# DISTRIBUTION OF SPERM WHALE STOCKS IN THE NORTH PACIFIC

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## ABSTRACT

Two contrary opinions on the segregation pattern of sperm whale stocks in the North Pacific, i.e. longitudinal vs. latitudinal, were tested using whaling operation data, results of recent sighting cruises, and movements of marked whales.

While Japanese coastal sperm whaling was exploiting the breeding schools, the operation gradually changed from summer to winter and from north to south. In the late 1950s and 1960s most of the whales were taken during summer in the cold Oyashio Current area. During the 1970s whales were taken in the warm Kuroshio Current area in summer and in the Oyashio area in other seasons. In the 1980s most of the whaling occurred in the Kuroshio Current area during the winter. The last phase is certainly undesirable for the industry using whaling stations opened for the northern ground. In recent years sperm whale sightings are rare in summer in the previous whaling grounds north of the Kuroshio Current and its extension.

These changes in the whaling operation and the whale distribution are explained by assuming two latitudinally segregating sperm whale stocks and earlier depletion of the northern one. In the summer adult males move to colder waters segregating from their breeding population as well as adult males of different stocks. This is supported by additional information from blood types, movement of marked whales, operation of Japanese pelagic whaling, and recent whale sightings. We further deduced that the eastern North Pacific is probably inhabited by a single sperm whale stock, although presence of some local stocks is not fully excluded.

The present study also indicates the importance of ocean currents and water masses for the evolution of sperm whale stocks, and provided an example that a habitat vacancy produced by the depletion of one stock is not easily reoccupied by nearby stocks. The successive exploitation of different components of one stock or exploitation of more than one stock with overlapping time period could have masked possible changes in the population structure and some density dependent life history parameters.

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Fig. 1. Japanese whaling stations that have been used for processing sperm whales during the 1955 to 1986 seasons.

## INTRODUCTION

Two contradictory opinions have been published on the segregation of sperm whale stocks in the North Pacific. One assumed that stocks were segregated longitudinally. The others believed that the stocks were segregated latitudinally, although recognizing the presence of some longitudinal segregation.

Although Kasahara (1950) did not clearly state about the stock identity in his study on whale stocks and whaling in Japan, he drew a diagram of sperm whale migration in the western North Pacific. It shows as if he believed that most breeding schools of sperm whales winter in the Bonin Islands

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waters and summer off Sanriku/Hokkaido waters, but that some females winter off Sanriku/Hokkaido waters and summer in the central and northern Kuril Islands area. Then Klumov (1955) presented a hypothesis that there are two breeding stocks one summering in the northern Kuril Islands and the other in the southern Kuril Islands, with similar latitudinal stock segregation in the eastern North Pacific. An exwhaler Watase (1963) published a similar hypothesis. He thought that the breeding schools of the southern stock segregate to the south of the Kuroshio Front with a northern range reaching 40°N in summer (off Sanriku, see Fig. 1) following the shift of the Kuroshio Front, while those of the northern stock principally inhabit waters north of the Oyashio Front. He thought the breeding schools of the two stocks intermingle in the summer in latitudes between 39° and 40°N off the Pacific coast of Japan, although the northern stock will move further south in winter. He also reported an autumn migration of a limited number of singletons or groups of large males to the coastal Oyashio Current area, but its relationship to these stocks was not explained. In the same year, Fujino (1963) found a significant difference in the blood type composition between sperm whales taken by Japanese coastal fishery (both sexes, taken from June to November) and males taken by the pelagic fishery in the central Aleutian Islands/Bering Sea area (51°-53°N, 172°E-165°W) in May to August, and concluded that the western North Pacific is inhabited by two sperm whale stocks and the northern stock migrates in autumn to Japanese waters but the southern stock does not migrate to the Aleutian waters. He also analyzed the movement of marked whales and concluded that sperm whales in the Bonin Islands area belong to the southern stock. Although he does not seem to have clearly mentioned that the northern stock migrating off the Pacific coast of northern Japan includes both sexes, an important factor for the interpretation of the result, his data support that case (see Discussion).

Other studies have proposed a single sperm whale stock in the entire latitudinal range off the east coasts of Japan and Kuril Islands. Masaki (1970) analyzed mark-recapture data, blood types, catch distribution, size composition, and density hiatus appearing in the whale sightings, and assumed three longitudinally segregating stocks in the entire North Pacific, with boundaries at around 170°E-180°E and 150°W-160°W. Later, Ohsumi and Masaki (1977) recognized a hiatus in the female catch in Japanese pelagic whaling in longitudes around 160°W-175°W, and considered it to represent a stock boundary. Although such information was not available to the west of 160°E, they considered from mark recapture data that sperm whales migrating off the Pacific coast of northern Japan and Kuril Islands represent a single stock (western North Pacific stock). They ignored an apparent density hiatus of females appearing in their data at  $35^{\circ}$ – $40^{\circ}$ N and west of  $165^{\circ}$ W, and concluded that there were two (eastern and western) sperm whale stocks in the entire North Pacific. Bannister and Mitchell (1980) analyzed the catch of 19th century whaling between 20°-40°N to find a density hiatus at 145°E, and assumed

three longitudinally segregated sperm whale stocks, i.e. to the west of  $145^{\circ}$ E, in  $145^{\circ}$ E $-179^{\circ}$ E, and in  $179^{\circ}$ E $-150^{\circ}$ W. The current management of the sperm whale population by the International Whaling Commission (IWC) is based on the assumption of two whale stocks in the entire North Pacific, a distribution which has been adopted since the 1979 season (IWC, 1979) and is close to Ohsumi and Masaki (1977).

Ohsumi (1980b) indicated historical changes in the season and fishing ground of Japanese coastal whaling during the past 29 years and attributed them firstly to oceanographic changes, but later to the combination of changes in the oceanography, selectivity between whale species, and decline in sperm whale availability due to the operation of USSR pelagic whaling off Japan (Ohsumi, 1981b). A major oceanographic factor known to affect the Japanese coastal whaling is the fluctuation of the Kuroshio Current as indicated by Uda (1954) and Ohsumi (1980b). The cycle, however, is believed to be 8 to 10 years (Uda, 1954). Since the studies of Ohsumi (1980b, 1981b), sperm whaling has continued in Japanese coastal waters and resulted in a further southward shift of the fishing ground and delay of the peak season (USSR pelagic whaling lasted till 1979, and exploitation of North Pacific sei whales till 1976). If such an uni-directional long time change of the fishery is attributable to change in some oceanographic condition, the total of such change must have been extremely large and should have caused a significant climatic change in the region. Such a change has not been detected.

Under these circumstances, the present study attempts to examine if either of the above two groups of hypotheses on the sperm whale stock off the Pacific coast of Japan can better explain the observed changes in the fishery and in the distribution of sperm whales. In addition we use analogy with the western North Pacific to consider the sperm whale distribution in the eastern North Pacific.

## MATERIALS AND METHODS

Statistics of Japanese land based fishery

The position, number and date of sperm whale catch by the Japanese coastal whaling are used to analyze the historical change in the distribution of the species off Japan. Catch positions of individual whales are available for seasons 1973 to 1985/86, but the corresponding data for 1955 to 1972 seasons are only available by months and by whaling stations (compiled by the Japan Whaling Association). We quoted from Kasahara (1950) the sperm whale catch statistics before World War II, when the species was hunted without regulation of fishing season or of catch quota. These are used in Tables 2 to 11 and Figs 2 to 4. Catch was regulated by national quota in 1959 to 1966, and by agreement between related nations or by IWC since 1970 (Ohsumi, 1980c). The actual figure of the quota varied by the government policy, agreement between countries, or allocation of IWC quota between coastal and

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pelagic fisheries. The reported catch agreed with the quota with a small number of differences. These statistics are used as an indicator of peak month of sperm whale catch, although we believe (without documented evidence) that there has existed unknown number of significant under-reporting in the postwar coastal operations under quota system. Sex ratio or body length compositions are not analyzed in detail. The body length must have been skewed by the misallocation of body length due to the body length regulation ( $\geq$ 30 feet in 1938 to 1948,  $\geq$ 35 feet in 1949–1972, and  $\geq$ 30 feet since 1973, Ohsumi (1980c)). Sex ratio of the catch will not represent the ratio in the population in the whaling ground due to the size selection of the fishery or catch quota by sex (Table 1).

#### Catch by Kuril Islands land based fishery

Sperm whale catches by the USSR land based fishery summarized by month and land station during five years (1950, 1951, and 1962 through 1964) are used to see the difference of migration timing between sexes (Fig. 8). The IWC body length regulation was the same as for Japanese coastal whaling during the period, although the selectivity for larger whales or between sexes could be different.

## Catch by Japanese pelagic fishery

Catch of sperm whales by sex, year, and two degree squares of latitude and longitude have been cited from Smith (1980) and Shimadzu (1987), and used to find density hiatus or geographical variation in sex ratio. These data are used in Figs 9 and 15. The range of Japanese pelagic whaling was modified several times by the Government during the period (Ohsumi, 1973). The limit was (1) north of 45°N in 1952–1966, (2) north of 50°N (west of 159°E), north of 45°N (159°–170°E) and north of 40°N (east of 170°E) in 1967 to 1971, (3) north of 50°N (west of 159°E), north of 45°N (159°–165°E), north of 20°N (165°E–150°W), and north of 35°N (east of 150°E) since 1972. In addition to these regulations Japanese factory ship operation was prohibited, since 1972, after 1 August in a small area off Japan surrounded by 20°N, 45°N, 165°E, and 170°E. The size limit was 35 feet in 1949–1951, 38 feet in 1952–1972, and 30 feet since 1973 (Ohsumi, 1980c), but there are some doubts on the reliability of the length statistics near the above size limits (Allen, 1980).

