



All units are equal in humpback whale songs, but some are more equal than others

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Abstract

Flexible production and perception of vocalizations is linked to an impressive array of cognitive capacities including language acquisition by humans, song learning by birds, biosonar in bats, and vocal imitation by cetaceans. Here, we characterize a portion of the repertoire of one of the most impressive vocalizers in nature: the humpback whale. Qualitative and quantitative analyses of sounds (units) produced by humpback whales revealed that singers gradually morphed streams of units along multiple acoustic dimensions within songs, maintaining the continuity of spectral content across subjectively dissimilar unit “types.” Singers consistently produced some unit forms more frequently and intensely than others, suggesting that units are functionally heterogeneous. The precision with which singing humpback whales continuously adjusted the acoustic characteristics of units shows that they possess exquisite vocal control mechanisms and vocal flexibility beyond what is seen in most animals other than humans. The gradual morphing of units within songs that we observed is inconsistent with past claims that humpback whales construct songs from a fixed repertoire of discrete unit types. These findings challenge the results of past studies based on fixed-unit classification methods and argue for the development of new metrics for characterizing the graded structure of units. The specific vocal variations that singers produced suggest that humpback whale songs are unlikely to provide detailed information about a singer’s reproductive fitness, but can reveal the precise locations and movements of singers from long distances and may enhance the effectiveness of units as sonar signals.

Keywords Acoustic communication · Cetacean · Mysticete · Vocal learning · Bioacoustics

Readers familiar with George Orwell’s *Animal Farm* will have recognized the title of this paper as an allusion to a crucial revision made to the barnyard moral code near the end of his novella (Orwell 1945). In Orwell’s fable, a group of animals rebel against their caretakers and create their own society, the foundation of which rests on adherence to seven commandments. The most important of these commandments is that “all animals are equal.” Unfortunately, not all animals on the farm are content to abide by these rules, and in a bid to justify their law-breaking ways, the pigs on the farm secretly revise this last commandment, converting it into the maxim that “all animals are equal, but some animals

are more equal than others.” This oxymoronic change ultimately derails the society the animals have constructed.

Fifty years ago, a small group of researchers reported that humpback whales were producing some of the most complexly structured vocal sequences ever observed in nature (Payne and McVay 1971; Winn et al. 1970). They described these sequences as “songs,” giving birth to a new way of thinking about the mental status of whales and raising the intriguing question of why whales sing. Although initially described as a “barnyard chorus” (Kibblewhite et al. 1967), scientists quickly came to view whale songs as the underwater analogues of bird songs (Payne et al. 1983; Winn and Winn 1978). As a result, most explanations for why humpback whales sing have focused on functions proposed for bird songs: attraction of mates and repulsion of competitors (Herman 2017). Underlying current hypotheses for the reproductive function(s) of humpback whale songs is the foundational assumption that singers combine sounds (called “units”) into patterned sequences (“phrases” and “themes”) to construct advertisement displays (songs) that can reveal

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the fitness of the singer to listening conspecifics. From this perspective, units within songs are like the quills within a peacock's tail or the tines in a deer's antlers: functionally equal elements that only achieve their utility when perceived en masse (Tyack 1981).

Contrary to this view, acoustic analyses of humpback whale songs suggest that singers vary the characteristics of units extensively and progressively both within and across songs (Cato 1991; Mercado et al. 2005), and that some units are much more likely to remain detectable after long range transmission than are others (Au et al. 2006; Gong et al. 2014). It is unclear how an “acoustic peacock tail” with colors and patterns that constantly change, both as a function of a listener's position and depending on the time period within which the display is observed, could possibly provide a reliable basis upon which listening whales might assess the relative fitness of a singer, especially given that social interactions between specific whales rarely persist for longer than a day or two in contexts where singing is prevalent (Clapham et al. 1992). Put another way, if units within songs are not functionally equivalent, then this calls into question the claim that humpback whales are simply chaining units in complex combinations (i.e., phrases, themes, songs) to advertise their superior vocal abilities, and raises the possibility that humpback whales are using their songs in ways that birds are not. All units within humpback whale songs cannot be functionally equal if some units are much less detectable than others. Something is awry in the oceanic barnyard.

Vocal versatility is relatively rare in the natural world (Freeberg et al. 2012; Janik and Slater 1997). While many mammals can produce a variety of complex sounds, most have only a limited ability to flexibly modify the size and composition of their vocal repertoire. Notable exceptions to this general trend are humans, bats, and cetaceans, which have the capacity to flexibly adjust their sound repertoires throughout their lifespan (Mercado et al. 2014). Identifying exactly how a given species' vocal repertoire changes over time is a critical step toward understanding both how individuals control those changes as well as for understanding the functional relevance of their dynamic repertoires. Historically, researchers have often characterized animals' repertoires by subjectively sorting recorded vocalizations (reviewed by Kershenbaum et al. 2016). Subjectively identified sound categories may then be validated using either statistical or computational methods (e.g., Fischer et al. 2013; Keenan et al. 2020; Wadewitz et al. 2015). Occasionally, the validity of such categories may also be assessed by testing whether animals can sort their own vocalizations in the same way as human observers (e.g., Bloomfield et al. 2003, 2008), by correlating sound types with their use in particular behavioral contexts (e.g., Clark 1982; Elie and Theunissen 2016), or by identifying neurons that show categorical responses

to different sound types (e.g., Shepard et al. 2015). Efforts to develop more data-driven, biologically-relevant descriptions of vocal repertoires have increased in the past decade (e.g., Cazau et al. 2016; Fischer et al. 2017; Hyland Bruno and Tchernichovski 2019; Schneider et al. 2019), but such objective techniques have rarely been applied in analyses of humpback whale songs.

Past auditory categories used to classify humpback whale song units have been categories of convenience. Most categories (e.g., *moans*, *cries*, and *groans*) existed before researchers ever discovered that whales sing. Winn and Winn (1985) reported that the seven basic unit categories that they identified (*cries*, *chirps*, *yups*, *oos*, *moans*, *snores*, and *surface ratchets*) were present in songs that they recorded across 12 years, two oceans, and five geographic locations, with only two of those categories (*chirps* and *surface ratchets*) not being present in all songs. In contrast, other researchers have found that unit categories identified in 1 year are often difficult to reliably apply to songs recorded a decade later (Cato 1991; Mercado et al. 2005). Given that it is not yet possible to experimentally identify the categories of units that are most salient from a humpback whale's perspective, it is important to closely consider the acoustic variations that singing humpback whales produce, and to take those characteristics fully into account when analyzing songs. The first aim of this study was to clarify whether singing humpback whales construct songs using a fixed “dictionary” of stereotyped unit types that is stable over time (as suggested by Garland and McGregor 2020; Helweg et al. 1992; Winn and Winn 1985), or whether they use a more graded vocal repertoire that they can dynamically adjust within songs and across years (Cato 1991; Mercado et al. 2005; Payne and Payne 1985).

A second aim of this study was to evaluate variations in the functional utility of different units within the repertoire used by singing humpback whales. Traditionally, researchers evaluating the functionality of units within humpback whale songs have treated them as analogous to notes in a musical piece (Gray et al. 2001; Payne 2000; Rothenberg and Deal 2015), letters within an alphabet (Malige et al. 2020; Miksis-Olds et al. 2008; Suzuki et al. 2006), or words within a dictionary (Allen et al. 2017). From these perspectives, changes in unit duration, pitch, frequency content, or intensity have no bearing on the functionality of units—all that is necessary is that a discrete sound be present for it to contribute to the information content or aesthetic of a song. Most researchers studying humpback whale songs have largely discounted the possibility that the functional roles played by individual units might vary across contexts or within songs (for exceptions, see Maeda et al. 2000; Mercado 2018b; Winn and Winn 1978). If singing humpback whales are using acoustically different units within songs for different functions, then this should

be evident from systematic differences in how they produce, distribute, and vary the acoustic characteristics of units (e.g., see Clark and Ellison 2004; Simmons and Stein 1980). Identifying systematic differences in the relative intensity, frequency, and localizability of units, in particular, is critical to evaluating whether units are functionally heterogeneous.

A final aim of the current study was to assess whether units vary along acoustic dimensions that affect how precisely listeners might localize the sources of units (or of echoes generated by units) from long distances. All current functional hypotheses for song function require that listening whales are able to track the locations of individual singers that cannot be seen (Herman 2017; Mercado 2018b), a task which can be quite challenging over long distances in shallow water environments (Frankel et al. 1995; Mercado and Frazer 1999; Mercado et al. 2007). Loud, sustained units that vary little in frequency over time will be highly detectable at long ranges, but may provide little information about the location of a singer (Barclay 1986; Simmons et al. 2014; Simmons and Stein 1980; Slabbekoorn et al. 2002). Intense units that sweep across a broad range of frequencies will often travel shorter distances before dropping below noise levels, but can provide more information about a singer's distance and bearing (Branstetter and Mercado 2006; Mercado et al. 2007, 2008; Schneider et al. 2014). Additionally, the specific frequencies produced within a unit will determine the distances from a singer at which that unit will be detectable (Frazer and Mercado 2000; Mercado and Frazer 1999; Mercado et al. 2000). Au et al. (2006) noted that even at close ranges, certain units (specifically, “vibrating upsweeps”) were better for precisely tracking the positions of singers than others. Thus, the acoustic variations evident across units not only affect their resilience when propagating long-distances underwater, but also determine the kinds of information that units can provide to listeners. Here, we show that singers vary the acoustic characteristics of units within songs in ways that are unlikely to reliably reveal individual differences in the biological fitness of singers, but that can enhance the efficacy of units as cues to the locations and movements of singers and as echo-generating sonar signals that singers can use to detect and track distant conspecifics.

Identifying the ways that singers vary units is important not only for understanding the origins and nature of humpback whale songs, but also for improving the validity and reproducibility of song analyses. In particular, methodologies that emphasize the acoustic dimensions along which individual singers change units can reduce reliance on subjective criteria for sorting and labeling units, as well as the inevitable biases introduced by human categorical perception, thereby increasing opportunities for

discovering the functional relevance of unit variations to humpback whales.

Method

Recordings

Past quantitative analyses of humpback whale song units (see Table 1) have focused heavily on summarizing basic acoustic features such as unit duration, patterns of frequency modulation, and bandwidth, ostensibly to create an “acoustic dictionary” of sounds produced by singing humpback whales. Because constructed unit dictionaries are typically used to transcribe sequences of unit types from recordings of many different singers, they tend to emphasize prototypical features of subjective categories of units sampled from several different singers recorded across multiple years (Allen et al. 2017; Murray et al. 2018). This nomothetic approach to describing the vocal repertoire of singing humpback whales aims to provide a universal characterization of units and song structure that generalizes to all members of the species (for an overview of nomothetic approaches, see Beltz et al. 2016).

In contrast, the goal of the current analysis was to collect detailed measures of variations in units produced by individual singers, and then to compare similarities and differences in unit characteristics produced in different time periods and populations (i.e., to analyze the overall structural variability of units used by individual singers). This idiographic approach to unit characterization emphasizes variability in the vocal behavior of individuals rather than summaries of salient features of “unit types” or criteria for determining the number of types in the species repertoire (for an overview of idiographic approaches, see Molenaar 2004). Consequently, the recordings selected for the current analysis were chosen to illustrate the acoustic variety of units produced by individual singers within a relatively short time period, rather than to describe the full range of vocalizations that singing humpback whales are capable of producing. We verified that the selected recordings contained units representative of those produced by several singers in a given locale and time period, and limited detailed analyses to those recordings with the highest signal-to-noise ratios.

Two archival recordings were obtained from the Macaulay Library, both made in the West Indies; the files are designated as catalog number 117770 (Perkins, 1970, Puerto Rico) and 110,858 (Perkins, 1973, British Virgin Islands). For specific recording information, see www.macaulay.library.org. Both recordings were originally included in analyses that focused on describing the complex sequential structure of humpback whale songs (Winn and Winn 1978). Based on analyses of at least 449

Table 1 Past quantitative analyses of unit repertoires used by singing humpback whales

Study	Year/Locale	Sampling approach	Songs analyzed	Units analyzed
Mednis, (1991)	1988/eastern Australia	Not indicated	64	Not indicated
Walker et al. (1996)	Not indicated	Not indicated	?	504
Mercado and Kuh, (1998)	1981–1995/Hawaii	Subjectively selected based on pitch and duration	?	242
Helweg et al. (1998)	1994/Southwest Pacific	Not indicated	71	4487
Maeda et al. (2000)	1991–1997/Ryuku Islands	Subjectively identified through aural and spectrographic analysis	19	4861
Cerchio et al. (2001)	1991/Kauai; Socorro, Mexico	Not indicated	159	4997
Mercado et al. (2005)	1981–1995/Hawaii	Subjectively sampled from representative phrases	37	813
Au et al. (2006)	2002/Hawaii	Not indicated	?	762
Suzuki et al. (2006)	1976–1978/Hawaii	Automated signal detection	16	12,703
Green et al. (2007)	1992/Hawaii	Automated signal detection	4	1183
Dunlop et al. (2007)	2002–2004/eastern Australia	Subjective sampling	0	88*
Rickwood and Taylor (2008)	Not indicated /eastern Australia	Automated signal detection	?	?
Picot et al. (2008)	Not indicated	Automated signal detection	?	505
Mercado et al. (2010)	2009/Puerto Rico	Automated signal detection	?	1221
Pace et al. (2010)	2008–2009/St. Marie Channel	Automated signal detection	?	424
Green et al. (2011)	1985–1995/Hawaii	Automated signal detection	?	8641
Stimpert et al. (2011)	2006/Stellwagen Bank	Subjectively selected, statistically clustered	0	964*
Rekdahl et al. (2013)	1997–2009/eastern Australia	Opportunistic selection	10	343*
Kaufman et al. (2012)	1973–1976/Puerto Rico, Lesser Antilles, Turks and Caicos	Automated signal detection	?	9545
Ou et al. (2013)	2002/Hawaii	Automated contour extraction	?	951
Adam et al. (2013)	2007–2009/St. Marie Channel	Subjectively selected based on signal-to-noise ratio	22	?
Fournet et al. (2015)	2012/Alaska	Subjectively selected based on signal-to-noise ratio	0	256*
Razik et al. (2015)	2008–2009/St. Marie Channel	Not indicated	?	?
Magnúsdóttir et al. (2015)	2008–2011/Iceland	Automated signal detection	?	2810
Cazau et al. (2016)	2008–2012/St. Marie Channel	Subjectively selected based on signal-to-noise ratio	4	2210
Allen et al. (2017)	2002–2014/eastern Australia	Subjectively sampled from representative phrases	76	6409
Murray et al. (2018)	2004,2011/eastern Australia	Not indicated	17	18,161
Pines (2018)	Not indicated /Hawaii	Automated segmentation	?	130
Rueda and Ryan (2020)	2016/northeast Pacific	Manually segmented and sorted, automated classification	1	4539
Malige et al. (2020)	2000–2001/Abrolhos bank off Brazil	Subjectively identified through aural and spectrographic analysis	19	5860
Schall et al. (2021)	2011–2018/Southern Ocean	Subjectively sampled, automated classification	302	29,304

