Stereotypical sound patterns in humpback whale songs: Usage and function

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Abstract

Humpback whales (*Megaptera novaeangliae*) produce cyclical, underwater sound sequences that are composed of a variety of structured sound patterns. These sequences have been described as songs and generally are assumed to serve a communicative function. Past studies of the sound patterns and individual sounds within songs often have described them as functionally homogeneous elements varied to convey information about the vocalizing whale. An alternative possibility is that different sounds and sound patterns within songs are functionally heterogeneous elements, some of which could vary for reasons unrelated to information content. To assess this possibility, we analyzed humpback whale songs recorded in Hawaii from 1992–1995 to determine whether whales consistently used some sound patterns more extensively than others, and to measure the stability of the acoustic features of sound patterns. We found that some 'dominant' sound patterns were consistently repeated for substantially longer periods and that other patterns were consistently repeated for shorter periods. We also found that spectral, temporal, and energetic features of sounds within dominant sound patterns were highly stereotyped. Comparisons of the sound patterns analyzed in this study with those described in past studies suggest that some sound patterns within humpback whale songs recur across years and populations. Our findings indicate that the detectability of different sounds and sound patterns within songs varies substantially. We speculate that differences in detectability reflect differences in functionality.

Key words: cetacean, communication, echolocation, mysticete, bioacoustics, *megaptera*, song.

Introduction

During the winter months, humpback whales (*Megaptera novaeangliae*) aggregate in tropical or sub-tropical waters. Behaviours associated with reproduction take place in these winter grounds, the most spectacular of which may be the production of underwater 'songs' by male whales. Extensive analyses of this unique vocal behaviour have revealed that: (1) males produce stereotyped, ordered sequences of sounds for long periods (Winn *et al.*, 1970; Payne & McVay, 1971), (2) at any given time, sequences produced by individuals within a wintering area are highly similar (Winn *et al.*, 1981; Payne & Guinee, 1983), and (3) whales continuously modify these sequences over time (Payne *et al.*, 1983; Payne & Payne, 1985). Explanations for the structural and acoustic features of humpback whale songs remain speculative. Because most researchers assume that songs are used primarily for long distance communication (Payne & McVay, 1971; Winn & Winn, 1978; Tyack, 1981; Helweg *et al.*, 1992; Frankel *et al.*, 1995; Cerchio *et al.*, 2001; Darling & Bérubé, 2001), song features often are interpreted in terms of how they might facilitate the transfer of information among whales (Winn & Winn, 1978; Frankel, 1995). Additionally, song properties could reflect strategies for collecting environmental information, if components of songs are used as echolocation signals (Winn & Perkins, 1976; Winn & Winn, 1978; Frazer & Mercado, 2000; *c.f.* Au *et al.*, 2001*b*). In the current study, we measured acoustic patterns in humpback whale songs recorded in Hawaiian waters during four consecutive years (1992–1995) to determine whether subcomponents of songs differ in their detectability after long-range propagation. Such analyses can provide important insights into the function(s) of humpback whale songs.

The basic characteristics of songs have been relatively well described. Individual sounds within songs, called units, range in duration from 0.1–10 s with most energy between 200–2500 Hz, and are separated by silent intervals of 0.1–6 s (Payne & Payne, 1985; Mednis, 1991). Source levels vary as a function of sound type, ranging from 155–189 dB re 1 µPa (Winn *et al.*, 1970; Friedl & Thompson, 1981;

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UNITS          =              {A,  B,  C,  D,  E,  F,  G}

SUBPHRASES     =                        {DE,  FF}

PHRASES        =              {BC,  DEDEFF,  GGGGGGG,  AAAA}

THEMES         =        {BCBCBC,  DEDEFFDEDEFF,  GGGGGGG,  AAAA}

SONG           =              AAABCBCDEDEFFDEDEFFGGGGGGG

SONG   SESSION =        ..A..BC..DEDEFF..G..A..BC..DEDEFF..G..

SOUND  PATTERNS =             {A,  BC,  DEDEFF,  G}
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Figure 1. Representation of the types of structural components typically present in sequences of sounds produced by singing humpback whales. Each letter represents one sound. Each individual sound is called a unit (different letters correspond to aurally distinctive sound units). Repeated groups of units are called phrases. Some phrases consist of repeated groups of subphrases. A theme is a set of repeated phrases. Songs consist of repeated theme sequences within a song session. We use the term 'sound pattern' to refer to any sound or set of sounds that is consistently repeated within a song session.

Cato, 1991; Abileah *et al.*, 1996; Au *et al.*, 2001*a*). Sounds are typically produced in predictable patterns, called phrases, which may be repeated multiple times (Fig. 1); sub-components of phrases have been described as clusters, subphrases, and motifs (Payne & McVay, 1971; Winn & Winn, 1978; Tyack, 1982). Sets of repeated phrases (called themes) generally are produced in a fixed order, although specific themes may be omitted from one song to the next and whales occasionally alternate between two themes (Payne *et al.*, 1983; Helweg *et al.*, 1990). A continuous sequence of song cycles makes up a song session (Payne & McVay 1971). In the current paper, we use the term 'sound pattern' to refer to any sound or set of sounds that is consistently repeated within a song session (Fig. 1).

Repeated sound patterns appear to be the fundamental component from which songs are composed, because they are more consistent in duration and structure than either units or themes (Thompson, 1981; Frumhoff, 1983; Payne *et al.*, 1983). Whales may repeat patterns precisely or may gradually modify features of pattern components with each repetition (Payne & Payne, 1985; Guinee & Payne, 1988). Sound patterns may change through the modulation, addition, and deletion of individual sounds (Payne *et al.*, 1983). Most of the changes in songs that occur across years can be traced to such modifications (Guinee & Payne, 1988). As patterns become older (i.e., having been produced for several years), they tend to become longer in total duration (Payne *et al.*, 1983; Payne & Payne, 1985; Cerchio *et al.*, 2001). It has been suggested that the varying features of song sound patterns are the result of runaway sexual selection for song complexity (Tyack, 1981; Cerchio *et al.*, 2001), reflect the age or status of the singer (Darling & Bérubé, 2001), and serve to increase the likelihood that information

being broadcast by the singer is reliably received (Winn & Winn, 1978).

The functional role of sound patterns and individual sounds within humpback whale songs is currently unknown. Tyack (1981) suggested that individual sounds within songs were likely of little relevance independent of their role as pattern components due to their high variability. Alternatively, it has been suggested that some differences in individual sounds could be correlated with physical characteristics of singers, such as size, and could convey information about a singer's fitness (Frankel, 1995). It generally has been assumed that sound patterns within songs (and individual sounds within patterns) are functionally homogeneous. Although this assumption is not unreasonable, it should be closely scrutinized. An alternative possibility is that different types of sounds or sound patterns within humpback whale songs could serve different functions.

How might one test the hypothesis that sounds and sound patterns within humpback whale songs are functionally equipotent? One way is to examine the predictability and detectability of different song components. Other factors being equal, sound patterns that are repeated many times are more likely to be received by listening whales than patterns that are produced infrequently. Sounds produced at high intensities are more likely to be detected at long ranges than are low intensity sounds. If the detectability of song components varies considerably after long-range propagation, and whales can be shown to respond to songs at long ranges, then this could provide a basis for rejecting the hypothesis that song components are functionally homogeneous. For example, if certain components of songs are undetectable at a range of 2 km because of transmission loss, then whales that respond to

songs from this or greater distances cannot evaluate the sounds they do not hear in the same way that they evaluate detectable sounds. Similarly, if a singing whale produces a particular sound pattern only once or twice within a 1 h period, listening whales cannot assess this pattern in the same way that they can assess a pattern produced hundreds of times during this period.