#### Mark-recapture data

Data include all the available records of whales marked by Canada, Japan, USA or USSR and recovered before 1987 by these countries. The female records were provided by Shimadzu (1987), and male records were compiled from published records of Omura and Ohsumi (1964), Ivashin and Rovnin (1967), Ohsumi and Masaki (1975), Ivashin (1983), and Japanese and USSR progress reports to IWC. Only recoveries made on 11th day or later

from the date of marking are used (Figs 10 to 14).

## Whale sighting data

Sightings of sperm whales were recorded during eleven whale sighting cruises conducted in early summer to autumn in 1983 to 1986 using chartered whale catcher boats *Toshimaru No. 15* (September to October in 1985 and 1986), *Toshimaru No. 18* (June to September in 1986), *Toshimaru No. 25* (June to August in 1983, June to September in 1984 and 1985, May to June in 1986), *Shonanmaru* (June to July in 1983, June to August in 1984, June to September in 1985), and *Kankimaru No. 58* (September to October in 1986). The method of sighting is described in Kasuya (1986a), and is identical to that used in the Antarctic minke whale assessment cruises (Best and Butterworth, 1980). The vessels surveyed 74,274 nautical miles of prefixed trackline spending a total charter period of 761 days. Only presence of sighting effort in squares of one degree longitude and latitude, position of sperm whale sighting and the estimated body length are used in the present study.

## RESULTS

## Changes in the fishing season

Ohsumi (1980c) summarized the history of legal regulation of the sperm whaling season. Until 1951 season, there was no regulation of sperm whaling season in the Japanese coastal waters. The season was set since 1952 at eight months of April to November, and then altered to May–December (1966– 1975) or August–March (1976/77 to present) (Table 1). The industry could operate whaling in any particular period described above. Each whaling company owned several land stations at different latitudes along the Pacific coast of Japan, and operated simultaneously one or two of them according to the seasonal movement of the whaling ground and target species. Although no sperm whales were landed at stations in Kii from 1964 to 1975 (Table 1), the stations were used during the period for short Bryde's whale seasons. Four land stations are currently in use for sperm whaling, i.e. at Ohsawa (Nitto Whaling), Ayukawa (Nihon Whaling), and Wadaura (Nitto Whaling being lent by Gaibo Whaling), and Taiji (Nihon Whaling).

Annual trend in the season of the sperm whale catch from 1955 to 1972 is shown in Table 2 (data of several years are grouped according to the change in the regulation of the fishing season) and that from 1973 to 1985/86 in Fig. 2. The peak catch gradually moved from August/September in 1955–1960 to October/November in 1970–1972 seasons. Even after 1973 season, when detailed catch data became available including the positions of individual whales, this trend in the annual shift of the fishing season further continued, to reach a peak in March in recent years (Fig. 2). It is notable that such uni-directional change of the peak season preceded the alteration of legal regulation. Possibly the legal regulation followed the need of the industry.

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Year	Kii 33.5°N	Boso 35°N	Sanriku 38°–40.5°N	Hokkaido 43°–43.1°N	Fishing season	Catch*
1955	2	_	8	4	Apr. – Nov.	1,506
1956	2	_	8	5	Apr. –Nov.	2,125
1957	1	-	8	5	Apr. – Nov.	2,361
1958	2	1	8	5	Apr. – Nov.	2,588
1959	2	1	8	5	Apr. – Nov.	2,111
1960	2	1	8	5	Apr. – Nov.	2,121
1961	3	-	8	5	Apr. – Nov.	2,110
1962	3	_	8	5	Apr. – Nov.	1,685
1963	2	-	6	5	Apr. – Nov.	1,715
1964	-	-	5	5	Apr. – Nov.	1,800
1965		_	4	4	Apr. – Nov.	1,800
1966	-	-	4	2	May – Dec.	2,101
1967	-	_	4	2	May – Dec.	2,635
1968	_	-	4	2	May – Dec.	3,747
1969	-	-	4	2	May – Dec.	3,667
1970	-	-	4	1	May – Dec.	3,484
1971	-	_	4	1	May – Dec.	3,328
1972		-	4	1	May – Dec.	3,020
1973	-	-	4	1	May – Dec.	2,436
1974	_	-	4	1	May – Dec.	2,361
1975	-	-	4	1	May – Dec.	2,307
1976/77	1	-	4	1	AugMar.	2,487
1977/78	1	1	2	_	AugMar.	2,017
1978/79	1	1	2	_	AugMar.	1,730
1979/80	1	1	2	-	AugMar.	1,269
1980/81	1	1	2	-	AugMar.	1,192
1981/82	1***	1	2	-	AugMar.	869
1982/83	1	1	2	_	AugMar.	439
1983/84	1	1	2	-	AugMar.	393
1984/85	1	1	2	-	AugMar.	400
1985/86	1	1	2		AugMar.	400

#### TABLE 1. NUMBER OF WHALING STATIONS\*\* THAT OPERATED SPERM WHALING OFF . THE PACIFIC COAST OF JAPAN AND RELATED WHALING REGULATIONS

\* Take of females exceeding 15% of the quota has been prohibited since 1979/80 season.

\*\*\* Given for geographical regions.
 \*\*\* Operated using a station in Bonin Islands (26.6°N) instead of the Taiji station on the Kii Peninsula.

#### TABLE 2. MONTHLY CATCH OF SPERM WHALES IN JAPANESE COASTAL WHALING OFF THE PACIFIC COAST OF JAPAN, EXPRESSED AS THE PERCENTAGE OF ANNUAL CATCH

Year						Month				
1 Cal	Apr.	Мау	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total*
1955-60	6.5	6.3	6.8	9.4	22.2	26.6	13.6	8.6		100 (12,837)
1961-65	1.4	3.4	5.5	9.0	20.6	34.5	17.3	8.4	-	100 ( 9,099)
1966-69	_	1.4	3.4	2.9	16.5	24.8	22.1	19.1	9.8	100 (12,150)
1970 - 72	-	1.5	1.6	3.4	8.7	20.8	29.3	22.7	12.0	100 ( 9,831)

\* In parentheses are total number of catch representing the monthly catch.



Fig. 2. Monthly distribution of sperm whale catch by Japanese coastal whaling.

The shift of the peak fishing season continued even after the ban on catching sei whales in 1977.

## Whaling ground

The whaling companies gradually closed their stations in northern Japan from 1963 through 1977, and several major companies ceased coastal whaling during the period, although this change might not be attributable solely to availability change of sperm whales but also to that of sei whales or to prefer-

Land stations by region	Kii 33.5°N	Boso 35°N	Sanriku 38°–40.5°N	Hokkaido 43°–43.1°N	Total
1955-60	1.9	0.4	32.1	65.6	100
1961-65	0.7	0	46.3	53.0	100
1966-69	0	0	71.4	28.6	100
1970-72	0	0	88.5	11.5	100

TABLE 3. NUMBER OF SPERM WHALE LANDINGS BY REGION AND WHALING SEASONS, EXPRESSED AS THE PERCENTAGE OF THE ANNUAL CATCH (BASED ON THE SAME DATA AS TABLE 2)

ence of industry for pelagic whaling over land based operation. Since 1977, coastal sperm whaling has been operated by two companies using four stations (Table 1).

Most of the sperm whale catch (65%) was landed at stations in Hokkaido (north of 43°N) during 1955–1960, but the proportion continued to decline after this and landings in Sanriku (38°–40.5°N) increased to attain 88% of the total sperm whale catch in 1970–1972 seasons (Table 3). This trend further continued in 1973 through 1985/86 seasons. In 1973 the major ground was in the latitudes of  $34^{\circ}$ – $39^{\circ}$ N with a peak in  $37^{\circ}$ – $38^{\circ}$ N (Figs 3 and 4). In 1977/ 78 season the catch occurred also in the additional latitudes of  $32^{\circ}$ – $33^{\circ}$ N or between Boso and Bonin Islands. Then during 1978/79 through 1982/83 seasons catch in the northern ground ( $34^{\circ}$ – $39^{\circ}$ N) declined and became almost negligible since 1983/84 season. The operation in 1981/82 season was exceptional because a station in the Bonin Islands was used only for one season. Recent catches occur in winter and mostly in  $29^{\circ}$ – $33^{\circ}$ N and  $130^{\circ}$ – $145^{\circ}$ E, which is quite different from the operation in the 1950s and 1960s done in summer and in higher latitudes.

The above change is hard to attribute to short cyclic fluctuations in oceanographic conditions because it lasted too long (over 30 years), nor to a selectivity change between whale species because the change continued both before and after the ban on catching sei whales in 1977. If we consider the fact that the two whaling stations (Taiji and Wadaura) in the south can process only meat, and that the other parts of the carcass (viscera, blubber and bone) have to be transported for the final processing to the northern stations in Sanriku (Ayukawa and Ohsawa), which in a straight line are 500 to 700km apart from the corresponding southern ones, we can reasonably presume that above mentioned change in the fishing ground is due to a decline in availability of sperm whales in the northern ground.

#### Seasonal and latitudinal changes in the coastal operation

Latitudinal and monthly distributions of the catch are shown in Tables 5 to 11. Several fishing seasons are combined according to the above mentioned changes in the regulation of whaling season and latitudinal range of operation.



Fig. 3. Latitudinal distribution of sperm whale catch by Japanese coastal whaling.

Some catches for research purposes are included.

Data from biologists indicate that the sperm whale catch was composed mostly of females in summer off Hokkaido (>43°N) and Sanriku  $(38^\circ-41^\circ N)$ (Table 4) or in winter (January and February) in  $36^\circ-40^\circ N$  (Ohsumi and Satake, 1980). These agree with the analysis of prewar statistics by Kasahara (1950; see Table 5) or postwar statistics by Ohsumi (1980b), and indicate that

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the catches are plotted for other seasons. Each mark represents one sperm whale.

the fishery exploited the breeding schools.