*Vocalizations analyzed were not from actual recordings of songs, but were described as being perceptually similar to units within songs

songs produced by 184 different singers over a period of 10 years (Winn et al. 1981; Winn and Winn 1978), Winn and colleagues concluded that all humpback whale singers use a fixed repertoire of unit types to construct their songs (Winn and Winn 1985). This conclusion appears to have been based on subjective impressions (both aural and

visual) of units, because none of their published reports include any detailed acoustic measurements of units. The two recordings from the West Indies analyzed in the current study provided a way to evaluate Winn and Winn's (1985) description of the unit repertoire using an unbiased sample of unsorted units (i.e., a sample selected by other

researchers for reasons unrelated to the goals of the current study).

Two additional recordings from Colombia (made in 2013 and 2019) were also analyzed in-depth (see Perazio et al. 2018 for details of how these recordings were made). Like the West Indies sample, these two recordings were selected from a larger database (39 songs recorded from ~28 singers) originally used to analyze the structure of humpback whale songs (Mercado and Perazio 2021; Perazio et al. 2018). Qualitative and quantitative comparisons of songs from this larger database confirmed that different singers used similar unit repertoires within each year (Mercado and Perazio 2021).

Each of these four recordings contained at least two full song cycles, with a single singer clearly audible, making it possible to assess intraindividual variations in units within songs as well as across consecutive songs. All of the recordings were made using a single hydrophone suspended from a boat. The singing humpback whales featured in these recordings are presumed to be adult males, because most identified singers to date have been found to be adult males (Herman, 2017). The recordings are most likely from different singers because there is no known exchange of individuals between Colombia and the West Indies, and because the probability of two singers recorded in different years being the same singer is low (Cerchio et al. 2001).

An archival set of unit measures collected from 19 songs (4681 units) recorded off the coast of Japan over a period of 7 years (Maeda et al. 2000) were also reanalyzed for comparison with the units measured in the current study.

Constructing the unit database

Units within humpback whale songs have been described as “the best-defined element of the humpback whale song” (Malige et al. 2020). They are traditionally defined as any sound produced by a singer that human listeners perceive as continuous (Payne and McVay 1971). This seemingly straightforward designation can be problematic, however, because sometimes singers’ vocalizations contain short-duration, silent gaps that are near the threshold of audibility (Fig. 1A). Additionally, units can differ dramatically in duration and intensity, such that some are much less evident than others (Fig. 1B). One observer’s unit is another’s series of units or no unit at all. For instance, in a recent comparison of song transcription between an expert analyst and a less experienced observer, the expert identified 1614 units while the less experienced observer found 1855 units in the same recording (Malige et al. 2020). In the current study, units were identified based on aural and visual impressions of phrases (via spectrographic and waveform representations), and isolated by manually selecting waveform segments using

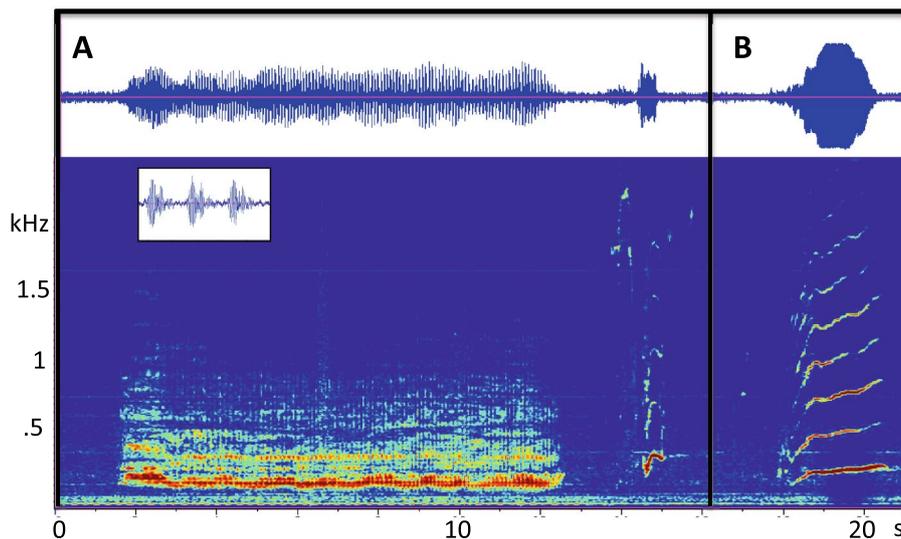


Fig. 1 Waveforms (*upper panel*) and spectrograms (*bottom panel*) of four units produced by a singing humpback whale. **A** Depicts two units with multiple “subunits.” The first unit is a click train containing ~100 individual clicks (shown in the inset waveform) and the second includes four rapid frequency jumps (from 3.2, to 3.9, to 3.2, to 0.5 kHz), followed by two tone pips in the upper register that sound similar to the initial frequency jumps. To most human listeners, both of these vocalizations are continuous, but acoustically they are not. **B** Shows two units that differ by more than an order of magnitude in

duration and intensity. The first, a 1.5 kHz, 10 ms tone pip, is a unit that is likely to be missed by observers who are not expecting it or who are not recording a singer in quiet conditions at short distances. This unit is so faint that it is visually undetectable within the waveform, even though it was recorded from the same distance as the second unit. Note also that if the temporal gap between these two units were slightly shorter, then the units would perceptually merge and be classified as a single unit, like the second unit in (A)

Raven (ver 1.5) to yield a series of time stamps indicating when units began and ended within each recording. No minimum duration threshold was used in classifying a sound as a unit, but a minimum interval of 10 ms was used for separating consecutive units.

The earliest published descriptions of whale songs classified units in terms of their aural and spectrographic features (Payne and McVay 1971; Winn et al. 1970; Winn and Winn 1978), an approach that continues to be popular (Allen et al. 2017; Garland et al. 2017; Malige et al. 2020). As part of this process, units have often been partitioned into broad classes. Winn and Winn (1985) identified three basic kinds of units: high, low, and changing frequencies. Mednis (1991) recommended dividing units into four main types—harmonic, broadband with spectral lines, broadband impulsive, and complex—as did Maeda et al. (2000), whose four types included harmonic, amplitude-modulated, impulsive, and complex (see also, Pace et al. 2010). Au et al. (2006) described two broad groups: tonal units with higher frequency harmonics and broadband units with weak harmonics and gurglelike features. Similarly, Allen et al. (2017) split units into those that were contoured (revealing narrow frequency peaks in spectrograms) versus those that were not. Magnúsdóttir et al. (2015) identified five major classes of units produced by singers in Iceland: high-frequency harmonic units; mid-frequency harmonic units with decreasing frequency modulation; mid-frequency harmonic units with increasing frequency modulation; low-frequency harmonic units; and complex and impulsive low frequency units (see also Clark 1982). All of these divisions correspond to variations in the fundamental frequencies of pulsed sounds (Killebrew et al. 2001; Mercado et al. 2010; Murray et al. 1998), with higher pulse rates generating more widely spaced spectrographic bands and lower pulse rates producing images that may appear more “noisy” depending on pulse characteristics and how analysis parameters are selected (Mercado and Kuh 1998). Pulse-rate dependent variations in the aural and spectrographic features of song units are generally comparable to differences observed across human vocal registers, with low pulse-rate units being comparable to “vocal fry” and higher-rate units falling in the whistle register (Mercado et al. 2010). Within these broad categories of units, there is little agreement about how many different unit types singers produce (see Table 2), or even about what aspects of units should be considered when classifying them (Cholewiak et al. 2013; Mercado and Handel 2012). Differences between investigators’ categories of units may partly be a result of analyses focused on data from a sample restricted to a single population or to a small number of years, or may simply result from idiosyncratic perceptual biases.

In the current study, units were subjectively classified into categories (10–16) identified by Winn and Winn

Table 2 Number of unit categories reported for humpback whale songs

Study	# of years spanned	# of unit categories
Winn and Winn (1985)	12	51
Mednis (1991)	1	12
Cato (1991)	2	15
Helweg et al. (1998)	1	17
Maeda et al. (2000)	7	32
Au et al. (2006)	1	9
Suzuki et al. (2006)	3	33
Rickwood and Taylor (2008)	1	10
Picot et al. (2008)	1	13
Miksis et al. (2008)	1	17
Pace et al. (2010)	2	21
Ou et al. (2013)	1	12
Magnúsdóttir et al. (2015)	3	14
Allen et al. (2017)	12	149
Garland et al. (2017)	7	58
Murray et al. (2018)	2	81
Pines (2018)	1	60
Allen et al. (2019)	13	142
Warren et al. (2020)	3	71
Rueda and Ryan (2020)	1	22
Malige et al. (2020)	2	15
Schall et al. (2021)	5	12

(1978), based on their published descriptions of song phrases (see Table 3). Generally, unit categories identified by Winn and colleagues correspond to differences in the register (upper, middle, lower), duration (long, short), and frequency modulation (up, down, variable) of units (see Helweg et al. 1998; Magnúsdóttir et al. 2015 for similar categorization schemes). In some instances, Winn et al. identified unit similarities across registers through phonetic similarities in category labels (e.g., *chirps* versus *ups* and *yups*, or *whos* versus *oos*). For instance, *ups* are lower-pitched *chirps*, and *yups* are lower-pitched *ups*. In other cases, however, such similarities were not acknowledged (e.g., *ees* and *oos* are lower-pitched *cries*, and *groans* are lower-pitched *wavers*). For recordings from the West Indies, units that were not perceptually matched to one of Winn and colleagues’ categories were labeled as being either a hybrid of two or more categories, or were designated as “none of the above.” For recordings from Colombia, units were classified into the categories identified by Winn and colleagues based on their perceptual similarities to sounds recorded in the West Indies. Units from Colombia that did not match West Indies-based categories were classified as either belonging to a new category or as hybrids.

Table 3 Basic unit categories identified by Winn and Winn (1985)

Unit Type	Characteristic features
Upper Register Units	Spectral energy > 600 Hz
*Cries	Tonal, duration > 0.5 s, often modulated
Chirps	Tonal, duration < 0.5 s, usually rapidly modulated
Middle Register Units	Spectral energy between 250–600 Hz
*Moans	Multiple harmonics, duration > 0.5 s, frequency modulated
Groans	Multiple harmonics, duration > 0.5 s, constant frequency
*Oos	Tonal, duration > 0.5 s, increasing frequency modulation
Ees	Tonal, duration > 0.5 s, decreasing frequency modulation
Wos	Tonal, duration > 0.5 s, increases then decreases in frequency
Reverse Wos	Tonal, duration > 0.5 s, decreases then increases in frequency
Whos	Pulsive, duration < 0.5 s, increasing frequency modulation
Ups	Tonal, duration < 0.25 s, increasing frequency modulation
Wavers	Tonal, duration > 1.0 s, tremolo
Broken Wavers	Tonal, duration > 1.0 s, multiple frequency jumps
Lower Register Units	Spectral energy < 250 Hz
*Yups	Pulsive, duration < 0.5 s, increasing pulse rate
*Snores	Pulsive, duration < 3 s, variable pulse rates
Surface Ratchets	Pulsive, duration > 4 s

*Units of this type were consistently present in every year analyzed

Characterizing variations in humpback whale song units

Three different approaches were used to characterize the acoustical properties of sorted and unsorted units, focusing on: (1) a subset of traditional and novel measures of the absolute features of isolated units; (2) graded variations in the acoustic properties of units within and across songs; and (3) acoustic relationships between temporally adjacent unit types. Most of the measured properties can be related to features that are detectable aurally from recordings and visually in spectrograms, though not necessarily to existing subjective categories of units.

Modern bioacoustic analyses focus heavily on quantitative measures of features that are salient within spectrograms, especially spectral features that vary over time (referred to as “frequency contours”). Frequency contours are perceptually salient, often appearing as horizontal lines or curves within spectrograms (see Fig. 1). Most past attempts to quantitatively characterize and classify humpback whale song units have emphasized contour-related measures (e.g., Allen et al. 2017; Helweg et al. 1998; Ou et al. 2013). Automatic or manual extraction of frequency contours can be effective for characterizing a subset of units, but the wide range of fundamental frequencies produced by singing humpback whales (~8–6000 Hz) in combination with nonlinear frequency jumps, chaotic segments, and acoustically complex pulse trains, complicate the application of this approach to many units. To address this complication, some researchers have pre-sorted units and developed different techniques for

measuring “harmonic” or “contoured” units versus other units that do not produce clearly delineated horizontal lines or curves within spectrographic images (Allen et al. 2017; Maeda et al. 2000). The current analysis instead analyzed all units with measures that do not require tracing frequency contours or subjectively sorting units and that are less likely to vary as a function of spectrographic resolution, including the frequency with peak energy, duration, direction of pulse-rate modulation, and root-mean-square (RMS) amplitude. We also included measures of spectral shape and pitch saliency (described further below), as the relative tonality or noisiness of vocalizations has been found to be an important distinguishing feature of sounds produced by singing birds (Elie and Theunissen 2016; Tchernichovski et al. 2000), and humpback whales (Mercado 2016; Rickwood and Taylor 2008).

