A Description of the Song Unit Repertoire and Rate of Change of Southeastern Pacific Humpback Whales at Their Breeding Area in the Gulf of Chiriquí, Panama

A Description of the Song Unit Repertoire and Rate of Change of Southeastern Pacific Humpback Whales at Their Breeding Area in the Gulf of Chiriquí, Panama

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Abstract

Male humpback whales (*Megaptera novaeangliae)* are known to produce long and complex songs during their breeding season. Every year, each humpback whale breeding population around the world sings a unique song, which can vary slightly or rapidly from that of the previous year. The degree of difference in a population's song from year-to-year depends on the level of connectivity with other humpback whale populations. In this study, I use novel methods of classification and calculation to describe the repertoire of units that make up the song of Southeastern Pacific humpback whales, also known as the Breeding Stock G (BSG) at their breeding area in Gulf of Chiriquí, Panama from 2007 to 2023. The unit repertoire of BSG whales consisted of a total 47 distinct unit types. Most unit types had a peak frequency below 5 kHz and a duration greater than 1sec. The most used units were those with a flat and tonal contour, and dense presence of harmonics. The composition of new, constant, and recalled units varied within and between year periods. However, in most periods, the song was primarily composed of constant (used in two consecutive years) and recalled units (seen in previous years but not the year directly before), indicating a slow pace of change until recent years. We see that the pace of change is generally driven by gradually phasing out units, but that at least two instances a change was driven by the addition of new units, causing a relatively rapid change in the song that suggests an instance of song 'revolution'. This study provides the first unit repertoire analysis for this humpback whale population and supports the hypothesis that changes in song unit composition are generally gradual, with a few instances of relatively rapid change, which suggest the arrival of males from other breeding populations at either their breeding or feeding areas.

Ultimately, the continuing long-term monitoring of the songs of this population will help us to understand the potential effects of climate change and human activities in their communication.

Key words: Bioacoustics, Whale Song, Cetaceans, Marine Biology, Population Ecology

1. Introduction

Humpback whales are highly vocal animals, with males producing long complex song displays primarily during the breeding season as first described in Payne and McVay (1971). The structure of humpback songs is traditionally described in a hierarchical fashion from subunits, units (made of subunits), phrases (made of units), and themes (made of one or multiple phrases) (Payne and McVay, 1971; Norris et al., 2000; Cholewiak et al., 2012). Humpback whales are open learners and appear to learn their song via cultural transmission, with all males in a breeding area conforming to the same song over time (Cholewiak et al., 2012). Most humpback whale populations experience slow changes in their song (Payne and Payne, 1985; Herman, 2017). These small year-to-year variations in song structure can result from vocal interactions between males from the same population which frequent different sub-areas at their common breeding area or during their migration (i.e., Darling et al., 2019; Shultze et al., 2022). However, in the South Pacific, several events of song 'revolution' have been reported from western to eastern populations (Noad et al., 2000; Garland, et al., 2011, 2013; Schulze et al., 2022). A song revolution is described as a rapid replacement of one song type with an entirely novel song, introduced from a male(s) from a neighboring breeding population (Noad et al., 2000). The best studied case is the song spread from eastern Australia to French Polynesian whale populations

(Garland et al., 2011, 2013). More recently, this eastern pattern has been extended into the eastern Pacific Ocean (Ecuador) (Schulze et al., 2022). In addition, an independent study discovered at least three humpback whales from different breeding populations at the same feeding areas in Antarctica (Schall et al., 2022), suggesting the potential for circumpolar Southern Hemisphere cultural transmission of song culture (Schulze et al., 2022). Therefore, the rate at which a song changes within a breeding area changes depending not only on the level of contact between individuals but also on where those individuals are coming from (Eriksen et al., 2005).

Distinct Population Segement 13 (DPS 13), or Breeding Stock G (referred to hereafter as BSG), is one of 14 distinct population segments of humpback whales recognized worldwide (Bettridge et al., 2015) (Fig. 1). These whales migrate from feeding areas in the Southern Hemisphere, specifically off the Antarctic Peninsula and the Fuegian Archipelago in Chile (Rasmussen et al., 2007; Acevedo et al., 2017) (Fig. 2), to various locations along the Pacific coast of South and Central America. In Central America they are observed between the end of June and mid-November (Rasmussen et al., 2007, Rasmussen et al., 2012). In the Southern Hemisphere, the best studies of humpback whales are from the western Pacific Ocean (DPS 10, 11, and 12) (i.e., Noad et al., 2000; Garland et al., 2011, 2013). In contrast, there are a few humpback whale song studies from the eastern Pacific Ocean (DPS 13) (i.e., Ecuador: Shultze et al., 2022; Colombia: Perazio et al., 2018; Panama: Oviedo et al., 2008; Costa Rica: Chereskin et al., 2019). Shultze et al. (2022) recently showed a potential song transmission from western Australia to Ecuador, which could result in occasional but rapid changes in the song of BSG whales in other breeding areas as well.

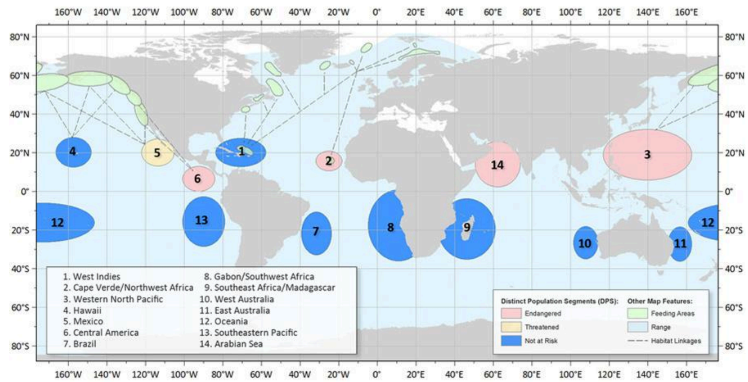


Figure 1. Distinct Population Segments Identification Map by NOAA. Last updated by Office of Protected Resources on 11/23/2020.