Current data suggest that sounds and sound patterns within humpback whale songs differ in their detectability. Different sound types are produced at different source levels (Winn *et al.*, 1970; Mednis, 1991), and some sound patterns within songs are produced more predictably than others (Winn *et al.*, 1970; Frumhoff, 1983). It is not clear from these past studies whether singing humpback whales are consistently using some sound patterns more extensively than others, or whether particular sounds within patterns are consistently higher in intensity. These factors are critical to determining the functionality of song components.

To further assess the assumption that different individual sounds or sound patterns within songs are functionally homogeneous, we first measured the amount of time singing humpback whales spend producing different sound patterns. We then analyzed the acoustic features of sound patterns that whales spend the greater percentage of time producing. Finally, we compared sound patterns analyzed in the current study with descriptions of sound patterns reported in prior studies to assess similarities in sound patterns across years and populations.

Materials and Methods

Recordings of humpback whales were made by researchers from the Kewalo Basin Marine Mammal Laboratory using an uncalibrated Labcore customized hydrophone (sensitive to 12 kHz) that was deployed from a small boat positioned less than 50 m from the singing whale. The hydrophone was attached to an Archer customized mini-amplifier (Catalogue no. 227–1008B) that was connected to a Marantz cassette recorder (Model PMD430) having a frequency response flat to 17 kHz. A database of over 100 recordings spanning 14 years was pre-analyzed to identify recordings suitable for the current analysis. A subset of recordings was chosen from this database based on three criteria: (1) only recordings in which a single vocalizing whale could be easily identified were selected. This was a necessary prerequisite for the use of automated analysis techniques (described below), (2) recordings spanned at least three consecutive seasons, to take into account across-season variability, and (3) to minimize redundancy, recordings were chosen that

contained songs from years that had not been previously described by other investigators. Fifteen recordings were identified that met these criteria: four recordings each, made in 1992, 1993, and 1995, and three recordings made in 1994. Recordings were not evaluated based on the number of songs or themes present on the recording. Rather, each recording provided an opportunistic sample of a portion of a single song session.

All whales were recorded near the Kawaihae Harbor on the north-western coast of the island of Hawaii, in waters less than 180 m deep. For purposes of the current analysis, no attempt was made to identify singers. Although it is possible that an individual singer may be represented on more than one of the recordings, the probability is low. It is also possible that songs produced by whales frequenting Kawaihae Harbor may differ systematically from songs produced by whales in other regions. Assessing this possibility is beyond the scope of the current analysis. Because a small sample of songs was examined from a restricted locale, it is not possible to determine whether our sample is representative of the Hawaiian population, or global humpback whale populations.

Recordings from each year first were analyzed aurally to subjectively identify the 'types' of sound patterns present in a given year. Tapes were digitized using a Sun Ultra-2 Workstation that sampled incoming signals at a rate of 8012 Hz. Each recording was collected in 10 min segments using a sound processing program available in the OpenWindows (Ver. 3.5.1) environment called 'audiotool'. The durations of themes (i.e., sets of repeated sound patterns) were then measured by manually selecting each theme and recording the duration of the selection displayed by the audiotool utility. The beginning and end points of themes were subjectively identified based on aural impressions. The percentage of the total recording duration that each theme accounted for was then calculated. All measurements were made by a single investigator (EM); however, recordings from 1995 also were measured by a second individual, so that variability resulting from inter-individual subjectivity could be assessed.

Additional analyses of sound patterns were performed with Matlab (Ver. 4.0) and Osprey (Ver. 1.1). This software created spectrographic representations of sound patterns and analyzed acoustic features of patterns in greater detail. Matlab script files were developed to measure acoustic features of sound patterns automatically. The script files first isolated individual sounds by searching waveforms for amplitudes above a set threshold that continued for a period greater than 0.1 s (the shortest song unit duration described in the literature). Because recordings were collected near individual singers,

threshold levels were far above ambient noise levels, minimizing false detections. Once individual sounds were isolated, the durations and intervals of silence between sounds were measured automatically. Next, a separate script file was used to measure the peak frequencies and the energy of each sound automatically, and to estimate the pulse repetition rate (PRR) of each sound. Measurements of total energy for each sound were calculated using the entire sound waveform. Because the recordings were not made with calibrated equipment, energy measurements were only useful for comparing relative differences in amplitude among sounds, and did not estimate the actual energy within sounds. Spectral analyses were made using Matlab's power spectral density function ('psd') using a frame size of 512. Estimates of PRR were calculated by automatically isolating three small segments of each sound, and using cross-correlation ('xcorr') or cepstral analysis ('rceps') to measure the pulse repetition rate within the segments (these techniques are often used in automated speech recognition). Segments corresponded to: (1) an area containing the maximum amplitude of the signal, (2) the middle of the signal, and (3) a segment just after the beginning of the signal. In general, measuring the PRR of a sound automatically was difficult because the precision of estimation was highly dependent on sound type, the length of the segment, and the acoustic features of the segment.

The sound patterns analyzed were compared with those described in other studies by directly comparing spectrograms, and when spectrograms were not available, by comparing descriptions of sound patterns. Spectrographic and verbal descriptions of sound patterns presented in the following studies were considered: Payne & McVay (1971), Winn & Winn (1978), Thompson (1981), Winn *et al.* (1981), Thompson & Friedl (1982), Payne *et al.* (1983), Frumhoff (1983), Payne & Payne (1985), Winn & Winn (1985), Guinee & Payne (1988), Chu (1988), McSweeney *et al.* (1989), Helweg *et al.* (1990), Dawbin & Eyre (1991), Cato (1991), Mednis (1991), Gill *et al.* (1995), Jenkins *et al.* (1995). Quantitative measures of sound patterns reported by Cerchio *et al.* (2001) were also analyzed. Collectively, these studies describe sound patterns from a variety of years and populations.

Results

A total of 9.3 h of recordings was analyzed: 2.3 h from 1992, 2.5 h from 1993, 1.8 h from 1994, and 2.7 h from 1995. The number of sound pattern types identified on a recording by the primary investigator ranged from 2 to 9; the second observer was more discriminating, identifying as many as 12 pattern types in recordings from 1995.

Comparisons of the pattern types from 1995 identified by each observer revealed four types that were directly comparable. The remaining types identified by the second observer appeared to correspond to sub-types within the primary investigator's categories. Such inter-observer differences highlight the limitations inherent to subjective classification of humpback whale sound patterns. Although the two observers did not form identical categories for sound patterns from 1995, the categories were deemed sufficiently similar to allow for replicable analyses of pattern usage. It was assumed that sound patterns from other years had analogous properties.

In 1992 and 1995, certain sound pattern types clearly accounted for a greater percentage of total recording duration, and other patterns accounted for only a small percentage of total duration (see Fig. 2). Differences in usage also were evident to a lesser extent in recordings from 1993 and 1994. Only two sound patterns were consistently present across all four years. The percentage of time spent on these two patterns was relatively stable across recordings (see Table 1). One of these sound patterns appeared similar to patterns described as 'ratchets' in previous studies (Winn *et al.*, 1970; Payne & Payne, 1985; Helweg *et al.*, 1990; Cerchio *et al.*, 2001). The second pattern also appears to have been described in previous studies (discussed below). Other sound patterns showed similarities across years, but clearly were being modified over time in terms of the number and characteristics of their constituent units (Payne *et al.*, 1983; Payne & Payne, 1985).

