COMPARISON OF SONGS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) RECORDED IN JAPAN, HAWAII, AND MEXICO DURING THE WINTER OF 1989

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ABSTRACT

Recordings of humpback whale (*Megaptera novaeangliae*) song were obtained between 10 March and 14 April 1989 from the Bonin Islands and the Ryukyuan Islands of Japan, the Hawaiian Islands, and the southeastern Baja Peninsula of Mexico. Through analyses of the song samples obtained, seven "themes" were identified in Hawaiian and in Bonin song and six in Mexican song. Theme similarities across these three regions arranged themselves hierarchically: Hawaii and Mexico shared five themes in common, and did not share three ; Hawaii and Bonin shared four themes and did not share three; and Mexico and Bonin shared three themes and did not share six. Three themes appeared in all three regions. The song samples from Ryukyu were all of short duration and were likely an incomplete record of the entire song repertoire. Nevertheless, of the three themes identified in the Ryukyuan samples, two appeared in Bonin song and none in Mexican and Hawaiian song. Overall, the thematic data suggested that there is acoustic contact during some portion of the migratory cycle among the whales wintering in Mexico, Hawaii, and the Bonin Islands.

Key words: humpback whale, acoustic communication, stock identity, song dialects

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate annually between high-latitude summer grounds where feeding occurs and low-latitude winter grounds. The behavior of the whales on the winter grounds (e.g., Herman, Forestell and

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Antinoja, 1980; Tyack, 1981; Darling, Gibson and Silber, 1983; Glockner and Venus, 1983; Baker and Herman, 1984) and their reproductive physiology during the winter months (Chittleborough, 1955, 1958, 1965) suggest that reproductive activities are predominant during the winter season.

Humpback whales produce a complex vocalization first characterized as "song" by Payne and McVay (1971). Singing peaks during the winter months (Winn and Winn, 1978; Thompson and Friedl, 1982; Helweg, 1989), although it has been reported occasionally late in the fall on the feeding grounds (Matilla, Guinee and Mayo, 1987; McSweeney, Chu, Dolphin and Guinee, 1989) and along migratory pathways (Tyack and Whitehead, 1983; Kaufman and Jenkins, 1985). The singing whales that have been sexed have proven to be male (Winn, Bischoff and Taruski, 1973; Glockner, 1983). The correlation of song production and seasonal gonadal activity suggests that song plays a role in the mating system, although that role is not yet established (cf. Tyack, 1981, 1983; Baker and Herman, 1984; Mobley, Herman and Frankel, 1988).

Humpback song is dynamic; songs in a given geographical region change during the course of each winter season, yet at any given time singers within the region appear to converge on the same or nearly the same rendition (Winn and Winn, 1978; Guinee, Chu and Dorsey, 1983; Payne, Tyack and Payne, 1983; Payne and Payne, 1985). The function of the seasonal changes in song and of the convergence of most singers on the current rendition remain speculative (cf. Winn and Winn, 1978; Frumhoff, 1983; Payne and Guinee, 1983; Payne *et al.*, 1983; Payne and Payne, 1985; Chu and Harcourt, 1986).

Previous studies have found substantial song differences between geographically isolated stocks of humpbacks in separate oceans: in particular, the North Atlantic, North Pacific, and South Pacific Oceans (Winn, Thompson, Cummings, Hains, Hudnall, Hays and Steiner, 1981; Payne and Guinee, 1983; Kaufman and Jenkins, 1985). Similarities in the songs of whales in different wintering areas within an ocean have also been found (Winn and Winn, 1978; Payne and Guinee, 1983). These authors have suggested that whales in different wintering areas singing the same rendition of song must be in acoustic contact during some portion of their annual cycle when song is produced. Contact may occur in the summer feeding grounds, during migration, through visits to more than one wintering ground during a season by some whales, and through visits to different wintering grounds in different seasons by some whales.

Payne and Guinee (1983) found that humpback songs recorded at about the same time near Maui in the Hawaiian Isalands and at Isla Socorro off the west coast of Mexico were similar to each other, suggesting that the whales in these two areas may constitute one stock. In this paper, we extend the North Pacific analysis by comparing songs recorded at about the same time in Hawaii, Mexico, and Japan.

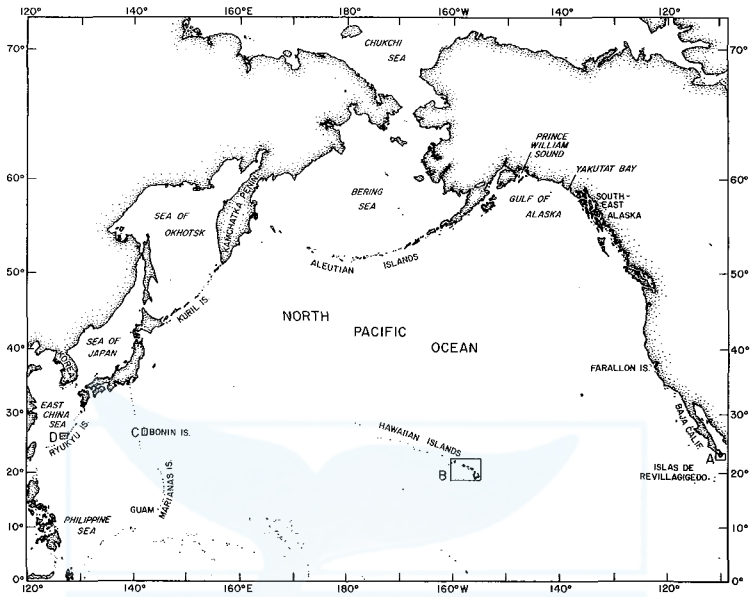

Fig. 1. The North Pacific Ocean, showing documented summer feeding sites for humpback whales from the western Gulf of Alaska through to southeast Alaska and the Farallon Islands (see text). Additionally shown are the locations of the four wintering areas from which songs were obtained in Mexico, the Hawaiian Islands, the Bonin Islands, and the Ryukyuan Islands.

