005)**,** where “mean string” was used to calculate the LD, also, themes always seem to be sung in a particular order in most of the studies which used LD calculations so far (e.g. GARLAND et al., 2013)). Previously, the LD was predominantly applied on a specific string of elements, well defined in length and content. In my case, though, in the recordings, the unit sequences are somewhat arbitrary long, thus the sequence of elements is unpredictably interrupted, which did not seem to affect the final comparison. Additionally, as concluded in Chapter II, the sequence of themes is not a stable feature of the humpback whale song. This was also a variable that could have heavily influenced the distance estimation since the Levenshtein distance method is mostly relying on tracking the sequence itself. However, this also seemed not to diminish the accuracy of the method.

On the other hand, we have the Density matrix, which uses the average values of all the cross-correlation matrices separately, and in this way, a lot of information is lost, and we can notice the shrinking of a value range. Because of this, in the Density matrix, we can see very little detail, thus differences between recordings are shown poorly. An important advantage of the Density matrix method is the simplicity of its calculation, as it is calculated basically as a “by-product” of the cross-correlation method, which proved very useful (Chapter II, section 4.3). The Density matrix can be used for the overall estimation of correlations among different recordings (songs), and potentially, by using different color pallets and contrast in the figure, more information can be extracted from it. Moreover, it shows all the strongest correlations, although, again, not in much detail.

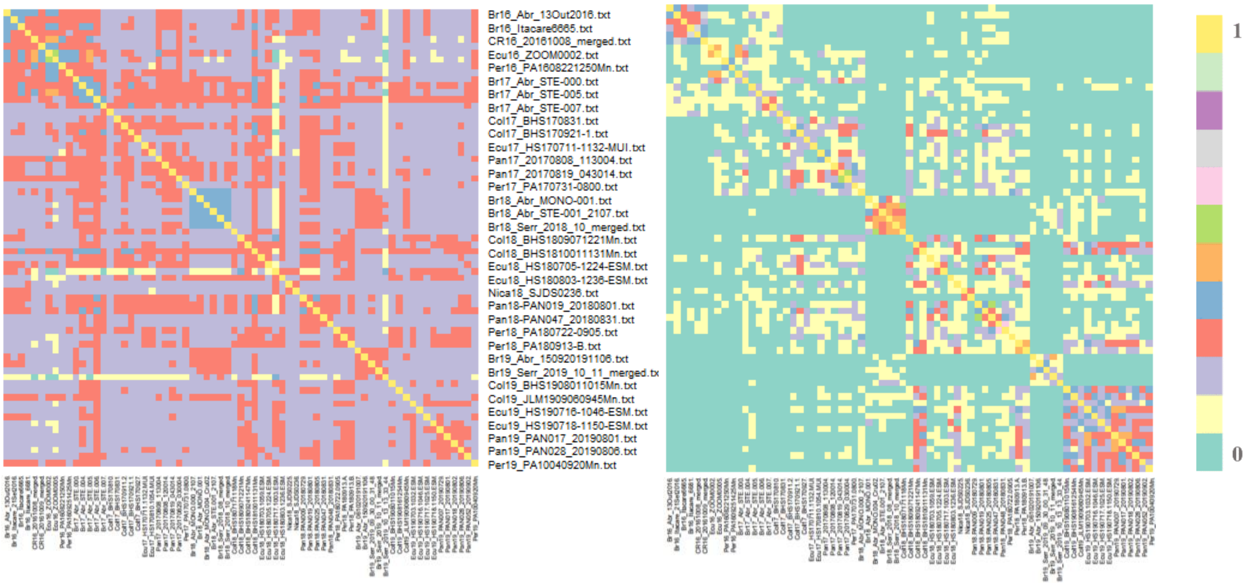


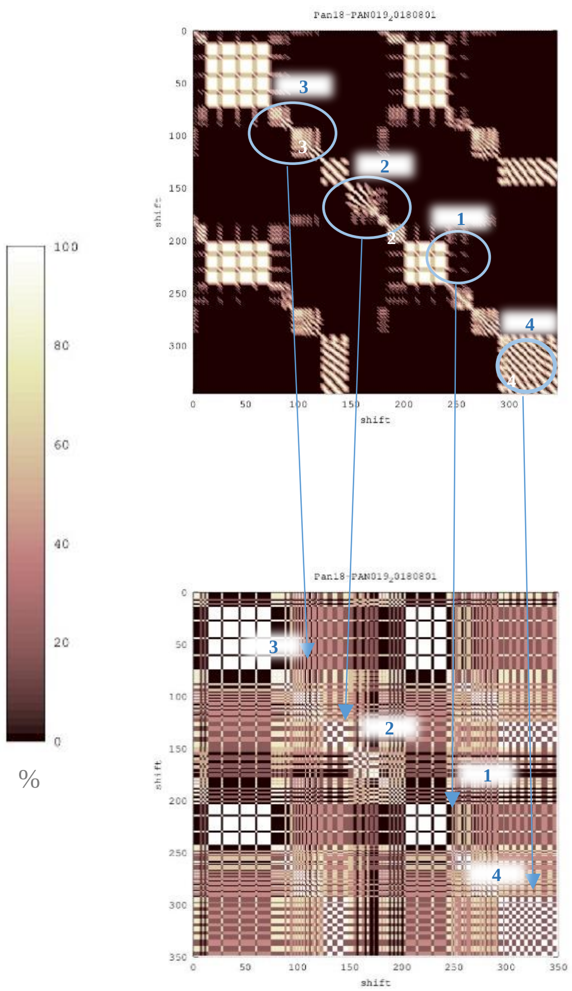
Figure 5 General data set: Density vs. LSI matrix

On the left, we can see the Density matrix heat map, which values correspond to the average of cross-correlation matrices of each pair of recordings from the dataset, multiplied by 100. On the right is the heat map of the Levenshtein similarity index (LSI) calculation, as well applied on all the recording in the dataset. Data are organized in the same order for both matrices: by year and geographical distance. In both, we can see the diagonal has the maximum similarity. However, much more detailed structure is visible in the LSI matrix. The contrast in visualization of the two matrices depend on the value span, which is highly reduced in the Density matrix, by averaging the values.

The overall comparison between the two methods' performances can be seen in Table 1, below, with the detailed focus on 9 specific categories (e.g. data preparation, limitations of input data, number of researchers needed, etc.). Figure 6 represents the Key and the Levenshtein matrices of the same recording, demonstrating a practical comparative performance of the two methods and their results.

Table 1 Levenshtein vs. Key methods comparison for obtaining recurrence plots

Category	**Levenshtein Matrix**	**Key Matrix**
Data preparation	Can be used without unit classification	Needs unit Key classification
Researchers involved in data preparation	If the unit classification is done without the key, at least two	One
Data input limits	Computation takes longer with longer samples/extract	Preparation in unit translation is time-consuming
Computation time	A tradeoff between extract size and clarity of the matrix	Fast
Method design complexity	Slightly more complicated	Slightly less complicated
Computation complexity	More complex	Less complex
Clarity of representation	High contrast between the structure and the background	Much detailed background, sometimes hard to confine the structure
Detail representation	Somewhat detailed	Very detailed (5-level)



Levenshtein matrix

- Clear difference between background and the song elements (1)
- Able to show transitional areas (phrases) (2)
- Clear boundaries between song elements (3)
- Blurred details within elements (4)
- Elements' structure lost in simplification of visual representation (4)

Key matrix

- Busy background hinders clear song element visual delineation (1)
- Not showing transitional areas (phrases) (2)
- Falsely could show several elements as one (3)
- Clear details within elements, facilitating tracking the same types (themes) (4)

Figure 6 Examples of each matrix method performance

Levenshtein (up) and Key matrix (down) of the same recordings, showing examples of the performance details of two methods. On the side are listed the positive and negative sides of both.

4.3 SEASONAL VERSATILITY AND COMPLEXITY

4.3.1 Versatility

Song versatility is a sensible method that calculates the ratio of the number of different elements and the number of all elements in the song. In our case, we counted the unit types divided by all units contained in every song of each recording. The song extraction was performed as explained in Chapter III, Section 5. After getting these values, the average per breeding stock per year (2016- 2019) was calculated and plotted (Figure 7).

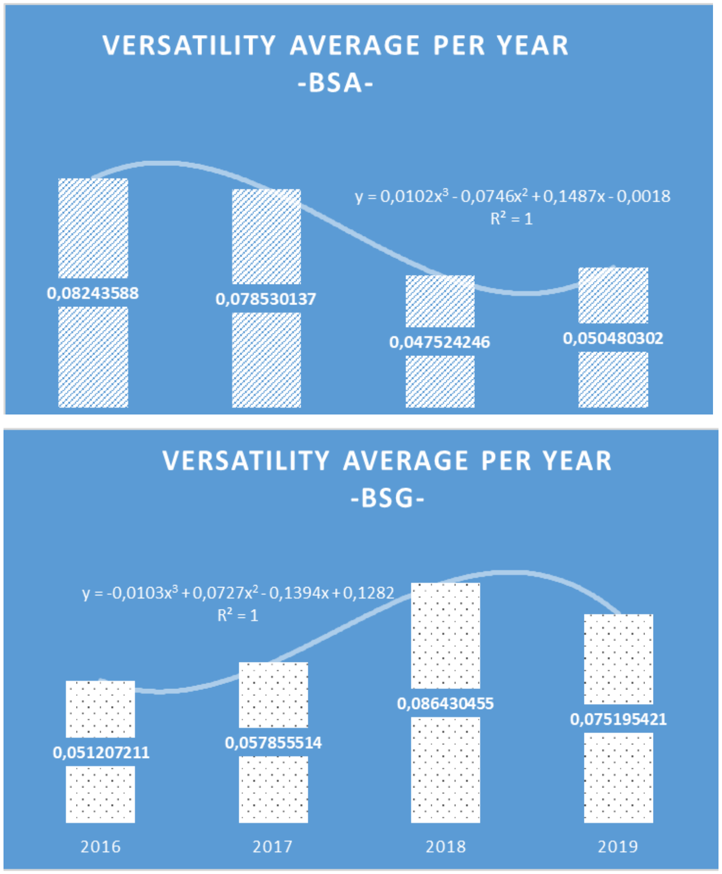


Figure 7 Versatility Index BSA vs. BSG, 2016- 2019

Noticeable is the change of Versatility Index pattern within the 4-year period in both cases, also interestingly, the patterns of two stocks appear like mirror images (breeding stock A on top, breeding stock G bottom).

As stated earlier, from the results of our other Chapters, we concluded that the year 2018 in BSA started with a brand new, revolutionary song- thus a revolution likely took place between breeding seasons 2017 and 2018 (GONÇALVES, et al., in prep.). In the BSG, the revolution of the same year, as suggested by some of the methods applied in this thesis, took place midseason, only bringing its final product in 2019. What we can read from our graph in Figure 6, is that the Versatility indeed follows the path of revolution, indicating

that the reduction of the song versatility is in synchrony with it. Thus, revolution indeed seems to diminish the versatility of the humpback whale song, and this result corresponds to similar conclusions suggested by the literature (ALLEN et al., 2018).

Moreover, it is interesting to notice the opposite trends of song versatility comparing both breeding stocks, throughout 4 seasons. The two trends are mirror images of themselves. One important conclusion to draw from this is that it seems that the fluctuation in versatility is changing in a 3-year time, in both stocks. A longer time-scale of data is needed to make a more robust conclusion about this phenomenon.

4.3.2 Complexity- Principal component analysis

Four variables were used for the PCA analysis: number of themes per song, number of unit types per song, the average number of units per theme, the average number of unit types per theme. The number of units per song was not included in the analysis, as we find that characteristic too variable while carrying no important information for this purpose. This observation emerged from what we learned from the recurrence plots- that songs are very variable in length (unit-wise) and structure, within the same seasonal dataset, even within a single recording (individual whale singer).

In Table 2, we can see the factor loadings for the 4 variables used in the PCA. Additionally, LDA was applied. As 81% of the variance in the original variables is explained by the first two PCs (it gave a high confidence level, Figure 7), we decided a 2-dimensional graph will be sufficient to demonstrate the relation among the songs. In Figure 9, we can see a plot with PC1 and PC2, corresponding to the factor loadings shown in Table 2. In the same figure, on the right-hand side, the centroids for the same PC1 and PC2 values, estimated per seasonal datasets are shown.

Table 2 PCA factor loadings

Variable	**PC1 (52%)**	**PC2 (29%)**
No. of themes per song	**0,639044485**	0,492398585
No. of unit types per song	0,109718396	**0,655693998**

Average no. of units per theme	-0,547172651	0,548583286
Average no. of unit types per theme	-0,52932609	0,163295413

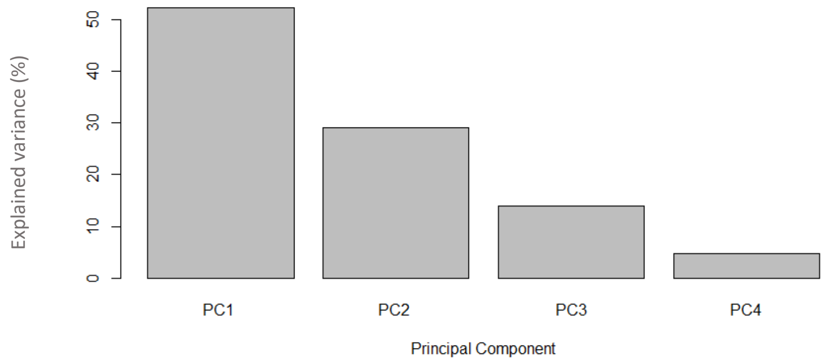


Figure 7 Importance of Principal Components

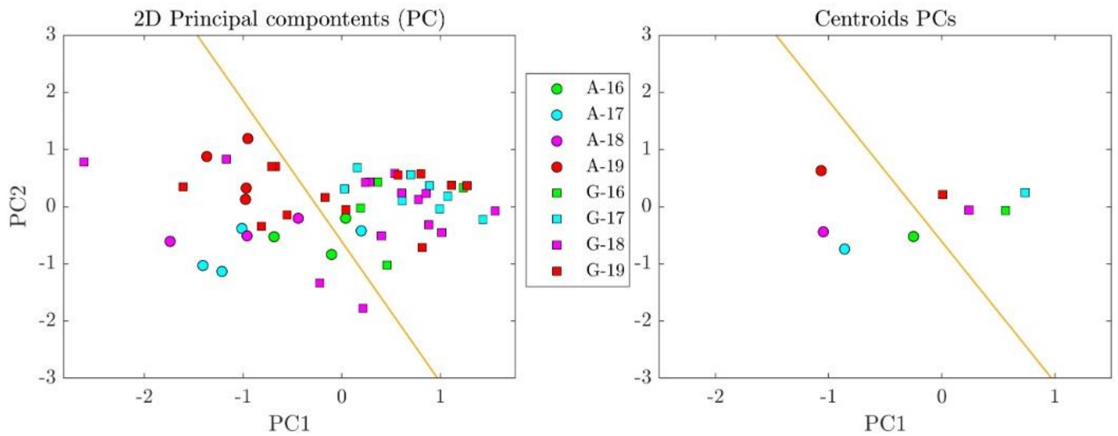


Figure 8 PCA with 4 variables

On the left- 4 variables were taken from 53 randomly chosen songs, and after a PCA transformation, a scatter plot in 2-D space was built (PC1 vs PC2 plot). Right- estimated centroids per seasonal datasets, from the songs plotted on the left graph. In both graphs, the yellow line represents the Linear discriminant function explaining well the difference between two breeding stocks in all 4 seasons- BSA and BSG

Finally, centroids of PC1 scores were plotted against the years of data sampling (2016-2019), representing song complexity, as done by Allen et al. (2018) (Figure 9). This plot was built in order to examine if the alternative variables we used here, and the method of building the sample batch would be able to demonstrate clear patterns in song complexity corresponding to the events of song evolutions/ revolutions. In the same figure, the cut-off values for two methods, Levenshtein Similarity Index, and Jaccard Similarity Index were used to indicate the events of song revolutions/evolutions, labeled as surfaces of different shades of blue: light- evolution, dark- revolution. Both methods are telling a similar story, except for the season between 2018-2019 for BSA. However, PC1 values do not seem to match, especially when considered in the same manner as in Allen et al. (2018) (revolution reduces complexity).

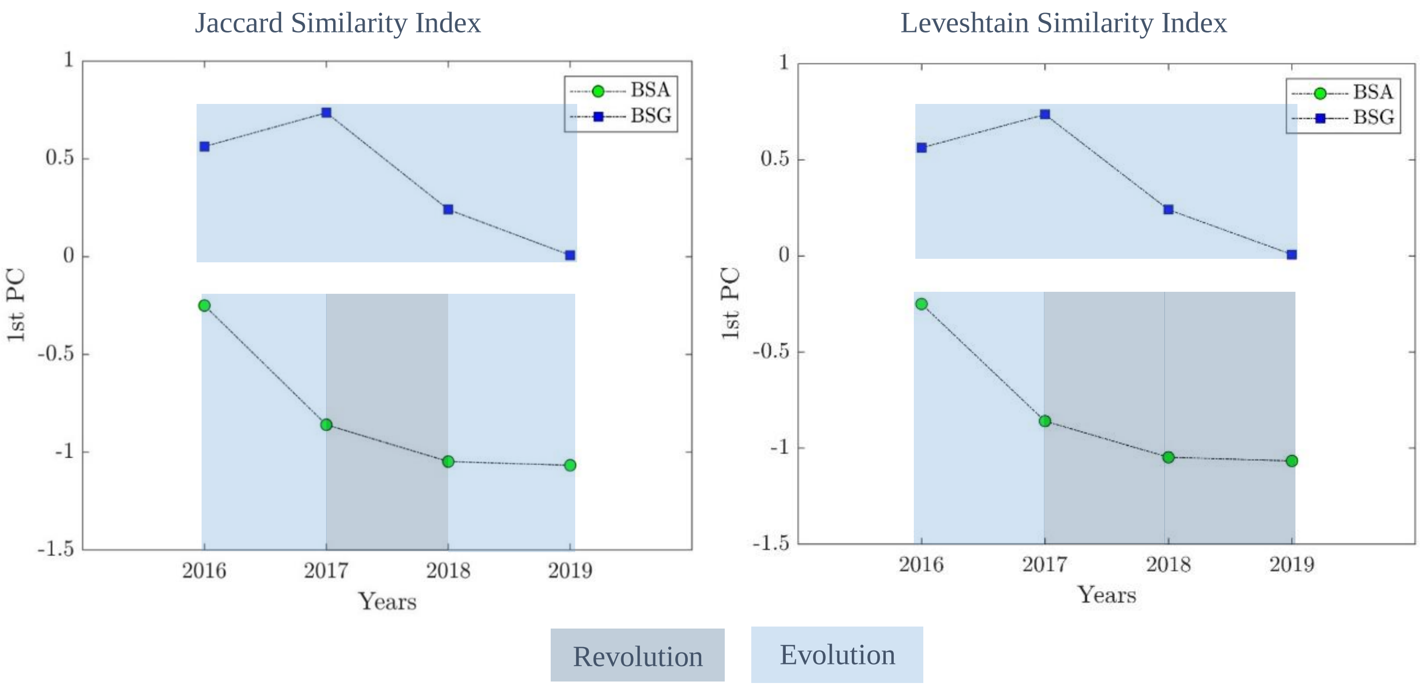


Figure 9 Song complexity for BSG and BSA, 2016-2019

Song complexity expressed through PC1 centroid values of two stocks, were plotted against the years of data-sampling. On the right side are the events of song revolutions and evolutions labeled based on the Jaccard Similarity Index cut-off value (Evolution >0.16), while on the left side is the same graph with the Levenshtein Similarity Index cut-off value (Evolution > 0.04) for determining the same song dynamic events. The results overlap, except for the period between seasons 2018-2019 BSA song.

In Figure 10, we compared results of different methodologies, applied to the same dataset, but on the different hierarchical levels of the song: Jaccard Similarity Index, comparing unit dictionaries, Levenshtein Similarity Index, comparing songs, and Song complexity, expressed as centroids' PC1 values for both stocks, with revolution/evolution labels (Figure 10). In the graph, each method was compared by stock, but also including all available data. Finally, on the far right of the figure, centroids per seasonal datasets are plotted on the PC1 and PC2 (data from randomly selected songs), with the linear discriminant analysis function separating songs of the two breeding stocks, across all 4 seasons.

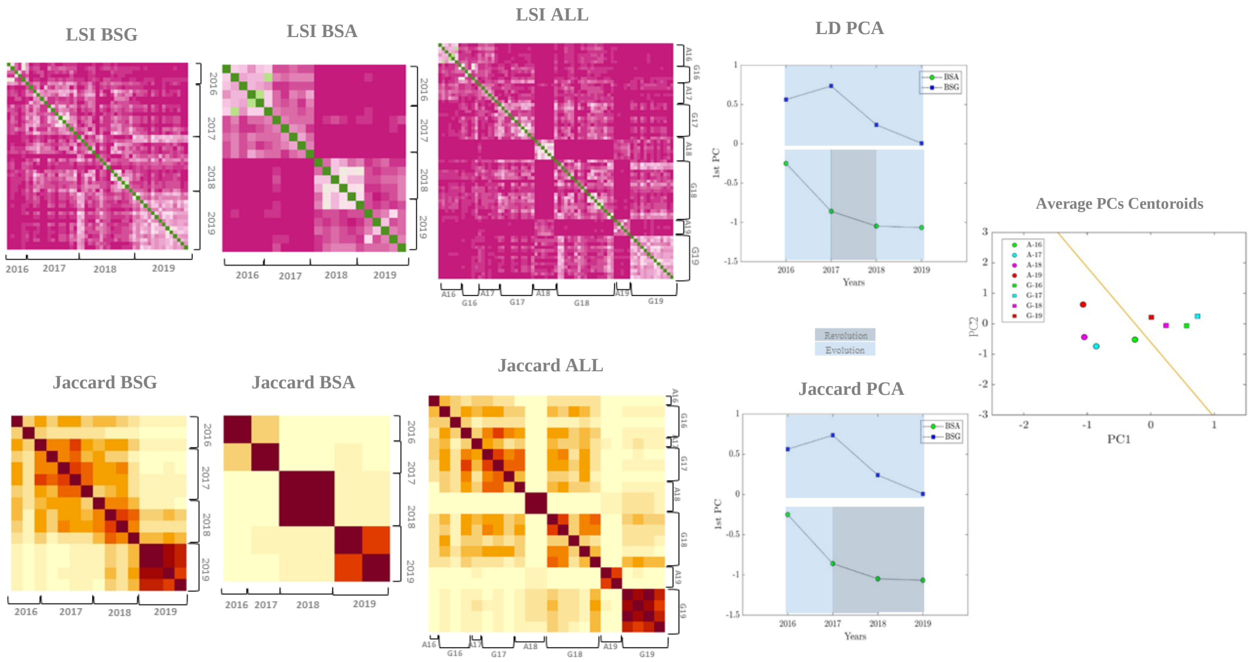


Figure 10 Comparison across methodologies

On the upper row are the heat maps built based on the Levenshtein Similarity Index (LSI) calculation of song comparisons (pink figures). The heat maps presented on the bottom row are calculated based on the Jaccard Similarity Index, comparing unit dictionaries (orange figures). The last two graphs of each row are the principal component values, plotted against the years, where in each event of song revolutions/evolutions are marked based on the two methodologies' cut-off values- uppers, Levenshtein Similarity (LD), bottom- Jaccard Similarity Index. The far-right graph in the middle shows an average centroid PC dot per seasonal dataset (2016-2019), for PC1 and PC2, with an LDA yellow line nicely separating between breeding stocks. (BS)A and (BS)G are the two breeding stocks from my dataset.

5 DISCUSSION

As the main goal of this chapter was to compare our newly established methods to the ones that already proved productive, in addition, we wished to explore possibilities of using different robust and repeatable method-independent song-describing variables. The established methodology was slightly modified to fit my dataset, but only to the level where the results were still comparable. The comparison was conducted by contrasting the Key vs. Levenshtein methods, for higher hierarchical levels delineation within recordings of humpback whales, also including the unit dictionaries comparison using Jaccard Similarity Index. Further, these same metrics were implemented in order to assess and compare song dynamics across stocks and years, while summing-up by Complexity scores based on the PCA, applied to some very basic variables.

5.1 KEY AND LEVENSHTEIN MATRIX METHODS

The primary advantage of the Key and the Levenshtein matrix method is providing visual recording representations, which demonstrate the repetitiveness of the songs contained in the recordings of any length. This was discussed in detail in Chapter II for the Key, and Chapter III for the Levenshtein matrix method. However, in this chapter, we used these methods' possibility for delineating the songs in their original (unaltered) form, in order to automatically and unbiasedly extract the songs contained in the recordings. This is one of the biggest challenges of the field of humpback whales song research, and in this chapter, we offered a solution, which has the potential to unify all the future results and make them comparable, without the waste of repeating work effort to adjust metric-specific results (which was one of the goals of this chapter). Having an automated method to delineate songs will further improve comparisons, making sure that the songs are delineated by the same criteria which will set a more realistic base for comparison. Further, this method helped us visualize the variable nature of the content of the song, in specific, the theme content (by its visual patterns), and their order in the songs. We learned that themes can be sung in a particular strict order (Chapter III), but it is not always the case (Chapter II). Moreover, we learned that this visual representation, thus our interpretation, heavily depends on the methods used to label the units and to calculate the distance between the song elements, used for building the matrices. If we take into consideration that the same dataset was used in this research, and it was processed by the same researchers, yet the final results varied so much, we can conclude with certainty that results will be based on the method in use. However, automatic song cutting offers a solution for unifying the song assessment method. Namely, it has the potential to be applied to any kind of distance matrix, yet, this option still needs to be explored. Once having songs extracted, based on a string of units, we can easily calculate certain song properties. Exactly in this way, we extracted some of the basic variables, like the number of units contained in a theme, the number of themes contained in the song, and so on, and so we were able to construct the Versatility index and Complexity score based on the PC1.

5.2 SONG VERSATILITY AND COMPLEXITY (PCA)

Although long in use for animal songs, in humpback whales, the Versatility index was not used so far, and the Complexity scores were built by Allen and colleagues (ALLEN et al., 2018), with slightly different criteria, and once again, based on a calculation-defined best song representatives (choosing “set medians” based on the highest LSI scores).

The Versatility Index metric appeared very useful in showing events of revolution and evolution, if we consider that the song complexity, in this case, expressed through the song Versatility, is reduced during a revolution, and keeps growing in periods of more gradual change (evolutions) (ALLEN et al., 2018). However, if we interpret the revolution/evolution events based on the results from other methods we put in practice on the BSA data, and apply those to the Versatility graph, what this graph implies is that the revolution is actually just a final stage of a longer process of song versatility/complexity reduction. The BSG versatility graph is slightly less simple to interpret, as the 2018 revolution likely took place midseason, having the final revolutionized song in 2019- the year we see the versatility dropping. Altogether, considering the simplicity and objectivity of the method, and yet, apparent ability to explain these complex events of humpback whale song dynamics, we deem it useful.

Different methods though gave us different data interpretations on song dynamics and slightly deeper insight. For example, based on the PCA we were able to discriminate among the songs of two different stocks clearly, and this difference was present over the course of all 4 years (Figure 8, right), with slight variability dependent on the level of change the songs went through between the seasons. Namely, this analysis potentially helped us observe how the animal interaction quantitatively modifies the song. If we look at the data distribution (Figure 8, left), patterns overlap with the ones presented in Figure 10. In detail, as for the BSA song, we can observe that some dots ended up on the other side of the LDA line, the BSG side, specifically, 2016 and 2017 songs. Recalling the event of the BSG whale being observed in BSA of the same season (FÉLIX et al., 2020), we could interpret this “migration” of Brazilian songs on the graph as an illustration of the BSG whale migration to Brazil in real life. In Figure 10, we can see similar results of these two seasons song of two stocks as being highly similar. As for the next two seasons, 2018 and 2019, the song “migrations” took place in the opposite direction- we can observe that some dots of BSG appear on the BSA side of the LDA line. Again, if we recall the Chapter II discovery of an entire BSA 2018 theme in the BSG 2019 song, the configuration of BSG 2019 dots on the PCA graph makes more sense. Additionally, based on the Jaccard Similarity Index heat map (Figure 11), we can see how BSA 2018 song gradually transformed into BSG 2019 song. From here, we might understand why BSG songs appear on the BSA side of the LDA line. However, it is important to take into consideration that the plotted songs were randomly picked from the dataset, thus the choice of the songs could have had a certain influence on the resulting plot. By determining centroids per seasonal dataset, all these details in data organization are reduced. In Figure 10-left, we can see the overall song dynamics in both stocks in the course of 4 seasons, but also the power of the PCA in combination with LDA to discriminate between different songs of different stocks based on complexity metrics (or to group them correctly).

