

Songs of humpback whales *Megaptera novaeangliae* in the Ryukyu and Bonin regions

Hidemasa Maeda¹, Naoto Higashi², Senzou Uchida³, Fumihiko Sato⁴, Manami Yamaguchi⁵, Takashi Koido⁶ and Akira Takemura⁷

¹Graduate School of Marine Science and Engineering, Nagasaki University, 1-14, Bunkyo-Machi, Nagasaki 852-8131, Japan

^{2,3}Okinawa Exipo Aquarium, Motobu-cho, Okinawa 905-0206, Japan

^{4,5}Ogasawara Marine Center, Byobubani, Chichijima, Ogasawaramura, Tokyo 100-2101, Japan

^{6,7}Faculty of Fisheries, Nagasaki University, 1-14, Bunkyo-Machi, Nagasaki 852-8131, Japan

Abstract. Changes in the songs of humpback whales *Megaptera novaeangliae* in the Ryukyu and Bonin regions of Japan were examined, and songs from the two regions were compared. Eighty-four song sessions in the Ryukyu region, from 1991 to 1997, and eleven song sessions in the Bonin region, from 1992 to 1995, were analyzed. The mean number of theme types was 6.9 for the Ryukyu samples and 7.6 for the Bonin samples. Song similarities were higher within winter than between winters and similarity declined as the number of intervening years increased, indicating that in these regions songs change with time. Song similarities for consecutive years varied, suggesting that the rate of change varies annually. Songs in the same year were very similar in both the Ryukyu and Bonin samples, furthermore site-specific theme types were not found. These results suggest there may be acoustic contact between animals using the two regions, supporting a previous photographic study which indicated that humpback whales migrate between these two regions.

Key words: acoustic contact, *Megaptera novaeangliae*, migration, song similarity.

Humpback whales *Megaptera novaeangliae* migrate between high-latitude summer feeding regions and low-latitude wintering regions where calving and mating take place (Baker and Herman 1984). Known North Pacific feeding regions include: the Sea of Okhotsk, the area of the Aleutian chain, the Bering Sea, the gulf of Alaska, off the south-east Alaskan coast, and off central California (e.g. Nishiwaki 1966; Ohsumi and Masaki 1975; Nemoto 1978; Darling and Jurasz 1983; Baker et al. 1986). Wintering has been observed in three regions, around the main Hawaiian Islands, off coastal Mexico, and in southern Japanese waters around the Ryukyu and Bonin Islands (e.g. Nishiwaki 1966; Ohsumi and Masaki 1975; Herman and Antinoya 1977; Baker and Herman 1981; Darling and Jurasz 1983; Urban and Aguayo 1987; Darling 1991; Darling and Mori 1993). The migration of whales wintering around Hawaii and off Mexico to their feeding regions, has been well studied (e.g. Baker et al. 1986; Darling and Jurasz 1983; Darling and McSweeney 1985; Calambokidis et al. 1997),

but little is known about the migration of whales wintering in the Ryukyu and Bonin regions.

Humpback whales produce long complex vocalizations on their wintering regions (Payne and McVay 1971). These vocalizations are in the form of long repeated patterns and are commonly referred to as "songs". These songs are thought to function in relation to breeding behavior, as only mature males sing (Winn et al. 1973; Winn and Winn 1978; Glockner 1983), and because complete songs are frequently recorded during the winter breeding season (Winn and Winn 1978; Thompson and Friedl 1982). Moreover, songs may serve to proclaim territory, because singing males are usually solitary (Winn and Winn 1978; Tyack 1981).

During the course of each winter male humpback whales are known to change their songs, and the songs of different males steadily converge becoming progressively more and more similar (Winn and Winn 1978; Winn et al. 1981; Guinee et al. 1983; Payne et al. 1983; Payne and Payne 1985). Between geographically isolated oceans, whale songs differ significantly, however within the same ocean males wintering in different regions sing very similar songs (e.g. Winn and Winn 1978; Winn et al. 1981; Payne and Guinee 1983; Helweg et al. 1990; Cerchio 1993; Helweg et al. 1998).

Helweg et al. (1990), who compared songs among the Hawaiian, Mexican, Bonin, and Ryukyu regions, found various common themes. Males in the Hawaiian, Mexican, and Bonin regions shared three common themes, however there were no over-lapping themes between songs recorded in the Ryukyu region and in the Hawaiian and Mexican regions. Helweg et al. (1990) also found two common themes in the songs of males in the Ryukyu and Bonin regions.

The aims of this study were to study humpback whale songs in the Ryukyu and Bonin regions, to clarify song changes taking place within and between years, and to compare the songs between the two regions. Possible contact between whales in the North Pacific Ocean is discussed while comparing the songs recorded during this study with those from previous studies of the Hawaiian and Mexican regions.

