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After 41 years of operation, the Whales Research Institute (WRI) closed in October 1987 while this volume was in press. This volume was completed by the Editorial Board, using the remaining funds in the WRI budget and with the cooperation of the new Institute of Cetacean Research, which was established to replace the WRI. The present Editorial Board will be dissolved upon the publication of this volume. We hope that the Director of the Institute of Cetacean Research will establish a new journal to replace the Scientific Reports of the Whales Research Institute (SRWRI).

The Editorial Board, SRWRI

THE SCIENTIFIC REPORTS OF THE WHALES RESEARCH INSTITUTE

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DISTRIBUTION AND MIGRATION OF THE WESTERN PACIFIC STOCK OF THE GRAY WHALE*

HIDEO OMURA**

ABSTRACT

There are two geographically isolated stocks of gray whales in the North Pacific. One is the eastern stock which migrates between the Bering and Chukchi Seas and Baja California, or California stock, and the other is the western stock which has been thought to migrate between Okhotsk Sea and south coast of Korean Peninsula. This stock was called Korean stock because south coast of Korean Peninsula has long been thought to be its calving ground.

In recent years papers from China reported that in the past gray whales also occurred in the Yellow Sea and East and South China Seas. In the light of these information the Japanese catch and other materials were studied and these supported these information.

In relation to the migration of these gray whales the difference of the ocean structure between the eastern and western North Pacific was noted. In the latter the continental shelf is well developed. The gray whale is thought to have lived in shallow water and migrated directly across the East China Sea between Kyushu and South China, from east to west or reverse way, while some whales have migrated along the coast of the Yellow Sea.

INTRODUCTION

The gray whale, *Eschrichtius robustus* (Lilljeborg, 1861), is the sole member of the family Eschrichtiidae and is considered to be the most primitive surviving baleen whale. There are presently two geographically isolated stocks: an eastern Pacific stock, which migrates between Baja California and the Bering and Chukchi Seas, and a western Pacific stock, which migrates between South Korea and the Okhotsk Sea. These may be designated the California stock and the Korean stock, respectively, on the basis of their breeding grounds (Rice and Wolman, 1971).

The California stock was once reduced heavily by whaling in the 1850s as well as by the operation of floating factories after the turn of the century. Even so this stock made remarkable recoveries. Since it was afforded protec-

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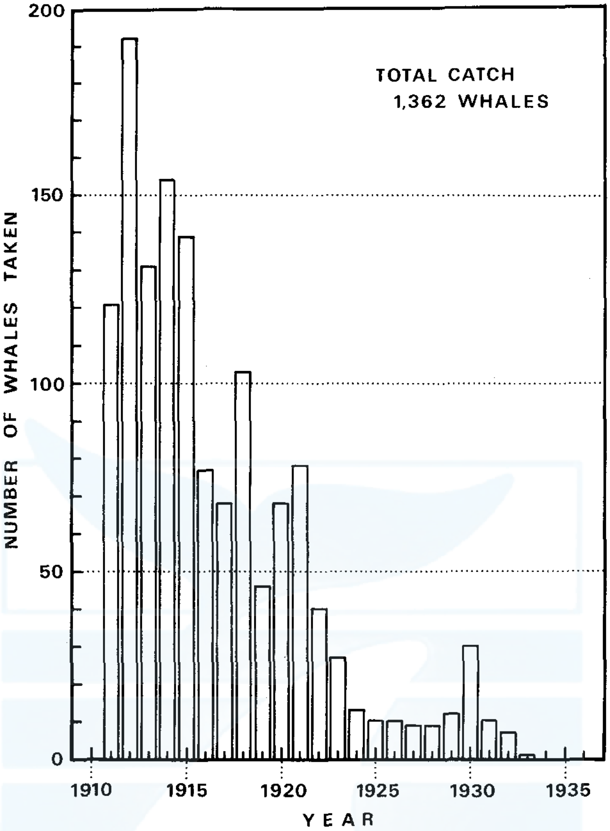

Fig. 1. Catches of gray whales in the western North Pacific region.

tion from commercial whaling in 1946 by the International Convention for the Regulation of Whaling, the population has recovered steadily. The stock has been classified as a Sustained Management Stock since 1978, based on the understanding that it had remained stable at about 11,000 whales over an 11 years period with approximately constant catches (IWC, 1986).

The western Pacific stock of the gray whale was hunted twice in the history of whaling. Prior to the turn of the century whales were taken in Japan using hand harpoon and net (net whaling). This whaling was conducted in two regions of Japan, one the Pacific side and the other on the coasts of southern Sea of Japan and eastern East China Sea (off Kyushu and Yamaguchi prefecture). Right whale (*Eubalaena glacialis*), humpback whale (*Balaenoptera novaeangliae*) and fin whale (*B. physalus*) were the major targets of this whaling, but the gray whale and other species of whales were also taken (Omura, 1984).

Gray whales in the above two regions may represent different populations. The gray whales coming to the Pacific side is thought to have followed a migration route along the east coast of Japan (Nishiwaki and Kasuya, 1970;

Omura, 1974, 1984; Bowen, 1974). Bowen (1974) describes further that those gray whales should be regarded as strays from the Bering Sea. Migration of these whales, however, is not discussed in detail in the present paper. The gray whales coming to the coasts of Kyushu and Yamaguchi prefecture are portion of those whales migrating in the waters adjacent to Korea (Omura, 1984).

After the turn of the century (in the years 1911 – 1933) gray whales were hunted heavily by modern catchers on the coast of Korea, and once the stock was thought to be exterminated (Mizue, 1951; Bowen, 1974), but this was not the case and some still survive (Brownell and Chun, 1977; Yablokov and Bogoslovskaya, 1984) (Fig. 1).

The calving ground of the western Pacific stock was once believed to be the southern coast of South Korea (Andrews, 1914; Mizue, 1951; Rice and Wolman, 1971; Omura, 1984; Yablokov and Bogoslovskaya, 1984). Wang (1984), however, noted the occurrence of gray whales in the Yellow Sea, the East and South China Seas and described that the calving grounds of these whales are possibly in Baya Bay and Wailuo Harbour. In the light of these reports I have tried to make clear their migration route using data in hand.

MIGRATION OF GRAY WHALES ALONG THE KOREAN PENINSULA

Andrews (1914) who firstly investigated gray whales at Ulsan, Korea, during a period in January and February 1912 states as follows:

"In November and December, when the females are taken, almost every individual will be found to be carrying young nearly for birth. As these would necessarily be delivered within two or three weeks after passing Ulsan, the birth must occur in the bays among the numerous small islands at the extreme southern end of the peninsula."

In fact he examined 24 gray whales during his stay at Ulsan, in which 21 whales were males and 3 were females. One of the females contained a fetus 476cm long. The mean body length at birth of the gray whale fetus is 4.9 meters for the California stock whales (Rice and Wolman, 1971). This fetus, therefore, can be regarded as near term. This is, however, the only fetal record he had. It is clear, therefore, that the statement was based largely on information supplied from others, especially a Norwegian whaling gunner H. G. Melsom, who worked with him.

As already stated a portion of the Korean stock had migrated to the north coast of Kyushu, where they were taken by net whaling prior to this century. No catch statistics by species in Kyushu are available (Omura, 1984), but it is clear that gray whales (Ko-kujira) were also taken at Ikitsuki Island in addition to right, humpback and fin whales (Yamada, 1983)*. There the

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* An English translation from a Japanese old book entitled 'Isanatori-ekotoba', which means "Whaling, explained with pictures". In the translation this was erroneously written as 'Yogiotoru eshi'.

TABLE 1. CATCHES OF GRAY WHALES BY JAPANESE WHALE CATCHER (AFTER KASAHARA, 1950)

Year \ Area	XII	XIII	XI	XIV	Total	F. and W.[1]
1910						6
1	13	106	2	–	121	121
2	?	?	?	–	192[2]	193
3	?	?	?	–	131[2]	131
4	30	109	15	–	154	155
5	–	130	9	–	139	139
6	41	36	–	–	77	78[3]
7	13	53	–	2	68	69
8	10	91	–	2	103	104
9	11	35	–	–	46	46
1920	14[3]	52[3]	2	–	68[3]	68
1	53	23	2	–	78	78
2	19	19	–	2	40	40
3	23	4	–	–	27	27
4	13	–	–	–	13	17
5	–	10	–	–	10	10
6	1	9	–	–	10	11
7	3	6	–	–	9	10
8	–	9	–	–	9	9
9	–	11	–	1	12	12
1930	–	30	–	–	30	30
1	–	10	–	–	10	11
2	–	7	–	–	7	7
3	–	1	–	–	1	2
Total	244	750	38	7	1,362	1,374

(1) Cited from Rice and Wolman (1971) which includes catches of gray whales in other areas, e.g. Okhotsk Sea.
(2) Cited from other sources kept at the Japan Whaling Association.
(3) Corrected in this table.
For the areas see text and Fig. 2.

whale migrating from north to south was called as the Down-going whale and that coming from south to north as the Up-going whale. This is applied to above four species of whales, including the gray whale. Hence the island was on the route of the southward and northward migration of the gray whale, while it is situated more southerly than the south coast of Korea.

Kasahara (1950) analyzed the catch statistics of Japanese coastal whaling between 1911 and 1949. A total of 83 land stations were operated by Japanese industry during the period in the western Pacific. He grouped these land stations into 16 areas and made clear the yearly catches of each species in each area in his Table 10.

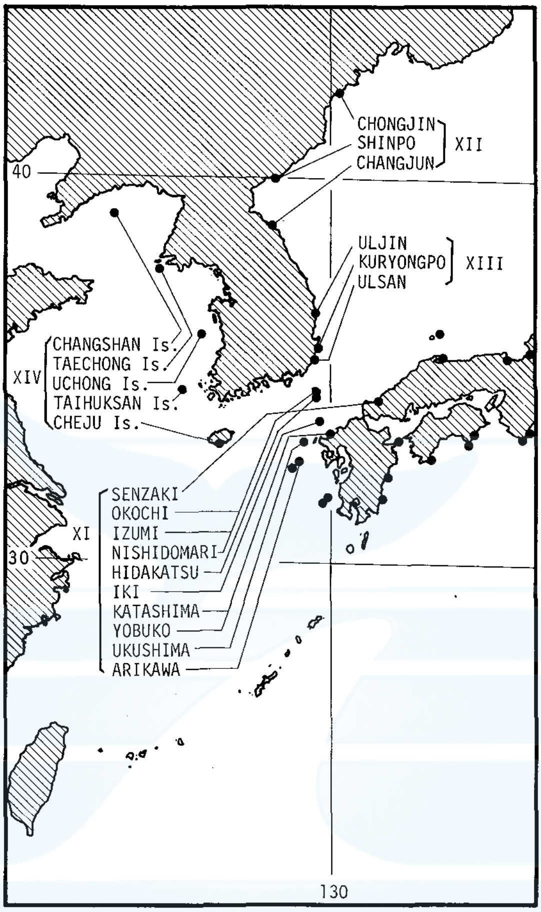

Fig. 2. Positions of land stations concerned with catches of gray whales (after Kasahara, 1950).

Table 1 was rearranged from his Table 10, extracting areas where gray whales were mostly taken during this period.

As to the Kasahara's area some explanation may be needed here (Fig. 2). Area XII means northeast Korea and includes land stations at Chongjin, Shinpo and Changjun. Area XIII means southeast Korea and includes Uljin, Kuryongpo and Ulsan. Area XI means North Kyushu and includes Senzaki, Okochi, Izumi, Nishidomari, Hidakatsu, Iki, Katashima, Yobuko, Ukishima and Arikawa. Area XIV means Yellow Sea and includes Cheju Island, Taihuksan, Uchong Island, Taechong Island and Changshan Island (Kantoshu).

As seen in Table 1 gray whales were mostly taken in Area XIII or southeast coast of Korean Peninsula and Ulsan was the center. This was followed by the Area XII or northeast coast of Korean Peninsula, and then North Kyushu. It is noted, however, some gray whales were taken in the Yellow Sea.

This supports the recent reports of Wang (1978, 1984) that gray whales occur in the Yellow Sea.

In this connection I recall a whale observed by Professor K. Uchida of the Kyushu University. He was a famous ichthyologist who studied fish larvae. Prior to 1945 he worked at the Fisheries Research Laboratory at Pusan, Korea and made an expedition to collect fish larvae in May 1930 in the Yellow Sea. He positively identified a gray whale during this expedition near Inchon, an island locally called "Chanchangon" and situated at northwest of 60 nautical miles from Inchon. His observation of the whale is well described in his book (1964). He observed clearly the fluke-lifting behaviour of a gray whale. He also writes that the area was said to be a gathering place of whales.

Andrews (1914) writes that Captain H.G. Melsom has often observed them (gray whales) in this vicinity, but because of the abundance of other and more valuable species, they are not killed at this time by the Japanese. This was written about the whaling off the south coast of Korean Peninsula, but it is thought this was applicable also to the Yellow Sea, because the main catches in this area were fin whales.

It is possible, therefore, that the so-called Korean stock of gray whales, or at least a portion of them, entered into the Yellow Sea and hence migrated south along the east coast of China, as shown in Fig. 2 of Wang (1984). It is also possible that some whale went westwards from south coast of Korean Peninsula to the east coast of China, across the southern border of the Yellow Sea.

MIGRATION ROUTE OF GRAY WHALES THROUGH THE COAST OF NORTHERN KYUSHU

Gray whales migrating to the northern Kyushu is a part of the Korean stock and its migration past Ikitsuki Island was noted above. However, the migration of these individuals are very difficult to be understood. Fig. 7 of Omura (1984) shows only the distribution of gray whales then known to him. In the case of humpback, fin and right whales it is possible that they migrated further south through the west coast of Kyushu. At Kasasa, a fishing village on the west of Kagoshima prefecture, these three species of whales were sometimes taken accidentally entangled in fishing nets (Nasu, 1974; Anon., 1978).

Gray whales, on the other hand, have never been noticed by villagers of Kasasa. It is possible, therefore, that gray whales took different course of migration from the above three species.

In this connection this problem should be considered in relation to the depth of the ocean. It is well known that the gray whale relies upon the benthic animals for food, though peripheral areas and pelagic resources are also exploited (Nerini, 1984). This does not mean, however, that they also live in pelagic seas. The California stock of gray whales migrates along the coastal

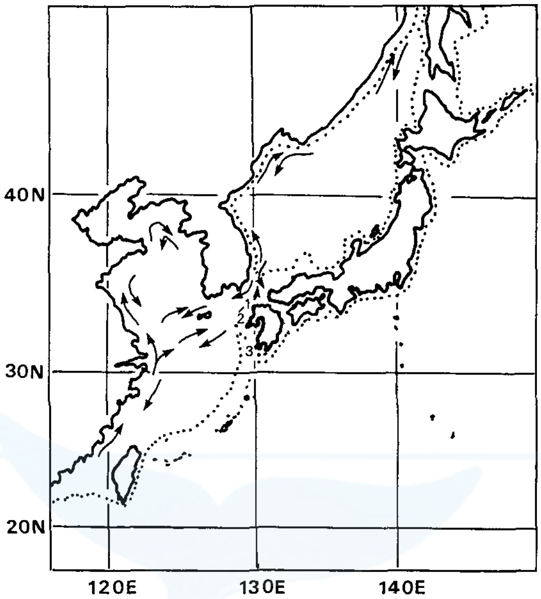

Fig. 3. Migration of the western Pacific stock of gray whales. (Excludes those occurring on the Pacific side of Japan).
1. Ikitsuki Island
2. Goto Island
3. Kasasa, Kagoshima prefecture

waters, and even in the eastern Bering Sea they travel within 2km from shore to Nuvivak Island after passing through Unimak Pass in the northbound migration. They migrated offshore only from that island to waters around St. Lawrence Island (Braham, 1984).

In comparing the migration of the eastern and western stocks of the gray whale we should consider the difference of the ocean structure between the eastern and western North Pacific. In the eastern North Pacific the continental shelf is less developed and the deep sea is close to the continent. On the contrary in the western North Pacific the continental shelf is well developed, and the Yellow Sea and most parts of the East China Sea are shallower than 200 meters.

The gray whale is thought to have evaluated to live in shallow water. In Fig. 3 the continental shelf or 200 meter depth line is shown by dotted line. As seen in this figure most part of the East China Sea is shallower than 200 meters, and the 200 meters line extends from east side of Formosa to the south side of Kyushu, but a tongue of deep water projects along southwest Kyushu as far north as it reaches westside of the Goto Islands, a group of small islands situated southwest of Ikitsuki Island. The gray whale, therefore, is thought to travel westwards, instead of southwards, avoiding this deep water, from Ikitsuki until it reaches to the coast of China. Such migrations directly crossing the East China Sea, from east to west or reverse way can not be denied. In this case they travel about 400 nautical miles of offshore.

Wang (1984) speculated that the western Pacific stock of the gray whale migrated in the former times through the waters off the east coast of China, and entered the calving grounds in the coastal waters of Guangdong Province. He also extended the speculation that these calving grounds are possibly in Baya Bay and Wailuo Harbour and that a few individuals probably reached occasionally as far south as 20°N in the adjacent waters of the east coast of Hainan Island.

In the light of the above knowledge of the distribution of the two gray whale stocks the names of "California" and "Korean" stocks seem to be inappropriate. The better expression will be "eastern Pacific" and "western Pacific" stocks of the gray whale.

Present size of the western Pacific stock of the gray whale, however, has been reduced to such a low level that it can no longer function as a significant part of its ecosystem (Brownell, 1977). Yablokov and Bogoslovskaya (1984) referred to a statement of Berzin (1978) that they were not recovering and the number continuing to decline.

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OSSIFICATION PATTERN OF THE VERTEBRAL EPIPHYSES IN THE SOUTHERN MINKE WHALE

HIDEHIRO KATO*

ABSTRACT

The pattern of fusion of the vertebral epiphyses to the centrum in the southern minke whale was examined using materials collected during the 1978/79 and 1979/80 Antarctic whaling expeditions. The fusion of the vertebral epiphysis to the centrum proceeds from the center of epiphysis to the peripheral on each vertebra regardless of the position on the vertebral column. On a vertebral column, epiphyseal fusion starts at anterior cervical then at posterior caudal vertebra, and is completed on the middle or posterior dorsal vertebrae. The fusion is completed on the entire vertebral column at ages of 23–36 years (males) or 28–36 years (females), and it has little correlation with the body length.

INTRODUCTION

The southern minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) is the only species which is currently exploited by the pelagic whaling in the Antarctic. Because of its importance in the stock management and study of the antarctic ecosystem, various studies attempted to clarify historical changes in their growth. For example, the decline of age at sexual maturity with time prior to the full exploitation started in 1971/72 has been suggested (Masaki, 1979; Best, 1982; Kato, 1983, 1987), which was thought to have resulted from the decline of possible competitative whale stocks such as blue (*B. musculus* (Linnaeus, 1758)) and fin whale (*B. physalus* (Linnaeus, 1758)).

Recently Kato (1987) compared growth curves between year classes of the southern minke whale and found the recent year-classes grew faster than the earlier ones. He analysed and suggested a possible change in the body length at the attainment of physical maturity with year-class. Although the examination of epiphyseal fusion to centrum is essential for the identification of physical maturity of whales, our information has been very fragmental on age, body length and progression of such change on the vertebral column. Kato (1987) analysed some of these aspects of southern minke whales using only the middle dorsal vertebrae, but he didn't present technical bases that this vertebral part can be used as a mark of the physical maturity. This study presents such basic information missing from the study of Kato (1987).

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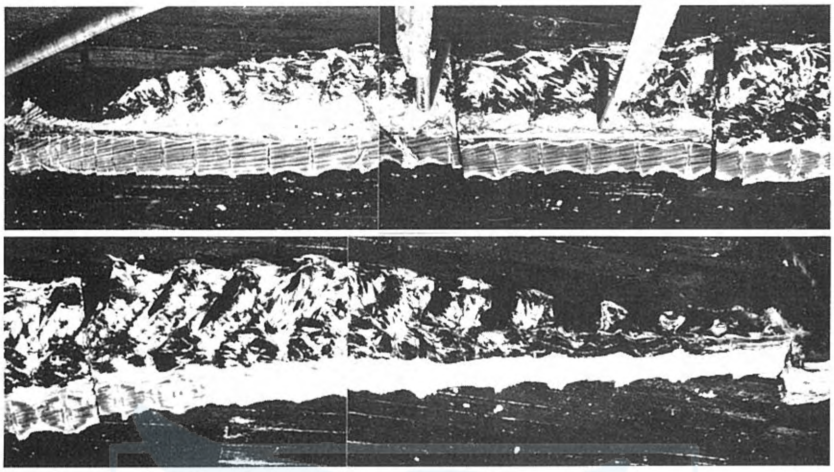

Fig. 1. Vertebral column of the southern minke whale bisected on the deck of *Nisshin-maru* No. 3 for the present study.

MATERIAL AND METHOD

Materials were collected from 45 males and 51 females caught by 1978/79 and 1979/80 Antarctic whaling expeditions of the *Nisshin-maru No. 3* to the south of 60° S and between 0° to 130°E (Areas III and IV). Age was determined counting growth layers in earplug and assuming annual deposition of the layer (Best, 1982; Kato and Best, unpublished). The layers were counted with stereoscopic microscope (6~10×) by myself. Female maturity was determined by examining ovaries, most of which were done by myself and some by Drs S. Ohsumi (Far Seas Fish. Res. Lab.) and Y. Masaki (South-East Regional Fish. Res. Lab.). Male maturity was not analysed in the present study.

For the present study the vertebral columns of animals which were randomly selected from the catch were cut into three or four segments with an electric chain saw (valid length = 2.5m) after stripping off the muscles, then they were bisected along the axis with the same saw (Fig. 1). Using the method I was able to examine small caudal vertebrae burried between the tail flukes. The cut surface was observed by naked eyes and classified into four stages after Laws (1961) (Fig. 2):

UTC;	unfused, thick cartilage present
UFC;	unfused, thin cartilage present
FJV;	fused, join visible
FJI;	fused, join invisible

The stage of *UTC, UFC, FJV* and *FJI* are equivalent to those of *N, n, a* and *A* of Ohsumi, Nishiwaki and Hibiya (1958) respectively.

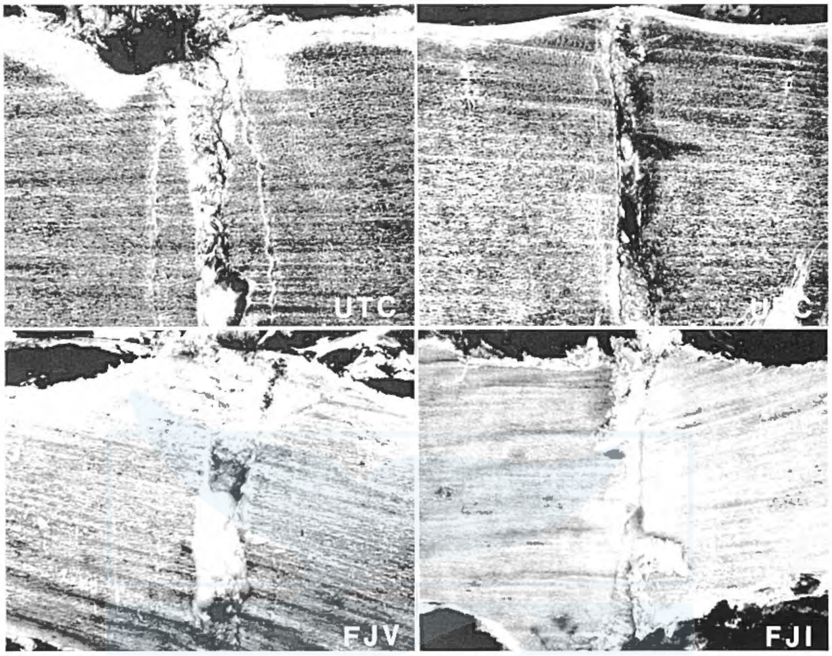

Fig. 2 Typical examples of the epiphyseal fusion stages used in the present study. *UFT*, unfused with thick cartilage; *UTC*, unfused with thin cartilage; *FJV*, fused with join visible; *FJI*, fused without visible join.

The epiphyseal fusion was examined on both center and ventral margin of the posterior epiphysis. Such observation was initially made on all the vertebrae of the sampled animals and recorded on the factory ship. However results on the 12 selected vertebrae are used in the following analyses. These vertebrae are:

1st, 4th and 7th cervical vertebrae;
2nd, 6th and 10th dorsal vertebrae;
2nd, 6th and 10th lumber vertebrae;
3rd, 10th and 17th caudal vertebrae.

Physically mature individuals were defined as those where epiphyseal fusion was completed on the above 12 vertebrae (stage *FJI*). All the other stage were defined as physically immature.

RESULT

Firstly I compared epiphyseal fusion between center and ventral margin of the same epiphysis. The result is grouped for the three vertebral segments of cervical, dorsal, lumber and caudal vertebrae and shown in Table 1. Majority

TABLE 1. COMPARISON OF EPIPHYSEAL FUSION STAGES* BETWEEN THE CENTER AND PERIPHERAL OF A EPIPHYSIS.

Vertebral segment	fusion at epiphyseal center	fusion at epiphyseal peripheral*			
		UTC	*UFC*	*FJV*	*FJI*
Cervical	*UTC*	25	–	–	–
	UFC	4	70	–	–
	FJV	–	5	118	–
	FJI	–	–	1	415
Dorsal	*UTC*	436	–	–	–
	UFC	6	169	–	–
	FJV	–	85	123	–
	FJI	–	–	59	107
Lumber	*UTC*	402	–	–	–
	UFC	28	128	–	–
	FJV	–	59	123	–
	FJI	–	–	98	260
Caudal	*UTC*	269	–	–	–
	UFC	53	116	–	–
	FJV	4	46	140	–
	FJI	–	–	184	811

* *UTC*, unfused with thick cartilage; *UFC*, unfused with thin cartilage; *FJV*, fused with join visible; *FJI*, fused with join invisible.

of the vertebrae showed the equal stage of fusion between the center and peripheral (ventral). Such vertebrae comprised 85.5% of the total data sets (4,344) or 77% of 2,751 vertebrae excluding those with fully fused epiphyses. However, 14.5% of them showed more advanced stage of fusion at the epiphyseal center and none of them showed the opposite case. Agreement of the two observations was lower on the posterior vertebral column; 95.5% in cervical vertebrae, 82.9% in dorsal vertebrae, 77.5% in lumbar vertebrae, and 64.7% in caudal vertebrae (excluding observations on vertebrae with fully fused epiphyses).

It is important to note that if the two observations disagreed the fusion near the peripheral of epiphysis was always less advanced. This indicates that the fusion of the vertebral epiphysis proceeds from its center to the peripheral, and that the progress is slower on the posterior vertebrae. Epiphyseal fusion completes at the marginal of each epiphysis. In the following analyses, I used only the status of epiphyseal fusion at the peripheral part.

Table 2 shows the progress of epiphyseal fusion with increasing body length. The fusion begins at the anterior cervical vertebrae in both sexes, and cervical epiphyses were completely fused to the centrum even on the smallest male sample (22ft in body length). Epiphyseal fusion on the posterior caudal vertebrae starts at a body length of about 27ft for both sexes. After then, the fusion proceeds with increase of body length towards the middle vertebral column. However, there are considerable individual variations in the stage of the epiphyseal fusion among the individuals of the same body length and sex. For example, some individuals almost completed fusion while others had only started the process on the dorsal and lumber vertebrae at the body length classes between 27ft and 29ft in males, and between 28ft and 31ft in females. However the ossification is usually advanced on older individuals of the body length classes above.

Then, the individual data were rearranged according to their age to produce Table 3 (individuals without sufficient age information were excluded). It was confirmed again that the fusion of epiphyses begins firstly at the anterior cervical at about age two years, and subsequently at the posterior caudal at about age 10 years in both sexes. The fusion proceeds with age from the both ends toward the middle region of the vertebral column and have been completed at the middle or posterior parts of the dorsal region. The youngest physically mature animals appeared at 23 years and 28 years in males and females respectively, while the oldest physically immature animals were 36 years in both sexes. However, the differences between sexes may not be significant.

DISCUSSION

Although histological technique will be desirable for the observation of epiphyseal fusion as by Wheeler (1930), it was not applicable in the present study. I cannot deny, therefore, misclassification of some stages of fusion, especially between later stage of *UFC* (unfused, thin cartilage present) and beginning of *FJV* (fused, join visible). However, as shown in Fig. 2, the presence or the absence of cartilage on the joining line can be easily recognized without histological section if observed carefully. Thus I consider the present method is adequate for the present study.

Mackintosh and Wheeler (1921) had preliminarily examined the physical maturity status of blue and fin whales by the epiphyseal fusion on some parts of the vertebral column, based on the suggestion given by an earlier work (Flower, 1864). Wheeler (1930) examined further the nature of the ossification pattern on column in southern fin whale, and found in female that the epiphyseal fusion starts from both ends of the column and is completed at the anterior dorsal vertebrae. Later Ohsumi *et al.* (1958) confirmed similar pattern of ossification in the North Pacific fin whale using a larger sample size and detailed observation.

The present study compared ossification pattern with absolute age by earplug growth layer counts, though both Wheeler (1930) and Ohsumi *et al.* (1958) used number of ovulation, and confirmed, for the southern minke whales, similar pattern of the ossification of the vertebral column to that in fin

TABLE 2. RELATIONSHIP BETWEEN EPIPHYSEAL FUSION STAGES AND BODY LENGTH

MALE

BL (ft)	Position on vertebral column*											
	C			D			L			Ca		
	1	4	7	2	6	10	2	6	10	3	10	17
22	●	–	–	–	–	–	–	–	–	–	–	–
24	▲	▲	▲	–	–	–	–	–	–	–	–	–
25	▲	△	△	–	–	–	–	–	–	–	–	–
	●	△	△	–	–	–	–	–	–	–	–	–
	●	▲	△	–	–	–	–	–	–	–	–	–
26	▲	▲	△	△	–	–	–	△	△	△	▲	△
	●	●	△	△	–	–	–	–	–	–	△	△
	●	●	△	△	–	–	–	–	–	△	△	△
27	●	△	△	–	–	–	–	–	–	–	–	–
	●	●	△	–	–	–	–	△	▲	△	●	●
	●	●	●	▲	–	–	–	–	–	△	▲	●
	●	●	●	△	–	–	–	–	△	△	▲	●
	●	●	▲	▲	–	–	–	–	▲	●	●	●
	●	●	●	▲	▲	△	△	●	●	●	●	●
	●	●	▲	▲	▲	▲	▲	●	●	●	●	●
	●	●	●	●	▲	▲	▲	▲	●	●	●	●
	●	●	●	●	●	▲	▲	●	●	●	▲	●
28	●	●	▲	△	–	–	–	–	–	–	△	–
	●	●	△	–	–	–	–	–	–	–	▲	▲
	●	▲	△	–	–	–	–	–	△	△	▲	●
	●	▲	△	△	–	△	–	–	△	●	●	●
	●	●	△	△	–	–	–	–	▲	●	●	●
	●	▲	▲	–	–	–	–	△	▲	▲	●	●
	●	●	●	▲	△	△	△	▲	▲	●	●	●
	●	●	●	△	△	△	▲	▲	▲	●	●	●
	●	▲	▲	▲	△	▲	▲	▲	●	●	●	●
29	●	△	△	–	–	–	–	–	–	–	△	–
	●	▲	△	–	–	–	–	–	–	●	●	–
	●	▲	△	△	–	–	–	–	▲	▲	●	●
	●	●	△	△	△	△	△	▲	●	●	●	●
	●	●	●	▲	△	△	▲	▲	●	●	●	●
	●	●	▲	▲	△	▲	▲	▲	●	●	●	●
	●	●	▲	▲	▲	▲	●	●	●	●	●	▲
	●	●	●	▲	▲	▲	▲	●	●	●	●	●
	●	●	●	●	▲	▲	▲	●	●	●	●	●
	●	●	●	●	▲	▲	▲	●	●	●	●	●
30	●	●	●	▲	△	–	△	▲	▲	▲	●	●
	●	●	▲	▲	△	▲	▲	▲	●	●	●	●
	●	●	●	●	●	●	●	●	●	▲	●	●
	●	●	●	●	●	●	●	●	●	●	●	●
	●	●	●	●	●	●	●	●	●	●	●	●
32	●	●	●	▲	△	△	△	△	▲	●	●	●

FEMALE

BL (ft)	Position on vertebral column												No. Ovulations
	C			D			L			Ca			
	1	4	7	2	6	10	2	6	10	3	10	17	
24	▲	△	–	–	–	–	–	–	–	–	△	△	0
25	●	△	–	–	–	–	–	–	–	–	△	△	–
	●	△	–	–	–	–	–	–	–	–	△	△	0
	●	●	△	△	–	–	–	–	–	–	–	△	0
26	●	▲	△	–	–	–	–	–	–	–	–	△	0
	●	●	●	▲	–	△	△	△	▲	●	●	●	20
27	▲	△	△	–	–	–	–	–	–	–	–	△	0
28	△	△	△	–	–	–	–	–	△	△	△	▲	0
	▲	▲	△	–	–	–	–	–	–	△	▲	–	1
	–	▲	△	–	–	–	–	–	–	▲	▲	●	9
	▲	▲	△	–	–	–	–	–	△	▲	▲	▲	12
	●	▲	△	△	–	–	△	△	▲	▲	●	●	5
	●	●	●	●	●	▲	▲	●	●	●	●	●	23
	●	●	●	●	▲	●	●	●	●	●	●	●	16
29	●	▲	△	–	–	–	–	–	△	△	▲	▲	7
	●	△	–	–	–	–	–	–	△	▲	▲	▲	2+
	▲	▲	▲	△	△	△	△	△	▲	▲	▲	●	23
	●	●	▲	▲	△	△	△	△	△	▲	▲	●	12
	●	●	●	▲	△	△	▲	△	▲	●	●	●	21
	●	●	▲	▲	△	▲	▲	▲	●	●	●	●	18
	●	●	●	▲	△	▲	▲	●	●	●	●	●	17
	●	●	▲	▲	▲	▲	▲	▲	●	●	▲	△	17
30	▲	△	–	–	–	–	–	–	–	–	▲	△	17
	●	–	–	–	–	–	–	–	–	–	▲	△	6
	●	▲	△	△	–	–	–	–	–	–	▲	●	4
	●	●	▲	▲	–	–	–	–	–	–	▲	●	4+
	●	●	▲	△	–	–	–	–	–	▲	△	△	9
	●	●	●	△	△	–	–	△	△	●	●	●	10
	●	●	▲	△	–	–	△	△	●	●	●	●	28
	●	▲	▲	△	△	△	▲	▲	●	●	●	●	19
	●	●	▲	▲	△	△	▲	▲	●	●	●	●	13
	●	●	●	▲	△	△	▲	▲	●	●	●	●	19
	●	●	●	●	▲	▲	●	●	●	●	●	●	26
	●	●	●	●	●	▲	▲	●	●	●	●	●	30
	●	●	●	●	●	●	●	●	●	●	●	●	28
	●	●	●	●	●	●	●	●	●	●	●	●	36
	●	●	●	●	●	●	●	●	●	●	●	●	29
30	●	▲	–	–	–	–	–	–	–	–	▲	△	9
	●	▲	▲	△	–	–	–	△	△	△	●	●	10
	●	●	△	–	–	–	–	△	△	●	●	●	13
	●	●	●	▲	–	–	△	▲	●	●	●	●	22
	●	●	●	●	–	–	△	▲	●	●	●	●	24
	●	●	▲	△	△	▲	▲	▲	●	●	●	●	14
	●	●	▲	▲	▲	▲	▲	●	●	●	●	●	28
	●	●	●	●	▲	●	●	●	●	●	●	●	30
	●	●	●	●	●	●	●	●	●	●	●	●	–
	●	●	●	●	●	●	●	●	●	●	●	●	28
	●	●	●	●	●	●	●	●	●	●	●	●	21
	●	●	●	●	●	●	●	●	●	●	●	●	33

32	●●●	●●●	●●●	●●●	41
33	●●●	●●●	●●●	●●●	32
34	●●●	●●●	●●●	●●●	–

* Symbols used are; C, crevical; D, dorsal; and Ca, caudal vertebrae. Hyphen indicates stage unfused with thick cartilage (*UTC*), open circle unfused thin cartilage (*UFC*), closed triangle fused join visible (*FJV*), closed circle fused join invisible (*FJI*).