In the late 1950s, sperm whaling started in April and slightly over half of the total catch was obtained off Sanriku (April to June), then the ground shifted to Hokkaido to the north (July to October), but this pattern changed from the late 1960s so that greater catches were made off Sanriku in any month (Table 6). And in the three years of 1973 to 1975 when individual catch positions became available, the season started in May at  $34^\circ$ - $39^\circ$ N, then the area of peak catch shifted in summer slightly to the south ( $33^\circ$ - $36^\circ$ N), and again returned to the north ( $37^\circ$ - $39^\circ$ N) in autumn (Table 7). The last feature was the same in the 1976/77 and 1977/78 seasons when the fishing season was extended to March (Table 1). Most of the winter (December–March) catch

 TABLE 4. PROPORTION OF FEMALES IN THE CATCH OF JAPANESE COASTAL

 SPERM WHALING EXAMINED BY BIOLOGISTS, 1960 THROUGH 1965

Land stations	Sex	May	June	July	Aug.	Sep.	Oct.	Nov.	Total
Hokkaido	male	0	8	39	246	444	200	20	957
	female	0	0	64	371	1345	691	73	2544
	(%)	-	0	63	60	75	78	79	73
Sanriku	male	16	52	111	218	93	49	15	554
	female	4	77	130	351	202	124	78	966
	(%)	20	60	54	62	68	72	84	64

TABLE 5. PROPORTION OF FEMALES IN THE CATCH OF JAPANESE COASTAL SPERM WHALING IN 1940 THROUGH 1948, WHEN THERE WAS NO REGULATION OF SEASON OR QUOTA (EXTRACTED FROM TABLE 29 IN KASAHARA, 1950)

Month		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Kuril Is	М	_	_	_	1	144	338	440	558	189	40	2	1
	F	_	_	-	-	-	11	62	101	1	4	_	_
	%	-	-	-	0	0	3	12	15	1	9	0	0
Hokkaido	М	-	6	8	14	35	44	27	33	268	257	71	16
	F	_	3	빗민	13		9	16	10	130	179	105	18
	%	_	- 33	ST 0	48	24	A(17)	37	23	33	41	60	52
Sanriku	М	100	73	75	90	155	357	444	421	330	448	422	255
	F	124	69	37	38	143	221	526	661	528	534	522	151
	%	55	49	33	30	48	38	54	61	62	54	55	37
Boso	М	16	20	11	43	56	12	12	1	3	1	2	14
& Kii	F	4	3	3	24	13	1	5	_		_	_	-
	%	20	13	21	36	19	8	29	0	0	0	0	0
Bonin Is	Μ	17	55	148	116	17	_		-	_	-	-	_
	F		56	209	196	65		_	_		_	_	_
	%	0	50	59	63	79	_	_	_		_	_	_

M: number of males, F: number of females, %: female proportion in %.

occurred at 36°-40°N (Table 8).

Off the Pacific coast of Japan the fronts of the cold Oyashio Current and warm Kuroshio Current situates at around 35°N and 40°N, respectively, and the surface water temperature in the intermediate area alternates seasonally close to either of the two currents with considerable annual and local variations

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Whaling stations	Apr.	Мау	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
1955 to 1960												
Hokkaido	341	280	264	781	2211	2792	1419	334				8422
Sanriku	314	500	548	420	625	612	332	770				4121
Boso	40	8										48
Kii	144	21	66	8	7							246
1961 to 1965												
Hokkaido	44	31	155	416	770	1883	1061	466				4826
Sanriku	37	269	336	401	1103	1255	515	295				4211
Kii	45	10	5	2								62
1966 to 1969												
Hokkaido		5	81	52	235	880	1086	896	236			3471
Sanriku		161	330	306	1765	2138	1603	1425	951			8679
1970 to 1972												
Hokkaido		17	51	53	65	126	414	376	16			1130
Sanriku		128	109	283	792	1920	2458	1848	1163			8701

TABLE 6. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE COASTAL WHALING IN THE PACIFIC, 1955 TO 1972 SEASONS

# TABLE 7. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE COASTAL WHALING IN THE PACIFIC, 1973 TO 1975 SEASONS

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
43°-44°N		1				7				<u> </u>		8
42°-43°N	1	5	8	7	14	8						43
41°-42°N	4	5	2	2	14	3						30
40°-41°N	2		S 4	UTEIC	FCE			SEANC				19
39°-40°N	3	1			4	23	67	98				196
38°–39°N	12	10		1	3	151	228	283				688
37°–38°N	16	21	2	4	26	297	645	861	10			1882
36°-37°N	26	18	8	29	91	867	1036	1078	33			3186
35°-36°N	33	57	56	56	183	184	75		25			669
34°–35°N	19	97	34	40	127	37		8				362
33°–34°N	4	16	17	14	28	19						98
32°33°N			1		5							6
31°-32°N			1									1
Total	120	231	133	154	496	1596	2051	2339	68			7188

(Mizuno and White, 1983), and possibly with a cyclical fluctuation of 8 to 10 years (Uda, 1954). The boundary area probably corresponds to the western part of the Subarctic Boundary of Favorite, Dodimead and Nasu (1976). The seasonal shift of the sperm whaling ground shown above is the reverse of the seasonal movement of the oceanography, and can be explained only by assuming that there were two groups or stocks of female sperm whales mainly inhabiting each in the Kuroshio and Oyashio Currents. The industry exploited more northern stock individuals in summer and autumn in postwar period

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
40°-41°N									51	6	9	66
39°40°N						6		7	315	75	26	429
38°–39°N				3				38	146	182	129	498
37°-38°N				3		43	116	385	95	213	203	1058
36°-37°N						7	270	647	416	562	216	2118
35°-36°N						25	18	3	53	8	8	115
34°35°N						51	18		26			95
33°34°N				1	3	23	34		22			83
32°–33°N					11	18	20					49
31°–32°N 30°–31°N							2					2
29°–30°N 28°–29°N 27°–28°N											1	1
Total				7	14	173	478	1080	1124	1046	592	4514

TABLE 8. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESECOASTAL WHALING IN THE PACIFIC, 1976/77 AND 1977/78 SEASONS

 TABLE 9. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE

 COASTAL WHALING IN THE PACIFIC, 1978/79 THROUGH 1980/81 SEASONS

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
40°-41°N		—H <sub>x</sub>	即回	リ法ノ	V E	本照	家類的	托凡	T	77	15	92
39°-40°N							IN RES			41	60	102
38°39°N				4		1		23	27	91	130	276
37°–38°N				1	1	2	1	86	83	113	244	531
36°-37°N					1		25	143	251	101	131	652
35°-36°N					3	4	43	66	57	102	34	309
34°–35°N					3	47	74	41	26	188	118	497
33°34°N					5	61	109	112	71	150	441	949
32°–33°N					4	13	109	86	37	87	161	497
31°32°N				2	7	11	6	15	9	6	1	57
30°-31°N					4	16	3	3				26
Total				7	28	155	371	575	561	956	1335	3988

before the 1960s, and started in the early 1960s to take a significant catch from the southern stock on the summering ground and from the northern stock on the wintering ground. This interpretation have some agreement with

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
41°–42°N 40°–41°N						2						2
39°-40°N										12	43	55
38°39°N						4				8	60	72
37°–38°N										11	36	47
36°-37°N											34	34
35°-36°N						1				4	22	27
34°-35°N						8	6		16	32	35	97
33°34°N						12	10	19	41	42	79	203
32°-33°N						21	8	5	8	25	24	91
31°–32°N						33	26	35	24	30	2	150
30°-31°N						5	19	21	11	13		69
29°–30°N							21	10	9	1		41
28°–29°N						2	3			22		27
27°–28°N						7	4	3	22	47	50	133
26°–27°N						17	10	2	36	34	48	147
25°-26°N					3	1		1	10	17	6	38
24°25°N					1							1
Total					4	113	107	96	177	298	439	1234

 TABLE 10. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE

 COASTAL WHALING IN THE PACIFIC, 1981/82 AND 1982/83 SEASONS

 TABLE 11. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE

 COASTAL WHALING IN THE PACIFIC, 1983/84 TO 1985/86 SEASONS

Latitude	Мау	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Toțal
40°-41°N		ń	n.a→a			л <b>— н</b> — а	± + + − − −	TT of the Ta		7	34	41
39°–40°N 38°–39°N											19	19
37°–38°N								20		3	7	30
36°-37°N							2	14		5		21
35°36°N						5	1	12		5		23
34°–35°N						12	3	23	53	7	67	165
33°34°N						31	22	25	18	65	60	221
32°33°N						21	8	4	29	42	28	132
31°-32°N						33	47	46	35	36	49	246
30°-31°N						29	75	30	31	42	41	248
29°-30°N						20	17	7			2	46
Total						151	175	181	166	212	307	1192

the previous analyses of fishery oceanography. Uda (1954) states that sperm whales are scarce in the middle of the Kuroshio Current System (Kuroshio Current and Kuroshio Extension), but are dense on both sides of the current. Several authors indicated bimodal catch of sperm whales off the Sanriku coast; July–August and October–November (Kasahara, 1950), or July–early September and early October–late November (Uda and Dairokuno, 1957). Although it is unclear if their ocean-ographical terminology accurately corresponds to ours, there seems to be some similarity with the result of the present study.

In the 1978/79 season the industry started operating both in the southern  $(32^{\circ}-35^{\circ}N, autumn)$  and northern  $(36^{\circ}-39^{\circ}N, winter)$  latitudes (Table 9), and this pattern lasted till the 1980/81 season. Although this pattern was principally retained in the 1981/82 season, the industry took sperm whales in autumn/ winter using a land station in the Bonin Islands with resultant catch in 25°-30°N only in this particular year (Table 10 and Fig. 4). Sperm whales taken from the northern stock on their wintering ground  $(35^{\circ}-40^{\circ}N)$  continued till the 1982/83 season, but it became negligible from the 1983/84 season when the fishery expanded to the southwest (Table 11 and Fig. 4).