The stocks of humpbacks in the North Pacific Ocean

Fig. 1 shows areas of seasonal aggregations of humpback whales in the North Pacific Ocean and neighboring waters. Five summer feeding sites have been documented in the central and eastern North Pacific (Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke and Ostman, 1986): the Farallon Islands, southeast Alaska, Yakutat Bay, Prince William Sound, and the western Gulf of Alaska. Photographic identifications have revealed that individual whales tend to return to the same feeding site each year (Darling and Jurasz, 1983; Darling and McSweeney, 1985; Baker *et al.*, 1986), resulting in an apparent segregation of feeding stocks. The historical feeding range of humpback whales extended beyond the western Gulf of Alaska through the Aleutian Islands and northward into the Bering and Chukchi Seas, as well as into the Okhotsk Sea and along the Kamchatka Peninsula (Kellogg, 1929; Nishiwaki, 1966; Tomilin, 1967; Nikulin, 1969; Nemoto, 1978; Rice, 1978). The degree of current use of these areas is not known.

Three primary winter aggregations have been identified. One is located in Mexican waters around the Baja Peninsula, Gulf of California, and Islas de Revillagigedo (Urban and Aguayo, 1987). A second, reportedly larger, aggregation forms around the waters of the main Hawaiian Islands (Herman and

Antinoja, 1977; Herman *et al.*, 1980; Baker and Herman, 1981; Darling and Jurasz, 1983). A third wintering ground was traditionally located south of Japan, among the Bonin, Ryukyuan, and Marianas Islands (Townsend, 1935; Dawbin, 1966; Nishiwaki, 1959, 1960, 1962, 1966; Tomilin, 1967; Nikulin, 1969). The western population was greatly reduced by commercial whaling (Tomilin, 1967), and was unaccounted for as late as 1984 (Johnson and Wolman, 1984). Recent sightings indicate, however, that humpback whales are returning to the Bonin and Ryukyuan winter grounds.

Exchange among the wintering grounds *between* seasons has been documented for Hawaiian and Mexican whales, although it appears to be a relatively rare occurrence (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985). Travel between Mexico and Hawaii *within* a season has been reported only once thus far, using photographic data from several laboratories and the archival laser disc records of the National Marine Mammal Laboratory.[1)] There are, as yet, few photographic records of humpback whales from Japanese waters, but it seems likely that the between- or within-season exchange between Hawaii and Japan would be no more frequent than that observed between Hawaii and Mexico.

Humpback whale song

Payne and McVay (1971) contended that the long, complex, vocalizations of the humpback whale in or near the winter grounds could be classified as "song" according to a definition of song as a series of sounds repeated in a recognizable sequence or pattern in time (Broughton, 1963). Payne and McVay (1971) and Payne *et al.* (1983) further described the hierarchical organization of humpback whale song: at the lowest level were discrete notes, or units, defined as "the shortest sounds in the song which seem continuous to the human ear" (Payne *et al.*, 1983, p. 15); small repeated groups of units were organized into phrases, often consisting of two subphrases, each containing repeated sounds; groups of phrases made up a theme; and, finally, the song itself was "a series of different themes given in a predictable order" (Payne *et al.*, 1983, p. 17). A song typically may last for perhaps 8 to 12 minutes. Successive songs sung without pause constituted a song session.

Transitional phrases may occur at the junction between themes (Payne, *et al.*, 1983). These transitions are often composed of the first subphrase of the preceding phrase and the second subphrase of the following phrase (Frumhoff,

1) Identification of a single humpback whale traversing from Mexico to Hawaii during the 1986 winter season was made by the National Marine Mammal Laboratory, Seattle, using their computer photographic identification system and photographic records from Mexico in 1986 supplied by the Universidad Autonoma de Mexico, and records from Hawaii for that same year, supplied by the Pacific Whale Foundation. Additionally, the same whale was photo-identified in previous years in Hawaii by the Kewalo Basin Mammal Laboratory, by the Center for Whale Studies, and by the West Coast Whale Research Foundation.

1983). Phrases within a theme may vary in the repetition rate of the subphrases or of the units (Payne and McVay, 1971; Payne, 1978).

The singing whale is most often alone (Winn and Winn, 1978; Tyack, 1981). The whale may remain submerged in a particular small area for long periods, surfacing at intervals of perhaps 8 to 15 min and then diving again after a short respiratory bout. Swimming while singing has been reported occasionally, as has singing in the company of other whales (Tyack, 1981; Baker and Herman, 1984; Frankel, Clark, Herman, Gabriele, Hoffhines, Freeman and Patterson, 1989). During some years of our observations in Hawaii, surfacing could be predicted by a series of "ratcheting" sounds, apparently similar to those described by Winn and Winn (1978) as preceding surfacing of North Atlantic humpback whales in the winter grounds near Puerto Rico. The ratchet sounds we have observed during 1987 to 1989 had a creaking, staccato character, and were usually followed by one or more short, higher frequency "whines". There is commonly a marked attenuation of sound prior to and during surfacing.