Measures of spectral peaks, duration, and RMS amplitude were automatically collected from waveforms and spectrograms using Raven software (ver 1.5). Measures of modulation direction were judged based on visual inspection of spectrograms or through listening, and numerically coded as follows: increasing = 0.5; decreasing = -0.5; increasing-then-decreasing = 0.25; decreasing-then-increasing = -0.25; constant = 0. This simplified coding of frequency modulation made it possible to statistically describe general properties of sets of units as well as to correlate measures of modulation direction with other acoustical measures. Unit spectra were also generated with Raven (Hanning window, size = 4096; 50% overlap) after which the spectral shape of each unit type was characterized using peak frequencies measured in

four discrete bands (20–250 Hz; 251–500 Hz; 501–800 Hz; and > 800 Hz) previously identified as regions where peaks often occurred (Mercado 2016, 2018a, 2010; Mercado et al. 2005; Perazio and Mercado 2018; Ryan et al. 2019). The spread (i.e., bandwidth) of each spectral peak was measured in terms of the adjacent frequencies with levels 6 dB lower than the peak value, as well as frequencies with levels 20 dB lower than the peak value (or the lowest value before a reversal in the shape of the spectrum).

In addition to these standard bioacoustic measures, two novel metrics were developed to characterize subjectively salient features of units. Pitch saliency (or spectral continuity, Tchernichovski et al. 2000), relates to the “noisiness” of a vocalization. In birds, high pitch saliency was shown to be important for transmitting information that identified individuals over long distances (Mouterde 2020; Mouterde et al. 2014). The specific metrics used to calculate pitch saliency in bird sounds (e.g., Elie and Theunissen 2016) are inadequate for analyzing humpback whale song units because of the extreme range of fundamental frequencies produced by singers. Here, pitch saliency was estimated by first calculating the duty cycle of a unit (using Matlab’s *dutycycle* function, which determines the ratio of pulse width to pulse period for each positive-polarity pulse within a waveform), after which the standard deviation of duty cycle measures across the waveform was calculated. The duty cycle of a waveform measures the proportion of time within a fixed frame (the signal period) that the frame is filled by a pulse. For humpback whales and other cetaceans, duty cycle tends to be higher for more sinusoidal vocalizations (with high pitch saliency) and lower for more “noisy” or pulsive signals (Mercado et al. 2010; Murray et al. 1998). Additionally, units that are highly tonal will generally have a more consistent duty cycle, whereas more noisy units will show greater variability in duty cycle as the signal progresses. Consequently, units with less variable duty cycle measures have higher overall pitch saliency.

To characterize the degree of frequency modulation within units (e.g., the complexity of frequency contours and variety of production modes), the sample entropy of the spectrum of each unit was calculated using the Matlab function *sampen* (Martínez-Cagigal 2018). Sample entropy is a unit-less measure that takes on values between 0 and $\log(2/((N-m-1)*(N-m)))$, where N = sample length, and m = the embedding dimension (Martínez-Cagigal 2018; Richman and Moorman 2000). Units with high spectrotemporal variability typically have multiple irregularly spaced spectral peaks (higher spectral sample entropy), whereas units that vary little in frequency content over time, tend to have more regular peaks (lower spectral entropy). Unlike Weiner entropy, which measures the randomness of a sound (Tchernichovski et al. 2000), *spectral entropy* can be low for both tonal and chaotic sounds, because such sounds are

often associated with a uniform spectral shape over time. Additionally, whereas spectral continuity measures will be dramatically affected by phenomena such as octave jumping, or transitions between pulsive versus tonal sound production (S. O. Murray et al. 1998), spectral entropy characterizes the overall spectral shape of a sound and so is minimally affected by such discrete transitions. Like pitch saliency, variations in frequency modulation within bird calls have been found to facilitate discrimination of degraded signals after long distance transmission (Mouterde, 2020; Mouterde et al. 2014; see also Maciej et al. 2011).

Comparing the detectability and localizability of unit variants

Payne and McVay (1971) noted in their first description of humpback whale song that some phrases contained brief units that were “a faint pulse” and that other phrases contained sounds that were “hard to detect in poor recordings.” They contrasted these brief, faint units with others that were loud and sustained or loud and frequency modulated. Au et al. (2006) similarly reported that the average source levels of some unit types consistently were 10–20 dB lower and were 50% or more shorter in duration than other unit types. Unquestionably, such large differences in vocalizations can dramatically affect their likelihood of remaining detectable after long-range propagation underwater. The differential drop out of different unit types is readily apparent in the songs of distant singers that are audible in the background of recordings of nearby singers. There have been no systematic comparisons of songs recorded at both long and short distances to confirm anecdotal observations and theoretical predictions that some units have greater propagation potential than others, but the fact that many of the faintest unit types (e.g., see Fig. 1B) are not even noted in published descriptions leaves little doubt that there are large differences in the detectability of units. Additionally, some distinctive units may be produced only once or twice within an hour-long recording of song, whereas others may occur hundreds of times (Allen et al. 2019; Maeda et al. 2000; Malige et al. 2020; Murray et al. 2018). Differential usage of subsets of the unit repertoire further suggests that some units may be more essential to the function(s) of songs than others (Allen et al. 2019; Maeda et al. 2000; Murray et al. 2018). Sounds that are brief, faint, and infrequently produced within songs are unlikely to play the same functional role as louder, sustained units that are frequently produced (Mercado et al. 2003). More importantly, units that are not detected by receivers cannot play the same functional role as units that are detected.

Histograms describing the usage of different unit types, the amount of time singers spent producing different units, and energy distributions across units were used to assess

variations in the detectability of unit types within individual songs. These measurements were used to test the following hypotheses: (1) singers consistently produced some unit types more frequently than others, (2) singers spent more time producing the unit types that they used the most (i.e., longer duration units were more likely to be produced repetitively); and (3) singers produce different unit types at substantially different intensity levels. Past reports of these properties of songs have been either anecdotal (Payne and McVay 1971), or have summarized measurements of units from multiple singers (Au et al. 2006), making it difficult to evaluate the extent to which individual singers vary the detectability of units within a song. The goal of the current analysis was to reveal variations in the detectability of all units within two consecutive songs produced by an individual singer, for multiple singers. This approach focuses on characterizing variations in units that listening whales might actually be exposed to rather than describing statistical measures of sets of units that no listener might ever encounter when hearing a song.

A basic assumption underlying most bioacoustic analyses of vocal repertoires is that individual sounds are functional elements, each of which is independently processed by a listener. An alternative possibility, however, is that the acoustic context within which a vocalization occurs can determine how that vocalization is perceived and processed. For example, echolocating bats vary their vocalizations based on both the environmental context within which they are flying and on their positions relative to potential prey (Obrist 1995). When foraging bats modulate their vocalizations in real-time, it is not to communicate different messages to insects or to advertise their fitness, but to calibrate the kinds of spatial information that they can garner from streams of returning echoes. In this context, the variability of sequentially produced vocalizations is related more to continuous processes of spatial perception than to message encoding.

Variations across consecutive units and phrases within humpback whale songs suggest that relative temporal and spectral properties of adjacent units may be more stable over time than the absolute features of units (Green et al. 2011; Mercado 2016; Mercado and Perazio 2021). Such relationships can emerge when pairs of sounds are transposed in frequency together (e.g., Weisman and Ratcliffe 2004), when vocal sequences are temporally compressed or expanded (Brown and Miller 2007; Buck and Tyack 1993; Deecke and Janik 2006), or when different sounds in a sequence are produced using different mechanisms (e.g., during bidirectional sound production, Eklund 2008). Additionally, recent structural analyses suggest that singers gradually change the acoustic features of units used in consecutive phrases throughout song production (Mercado, 2021a; Mercado and Perazio 2021), a process hereafter referred to as morphing.

To more clearly characterize how singers morph units over time within individual songs, recordings were edited to segregate sequences of acoustically similar units while maintaining the order in which units were produced. Spectrograms of unit sequences spanning a minute or less were visually and aurally inspected and units that were most perceptually similar were associated with a particular stream (Bregman 1978, defines "streams" within an auditory scene as parts of the scene that group together perceptually). Units from each stream were then combined by removing intervening units and silent intervals (see Fig. 2 and Supplemental Fig. S1). In this way, every unit within a song was associated with a particular stream. Unlike song phrases, which are identified based on temporally distal comparisons of sequential patterns of units, streams were constructed based on local comparisons of the acoustic similarities of pairs of units, with emphasis on matches in spectral content. Measurements of unit variations along multiple acoustic dimensions were collected from each constructed stream, including: (1) similarities in spectral shapes across different frequency bands; (2) variations in spectral peaks across streams; and (3) inter-onset intervals between perceptually similar units (i.e., the duration between the onsets of units with matching acoustic features). The goal of analyzing unit variations within streams was to identify the extent to which unit types transformed within songs, as well as the overlap in acoustic features present before and after such transformations.

If singing humpback whales continuously and progressively vary the acoustic properties of "repeating" units within songs, then these changes will directly affect the spatial information that listeners can extract from units, and that singers can extract from echoes, in much the same way that the variations made by echolocating bats determine the spatial information that they can extract from echoes. In particular, shifts in focal frequencies can affect a listener's ability to assess the distance a unit or echo has traveled (Mercado et al. 2007, 2008), variations in frequency modulation can affect a listener's ability to resolve a singer's bearing and a singer's ability to resolve a target's bearing (Simmons and Stein 1980), and changes in the rate at which acoustically matching units are produced can affect the resolution with which listeners can track the movements of a singer, and the accuracy with which singers can track the movements of conspecifics using echoes.

Results

Acoustic variations in humpback whale song units

Figures 3 and 4 show units from Winn and Winn's (1985) categories sampled from singers recorded in the West Indies.

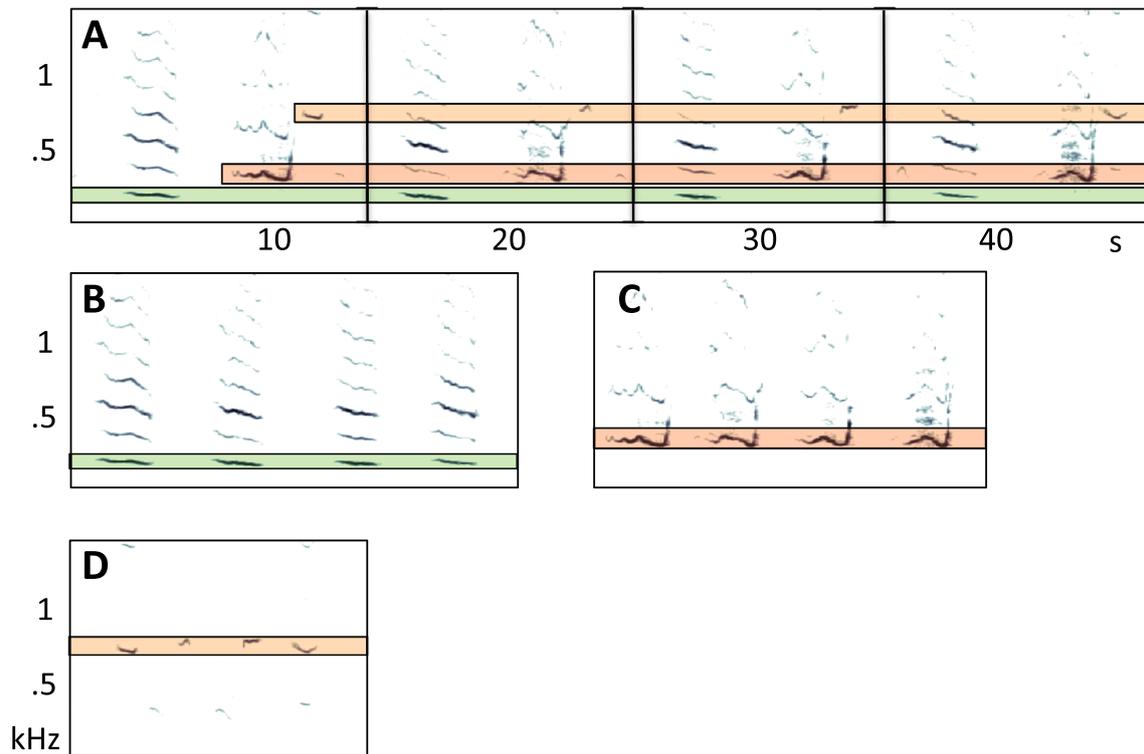


Fig. 2 **A** Humpback whale songs often include repeating patterns of units, called phrases, which are visually salient in spectrograms (separated here by vertical lines). Such sequences can be divided into separate streams of acoustically similar units (indicated by horizontal shaded regions). Streams can be digitally separated by deleting all

units from a song segment other than those that are most similar (**B–D**), to facilitate the detection of systematic changes in units over time. For example, the stream segments in **B**, **C** show a decrease in unit duration and variations in frequency modulation across repetitions, while the stream in **D** shows shifts in frequency content

Most units (96%, $n = 1861$) could be sorted into the subjective categories that they identified, although exemplars of unit types from each year were clearly distinguishable. Units that could not be classified consisted mainly of *hybrid* units, having properties of two or more different categories (74%). Most units recorded in Colombia (72%, $n = 1802$) could also be subjectively sorted into the types identified by Winn and colleagues, although again Colombian units from each category differed acoustically from those recorded in the West Indies (Supplementary Figs. S2 and S3). Two unit types produced by Colombian singers were not evident in recordings from the West Indies.