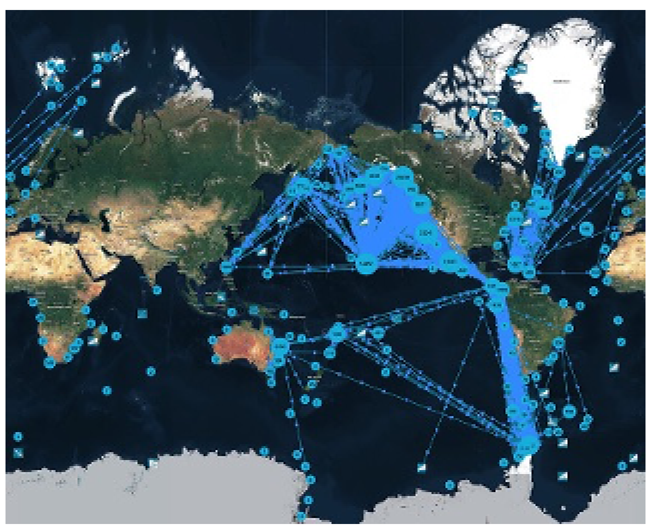


Figure 2. Global migratory patterns of whales from Happywhale database.

https://happywhale.com/whaleid

There are only three studies describing the song for BSG whales in Central America, one done at the Archipelago de las Perlas in Panama, which reported the song consisted of three themes (Oviedo et al., 2008), and another done in Caño Island, Costa Rica, where it was reported the song consisted of four themes, ten phrases, and twelve units. The authors also found a new phrase appearing at the end of the season, which became common once it was incorporated into the song (Chereskin et al., 2019). The third study was by undergraduate UVM student Kate Ziegler as part of her 2018 Honors Thesis, studying the song structure of BSG at the Gulf of Chiriquí from 2016 through 2018. Ziegler (2018) found that the song consisted of four themes and 22 units, and that on average 57% of phrases in the song of any given year were new compared with the previous year. Furthermore, she found that BSG whales from Chiriquí and the neighboring breeding area in Caño Island, Costa Rica shared at least 50% of their song repertoire in 2016 and 2017, suggesting that BSG males likely remain in the same breeding area which can lead to only slightly different song repertoires across breeding areas. The main goal of this Honors Thesis is to describe the unit repertoire of BSG whales in the Gulf of Chiriquí using a database of recordings from 2007 through 2023. Units are the building blocks of the humpback whale song, and determining how unit composition varies between years can help us to better understand the pace of change of the song in this breeding area.

Hypothesis: I hypothesize that, like other humpback whale populations (Noad et al., 2000), the pace of song change at the Gulf of Chiriquí will be gradual, with progressive changes in the proportion of stable, new, and recalled units (Winn et al., 1978; Payne and Guinee, 1983; Garland et al., 2020).Song revolutions require the arrival of males from other breeding populations in the Southern Hemisphere (Fig. 2), and while these events do occur, they are relatively rare (Schall et al., 2022; Schulze et al., 2022). I do anticipate a potential song revolution around the 2016-2019 time period, as seen at the phrase level in Ziegler et al (2021). An increase in anthropogenic noise (Affatati et al., 2022; Chapman and Price, 2011) could lead to an increased rate of change in unit repertoire (Parks et al. 2007; Parks et al. 2012), as well as changes in the average peak frequency and duration of song units over time.

Predictions: Based on this hypothesis, I predict that (1) unit presence will vary between years, with similar proportions of newly introduced and phased-out units possibly increasing over time, with potential for rapid change driven primarily by the introduction of new units in the 2016-2019 time period, and that (2) the average peak frequency and duration of the unit repertoire will change over time to accommodate increased anthropogenic noise.

2. Significance

The results of this study will provide important information about the pace of change of BSG whales at the northernmost part of their distribution and contribute to our overall understanding of cultural transmission in humpback whales. Furthermore, as the ocean gets warmer and noisier, there is potential for ambient and anthropogenic noise to reduce the range at which these animals communicate (Affatati et al., 2022). A noisier ocean could result in selection for songs made up of units with contours and acoustic features that may facilitate easier individual-to-individual transmission, but with a cost in unit richness and complexity that may impact observed cultural transmission of their songs (Allen et al., 2018). For example, North Atlantic right whales and blue whales have been known to modify their vocal communication to increase probability of detection by increasing the amplitude, the duration, and the frequency range of a signal (Parks et al. 2007, Parks et al. 2012, McDonald et al., 2009). By understanding the makeup of their song unit repertoire and addressing how humpback whale song unit composition shifts over time, this study will lay the groundwork for the development of models to predict the direction of these changes in future.

Classification is a point of much dialogue within the field of humpback whale bioacoustics, and studies do not often agree on the best method for categorizing song components. Some state that acoustic parameters were measured in their process of classification, but do not list the parameters in question (i.e. Rekdahl et al., 2018; Maeda et al., 2000). Others assign arbitrary names or symbols to song components, but do not provide a key for identification in other studies (i.e. Winn et al., 1980; Mednis 1991). Still others list the acoustic parameters used for classification, but do not provide the thresholds needed to repeat this classification (e.g. what duration class designates one unit classification vs another) (i.e. Magnusdottir et al., 2015). This disparity in methods makes it difficult to compare song repertoires across multiple populations and years. Though scientists agree that there is a need for standardized classification methods, no concrete guidelines have been developed (i.e. Cholewiak, Sousa-Lima, & Cerchio, 2013). Only one study has recently provided a framework for standardized classification, Djokic (2019). Here, I extend Djokic's work to outline a clear and self-descriptive method of classifying units, as well as an equation for the calculation of rate of change between years and periods. Together, these frameworks will serve as a starting point for methods that allow for better comparisons of song repertoires, leading to a broader knowledge of the humpback whale metapopulation worldwide.

