Aquatic Mammals 1999, **25.1**, 35–42

An introduction to the structure of humpback whale, *Megaptera novaeangliae*, song off Ryukyu Islands, 1991/1992

Shane Guan[1], Akira Takemura and Takashi Koido

Laboratory of Fisheries Science, Faculty of Fisheries, Nagasaki University 1–4, Bunkyo Machi, Nagasaki 852, Japan

Abstract

Humpback whale, *Megaptera novaeangliae*, songs were recorded off Ryukyu Islands, Japan, during the 1991 and 1992 winter-spring breeding seasons. Each song was composed of six fundamental themes, each theme was constructed by repeating certain phrases, which were composed of a series of units emitted in a particular sequence. Sixteen different units were recognized among songs recorded during the research period. Among them 13 units were found in 1991 and 14 in 1992 with 11 being shared in both seasons. Besides six fundamental themes, we also found 3 optional themes, themes did not usually occur in a typical full song, in our two-year sample. The average song duration was 7.76 ($\pm$ 1.81) min in 1991 and 11.94 ($\pm$ 4.62) min in 1992.

A visual comparison of sound spectrograms of humpback whale songs from this research with those of Hawaii and Eastern Pacific waters showed remarkable similarity in acoustical characteristics, supporting the notion of overlapping of the humpback population throughout the North Pacific Ocean.

Introduction

Humpback whales, *Megaptera novaeangliae*, produce long and stereotyped sounds during their winter-spring breeding seasons (Winn *et al*., 1970). These sounds are emitted in a highly patterned repeated sequence which lasts from 6 to 30 min. Due to the repeatability of these vocal series, Payne & McVay (1971) defined them as 'songs'. A song is composed of units (or 'syllables' of Winn & Winn (1978)). A unit is defined as 'the shortest sound that is continuous to our ears when heard in ''real time'' ' (Payne & McVay, 1971:590). Units in turn create 'phrases' ('motifs' of Winn & Winn (1978)), phrases create 'themes' ('phrases' of Winn & Winn (1978)), and a 'full song' can typically be composed of 5 to 6 themes (Payne & McVay, 1971; Winn & Winn, 1978).

Unit, phrase, and thematic construction of songs change progressively through different breeding seasons (Payne, 1978; Winn & Winn, 1978; Winn *et al*., 1981; Guinee *et al*., 1983; Payne *et al*., 1983; Payne & Payne, 1985). The fact that all observed singing whales were male (Winn *et al*., 1973; Darling *et al*., 1983; Glockner, 1983) and that the songs were usually only heard from late autumn through early spring within the waters of low latitude breeding grounds suggests that the main functions of songs are for male humpbacks to attract females (Winn & Winn, 1978; Tyack, 1981), and to maintain space among competing males (Winn & Winn, 1978; Tyack, 1981; Frankel *et al*., 1995).

In the North Pacific Ocean, the breeding grounds for humpback whales are divided into three major regions: (1) the central Pacific region, around the waters of the Hawaiian Islands (Herman & Antinoja, 1977; Baker & Herman, 1981, 1994; Darling & Jurasz, 1983); (2) The eastern Pacific region, which includes Baja Peninsula and Islas Revillagigedo off Mexico (Urban & Aguayo, 1987); and (3) the western Pacific region, which includes the Bonin (Ogasawara) Island chain south of Japan and Ryukyu (Okinawa) Islands east of Taiwan (Nishiwaki, 1959, 1961; Tomilin, 1967; Darling & Mori, 1993).

During the past twenty-five years or so, much research has been done on analyzing the structure and composition of humpback whale songs recorded in the central and eastern Pacific breeding grounds (Hawaii: Payne, 1978; Frumhoff, 1983; Guinee *et al*., 1983; Payne *et al*., 1983; McSweeney *et al*., 1989; Hawaii and Pacific Mexico: Winn *et al*., 1981; Hawaii and Islas Revillagigedo: Payne & Guinee, 1983). For the western Pacific region, however, our knowledge of this subject is incomplete (e.g., Helweg *et al*., 1990). We present here a detailed study of the structure of humpback whale song in the Western Pacific.