Based on our PCA graph of the first level, two variables, in particular, were very powerful to demonstrate these clear membership of songs to different stocks (81% of explained data variance) - number of themes per song and the number of unit types per song. This is a very promising finding, as these variables are very simple and sensible to extract from recordings, but are dependent on the unit determination method. Thus, once agreed upon unit determination, this method is easy to replicate.

However, with the idea to replicate the Allen et al. (2018) methodology, where the authors took the PC1 values as a song Complexity score and plot it against the years while using Levenshtein Distance to determine song evolutions and revolution events across seasons, our final plot was unquestionably less straightforward. In our graph, the PC1 values of centroids were plotted against the 4 years of my dataset (Figure 9).

Because of various methodologies we used to access our data, we consulted two, Levenshtein Similarity Index values, as well as Jaccard Similarity Index values, to determine the events of song revolutions and evolutions, based on different cut-off values. Density scores were omitted from this process, as they were a product of intense averaging, thus a lot of information is lost this way (see Section 4.2).

Our graph (Figure 8) is plotted for the comparison of two different stocks, which, as we can see in the mentioned graph, means different song Complexity patterns change over the season. More than the pattern, values of Complexity differ as well, as BGA songs are always sitting on the positive side of the graph, oppose to the BSG song, which illustrates a well-defined difference between the two stocks' songs.

While complexity in BSG songs is in a constant decline (of different intensity), BSA song appears more variable, increasing in complexity in one season (2017). These patterns do not go in hand with the conclusion driven by Allen et al. (2018), where they claim the complexity is reduced in the events of the song revolution. Namely, it appears that independent of the variation of song complexity, only evolution took place in BSG song in the course of 4 seasons of our research, according to both methods' cut-off values we used- Jaccard Similarity Index and LSI.

This is not the case for the BSA song. Namely, the two methods brought us different results for BSA song across seasons, specifically telling contradicted information for the period between 2018 and 2019, where Jaccard Similarity Index claims revolution, while by LSI it stayed undetected. An explanation for these different conclusions might lie in the "unpatterned theme" (*sensu* PAYN; PAYNE, 1985) used in this season, which carried an extraordinary number of unit types. It for sure had a major influence on the song specifics, particularly the ones we measured, and because of it, we are also unable to claim which process exactly generated the 2019 BSA song. This reminds us that humpback whale song has many layers of change, and disregarding some of them can interfere with our conclusion about it in a long run. Unpatterned themes are one of them, and although rare, they might be a valuable piece of information concerning the dynamics of the humpback whale song.

A similar problem exists in the BSG song- namely, although neither of the cut-off values of the two methods marked the 2018-2019 season as a revolution event, on the heat maps we are encountering a different situation (Figure 10). In these graphs, LSI as well as Jaccard Similarity Index, the song 2019 is strongly visually divided from 2018 one. For now, we will focus on the Jaccard Similarity Index heat map for simplicity (Figure 11) (in Figure 10 we can see it is representing similarly the situation to LSI heat maps).

In the figure below (Figure 11), the BSG 2018 location orders were rearranged in a way to clearly visualize the gradual increase of similarity toward the 2019 song, while not losing it within the seasonal dataset (2018 locations' songs are highly similar between themselves). We can also see that the level of similarity between songs of these particular locations in the 2018 and 2019 datasets is higher than with any of the previous year's songs. In addition, the level of similarity with the 2019 locations is notably higher than within any other songs earlier (intensely dark red patch). This is obvious in all heat maps in Figure 10, across the general dataset. From the reasons stated above, we are of an opinion that the BSG 2019 is the song of revolution, that actually started in the preceding season. However, non of the methods managed to detect it directly.

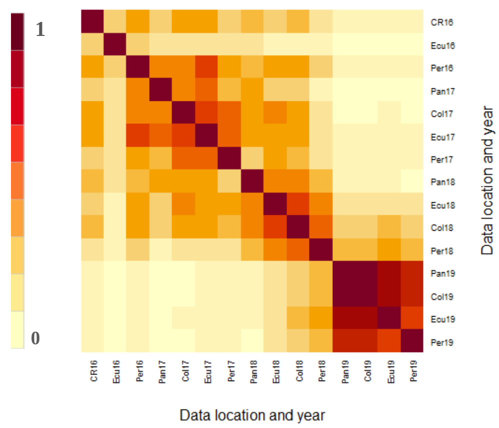


Figure 11 BSG 2016- 2019 unit dictionary Jaccard Similarity Index heat map

This brings us to the previous discussion about random data sampling. Namely, as the data for plotting PCA were randomly chosen from the general dataset table, what could have happened is that the songs chosen were the hybrid songs, the ones assembled of parts of the new and old song together. In this case, the intense jump or decrease in song complexity is not visible, as it is rather gradual. However, if a different song was picked for the analysis, not the hybrid one, we would maybe be able to clearly detect the revolution that plausible took place between those seasons.

Nonetheless, even if the revolution/evolution events were labeled the same by both methods for all 4 years for both breeding stocks or our observations would overlap with obtained results, their incoherence to the song complexity would not change.- seems the two- complexity and dynamic events- are following independent paths.

Revisiting the problem of an unpatterned theme, the item that should be added to this list of the small-scale-high-impact song phenomenon are hybrid songs. The hybrid songs might be used as incentives for an event of revolution. However, should be borne in mind that picking song representatives, depending on the methodology, can influence the results, and our conclusions on humpback whale song nature in a different, unpredictable manner. One possibility of overcoming this methodological obstacle is using for example Monte Carlo Simulation, to predict possible outcomes, based on the chosen songs. All in all, we would like to advocate for using songs in their most original form, keeping their variabilities and heterogeneity, as those are a genuine part of humpback whale vocalizations.

To conclude, these results suggest that in the songs of humpback whales of Latin America, complexity does not seem to follow the overlapping pattern of revolution/evolution events as the ones of Australia (complexity increase- evolution, decrease- revolution, *sensu* ALLEN et al., 2018). However, it should be taken into consideration the influenced by the methodological approach and result interpretations, as discussed earlier.

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GENERAL CONCLUSION

1 MAIN FINDINGS AND RECOMMENDATIONS

- In the same recording, the song (and theme) structure differs with every repetition, in size, and/or organization (independent of the assessment methodology). This is already suggested by previous work (ex. CERCHIO et al, 2001; CHOLEWIAK et al, 2003), but not fully accepted by the general research community, as the measurement of song similarity still heavily relies on this metric. From the results delivered in my work, this variability of song rigidness seems stock and season-dependent.
- Due to the intra-recording variation, it is of great importance to have a reliable method to unbiasedly and confidently determine the real beginning and endpoints of every song within the recording. Only then would comparisons across songs give realistic information. Otherwise, there is a risk of false comparison, contrasting elements of different hierarchical levels, also possible heavy bias determining what the song is, while averaging for the optimal representative.
- The source of variation of theme order within the song, or on the contrary, stereotypy, is still unknown. These could be individual differences or the property of the seasonal song, thus a cultural trait. This matter, in general, was not investigated much so far, as the observation itself was mostly neglected.
- Recurrence plots proved as a solid methodology in visualizing the repetitive structure of humpback whale song, but more than that, its hierarchical organization, which is repeated in a slightly less predictable manner than earlier believed. Visualizing songs in this way sheds light on the previously less known inter and intra-individual performing variations. Moreover, using recurrence plots, we were able to unbiasedly determine the beginning and endpoint of every song repetition within a recording.
- Within each stock (BSA and BSG), the order of themes might be stereotyped, variable (confirmed in this study), or possibly switched from stereotyped to a variable within a season (assumption), in addition to not knowing if these properties are song or individual singer related. Thus, we are proposing a new definition of a seasonal song*: a collection of themes sung in a particular season*.
- A more general and comparable metric or a system of evaluation is needed to determine if a certain seasonal song (*sensu collection of themes sung in a particular season*) is a product of a revolution or an evolution process. So far, the most important element in determining evolution or revolution was to identify the source of the new song (stock of origin), next to the total song change in the stock (thus, the rate of change of 100%), which, as discussed in the text, is metric-dependent and thus unreliable.
- A complicated case of defining a song as a revolution or evolution process we found in the example of the BSA 2019 song, which interpretation remains uncertain in this sense. This is because of the unpatterned theme that is a part of this song. Namely, an unpatterned theme brings an intense level of variability to the song, however, we cannot claim that all the song variability is sourced in this unpatterned theme. Thus, without altering the song content, we are not able to pinpoint the source of the intensive change that is visible in the BSA song from the 2018 to 2019 season.

- Revolution can also be treated as a final step of a cycle of song evolution. This conclusion comes from comparing our results to the ones of Noad (et al., 2000), where the entire process of song change took roughly 3 years. This pattern of song change is confirmed in our study by the Versatility index graph, where we can see the unidirectional flow of the song versatility (reduction or growth) in 3 consecutive years, after which it suddenly changes. Thus, this moderate change of unidirectional flow of song versatility can be interpreted as an evolution, where after its final step –a revolution- the song shifts its versatility towards growth or reduction.
- We calculated the cut-off values that could determine the events of evolutions/revolution, for two measures of similarity Levenshtein distance (0.04) and Jaccard Index (0.16). These values were calculated as the average value of song change for seasons 2 years apart (evolution) (e.g. 2016 vs. 2018). The reasoning behind sits in the time-frame under which the change is observed- if we compare season after season, we can theoretically only notice a partial change, where in a longer-span, of a minimum of 2 years, we can indeed conclude if the song is totally changed or only partially.
- In future comparisons, when similarity drops below the given value (Levenshtein distance < 0.04, Jaccard Index < 0.16) from one year to the next, thus different from the standard rate of change, it should be considered as a radical change, thus a revolution. Otherwise, the song is changing at a predictable pace and should be taken as an evolution product.
- We propose that a *song revolution occurs when the metric of similarity, from one season to the next, falls below a value characteristic for a 2-year period (e.g. from 2016 to 2018), and the change is adopted, at least, by all sampled individuals from a stock.*
- *The cultural revolution*, consequently, is composed of a song revolution as defined above, plus the identification of the stock where the new song type originated (cultural pathway identification).
- Based on our data, we are suggesting that a song revolution can happen in two different modes- a midseason revolution and an instant revolution, depending on the existence of a hybrid song type. Should be bared in mind the influence that the song sampling method has on detecting the hybrid song.
  - To diminish the influence of song sampling on the ability to track the hybrid song, the unit dictionaries comparison can serve as an alternative, as the dictionaries would show all the unit types used in the particular season, without a need to determine the actual hybrid songs. This means that all songs' content will be presented in the dictionary, independent of the quantity of each song "type" representation in my dataset.
    - Thus, in a sense, in specific seasons, we can talk about "hybrid dictionaries", the ones assembled of a combination of unit types from the previous and a consecutive year, when available. Comparison between dictionaries, using Jaccard Similarity Index, would further show a gradual change in the unit composition, in the case of midseason revolution, or a radical one if the change happened off the breeding ground. (These conclusions are driven only based on the specificities of my dataset).

- The conclusion from our research is that the song revolution can be detected in the unit content, as changing types of units used in the song will surely mean changes on a phrase and theme level. What in theory could happened, when detecting a revolution through unit type repertoire (dictionary), is a certain level of false negatives since some unit types can be recycled, but as a part of a different phrase. This is why we calculated cut-off values, that should be different from 0. Again, a more solid definition of what a song revolution means is necessary.
- Previous works suggested that the song revolution coincides with low song complexity (ALLEN et al., 2018). However, in our data, a drop in complexity, expressed by a complexity score, where the most relevant metrics were the number of themes per song and the number of unit types per song, happened during both processes - evolutions and revolutions (as per our interpretations of these events).
  - Yet, the situation can be slightly more complicated, due to the presence of hybrid songs and unpatterned themes, which increase unit repertoire size. For example, BSA 2019 song had an unpatterned theme, and using the Jaccard Similarity Index method, it was considered a revolution. In contrast, BSG 2018 song was not recognized as a revolution (considering versatility and complexity scores), although it showed hybrid songs and a large repertoire size (and we are aware from the experience of listening to the songs of that season and the previous one, that the song intensively changed in the year 2018).
  - Additionally, it is hard to tell if the sample song is indeed the ending stage of the revolution (or alternatively a sample from an ongoing process).
  - In the example of the song revolution from BSA 2017 – 2018 season we had in the dataset, the repertoire size was heavily reduced and entirely replaced. This was not the case with the 2018 BSG total song change, where the number of unit types decreased, but not as much.
- I found evidence of structural similarities – a Syntax? - across the dataset. This opens up new questions of the existence of some sort of "grammar" of the humpback whale song, or the rules they might follow in constructing the songs, and while using different unit types, they might be organizing them in the same way under these rules.
- Unit types can be determined using 5 major characteristics: Contour, Sound type, Peak Frequency, Length, and Harmonics when used as categorical values. This is far less detailed than standard 14 variables unit classification (Dunlop et al, 2007), however appears sufficient for this type of analysis.
- These categorized values can further be used to calculate the distance (or similarity) between unit types. This plays a great role in building recurrence plots directly from the string of units, also shortening the procedure usually taken to compare units between themselves in the quantitative matter (ex. ALLEN et al., 2017; GARLAND et al., 2017).
- Seasonal unit repertoire alone can give great insight into two stocks interaction, and song dynamics within the breeding area. This approach was not taken so far, as the comparisons were usually relying on songs or themes. However, the unit dictionary is the simplest possible and least biased approach, delivering most realistic acoustic representation of humpbacks vocalizations, as units are easiest to determine out of all hierarchical levels of their song.

- Surprisingly, the change in song type directly means change in the unt types in use. Thus, every time the song changes entirely, so does the unit dictionary of the stock for that season (not including universal unit types). As the songs were not analyzed solely based on the unit types they are composed of (unit dictionary) in the past studies, we were not aware of this humpback whale song property so far.
- Songs with larger unit repertoires usually have more complex visual representations (recurrence plots) and are less repetitive. Accordingly, fewer themes can "fit" in the same recording time, compared to some more simple songs, comprised of only a few unit types. This is explained by the higher frequency of repetition, inversely proportional to the length of the song (in the number of units).
- We found different kinds of transitional phrases in my dataset. The "standard" transitional phrases, comprised of units from flanking themes, but also those comprised by units from themes positioned distantly within the song. To the best of our knowledge, this second type of transitional phrase between themes is not yet described.
- 15 minutes long recording of a humpback whale song is the minimum recording duration that can be of use to confidentially assess the song unit content. This is valuable information, as giving a solid time frame of the usable recording, potentially notably expands usable datasets that were considered futile so far.
- BSG and BSA are in acoustic contact (the least, if not individual exchange between stocks), in a rate variable per season, judging based on the song similarities. There are seasons, like 2016 and 2017, that songs are highly similar, which indicates close acoustic contact of stocks. In other seasons, like 2018, songs evolved apart notably. Then again, the 2019 BSG song shows traces of BSA 2018 song, suggesting once again contact between breeding stocks.
- In the years for which there were individual ID matches of whales between stocks, or on feeding grounds, seems this mixing echoed in song similarity between stocks.
- Next to the off-feeding season contact of animals (inter-stock visits of individuals), we can conclude that the feeding grounds are one of the most important points for vocal cultural or individual exchange (immigration/emigration to another breeding stock events) for the species of humpback whales. BSG and BSA have very restricted contact opportunities, basically limited to the feeding ground interaction around the Antarctic continent, and as such are especially convenient research subjects for this matter. Although they are thought to segregate themselves there as well, our results show that they most probably do mix. Variable levels of song similarities across years highlight the importance of feeding grounds for humpback whale culture studies.
- CA shows very little dictionary overlap with other Latin American stocks in the year 2018, as expected, based on their temporal segregation from other stocks. Hypothetically, the overlapping uni types could be Universal uni types- ones that appear often in all the songs, unrelated to the song type. However, further research is needed for a more solid conclusion, optimally song comparison between reliably independent stocks (not in the acoustic contact).

- We found song elements from Brazil 2018 revolutionized song in the BSG 2019 song. This is a piece of evidence that the humpback whale culture can be passed on geographically in both directions (eastward, GARLAND et al. 2011, westward, this study). In both scenarios, the song seems to be passed from larger to smaller breeding stocks.
- One particular theme that originated in BSA 2018 (revolutionized song) was found in BSG song the next season. This particular theme could give us an insight into the mechanisms of song dynamics: why the entire theme, why that particular theme, and why it was integrated into the other song in the way it did (position)? Moreover, it was the only theme that persisted throughout BSA 2019 song. This theme can be taken as evidence that song learning is a cultural trait - it was evidently originated in BSA and passed on to BSG in the following season. This suggests that certain acoustic properties or acoustic arrangements are preferred over others by whales and are passed on from one stock to the other.
- Systematic acoustic monitoring of this part of the world is needed, for the acquisition of high-quality data, which will provide more information on the song dynamics of these two stocks, and consequently their interaction and the mechanism of song evolution. Besides, quantity, in this case, means quality, as longer and better recordings can lead to a more detailed investigation and more robust inferences. These high-quality, long recordings would likely be data from autonomous fixed systems, as an array of synchronized systems could even follow an individual’s song, allowing finer spatial- and time-scale data.

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Chapter I

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Chapter II

-Comparison of the song structure and composition of different stocks of humpback whales-

R. S. Sousa-Lima [1,2], F. Malige [3], J. Patris [3], J. Oña [4], E. Duque –Mesa [5], L. May-Collado [6], C. Castro [7], M. Rossi- Santos [8], A. S. Pacheco [9], S. Silva [10], M. C. C. Marcondes [11], K. Rasmussen [12], D. Venturini [13], J. De Weerdt [14], M. I. C. Gonçalves [1,15,16], J. E. Baumgarten [16,17], L. R. Padovese [18],

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Chapter III

-Use of recurrence plots for identification and extraction of patterns in humpback whale song recordings-

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Chapter IV

-Comparison of methodologies for the assessment of humpback whale song dynamics-

R. S. Sousa-Lima [1,2], F. Malige [3], J. Patris [3], I. Sanchez-Gendriz [4] , J. Oña [5] , E. Duque- Mesa [6], L. May-Collado [7], C. Castro [8] , A. S. Pacheco [9], S. Silva [10], M. C. C. Marcondes [11], M. Rossi- Santos [12], D. Venturini [13], K. Rasmussen [14], J. De Weerdt [15], M. I. C. Gonçalves [1,16,17] , J. E. Baumgarten [17,18] , L. R. Padovese [19]

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APPENDIX

Content

Dataset
-Technical details on recordings and equipment-

Year	Stock	Country	Location	Date	Duration (min)	Sampling rate (Hz)	Equipment	Institution/ Researcher
2016	**A**							
		Brazil			95			
			Abrolhos					
				October, 13		44800	Go Pro 4	Daniel Venturini
				November		44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional ; Recorder Sony HI-MD-MZ-NH1	IBJ
			Bahia			44800	Hydrophone HTI-96-min ;Recorder TASCAM DR- 40	Marcos Rossi Santos
				Jul, 21				
				August, 9				
				September, 21				
				Unknown				
	G							
		Costa Rica			100	4100	RUDARs & SM2M, autonomous	Laura May- Collado
			El Jardin					

				October 8 , 9				
		Ecuador			20	44100	Hydrophone to be confirmed; Recorder Sony TCD-D7	Cristina Castro
			Machalilla					
				August 30, 31				
		Peru			88	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional ; Recorder Zoom H4n Pro	Aldo Pacheco
			Cabo Blanco					
				August, 22				
				September, 25				
					Total = 303			

Year	Stock	Country	Location	Date	Duration (min.)	Sampling rate (Hz)	Equipment	Institution/ Researcher
2017	**A**							
		Brazil			74	44100	Hydrophone Aquarian Audio H2a; Recorder Zoom H4nPro	IBJ
			Abrolhos	October 16, 18				
	G							
		Colombia			62	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Marantz solid state PMD661.	Esteban Duque Mesa
			Bahía Solano	August, 10 ,31				
				September, 11, 21, 27				
		Ecuador			94	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; tape recorder	Javier Oña
			Esmeraldas	Jul, 11				
				August, 10				
		Panama			81		Hydrophone High Tech Inc.; Recorder Zoom H4n	Kristin Rasmussen
				August, 8,8,19,29				
		Peru						
			Cabo Blanco	July, 31	35	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Zoom H4n Pro	Aldo Pacheco
					Total = 346			

Year	Stock	Country	Location	Date	Duration (min.)	Sampling rate (Hz)	Equipment	Institution/ Researcher
2018	A							
		Brazil						
			Abrolhos	July, 21x2	91	44100	Hydrophone Aquarian Audio H2a-XLR; Recorder Zoom H4nPro	IBJ
				Unknown				
				September, 22				
			Serra Grande	August, 13	90	16000	Oceanpods, produced by LACMAM - USP	Maria Isabel Gonçalves
				October, 1				
	G							
		Colombia			86	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Marantz solid state PMD661	Esteban Duque Mesa
			Bahía Solano	July, 17				
				September 7, 24				
				October, 1				
		Ecuador			63	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; tape recorder	Javier Oña
			Esmeraldas	Jul, 11				
				August, 10				
		Panama			88	48000	Hydrophone Cetacean Research Technology C57, Cylindrical; Recorder Zoom H4n	Kristin Rasmussen
				July, 29				
				August, 1,5,31,31				

		Peru						
			Cabo Blanco	July, 22	38	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Zoom H4n Pro	Aldo Pacheco
				September 13,13				
	CA	Nicaragua						
			Padre Ramos	April, 7, 8	87	96000	Hydrophone Tascam DR-05; Recorder Zoom H2a	Joelle De Weerdt
					Total = 543			

Year	Stock	Country	Location	Date	Duration (min.)	Sampling rate (Hz)	Equipment	Institution/ Researcher
2019	**A**							
		Brazil				44100	Hydrophones Aquarian Audio H2a-XLR/ CR1 Cetacean Research Technology ;Recorders Zoom H4n Pro / H1n	IBJ/ LaB
			Abrolhos	September, 15	69			
				October, 6				
			Serra Grande	September, 30	90	16000	Oceanpods , produced by LACMAM - USP	Maria Isabel Gonçalves
				October, 11, 13				
	G							
		Colombia				44100		Esteban Duque Mesa
			Bahía Solano		105		Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Marantz solid state PMD661.	
				August 1 ,16				
				September, 6				
		Ecuador			122	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; tape recorder	Javier Oña
			Esmeraldas					
				Jul, 3,16,17,18				
		Panama			108	48000	Hydrophone C57 Cetacean Research Technology,	Kristin Rasmussen

							cylindrical; Recorder Zoom H4n	
				July, 29				
				August, 1, 2, 6				
				September, 2				
		Peru			32	44100	Hydrophone Aquarian Audio H2a-XLR, omnidirectional; Recorder Zoom H4n Pro	Aldo Pacheco
			Cabo Blanco	October, 4				
					Total = 526			

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MEMORANDUM OF UNDERSTANDING FOR SCIENTIFIC COOPERATION BETWEEN UFRN LABORATORY OF BIOACOUSTICS, AND */name of your institution/*

Dr. Renata Sousa-Lima, UFRN LABORATORY OF BIOACOUSTICS and MSc. Divna Djokic, Ph.D. candidate of UFRN Program on Psychobiology, Brazil, and */your name and name of your institution, country/* agree to this Memorandum of Understanding.

The Memorandum of Understanding (MOU) establishes the following:

FIRST - OBJECTIVE OF THE AGREEMENT:

To establish a mutually beneficial relationship built on scientific cooperation. Areas of cooperation between **UFRN Laboratory of Bioacoustics, Brazil** and the ***/name of your institution, country/*** (hereafter referred to as scientific collaboration) includes the exchange of acoustic samples, participation in publications, and sharing of technical information about humpback whale songs in breeding */and feeding/* grounds off the coast of /*Your Country/* and Brazil.

SECOND - GOALS AND FORMS OF COOPERATION:

The signing institutions and responsible researchers agree to provide the opportunity, when appropriate, for the following activities towards the completion of the objective of this MOU.

1. Exchange acoustic samples of humpback whales collected by the /*name of your institution/*
2. Elaborate and author jointly scientific publications according to ¨Best Practice Guidelines on Publishing Ethics¨.
3. Exchange technical information during the duration of Divna Djokic`s Ph.D. project, such as preliminary reports and progress reports in the use of acoustic data and analyses.

THIRD - IMPLEMENTATION OF THE MEMORANDUM OF UNDERSTANDING:

The objectives of the MOU will be implemented and regulated in the following manner:

Exchange of Acoustic Samples:

- The Ph.D. student may use acoustic samples specifically for her academic project in the department and school of her university. Acoustic samples will be shared according to the research goal and interest of both parties.

- Preliminary reports or notes about acoustic analyses of the data will be shared with /*name of your institution/*. This form of cooperation will allow the use of those information for academic purposes and the training of future students interested in acoustics.