3. Materials and Methods

3.1 Study Area

This study took place in the waters around the archipelago of Islas Secas in the Gulf of Chiriquí of Western Panama (depth <300m). The Gulf of Chiriquí is an important breeding area for BSG humpback whales and has a notably high annual proportion of mother-calf pairs (Rasmussen and Palacios 2013). Findings from a 2017 photo-identification study suggest that southern humpbacks (BSG) are more likely to migrate to this area than their northern counterparts, which is consistent with a previous genetic study done in the area (Acevedo et al., 2017). This latitudinal preference may reflect behavioral or migratory patterns, or maternal fidelity and natal philopatry, both of which vary regionally (Baker et al. 1990, 1994; Medrano-González et al. 1995; Palumbi and Baker 1994; Pardini et al. 2001; Baker et al. 2013; Carvalho et al. 2014).

3.2 Recordings

Humpback whale songs were recorded from the boat using handheld hydrophones from various companies but primarily a SQ26-08 plug-in powered hydrophone (effective sensitivity of -194dB, re 1V/µPa, frequency response of 2 Hz to 50 KHz) connected to a Zoom H4n Pro at a 48kHz sampling rate. Recordings were obtained primarily from late July to early September in four periods of three consecutive years (2007- 2009, 2013-2015, 2017-2019, and 2021-2023) by Kristin Rasmussen, MSc. of Panacetacea, and used with her permission. Only songs with a signal-to-noise ratio (SNR) greater than 6 dB were selected for the identification of units (Chereskin et al., 2019). The acoustic files were opened in RAVEN 1.6 build 37 (Bioacoustics Research Program, 2014) and a spectrogram was generated using a fast Fourier transform (FFT) size of 2,048 points, an overlap of 50%, and a 512-sample Hann window. Figure 3 shows all the locations where the hydrophone was deployed across all years (red= songs detected, black=no songs detected) and Table 1 shows the sampling effort by year.

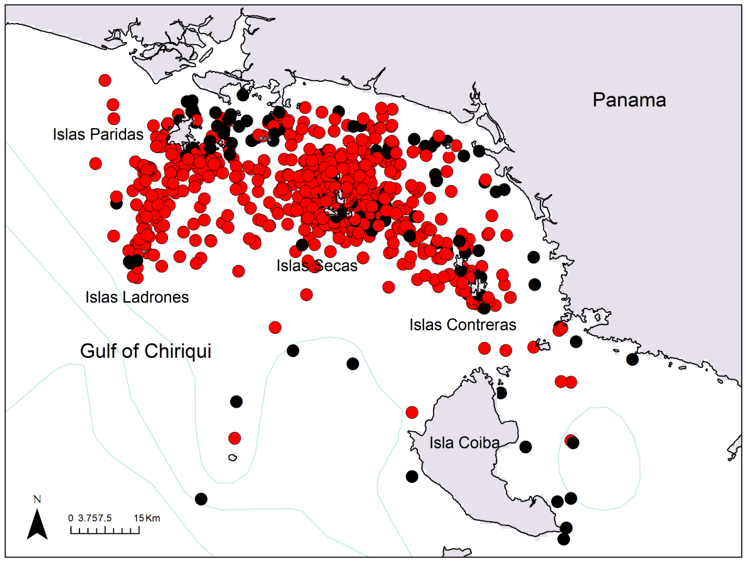


Figure 3. Summary of hydrophone deployment from 2007 through 2023. Black dots signify a deployment with no song detected, red dots signify deployment with song observed. Figure made by Kristin Rasmussen, Msc.

Table 1. Recording efforts detailing months included per year, number of files recorded, and total recorded time. Years without recordings were due to lack of recording equipment (2010-2012) or no surveys run that year (2016, 2020).

Year	Months Included	# Recording Files	Total Duration (sec)
2007	Aug	3	5355
2008	July, Aug Sep, Oct	3	3182
2009	July, Aug, Sep	2	2048
2010	-	-	-
2011	-	-	-
2012	-	-	-
2013	Aug, Sep	1	813
2014	July, Aug, Sep	3	3947
2015	Aug, Sep	3	3974
2016	-	-	-
2017	July, Aug, Sep	3	5473
2018	July, Aug, Sep	3	3646
2019	July, Aug, Sep	2	3620
2020	-	-	-
2021	Feb	2	485
2022	Mar	1	21
2023	July, Aug	2	1400

3.3 Unit Classification and Analysis

From selected songs, units were identified and annotated in the spectrogram, and then classified using a modified version of the classification key by Djokic (2019) (Table 2). This key allows for natural variation in unit structure while still allowing for the grouping of like terms (Helweg et al., 1998; Rekdahl et al., 2018b). Table 2 shows the classification criteria based on contour shape, duration, and peak frequency (the frequency with most energy).

Table 2. Unit classification criteria based on Djokic (2019). Numbers in parentheses represent the corresponding code for each criteria category.

Criteria	Subcategories	Definition
Contour	Upsweep (1)	Contour increasing in frequency
	Down sweep (2)	Contour decreasing in frequency
	Flat or continuous (3)	Continuous frequency with the dominant frequency varying between 100Hz
	Arc (4)	Increasing and then decreasing in frequency
	U-shaped (5)	Decreasing and then increasing in frequency
	Frequency-variable with tail (6)	Shape "N" is repeated once or more, and the final part of the unit doesn't resemble the rest and looks like a tail
	Frequency-variable with high tempo (7)	Indicating fast changes in frequency
	Fuzzy (9)	Broadband, cloudy, similar to deterministic chaos ("segments of non-random noise centered around a portion of the fundamental frequency" (Riede et al. 2004))
Signal type	Tonal (1)	Narrow band frequency
	Pulsed sounds (2)	Rapid pulses or no well-defined contour
	Mixed (3)	Contains both tonal and pulsative sounds that can grade into one or the other
	Noisy tonal (4)	A tone with non-linear phenomena, primarily deterministic chaos
	Raspy (5)	Non-tonal, looks fuzzy
Peak frequency	Below or equal to 5kHz (1)	Self-explanatory
	Above 5kHz (2)	Self-explanatory

Duration	Below or equal to 1sec (1)	Self-explanatory
	Above 1 sec (2)	Self-explanatory
Harmonics presence	Dense (1)	Multiple harmonics close to each other less than 500 Hz between bands
	Sparse (2)	Multiple harmonics separated by 500 Hz or more
	No harmonics or sidebands (3)	Self-explanatory