Source levels for humpback song are relatively loud, on the order of 155 dB (re 1 μPa at 1 m) (Levenson, 1972). Payne and Guinee (1983) argued, however, that humpback song can probably be heard by other whales only at distances of less than 20 km, based on the model of sound propagation developed by Payne and Webb (1971). Winn and Winn (1978) reported hearing humpback whale song on listening hydrophones at a distance as great as 32 km and Frankel *et al.*, (1989), using a three-element hydrophone array, have located some singing whales at distances estimated as 20 km. These various theories and data suggest that acoustic contact between humpback whales, for song vocalizations, is probably limited to relatively short ranges of, say, less than 40 km.

MATERIALS AND METHODS

Because humpback whale song may change to varying degrees over the course of a winter season, we chose to compare songs obtained at roughly comparable points in time from the different geographic regions. Table 1 lists the locations and dates within the Mexican, Hawaiian and Japanese regions from which our 1989 song samples were obtained, and gives the duration of each sample. Fig. 2 provides detailed maps of the specific location from which song samples were obtained within each region. Song samples were obtained in Mexico on March 10 and 11; in Hawaii on March 12 and 15, and on April 4; in the Ryukyuan Islands on March 19, 22 and 23 March; and in the Bonin Islands on April 14. Thus, with the exception of the Bonin songs and one Hawaii song, samples of song were available within the 3-week interval from March 10 to March 24. Earlier (1979) comparisons of Mexican and Hawaiian song (Payne and Guinee, 1983) were similarly based on recordings made in the month of March. The

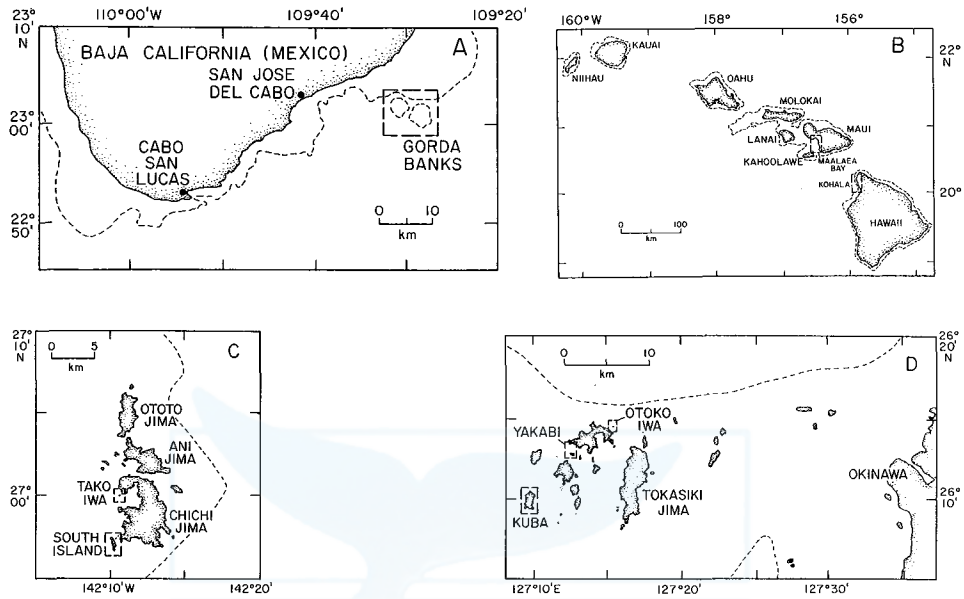

Fig. 2. Details of the study regions from which recordings were made. Each corresponds to an inset box on Fig. 1 but is not identical to the area delimited by the box in Fig. 1. The specific recording sites are shown in boxes and correspond to the locations given in Table 1. The dotted lines indicate the 200m isobath.

TABLE 1. DATES, LOCATIONS AND DURATIONS OF 1989 HUMPBACK WHALE SONG SAMPLES, AND THE RESEARCH GROUP PROVIDING EACH SAMPLE.

Date	Region (location)	Duration (min:sec)	Code	Group
10 March	Mexico (Gorda Bank)	5:13	MEX310A	CWR; UNA
10 March	Mexico (Gorda Bank)	20:20	MEX310B	CWR; UNA
11 March	Mexico (Gorda Bank)	27:05	MEX311	CWR; UNA
12 March	Hawaii (South Kohala)	30:00	HI312	KBMML
15 March	Hawaii (South Kohala)	26:24	HI315	KBMML
4 April	Hawaii (Maalaea)	31:20	HI404	PWF
19 March	Ryukyu (Otoko Iwa)	4:57	RYU319	TA; TN
22 March	Ryukyu (Kuba)	2:23	RYU322	TA; TN
23 March	Ryukyu (Yakabi)	2:56	RYU323	TA; TN
14 April	Bonin (South Island)	32:09	BON414A	PWF
14 April	Bonin (Takojima)	18:00	BON414B	PWF

Group codes: CWR = Center for Whale Research; UNA = Universidad Nacional Autononoma de Mexico; KBMML = Kewalo Basin Marine Mammal Laboratory; PWF = Pacific Whale Foundation; TA = Toba Aquarium; TN = Tsuneo Nakamura (Volvox).

hydrophones and recording equipment used by the various research groups to obtain the 1989 songs varied, but reportedly all systems had frequency responses flat from 50 Hz to at least 10,000 Hz.

The samples from Hawaii and the Bonin Islands contain full songs without interruption. Although the Mexican song samples were interrupted at several points when the research group pursued fluke photography as the singers surfaced, two of the song sessions are long enough (*ca.* 20 to 27 min) to make it likely that all sounds made by the whales are represented in the song samples (K. Balcomb, pers. comm.). The three samples from Ryukyu were all of short duration, but one (RYU319) does contain a cycle of themes that returns beyond the "starting" theme.