[1]Present address: U.S. Fish and Wildlife Service-Fisheries, 4401 Fairfax Dr, Arlington, VA 22203, USA.

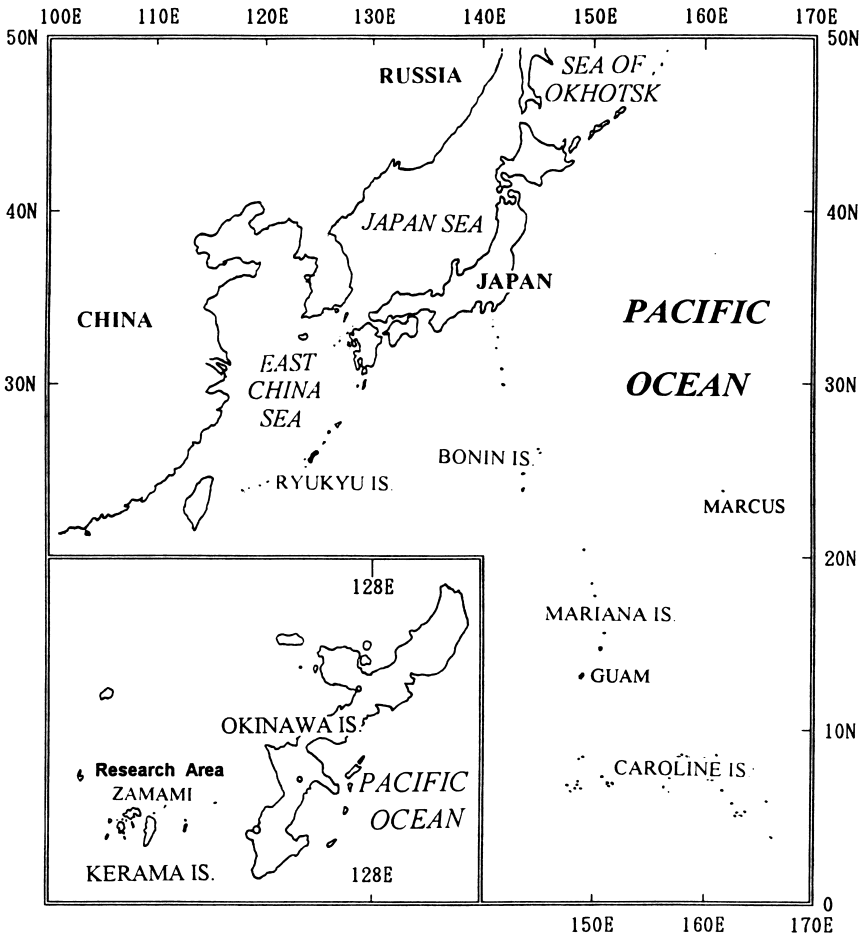

Figure 1. Winter-spring breeding grounds of humpback whale in the northwestern Pacific Ocean. Also showing Zamami, Ryukyu Islands where recordings were made.

Methods

Forty-four field surveys were conducted to collect humpback whale song recordings off Zamami, Ryukyu Islands, Japan (Fig. 1) during the 1991 (January 10 to March 13, 13 surveys) and 1992 (January 21 to March 26, 31 surveys) winter-spring breeding seasons. An SW-1020 Oki Underwater Sound Level Meter (hydrophone) was used as the listening device. Opportunistic recordings were made when a song was heard, although in most cases no whale was sighted. Each uninterrupted recording period was defined as a recording session. Songs were recorded on a Sony TCD-D3 digital audio tape (DAT) recorder.

Sound analysis was conducted by using a sound spectrograph (RION SG-07) which was set to the essential flat frequency response from 30–2500 Hz with an effective bandwidth of 15 Hz (analyzing time 7.2 seconds). For sounds exceeding the upper limit of 2.5 kHz, the flat response was switched into a 85–8000 Hz range with an effective bandwidth of 45 Hz (analyzing time 2.4 seconds). Measurements of frequencies and duration were carried out manually by using a ruler. Narrow band spectra were used to gain the finest resolution of frequency and intonation of the sounds.