The characterizations of units using the criteria in Table 2 resulted in each unit to be associated with a five-digit code that described each unit's contour as its name. Additionally, each unit was assigned the following category within a year (1) new is the unit was new for that particular year and was not present in previous years), (2) stable is when a unit was present in two consecutive years, and (3) recalls, if the unit was not present in the previous year but was present in the year before that. Finally, the pace of song unit change was calculated for each year-to-year transition as the number of units phased out (no longer present in that year from the previous) from the first year subtracted from the number of new and constant units in the second year, and then divided by the total number of units present in both years. For example, if for 2018 the number of phased-out units (no longer present from the previous year) from 2017 was 3 and the number of new units in 2018 was 2, out of a total of 12 units between the two years, the pace of change would be (2-3)/12=-0.083, which means the song changed only 8% in its unit composition between those years, and the change was driven primarily by the number of phased-out units. It is important to highlight that, as shown in Table 2, the recording time and, consequently, whale song representation for each year varied considerably among years (from 13 minutes in 2013 to

89 minutes in 2007 and 2017). Therefore, I used the proportion of units to calculate the composition of new, stable and recall units for each year.

4. Results

4.1. Unit repertoire composition

A total of 28 song files were analyzed for this study representing four sets of three consecutive years: 2007-2009, 2013- 2015, 2017-2019, and 2021-2023. From these files a total of 381 units were classified into 47-unit types (Fig. 4, Table 2). The most common unit type was 31121, which was present in the first eight years of the study. This unit is characterized by a flat and tonal contour with dense harmonics, a peak frequency below 5 kHz and duration above 1 second. Because of differences in recording effort and quality, the amount of identified unit types in each year ranged from 1 in 2013 (13 min) to 31 in 2023 (23 min) (Fig. 4).

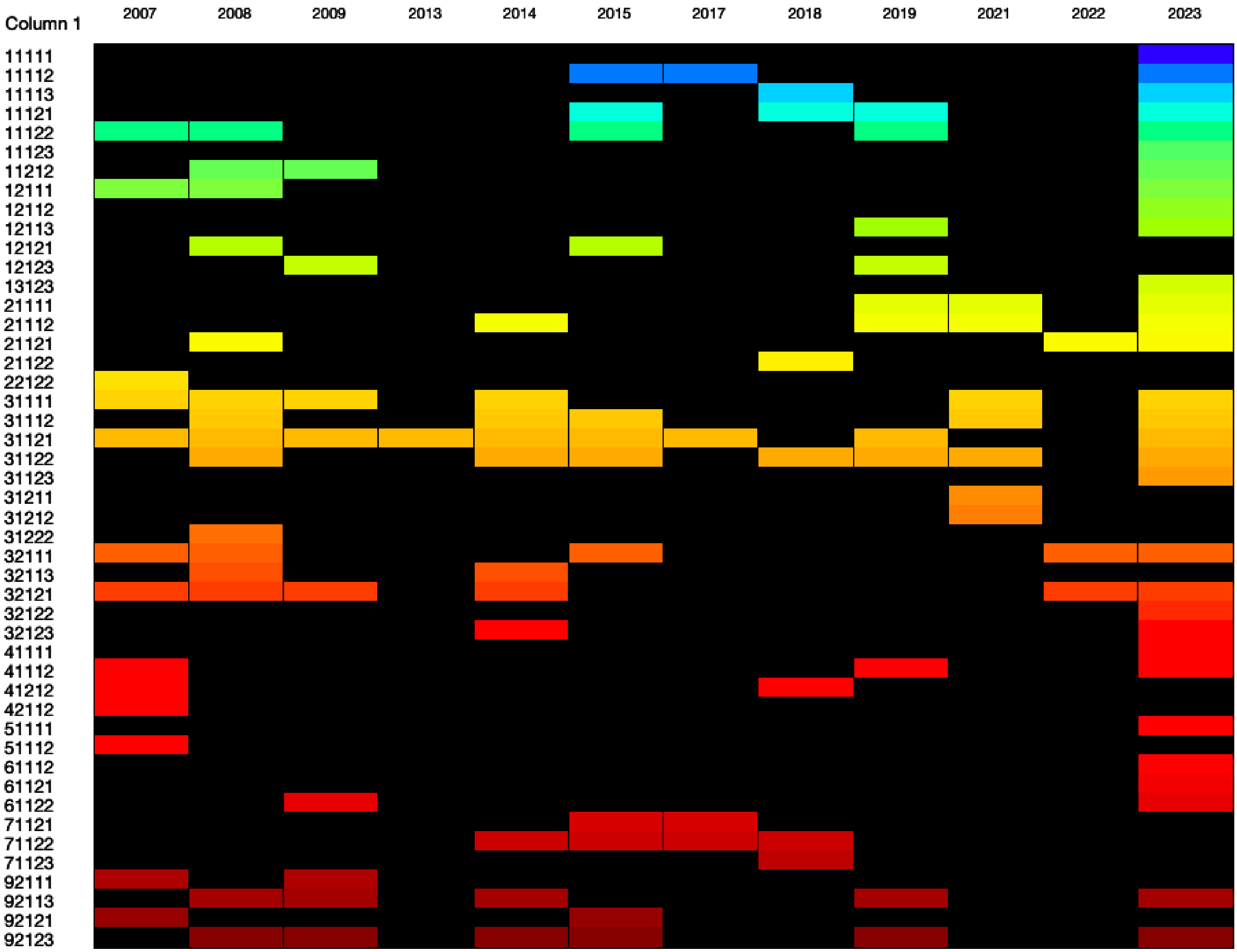


Figure 4. Presence-absence of song unit types for the four sets of consecutive years. Each unit has its own distinct color, and as shown in the figure most units were present in multiple years.

The composition of new, stable, and recalled units varied between and within periods (Fig. 5). Between periods, as expected, 100% of units were new in the period of 2007-2009, for 2013-2015 the song consisted of similar proportions of new (44%) and stable units (55%), in

2017-2019 the song consisted primarily of stable units (71%) with a small proportion of new units (29%) and in the period of 2021-2023, the song has a slightly higher proportion of new (38%), followed by stable (32%) and recall (29%) units.