Sonograms of representative phrases from each theme, as well as of "atypical" transitional phrases, were made on a Kay (Series 7800) SonoGraph. Previously published sonograms of humpback song have typically limited the upper frequency to 2.0 kHz (Payne and McVay, 1971), or 2.5 kHz, and have provided tracings only of the fundamental frequency (e.g., Frumhoff, 1983; McSweeney *et al.*, 1989; Payne and Guinee, 1983; Payne *et al.*, 1983). We chose instead an upper frequency limit of 4 kHz (using an effective bandwidth of 150 Hz) because several subphrases had fundamental frequencies close to or above 2.5 kHz, and a great deal of sound energy lay in harmonics. The harmonic structure of the songs proved helpful in discriminating similarities and differences between phrases.

The obtained sonograms were used to identify units, subphrases, phrases and themes. There was some variation in the repetition rate of subphrases within phrases, and phrases within themes, but this variation occurred both within and between songs. The variation was ascribed to idiosyncrasies of particular whales rather than to a group characteristic and was not taken into consideration in the analyses of similarties and differences across regions.

Using HI315 (Table 1) as the reference song, the first theme following the surface ratchet was labelled A. This is the same criterion as used by Winn and Winn (1978) in their song analyses. Successive themes were labelled B, C, D... etc. The ratcheting sound appeared in the songs from the island of Hawaii (HI312 and HI315) and in the Bonin songs, but not in the Mexican or Ryukyuan song, nor the Hawaiian sample from Maui (HI404). The A theme was then searched for in the songs from Mexico and succeeding themes from that region were identified according to the labels used for HI315, or were given new labels if they did not appear in the Hawaii song. The Bonin themes were then analyzed using the labels identified in the Hawaiian and Mexican songs, with new labels added as needed. Finally, the Ryukyuan themes were analyzed using the labels available from the previous three regions, with one new label necessary in this last step. These procedures allowed for a comparison of theme sequences as well as theme differences.

TABLE 2. SHARED AND UNIQUE SONG THEMES

Theme	Hawaii	Mexico	Bonin	Ryukyu
A	X	X	X	
B	X	X		
C	X			
D	X	X	X	
E	X	X	X	
F[1)]	X		X	
G	X	X		
H		X		
I			X	X
J			X	X
K			X	
L				X

1) Ratchet sound.

RESULTS

Comparison of themes across regions

Themes from all of the song samples available in a region (Table 1) were combined to identify the themes present in that region, as shown in Table 2. A total of 12 different themes (A-L) were identified across the four regions. Hawaiian and Bonin song each contained seven themes and Mexican song six. Ryukyuan song contained only three themes but, as was noted, all song samples were of short duration.

The data yielded a hierarchy of theme similarities across regions: Hawaii and Mexico shared five themes and did not share three; Hawaii and Bonin shared four and did not share three; Mexico and Bonin shared three and did not share six; and Bonin and Ryukyu shared two and did not share six. The themes present in Ryukyuan song did not overlap with any present in Hawaiian or Mexican song. Three themes (A, D, and E) were common to Hawaiian, Mexican and Bonin song; those three are referred to here as "pan-Pacific" themes.

Fig. 3 shows sonographic records of these three pan-Pacific themes. The versions from the various regions appear very similar. Frumhoff (1983, p.83) defined "fundamental" themes as those "present in all songs of a least 90% of the song sessions recorded in both that season and at least one contiguous season." Whether the pan-Pacific themes can be termed "fundamental" in Frumhoff's sense must await data from additional seasons and from additional recordings.

The finding that no Ryukyuan theme appeared in the Hawaiian or Mexican samples, and vice-versa, suggests that the whales visiting the Ryukyuan Islands may be acoustically isolated from those visiting Hawaii or Mexico. At the same time, the very short and likely incomplete song records from the Ryukyuan Islands, the presence of two of three Ryukyuan themes in Bonin song, and the

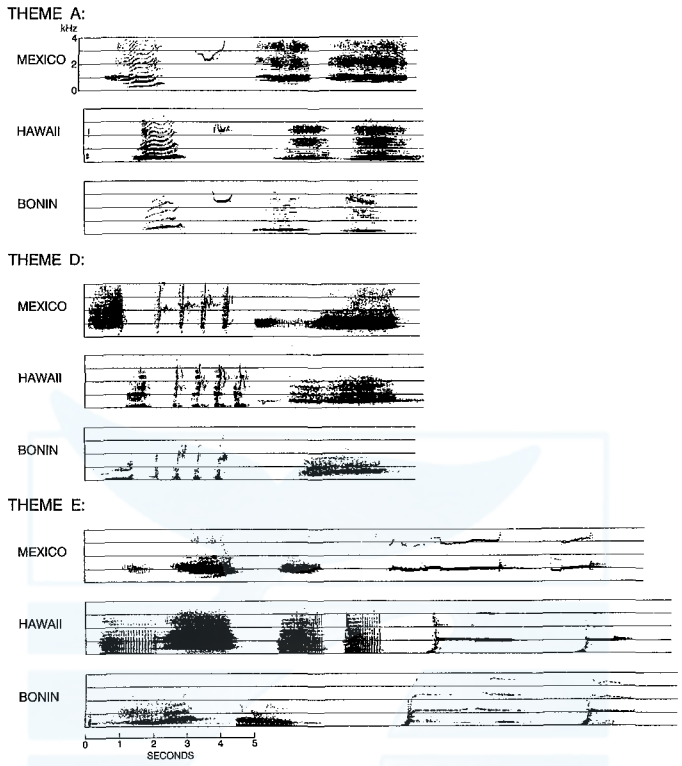

Fig. 3. Comparison of sonograms of "pan-Pacific" themes shared by song recorded in Japan, Hawaii and Mexico. Component subphrases of each theme are shown once in the figure although some may be repeated within any given phrase. Effective filter bandwidth of Kay SonoGraph was 150 Hz. Vertical scale is in 1000 Hz increments. Time is shown on horizontal axis.

partial overlap of Bonin with Hawaiian and Mexican song, weakens any case for acoustic isolation.