Differences in the percentage of total recording duration of a sound pattern may be accounted for by: (1) the number of times different themes occurred in recordings, or (2) the average duration of different themes. The number of times a theme containing a sound pattern occurred in recordings was positively correlated with the percentage of time spent on that pattern, as was the average amount of time spent continuously on each sound pattern (see Table 2). Overall, the percentage of time each sound pattern accounted for in recordings was more closely correlated (t=4.5, df=63, $P<0.01$)[1] with the average amount of time spent on each pattern (r=0.86) than with the number of times a theme occurred in recordings (r=0.66). In other words, sound patterns typically accounted for a larger percentage of song time because they were

[1]Because the average amount of time spent continuously on each sound pattern was correlated with the number of times a theme containing that pattern occurred, a specialized t-test was used to assess which of these two variables was more correlated with the percentage of time each sound pattern accounted for in recordings (see McNemar, 1969, pp. 158).
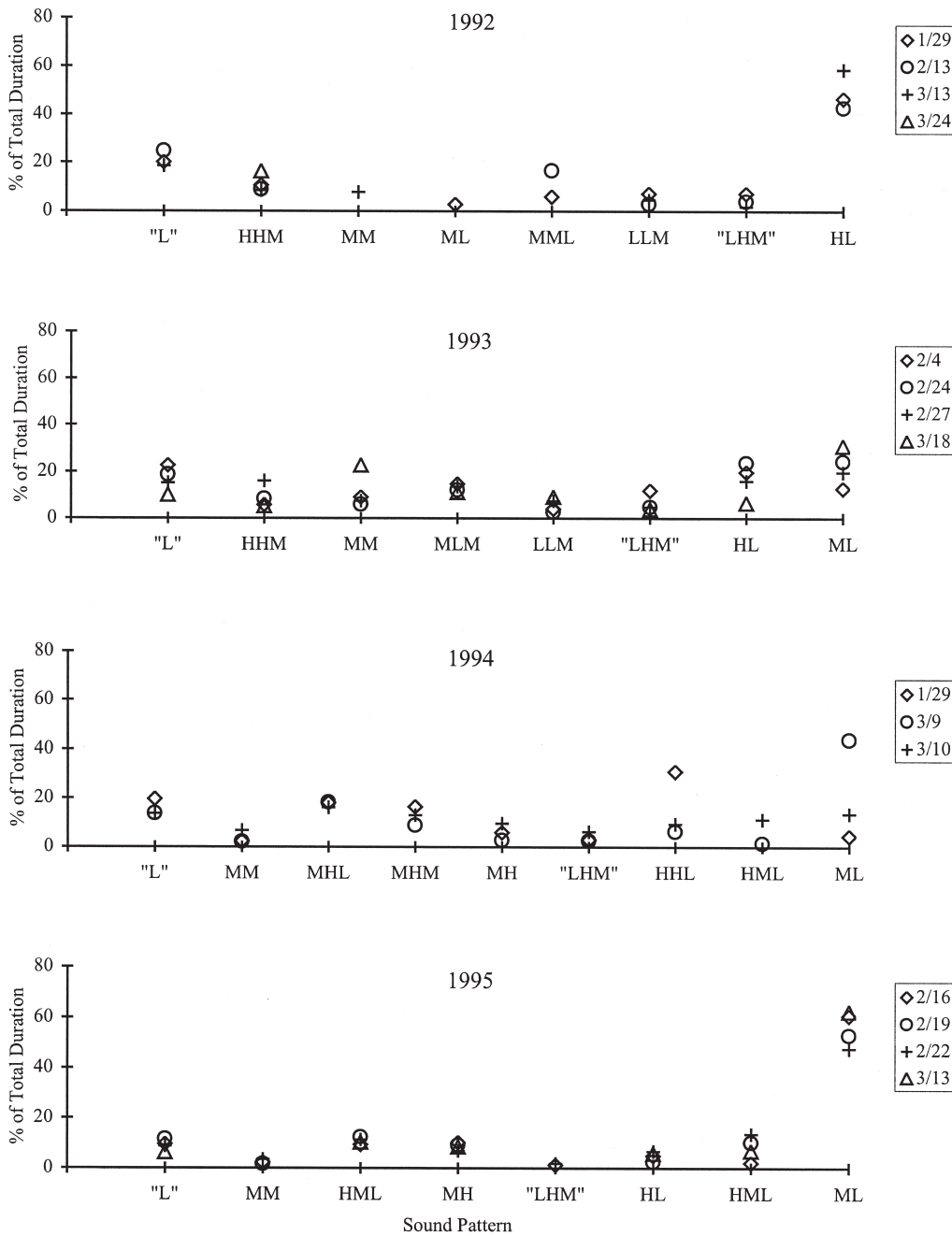
Figure 2. Percentage of time each sound pattern occurred in each recording. Singing humpback whales consistently produced some 'dominant' sound patterns for substantially longer periods; other patterns were consistently repeated for shorter periods. Sound patterns are denoted using an ordered letter code corresponding to the gross PRR characteristics of individual sound types within the pattern (L=low, M=medium, H=high). These labels simply identify specific patterns, and are not intended to precisely describe patterns. Sound patterns are arranged along each abscissa in the order they typically occurred within a song; ratchets (L) were arbitrarily designated as the first pattern in this cycle. Quotes (e.g., "L") indicate that subjectively a pattern was highly similar across all recordings and years. The four classifications of sound patterns in 1995 that were found to be directly comparable across both observers were MM, LHM, HML, and ML.

Table 1. Summary statistics for humpback whales sound pattern usage from 1992–1995 in Hawaiian waters.

1992	'L'	HHM	MM	ML	MML	LLM	'LHM'	HL	
x	2.4	1.2	2.2	0.5	4.4	0.9	0.7	5.6	
n	8	14	1	2	10	5	6	8	
%	14	12	2	1	33	3	3	33	
1993	**'L'**	**HHM**	**MM**	**MLM**	**LLM**	**'LHM'**	**HL**	**ML**	
x	2.4	1.5	1.3	2.0	0.9	0.9	2.0	2.3	
n	11	10	12	10	10	12	13	14	
%	17	10	11	13	6	7	17	21	
1994	**'L'**	**MM**	**MHL**	**MHM**	**MH**	**'LHM'**	**HHL**	**HML**	**ML**
x	2.0	0.5	2.0	1.3	0.7	0.6	2.3	0.9	2.3
n	9	7	10	11	9	7	8	4	10
%	16	3	18	13	6	4	17	3	21
1995	**'L'**	**MM**	**HML**	**MH**	**'LHM'**	**HL**	**HML**	**ML**	
x	1.2	0.4	1.6	1.2	0.2	0.9	0.9	4.0	
n	12	7	11	12	6	10	15	23	
%	9	2	11	9	1	5	10	56	

As in Figure 1, sound patterns are denoted using a three-letter code describing the PRR of constituent units (L=low, M=medium, H=high; quotes indicate that the pattern occurred in all years). Rows labeled 'x' show the average amount of time spent continuously on each sound pattern (in min) for each year. The average includes complete themes, as well as partial themes present at the beginning and end of recordings. Rows labeled 'n' show the total number of occurrences of each theme in recordings from each year, and rows labeled '%' show the percentage of total recording duration each theme accounted for in each year. Theme durations ranged from 11 s to just over 11 min. Interestingly, there appears to be a tendency for short and long duration themes to alternate in song cycles.

repeated many times within a theme, rather than because a particular theme was produced more often than others.