Materials and methods

We recorded songs of humpback whales around the Kerama Islands, in the Ryukyu region, from 1991 to 1997, and around the islands of Chi-chi and Ha-ha in the Bonin region from 1992 to 1995 (Table 1; Fig. 1). After confirming that humpback whales were singing, songs were recorded from a drifting boat with the engine switched off. In the Ryukyu region we recorded songs using an Oki ST-1020 hydrophone with a 30 m cable, an Oki SW-1020 preamplifier and a Sony TCD D-3 digital audio tape deck. This recording system was flat, with a frequency response of 3 dB from 20 Hz to 22 kHz. In the Bonin region we used a Sony TC-D5M cassette tape deck, with an unspecified hydrophone and preamplifier.

Aural and spectrographic analysis of the songs (using a Kay CSL model 4300b), revealed that most of the sound energy lay below 4,000 Hz, thus we chose an upper frequency limit of 4,000 Hz using an effective bandwidth of 14 or 29 Hz.

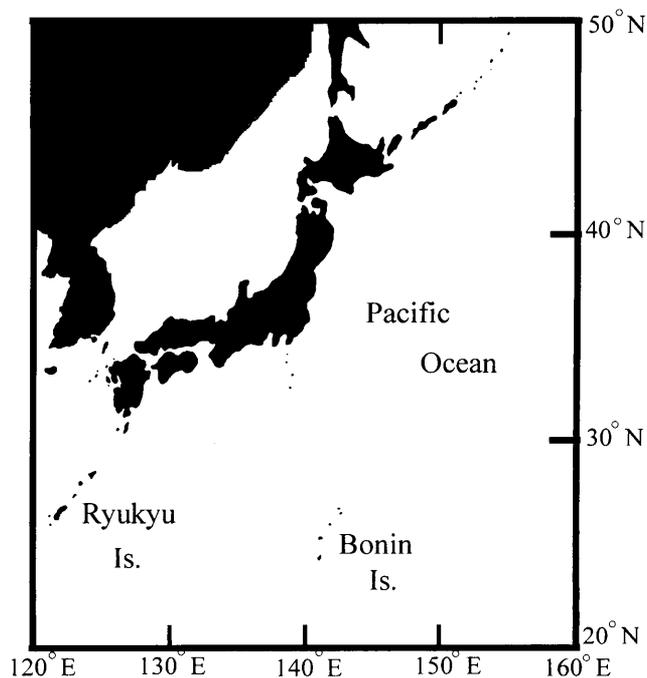
Based on the terminology used by Payne and McVay (1971), we defined a unit as the shortest sound interval that appears continuous to the human ear. Repetition of several units of the same type was defined as a phrase, and a sequence of several phrases of the same or similar types was defined as a theme. A series of several different themes was defined as

Table 1. Summary of recording efforts of humpback whale songs in the Ryukyu and the Bonin regions.

Region	Year	Period	Days	Duration (min)
Ryukyu	1991	10 Jan. – 13 Mar.	13	669
	1992	21 Jan. – 26 Mar.	31	1514
	1993	20 Jan. – 6 Apr.	21	593
	1994	2 Feb. – 29 Mar.	24	1074
	1995	9 Feb. – 27 Mar.	14	702
	1996	25 Feb. – 28 Mar.	9	313
	1997	4 Feb. – 30 Mar.	20	843
Bonin	1992	10 Feb. – 11 May	12	542
	1992/93	22 Dec. – 22 Apr.	13	974
	1994	3 Mar. – 24 Apr.	8	433
	1995	22 Jan. – 12 Mar.	5	229

a song, and a series of songs which did not pause for more than one minute was termed a song session.

We categorized units into unit types. We were able to distinguish unit types from each other by the contours produced on a sound spectrogram. Although contours within the same unit type varied slightly, this variation was generally small compared with those between different unit types. We classified phrases as belonging to the same phrase type when they consisted of the same unit types, and classified themes into the same theme types when they were in the same position in the song and consisted of the same or similar phrase

**Fig. 1.** The locations of the Ryukyu and Bonin Island study regions.

types. When different phrase types occurred alternately, we regarded them as one theme type. We coded unit types by using alphabets, and described phrase and theme types in each song using coded unit types (see Tables 2 and 3).

Earlier studies have considered "ratchet sounds" to be related with surfacing (Winn and Winn 1978; Helweg et al. 1990; Cerchio 1993), however, because we found "ratchet sounds" to occur in singly or together with other unit types each year and to make up phrase types or theme types, we have treated them as one kind of unit type.