Fig. 4 shows sonographic records of the four themes (B, C, G and H) present in Hawaiian and/or Mexican song, but not in songs from the western Pacific. Hawaiian and Mexican song share two of these themes (B and G). Mexican song contains the unique theme H and Hawaiian song the unique theme C.

Fig. 5 shows theme F, the surface-ratchet sound, present in Hawaiian and Bonin song but not in Mexican or Ryukyuan song. As we noted earlier, the ratchet sound reliably predicted the surfacing of a singing whale in the Hawaiian songs of 1989, as well as in songs of 1988. A ratcheting sound was also reported by Winn and Winn (1978) as preceding surfacing of singing whales in the Puerto Rico Silver Bank region. Sonograms available in Winn and Winn (1978) suggest a similarity of the North Atlantic ratchet to the North Pacific sound, but it is

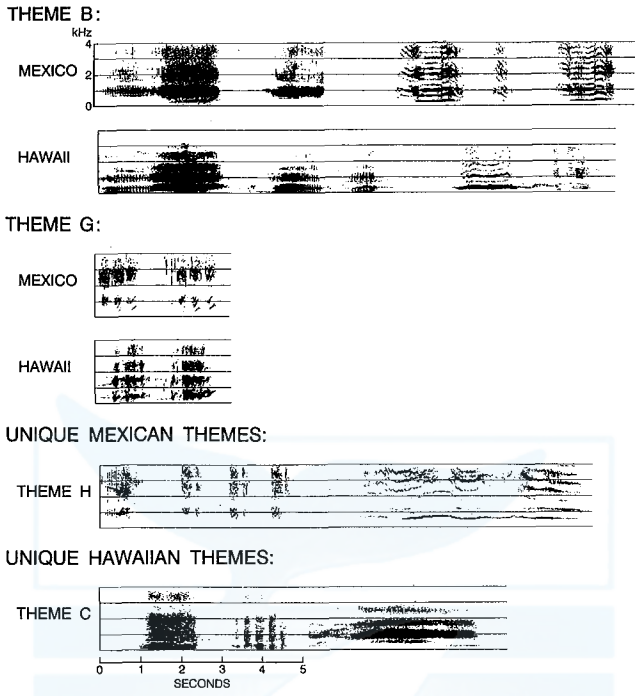

Fig. 4. Sonograms of themes found in Mexican or Hawaiian song, or both, but not present in song from Japan, prepared as in Fig. 3.

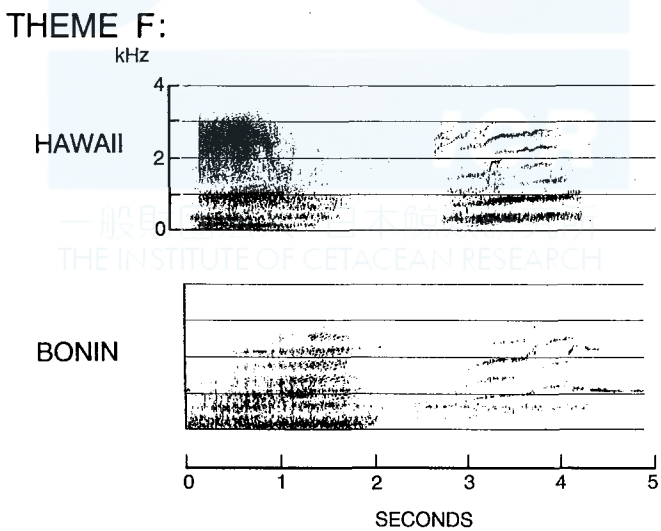

Fig. 5. Sonograms of theme F, the "surface ratchet," common to Hawaiian and Bonin song, but not present in song from Mexico or Ryukyu, prepared as in Fig. 3.

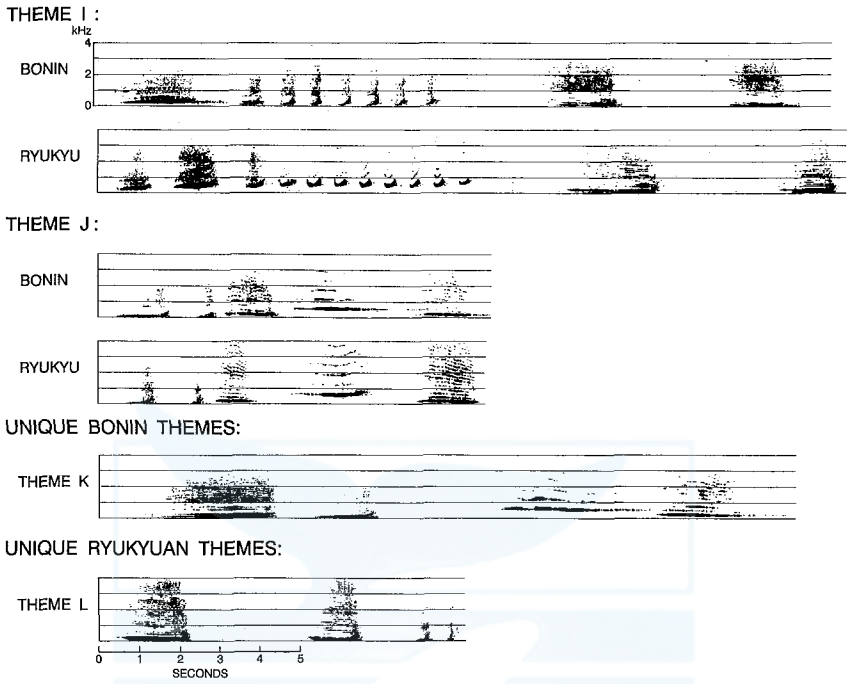

Fig. 6. Sonograms of themes found in Ryukyuan or Bonin song, or both, but not present in song from Hawaii or Mexico, prepared as in Fig. 3.

difficult to make a firm judgment from the quality of the available sonograms.