This research adopts Payne & McVay's (1971) nomenclature, i.e., 'units', 'phrases', and 'themes' for song structure analysis. All detectable whale sounds were classified by giving each distinguished unit an alphabetic name based on its contour, duration, and fundamental frequency. The whales combined these units into phrases, which were repeated to form themes. Each theme was given a number based on its phrase. The terminal theme,

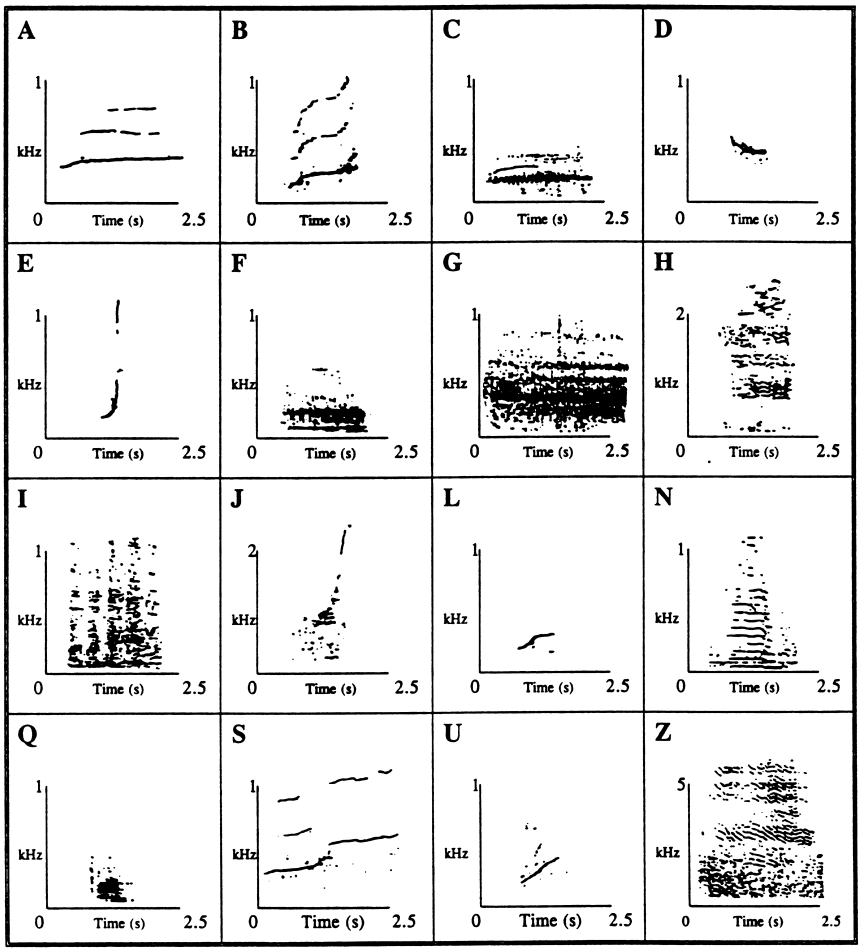

Figure 2. Sonograms of sixteen units which composed humpback whale songs in 1991 and 1992 breeding seasons. Units A, B, C, D, E, F, G, H, J, L, and S were found in both seasons; units I and N were only found in 1991 breeding season; units Q, U, and Z were only found in 1992 season.

i.e., Theme 6 was defined on the basis of similarity of sound spectrograms with the 'surface ratchet' identified in other previous studies (Winn & Winn, 1978; Winn *et al.*, 1981; Helweg *et al.*, 1990). Although this 'surface ratchet' may have nothing to do with the whales' surfacing behavior (P. Tyack, WHOI, pers. comm., 1997), nor were we able to confirm whether the singers emerged after Theme 6 because in most cases there was no whale in sight during the recordings. The universal presence of this theme (Winn & Winn, 1978; Winn *et al.*, 1981; Helweg *et al.*, 1990) led us to define the theme following 'surface ratchet' as Theme 1. Themes occurring after Theme 1 were numbered consecutively. When a song was recorded uninterrupted from the beginning of Theme 1 to the beginning of the next Theme 1, it was defined as a full song. A song session was defined as several full songs being emitted in a consecutive way, presumably from a single whale.