TABLE 3. RELATIONSHIP BETWEEN EPIPHYSEAL FUSION STAGES AND AGE.

MALE

		Position on vertebral column*											
Age	BL	C			D			L			Ca		
	(ft)	1	4	7	2	6	10	2	6	10	3	10	17
2	25	●	△	△	–	–	–	–	–	–	–	–	–
	25	●	▲	△	–	–	–	–	–	–	–	△	△
4	26	●	●	△	△	–	–	–	–	–	–	△	△
5	29	●	△	△	–	–	–	–	–	–	–	△	△
7	26	●	●	△	△	–	–	–	–	–	△	△	△
8	28	●	●	△	–	–	–	–	–	–	–	▲	▲
9	26	▲	▲	△	△	–	–	–	△	△	△	▲	△
	29	●	●	●	▲	△	△	△	▲	▲	●	●	●
12	29	●	▲	△	–	–	–	–	–	–	●	●	–
	28	●	●	△	△	–	–	–	–	▲	●	●	●
14	27	●	●	●	△	–	–	–	–	–	△	▲	●
	27	●	●	●	▲	–	–	–	–	–	△	▲	●
16	28	●	●	●	△	△	△	▲	▲	▲	●	●	●
17	30	●	●	▲	▲	△	▲	▲	▲	●	●	●	●
19	29	●	▲	△	△	–	–	–	–	▲	▲	●	△
	28	●	▲	▲	▲	△	▲	▲	▲	●	●	●	●
	29	●	●	▲	▲	▲	▲	●	●	●	●	●	▲
21	32	●	●	●	▲	△	△	△	△	▲	●	●	●
23	30	●	●	●	▲	△	–	△	▲	▲	▲	●	●
	30	●	●	●	●	●	●	●	●	●	●	●	●
26	27	●	●	●	▲	▲	△	▲	●	●	●	●	▲
29	29	●	●	●	▲	▲	▲	▲	●	●	●	●	●
30	30	●	●	●	●	●	●	●	●	●	●	●	●
36	27	●	●	●	●	▲	▲	▲	▲	●	●	●	●

FEMALE

		Position on vertebral column*											
Age	BL	C			D			L			Ca		
	(ft)	1	4	7	2	6	10	2	6	10	3	10	17
4	25	●	△	–	–	–	–	–	–	–	–	–	–
5	27	▲	△	△	–	–	–	–	–	–	–	–	–
7	30	●	●	▲	▲	–	–	–	–	–	–	△	●
10	28	▲	▲	△	–	–	–	–	–	–	△	▲	–
11	31	●	▲	–	–	–	–	–	–	–	–	▲	△
	30	●	▲	△	△	–	–	–	–	–	–	▲	●
13	30	●	●	–	–	–	–	–	–	–	–	▲	△
14	31	●	▲	▲	△	–	–	–	△	△	△	●	●
15	30	▲	△	–	–	–	–	–	–	–	–	▲	△
	28	●	▲	△	△	–	–	△	△	▲	▲	●	●
16	29	●	△	–	–	–	–	–	–	△	▲	▲	●
	28	▲	▲	△	–	–	–	–	–	△	▲	▲	▲
17	28	–	▲	△	–	–	–	–	–	–	▲	▲	●
18	30	●	●	●	▲	△	△	▲	●	●	●	●	●
19	31	●	●	△	–	–	–	–	▲	●	●	●	●
21	29	●	▲	△	–	–	–	–	–	△	△	▲	△
	30	●	●	▲	△	–	–	–	–	–	▲	△	△
	28	●	●	●	●	▲	●	●	●	●	●	●	●
22	31	●	●	▲	△	△	▲	▲	▲	●	●	●	●
24	30	●	●	●	△	△	△	△	△	△	●	●	●
	29	●	●	▲	▲	△	△	△	△	△	▲	▲	●
25	29	●	●	●	▲	△	▲	▲	●	●	●	●	●
	30	●	●	●	●	●	▲	▲	●	●	●	●	●
26	29	●	●	●	▲	△	△	▲	△	▲	●	●	●
28	31	●	●	●	▲	–	–	△	▲	●	●	●	●
	30	●	▲	▲	△	△	△	▲	▲	●	●	●	●
	30	●	●	●	●	●	●	●	●	●	●	●	●
29	34	●	●	●	●	●	●	●	●	●	●	●	●
30	26	●	●	●	▲	–	△	△	△	●	●	●	●
31	31	●	●	●	●	●	●	●	●	●	●	●	●
32	30	●	●	▲	▲	▲	▲	▲	▲	●	●	▲	–
34	30	●	●	●	●	●	●	●	●	●	●	●	●
35	28	●	●	●	●	●	▲	▲	●	●	●	●	●
36	30	●	●	●	●	▲	▲	●	●	●	●	●	●
38	30	●	●	●	●	●	●	●	●	●	●	●	●
41	31	●	●	●	●	●	●	●	●	●	●	●	●
42	33	●	●	●	●	●	●	●	●	●	●	●	●

* For symbols see Table 2.

whale above. Some differences exist, however, between fin and minke whale; in the fin whale the epiphyseal fusion firstly commences at posterior parts of caudal vertebrae while it firstly starts at the anterior of the cervical in minke whales; the fusion is completed among the anterior dorsal vertebrae for fin whale rather than the posterior dorsal as in minke whale.

As stated by Wheeler (1930) and Mackintosh (1942) the completion of epiphyseal fusion bears relation to number of ovulation and little to the body length. It was considered, in fin whale, that the ossification was completed at 13–16 ovulations (Wheeler, 1930; Peters, 1939; Nishiwaki and Oye, 1939; Brinkman, 1948; Ohsumi, *et al.*, 1958); based on the evidence of ossification at the particular vertebrae. By converting these values of ovulation to absolute age by average annual ovulation rate reported (0.67-0.71; Laws, 1961; Lockyer, 1971; Gambell, 1973) and assuming average age at sexual maturity in the 1930–1950s to be age 11-12 years (from studies by Lockyer (1984) and Ohsumi (1986)), the values can be roughly calculated to be age 28-36 years. These ages for fin whale is similar to those in the present study for minke whale (age 23-26 years), though the maximum life span for the former is about twofold to the latter (Ohsumi, 1979).

However, it is still not clear whether completion of epiphyseal fusion of individual depend on time after sexual maturation or absolute age. Moreover, another aspect should be considered; the relationship between the physical maturity and changes in density. For example, Kato (1987) found that density dependent changes in growth parameters such as age at sexual maturity and growth rate and suggested increase in body length at physical maturity with density in the southern minke whale stocks. These aspects are desired to be examined further in the future study.

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BRYDE'S WHALE IN THE COASTAL WATERS OF EASTERN AUSTRALIA

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ABSTRACT

While documented capture of *B. edeni* in eastern Australian waters is limited to only a few records, inshore observations suggest that the species is not uncommon. Aspects of osteology and baleen morphology in two large stranded whales now housed in the Queensland Museum confirm their identity as Bryde's whales. Breaching behaviour and the "working" of fish schools is discussed.

INTRODUCTION

Bryde's whale (*Balaenoptera edeni* Anderson, 1878) is widely distributed between latitudes 40°N and 40°S (Omura, 1959). Although Bryde's whale has been captured in the south-west Pacific Ocean to the east of Australia (Kawamura, 1980) very few captures have been reported from the waters adjacent to the east Australian mainland which lies between latitudes 11°37'S and 39°04'S (Fig. 1). Information will be presented in this paper detailing Bryde's whale captures, strandings and field observations in the coastal waters of eastern Australia. Specimens mentioned in this paper are lodged in the following collections: Queensland Museum (J or JM), Victorian Museum (C).

CAPTURES

Between 1952 and 1962 shore stations at Tangalooma (27°11'S, 153°23'E) and Byron Bay (28°37'S, 153°38'E) processed 7423 humpback whales (Paterson and Paterson, 1984) and the industry was based almost exclusively on that species. However, Bryden (1978) noted that on 14 September 1962 a 42 foot 3 inch [12.87 m] male sei or Bryde's whale was captured by the chaser *Norfolk Whaler* five miles north of Cape Byron and Best (1977) noted that he had received data concerning two Bryde's whales captured from the east Australian shore stations in the early 1960s. Those captures and the small numbers captured from the shore station at Carnarvon in Western Australia (Chittleborough, 1959) occurred during the decline in humpback whale stocks in Australian waters and may have been associated with attempts to

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**Queensland Museum, PO Box 300, South Brisbane, Queensland 4101 Australia*

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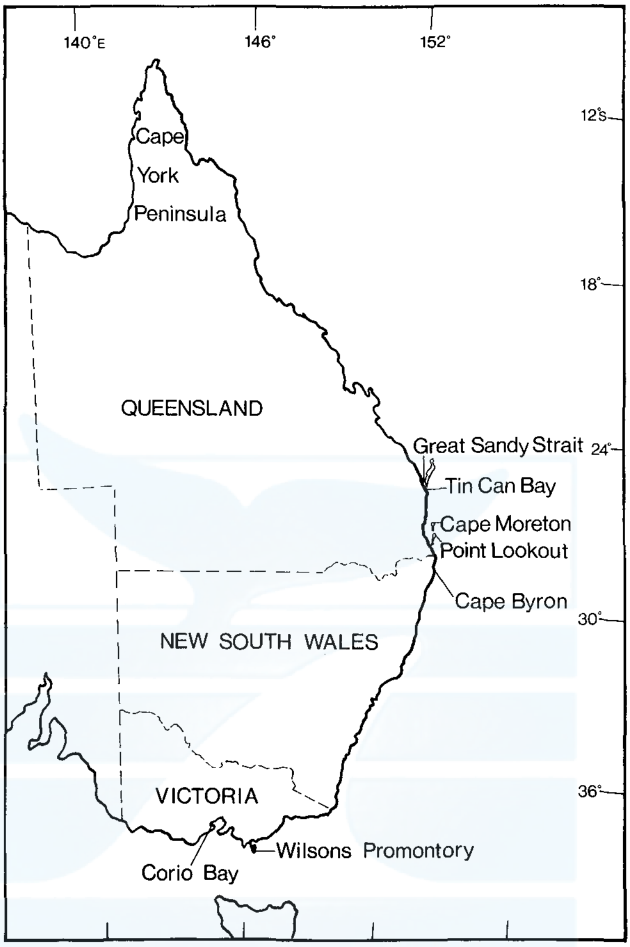

Fig. 1. Eastern Australian mainland showing localities mentioned in text.

diversify the operations of the shore stations. No systematic survey of Bryde's whale abundance was conducted and in 1962, when humpback whale stocks were commercially exhausted, the east Australian shore stations ceased all whaling activity.

STRANDINGS

Skeletal elements of two whales, positively identified as Bryde's whales at the time of stranding by the characteristic three longitudinal ridges on the dorsal aspects of their heads (Omura, 1962) have been deposited in the Victorian and Queensland Museums (Table 1 and Figs 2 and 3). The two specimens are

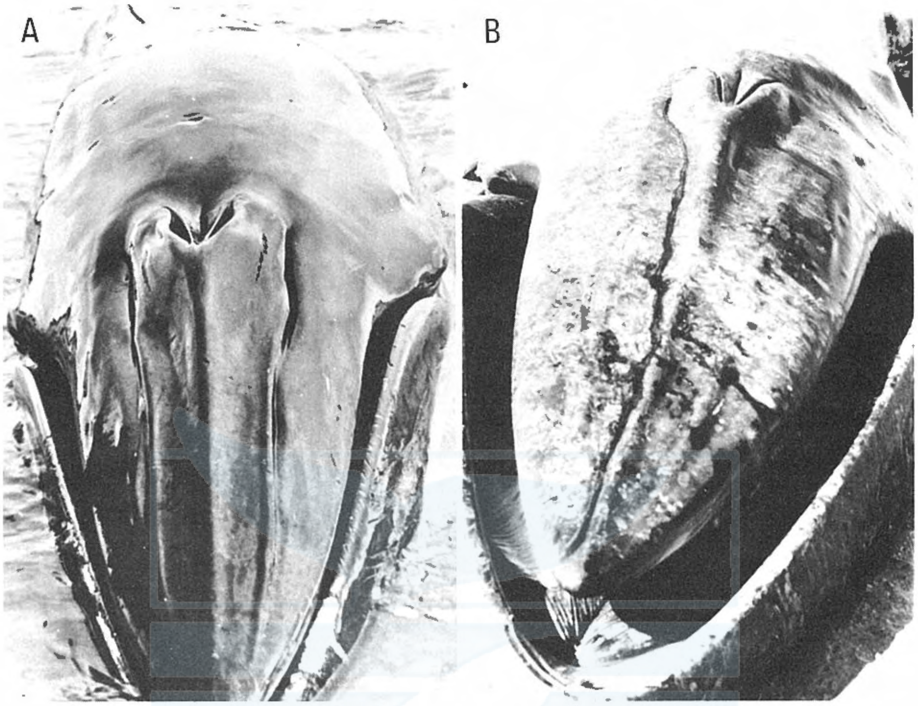

Fig. 2. Bryde's whales stranded on the east Australian coast.
A. Specimen C8841, from Victoria. B. Specimen JM4386, from Queensland.
See Table 1 for locality details.

TABLE 1. BRYDE'S WHALES STRANDED ON THE EAST AUSTRALIAN COAST

Registration Number	Date and location of stranding	Specimen details	Reference
C8841	25.vii.1968 Limeburner Creek, Corio Bay, Victoria (38°04'S, 144°24'E)	Male, 6.1 m long, Post cranial skeleton not collected.	Dixon (1970)
JM4386	30.x.1982 Stewart Island, Great Sandy Strait, Queensland (25°38'S, 152°57'E)	Sex unknown, 14.35 m long., Almost complete skeleton but some caudal vertebrae missing.	Paterson (1984)

from animals of disparate physical maturity. Watson (1981) noted that the maximum lengths of male and female Bryde's whales are 14.3 and 14.6 m respectively but the maximum lengths of male and female Bryde's whales

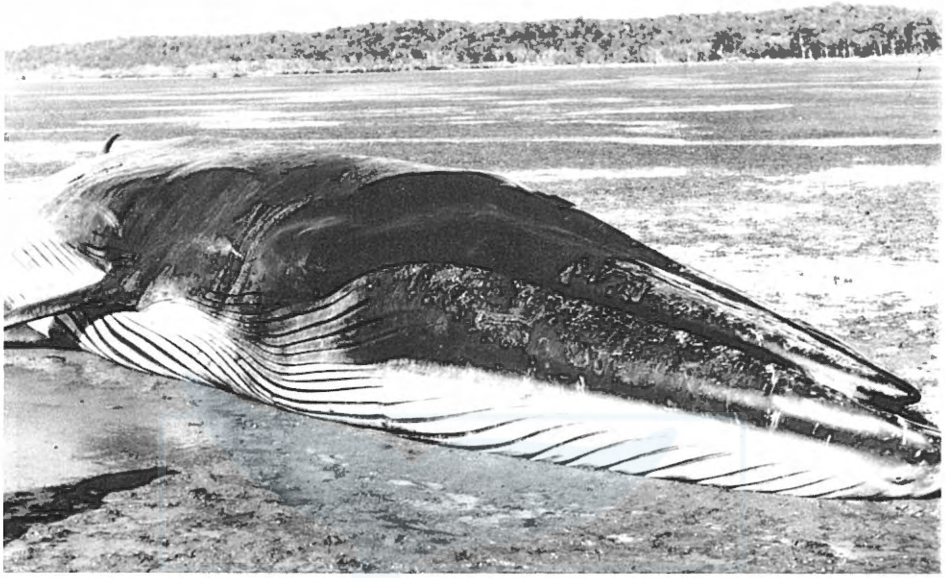

Fig. 3. Bryde's whale JM4386, stranded at Stewart Island, Great Sandy Strait, Queensland.

captured from the Great Barrier Island shore station in New Zealand between 1956 and 1961 were 14.6 and 14.9 m respectively (Gaskin, 1968). C8841 measured 6.1 m in length and the incomplete fusion of its cranial sutures indicates that the animal was juvenile whereas JM4386 measured 14.35 m in length and the lumbo-caudal portion of its vertebral column shows gross change of spondylitis deformans with associated spinal canal stenosis. Those pathological changes are considered to be a mainfestation of advanced age (Paterson, 1984) and are probably caused by repetitive vertebral ligamentous traction (Lagier, 1977).

Omura (1959) and Omura, Kasuya, Kato and Wada (1981) after detailed studies of Bryde's whales from the north and south Pacific Ocean and the Indian Ocean considered that the appearances of the anterior aspects of the nasal bones were the most distinctive osteological characteristic of Bryde's whales with regard to differentiation from sei whales (*Balaenoptera borealis* Lesson, 1828). The anterior margins of the nasal bones are concave and inclined forwards on their outer aspects in all specimens of Bryde's whales examined by Omura whereas those of sei whales are convex or straight and never inclined forwards on their outer aspects. The skull of JM4386, showing the characteristic nasal bones, is illustrated in Fig. 4. The skull of C8441 has been examined and its nasal bones are consistent with Omura's description of Bryde's whale.

Part of a baleen plate from JM4386 is shown in Fig. 5. The incomplete

Fig. 4. Dorsal view of the skull of Bryde's whale JM4386.

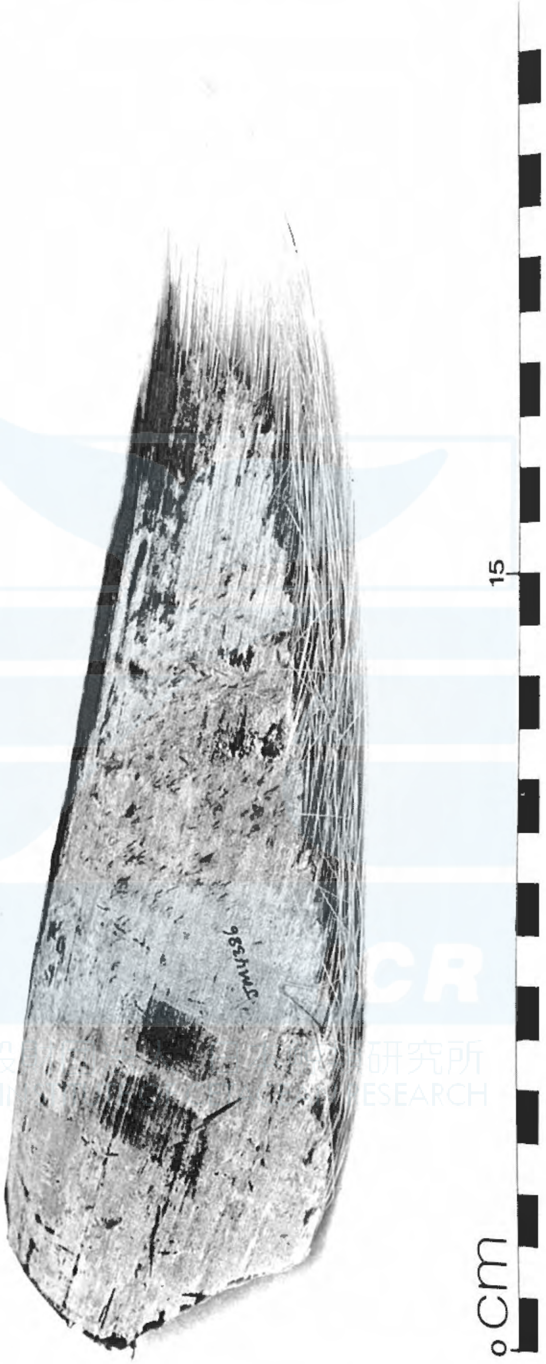

Fig. 5. Baleen sample from Bryde's whale JM4386.

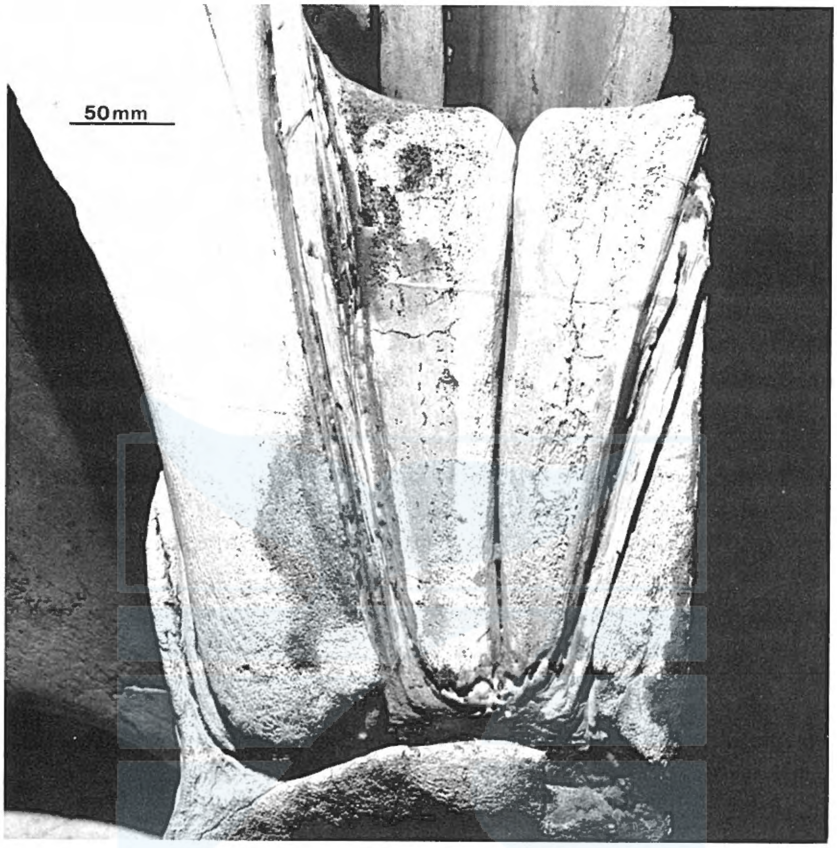

Fig. 6. Dorsal view of the nasal bones of Bryde's whale J21713 (the skull had been sawn longitudinally to allow its wall mounting).

nature of this sample precluded a determination of the affinities of JM4386 with Best's (1977) "inshore" and "offshore" forms.

Specimen J21713 in the Queensland Museum is from a whale which stranded at Tin Can Bay Inlet (25°51′S, 153°02′E) in 1965. No baleen samples or diagnostic photographs of the stranded animal are available for study. The specimen was considered to be that of a sei whale and was mounted and displayed in the Queensland Museum. The Museum has recently been relocated and the opportunity has arisen to examine the specimen in detail. The nasal bones are illustrated in Fig. 6 and their appearance is typical of a Bryde's whale. Omura *et al.* (1981) noted that the vertebral count of Bryde's whales is 54–55 and that of sei whales 56–57. Some vertebrae of JM4386 and J21713 are missing, the vertebral count being 49 in each specimen. Specimens of both Bryde's and sei whales examined by one of us (S.V.D.) in 1987, in the Rijksmuseum Van Natuurlijke Histoire, Leiden, Nederland (including the Palau Sugi specimen referred to by Omura, 1959) have confirmed the identity of JM4386 and J21713 as Bryde's whales.

FIELD OBSERVATIONS

One of us (R.A.P.) has monitored the annual migration of humpback whales from Point Lookout (27°26′S, 153°33′E) and Cape Moreton (27°02′S, 153°28′E) during the months of June to October yearly since 1978 (Paterson, 1987). During this period (an approximate total of 320 watching days) incidental sightings of minke and Bryde's whales were recorded. The latter were positively identified when the characteristic rostral ridges, described above, were seen. It was not uncommon for Bryde's whales to be seen close inshore near the headland at Point Lookout and in the surf-lines along adjacent beaches.

Kawamura (1980) noted that Bryde's whales have peak feeding periods during early morning and late afternoon and the Point Lookout observations appeared to support those findings but if schooling fish were present at other times during the day behaviour considered characteristic of feeding was observed. The behaviour included surface rushes, lunging and circling. On occasions fish were seen leaping as the whales swam quickly through densely packed schools.

Watson (1981) noted that Bryde's whales seldom show their flukes and fluke raising was not observed during any of the Point Lookout sightings. Breaching was occasionally seen but it was not acrobatic, as is that of humpback whales. When a Bryde's whale breached it usually emerged partially from the water and returned in the reverse direction but on two occasions Bryde's whales were seen to leap clear of the water in a horizontal position and re-entered by a "belly-flop".

Singles and pairs were the most common groupings and pairs occasionally "worked" adjacent schools of fish. As mentioned above, observations were conducted at Point Lookout from June to October and no assessment was made of Bryde's whale occurrence during the other months of the year. At this latitude in eastern Australia the sea is warmest in February and coldest in August. The average surface temperatures for February and August were reported as 24.3°C and 18.9°C (Paterson, 1986). Although Bryde's whales were seen in all months from June to October they were most frequently seen during August and September. Bryden (1978, pls 1–3) showed a photograph of a Bryde's whale seen near Cape Moreton (27°02′S, 153°28′E) during aerial observations in September 1976.

As Bryde's whales seen on successive days at Point Lookout may have been the same animals it was not possible to estimate their abundance. However, the observations indicate that Bryde's whales frequent the inshore waters of eastern Australia between latitudes 27°S and 28°S at least during the winter and spring months.

ACKNOWLEDGEMENTS

Mr Malcolm Cox of Project Jonah, Brisbane initially identified specimen JM4386 and kindly allowed reproduction of his original photographs. Dr Chris Smeenk, Curator of Mammals at the Rijksmuseum van Natuurlijke Histoire, Leiden, Holland is gratefully acknowledged for his hospitality and assistance while examinations were made of specimens in his care. Miss Joan Dixon, Curator of Mammalogy at the Museum of Victoria gave every assistance with regard to specimen C8841 and provided the relevant photograph. Mr Carlos Picasso of the Queensland Museum photographed the specimens in that Museum. Drs Hideo Omura and Seiji Ohsumi were most helpful with advice in relation to our enquiries.

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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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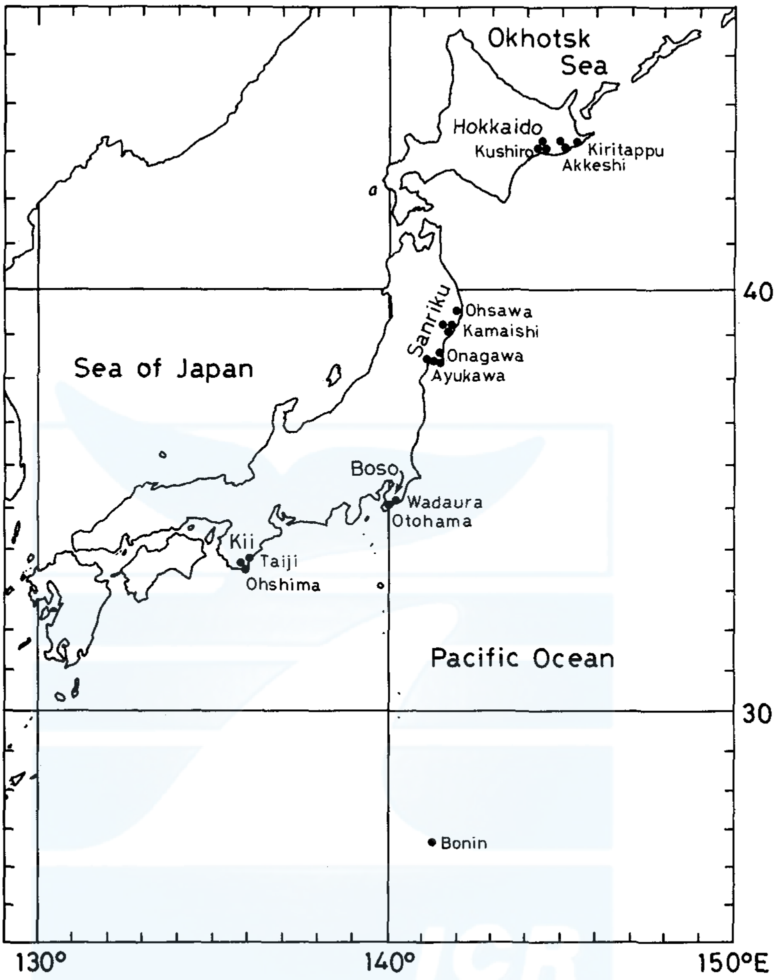

Fig. 1. Japanese whaling stations that have been used for processing sperm whales during the 1955 to 1986 seasons.

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 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°–40°N and west of 165°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°E, in 145°E–179°E, and in 179°E–150°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 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 (≥30 feet in 1938 to 1948, ≥35 feet in 1949–1972, and ≥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.

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

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	Aug.–Mar.	2,487
1977/78	1	1	2	–	Aug.–Mar.	2,017
1978/79	1	1	2	–	Aug.–Mar.	1,730
1979/80	1	1	2	–	Aug.–Mar.	1,269
1980/81	1	1	2	–	Aug.–Mar.	1,192
1981/82	1***	1	2	–	Aug.–Mar.	869
1982/83	1	1	2	–	Aug.–Mar.	439
1983/84	1	1	2	–	Aug.–Mar.	393
1984/85	1	1	2	–	Aug.–Mar.	400
1985/86	1	1	2	–	Aug.–Mar.	400

* 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									
	Apr.	May	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.