The above analysis is summarized as follows. Although both stocks had been hunted by Japanese coastal whaling since before World War II, in the postwar period before the early 1950s most of the sperm whales were caught from the northern stock. A significant number of whales started to be taken from the southern stock probably in the late 1950s in the northern part of its summer range, while operations in other seasons took mainly from the northern stock. However, the proportion of whales from the southern stock probably did not show rapid increase till the 1978/79 season, because the take from the northern stock on the wintering ground continued by extending the fishing season to March. Exploitation of the southern stock for the entire whaling season started in late 1970s, and the hunting of the northern stock became negligible since the early 1980s.

#### Other information on sperm whale distribution

Fig. 5 shows the distribution of sperm whales taken in Japanese waters by American whaling operations during the middle 18th to early 20th centuries (Townsend, 1935). The catch off the Pacific coast of Japan occurred in those days in two isolated areas, one in 35°–40°N and west of 150°E, and the other in an area extending from 28°N, 135°E to 30°N, 180°. The main season for the former ground was May–July, and that for the latter was April–July (west of 143°E) or June–September (east of 143°E). The former ground probably represents sperm whales of the northern stock which winter there and have been hunted by modern coastal whaling in the early summer of the 1973– 1975 seasons and in the winter of the 1977–1983 seasons. However, there remains a possibility that some individuals from the southern stock are included in the periphery of the main range. The hiatus in distribution between the two fishing grounds roughly corresponds to the low density area



Fig. 5. Distribution of sperm whale catches from the records of 19th century American whale fishery. Plots represent positions of vessels on days when one or more sperm whales were taken (modified partial reproduction of Townsend, 1935).

in the middle of the Kuroshio Current System indicated by Uda (1954). Although the northern range of the southern stock of females approximately coincides with the Kuroshio Front, its primary habitat will be to the south of the Kuroshio Current and its extension.

Recent whale sighting cruises in summer off the Pacific coast of Japan indicate that most sperm whale sightings are limited to the south of the fronts of the Kuroshio Current System, and that the density is high to the south of these currents, which agrees with the feature observed in America whaling and recent Japanese coastal whaling operations. Spending a considerable sighting effort off the Pacific coast of northern Japan, we have confirmed that recent sperm whale density is extremely low in summer to the north of 35°N (past coastal whaling grounds off Sanriku and Hokkaido) (Figs 4, 6 and 7).

In the northern North Pacific and Bering Sea only 15 sperm whales in 4 schools have been sighted during five Dall's porpoise sighting cruises with a total period of 202 days from May to October, i.e. 17 August to 19 September 1982 (Kasuya, 1982a; Kasuya and Ogi, 1987), 10 August to 11 September 1983 (Ogi, 1983; Kasuya and Ogi, 1987), 10 May to 20 June 1984 (Miyazaki, Fujise, Komuro and Taketomi, 1984), 6 August to 16 September 1985 (Ogi, Tanaka, Kuramochi and Yamamoto, 1986; Kasuya and Ogi, 1987), and 9 August to 6 October 1986 (Yoshioka, Ogura and Shikano, 1987). Because



Fig. 6. Distribution of sperm whales observed during the whale sighting cruises in 1983 to 1986, May to July. Star indicates school containing individuals 46 feet or over in body length, and closed circle school of smaller whales. Shaded area represents one degree squares of latitude and longitude not surveyed.

Dall's porpoises are distributed to the north of the Subarctic Boundary (Kasuya and Jones, 1984), the survey area covered past grounds for sperm whales to the north of 40°N. Although all the cruises had experienced whale biologists on board, only the 1982 cruise had an observer with experience of commercial whaling. The target species of the cruise was the Dall's porpoise which was usually sighted within 0.5 nautical miles from the trackline (Bouchet, Ferrero and Turnock, 1986; Kato and Miyazaki, 1986). These factors could have caused a lower sperm whale sighting efficiency of the cruises compared with those off Japan (Figs 6 and 7). However, we still consider that these data indicating low sperm whale density in the previous whaling grounds are significant, because the number was less than one fourth of the sum of the blue, fin, sei and humpback whales identified to species (51 individuals in 20 schools). The historical southward shift of the sperm whaling ground. (Ohsumi and Masaki, 1977) will therefore indicate the density decline in the northern grounds.

It will be concluded from this that the sperm whales that once wintered



Fig. 7. Distribution of sperm whales observed during the whale sighting cruises in 1983 to 1986, August to October. For marks see Fig. 6.

in the western North Pacific north of 35°N and were hunted by the Japanese and USSR coastal and pelagic whaling operations have been extremely depleted.

## Segregation of adult males

Table 12 shows the frequency of estimated body lengths of sperm whales listed in Figs 6 and 7. The majority of them were individuals below 40 feet (12.1m) and about 5% of the individuals with body length estimates were calves ( $\leq 20$  feet), indicating that the North Pacific area south of the Kuroshio Current System is inhabited in early summer to autumn season by breeding schools of the sperm whale.

However, some sperm whales have been estimated at over 46 feet (13.9m) in body length, which are expected to be mature males in the North Pacific and Southern Hemisphere (Ohsumi, 1966; Best, 1979) (Table 13). These individuals were singletons or found with relatively large individuals (over 42 feet or 12.7m), suggesting that adult males were solitary or formed schools with pubertal males but they were not in breeding schools. This agrees with the observation of sperm whales off the Galapagos Islands that the mature males are associated with a particular group of females only for a periods of hours at a time (Whitehead, 1987). Although all six schools of adult males in June and July were sighted in latitudes similar to that of the breeding schools (Fig. 6), many of those in August tended to be segregated

Body length	May to July	August to Oct.	Body length	May to July	August to Oct.
≤13	8	4	36	40	6
14			37	40	8
15	2	2	38	45	8
16	1		39		
17	3	5	40	42	8
18	3		41	8	
19			42	27	3
20	13		43	5	6
21			44	3	2
22			45	4	4
23	1	2	46	5	
24			47		
25	7	1	48	3	
26	2 3	2 2	49	1	
27			50	2	6
28	18	17	51		5
29		3	52		8
30	40	31	53	1	2
31	15	16	54		1
32	32	24	55		1
33	57	25	Total	543	256
34	34	19	Calves*	62	34
35	78	35			

#### TABLE 12. COMPOSITION OF ESTIMATED BODY LENGTHS (IN FEET) AND NUMBER OF CALVES IN THE SPERM WHALE SIGHTINGS IN FIGS 6 AND 7

\* Number of calves, includes both those having body length estimation and listed in the frequency and those without length estimation.

# TABLE 13. POSITION AND SCHOOL STRUCTURE OF LARGE MALE SPERM WHALES (≥46 FEET) IN TABLE 12, FIG. 6 AND FIG. 7

Date	Position	School size	Body length composition (ft)
15 June '83	30°29'N, 137°32'E		53
23 June '86	24°59'N, 147°57'E	1	48
3 June '84	31°31'N, 143°26'E	1	50
9 July '83	22°33'N, 158°05'E	5	46×2, 48×2, 50
16 July '84	12°36'N, 147°41'E	9	42×3, 44×3, 46×3
22 July '84	15°51'N, 158°47'E	1	49
6 Aug. '86	26°37'N, 142°44'E	9	50×4, 51×3, 52×2
13 Aug. '84	34°23'N, 152°36'E	9	50×2, 51, 52×4, 54, 55
13 Aug. '84	34°29'N, 152°24'E	1	53
18 Aug. '84	38°11'N, 157°26'E	1	52
18 Aug. '84	38°03'N, 157°15'E	2	51, 52
18 Aug. '84	37°57'N, 157°21'E	1	53



Fig. 8 Catch of sperm whales by USSR coastal whaling off the Kuril Islands in 1950, 1951, and 1962 through 1964, expressed by sex, month and position of land stations (compiled from USSR IWC/NP Forms). Closed circle and solid line: proportion of females in the catch; open circle and dotted line: number of female catches (actual number); triangle and dotted line number of male catches (×0.25 for 46°-50°N, ×0.5 for other areas).

to the north  $(34^\circ - 40^\circ N)$  of the breeding schools (Fig. 7).

The breeding of sperm whales is seasonally diffuse, and in the northern hemisphere conceptions occur most frequently in April–May and least in October–November (Ohsumi, 1965; Shimadzu, 1987). The distribution of adult males appearing in our sighting records suggests that adult males of the southern stock leave the breeding ground after the mating peak and migrate to northern latitudes. However, we consider from their presence in  $34^\circ$ – $40^\circ$ N in August that they may not migrate so far north as the Bering Sea/Aleutian Islands waters (>50°N) but probably remain during summer in the Oyashio Current and its eastern extension (Subarctic Current) in  $40^\circ$ – $50^\circ$ N, or just to the north of the front of the Kuroshio Current System at  $35^\circ$ – $40^\circ$ N.