Themes containing sound patterns that accounted for a greater percentage of total recording duration in a year were analyzed using automated techniques

Table 2. Correlations between usage and repetition of patterns and themes by humpback whales in Hawaiian waters, 1992–1995. r_{np} denotes the correlation between the number of times a theme containing a sound pattern occurred in recordings and the percentage of time spent on that pattern. r_{rp} denotes the correlation between the average amount of time spent continuously on each pattern and the overall percentage of time spent on that pattern.

Year	r_{np}	r_{rp}
1992	0.58	0.92*
1993	0.61	0.94*
1994	0.69*	0.96*
1995	0.91*	0.98*

*$P<0.05$.

(described above) to assess how individual sounds within the patterns varied with repetition. Both spectral and temporal features of sound patterns from such themes were highly stable across within-song repetitions (Figs 3, 4). Additionally, there were predictable differences in energy levels that were associated with particular units within these themes. Sounds that had a low PRR (<100 pps) typically had much less total energy than sounds with higher PRRs (Figs 5, 6). Sound patterns that only accounted for a small percentage of the total duration of recordings also had interesting similarities. For example, rapid bursts of short duration units were a common component of such patterns (Fig. 7).

Past descriptions of sound patterns within humpback whale songs were surprisingly similar to the patterns analyzed in the current study. For example, Theme I in Payne & McVay (1971), recorded in the West Indies, appears quite similar to the sound pattern shown in Figure 4. McSweeney et al. (1989) described a similar two-sound pattern recorded from a whale in Hawaii in 1981. Preliminary analyses of Hawaiian songs recorded by researchers from KBMML in 1981 confirmed
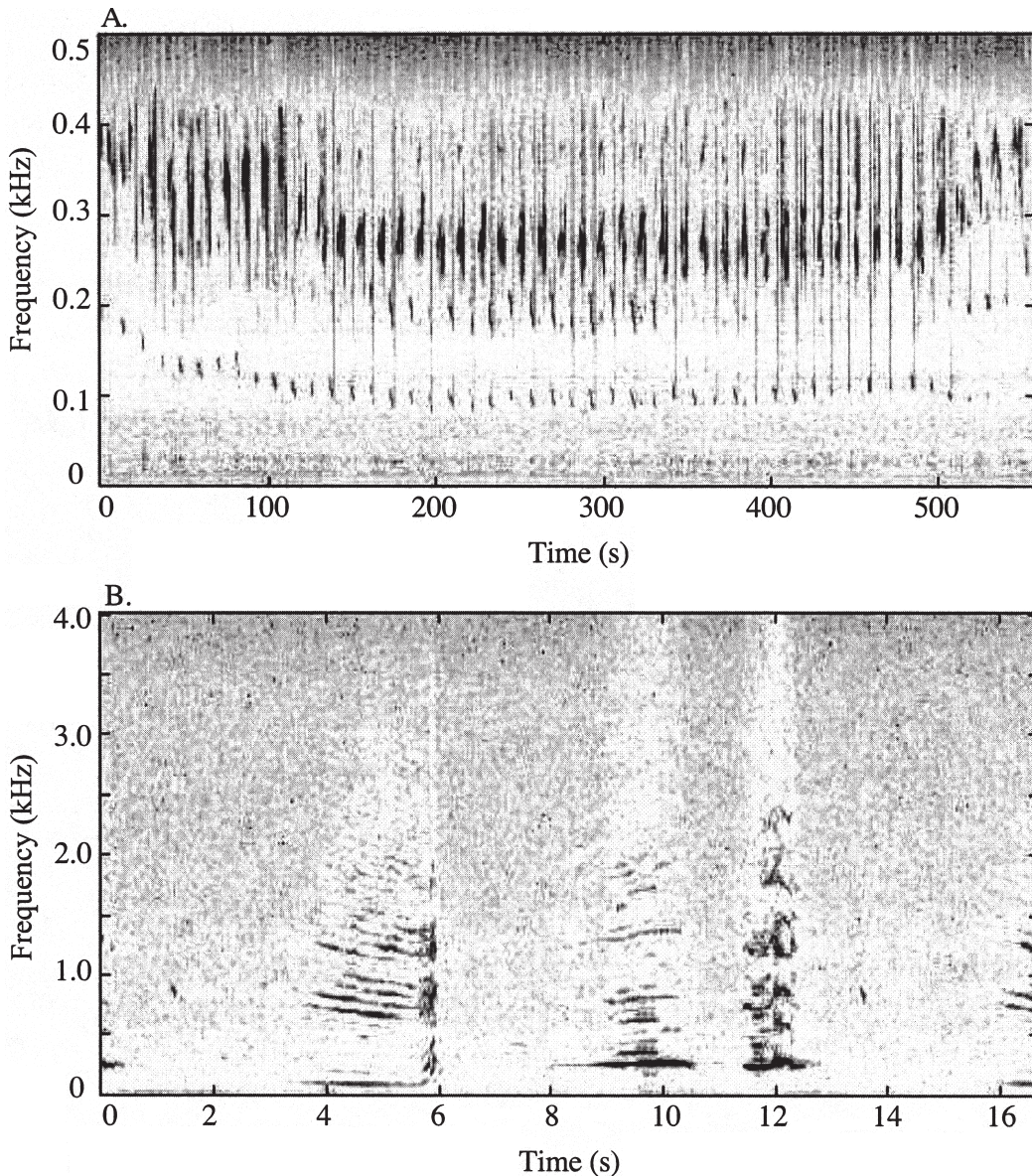
Figure 3. Spectrograms of the 1992 MML sound patterns showing: (A) a nine min theme from the 24th March recording. The spectrogram shows a theme that has been 'compressed' by decimating the recorded signal by a factor of eight; note that the decimation process tends to spread spectral energy across a wider bandwidth. Frequency and time scales have been adjusted to reflect the spectral and temporal features of the original signal. This spectrogram reveals high stereotypy across pattern repetitions. (B) an individual 1992 MML pattern sampled from the theme shown in (A). In this spectrogram, the low-PRR unit precedes the two medium-PRR units to emphasize one kind of bias that subjective classification can introduce (i.e., the designation of the 'first' and 'last' units in such patterns is arbitrary, MML=LMM=MLM).