Fig. 6 describes four themes (I, J, K and L) present in Ryukyuan and/or Bonin song, but not present in Hawaiian or Mexican song. Ryukyan and Bonin song shared themes I and J. Additionally, Bonin song contains one unique theme (K). Ryukyuan theme L was not present in RYU322 or RYU323, and was produced only once in RYU319.

Comparisons of theme sequences within regions

Table 3 shows the sequence of themes in each song sample. The sequences are arranged to highlight corresponding theme sequences across the different recordings within each region. In Hawaii, the sequence DEFAB appears in the song of HI312 and of HI315. HI404 shares the sequence BCDE with HI315. The short sequences BD and DE are shared by all three samples.

The Mexican song samples show an apparent lesser degree of correspondence across song samples. The longest shared sequence is BED, found in MEX310B and MEX311. The two-theme sequence AB is found in all three samples. Again, however, the short duration of MEX310A limits this type of analysis.

TABLE 3. THEME SEQUENCES OF EACH SAMPLE OF SONG FROM EACH REGION. IDENTICAL THEMES OR THEME SEQUENCES WITHIN EACH REGION ARE ALIGNED TO HIGHLIGHT SIMILARITIES.

HI312				B		D	E		D	G	B	D	E	F	A	B										
HI315	B	F	A	B	C	D	E					D	E	F	A	B	D									
HI404				B	C	D	E				B	D														
MEX310A						A	B																			
MEX310B						A	B	E	D//				B	E	D	E	D									
MEX311	B	E	D	H	G	A	B//		D	H	G	A	B	E	D				H	G	A					
BON414A									K	F	A	D	E	I	J	K	F	A	D	E	I					
BON414B	E	D	E	F	A	D	E	D		F	A	D	E	I	J		F	A	D	E	I	J				
RYU319			I	L	J	I	J																			
RYU322						I	J																			
RYU323							J																			

Note: Gaps between themes do not represent gaps in taping.
Actual breaks in taping are indicated by "//"

The two Bonin samples share a six-theme sequence FADEIJ. The shorter sequence FADE was found twice in BON414A and three times in BON414B. The Ryukyuan song samples are short and generalizations are difficult. Nevertheless, similarities are seen across samples in the sequence IJ, shared by two song samples.

It is apparent that longer sequences (three or more themes) are not shared across the different regions, but several two-theme sequences are. Hawaii, Mexico and Bonin song all share the sequences DE and the inversion ED. Additionally Hawaii and Mexico share the sequence AB. Finally, Bonin and Ryukyu share the sequence IJ.

Inverted theme sequences are rare. Payne *et al.* (1983) found only five theme inversions among 1196 two-theme sequences recorded during the 1976-77 winter season in Hawaii. In our *within*-region data, inversion of DE and ED is relatively rare. Thus, in the Hawaiian songs, DE appears five times and ED twice. Similarly, in Bonin song DE appears six times and ED twice. In Mexican song, a reverse trend occurs: ED is the more common theme, appearing five times while DE appears only once.

Fig. 7 graphs the two-theme transitions from Hawaii, Mexico and Bonin for those song sessions having the greatest number of theme sequences: HI315, MEX311 and BON414B, respectively. The graphs reveal the general orderliness in which themes are sequenced, especially for MEX311. Additionally, the figures show the inversions of themes E and D in songs of individual whales from Hawaii and Bonin and theme omissions by these same whales. Theme omissions, e.g., singing the sequence BD rather than BCD, are not unusual (Payne *et al.* 1983, Fig. 2) although omission of a fundamental theme is considered aberrant (Frumhoff, 1983).

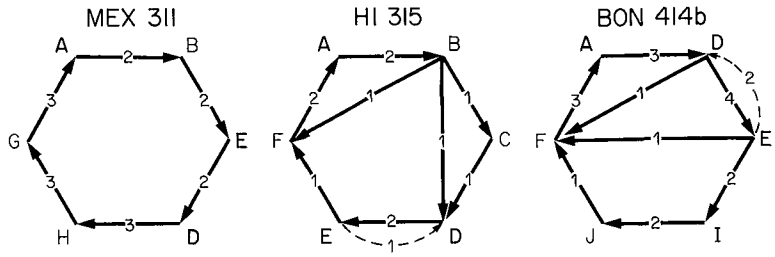

Fig. 7. Theme transitions of selected samples from Mexico, Hawaii and Bonin regions, based on data in Table 3. Frequency of transition is indicated within each arrow. Solid lines indicate usual transition order; theme reversals are indicated by dashed lines.

Unique sound units

Despite the great variability of sounds produced during a singing session, the introduction of new or unusual sounds is rare (Frumhoff, 1983). The basic "library" of sounds available to singers appears to remain relatively constant. Variability and progressive change occur mainly by recombination of basic units or phrases. Novel sounds tend to become incorporated rapidly into the songs of whales in a common wintering ground (Payne *et al.*, 1983). The presence of a few sound units in one wintering ground that do not appear in another wintering ground, while at the same time the remaining sound units are shared, may indicate that those novel sounds were developed in the winter grounds themselves when whales are acoustically isolated (because of the great distances involved) from whales in other wintering grounds.