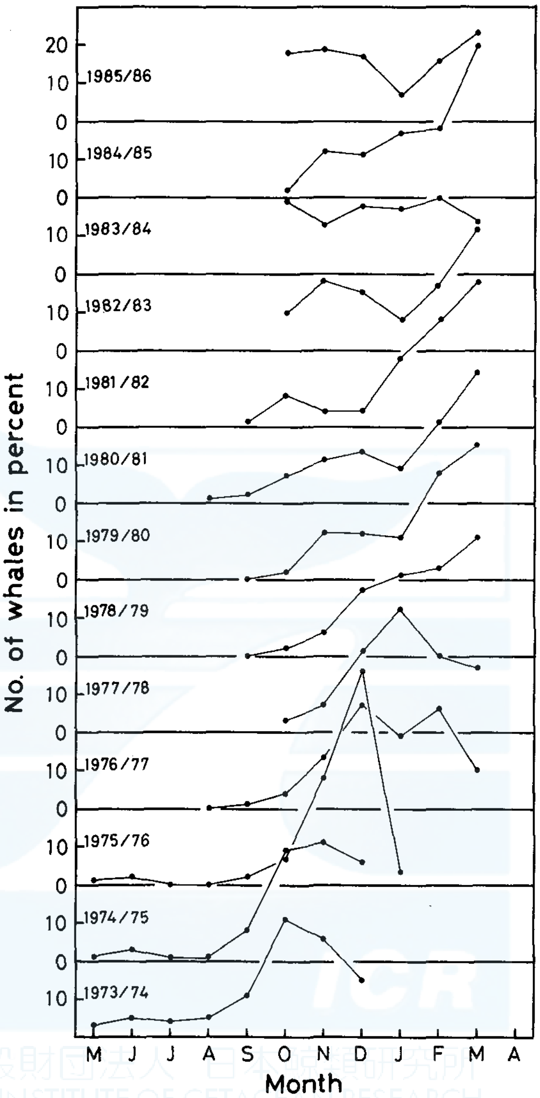

Fig. 2. Monthly distribution of sperm whale catch by Japanese coastal whaling.

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-

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)

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

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°–39°N with a peak in 37°–38°N (Figs 3 and 4). In 1977/78 season the catch occurred also in the additional latitudes of 32°–33°N or between Boso and Bonin Islands. Then during 1978/79 through 1982/83 seasons catch in the northern ground (34°–39°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°–33°N and 130°–145°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.

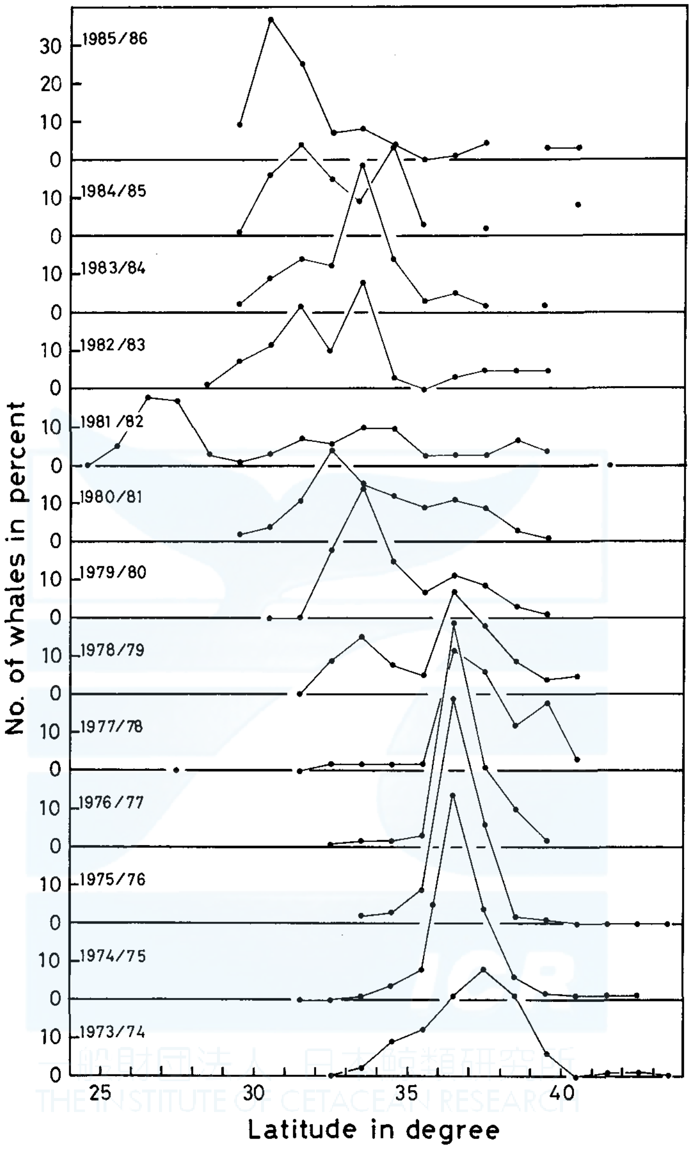

Fig. 3. Latitudinal distribution of sperm whale catch by Japanese coastal whaling.

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°–41°N) (Table 4) or in winter (January and February) in 36°–40°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

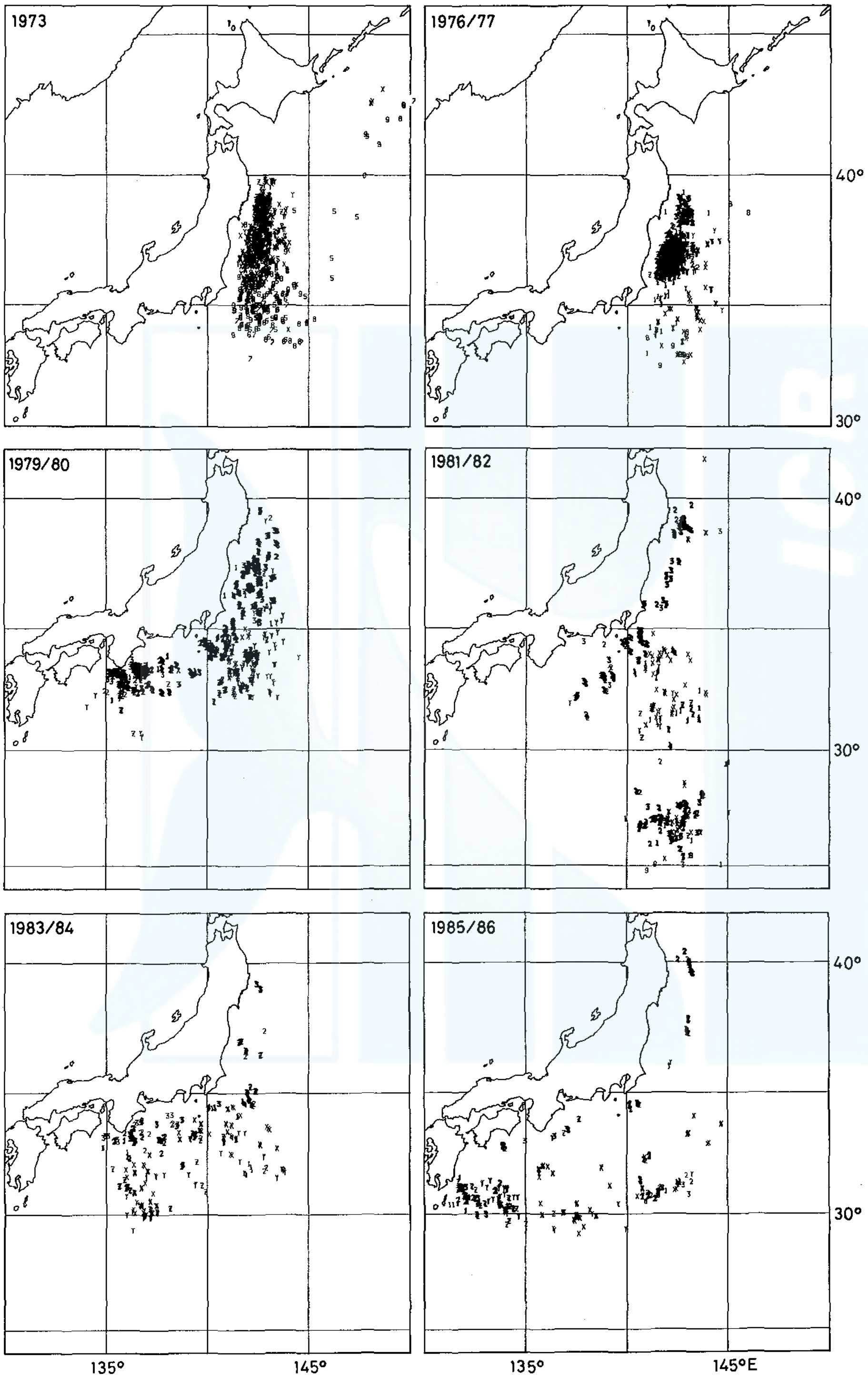

Fig. 4. Position of sperm whale catch by Japanese coastal whaling in some selected years. Each mark represents one sperm whale. Numerals (1 to 9) and alphabets (X, Y, Z) indicate month of the year (January to September, October to December). Every second individual has been plotted (being selected by the order of processing) for 1973 and 1976/77 seasons, but all 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°–39°N, then the area of peak catch shifted in summer slightly to the south (33°–36°N), and again returned to the north (37°–39°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	M	–	–	–	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	M	–	6	8	14	35	44	27	33	268	257	71	16
	F	–	3	–	13	11	9	16	10	130	179	105	18
	%	–	33	0	48	24	17	37	23	33	41	60	52
Sanriku	M	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 & Kii	M	16	20	11	43	56	12	12	1	3	1	2	14
	F	4	3	3	24	13	1	5	–	–	–	–	–
	%	20	13	21	36	19	8	29	0	0	0	0	0
Bonin Is	M	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

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

Whaling stations	Apr.	May	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 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						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		4	1	1			11				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

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

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							2					2
30°–31°N												
29°–30°N												
28°–29°N												
27°–28°N											1	1
Total				7	14	173	478	1080	1124	1046	592	4514

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										77	15	92
39°–40°N							1			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

TABLE 10. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE COASTAL WHALING IN THE PACIFIC, 1981/82 AND 1982/83 SEASONS

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
41°–42°N						2						2
40°–41°N												
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 11. LATITUDINAL DISTRIBUTION OF THE SPERM WHALE CATCH BY JAPANESE COASTAL WHALING IN THE PACIFIC, 1983/84 TO 1985/86 SEASONS

Latitude	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
40°–41°N										7	34	41
39°–40°N											19	19
38°–39°N												
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°–35°N, autumn) and northern (36°–39°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°–40°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

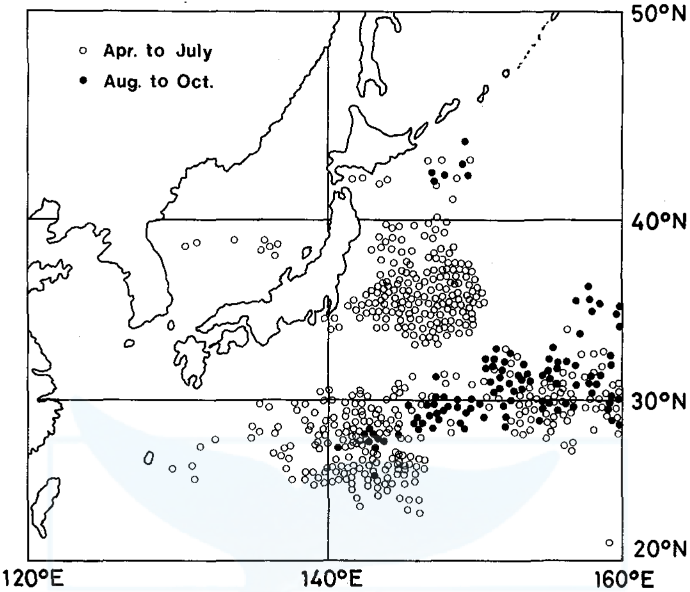

Fig. 5. Distribution of sperm whale catches from the records of 19th century American whale fishery. Plots represent positions of vessels on days when one or more sperm whales were taken (modified partial reproduction of Townsend, 1935).

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

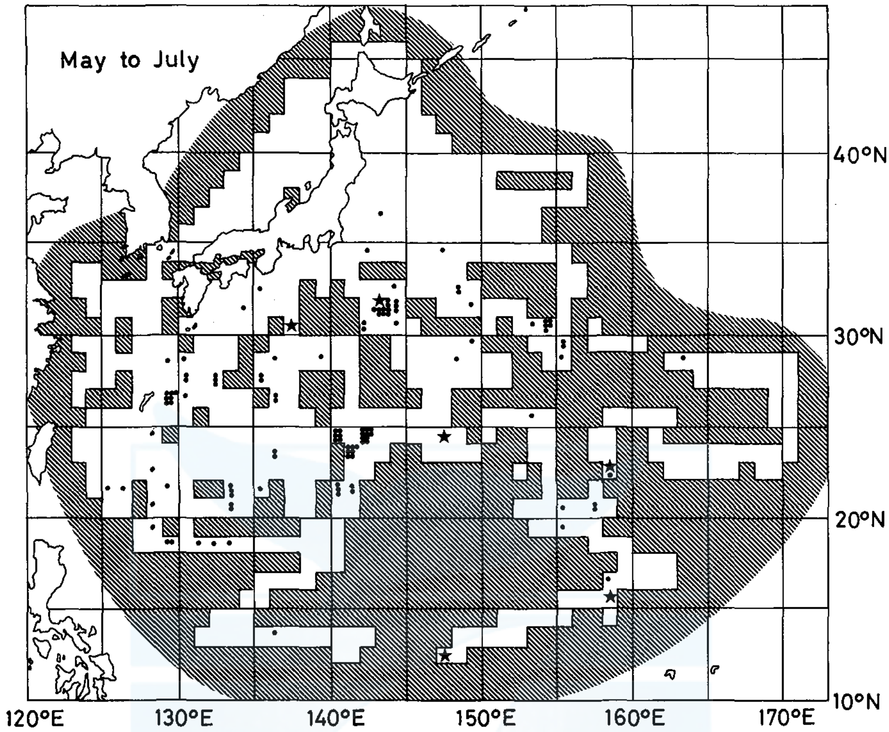

Fig. 6. Distribution of sperm whales observed during the whale sighting cruises in 1983 to 1986, May to July. Star indicates school containing individuals 46 feet or over in body length, and closed circle school of smaller whales. Shaded area represents one degree squares of latitude and longitude not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

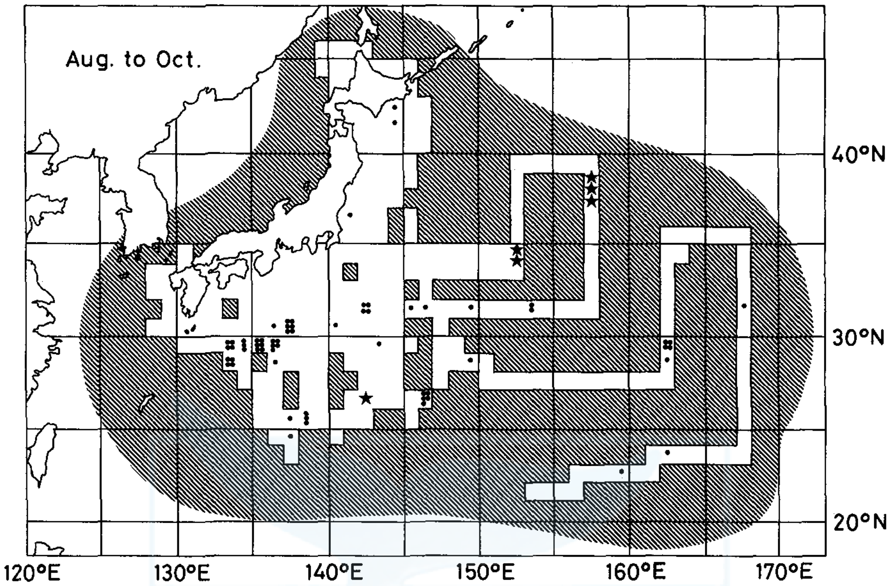

Fig. 7. Distribution of sperm whales observed during the whale sighting cruises in 1983 to 1986, August to October. For marks see Fig. 6.

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 (≤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

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

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	2	49	1	
27	3	2	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			

* 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	1	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

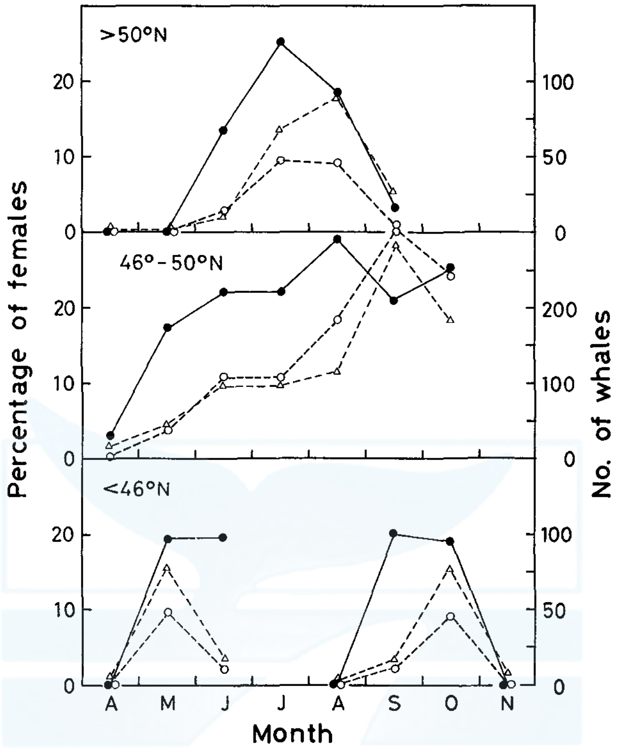

Fig. 8 Catch of sperm whales by USSR coastal whaling off the Kuril Islands in 1950, 1951, and 1962 through 1964, expressed by sex, month and position of land stations (compiled from USSR IWC/NP Forms). Closed circle and solid line: proportion of females in the catch; open circle and dotted line: number 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°–40°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°–40°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°–50°N, or just to the north of the front of the Kuroshio Current System at 35°–40°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°–51°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°–52°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°–44°N. The latitudes of low sperm whale catch correspond to a very distinct hiatus in whale sightings in 30°–40°N and 154°E–175°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°–55°N and south of 30°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

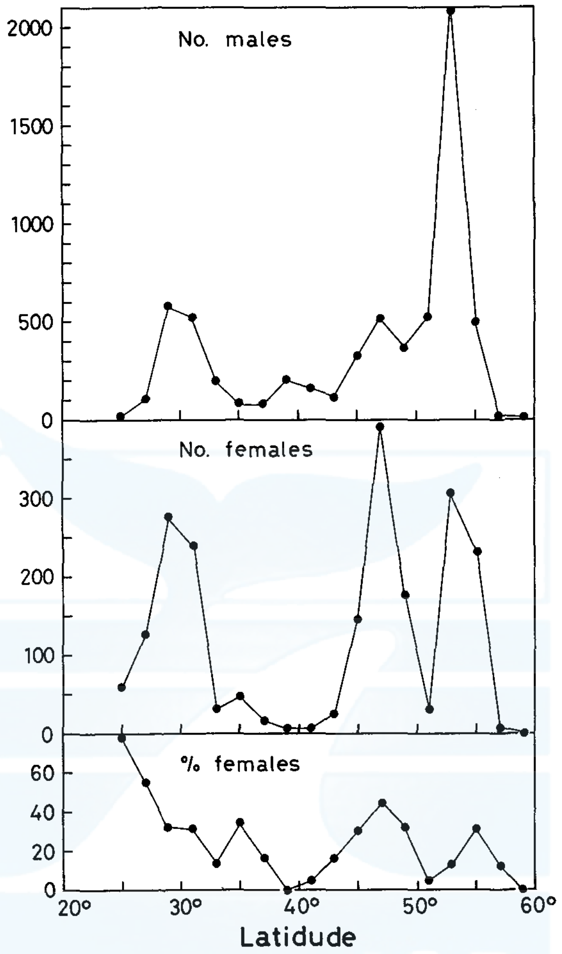

Fig. 9. Latitudinal distribution of sperm whale catch by Japanese pelagic whaling in 1966–1977, between 158°E and 180° longitude (compiled from Smith, 1980).

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

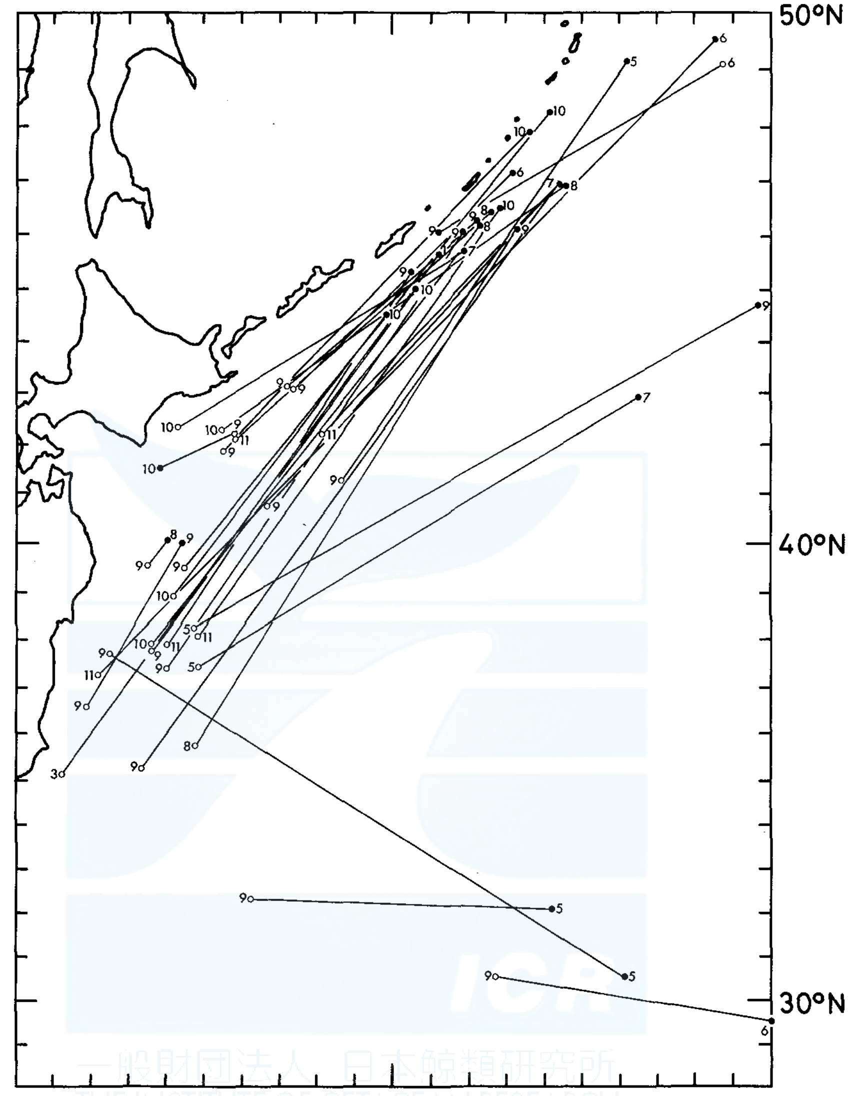

Fig. 10. Movement of marked female sperm whales, USSR marks only. Includes only marks recovered over 10 days after marking. Closed circle represents position of marking, open circle position of recovery, and numeral by the circle month of marking or recovery. For movement outside of this range see Table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

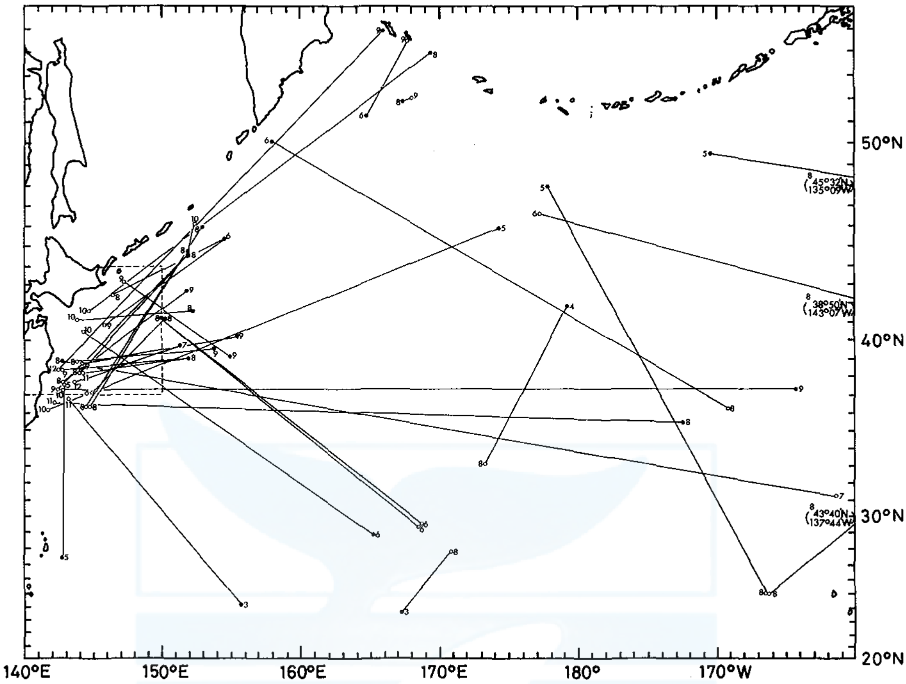

Fig. 11. Movement of marked female sperm whales, Canadian, Japanese, USA and USSR marks (excluding those listed in Fig. 10). Recoveries within 10 days or less from marking or movement within the dotted area are excluded. For movement outside this range see Table 14, and for symbols see Fig. 10.

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°N and south of 30°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°–40°N latitudes or between these latitudes (30°–40°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°E–180° in higher latitudes (40°–50°N) or between 160°W–170°W in lower latitudes (20°–30°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. ≥46 feet (13.9m) as mature and ≤45 feet (13.6m) as immature. There are

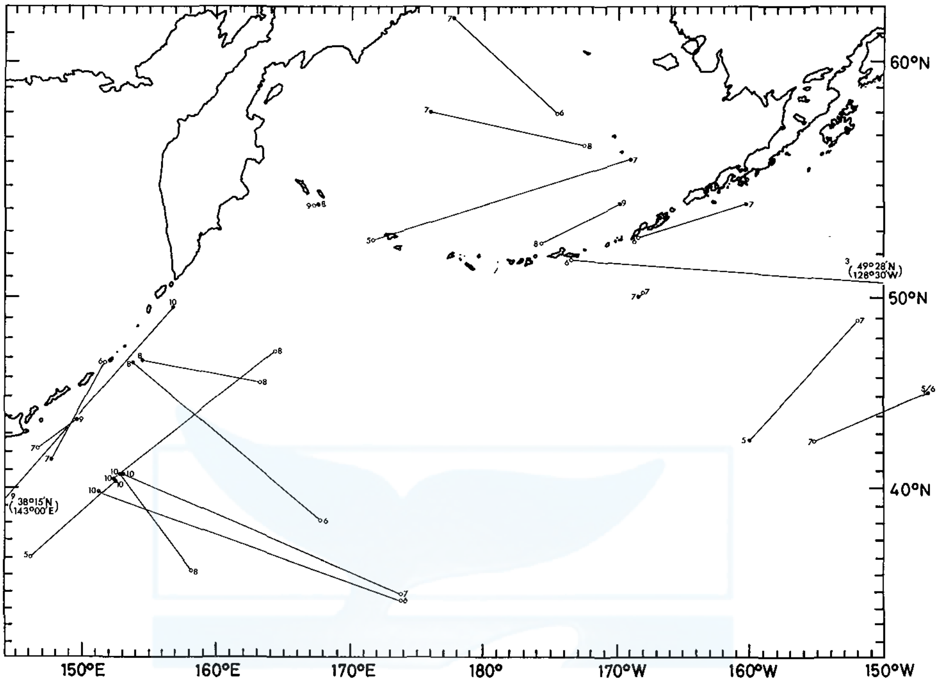

Fig. 12. Movement of marked adult male sperm whales (≥46 feet at recapture), using Canadian, Japanese and USSR marks recovered over 10 days after marking. For symbols see Fig. 10.

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

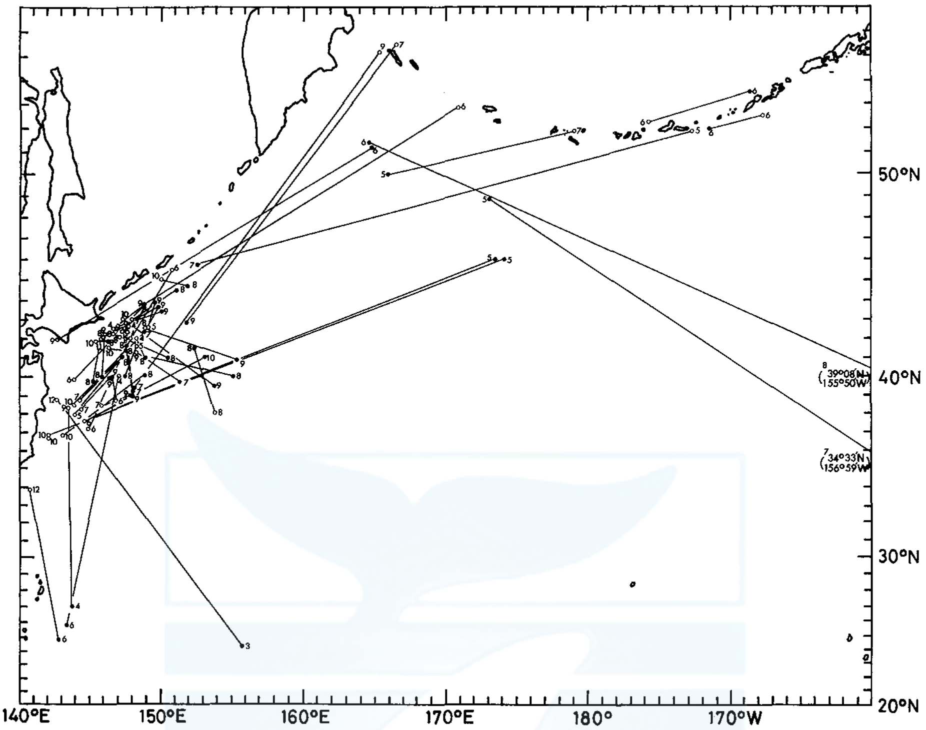

Fig. 13. Movement of marked immature male sperm whales (≤45 feet at recovery), using Japanese marks recovered over 10 days after marking. For movement outside this range see Table 14, and for symbols see Fig. 10.

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

The movement of immature males (≤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.

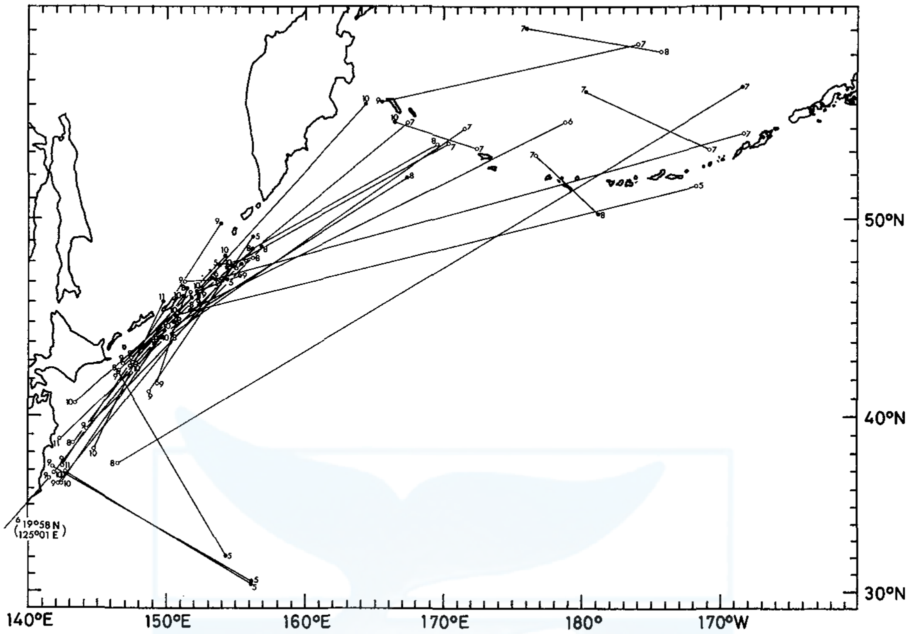

Fig. 14. Movement of marked immature male sperm whales (≤45 feet at recapture), using USSR marks recovered over 10 days after marking. For movement outside this range see Table 14, and for symbols see Fig. 10.

