



Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages

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Humpback whale song, a male breeding display, shows a remarkable degree of similarity among distant breeding assemblages, despite constant progressive change. It has been hypothesized that whales maintain continuity through cultural transmission via migratory movements of males. We examined songs of whales breeding off Hawaii and Mexico to determine whether they changed similarly in both areas during the course of a breeding season. Songs recorded off Kauai, Hawaii (11 individuals) and Isla Socorro, Mexico (13 individuals) during winter and spring of 1991, were compared qualitatively and quantitatively. We measured 44 acoustic variables describing all known levels of song structure for each singer and we grouped these variables into six categories. We used two-factor analyses of variance to assess change across the season in each area, comparing the two regions and two 3-week periods (January/February and April). Twenty-seven variables changed significantly during the 12-week study in at least one area. Variables within categories displayed similar trends of change. Time and frequency characteristics describing the structure of song elements (units and phrases) changed synchronously in each area, with 21 of 25 variables displaying significant differences between periods and no interaction with region. Structures of song patterns, as defined by frequency of occurrence and number of unit and phrase types, changed differently in each area, with five of 12 variables indicating a significant interaction between region and period. Our results may suggest cultural transmission during the season, since many variables changed in similar manners. We propose an alternative hypothesis, that whales may be predisposed to gradually change certain features of song independently of cultural influences; change of structural elements may be governed by a discrete set of rules, or according to an innate template. Therefore, continuity of song patterns across the ocean basin may be due to a combination of mechanisms, only partially involving cultural transmission. We assess these hypotheses in relation to humpback whale behaviour and population structure, and cultural transmission and evolution of avian song.

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Humpback whales, *Megaptera novaeangliae*, migrate annually between summer feeding areas in subpolar or cold-temperate waters and tropical or subtropical winter areas. In the North Pacific, humpback whales spend summer and autumn off Alaska and central North America (Baker

et al. 1986; Calambokidis et al. 1996, 1998) and migrate in late autumn to spend winter and spring off the Hawaiian Islands, Mexico, and southern islands of Japan (Darling & Jurasz 1983; Darling & McSweeney 1985; Baker et al. 1986; Darling & Cerchio 1993; Darling & Mori 1993). At these locations calving and presumably mating occur (Darling 1983; Baker & Herman 1984). While in their winter breeding areas, humpbacks sing lengthy, complex songs (Payne & McVay 1971; Winn & Winn 1978). Only males have been documented singing (Darling et al. 1983; Glockner 1983), and it has been hypothesized that songs are important to male breeding

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success (Herman & Tavalga 1980; Tyack 1981; Darling 1983). Herman & Tavalga (1980) and Clapham (1996) suggested that humpback breeding behaviour is similar to that of lekking animals, and indicated that song may function as an intersexual signal. Darling (1983) suggested that song is an acoustic display that may determine dominance rank among males, thereby emphasizing an intrasexual function.

Payne & McVay (1971) first described the structure of humpback whale song as an ascending hierarchical series of units, phrases, themes and songs, a categorization still recognized today. A 'unit', analogous to a note, is a signal that appears aurally continuous. Units have fundamental frequencies ranging from 30 Hz to greater than 10 000 Hz (observed in this analysis) and are structurally diverse. Different units are organized into distinct, stereotyped patterns, termed 'phrases', with 2–20 or more units, and lasting approximately 5–30 s. Several distinct phrase types are usually found in a whale's repertoire, each characterizing a different 'theme'. A theme is typically a repetitious series of similar phrases, and three types of themes have been described: static, shifting and unpatterned (Payne & Payne 1985). A 'song' consists of several different themes sung in a consistent, cyclical order (Payne & McVay 1971; Frumhoff 1983; Payne et al. 1983). Songs are usually repeated without pauses, and a group of consecutive songs is a 'song session'. This organization of song patterns is similar to the 'eventual variety' model described for some songbirds (Kroodsma 1982), although the terminology for song elements is different.

All males within a region (e.g. the Hawaiian Islands), sing very similar songs at any given time (Payne 1978; Winn & Winn 1978); however, the songs progressively change during the breeding season, and all males in an area incorporate the same changes into their songs (Payne et al. 1983; Payne & Guinee 1983; Payne & Payne 1985). Change is gradual, but changes accumulate over several seasons so that songs recorded 4–5 years apart are very different (Payne et al. 1983; Payne & Payne 1985). Songs change at all studied levels of structure: units, phrases, themes and songs (Payne et al. 1983). Most changes in the song occur throughout winter when singing is a prevalent behaviour, whereas songs change little during intervening summers (Payne et al. 1983) when singing is relatively uncommon (Mattila et al. 1987; McSweeney et al. 1989). Guinee et al. (1983) reported that known individual males change their songs throughout the breeding season and years, so that at any given time, a male's songs more closely resemble the songs of whales around him than his own songs from previous years or months. They interpreted this as evidence of learning and cultural transmission among individuals, and therefore indicated that progressive change is an example of cultural evolution. This type of rapid cultural evolution, where individuals progressively change their songs over the course of a season, has been documented for only two other animal species, both of which are songbirds: the yellow-rumped cacique, *Cacicus cela* (Feeke 1977, 1982; Trainer 1989), and the village indigobird, *Vidua chalybeata* (Payne 1979, 1985).

Geographically isolated groups of humpback whales in separate ocean basins (i.e. separate populations) use the same general song structure, but sing songs with different content. Conversely, whales in the same ocean basin sing very similar songs (Winn et al. 1981; Payne & Guinee 1983). Payne & Guinee (1983) compared songs recorded off Maui, Hawaii and the Islas Revillagigedos, Mexico, 4800 km apart, during 1977 and 1979. In 1979, the only year with a sample size adequate for detailed comparison, all of seven themes were common to both areas and quantitative analysis of 14 variables showed few significant differences between regions. From 1977 to 1979, the variables also changed qualitatively in the same ways in both areas. These results suggested cultural transmission between whales in these two distant areas, and Payne & Guinee proposed three hypotheses concerning the mechanism. First, singers may exchange information while in high-latitude feeding areas or during migration. Second, singers may visit different breeding areas in subsequent winters, bringing with them song changes they learned the previous year. Third, singers may visit different winter areas within a single breeding season (i.e. travelling between Mexico and Hawaii).

The objective of this study was to track progressive change in songs from both Hawaii and Mexico during a single breeding season, and thereby assess the mechanism by which humpback whales maintain continuity of song pattern over a large geographical range despite continual change. We propose three alternative hypotheses and sets of predictions based on the information currently available on song and cultural evolution. (1) Based on the first and second hypotheses of Payne & Guinee (1983), if whales in Hawaii and Mexico were isolated from each other during the breeding season, there could be no cultural transmission between areas. In the absence of cultural transmission, continuous independent innovations and changes (cultural evolution) will lead to song divergence within a season. Therefore, even if innovations occur at random, we would predict divergence in at least 50% of song changes (given equal chance for a quantitative variable to change in one direction or the other). (2) Conversely, if whales moved between areas during the breeding season (hypothesis three of Payne & Guinee), there would be the opportunity for cultural transmission among individuals from both areas. We would then predict the same changes to appear in each area. In this scenario, we expect absolute differences between songs from each area at any specific time due to a delay in transmission of changes as individuals travelled between Hawaii and Mexico. However, quantitative variables would change in the same manner in each area (i.e. increasing or decreasing). (3) A third mechanism not considered by Payne & Guinee, is that individual whales may be predisposed to change songs in similar ways in the absence of cultural transmission. Macrogeographical comparisons of populations in different ocean basins indicate that basic song structure follows an innate template, with a repetitive, nested hierarchy of levels. It is feasible that all populations also adhere to a discreet set of rules for temporal change, at least for some aspects of song. Individuals may change specific song elements