- During the elaboration of scientific documents, such as articles or short communications, /*name of your institution/* must be involved during the entire process and as co-author, taking into account the four following criteria according to ¨Best Practice Guidelines on Publishing Ethics¨:

1. Substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data for the work; and
2. Drafting the work or revising it critically for important intellectual content; and
3. Final approval of the version to be published; and
4. Agreement to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

<u>FOURTH - DURATION AND RENEWAL OF MOU</u>

a. The agreement shall come into effect on */put date/* Changes to this agreement shall be made by mutual consent between both parties. In cases of disagreement, the Institution wishing to depart from the agreement shall, wherever possible, give three months' notice of its intention to do so.

b. Correspondence about this agreement shall be conducted between the representatives /*name of your institution/* and UFRN Laboratory of Bioacoustics, Brazil

Natal, RN, Brazil

Sincerely,

MSc. Divna Djokic

Ph.D. Candidate

UFRN PhD program on Psychobiology, Brazil ____________________

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/Your name and

name of your institution/

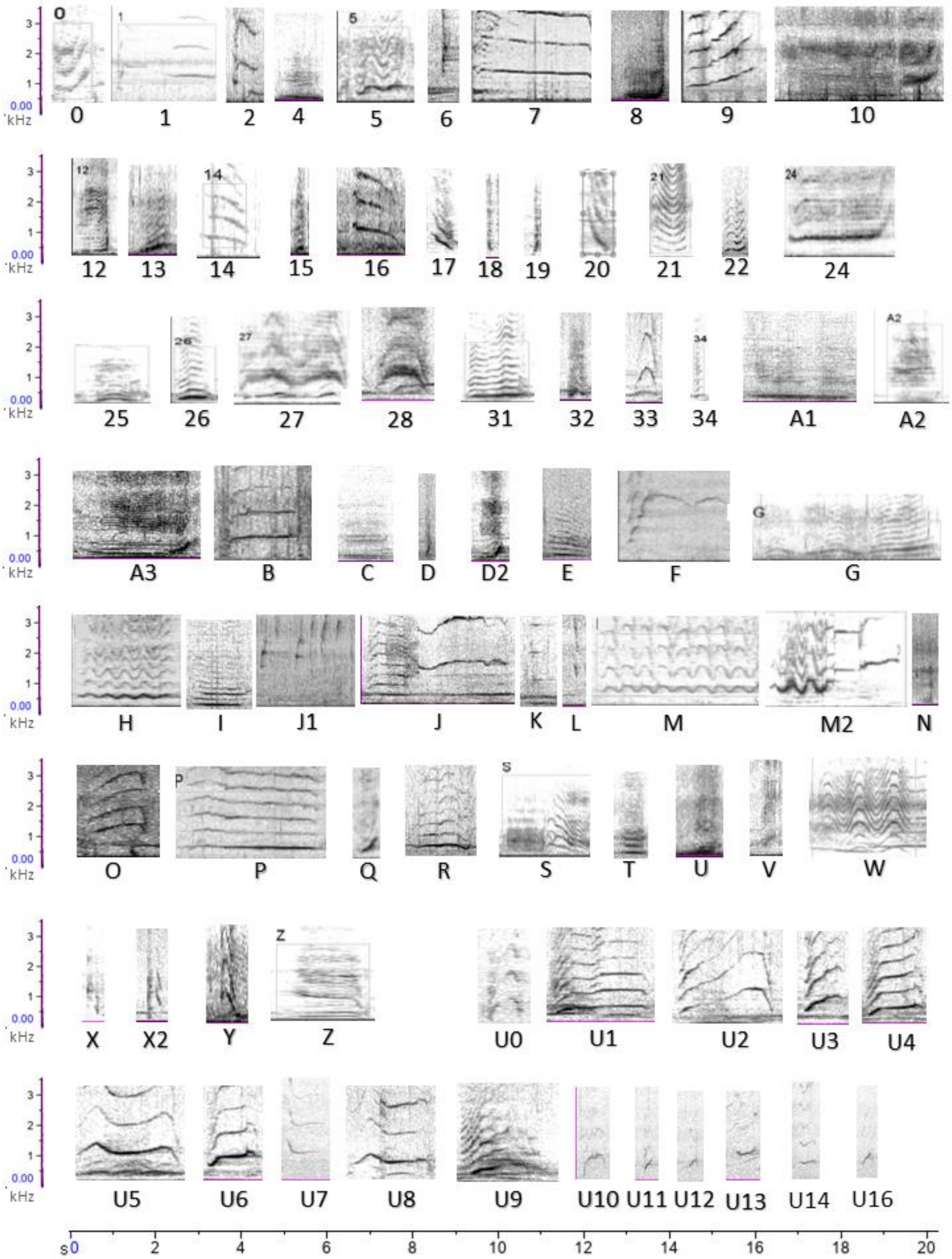
General Unit Dictionary

Unit	Contour	Sound type	Peak F	Length	Harmonics
U3	1	1	3	1	1
6	1	1	3	1	2
J1	1	1	3	3	2
V	1	2	2	1	3
T	1	2	3	1	2
8	1	3	1	2	3
A3	1	3	2	2	3
10	1	3	3	2	2
Q	1	4	2	1	1
O	1	4	2	2	1
9	1	4	3	2	2
U6	1	4	3	2	1
U11	1	4	3	3	2
D	1	5	1	2	1
D2	1	5	2	1	3
19	1	5	2	3	3
0	1	5	3	2	2
L	1	5	3	3	3
U7	2	1	2	2	2
14	2	1	3	2	2
U12	2	1	3	3	2
17	2	4	2	1	1
P	2	4	2	2	1
20	2	4	3	1	1
16	2	4	3	2	2
18	2	5	2	1	1
E	2	5	2	2	1
Z	2	5	3	2	1
K	3	1	3	1	2
I	3	4	1	2	1
2	4	1	3	1	2
U2	4	1	3	2	1
7	4	1	3	2	2

33	4	1	3	3	2
X2	4	3	2	1	3
X	4	3	3	1	3
26	4	4	2	1	2
13	4	4	2	2	2
U0	4	4	3	1	1
U10	4	4	3	1	2
U1	4	4	3	2	1
15	4	5	2	1	1
32	4	5	2	1	3
25	4	5	2	2	1
31	4	5	2	2	2
U13	5	1	3	2	2
21	5	4	2	1	1
M2	6	1	2	2	2
F	6	1	3	1	2
1	6	1	3	2	2
12	6	3	2	2	1
R	6	4	2	2	1
J	6	4	3	2	1
U5	6	4	3	2	2
M	7	1	2	2	2
U4	7	1	3	1	1
B	7	1	3	2	2
U9	7	1	3	2	1
28	7	3	3	1	2
A2	7	3	3	2	1
27	7	3	3	2	2
22	7	4	2	1	1
G	7	4	2	2	1
U14	7	4	2	2	2
W	7	4	3	2	1
U8	7	4	3	2	2
34	7	5	3	3	2
S	8	3	2	2	1
Y	8	4	2	1	1
H	8	4	2	2	1
5	8	4	2	2	2

C	9	2	1	2	3
U	9	2	1	3	3
4	9	2	2	2	3
N	9	2	2	3	3
23	9	5	1	1	3
A1	9	5	2	2	3
24	9	5	3	2	3

Spectrograms of all unit types 2016- 2019

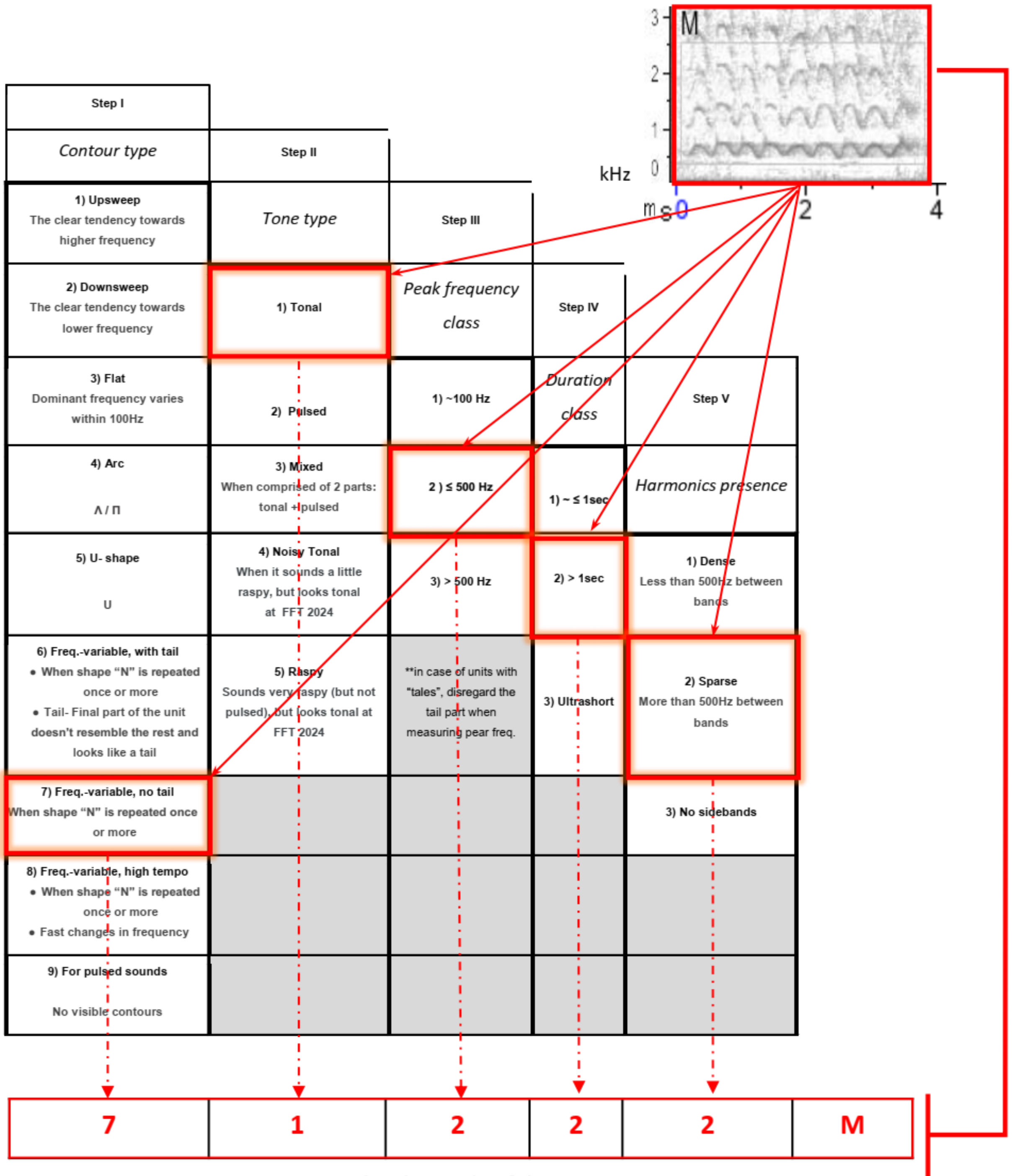


Unit Classification Key

The Key is organized based on the 5 major unit characteristics: *Contour type, Sound type, Peak frequency classy, Duration class and Harmonics presence*. From each step, one category should be chosen, based on the specific unit's characteristics. Finally, the unit will be determined as a 5-digit code, which will give units name (letter, number, or the mix of two), and its position in the unit dictionary. *Flat contour type was determined as shown in the table, yet we would recommend the future use of logarithmic factor for the mentioned 100Hz variation

Step I				
Contour type	**Step II**			
1) Upsweep **The clear tendency towards higher frequency**	*Tone type*	**Step III**		
2) Downsweep **The clear tendency towards lower frequency**	**1) Tonal**	*Peak frequency class*	**Step IV**	
3) Flat **Dominant frequency varies within 100Hz**	**2) Pulsed**	**1) ~100 Hz**	*Duration class*	**Step V**
4) Arc **∧ / ∏**	**3) Mixed** **When comprised of 2 parts: tonal + pulsed**	**2) ≤ 500 Hz**	**1) ~ ≤ 1sec**	*Harmonics presence*
5) U- shape **U**	**4) Noisy Tonal** **When it sounds a little raspy, but looks tonal at FFT 2024**	**3) > 500 Hz**	**2) > 1sec**	**1) Dense** **Less than 500Hz between bands**
6) Freq.-variable, with tail ● **When shape "N" is repeated once or more** ● **Tail- Final part of the unit doesn't resemble the rest and looks like a tail**	**5) Raspy** **Sounds very raspy (but not pulsed), but looks tonal at FFT 2024**	**in case of units with "tales", disregard the tail part when measuring pear freq.	**3) Ultrashort***	**2) Sparse** **More than 500Hz between bands**
7) Freq.-variable, no tail **When shape "N" is repeated once or more**			*When the value is notably shorter than 1 second.	**3) No sidebands**
8) Freq.-variable, high tempo ● **When shape "N" is repeated once or more** ● **Fast changes in frequency**				
9) For pulsed sounds **No visible contours**				

Example of a unit classification procedure using the Key

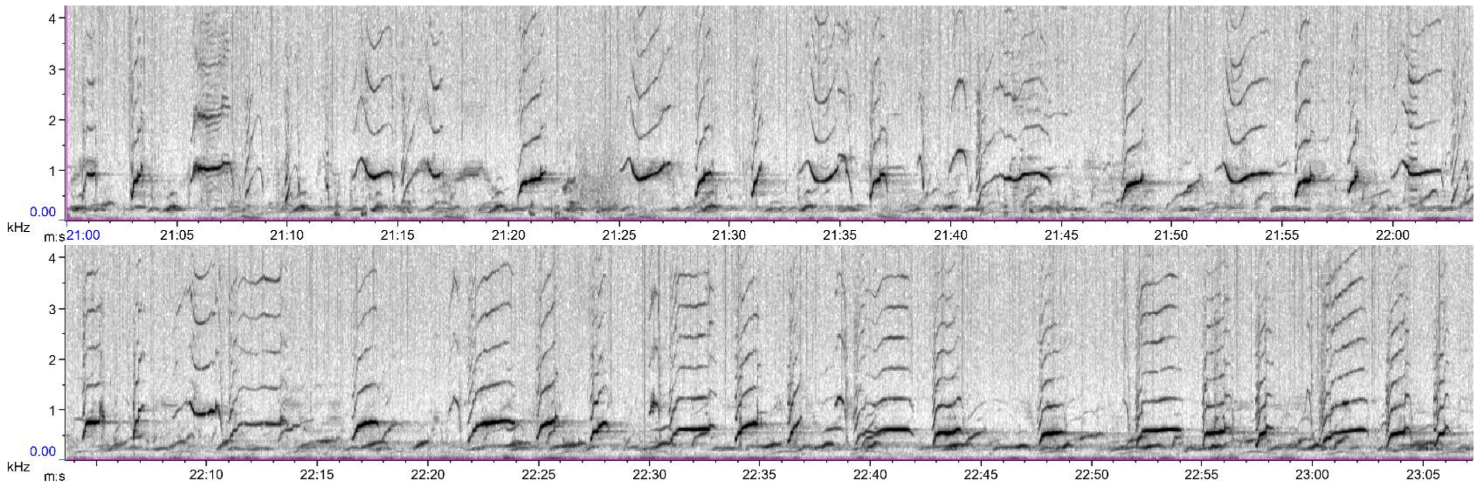


5-digit key code of the unit M

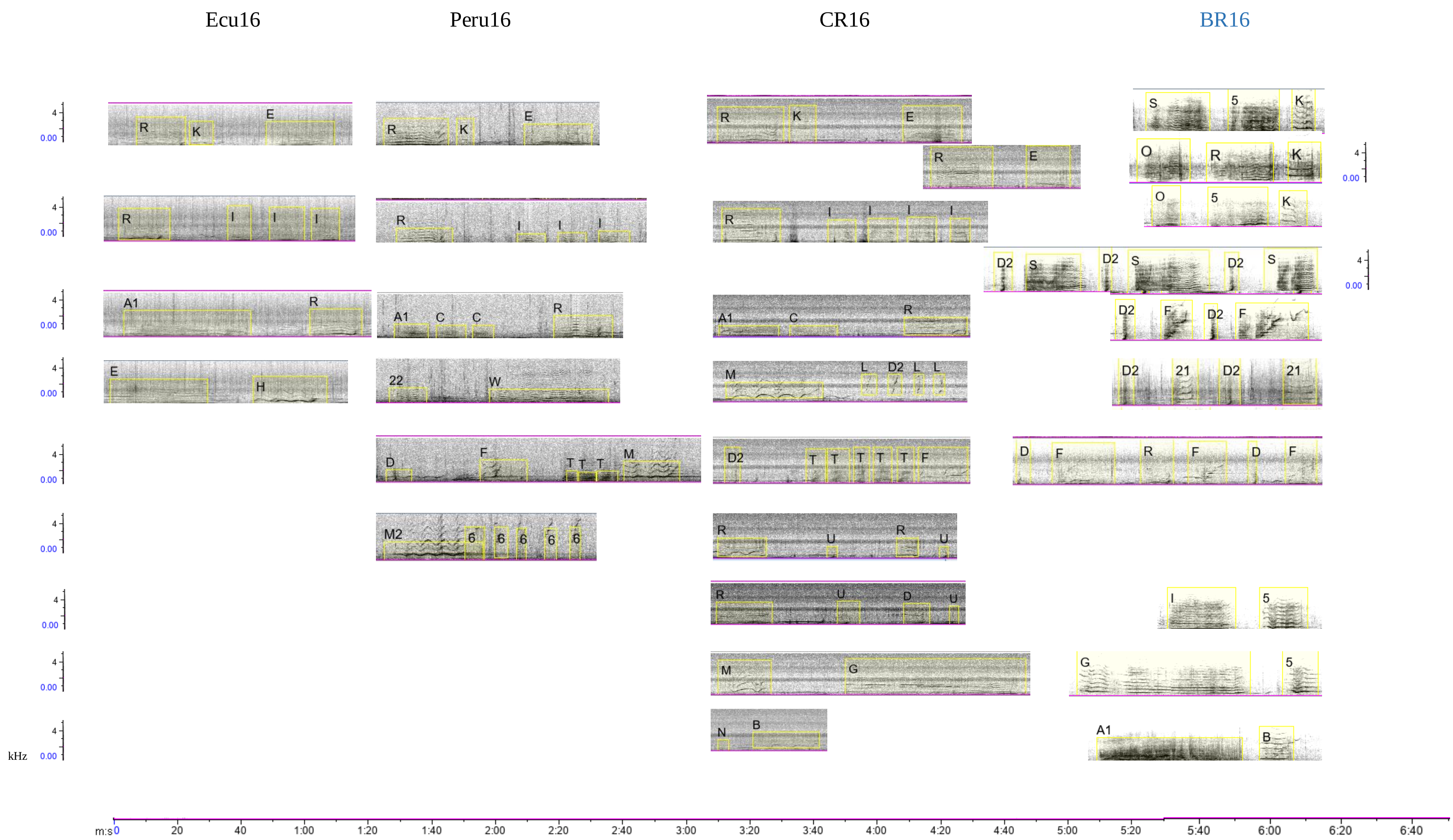
Jaccard Similarity Index unit dictionaries comparison

	Br16	CR16	Ecu16	Per16	Br17	Pan17	Col17	Ecu17	Per17	Br18a	Br18s	Pan18	Col18	Ecu18	Per18	Br19a	Br19s	Pan19	Col19	Ecu19	Per19
Br16	1	0,380952	0,266667	0,230769	0,28	0,173913	0,259259	0,178571	0,08	0	0	0,230769	0,194444	0,1875	0,178571	0,027778	0,026316	0,033333	0,033333	0,064516	0,038462
CR16	0,380952	1	0,294118	0,458333	0,346154	0,304348	0,423077	0,5	0,304348	0	0	0,4	0,393939	0,322581	0,241379	0,025641	0	0,133333	0,133333	0,16129	0,111111
Ecu16	0,266667	0,294118	1	0,315789	0,136364	0,25	0,227273	0,238095	0,176471	0	0	0,190476	0,16129	0,148148	0,130435	0	0	0	0	0	0
Per16	0,230769	0,458333	0,315789	1	0,266667	0,571429	0,538462	0,695652	0,5	0	0	0,407407	0,441176	0,419355	0,258065	0	0	0,15625	0,15625	0,147059	0,137931
Br17	0,28	0,346154	0,136364	0,266667	1	0,222222	0,428571	0,392857	0,32	0,038462	0,038462	0,357143	0,4	0,333333	0,181818	0,102564	0,071429	0,121212	0,121212	0,181818	0,137931
Pan17	0,173913	0,304348	0,25	0,571429	0,222222	1	0,521739	0,619048	0,4	0	0	0,434783	0,333333	0,258065	0,133333	0,027027	0,025641	0,032258	0,032258	0,030303	0
Col17	0,259259	0,423077	0,227273	0,538462	0,428571	0,521739	1	0,708333	0,590909	0	0	0,481481	0,5	0,533333	0,242424	0,071429	0,044444	0,083333	0,083333	0,108108	0,060606
Ecu17	0,178571	0,5	0,238095	0,695652	0,392857	0,619048	0,708333	1	0,619048	0	0	0,5	0,470588	0,451613	0,212121	0,047619	0,022222	0,117647	0,117647	0,111111	0,096774
Per17	0,08	0,304348	0,176471	0,5	0,32	0,4	0,590909	0,619048	1	0	0	0,269231	0,375	0,444444	0,214286	0,055556	0,025641	0,142857	0,142857	0,133333	0,12
Br18a	0	0	0	0	0,038462	0	0	0	0	1	1	0	0	0	0	0,142857	0,133333	0,181818	0,181818	0,217391	0,1
Br18s	0	0	0	0	0,038462	0	0	0	0	1	1	0	0	0	0	0,142857	0,133333	0,181818	0,181818	0,217391	0,1
Pan18	0,230769	0,4	0,190476	0,407407	0,357143	0,434783	0,481481	0,5	0,269231	0	0	1	0,580645	0,571429	0,344828	0,04878	0,046512	0,121212	0,121212	0,147059	0,064516
Col18	0,194444	0,393939	0,16129	0,441176	0,4	0,333333	0,5	0,470588	0,375	0	0	0,580645	1	0,71875	0,612903	0,058824	0,037037	0,333333	0,333333	0,351351	0,294118
Ecu18	0,1875	0,322581	0,148148	0,419355	0,333333	0,258065	0,533333	0,451613	0,444444	0	0	0,571429	0,71875	1	0,551724	0,065217	0,040816	0,228571	0,228571	0,25	0,181818
Per18	0,178571	0,241379	0,130435	0,258065	0,181818	0,133333	0,242424	0,212121	0,214286	0	0	0,344828	0,612903	0,551724	1	0,023256	0	0,407407	0,407407	0,428571	0,36
Br19a	0,027778	0,025641	0	0	0,102564	0,027027	0,071429	0,047619	0,055556	0,142857	0,142857	0,04878	0,058824	0,065217	0,023256	1	0,724138	0,076923	0,076923	0,1	0,027027
Br19s	0,026316	0	0	0	0,071429	0,025641	0,044444	0,022222	0,025641	0,133333	0,133333	0,046512	0,037037	0,040816	0	0,724138	1	0,047619	0,047619	0,069767	0
Pan19	0,033333	0,133333	0	0,15625	0,121212	0,032258	0,083333	0,117647	0,142857	0,181818	0,181818	0,121212	0,333333	0,228571	0,407407	0,076923	0,047619	1	1	0,9	0,777778
Col19	0,033333	0,133333	0	0,15625	0,121212	0,032258	0,083333	0,117647	0,142857	0,181818	0,181818	0,121212	0,333333	0,228571	0,407407	0,076923	0,047619	1	1	0,9	0,777778
Ecu19	0,064516	0,16129	0	0,147059	0,181818	0,030303	0,108108	0,111111	0,133333	0,217391	0,217391	0,147059	0,351351	0,25	0,428571	0,1	0,069767	0,9	0,9	1	0,7
Per19	0,038462	0,111111	0	0,137931	0,137931	0	0,060606	0,096774	0,12	0,1	0,1	0,064516	0,294118	0,181818	0,36	0,027027	0	0,777778	0,777778	0,7	1

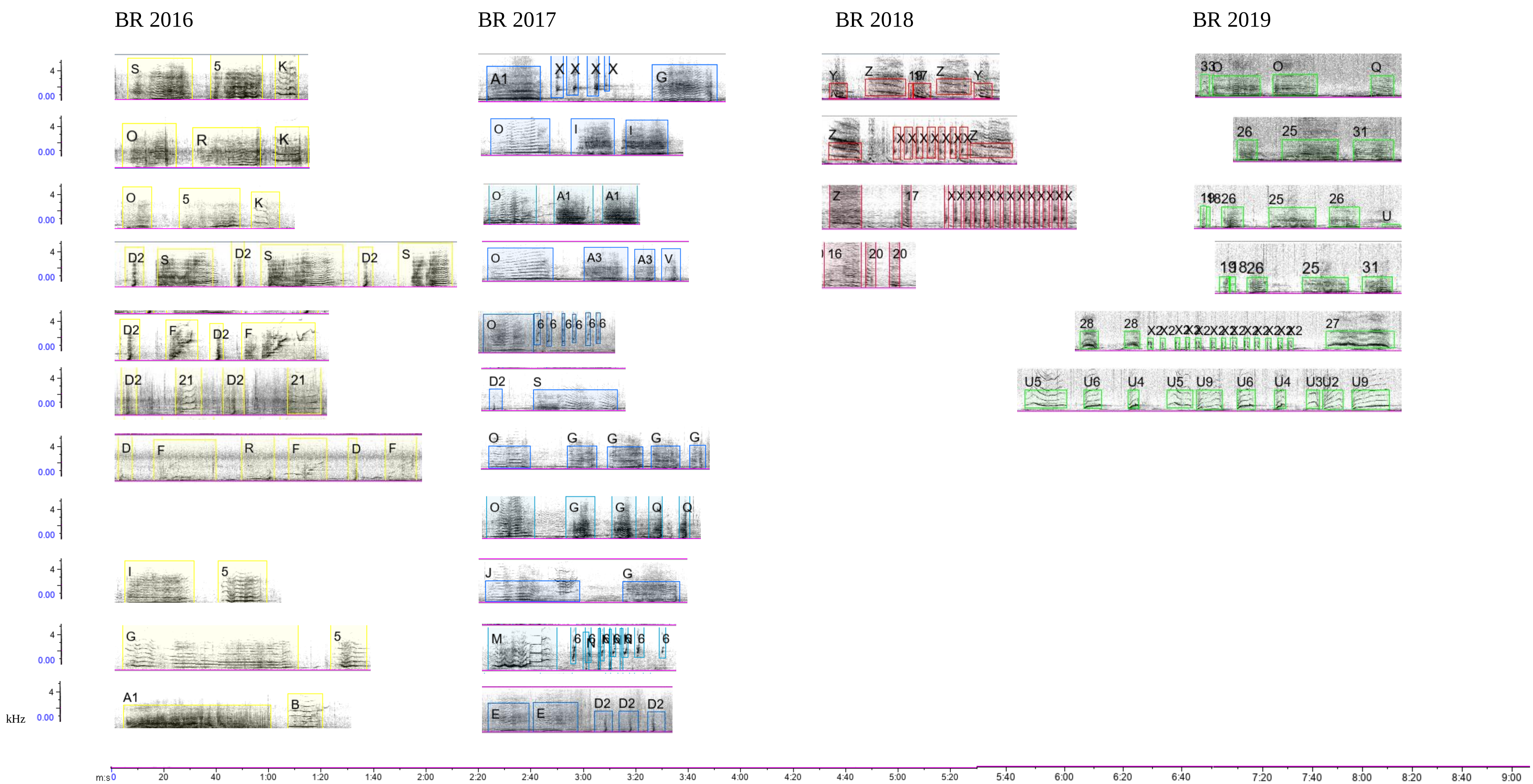
Unpatterned theme sample from BR 2019 song