Sexual segregation of sperm whales in the Oyashio Current area is seen in the operations of USSR coastal whaling off the Kuril Islands (Fig. 8). The season of female catch was shorter, and the female proportion in the catch

was lower in the northern Kuril Islands. The peak of female catch in the northern Kuril Islands was slightly earlier than that of the males in the same region  $(50^\circ - 51^\circ N)$ . Such features are expected when females are segregated to the south and arrive later and return to the south earlier than the males. The seasonal change in the sex ratio is apparent only in the northern part. suggesting that male density is probably higher off the northern Kuril Islands than the south. Off the Pacific coast of northern Japan and during the same period (early 1960s), the female proportion was slightly higher off the northern (Hokkaido) land stations than those off the southern (Sanriku) ones, and it increased from summer to autumn/early winter in both areas (Table 4). The similar seasonal trend is observed in the prewar catch in the 1940s (Table 5). The absolute value of the sex ratio is not directly comparable between the Kuril and Japanese coastal fishery, or between prewar and postwar operations off Japan, because both the selectivity of sexes and availability of whales might be different. However, the above feature suggests that one of the concentrations of female sperm whales in the western North Pacific exists in the summer season off the Kuril Islands area, and that it migrates off Hokkaido and Sanriku waters in autumn/winter season. The period of high male proportion was probably longer off Hokkaido (May to August) than off Sanriku (March to April) during the 1940s (Table 5). This suggests that more males were distributed off Hokkaido (and possibly to further north) than off Sanriku.

Supporting evidence for this is found in the catch of sperm whales by Japanese pelagic whaling presented by Smith (1980). If the catch between 158°E and 180° is totalled latitudinally from his data, there appears in both sexes two major latitudinal concentrations of the catch (Fig. 9). There is a small hiatus in the catch, especially of females, in  $50^{\circ}-52^{\circ}N$  and west of 172°E. We consider this relates to a local intrusion of cold water in the region (see below). Ignoring this small hiatus, we find larger hiatus in the catch in latitudes  $32^{\circ}-44^{\circ}N$ . The latitudes of low sperm whale catch correspond to a very distinct hiatus in whale sightings in  $30^{\circ}-40^{\circ}N$  and  $154^{\circ}E-175^{\circ}E$  apparent in Ohsumi, Masaki and Wada (1977), and to the waters between the front of the Kuroshio Extension (Mizuno and White, 1983) and the Subarctic Boundary (Favorite *et al.*, 1976). The proportion of females in the catch is high on both sides of these latitudes, or in  $45^{\circ}-55^{\circ}N$  and south of  $30^{\circ}N$ .

The distribution of the catch of female sperm whales by the Japanese pelagic fishery (Smith, 1980; Shimadzu, 1987) also shows geographical concentrations, two in the western North Pacific and one in the eastern North Pacific (Fig. 15). The two in the western North Pacific correspond to the above mentioned latitudinal concentrations of female sperm whales. Although the southwestern extension of the northern female concentration is unclear in Smith (1980) and Shimadzu (1987) due to the prohibition of pelagic whaling in the eastern area by the Japanese Government (see Materials and Method), the above analysis of the catch of USSR and Japanese coastal fisheries suggests



Fig. 9. Latitudinal distribution of sperm whale catch by Japanese pelagic whaling in 1966–1977, between 158°E and 180° longitude (compiled from Smith, 1980).

that it will have extended to the southern Aleutian Islands (Fig. 15).

From these analysis we conclude that there are two concentrations of female sperm whales in the western North Pacific, one in the Western North Pacific Gyre to the north of the Oyashio Front or Subarctic Boundary and the other to the south of the front of the Kuroshio Current System. Ohsumi and Nasu (1970) indicated that the northern limit of summer range of the former concentration coinsides with the surface water temperature of 9°C. Adult males are segregated in non-mating season to the north of these female concentrations. There is some overlap between the ranges of adult males and their breeding population even in the non-breeding season. The summer ranges of adult males of the southwestern North Pacific stock and adult females of the northwestern North Pacific stock overlap considerably, although



Fig. 10. Movement of marked female sperm whales, USSR marks only. Includes only marks recovered over 10 days after marking. Closed circle represents position of marking, open circle position of recovery, and numeral by the circle month of marking or recovery. For movement outside of this range see Table 14.

the overlap between individuals of the corresponding sex or growth stages from different stocks seems to be less common. This segregation will be further analyzed using information on movement of marked whales (see below).



Fig. 11. Movement of marked female sperm whales, Canadian, Japanese, USA and USSR marks (excluding those listed in Fig. 10). Recoveries within 10 days or less from marking or movement within the dotted area are excluded. For movement outside this range see Table 14, and for symbols see Fig. 10.

# Evidence from the movement of marked whales

If the widely accepted assumption of a single sperm whale stock in the western North Pacific is correct, there will be a significant number of marked whales moving between north of  $40^{\circ}$ N and south of  $30^{\circ}$ N. However, if there are two latitudinally segregated sperm whale stocks, we will see no mixing between the two isolated latitudes. We do not consider the movement within  $30^{\circ}-40^{\circ}$ N latitudes or between these latitudes ( $30^{\circ}-40^{\circ}$ N) and either of the ranges of the two hypothetical stocks to be meaningful. The intermediate latitudes can be seasonally inhabited by the two stocks, or simultaneously by schools of the two stocks. It is also important to note that since such marking data have been collected over many years they exaggerate the intermingling between stocks in a season of a particular year.

Large numbers of recaptures of marked females off Hokkaido and Sanriku (Figs 10 and 11) are due to a high sperm whale catch in the area. Their movement indicates that breeding schools taken off the Pacific coast of Japan have a connection with those in the northwestern North Pacific or southwestern North Pacific including those in the Bonin Islands waters. The females off Japan and the Kuril Islands waters migrate to 160°W–170°W,

while females from the eastern North Pacific waters migrate  $170^{\circ}E-180^{\circ}$  in higher latitudes ( $40^{\circ}-50^{\circ}N$ ) or between  $160^{\circ}W-170^{\circ}W$  in lower latitudes ( $20^{\circ}-30^{\circ}N$ ). No direct connection of female sperm whales is indicated between western and eastern North Pacific. This does not support the assumption of two stocks in lower latitudes of the western North Pacific (Bannister and Mitchell, 1980), but agrees rather well with the conclusion of Ohsumi and Masaki (1977) that sperm whales in the western and eastern North Pacific intermingle in the central North Pacific, although their deduction of a single stock in the entire latitudinal range of the western North Pacific disagrees with ours.

Available data indicate no female movement between north of 40°N and south of 30°N. We consider that this is indirect support of the presence of latitudinally segregated sperm whale stocks in the western North Pacific. There is one female that was marked by Japan in May 1967 in 48°00'N, 177°49'E and recovered in August 1976 in 25°01'N, 166°27'W. Although this might appear to represent an example that violated this hypothesis, we interpreted this in another way. It was recovered with a female that was marked by USSR in August 1960 in 43°40'N, 137°44'W, thus the school could have belonged to the eastern North Pacific stock of Ohsumi and Masaki (1977), which might have a wider latitudinal range (see below).

Movement of female sperm whales from the summering ground off the Kuril Islands to the wintering ground off Hokkaido and Sanriku (northwestern North Pacific stock) is indicated by numerous whale mark recoveries. Movement of females of another stock (southwestern North Pacific stock), which may winter in the Bonin Islands waters or further south, to Sanriku/Hokkaido waters for summering is indicated by six females (Figs 10 and 11).

Ohsumi and Masaki (1975) considered a Japanese whale mark No. 7741 to indicate female movement between the Bering Sea and the Gulf of Alaska. However, accepting that such a rare case may occur, we ignored this particular mark return and considered that there are currently no reliable evidence supporting such movement. This mark was recorded to have been fired at a fin whale but reportedly recovered from a female sperm whale by a USSR factory ship which processed both fin and sperm whales on that day (Shimadzu, 1987). We also ignored another Japanese mark No. 8394 apparently indicating movement of a sperm whale of unknown sex between the Bering Sea (52°15'N, 176°00'W) and the central North Pacific (37°11'N, 176°10'E). This was fired in the Bering Sea in 1961 at an 11m sperm whale and recovered by a USSR fleet in 1972, but no information was provided on the sex, body length, or how it was recovered. It is possible that the mark was recovered from a cooker. The movement of this mark, if it is accepted, does not change our conclusion.

Since the distribution of adult males is different from that of the pubertal or juvenile males (Best, 1979; Ohsumi, 1966), we analyzed movement by growth stages, roughly classifying the maturity from body length at recapture, i.e.  $\geq$ 46 feet (13.9m) as mature and  $\leq$ 45 feet (13.6m) as immature. There are



Fig. 12. Movement of marked adult male sperm whales (≥46 feet at recapture), using Canadian, Japanese and USSR marks recovered over 10 days after marking. For symbols see Fig. 10.

20 whale marks recovered from adult male sperm whales, five from the Bering Sea, 10 from the Kuril Islands and Pacific coast of Japan, and five from the eastern North Pacific. And there are no mark returns indicating movement between any of these areas (Fig. 12). We consider this significant as an indication of segregation between adult males of different stocks.

Two concentrations of adult males identified in the summer season in the western North Pacific and Bering Sea are located to the north of the summer range of breeding schools of the corresponding female populations mentioned above, i.e. the Bering Sea adult male concentration to the north of the females of the northwestern North Pacific stock summering in the western Aleutian/Kuril Islands area, and the Kuril Islands/Hokkaido/Sanriku concentration to the north of the females of the southwestern North Pacific stock summering in the Kuroshio Current System (Fig. 15). This suggests that adult males from each of the two western North Pacific stock migrates after the mating season to the north of the female range. This will function to decrease competition for food resources between adult males and breeding schools of the same stock (Best, 1979).

The summer range of the adult males from the southwestern North Pacific stock mostly overlaps with that of the females of the northwestern



Fig. 13. Movement of marked immature male sperm whales ( $\leq$ 45 feet at recovery), using Japanese marks recovered over 10 days after marking. For movement outside this range see Table 14, and for symbols see Fig. 10.

North Pacific stock. We do not consider that this will mean free interbreeding between stocks (see Discussion).