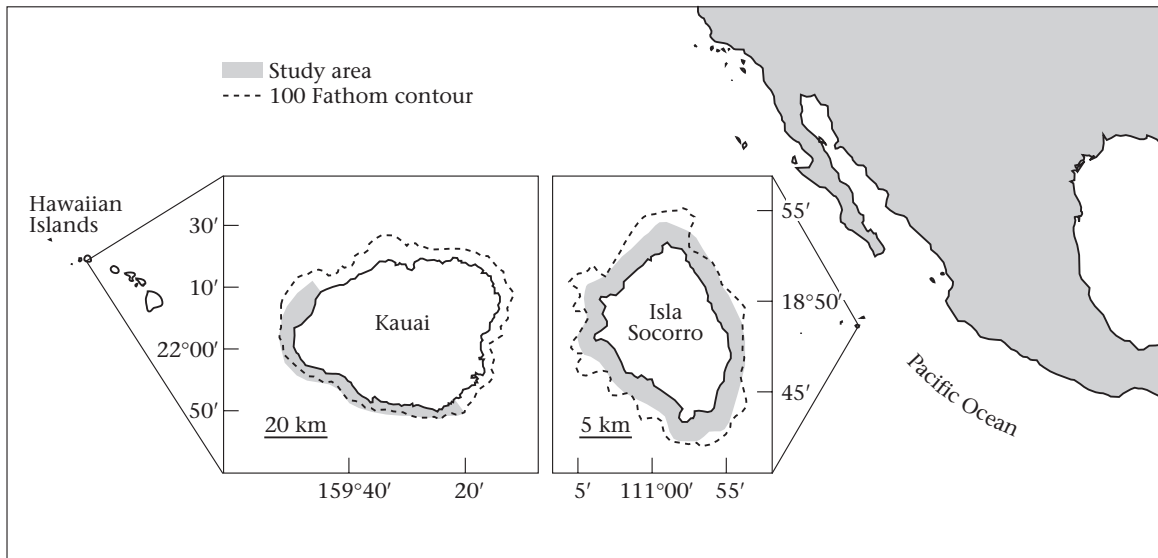


Figure 1. Study region of the North Pacific indicating Kauai and Isla Socorro, and details of each island. Shaded areas indicate study range off each island where most recordings were made. Outer boundary of shading does not necessarily indicate offshore extent of range.

following an innate template, or alternatively, a flexible set of rules governing change may be learned from conspecifics. In this case, we would expect simultaneous change between Mexico and Hawaii, with few quantitative differences between areas, low variability among individuals, and maintenance of similar songs with a minimum of cultural exchange.

METHODS

Study Sites

We recorded humpback whale songs off the island of Kauai ($21^{\circ}55'N$, $159^{\circ}40'W$) in the Hawaiian Islands and Isla Socorro ($18^{\circ}45'N$, $111^{\circ}00'W$) off the coast of Mexico in the Archipiélago Revillagigedo, approximately 4800 km from Kauai (Fig. 1). The study area off Kauai was the south and west coasts out to approximately 12 km offshore, although most recordings were made off the west coast within 3–5 km of shore (Fig. 1). Off Socorro, the study area ranged around the entire island to 10 km offshore, although recordings occurred primarily off the southwest coast within 5 km of shore (Fig. 1).

Song Collection

From 21 January to 19 April 1991, we made focal animal recordings of humpback whales off Kauai (Table 1). Recordings were conducted from an inflatable boat using a modified 41C Sonobuoy hydrophone, a home-built power supply, and a Sony TC-D5M or Marantz PMD430 cassette tape deck. System frequency response was flat ± 3 dB from approximately 50 to 15 000 Hz for the Sony deck, and 50 to 17 000 Hz for the Marantz deck, however response for both systems was as low as 20 Hz. Concurrently, we recorded songs off Socorro using a

similar Sonobuoy hydrophone, power supply and Sony TC-D5M cassette tape deck. A sample was defined as a continuous recording session of a single individual, lasting more than 45 min and having at least three complete songs (with one exception as described in Results).

Humpback whales tended to sing while solitary and singing whales were usually separated by one to several kilometres. All singers also tended to breathe during the same recognizable theme of the song. Therefore, it was relatively easy to identify which whale in an area was being recorded. We typically began recording within 50 m of a singer, and terminated the recording if the singer moved beyond sighting range and/or the signal-to-noise ratio degraded below the point at which the focal singer was easily distinguishable from noise or other singers. Care was taken while positioning the boat for recording so as not to disturb the singer. Typically the whale showed no obvious sign of awareness of the drifting and silent recording boat. In the recording of over 300 whales off Kauai during 5 years, there were perhaps five occasions where the animal clearly became aware of the recording boat by coincidentally swimming close to the boat; on only one of those did the animal stop singing, after which he circled and investigated the boat with apparent curiosity. More typically, after discovering the boat the singer slowly moved ca. 100 m away without interrupting his song sequence.

Individual singers were identified by photographs of the pigmentation patterns on the underside of their flukes (Katona et al. 1979). If a whale was recorded on more than one occasion, only one sample was used in the analysis. Whales recorded but not photographed may have been recorded previously. To account for this, we determined the probability of repeat (nonindependent) samples by calculating the proportion of individually identified (photographed) whales recorded more than once.

Table 1. Samples of humpback whale song recorded off Kauai and Socorro in 1991 and used in analysis

Island	Period	Date	Singer	ID	Sample duration (min)	Complete songs	Incomplete songs or fragments
Kauai	1	29 January	KI-91-04	—	33	2	4
		1 February	KI-91-05	SC-200	121	11	5
		1 February	KI-91-06	—	112	7	9
		6 February	KI-91-07	—	75	5	3
		16 February	KI-91-10	—	83	7	2
Kauai	4	4 April	KI-91-40	—	61	3	2
		4 April	KI-91-42	SC-117	82	6	2
		8 April	KI-91-46	SC-378	90	5	2
		10 April	KI-91-52	SC-381	113	6	2
		11 April	KI-91-53	—	80	6	2
		17 April	KI-91-57	SC-266	77	7	2
Socorro	1	28 January	SO-91-01	JJ-007	46	6	2
		2 February	SO-91-04	—	46	6	2
		3 February	SO-91-05	—	46	8	2
		8 February	SO-91-08	JJ-155	92	14	2
		8 February	SO-91-09	—	91	8	5
		11 February	SO-91-10	—	93	8	2
		16 February	SO-91-12	—	66	7	3
		31 March	SO-91-70	—	59	4	2
Socorro	4	3 April	SO-91-75	JJ-135	70	5	4
		6 April	SO-91-81	JJ-142	80	6	2
		11 April	SO-91-88	JJ-121	54	5	3
		17 April	SO-91-95	JJ-170	86	12	2
		20 April	SO-91-97	JJ-127	85	5	5

Period 1: 27 January–16 February; Period 4: 31 March–20 April. ID: Only those individuals that were photographically identified were assigned an identification number.

Qualitative Song Structure

For preliminary analysis, we arbitrarily chose 11 samples, spanning the entire study period (six samples from Kauai recorded on 1, 16 and 25 February, 22 March, 4 and 17 April; and five samples from Socorro recorded on 2 and 27 February, 24 March, 16 and 20 April). Sound spectrograms of these tapes were made at the Animal Communication Laboratory of the University of California, Davis, U.S.A., using a PAR 4512 spectrum analyser. Analysis band ranged from 0–2000 Hz (sampled at 4000 Hz) to 0–10 000 Hz (sampled at 20 000 Hz), depending on the highest fundamental frequencies of signals analysed and Fast Fourier Transform (FFT) size was 1024 points. We categorized all phrase types, and determined the general sequence of themes from these spectrograms.

Quantitative Measures

For quantitative analysis we chose variables describing all known levels of song structure (unit, phrase, theme and song). Some variables were chosen because qualitatively they appeared to change during the study period in at least one area, thereby allowing an investigation of cultural transmission between areas. For other variables, such as phrase durations, it was impossible to determine whether there was any change through time. We measured 44 variables for each individual (Table 2). We grouped these into six categories: (1) phrases and song durations, (2) peak frequencies of phrases, (3) phrase

repetitions, (4) unit structure, (5) phrase structure and (6) theme and song structure. By grouping variables in this manner, it was possible to test whether similar variables changed through time in similar ways (e.g. durations of seven different phrase types). This also allowed comparison of different groups of variables (e.g. phrase durations versus phrase structure).

We viewed continuous sound spectrograms of recordings on a personal computer equipped with real-time digital signal processing software (Engineering Design, Inc., Belmont, Massachusetts, U.S.A.). Analysis band ranged from 0–1000 Hz (sampled at 2500 Hz) to 0–12 000 Hz (sampled at 30 000 Hz) depending on the highest fundamental frequency of the signals, FFT size was 512 points, and frequency resolution varied accordingly from 5 to 59 Hz. We made measurements of time and frequency domain variables from the 16-colour display. All frequency measurements were made on the fundamental frequency of a unit, and all measurements of the same variable were made with the same analysis parameters.