Figure 5 shows average spectra of the five major unit types described by Winn and Winn (1985) as being present in all humpback whale songs, revealing two broad classes of units—those with most energy focused in narrow spectral peaks (e.g., *oos*) and those with energy spread across a broader range of frequencies (e.g., *moans*, *snores*). For some categories (e.g., *yups*, *groans*), all units within the category had highly similar spectral shapes across locations and years, whereas for others (e.g., *snores*, *cries*), spectral shape varied substantially across different units within the category (see Supplemental Figs. S4–S7). Peaks measured from the average spectra of all

units within each category were not consistent across recordings (Table 4).

Units from a given locale and year could be subjectively sorted into a relatively small number of auditory categories (~9–15) based on the spectral content, timbre, and durations of those units, consistent with past reports. However, comparisons of unit variations within and across singers showed that the acoustic properties of units falling within each subjective category varied substantially over time, such that a unit categorized as one type in a year might be categorized as a different type in a different year, and two units with distinctly different acoustic features might be classified as being in the same category within or across years. Unit repertoires produced by individual singers, even over a relatively short time period, were variable and graded rather than stereotyped and discrete.

Variations relevant to the detectability and localizability of units

Determinants of detectability

Singers consistently produced some unit types more often than others (Fig. 6A), and the types that they produced most

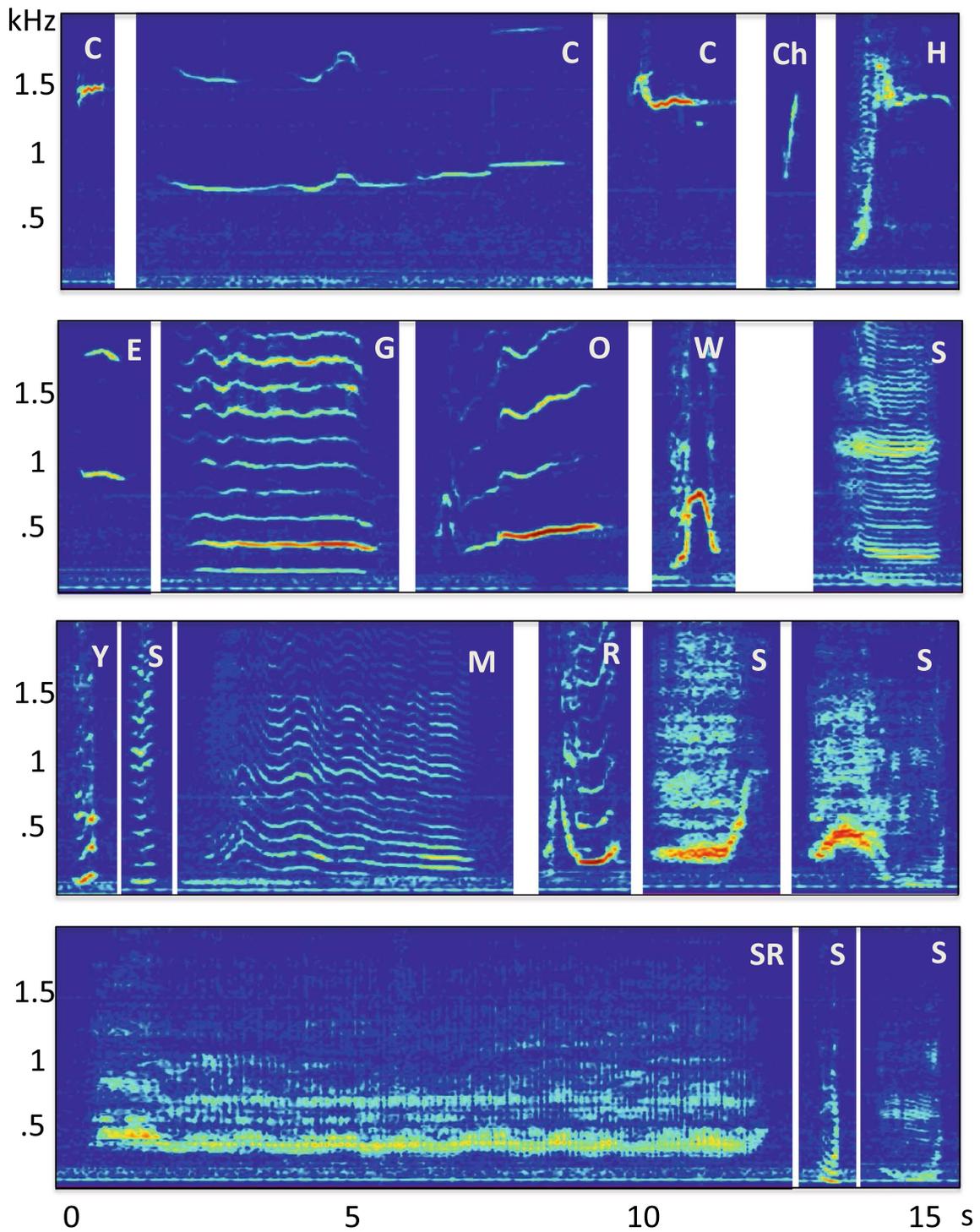


Fig. 3 Spectrograms of exemplars of each unit type identified by Winn and Winn (1985) produced by a singing humpback whale recorded in the West Indies in 1973. The *top row* shows upper register units, increasing in bandwidth from left to right: C=cry; Ch=chirp; H=hybrid. The *second row* illustrates middle register units: E=ee; G=groan; O=oo; W=wo; S=snore. The *third row* includes units with both lower and middle register elements: Y=yup;

M=moan; R=reverse wo. The *last row* shows lower register units: SR=surface ratchet. Note that units within most categories are not stereotyped and may vary in frequency content, modulation, and duration (e.g., compare the three different exemplars of cries, and the six different exemplars of snores, which vary along multiple acoustic dimensions)

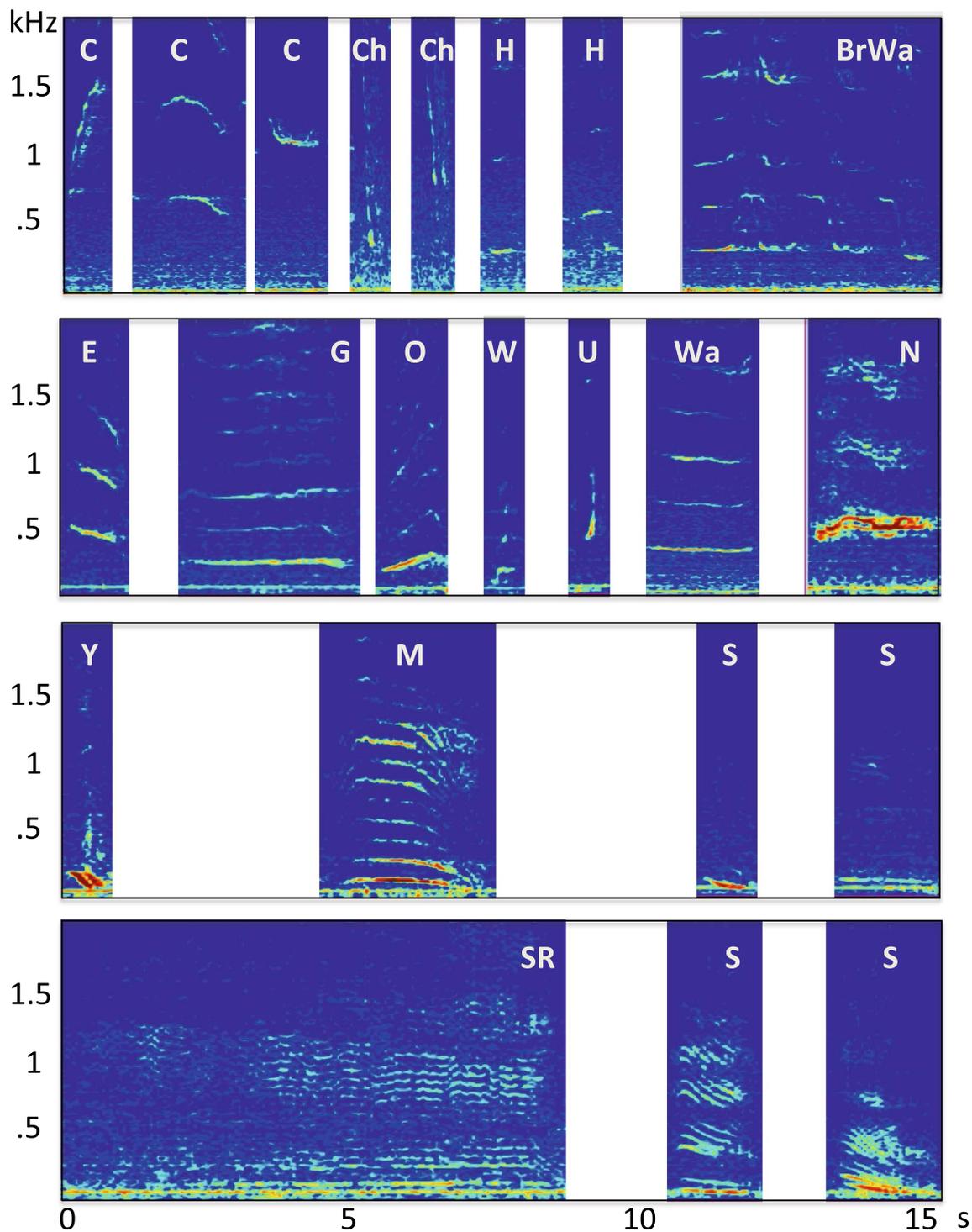


Fig. 4 Spectrograms of exemplars of each unit type identified by Winn and Winn (1985) produced by a singer recorded in the West Indies in 1970. Exemplars are arranged spatially such that those most similar to unit types present in 1973 (Fig. 3) are in similar locations (white spaces between exemplars thus correspond either to unit types that were not present or to differences in exemplar duration). The *top row* shows upper register units: C=cry; Ch=chirp; H=hybrid; BrWa=broken waver. The *second row* illustrates middle regis-

ter units: E=ee; G=groan; O=oo; W=who; U=up; Wa=waver; N=no category identified. The *third row* includes units with both lower and middle register elements: Y=yup; M=moan; S=snore. The *last row* shows lower register units: SR=surface ratchet. Note that none of the units within any category are an exact match for the corresponding categories identified in 1973 (compare with exemplar units shown in Fig. 3), and are similar mainly in terms of their tonality, pitch, direction of frequency modulation, or duration

frequently accounted for the greatest proportion of song duration (Fig. 6B). Units subjectively classified as *snores*, *moans*, *groans*, and *oos* collectively accounted for more than half of all units produced within the West Indies songs, as well as from songs recorded in Colombia in 2013. Singers spent the most time producing units with peak frequencies between 100 and 450 Hz, a pattern also evident in units recorded off the coast of Japan (Maeda et al. 2000; Fig. 7C).

Some unit types were produced more energetically than others (Fig. 6C), consistent with intensity differences measured from recordings of Hawaiian singers (Au et al. 2006). The highest intensity units produced by singers recorded in the West Indies included units subjectively classified as *oos*, *groans*, and *yups*, while in Colombia the most intense units were *ees* and *cries* in 2013, and *yups* and *ups* in 2019. The faintest units recorded in the West Indies were *chirps* and *ratchets*. *Chirps*, *moans*, *whos*, and *snores* were the least intense units recorded in Colombia.

Distributions of unit acoustic features, including estimates of pitch saliency and spectral entropy, were generally comparable across years and populations (Fig. 8). Lower-register, broadband units had the lowest pitch saliency. Units with mixed characteristics had the highest spectral entropy (e.g., hybrid units like the example shown in Fig. 3, and *broken wavers*, as shown in Fig. 4). In the West Indies and Colombian recordings, singers produced more than double the number of units with broadband spectral shapes (including both low pulse-rate and frequency modulated units) compared to units with narrow peaks (tonal, constant-frequency units; see Fig. 8, *middle row*). Differences in the time spent producing broad versus narrowly peaked units were even larger (e.g., in 1970, the singer spent only 7% of production time on narrowly peaked units). Narrowly peaked units also were the least likely to repeat and had the longest intervals before recurring. For example, the median inter-matching-unit-interval for *groans* was 21 s in 1970 and 10 s in 1973. Short duration units with broadly-peaked spectral shapes (e.g., *chirps*), were the most likely to repeat at short intervals (between 0.5–3.5 s), while mid-register, broadly-peaked units (e.g., *ees*, *oos*, and *moans*) recurred at intervals of ~4–7 s.

Variations in the number, intensity, duration, peak frequency, and timing of units within humpback whale songs directly affect the likelihood that specific units and echoes from those units would remain detectable after long-distance transmission (Table 5), with some units within songs being much less likely to be detectable at long ranges than others.