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

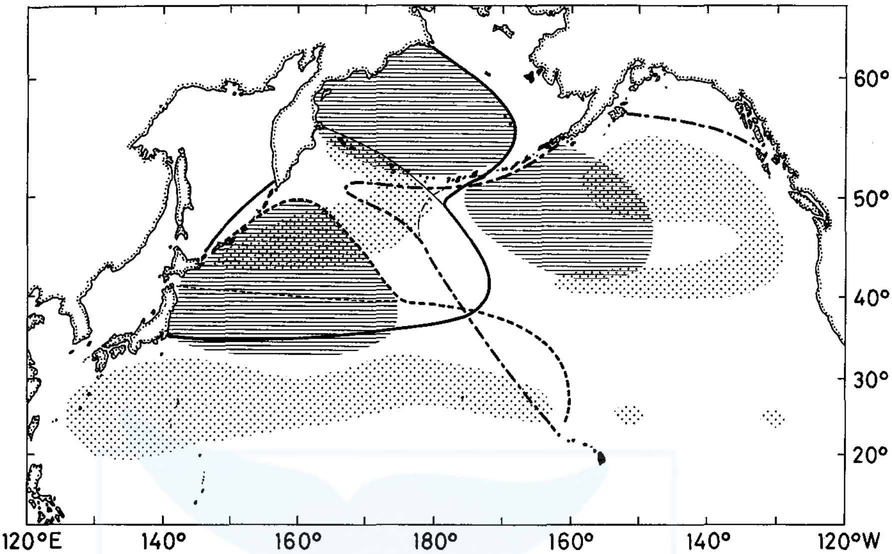

Fig. 15. Distribution of three sperm whale stocks in the North Pacific suggested in the present study. Solid line: northwestern North Pacific stock; Dotted line: southwestern North Pacific stock; Chain: eastern North Pacific stock. For each stock, thick line indicates a total geographical range for the stock (based on mark-recapture 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

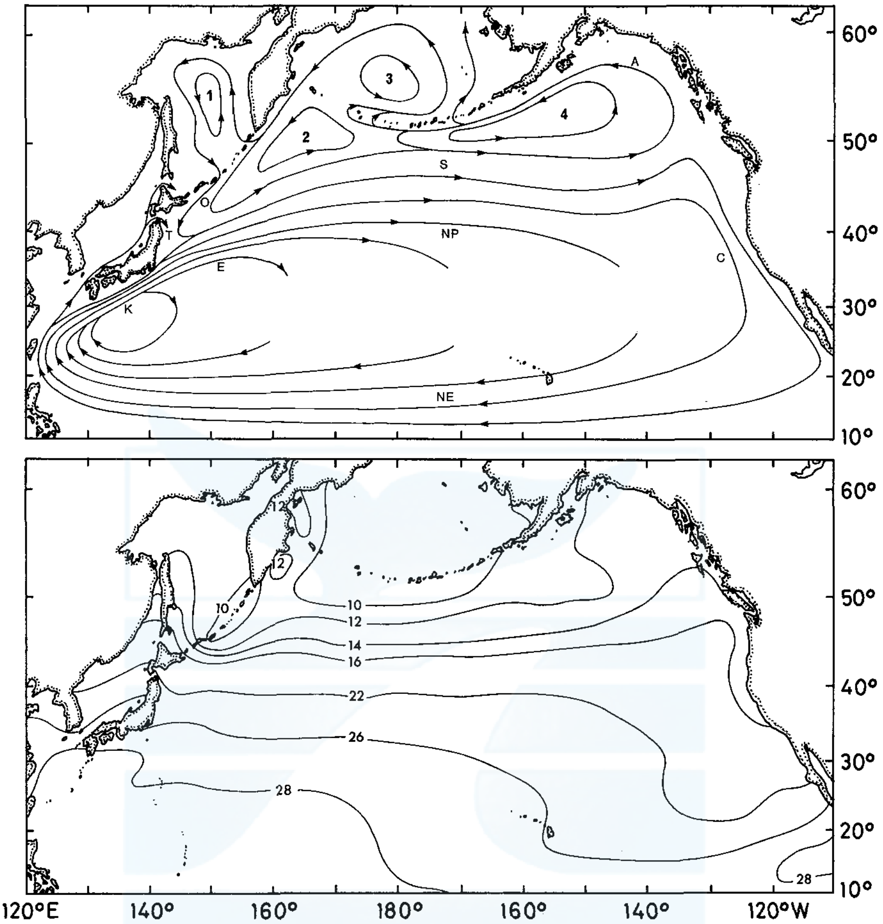

Fig. 16. Top. Major current systems in the North Pacific in July through September (based on Dodimead *et al.*, 1963; Favorite *et al.*, 1976; Maritime Safety Agency, 1982). Keys: 1=Okhotsk Sea Gyre, 2=Western North Pacific Gyre, 3=Bering Sea Gyre, 4=Alaskan Gyre, A=Alaskan Stream, C=California Current, 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°N) in March and May were recovered in the southern hemisphere (4°–5°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.

TABLE 14. MOVEMENT OF MARKED SPERM WHALES IN THE EASTERN NORTH PACIFIC NOT LISTED IN FIGS 10 THROUGH 14

Mark no.	Marking		Recapture		
	date	position	date	position	body length
Females					
J9729	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

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

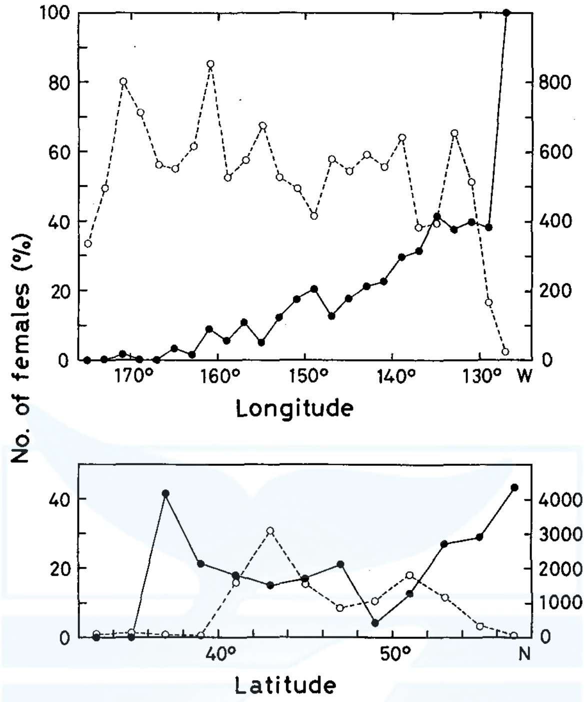

Fig. 17. Sexual segregation of sperm whales in the eastern North Pacific appeared in the catch of Japanese pelagic fishery from 1966 through 1977 (data are based on Smith, 1980). Open circle and dotted line indicate total number of sperm whales caught, closed circle and solid line percentage of females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

Top. Longitudinal segregation of female sperm whales in the eastern North Pacific north of 40°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°W and north of 40°N, and east of 160°W and south of 40°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. commn 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 cookie-cutter 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).

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 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°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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SEGREGATION OF TWO FORMS OF SHORT-FINNED PILOT WHALES OFF THE PACIFIC COAST OF JAPAN*

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ABSTRACT

Two forms of the short-finned pilot whale are known off the Pacific coast of Japan. The northern form, having larger body size, distinct saddle mark and round contour of the head seen from the top, inhabits the coastal waters between fronts of the cold Oyashio Current and warm Kuroshio Current, or 12°–24°C in surface water temperature and 35°–43°N in latitude. The southern form, having smaller body size, indistinct saddle mark and square shaped contour of adult male head, is known from wide range of the coastal and offshore waters south of the Kuroshio Front (over 18°C and south of 39°N) with some degree of possible density gap within the range. Their geographical ranges may occasionally overlap in the boundary area, but mixed schools of two forms are believed to be very rare. The geographical and social segregation, individually identifiable morphological differentiation, and similarity in their life history characteristics suggest that they can be dealt as separate subspecies or local stocks of the short-finned pilot whale. Although north/south segregation of the corresponding forms might exist in the eastern North Pacific, current information is insufficient for further consideration.

INTRODUCTION

Yamase (1760) described two kinds of pilot whales off Taiji on the Pacific coast of central Japan, the one *Shiho goto* was larger and had white dorsal patch, and the other *Naisa goto* was smaller and had no dorsal mark. Gray referred similar distinction for Japanese pilot whales, and named his *Naisa gota* (appeared in his 1846 and 1866 papers) or *Naisa goto* (in his 1846 paper) as *G. sieboldii* Gray, 1846 and *Shibo golo* (in 1846, 1866 and 1871 papers) as *G. sibo* Gray, 1871. The minor difference in the spelling is not important. The *Ohnan goto* of Yamase (1760) and Gray (1866) is now considered to represent the false killer whale *Pseudorca crassidens* (Owen, 1846). Recent Japanese whalers who hunted pilot whales also distinguished two pilot whales *Tappa-*

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naga (=having long flipper) off northern Japan and *Ma-gondo* (=common pilot whale) off central and southern Japan. Since the last century this caused confusion for Japanese whale taxonomists, and caused the use of various scientific names as reviewed by Hawley (1960) and Kasuya (1975).

Nishiwaki, Kasuya, Brownell and Caldwell (1967) examined pilot whale skulls taken off Izu coast (34°30′N) and Taiji (33°35′N) to find that the pilot whales off the Pacific coast of central Japan which was called by the vernacular name of *Ma-gondo* and had been considered to represent *Globicephala melaena* (Traill, 1809) was actually *G. macrorhynchus* Gray, 1846. Kasuya (1975) examined statistics of pilot whale catch by Japanese small-type whaling and the skulls taken by the fishery off the Pacific coast of northern Japan, found that all the specimens examined by him possessed characteristics of rostral region of *G. macrorhynchus* described by Bree (1971), and concluded, acknowledging the possibility of presence of some local stocks, that *G. macrorhynchus* is the only confirmed member of recent pilot whale fauna in the western North Pacific. Although *G. melaena* survived in the northern Sea of Japan till the 12th century and the current existence was not fully denied (Kasuya, 1975), no supporting evidence was collected after the study and there was accumulated indications suggesting the absence of *G. melaena* in the Bering Sea and northern North Pacific (see below).

In 1982, some of the Japanese small-type whalers resumed harvesting pilot whales off the southern part (38°N to 40°N) of the Sanriku region (Pacific coast of northern Japan between 38°N to 41°30′N) as reviewed by Kasuya and Tai (1986), and some of the catch were examined by Miyazaki (1983). He reported that two kinds of pilot whales were taken in the season. The one (southern form of this study) was a type that was common off the Pacific coast of central and southern Japan (Izu and Taiji) and studied by Nishiwaki *et al.* (1967), Yonekura, Matsui and Kasuya (1980), Kasuya and Matsui (1984), Kasuya and Marsh (1984) and Marsh and Kasuya (1984). The other (northern form of this study) was new to him. Although, both forms shared skull characteristics of *G. macrorhynchus* described by Bree (1971), the latter was easily distinguished from the former by distinct saddle mark and larger body size (Miyazaki, 1983; Kasuya, 1986b).

In the present study, we analyze distribution and segregation of the two forms of short-finned pilot whales using sighting records in the western North Pacific collected since the finding of Miyazaki (1983), and some additional records of previous sightings, some of which are identifiable to two forms based on photographic or other records.

MATERIALS AND METHODS

Identification of two forms

The short-finned pilot whale identified in this study as "northern form" represents those being recognized by Japanese whalers as *Tappa-naga*, and its

Fig. 1. Difference of saddle mark between the two forms of short-finned pilot whales off the Pacific coast of Japan. A and B: northern form, C and D: southern form.

counterpart "southern form" represents *Ma-gondo* of the whalers. Compared with the southern form, the northern form has larger body by about 1 m (female) to 2 m (male) (Kasuya, 1986) and round contour of head viewed from the above. Adult males of the southern form has square shaped head (Yonekura, Matsui and Kasuya, 1980). The dorsal fin of adult males of the northern form tends to be narrower than that of the southern form, but the difference is indistinct. Miyazaki (1983) reported slight difference in the flipper length (longer in the northern form).

The saddle mark of the northern form is usually more light varying in color from pure white to very light grey, and that of the southern form is grey or dark grey and almost unrecognizable on the carcass (Yonekura, *et al.*, 1980). However, the absolute brightness is an inferior cue especially for the ship board observers because its visual character changes by weather condition, direction of sun, and depth of whales in the water. The eye patches are slightly more bright in the northern form, but they are indistinct and are not suitable for the identification purpose. The size of saddle mark is variable among northern form individuals.

The best external characteristics that separate the two forms are not the size or brightness of the saddle mark, but the direction and distinctness of the posterior boundary of the saddle mark (Fig. 1). On the northern form the posterior boundary of the saddle mark is clearly bounded by the posterior black area of the body and directed anterio-ventrally, and additionally the saddle mark does not extend posteriorly beyond the level of anus but extend anteriorly usually beyond the level of posterior margin of the dorsal fin. On the southern form, however, it extends posteriorly to the mid-length of tail

TABLE 1. LIST OF CRUISES CONDUCTED BY THE JAPAN FISHERY AGENCY AND USED TO COLLECT DATA IN FIG. 2 OF THIS STUDY

Name of vessel	Year	Month	Pilot whale sightings*	Reference for cruise track line
Konanmaru No. 25	1982	1-3	present	Miyashita (1986b)
Toshimaru No. 15	1983	1-3	absent	Miyashita (1986b)
Toshimaru No. 15	1984	1-3	present	Miyashita (1986b)
Toshimaru No. 15	1985	1-3	absent	Miyashita (1986b)
Toshimaru No. 25	1986	5-6	present	Miyashita and Kasuya (1987)
Shonanmaru	1983	6-7	present	Miyashita (1985)
Toshimaru No. 25	1983	6-8	present	Miyashita (1985)
Shonanmaru	1984	6-8	absent	Miyashita (1986a,b) Kasuya (1986a)
Toshimaru No. 25	1984	6-9	present	Miyashita (1986a,b) Kasuya (1986a)
Toshimaru No. 25	1985	6-9	present	Miyashita (1986b)
Toshimaru No. 18	1986	6-9	present	Miyashita and Kasuya (1987)
Shonanmaru	1985	7-9	present	Miyashita (1986b)
Toshimaru No. 15	1985	9-10	absent	Miyashita (1986b)
Toshimaru No. 15	1986	9-10	present	Miyashita and Kasuya (1987)
Kankimaru No. 58	1986	9-10	present	Miyashita and Kasuya (1987)

* Pilot whale sightings in the area indicated in Fig. 2.

peduncle. The posterior and ventral boundaries of the saddle mark of the southern form gradually fades into the black body color making it difficult to define the boundary. The saddle marks of live pilot whales in Figs 1 and 2 of Plate I in Yonekura *et al.* (1980) are now clear to represent those of northern forms, but other photographs of the carcasses and a drawing in text-Fig. 2 of their study represent the southern form.

Using above criteria, Kasuya (1986b) could identify all the postnatal northern forms used in his study (about 300 individuals over 1.5 years old), and found no individuals that could be considered as intermediate of the two forms of the short-finned pilot whale. However, none of the four full term fetuses of northern form (165 to 185 cm in body length) had recognizable saddle mark (Kasuya, unpublished) and the distinction of the two forms appeared to be difficult except for the larger body size of the northern form (Kasuya, 1986b). This suggests that the distinction of two forms by the saddle mark becomes possible at an age between 0 and 1.5 years or well before the mean age at weaning 2.4–3.1 years (Kasuya, 1986b), which causes no difficulty in the identification of northern form schools.

Source of sighting data

Main body of the data used in this study was the results of whale sighting cruises conducted by Japan Fishery Agency in 1982 through 1986 (Table 1).

TABLE 2. DALL'S PORPOISE SIGHTINGS AND HARPOONING CRUISES IN THE WESTERN NORTH PACIFIC AND BERING SEA, WHICH PROVIDED INFORMATION ON PILOT WHALE DISTRIBUTION FOR THE PRESENT STUDY

Name of vessel	Year	Month	Pilot whale sightings	Reference for cruise track line
Hoyomaru No. 67	1979	6-8	none*	Miyazaki, Jones and Beach (1984)
Hoyomaru No. 12	1982	8-9	2 schools off Japan	Kasuya and Ogi (1987)
Hoyomaru No. 12	1983	8-9	none	Kasuya and Ogi (1987)
Hoyomaru No. 53	1984	5-6	none	Miyazaki and Fujise (1985)
Hoyomaru No. 12	1985	8-9	none	Kasuya and Ogi (1987)
Hoyomaru No. 12	1986	8-10	present	Yoshioka *et al.* (1987)

* Personal communication of Dr N. Miyazaki.

In these cruises the sighting of whales was conducted along pre-fixed track line using the method that had been used in the Antarctic minke whale assessment cruise (Best and Butterworth, 1980), and all the marine mammal sightings were recorded. The trackline was designed systematically to cover evenly the survey area. Instruction was given since 1984 to biologist on board or to captain of the vessel to distinguish the two forms of short-finned pilot whales and to take photographs of those individuals for later confirmation. Some additional photographs or sketches were left by observers of earlier cruises at voluntary base.

Additional information was available from published reports of five cruises conducted by Japan Fishery Agency for Dall's porpoise sightings and harpooning in the western North Pacific (Table 2). Among these cruises pilot whales were sighted only during the 1982 and 1986 cruises, but information obtained from other cruises was also valuable as the indication of absence of pilot whales in the surveyed area. Biologists were on board of these five cruises.

In addition to above cruises, sightings data collected during 4 cruises of the *Hakuhomaru* and 4 cruises of the *Tanseimaru* (both were conducted by the Ocean Research Institute, University of Tokyo), and each cruise of the *Hayachinemaru* and *Koeimaru* were used. These cruises (conducted in 1967 to 1985) were selected from many other similar kind of cruises by the presence of at least one pilot whale sighting. Kasuya or some trained observers were on board of these cruises to collect records of whale sightings. Two schools of the northern form and one school of unidentified form were cited from Ogi (pers. commn in 1985) and Kuroda (1956), respectively. Some of these sightings were identified to the whale types using photographs.

Catch of drive fisheries or of small-type whaling in Kasuya and Marsh (1984) or in Kasuya and Tai (1986) were used as well as a stranding in Kasuya and Marsh (1984) as the indication of occurrence of the species.

The surface water temperature was recorded at the position of sighting for many of the above records.

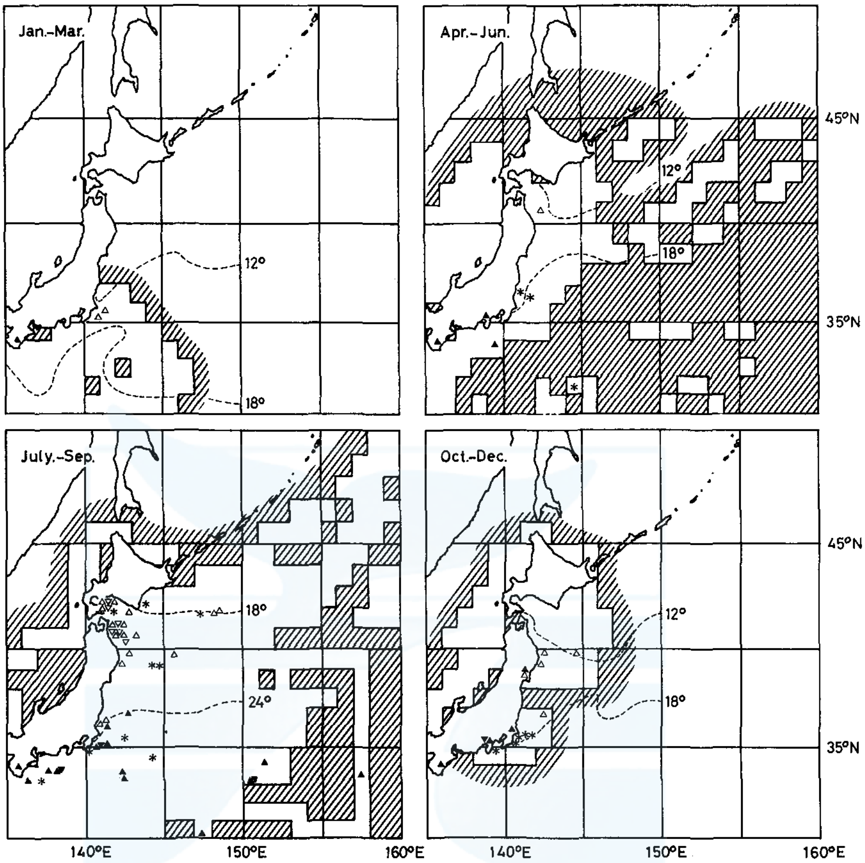

Fig. 2. Sightings of short-finned pilot whales and surveyed area (inside of the shaded area indicated by one degree squares). Open triangle: school of northern form, Closed triangle: school of southern form, Star: school of unidentified form. Marks inside the coast line represent catch or stranding. The isotherms indicate ten years mean of surface water temperature in March, July, September, and December (Japan Oceanographic Data Center, 1978).

RESULTS

Geographical segregation

The surveyed area and sightings of pilot whales are indicated by seasons in Fig. 2. In winter (January to March), the sighting effort was limited to the south of 37°N. Northern forms were sighted twice off the Boso Peninsula at between 35°N and 36°N. In spite of extended sighting effort no southern forms were sighted to the north of 30°N, but several sightings were recorded to the south of the latitude (Table 4, for further details of these sightings see Miyashita (1986b)). In this season the drive fishery off Taiji (33°35′N) captured schools of the southern form, indicating their presence in the coastal waters of the latitude.

In spring (April to June), the sighting effort expanded to wider geographical area, although the total surveyed areas was still limited. Northern forms were sighted off northern Japan at latitudes between 40°N and 41°N. A school of southern form was sighted at about 34°N. Several additional sightings of the form were recorded to the south of 30°N (Miyashita, 1986b). Drive fishery at Taiji (33°35′N) and at Arari (34°50′N) on the Izu coast captured schools of the southern form in this season. These suggest a northward expansion of the concentration of southern form whales in the spring season. A school of unidentified form in Fig. 2 (5th May 1986) in the coastal waters in 36°–37°N and 141°–142°E was recorded by the captain of the *Toshimaru No.25* as the southern form. Although the surface water temperature at the position (8.6°C) appeared to be too low for the southern form, this position was just to the inshore colder side of a very distinct water front (surface water temperature decline of 12.3°C in 24 n.m.), and both forms could have been present at the spot. Since the correctness of the identification could not be supported by photographs or subsequent sightings (the cruise had only one sighting of pilot whales), we tentatively dealt the school as unidentified.

In summer months (July to September), the sighting effort expanded widest. Northern forms were sighted in the Japanese coastal waters between 36°N and 43°N, and west of 149°E longitude. Most of these sightings were concentrated within about 100 nautical miles from the coast. In spite of considerable amount of sighting effort (three 40 to 45 days cruises in August through September, and two similar cruises in May through August), there were no sightings of pilot whales in the Bering Sea and western North Pacific west of 175°E in the Subarctic Convergence Zone and north of it (Table 2). Pilot whales of unidentified form were sighted south of the Subarctic Convergence in the central North Pacific in August (Table 3). These data suggest that short-finned pilot whales do not usually enter into the Subarctic Convergence Zone in the North Pacific and the long-finned pilot whale does not exists in the Bering Sea and northern North Pacific.

In the same season, southern forms were sighted to the south of 37°N. Segregation between the two forms is clear (Fig. 2). At Taiji (33°35′N), the drive fishery captured southern form schools. Although density seemed to be low south of 25°N or east of 152°E suggesting the maximum range of the population in the western North Pacific (IWC, 1987), firm conclusion was hard to be drawn due to the limited sighting effort in the offshore waters. In addition to this, there is an apparent density hiatus in the Kuroshio Current area and the distribution seems to be discontinuous between coastal area and offshore Kuroshio Counter Current area. The sighting trackline was arranged systematically for even coverage of the area, so the density hiatus does not seem to be an artifact of uneven sighting effort (for details see Miyashita, 1986b). Further study is needed to confirm more than one stocks of the southern form short-finned pilot whales in the western North Pacific.

TABLE 3. SIGHTINGS OF PILOT WHALES DURING THE CRUISES DEALT IN THE PRESENT STUDY, OUTSIDE OF THE RANGE IN FIG. 2 AND NORTH OF 35°N. NONE OF THE WHALE TYPES WERE IDENTIFIED

Date of sighting	Position of sighting	Area	Water temp.	Name of vessel
2 Aug. 1967	42°04′N, 175°00′E	w. N. Pac.	19.6°C	Hakuhomaru
2 Aug. 1967	41°57′N, 171°54′E	w. N. Pac.	22.9°C	Hakuhomaru
3 Aug. 1967	41°56′N, 165°17′E	w. N. Pac.	19.9°C	Hakuhomaru
28 Aug. 1971	39°04′N, 134°36′E	S. of Japan	24.5°C	Hakuhomaru

In autumn months (October to December), sighting effort was limited to the Pacific coast between 34°N and 39°N, and there were sighted three schools of northern forms (to the north of 36°N). Northern forms were caught by Japanese small-type whaling off the Pacific coast in October and November in latitudes between 37°N and 40°N (Miyazaki, 1983; Kasuya and Tai, 1986). Southern forms were not sighted in the coastal waters south of 36°N in this season, but the presence was indicated by the stranding of a school at Choshi (35°43′N), and frequent catch by the drive fishery on Izu coasts (34°40′N) and at Taiji (33°35′N) (Kasuya and Marsh, 1984). Miyazaki (1983) reported catch of the southern form by small-type whaling off Sanriku (38°N to 40°N) in October 1982. However, this was possibly a rare incident for the region in this season, because such case did not occur during the following four pilot whaling seasons (Kasuya, 1986; unpublished; Kasuya and Tai, 1986) and because it was the first case for the gunner to hunt such short whales of adult shape (Mr Y. Toba, pers. commn in 1983).

There are reasons to believe that northern forms may occasionally occur off Taiji (33°35′N) on the Pacific coast of central Japan (see Discussion).

In the Sea of Japan, we have only one record of sighting of pilot whales of unknown form (Table 3). The species seems to be uncommon in the area as already mentioned by Kasuya (1975). We do not have data to indicate which form of pilot whales are distributed in the Sea of Japan.

Thermal segregation

Table 4 shows number of short-finned pilot whale sightings by surface water temperature, type of whales and season. Southern forms were sighted at the water temperature between 24° and 31°C in summer, and between 20° and 24°C in winter. The observed seasonal difference of the low temperature limit was 4°C (lower in winter), while the geographical northern range shifted to the south by about 9° in latitude. The actual thermal difference in the habitat between winter and summer must have been larger, because there were frequent winter drives of this form at Taiji (33° 35′N) where surface water temperature could be below 20°C (Fig. 2). This indicates that the seasonal change of the geographical range of southern form short-finned

TABLE 4. MONTHLY SURFACE WATER TEMPERATURE AT THE POSITION OF SHORT-FINNED PILOT WHALE SIGHTING IN FIG. 2 (WITHOUT PARENTHESIS) AND THOSE IN THE WATERS SOUTH OF 30°N LATITUDE MADE BY CRUISES LISTED IN TABLE 1 (IN PARENTHESES)

W.T.*	Northern form				Southern form			Unidentified		
(°C)	1-3	4-6	7-9	10-12	1-3	7-9	10-12	4-6	7-9	10-12
8								1**		
14									1	
15		1								
16	1							1		
17	1			1						1
18										
19			6							
20			1		(2)					1
21			1		(3)			1		
22			4		(2)				1	2
23			4		(1)					
24						4				
25						1			1	
26						2(2)	(1)		1	
27						5(7)				
28						4(1)		(2)	1	
29						(2)				
30						(1)				

* Water temperatures between n° and n+1°C indicated by n (n being integer).

** Captain of the research vessel (*Toshimaru No. 25* cruise in 1986) recorded this as a southern form school (see text).

pilot whales is not large enough to retain a constant surface water temperature environment for the stock. In other words, some additional factors such as basithermo structure or food availability is also controlling the distribution and their distribution does not always cover the whole geographical range permitted by their thermal tolerance.

Northern forms, on the other hand, were sighted at the surface water temperature between 19°C and 24°C in summer, and at between 15°C and 18°C in other seasons (Table 4). Accumulation of more data may give wider thermal range, especially for the lower limit. Kasuya and Tai (1986) reported that the water temperature at the position of northern form catch (38°N to 40°N) in October and November ranged from 12°C to 21°C with a peak frequency of catch at 16°–17°C. The surface water temperature of 10°–15°C corresponds to the front of the cold Oyashio Current in the area. The summer sightings of three pilot whale schools of unidentified form at 41°–43°N will represent the northern form. We consider that northern forms move in the fall to the southern wintering ground (north of 35°N and south of the Oyashio

Front) from their summering range expanded probably up to 43°N accompanying the seasonal shift of the Oyashio Front. Their southern range does not change seasonally so much as the northern range, and they endure the seasonal change of the surface water temperature between 12° and 24°C (Fig. 2).

The segregation between the northern and southern forms of short-finned pilot whales is usually distinct geographically and thermally. Although there exist some examples of geographical or possible social intermingling, such cases seem to be rare and unusual as discussed below.

DISCUSSION

The characteristics that we have used in the present study to separate two forms of short-finned pilot whales off the Pacific coast of Japan are similar to those used by Yamase (1760) to describe two kinds of pilot whales off Taiji (33°35′N) on the Pacific coast of Japan. Gray's (1846; 1866) description of the pilot whales off Japan is almost identical to that of Yamase (1760). This lead us to consider that our "southern form" is equivalent to their *Naisa goto* or *Naisa gota* which was named as *G. sieboldii* Gray, 1846, and our "northern form" is equivalent to their *Shiho goto* or *Shibo golo* named as *G. sibo* Gray, 1871. Both of these scientific names have been correctly considered by Bree (1971) to be junior synonyms of *G. macrorhynchus* Gray, 1846.

The next question will be if the northern form individuals still occur off Taiji which situates further south of the ordinally range of the northern form confirmed in the present study. There are evidences supporting this. In winter, a belt of cold coastal water below 18°C extends from 35°N (the ordinary southern range of the northern form in both summer and winter) to 33°N (south of Taiji at 33°35′N) along the Pacific coast of Japan. Thus it is expected for some northern form individuals to stray to the waters off Taiji. An ex-whaler and a present dolphin meat dealer Mr M. Mizutani of Taiji Town and Mr Y. Seko of the Taiji Fish Market gave us the description of the northern form correctly and told their belief that one of the small-type whaling vessels at Taiji caught the northern form pilot whale (their *tappa-naga*) once (Mizutani) or several times (Seko) after World War II. Since the meat of southern forms is esteemed over that of northern forms, their identification can be trusted. As the small-type whaling ceased operation off Taiji since 1978, the catch could have been before the date.

In their sample of more than 500 southern form short-finned pilot whales, Kasuya and Marsh (1984) found only one male of putative northern form and excluded it from their analysis. This male was found in an aggregation of about 230 southern form individuals caught at Taiji in June 1975, and examined by their colleague. It was 5.8 m in body length, or 0.6 m larger than the largest southern form in their sample. The testis (1.7 kg) was at the lower limit of the testis weight (1.7–3.0 kg) of southern forms measuring over 5 m in body length, but it was of reasonable weight for the northern form of that body size (Kasuya, 1986b). The lack of observation of saddle mark or age estimate inhibited reliable classification of the whale type. Yonekura *et al.* (1980) did not recognize among their sample of 211 individuals (most of them were not included in Kasuya and Marsh (1984)) any individuals which could be classified to the northern form.

Only confirmed records of southern forms off the Sanriku coast (33°–37°N) were seven individuals taken by a small-type whaling vessel at Ayukawa (38°15′N) on 5th November 1982, examined by Dr N. Miyazaki (1983) and aged by Kasuya (1986b). These individuals were apparently taken from a school of the same form (Y. Toba, pers. commn in 1984). These were no additional records of such incidence during the five years operation of the whaling in October and November, 1982 to 1986. Kasuya (1986b) identified about 300 individuals taken by the small-type whaling off Sanriku during the period as the northern form based on the pigmentation, and confirmed it using body length on age relationship. These suggest that the two forms of short-finned pilot whales rarely form a common school even though their range of distribution may occasionally situate close or overlap in the boundary area.

Although there exist opinions to consider that the saddle mark of the short-finned pilot whale may change brightness or shape by growth or physiological conditions (see below), currently available data indicate that the feature of saddle mark we have described above is a stable characteristics to identify individually two forms of short-finned pilot whales off Japan with possible exception of newborn individuals. The whale type of newborns is identifiable only by body size assisted by the age information (Kasuya, 1986b). The life history of northern form short-finned pilot whales off Japan differs from that of the southern form (Kasuya and Marsh, 1984) only in the larger body size and later mating peak (May vs. September), and all the life history characteristics that were found by them to be peculiar to the short-finned pilot whale are shared by both northern and southern forms (Kasuya, 1986b). Kasuya (1986b) speculated from these some ecological mechanisms which might inhibit free interbreeding between the two forms, and considered that the degree of differentiation between the two forms will be at the level of subspecies or local stocks. Wada (1988) arrived at the similar conclusion through the analysis of isoenzymes.