The duration of each theme was measured and the percentage of its average duration in a full song was calculated. Sound spectrograms of full songs were printed on recording papers (RION RP-08) and were later photocopied and carefully put together to be made into an uninterrupted scroll for sequence studies.

For the preliminary statistical analysis, we calculated the mean value of all parameters, such as fundamental frequencies and duration, from a song or song session. By doing so we were able to minimize the bias caused by certain

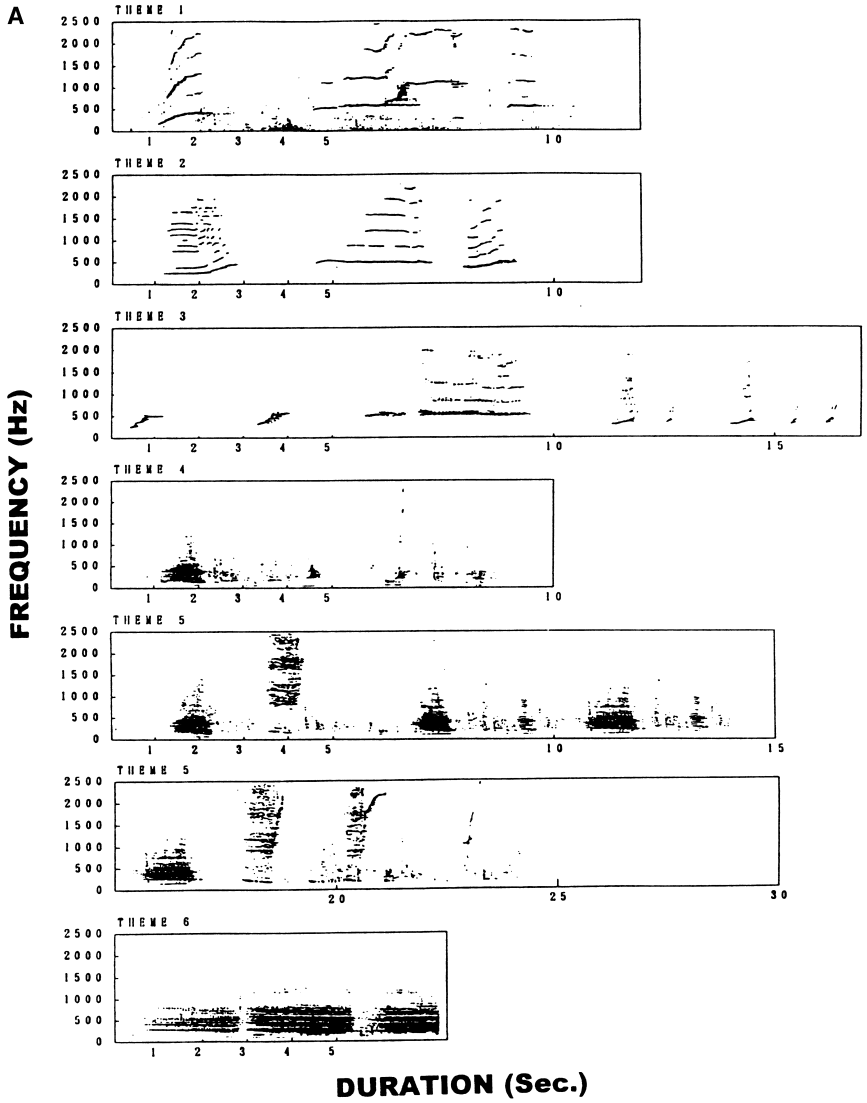

Figure 3A. Sonograms of phrases for six basic themes ('fundamental themes') in 1991 breeding season.

individuals which might contribute more songs in our recordings.

Results

The total of 44 surveys contained 84 recording sessions (23 in 1991 and 61 in 1992) and yielded 16 hours of data for 1991 and 29 hours for 1992. A total of 50 full songs were found in the recordings from both years. Sixteen different units for the humpback whale songs were recognized (Fig. 2). Among them 13 units were found in 1991 and 14 in 1992 with 11 being shared in both seasons. For most units their fundamental frequency fell in the range 0–2500 Hz. Although Unit Z covered a range of 0–8000 Hz, this unit was only detected in 1992 and was very rare.

