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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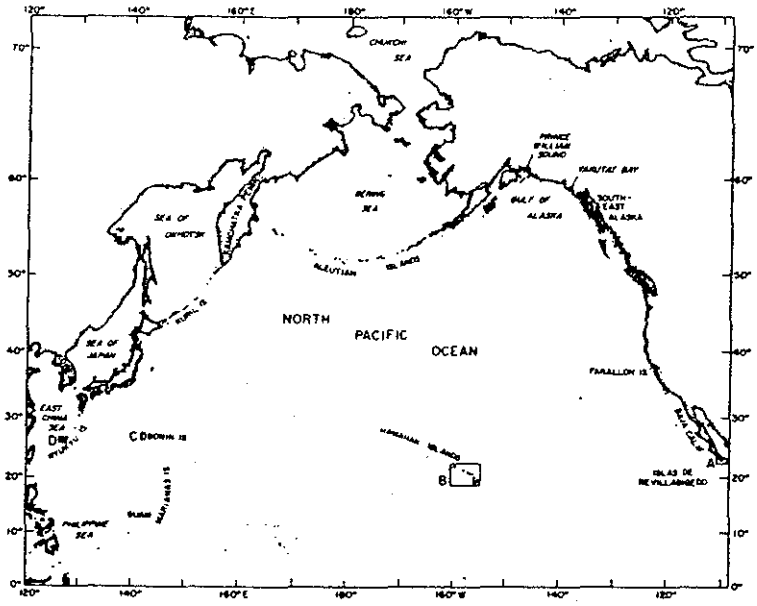

Fig. 1. The North Pacific Ocean, showing documented summer feeding sites for humpback whales from the western Gulf of Alaska through to southeast Alaska and the Farallon Islands (see text). Additionally shown are the locations of the four wintering areas from which songs were obtained in Mexico, the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

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

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.

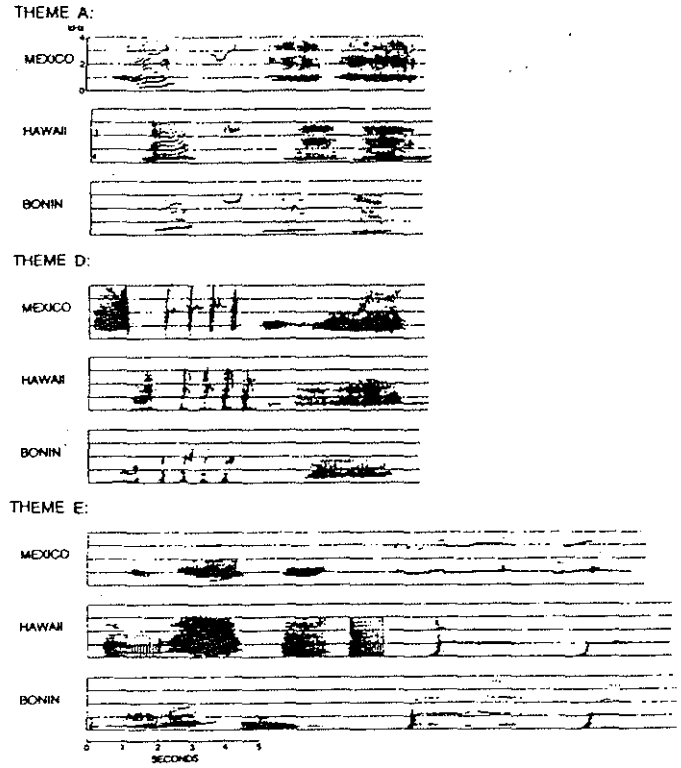

Fig. 3. Comparison of sonograms of "pan-Pacific" themes shared by song recorded in Japan, Hawaii and Mexico. Component subphrases of each theme are shown once in the figure although some may be repeated within any given phrase. Effective filter bandwidth of Kay SonoGraph was 150 Hz. Vertical scale is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

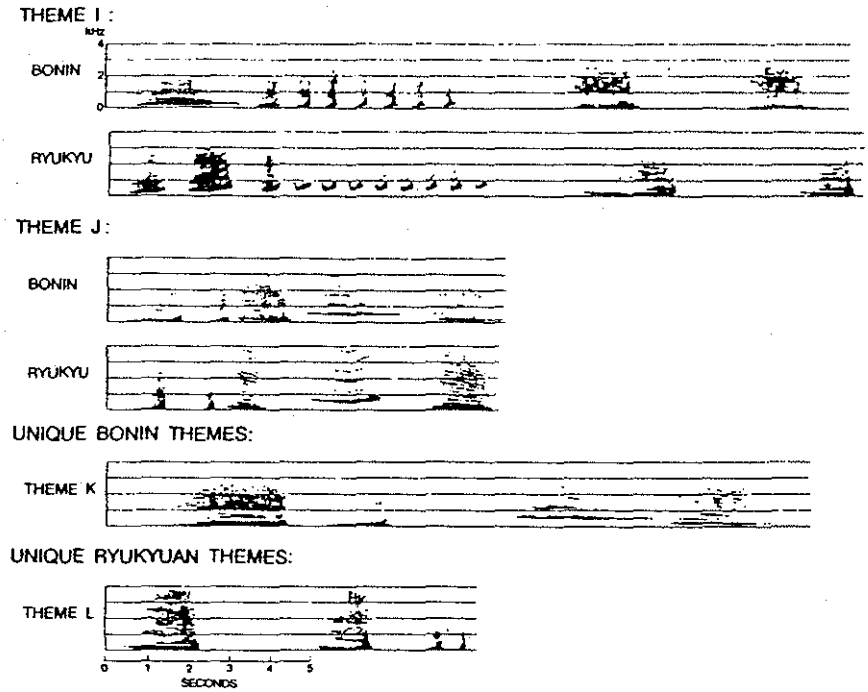

Fig. 6. Sonograms of themes found in Ryukyuan or Bonin song, or both, but not present in song from Hawaii or Mexico, prepared as in Fig. 3.

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.

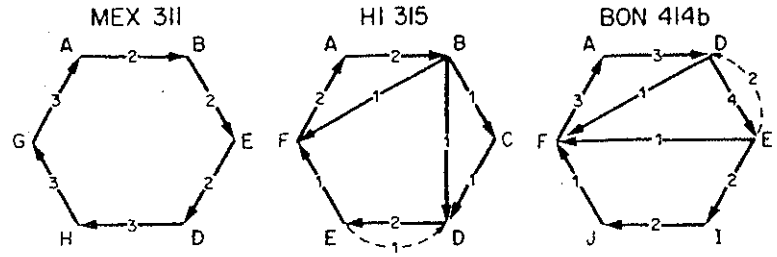

Fig. 7. Theme transitions of selected samples from Mexico, Hawaii and Bonin regions, based on data in Table 3. Frequency of transition is indicated within each arrow. Solid lines indicate usual transition order; theme reversals are indicated by dashed lines.

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.

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

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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