Two types of short-finned pilot whales have been distinguished in the eastern North Pacific using various independent characteristics, e.g. body size and head shape (Mitchell, 1975) and skull morphology (Polisini, 1980). Published studies on the pigmentation of short-finned pilot whales in these warters are confusing. Yablokov and Evans (1981) described individual variation of the saddle mark of short-finned pilot whales in the southern California Bight, and Leatherwood, Reeves, Perrin and Evans (1982) and Evans, Thomas and Kent (1984) questioned its stability and the usefulness for stock identification. The latter authors, however, suggested in the same study a possibility of geographical variation of the pigmentation pattern, indicating that the short-finned pilot whales in the eastern tropical Pacific usually have no or only faint markings on the dorsal surface. The apparent disagreement of opinions probably came from the mixing of some minor individual variation of pigmentation in a single population and more stable difference between stocks.

A short-finned pilot whale photographed off Baja California and the Gulf of California by T. Arnbom (pers. commn in 1986) and Leatherwood *et al.* (1982) had saddle mark similar to that of the present northern form, and a school of 35 pilot whales sighted off Seattle (48°28′N, 133°51′W) in August had apparently similar saddle mark with the northern form sighted off Japan (39°50′N, 145°42′E) in August during the same cruise (Yoshioka, Ogura and Shikano, 1987). We confirmed the photographic records of these sightings. While describing the external morphology of *G. scammonii*, which was identified by Bree (1971) as a junior synonym of *G. macrorhynchus*, Scammon (1874) made no comment on the saddle mark of the type specimen taken by him off Baja California (31°N). His detailed description of the variation of killer whale saddle mark in the same book suggests that he would have mentioned the saddle mark of the type specimen if it had such clear one as found on short-finned pilot whales off northern Japan or off the coast of North America. These suggest, as well as a comment in Evans *et al.* (1984), the presence of geographical segregation of two forms of the short-finned pilot whale in the eastern North Pacific. Although information on other biological feature of these individuals is needed for further consideration, there is a possibility that each of them corresponds to the southern and northern forms off Japan. The short-finned pilot whale in the North Pacific could have evolved two geographical forms (or subspecies), one in the tropical waters and the other in the temperate waters north of it.

We do not have information on the morphology of pilot whales sighted in the central northern North Pacific (Table 3). The latitudes of sightings (39°–42°N), which were just to the south of the Subarctic Convergence Zone, leave possibility for them being either of the two forms of the present study. However, in view of the concentration of northern forms in the Japanese coastal waters and the apparent discontinuity of distribution in the offshore waters, we consider that the Japanese coastal individuals of the northern form will constitute a local stock of relatively small population size. Miyashita (1986b) estimated the population as about 5,000 individuals.

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GENETIC DIFFERENTIATION BETWEEN TWO FORMS OF SHORT-FINNED PILOT WHALES OFF THE PACIFIC COAST OF JAPAN*

SHIRO WADA**

ABSTRACT

The northern and southern forms of the short-finned pilot whale off the Pacific coast of Japan were examined by horizontal starch gel electrophoresis on 36 enzyme loci using 371 specimens. Two and five loci were variable in the northern and southern forms, respectively. The proportion of polymorphic loci under the 0.95 criterion and the value of the average heterozygosity per locus were 0.028 and 0.009 in the northern form and 0.056 and 0.008 in the southern form, respectively. No significant deviation in genotype frequencies from the Hardy-Weinberg expectations was seen in either form. Significant between-form difference in genic proportions revealed that the northern form is genetically isolated from the southern form. From the value of Nei's genetic distance, 0.0004, the degree of genetic differentiation between two forms was considered to be of the local population level.

INTRODUCTION

The short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846, is one of the important objective species for the coastal whaling in Japan, which has been harvested in two different fisheries. Two forms segregate geographically and thermally off the Pacific coast of Japan (Kasuya, Miyashita and Kasamatsu, 1987). The northern form, *tappanaga*, having been harvested by the small-type whaling (Kasuya and Tai, 1986), distributes off the Pacific coast of northern Japan between 35°N and 42°N in the surface water temperature range of 12–24°C, while the southern form, *magondo*, having been harvested by the small-type whaling and the drive fishery at Taiji (Kasuya, 1986b), distributes in the waters south of the major range of the northern form and waters over 18°C.

Form-identification is easy from the difference of external characteristics. The northern form has a larger body size, a distinct saddle mark and a round contour of the head, while the southern form has a smaller body size, an

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indistinct saddle mark and a square contour of adult male head (Kasuya *et al.*, 1987). However, the life history parameters of the two forms differ significantly only in those concerning to body size and to breeding season (Kasuya, 1986a). Both forms share the skull characteristics of *G. macrorhynchus* described by Bree (1971). From these, Kasuya (1986a) suggested that they can be dealt with as separate geographical forms or subspecies.

Electrophoretic survey on a large number of loci for genetic variability or genetic differentiation in cetacea have been reported on rather limited number of species; on minke whale by Wada and Numachi (1979), Simonsen, Kapel and Larsen (1982), and Wada (1982; 1983a; 1984); on fin and sei whales by Daníelsdóttir and Arnason (1987); on fin, sei, Bryde's and minke whales by Wada (1987); on striped dolphin by Wada (1983b); on Dall's porpoise by Winans and Jones (in press); on long-finned pilot whale by Andersen (1987); on 12 species of toothed whale by Shimura and Numachi (1987).

The aim of the present study is to evaluate the magnitude of genetic differentiation between two forms of short-finned pilot whales and to consider their taxonomic relationship from the viewpoint of biochemical genetics.

MATERIALS AND METHODS

Tissue samples, liver and skeletal muscle, of 204 northern forms were collected by Dr T. Kasuya and his co-workers as a part of their biological samplings from the whales caught by the small-type whaling off the Sanriku region and landed at Ayukawa in October and November 1983 (105 specimens) and 1984 (99 specimens).

Tissue samples of 167 southern forms were collected by myself from the whales driven at Taiji and flensed on 7–8 October 1984 (68 specimens from four schools in a single drive of 92 whales) and 11–12 November 1985 (99 specimens from a single drive of about 120 whales which might have been mixed with a few members of a previous drive). Form-identification for the specimens in 1984 was done by Dr N. Miyazaki and for those in 1985 by myself. All tissue samples were stored at −20°C until use.

Methods of sample and gel preparations, and electrophoresis followed the procedures described in Numachi (1974), and Shimura and Numachi (1987), and that of gel preservation in Numachi (1981). Of the 32 enzymes examined, the following three loci and five enzymes showed an indistinct electrophoretic pattern, and therefore I didn't use them in the present study though the last three enzymes were found to be variable; *Adh–2*, *Ak–1*, *Pgm–2*, Aconitase, Fumarase, Peptidases B, C and D. Table 1 shows buffers and tissues used for 36 loci on which reliable genotyping was possible. Recipes for the 100 ml reaction mixture for staining enzymes, prepared according to Harris and Hopkinson (1976) in principle are listed in Table 2.

In case of multi-loci enzymes, a most anodally migrating locus was named as 1, lesser anodal locus as 2, and so on. At a variable locus, alleles were named alphabetically as *c*, *s*, *n* and *f* from cathode to anode. The *n* allele denotes the most frequent allele in a variable locus, or denotes the single one in a monomorphic locus.

Genotype and allele frequencies were analysed using the *G*-test (Sokal and Rohlf, 1969) for a deviation in genotype frequencies from the Hardy-Weinberg expectations within a form (G_D), and for between-form heterogeneity in gene frequencies (G_H) based on the *R* (number of alleles) × *C* (number of forms) contingency table format. *G*-values were compared with the critical values of Chi-square under (number of genotypes)−(number of alleles) degrees of freedom for G_D, and under $(R-1) \times (C-1)$ degrees of freedom for G_H.

RESULTS

Genetic variability

Genetic variation was found at two loci, *Ada* and *Sod–1*, in the northern form and at five loci, *Ada*, *Mdh–1*, *6Pgd*, *Pgm–3* and *Sod–1*, in the southern form. These loci were all biallelic. The northern form had the same alleles as the southern form at all loci except *Ada*, where a variant allele in the former (Ada^s gene) was different from that in the latter (Ada^c gene). Heterozygotes at *Ada* and *Pgm–3* showed a two-banded pattern and those at *Mdh–1*, *6Pgd* and *Sod–1* showed a three-banded pattern, suggesting that the enzymes controlled by the former two and the latter three loci are monomer and dimer, respectively (Fig. 1). The remaining 31 loci were fixed for a single allele in both forms, so that the subunit structure of enzymes controlled by these loci was unknown. These results on the southern form agreed substantially with those in Shimura and Numachi (1987) except a considerable gene frequency difference at *Ldh–A* (their *Ldh–1*) and *Pgm–2*, probably due to difference of sample size between the two studies.

The observed genotype frequencies at five variable loci agreed well with the Hardy-Weinberg expectations. Although the expectations for rare genotypes were less than five, the G_D values for 7 cases, ranged from 0.01 to 0.97, were all less than the critical values of Chi-square at the 5% level of significance (Table 3). This suggests that each sample is homogeneous.

Number of polymorphic loci under the 0.95 criterion ($P_{.95}$: loci on which the most frequent allele is less than or equal to 0.95) was very small, only one (*Ada*) in the northern form and two (*Ada* and *Sod–1*) in the southern form, though *Sod–1* of the former was nearly polymorphic. The $P_{.95}$ values were therefore 0.028 and 0.056 in the northern and southern forms, respectively. The level of average heterozygosity per locus (*H*) was also low due to low frequencies of variant genes. The estimates of *H* value calculated in the northern and southern forms were 0.009 ± 0.007 (SE) and 0.008 ± 0.005 (SE), respectively. Standard error (SE) of *H* was calculated using a formula of Nei and Roychoudhury (1974).

TABLE 1. LOCI EXAMINED AND ELECTROPHRETIC CONDITIONS FOR THE SHORT-FINNED PILOT WHALES

Enzyme (abbreviation)	Locus	Tissue used	buffer
Adenosine deaminase (ADA)	*Ada*	Liver	AC70
Alcohol dehydrogenase (ADH)	*Adh-1*	Liver	AC70, Mg, NAD
Adenylate kinase (AK)	*Ak-2*	Muscle	AC70
Aldolase (ALD)	*Ald*	Muscle	AC70, Mg
Creatine kinase (CK)	*Ck-1*	Liver	TEB87
	Ck-2	Muscle	TC86
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	*Gapdh*	Liver	TC86, EDTA, NAD
α-Glycerophosphate dehydrogenase (GDH)	*Gdh*	Liver	AC70, Mg, NAD
Glutamate dehydrogenase (GLUDH)	*Gludh*	Liver	TEB87
Glutamate oxaloacetate transaminase (GOT)	*Got-1*	Liver	TC80
	Got-2	Liver	AC70
Glucosephophate isomerase (GPI)	*Gpi*	Liver	TC80
Hexokinase (HK)	*Hk*	Liver	TC86
Isocitrate dehydrogenase (IDH)	*Idh-1*	Liver	AC70, Mg
	Idh-2	Liver	AC70
Lactate dehydrogenase (LDH)	*Ldh-A*	Liver	AC60
	Ldh-B	Liver	AC60
Malate dehydrogenase (MDH)	*Mdh-1*	Liver	AC60
	Mdh-2	Liver	AC60
Malic enzyme (ME)	*Me*	Liver	AC60
Mannosephosphate isomerase (MPI)	*Mpi*	Liver	AC70
NADP-dependent dehydrogenase (NDH)	*Ndh*	Liver	AC70, NADP
Peptidase-A (PEPA)	*PepA*	Liver	AC60
Peptidase-E (PEPE)	*PepE*	Muscle	AC60
Peptidase-S (PEPS)	*PepS*	Liver	TC80, Mg
6-Phophogluconate dehydrogenase (6PGD)	*6Pgd*	Liver	AC70, NADP
Phophoglucomutase (PGM)	*Pgm-1*	Liver	AC70
	Pgm-3	Liver	TC80
Pyruvate kinase (PK)	*Pk*	Muscle	AC60, Mg
Sorbitol dehydrogenase (SDH)	*Sdh*	Liver	AC70, Mg, NAD
Superoxide dismutase (SOD)	*Sod-1*	Liver	AC60
	Sod-2	Liver	AC60
	Sod-3	Liver	AC60
	Sod-4	Muscle	AC60
Xantine oxidase (XOD)	*Xod*	Liver	TEB87
Xylulose reductase (XR)	*Xr*	Liver	AC70, Mg, NADP

AC: amine-citrate buffers originally used in Clayton annd Tretiak (1972), slightly modified by Numachi, Nagahora and Iwata (1979).
Gel: 0.002 M citric acid. Electrode: 0.04 M citric acid.
AC60: adjusted with N-(3-Aminopropyl)-morpholine to pH 6.0.
AC70: adjusted with N-(3-Aminopropyl)-diethanolamine to pH 7.0.
TC: tris-citrate buffers.
TC80: originally used in Clayton and Tretiak (1972). Gel: 0.002 M citric acid. Electrode: 0.04 M citric acid. Both solutions were adjusted with Tris (hydroxymethyl) aminomethane to pH 8.0.
TC86: described in Harris and Hopkinson (1976). Electrode: 0.083 M citric acid adjusted with 0.661 M Tris (hydroxymethyl) amino-methane to pH 8.6. Gel: 27.5 times dilution of electrode buffer.

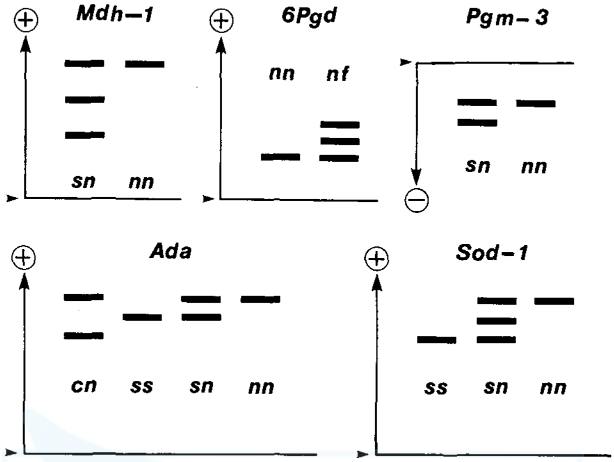

Fig. 1. Electrophoretic patterns at five variable loci in the short-finned pilot whales off the Pacific coast of Japan. The genotype of each phenotype is shown in italic. ▶: sample origin, ⊕: anode, ⊖: cathode

Genetic differentiation

A significant difference in gene frequencies between the two forms was found in the following three loci, *Ada*; G_H = 48.03, d.f. = 2, $P<0.001$, *Mdh–1*; G_H = 10.55, d.f. = 1, $P<0.01$, *6Pgd*; G_H = 4.80, d.f. = 1, $P<0.05$, but the differences at *Pgm–3* and *Sod–1* were not significant. An overall G_H value for the five variable loci was 66.96 (d.f. = 6, $P<0.001$), which indicates that the two forms are genetically isolated stocks.

The extent of genetic differntiation between two forms was measured by Nei's (1972) genetic distance (*D*), which represents the average number of electrophoretically detectable allelic substitutions per locus. It ranges from 0 (all populations share the same alleles in the same frequencies at all loci) to infinite (each population is fixed for an unique allele at all loci). The estimate of *D* value calculated using 36 loci was 0.0004.

(Footnote continued)

TEB: described in Harris and Hopkinson (1976). Stock: 0.9 M Tris (hydroxymethyl) aminomethane-0.02 M ethylenediamine tetraacetic acid disodium salt (EDTA-2Na)-0.5 M boric acid, pH 8.7. Anodal electrode: 7 times dilution of stock; cathodal electrode: 5 times dilution of stock. Gel: 20 times dilution of stock.
EDTA: gel contains 0.242 mM or 9 mg/100 ml EDTA-2Na.
Mg: gel contains 10 mM magnesium chloride.
NAD: gel and electrode buffers contain 4 mg/200 ml nicotinamide adenine dinucleotide. For GAPDH only, 15 mg/200 ml was used.
NADP: gel and electrode buffers contain 4 mg/200 ml nicotinamide adenine dinucleotide phosphate.

TABLE 2. STAIN RECIPIES FOR THE 100ml REACTION MIXTURE

Enzyme6)	Substrate(s) 1)	Buffer	Coenzyme and coupling dye 2)	Iron 3)	Linking enzyme 4)	Other components 5)
ADA	40mg Adenosine	0.05M Phosphate, pH7.4	NBT, PMS	−	1u XOD 1u NP	2g Agar
ADH	1ml l-octanol 9ml 95% ethanol	0.1M Tris-HCl, pH8.7	NAD*, NBT, PMS	−	—	—
AK	500mg D-glucose 100mg ADP	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	100u HK 60u G6PD	2g Agar
ALD	200mg Fructose-1,6-diphosphate	0.1M Tris-HCl, pH8.0	NAD, NBT, PMS	−	100u GAPDH	500mg Na arsenate
CK	100mg Creatine phosphate 500mg D-glucose 100mg ADP	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	100u HK 60u G6PD	2g Agar
GAPDH	400mg Fructose-1,6-diphosphate	0.1M Tris-HCl, pH8.0	NAD*, NBT, PMS	−	25u ALD	500mg Na arsenate
GDH	2g α-glycerophosphate	0.1M Tris-HCl, pH8.7	NAD, NBT, PMS	−	—	1g EDTA-2Na
GLUDH	2g L-glutamate	0.1M Tris-HCl, pH8.0	NAD, NBT, PMS	−	—	—
GOT	75mg 2-oxoglutaric acid 225mg L-aspartic acid	adjusted to pH7.5 with 2M KOH	500mg Fast blue BB	−	—	100mg EDTA-2Na 3g Na phosphate monobasic
GPI	100mg Fructose-6-phosphate	0.1M Tris-HCl, pH7.4	NADP, NBT, PMS	−	60u G6PD	2g Agar
HK	2g D-glucose 200mg ATP	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	60u G6PD	2g Agar
IDH	200mg DL-isocitrate	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	—	—
LDH	2ml 50% DL-lactate	0.1M Tris-HCl, pH8.7	NAD, NBT, PMS	−	—	—
MDH	2g DL-malate	0.1M Tris-HCl, pH8.7	NAD, NBT, PMS	−	—	—
ME	2g DL-malate	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	—	—
MPI	100mg D-mannose-6-phosphate	0.1M Tris-HCl, pH7.4	NADP, NBT, PMS	−	60u G6PD 50u GPI	—
NDH	—	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	—	—
PEPA	100mg Glycyl-DL-glycine	0.05M Phosphate, pH7.4	75mg Dianisidine-HCl	+	10u AAO 100u POD	2g Agar
PEPE	100mg L-leucyl-β-naphtyl-amide as substrate in the same buffer and reagent mixture as PEPA					
PEPS	100mg L-leucyl-l-leucine as substrate in the same buffer and reagent mixture as PEPA					
6PGD	100mg 6-phospho-gluconate	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	—	—
PGM	200mg D-glucose-1-phosphate*	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	60u G6PD	—
PK	100mg Phosphoenol pyruvate 500mg D-glucose 100mg ADP	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	++	100u HK 60u G6PD	2g Agar
SDH	3g D-sorbitol	0.1M Tris-HCl, pH8.0	NAD, NBT, PMS	−	—	—
SOD	—	0.1M Tris-HCl, pH8.7	NBT, PMS	−	—	500mg EDTA-2Na
XOD	250mg Hypoxanthine	0.1M Tris-HCl, pH8.0	NBT, PMS	−	—	—
XR	3g D-xylitol	0.1M Tris-HCl, pH8.0	NADP, NBT, PMS	+	—	—

1) ADP: Adenosine-5′-diphosphate; ATP: Adenosine-5′-triphosphate; *: containing D-glucose-1,6-diphosphate. Ca. 1%.
2) NAD: 30mg Nicotinamide adenine dinucleotide; NAD*: 90mg; NADP: Nicotinamide adenine dinucleotide phosphate; NBT: 20mg Nitroblue tetrazolium; PMS: 5mg Phenazine methosulfate.
3) +: 10mM $MgCl_2$; ++: 10mM $MgCl_2$, 150mg KCl.
4) NP: Nucleoside phospholylase; G6PD: Glucose-6-phosphate dehydrogenase; AAO: Amino acid oxidase; POD: Peroxidase.
5) EDTA: Ethylenediaminetetraacetic acid.
6) see Table 1

TABLE 3. GENOTYPE AND ALLELE FREQUENCIES FOR FIVE VARIABLE LOCI IN THE NORTHERN AND SOUTHERN FORMS OF THE SHORT-FINNED PILOT WHALE OFF THE PACIFIC COAST OF JAPAN

Locus	Form	Genotypes					Allele frequencies			GD value
		cn	*ss*	*sn*	*nn*	Total	*c*	*s*	*n*	
Ada	N	0	1	17	51	69	.000	.138	.862	0.64
	S	13	0	0	86	99	.066	.000	.934	0.91
			ss	*sn*	*nn*	Total		*s*	*n*	
Mdh-1	N		0	0	154	154		.000	1.000	
	S		0	8	159	167		.024	.976	0.20
			nn	*nf*	*ff*	Total		*n*	*f*	
6Pgd	N		204	0	0	204		1.000	.000	
	S		164	3	0	167		.991	.009	0.03
			ss	*sn*	*nn*	Total		*s*	*n*	
Pgm-3	N		0	0	204	204		.000	1.000	
	S		0	2	165	167		.006	.994	0.01
			ss	*sn*	*nn*	Total		*s*	*n*	
Sod-1	N		0	18	186	204		.044	.956	0.83
	S		1	16	150	167		.054	.946	0.97

S: southern form. N: northern form. GD: *G*-value for deviation in genotype frequencies from the Hardy-Weinberg expectations within a form.

DISCUSSION

Reliable estimates of average heterozygosity for marine mammals have been reported from nine species of pinniped, four species of baleen whale and 12 species of toothed whale. Table 4 summarises the level of their genetic variabilities. Mean *H* value for pinnipeds is 0.019, ranging from 0 in northern elephant seal, *Mirounga angustirostris* (Bonnell and Selander, 1974) to 0.047 in ribbon seal, *Phoca fasciata* (Fujio and Saito, 1986). Wada (1987) calculated *H* values for three stocks of fin whale, *Balaenoptera physalus*, two stocks of sei whale, *B. borealis*, five stocks of Bryde's whale, *B. edeni*, and three stocks of minke whale, *B. acutorostrata*, which allowed to calculate the mean values of *H* for fin, sei, Bryde's and minke whales as 0.017, 0.021, 0.022 and 0.051, respectively. Simonsen *et al.* (1982) reported $H = 0.046$ for the Atlantic minke whales. Using these values, the mean *H* values for four stocks of minke whales and four baleen whale species have been calculated as 0.050 and 0.028, respectively.

On toothed whales, Wada (1983b) reported the *H* value in striped dolphin, *Stenella coeruleoalba*, off the Pacific coast of Japan as 0.021. Shimura and Numachi (1987) calculated *H* values on 12 species in 11 genera from 4 families, which ranged from 0 in finless porpoise, *Neophocaena phocaenoides*, to 0.154 in Dall's porpoise, *Phocoenoides dalli* (*dalli*-type). Winans and Jones (in press) also

TABLE 4. SUMMARY OF THE GENETIC VARIABILITY IN MARINE MAMMALS

Species	No. loci examined	$P_{.95}$	H	Reference
Seals				
Mirounga angustirostris	24	0.000	0.000	Bonnell and Selander (1974)
M. leonina	18	0.278	0.030	McDermid, Ananthakrishnan and Agar (1972)
Odobenus rosmarus rosmarus	32	0.094*	0.026	Simonsen, Born and Kristensen (1982)
Pagophilus groenlandicus	21	0.048*	0.007	Simonsen, Allendorf, Eanes and Kapel (1982)
Cystophora cristata	21	0.048*	0.009	Simonsen, *et al.* (1982)
Pusa hispida	21	0.095*	0.009	Simonsen, *et al.* (1982)
Phoca fasciata	34	0.147	0.047	Fujio and Saito (1986)
P. viturina stejnegeri	34	0.059	0.023	Fujio and Saito (1986)
P. largha	34	0.059	0.017	Fujio and Saito (1986)
Baleen whales				
Balaenoptera physalus$^{1)}$	45	0.138*	0.017	Wada (1987)
B. borealis$^{2)}$	45	0.158*	0.021	Wada (1987)
B. edeni$^{3)}$	45	0.114*	0.022	Wada (1987)
B. acutorostrata$^{1)}$	45	0.207*	0.051	Wada (1987)
B. acutorostrata	21	0.095*	0.046	Simonsen, *et al.* (1982)
Toothed whales				
Berardius bairdii	18	0.056	0.016	Shimura and Numachi (1987)
Globicephala macrorhynchus (N.F.)	36	0.028	0.009	Present study
G. macrorhynchus (S.F.)	36	0.056	0.008	Present study
G. macrorhynchus (S.F.)	19	0.263	0.054	Shimura and Numachi (1987)
Peponocephala electra	19	0.105	0.035	Shimura and Numachi (1987)
Pseudorca crassidens	19	0.211	0.051	Shimura and Numachi (1987)
Stenella coeruleoalba	15	0.130	0.021	Wada (1983b)
S. coeruleoalba	19	0.263	0.089	Shimura and Numachi (1987)
S. attenuata	19	0.263	0.089	Shimura and Numachi (1987)
Tursiops truncatus	19	0.105	0.039	Shimura and Numachi (1987)
Lagenorhynchus obliquidens	19	0.316	0.093	Shimura and Numachi (1987)
Steno bredanensis	19	0.053	0.007	Shimura and Numachi (1987)
Phocoena phocoena	18	0.167	0.047	Shimura and Numachi (1987)
Phocoenoides dalli (*dalli*-type)	26	0.231	0.058	Winans and Jones (in press)
P. dalli (*dalli*-type)	19	0.421	0.154	Shimura and Numachi (1987)
P. dalli (*truei*-type)	19	0.474	0.147	Shimura and Numachi (1987)
Neophocaena phocaenoides	18	0.000	0.000	Shimura and Numachi (1987)

* under the 0.99 criterion
1) mean value for three stocks. 2) mean value for two stocks. 3) mean value for five stocks.
N.F. = the northern form. S.F. = the southern form.

examined other specimens of the latter species from three areas in the North Pacific and Bering Sea, and calculated H value as 0.058. However, there are large differences in the reported values of $P_{.95}$ and H for *S. coeruleoalba*, *P. dalli* (*dalli*-type) and *G. macrorhynchus* between authors (Table 4). However, comparing the common loci only, these studies show very similar results apart from a few loci where sample size is small. The mean of the above 17 H values for 13 toothed whale species (Table 4) is 0.054, which is higher than that for pinnipeds ($\bar{H}$ = 0.019), baleen whales ($\bar{H}$ = 0.028) and 184 mammalian species ($\bar{H}$ = 0.041; Nevo, Beiles and Ben-Shlomo, 1984).

Selander and Kaufman (1973) suggested that large, mobile animals generally have lower levels of genetic variability than smaller, less mobile ones. However, both forms of the short-finned pilot whale showed almost the lowest levels of genetic variability among cetacean species, which were lower than Baird's beaked (*Berardius bairdii*), Bryde's, sei and fin whales that have a larger body size thereby a lower level of genetic variability than the pilot whales is predicted.

Nei (1975) showed the D values to correlate with the systematic distance, i.e., 0–0.058 of interpopulation level, 0.004–0.351 (mainly 0.1–0.2) of intersubspecies level and 0.05–2.73 (mainly 0.5–2.0) of interspecies level. However, Avise and Aquadro (1982) showed that the degree of genetic differentiation differ considerably from species to species, and that the mean D value between species was 1.75 in amphibia, 0.67 in reptilia, 0.41 in mammalia and 0.08 in Aves.

In cetacea, however, much smaller D values have been reported between populations. Among five stocks of Bryde's whale in the Indian and Pacific Oceans, Wada (1987) obtained $\bar{D}$ = 0.0029, ranging from 0.0003 to 0.0050. The D value between two color types of the Dall's porpoise was 0.004 (Shimura and Numachi, 1987). Andersen (1987) calculated the genetic distance among nine schools of the long-finned pilot whale, *Globicephala melaena*, around the Faroe Islands. The largest D value estimated from her gene frequency data is 0.0032. The D value of 0.0004 calculated in the present study was in the lower range of above values.

Nei and Roychoudhury (1974) and Nei (1978) studied on the sampling variance of D, and decomposed a total variance into the intralocus and interlocus variances. The former is due to a restricted number of genes sampled for each locus, and is almost negligible when the sample size is more than 50. The latter is due to a restricted number of loci sampled from the genome. Therefore, the reliability of the estimate of D mainly depends on the number of loci or chance of sampling particular loci.

In cetacea examined to date, the most frequent allele at each locus was common in all populations within a species except in minke whales. This yielded a small value of a single-locus distance; the largest ones between populations were 0.0034 at *Me* in fin whale, 0.0150 at *Ada* in short-finned pilot whale, 0.0211 at *Pgm–3* in Dall's porpoise, 0.1164 at *Sdh* in sei whale and 0.1316 at *Pgm–1* in Bryde's whale. If a hypothetical D is calculated between the two forms of the short-finned pilot whales off Japan assuming an additional 37th locus with a single-locus distance value of 0.15, tenfold of the actually observed value, the estimate of D over all loci increases from 0.0004 to 0.0040. Even under this extreme assumption, the D value is still smaller than the smallest ones obtained from species comparison; D = 0.026 between striped dolphin, *Stenella coeruleoalba* and spotted dolphin, *S. attenuata*, and D

= 0.047 between sei and Bryde's whales. From this, I conclude that the extent of genetic differentiation between the two forms of the short-finned pilot whale is nothing more than the level of interpopulation. It is quite reasonable to say that their current taxonomic relationship is the two local forms within a species. This conclusion coincides with the results of the comparative studies on life history parameters (Kasuya, 1986a) and on morphology and segregation (Kasuya *et al.*, 1987) between the two forms.

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RE-EXAMINATION OF LIFE HISTORY PARAMETERS OF LONG-FINNED PILOT WHALES IN THE NEWFOUNDLAND WATERS*

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ABSTRACT

Age dependent life history parameters of the long-finned pilot whale were analyzed using recent technique of aging which allowed accurate age estimate for old individuals and materials taken in 1954 from the drive fishery off Newfoundland and once used by Sergeant (1962). In both sexes mean growth ceases at ages between 21 and 25 years, when natural mortality increases. Males live to age 36 years or about 10 years shorter than females. Natural mortality is dependent on age in both sexes, and male mortality exceeds that of females of the same age, thus causing age related decline of male proportion in the population. Pregnancy rate is not apparently dependent on age of females and the possibility of a large proportion of postreproductive females is rejected, which is different from feature known on the short-finned pilot whale. Additionally, long-finned pilot whales differ from short-finned pilot whales in the younger age at maturation, shorter longevity and higher proportion of adult males, suggesting less specialized reproductive strategy and difference in the social structure.

INTRODUCTION

A study on life history and reproductive biology of the long-finned pilot whale, *Globicephala melaena* (Traill, 1809), was published by Sergeant (1962) using materials obtained from the drive fishery off Newfoundland. This was the first delphinid biology based on reliable age determination. However, as recognized by himself, the age of older individuals tended to be under estimated due to the decrease of readability of dentine layers or cessation of the deposition at an age between 8 and 16 years, and reliable life history parameters were not available for older individuals. Recent study of Martin (1987) on long-finned pilot whales mass stranded on the British coast probably retained similar problem (IWC, 1987).

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After Sergeant (1962), there was a progress in age determination technique of toothed whales (Perrin and Myrick, 1981), and Kasuya and Matsui (1984) established age determination method for the short-finned pilot whale, *G. macrorhynchus* Gray, 1846, using annual growth layers in dentine and cementum apparent in decalcified and haematoxylin stained longitudinal section of the tooth. Based on this aging technique, Kasuya and Marsh (1984), Marsh and Kasuya (1984) and Kasuya (1986) analyzed the life history and reproductive biology of short-finned pilot whales taken by the drive fishery or small-type whaling with harpoon gun off the Pacific coast of Japan. These studies showed that the short-finned pilot whale exhibits a large longevity difference between males (46 years) and females (63 years), age dependent change in the pregnancy rate, and post-reproductive life time of females extending over 20 years. Marsh and Kasuya (1986) indicated further need to examine the presence of postreproductive females in *g. melaena*.

We reanalyzed in the present study some of the life history parameters of the long-finned pilot whale using materials of Sergeant (1962) and age determination method of Kasuya and Matsui (1984), and compared them with the results of short-finned pilot whales off Japan to find difference of the reproductive strategy between the two pilot whale species.

MATERIALS AND METHODS

This study is based on teeth of 437 long-finned pilot whales obtained from the drive fishery off Newfoundland and some accompanying biological data (Table 1). They were collected in June to October 1954 and were the major portion of the materials used by Sergeant (1962) for the study of age and growth. The teeth had been preserved in glycerin with a tag having specimen number, body length (measured to a nearest inch), sex and date on it.

Information was not available for male maturity. The reproductive status data of females (usually pregnancy and lactation only) were available for some limitted number of individuals. Although these data did not seem to be biased to certain body length classes (Fig. 2), our data contained high proportion of females of unknown reproductive status and very low number of resting females (adult females neither pregnant nor lactating), the former being close to the sum of the females in pregnancy or in lactation, and the latter amounts only 16% of the pregnant females (Table 2). This was because only females which were obviously pregnant or lactating were fully recorded and mature females of another reproductive status (resting) were underrecorded in the sample (Sergeant, 1962: p.56). Therefore mature females of unknown reproductive status were more likely to be in the resting status rather than pregnant or lactating.