Determinants of localizability

Multiple streams of morphing units were evident within each recording. In several streams, singers morphed units so extensively that the units spanned multiple subjective

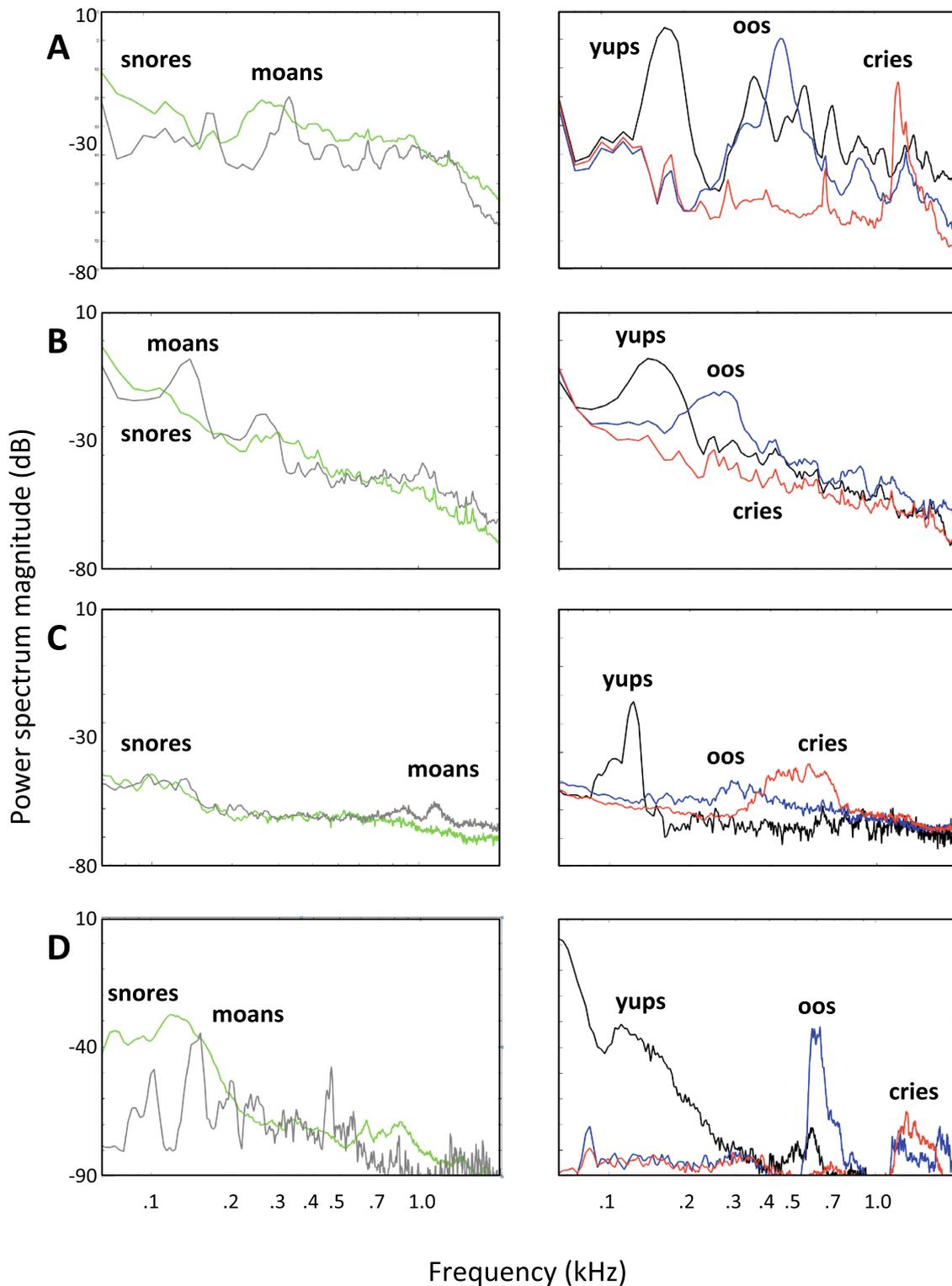
categories (Figs. 9 and 10; see also Supplemental Figs. S8 and S9); units were morphed along multiple dimensions, including intensity, frequency contour, duration, spectral shape, and pitch saliency. The rates and degree of unit transformations varied within and across streams. For some streams, spectral shape was maintained across transitions between subjectively distinctive units within a stream (Fig. 9B), whereas for others, spectral shape changed in parallel with other acoustic transformations (Fig. 9C).

Qualitative comparisons between streams from 1970 and 1973 revealed that unit morphing did not follow fixed trajectories. For instance, in streams from 1970, *oos* morphed into *groans* (Fig. 10B), while in 1973 they morphed into *snores* (Fig. 9C). However, some common transformations were evident across years. In both 1970 and 1973, for example, *snores* became *ratchets* that morphed into *moans* and then into *yups*. Comparisons of morphing trajectories across consecutive songs (e.g., Figs. 9A and 10A) revealed highly similar trajectories, ruling out the possibility that unit transformations arose from propagation-related distortion and demonstrating that singers precisely controlled how they modulated the transforming characteristics of units within song sessions. The specific morphing trajectories recorded in Colombia differed from those seen in West Indies recordings (see Supplemental Figs. S8 and S9).

Transformations in the spectral, temporal, and spectrotemporal properties of units across “repetitions” likely affected the positions within the area surrounding a singer from which listening whales could potentially localize a singer’s position (Table 5), both in terms of determining the range of the singer and the bearing from which a unit originated. Morphing of units within streams may have similarly affected the locations from which singers could detect and localize unit-generated echoes from conspecifics.

Discussion

Based on qualitative and quantitative analyses, we conclude that singing humpback whales are capable of flexibly modulating units along multiple acoustic dimensions within individual songs, but do so within relatively fixed spectral and temporal constraints. We found that singers vary the acoustic characteristics of units in ways that suggest that there are systematic differences in the functional utility of unit “types” that are consistent within and across songs (i.e., all units are NOT equal). In particular, some units have greater potential for remaining detectable after long-range transmission and/or for providing spatial information. Collectively, these findings suggest that the dynamic, intergraded repertoires of units produced by individual singers may be an adaptation that facilitates long-distance transmission in highly reverberant sound channels.



One limitation of the current analysis is the focus on a small number of songs produced by at most four singing humpback whales in a few locations and years. Clearly, analyzing a larger number of songs produced by more individuals in a greater variety of contexts would provide a more

comprehensive characterization of the full range of units that singers are capable of producing. We cannot say whether the intra-individual variations in unit repertoire described here are representative of humpback whales as a species. They may not even be representative of the variability produced

Fig. 5 Spectra of five unit types noted by Winn and Winn (1985) as being present in all song forms recorded from all populations in all years: *snores* (green), *moans* (gray), *yups* (black), *oos* (blue), and *cries* (red). Each spectrum line is the average across all units of that type within a recording (FFT=4096; Hanning window), plotted on a log frequency scale. **A** Spectra in the *top row*, from the 1973 West Indies recording show that *snores* and *moans* span a broad range of frequencies, whereas energy is focused within a narrow peak for *yups*, *oos*, and *cries*. Most units within songs follow one of these two trends in terms of spectral shape (i.e., the number, distribution, and width of peaks within the spectrum). **B** Spectra in the *second row*, from the 1970 West Indies recording reveal that although the same five unit types can be subjectively identified across years, the spectral shapes associated with each type do not necessarily match across years (or whales), and that some unit types (e.g., *cries*) may be broadband in 1 year and narrowband in another. **C** Spectra in the *third row*, from the 2013 Colombia recording, similarly suggest that spectral shapes of unit types are not stereotyped across populations (or locations). **D** Spectra in the *fourth row*, from the 2019 Colombia recording, show that *oos*, *cries*, and *moans* recorded in that year were spectrally more similar to unit types produced in the West Indies in 1973 than to those produced in Colombia in 2013

by these specific individuals within the song sessions within which they were recorded. Given that all four recordings showed similar distributions of acoustic measures and gradual morphing of unit characteristics within songs, however, we are confident that the analyses accurately characterize what singers are capable of vocally achieving. Comparisons with findings from earlier quantitative analyses of units (e.g., Maeda et al. 2000; Mercado et al. 2005) further suggest that the basic acoustic features of units analyzed here are comparable to those measured from other populations of singers.

How singers morph units

The most important new finding of this study is that individual singers are continuously morphing unit “types” within songs along multiple acoustic dimensions. In other words, traditional categories of units do not represent discrete types, but are instead points along a continuum of vocalizations that singers progress through while producing songs. Singers vary the rate at which they progress along this continuum, sometimes repeating units with similar characteristics several times before moving on. Many of the unit “types” identified in past studies likely correspond to only the most frequently reproduced sounds. Although frequently produced unit forms may be amenable to either manual or automated sorting in any given year, this approach obscures any comparisons of unit properties within and across individuals, years, or populations. Characterizing song units in terms of familiar auditory categories is like describing star clusters as constellations; the approach may have mnemonic value, but its scientific relevance is questionable. Supplementing subjective classification systems with spectrographic or statistical measures that describe features of different sound types does not adequately address the problem, because this

approach fails to account for the graded structure of singers’ vocalizations. Units within humpback whale songs are not simply graded in the sense that some unit types are harder to distinguish or are more variable than others. They are graded in that singers are able to morph units continuously across even the most discrete unit “types” (see also Chabot 1988; Clark 1982; Fournet et al. 2015, 2018; Rekdahl et al. 2013). Singers not only are able to transform units in this way, they constantly do so, often within multiple parallel streams of acoustically related units. Characterizing this sort of dynamic vocal process in terms of subjective categorical criteria that may have little biological relevance may increase the difficulty of understanding what humpback whales are doing when they sing.

Singing humpback whales changed frequencies within streams of similar units in three main ways. First, they varied the degree and direction of frequency modulation across “repeated” unit forms, thereby changing the bandwidth of spectral peaks within which acoustic energy was concentrated. Second, they continuously shifted the peak frequencies within some streams while maintaining fixed peaks in others (e.g., see Supplementary Fig. S1). Finally, they switched between focusing energy at the fundamental frequency of a repeated unit and emphasizing specific harmonics or other frequency bands (Cazau et al. 2013; Mednis 1991; Mercado 2020; Mercado and Handel 2012; Mercado et al. 2010). This type of shifting between frequency bands may play a more significant role in humpback whale songs than has been previously recognized, because the frequencies that singers emphasize determine not only how detectable units are at different distances (Frazer and Mercado 2000; Mercado and Frazer 1999; Mercado et al. 2007), but also how consecutive units interact as they propagate long distances underwater (Mercado 2016, 2018b, 2021b). Singers also gradually expanded or compressed the duration of units within streams across repetitions. These graded changes in units produced within songs parallel the kinds of variations in unit repertoires that have been observed in cross-year comparisons of units (Cato, 1991; Maeda et al. 2000; Mercado et al. 2005; Payne and Payne 1985; Winn and Winn 1978). Thus, the repertoires of units produced by singing humpback whales are best described as graded and dynamic, rather than as a stable lexicon of distinctive types.

Despite the seemingly limitless ways in which singers can modify units over time, the changes that they actually make to units within their repertoires are apparently not arbitrary, but instead involve concentrating energy into somewhat predictable frequency bands and transforming the distribution of spectral energy within units in predictable ways. Singers consistently concentrated energy in either 2–4 narrow frequency bands or 1–3 broader spectral bands (see also Allen et al. 2019; Maeda et al. 2000; Murray et al. 2018). Although spectral peaks and bandwidths were highly similar across

Table 4 Spectral peaks from cumulative spectra for each unit type

Sound types	BAND1	BAND2	BAND3	BAND4
West Indies, 1970				
Cry				2000
Chirp			700	1200
Hybrid		530		
Ee		440		1100
Groan	230	460	690	930
Oo		280		
Who	180	400	590	
Snore	70	300		
Yup	140	420		
Moan	140	260		
Waver			630	1200
Broken Waver			600	1300
Up			680	
Surface Ratchet	250			
Not Classifiable		500		1100
West Indies, 1973				
Cry				1300
Chirp				1400
Hybrid		270		1500
Ee			550	1700
Groan	180	370	550	1600
Oo		330	460	1400
Wo		260	670	830
Snore	65	280	430	
Yup	170	380	580	
Moan	170	340	500	
Reverse Wo		290	480	920
Surface Ratchet		320		
Colombia, 2013				
Cry		430	570	
Chirp				1600
Ee		310		
Groan	145	460		
Oo	170	270		
NoisyD		430		
Reverse Wo	160	420		
Yup	120			
Moan	120	460		
Snore	30			
Not classifiable		410		
Colombia, 2019				
Cry				1500
Chirp				2400
Hybrid	150		880	
Ee			800	1600
Oo			580	
Wo		360		
Reverse Wo		320		
Groan	150			

Table 4 (continued)

Sound types	BAND1	BAND2	BAND3	BAND4
Moan	140		470	
Who	170			
Up	150			
Yup	60			
Snore	120			
Surface Ratchet		240	790	
Noisy			680	
Screeal			840	1700

*Note peaks could include multiple sound type variants. Bolded values indicate the spectral peak with the maximum energy

consecutive songs, they were not identical, suggesting that singers may adjust the spectral properties of unit sequences within and across song sessions (Magnúsdóttir et al. 2015; Mercado 2018a, 2021b; Mercado et al. 2005; Mercado and Perazio 2021). Differences in spectral shape trajectories across years and populations further suggest that singers are not constrained to producing units with fixed spectral content, but instead may flexibly modify morphing trajectories across songs. Without knowing how singers perceive unit sequences, it is difficult to know how extensive unit transformations would need to be before a whale would perceive that the acoustic features of units have changed. More importantly, there is no way to know if singing humpback whales perceive different units as falling within categorically different sound types: 8 subjective categories formed by a human observer may correspond to 0 (or 80) categories perceived by a singing humpback whale.