Statistical Analyses

We examined both regional and temporal variation of song variables in a two-factor design. We divided the study duration into four 3-week sample periods starting from 27 January 1991. We restricted quantitative analysis to the first period, 27 January–16 February, and the fourth period, 31 March–20 April (i.e. the beginning and end of

Table 2. Results of two-factor ANOVAs for all variables comparing differences between periods and islands

Variable	ANOVA <i>P</i> values		
	Period	Island	Interaction
Phrase and song durations			
1 Phrase R	0.24	0.16	0.67
2 Phrase RT	<0.001	0.002	0.39
3 Phrase 1a	<0.001	0.99	0.50
4 Phrase 1b	<0.001	0.39	0.06
5 Phrase 2A	0.02	0.10	0.35
6 Phrase 2B	0.12	0.55	0.50
7 Phrase 3B	0.003	0.02	0.43
8 Song: all songs	0.001	0.01	0.93
9 Song: typical songs	0.06	0.01	0.98
Peak frequencies			
10 Peak frequency 1a/theme	0.001	<0.001	0.90
11 Peak frequency 3B/phrase	0.01	0.07	0.57
Phrase repetitions/song			
12 Phrase R	0.04	<0.001	0.98
13 Phrase 1a/b	0.01	0.17	0.87
14 Phrase 1a	0.003	0.72	0.15
15 Phrase 1b	0.03	0.003	0.06
16 Phrase 2A	0.66	0.46	0.07
17 Phrase 2B	0.26	0.20	0.34
18 Phrase 3B	0.53	0.44	0.10
Unit structure			
19 1a unit 2: unit duration	<0.001	0.01	0.35
20 1a unit 2: average slope	0.005	0.41	0.83
21 1b unit 2: initial frequency	0.01	0.17	0.27
22 1b unit 2: frequency range	<0.001	0.01	0.20
23 1b unit 2: unit duration	<0.001	0.001	0.42
24 1b unit 2: average slope	0.94	<0.001	0.84
25 2A unit 1: initial frequency	<0.001	0.03	0.35
26 2A unit 1: frequency range	<0.001	0.19	0.53
27 2A unit 1: unit duration	0.001	0.89	0.83
28 2A unit 1: average slope	<0.001	0.19	0.64
29 2A unit 2: initial frequency	<0.001	0.10	0.27
30 2A unit 2: frequency range	<0.001	0.50	0.98
31 2A unit 2: unit duration	<0.001	0.20	0.09
32 2A unit 2: average slope	<0.001	0.44	0.37
Phrase structure			
33 Number of units RT	0.12	0.79	0.99
34 Number of units 1a	0.002	0.04	0.002
35 Number of units 1b	0.02	0.42	0.03
36 Number of units 2AS2	0.13	0.13	0.24
37 Number of units 3BS1	0.001	0.54	<0.001
38 Proportion of ascending units 2AS2	0.21	0.84	0.19
39 Proportion of low-frequency units 3BS1	<0.001	0.01	0.11
40 Proportion of discrete units 3BS1	0.05	0.03	<0.001
Theme and song structure			
41 Proportion of songs with theme 2B	0.17	0.003	0.06
42 Proportion of songs with theme 3A	0.001	0.002	0.01
43 Proportion of songs with 2B–1 transition	0.07	0.36	0.89
44 Proportion of 1a phrase types in theme 1	0.002	0.001	<0.001

P values for period, island and interaction terms are indicated. Significant *P* values are indicated in bold after application of sequential Bonferroni adjustment for experimentwide error (Rice 1989; Chandler 1995).

the entire study period). We analysed samples recorded in each period off both islands (Table 1).

For each singer, we calculated means, standard deviations and coefficients of variation for each variable. We used means for each singer as samples in all statistical analyses to eliminate bias towards long samples. We used a model I two-factor analysis of variance (ANOVA) to test for differences between islands, between periods, and for

interaction between the two factors. We first tested data for normality and heterogeneity of variance; if necessary, we transformed and rechecked the data. To control for experimentwide error and inflated alpha values due to multiple tests, we used a sequential Bonferroni adjustment to determine significance at $P=0.05$ (Rice 1989; Chandler 1995). We treated each related group of variables as a separate experiment for application of the

sequential Bonferroni correction. Although the use of means for individuals has the side effect of masking variability within the songs of an individual, we believe the use of individual means was justified given that we were attempting to characterize population and temporal trends.

Interpretation of results fell into three major categories: no change, similar change and different change over time. If an ANOVA yielded no significant difference between periods and no interaction, we concluded that the variable either did not change through time, or contained too much variation within cells (among individuals) to yield a significant result. If there was a significant difference between periods and no interaction, we concluded that the variable changed through time in the same manner in each area (i.e. both increased or both decreased). We further classified the variable as to whether the mean was significantly larger off one island. Finally, if the ANOVA yielded a significant interaction between the two factors, we concluded that the variable changed differently through time in the two areas. We then examined the cell means to determine whether the variable changed in divergent ways (i.e. increasing in one area and decreasing in the other), or if it changed in one area while remaining relatively stable in the other area.

RESULTS

Recording Sessions

We recorded acceptable samples (>45 min) of 36 whales off Kauai and 59 whales off Socorro between 21 January and 20 April 1991. We chose 24 recording sessions for quantitative analysis, 11 from Kauai and 13 from Socorro (Table 1). We included all usable recording sessions in the first period in the analysis, and to increase the Kauai sample size, we included a recording of singer KI-91-04 even though it was 33 min in duration. We chose six sessions from the fourth period (based upon length of recording, recording quality, and whether the whale was identified) so sample sizes among cells in ANOVAs would be relatively equal. We analysed a total of 31 h of recordings and 159 complete songs. We made measurements on 7963 phrases and 4997 units.

The rate of re-recording identified (photographed) singers was 0.10 off Kauai and 0.17 off Socorro. In the quantitative analysis, six samples off Kauai and six off Socorro were from unidentified singers (Table 1), introducing the potential of nonindependent samples in the preceding probabilities. Having two samples from the same individual would violate the assumption of independence and bias results toward the re-recorded individual. The actual probability of re-recording an individual is probably less than that calculated for identified singers due to individual differences in behaviour. Singers recorded more than once may have a greater probability of being resighted and re-recorded because they may have a tendency to remain in the study area longer, or may sing for longer periods, allowing more opportunities for

recording. Therefore, we do not consider this to be a significant bias.

Qualitative Song Structure

We identified six different themes qualitatively, all of which occurred in both areas, and we labelled these to reflect historical continuity (Fig. 2). We examined sound spectrograms of songs recorded off Kauai in 1989 and 1990 (S. Cerchio, unpublished data) to determine how single themes differentiated into two or more separate themes by 1991. The label of each theme in 1991 reflects its origins and sequence in the song. Thus, themes 2A and 2B were derived from the same theme of 1989, as well as themes 3A and 3B. We labelled theme R to reflect its ratchet-like aural quality. Because whales usually surfaced to breathe during this theme, we arbitrarily chose this theme as the starting point in the song.

Theme structure varied among the different themes. Themes 2A, 2B, 3A and 3B were 'static themes' (Payne & Payne 1985); phrase structure remained consistent with each consecutive repetition in a song. Theme R and theme 1 were 'shifting themes' (Payne & Payne 1985); phrase structure changed slightly with each consecutive repetition of the phrase, so that the phrase type changed progressively from the beginning to the end of the theme. Theme R began with pulse trains of broadband clicks; with consecutive repetitions of the phrase, the pulse trains became longer and the pulse rate increased so that the unit resolved into multiple frequency bands in a 512 point FFT spectrogram (Fig. 2). The unit also split into multiple units; we labelled these phrases in the latter part of the theme phrase type RT for ratchet transition. We subdivided theme 1 into phrase types 1a and 1b (lower case letters were used to distinguish this division from that used for separate themes). With each repetition of phrase type 1, the component units progressively dropped in peak frequency and frequency range. If the frequency range of the second unit exceeded 500 Hz, we labelled the phrase 1a; once the second unit flattened out with a frequency range at or less than 500 Hz, the phrase was labelled 1b (Fig. 2). At the beginning of the sample period this division was less pronounced and there were often sequences where a whale would alternate between phrase types 1a and 1b. By the end of the sample period the division became quite distinct and rarely did a whale repeat a 1a phrase once it began singing 1b phrases, suggesting that this theme was in the process of differentiating in 1991. Examination of spectrograms of songs recorded off Kauai in 1992 (S. Cerchio & T. F. Norris, unpublished data) confirmed that this theme was differentiating into two separate themes.