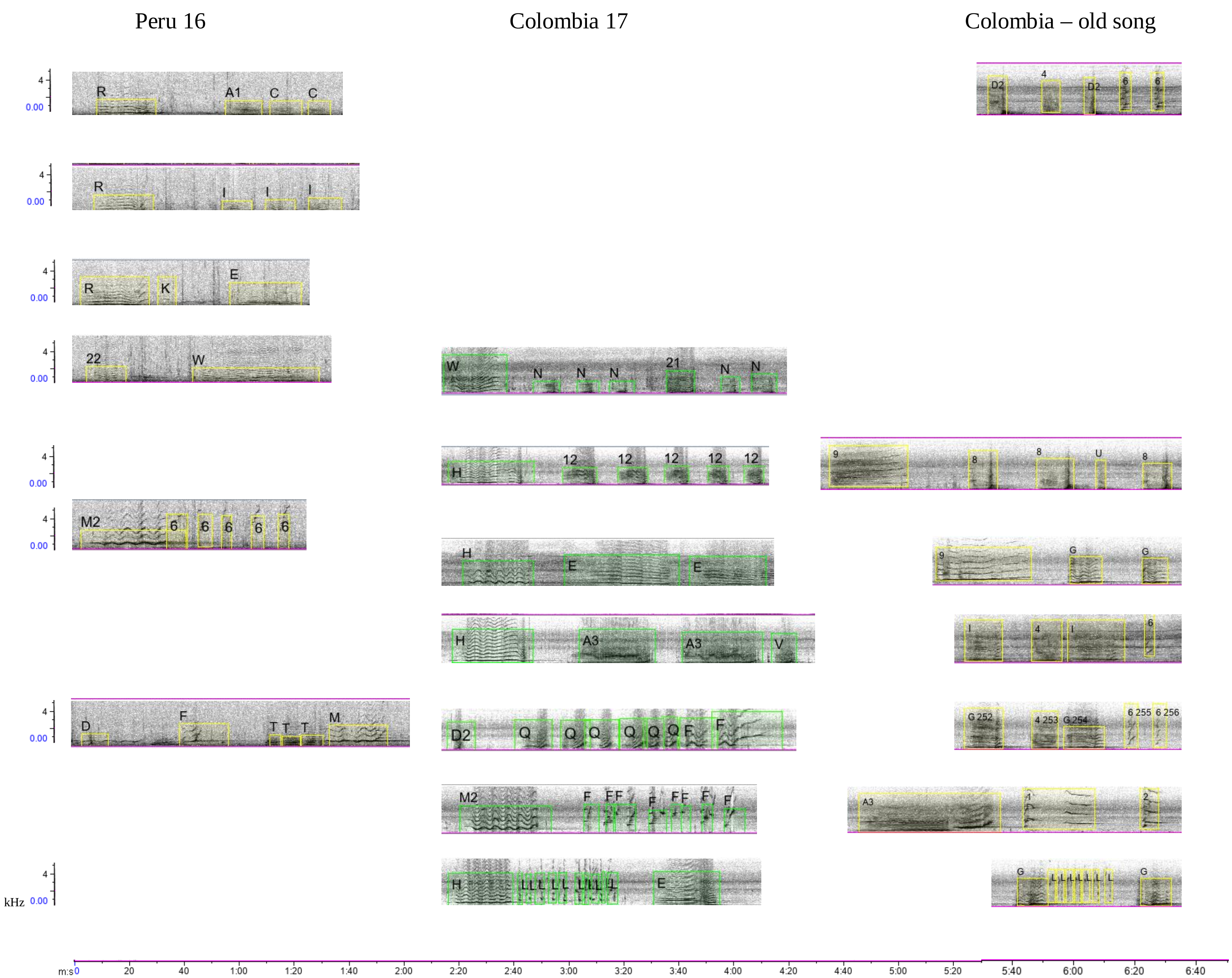
Phrases in 2016

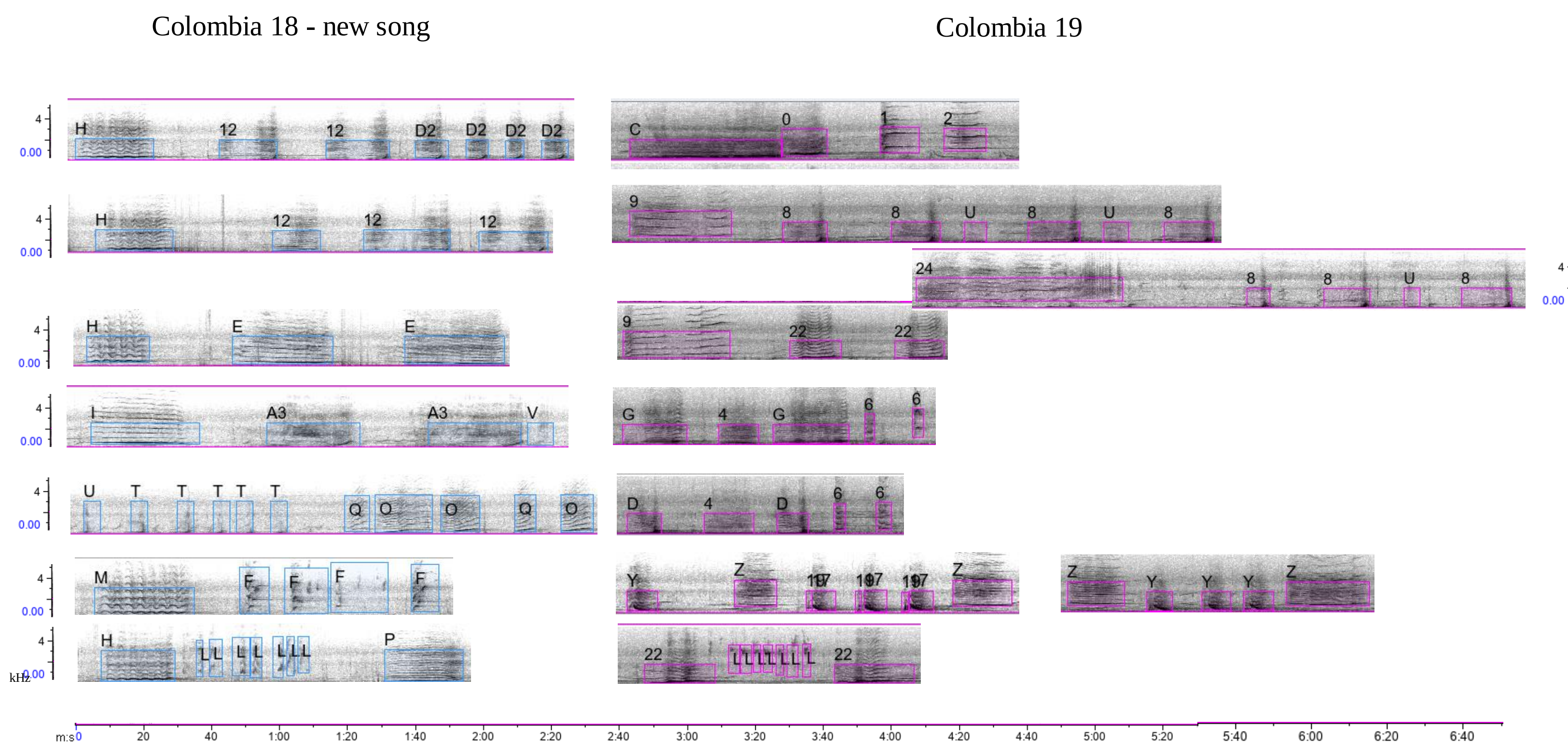


BSA phrases 2016- 2019



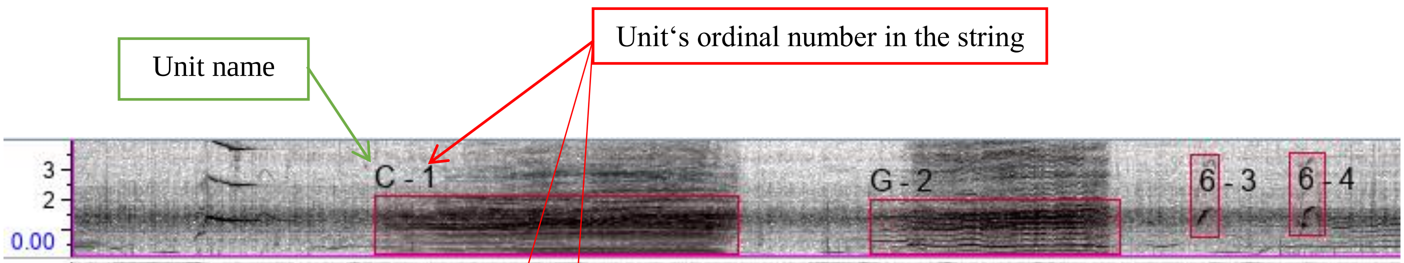
BSG – all phrases 2016-2019



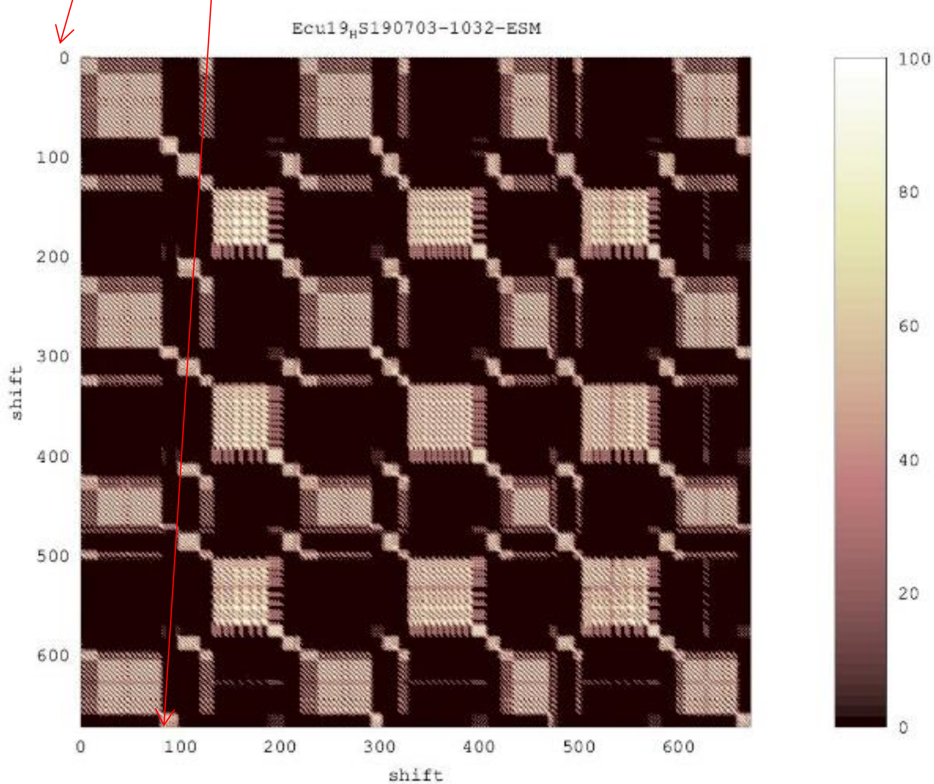

Colombia 18 - new song
Colombia 19
kHz
m:s

Key and Levenshtein matrices vs. Spectrogram

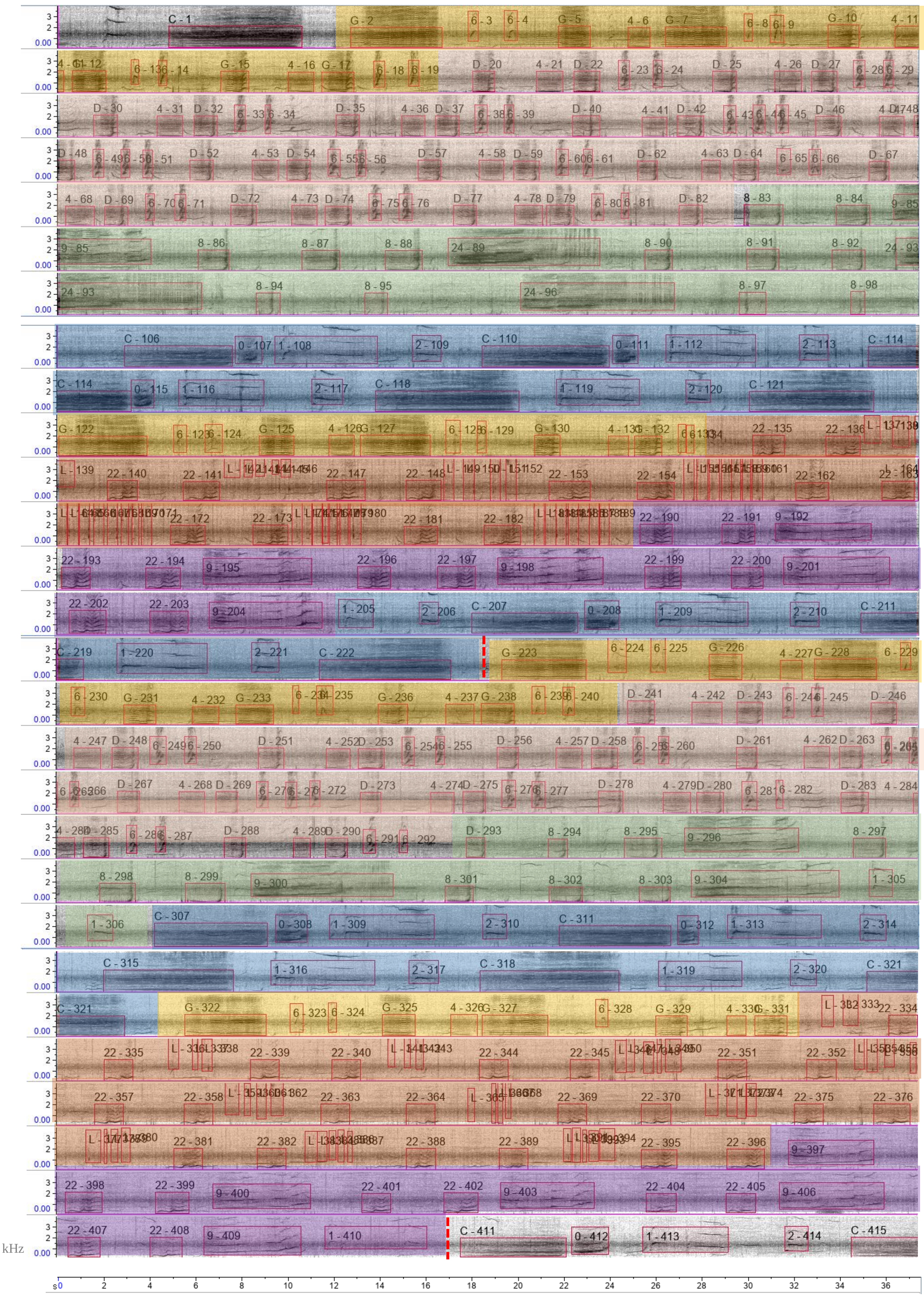
In the figure below, one can see a representation of how both types of matrices (Levenshtein and Key) are able to delineate songs and themes within a longer recording. In this particular case, the song from **Ecuador 2019, 1032**, is presented. In the first part of the section are the spectrograms of the first two song repetitions, and themes within are labeled by color. On the 3rd page, one will find string of units for the first song repetition and how they correspond to the matrices on the right side. The Levenshtein matrix is not able to tell between different theme types, however Key matrix is. The smaller squares of different colors represent diff. theme types, and the big dashed square presents a song.



Unit’s ordinal number is also visible in the table with the unit string of the first two songs on the 3rd page, in addition, it is also necessary to confirm the reliability of the matrices, as you can read the unit’s ordinal position on the axis of the matrices. Interesting to notice is how the last theme is omitted from the second song repetition.



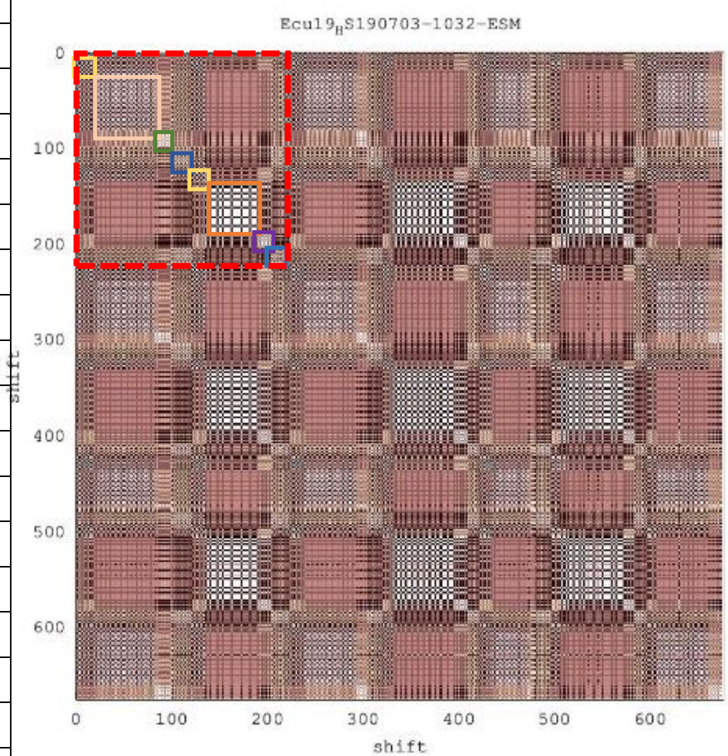
Ecuador 2019- 1032



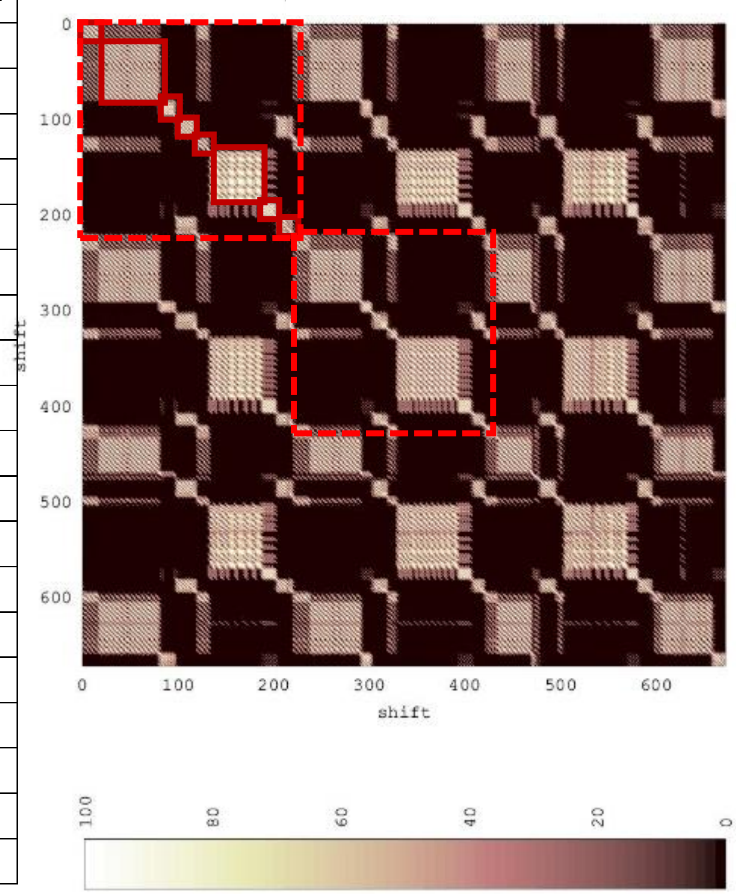
Unit string

unit	no.	unit	no.	unit	no.	unit	no.	unit	no.	unit	no.
C	1	4	41	6	81	G	121	9	161	22	201
G	2	D	42	D	82	6	122	22	162	9	202
6	3	6	43	8	83	6	123	22	163	22	203
6	4	6	44	8	84	G	124	9	164	22	204
G	5	6	45	9	85	4	125	9	165	2	205
4	6	D	46	8	86	G	126	1	166	C	206
G	7	4	47	8	87	6	127	2	167	0	207
6	8	D	48	8	88	6	128	C	168	C	208
6	9	6	49	24	89	G	129	0	169	2	209
G	10	6	50	8	90	4	130	1	170	C	210
4	11	6	51	8	91	G	131	22	171	1	211
G	12	D	52	8	92	6	132	22	172	2	212
6	13	4	53	24	93	6	133	L	173	C	213
6	14	D	54	8	94	22	134	L	174	0	214
G	15	6	55	8	95	22	135	L	175	1	215
4	16	6	56	24	96	L	136	L	176	2	216
G	17	D	57	8	97	L	137	L	177	C	217
6	18	4	58	8	98	L	138	L	178	0	218
6	19	D	59	9	99	22	139	L	179	C	219
D	20	6	60	1	100	22	140	L	180	2	220
4	21	6	61	2	101	L	141	22	181	C	221
D	22	D	62	C	102	L	142	22	182		
6	23	4	63	0	103	L	143	L	183		
6	24	D	64	1	104	L	144	L	184		
D	25	6	65	2	105	L	145	L	185		
4	26	6	66	C	106	22	146	L	186		
D	27	D	67	0	107	22	147	L	187		
6	28	4	68	1	108	L	148	L	188		
6	29	D	69	2	109	L	149	L	189		
D	30	6	70	C	110	L	150	22	190		
4	31	6	71	0	111	L	151	22	191		
D	32	D	72	1	112	22	152	9	192		
6	33	4	73	2	113	22	153	22	193		
6	34	D	74	C	114	L	154	22	194		
D	35	6	75	0	115	L	155	9	195		
4	36	6	76	1	116	L	156	22	196		
D	37	D	77	2	117	L	157	22	197		
6	38	4	78	C	118	L	158	9	198		
6	39	D	79	1	119	L	159	22	199		
D	40	6	80	2	120	L	160	22	200		

Key matrix

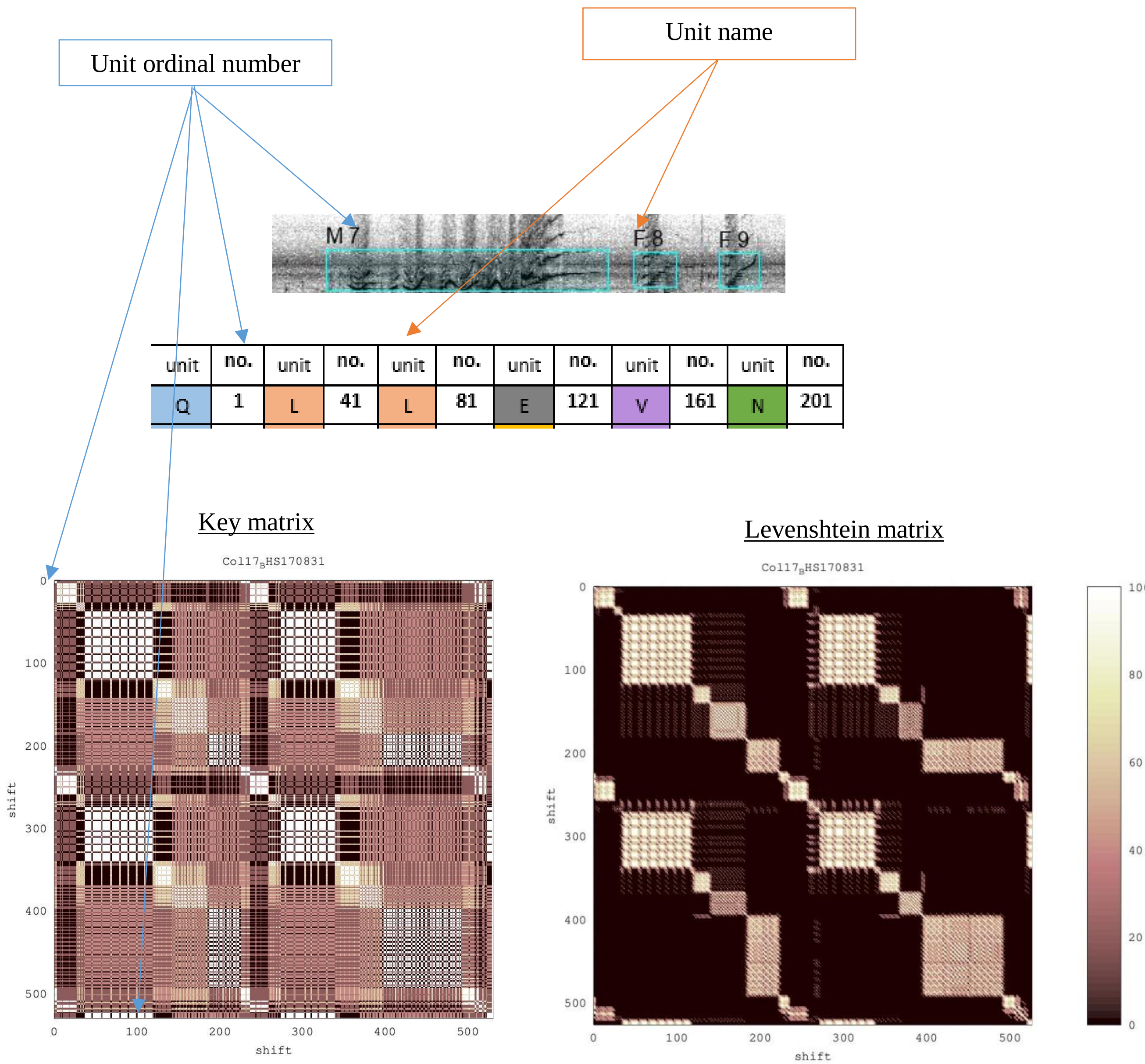


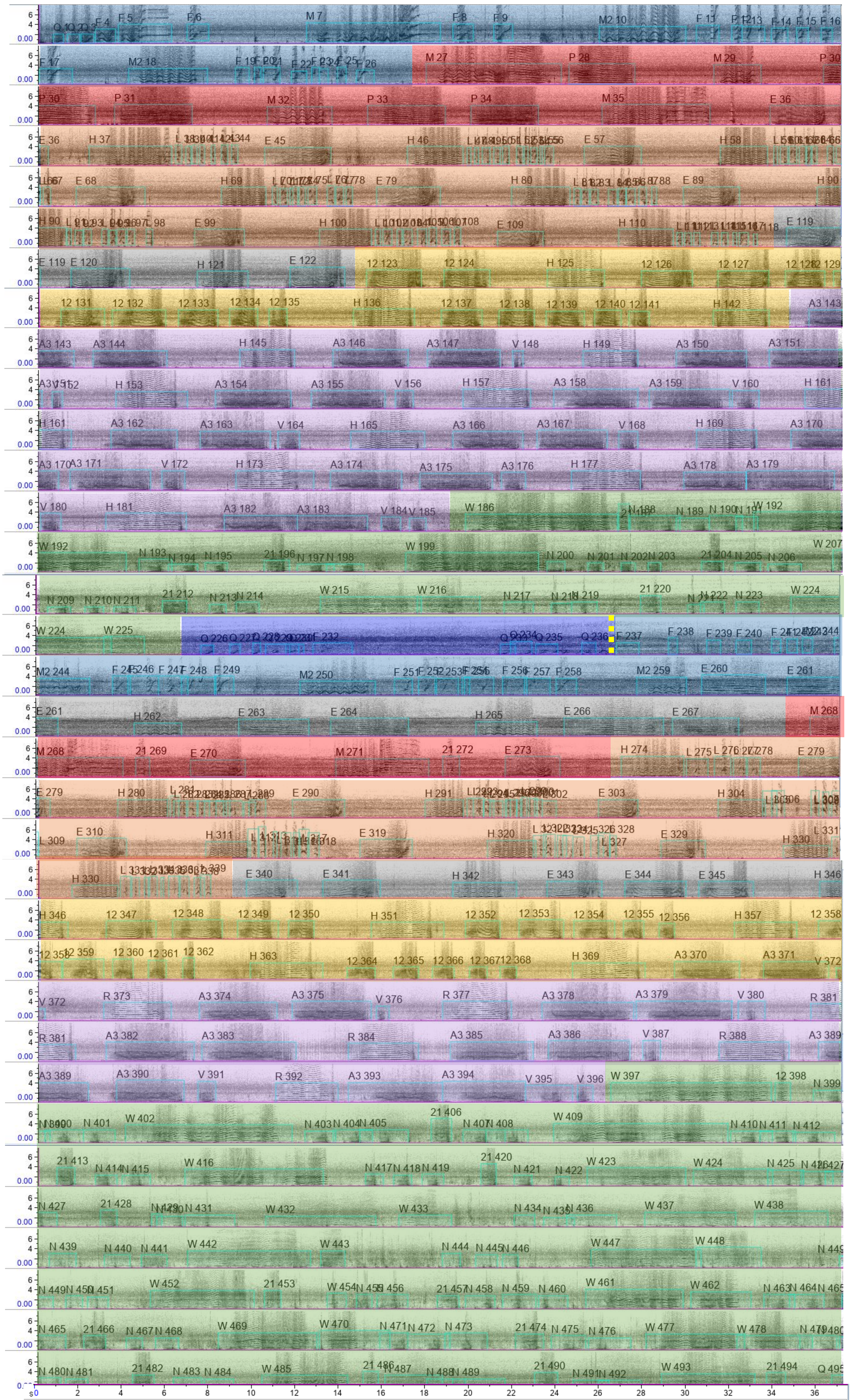
Levenshtein matrix



Validity of the Key matrix method for accessing different theme types, and song repetitions

A recording from **Colombia in 2017, 0831,** is presented as an example, by the spectrogram of the whole recording, 23 minutes long, containing two songs. This section will demonstrate how well in detail the Key matrix recording representation is overlapping with the situation on the spectrogram of the same recording, shown through the correspondence of the unit string of the first song, which can be found on the third page of this section, in the table on the left. Colors in the table and the matrix squares, correspond to the ones on the spectrogram, labeling different theme types.