Six themes were recognized in each of the two years (Figs. 3A and 3B). The mean phrase duration ranged from 7.0–23.4 s, the mean repetition of phrases in a theme ranged from 5–19, the mean theme duration ranged from 20.5–202.4 s, and the percentage of duration for a particular theme in a song ranged from 4.3% to 29.8% (Table 1).

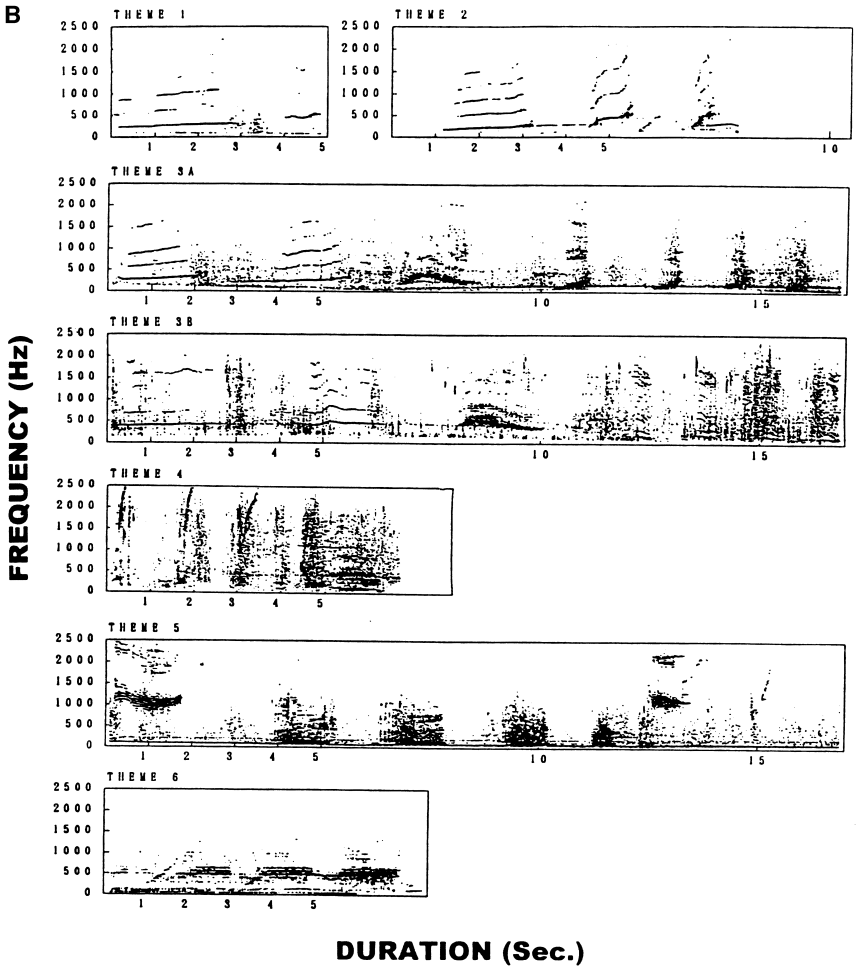

Figure 3B. Sonograms of phrases for six basic themes ('fundamental themes') in 1992 breeding season.