The teeth had been cut transversely near the cingulum for the previous age determination. For the present age determination, we usually used only the root portion of the tooth. The crown side of old individuals did not usually

TABLE 1. MATERIALS USED IN THE PRESENT STUDY

Sex	Month*	With age and body length	With age but without body length**	Total
Male	July	43	0	43
	August	101	1	102
	Sept.	8	0	8
	Oct.	0	0	0
	Total	152	1	153
Female	July	67	1	68
	August	200	6	206
	Sept.	8	2	10
	Total	275	9	284

* All the materials were collected in 1954.

** Used for only age composition and age dependent sex ratio analysis.

have the most recent layers due to sawing off. The few exceptions were for 0 to 2 years old young tooth where the crown side of the tooth was used because the root was too short and thin. Either root or crown portion of the tooth was firstly rinsed in running water for one to two nights to remove the glycerin, longitudinally half sectioned, glued on a plastic plate, polished to a thickness of about 30 to 40 μm, decalcified in 5% formic acid for several hours, stained with Mayer's haematoxylin and mounted with Canadian balsam (Kasuya and Matsui, 1984).

Kasuya aged all the individuals without referring to any data of the specimen (including the date of sampling) and using method of Kasuya and Matsui (1984) outlined below:

(1) To have three independent counts for both cementum and dentine.

(2) To choose the middle figure as the best for each tissue.

(3) To use the best dentinal count if the pulp cavity is wide and the deposition of dentine was considered to be continuing on the entire pulp wall (open pulp cavity) or on part of the wall (closing one), or to use the best cemental count if the pulp cavity was narrow and lined by thin uniformly stainable dentine suggesting cease of the deposition (closed pulp cavity).

(4) A pair of stainable and unstainable layer was assumed to represent one year as deduced by Sergeant (1962), and any age between n and n+1 year was expressed by n+0.5 (n being an integer).

After aging all the individuals, the body length was plotted on age, and five individuals (two females and three males, see Figs 3 and 4) were found in the body length/age relationship to be apart from rest of the individuals. These individuals were excluded from the subsequent analyses, but ages of rest of the individuals were accepted as they stand (including 10 individuals having no body length data).

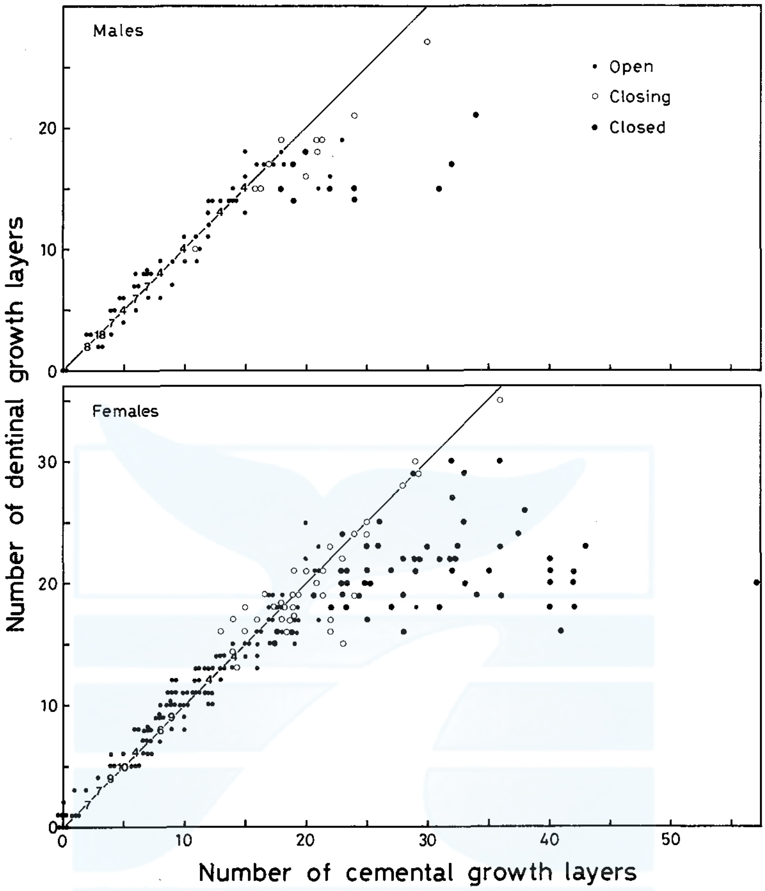

Fig. 1. Scatter plot of number of dentinal growth layers on that of cemental layers in the same tooth slide. Symbols distinguish the condition of pulp cavity. Numerals represent the number of individuals having open pulp cavity, and each of other mark represents one individual. The solid line represent equal deposition of layers in both issues.

RESULTS

Comparison between dentinal and cemental layer counts

Fig. 1 compares the number of growth layers in cementum and that in dentine of the same teeth. Since these tooth had been cut transversely to remove a piece of thin section for the previous age determination (Sergeant, 1962), we could not confirm on most of the present preparations if all the cemental or postnatal dentine layers were present (neonatal line in dentine could be identified only on the slide of juveniles prepared from the crown portion of the tooth). Although this did not necessarily imply loss of the first postnatal growth layer in either of the tissues, we were uncertain on tooth showing disagreement of counts in the two tissues if it came from the error of reading or from the deficit of the preparation. The readability of cemental and dentinal layers was slightly inferior to that of the short-finned pilot whales studied by Kasuya (1986) and Kasuya and Matsui (1984).

Admitting possible minor disagreement expected from the above deficit, we considered that growth layer counts in the two different tissues in a tooth slide were similar on most of the teeth having open or closing pulp cavity, but the correlation was lost on teeth with closed pulp cavity. The number of cemental layers exceeded that of the dentinal layers after ages between 15 to 20 years, and the magnitude of the disagreement increased with increasing age (Fig. 1).

We conclude therefore that growth layers in the two dental tissues are deposited at a same rate on young individuals, but on older individuals only the cemental layers continue deposition. And we assumed without direct evidence that the rate of cemental layer deposition stays same (annual) for the entire lifetime after the start of its deposition in early postnatal time (Kasuya and Matsui, 1984).

Body length composition and neonatal length

Body lengths of the 152 males ranged between the half-foot length groups of 5.5–6.0 feet (1.68–1.83m) and 19.5–20.0 feet (5.94–6.10m) (Fig. 2). A peak of large individuals was present between 17.5 and 19.0 feet (5.33 to 5.79m)

Body lengths of the 275 females were found between length groups of 6.0–6.5 feet (1.83–1.98m) and 16.0–16.5 feet (4.88–5.03m). A peak of larger individuals was present at lengths between 14.0 and 15.0 feet (4.27 to 4.57m), which was about 1 m smaller than that of the male. These features are similar to the body length frequencies presented by Sergeant (1962).

We had five (three female and two male) postnatal individuals having no neonatal layer in dentine, an indication of newborn calves (Kasuya and Marsh, 1984). Their body lengths were 175 and 198cm in males, and 173, 183, and 183cm in females (Figs 3 and 4). Mean of the five body lengths was 182.4cm. The range was nearly within the range of neonatal lengths of both sexes (165 to 191 cm) reported by Sergeant (1962), and the mean was close to the mean neonatal lengths (174 cm in females and 178 cm in males) estimated by him. We found no reason to change the neonatal length estimate of Sergeant (1962).

Male growth

The correlation between body length and age was very good before age 20 years, with most of the plots within the range of 70 cm, but it was apparently lost after an age between 21 and 25 years (Fig. 3). The male growth is rapid till the age of 2.5 years, or the body length of 2.7 to 3.3 m. After this

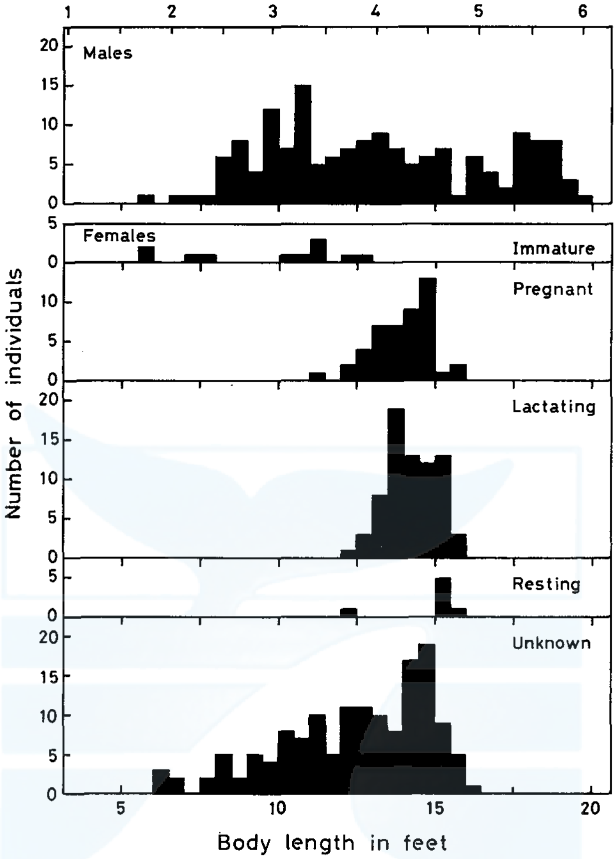

Fig. 2 Body length frequency of materials used in the present study. Scale at the top indicates body length in meter.

age, males grew at a slower but almost constant rate till the age of about 20 years. The inconspicuous secondary growth spurt probably started at about 12-13 years.

Although the mean body length seemed to stop increasing at an age between 21 and 25 years, and the mean body length of males over 25 years was 557 cm (n=5), we were unable to consider this figure as a reliable estimate of the mean asymptotic length of males due to the small sample size (Appendix Table 1).

The age at the start of secondary growth spurt (12-13 years) probably corresponds to the mean age at the attainment of breeding maturity 12 years estimated by Sergeant (1962). Due to the lack of adequate number of samples on age and maturity, Sergeant (1962) firstly estimated the mean age of breeding maturity (12 years) from a limited number of samples with good age estimate, then he read the mean body length of 4.88 m at breeding maturity on his mean growth curve corresponding to the age at the attainment of

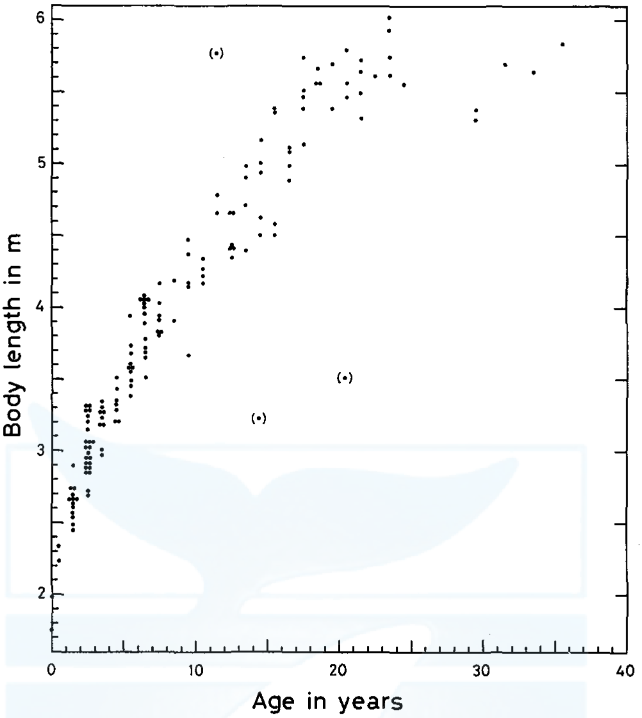

Fig. 3. Scatter plot of body length on age, males. Each mark represents one individual. Marks in parentheses indicate ages that were not used in the present alalyses.

breeding maturity. If the same method was adopted to the growth curve constructed in the present study, males were estimated to attain the length of 4.3 to 4.9 m at the mean age of breeding maturity (12 years). The middle value of this range, 4.6 m, was about 30 cm smaller than the estimate of Sergeant (1962). We consider that the difference is significant in view of the narrow individual variation of body length (see above).

This disagreement probably came from the overestimation of male growth by Sergeant (1962) due to the underestimation of age of many individuals over 8 to 16 years. Therefore, the present estimate of 4.6 m can be a better estimate of the mean male length at age 12 years (age at breeding maturity estimated by Sergeant (1962)). However, in view of slow and complicated procedure of maturation of males of the short-finned pilot whale (Kasuya and Marsh, 1984) and rather limited number of samples available for the long-finned pilot whale study (Sergeant, 1962), we feel that parameters relating to male maturity of the latter species require further investigation.

Female growth curve

Female body length increased almost at the same rate as that of the

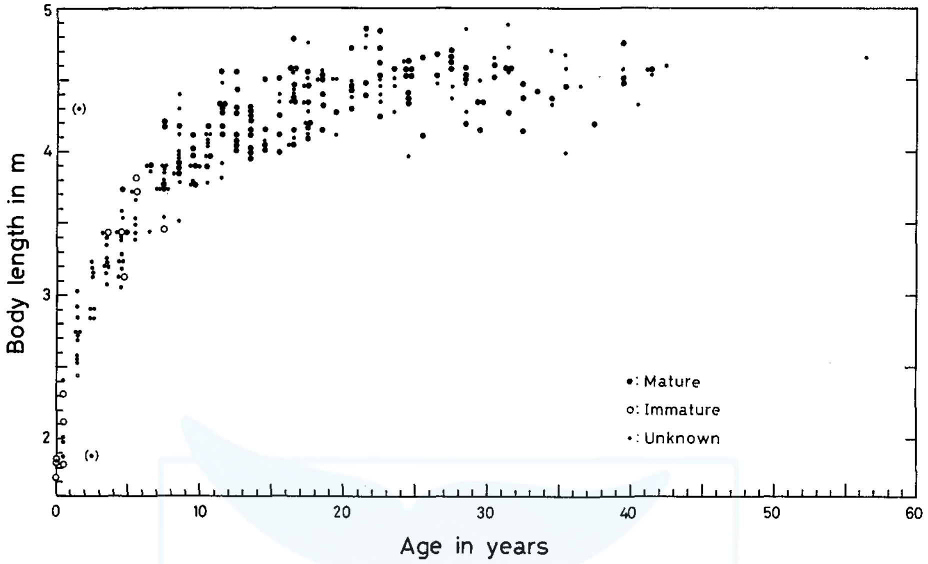

Fig. 4 Scatter plot of body length on age, females. Each mark represents one individual. Marks in parentheses indicate ages that were not used in the present analyses.

males till the age of 6 years (mean age of females at sexual maturity, see below) as indicated by Sergeant (1962) (Fig. 4), then the growth rate declined rapidly with increasing age, and the mean body length apparently ceased to increase at an age between 21 and 25 years. The mean body length of females over 25 years was 488.8cm (n=53, sd=18.6). This is the mean asymptotic length of females of this population.

Both mature and immature females were present at the body lengths between 11.0 and 13.0 feet (3.35 and 3.96m), and at the ages between 4 and 8 years (Figs 4 and 5). These ranges did not differ from corresponding figures estimated by Sergeant (1962). His estimation of the mean age and body length of females at the attainment of sexual maturity were 6 years and 12 feet (3.66m), respectively.

Age related change in female reproductive activity

Three resting females identified as senile by Sergeant (1962) were aged by us at 22.5, 30.5, and 41.5 years, and they were not always old. Marsh and Kasuya (1984) indicated the difficulty of identifying postreproductive females by macroscopic observation of ovaries. The oldest females of the present study at the pregnant, lactating, or resting status were aged at 39.5, 39.5 and 41.5 years, respectively (Fig. 5), which were close each other. Ages of three resting femals having corpus luteum of ovulation were 4.5, 24.5, and 25.5 years, and the age of a lactating female having corpus luteum of ovulation

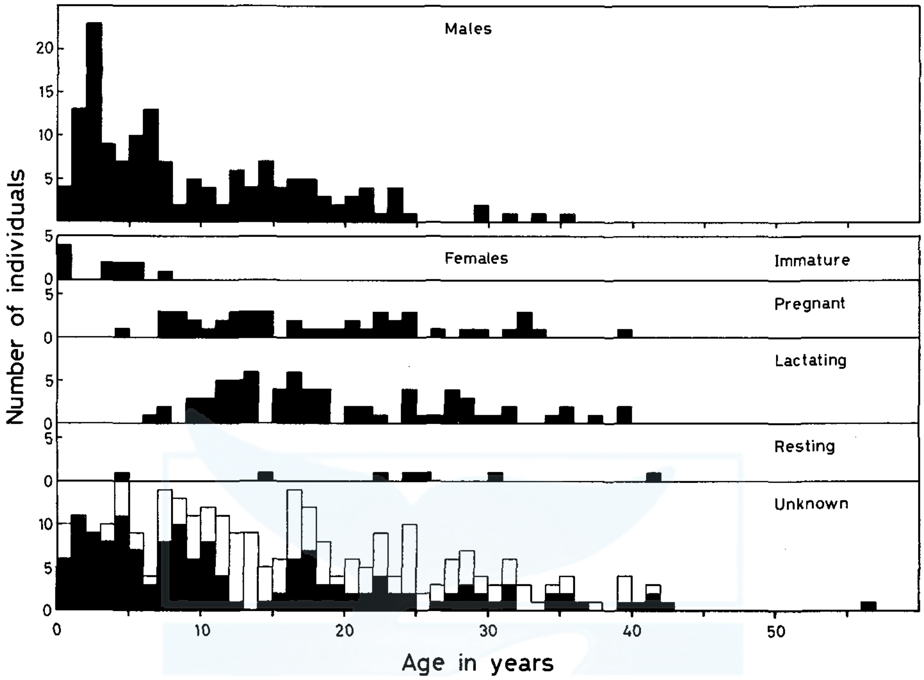

Fig. 5. Age composition and reproductive status of the long-finned pilot whale sample. White square at the bottom indicates sum of the females of known reproductive status.

was 31.5 years. These ages are younger than that of the oldest confirmed pregnancy.

Table 2 lists two kinds of pregnancy rates; (1) proportion of pregnant females in sexually mature females of known reproductive status, and (2) proportion of pregnant females in all the females including both immature and unknown reproductive status. Since females of unknown reproductive status in our sample probably tended to include more resting females than the pregnant or lactating ones (see above), the former figure will overestimate level of the apparent pregnancy rate of the sample, and this underrepresent, if it exists, the age dependent decline in the pregnancy rate. To the contrary, the latter will underestimate the apparent pregnancy rate (the degree of which will depend on the number of pregnant females classified to the unknown category), but will better reflect the age dependent change in the pregnancy rate if it exists.

None of the two pregnancy rate series in Table 2 showed significant age dependent change (Chi-square tests for ages over 10 years, $p > 0.5$). Thus, we were unable to conclude that the females of long-finned pilot whales off Newfoundland exhibit age dependent decline of reproductive activity, which was very distinct in the short-finned pilot whale populations off Japan and

TABLE 2. AGE DEPENDENT CHANGE IN APPARENT PREGNANCY RATE IN *GLOBICEPHALA MELAENA*.

Age (years)	Immature	Mature*				No. data	Pregnancy rate (%) **	
		P	L	R	T		(1)	(2)
0–10	11	8	6	1	15	75	53.3	8.8
10–20	0	17	37	1	55	28	30.9	20.5
20–30	0	14	19	3	36	20	38.9	25.0
30–40	0	6	9	1	16	10	37.5	23.1
40–50	0	0	0	1	1	4	0	0
50–60	0	0	0	0	0	1	–	0
Total	11	45	71	7	123	138	36.6	16.5

* P=pregnant, L=lactating, R=resting, T=total.

** (1) indicates proportion of pregnant females in mature females of known reproductive status, and (2) that in total females including females of immature and unknown maturity.

was an indication of the presence of postreproductive females (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; Kasuya, 1986).

The uncertainty that surrounds above analysis comes from the adult females of unknown reproductive status. If a 39.5 years old pregnant female is excluded, then all the 18 females over 33.5 years are non-pregnant or of unknown reproductive status (Appendix Table 2). Females of the latter category has high probability of not being pregnant, and might leave a possibility for postreproductive females. However, even under extreme assumption that they were all in the resting status, the number of pregnant females in the total females over 35 years (1/15) was not significantly different from that at 10-35 years (36/119) (Chi-square test, $0.2 > p > 0.1$), making it impossible to conclude the presence of significant number of postreproductive females in the population.

From the above analyses we conclude that the population of long-finned pilot whales has high reproductive capacity till the observed oldest age, although a larger sample may perhaps prove the presence of some postreproductive females among old females.

Sex ratio, age composition and mortality rate

The proportion of females in the sample increased from parity at ages below 10 years to 100% at age over 36 years (Table 3 and Appendix Table 2), or about 5 years earlier than the corresponding age for the short-finned pilot whale populations off Japan (Kasuya and Marsh, 1984; Kasuya, 1986). The decline of male proportion with increasing age will reflect the sexual difference of mortality rates and longevity (see below).

Sergeant (1962), using cementum age of limited number of selected individuals, showed that males lived to age of only 36 to 40 years while females did to age of 46 to 50 years. Ages of the oldest individuals of the present

TABLE 3. AGE RELATED CHANGE OF THE SEX RATIO IN *GLOBICEPHALA MELAENA.*

Age (years)	No. females	No. males	Total	Females (%)
0– 5	55	56	111	49.5
5–10	51	37	88	58.0
10–15	46	23	69	66.7
15–20	44	19	63	69.8
20–25	34	13	47	72.3
25–30	22	2	24	91.7
30–35	16	2	18	88.9
35–40	10	1	11	90.9
40–45	5	0	5	100.0
45–50	0	0	0	–
50–55	0	0	0	–
55–60	1	0	1	100.0
Total	284	153	437	65.0

material were 35.5 years in males and 56.5 years in females. However, the age of the oldest female seemed to be an outlier, and the ages of the next oldest male and female were 33.5 and 42.5 years, respectively (Appendix Table 2). Thus reasonable longevity difference between sexes of the long-finned pilot whale will be about 10 years as suggested by Sergeant (1962).

Age frequencies plotted on a logarithmic scale (Fig. 6) showed an apparent gradient change in both sexes at an age between 21 and 25 years. Additionally, there was observed in the male age composition a slight depression at ages between 8 and 17 years or at the age of puberty, suggesting a possible segregation of some pubertal males from the breeding schools. The similar feature was indicated for short-finned pilot whales off Japan (Kasuya and Marsh, 1984).

Ignoring the slight underrepresentation of pubertal males indicated above, we estimated the apparent annual mortality rate of males as about 0.07 at ages below 25 years (Table 4). The corresponding figure for ages between 21 and 36 years (the oldest male age) was calculated to be about 0.15 using very limited number of samples. For females, we estimated the corresponding figure of the mortality rates to be slightly over 0.02 (< 25 years) and about 0.1 (from 21 to the oldest individual). The male apparent mortalities are always higher than that of the females of the same age, as observed on the short-finned pilot whale off Japan (Kasuya and Marsh, 1984; Kasuya, 1986).

DISCUSSION

We re-examined several biological parameters of long-finned pilot whales off the Newfoundland waters using materials once used by Sergeant (1962) and

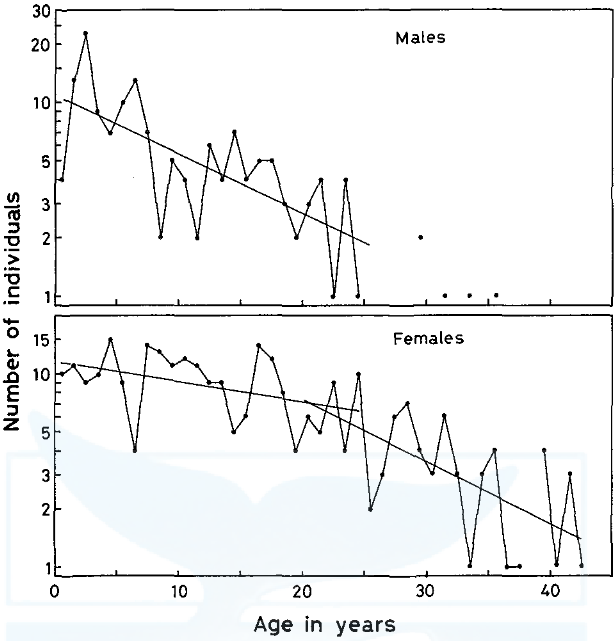

Fig. 6. Age frequency of long-finned pilot whale samples plotted on logarithmic scale. Straight line indicate linear regression of the frequency on age (see Table 4).

recently improved age determination method, which could give higher ages for many of individuals aged over 10 years by the previous method of aging using only dentinal layers. Among biological parameters examined, we found no reason to alter the previous estimate of Sergeant (1962) on neonatal body length, longevity, female age at the attainment of sexual maturity, and juvenile sex ratio. The growth curves of both sexes were altered slightly, and the mean asymptotic length of females and the age at the length were newly estimated in the present study.

In particular, we obtained new estimate of age composition of the catch and biological parameters derived from it. These allowed us to compare some life history parameters of long-finned pilot whales in the Newfoundland waters and those of short-finned pilot whales off Japan studied by Kasuya and Marsh (1984), Marsh and Kasuya (1984) and Kasuya (1986).

Apparent mortality rates calculated above are sums of natural mortality rate, fishing mortality rate and annual change in recruitment. Effect of the fishery on the latter two components is probably significant in the population of long-finned pilot whales, which had long history of hunting of relatively small scale (probably less than 500 individuals per year) by highly selective harpoon fishery and 3 years large scale harvest just prior to the commencement of present sampling (about 3,000 individuals per year) by less selective

TABLE 4. APPARENT ANNUAL MORTALITY RATES OF *GLOBICEPHALA MELAENA* ESTIMATED FROM AGE COMPOSITION.

Method		A	B
Female	0 – 25 years	0.0231	0.0201 ±0.0090
	21 – 43 years	0.0696	0.0682 ±0.0160
	21 – 57 years	–	0.0985 ±0.0122
Male	0 – 25 years	0.0683	0.0716 ±0.0115
	21 – 36 years	–	0.1497 ±0.0507

A: From the gradient of the linear regression in Fig. 6.
B: By segment analysis (Robson and Champman, 1961), best point estimate and standard error.

(Kasuya and Marsh, 1984) drive fishery (Sergeant, 1953; 1962; Mercer, 1975).

We consider that the drive fishery could have decreased absolute number of recruitment in the last 2 years preceding the sampling, but did not cause severe change in the age composition of older individuals. Thus we feel that the present age composition data are not suitable for the analysis of age dependent change in juvenile mortality rate.

To the contrary, the history of harpoon fishery over 7 years could have selectively killed larger individuals and changed the age composition and sex ratio of older individuals as observed on the short-finned pilot whales off Japan (Kasuya and Marsh, 1984). This causes difficulty to make meaningful comparison of apparent age dependent mortality rates between sexes. However, we consider that the present sample size is probably large enough to give a rough estimate of the maximum age which is allowed physiologically for the species, and that our finding of the shorter longevity of males allows our deduction of above result that males will have natural mortality rate exceeding that of the females of same age.

Ages of the oldest individuals in the sample of long-finned pilot whales were younger than those of short-finned pilot whale populations off Japan by 6 (including an outlier) or 20 years (excluding an outlier) in females or by 10 years in males, and were close to those of less specialized delphinid species such as striped dolphin, *Stenella coeruleoalba*, and spotted dolphin, *S. attenuata*, studied by Kasuya (1985). The difference of longevity between the two pilot whale species was in parallel with that of the age at sexual maturity (*G. melaena* of shorter life matures younger). Although reliable estimates of natural mortality rate are not available for either of the two pilot whale species, above longevity difference suggests a higher natural mortality of the long-finned pilot whale.

Although there remains a possibility that a larger sample may find some postreproductive females in old age classes, we have been unable to confirm age dependent decline of pregnancy rate in the long-finned pilot whale. This is in clear contrast with the life history observed on the short-finned pilot whale populations off Japan, where the confirmed pregnancy occurred below age of 36 years and lactation below 51 years while females lived for 63 years, and additionally their pregnancy rate declined with increasing age for all the age range over 8 years (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; Kasuya, 1986). We conclude therefore that female long-finned pilot whales have a shorter lifespan and breed till older age at a more constant rate than the short-finned pilot whale. We do not have data to compare the absolute annual pregnancy rates of the two species. Not denying the possibility that the above features of reproduction of long-finned pilot whale could have been enhanced in some degree by the continued expolitation, we suggest that the differences indicated between the two pilot whale species are principally species specific.

In a short-finned pilot whale population off Japan, individuals become reproductive at the mean ages of 9 years (female) and 17 years (male), and the sex ratio of adult individuals is 0.27 (adult males/adult females) (Kasuya and Marsh, 1984). In the population of long-finned pilot whales, males mature at a lower age (probably at 12 years) relative to the age of female maturity (6 years), and the natural mortality rate of both sexes appear to increase at a similar age (21-25 years) while there is large difference in the short-finned pilot whale off Japan (28 years in males and 46 years in females). These resulted in the higher adult male ratio of 153/220=0.70 (estimated from the age composition), which is closer to those of more generalized delphinids, e.g. 0.77 of *Stenella attenuata* (Perrin, Coe and Zweifel, 1976), 0.91 of *S. longirostris* (Perrin, Holts and Miller, 1977) and 1.1 (=1278/1191) of *S. coeruleoalba* (Miyazaki and Nishiwaki, 1978)

Above analyses indicate that the long-finned pilot whale has life history parameters which are apparently less specialized than those of the short-finned pilot whale, and that its reproductive strategy and social structure will not be the same with those of the short-finned pilot whale. The cohesive matrilineal school structure and long maternal care of the latter species (Kasuya and Marsh, 1984) may not be so pronounced in the long-finned pilot whale population off Newfoundland.

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APPENDIX TABLE 1. AGE–LENGTH KEY OF *GLOBICEPHALA MELAENA* (CM).

Age (years)	Males			Females		
	no. samples	mean	sd	no. samples	mean	sd
0.5	4	207.8	23.0	10	199.3	21.4
1.5	13	264.3	11.4	11	270.6	16.7
2.5	23	303.0	17.9	8	302.0	15.4
3.5	9	319.7	12.3	10	327.1	11.9
4.5	7	332.9	10.6	15	333.5	17.9
5.5	10	360.1	15.0	8	358.9	14.5
6.5	13	387.7	17.9	4	376.5	19.4
7.5	7	393.1	11.7	14	379.5	19.4
8.5	2	405.0	14.0	13	398.4	22.2
9.5	5	416.8	26.9	9	389.4	11.2
10.5	4	425.0	6.3	10	401.1	11.0
11.5	2	471.5	6.5	10	422.2	21.9
12.5	6	448.3	12.1	8	421.9	18.4
13.5	4	474.3	22.8	9	413.4	12.3
14.5	6	481.8	23.0	5	415.0	18.0
15.5	4	495.3	41.8	6	426.2	17.2
16.5	5	508.2	16.1	14	436.4	21.4
17.5	5	544.4	19.7	12	435.9	18.0
18.5	3	559.3	4.7	7	441.7	13.6
19.5	2	553.5	15.5	4	434.5	16.5
20.5	3	560.3	13.8	6	445.3	13.3
21.5	4	554.0	15.6	5	464.6	18.3
22.5	1	561.0	–	9	451.2	18.0
23.5	4	582.3	15.8	4	444.0	12.3
24.5	1	556.0	–	10	444.8	18.9
≥25.5	5	557.2	19.8	53	448.8	18.6

APPENDIX TABLE 2. AGE AND REPRODUCTIVE STATUS OF *GLOBICEPHALA MELAENA*.

Age (year)	Females						Males
	immat.	mature			unknown	total	
		preg.	lact.	rest.			
0.5	4				6	10	4
1.5					11	11	13
2.5					9	9	23
3.5	2				8	10	9
4.5	2	1		1*	11	15	7
5.5	2				7	9	10
6.5			1		3	4	13
7.5	1	3	2		8	14	7
8.5		3			10	13	2
9.5		2	3		6	11	5
10.5		1	3		8	12	4
11.5		2	5		4	11	2
12.5		3	5		1	9	6
13.5		3	6			9	4
14.5		3		1	1	5	7
15.5			4		2	6	4
16.5		2	6		6	14	5
17.5		1	4		7	12	5
18.5		1	4		3	8	3
19.5		1			3	4	2
20.5		2	2		2	6	3
21.5		1	2		2	5	4
22.5		3	1	1**	4	9	1
23.5		2			2	4	4
24.5		3	4	1*	2	10	1
25.5			1	1*		2	
26.5		1	1		1	3	
27.5			4		2	6	
28.5		1	3		3	7	
29.5		1	1		2	4	2
30.5			1	1**	1	3	
31.5		1	2*		3	6	1
32.5		3				3	
33.5		1				1	1
34.5			1		2	3	
35.5			2		2	4	1
36.5					1	1	
37.5			1			1	
38.5							
39.5		1	2		1	4	
40.5					1	1	
41.5				1**	2	3	
42.5					1	1	
56.5					1	1	
Total	11	46	71	7	149	284	153

* Includes one female having corpus luteum of ovulation.
** Classified as "senile" by Sergeant (1962).