One of the most challenging aspects of describing the graded repertoires produced by singing humpback whales is that individual whales continuously modify the acoustic details of the units that they produce within and across songs (Cato 1991; Guinee et al. 1983; Payne et al. 1983). Although subjective criteria for sorting units can be statistically mapped onto variations in acoustic parameters (Maeda et al. 2000; Magnúsdóttir et al. 2015; Schall et al. 2021), this mainly serves to demonstrate that human auditory perception is systematic rather than random or illusory (i.e., people can hear differences because there are differences). Recent techniques for classifying the graded vocal repertoires of primates are better able to account for fuzzy boundaries between categories (Fischer et al. 2017; Wadewitz et al. 2015), but still depend on subjective or functional criteria for separating overlapping clusters of similar vocalizations, and assume that the acoustic features that define categories are stable. Techniques for quantitatively characterizing progressive variations in vocalizations over time provide a way to track trajectories of change within single streams (Clink et al. 2018; Clink and Klinck 2021), but are less able

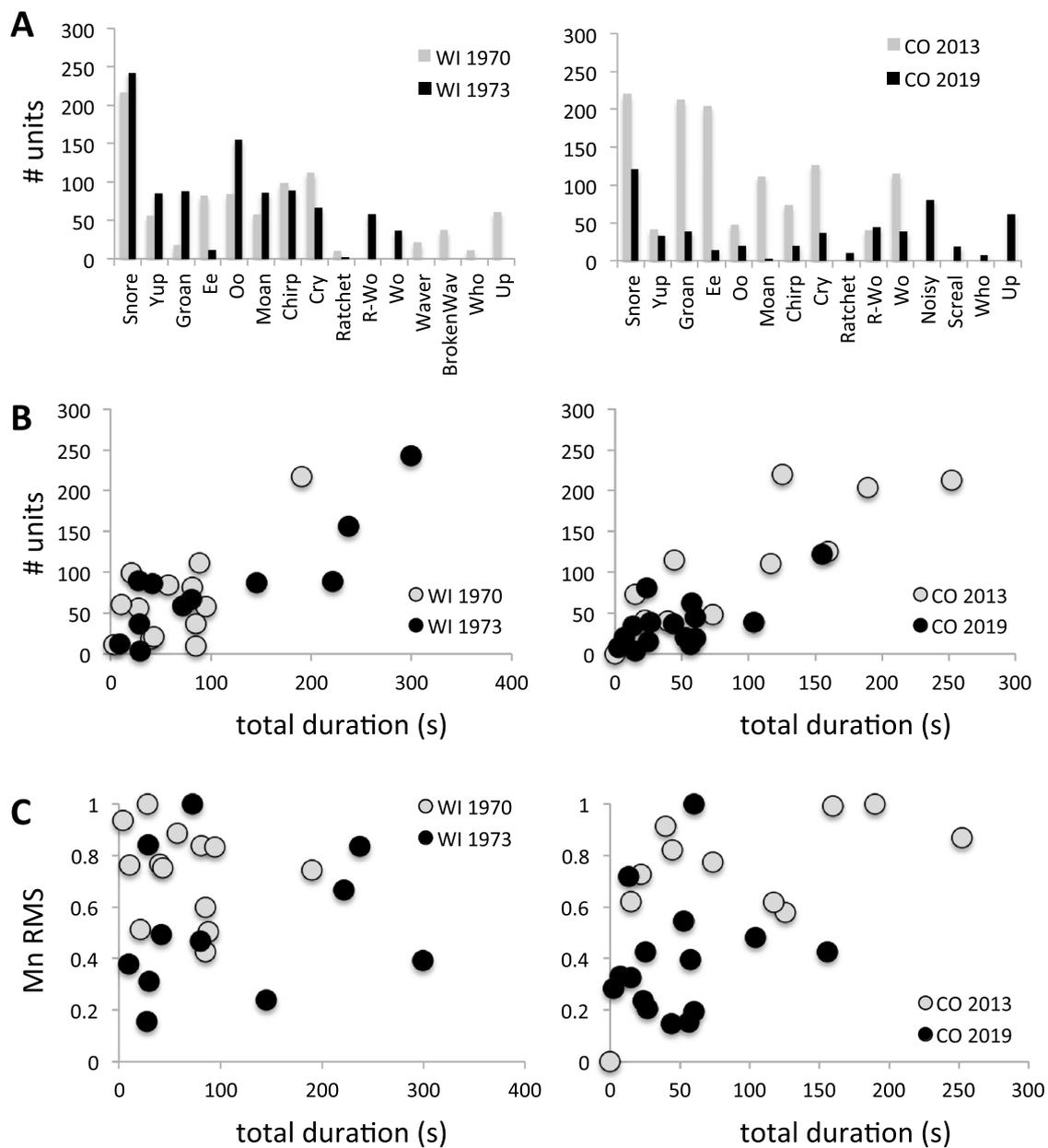


Fig. 6 **A** Singers consistently produced some unit types more frequently than others, and **B** often spent more time producing the units that they used the most. **C** Different unit types were produced at substantially different intensity levels, regardless of how much time sing-

ers spent producing them. Note that in these plots mean RMS values for each unit type were normalized by dividing the means by the maximum mean RMS value

to capture progressive transformations when multiple, co-occurring streams are present, as was the case in the humpback whale songs analyzed here. New analytical techniques are needed for objectively identifying and measuring different morphing trajectories within songs, such as those that have been developed to describe the ontogeny of songs in birds (Hyland Bruno and Tchernichovski 2019; Tchernichovski et al. 2001). For example, Mercado and Perazio (2021)

analyzed variations in unit morphing trajectories produced by singing humpback whales in Columbia across consecutive years by fitting simple mathematical functions to time series of peak frequencies measured from streams of units. These analyses revealed that singers gradually decreased the frequency content of some unit streams while simultaneously maintaining a stable peak frequency in others. This pattern was present across years, suggesting that singers may

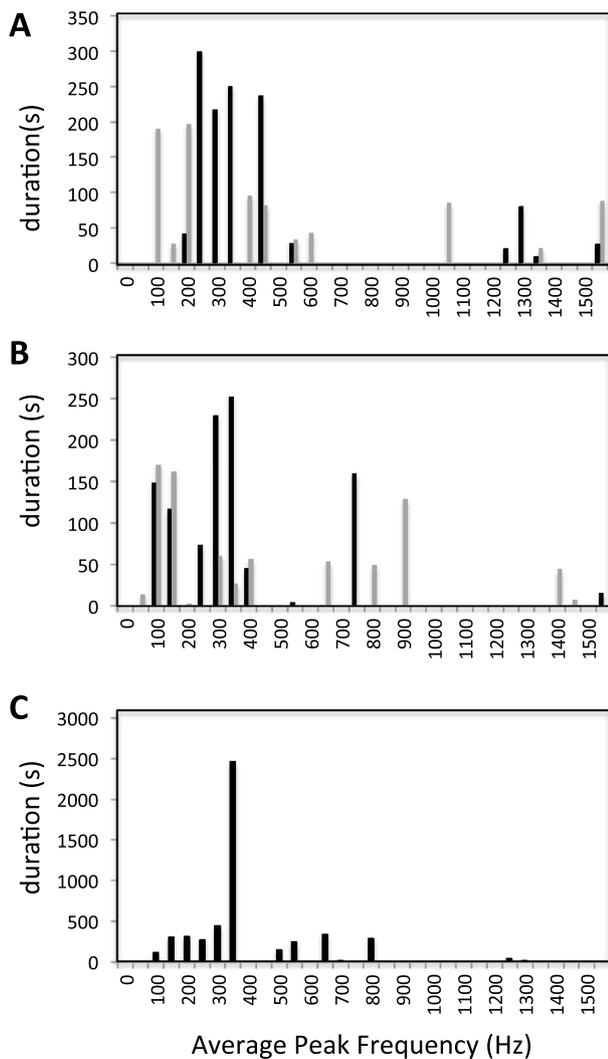


Fig. 7 **A** Histogram plots showing the amount of time singers recorded in the West Indies in 1973 (black) and 1970 (gray) spent producing units with different peak frequencies show that most peaks were between 100 and 450 Hz. **B** Histograms from units recorded in Colombia in 2013 (black) and in 2019 (gray) show a similarly disproportionate distribution of unit peak frequencies, but with relatively more time spent producing higher frequency units. **C** The distribution of unit peak frequencies produced within 19 songs spanning 7 years (recorded near Japan; Maeda et al. 2000), also shows a preponderance of time being spent on units with peak frequencies between 150–350 Hz

be physically or functionally constrained in terms of how they morph units within particular streams.

One implication of the finding that singers' unit repertoires are graded and dynamic rather than fixed and discrete is that results from past studies employing fixed, whole-unit classification methods are questionable. Because the first step in thematic analyses of songs involves assigning each unit a label or symbol designating its type, the form of the resulting symbol sequences depends heavily on how units

are sorted. For example, if broad categories are used to sort units, then a phrase might be coded as the sequence “aabbb,” whereas if more narrow categories were used, then the same sequence might become “abccd.” And, if the temporal gap between the third and fourth units is sufficiently short, some observers may code the same unit sequences as “abcd,” resulting in three different strings for a single instance of a phrase. This problem is compounded when “repeated” phrases contain units that are morphing at different rates, a situation that can lead observers to assign qualitatively distinctive units the same label (e.g., “snores”) simply because they occur in the same position within a phrase (e.g., see Malige et al. 2020). The dynamic changes that singers make to unit sequences within songs also raise questions about the nature of phrases and whether they should be “considered the salient element of repetition within humpback song” as proposed by Cholewiak et al. (2013).

Units versus phrases: which level is more functionally relevant?

Phrases have been the focus of many past studies investigating song characteristics, song comparisons, song development, and song learning, and it is widely accepted that singers order their units into specific phrases that they repeat (e.g., Cholewiak et al. 2013; Payne and McVay 1971; Suzuki et al. 2006). Although there is no question that repeating patterns are present within songs, it is less clear whether phrases are functionally relevant components of songs. Cholewiak et al. (2013, 2018) have argued that phrases should be viewed as analogous to bird songs because their timing is stable and because singers often repeat phrases multiple times before switching between them in a manner similar to some species of birds. However, there are many examples of patterned sound production in nature in which stably repeating sequences are functionally irrelevant. For example, a snoring human may produce sounds that alternate in predictably timed patterns and that change in predictable ways depending on a sleeper's body position. The stable sequences of units within song phrases might similarly be a side effect of concurrent stream production. Mercado and Perazio (2021) found that the ordering and timing of units within phrases could be the result of bidirectional sound production (see also Mercado and Handel 2012). Their analyses revealed that singers morphed putative “ingressive” sounds differently than they morphed “egressive” sounds. This finding suggests that streams of units identified in the current study may also be linked to different directions or modes of sound production. If phrase structure is a side-effect of bidirectional production mechanisms and/or overlapping unit streams that are temporally correlated, then measures of phrase structure can reveal variations in production over time and thus can be scientifically informative. On the other

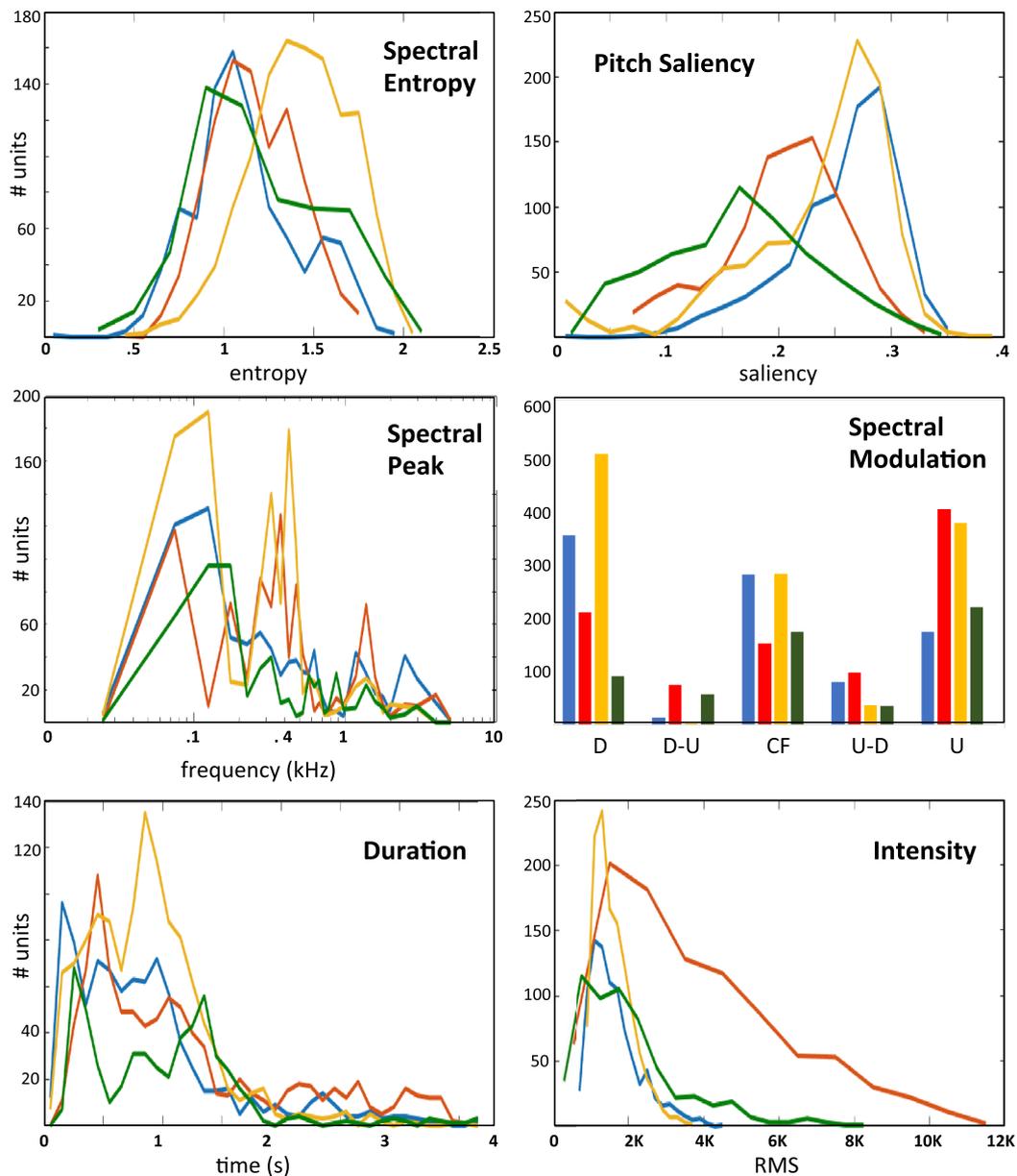


Fig. 8 Histogram plots for six of the acoustic measures collected from units in 1970 (blue), 1973 (red), 2013 (orange), and 2019 (green). Distributions of two acoustical properties related to spectral shape are shown in the *first row*. Two acoustical properties related to frequency content and contours are shown in the *middle row*. Note that the frequency scale is logarithmic and that some frequencies are much less likely to be focal frequencies than others. D=down-swept (decreasing frequency modulation); D-U=down-swept, then up-

swept; CF=constant frequency; U-D=up-swept, then down-swept, and U=up-swept (increasing frequency modulation). Finally, distributions of duration and intensity are shown in the *third row*. Units of durations greater than four seconds (range=11.7 s) are excluded from plots, but occur about as often as units lasting between 3.5–4 s. Longer duration units were excluded to more clearly reveal the multimodal distribution of unit durations less than 1.5 s

hand, if the continuity of gradually morphing units across repeated phrases is ignored, then phrase-based analyses can distort cross-song comparisons and provide a misleading picture of how humpback whales organize and change songs over time (Mercado and Perazio 2021). Given that singers are morphing units across phrases, in many cases the phrases

within song are not technically repeating, such that categorizing phrases into “types” becomes just as problematic as categorizing units into types. Overall, it remains uncertain whether phrases (or themes) are structural features that humpback whales recognize, and it is possible that phrases

play no functional role beyond those served by individual units or streams of units.