The numbering of themes for 1992 was based on similarities with 1991 themes. The phrase for theme 2 was ABB in both 1991 and 1992. Theme 6 was GGG in both years. The other four themes changed from 1991 to 1992. In 1991, Theme 1 contained 2 units 'A' and 'D', while in 1992 it had 3 units, 'B', 'S', and 'D'. The number of composing units of Theme 3 varied the most, even within the same song, when compared with other themes. In 1991 it had two forms: 3A and 3B. Theme 3A started with one or two A units, followed by a Unit C, and then 3 to 11 L Units; Theme 3B had the same beginning of 3A, but the units following Unit C were C Units instead of L. Interestingly, Theme 3A was heard only on February 7 and March 7, 1991, while Theme 3B was detected on all recording days except on March 7. In 1992 there was only one form of Theme 3 which was similar to Theme 3A of the previous season. It started with one or two U Units, followed by an Unit C, and then 6 to 14 L Units. Theme 4 was the most stable theme and had very little variation through both seasons. The phrase of this theme had 4 units, one 'F' and three 'E's. Theme 5 contained the longest phrase, which lasted for about 20 to 30 seconds. In 1991, the phrase of this theme was 'HFFFFJJJJ'; while in 1992 it became 'FHFQFQFJJJJ'. In some of the songs in 1992 the second 'Q' and the fourth 'F' were sometimes omitted, and the last two 'J's appeared in the form of so called 'complex Hj' units, which means they look like a combination of two 'H' units and 'J' joined together on the sonogram. Theme 6 was designated the last theme of a full song, and contained only one G Unit. After Theme 6 the song

Table 1. Average duration and average repetition of phrases and themes for the humpback whale full songs (n=16 in 1991 and 34 in 1992)

Theme number	Phrases		Themes	
1991	Average duration (sec.)	Average repetition	Average duration (sec.)	% of length in full songs
Theme 1	4.5 ± 5.2	1 ± 1	14.1 ± 16.2	2.9
Theme 2	8.7 ± 1.1	16 ± 5	141.9 ± 42.7	29.5
Theme 3	18.8 ± 2.7	5 ± 2	94.7 ± 32.8	19.7
Theme 4	8.6 ± 1.3	7 ± 2	56.7 ± 20.0	11.8
Theme 5	23.1 ± 5.8	5 ± 2	109.0 ± 28.1	22.7
Theme 6	10.8 ± 2.8	4 ± 2	46.1 ± 17.4	9.6
1992	Average duration (sec.)	Average repetition	Average duration (sec.)	% of length in full songs
Theme 1	10.0 ± 2.3	12 ± 8	121.9 ± 84.1	17.0
Theme 2	10.2 ± 2.8	19 ± 16	183.7 ± 157.4	25.6
Theme 3	22.9 ± 5.9	4 ± 2	94.4 ± 39.5	13.1
Theme 4	11.1 ± 8.2	5 ± 3	49.6 ± 30.2	6.9
Theme 5	23.5 ± 3.1	9 ± 5	209.8 ± 120.5	29.2
Theme 6	13.8 ± 7.4	4 ± 3	55.3 ± 36.3	7.7

was recycled into Theme 1. There was no apparent interval between these two themes in most cases.

Besides the above-mentioned six themes, which we refer to as 'fundamental themes' (Frumhoff, 1983) due to their occurrence in all full songs through both seasons, we also found 3 'unusual' themes in 1991 and one in 1992. These 'unusual' themes were only heard on a few days in a year, and they were termed 'optional themes' (Payne, 1978). Two optional themes of 1991 occurred between Themes 2 and 3, another one was heard between Themes 3 and 4. In 1992, the only optional theme was detected after Theme 6.

A song usually lasted for about 10 minutes, and its length usually depended on the number of repeats of each phrase within a theme. We recorded 16 full songs in 1991 and 34 full songs in 1992. The average duration of full songs calculated from the mean values of song sessions was 7.76 min (n=8, range: 6.68–11.01 min) in 1991 and 11.94 min (n=29, range: 3.97–24.28) in 1992. The difference of song duration between 1991 and 1992 was significant when tested by t-test ($P<0.001$, df=35).

Discussion

This work represents a detailed analysis of the structure of humpback whale songs of the Ryukyu breeding ground in 1991 and 1992 seasons. Our results of the thematic structure, the duration, and the progressive change of humpback songs in two consecutive seasons showed the similar characteristics of songs reported in other breeding grounds. In general, our understanding of this species in the western North Pacific Ocean falls behind when compared with that of central and eastern North Pacific conspecific.