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DISTRIBUTION AND ABUNDANCE OF DALL'S PORPOISES OFF JAPAN*

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ABSTRACT

Results of nine whale sighting cruises in the Japanese coastal waters in 1983 through 1986 and some additional cruises provided following conclusion. Dall's porpoises inhabit waters below 24°C, but the upper temperature limit is lower in winter. *Dalli*-type individuals occur throughout the range of the species, but the majority of them winter in the Sea of Japan, and summer in the Okhotsk Sea and Pacific coast of Japan. *Truei*-type individuals inhabit only waters off the Pacific coast of northern Japan and southern Kuril Islands. They winter off the Pacific coast of Japan, and summer mainly in the waters between 40° and 45°N and west of 155°E. A minimum estimate of the number of *dalli*-type that winter in the eastern Sea of Japan is about 46,000 individuals, of these about 15,000 migrate through the Tsugaru Strait to the Pacific coast of Japan with the major portion of the stock summering in the Okhotsk Sea and northern Sea of Japan. The number of *truei*-types in the nearshore surveyed area is estimated at about 26,000, and the extraporation of the density to the offshore range of the type provides an estimation of total *truei*-type population of about 58,000 individuals. The continuation of current Japanese harpoon fishery will further deplete the stock(s) of Dall's porpoises.

INTRODUCTION

The Dall's porpoise, *Phocoenoides dalli* (True, 1885), includes two major color morphs designated as *dalli*-type and *truei*-type (Houck, 1976; Kasuya, 1978), the former being mainly distributed in the cold waters of the North Pacific and the latter in a limited area of the northwestern North Pacific (Nishiwaki, 1972; Ohsumi, 1975; Kasuya, 1978, 1982). Considering distribution of these color types and their seasonal movement, Kasuya (1978) suggested the presence of at least three local stocks of the Dall's porpoise in the northwestern North Pacific and the adjacent seas, i.e. 1) off the Pacific coast of northern Japan and southern Kuril Islands, 2) offshore northwestern North Pacific and the Bering Sea, and 3) in the Sea of Japan and the Okhotsk Sea. He considered

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that all the *dalli*-type individuals in the *truei*-type range off the Pacific coast of Japan would not be the members of Japanese east coast stock, but that at least some of them, especially those in the schools containing no *truei*-types, would be migrants from the offshore stock in the northwestern North Pacific and the Bering Sea or from the Sea of Japan-Okhotsk Sea stock. A similar view was presented by Miyazaki and Fujise (1985).

Recent data on the distribution of mother-calf pairs, parasite load, electrophoretic analysis of isoenzymes and pollutant levels in Dall's porpoise suggest that the hypothetical stock of Kasuya (1978) in the northwestern North Pacific and the Bering Sea probably includes two or more stocks, each breeding in the Bering Sea, south of the western Aleutian Islands, and perhaps off the east coast of northern Kuril Islands, respectively (Kasuya and Ogi, 1987; Subramanian, Tanabe, Fujise and Tatsukawa, 1986; Walker, 1987; Winans and Jones, in press). Additionally, Yoshioka, Ogura and Shikano (1987) presented data suggesting another apparently isolated breeding ground in the Gulf of Alaska.

Subramanian, Tanabe, Fujise and Tatsukawa (1986) found that the PCB/DDE ratio in the *dalli*-types taken in summer off the Pacific coast of Hokkaido was closer to those in the Sea of Japan than the *truei*-types in the same region, and considered that the *dalli*-types in the two locations could have shared a common feeding area. This suggests that the *dalli*-types migrate seasonally between the Sea of Japan and the Pacific coast of northern Japan.

The number of Dall's porpoises in the principal area of *truei*-type distribution has been estimated, using sightings data pooled for the months April to August since 1980, as about 64,000 (Kato, 1986) or about 125,000 individuals (Kato, 1987).

The present study analyzes the distribution and segregation of two types of Dall's porpoises in the Japanese waters using data obtained through nine whale sighting cruises in the western North Pacific, Sea of Japan and the Okhotsk Sea. The population of the two types of Dall's porpoises in the area is estimated using line transect methodology.

MATERIALS AND METHODS

The main body of data was obtained from the nine whale sighting cruises conducted using two whale catcherboats (*Toshimaru No. 15*, 647.3 gross tons, 3,480 HP; *Toshimaru No. 25*, 739.9 gross tons, 3,600HP) chartered by the Japan Fisheries Agency in 1983 through 1986 (Table 1). Other sighting cruises in which no Dall's porpoises were observed were excluded. The seasons covered were nine months of the year, excluding April, November and December.

In these cruises, survey was conducted along predetermined track line placed systematically perpendicular to the coast line. Two mast-top observers and three to six upper wheel-deck observers conducted sightings during

TABLE 1. WHALES SIGHTING CRUISES USED IN THE PRESENT STUDY

Cruise no.	Period*	Year	Name of vessel	Biologists on board	Number of schools sighted			
					D	T	M	U
1	12 Jan. – 24 Mar.	1983	Toshimaru No. 15	S. Shiraga	0	0	0	3
2	11 Jan. – 10 Mar.	1984	Toshimaru No. 15	S. Nishiwaki	24	0	0	3
3	10 Jan. – 10 Mar.	1985	Toshimaru No. 15	H. Shimada	1	0	0	0
4	2 May – 30 June	1986	Toshimaru No. 25	–	85	71	1	0
5	9 June – 4 Sep.	1984	Toshimaru No. 25	T. Kasuya (7 July–6 Aug.)	9	47	2	5
6	10 June – 5 Aug.	1983	Toshimaru No. 25	–	9	38	0	0
7	8 June – 5 Sep.	1985	Toshimaru No. 25	Y. Fujise (88 June–8 July), F. Kasamatsu (6–20 Aug.), H. Kishino (6–20 Aug.)	47	24	1	9
8	1 Sep. – 30 Oct.	1985	Toshimaru No. 15	T. Miyashita (1–30 Sep.)	24	5	0	0
9	1 Sep. – 30 Oct.	1986	Toshimaru No. 15	H. Shimada, M. Ichihara (2 Sep.–8 Oct.)	34	16	4	6

D: *dalli*-type Dall's porpoise. T: *truei*-type Dall's porpoise. M: mixed school of the two color types. U: school of unknown color type. *: Total period of the cruise including the period that cruised out side the ranges of Figs 2 to 7 and had no Dall's porpoise sightings.

daytime from 15 minutes after sunrise to 15 minutes before sunset except during poor weather condition (Kasuya, 1986). The method of sighting was basically the same with that used for the Southern Hemisphere minke whale assessment cruises and described by Best and Butterworth (1980).

Sighting effort has usually been discontinued when visibility is less than 1.0 nautical mile (n. m.) or the sea state is Beaufort 5 or over. The vessel remained at the termination position until the weather changed, as far as time permitted. Only sighting effort during searching mode under good weather conditions and with mast-top observers was used as the primary sighting effort, and sightings made under these condition are designated as primary sightings. We used only primary sightings and accompanying effort data for the estimation of abundance. Any sightings other than primary sightings were dealt as secondary sightings and used only for the analyses of distributional ranges.

All the marine mammals sighted were attempted to approach for identification of species, color types of Dall's porpoise and school composition. The following data were collected by the biologist and the captain for each sighting; sighting time, sighting cue, angle from the bow of the vessel to the school, radial distance, position and swimming direction of the school when first seen, and estimated size composition. Surface water temperature at the position of school was recorded, except for the 1983 and part of the 1984 cruises of *Toshimaru No. 25*. Radial distance between the vessel and Dall's porpoise school was estimated usually when school was within about 0.5 n. m., but when school was apart for over the distance it was estimated from the vessel speed (15 knot for closure) and the time required for closure to a certain

TABLE 2. NUMBER OF DALL'S PORPOISE SIGHTINGS IN THE JAPANESE COASTAL WATERS BY AREA, MONTH AND COLOR TYPE MADE DURING THE NINE CRUISES IN TABLE 1

Area & Month	*dalli*-type		*truei*-type		mixed		U	Total*	
	no.	%	no.	%	no.	%	no.	no.	%
Pacific									
March	–	–	–	–	–	–	3	–	–
May	4	5.3	70	93.3	1	1.3	–	75	100
July	18	15.3	98	83.1	2	1.7	5	118	100
August	21	63.3	11	33.3	1	3.0	1	33	100
September	18	64.3	6	21.4	4	14.3	2	28	100
October	35	77.7	10	22.2	–	–	4	45	100
Sea of Japan									
March	25	100.0	–	–	–	–	3	25	100
May	22	100.0	–	–	–	–	–	22	100
June	56	100.0	–	–	–	–	–	56	100
July	8	100.0	–	–	–	–	2	8	100
October	2	100.0	–	–	–	–	–	2	100
Okhotsk Sea									
May	3	75.0	1	25.0	–	–	–	4	100
July	18	100.0	–	–	–	–	6	18	100
October	3	37.5	5	62.5	–	–	–	8	100
Total	233		201		8		26	442	

U: school of unidentified color type. mixed: school of the two color types.
*: excluding school of unidentified color type.

position from the school where the rest of distance could be estimated visually. However, the majority of the Dall's porpoise sightings occurred within the former range.

School size was estimated by the two mast-top observers. Calves were identified by their small size and close association with a larger individual (presumably the mother). Color type of the porpoise was identified by the biologist on board or by the captain. When color type was not recorded for all the members of a Dall's porpoise school, we considered that all individuals in the school were of the same color type. This could have underestimated the proportion of mixed schools composed of both color types. Since 1983 summer cruise, an attempt was made to photograph all the marine mammal sightings for later confirmation of the species identificaiton.

The surface isotherm was drawn based on surface water temperature hourly recorded. Although this does not reflect the actual isotherm at any particular moment, it is useful to indicate the relationship between the distribution of Dall's porpoise and surface water temperature.

Additional data recorded by the officers of research vessels include position of the vessel and hourly meteorological records from 4 a.m. to 8 p.m.

TABLE 3. OCCURRENCE OF DALL'S PORPOISE SCHOOLS OFF THE PACIFIC COAST OF JAPAN IN RELATION TO THE SURFACE WATER TEMPERATURE AT THE POSITION OF SIGHTING. NOON POSITIONS INCLUDE ALL RECORDS FOR DAYS WITH ORDINARY SIGHTING EFFORT DURING THE CRUISES IN TABLE 1*

Surface water temperature (°C)	May			July			August			September			October		
	N	D	T	N	D	T	N	D	T	N	D	T	N	D	T
3.0– 3.9	1	2	3												
4.0– 4.9	1		1												
5.0– 5.9	2		10												
6.0– 6.9	2	1	8												
7.0– 7.9	5	1	12												
8.0– 8.9	2	1	9	1											
9.0– 9.9	1		7		1										
10.0–10.9			7	2	1									3	
11.0–11.9	1		2			10								2	
12.0–12.9			5			2		2		1	1		3		1
13.0–13.9			5					1			9		4	11	1
14.0–14.9	1					7	1	3		1	2	4	8	13	1
15.0–15.9	1		1	2		1		5		1	1	1	7	2	2
16.0–16.9	1					1		2		2	3	2	7		
17.0–17.9						1		1		2	2	1	10	2	3
18.0–18.9	3		1			1		1		7	3	1	10	2	1
19.0–19.9				3	1	1		1		7		1	4		
20.0–20.9	1			3		1	1	2		11	1				
21.0–21.9						1	5	1		6					
22.0–22.9				3			5		1	6			1		
23.0–23.9				3		1	3	1	1	1					
24.0–24.9				4	1	4	3			3					
25.0–25.9				3			3			4					
26.0–26.9				9			2						1		
27.0–27.9				3			6			2					
Total	22	5	71	36	4	31	29	20	2	54	22	10	55	35	9

N: number of noon positions, D: number of *dalli*-type schools, T: number of *truei*-type schools.
*: mixed schools are included into schools of each color type.

in local time during steaming, and when the activity of the vessel changed.

The northeastern range of *truei*-type porpoise was determined using information recorded by biologists on board several Dall's porpoise research vessels operated by the Japan Fisheries Agency during transits to the northwestern North Pacific and Bering Sea. These cruises and the references where details of the cruise including track lines and sightings are available are as follows;

May to June, 1984: Miyazaki, Fujise, Komuro and Taketomi (1984)
June to August, 1978: Miyazaki, Jones and Beach (1984), Kasuya and Ogi (1987)

TABLE 4. OCCURRENCE OF DALL'S PORPOISE SCHOOLS IN THE SEA OF JAPAN IN RELATION TO THE SURFACE WATER TEMPERATURE AT THE POSITION OF SIGHTING. NOON POSITIONS INCLUDE ALL RECORDS FOR DAYS WITH ORDINARY SIGHTING EFFORT DURING THE CRUISES IN TABLE 1

Surface water temperature (°C)	March		May		June		July		October	
	N	D	N	D	N	D	N	D	N	D
2.0– 2.9			1							
3.0– 3.9										
4.0– 4.9										
5.0– 5.9										
6.0– 6.9				1						
7.0– 7.9						1				
8.0– 8.9		2	2	15	3	6				
9.0– 9.9		7	1	7		12				
10.0–10.9	3	14			1	10				
11.0–11.9	1	1			1	18			1	
12.0–12.9	3	1			1	7	1			
13.0–13.9	2				1	2		2		1
14.0–14.9					1		1	3	1	
15.0–15.9					1		2	3	5	
16.0–16.9					4		1		2	
17.0–17.9					2					
18.0–18.9					4				1	
19.0–19.9					6					1
20.0–20.9					4				3	
21.0–21.9									1	
22.0–22.9									3	
23.0–23.9									4	
24.0–24.9									1	
Total	9	25	4	23	29	56	5	8	22	2

N: number of noon positions, D: number of *dalli*-type schools.

August to September, 1982: Kasuya and Jones (1984), Kasuya and Ogi (1987)

August to September, 1983: Ogi and Fujise (1984), Kasuya and Ogi (1987)

August to September, 1985: Ogi, Tanaka, Kuramochi and Yamamoto (1986), Kasuya and Ogi (1987).

SURFACE WATER TEMPERATURE

Sea of Japan-Okhotsk Sea dalli-*types*

Only *dalli*-type individuals were sighted in the Sea of Japan. Although *truei*-types were sighted in summer months near the southeastern border of

TABLE 5. OCCURRENCE OF DALL'S PORPOISE SCHOOLS IN THE OKHOTSK SEA IN RELATION TO THE SURFACE WATER TEMPERATURE AT THE POSITION OF SIGHTING. NOON POSITIONS INCLUDE ALL DAYS WITH ORDINARY SIGHTING EFFORT DURING THE CRUISES IN TABLE 1*

Surface water temperature (°C)	May			July			October		
	N	D	T	N	D	T	N	D	T
2.0– 2.9	2								
3.0– 3.9									
4.0– 4.9	1								
5.0– 5.9									
6.0– 6.9		3							
7.0– 7.9	2		1						
8.0– 8.9				1	1			3	
9.0– 9.9							1		1
10.0–10.9							1		
11.0–11.9					1				1
12.0–12.9				2	11		1		3
13.0–13.9					5				
Total	5	3	1	3	18		3	3	5

N: number of noon positions, D: number of *dalli*-type schools, T: number of *truei*-type schools.
*: mixed school of the two color types are included into schools of each color type.

the Okhotsk Sea (Figs 2 and 6), the primary color morphs of the Dall's porpoise inhabiting the sea was considered to be *dalli*-type. In these two waters, the survey was conducted in surface water temperature between 2° (May) and 25°C (October), and the Dall's porpoise occurred in the temperature range of 6° (May) to 20°C (October) (Tables 4 and 5).

Sighting effort below 6°C was about 6 hours (one day) in the Sea of Japan and 18 hours (three days) in the Okhotsk Sea resulting in a survey distance of about 290 n. m. The absence of Dall's porpoise during the period suggests that *dalli*-type Dall's porpoises in the Sea of Japan and Okhotsk Sea may be uncommon in the waters below 6°C. Further definition of the lower temperature bound of the species is not possible due to the limited survey effort near the northern limits of the species.

The comparison between distribution of surface water temperature at the noon position (indication of effort distribution) and the temperature at the position of the Dall's porpoise sightings suggests that *dalli*-type Dall's porpoises are rare in waters over 16°C in the Sea of Japan and in the Okhotsk Sea (Tables 4 and 5). If one exceptional October record between 19° and 19.9°C is excluded, the upper bound of surface water temperature for the distribuion of the species in the Sea of Japan varied from about 13°C in March, 14°C in June, and to 16°C in July and October (Table 4 and 5, and Fig. 1). This change will be more enhanced if an exceptional record in October is taken into consideration. Thus we consider that Dall's porpoises do not change the geographical distribution seasonally so much as expected from the change in the surface water temperature, but they tend to live in higher water temperature in the summer season than in the winter.

The number of *dalli*-type sightings relative to the quantity of survey effort in certain water temperature range (represented by the number of noon position at certain surface temperature) was high in the temperature ranges of 7°–11°C in March, 8°–13°C in June, and 12°–16°C in July, indicating a temperature increase of 3°–5°C during the three months. Although data were scanty in May and October, the feature was probably close to March and July, respectively.

Pacific coast truei-*types*

Although six schools of *truei*-types were sighted in May and October in the southern Okhotsk Sea (Figs 2 and 6, and Table 5), they were very close to the boundary to the Pacific Ocean. Therefore we consider they have not altered our general concept that the southern Okhotsk Sea is primarily inhabited by *dalli*-types (Kasuya, 1978).

Off the Pacific coast survey was conducted within the surface water temperature of 3° to 28°C (May to October), and *truei*-type individuals were sighted at temperature below 25°C (Tables 3 and 5). The lower bound of distribution was not detected, because the surveyed area was limited well to the south of the northern range of distribution of *truei*-types indicated in Fig. 8.

The upper bound of the temperature range in May (19°C) increased to 25°C in July, and this was followed by a gradual decline to 24°C in August, 20°C in September, and to 19°C in October (Table 3). Three schools of Dall's porpoise of unknown color type were sighted in March at about 35°N off the Pacific coast of Japan (Fig. 1). Surface water temperatures for these sightings were between 12° and 13°C. Thus it is suggested that seasonal migration of *truei*-type Dall's porpoises is less than the magnitude of seasonal change of surface water temperature, and that they inhabit waters of relatively high temperature in summer season. A similar trend was indicated on *dalli*-types in the Sea of Japan-Okhotsk Sea (see above), but the absolute temperature ranges were several degrees higher in the Pacific *truei*-types.

The water temperature range of high sighting frequency was between 5° and 14°C in May and did not seem to fluctuate seasonally, which appeared to be different from feature in the Sea of Japan-Okhotsk Sea stock.

Pacific coast dalli-*types*

Although, upper bounds of the temperature range of Pacific *dalli*-type sightings in July through October did not significantly differ from that of *truei*-types in the same area, it was considerably lower in May and the range of the most preferred temperature seemed to be lower than that of *truei*-type in August through October (Table 3).

This will reflect the distribution of *dalli*-types in the northern part of the surveyed area. The factors controlling this geographical segregation were unclear.

GEOGRAPHICAL RANGE

Sea of Japan-Okhotsk Sea dalli-*types*

Data are available for February/March (Fig. 1), May (Fig. 2), June (Figs 2 and 5), July (Fig. 5), and October (Fig. 6) to indicate seasonal change of Dall's porpoise distribution in the Sea of Japan and Okhotsk Sea.

The currently confirmed southern limit of the distribution in the Sea of Japan has been between 35° and 36°N. A small number of individuals was recorded in winter from northern Kyushu at latitude of about 34°N during the extensive sighting survey of dolphins in the Iki Island area between southern Sea of Japan and the East China Sea (Kirishima, 1986). Thus, we consider that the southern limit of Dall's porpoise in the Sea of Japan is in the Tsushima Strait between Korea and Kyushu in western Japan, and that they do not migrate to the East China Sea. Dall's porpoises have not been recorded from China (Zhou, 1986).

The southern limit moved with the progress of season from the Tsushima Strait to 40°N in early June (Fig. 2), and to 43°N in early July (Fig. 5). In October some sporadic sightings of the *dalli*-type were recorded in the northeastern part of the Sea of Japan between 41° and 43°N (Fig. 6). Noguchi (1946) reported past records of dolphin fishery off Tajima (35°30′N) in the southern Sea of Japan. The records indicated that the season of Dall's porpoise hunting ended while the Pacific white-sided dolphin started in early May. No data are available to indicate southward movement in the autumn/winter season.

Although the majority of Dall's porpoise in the Sea of Japan leave there in summer months and enter the Okhotsk Sea (Kasuya, 1978; 1982), some individuals may summer in the Tatarskii Strait region where the surface water temperature remains below 17°C.

Pacific coast truei-*types*

Data on the seasonal change of Dall's porpoise distribution off the Pacific coast of Japan were available in March (Fig. 1), May (Fig. 2), July (Figs 3, 4 and 5), August (Figs 3, 4 and 5), September (Figs 6 and 7), and October (Fig. 7).

Truei-types were not observed in the Sea of Japan (Table 2), and the western limit observed in the present study was about 30 n. m. northeast of the eastern entrance of the Tsugaru Strait (Fig. 3). Kawamura, Nakano, Tanaka, Sato, Fujise and Nishida (1983) reported the occurrence of *truei*-types in the Tsugaru Strait area at 41°30′N, 141°00′E in June and December. This

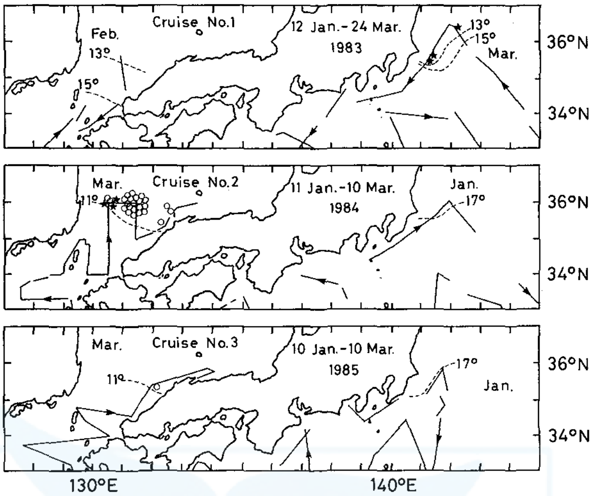

Fig. 1. Southern limits of Dall's porpoises in winter season observed during three whale sighting cruises of the *Toshimaru No. 15* (January, February and March in 1983, 1984 and 1985). Solid line indicates track line cruised with ordinary sighting effort, dotted line the surface water isotherm in centigrade, open circle sighting of *dalli*-types, and star that of type unidentified Dall's porpoises. Dall's porpoise schools of secondary sighting included.

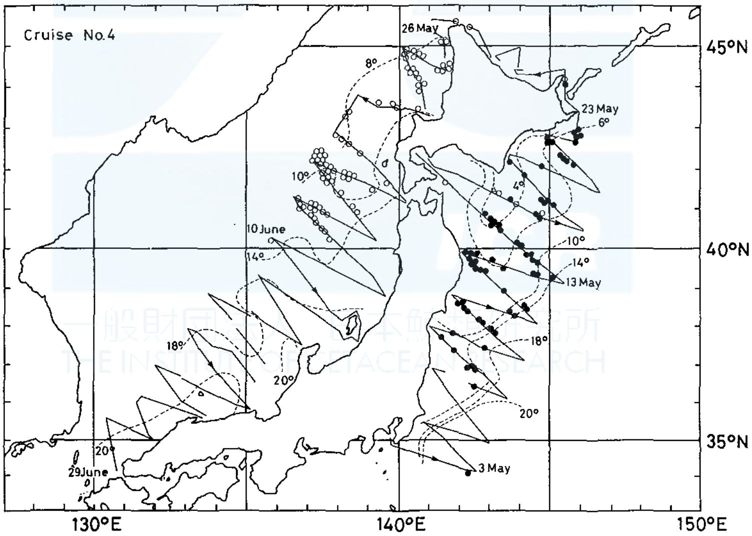

Fig. 2. Dall's porpoise sightings, surface water isotherms (dotted lines, in centigrade), and the track lines of the *Toshimaru No. 25* cruised with ordinary sighting effort in May through June, 1986 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

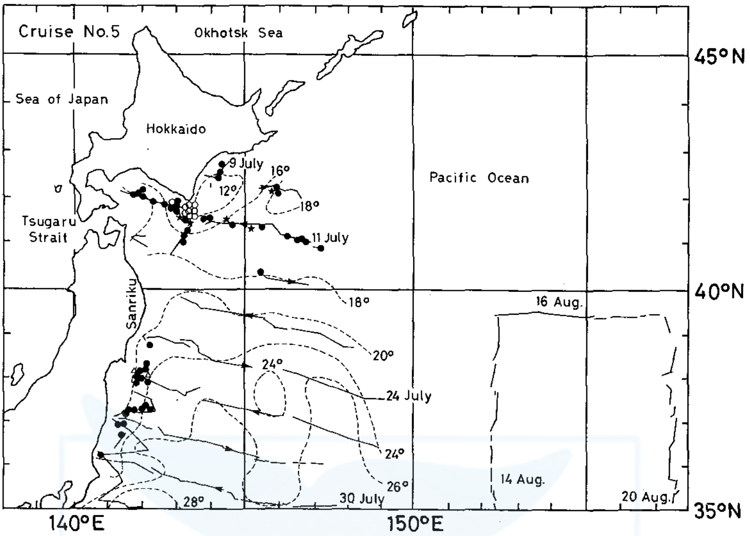

Fig. 3. Dall's porpoise sightings, surface water isotherms (dotted lines in centigrade), and the track lines of the *Toshimaru No. 25* cruised with ordinary sighting effort in July through August, 1984 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

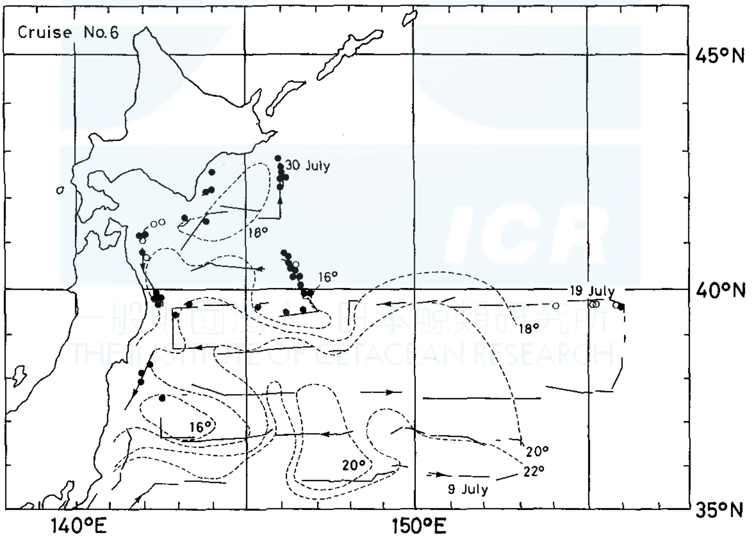

Fig. 4. Dall's porpoise sightings, surface water isotherms (dotted lines in centigrade), and the track lines of the *Toshimaru No. 25* cruised with ordinary sighting effort in July through August, 1983 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

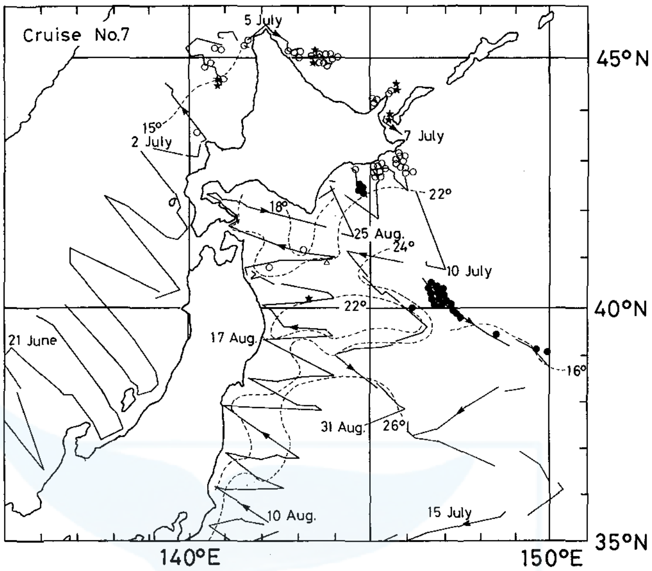

Fig. 5. Dall's porpoise sightings, surface water isotherms (dotted lines in centigrade), and the track lines of the *Toshimaru No. 25* cruised with ordinary sighting effort in July through August, 1985 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

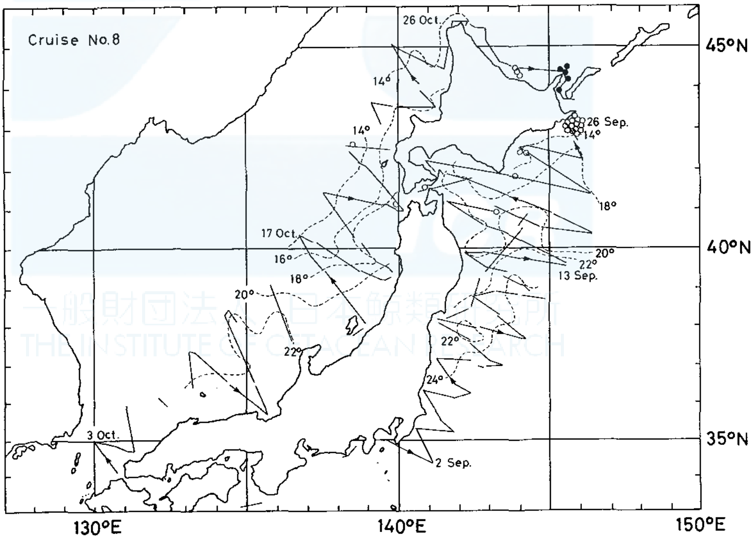

Fig. 6. Dall's porpoise sightings, surface water isotherms (dotted lines, in centigrade), and the track lines of the *Toshimaru No. 15* cruised with ordinary sighting effort in September through October, 1985 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

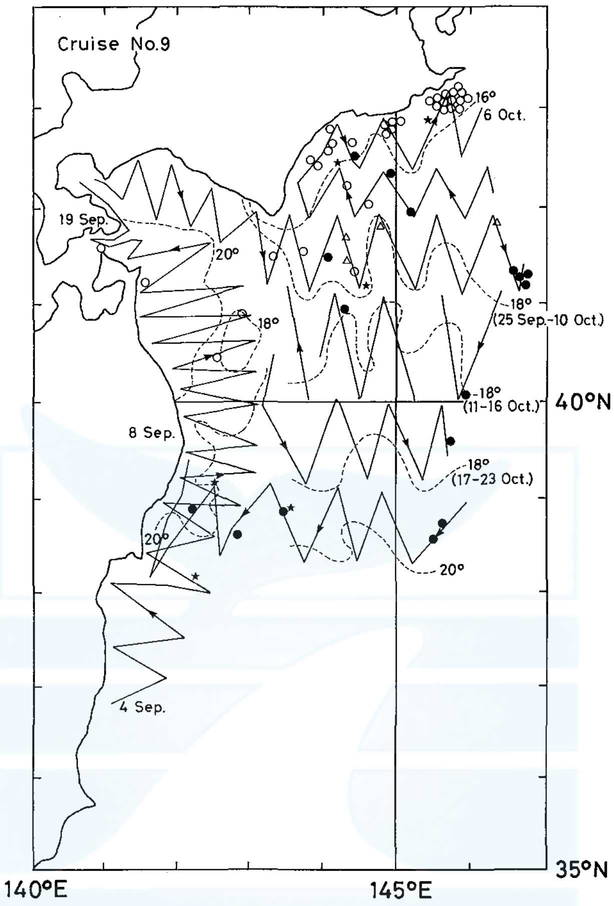

Fig. 7. Dall's porpoise sightings, surface water isotherm (dotted lines in centigrade), and the track lines of the *Toshimaru No. 15* cruised with ordinary sighting effort in September through October, 1986 (solid line and arrow head). Open circle indicates school of *dalli*-types, closed circle that of *truei*-types, open triangle that containing two color types, and star that of unidentified color types. Secondary sightings of Dall's porpoise schools included.

is the confirmed western limit of the color type in the Tsugaru Strait area.

The southernmost sighting of *truei*-types was recorded in May at about 34°N and at the water temperature of about 24°C (Fig. 2 and Table 3). This was an isolated southern record for the season and we do not consider it to represent the ordinary range of the color type in the season (Fig. 2). The next southern records (three schools of unknown color type) were obtained in March in between 35° and 36°N (Fig. 1) and this agreed with the previously reported range of the species off the Pacific coast of Japan (Kasuya, 1978).