We defined a "full song" as a song that was recorded completely from the beginning of the first theme type to the end of the last one. We arbitrarily chose the theme type containing ratchet sounds as the last theme type of a song, and thus the following theme type became the first theme type of the subsequent song. Theme types which occurred after the first theme type were numbered successively.

Incomplete recordings, which started or ended halfway through a song, were excluded from the analyses. We also excluded songs that were not recorded clearly, because of the intrusion of other whale songs or other prominent noises. When more than one full song was recorded during one song session, only one full song was used for the subsequent analysis.

In order to assess how songs change with time, and to compare songs between the Ryukyu and Bonin regions, we calculated a phrase and unit type similarity index by grouping songs by month, year and region. We scored the presence (one) or absence (zero) of each phrase or unit type in each song. As a similarity index, we used Jaccard's coefficient (Sneath and Sokal 1973), which is expressed as the number of phrase or unit types common to two songs, divided by the total number of phrase or unit types present in both songs. A similarity index ranges between zero and one, and is close to one when two songs are very similar, and close to zero when two songs are dissimilar. We calculated the mean similarity indices for every pair of songs both within and between song groups, based on the un-weighted pair-group method using arithmetic averages (Sneath and Sokal 1973). We compared mean similarity indices within and between song groups using non-parametric statistical techniques (Siegel 1956).

Results

General description

Songs consisted of five to eight theme types, many of which included several phrase types (Tables 2 and 3; Figs. 2 and 3). Although songs varied even in the same year within the same region, we selected a standard song for a season in a region based on phrase type, that is, a song consisting of the most common phrase type was regarded as a standard song. For instance, in the 1991 four phrase types (A^nD^n , ABB , B^nCL^n , $H^nQ^nJ^n$) were common in the Ryukyus. Thus, the song shown in Fig. 2 was selected as a standard song. Following this procedure the standard songs in Figs. 2 and 3 were selected, and were compared with each other.

The mean number of theme types constituting a song was 6.9 ± 0.9 (*SD*) for the Ryukyu samples (Fig. 2) and 7.6 ± 0.9 (*SD*) for the Bonin samples (Fig. 3), both of which were in the range of song variation previously reported in other regions. Some songs consisting of five theme types, were actually eight-theme-type songs lacking the third, fourth, and fifth theme

Table 2. Phrase types in each theme type for the Ryukyu sample.

Theme type order	1991 (n=11)	1992 (n=23)	1993 (n=5)	1994 (n=15)
1st	A ⁿ D ⁿ , A ⁿ	A ⁿ D ⁿ , A ⁿ	A + A ⁿ	A + A ⁿ
2nd	ABB, ABL, ALL	BSD, BSB, BD, SD	X ⁿ TB ⁿ	X ⁿ M ⁿ , B ⁿ X ⁿ T ⁿ , B ⁿ X ⁿ , M ⁿ
3rd	A ⁿ CF ⁿ , A ⁿ CL ⁿ , B ⁿ CL ⁿ , ABCF ⁿ	BAB, BOB	BAB, BOB	B ⁿ LM ⁿ *2
4th	K ⁿ F ⁿ *1	CL ⁿ , B ⁿ C ⁿ L ⁿ	B ⁿ CL ⁿ , K ⁿ L ⁿ	LY ⁿ L ⁿ T ⁿ , LY ⁿ L ⁿ , T ⁿ L ⁿ *2
5th	E ⁿ Q	QE ⁿ	K ⁿ R ⁿ , K ⁿ R ⁿ L ⁿ	K ⁿ R ⁿ L ⁿ , K ⁿ R ⁿ , K ⁿ L ⁿ *2
6th	H ⁿ Q ⁿ J ⁿ , H ⁿ Q ⁿ , QH ⁿ Q ⁿ J ⁿ	QHQ(FQ) ⁿ Hj ⁿ J ⁿ , QHQ(FQ) ⁿ , QHQ(FQ) ⁿ J ⁿ , QHQ(FQ) ⁿ Hj ⁿ , QHjJ ⁿ	Fj ⁿ Q ⁿ	Fj ⁿ Q ⁿ , Tj ⁿ Q ⁿ
7th	Ra ⁿ	Ra ⁿ	H ⁿ Q ⁿ	H ⁿ Q ⁿ , HFQ, FQ, HF
8th			Ra ⁿ	Ra ⁿ