A tentative visual comparison of our sound spectrograms with those from Cerchio's (1993) work showed that the humpback whale song structure in the Ryukyu area shared remarkable similarity with those recorded off Hawaii and Isla Socorro in 1991. This similarity supports the existence of 'pan-Pacific themes', themes shared by humpback whales in the North Pacific, raised by Helweg *et al*. (1990). It also supports the hypothesis that there're contacts among humpback whales in North Pacific (Helweg *et al*., 1990), and indicates a possibility of overlapping of the humpback whale population throughout the North Pacific instead of just central and eastern Pacific, as suggested by most photo-identification studies (Darling & Jurasz, 1983; Darling & McSweeney, 1985; Baker *et al*., 1986) and song analysis (Payne & Guinee, 1983). Although direct evidence supporting the interchange of humpback whales between Bonin Island, Japan and Hawaii was found by matching the photo of only one individual (Darling & Cerchio, 1993) in 1990 and 1991, the scale of such interchange might be larger.

It is very interesting to note the difference in song duration between 1991 and 1992. Such difference in mean song length within the same population in two consecutive years was also noted by Payne *et al*. (1983). Chu (1988) suggested that the duration of a song implies the physical condition of the

singing whales, because longer songs were probably emitted by stronger whales with better diving ability (Chu & Harcourt, 1986; Chu, 1988). On the other hand, one may consider that the shorter songs may be favored because of the faster turning rate, as suggested by Clapham (1996). If song length does provide cues to the physical condition of the competing males, it may indicate that the environment conditions favored singing more in one year than the other in the Ryukyu area.

Acknowledgements

Many thanks to Senzo Uchida, Chief of Okinawa Expo Aquarium, and Naoto Higashi, researcher of Okinawa Expo Aquarium, who generously provided us with many recordings of this work. This work would have been impossible without Yukinobu Taira, Captain of the R/V Koufukku Maru, who operated the boat during the two recording seasons. Kazuaki Watanabe and Kiwamu Miyai, former students of the Fisheries Faculty, Nagasaki University, made some of the recordings in 1991 and 1992 breeding seasons. We are grateful for the proof-reading by Dr. Arch McCallum of the College of Charleston, William Roumillat of the South Carolina Department of Natural Resources, Marine Resources Division, Myra Brouwer, Michael Janech, and Shannon Lund of the Grice Marine Laboratory. We would also like to thank Dr Peter Tyack and two anonymous reviewers. This research was supported by a grant from the Tokai Foundation, Japan.

References

Baker, C. S. & Herman, L. M. (1981) Migration and local movement of humpback whales through Hawaiian waters. *Can. J. Zool.* **59,** 460–469.

Baker, C. S. & Herman, L. M. (1984) Alternative population estimates of humpback whales (*Megaptera novaeangliae*) in Hawaiian waters. *Can. J. Zool.* **62,** 1922–1937.

Baker, C. S., Herman, L. M., Perry, A., Lawton, W. S., Straley, J. M., Wolman, A. A., Kaufman, G. D., Winn, H. E., Hall, J. D., Reinke, J. M. & Ostman, J. (1986) Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Mar. Ecol. Progress Series* **31,** 105–119.

Cerchio, S. (1993) Geographic variation and cultural evolution in songs of humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific. Masters Thesis, San Jose State University. 68 pp.

Chu, K. (1988) Dive times and ventilation patterns of singing humpback whales, (*Megaptera novaeangliae*). *Can. J. Zool.* **66,** 1322–1327.

Chu, K. & Harcourt, P. (1986) Behavioral correlation with aberrant patterns in humpback whale songs. *Behav. Ecol. Sociobiol.* **19,** 309–312.

Clapham, P. J. (1996) The social and reproductive biology of humpback whales: an ecological perspective. *Mammal Review* **26,** 27–49.

Darling, J. D. & Cerchio, S. (1993) Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Mar. Mamm. Sci.* **9,** 84–89.

Darling, J. D. & Jurasz, C. M. (1983) Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 359–368. Westview Press: Boulder.

Darling, J. D. & McSweeney, D. J. (1985) Observations on the migrations of North Pacific humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* **63,** 308–314.

Darling, J. D. & Mori, K. (1993) Recent observations of humpback whales (*Megaptera novaeangliae*) in Japanese waters off Ogasawara and Okinawa. *Can. J. Zool.* **71,** 325–333.