A complete song was defined as in Frumhoff (1983): a sequence of 'at least three themes which are repeated in the same order two or more times during a recorded song session'. The following was a typical theme sequence constituting a complete song with all themes present: R-1-2A-2B-3A-3B-R. Themes 2B and 3A were often excluded resulting in the following song sequences: R-1-2A-2B-3B-R or R-1-2A-3B-R. These sequences were all considered 'typical' songs. There was one common theme

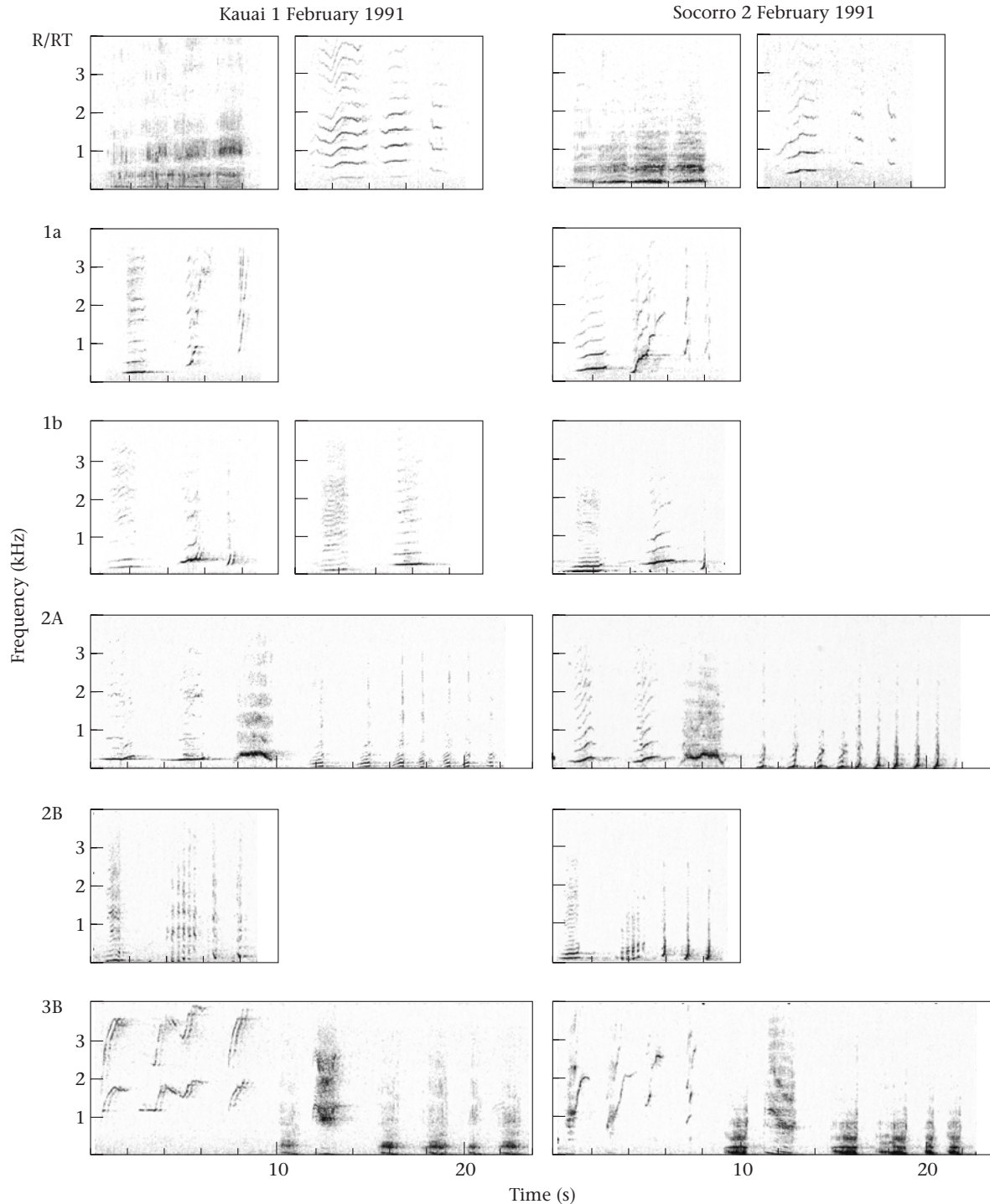


Figure 2. Sound spectrograms (8 kHz sampling rate, 512 point FFT, 50% overlap) of exemplary phrase types R, RT, 1a, 1b, 2A, 2B and 3B recorded from singer KI-91-05 off Kauai on 1 February 1991, and singer SO-91-04 off Socorro on 2 February 1991. Both regions shared all phrase types, including one not shown, 3A, which was relatively rare in both samples. Theme R and 1 were shifting themes, in which the phrase structure progressively changed with each repetition of the phrase (from R to RT, and from 1a to 1b). Themes 2A, 2B and 3B were static themes in which the phrase structure remained relatively stable with each repetition. Noticeable differences between the exemplary phrases for each region were typically no greater than qualitative differences between individuals within regions.

reversal, or aberrant transition as defined by [Frumhoff \(1983\)](#), in which a whale followed theme 2B with theme 1, skipping the sequence 3A–3B–R. This resulted in two ‘atypical’ songs as follows: R–1–2A–2B and 1–2A–2B–

(3A)–3B–R (note: 3A was often absent). Occurrences of the 2B–1 transition were included in quantitative analysis (see below). Other aberrant theme transitions occurred, but were uncommon, appearing in the session of only

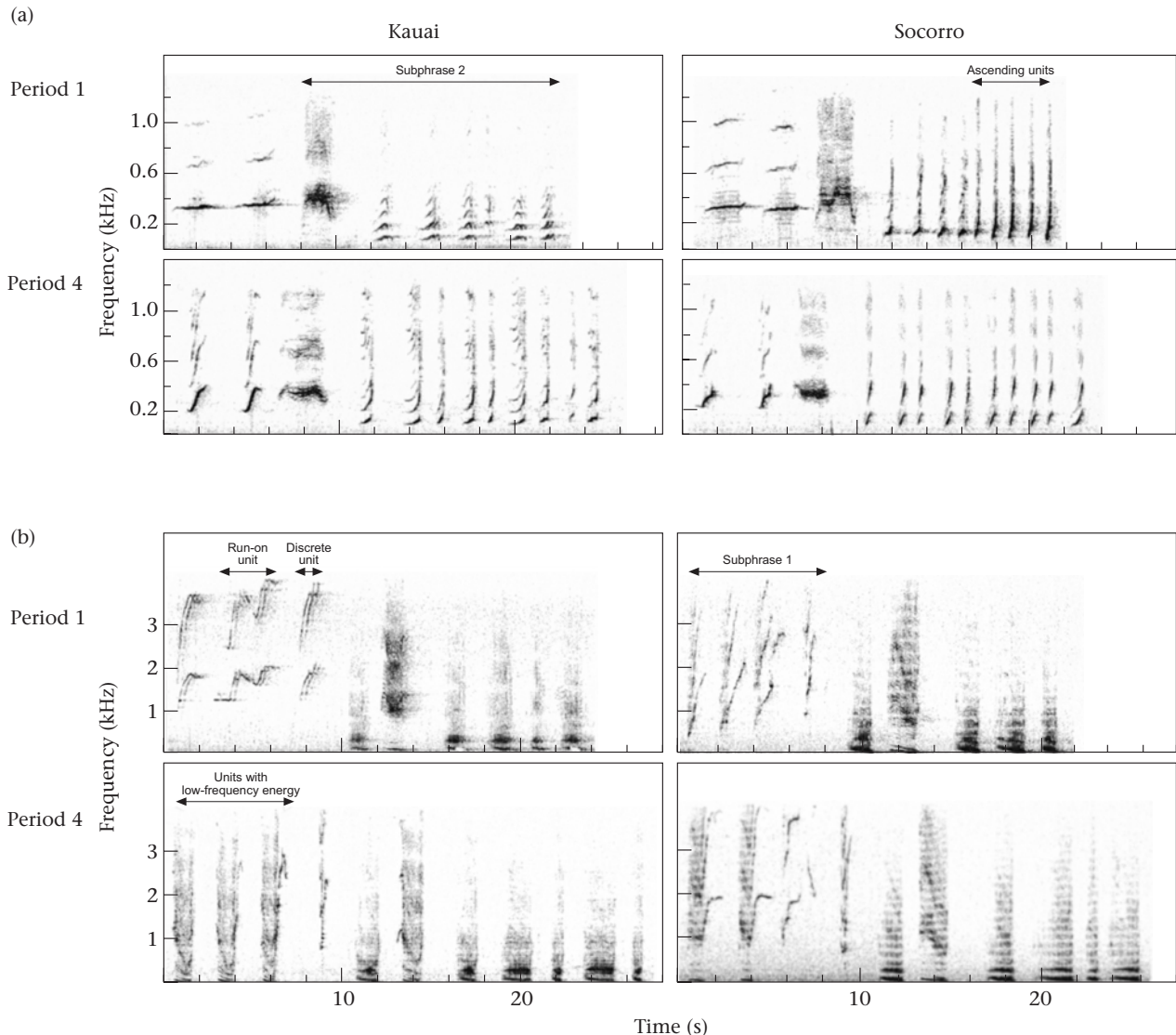


Figure 3. Songs changed over the 12-week study in both regions. Exemplary phrases for two phrase types were chosen from different individuals recorded in Period 1 and Period 4 to illustrate the changes in each region (specific phrases were chosen to best reflect mean values of variables measured for each region and period). (a) Phrase type 2A (2.8 kHz sample rate, 512 point FFT, 75% overlap) illustrating the following changes: an increase in duration in both regions, a dramatic change in the first two units in both regions, an increase in the number of units in subphrase 2 that occurred only in Kauai, and a decrease in the proportion of ascending units that occurred only in Socorro. (b) Phrase type 3B (8 kHz sample rate, 512 point FFT, 50% overlap) illustrating the following changes: an increase in duration in both regions, increase of units in subphrase 1 from three to four that occurred in Kauai, an increase in the proportion of units with broadband low-frequency energy in subphrase 1 that occurred in both regions, and an increase in the proportion of 'discrete' units that occurred in Kauai, while decreased in Socorro (not readily apparent from examples).

one or two singers. These transitions were not considered in quantitative analysis due to their low frequency of occurrence.