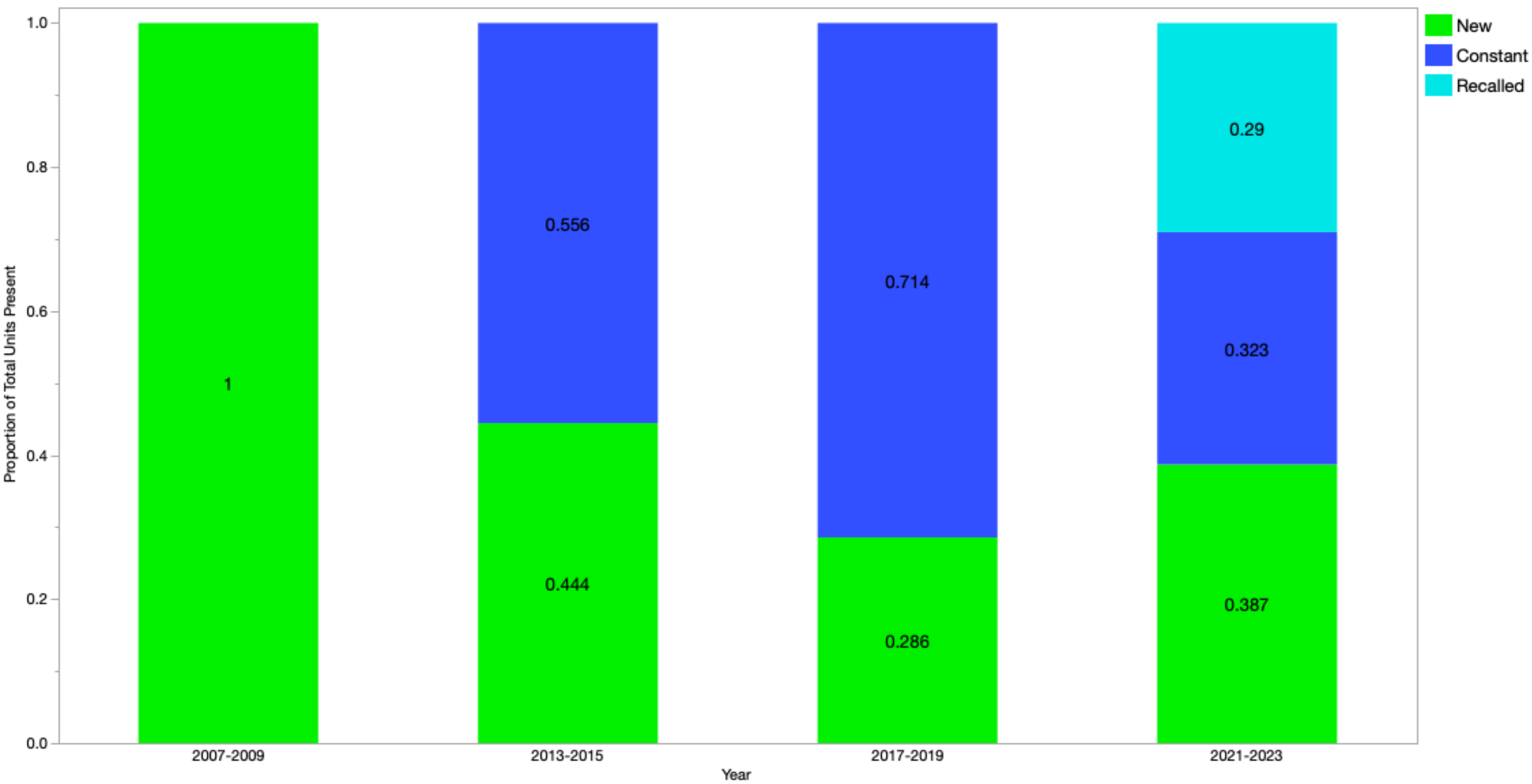


Figure 5. Proportion of new, stable, and recall units in the song of BSG humpback whales for four periods of three consecutive years.

Figure 6 shows the variation of song unit types within each period. In the first year of survey, 2007, the song consisted only of new units (due to 2007 being the first year studied). The proportion of new vs stable units changed in 2008 including 57% of new and 43% of stable units, and in 2009 the song consisted primarily of stable units (67%) with a few new and recall units.

In the next period, starting with 2013, the song consisted 100% of recalled units (as the first of its period); in 2014, the song continued to consist primarily of recalled units (64%), follow by new units (28%) and a few stable units (9%); and in 2015, the song consisted primarily of stable units (42%) followed by recalled units (33%), and new units (25%). For the next period, starting with 2017, the entirety of the song was made of recalled units (as the first of its period); in 2018, the song unit composition changed drastically, consisting of 57% new units, follow by 29% recalled units and 14% stable units, and in 2019, the song consisted primarily of recalled units (73%), followed by constant units (18%) and new units (9%). In the last period, starting with 2021, the song consisted of 71% recalled units, followed by 29% new units, and in both 2022 and 2023 the song maintained a high percentage of recalled units (67% and 58%, respectively) followed by new units (33% and 32%, recspectively), and 10% constant units in 2023.