Darling, J. D., Gibson, K. M. & Silber, G. K. (1983) Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii, 1977–79. In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 201–222. Westview Press: Boulder.

Frankel, A. S., Clark, C. W., Herman, L. M. & Gabriele, C. M. (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. *Can. J. Zool.* **73,** 1134–1146.

Frumhoff, P. (1983) Aberrant songs of humpback whales (*Megaptera novaeangliae*): Clues to the structure of humpback songs. In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 81–127. Westview Press: Boulder.

Glockner, D. A. (1983) Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 447–464. Westview Press: Boulder.

Guinee, L. N., Chu, K. & Dorsey, E. M. (1983) Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 59–80. Westview Press: Boulder.

Helweg, D. A., Herman, L. M., Yamamoto & Forestell, P. H. (1990) Comparison of songs of humpback whales (*Megaptera novaeangliae*) recorded in Japan, Hawaii, and Mexico during the winter of 1989. *Scientific Reports of Cetacean Research, Tokyo* **1,** 1–20.

Herman, L. M. & Antinoja, R. C. (1977) Humpback whales in the Hawaiian breeding waters: Population and pod characteristics. *Scientific Report of the Whales Research Institute, Tokyo* **29,** 59–85.

McSweeney, D. J., Chu, K. C., Dolphin, W. F. & Guinee, L. N. (1989) North Pacific humpback whale songs: A comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. *Mar. Mamm. Sci.* **5,** 130–148.

Nishiwaki, M. (1959) Humpback whales in Ryukyuan waters. *Scientific Reports of the Whales Research Institute, Tokyo* **14,** 49–87.

Nishiwaki, M. (1961) Ryukyu whaling in 1961. *Scientific Reports of the Whales Research Institute, Tokyo* **16,** 19–28.

Payne, K., Tyack, P. & Payne, R. (1983) Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 9–57. Westview Press: Boulder.

Payne, R. (1978) Behavior and vocalization of humpback whales (Megaptera sp.). In: K. Norris & R. Reeves (eds) Report on a Workshop on Problems Related to Humpback Whales (*Megaptera novaeangliae*) in Hawaii, pp. 56–78. US Department of Commerce, NTIS PB 280 794.

Payne, R. & Guinee, L. (1983) Humpback whale (*Megaptera novaeangliae*) songs as an indicator of 'stocks'. In: R. Payne (ed.) *Communication and Behavior of Whales*, AAAS Selected Symposia Series, pp. 333–358. Westview Press: Boulder.

Payne, R. & McVay, S. (1971) Songs of humpback whales. *Science* **173,** 585–597.

Payne, R. & Payne, K. (1985) Large scale changes over 17 years in songs of humpback whales in Bermuda. *Z. Tierpsychol.* **68,** 89–114.

Tomilin, A. G. (1967) Mammals of the U.S.S.R. and adjacent countries. Vol. IX. Cetacea. (trans. from Russian.) Israel Program for Scientific Translations. Jerusalem, Israel.

Tyack, P. L. (1981) Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ethol.* **80,** 190–204.

Urban, J. R. & Aguayo, A. L. (1987) Spatial and seasonal distribution of the humpback whale, *Megaptera novaeangliae*, in the Mexican Pacific. *Mar. Mamm. Sci.* **3,** 333–344.

Winn, H. E. & Winn, L. K. (1978) The song of the humpback whale *Megaptera novaeangliae*, in the West Indies. *Mar. Biol.* **47,** 97–114.

Winn, H. E., Bischoff, W. L. & Taruski, A. G. (1973) Cytological sexing of Cetacea. *Mar. Biol.* **23,** 343–346.

Winn, H. E., Perkins, P. J. & Poulter, T. C. (1970) Sound of the humpback whale. In Proceedings of the Seventh Annual Conference on Biological Sonar and Diving Mammals, pp. 39–52. Stanford Research Institute, Menlo Park.

Winn, H. E., Thompson, T. J., Cummings, W. C., Hains, J., Judnall, J., Hays, J. & Steiner, W. W. (1981) Song of the humpback whale: Population comparisons. *Behav. Ecol. Sociobiol.* **8,** 41–46.