Quantitative Analysis

Most phrase types underwent noticeable change during the study period in both areas (Fig. 3, Tables 2 and 3). Means of variables changed in one of four ways between periods and areas. (1) Variable means increased or decreased the same amount in each area, yielding a significant difference between periods, no difference

between areas, and no interaction (Fig. 4a, Table 2, variable 3). (2) Variable means increased or decreased in like directions in both areas, however, area means differed, yielding a significant difference between periods and areas, but no interaction (Fig. 4b, Table 2, variable 10). (3) Variable means increased or decreased in only one area, yielding a significant interaction (Fig. 4c, Table 2, variable 34). (4) Variable means increased in one area and decreased in the other, again yielding a significant interaction (Fig. 4d, Table 2, variable 40). A variable was scored as undergoing 'similar change' if the first or second pattern was observed (Fig. 4a, b), or 'different change' if the

Table 3. Interpretive summary of statistically significant results: change over time and differences between areas

Temporal trend:	Similar change		Different change		
	Island means similar	Island means different	Change was opposite	Change in KI only	Change in SO only
Island trend:					
Variable category					
Phrase and song durations	4	1			
Peak frequencies/phrase	1	1			
Phrase repetitions/song	1				
Unit structure	12	1			
Phrase structure	1		1	2	
Theme and song structure				1	1

Results were grouped into two major categories of temporal trend, 'similar change' or 'different change' between the regions. If a variable changed in the same manner, increasing or decreasing in each area, it was scored as undergoing 'similar change'; variables were then further classified by 'island trend' as to whether the 'island means were similar' (see Fig. 4a) or 'different' (see Fig. 4b) during each period. If a variable changed divergently between areas ('change was opposite', see Fig. 4d), or changed in only one area ('change in KI only' or 'change in SO only', see Fig. 4c), and resulted in a significant interaction term, it was scored as a 'different change'. Tabulated values represent the number of variables within each category that displayed the specified trend and were statistically significant. KI=Kauai, SO=Socorro.

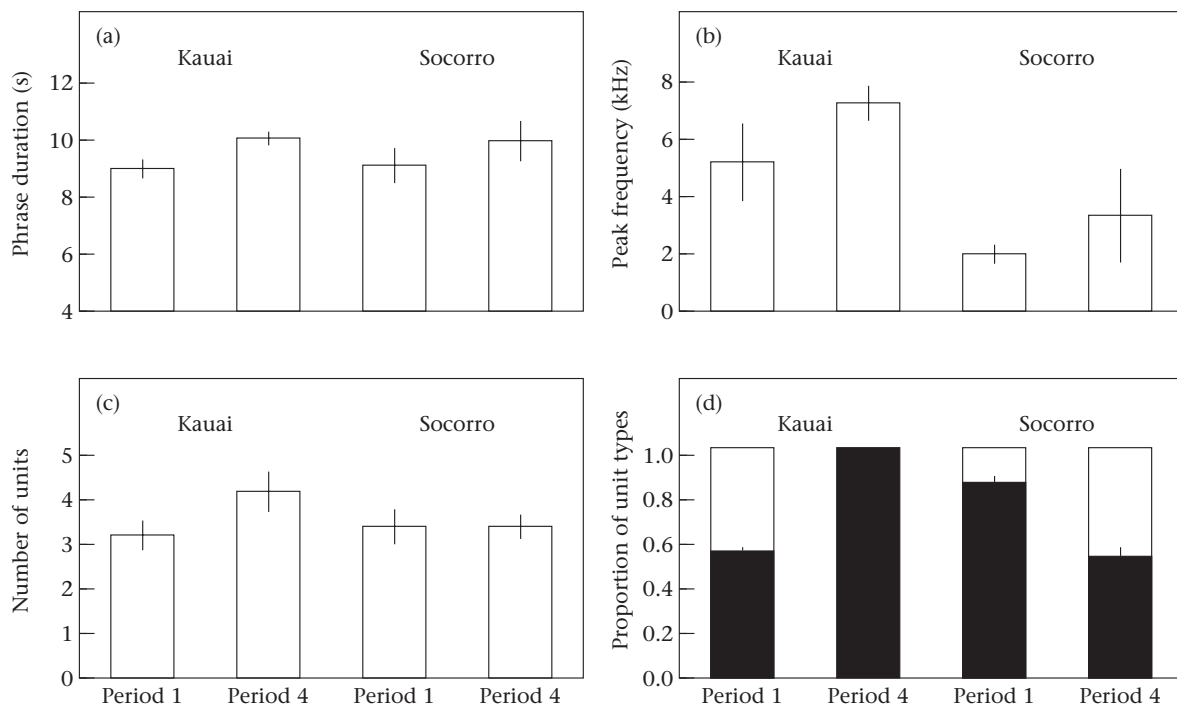


Figure 4. Examples illustrating four trends of change in quantitative variables. Variable means either (a) changed similarly in each area, with no difference between islands (illustrated by phrase duration of phrase 1a, variable 3, which increased equivalent amounts in each area), (b) changed similarly in each area, with a significant difference between island means (illustrated by the peak frequency per theme for theme 1a, variable 10, which started with different values in each area and increased proportionally in both), (c) changed differently, changing off one island but not the other (illustrated by the number of units in phrase 1a, variable 34, which increased in Kauai, but remained stable in Socorro), or (d) changed differently, increasing off one island and decreasing off the other (illustrated by the proportion of phrases 3BS1 with discrete, ■, versus run-on, □, units, which increased in Kauai, whereas decreased in Socorro, variable 40). Means for each individual were used as samples, and sample size was as indicated in Table 1. Error bars represent one standard deviation.

third or fourth pattern was observed (Fig. 4c, d). Twenty-seven variables yielded significant period or interaction terms, indicating change over time, and four additional variables yielded marginal significance (Table 2).

We measured the six categories of variables examined as follows (see Table 2 and Appendix, Table A1).

(1) We measured phrase durations (variables 1–7) from the start of one phrase to the start of the next, for all

phrase types described (except 3A due to its rarity); we examined song duration for all songs combined (variable 8) as well as for typical songs only (variable 9).

(2) Peak frequencies (variables 10–11) represented the highest frequency of a unit per theme for theme 1a, and per phrase for theme 3B.

(3) Phrase repetitions (variables 12–18) were the counts of a given phrase type per song.

(4) Unit structure was described by frequency and duration measurements made on two units from a shifting theme (theme 1; variables 19–24) and two units from a static theme (theme 2A; variables 25–32). Unit 2 of phrase type 1a was a highly variable unit that changed in frequency as the theme progressed; therefore, we excluded frequency range from analyses. We also excluded initial frequency due to possible measurement bias resulting from the large frequency band required to view the unit and thus poor frequency resolution.

(5) We evaluated phrase structure (variables 33–40) by the number and types of units that composed a phrase. We measured number of units in phrase types RT, 1a and 1b, as well as for subphrase 2 of 2A (abbreviated 2AS2) and subphrase 1 of 3B (abbreviated 3BS1). We measured relative proportions of different types of units in a phrase for 2AS2 and 3BS1. In 2AS2, we measured the proportion of rapidly ‘ascending’ units (strongly frequency modulated with characteristic ‘whoop’ sound; Fig. 3). We categorized units in 3BS1 by whether they contained broadband low-frequency energy (< approximately 500 Hz) before sweeping up (Fig. 3). We also classified the entire subphrase of 3BS1 by the presence of ‘discrete’ versus ‘run-on’ units (Fig. 3), so that phrases containing one or more units where frequency swept up, down and then up again were classified as ‘run-on’.

(6) We evaluated theme and song structure (variables 41–44) by the frequency of occurrence of specific themes (2B and 3A), an aberrant theme transition (2B–1), and specific phrase types (1a versus 1b).