that this two-sound pattern had acoustic features comparable to the 1995 two-sound pattern. Sound patterns involving alternating tonal and pulsive sounds appear to be a staple across years and populations, also being reported by Winn & Winn (1978), Payne *et al.* (1983), Cato (1991), and Mednis (1991). Another pattern (Theme 2 in Winn & Winn, 1978), recorded in the West Indies, appears
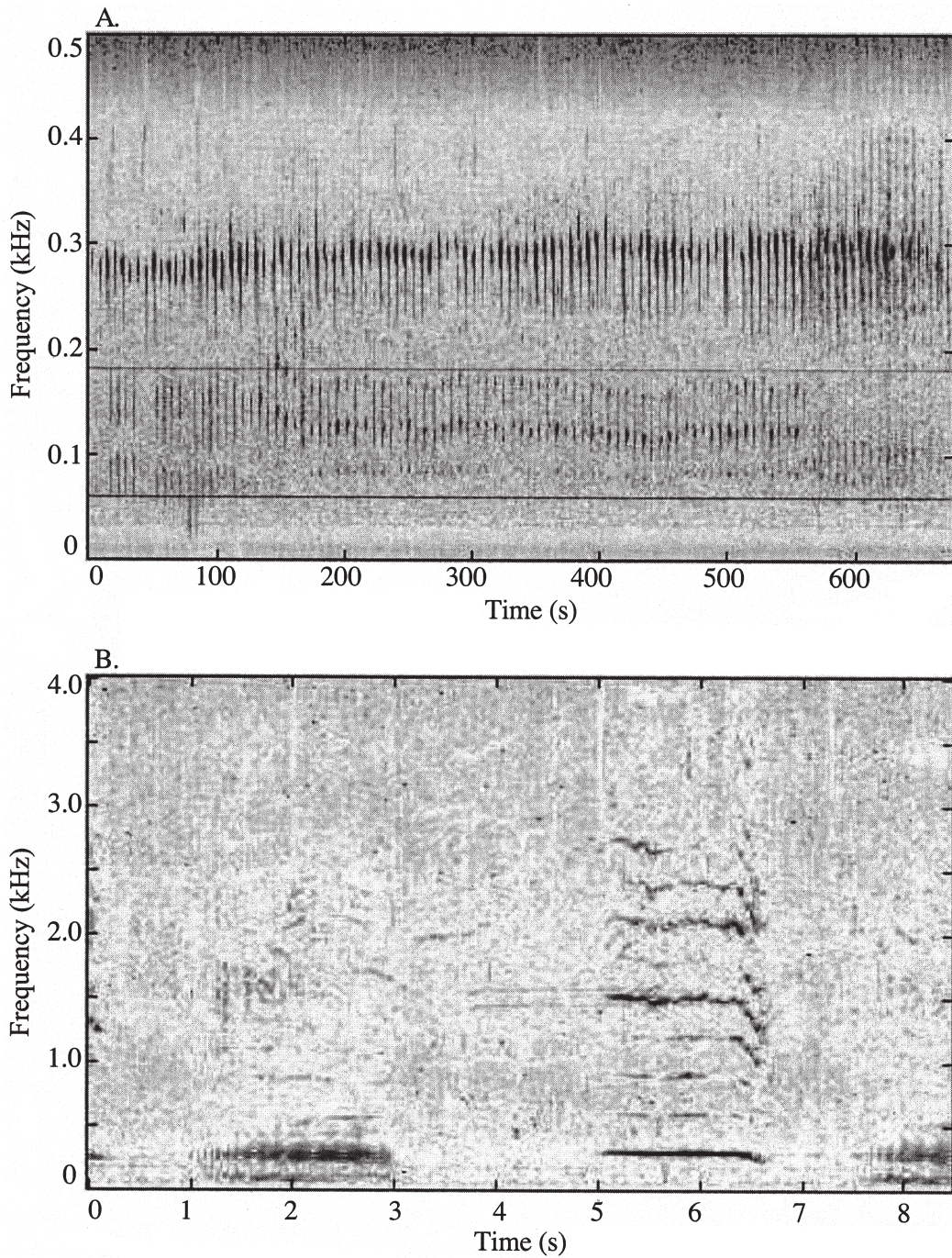
Figure 4. Spectrograms of the 1995 ML sound pattern showing: (A) an 11 min theme from a 19 February recording. As in Figure 3, the spectrogram shows a theme that has been 'compressed' via decimation. Again, high temporal and spectral stereotypy across pattern repetitions is evident. (B) an individual 1995 ML pattern sampled from the theme shown in (A); the low-PRR unit is again shown preceding the medium-PRR unit.
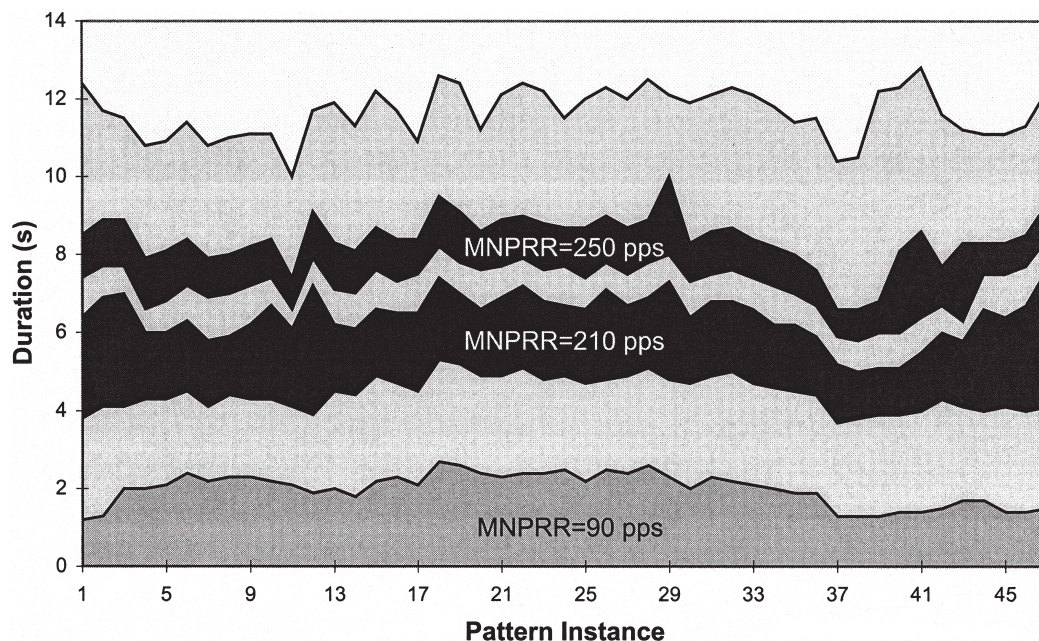
Figure 5. Representation showing the temporal and energetic stability of repeated 1992 ML sound patterns (adapted from Mercado & Frazer, 2001). In this graph, the ordinate corresponds to the temporal properties of a single pattern. The bottom band (medium grey) corresponds to the duration of the 'first' sound in the pattern (as shown in Fig. 3B), the next band up (light grey) corresponds to the subsequent interval of silence, the next band (dark grey) corresponds to the 'second' sound, and so on. The relative darkness of each band symbolically represents the relative amount of acoustic energy being produced during each temporal interval (darker bands are more energetic). MNPRR=the average PRR for each sound across patterns. Energy in the higher PRR sounds (mean=2.3 ± 1.0 and 1.7 ± 0.9) was over ten times greater than that of the lower PRR sound (mean=0.15 ± 0.08).

similar to the sound pattern shown in Figure 7A. Spectrograms of patterns recorded from singers in Australian waters (described as 'n-chugs,' 'yaps,' and 'n-whistles') also appear similar to this sound pattern (Mednis, 1991; Gill *et al.*, 1995). Although other patterns occurring across populations and years were found, the quality of spectrograms and descriptions limited the extent to which such similarities could be meaningfully assessed.