The movement of immature males ( $\leq$ 45 feet or 13.6m) in the western North Pacific has characteristics of both females and adult males, or in other words it is intermediate of the two in many cases. Many of such male recaptures show movement within the range inhabited by the females, i.e. between Sanriku/Hokkaido area and south of the western Aleutian Islands area or between Sanriku/Hokkaido area and Bonin Islands/western Taiwan area. However, some of the immature males showed movement between the Bering Sea and female range south of the western Aleutian Islands or movement within the Bering Sea as seen in the adult males. Another seven immature males probably of the northwestern North Pacific stock moved to waters surrounding the eastern Aleutian Islands near to 170°W. These indicate as suggested by Best (1979) that males leave the breeding school at the puberty and tend to migrate to higher latitudes, and provides support for the assumption that the adult male sperm whales migrating into the Bering Sea are those from the western North Pacific stock.



Fig. 14. Movement of marked immature male sperm whales ( $\leq$ 45 feet at recapture), using USSR marks recovered over 10 days after marking. For movement outside this range see Table 14, and for symbols see Fig. 10.

Although further accumulation of data, which is unlikely given the current situation of whaling, may show some adult or pubertal males migrating between the Bering Sea and the Gulf of Alaska through the eastern Aleutian Islands, currently available data do not indicate such movement.

## Identity of eastern North Pacific sperm whales

This subject is analyzed using only the catch distribution of sperm whales by Japanese pelagic whaling reported by Smith (1980) for 1966 to 1977 and Shimadzu (1987) for 1966 to 1979, the movement of marked whales, and the analogy with the stocks in the western North Pacific.

The female catch by Japanese pelagic whaling in the eastern North Pacific (June to September in 1966–1979) concentrated in two latitudinal zones centered at 43°N and 52°N, which merged at the eastern part (Fig. 15). The presence of two latitudinal concentrations does not seem to be the artifact of biased fishing season, because this pattern appears in July and August of the monthly total of the 14 years catch or yearly totals of the seven whaling seasons when a considerable catch has been made in the eastern North Pacific (Appendix Figs 1.1 to 2.15 of Shimadzu, 1987). Rather, we consider that this female concentration relates to the relatively warm area of the Alaskan Stream, and that the low catch of females in the western part of



Fig. 15. Distribution of three sperm whale stocks in the North Pacific suggested in the present study. Solid line: northwestern North Pacific stock; Dotted line: southwestern North Pacific stock; Chain: eastern North Pacific stock. For each stock, thick line indicates a total geographical range for the stock (based on markrecapture data), thin line northern or western limit of females in summer season (based on mark-recapture data), shaded area major concentration of adult males in summer after mating season (based on mark-recapture and sightings data), dotted area high concentration of females in summer season (constructed from Smith, 1980, Shimadzu, 1987, USSR coastal fishery off Kuril Islands, and whale sighting data).

the Alaskan Gyre relates to the low water temperature (Fig. 16). We find a similar hiatus in female distribution in the western part of the Western North Pacific Gyre (see above) and will interprete it in the same manner as the effect of the intrusion of cold water indicated by Favorite *et al.* (1976).

From analogy with the western North Pacific female concentrations, we presume that the summer concentration of females in the Alaskan Gyre represents the breeding population of a sperm whale stock in the eastern North Pacific. Shimadzu (1987) reported a small scale concentrations of female catch in July 1978 around 25°N, 130°W and 25°N, 152°W (Fig. 15). We wondered if these female concentrations represent a breeding population of another sperm whale stock in the eastern North Pacific. However, there is no supporting evidence at present for that assumption. Rather, the currently available marking data of females and the movement of an immature male that wintered in the southern Mexican waters (17°N) and summered in the Alaskan Gyre (46°N) (Table 14) suggest a single sperm whale stock distributed widely in the eastern North Pacific, i.e. breeding schools moving between Mexican waters, Hawaiian ground, Alaskan Gyre, and waters to the south of



Fig. 16. Top. Major current systems in the North Pacific in July through September (based on Dodimead *et al.*, 1963; Favorite *et al.*, 1976; Maritime Safety Agency, 1982). Keys: 1=Okhotsk Sea Gyre, 2=Western North Pacific Gyre, 3=Bering Sea Gyre, 4=Alaskan Gyre, A=Alaskan Stream, C=California Current, E=Kuroshio Extension, K=Kuroshio Current, NE=North Equatorial Current, NP=North Pacific Current, O=Oyashio Current, S=Subarctic Current, T=Tsugaru Current.

Bottom. Fifteen years (1966–1980) mean of the surface water temperature (°C) in the North Pacific in August (after Maritime Safety Agency, 1982). The surface water temperature in February will be about 10°C lower than that in August in the middle latitudes (30°–40°N).

the eastern Aleutian Islands.

Quite different from the two sperm whale stocks in the western North Pacific, the movement of marked whales in the eastern North Pacific does not demonstrate post-mating latitudinal segregation between adult males and breeding population, but suggests segregation of adult males to the west of the concentration of the breeding schools. This agrees with the fact that the

latitudinal segregation of males was unclear in the catch of the Japanese Pelagic fishery in the eastern North Pacific but the proportion of males was high in the western part of the Gulf of Alaska (Fig. 17). This segregation pattern has been mentioned by Ohsumi and Nasu (1970). As mentioned above, the western part of the Alaskan Gyre is covered, in July to September, by water which is a few degrees colder than the surrounding area of the Gulf of Alaska (Fig. 16). We consider that the above adult male segregation relates to the presence of this cold water area and has the same biological significance as in the north/south segregation of sperm whales in the two western North Pacific stocks (see above). The range of pubertal males of this stock probably extends further to the west along the southern coast of Aleutian Islands (indicated by 44 feet and 35 feet males in Fig. 13). Although the Aleutian Islands may not absolutely inhibit the migration of sperm whales (see above), the relatively shallow water depth (<500m) may decrease the chance of their migration between the Bering Sea and the North Pacific through the eastern Aleutian Islands.

Two whales (a juvenile male and a female) marked in the northern hemisphere ( $<10^{\circ}N$ ) in March and May were recovered in the southern hemisphere ( $4^{\circ}-5^{\circ}S$ ) in November and March, respectively (Table 14). We do not know the relationship between these individuals and the eastern North Pacific sperm whale stock, but there may remain some possibility that there is one sperm whale stock in equatorial waters or that the range of a southern hemisphere stock seasonally crosses the equator in the eastern Pacific.

Mark no.	Marking		Recapture		
	date	position	date	position	body length
Females		STITUTE OF CETACE			
19729	29/05/1965	54°10'N, 141°50'W	26/06/67	46°20'N, 134°26'W	11.6m
A439*	10/12/1965	35°58'N, 120°43'W	17/07/71	48°35'N, 131°26'W	11.6m
A444*	10/12/1965	35°58'N, 120°43'W			
R610187	19/08/1963	40°00'N, 145°08'W	10/06/68	43°37'N, 131°19'W	10.5m
R610852	08/05/1963	49°53'N, 129°20'W	22/07/65	48°55'N, 127°57'W	10.7m
RE1725	07/05/1975	02°52'N, 094°55'W	20/03/76	04°40′S, 082°50′W	9.8m
Males					
R610203	18/08/1963	39°23'N, 144°27'W	30/06/66	44°11′N, 142°22′W	11.4m
R610675	01/03/1966	17°11'N, 102°32'W	25/06/66	46°43'N, 141°27'W	11.2m
RE1885	29/03/1975	09°07'N, 093°55'W	09/11/75	04°12'S, 083°20'W	9.8m

 TABLE 14. MOVEMENT OF MARKED SPERM WHALES IN THE EASTERN

 NORTH PACIFIC NOT LISTED IN FIGS 10 THROUGH 14

\*: recovered from same individual. A: US mark. J: Japanese mark. R: USSR mark.



Fig. 17. Sexual segregation of sperm whales in the eastern North Pacific appeared in the catch of Japanese pelagic fishery from 1966 through 1977 (data are based on Smith, 1980). Open circle and dotted line indicate total number of sperm whales caught, closed circle and solid line percentage of females in the catch.

Top. Longitudinal segregation of female sperm whales in the eastern North Pacific north of  $40^{\circ}$ N (Gulf of Alaska area).

Bottom. Latitudinal segregation of female sperm whales in the principal range of the eastern North Pacific stock (Pacific areas east of  $170^{\circ}$ W and north of  $40^{\circ}$ N, and east of  $160^{\circ}$ W and south of  $40^{\circ}$ N).

#### DISCUSSION

## Stock boundaries

Klumov (1955) assumed two breeding stocks of sperm whales summering off the northern and southern Kuril Islands. His southern stock might correspond to some females of our southwestern North Pacific stock migrating to southern Kuril Islands north of its ordinary summer range, and the northern stock to our northwestern North Pacific stock. However, it is also possible to presume that he had just identified two latitudinal concentrations of females of the northwestern North Pacific stock (Fig. 15). Our study failed to find support for the two female stocks considered by Klumov (1955) to be segregated latitudinally in the eastern North Pacific.

In an isozyme analysis of North Pacific sperm whales, Wada (1980)

compared the gene frequency of the North Pacific sample from the central sectors with several subsamples extracted from it, and concluded that the central North Pacific sample represents more than one stock. This supports our contention that the central North Pacific is a mixing area for eastern and western stocks.