Within categories, variables tended to display the same patterns of change, although all categories did not follow either similar or different change (ANOVA results, Table 2; interpretive summary, Table 3; variable statistics, Appendix, Table A1). Variables of phrase and song duration (5 of 9), peak frequencies (2 of 2), and unit structure (13 of 14) changed similarly in each area, yielding a statistically significant change between periods with no interaction (Table 2). Furthermore, most of these variables changed to the same degree in both regions with few significant differences between the regional means (Table 3). In addition, the means of three variables of phrase/song duration (5, 6 and 9) revealed the same trend of similar change, although nonsignificant for period due to variation within cells (marginally significant at $\alpha=0.10$ for variables 5 and 9). Conversely, variables of phrase structure (3 of 8) and theme and song structure (2 of 4) changed differently with highly significant interaction terms (Table 2); most changed off one island only, whereas one (variable 40) changed divergently (Table 3). In addition, one variable of phrase structure (35) and one of theme structure (41) had a marginally significant

interaction term. Phrase repetition was the only variable group that did not follow one predominant pattern of change and yielded only one significant period result, probably due to high variation among individuals.

DISCUSSION

It has been reported previously that the songs of humpback whales are similar in Hawaii and Mexico and that they change in similar ways across seasons (Winn et al. 1981; Payne & Guinee 1983). We have established that these songs also change in similar ways during a single season, at least for some sets of variables. Existing literature considers only cultural transmission and cultural evolution when discussing populationwide continuity and temporal change in song. Given this mechanism, if whales off Kauai and Socorro were isolated during the breeding season, and cultural evolution occurred throughout the season, we would expect substantial divergent change of song variables between areas. Conversely, if there were cultural transmission between areas, we might expect all or most variables to change similarly in the two areas with one region lagging behind the other. Our results are not consistent with such simple explanations; some variables changed similarly, whereas others changed differently. We now assess the three alternative hypotheses proposed in the Introduction, discussing each hypothesis separately.

Cultural Transmission between Seasons, Cultural Isolation during Seasons

Traditions diverge when undergoing cultural evolution in geographically isolated areas (Mundinger 1980; Lynch 1996). Thus, one of our most significant observations was the large number of acoustic feature variables that changed in the same manner in both regions (22 of 44, Table 3). Furthermore, only five variables displayed a significant interaction term (Table 2), and only one variable (variable 40) changed in divergent directions (Table 3). At face value these results argue strongly against cultural isolation during the season. The high degree of continuity in song changes ‘during’ a single season indicates that maintenance of song similarity across the eastern North Pacific cannot be explained solely by the movement of individuals ‘between’ seasons and the associated staccato cultural transmission. Either cultural transmission during a season, or a mechanism that does not involve cultural transmission, must be at work.

Cultural Transmission of Song Changes during a Season

Within-season movement of individuals

Payne & Guinee (1983) first suggested that male humpback whales may move between Hawaii and Mexico during a breeding season. In this scenario, new traditions (changes in various elements of the song) would be

generated in each area and transmitted to the other area via meme flow (the transfer of a tradition between populations) and cultural diffusion (the spread of a tradition through the recipient population) during the breeding season (Mundinger 1980; Lynch 1996). Our data potentially support this hypothesis, because at least three groups of variables changed similarly in each area during the season.

However, there are at least four problems apparent with this hypothesis. First, there is little existing evidence of movements of individuals from Hawaii to Mexico within a breeding season. Early photographic mark-recapture comparisons found little tendency for exchange (Baker et al. 1986; North Pacific Humpback Whale Working Group et al., unpublished data), although these may be biased due to small samples from Mexico. More recently, in a 3-year comparison of 1144 individuals from Hawaii and 530 from Mexico, Calambokidis et al. (1998, in press) found no within-season transits, and across-season exchange between the breeding areas was an order of magnitude less than within either area. Calambokidis et al. concluded that Hawaii and Mexico represent distinct subpopulations with only limited exchange of individuals.

Second, in our analysis not all variables changed similarly in each area. At least three variables associated with phrase structure and two variables of theme and song structure changed differently (Table 3). If small changes in phrase duration were thoroughly integrated into the recipient population through meme flow and cultural diffusion, then changes in phrase structure of the same phrases should be integrated as well. This was not the case, as illustrated by phrases 1a and 3B (Table 2 and Appendix, Table A1, variables 3, 19, 20 and 34, and variables 7, 37 and 40, respectively).

Third, considering the size of the North Pacific population, 3000–4000 for the Hawaiian Islands (Cerchio 1998; Calambokidis et al. 1998) and 1500 to over 2000 for Mexico (Urban et al. 1994, 1999; Calambokidis et al. 1998) and distances between breeding areas, cultural transmission would probably result in greater variation among individuals and areas than that shown by many of the variables we examined. Thousands of males, spread over distances of 100–500 km within breeding areas and up to 5000 km between breeding areas, are simultaneously transmitting and receiving song information. It seems unlikely that all individuals in different breeding areas could synchronously change their songs and maintain low interindividual variability via cultural transmission alone. Yet, variation among individuals and between areas was low for many variables, particularly variables of phrase duration and unit structure (detailed data on within- and between-individual variation are presented in Cerchio 1993).

Finally, if meme flow and cultural diffusion were responsible for transmission of song changes between Hawaii and Mexico, we would expect a change to occur later in one area than in the other area. Assuming an average travelling speed of 5 km/h (Bauer 1986; Gabriele et al. 1996), a whale would travel the 4800 km between Kauai and Socorro in approximately 40 days. During

transit, song changes would continue to progress at the whale's origin. After arriving at its destination, there would be an additional delay before information from the individual's origin was transmitted and fully integrated into the recipient population. Therefore, we would expect similar change in each area with significant differences due to time lags between islands. However, this was not evident in our data; most variables that changed similarly did not differ significantly between areas (Table 3). It is therefore difficult to attribute these similarities between Kauai and Socorro to within-season movements and cultural transmission.

Open-ocean singing

An alternative mechanism for within-season cultural transmission does not require individuals to move between the breeding areas: it has been suggested that males may sing in the open ocean between Mexico and Hawaii and transmit changes via long-distance sound propagation. Low-frequency signals (below 100 Hz) in humpback song may travel great distances (i.e. many hundreds of kilometres), similar to those of blue, *Balaenoptera musculus*, and fin whales, *B. physalus* (Cummings & Thompson 1971; Payne & Webb 1971; Clark & Fristrup 1997; Clark & Ellison, in press); however, much of humpback song energy occurs at higher frequencies (e.g. 500–10 000 Hz), which do not propagate as well due to absorption and scattering attenuation. Therefore we expect high-frequency detail in song to be lost over relatively short distances (i.e. tens of kilometres) as demonstrated by Clark & Ellison (in press). The units we documented changing synchronously off Kauai and Socorro had upper frequencies above 500 Hz, which are too high for long-distance propagation. In three studies using deep-water, bottom-mounted hydrophone arrays, detections of humpback whale song were limited to signals below 300 Hz and maximum distances ranging from 80 km to 'a few hundred kilometers' (Clark 1995; Abileah et al. 1996; Watkins et al. 2000). Furthermore, humpbacks are near-surface vocalizers, and thus, probably very little sound energy makes it into the deep sound channel (Watkins et al. 2000); W. A. Watkins (personal communication) estimates that most energy in song is lost after 30–50 km, with maximum detections limited to 100–300 km, even under ideal conditions.

Although it is unlikely that song could propagate thousands or even hundreds of kilometres, a string of singers, spread out in the open ocean in relatively close proximity, may transmit changes from one to another in a chain (C. W. Clark, personal communication). This is plausible, particularly in regions such as the Caribbean or among the Hawaiian Islands, where islands are relatively close together, whales may regularly transit between them, and whales singing at island shelf breaks can gain access to the deep sound channel (Clark & Ellison, in press). However, this mode of communication seems less likely between Hawaii and Mexico given the current evidence. Humpback whales have been documented singing during migration in the North Atlantic (Clapham & Mattila

1990), and three studies have indicated the presence of deep-water singers in the eastern North Pacific, using towed hydrophone arrays during oceanic surveys (Norris et al. 1999, 2000) and bottom-mounted hydrophone arrays (Ableah et al. 1996; Watkins et al. 2000, personal communication). All three studies reported open-ocean singers in roughly the same regions, either north of Hawaii (up to 40°N) and/or west of California (close to 130°W), strings of detections on longitudinal lines, and movements of singers in north–south directions. It was proposed that these represent whales singing along migratory routes to/from Hawaii and Alaska, and the Islas Revillagigedo and Alaska (Norris et al. 1999). None of these studies indicated detections on latitudinal lines between Mexico and Hawaii, nor were east–west movements detected, despite considerable east–west coverage in all three studies. This lack of detections is congruent with the absence of documented transits in mark–recapture studies. Since the acoustic studies were not designed to search specifically for singers in this region, and therefore were less than ideal for detecting such singers, the possibility remains and warrants further investigation. If in the future, more directed research indicates an abundance of singers in the latitudinal expanse between Mexico and Hawaii, then this hypothesis will gain further support. Regardless, we find it difficult to conceive of an adaptive explanation for singing in this open-ocean expanse, unless males (and oestrous females) were en route between breeding areas; however, mark–recapture evidence argues against extensive exchange. It is also possible that migratory routes for the respective areas cross in higher latitudes (Norris et al. 1999), allowing another opportunity for cultural exchange without within-season movement. All of these possibilities for within-season cultural transmission predict time lags in the appearance and progression of a change between distant areas, and therefore are not congruent with the synchronicity of change we have documented.