A recent report by Cerchio *et al.* (2001) describes songs produced by humpback whales (n=95) in Kauai and Mexico during 1991. Data from the appendix of Cerchio *et al.* were used to estimate the amount of time whales spent producing particular sound patterns within individual songs (Fig. 8). Cerchio *et al.* used different sampling and analysis techniques from the ones used in the current study to characterize songs. Even so, the percentage of time whales spent producing particular sound patterns was highly similar for both data sets (Fig. 8). In 1991, whales from Kauai and Mexico: (1) spent about 15% of their singing time producing ratchets, compared to 14% for whales off Hawaii in 1992, (2) spent the smallest percentage of time (7%) producing a pattern similar to the reduced-usage patterns

shown in Figure 7, and (3) spent the greatest percentage of time (28%) producing the sound pattern that preceded the ratchet pattern, as did whales off Hawaii from 1992 to 1995.

Discussion

Our results indicate that the detectability of different sounds and sound patterns within humpback whale songs varies substantially, contrary to what one would expect if songs are comprised of functionally homogeneous elements. We found that some singers consistently produce particular sound patterns for substantially longer periods than other patterns. One sound pattern (Fig. 4) accounted for $\geq 50\%$ of total recording time in 1995, for all four recordings analyzed. Researchers previously have observed that singers may extensively repeat certain sound patterns. For example, Thompson (1981) discussed songs recorded in Tonga in which one theme constituted 58% of the total duration of songs, and Gill *et al.* (1995) referred to 'dominant' themes in songs recorded near New Caledonia. We found similarly skewed distributions of sound pattern usage in data on humpback whale songs
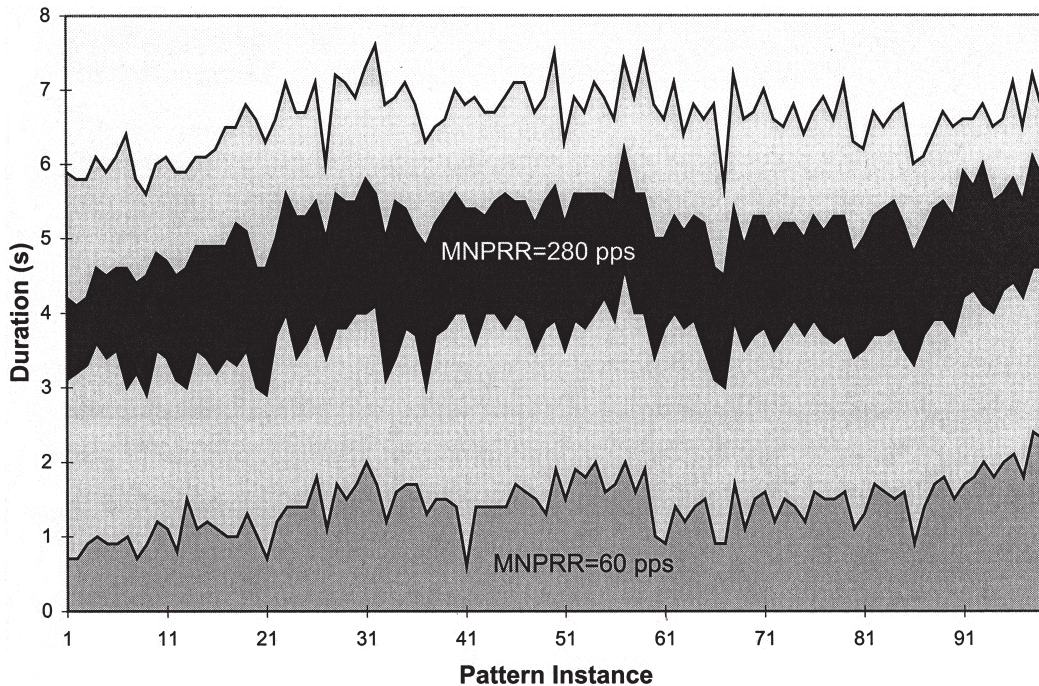
Figure 6. Representation showing the temporal and energetic stability of repeated 1995 ML sound patterns (adapted from Mercado & Frazer, 2001). MNPRR = the average PRR for each sound across patterns. Energy in the higher PRR sound (mean = 0.45 ± 0.2) was over three times greater than that of the lower PRR sound (mean = 0.14 ± 0.19).

(n = 159) reported by Cerchio *et al.* (2001). Our automated analyses revealed that the spectrotemporal structure within dominant themes is highly stereotyped.

Other sound patterns (e.g., Fig. 7), which were consistently produced in every song in all recordings from 1995, typically accounted for less than 5% of total recording time. Such reduced-usage sound patterns could be analogous to transitional phrases, i.e., phrases that combine elements of preceding and succeeding patterns (Payne *et al.*, 1983; Frumhoff, 1983). However, the patterns we observed often contained unique sound types. Additionally, reduced-usage sound patterns were consistently repeated within and across songs, which is atypical of transitional phrases. We found that certain reduced-usage patterns remained stable in form and usage across four years. Researchers previously have described sound patterns that were only produced once within each song, or that were repeated few times (Payne & McVay, 1971; Payne *et al.*, 1983; Cato, 1991; Mednis, 1991). We also discovered reduced-usage sound patterns in Cerchio *et al.*'s (2001) data set. The reduced-usage patterns described by Cerchio *et al.* are acoustically similar to the reduced-usage patterns we identified.

These differences in sound pattern usage suggest that long duration themes play a different role from shorter duration themes. By producing a sound pattern numerous times, a whale can increase the likelihood that the pattern will be received (Winn & Winn, 1978). In comparison, patterns that are produced infrequently will typically have a lower probability of being received (assuming the propagation range of the infrequent pattern is comparable to that of the frequent pattern). If a sound pattern is repeated at a set rate, then this will further enhance the detectability of that pattern because of the increased temporal predictability of the signal. The stereotyped acoustic structure of dominant sound patterns (i.e., patterns consistently repeated for longer periods) should thus increase the detectability of these patterns.