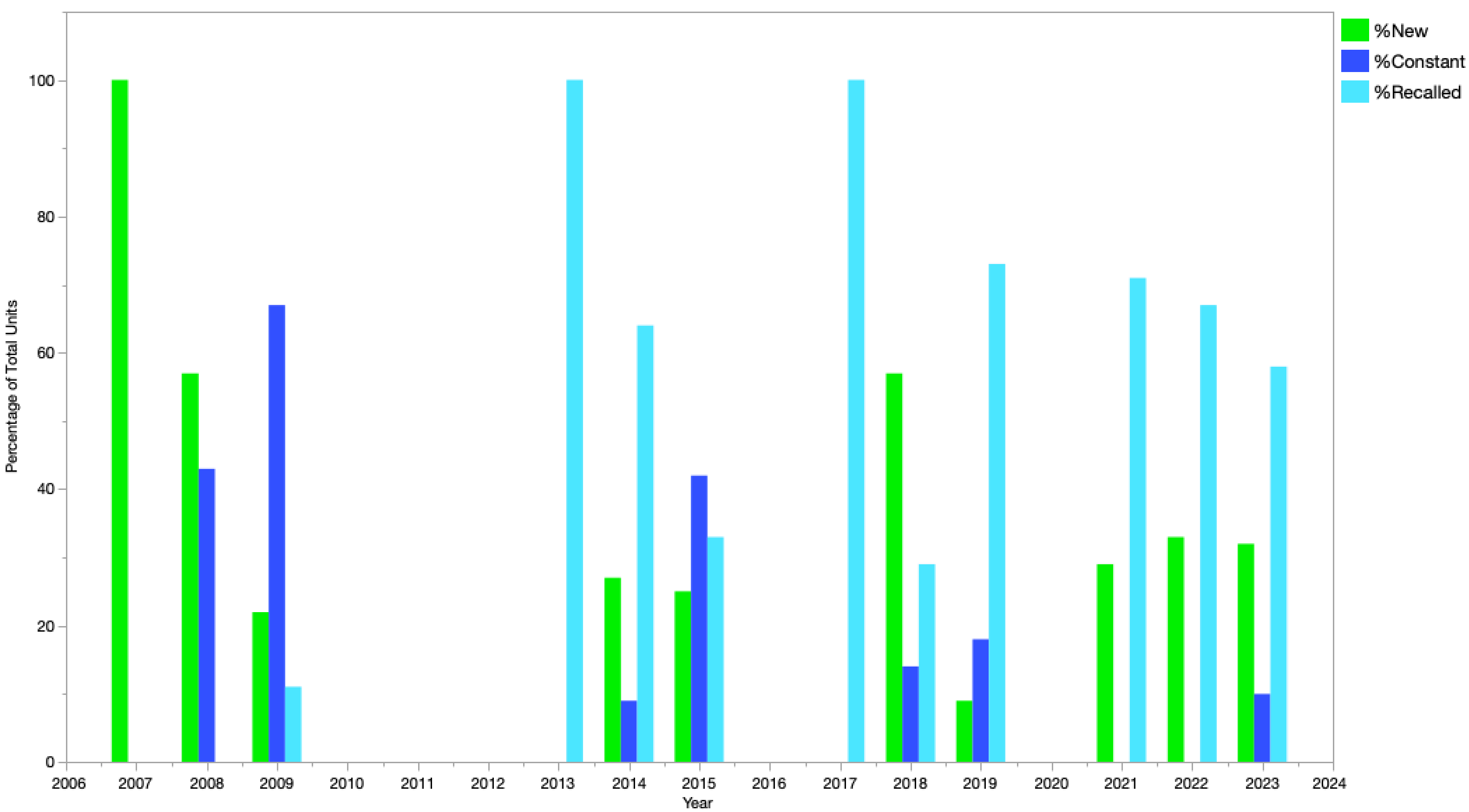
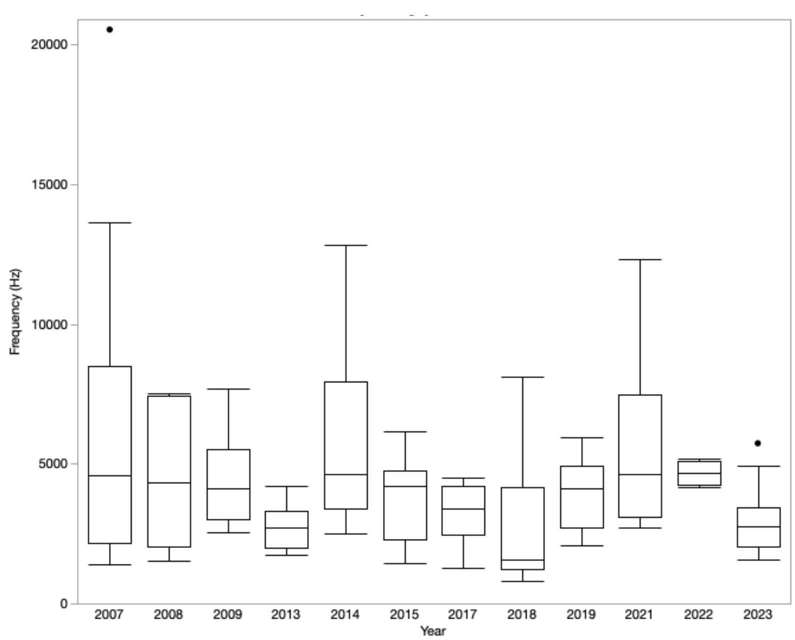


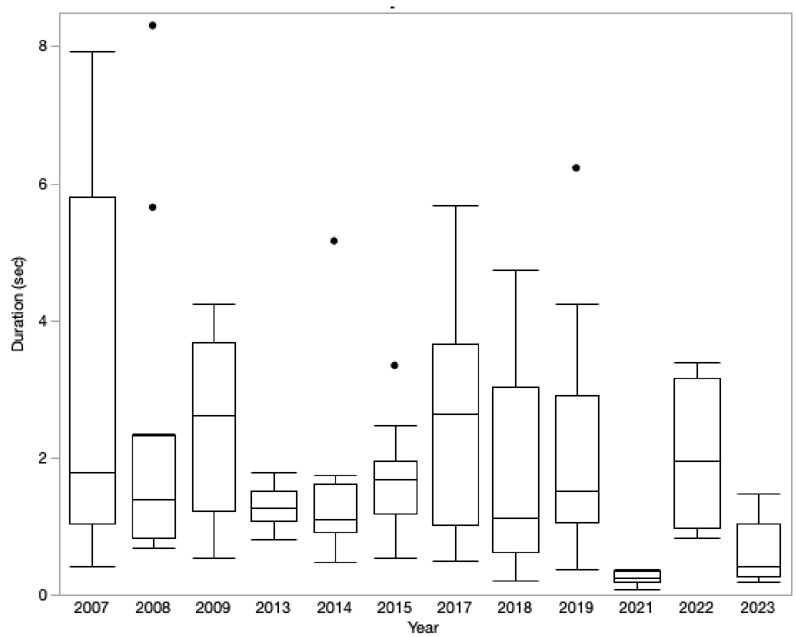
Figure 6. Percentage of new, stable, and recalled units in the repertoire for each year. Apart from the period of 2007-2009 and 2018, it seems that males in this population tend to primarily use recycled units from previous years to build their songs.