Predisposition for Progressive Temporal Change

As an alternative hypothesis to explain continuity of songs between Hawaii and Mexico, some features of humpback whale song may undergo change according to predetermined patterns in the absence of cultural influences. Variables such as phrase duration and unit structure (all time and frequency measurements) effectively describe the structural elements, or building blocks of song. These structural elements may change according to an innate template, or a set of rules that is learned (e.g. as a juvenile). Overlaying this process, the arrangement of these elements, or the actual patterns of song (as described by frequency of occurrence and number of elements: phrase structure and song structure variables) may be culturally transmitted among individuals, and changes would be the result of cultural evolution. The similarities between songs in Hawaii and Mexico, therefore, would be due to a combination of mechanisms, only partially involving cultural transmission.

This hypothesis is supported by the low level of variation in mean phrase durations among areas, among individuals, and within individuals. As a general rule, we propose individuals may increase duration of phrases at a fixed rate, independent of information they receive from other whales. This should be testable by comparing the mean phrase durations of known whales recorded more than once, with the prediction that similar rates of change would be observed for different individuals as well as different phrase types. Payne et al. (1983) found mean phrase duration of most phrase types increased during two consecutive seasons, and Frumhoff (1983) reported phrase duration among individuals was the least variable of five measures of song structure. To date there have been no analyses indicating a phrase to shorten in duration through time. These findings are consistent with the proposed hypothesis.

This hypothesis also could explain the similar change between areas and low variation in unit structure measurements, particularly of the static theme 2A. It is difficult, however, to propose a general rule that would govern change in all units. Unlike phrase durations, different units changed in different ways (e.g. units in 1a and 1b increased in duration, whereas units in 2A decreased in duration). Perhaps change in a specific unit (e.g. an increase in frequency range) is initiated culturally, via innovation. Individual whales then continue to progressively change the unit (continue to increase the frequency range) at a predetermined rate. This also is testable with multiple samples from known individuals.

It is not implied here that innate (or previously learned) mechanisms exclusively govern change, nor that geographical continuity is maintained predominantly thus so. Rather, we suggest that a set of rules for change may facilitate the maintenance of similarity despite limited cultural exchange and continual temporal variation. Cultural transmission remains necessary for whales from Mexico, Hawaii and Japan to maintain continuity over decades, and the predominant route between breeding regions may be between-season exchange. Limited evidence suggests that humpback whale populations from Japan and Hawaii share fewer similarities in song structure than those between Hawaii and Mexico (Helweg et al. 1990; this study). If whales from two regions only share a portion of their respective phrase repertoire in some years (indicating isolation during those years), then our hypothesis will make the following prediction: shared phrases will evolve in similar manners despite lack of cultural exchange, and region-specific phrases will eventually be introduced into the other region across years. This may be testable by tracking changes over several years in Japan and Hawaii.

To our knowledge there are no examples of animal populations that are ‘programmed’ to continuously change a tradition. In all examples cited, it is accepted that change of a tradition through time results from cultural mutation (mistakes or innovations) and imitation, the characteristic processes of cultural evolution (Jenkins 1977; Payne 1979; Ince et al. 1980; Mundinger 1980; Slater et al. 1980; Payne et al. 1981; Feeles 1982;

Payne 1985; Lynch et al. 1989; Trainer 1989; Lynch 1996). If certain elements of humpback whale song follow a predetermined pattern of change, it could be a unique phenomenon. This idea is somewhat speculative, and the hypothesis requires further testing. Our sample of individuals is relatively small and represents the events of only one breeding season. These results need to be replicated in other years with larger samples to determine general 'rules of change'.

Adaptive Significance of Song and Rapid Change in the Breeding System

We must also consider what role vocal learning and cultural transmission play in a species' mating system and what drives rapid cultural evolution. There are two examples of songbirds in which rapid temporal change has been attributed to the traditional processes of cultural transmission and evolution, the yellow-rumped cacique (Feeke 1977, 1982; Trainer 1989) and the village indigobird (Payne 1979, 1985; Payne & Payne 1998). These studies provide insight into the evolution of this behaviour in these systems. As with humpback whales, songs of individual indigobirds and caciques are similar within a social group and progressively change in a synchronous manner (Payne 1985; Trainer 1989). Payne (1985) and Payne & Payne (1998) reported that male village indigobirds with the most matings initiated changes in songs and were imitated most. Trainer (1989) did not directly observe this in caciques, but proposed a process based on preferential adoption of songs of successful males by less successful males, who attempt to confer the same selective advantage upon themselves. After being copied widely by other males in the social group, a dominant male responds by making new improvisations, which in turn are imitated and spread throughout the breeding group; thus there is continual incentive to improvise, and the repeating cycle results in nonrandom, directional change. This model of rapid change due to cultural transmission works within the behavioural context of caciques and indigobirds. In both species, social organization is characterized by local neighbourhoods with distinct dialects, and neighbourhoods are composed of a relatively small number of closely associated individuals (Feeke 1982; Payne 1985; Trainer 1989). In each species, males that switch neighbourhoods usually learn the new dialect, rather than introducing songs from their previous neighbourhoods (Payne 1985; Trainer 1989).

Song behaviour in humpback whales resembles that of caciques and village indigobirds in many respects: all males in a region share the same song patterns, songs gradually change throughout the season, males continue to learn songs as adults, incorporating changes into their own songs, and these changes accumulate through time (Payne 1979, 1985; Guinee et al. 1983; Payne et al. 1983; Payne & Payne 1985). Humpback whales also share many of the reproductive behaviours noted for caciques and village indigobirds: the mating system is presumed to be polygynous (Darling 1983), males are not territorial (Tyack 1981), there is a high level of male–male competition (Tyack & Whitehead 1983; Baker & Herman 1984),

and there is a high degree of dispersal of males throughout the breeding areas (Darling & McSweeney 1985; Darling & Cerchio 1993; Cerchio et al. 1998).

Although these characteristics fit well the behavioural trends proposed by Trainer (1989), it is intuitively difficult to apply her model to humpback whales due to several distinct differences. Songs of humpback whales differ from cacique and village indigobird song in that humpbacks appear to have no distinct local dialects. Different dialects in cacique and indigobird populations consist of distinct sets of songs with different patterns of notes (Payne 1985; Trainer 1989). In both species, neighbouring dialects may share some songs, whereas more distant dialects several kilometres apart share few, if any. Conversely, in humpback song there is relatively little variation over an extensive geographical area. Helweg et al. (1990) reported possible evidence for song dialects among humpback whales from Japan, Hawaii and Mexico: songs in 1989 from Hawaii and Mexico shared only five phrase types, and did not share three phrase types. However, Payne & Guinee (1983) found songs shared all phrase types in 1979, and we have shown that songs from Hawaii and Mexico shared all phrase types in 1991. Furthermore, qualitative analysis of long song sessions in 1989 (the same year as Helweg et al.) from Kauai ($N=6$) and Socorro ($N=5$), indicated that the two regions shared all of seven phrase types (S. Cerchio & J. K. Jacobsen, unpublished data). Therefore, it is likely that the results of Helweg et al. were artefacts of their small sample size ($N=3$ samples per region) and use of incomplete songs (recording sessions of 5–30 min). Thus we have established that songs from Hawaii and Mexico do not represent dialects, in the sense that all song patterns (phrase types) are shared and change similarly for many variables.

Humpback whale songs also differ from cacique and indigobird songs in the number of individuals that share the same songs. Both bird species breed in relatively small colonies or neighbourhoods, providing the opportunity for close association among individuals; therefore, copying the song of a successful male could have an immediate and significant impact on reproductive success of subordinate males. Conversely, it is apparent that thousands of whales spread across the North Pacific share the same songs. Therefore, it is difficult to conceive of how a dominant male's song in Hawaii would have any relevance to males in Mexico. If copying dominant males were the sole driving force for cultural evolution, then one would expect highly divergent change in these distant areas and the rapid development of regional dialects. We conclude that some mechanism other than that proposed by Trainer (1989) is driving rapid temporal change in humpback whales.