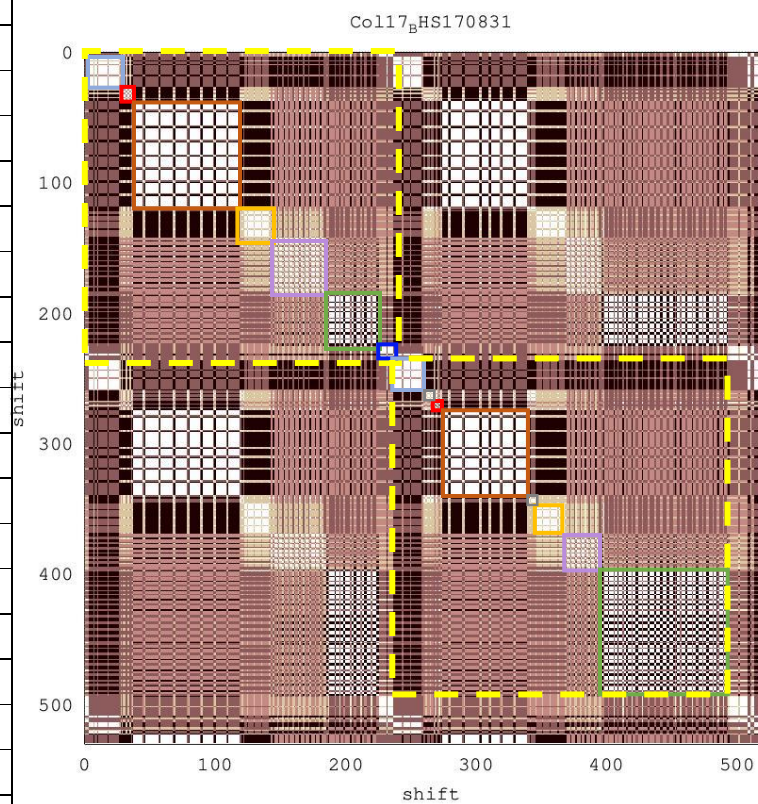


6
4
0.00
s 0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36

Unit string

unit	no.	unit	no.	unit	no.	unit	no.	unit	no.	unit	no.
Q	1	L	41	L	81	E	121	V	161	N	201
Q	2	L	42	L	82	12	122	H	162	N	202
Q	3	L	43	L	83	12	123	A3	163	N	203
F	4	L	44	L	84	H	124	A3	164	N	204
F	5	E	45	L	85	12	125	V	165	21	205
F	6	H	46	L	86	12	126	H	166	N	206
M	7	L	47	L	87	12	127	A3	167	N	207
F	8	L	48	E	88	12	128	A3	168	W	208
F	9	L	49	H	89	H	129	V	169	W	209
M2	10	L	50	L	90	12	130	H	170	N	210
F	11	L	51	L	91	12	131	A3	171	N	211
F	12	L	52	L	92	12	132	A3	172	N	211
F	13	L	53	L	93	12	133	V	173	21	212
F	14	L	54	L	94	12	134	H	174	N	213
F	15	L	55	L	95	H	135	A3	175	N	214
F	16	L	56	L	96	12	136	A3	176	W	215
F	17	E	57	L	97	12	137	A3	177	W	216
M2	18	H	58	E	98	12	138	H	178	N	217
F	19	L	59	H	99	12	139	A3	179	N	218
F	20	L	60	L	100	12	140	A3	180	N	219
F	21	L	61	L	101	A3	141	V	181	21	220
F	22	L	62	L	102	H	142	H	182	N	221
F	23	L	63	L	103	A3	143	A3	183	N	222
F	24	L	64	L	104	A3	144	A3	184	N	223
F	25	L	65	L	105	H	145	V	185	W	224
F	26	L	66	L	106	A3	146	V	186	W	225
M	27	L	67	L	107	A3	147	21	187	Q	226
P	28	E	68	E	108	V	148	N	188	Q	227
M	29	H	69	H	109	H	149	N	189	Q	228
P	30	L	70	L	110	A3	150	N	190	Q	229
P	31	L	71	L	111	A3	151	N	191	Q	230
M	32	L	72	L	112	V	152	W	192	Q	231
P	33	L	73	L	113	H	153	N	193	F	232
P	34	L	74	L	114	A3	154	N	194	Q	233
M	35	L	75	L	115	A3	155	N	195	Q	234
E	36	L	76	L	116	V	156	21	196	Q	235
H	37	L	77	L	117	H	157	N	197	Q	236
L	38	L	78	E	118	A3	158	N	198		
L	39	E	79	E	119	A3	159	W	199		
L	40	H	80	H	120	H	160	21	200		

Key matrix

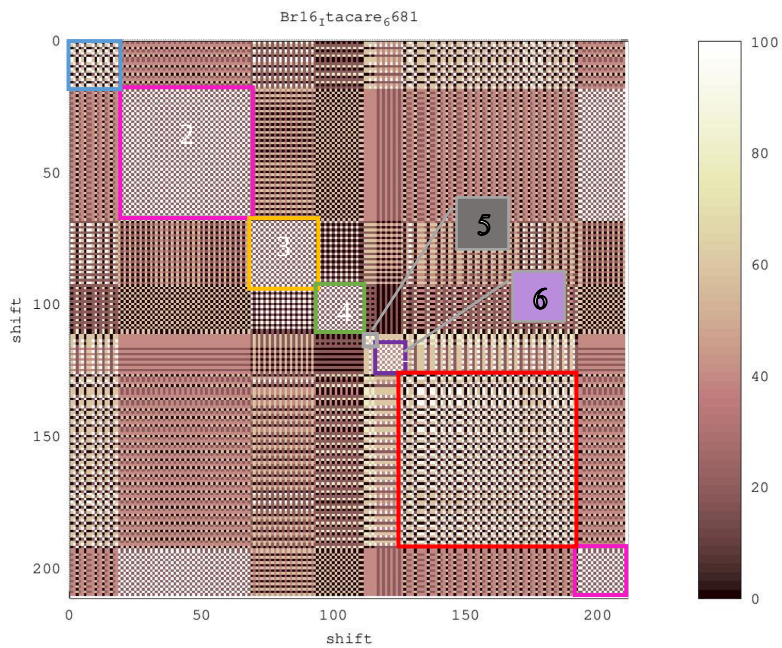


Syntax vs. Unit structure in the matrix representation

An example of how the Key matrix “understands” structure (syntax) vs. unit types- Brazil 2016, 6681 recording.

As you could notice, themes 2, 3, 4, 5 and 6 are all made of only 2 unit types, different ones. As you can see in the matrix below, it represents these themes as equal, although they are made of different unit types. However, from this example we can see how the matrix "reacts" on the syntax, rather than unit type. Moreover, themes 1 and 7 are also represented very much alike, and by their composition (in the spectrogram), you can understand why (S + 5+ K and O + 5+ K).

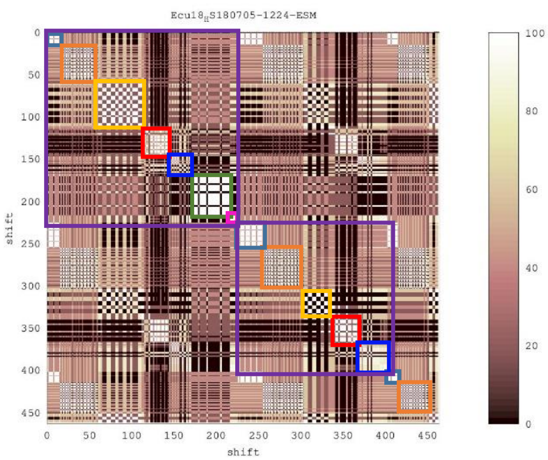
<u>Key matrix</u>



Variable theme order

In this section, different Key matrices are demonstrating how the theme order is rather a flexible song character, even within the same song session, thus, should be treated as such. The theme order is stereotyped, but not necessarily fixed. Because of this song property, in the text was insisted on excluding the order of themes as an important specificity determining a song type.

Example 1, Ecuador 2018



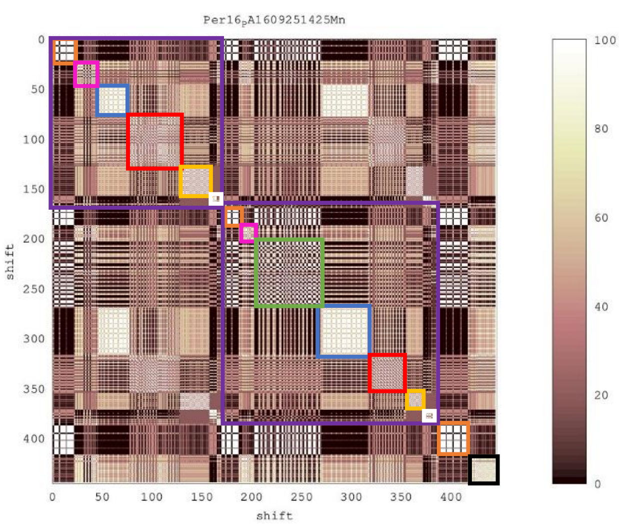
<u>1st song theme order</u>:

Gray-orange-yellow-red-blue-green-pink

<u>2nd song:</u>

Gray-orange-yellow-red-blue

Example 2, Peru 2016



<u>1st song theme order</u>:

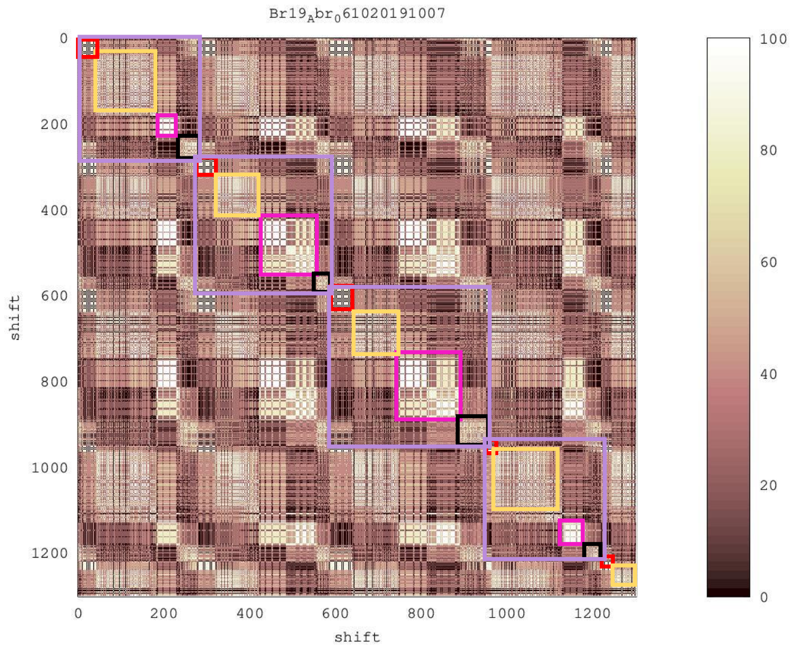
Orange-pink-blue-red-yellow-white

<u>2nd song:</u>

Orange-pink-green-blue-red-yellow-white

<u>3rd song, beginning:</u>

Orange-black

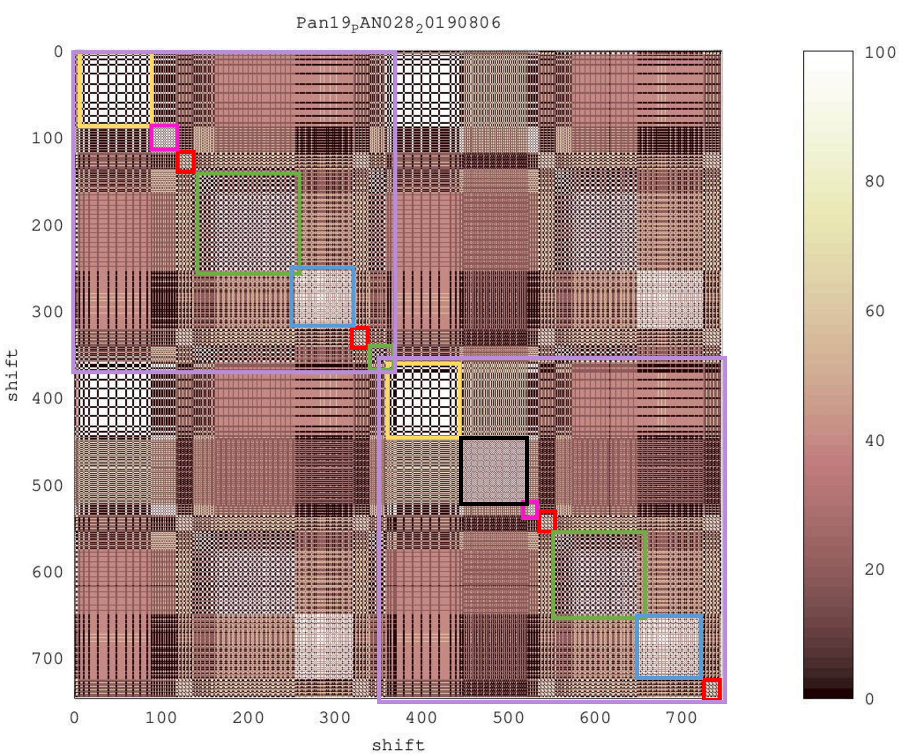


<u>An example where the themes are in the same order in all 4 song renditions</u>:

Red-yellow-pink-black(unpatterned)

(You can notice how the same themes defer in length (square size) in every song repetition)

Example 4, Panama 2019

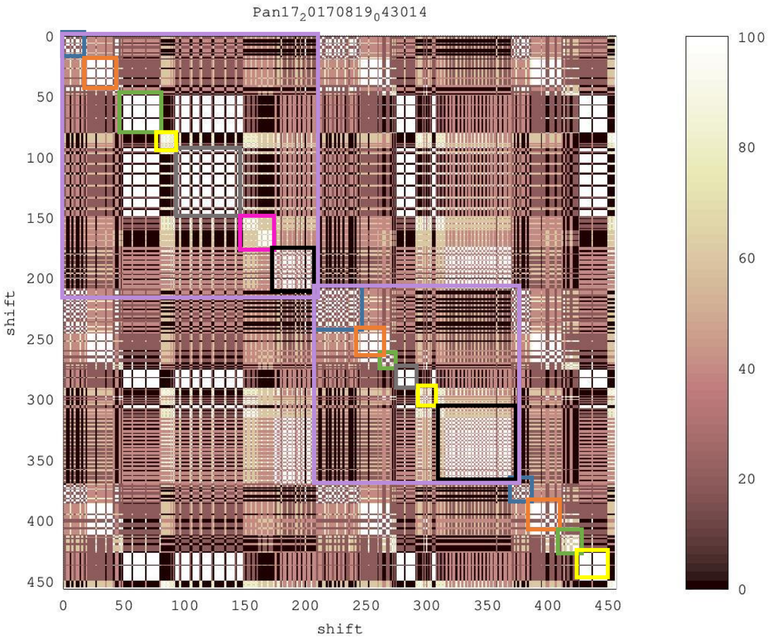


<u>1st song theme order:</u>

Yellow-pink-red-green-blue-red-green

<u>2nd song:</u>

Yellow-black-pink-red-green-blue-red-?



<u>1st song theme order:</u>

Blue-orange-green-yellow-gray-pink-black

<u>2nd song:</u>

Blue-orange-green-gray-yellow-black

<u>3rd song, beginning:</u>

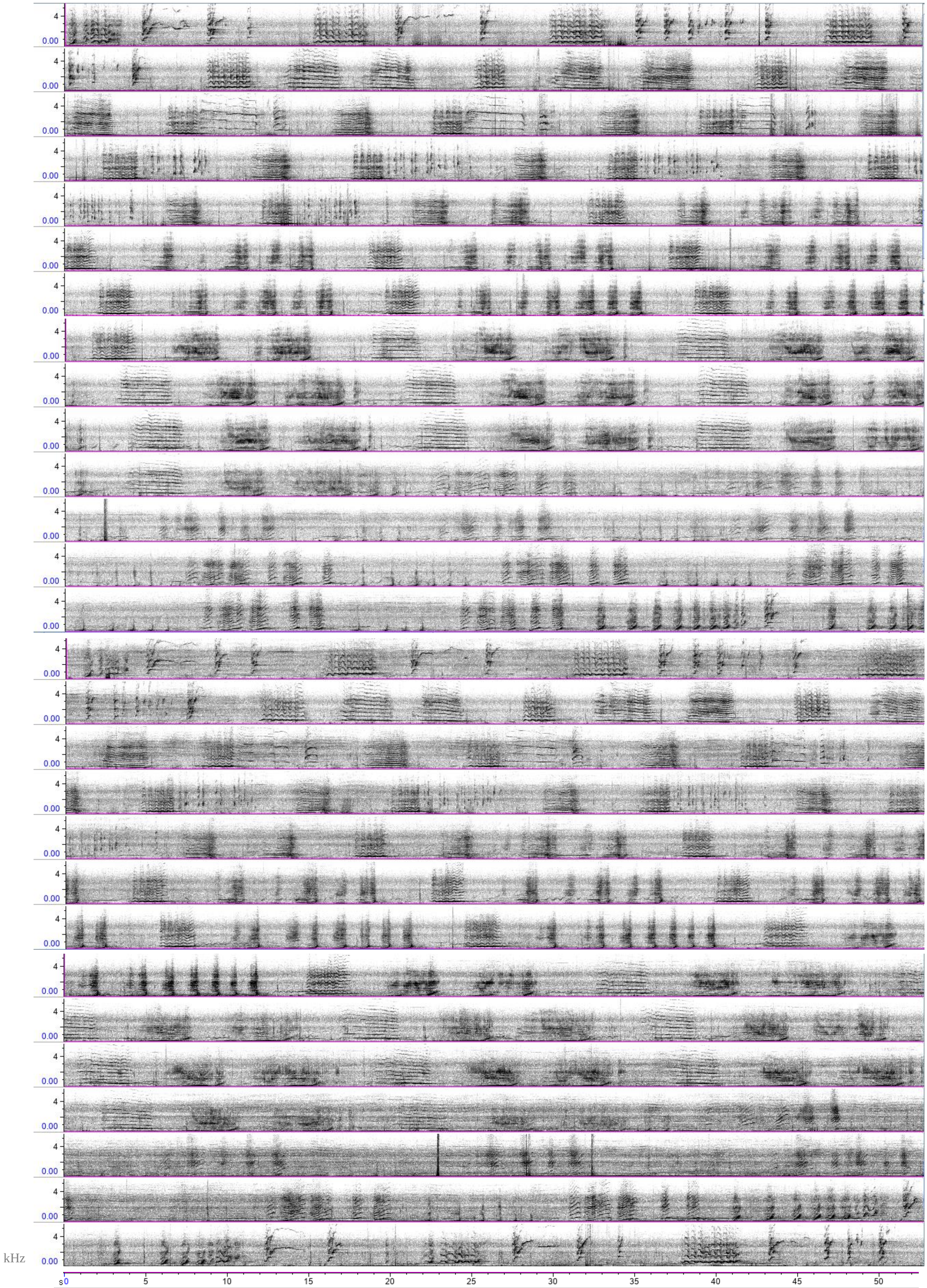
Blue-orange-green-yellow-?

Spectrograms of (di)similar matrices

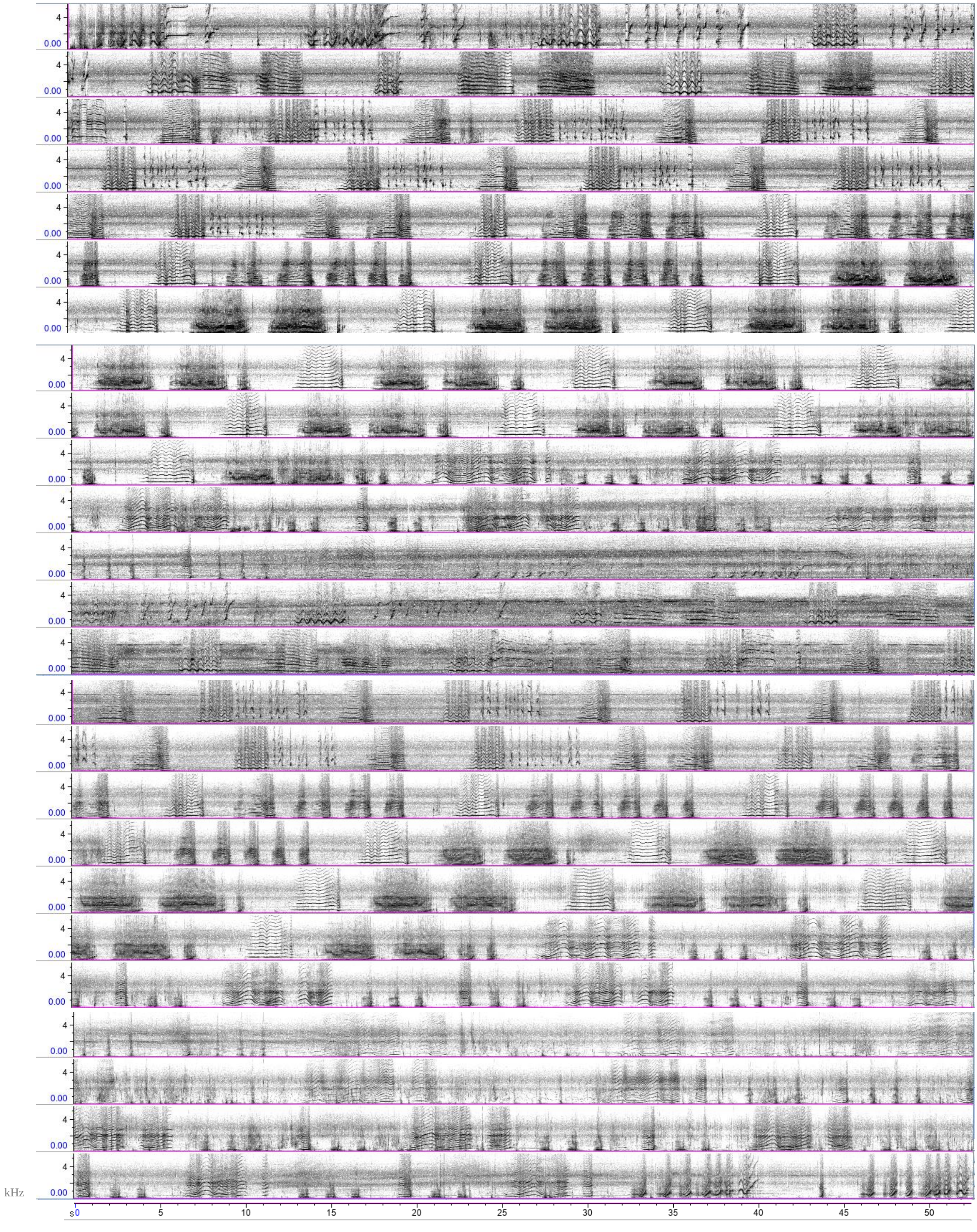
Comparison of the spectrograms of different recordings, which are very similar as of the same location in consecutive years (Colombia 2017 and Colombia 2018-old song). One more recording, Brazil 2017, is presented by the spectrogram of its distinctive song. However, slight overlaps in the song structure between two locations are visible.

Finally, on the last page of this section you can see how this similarity/dissimilarity in the song structure corresponds to the similarity in the matrix visual structure representation (Key and Levenshtein). Matrices are to the scale.