Song transmission

Frequency of repetition is not the sole determinant of sound pattern detectability. Other factors such as energy levels of sounds within the pattern, water depth, signal bandwidth, and signal directionality also must be taken into account when assessing
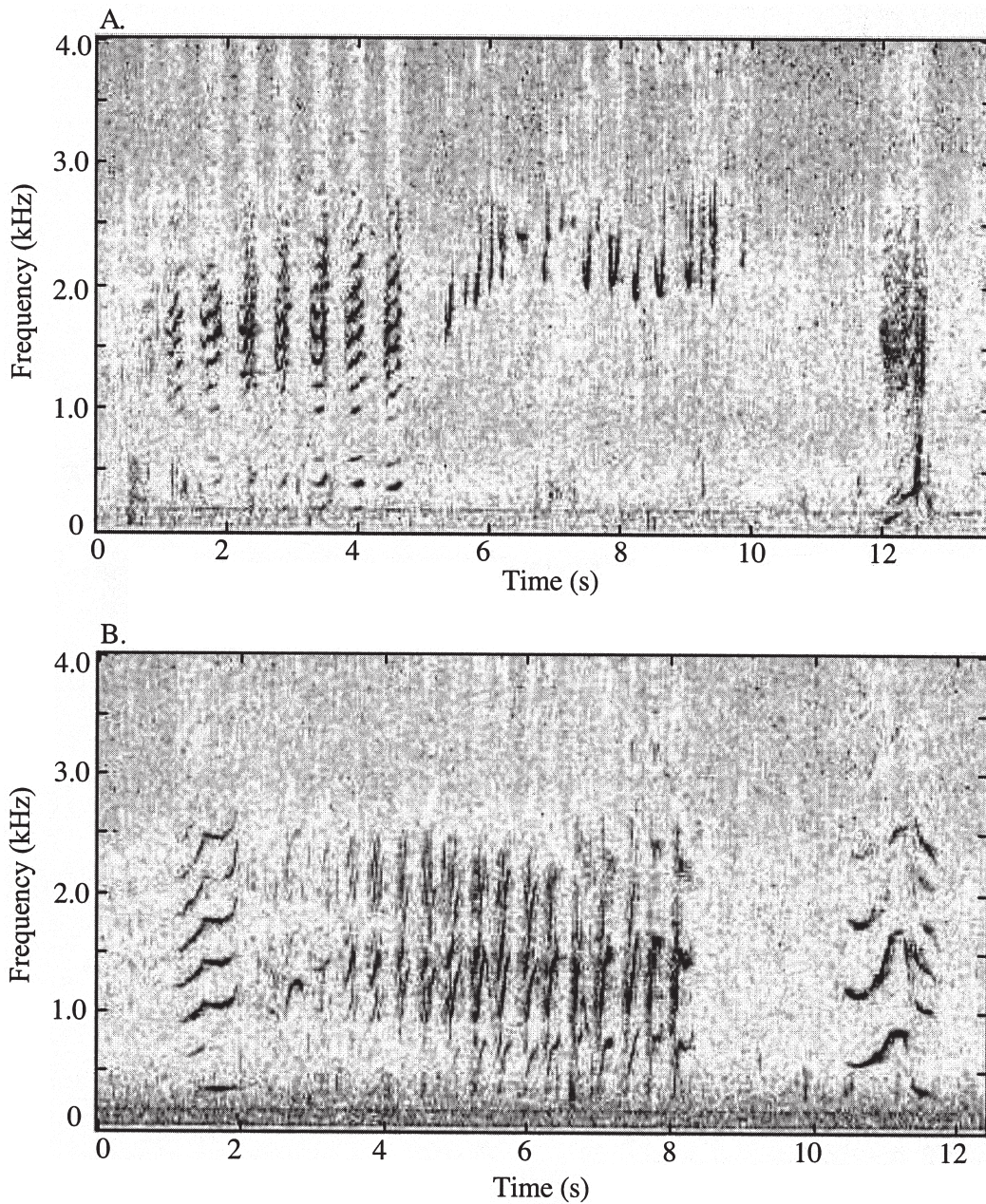
Figure 7. Spectrograms showing (A) the 'LHM' sound pattern from 1994, and (B) the 'MM' sound pattern from 1994. Both sound patterns consistently accounted for only a small percentage of total recording duration. Interestingly, both patterns were the only patterns that contained rapid clusters of units.

underwater transmission of humpback whale songs (Mercado & Frazer, 1999). Because our recordings were collected with uncalibrated hydrophones, we could not use them to estimate how far particular sound patterns travelled. However, because the frequency response of the recording system was flat within the frequency range we analyzed, and recordings were collected from isolated singers, we can assess which components of sound patterns propagated the farthest.
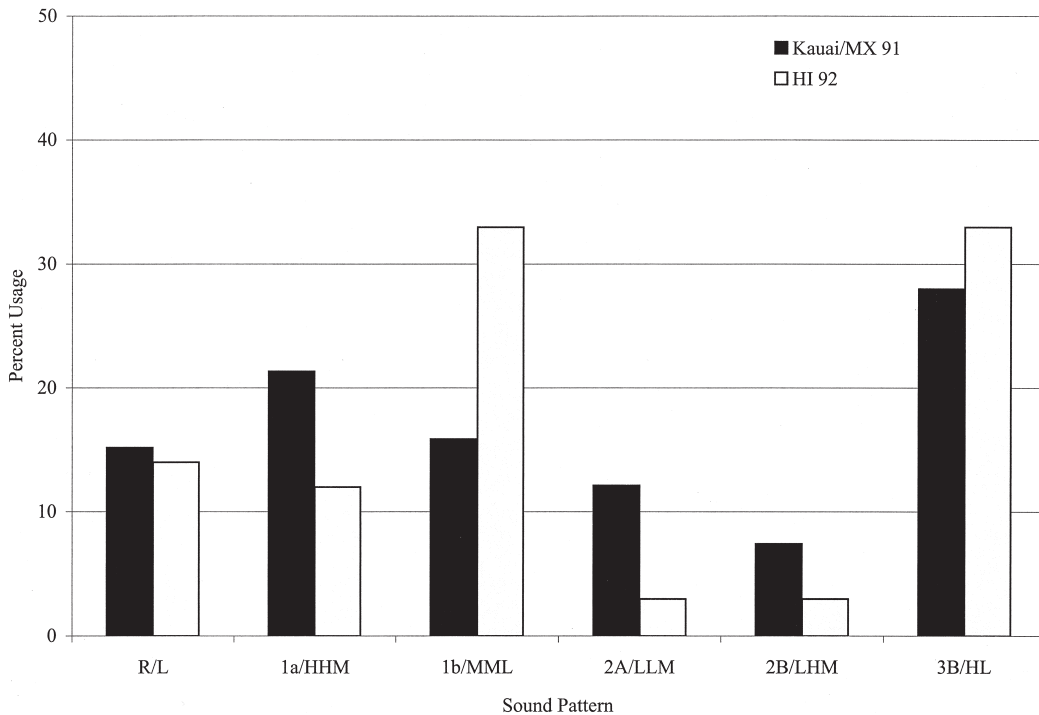
Figure 8. Comparison of sound pattern usage by whales recorded in waters off of Mexico and Kauai in 1991 (derived from Cerchio *et al.* 2001, Appendix, p. 329) with pattern usage by whales recorded in waters off of the coast of Hawaii in 1992. Cerchio *et al.* labeled sound patterns from 1991 that occurred sequentially after the ratchet pattern (R) as 1a, 1b, 2A, 2B, 3B. Six sound patterns that occurred sequentially in all songs recorded off Hawaii in 1992 (Fig. 2) were compared with the patterns described by Cerchio *et al.* Data for Kauai/MX 91 represent the average percentage of time whales (n=95) spent producing a particular pattern within individual songs across all locales and recording periods, as estimated from mean phrase durations and mean number of phrase repetitions/song. Usage of ratchets is highly similar across groups. The sound pattern preceding the ratchet (3B/HL) is dominant in both data sets, and the sound pattern least used by whales in all locales (2B/LHM) precedes use of the dominant pattern.

Winn & Winn (1978) suggested that because low frequencies within humpback whale songs are attenuated less than high frequencies during propagation, higher frequency units might be used for transmission over short ranges whereas lower frequency units might be used for longer ranges. Contrary to this notion, empirical and theoretical data show that when whales sing in shallow water environments in Hawaii, the lowest frequencies they produce will not propagate as far as the higher frequencies they produce (Jensen & Kuperman, 1983; Urick, 1983; Mercado & Frazer, 1999). No single frequency will propagate optimally to all positions within the water column. Thus, increasing the range of frequencies produced within a sound pattern can increase the number of positions within a shallow water environment from which the pattern can be detected.