Our conclusion on sperm whale stocks in the western North Pacific agrees with the hypothesis presented by Watase (1963). Although he did not present the basic data used to construct the hypothesis, he wrote that the size of breeding schools is larger in his "northern stock" than the "southern stock". He told us that the southern stock schools were frequent in the protrusion of the Kuroshio Current into the Oyashio Front and that of the northern stock to the north of it. The southern individuals had light brown color while northern ones dark brown body (he was uncertain if it reflected the real body color difference or difference in the color of sea water). Such difference will appear even from different degree of diatom infection. He also stated that the northern stock schools were tighter than those of the southern stock when chased by the catcher boat, although he was not sure if it reflects the real behavior difference of whales or difference in the ocean structure and sound conductivity (S. Watase, pers. commn in 1987). After mentioning the loose dispersed schools of the southern type which might correspond to the above mentioned school difference of Watase, Mr K. Yamamura of the Japan Whaling Association stated that it was the general belief of his colleagues (confirmed by his observations made while he was working at an Onagawa land station on the Sanriku coast) that individuals of the southern type had a greater number of healed or unhealed oval scars than the northern type and the skin looked unclean (pers. commn in 1987). Mr Y. Yanagihara, gunner of the Sanyo Whaling, believed that the southern type has slender body and is hard to harpoon because of the smartness and/or the school members that tend to scatter during the chase (pers. comm in 1987). This was partially confirmed by Dr H. Kato, the Whales Research Institute, that an adult male (16.8m) of the southern type identified by the station staff had smaller mandibular teeth and much slender lower jaw (0.86 time in the absolute diameter at mid-symphysis) than the northern type adult male (17.6m) taken from different herds and processed on a same day in November 1987 at the Ohsawa Station (pers. commn in 1987).

We presume that their southern type corresponds to the southern stock of Watase (1963) and that the scars would be equivalent to bites of the cookiecutter shark, *Isistius brasiliensis*, known on various cetaceans in warm waters (Jones, 1971). The recognition of two stocks (or types) of sperm whales off the Pacific coast of Japan was probably common among whalers, although it was not always clear from their description if the characteristics were a valid basis for separating the stocks. Yamamura also stated that the southern type arrived off Sanriku in early summer but that the date was delayed about two weeks every year in the early 1970s. This agrees with our analysis of catch statistics,

and probably reflects a change in the timing of migration accompanied by the density decline in the peripheral habitat. We consider that the two sperm whale types described by them represent two stocks identified by us in the western North Pacific. Adult males, solitary or in small schools, reported by Watase (1963) to migrate off Hokkaido in autumn possibly represent adult males from the southwestern North Pacific stock that summered in the cold Oyashio Current area.

Blood type analysis by Fujino (1963) was probably the first to give a scientific basis for distinguishing two sperm whale stocks off Japan. Using 198 blood samples (all males) from the Bering Sea/Aleutian Islands waters (>51°N) and 121 samples off the Hokkaido/Sanriku area (26% were males and 72% were taken in August/September), he found that the former sample contained no Ju2-positive individuals but the latter contained about 42% of such individuals. He further confirmed that blood type frequency did not significantly differ between the sexes of the pooled Japanese coastal sample, and that the proportion of Ju2-positive individuals in the Japanese coastal sample decreased from 46/87 (53%) in August/September to 4/29 (14%) in October/ November. Finally he concluded after examining mark recapture data that members (sex is not stated by him) of the stock in the Bering Sea/Aleutian waters migrated in autumn to northern Japan, and that adult males of the Japanese coastal stock (with high Ju2-positive frequency) would migrate to Kuril and Kamchatka waters but not to the central Aleutian waters.

Examination of data presented in Tables 4 and 6 of Fujino (1963) reveals that his October/November sample contained a minimum number of 5 females in 1959 and 14 in 1961 and 2 of these were Ju2-positive, i.e. the minimum number of Ju2-negative females was 17 and the positive ones were actually 2 females. For safety we compared this minimum ratio (17:2) for females with 41:46 (negative:positive) of the August/September sample (which includes both sexes, and was collected in 1962 except for 2 in 1961) to find a highly significant difference (Chi-square test, p<0.001). Thus we conclude that data presented by Fujino (1963) support our conclusion on the presence of two breeding stocks of sperm whales off the Pacific coast of northern Japan.

We have concluded that many female sperm whales summering off the Sanriku coast winter in the lower latitudes (20°-30°N) of the western North Pacific and belong to the southwestern North Pacific stock, which contains a high proportion of Ju2-positive individuals (Fujino, 1963). If adult males from this stock had migrated to the Aleutian Islands area, Fujino (1963) should have detected some Ju2-positive individuals in the sample from the region. The absence of such individuals in his sample must indicate the correctness of our conclusion on the segregation pattern of adult males of the two sperm whale stocks in the western North Pacific. At the same time this indicates the presence of some yet unknown mechanism that inhibits free interbreeding between males of southwestern North Pacific stock and females of the northwestern North Pacific stock in their overlapping summer range

(small scale interbreeding may occur between stocks).

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The first of the possible factors will be the timing of migration and breeding peak. The northward migration of adult males and the overlap of distribution between sexes of different stocks occurs after the conception peak of the species (see above). This alone can decrease the chance of interbreeding. The second is the social barrier inhibiting the free interbreeding between stocks. Killer whales, Orcinus orca, off Vancouver Island are known to have three communities each consisting of 3 to 12 pods and having occasionally overlapping ranges (Bigg, 1982; Ford and Fisher, 1983). Although pods within community regularly associate with one another and may interbreed (cows in a pod without bull produced calves), pods in different communities do not presumably due to cultural or behavioral differences (Bigg, Ford and Craeme, 1985). If this happens to the sperm whale, it will contribute to inhibit free interbreeding between different stocks. The third possibility relates to the synchlonize of migration and the cycle of reproductive activity in individual males. The social structure of elephants has some similarity to that of the sperm whales (Best, 1979). Adult males of the Asiatic elephant, Elephas *maximus*, live apart from matriarchal group of cows and calves, and join it only when it passes his territory while he is in heat which is thought to come annually or biannually (Eisenberg, 1981). Dugongs, Dugong dugon, have no sharply defined breeding season, but the males are not continuously in breeding condition and their reproductive activity in a population is not synchronized (Marsh, Heinsohn and Marsh, 1984). Although nothing is known on the reproductive cycle of individual males of sperm whales in the North Pacific, these example will suggest a possibility that males migrating to the higher latitudes are in cycle of lower reproductive activity, and that they may return to the breeding ground at the arrival of the heat as suggested by our sighting data.

A possible ratio of the two stocks constituting the Japanese coastal catch can be estimated using data from Fujino (1963) and with the unconfirmed assumptions mentioned below. The proportion of Ju2-positive individuals in his combined Hokkaido/Sanriku sample was 2/5 in June and July, 46/87 in August and September, and 4/29 in October and November. Assuming as suggested from his sample that the northwestern North Pacific stock contains no Ju2-positives, assuming as an unconfirmed extreme case that all the individuals from the southwestern North Pacific stock are Ju2-positive, and using the monthly catch reported by the industry (Table 2), we roughly estimate the contribution of the southwestern stock in the late 1950s as (0.065 + 0.063 + $0.068 + 0.094) \times 2/5 + (0.222 + 0.266) \times 46/87 + (0.136 + 0.086) \times 4/29$ = 0.40, and that of the northeastern stock as 1 - 0.40 = 0.60. Since the blood type composition was probably different between Hokkaido and Sanriku samples, further improvement of above estimate requires larger sample and calculation by each geographical area. If Ju2-negative individuals exist in the southern stock, the above calculation will underestimate its contribution to

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the catch. The proportion of the northwestern North Pacific stock in the catch was probably higher in earlier years when the industry landed most of the sperm whales in Hokkaido, and it could have increased again during the 1976/77 to 1977/78 seasons when they hunted sperm whales wintering off Sanriku coast. It must have become almost negligible since the 1983/84 seasons (see above).

## Oceanographic factors

The effect of oceanography on migration and segregation of toothed whale stocks has been demonstrated by several studies in the northwestern North Pacific. With the exception of finless porpoises, *Neophocaena phocaenoides*, which live in coastal waters of wide thermal range (Kasuya and Kureha, 1979), most other toothed whales in the area inhabit either warm waters under the influence of Kuroshio Current or cold waters such as the Oyashio Current area (Kasuya, 1980; 1982b).

The Dall's porpoise, Phocoenoides dalli, is one of the best studied cold water species. Its distribution is limited to north of the Subarctic Boundary, and the breeding population of each stock segregates into particular water domains such as the Okhotsk Sea Gyre, Oyashio Current, Western North Pacific Gyre, Bering Sea Gyre, and Alaskan Gyre (Kasuya and Ogi, 1987; Miyashita and Kasuya, 1987; Yoshioka, Ogura and Shikano, 1987). One population of the Dall's porpoise in the Oyashio Current has successfully expanded its habitat to the Japanese coastal waters between the fronts of cold Oyashio and warm Kuroshio Currents, but is still unable to intrude into the proper Kuroshio current area. The Baird's beaked whale, Berardius bairdii, was considered from its breeding season probably to have evolved in higher latitudes (Kasuya, 1977), which was supported by the distribution in the northern North Pacific. This cold water species in the North Pacific has developed a local stock in Japanese coastal waters near the southwestern range, or between the fronts of Kuroshio and Oyashio Currents (Kasuya, 1986a). Although these whales commonly occur in an area with high  $(>20^{\circ}C)$ surface water temperature in summer, they are still unable to expand their habitat in the main Kuroshio Current area and their range is limited to the area north of 35°N.

An opposite example is found with the short-finned pilot whales, *Globicephala macrorhynchus*, inhabiting tropical and temperate waters of the world. In the northwestern North Pacific, the majority of the individuals (southern form) live in a vast range to the south of the fronts of Kuroshio Current and its extension. However the species has developed a morphologically distinct local form (northern form) in colder waters off Japan between the fronts of Kuroshio and Oyashio Currents (Kasuya, 1986b; Kasuya, Miyashita and Kasamatsu, 1988). Northern forms are not distributed in the Oyashio Currents and its eastern extension. Although an apparently similar form (having distinct saddle mark) has been sighted in the northeastern

North Pacific from Washington coast to Baja California, the distribution is apparently discontinuous between the two sides of the North Pacific and further study is needed on the systematic relationship between them (Kasuya *et al.*, 1988).