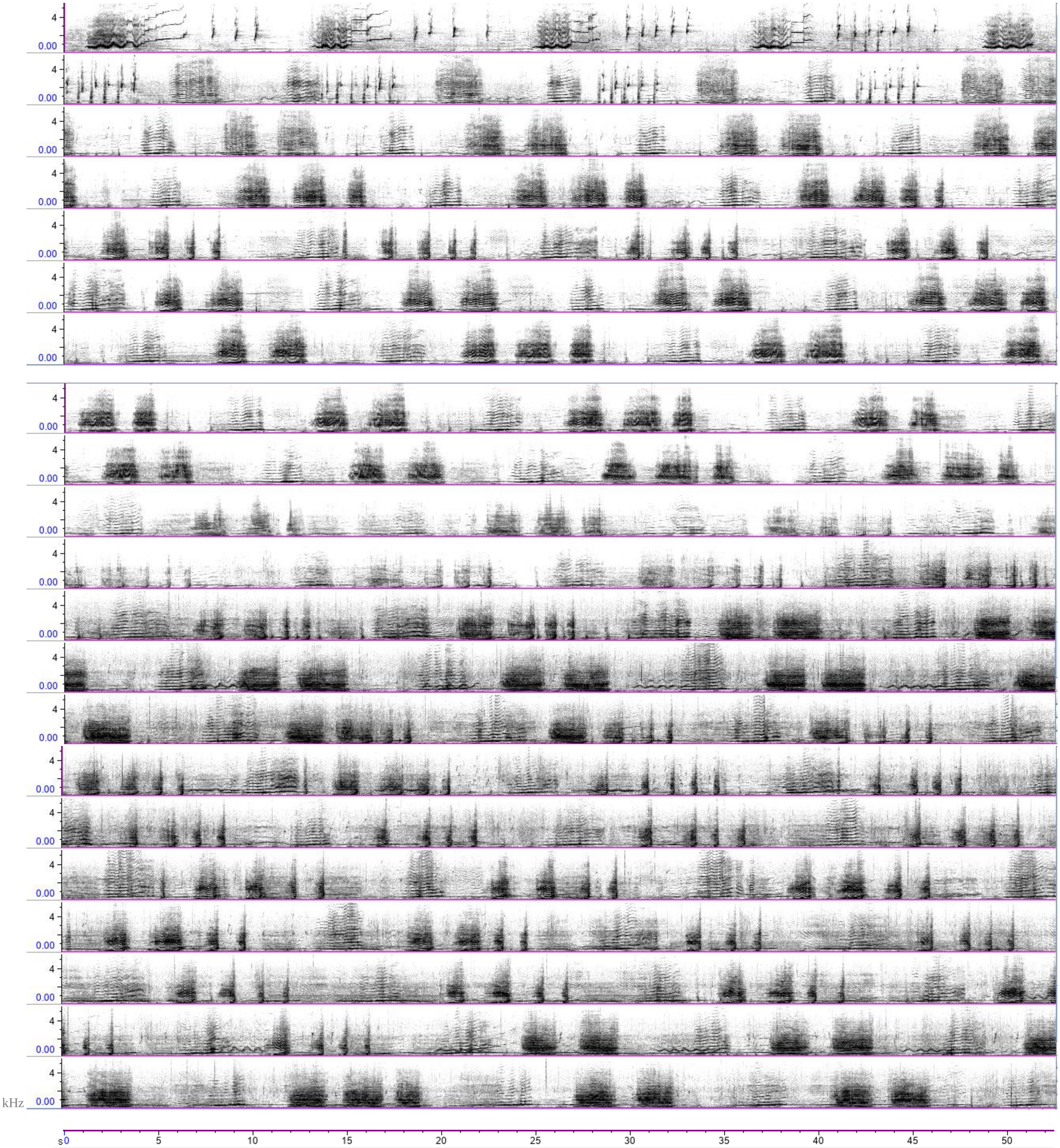
Colombia 2018, 1118- old song



Colombia 2017, 0831



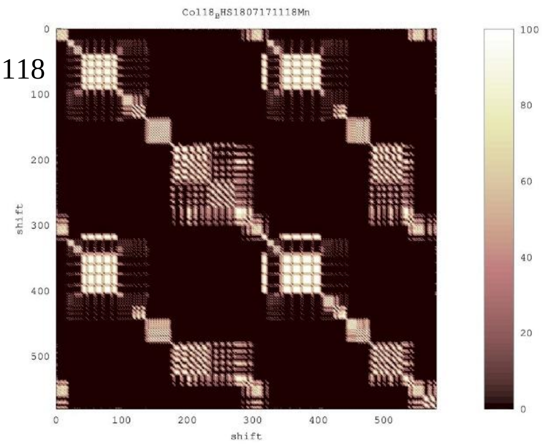
Brazil 2017, 004

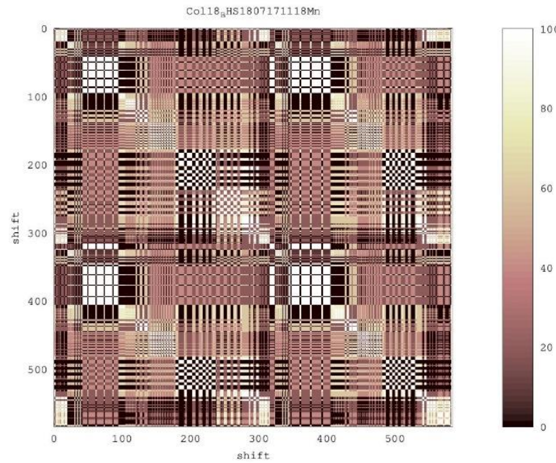


Levenshtein matrices

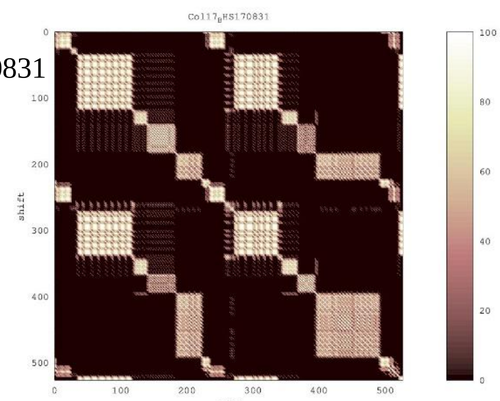
Key matrices

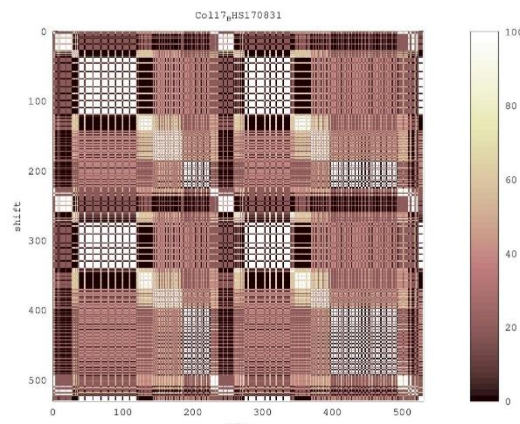
Colombia 2018, 1118



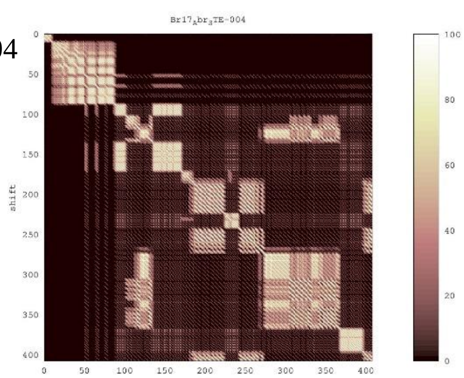


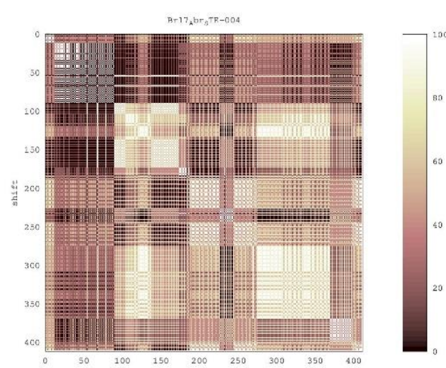
Colombia 2017, 0831





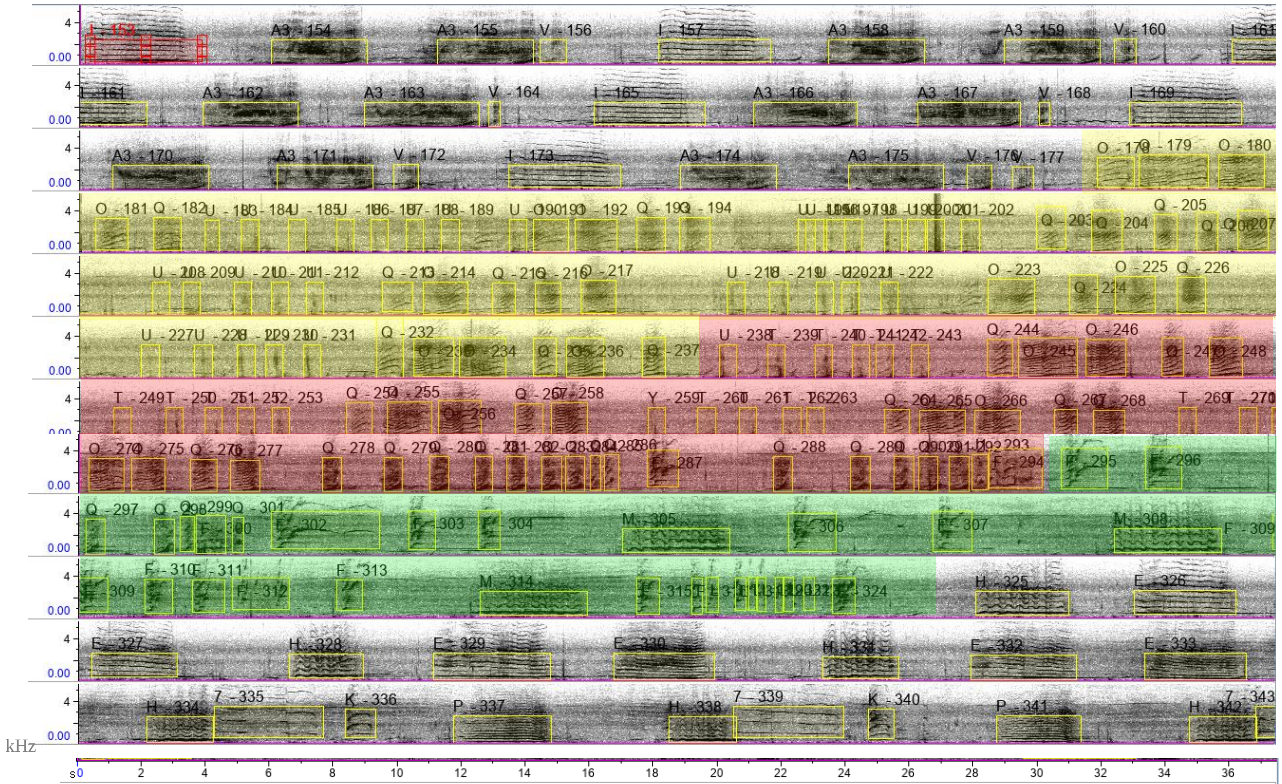
Brazil 2017, 004



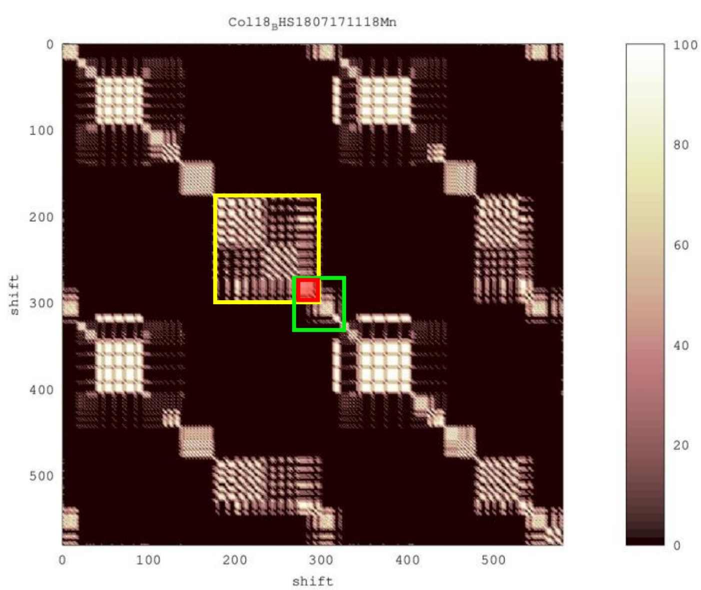


No-transitional traverse between themes

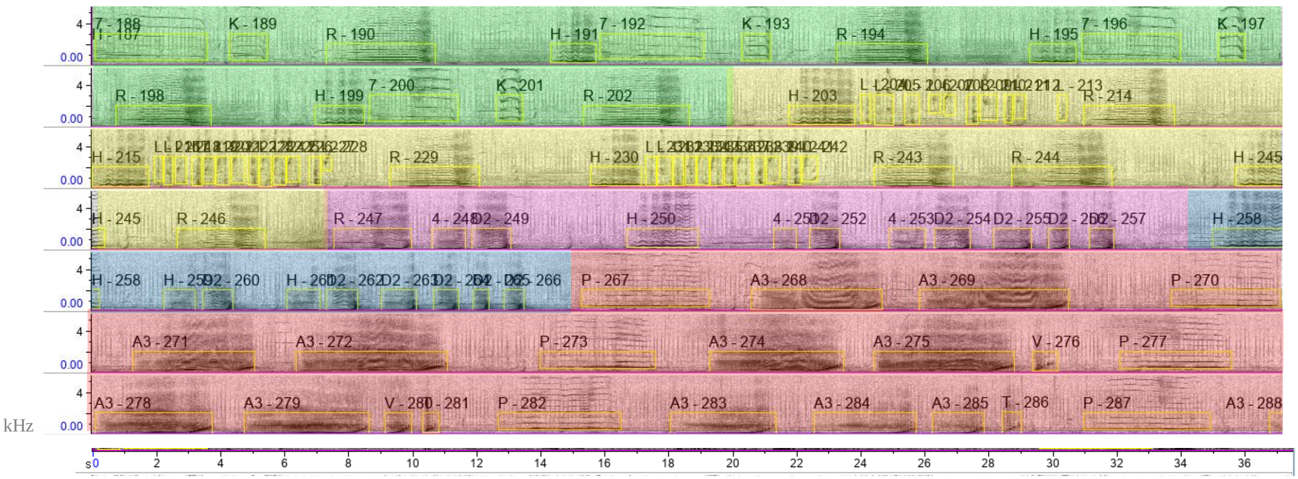
Colombia 2018, 1118



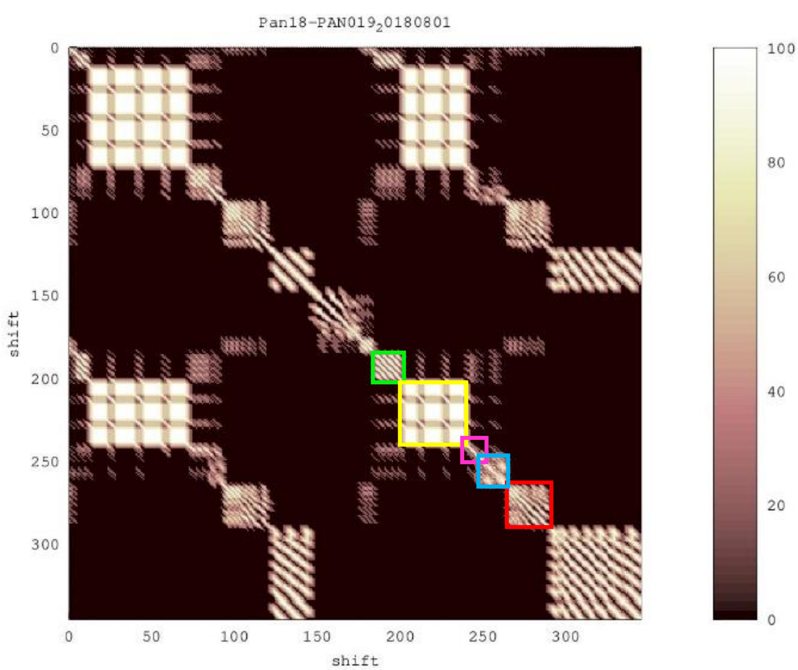
Red labels the no-transitional traverse, as it contains unit types Y and T, which are not present in the neighboring themes. However, this observation is apparently sensitive to unit classification method.



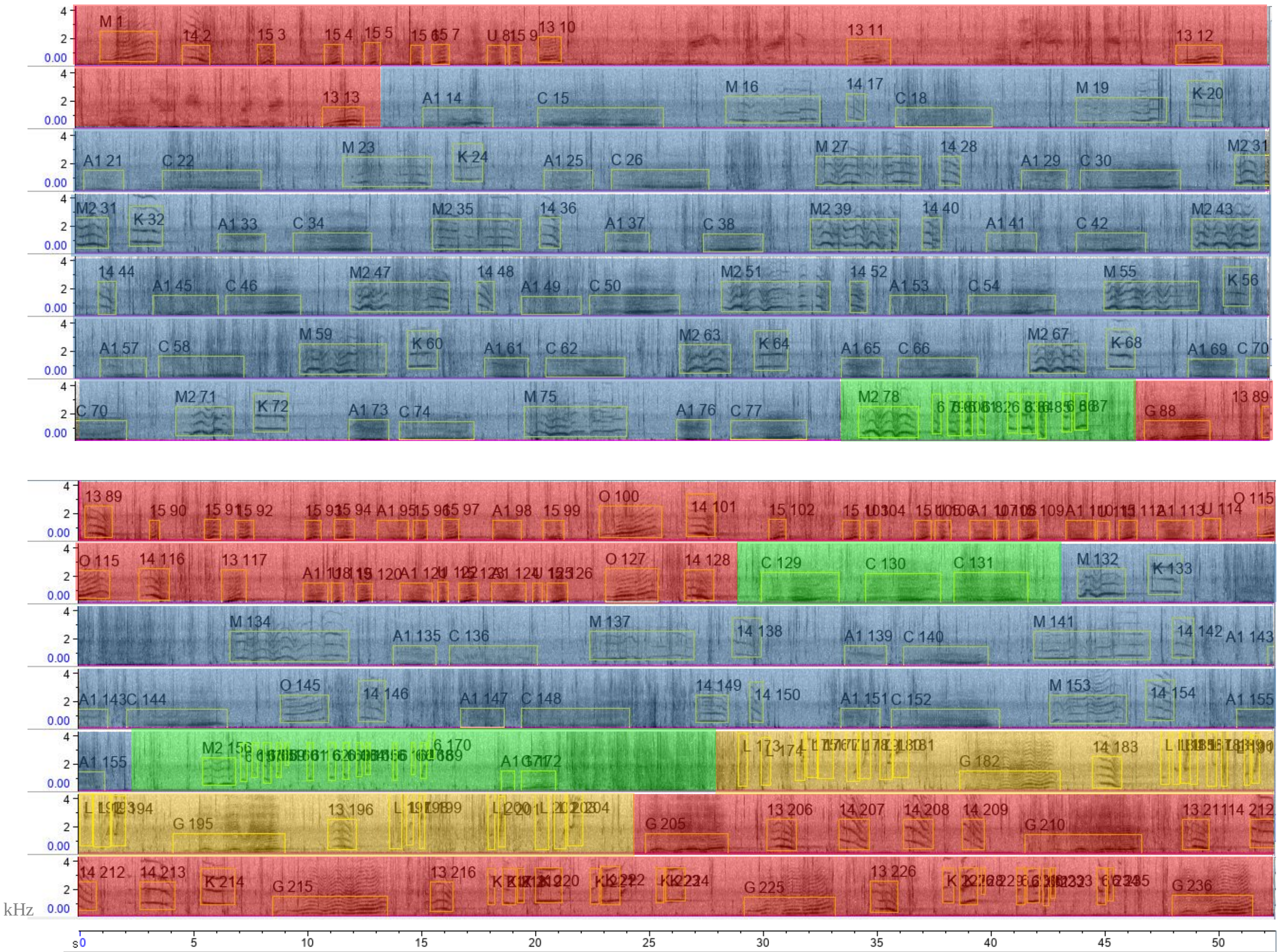
Panama 2018, 0801



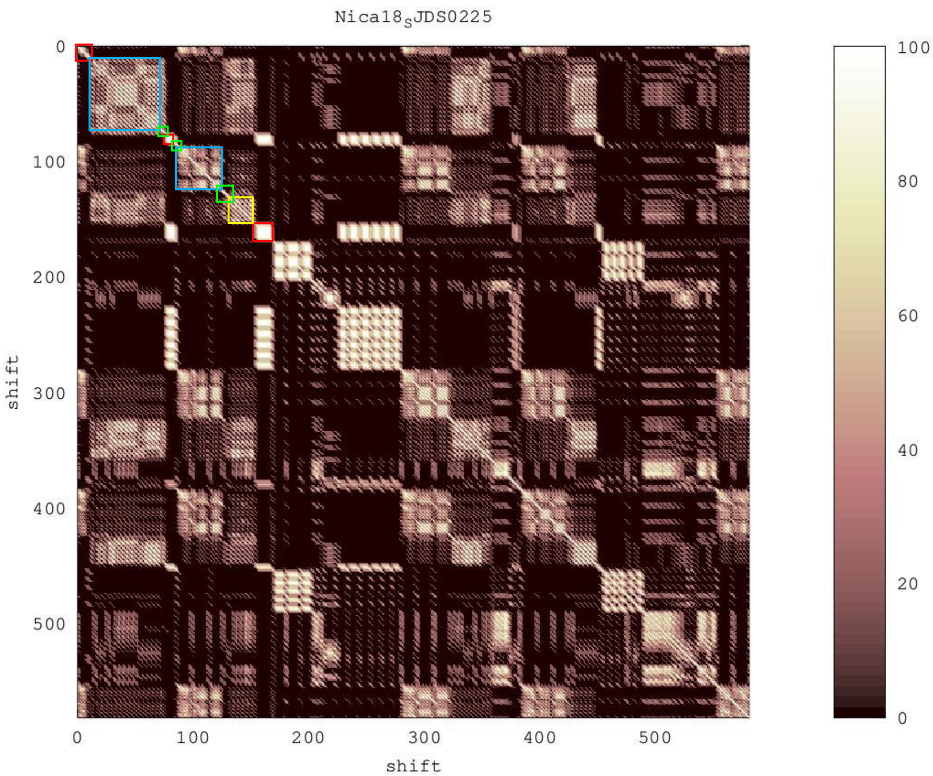
Pink part is what seems to be a no-transitional traverse, as in contains unit type 4, which is not present in the neighboring themes.



Nicaragua 2018, 0225

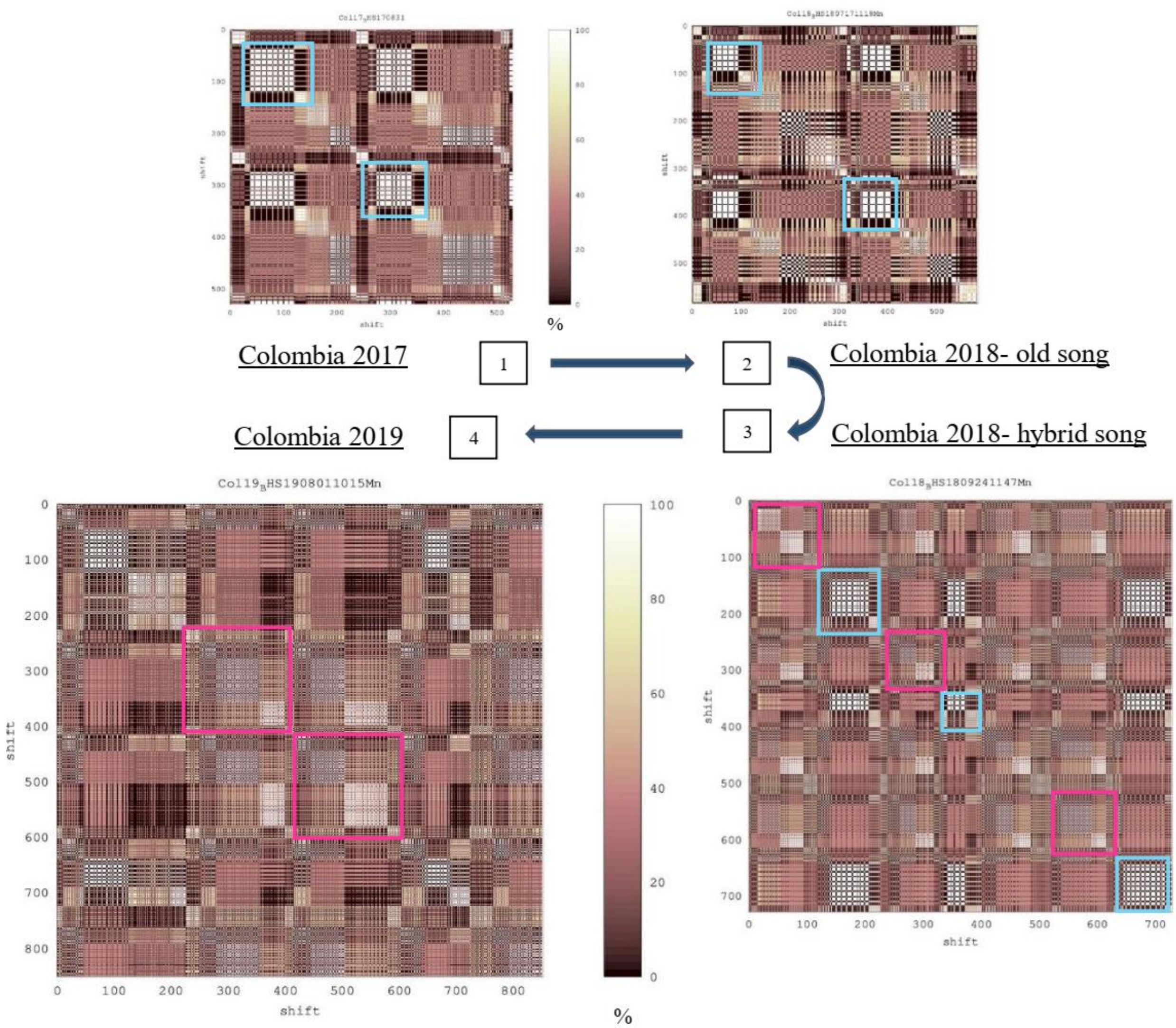


Green represents no-transitional traverses, and there are two different ones in this section of the recording. Ona type is apparent two times, containing units M2 and 6, while the second is composed of only one unit type- C. The Key matrix of this recording is on the next page.

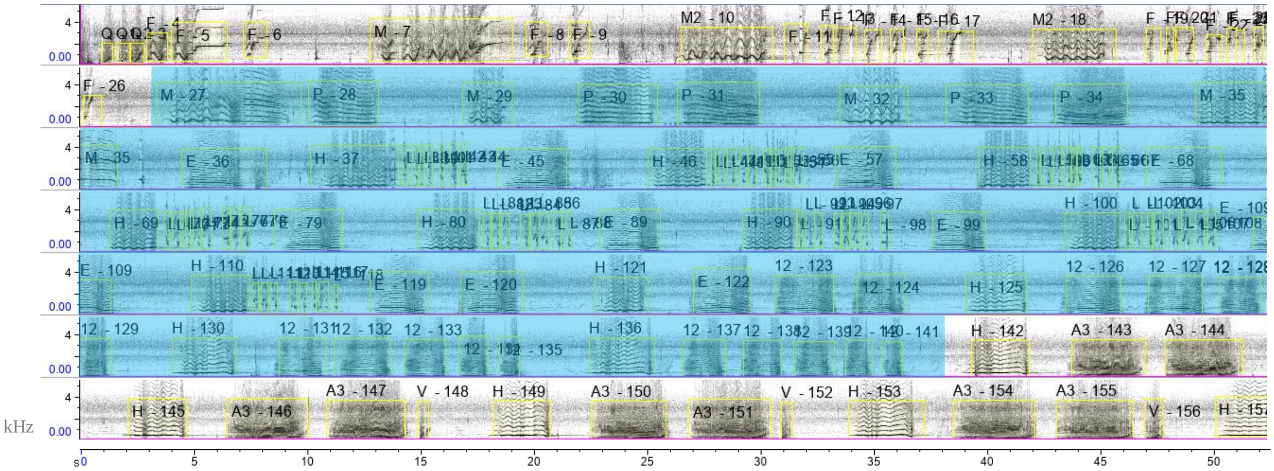

Nica18SJDS0225
shift
shift
0
100
200
300
400
500
0
100
200
300
400
500
100
80
60
40
20
0

Spectrograms with the Figure 10, Chapter II

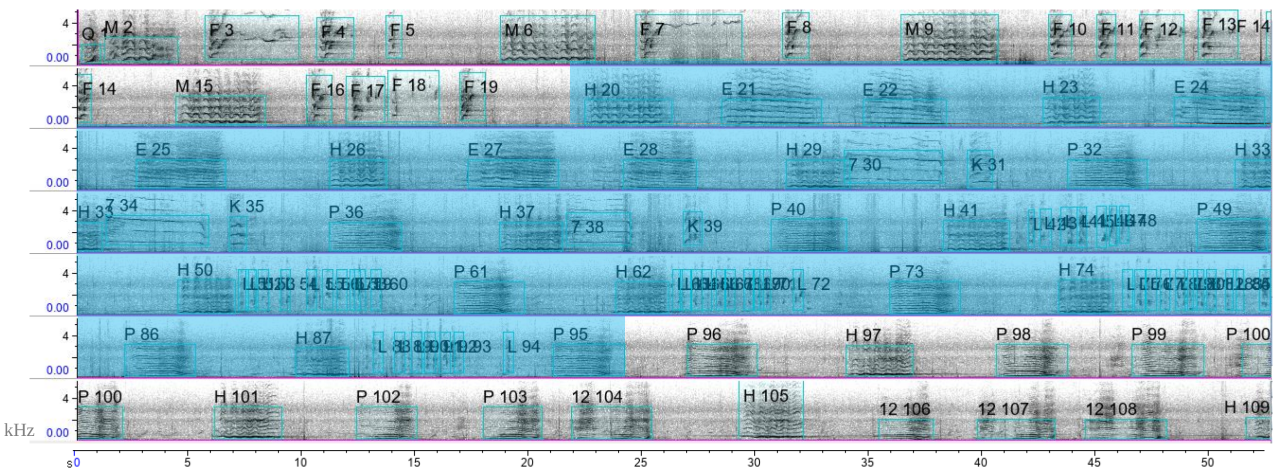
Spectrograms corresponding to the figure belowe - spectrograms are showing only parts of the entire recordings, demonstrated by the matrices.



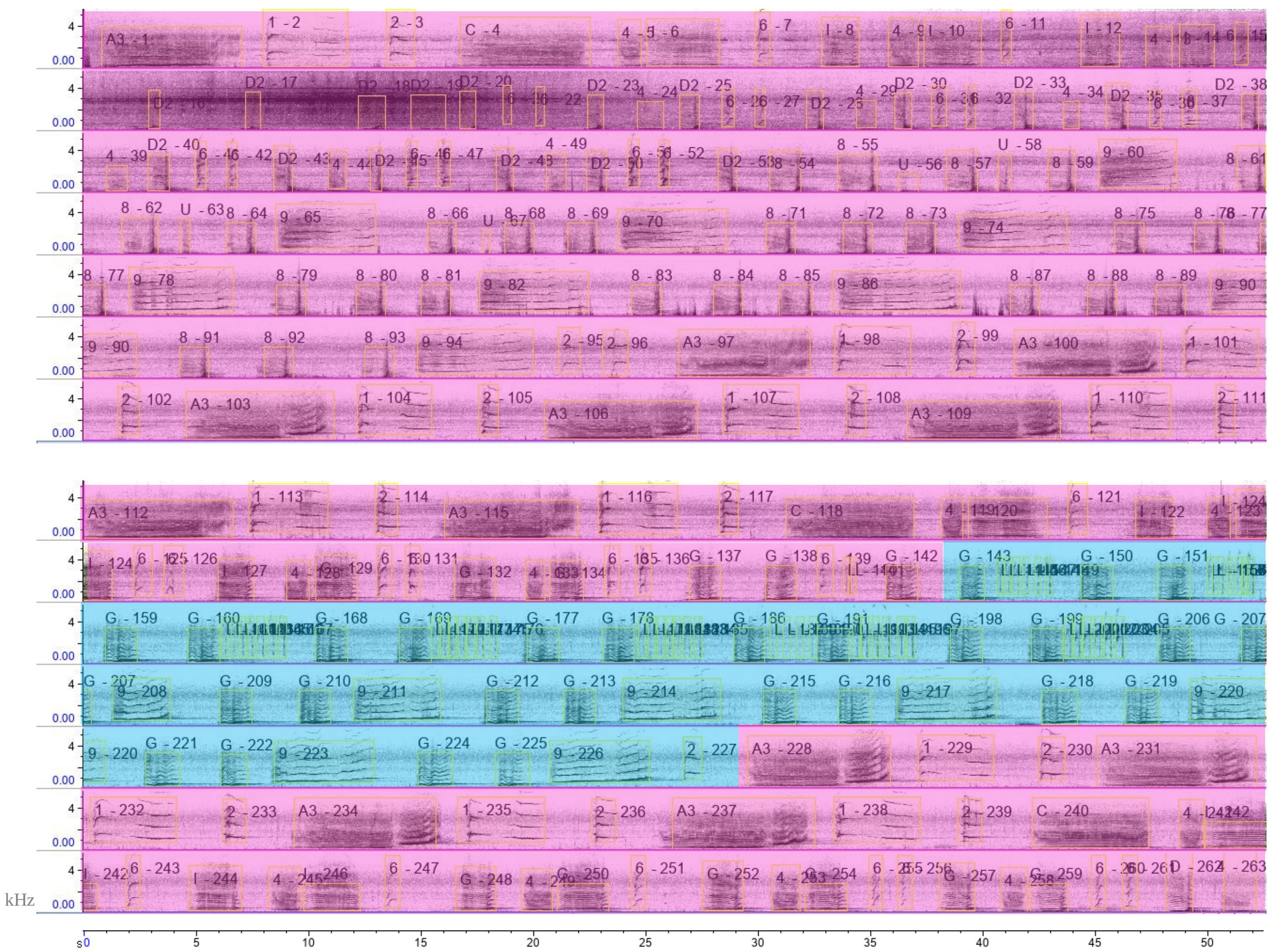
Colombia 2017, 0831 (step 1)