Although specific dialects in bird song may have no biologically adaptive significance, the 'ability' to sing the appropriate dialect may confer a selective advantage (Munding 1982). That male caciques and village indigobirds learn new dialects when they change song neighbourhoods supports this (Payne 1985; Trainer 1989). Similarly, singing the current version of the song may have an immediate social significance for male humpback

whales. Accordingly, K. Payne (personal communication) hypothesized that a selective advantage may lie with those males that can demonstrate conformity to the current version of the song as well as display innovation. If this hypothesis is correct, males would avoid singing both 'old' songs, and songs too different from conspecifics in the region. Therefore, we speculate that a female preference for 'constrained' novelty may have evolved and become linked with a male trait for continual change, and rapid progressive change could therefore be the result of Fisherian self-reinforcing selection. A runaway model of selection is also congruent with the high complexity of humpback song and broad variety of humpback vocalizations (in terms of frequency range and acoustic structure), traits that are highly derived in humpbacks and phylogenetically unique among Mysticeti. If it is adaptive to sing the current but ever-changing version of the song, and individuals move between distant breeding areas during a lifetime, it is reasonable that a mechanism would evolve to facilitate the ability of a male to sing the appropriate song. In such a scenario, a set of rules might exist that govern the temporal evolution of basic structural elements of song (e.g. phrase duration). Thus, individuals in Hawaii and Mexico could maintain similar songs with a limited amount of cultural transmission. Song exchange during the season would not be necessary to maintain continuity across the ocean basin; yearly exchange due to between-season movements would suffice.

Several predictions can be made from this hypothesis.

- (1) The same patterns of change between songs from Mexico and Hawaii should be evident in different years.
- (2) Humpback whale songs from Japan should also follow the same patterns within a breeding season, changing in phrase duration similarly with Hawaii and Mexico, but differently in phrase structure.
- (3) Known individuals may change phrase duration and other variables at a fixed rate.
- (4) Geographically isolated populations with different songs should also follow similar patterns of change.

Studies of macrogeographical variation (i.e. songs from different ocean basins) will reveal species-specific traits, such as innate structural rules or a predisposition to a specific pattern of change; studies of microgeographical variation (i.e. songs within an ocean basin) will reveal patterns of cultural transmission. Future studies should include detailed comparisons, such as presented here, of songs from different breeding areas within an ocean basin, and from different ocean basins, spanning several consecutive years. An effort should also be made to view results in the context of cultural evolution of behavioural traditions that have been studied more extensively (e.g. avian song).

On the Absence of Dialects and Implications for Population Structure

There exists some debate regarding the relationship of population genetic structure and geographical distribution of bird song dialects (Payne & Westneat 1988; Payne & Payne 1998); however, individuals with the same dialect are generally considered to be

inter-breeding, if not panmictic. That there appear to be no dialects in North Pacific humpback whale song suggests that whales wintering in Mexico, Hawaii and probably Japan compose a single population (first proposed by Payne & Guinee 1983). However, Calambokidis et al. (1998, *in press*) found limited exchange of photographically identified whales from Japan, Hawaii and Mexico. Also, Baker et al. (1998) found significant differences in mtDNA and nDNA markers among Hawaiian, Mexican and Japanese whales. These studies indicate that, although some genetic exchange exists among these breeding aggregations, they are not panmictic, and there is strong evidence for at least subpopulation division. Baker et al. (1998) also indicated male-biased gene flow as one potential explanation for the more prominent mtDNA stratification as compared to nuclear differentiation. Since song is a male-mediated measure of cultural exchange, the greater similarity of nuclear gene markers and continuity of song across the North Pacific basin are partially congruent. It is still difficult to reconcile the high degree of song similarity and synchrony of change with the apparent low degree of movement and gene flow between these breeding assemblages. The mechanism described herein, that of predisposition to temporal change of songs, can help to explain this discrepancy. The picture that is emerging in the North Pacific is one of a single large metapopulation, with at least three genetically distinct subpopulations; at least two, and probably all three subpopulations share a single vocal tradition that is maintained despite rapid temporal change and an apparent minimum of cultural exchange.

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Appendix

Table A1. Means and standard deviations for all variables in each area and period. Proportions were arcsine transformed

Variable	Kauai		Socorro	
	Period 1	Period 4	Period 1	Period 4
Phrase and song durations				
1 Phrase R (s)	10.93±1.14	11.74±0.52	10.45±1.49	10.82±1.21
2 Phrase RT (s)	11.05±0.93	13.05±0.69	10.29±0.53	11.76±0.59
3 Phrase 1a (s)	9.02±0.23	10.08±0.15	9.14±0.51	9.97±0.61
4 Phrase 1b (s)	8.76±0.35	9.99±0.15	8.96±0.25	9.52±0.67
5 Phrase 2A (s)	21.63±0.88	23.80±0.93	21.13±1.81	22.07±1.97
6 Phrase 2B (s)	8.86±0.51	9.12±0.59	8.84±0.62	9.46±0.71
7 Phrase 3B (s)	23.99±1.24	26.83±0.57	22.71±2.61	24.52±1.15
8 Song: all songs (min)	9.57±0.92	13.27±3.12	7.18±1.68	10.71±2.23
9 Song: typical songs (min)	11.97±2.31	13.95±2.43	8.92±2.49	10.83±2.06
Peak frequencies				
10 Peak frequency 1a/theme (kHz)	5.19±1.4	7.25±0.62	1.92±0.35	3.33±1.58
11 Peak frequency 3B/phrase (kHz)	3.34±1.03	4.29±0.38	2.97±0.37	3.60±0.81
Phrase repetitions/song				
12 Phrase R	10.09±0.97	9.21±0.53	8.36±1.19	7.44±1.17
13 Phrase 1a/b	22.15±11.45	33.92±9.05	15.65±4.10	28.82±13.61
14 Phrase 1a	12.62±4.64	17.34±5.41	7.73±2.81	20.35±10.3
15 Phrase 1b	10.4±6.40	17.85±4.78	8.02±1.39	8.49±3.36
16 Phrase 2A	4.36±2.01	3.03±0.67	2.87±1.12	3.66±1.37
17 Phrase 2B	4.72±1.49	4.52±1.32	7.28±4.07	4.9±2.07
18 Phrase 3B	6.53±1.07	8.88±3.57	7.47±2.36	6.37±1.70
Unit structure				
19 1a unit 2: unit duration (s)	1.74±0.37	2.65±0.25	1.22±0.14	2.39±0.47
20 1a unit 2: average slope (Hz/s)	1110 ±380	770 ±160	1000 ±110	710 ±290
21 1b unit 2: initial frequency (Hz)	308 ±23	270 ±64	301 ±61	216 ±15
22 1b unit 2: frequency range (Hz)	171 ±46	227 ±31	199 ±33	290 ±35
23 1b unit 2: unit duration (s)	1.92±0.23	2.78±0.18	1.51±0.27	2.16±0.43
24 1b unit 2: average slope (Hz/s)	69 ±11	75 ±28	141 ±53	143 ±19
25 2A unit 1: initial frequency (Hz)	241 ±25	180 ±19	251 ±16	206 ±16
26 2A unit 1: frequency range (Hz)	154 ±48	240 ±26	163 ±22	266 ±27
27 2A unit 1: unit duration (s)	1.49±0.16	1.18±0.14	1.49±0.28	1.15±0.18
28 2A unit 1: average slope (Hz/s)	105 ±31	213 ±17	118 ±30	239 ±46
29 2A unit 2: initial frequency (Hz)	241 ±22	180 ±19	246 ±23	205 ±14
30 2A unit 2: frequency range (Hz)	156 ±44	243 ±42	166 ±27	252 ±12
31 2A unit 2: unit duration (s)	1.63±0.31	1.00±0.10	1.36±0.21	1.04±0.10
32 2A unit 2: average slope (Hz/s)	103 ±12	252 ±49	130 ±33	250 ±30
Phrase structure				
33 Number of units RT	2.91±0.52	2.60±0.41	2.86±0.54	2.55±0.27
34 Number of units 1a	3.24±0.26	4.22±0.46	3.43±0.36	3.43±0.21
35 Number of units 1b	2.58±0.48	3.17±0.32	2.96±0.17	2.98±0.08
36 Number of units 2AS2	8.59±1.05	10.48±1.13	8.35±1.90	8.59±2.01
37 Number of units 3BS1	3.30±0.40	4.18±0.19	3.82±0.21	3.79±0.27
38 Proportion of ascending units 2AS2	0.29±0.10	0.30±0.01	0.40±0.05	0.16±0.08
39 Proportion of low-frequency units 3BS1	0.42±0.05	0.70±0.01	0.15±0.04	0.62±0.01
40 Proportion of discrete units 3BS1	0.55±0.02	0.99±0.03	0.85±0.03	0.52±0.04
Theme and song structure				
41 Proportion of songs with theme 2B	0.98±0.04	1.00±0.02	0.89±0.11	0.47±0.27
42 Proportion of songs with theme 3A	0.58±0.30	0.01±0.03	0.01±0.02	0.00±0.00
43 Proportion of songs with 2B-1 transition	0.22±0.10	0.01±0.08	0.35±0.11	0.10±0.42
44 Proportion of 1a phrase types in theme 1	0.55±0.05	0.49±0.04	0.48±0.07	0.70±0.05