Unlike in past analyses of humpbacks' unit repertoires, we did not divide recordings into songs, themes, or phrases prior to extracting and classifying units. Structurally partitioning unit sequences into phrases emphasizes inter-individual similarities while de-emphasizing intra-individual variations between units. Segregating unit sequences into coincident streams, in contrast, highlights the dynamic gradations that individual singers make to units as they progress through a song. It is well known that singing humpback whales often produce phrases in predictable orders. This predictable ordering of phrases is what originally led Payne and McVay (1971) to describe the vocal actions of whales as singing. How (or even if) the ordering of phrases is in any way related to the acoustic features of the units within the phrases, or to the trajectories along which units are morphed, remains unclear. Whereas phrases have been described as changing continuously and irreversibly across years (e.g., Payne and Payne 1985), recent analyses suggest that at least some aspects of unit morphing are stable across years and populations (Mercado and Perazio 2021). Consistent morphing trajectories across populations of humpback whales suggest that the dynamic characteristics of streams may be more universal than are the combinations of units found within phrases. Predictable trajectories also suggest that song structure is more constrained than has generally been assumed.

Singers often maintained stable spectral peaks within streams of units even when duration, intensity, pitch saliency, and direction of frequency modulation were all varying over time, suggesting that morphing of units is in some way constrained so that acoustic energy is consistently focused within specific frequency bands (Mercado and Perazio 2021; Perazio and Mercado 2018; Ryan et al. 2019). As units progressively morphed from one form into another (e.g., transforming from *oos* into *snores*), they often maintained similar spectral shapes despite large subjective changes in aural and spectrographic features. Furthermore, the spectral peaks where energy was most likely to be focused were relatively limited, with the bandwidths of individual peaks being more likely to change over time than were the positions of peaks. Importantly, the specific frequencies that singers favored varied over time and locales, suggesting that the peaks were not intrinsically constrained by sound production mechanisms, but could potentially be selected by singers (see also Magnúsdóttir et al. 2015; Mercado et al. 2005). Identifying relationships between the spectral shapes of units within and across phrases can potentially provide important clues about why singing humpback whales produce unit sequences in stereotypical orders (Mercado and Handel 2012), and about why singers continuously modulate the acoustic properties of their songs over time.

Why do singers morph units?

The varying social contexts within which animals produce different vocalizations can often be used to validate the functional relevance of variations within a vocal repertoire (Elie and Theunissen 2016; Green and Marler 1979). This is not an option for classifying units produced by singing humpback whales. Humpback whales do produce vocalizations that are acoustically similar to song units when they are not singing (Chabot, 1988; Dunlop et al. 2007; Fournet et al. 2015; Rekdahl et al. 2013; Winn et al. 1979), and vary their usage of those “non-song” vocalizations somewhat according to the social context within which they produce them (Rekdahl et al. 2015). In contrast, no obvious differences in the features of units have been reported across the wide variety of behavioral contexts within which whales sing: while alone and relatively stationary (Frankel et al. 1995; Tyack, 1981; Winn and Winn 1978); while swimming at a steady rate (Helble et al. 2015; Henderson et al. 2018; Noad et al. 2004); while interacting with other whales (both males and females, Darling and Berube 2001; Darling et al. 2006; Smith et al. 2008); and while foraging (Clark and Clapham 2004; Stimpert et al. 2012). Consequently, the factors that might drive singers to use functionally heterogeneous units within songs are unknown.

Historically, researchers have argued that vertebrates are most likely to use graded vocal repertoires for short-distance communication, when visual cues can resolve ambiguities (Green and Marler 1979). Singing humpback whales not only use graded, morphing units within their songs, but also dynamically shift how they morph units over time, such that the spectral shapes of unit types vary across years. The ways that singers morph units directly affect how those units propagate, which in turn determines what signals will effectively reach listeners as well as the kinds of information that received units, and echoes from units, provide (for a related discussion of how acoustic features affect the propagation potential of primate calls, see Brown and Waser 2017). Some of the observed variations in units affect their detectability, whereas others determine how precisely the origin of the units (or the echoes they generate) can be localized from different positions. This suggests not only functional heterogeneity across units, but also the adaptive specialization of certain unit characteristics to either facilitate spatial perception or to increase the efficacy of song transmission.

The complexity of the humpback whale's unit repertoire might seem to set them apart from other singing species, most of which construct songs using a relatively fixed set of vocalizations as adults. There is increasing awareness, however, that several species' vocal repertoires may be less discrete than was previously assumed, and that some species do use graded repertoires for long-distance communication (Fischer et al. 2017; Hammerschmidt and Fischer 1998;

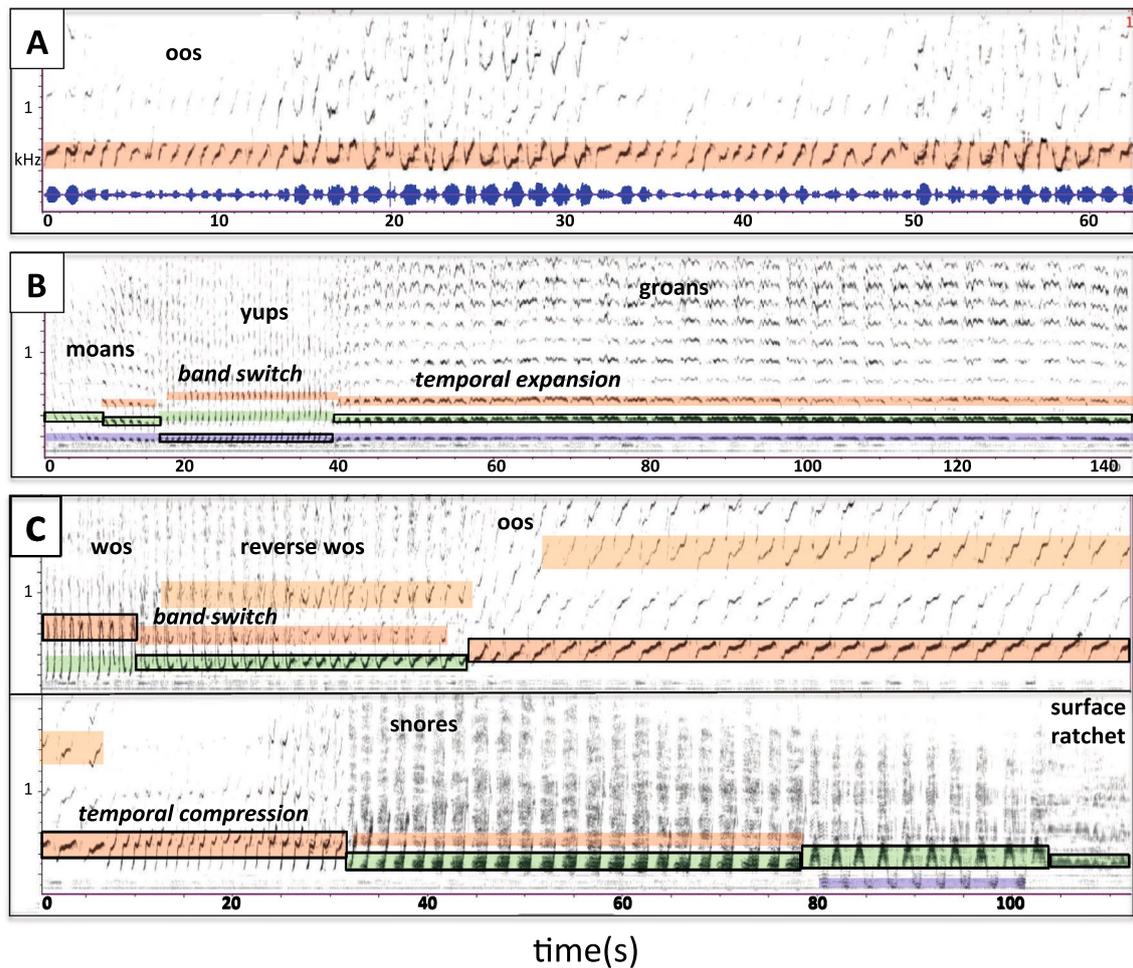


Fig. 9 Spectrograms of constructed streams of sequentially produced, perceptually similar units (i.e., units that look and sound alike) from songs recorded in the West Indies in 1973. **A** Shows *oos* gradually shifting in frequency modulation, duration, and intensity (blue waveform inset within the spectrogram), while maintaining a relatively constant concentration of spectral energy within a single band (colored rectangle). Streams across two consecutive song cycles are shown. **B** In this stream, *moans* shift from containing energy focused within two bands to three bands (colored rectangles) before transforming into shorter duration *yups*, which eventually morph into

groans that gradually expand in duration. Note that the distribution of spectral peaks varies little during these transformations, but that the band with maximal energy (outlined in black) shifts during transitions across unit types. **C** An extended stream involving changes in the frequency modulation, frequency usage, duration, and categories of units. Spectral energy is concentrated in two main bands throughout this stream, with the singer modulating spectral peaks continuously as the stream progresses. The differently colored shading within rectangles differentiates the four main frequency bands analyzed (see Table 4)

Keenan et al. 2013, 2020). Additionally, some species use sequences of progressively morphed sounds for long distance communication, including other baleen whales such as blue whales (Gavrilov et al. 2012; McDonald et al. 2009). For example, when female gibbons sing in tropical rainforests (presumably to communicate over long distances), they produce a predictably structured series of vocalizations that morph along a graded continuum, starting with longer duration narrowband sounds that gradually transform into shorter-duration broadband sounds (Clarke et al. 2006; Koda et al. 2013; Marshall and Marshall 1976; Mitani and Marler 1989; Raemakers et al. 1984). These cross-species similarities suggest that evolutionary forces may have led

to convergent acoustic coping strategies in animals that rely on long-range acoustic communication in complex environments such as rainforests or shallow coastal waters.

The question remains as to why humpback whales and other animals have evolved graded vocal repertoires for use in long-range acoustic communication. Green and Marler (1979) argued that using sound in this way should be maladaptive, given that the absence of visual cues would make many received signals ambiguous. Such ambiguities would be an issue even without accounting for propagation effects, which generally should further complicate interpretation of received signals. The situation faced by whales listening to singing humpback whales should be even more