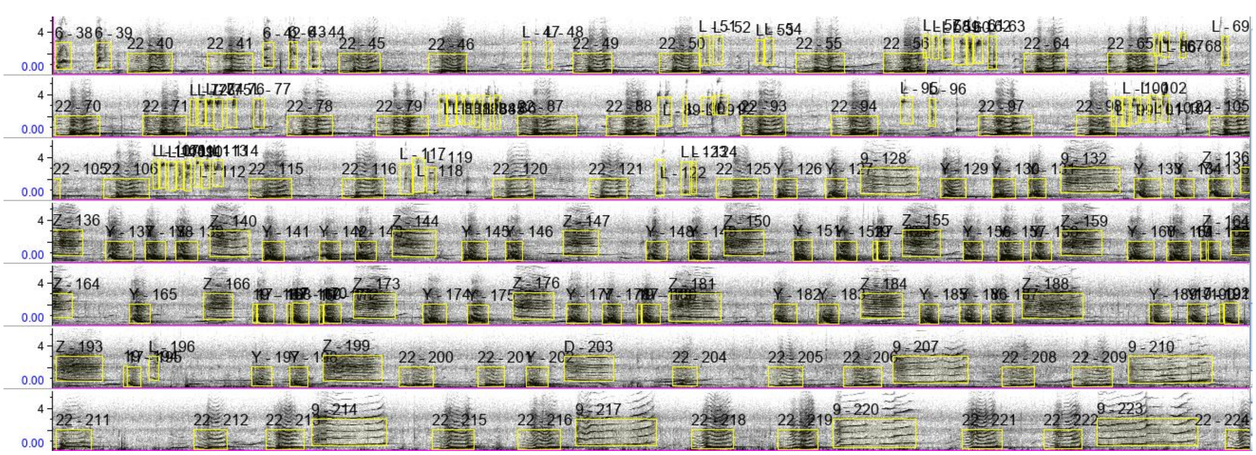
Colombia 2018, 1118- old song (step 2)

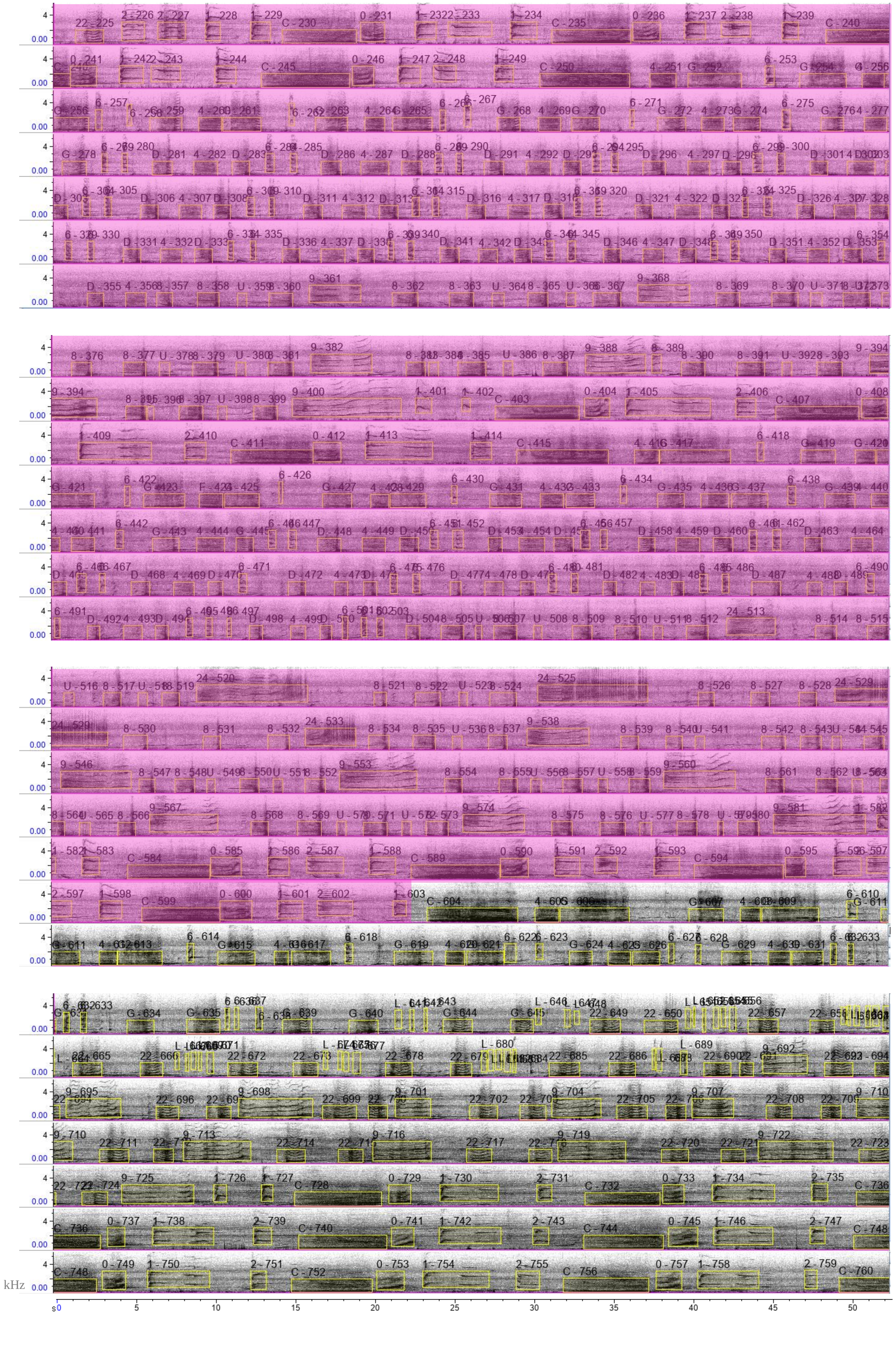


Colombia 2018, 1147- hybrid song (step 3)



Colombia 2019, 1015 (Step 4)

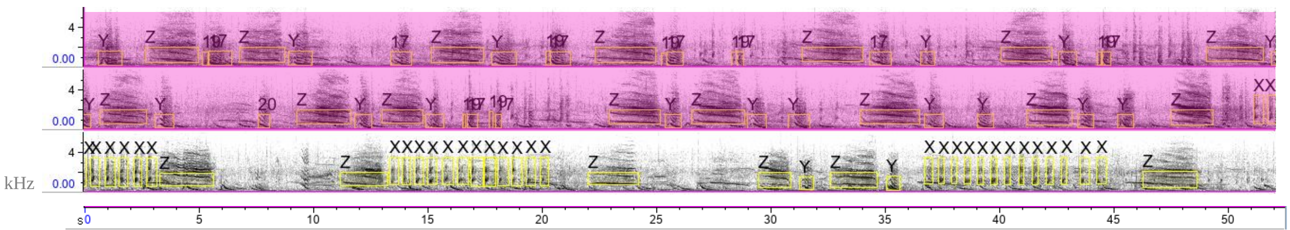



kHz
s
0 5 10 15 20 25 30 35 40 45 50

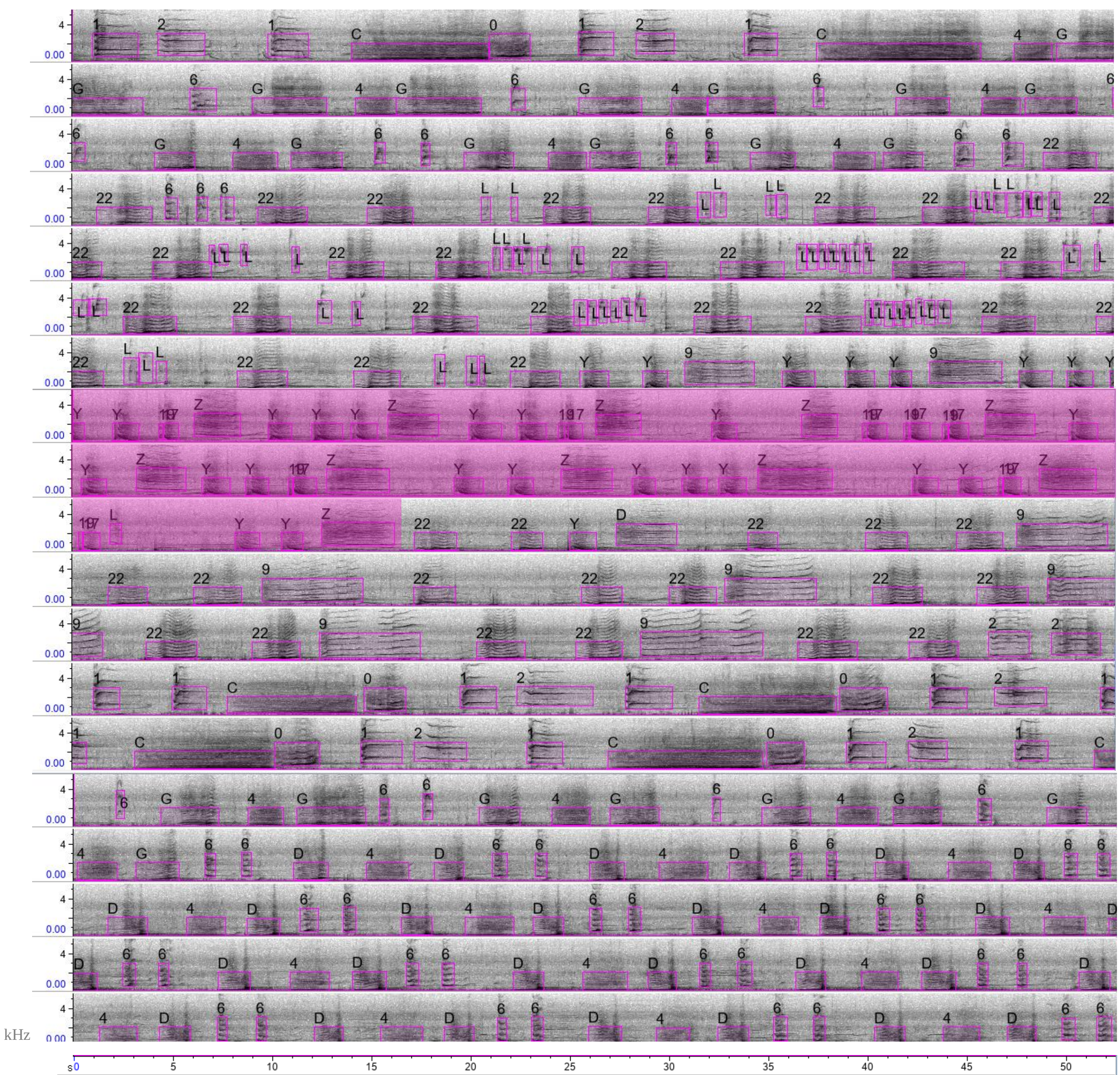
Forwarded theme

Brazil 2018 revolutionary song was composed of only 2 to 3 themes (depending on the singer). Spectrogram of Colombia 2019 song shows an insert of a longer recording, including one particular theme that was passed on from BSA 2018 to BGS 2019 song.

Brazil 2018

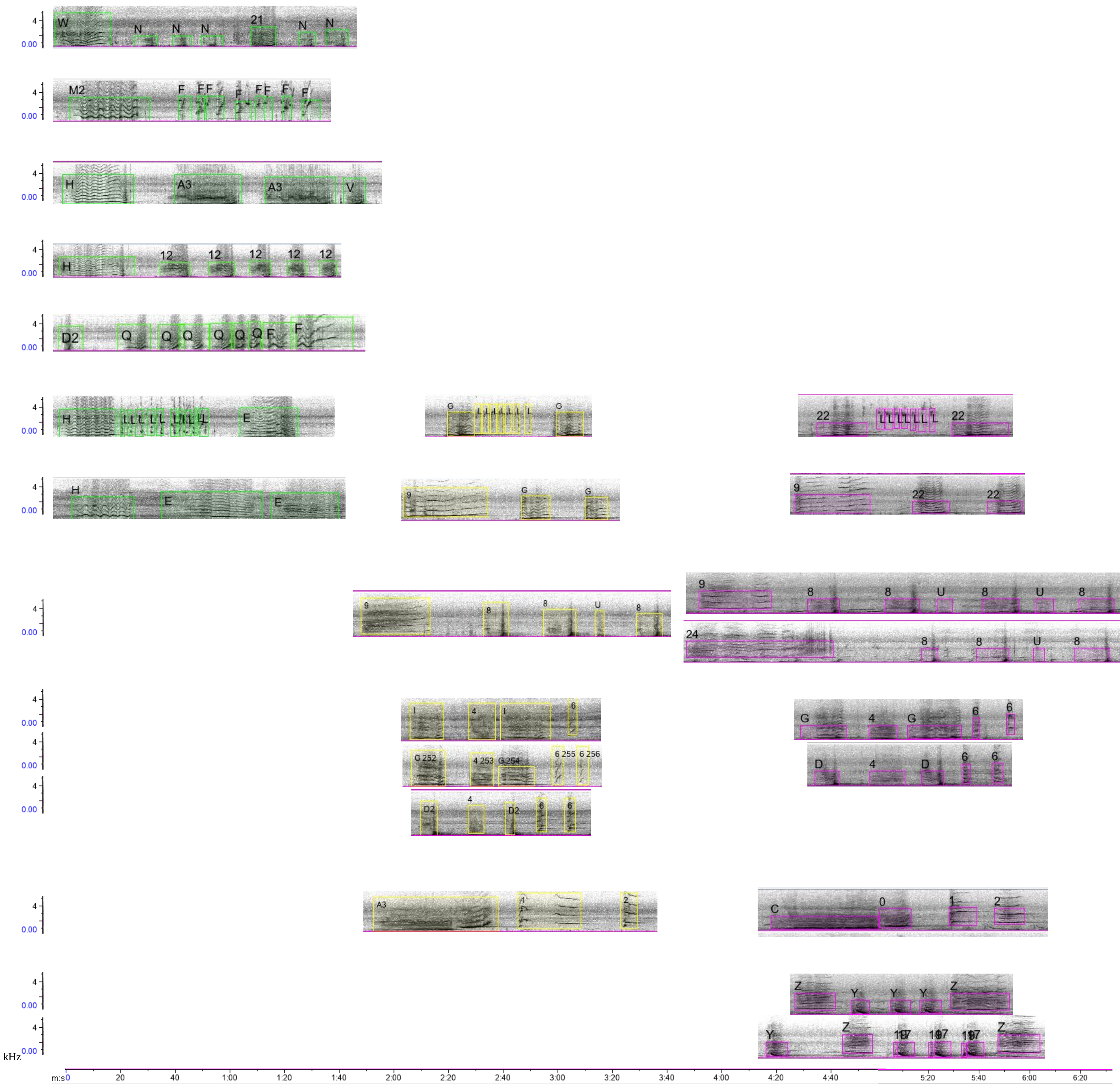


Colombia 19, 1015

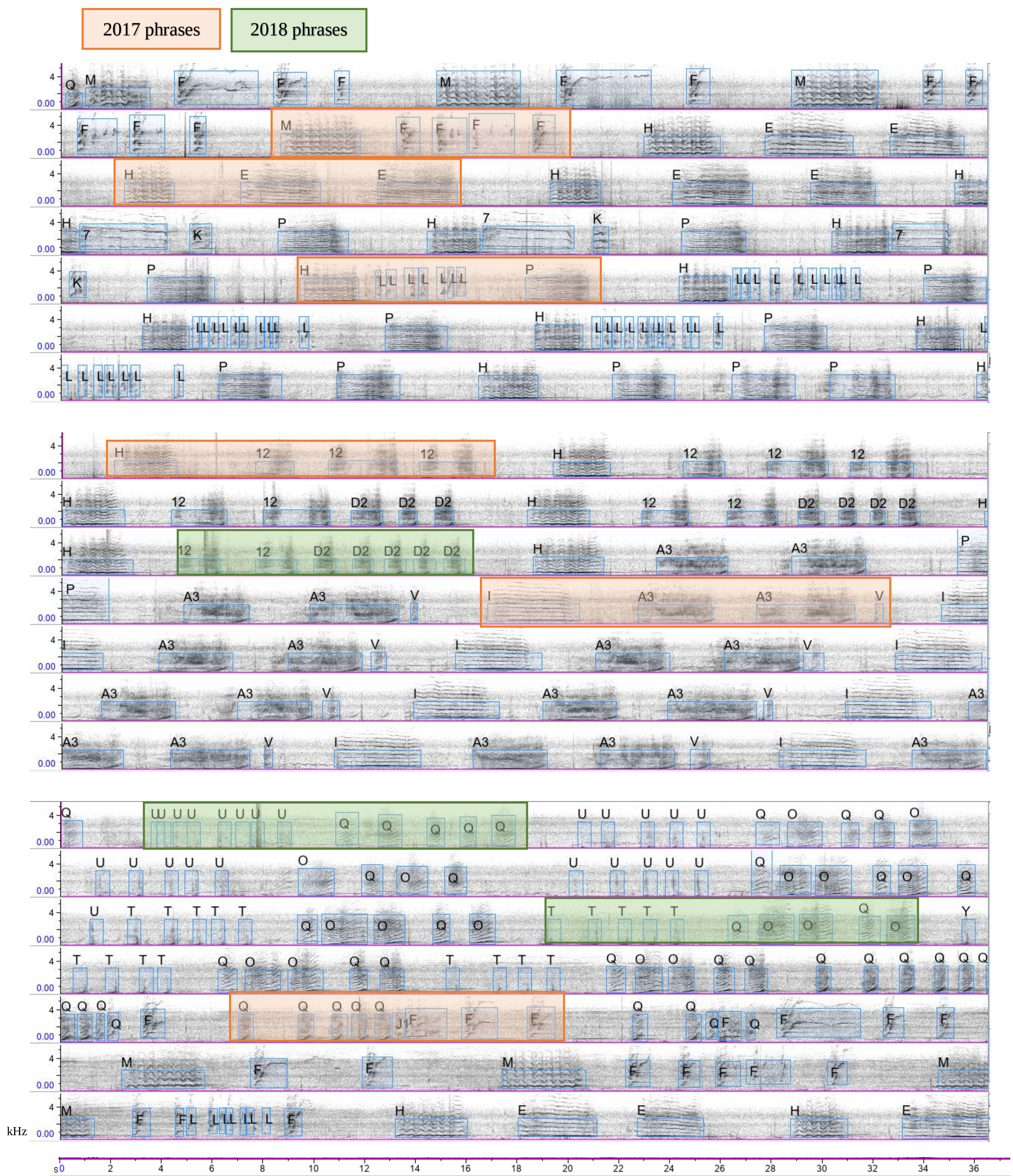


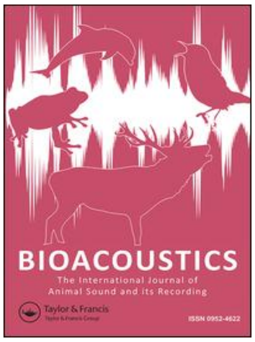
Phrase evolution through the hybrid song

Colombia 2017, 0831 | Colombia 2018, 1147- hybrid song | Colombia 2019, 1015



Colombia 2018, 1118-old song, contained both, 2017 and 2018 phrases





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Use of recurrence plots for identification and extraction of patterns in humpback whale song recordings

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Use of recurrence plots for identification and extraction of patterns in humpback whale song recordings

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ABSTRACT

Humpback whale song is comprised of well-structured distinct levels of organisation: combinations of sounds, repetition of combinations, and a sequence of repetitions, which have no clear silent intervals. This continuous sound output can be hard to delimit, rather, it could be interpreted as a long series of states of a system. Recurrence plots are graphical representations of such series of states and have been used to describe animal behaviour previously. Here, we aim to apply this tool to visualise and recognise structures traditionally used in inferences about behaviour (songs and themes) in the series of units manually extracted from recordings of humpback whales. Data from the Abrolhos bank, Brazil were subjected to these analyses. Our analytical tool has proven efficient in identifying themes and songs from continuous recordings avoiding some of the human perception bias and caveats. Furthermore, our song extraction is robust to errors coming from both manual and automated transcriptions, constructing a level of description largely independent of the first stage of analysis.

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Humpback whale; song; recurrence plot; song structure; sound visualisation; sound transcription; sound sequences

1. Introduction

Songs usually describe sequences of sounds showing some structure. Complex strings or sequences of sounds have evolved in many taxa (Kershenbaum et al. 2014) and animals may sing with varying degrees of complexity. Depending on the research question, one may or may not consider the adjacent acoustic context in which such songs, or sound sequences, are delivered, i.e., some are separated by silent intervals, but some are not. These long and continuous complex sequences of sounds impose the added challenge of limiting when one biological meaningful sequence ends, and another begins. The humpback whale male song is an example of such an animal acoustic output structure which is very hard to characterise due to the issues just described.

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Supplemental data for this article can be accessed here.

1.1. Structure of humpback whales songs

Schreiber (1952) was the first to describe sounds recorded in the ocean by the U. S. Navy in 1951 which were later attributed to humpback whales, *Megaptera novaeangliae* (Schevill and Watkins 1962). Nonetheless, the complex structure of the humpback whale acoustic display – the song – was noticed almost a decade later by Katy and Roger Payne in 1969 and formally published by Payne and McVay (1971). Three decades after that, genetic confirmation (Darling and Brub 2001) supported the behavioural and morphological evidence that only males sing (Darling (1983), Glockner (1983)).

According to Payne and McVay's description, singing males emit sound units that are arranged in phrases that are repeated to form a theme. Themes are sung in a fixed order which is a song, and a song session is the continued rendition of the song. Constant changes in the song throughout the singing season, called song evolution characterise the dynamic of singing activity in humpback whales (Payne et al. 1983). This hierarchical song structure that cycles in a fixed order was revised by Cholewiak et al. (2013) to incorporate multi-level variation in song structure and to address some caveats with the original structure and order proposition. Fundamental differences between bird song literature that inspired Payne and McVay (1971), such as the lack of silences between song renditions, hindered the acknowledgement that boxing humpback whale song into static artificial hierarchical levels was potentially misleading inferences (Cholewiak et al. 2013). Specially complicated is to arbitrarily define limits of songs and themes that would vary depending on who was describing it.

Methodology on humpback whale song elements identification (and extraction) is still advancing as consensus on the best protocols are not yet established. As the song and its elements vary in length and order (Cholewiak et al. 2013), it is challenging to manually identify them (and their limits) without subjectivity. Automating the process of song structure recognition would significantly reduce the frequent human bias. As a mean of going a step closer to this goal of automation, we propose a method based on the 'unit' level of the vocalisation. Unit is the best-defined element of the humpback whale song, and can be described as 'the shortest sound entity recognised by the human ear, separated from other sounds by a short period of silence' (Payne and McVay 1971). Even though classifying units can be a tricky process since there is some versatility in the renditions of the same unit, yet as an entity, the unit remains the most unambiguous element of the humpback whale song hierarchy.

In order to reliably define patterns of higher hierarchical level – themes and songs, as assemblies of units, we propose a new method to remove some of the human influence in defining the start and end points of songs. This is done by adopting a semi-automated protocol to detect, analyse or extract the aforementioned features from transcribed unit label strings.

1.2. Recurrence plots

Recurrence plots are used to visualise and analyse, at a global level, long series of states of a system (see definition by Eckmann et al. (1987) in the case of a general dynamical system). This tool and its graphical representation have been used in several scientific topics: first in medicine in Zbilut et al. (1990) and then in astronomy, neuroscience, mechanics, geology, climate changes (see review by Marwan et al. (2007)). This tool has recently been proposed to study structures in animal movements or communication in Ravignani and Norton (2017). It was used in acoustics – monitoring of air guns (Miralles et al. 2015), and bioacoustics – shrimps sound production (Hee-Wai et al. 2013). A closer application to our problem of analysing humpback whale songs has been to visualise structures of a music extract (Foote 1999) or to cut it automatically as in Foote (2000) or Paulus et al. (2010). It has recently been used to study the rhythm of humpback whale sound production in Schneider and Mercado (2018), without focusing on the spectral content of the sounds.

The main topic of this paper is to apply this tool to visualise and recognise the main structures (songs and themes) in unit series of humpback whales. We apply this method to data taken in Abrolhos bank, off the northeastern coast of Brazil (see section 2.1). These recordings were manually transcribed into a string of units named as letters (see section 2.2). On this input, a matrix of distances, based on the Levenshtein distance is computed as done in recurrence plots (see section 3). A method for the automatic extraction of songs in the series of units is proposed (see section 4) and tested on our data set in the final section 5.

2. Data collection and sound units transcription

2.1. Data collection

Data were collected in the Abrolhos bank, located off the Northeastern coast of Brazil (17^{o}S and 38^{o}W) where humpback whales come during the austral winter and which is considered the main calving grounds for the species in the western south Atlantic Ocean (Martins et al. (2001) and Andriolo et al. (2006)). During 2000 and 2001 research cruises, groups of humpback whales were sighted and monitored for acoustic activity using one HTI 90 min hydrophone connected to a portable DAT Sony TCD D-10 (sampling rate 48 kHz). Vocalising males were then identified and located by monitoring the amplitude decrease of an individual's sounds as it surfaced to breath. Silent approaches to these focal singers were performed using a small zodiac with an improvised sail. Songs were collected from the zodiac at distances that varied from 100 to 500 m to the focal male while its behavioural activity was continuously registered. Several recordings were made but only the best quality ones were used in our analyses. Selected recordings made in September of the year 2000 generated 3 high-quality audio files (recordings #1,2,3) lasting, respectively, 58 minutes, 1 h 37 min and 2 h and 7 minutes. In September 2001, the two selected audio files (recordings #4,5) were, respectively, 26 min and 1 h and 38 min long. Another study of song sessions in the same place in 2000 will serve as a comparison for the data we present (Arraut and Vielliard 2004).

2.2. Sound unit transcription

Classifying units into specific types is a complex problem, since there is a large versatility in the acoustical properties of a single unit (Janik 1999). First, there is a seemingly infinite number of different unit types used by whales, in an ever-changing song. Second, even the units belonging to the same type may vary to a certain level throughout the same song, in the recordings of different singers, and depending on the quality of the dataset. Thus, a different final product of classification can arise from the same dataset due to differences in the methods used to determine the units. The final number of different unit types in different studies varies greatly, from 12 to more than 100 (Pines 2018). Challenge to group the units by type (as similar or different) opens the debate on what is the acceptable level of variation within the same unit type.

In order to overcome this difficulty, we used the context i.e. the position of the unit in the song (or more commonly in the phrases within each theme), defined by the arrangement of adjacent units (Green et al. 2011). The context has proven as a good way to help determine the unit type (Cholewiak et al. 2013). For this work, all recordings were inspected by hand. Spectrograms were created using 1024 point FFTs, Hann window, 43.1 Hz resolution and 50% overlap (created by software Raven pro 1.5 – Cornell Lab of Ornithology, Ithaca, NY, (2014)), and subjected to aural and visual inspection by two trained analysts. Each analyst separately inspected and labelled the whole dataset. This procedure is a common protocol adopted by humpback whale song researchers (Payne and McVay (1971), Darling et al. (2019)). Our protocol for unit classification also takes context into consideration, i.e. where the unit is placed, so that other hierarchical levels of organisation can help define how much variation is allowed in a single unit type. Note that even when studies carry on unit annotation using computational methods, the results are usually validated using manual classification (Pace et al. (2010), Garland et al. (2013), Allen et al. (2017)).

The labelling was done in the following way: every unit type was attributed to an alphabet letter based on its distinctiveness from other units (Darling et al. 2019). Analysts considered visually and auditory perceptual characteristics for classification such as unit tonal or pulsed quality, its pitch content and frequency modulation pattern, its duration, and its placement within phrases (context). Each time the specific unit would arise in the recording, it was labelled in Raven, according to its type, minding its context (adjacent units). The final product of every separate recording would be a list of N consecutive letters, the way the units appeared in that specific humpback whale vocalisation (see Figure 1 and supplementary material #1). This list of letters (units) will, in the later steps of the method, serve as an input for computing recurrence plots (section 3). Finally, an

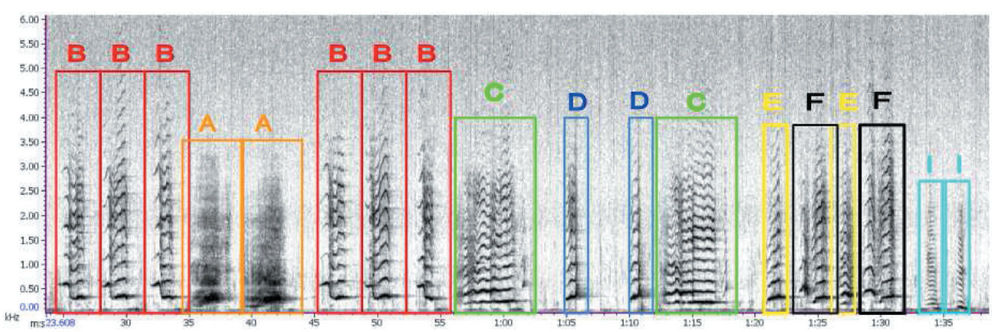

Figure 1. Time (min:sec)/frequency (kHz) representation of an extract of recording #3 (from Abrolhos Archipelago 2000), 1024 point FFTs, Hann window, 43.1 Hz resolution and 50% overlap. Unit transcription into letters is signalled above the boxes.

inexperienced analyst, using another software (Audacity, using a 8192 points FFT, Hanning window, 99% overlap) independently transcribed part of recording #3 into a series of units as a comparison with the first transcription and a check on the robustness of our method (see section 5.2).