Theme type order	1995 (n=9)	1996 (n=7)	1997 (n=14)
1st	A + A - ⁿ	A + A - ⁿ	A + A - ⁿ , A - ⁿ
2nd	X ⁿ N ⁿ	X ⁿ N ⁿ , PN ⁿ , X ⁿ NP ⁿ , BNPX ⁿ	L ⁿ P ⁿ , L ⁿ L ⁿ P ⁿ , FUP ⁿ
3rd	NB	BPN, NB *2	GBP ⁿ , G ⁿ AP ⁿ , G ⁿ P ⁿ , GAFF ⁿ , GAP + ⁿ
4th	T ⁿ L ⁿ , T ⁿ L ⁿ J, L ⁿ J	L ⁿ J *2	GBA, G ⁿ A, GS, G ⁿ W, GAB, GAW, GBS
5th	K ⁿ R ⁿ , K ⁿ R ⁿ L ⁿ J, R ⁿ	K ⁿ R ⁿ *2	ZA, ZS, ZW
6th	VL, VZ, VAZ	VZ, VAZ	Ra - ⁿ , Ra - ⁿ A, Ra - ⁿ W
7th	AZ	AZ, WZ	
8th	Ra ⁿ	Ra ⁿ	

Note: Figure in parentheses: number of song sessions, Capital alphabets: unit types, Ra: unit type Ratchet, n: repetition of a unit type or a set of several unit types, types, *1: phrase types of unique theme types, *2: phrase types of theme types that was absent in some songs, + or -: longer and shorter in duration, Comma appeared in several theme types: separation of different phrase types.

types (Tables 2 and 3; Figs. 2 and 3). Such simple songs did not coexist with eight-theme-type songs in a single song session. In the Ryukyu samples, two out of fifteen song sessions recorded in 1994 were simple, whereas four out of seven were simple in 1996. In the Bonin region, one simple song was recorded out of three sessions in 1994. Simple songs were not

Table 3. Phrase types in each theme type for the Bonin sample.

Theme type order	1992 (n=3)	1993 (n=3)	1994 (n=3)	1995 (n=2)
1st	A ⁿ D ⁿ , A ⁿ	A + A ⁿ	A + A ⁿ	A + A - ⁿ
2nd	BSB, BSD, BSP, BSDP	BSB, BSD, BSDP, X ⁿ TB ⁿ	X ⁿ , T ⁿ , X ⁿ M ⁿ , MN, NB	X ⁿ M ⁿ , NB, B ⁿ
3rd	BAB, BOB, BABP, BOBP	BOB, BAB	B ⁿ LPM ⁿ *1	B ⁿ LN ⁿ
4th	B ⁿ CL ⁿ , CL ⁿ	B ⁿ CL ⁿ , CL ⁿ	LY ⁿ LJ, L ⁿ J, T ⁿ *1	L ⁿ J, LY ⁿ LJ, T ⁿ
5th	K ⁿ L ⁿ , K ⁿ R ⁿ L ⁿ	K ⁿ R ⁿ L ⁿ , K ⁿ , K ⁿ R ⁿ	K ⁿ R ⁿ L ⁿ , K ⁿ R ⁿ *1	K ⁿ R ⁿ L ⁿ , K ⁿ R ⁿ LJ ⁿ , K ⁿ R ⁿ
6th	Q ⁿ E ⁿ , QE ⁿ P	Q ⁿ E ⁿ , Fj ⁿ Q ⁿ , Tj ⁿ Q ⁿ	Tj ⁿ Q ⁿ , (Tj ⁿ P ⁿ) ⁿ Q ⁿ	VP, VAZ, VZ
7th	QHjQ(FQ) ⁿ Hj ⁿ J ⁿ , QHjQ ⁿ , QHjJ ⁿ , QHj ⁿ (FQ) ⁿ J ⁿ , QHj ⁿ PHj ⁿ , QHj ⁿ (FQ) ⁿ Hj ⁿ	H ⁿ Q ⁿ	H ⁿ Q ⁿ , HFQ, F ⁿ Q, HF	AZ, FQ
8th	Ra ⁿ	Ra ⁿ	Ra ⁿ	Ra ⁿ

Note: Figure in parentheses: number of song sessions, Capital alphabets: unit types, Ra: unit type Ratchet, n: repetition of a unit type or a set of several unit types, *1: phrase types of theme types that was absent in the songs of some whales, + or -: longer and shorter in duration. Comma appeared in several theme types: separation of different phrase types.