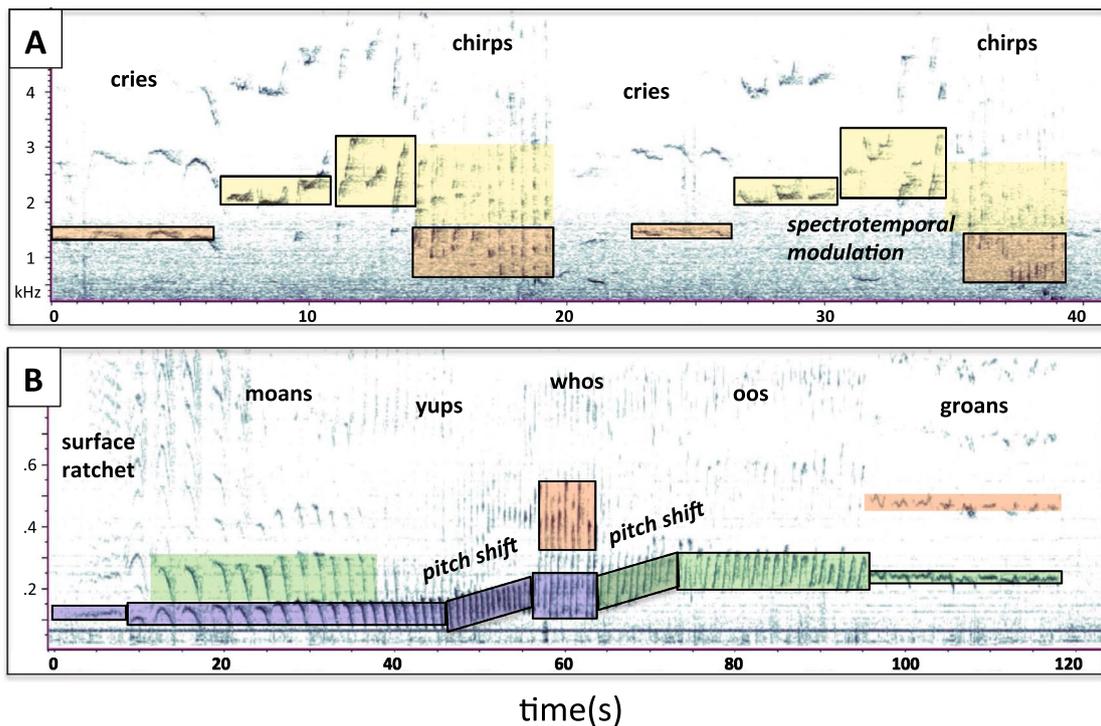


Fig. 10 Spectrograms of constructed streams of sequentially produced, perceptually similar units from songs recorded in the West Indies in 1970. **A** Shows *cries* changing in frequency modulation, duration, and bandwidth before morphing into *chirps*. Colored rectangles show the frequency range of two broad peaks defining the spectral shape of units, with the maximal band outlined. Streams across two consecutive song cycles are shown. **B** In this stream, the pulse rate of a *surface ratchet* increases, such that it transforms it into a shorter-duration *moan*. Units continue to compress temporally across repetitions, transforming into *yups*. Then, the peak band of the *yups*

begins to gradually shift to higher frequencies, until the *yups* morph into *whos*, which have a bimodal spectral shape. Next, spectral energy within *whos* is concentrated within a single, middle-register band that resumes an upward frequency shift, until the *whos* morph into *oos*. Finally, *oos* become longer-duration *groans*, with peak frequencies focused in a narrow band that falls within the peak band associated with the *oos*. As in the streams shown in Fig. 9, continuity of spectral shape is maintained within this stream across transitions between unit types

problematic, because the “boundaries” between fuzzy categories of units are not stable and therefore not reliable, and because humpback whales are constantly on the move, such that the distorting effects of propagation will also be continuously changing. Two main explanations have been proposed for why whales sing, either of which could potentially be related to singers’ dynamic vocal repertoires. First, humpback whales may sing to provide other whales with information about their reproductive fitness, in which case repertoire features are likely driven by sexual selection. Second, whales may sing to provide themselves or other whales with spatial information, with repertoire properties mainly driven by environmental factors.

Sexual selection?

Numerous species produce vocalizations (including songs) as part of their mating process (Bradbury and Vehrencamp 2011). In some cases, acoustic properties of vocal sequences are correlated with individuals’ reproductive success (e.g.,

Charlton et al. 2018), or with the likelihood that a potential mate will join the vocalizer (e.g., Toth and Parsons 2018). Accordingly, several researchers have proposed that humpback whale songs play a similar role, enabling other whales to judge the quality of a singer (Cerchio et al. 2001; Garland and McGregor 2020; Herman 2017; Payne 2000). In principle, singers that produce louder, longer, or lower songs might be more reproductively fit (Adam et al. 2013). Similarly, singers that produce songs of higher complexity, novelty, or accuracy might be more attractive to females (Garland and McGregor 2020; Payne 2000). Prerequisites for any such fitness information to be conveyed are that the relevant acoustic cues consistently predict differences in physical or cognitive capacities of individual singers and that those cues are reliably perceived and differentiated by listeners. In other words, indices of fitness must be consistently transmitted to be useful. By Green and Marler’s (1979) account, however, humpback whale songs should be the least reliable long-range communication signals on the planet—not what one would expect of an acoustic display that listening

whales use to make subtle distinctions about differences in the reproductive fitness of individual singers. Singers vary the duration and frequency content of songs and units within and across sessions, confounding cross-singer comparisons of any cues related to size or stamina. They also vary the form and amplitude of units so extensively that these features are unlikely to consistently correlate with any physical qualities of singers. No terrestrial animals use graded, constantly evolving sound repertoires in their sexual advertisement displays, even at close ranges, presumably because this makes it more difficult for listeners to discern and judge relevant differences between the displays. Add to this the fact that propagation-related distortion in shallow-water environments will degrade received songs in unpredictable ways, and the likelihood that any indices of a singer's quality will remain intact after long-distance transmission becomes quite low. For example, even minor fluctuations in the depth of a singing blue whale result in detectable differences in call intensity for a receiver (Bouffaut et al. 2021), making it unlikely that receivers can reliably estimate the size of a singer based on intensity. Signal complexity can support complex communication, if the properties of the signals are predictable. But, if much of the complexity received by a listener is unpredictable and/or not produced by the sender, then signal complexity increases the potential for confusion (e.g., intermittent gaps occurring within a phone call can make it impossible to have a conversation), making it unlikely that the complex signals convey complex messages.

One reason why many researchers believe that sexual selection drove the evolution of complexity in humpback whale songs is because adults are continuously and communally adopting new songs. Garland and McGregor (2020) describe this unique form of vocal variation as an unending “quest for novelty.” The idea is that singers whose songs stand out in a crowd will be more attractive to listening females, and thus will provide a reproductive advantage. Like Winn and Winn (1985), Garland and McGregor (2020) suggest that humpback whales construct songs from an innate, worldwide repertoire of discrete unit types, such that the only novelty within songs comes from which types are included and how they are arranged into patterns. The current analysis suggests, however, that the unit repertoire that singers use to construct songs is neither innate nor composed of discrete types. Some of the “universal types” identified by Winn and Winn could alternatively be viewed as a single type produced in multiple vocal registers, or for longer or shorter durations, while others (e.g., *snores*) include so many acoustically diverse variants that the only defining characteristic is that they do not fit into other categories.

The fact that singing humpback whales in acoustic contact maintain a common song form (i.e., share a common graded repertoire of units), despite continuously modifying their songs over time, has generally been interpreted

as strong evidence that singers vocally imitate novel songs (or singers) that they encounter (Laland and Janik 2006; Rendell and Whitehead 2001). It remains unclear, however, what aspects of song production singers actually copy. For example, if singers morph units along predictable acoustic continua (as suggested by Mercado and Perazio 2021), then all a listening singer would need to encode to recreate an experienced stream of units would be the form of the initial unit and the trajectory along which that unit was morphed. Using this information, a singer could potentially reproduce hundreds of unit variants without needing to recall anything about the detailed acoustic features of the previously perceived units (other than the initial unit). By encoding and reproducing two parallel streams of units in this way, a singer might also be able to reproduce complex sequential patterns of units (i.e., phrases and themes), without requiring any memories of the sequences of units within songs or any awareness of phrases or themes. Comparisons of similarities and differences between the unit sequences produced by different individuals or populations are insufficient for identifying what elements of songs humpback whales are vocally learning, especially when graded variations in the unit repertoires used by singers are not considered. More precise acoustic comparisons of unit characteristics produced before, during, and after a singer has been exposed to a song session containing novel songs are necessary to identify when and how singers adjust their production of units in response to hearing other singers.

Spatial localization?

Given that the acoustic characteristics of units affect the distances from which they will remain detectable (Au et al. 2006; Mercado and Frazer 1999), as well as the kinds of spatial information that units can provide when received, it seems likely that the complexities of long-distance acoustic transmission in variable ocean environments have strongly influenced the evolution of vocal control in humpback whales. We tentatively suggest that the complexity of humpback whale songs and unit repertoires did not evolve in response to the preferences of other whales, but was instead primarily driven by the properties of the sound channels within which humpbacks operate (see Table 5). More specifically, the current results suggest that singers dynamically morph units within songs to control the spatial information provided by those units.

There are two main ways that songs may be a useful source of spatial information to humpback whales. One is that songs can reveal the location and movements of a singer. Such information could potentially be used by listening females (as suggested by the lekking hypothesis, Herman 2017) or males as a homing beacon (Darling et al. 2012), and could enable singers to space themselves out (Frankel

Table 5 Potential effects of unit variations on detectability and localizability

Factors determining detectability	Predicted Effect
Number of times produced	Rare units will generally be less detectable
Intensity of production	Less intense units will be less detectable
Duration of each unit	Longer duration units will be more detectable
Peak frequency	Units with frequency content adapted to the context will be more detectable
Inter-matching-unit intervals	Longer intervals provide longer windows within which to detect echoes
Factors determining localizability	
Spectral entropy/pitch saliency	Higher spectral complexity provides more cues to changes in source location
Modulating spectral peaks (band switching)	Switching between different peak frequencies can increase the effective active space
Pitch shifting	Gradually increasing/decreasing peak frequency can progressively shift coverage of active space
Temporal expansion/compression	Increasing unit duration can expand the active space
Spectrotemporal modulation	Shifting spectral energy from narrowband peaks to broadband peaks can increase resolution of source bearing and distance, but at the cost of a smaller active space

et al. 1995). Information about the location of singers could also enable females with calves to avoid them (Craig et al. 2014). A second way that songs may function spatially is by revealing the locations of silent conspecifics (Frazer and Mercado 2000; Mercado 2018b), or seamarks (Clark and Ellison 2004), to singing humpback whales. In this scenario, singers listen for song-generated echoes from reflectors and use those echoes to detect and track other whales and/or to navigate. These two functions are not mutually exclusive. Importantly, the acoustic properties and auditory capacities that make it possible for a listener to passively detect and localize singers from a variety of locations are the same ones that would make it possible for a singer to detect and localize the sources of echoes. For example, units that are difficult for listeners to use to localize a singer will generate echoes that are difficult for the singer to use to localize targets, while units that are easy for listeners to localize should generate echoes that reveal more about the movements of targets. Consequently, any adaptations to a whale's vocal repertoire that facilitate transmission of spatial information to listeners will also potentially enhance a singer's capacity to extract spatial information from echoes generated by those same vocalizations.

As noted above, we propose that the progressive changes that singers make to units within songs may serve mainly to enhance the flexible transmission of spatial or other information rather than to advertise the relative fitness of singers. The changes that singing humpback whales make to their unit repertoires across days, months, and years, which are acoustically comparable to the changes they make to units within songs (Mercado 2021a), may also serve to enhance the reliability with which spatial cues can be transmitted to multiple locations surrounding a singer despite variations in bottom topography, water depth, the positions of potential listeners/targets, and the presence of other singers producing

potentially overlapping songs. One way to test this proposal is to collect recordings simultaneously from multiple positions around a singer, and then to estimate the range and bearing of the singer using only the information available at each of those positions. We predict that estimates of a singer's bearing and distance will vary in accuracy across different unit types (e.g., see Au et al. 2006) and locations, and that the optimal units for localizing the singer will be position-dependent, varying as a function of distance, bearing, and receiver depth (see Mercado and Frazer 1999). In that case, use of a graded vocal repertoire may increase the odds that at least a subset of the units produced by a singer will propagate effectively to (and from) the possibly unknown locations of conspecifics. It remains possible that gradations in unit repertoires could serve both sexual and spatial functions, or no function at all. Identifying factors that affect when and how singers adjust their morphing trajectories can provide new insights into what they hope to achieve by doing so.

Conclusions

In summary, singing humpback whales produce a large number of unit variants with ever-changing forms, while at the same time restricting the spectral content of units, (Magnúsdóttir et al. 2015; Mercado et al. 2005; Perazio and Mercado 2018). By analogy, it is as if a piano player had a fully functional piano, but each year chose to play songs using primarily four keys of the piano, selecting a slightly different set of four keys each year with which to perform songs. Four keys would still give the pianist a lot of flexibility with regards to the intensity, duration, timing, and combination of notes, but obviously using all the keys available would provide even more options. Humpback

whales produce an impressive range of fundamental frequencies (~8–6000 Hz), at high intensities, for hours at a time (Au et al. 2006; Mercado et al. 2010). Given singers' exquisite vocal control of unit features, it is unlikely that unit morphing is inadvertent or that large variations in the functional utility of units are accidental. A simpler explanation is that unit morphing contributes to the function of songs, possibly by increasing the number of positions from which listeners (singers and/or other whales) can reliably detect, localize, and track units and echoes generated by units.

Overall, the current analyses highlight the flexibility with which singing humpback whales can adjust unit features within and across songs, as well as the limitations of traditional approaches to characterizing the vocal repertoires used by singing humpback whales. Previous studies that have analyzed humpback whale songs by sorting units into discrete categories, either subjectively or computationally (including our own past analyses), do not adequately capture the ways in which singers flexibly and continuously vary units within songs. Given that phrase and theme structure are typically defined based on variations in constituent units, the current findings also call into question the adequacy of past structural analyses of humpback whale songs. Phrase-based analyses can reveal important information about the dynamics of song structure both within and across song sessions. At the same time, they can obscure the mechanisms that produce this structure (Mercado and Handel 2012; Mercado and Perazio 2021), the acoustic continuity within streams of morphing units, and key functional features of unit sequences (Mercado 2016, 2021b).

Methods that more precisely characterize the graded, dynamic nature of unit repertoires can potentially clarify why singing humpback whales continuously and progressively change their songs, which is a critical step toward identifying the acoustic dimensions of units that are most functionally relevant to humpback whales, as well as for understanding the drivers of song complexity. Recent analyses show that how singers arrange unit sequences is not determined by cultural conventions, but is instead predictable across years and populations (Mercado and Perazio 2021). Progressive variations in unit characteristics and combinations over time are what led researchers to conclude that singing humpback whales gradually replace their songs with new ones. There is no question that singers are constantly changing their songs, sometimes in dramatic ways. But, understanding how and why they do so requires more careful consideration of the nature of the acoustic changes that they make to units when they sing.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-021-01539-8>.

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Data availability All recordings analyzed in this paper are available either through the Macaulay Library at Cornell University or by request via C. Perazio.

Code availability Customized Matlab scripts used to analyze sounds are available from E. Mercado on request.

Declarations

Conflicts of interest The authors declare that they have no conflicts of interest.

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