4.2. Unit acoustic structure

Regarding other acoustic features of the units, all units in the songs of these whales independently of year had most of their energy below 5 kHz (Fig. 7a) and in most years unit duration was above 1 second, except for 2021 and 2023. Overall, as shown in Figure 8, the most common unit types were those with a flat and tonal contour, dense presence of harmonics, long duration, and low peak frequency.



a.



b.

Figure 7. Variation in song unit peak frequency (Hz) (a) and duration (s) (b) between years. The limits of the boxplots represent the upper and lower quartiles, with the horizontal line as the median and the whiskers as the range. Peak frequency over all years studied had an F ratio of 7.3220 and p-value of less than 0.001, indicating highly significant differences across at least some years. Duration over all years studied had an F ratio of 8.3213and a p-value of less than 0.0001, indicating highly significant differences across at least some years.

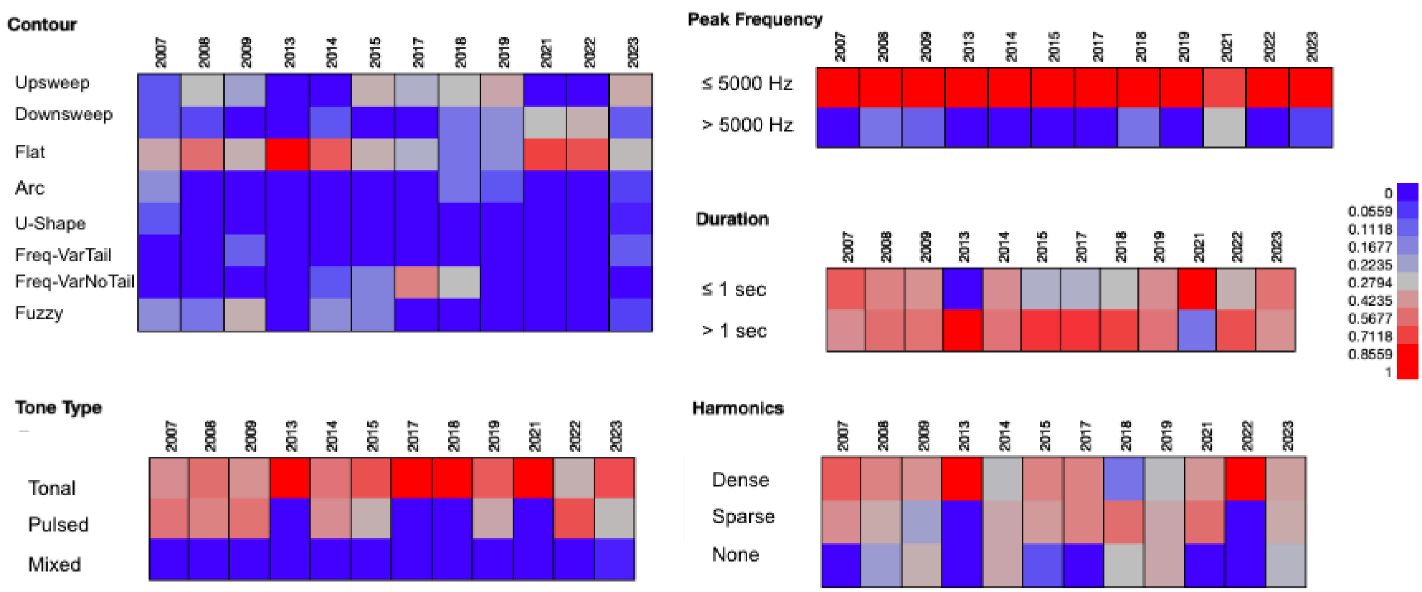


Figure 8. Number of units for each criterion normalized by dividing by the amount of time recorded per year.

Table 3. Estimation of the pace of change of the song, calculated as the number of recalled units plus the number of new units in year 1 to minus the number of phased-out units from year 2, all over the total number of units present over the two years. The green color highlights changes due to gain of units and the purple color highlights changes due to loss of units. The blue color highlights transitions of over one year.

Year Transition	New and Recalled Units	Phased-Out Units	Total Units	Unit Change
2007/2008	8	5	13	0.2307692308
2008/2009	3	8	11	-0.4545454545
2009/2013	1	8	9	-0.7777777778
2013/2014	10	0	10	1
2014/2015	7	6	13	0.07692307692
2015/2017	4	8	12	-0.3333333333
2017/2018	6	3	9	0.3333333333
2018/2019	9	5	14	0.2857142857
2019/2021	7	8	15	-0.06666666667
2021/2022	3	7	10	-0.4
2022/2023	28	0	28	1

4.3. Rate of unit change

Table 3 shows an estimation of the pace of change of the song calculated as the number of recalled plus new units in year 1 minus those present in year 1 but not in year 2 (coloquially called “phased out”), and both divided by the total number of new, recalled, and phased out units in both years. It is important to highlight that this estimation does not consider differences in sampling time, which could either overestimate or underestimate the degree of change from one year to the next. Overall, the transitions in which the song changed due to the addition of new units were 2007/2008, 2013/2014, 2014/2015, 2017/2018, 2019/2019, and 2022/2023, and in 2013/2014, 2022/2023, and 2017/2018 that change occurred relatively fast (though in the case of the 2013/2014 and 2022/2023 transitions, this fast change this was likely due to the disparity in recording time between years 1 and 2). The transitions with song change due to the loss of units were 2008/2009, 2009/2013, 2015/2017, 2019/2021, and 2021/2022, and the 2015/2017 and 2019/2021 transitions showed the slowest change in unit type composition.