We found only three instances of sound units unique to a given wintering ground in our song samples from Mexico, Hawaii and the Bonin Islands. The Bonin song sample coded BON414A contains a unit in Theme I that appears to be unique to this region. The unit is shown in Fig. 8a and can be described as a "pulsive scream" with a highly variable frequency structure. Furthermore, theme I contains a subphrase that is composed of a unit not found in either Mexican or Hawaiian song. This is the series of J-shaped units shown in Fig. 8b which, together, comprise the central subphrase of theme I.

The sample of Mexican song coded as MEX311 contains a complex unit, shown in Fig. 8c, that appears to be unique to the singers in Mexican waters. This unit is found in theme H and is distinguished by a rapid change of harmonic structure between the initial and subsequent subunits, as well as by a rapid traverse of frequency.

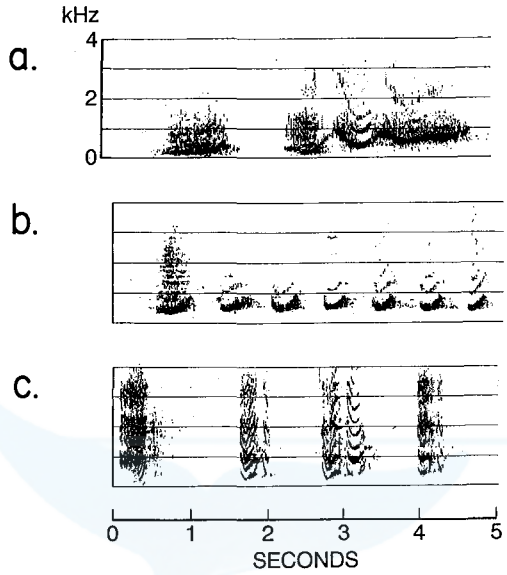

Fig. 8. Unique sound units in different wintering areas. *a*. The "pulsive scream" from Bonin theme I that is unique to the Bonin song samples. *b*. The J-shaped units that may comprise the central subphrase of theme I in Bonin song. *c*. The complex unit from Mexican theme H that is unique to the Mexican song samples.

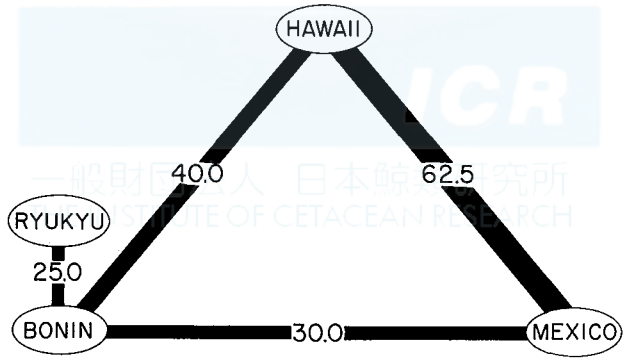

Fig. 9. The percentage of overlap of song themes from the five wintering areas, based on the data of Table 2. The width of the lines connecting paired regions is proportional to the percentage of overlap.

DISCUSSION

The comparison of themes across the different regions revealed varying degrees of theme overlap. Using the theme structure shown in Table 2, the percentage of overlap of two regions can be calculated as the number of shared themes divided by the total number of shared and unshared themes across the two regions, multiplied by 100. Fig. 9 illustrates the results obtained with this measure for each pair of regions. The largest overlap occurred for Hawaiian and Mexican song, then Hawaiian and Bonin song, then Mexican and Bonin song, and finally Bonin and Ryukyuan song. There was no overlap of Ryukyuan song with song from Hawaii or Mexico.

As we noted earlier, the Ryukyuan song samples we obtained were of very short duration, and it is probable that had longer samples been available more themes would have been found. Hence, at this time no firm conclusions are possible about the relationship between Ryukyuan song and songs from Hawaii or Mexico. The relationship between Ryukyuan song and Bonin song is probably closer than suggested by the low percentge of overlap shown in Fig. 9. Of the three Ryukyuan themes identified, two were also found in Bonin song. Ryukyu may not be a true winter terminus for humpback whales but only a temporary way-station along the migration route to the Bonin Islands or to points south, as was implied by Nishiwaki's (1959, 1960, 1962, 1966) data. In the future, further, detailed analysis of longer samples of Bonin song can help to answer questions about the degree to which whales visiting the Ryukyuan islands are affiliated with whales visiting the Bonin Islands.

The relatively large overlap of Hawaiian and Mexican song confirms earlier reports of Winn *et al.* (1981) and of Payne and Guinee (1983) of considerable song similarity across these regions. Spectrograms published in Payne and Guinee (1983) show that the seven themes found in 1979 Mexican song overlapped totally the seven found in Hawaiian song in that same year. This result is similar to our findings that five of six Mexican themes were found among the seven Hawaiian themes. Comparisons of the 1979 sonograms published by Payne and Guinee (1983) with those available here do not show any obvious similarity of themes, indicating that the song evolved considerably over the 10-year interval. This degree of change is not unexpected based on other analyses of progressive song change over years. (Payne *et al.*, 1983; Payne and Payne, 1985).