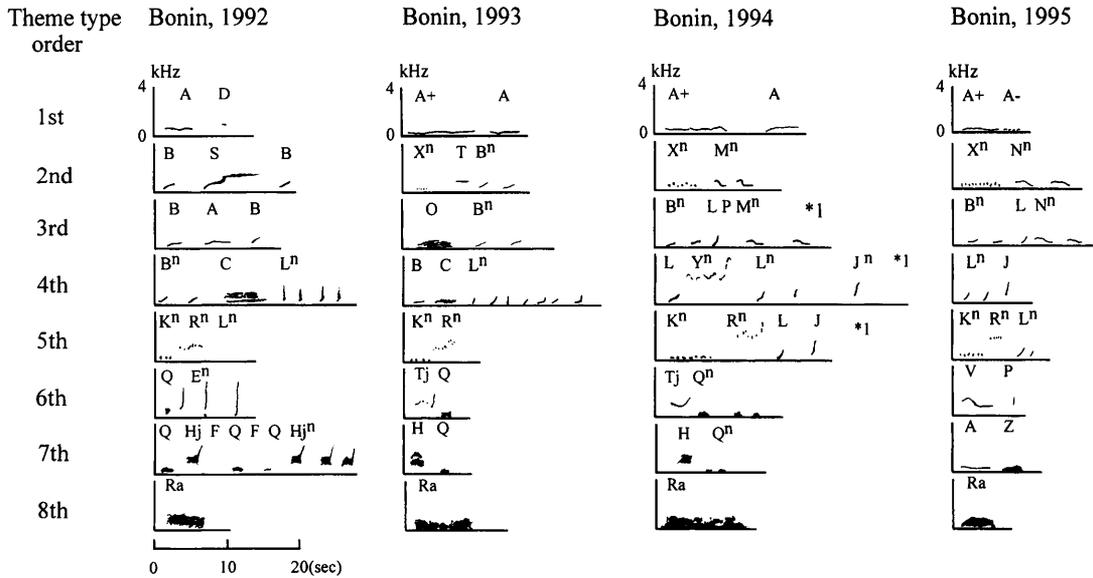


Fig. 3. Illustrated sound spectrograms of typical phrase types in each theme recorded in the Bonin regions from 1992 to 1994. *1 indicates phrase types in the theme types that were absent from some song sessions. Capital letters indicate unit types.

(TjQ)ⁿ in April. Such changes did not occur in other theme types in the 1993 songs (see Fig. 4).

Similarity indices for phrase types within months were significantly higher than those between months in the 1991, 1992 and 1995 Ryukyu samples, but were not significantly different from those between months in the 1993, 1994 and 1997 Ryukyu samples (see Table 4). Similarity indices for unit types within months did not differ significantly from those between months in any of the Ryukyu samples except in 1995. Insufficient data in 1996 in the Ryukyus, and in all other years in the Bonin samples, precluded statistical analysis of

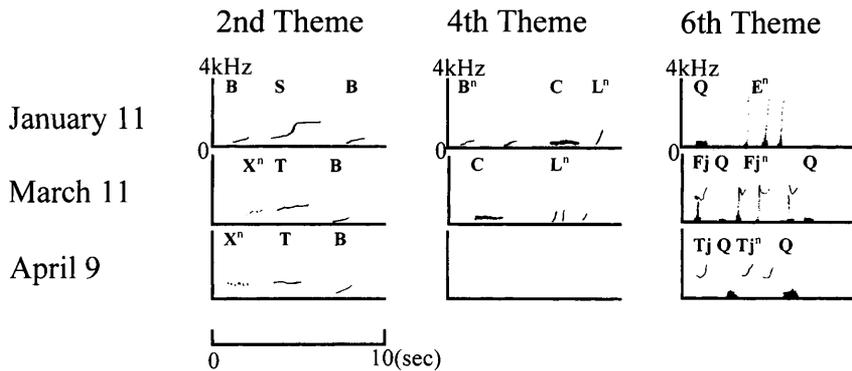


Fig. 4. Illustrated sound spectrograms of phrase types in the 1993 Bonin sample. Capital letters indicate unit types.

Table 4. Mean similarity indices of phrase and unit types within and between months and the results of Mann-Whitney *U*-test (*z*-value).

Region	Year	Number of songs				Phrase type			Unit type		
		J	F	M	A	within month	between months	<i>z</i> -value	within month	between months	<i>z</i> -value
Ryukyu	1991	0	3	8	0	0.73 (31)	0.60 (24)	2.83 *	0.92 (31)	0.95 (24)	1.12 ns
	1992	0	5	18	0	0.79 (163)	0.73 (90)	4.12 ***	1.00 (163)	1.00 (90)	0.00 ns
	1993	0	0	4	1	0.85 (6)	0.86 (4)	9 ¹ ns	0.93 (6)	0.93 (4)	12 ¹ ns
	1994	0	7	8	0	0.57 (49)	0.55 (56)	0.2 ns	0.81 (49)	0.83 (56)	0.63 ns
	1995	0	1	8	0	0.89 (28)	0.67 (8)	3.81 ***	0.98 (28)	0.85 (8)	4.26 ***
	1996	0	0	7	0	0.60 (21)	— (0)	— —	0.80 (21)	— (0)	— —
	1997	0	4	10	0	0.60 (51)	0.59 (40)	0.10 ns	0.83 (51)	0.84 (40)	0.68 ns
Bonin	1992	0	0	0	3	0.72 (3)	— (0)	— —	0.92 (3)	— (0)	— —
	1993	1	0	1	1	— (0)	0.50 (1)	— —	— (0)	0.73 (1)	— —
	1994	0	0	1	2	0.67 (1)	0.41 (2)	— —	0.89 (1)	0.54 (2)	— —
	1995	2	0	0	0	0.71 (1)	— (0)	— —	0.95 (1)	— (0)	— —