5. Discussion

1. Total Unit Presence

This study finds that Southeastern humpback whales reproducing in the Gulf of Chiriquí have a unit repertoire consisting of 47 unit types represented across 381 recorded discrete units. Other studies have reported a higher number of units and in a shorter period: for example, Magnusdottir et al., (2015) reported that the song of humpback whales singing at their feeding areas in Iceland had a total repertoire of 2,810 units. This discrepancy is likely due to differences in unit classification and in sampling effort, but more importantly likely because whales express a greater variation of songs in their feeding areas than in their breeding areas. Regarding classification of units, the authors used automatic unit detection, which is known to overestimate the number of units present. Maeda et al. (2000) found that humpback whale song consisted of 32 unit types over a 6-year period in the Ryukyu Islands of Japan, using a similarly automated classification method as Magnusdottir. In this study all unit types were classified manually by one person and then reclassified after revision by four other lab members until a consensus was reached.

The mean number of units present per year found in this study, 10 units, is similar to reported means in two of the three other studies of BSG song in Central America - 14 units in a study conducted in the Archipelago de las Perlas in Panama from 2006-2007 (Oviedo et al., 2008), and 12 units in a study conducted off of Caño Island, Costa Rica from 2016-2017 (Chereskin et al., 2019). Ziegler (2018) found 22 distinct units in the 2017 song repertoire of BSG at Cano Island in the Osa Peninsula, while only 4 were found in this study for 2017. This was likely another case of unit classification disparity.

2. Prevalent Qualities

Most units were present across all 4 time buckets (Fig. 4). The units present across the most years were units 31121 (9 years) and 31122 (7 years). These units both had the flat contour type, were tonal, had peak frequencies of less than or equal to 5000 Hz, were less than or equal to 1 sec in duration, and differed only in harmonics presence (with 31121 having dense harmonics and 31122 having sparse harmonics). Ross (2005) calculated an average ambient noise level of 50Hz in the North Pacific increasing by 5.5 dB/decade since the 1970s, though noise generated by ocean traffic in the North Pacific has become more variable of late (Andrew et al., 2011). This is well under the top of the range of peak frequencies of the two most heavily used units, and well under the average mean peak frequency for all years studied (Fig. 7a), indicating that selective environmental pressure may factor into unit use and retention.

Most of the units present were flat in contour, tonal, and with a low peak frequency and relatively low duration. These findings corroborate Perazio and Mercado's (2022) acoustic characterization of the BSG humpback whale songs from a breeding area in Colombia, where most of the energy was between 250 and 475 Hz. Low frequencies have lower transmission loss, and thus can be heard by conspecifics from farther away. Similar patterns have been found in other baleen whales: for example, Clark (1982) found that the calls of the bowhead whale and southern right whale remained lower in peak frequency in noisy environments. Sound propagation is known to increase with higher temperatures, and Beer's law states that sound intensity is inversely proportional to sound frequency and water density (which decreases with temperature) (Rafferty 2023). Therefore, a lower sound frequency has a higher intensity, especially in warmer water, and is likely selected for in long-distance communication (May-Collado et al., 2007).

2. Unit Composition and Rate of Change

Regarding the unit composition of new, stable, and recalled units, we found a tendency to recycle units from the previous and other past years. This suggests that whales have a limited number of units in their repertoire at a time, many of which are regularly used to form their songs. This would explain the slow gradual changes observed within and between year periods. The most drastic change in song unit composition compared to the other periods was within the periods of 2007-2009 and 2013-2015 (78%), likely due to a greater temporal difference between recordings. Otherwise, the changes between periods suggest gradual change. This is supported by studies in other humpback whale populations, such as those in the Northern Hemisphere that show a slow-evolving song (Zandberg et al. 2021). Darling et al. (2019) reported whale song with a varying rate of song change over three years across several studied populations of North Pacific humpback whales, but in this study, the last three periods of three consecutive years show similar patterns of unit composition, despite differences in proportion.

Interestingly, the years with most presence of new units correspond to moments of potential arrival of males from other populations. For example, in 2018 our lab detected a phrase previously described in Brazil the year before, suggesting either exchange due to an outside male arriving to the BSG breeding areas or vice versa (May-Collado personal communication). That same year, the song repertoire of BSG humpback whales in Ecuador matched those of whales in French Polynesia. Schulze et al. (2022) reported a song spread in an eastward direction around that time, with whales in Ecuador adopting a song from French Polynesia, suggesting vocal connectivity across the entire South Pacific Ocean basis. The transitions between 2017/2018 and 2018/2019, as well as the transition between 2022 and 2023, were found in this study to be periods of relatively high unit change caused by introduction of new units. Therefore, it is possible that, at least during the 2017 through 2019 period and potentially during the 2022/2023 period, there was a revolution of song across the entire Pacific Ocean. In general, southwestern humpback whale populations are more often described as "revolutionary" in their songs than their southeastern counterparts because they experience a lot of change over a short period of time (Zandberg et al. 2021) - the Schulze et al. (2022) report of song revolution in the east south Pacific appears to be a rare instance of revolution in this area, and this study corroborates that revolution, as well as Ziegler's (2018) findings for 2018-2019 at the phrase level.

6. Conclusion

The unit structure of the humpback population that winters off the Chiriquí Gulf of Panama is shown in this study to be variable over time in contour and duration, though relatively stable in peak frequency. The composition of new, constant, and recalled units varied between years and across periods, but most periods consisted mostly of constant units until the 2021-2023 period, indicating gradual change until the recent influx of new and recalled units. In the 2017/2018 and 2018/2019 transitions, as well as in the 2022/2023 transition, song change was relatively high and driven primarily by the introduction of new units, indicating that a song revolution had potentially occurred. From this information, we can better grasp the impact of environmental factors such as ambient noise (mostly anthropogenic), assume a relatively high level of connectivity between sub-populations in the breeding area, and better understand the effects of eastern song spread in regards to song revolution and population connectivity, allowing for better and more effective conservation efforts to take place.

Due to differences in acoustic recording effort and quality across years, the unit repertoire analysis resulting from this study is limited to very small sample sizes. However, the overarching purpose of the study was to test and advance a novel classification method of song units developed by Djokic (2019) and a novel equation for calculation of rate of song change at the unit level. Therefore, though the findings themselves may be skewed disproporitionately, this study still makes an important contribution to the study of humpback whale song.

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