The overlap between Bonin and Hawaiian song and between Bonin and Mexican song, especially the presence of the three pan-Pacific themes in the songs of all three regions, suggests that whales in these wintering grounds are in acoustic contact during some portion of their migratory cycle. The percentage of overlap of pairings of Mexico, Hawaii and Bonin song, as shown in Fig. 9, varies directly with the distance between these locations: approximately 3,160 km from Mexico to Hawaii, 3,940 km from Hawaii to Bonin, and 7,056 km from

Mexico to Bonin. The data thus suggest a decreasing degree of acoustic contact of the whales in these separated areas as a function of distance. The distance separating the winter grounds may not be the major variable determining song similarities and differences, however, and the data on the limitation in propagation distances of song (Frankel *et al.*, 1989; Payne and Guinee, 1983; Winn and Winn, 1978) make it unreasonable to assume that whales in one winter ground could be listening to whales in another winter ground. More important variables may be the degree of spatial separation of whales in the summer feeding grounds, the spatial separation of the migration routes taken by whales journeying to the different winter grounds, and the degree to which migratory interchange occurs between summer grounds and between winter grounds.

Whales visiting Hawaii and Mexico are known to appear in some of the same feeding sites in the summer, the western Gulf of Alaska, including Prince William Sound, and southeast Alaska, in particular (Baker *et al.*, 1986; Darling and Jurasz, 1983), allowing for song exchange during the late Fall months when some singing is heard (Matilla *et al.*, 1987; McSweeney *et al.*, 1989). Additionally, whales from the feeding grounds in Prince William Sound, the western Gulf of Alaska, and southeast Alaska may share portions of their migration routes during a journey to Hawaii or Mexico, allowing for song exchange during a time when singing has been heard (Tyack and Whitehead, 1983; Kaufman and Jenkins, 1985). Also, there is some dispersion of whales from a common feeding site to the different winter grounds of Hawaii and Mexico (Baker *et al.*, 1986; Perry, Mobley, Baker and Herman, 1988), so that a common late Fall song heard in a given feeding ground could appear in different winter grounds; additionally, some convergence of song could occur after return of whales from different winter grounds to the common feeding grounds, which would manifest itself in song similarity during the subsequent winter season. Finally, although apparently rare, visits between the Mexican and Hawaiian winter regions by indivisual whales during contiguous winter seasons has also been documented (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985), providing a further mechanism for song exchange, provided the song has not drifted too far during the intervening year. We also noted earlier the one case reported thus far of a whale visiting both Mexico and Hawaii in a single winter season.

It seems less likely that whales visiting the western Pacific winter grounds share a migration route with whales visiting the central or eastern Pacific grounds. Contact of Mexican/Hawaiian whales with Bonin whales may take place in the summer feeding grounds, however. Nishiwaki (1966) reported the recovery of six Discovery tags in the Ryukyuan Islands from humpback whales marked in the eastern end of the Aleutian chain. This feeding region may be close enough to the western Gulf of Alaska, a documented site to which some whales return from Hawaii (Baker *et al.*, 1986), to allow for acoustic contact.

Thus at least three mechanisms—contact in the feeding grounds, common migration routes, and interchange between winter sites by individuals—seem available for song exchange between Hawaii and Mexico. In the least, the first mechanism listed may also be available for song exchange between whales visiting Hawaii and the Bonin Islands. Our findings that the songs across the three regions are not identical, that some themes are not shared, and that some unique sound units occur in Mexican and Bonin song, suggest that acoustic contact across these three principal regions—Hawaii, Mexico and the Bonin Islands—is not complete, at least during the portion of the season when we sampled song.

A final consideration is the extent to which song similarity is correlated with genetic distance, and may therefore be an indicator of the separation of stocks. Baker, Palumbi, Lambertsen, Weinrich, Calambokidis and O'Brien (1990) examined mitochondrial DNA differences among humpback whales in the Farallon Islands near central California, the Hawaiian Islands, and southeast Alaska in the North Pacific, and the Gulf of Maine in the North Atlantic. They found the greatest genetic distance between the Gulf of Maine whales and those of the North Pacific, and considerably less disparity within regions of the North Pacific. Particularly, there was virtually no difference between the Hawaiian and southeast Alaska whales. It is interesting that photographic matches have shown that a majority of the photo-identified whales from southeast Alaska winter in Hawaii (Baker *et al.*, 1986; Darling and Jurasz, 1983; Darling and McSweeney, 1985; Perry *et al.*, 1988). The genetic distance between the whales of the Farallon Islands and those from Hawaii was greater than that between Hawaii and southeast Alaska but less than that between the North Atlantic and any region of the North Pacific. Photo-identification data suggests that whales from the Farallon Islands tend to winter in Mexico primarily (Calambokidis, Steiger, Cubbage, Balcomb, Bloedel and Bockus, 1989). The analyses of song differences in this paper, as well as earlier analyses by Payne *et al.* (1983) and Winn *et al.* (1981), reveal large song differences between North Atlantic and Mexican/Hawaiian whales and, in this paper, some differences between Hawaii and Mexico whales. Thus, genetic distance and song difference appear to be positively correlated, giving some support to the thesis of Payne and Guinee (1983) that song differences may be an indicator of separate stocks. If their thesis is correct, one would expect that mitochondrial DNA analyses of whales in Japanese waters would reveal a genetic distance from Hawaiian whales at least as great as that found between Hawaiian whales and those in the Farallon Islands. Efforts to obtain miotochondrial DNA data from whales in Japanese waters should thus prove fruitful for further understanding of stock separation and the relation of song differences to stocks. Additionally illuminating would be more extensive photographic analyses of whales in Japanese waters to search for individuals that might have appeared in other years in winter grounds to the east or in summer grounds shared with whales visiting Hawaii or Mexico.

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