Figure in parentheses: Number of pair songs used to calculate mean similarity index

J: January, F: February, M: March, and A: April

¹: *U*-value of Mann-Whitney test

For *z*-value: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant

For *U*-value: * $P < 0.05$, ** $P < 0.02$, *** $P < 0.002$, ns: not significant

similarity indices of phrase and unit types.

No full songs were recorded during January in the Ryukyu Islands, while two full songs were recorded during that month in the Bonin Islands. Using the Bonin samples to study changes in songs over the summer, we calculated similarity indices between April 1992 and January 1993, and those between April 1994 and January 1995. Between April 1992 and January 1993, the mean similarity index was 0.37 for phrase type and 0.70 for unit type. Between April 1994 and January 1995, the mean similarity index was 0.36 for phrase type and 0.71 for unit type. These “summer” values were higher than winter values between January 1993 and March 1993 (phrase type: 0.33; unit type: 0.56).

Comparison between years

The mean similarity indices for phrase types within years were found to be significantly higher than those between years in the Ryukyu and Bonin samples (see Table 5). Mean similarity indices for unit types within years were also significantly higher than those between years in all the Ryukyu samples. In the 1992–1993 and 1993–1994 Bonin samples, the mean similarity indices of unit types within years were significantly higher than those between years, however the value for the 1994–1995 Bonin samples did not differ significantly from that between years, possibly because the 1995 Bonin sample contained only two songs recorded during January. In the Ryukyu sample, the mean of the mean similarity indices of phrase and unit types decreased as the number of years separating them increased (Spearman rank correlation: phrase type: $r_s=1.00$, $n=6$, $P<0.01$; unit type: $r_s=1.00$, $n=6$, $P<0.01$; see Fig. 5). A similar trend was observed among the Bonin samples, but statistical analysis was not possible because of the small sample size.

To see whether songs change at the same rate between years, we compared similarity indices between consecutive years using the Ryukyu samples. This analysis revealed significant differences among similarity indices of phrase types for consecutive years (Kruskal-Wallis test $H=541.0$, $P<0.001$: 1991–1992, $n=253$; 1992–1993, $n=115$; 1993–1994, $n=75$; 1994–1995, $n=285$; 1995–1996, $n=133$; 1996–1997, $n=98$). There was also a significant difference among similarity indices of unit types for consecutive years in the Ryukyu samples (Kruskal-Wallis test $H=599.8$, $P<0.001$: 1991–1992, $n=253$; 1992–1993, $n=115$; 1993–1994, $n=75$; 1994–1995, $n=285$; 1995–1996, $n=133$; 1996–1997, $n=98$).

Similarity between regions

Most of the similarity indices for phrase and unit types within a region were significantly higher than those between regions (see Table 6). However, if small variations in phrase and unit types within seasons were ignored, neither the Ryukyu nor the Bonin region songs had site-specific theme types (Tables 2 and 3; Figs. 2 and 3). When comparing pairs of songs between the two regions, the highest similarity indices were 0.70 for phrase types (1993 sample) and 1.00 for unit types (1993 sample).

Discussion

Songs of humpback whales are highly variable. Even songs recorded in the same region during the same month vary slightly, thus it is not surprising that there is even greater variation between regions. It appears that humpback whales in the Ryukyu and Bonin

Table 5. Mean similarity indices of phrase and unit types within and between years and the results of Mann-Whitney *U*-test (z-value).

Region	Comparison	Phrase type			Unit type		
		within year	between years	z-value	within year	between years	z-value
Ryukyu	1991–1992	0.74 (308)	0.23 (253)	20.40 ***	0.99 (308)	0.76 (253)	20.31 ***
	1992–1993	0.76 (263)	0.23 (115)	15.47 ***	1.00 (263)	0.41 (115)	15.47 ***
	1993–1994	0.59 (115)	0.27 (75)	10.71 ***	0.83 (115)	0.61 (75)	8.21 ***
	1994–1995	0.63 (141)	0.09 (135)	14.28 ***	0.85 (141)	0.37 (135)	14.28 ***
	1995–1996	0.75 (57)	0.48 (63)	6.69 ***	0.90 (57)	0.68 (63)	6.29 ***
	1996–1997	0.60 (112)	0.14 (98)	12.49 ***	0.83 (112)	0.41 (98)	12.49 ***
Bonin	1992–1993	0.57 (6)	0.23 (9)	2 1**	0.77 (6)	0.49 (9)	6 1**
	1993–1994	0.46 (6)	0.21 (9)	0 1***	0.64 (6)	0.49 (9)	9 1*
	1994–1995	0.55 (4)	0.29 (6)	0 1*	0.73 (4)	0.59 (6)	8 1ns