Our analyses showed that certain sounds within dominant patterns have predictably lower energy levels than other sounds. In particular, in both sets of dominant patterns analyzed, one sound consistently was much lower in energy than other sounds in the pattern. Additionally, the energy in the quieter sound was spread across a wider spectral bandwidth and over equivalent or longer periods than other pattern components (Figs 3–4), such that the spectral energy at any particular frequency was quite low throughout the duration of the quieter sound. The potential range at which such low energy sounds can be detected should be greatly reduced relative to higher energy, higher-PRR sounds (Van Trees, 1968). Put another way, when singers produced dominant sound patterns in shallow waters off the coast of Hawaii, the higher-energy units within these patterns insonify a much greater volume of water than the lower-energy units.

The reduced propagation potential of low-energy sounds within dominant patterns suggests either

that these sounds are used for shorter ranges, or that they are non-functional. Most of the low-energy sounds identified in the current study were low-PRR signals that alternated with higher-energy, higher-PRR signals. Although similar low-energy sounds are present within other themes (Mercado, 1998), detailed comparisons of acoustic features across themes have yet to be made. To fully assess the relative detectability of various sounds and sound patterns produced by singing humpback whales, singers need to be recorded with an array of calibrated hydrophones, spread over a wide range of distances, depths, and environments.

Song production

Although it is not known with any certainty how humpback whales produce sounds, they are presumed to do so using a moving air stream (Sukhovskaya & Yablokov, 1979; Morris, 1986; Quayle, 1991; Reidenberg & Laitman, 1992). No air is released under water as whales sing, suggesting that air is being re-circulated. Such re-circulatory processes may sometimes be audible. For example, moths (*Acherontia atrops.*) produce sounds during both inspiration and expiration of air through a constricted tube (Ewing, 1989, p. 23). A tonal note is produced during expiration and a pulse train is produced during inspiration. It seems possible that sequences of alternating tonal and pulsatile units in humpback whale songs also might be related to internalized 'inspiration' and 'expiration' of air during sound production. The low-energy, low-PRR signals that we observed in dominant sound patterns are similar in many respects to surface ratchets. Given that ratchets are associated with surfacing, and by proxy with respiratory processes, we speculate that ratchets are the audible result of physiological processes related to the switch between internal air recirculation and respiration. Acoustic similarities between ratchets and 'growl' blow sounds made by right whales, *Eubalena australis*, (Clark, 1982) are consistent with the idea that ratchets are an acoustic side-effect of some pre- or post-respiratory, internal air transfer.

A clearer understanding of how humpback whales produce songs is needed to evaluate the hypothesis that pulsatile units within songs are physiological byproducts. Sound production mechanisms constrain what sound patterns a singing humpback whale can use, and therefore can influence whether a particular pattern is likely to be dominant or repeated less often. Conversely, on an evolutionary time scale, pressure to repeatedly use particular types of sound patterns may have played a critical role in shaping humpback whales' sound production mechanisms. Specializations in production mechanisms that facilitate the production of particular patterns might thus reflect the importance of those patterns.

Recurring patterns

We were surprised to discover that certain sound patterns appeared to recur across populations and decades. Past studies noted few similarities between sound patterns produced by different populations (e.g., Winn *et al.*, 1981). However, most past comparisons have been based on subjective impressions of themes produced by different populations within the same year. Quantitative comparisons of sound patterns produced by different populations within and across years have not been attempted. Comparing sound patterns is difficult because whales can gradually modify the units that make up the patterns. Additionally, it is unclear whether patterns that differ in a single unit, or in the repetitions of a unit, should be considered different patterns, or just gradations of a single pattern type. Despite such difficulties, researchers have consistently reported that at least one sound pattern (the surface ratchet) is produced intermittently across populations and among years (Payne & Payne, 1985; Helweg *et al.*, 1990; Cato, 1991; Jenkins *et al.*, 1995; Cerchio *et al.*, 2001). The current analysis suggests that at least two other sound patterns (Figs. 4B, 7A) are also occurring across populations and years. Better methods for quantitatively characterizing the structural features of sound patterns will need to be developed before comprehensive comparisons of patterns across individuals, populations, and years can be made. Identifying sound patterns that occur across populations could be particularly important for assessing hypotheses of song function, because such patterns reveal regularities in song production that supersede local conventions.

Song function

Lone humpback males can sing continuously for long periods of time (>2 h, Tyack, 1982; Winn & Winn, 1985). Because the period of peak singing is seasonal and coincides with periods of heightened reproductive potential (Dawbin, 1966; Chittleborough, 1958), and because singers are almost certainly exclusively males (Winn & Winn, 1978), song is thought to play an important role in the humpback whale mating system. Most researchers currently speculate that songs serve primarily for inter- and intra-sexual advertisement, informing females about the location and reproductive fitness of singers, and informing other males about the location of singers to produce spacing among multiple singers (reviewed by Helweg *et al.*, 1992; Clapham, 1996), or advertising the fitness of males (Darling & Bérubé, 2001). Additionally, males may use songs to locate other whales through

echolocation (Makris & Cato, 1994; Frazer & Mercado, 2000; Mercado & Frazer, 2001—see Makris *et al*., 1999; Au *et al*., 2001*b* for arguments against this hypothesis). The results of the current acoustic analyses provide new data with which to assess the potential function(s) of humpback whale song.

If song serves to communicate information to both males and females (Helweg *et al*., 1992; Frankel *et al*., 1995), then it is possible that different components of songs could be intended for different sexes. For example, Puerto Rican frogs (*Eleutherodactylus coqui*) produce a two-note advertisement call in which one note is a lower frequency signal that serves to space males apart from one another, and the other note is a higher frequency signal that serves to attract females (Narins & Capranica, 1978; Lopez & Narins, 1991). It is possible that lower PRR units in humpback whale sound patterns are lower in energy because they serve primarily to inform nearby males of a singer's proximity, whereas higher-energy sounds are produced to propagate as far as possible, thereby maximizing the probability that they are heard by distant females. If subsets of sounds within sound patterns are directed toward different sexes, then the apparent complexity of humpback whale sound patterns could be epiphenomenal. For example, phrases could be decomposable into two or more simpler sound sequences that are temporally overlapping, as is seen in Puerto Rican frogs.

If song serves to provide the singer with environmental information, then only a subset of the sounds being produced within songs are useful for this purpose. For example, lower-energy sounds in dominant sound patterns appear to be useless as sonar signals. In contrast, the higher-energy sounds within these patterns are suitable. The dominant themes we observed are similar in certain respects to the search signals used by some echo-locating bats (e.g., see Neuweiler, 1983). In particular, bat species that forage in open spaces tend to produce stereotyped sequences of constant-frequency sonar signals to optimize their long-range detection of targets (Simmons *et al*., 1978; Pye, 1980; Fenton & Bell, 1981; Feng & Tyrell, 1988). Bats have also been observed to use patterns of sonar signals that consist of alternating lower energy calls and higher energy calls (Obrist, 1995).

Our acoustic analyses cannot provide evidence that humpback whales use songs for a specific function. They can lead to testable predictions, potentially rule-out possibilities, and provide a useful basis for comparative analyses. Given that the sound patterns used by singing humpback whales differ in terms of their stability, predictability, and usage, it seems likely that they also differ in their function. Precise comparisons of sound patterns within song sequences produced by humpback whales in a wide range of contexts should further elucidate the potential functionality of humpback whale songs.

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