3. The Levenshtein distance recurrence plots

3.1. Definition of the Levenshtein distance recurrence plot of order n

To visualise the structures contained in a recording, we compute a distance matrix, using OCTAVE (Eaton et al. 2009) in the following way. Each recording is transcribed as a string of N letters representing sound units (see section 2.2). Then, we define $extract_i$ as an n-letter extract beginning with unit number i. The length of the extracts n is taken much smaller than the total length of the string N. The Levenshtein distances $d_{ij} = Levenshtein\ distance\ \left(extract_i, extract_j\right)$ between all pairs of n-letters extracts are computed.

The Levenshtein distance between two strings is the minimum number of insertions, deletions and substitutions necessary to transform one string into the other (Levenshtein 1965). Note that the computation of other types of distance matrix could be achieved choosing other distances between two strings of letters: Jaro-Winkler, Damerau-Levenshtein and Hamming distances for example.

For convenience, we defined a correlation index by:

$$c_{ij} = \frac{n - d_{ij}}{n}$$

Thus, the coefficients of the matrix satisfy $c_{ij} \in [0; 1]$. The coefficient 0 means maximum Levenstein distance and thus minimal correlation. The coefficient 1 means zero Levenstein distance and thus maximal correlation.

The resulting matrix (c_{ij}) is a square matrix of size $N - n + 1 \simeq N$, symmetrical, and has ones on its diagonal (maximal correlation between one element and itself). As an example, Figure 2 shows the graphical representation of this Levenshtein distance matrix of recording #2 (a total of $N = 1260$ units), with 5-letters extracts (n=5).

The result is a **recurrence plot** of a dynamical system (as defined in Eckmann et al. (1987)) in which a state is a vector of n letters. We call this special recurrence plot the Levenshtein distance recurrence plot of order n ($LDRP_n$).

The value of n is chosen by the analyst. In our data, the visual information is basically the same when n varies (see Figure 3). For low values of n, there are few levels of Grey. For high values of n, the resulting figure is more blurred (see Figure 3), and the computation of Levenshtein distance is rather time-consuming (the time of computation of the distance between two strings of n letters is proportional to n^2) (Wagner and Fischer 1974). The computation of the $LDRP_n$ for $n = 17$ and $N = 800$ in Figure 3, takes around 1 h in a domestic computer. The parameter n can be adapted depending on the use of the $LDRP_n$: visual analysis, extraction of structures, etc.

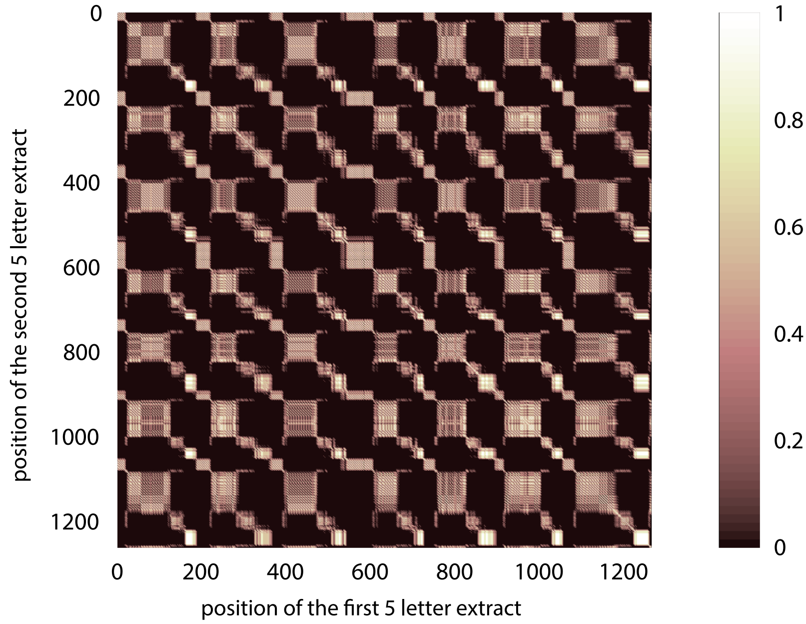

Figure 2. Example of a Levenshtein distance recurrence plot (5 letter extracts) created form recording number #2 from Abrolhos Archipelago (2000). The number of units of this recording is $N = 1260$. The coefficients of the matrix denote correlation between 5 letter extracts (0 is no correlation, 1 is maximal correlation).

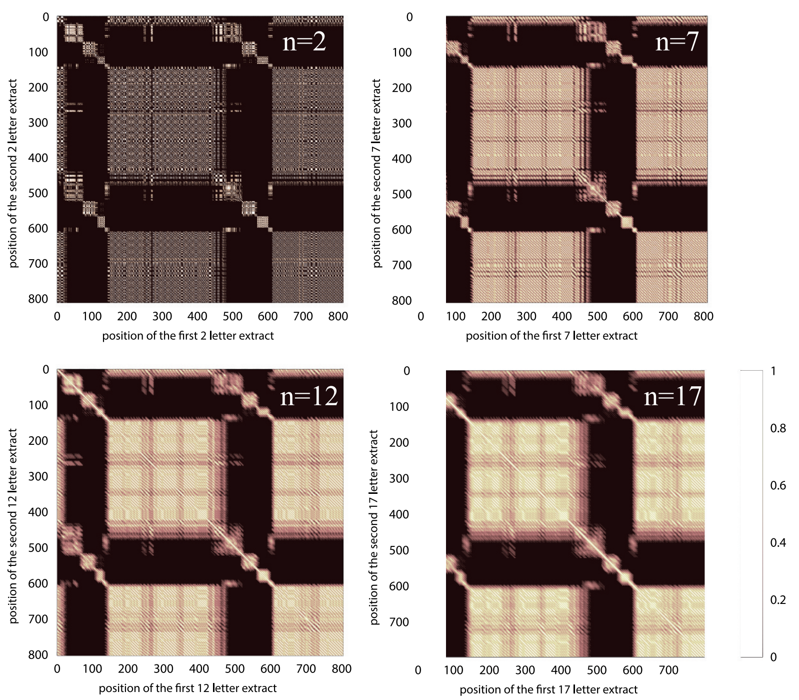

Figure 3. Recording #5 (from Abrolhos Archipelago 2001): Levenshtein distances recurrence plots for different values of the length n of the extract (2,7,12 and 17).

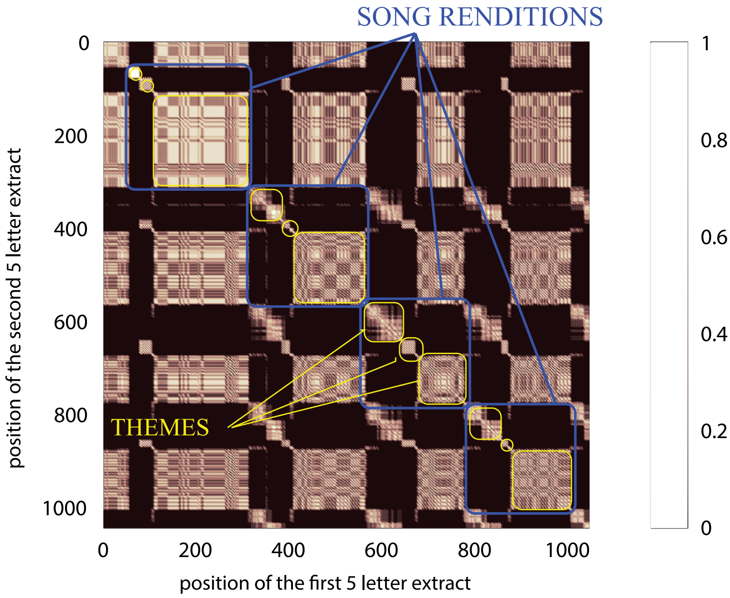

Figure 4. Recording #1 from Abrolhos archipelago, 2000: Levenshtein distances recurrence plot commented (n=5). The main structures of humpback whale sound production appear: songs in blue, themes in yellow.

3.2. *Visual identification of main structures in the recurrence plot*

Figures 2, 3 and 4 show obvious structures in the recording. On the diagonal of the matrix, squares represent auto-similar structures. Rectangles out of the diagonal show whether these structures correlate with each other. The high contrast of this representation is due to the sparsity of input representation (letters) added to the efficiency of the distance operator.

In Figure 4, we annotated the two different scales of structures found in all recordings of this study. First, a global pattern can be seen that is reproduced periodically (the 'period' can be seen in the horizontal or vertical regularly spaced correlations of parts of the recording). We thus define a **song as the largest repeated structure** that can be found in a recurrence plot. The song is repeated with a high level of similarity, apparent in the non-zero correlation with other songs. This structure is obvious in our representation, it is also in accordance with the general literature on humpback whale bioacoustics (Payne and McVay 1971; Mercado-III et al. 2003; Cholewiak et al. 2013).

A second scale of the structure is visible in the $LDRP_n$: each song is itself composed of several auto-similar parts or 'squares' (Figure 4). These parts are not repeated within a song (square 1 does not correlate with others during the same song). We define a **theme as the string of units corresponding to a 'square', or self-similar part of a song**. With this definition, we are consistent with general literature on humpback whales (Mercado-III et al. 2003) which states that a theme is a repetition of similar phrases composed of similar sound units. Nevertheless, it is difficult to see a distinctly visual signature of phrases in the recurrence plot. Anyway, the separation of themes in squares could help a humpback whale song analyst to identify phrases in each series of units corresponding to a square.

4. Automation of the extraction of songs

Based on the computation of the distance recurrence plots, we wrote a routine that separates songs in a fully automatic way. We defined the song as a structure that is repeated with a good amount of similarity, with the largest possible scale in our recording. The approximate size (in number of units) of a song can be estimated by a two-dimensional FFT of the Levenshtein distance recurrence plot of order *n* (see Figure 5, left). Then, the following algorithm for song extraction is proposed:

(1) Compute the Levenshtein distance recurrence plot for a given value of *n*
(2) Perform a 2D Fast Fourier transform of the matrix considered as an image. A peak at a frequency inverse to the mean length of the song can be seen (Figure 5, left). The abscissa of this peak is then measured to obtain an order of magnitude of the lengths of the songs.
(3) Read the first line of the Levenshtein distance recurrence plot and select the columns with non-zero correlation. Sum all these columns to improve the signal-to-noise ratio. The resulting column is represented in Figure 5, centre.
(4) Find sudden increases or upward steps in the resulting column using convolution with a step filter (Figure 5, right). Keep only the steps compatible with the average song size predicted by the 2D Fourier transform. Here, we defined the margin of acceptability at one-third of the average size given by FFT analysis.
(5) Extract the units transcribed from the recording between two upward steps: this is a song (Figure 6).

5. Results: song extraction

5.1. Extraction of songs in series of units from Abrolhos Archipielago in 2000/2001

We applied the algorithm presented in the previous section to the five recordings of our study. Visually, the same features corresponding to our definition of songs and themes appear in each Levenshtein distance recurrence plot. The recording #4 is too short and do not present a complete song and our routine consequently did not extract any song. In all

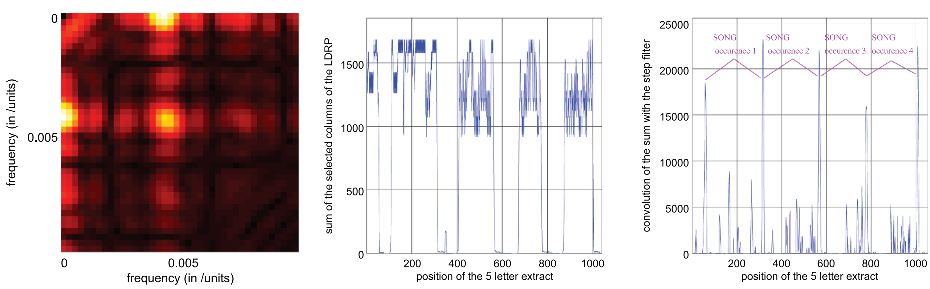

Figure 5. Steps in the extraction of the songs. **Left**: Step 2 of the algorithm, extract of the 2D fast Fourier transform of the Levenshtein distance matrix (for $n = 5$, recording #1). A peak is visible at a frequency of about 0.045 units^{-1} (which means a scale of 200 to 250 units of the recording) **centre**: Step 3 of the algorithm, the horizontal sum of selected columns of the recording 1, n=5. **Right**: Step 4 of the algorithm, each peak shows the transition between two songs.

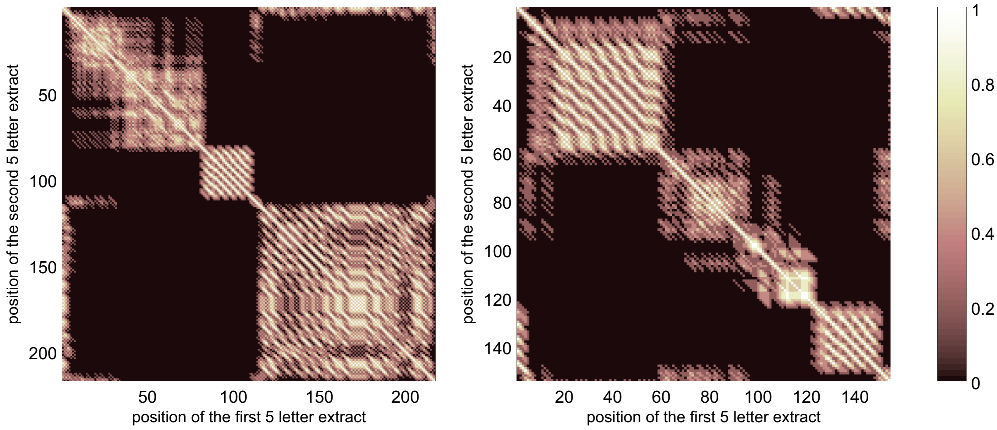

Figure 6. Two songs automatically extracted. **Left**: Recording #1 from Abrolhos archipelago, 2000: third song automatically extracted from Figure 4. In order to see clearly the song, the frame of the figure is chosen a bit larger for representation. **Right**: recording #2 from Abrolhos archipelago, 2000: zoom on the third song occurrence in the Levenshtein distance recurrence plot of Figure 2. Different types of transition between themes appear.

the other recordings, the extraction of songs was achieved successfully. In recording #5, only one song is present.

We compared the extraction of songs carried out by our routine, based on the Levenshtein distance recurrence plot, and songs delimited by a human expert. Comparison was performed for the recording #3. The analyst followed the instructions described in Cholewiak et al. (2013), the choice for the beginning point of the first song was the first complete theme (composed of the same type of letters). The extraction of the songs (presented in supplementary material #2) is equivalent by both methods. The only difference sits in a few transitional units (less than 5 units per song).

It is interesting to note that recurrence plots can show transitional phrases, which are combinations of units from the previous theme with ones from the next theme the male sings (Frumhoff 1983; Payne et al. 1983; Cholewiak et al. 2013). Transitional phrases appear in our recurrence plots as blurry areas around self-similar ‘squares’ that represent the themes. It is particularly clear in Figure 6 (right), where the three squares corresponding to themes numbers 1,2 and 3 inter-penetrate each other. On the contrary, the transition between themes in Figure 6 (left) is quite abrupt: the squares are well separated.

Once the songs are extracted, the automatic measurement of the songs’ parameters is easily done. As an example, we automatically computed songs’ length, alphabet (set of different units – or letters – used in the song), and importance of units (% of the number of occurrence of a particular unit in a song occurrence compared to the length of this song). These results are presented in Table 1 and Figure 7.

Figure 7 gives the percentage of each unit in the song occurrence of recording #1. The first occurrence of the song, in red (or circles), is quite different from the other songs. Indeed, during the first song occurrence, a series of units are masked by boat noise and were labelled with a special letter (H) in place of a whole theme containing the letters J,K, L,M,O,P. It can be seen in the Levenshtein distance recurrence plot where the first theme

Table 1. Mean and standard deviation of the songs' length for recordings #1,2,3 and 5.

Recording	Year	nb of songs	Mean length (in units)	Standard dev. (in units)
#1	2000	4	238	22
#2	2000	6	177	25
#3	2000	8	301	72
#5	2001	1	438	None

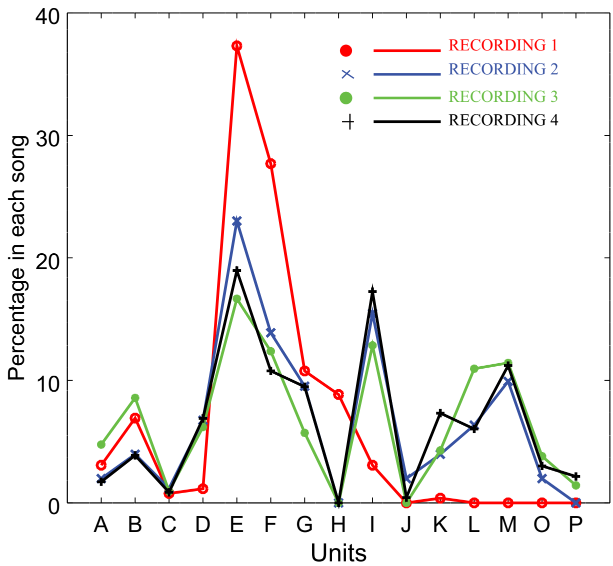

Figure 7. Percentage of each unit in the four song occurrences of recording #1 from Abrolhos archipelago, 2000 (colours are red, blue, green and black for song occurrences 1,2,3,4 respectively). The first occurrence of the song in the recording (see Figure 4), in red in this figure is quite different from the other occurrences in term of its units, due to boat noise that prevented an accurate identification of several units.

of the first rendition of the song does not correlate with any of the themes of other renditions (Figure 4). However, the recurrence plot still enabled us to extract the song structure accurately.

The results of Table 1, where the mean length of all the songs analysed is 255, compare well with the results of Arraut and Vielliard (2004), working with the same data but with manual analysis, where the mean song length is around 250–300 units.

5.2. Robustness of the extraction method

In order to test the robustness of our method of songs' extraction, we first checked that the extraction is not dependent on the order n of the Levenshtein distance recurrence plot $LDRP_n$. For each recording (#1 to #3) the number of songs extracted was the same for n going from 4 to 10.

We then checked that the extraction is not heavily dependent on the unit transcription. For recording #3, an inexperienced analyst transcribed part of it in a string of units. Even though the confirmed analysts transcribed 1614 units and the inexperienced one

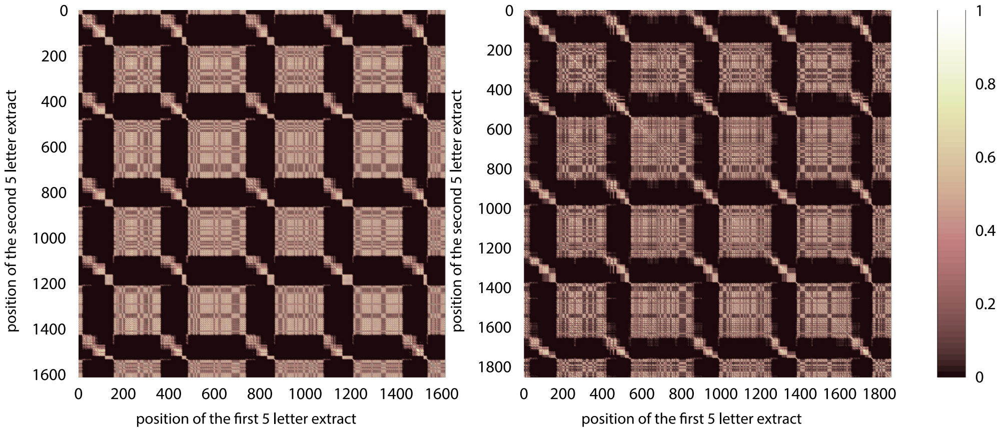

Figure 8. Recurrence plots of part of the recording #3 from Abrolhos archipelago, 2000, with $n = 5$. **Left**: transcription into units by confirmed analysts, **Right**: transcription into units by an inexperienced analyst.

1855, the recurrence plots have the same appearance (Figure 8). The automatic extraction of the song was then performed on these two strings of units and gave similar results: four songs are extracted in each case. The ratio r_u of the length of the song extracted from the series of units produced by the confirmed analysts and the length of the song extracted from the series of units produced by the inexperienced analyst (measured in unit) is very stable for each song extracted ($r_u = 0.86 \pm 0.006$). We also checked that the determination of the start and end of an automatically extracted song is consistent between the human transcriptions (with a ratio between songs' durations (measured in seconds) of $r_t = 1.01 \pm 0.04$ between the two human analysts). Thus, our method of song extraction is remarkably robust to differences in unit labelling due to the subjectivity or lack of training of the analyst.

In addition, we checked the robustness of our method to accidental errors in units transcription, not considering whether this was done automatically or manually. We applied the extraction routine to the strings of units of recording #1 and #2, gradually and randomly changing a percentage of these units (replacing it randomly by a unit from the same recording). For each percentage of error, the test was repeated 20 times and the number of extracted songs was noted. The result is visible in Figure 9, where for each percentage of errors in unit identification, the average number of extracted songs is plotted, along with the error bar corresponding to the variation across the 20 draws. We see that for less than 5% of randomly changed units, the results are very coherent with the original recording. Even as the rate of error grows, the number of extracted songs stays close to the nominal one (1 song of difference for up to 20% of errors).

Last, we applied the extraction routine to strings of units of recording #1 where we gradually and randomly removed a percentage of these units. In this case, until 40% of units were removed, the routine extracts the correct number of songs for more than 90% of the tries. Therefore, our extraction method is robust to missing units during the transcription, for example when the signal-to-noise ratio of the vocalisations of humpback whale is low. However, this was done for randomly chosen units and do not account

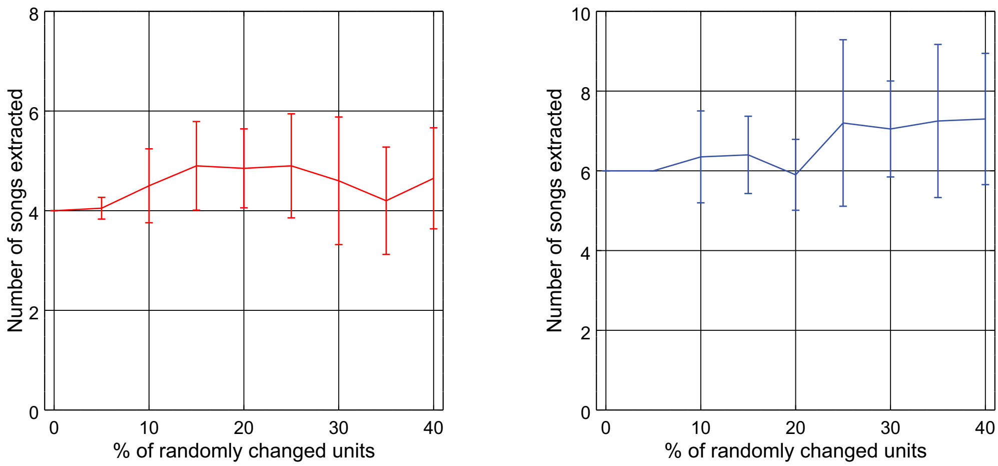

Figure 9. Number of song correctly found in function of the percentage of randomly changed units. The test is done on 20 random tries and the error bar quantifies the distribution of the results over the 20 tries. **Left**: Recording 1 from Abrolhos archipelago, 2000, **right**: recording #2 from Abrolhos archipelago, 2000.

for systematic errors (such as would happen if one type of unit only would be lost in the noise, which is not an improbable case).

6. Discussion

6.1. Use of recurrence plots

Recurrence plots are a very visual way of representing the sequence of units, allowing immediate global identification of the structures of the highly organised vocalisation emitted by male humpback whales, presented in the preceding sections. It helps with getting a qualitative view of their variability as well as the type of transition (abrupt versus gradual change) between these structures. It could be used as a valuable tool for every highly structured type of sound emission by animals and seems particularly well fitted to study the ever-changing structures of humpback whale songs.

Recurrence plots can also be used for automatic unsupervised selection of different structure levels in the recording translated as a series of units. The results of the previous section indicate that our method of extraction is quite robust to errors during manual or automatic transcription of the sound units into a string of letters. The quantification of errors detected for song unit classification systems in studies such as Dunlop et al. (2007), Ou et al. (2013) or Rekdahl et al. (2018) is usually from 10% to 20% which compares well with the percentage of errors that still enables us to automatically extract songs.

The use of recurrence plot to extract songs is still a work in progress but these results are encouraging. Even in the situation of different criteria for unit labelling in different recordings, the song session structure will probably still be visible. This is an additional benefit of the proposed recurrence plot methodology, as it undermines differences in unit labelling among studies. The plot gives a representation of each recording, rather independent of the string it was calculated from. In this way, the recurrence plots provide standardised limits of patterns in the recordings that can be further explored and compared.

This automated song extraction is the first step for many more studies regarding song analysis, and comparison between songs. The automated extraction of other structures (such as themes) could be performed based on this tool but is not as straightforward as songs extraction. Some of the difficulties of theme extraction are: blurred or imprecise transition between themes, unclear definition of a theme, very short or evanescent themes. Thus, any method of automated theme extraction would probably be rather ad hoc, which is the reason why we did not perform it on our limited set of data.

Finally, a matrix comparing two series of units extracted from two different recordings can be computed which shows the similarity between two recordings in term of song rendition. This type of analysis could enable people to compare quickly two song bouts distant in time or space.

6.2. Large scale automatic treatment of humpback whales' recordings

This study is a step towards the automatic treatment of large-scale recordings. Automatic tools to transcribe sounds into a string of letters such as the one developed in Dunlop et al. (2007), Glotin et al. (2009), Rickwood and Taylor (2008), Pace et al. (2012), Ou et al. (2013), Razik et al. (2015), Bartcus et al. (2015) or Rekdahl et al. (2018) could be used beforehand. Then, our method could be applied to extract, classify and compare songs and their features along with other approaches to visualise the structures of humpback whale's songs.

Finally, analysing humpback whale song structures with recurrence plots would be difficult in the case of a recording where many singers are vocalising together. In this case, the separation of these singers is a challenge that has to be addressed.

Highlights

- The complex hierarchical and cyclical structure of humpback whale song can be visually represented in recurrence plots.
- Recurrence plots of humpback whale singing provide insights into the intra-individual variation in song structures of a male.
- Our tool can help extracting structures, from long recordings, removing some human perceptual caveats.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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CERTIFICADO

Natal (RN), 05 de junho de 2018.

Certificamos que a proposta intitulada **"A transmissão dos padrões de canto da baleia jubarte (*Megaptera novaeangliae*) entre os dois estoques reprodutivos na América Latina – onde acontece?**", protocolo 031/2018, **CERTIFICADO nº 101.031/2018**, sob a responsabilidade de **Renata Santoro de Sousa Lima Mobley** - que envolve a produção, manutenção e/ou utilização de animais pertencentes ao filo Chordata, subfilo Vertebrata (exceto o homem), para fins de pesquisa científica (ou ensino) - encontra-se de acordo com os preceitos da Lei n.º 11.794, de 8 de outubro de 2008, do Decreto n.º 6.899, de 15 de julho de 2009, e com as normas editadas pelo Conselho Nacional de Controle da Experimentação Animal (CONCEA), foi aprovada pela COMISSÃO DE ÉTICA NO USO DE ANIMAIS da Universidade Federal do Rio Grande do Norte – CEUA/UFRN.

Vigência do Projeto	**Dezembro 2019**
RELATÓRIO	**JANEIRO 2020**
Espécie/Linhagem	**-**
Número de Animais	**Não houve utilização de animais.**
Idade/Peso	**-**
Sexo	**-**
Origem	**Banco de Abrolhos - Bahia**
Observação	**Análise de dados coletados de 2000-2005 (Instituto Baleia Jubarte) e 2015-2017**

Informamos ainda que, segundo o Cap. 2, Art. 13, do Regimento Interno desta CEUA, é função do professor/pesquisador responsável pelo projeto a **elaboração de relatório** de acompanhamento que deverá ser entregue tão logo a pesquisa seja concluída. **O descumprimento desta norma poderá inviabilizar a submissão de projetos futuros.**

José de Castro Souza Neto Júnior
Coordenador da CEUA-UFRN