Figure in parentheses: Number of pair songs used to calculate mean similarity index

!: *U*-value of Mann-Whitney test

For z-value: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant

For *U*-value: * $P < 0.05$, ** $P < 0.02$, *** $P < 0.002$, ns: not significant

Table 6. Mean similarity indices of phrase and unit types within and between regions and the results of Mann-Whitney test (z-value).

Year	Number of songs		Phrase type			Unit type		
	Ryukyu	Bonin	within region	between regions	z-value	within region	between regions	z-value
1992	23	3	0.75 (256)	0.38 (69)	12.75 ***	0.99 (256)	0.80 (69)	12.75 ***
1993	5	3	0.75 (13)	0.55 (15)	37 1*	0.86 (13)	0.76 (15)	64 1ns
1994	15	3	0.56 (108)	0.35 (45)	6.89 ***	0.81 (108)	0.65 (45)	5.77 ***
1995	9	2	0.84 (37)	0.26 (18)	5.97 ***	0.95 (37)	0.69 (18)	5.97 ***

Figure in parentheses: Number of pair songs used to calculate mean similarity index

!: *U*-value of Mann-Whitney test

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant

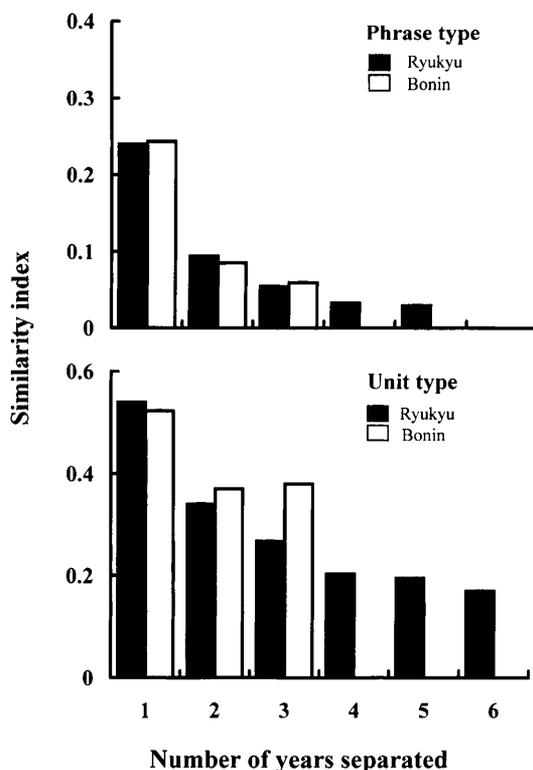


Fig. 5. Changes in song similarity indices between years. Each value was calculated by averaging the mean similarity index by the number of intervening years.

regions change their songs independently.

In the 1993 Bonin sample, three particular phrase types changed during the period from January to April, while others hardly changed during this period (Fig. 4). This observation confirms previous reports that song changes do not occur in all phrase types at the same time (Payne et al. 1983; Payne and Payne 1985; Cato 1991).

Comparisons of songs between years, revealed that in general songs within a year were significantly more similar than those between years, and that song similarity decreased with the number of intervening years, clearly indicating that songs change with time. Furthermore, there were significant differences among the similarity indices for consecutive years, indicating that the song changes did not occur at the same rate. Dawbin and Eyre (1991), who studied songs off the west Australian coast, reported that rapid change occurred from 1986 to 1987 but that only slight changes occurred from 1988 to 1990. In contrast, Payne and Payne (1985) reported that off the coast of Bermuda songs in consecutive years were very similar for nineteen years. Although we do not know what determines the rate of song change, it appears that the rate at which songs change may vary between years and between geographical regions.

Among the Bonin samples, the song recorded in January 1993 was more similar to songs recorded nine months earlier, in April 1992, than to the song recorded two months later in March 1993. Thus, the rate of change of songs appears to be much greater during winter

than across the whole of a summer. This supports Payne et al.'s (1983) and Payne and Payne's (1985) assertions that songs change, not due to forgetfulness during summer, but due to some other mechanism occurring mainly during winter.