These examples suggest that the Kuroshio and Oyashio Fronts have acted as strong barriers to the distribution of toothed whales, and that it has not been possible to cross both of the fronts and to enter into quite different water masses even for species that succeeded to overcome one of the two fronts. For this reason if such a boundary is once passed it could have contributed to the development of isolated whale populations.

Several gyres to the north of the Subarctic Boundary probably have worked also in a similar, but weaker way. The distribution of three sperm whale stocks in the North Pacific seems to be closely related to the gyres in the North Pacific, i.e. the concentration of breeding populations of the three sperm whale stocks has a tight connection each with the Western North Pacific Gyre, Alaskan Gyre, and with the wide circulation area centered at the Kuroshio Counter Current area and surrounded by Kuroshio Current, Kuroshio Extension, North Pacific Current, and presumably North Equatorial Current. The presence of only one recognized sperm whale stock in most of the latitudinal range of the eastern North Pacific probably relates to the absence of distinct ocean fronts in the region. Although there seem to be no distinct oceanographic barriers between female ranges of the southwestern North Pacific stock and eastern North Pacific stock, a significant isolation could probably have been maintained because (1) the major concentration of the latter stock occurs in the Alaskan Gyre and the low sperm whale density in the lower latitudes of the stock's range decreased the chances of mixing, (2) the segregation of eastern North Pacific stock females to the east of male range decreased chances of mixing (this also apply to isolation from the northwestern North Pacific stock), and (3) the mixing was limited due to the direction of seasonal migration that tended to be north/south rather than east/west.

The pantropical distribution of sperm whales suggests the tropical origin of the species. We believe that the sperm whales in the Okhotsk Sea or Sea of Japan can be excluded from the possible origin of the northwestern North Pacific stock, because the species is uncommon in these waters (Berzin, 1972), and they do not seem to have established their niche in the region. Thus, the northwestern North Pacific stock of the sperm whales could have probably originated either from the southwestern North Pacific stock or the eastern North Pacific stock. Since the north/south temperature boundaries seem to have blocked the dispersal of toothed whales more effectively than the boundary between the Western North Pacific Gyre and Alaskan Gyre (see above), we consider that the eastern North Pacific stock is more plausible as the origin of the sperm whale stock in the northwestern North Pacific.

There are two possibilities on the origin of the eastern North Pacific

stock of the sperm whale. One is to assume that the sperm whales in the Kuroshio Current System intruded into eastern North Pacific and established a niche in the Alaskan Gyre and the California Current possibly after the Würm Glacier Period which was the last glacier period ended about 10,000 years ago. Another possibility is that sperm whales immigrated in the cold California Current area across the equator from the South Pacific. Southern hemisphere sperm whales could have immigrated to the northern hemisphere more easily across the colder eastern equatorial waters during a period of cold climate. Similar incidents have been suspected for several cetaceans (Davies, 1963; Kasuya, 1975; Brownell, 1983). Although the chance of such immigration could have certainly occurred during the Würm Glacier Period, the chance probably lasted till the very recent time for such pantropical species as sperm whales. The movement of two juvenile sperm whales that were marked in the northern hemisphere in northern spring and recovered in the southern hemisphere in austral fall or spring provides an evidence of small scale (7° to 13° in latitude) transequatorial migration of breeding schools in the eastern tropical Pacific (Table 14). Larger scale transequatorial movement (from 21°N to 33°S in 4 years 3 months) of an immature male sperm whale was known from the eastern Atlantic (Ivashin, 1967), where the oceanographic structure is comparable to eastern tropical Pacific. These indicate that the large scale transequatorial immigration of sperm whales was possible in some geological age. Fujino (1963) indicated a highly distinct difference in blood type frequencies between two sperm whale stocks in the western North Pacific (no Ju2-positives vs. 53% or more). This leaves a possibility for eastern South Pacific sperm whales to be the origin of eastern North Pacific stock. Further analysis of genetic similarity between sperm whale stocks in the North Pacific and those in the eastern South Pacific will throw some light on the evolution of these stocks.

The niche previously occupied by the northwestern North Pacific stock of the sperm whale has become almost vacant after its depletion. However, so far we do not find the niche being reoccupied by sperm whales from some nearby stocks, e.g. the southwestern North Pacific stock or stock in the eastern North Pacific. This will be an example indicating that such vacancies are hard for other nearby stocks to reoccupy, especially when the nearby stocks are also depleted to some unknown degree. It can, however, reasonably be deduced from the above analyses that the range of each sperm whale stock and movement of the member whales are controlled by oceanographic conditions.

We have no data to indicate the possibility of a small local stock in Japanese coastal waters between the fronts of Kuroshio and Oyashio Currents as observed for Baird's beaked whales and short-finned pilot whales. Development of such a local sperm whale stock could have been inhibited by the earlier establishment of a Baird's beaked whale stock in the near shore deep waters or the current two sperm whale stocks partially overlapping off Japan. However, even if such a small local stock had evolved in a geological age

either from the southwestern or northwestern North Pacific sperm whale stock, it could have been exterminated by the intensive operation of Japanese modern whaling in coastal waters.

## Significance for management

IWC (1980) identified two human induced factors expected to cause pregnancy rate change in the sperm whale population, i.e. a decrease in the number of adult males relative to that of adult females, and a decrease in the female density. The first effect, decrease in pregnancy rate accompanied by a decrease in the adult male density, has not been detected in any sperm whale stocks, but the second has been detected in sperm whales off South Africa.

Best (1980) reported an increase in the apparent pregnancy rate of sperm whales that followed exploitation off Durban from about 17% in the early 1960s to 21% in the middle 1970s. Later, Best, Canham and Macleod (1984) further refined the analysis to reinforce the conclusion that the pregnancy rate increase was due to the improvement of reproductive potential of females of wide age range and not to the increased proportion of young adult females of high reproductive potential.

In the North Pacific, however, several attempts to detect the historical change in the sperm whale pregnancy rate were unsuccessful (Beddington, 1980; Masaki, 1980; Ohsumi, 1980a; Ohsumi, 1981a; Shimadzu, 1987). Several factors could have masked possible change in the pregnancy rate. They include (1) a very slight change in the timing of the sampling period, which included both mating and parturition seasons, could have easily changed the proportion of females in early or late pregnancy, (2) the difficulty in distinguishing females in early pregnancy and those having corpus luteum of ovulation, and (3) the proportion of unrecorded take of lactating females could have changed between years, fishing grounds and whaling fleets.

One of two additional factors could be that the whaling operation moved from north to south and from west to east. Thus the proportion of females from the more depleted stock gradually decreased in the catch and that of the less depleted one increased, and during this period the depletion of the latter stock could have progressed. Many authors have attempted to overcome this problem by dividing the female sample into 10 degree (or larger) cells of latitude and longitude, without recognizing the latitudinal segregation of the stocks. If the sample was divided into small areas or short time periods (month), it inevitably decreased the sample size in each cell and caused low precision, but too coarse cell divisions also could have masked the possible change in the pregnancy rate. A similar kind of effect is expected in the analysis of many population parameter changes expected to accompany exploitation (with exception of growth rate increase (Kasuya, unpub.)).

Another factor that could have caused an apparently stable pregnancy rate would be the combined effect of adult male depletion and the depletion

of females. Since adult males segregate, in summer, to the north or west of the female range of the corresponding stock, and whaling commenced earlier in the north/west and selectively hunted adult males which were larger in body size, the availability of adult males for reproduction could have decreased and the pregnancy rate could have declined before the large scale exploitation of females in the corresponding stock started. For example, hunting of adult males of the southwestern stock segregating in summer off Hokkaido and Kuril Islands continued from the start of Japanese coastal whaling in the 1910s (Table 5) to the end of pelagic whaling in the late 1970s (Ohsumi, 1980c). Although the exploitation of breeding females of the stock started at the same time off Sanriku (probably mainly in summer) and other Japanese whaling station to the south of Sanriku region, most intensive exploitation probably started in the late 1960s with the pelagic and coastal fisheries. The pregnancy rate analyses for this stock used data collected since 1972 (Masaki, 1980; Ohsumi, 1980a). Therefore, the annual trend in pregnancy rate would be hard to analyze without catch statistics by sex, maturity and stock, and the detection or prediction of the change would be extremely hard due to the opposite effects of the change in male availability and female density. The similar change could have occurred on the eastern North Pacific stock.

If the present hypothesis on the range of North Pacific sperm whale stocks is correct, the stock boundary currently in use for the management will have to be adjusted. The boundary between the eastern North Pacific stock and two stocks in the western North Pacific will be the Aleutian Islands and line connecting points 52°30'N, 175°E and 20°N, 160°W. The latter passes middle of the overlapping area of the stocks. We have no data on the boundary to the south of 20°N, but 160°W longitude will probably be adequate. The boundary between the breeding populations of two western North Pacific stocks will be at around 35°N in winter and 40°N in summer. Latitudinal boundary between the adult male populations of two western North Pacific stocks will be at about 50°N in summer and perhaps at around 35°N in winter to spring (mating season), but nothing is known on the boundary in the intermediate seasons. To make the problems more difficult is the range of pubertal males, which are expected to be distributed in either of the adult male or breeding female ranges and also in areas between the two ranges depending on their age. Thus, if a sample is collected in summer in the western North Pacific between 40°N and 50°N, it will be mainly composed of adult males of the southwestern North Pacific stock, and pubertal males and members of breeding schools (females and immature males) of the northwestern North Pacific stock. However, it will probably include also some members of breeding schools of the former stock in the southern part of the sampling area and some members of adult males from the latter stock in the northern part of the latitudes. Further study is needed for more precise determination of stock boundaries and their seasonal movement.

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