Although most similarity indices of phrase and unit types within regions were significantly higher than those between regions (Table 6), no site-specific theme types were identified. This similarity in the songs between the Ryukyu and Bonin regions seems to be similar to the relationship described by Cerchio (1993), who found that the songs of humpback whales in Hawaii and Mexico during 1991 consisted of six different themes, all of which were common to both regions.

The distance between the Ryukyu and Bonin regions is approximately 1,600 km, which makes it less likely that whales in one region are able to listen to the songs in other regions based on the limitation of song propagation (Winn and Winn 1978; Payne and Guinee 1983). Previous studies have found that songs differed significantly between geographically isolated oceans, while songs from different wintering regions within the same ocean were similar (e.g. Winn and Winn 1978; Winn et al. 1981; Payne and Guinee 1983; Helweg et al. 1990; Cerchio 1993; Helweg et al. 1998). It seems likely, therefore, that similarities in songs between the Ryukyu and Bonin regions are due to acoustic contact between individuals from the two regions during at least part of their life cycle.

Payne and Guinee (1983) have proposed three possible forms of acoustic contact: 1) individuals may move between wintering regions within the same winter; 2) individuals may migrate to different wintering regions in subsequent wintering seasons; 3) acoustic contact may occur in the feeding regions or while on migration between the feeding and wintering regions.

Some whales are known to migrate between the Ryukyu and Bonin regions within a single winter (Darling and Mori 1993; Mori 1994; Yamaguchi et al. 1995; Uchida 1997; Calambokidis et al. 1997). Although Yamaguchi et al. (1995) identified photographically a total of 592 whales in the Ryukyu and Bonin regions from 1987 through 1994, they were only able to match five individuals in both regions during the same winter. It seems, therefore that migration between the two regions does occur, but it does not occur frequently, making it unlikely that it is movement between the two regions during winter that maintains song similarity. Given that humpback whales in the same wintering region converge on almost the same songs during any given winter (Winn and Winn 1978; Winn et al. 1981; Guinee et al. 1983; Payne et al. 1983; Payne and Payne 1985), they may be in acoustic contact while in their feeding regions or while migrating between feeding and wintering regions. In fact, songs have occasionally been recorded in late autumn on the feeding regions (Mattila et al. 1987; McSweeney et al. 1989).

The main feeding regions of the humpback whales that winter off southern Japan remain unknown. However, some "Discovery-type" tag data has shown that whales tagged around the Aleutian Islands and in the Bering Sea move to the Ryukyu region, and that some whales tagged in the Bonin region also migrated to the Bering Sea (Nishiwaki 1966; Ohsumi and Masaki 1975). Yamaguchi et al. (1995) matched twenty-two whales as having occurred in both the Ryukyu and Bonin regions in different years during the period from 1987 to 1994, indicating that whales wintering in the Ryukyu and Bonin regions may be in contact while in a feeding region or while migrating between their feeding and wintering regions.

Furthermore, such contact may not be limited just to those whales in the western North

Pacific, it may also occur among humpback whales throughout the North Pacific Ocean. When we compared our sonograms of the 1991 Ryukyu songs (Fig. 2) with those of the 1991 Hawaiian and Mexican songs published by Cerchio (1993), we found that with the exception of one unique theme type, all the theme types were identical. Humpback whales from the eastern Aleutian Islands are known to migrate as far as the Ryukyu region (Nishiwaki 1966), and the eastern Aleutian Islands are very close to the western Gulf of Alaska, the feeding regions of some whales that winter in Hawaii and Mexico. Additionally, photographic studies indicate that whales wintering off Japan, Hawaii and Mexico regions all feed in the eastern and western Gulf of Alaska (Baker et al. 1986; Calambokidis et al. 1997). It is also known that North Pacific humpbacks tend to return to the same wintering region (Calambokidis et al. 1997). It appears then that all North Pacific humpback whales may make contact while on their feeding regions or while migrating between their feeding and wintering regions, and that it is this contact that results in the convergence of their songs.

Acknowledgements: We wish to thank Mr. Yukinobu Taira, captain of the R. V. Koufuku Maru, for his co-operation during data collection for this study. Mr. Shinji Ogasawara, associate professor of Faculty of Education Department of English, Nagasaki University, Mr. U. S. Rao, Research Associate of Laboratory of Plant Pathology & Genetic Engineering College of Agriculture, Okayama University, and Mr. Wendell Hoyseth, Fisheries and Ocean Canada kindly improved the English of a draft manuscript. Dr. Takashi Saitoh, editor-in-chief of Mammal study, anonymous referees and Dr. Mark Brazil helped to further improve the manuscript. Part of this study was sponsored by the Tokai Foundation.

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Received 15 April 1998. Accepted 22 May 2000.