The sourthern range of *truei*-types in the Japanese coastal Pacific waters moved from around 35°N in March to around 36°N in early May and early

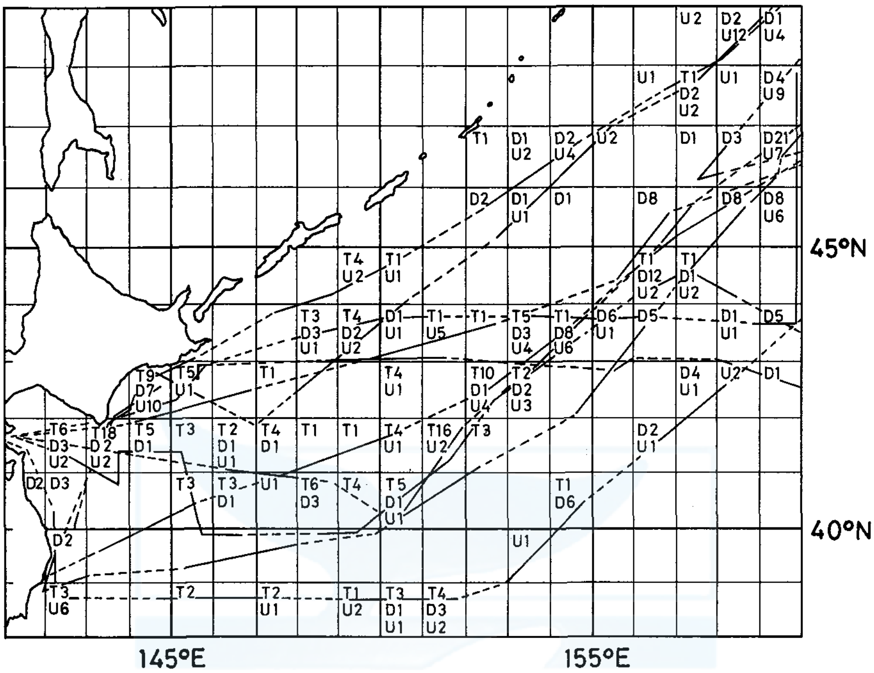

Fig. 8. Number of Dall's porpoise sightings off the Pacific coast of northern Japan and southern Kuril Islands in May through September appeared in the published records of the Dall's porpoise research cruises (Kasuya and Jones, 1984; Miyazaki *et al.* 1984a; Miyazaki *et al.*, 1984b; Ogi and Fujise, 1984; Ogi *et al.*, 1986). Secondary sightings included. Color type code: T, *truei*-type school; D, *dalli*-type school; U, school of unidentified type. Mixed schools of two color types are included into each type.

July (Figs 2 and 4), to 40°N in early August (Fig. 4). The southern limit of *dalli*-type in the coastal waters tended to be to the south of their range in the offshore waters (Figs 5 and 7). This reflects the presence of cold water in the coastal area.

Kasuya (1978) indicated that although the proportion of *dalli*-type catch increased with month the majority (about 96%) of Dall's porpoise catches off Sanriku Region between 37°30′N and 40°00′N were *truei*-types in January to March. The feature is similar in principle to our sighting data during May through July (Figs 2 to 4), but the predominance probably changes in August as seen in Figs 4 and 5.

In August, *truei*-types were absent in the coastal Pacific waters during the cruise no. 7 in 1985 (Fig. 5), but present during the cruise no. 6 in 1983 (Fig. 4) suggesting some annual fluctuation in the timing of seasonal movements and predominance change. *Truei*-types were almost totally absent from Japanese coastal waters in September of 1985 (cruise no. 8) and 1986 (cruise no. 9) (Figs 6 and 7). However, a survey in September and October 1986 (cruise no. 9) suggested that the porpoise had probably moved in summer to the offshore waters between 144° and 147°E and returned to coastal waters in October (Fig. 7). Some *truei*-types were sighted in late October in the boundary area between the southern Okhotsk Sea and Pacific Ocean at latitudes around 44°N (Fig. 6). We conclude therefore that *truei*-types predominates over *dalli*-types in the coastal waters along the Pacific coast of northern Japan during winter and spring seasons (probably, from November to July) but the predominance alters during a short summer/autumn period (September to early October) with possible annual fluctuation.

Information on the northern range of *truei*-types has been reported by biologists on board of five Dall's porpoise research cruises in the northwestern North Pacific and the Bering Sea (Fig. 8). Although Dall's porpoises were sighted almost continuously during the cruises in the area, the dominant color type altered rather sharply. The approximate positions of the change in the predominant color types of the Dall's porpoise are as follows (*truei*-type predominating on the southwestern side of the designated points);

1.	May	38°30′N, 152°00′E (Miyazaki, Fujise, Komuro, Taketomi, 1984).
2.	June	42°30′N, 153°00′E (Miyazaki, Fujise, Komuro, Taketomi, 1984).
3.	June	45°00′N, 150°00′E (Miyazaki, Jones and Beach, 1984).
4.	August	42°00′N, 143°30′E (Ogi, Tanaka, Kuramochi and Yamamoto, 1986).
5.	August	43°00′N, 154°00′E (Miyazaki, *et al.*, 1984).
6.	August	43°30′N, 152°00′E (Ogi and Fujise, 1984).
7.	August	44°00′N, 157°00′E (Kasuya and Jones, 1984).
8.	September	43°00′N, 145°00′E (Kasuya and Jones, 1984).
9.	September	43°00′N, 151°00′E (Ogi and Fujise, 1984).
10.	September	43°00′N, 153°30′E (Ogi *et al.*, 1986).

Two coastal points (nos 4 and 8 in the above list) reflect the local concentration of *dalli*-types mentioned below and may not be a good indicator of the eastern limit of the range of *truei*-types. The point no. 1 will possibly represent the eastern range of *truei*-types in May.

In other months (June to September), the observed northern boundary of distribution of *truei*-types was located between 42° and 45°N, and showed no north/south movement. This is in good contrast with the disappearance of most of *truei*-types from the Japanese coastal waters in September and October (see above).

The above analysis indicates that *truei*-type Dall's porpoise has seasonal northeast to southwest movement within their range between 35° and 45°N, and in late summer they almost disappear from a narrow Japanese coastal waters south of 43°N to concentrate in the northern and presumably slightly offshore waters. Northern limit of *truei*-types in the winter season is still to be examined.

Pacific coast dalli-*types*

Data on the distribution of *dalli*-type Dall's porpoise off the Pacific coast of northern Japan were obtained during cruises in March (no color type identification available, Fig. 1), May (Fig. 2), July (Figs 3, 4 and 5), August (Figs 4 and 5), September (Figs 6 and 7), and in October (Fig. 7).

About 4% of the catch of the winter operation of harpoon fishery off Sanriku were *dalli*-types (Kasuya, 1978), and there was no difference detected in the temperature preference between the two color types off the Pacific coast of Japan (see above). Therefore, we consider that the southern limit of the normal distribution of *dalli*-types would be at about 35°N as in the case for the *truei*-types.

Our data recorded small local concentrations of *dalli*-types to the east of the Tsugaru Strait as already indicated by Kasuya (1978) and Miyazaki and Fujise (1985). This concentration occurred in May along the southern coast of Hokkaido from the east of the Tsugaru Strait to 41°N, 145°E (Fig. 2). The feature was similar in July 1984, when we observed a concentration in 42°N, 143°30′E close to the southern coast of Hokkaido (Fig. 3). Such concentration possibly existed in August 1983 in the southeastern area of the Tsugaru Strait (Fig. 4).

The abundance and distribution of *dalli*-type individuals off the Pacific coast of Japan was high during the months when *truei*-types were becoming scarce in August (Fig. 5), almost absent (September, Figs 6 and 7), or probably just starting to reappear (October, Fig. 7). Among Dall's porpoise sightings in Fig. 5, all the 24 *truei*-type sightings occurred in July, 2 *dalli*-type sightings in the Pacific area in July, and 19 *dalli*-type sightings in August.

Our data confirmed that the distribution of *dalli*-types in the Pacific waters was continuous through the Tsugaru Strait to the Sea of Japan at least in May (Fig. 2), September (Fig. 7) and October (Fig. 6). However the density in the strait area appeared to be low. Similar observations have been made by Kawamura *et al.* (1983) in the Tsugaru Strait area. They recorded more *dalli*-types in the strait area in April through July than *truei*-types, but they considered that the frequency was low compared with that of other dolphin species.

We consider therefore that the distribution of *dalli*-type Dall's porpoises is continuous between the Sea of Japan and Pacific waters during spring and autumn season, and that most of the *dalli*-types in the latter area are probably migrants from the former waters. Thus, we presume that a portion of the putative Sea of Japan-Okhotsk Sea stock of Kasuya (1978) passes the Tsugaru Strait in spring to migrate to the Pacific coast of Japan and summer there while the majority of *truei*-types summer further offshore in the northern area. *Dalli*-types will return to the Sea of Japan in autumn preceding the arrival of *truei*-types. The bases for the above conclusion are summerized as follows;

(1) A small local concentration of *dalli*-types occurred in the waters east

of the Tsugaru Strait in May when the distribution of *dalli*-types was continuous through the strait between the Sea of Japan and Pacific coast of Japan (Fig. 2).

(2) The *dalli*-type range extended east/south before summer when the distribution of the species became discontinuous between the two seas (Fig. 5).

(3) The distribution of *dalli*-types was continuous through the Tsugaru Strait in September and October, when the migration of *dalli*-types in the southern Okhotsk Sea did not apparently reach to the west coast of Hokkaido (Fig. 6).

This migration pattern of the Dall's porpoise is similar to schematic drawing by Noguchi (1946), which has not received the attention of biologists, presumably due to the lack of presentation of basic data for the hypothesis.

Data are not available to determine whether *dalli*-types summering off the Pacific coast of northern Japan and in the southern Okhotsk Sea (they are considered to belong to Sea of Japan/Okhotsk Sea stock) intermingle in the waters adjacent to the southern Kuril Islands and eastern Hokkaido.

ABUNDANCE

Mathematical methodology

Population size (N) was estimated for the two color types and sub-areas defined below using following equation,

$$\mathrm{N} = \frac{n \cdot f(0)}{2 \cdot L} \cdot A \cdot s$$

where n represents number of primary sightings, A size of surveyed area (n. m.^{2}), L length of transect line (n. m.), $f(0)$ probability density function of the perpendicular distances evaluated at the origin, and s mean school size. The coefficient of variation (c.v.) for n, s and $f(0)$ were estimated by the equations of Anon. (1985a), then that of N by following equation,

$$\mathrm{c.v.(N)}^2 = \mathrm{c.v.(n)}^2 + \mathrm{c.v.(f(0))}^2 + \mathrm{c.v.(s)}^2$$

assuming each factor was independent statistics.

In this study we firstly fitted both Fourier series (FS) and negative exponential models (NE) to estimate $f(0)$ value, then chose the model with better fit for each data using the Chi-square goodness of fit test (Table 7). The probability of seeing a Dall's porpoise school on the track line was assumed as one. No smearing was done to eliminate the rounding error of sighting angle and radial distance estimate.

Sub-area definition

We used only data obtained through six spring/summer cruises (cruise nos 2, 4, 6, 8 and 9) which had relatively good coverage of the Dall's porpoise range of distribution and had a large number of sightings. Five sub-areas (two

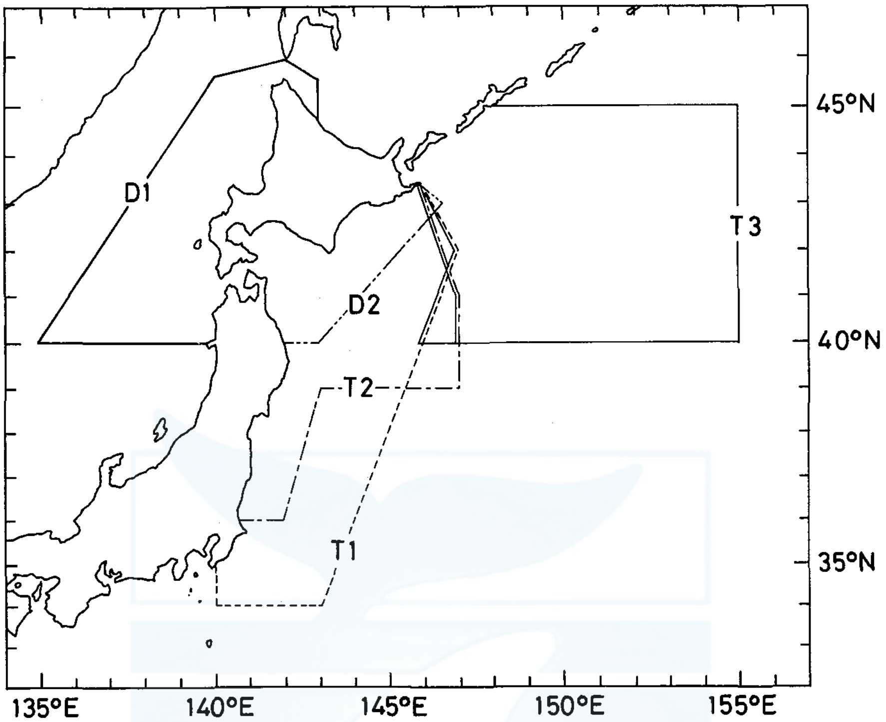

Fig. 9. Sub-areas defined to estimate the population of Dall's porpoises off Japan. D1, observed range of *dalli*-types in the Sea of Japan; D2, observed range of *dalli*-types off the Pacific coast of Japan; T1 and T2, observed ranges of *truei*-types off the Pacific coast of Japan; T3, known range of *truei*-type predominance but unsurveyed in the present study.

for *dalli*-type range and three for *truei*-type range) (Fig. 9 and Table 6) were defined to cover the whole range of Dall's porpoise sighting. Of these five sub-areas, four (D1, D2, T1 and T2) are areas covered by our sightings effort, but the remaining one (T3) is the unsurveyed area known to be inhabited by *truei*-types (see above). A minor modification is done for T3 to meet the boundary difference of T1 and T2. We have extrapolated the *truei*-type densities in the two surveyed sub-areas (T1 and T2) into the unsurveyed sub-area (T3) in order to obtain a rough estimate of the total population of *truei*-types. The methodological problem that surrounds this procedure will be discussed later.

School size

We used primary sightings of 143 *dalli*-type schools and 136 *truei*-type schools for the population estimate, but school size estimate was not available for one *dalli*-type school. There were three mixed schools of the two color types, and we regarded them as separate school for each color type.

TABLE 6. PARAMETERS FOR THE ESTIMATION OF DALL'S PORPOISE POPULATION IN THE SURVEYED AREA

Cruise number*	Sub-area	Period of data	Area (n. mile)^2	Transect length (n. mile)	no. of sightings**	Mean school size (c.v.)	Sighting rate*** (c.v.)
dalli-type							
4	D1	26 May – 11 June 1986	48,802	1,296	75	6.7 (0.07)	3.75 (0.19)
7	D2	7 July – 26 Aug. 1985	25,365	1,003	14	13.3 (0.19)	1.40 (0.40)
8	D2	16 Sep. – 30 Oct. 1985	25,365	1,398	17	9.6 (0.19)	1.36 (0.65)
9	D2	11 Sep. – 30 Oct. 1986	25,365	1,756	32	7.5 (0.16)	1.65 (0.33)
8+9	D2	11 Sep. – 30 Oct.	25,365	3,154	49	8.4 (0.13)	1.48 (0.30)
truei-type							
4	T1	2 May – 23 May 1986	93,718	2,296	68	6.4 (0.08)	2.92 (0.22)
5	T2	8 July – 3 Aug. 1984	74,311	1,124	35	3.5 (0.10)	2.94 (0.32)
6	T2	14 July – 3 Aug. 1983	74,311	836	33	9.7 (0.15)	3.95 (0.34)
5+6	T2	8 July – 3 Aug.	74,311	1,960	68	6.5 (0.13)	3.42 (0.24)

*: see Table 1. **: number of primary sightings; ***: number of primary sightings per 100 n. miles.

The size of 142 *dalli*-type schools ranged from one to 34 individuals, with the modal school size at four to six individuals in the three sub-area/cruises (Fig. 10). Mode was unclear in the Pacific sightings in sub-area D2. Mean school sizes of *dalli*-type were from 7.5 to 13.3 individuals in the Pacific sub-area D2 and 6.7 in the Sea of Japan sub-area D1. The first and last figures were significantly smaller than the largest figure for the Pacific sub-area (Mann-Whitney U-test, $p<0.04$), but other means were not significantly different each other ($p>0.19$).

The 136 primary sightings of *truei*-types ranged from one to 70 individuals (the second largest school was composed of 34 individuals). We excluded from the following analysis this largest school of 70 individuals recorded during the cruise no. 6 in sub-area T2, because we were uncertain if it was a real large school or included some nearby schools that should have been classified as secondary sightings. This exclusion decreased the mean school size from 11.5 (with the largest school) to 9.7 (used here). It could have also caused small degree of underbias in the population estimate (Tables 7 and 8) through the under representation of school density. However, we do not consider this effect very important, because the population estimate thus calculated still had extraordinarily large coefficient of variation (see below).

The modal figures of the *truei*-type school sizes varied between three to 10 individuals in the three sub-area/cruises (Fig. 10), and the mean values between 3.5 and 9.7 individuals (Table 6). Only the smallest mean school size (3.5 individuals) for cruise no. 5 in sub-area T2 was significantly smaller than any other values (Mann-Whitney U-test, $p<0.01$).

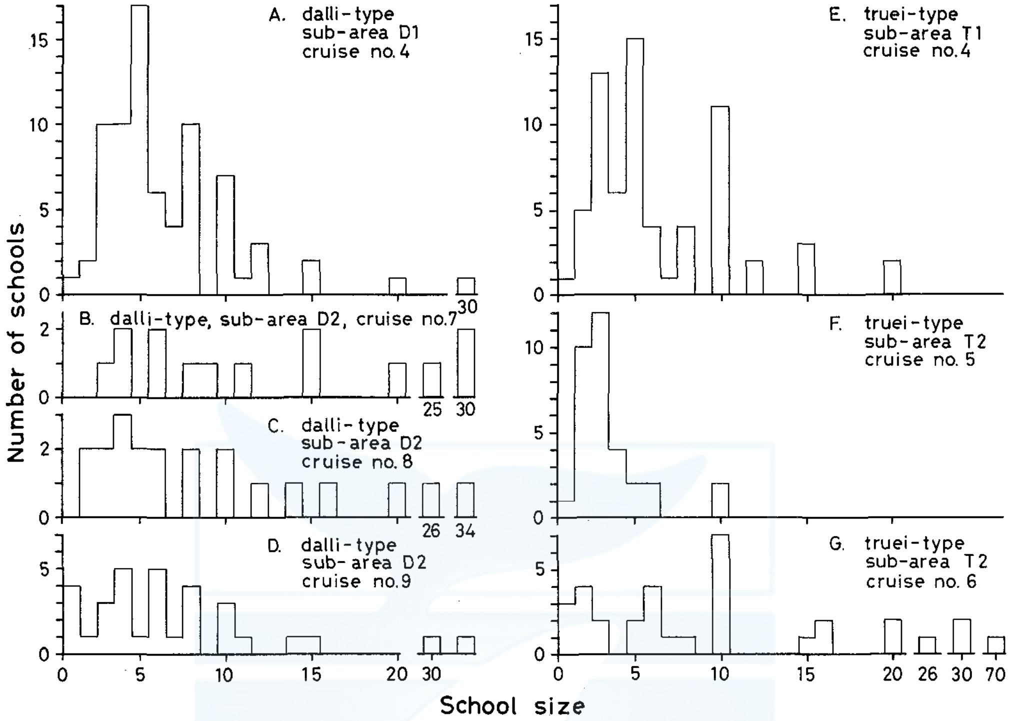

Fig. 10. School size composition of primary sightings of Dall's porpoises.

Sighting rate

The sighting rate (number of primary sightings per 100 n. m. of transect line) of the *dalli*-type schools was between 1.36 and 1.65 in the Pacific sub-area D2 (cruise nos 7, 8 and 9) and 3.75 in the Sea of Japan sub-area D1 (cruise no. 4) (Table 6). The figure for the Sea of Japan sub-area was significantly larger than any of the three corresponding figures of the *dalli*-type in the Pacific (Mann-Whitney U-test, $p<0.01$).

The three sighting rates for *truei*-type in the Pacific sub-area T1 and T2 ranged from 2.92 to 3.95 (Table 6), and the difference was not statistically significant (Mann-Whitney U-test, $p>0.14$).

Perpendicular distance

The distribution of perpendicular distances of *dalli*-type (Sea of Japan) and *truei*-type (Pacific) sightings during the cruise no. 4 (*Toshimaru No. 25*) had clear shoulder at 0.2 to 0.3 n. m. (Fig. 11 A and E), but different cruises by one vessel often had different distribution pattern as seen in the contrast between A or E and F or G in Fig. 11 (*Toshimaru No. 25* cruise). This suggests that the distribution pattern of the perpendicular distances is not dependent on the vessel but varies between cruises (presumably affected by observer or weather).

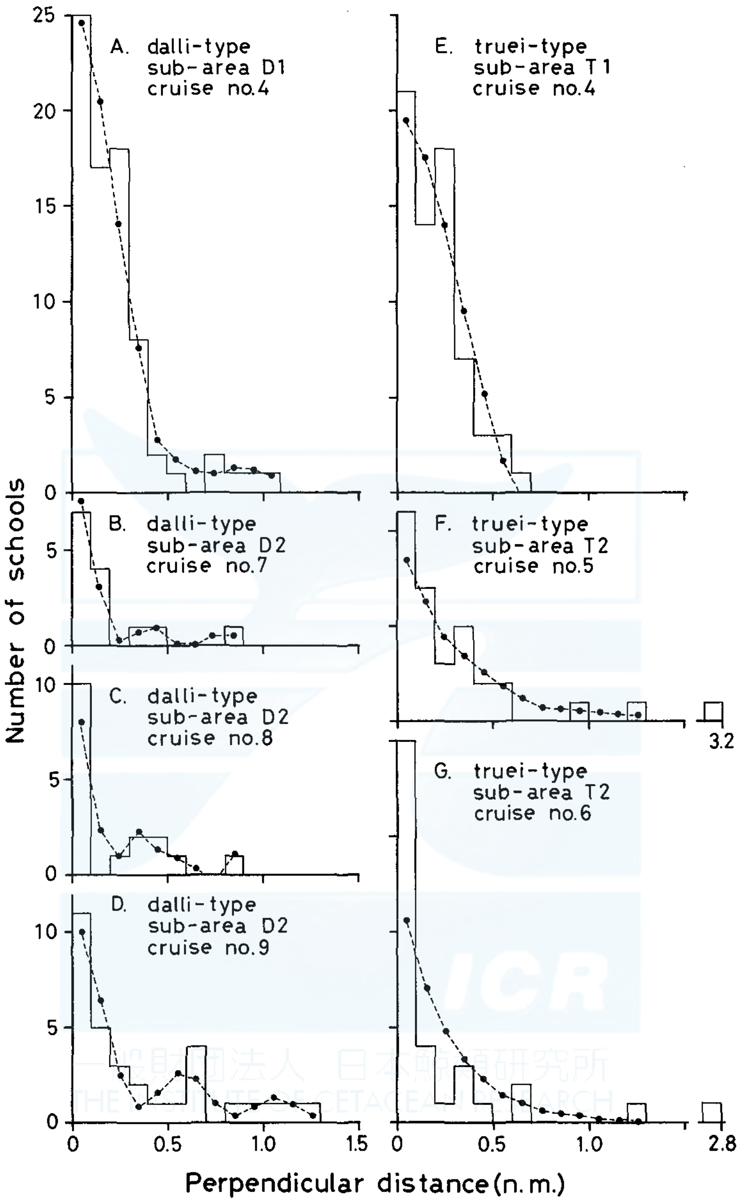

Fig. 11. Perpendicular distances of primary sightings of Dall's porpoises (white squares) and Fourier or negative exponential model fitted to them (closed circles and dotted line). For models used see Table 7.

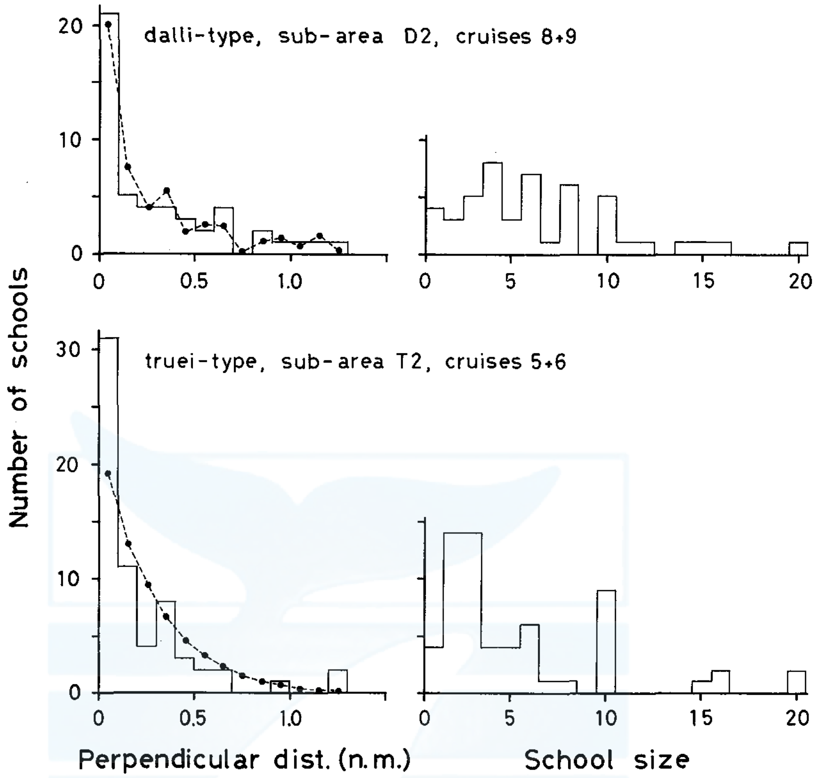

Fig. 12. Distribution of school size and perpendicular distance for *dalli*-types (sum of the cruise nos 8 and 9) and *truei*-types (sum of the cruise nos 5 and 6) off the Pacific coast of Japan. For marks see Fig. 11 and Table 7.

Population estimate

Either Fourier series or negative exponential model was selected for individual data set based on Chi-square goodness of fit test (Table 7). The Fourier series model showed better fit for *dalli*-type sightings in all sub-area/cruises and one *truei*-type data set (cruise no. 4, sub-area T1). Another *truei*-type data set (cruise no. 5, sub-area T2) showed better fit to the negative exponential model. And only negative exponential model could be successfully fitted to a *truei*-type data set in the Pacific sub-area T2 (cruise no. 6). The Fourier series model could not be fitted to this data set, because the terms of the Fourier series fit exceeded the number to satisfy the 'stopping rule' of Burnham, Anderson and Laake (1980).

Population of *dalli*-types in the Sea of Japan (for sub-area D1) was estimated at 31,789 individuals (with 95% confidence interval of 17,770 to 45,808) using data in May to June, 1986 (cruise no. 4) (Table 7). This value represents only a portion of the Sea of Japan-Okhotsk Sea stock of the Dall's porpoise (*dalli*-type), because it does not include individuals in the whole

TABLE 7. POPULATION ESTIMATE OF DALL'S PORPOISES IN THE SURVEYED AREA. f(0) WAS CHOSEN BY THE CHI-SQUARE FITNESS TEST

Cruise no. in Table 1	Sub-area	Period of data	f(0) (c.v. and model used)*	Chi-squ. goodness of fit**	Population size (c.v.)
dalli-type					
4	D1	May – June 1986	3.36 (0.09, FS)	0.816	31,789 (0.23)
7	D2	July – Aug. 1985	6.19 (0.24, FS)	0.600	14,579 (0.50)
8	D2	Sep. – Oct. 1985	5.69 (0.25, FS)	0.082	8,424 (0.72)
9	D2	Sep. – Oct. 1986	3.31 (0.21, FS)	0.430	5,737 (0.42)
8+9	D2	Sep. – Oct.	4.91 (0.19, FS)	0.247	8,126 (0.38)
truei-type					
4	T1	May 1968	2.94 (0.06, FS)	0.452	26,113 (0.25)
5	T2	July – Aug. 1984	2.88 (0.24, NE)	0.522	11,662 (0.41)
6	T2	July – Aug. 1983	3.87 (0.25, NE)	0.004	55,057 (0.45)***
5+6	T2	July – Aug.	3.36 (0.17, NE)	0.018	27,844 (0.32)***

*: FS, Fourier series model. NE, Negative exponential model.
**: probability of obtaining a deviation as great or greater than calculated Chi-square value.
***: low reliability due to poor model fit.

range of the stock considered to extend during the survey period to the Okhotsk Sea (Kasuya, 1978) and western part of the Sea of Japan (see Fig. 2) or to the Pacific coast of northern Japan (see above). At the time of the cruise (early June) the southern limit of distribution has already moved to 40°N from the southernmost limit at 35°N in winter season. The cruise (no. 4) proceeded from north to south against the seasonal movement of the Dall's porpoise (Fig. 2). This also could have caused some degree of underbias in the estimate of population size.

Three population estimates of *dalli*-types in the Pacific sub-area (D2) ranged from 5,737 to 14,579 individuals (Table 7), but none of these figures were statistically different ($p>0.33$). Since none of the parameters of *dalli*-type sightings during the two cruises of no. 8 and no. 9 in the Pacific sub-area D2 and in September and October, we combined the data to increase sample size and to decrease the confidence interval. The procedure gave *dalli*-type population of 8,126 with 95% confidence interval of 2,105 to 14,146 (Tables 6 and 7). This was not significantly different still from 14,579 estimated for July–August data of the same area. However, the September/October figure was only half of the July/August figure, and it is suggested that the difference may reflect in some degree the migration of the *dalli*-type individuals to the Sea of Japan in autumn (see above). Therefore, we considered that about 15,000 individuals of *dalli*-types in the Sea of Japan migrate through the Tsugaru Strait and spend summer off the Pacific coast of Japan. The rest of individuals in the stock will summer in the northern Sea of Japan or in the Okhotsk Sea (Kasuya, 1978).

The above population estimates of *dalli*-types in the Sea of Japan (D1) and Pacific (D2) area were made using data obtained in slightly different seasons of the year (late May to early June in the Sea of Japan, and early July to late August in the Pacific). Although there is some possibility that individuals counted in the Sea of Japan were again included in the population estimate for the Pacific area, we consider that the effect may not be very large compared with the individuals distributed in the western Sea of Japan or in the Okhotsk Sea far from the Hokkaido (Japanese) coast and excluded from the calculation. We note that the southern boundary of the Dall's porpoise in the Sea of Japan has almost passed the latitude of the Tsugaru Strait at the survey time in early June (Fig. 2). We have excluded some *dalli*-types found in the offshore unsurveyed *truei*-type area (T3), which belonging is still uncertain to us. Thus we consider that the currently available best figure of the minimum estimate of Sea of Japan-Okhotsk Sea stock of Dall's porpoises is about 46,000 (=31,789+14,579) individuals with 95% confidence interval of 26,290 to 66,445.

We obtained primarily three population estimates for *truei*-types in the surveyed area, one for May and two for July/August. Although their range was wide (11,662 to 55,057 individuals, Table 7), none of them were statistically different from others ($p>0.14$). Although the mean school sizes were different between the two cruises (nos 5 and 6) conducted in the same season (July/August) and in the some sub-area T2, we combined these data as in the *dalli*-type case (cruise nos 8 and 9) to improve the estimate of *truei*-type population size. This procedure provided an estimate of 27,844 individuals with 95% confidence interval of 10,380 to 45,308 (Tables 6 and 7). This figure (July/August, sub-area T2) is not significantly different from 26,113 (with 95% confidence interval of 13,522 to 38,704) estimated using May data in the sub-area T1.

Above estimates of *truei*-type population do not include individuals known to be distributed in their summering ground outside the present survey area. Extrapolation of the density data corresponding to the above three estimates to the unsurveyed area almost doubles the estimation of *truei*-type population (Table 8). This procedure assumes equal Dall's porpoise density in any particular moment for both surveyed and unsurveyed part of the sea. Table 9 compares, using data listed in Fig. 12, Dall's porpoise density between offshore and inshore Pacific areas off the northern Japan, which roughly correspond to T3 and T1 or T2 of this study, respectively. The ratios of *truei*-types: *dalli*-types in each of the area are 190:59 (northern offshore area), 186:51 (northern inshore) and 52:11 (southern inshore), and the *truei*-type proportion ranged from 76 to 82% showing no significant difference between the three areas. The density of Dall's porpoises were almost same between two northern areas while that in the southern area was lower than the two.

These suggest that the Dall's porpoise density in the present surveyed areas (T1 and T2) is almost same with that in unsurveyed area (T3) if averaged

TABLE 8. *TRUEI*-TYPE POPULATION ESTIMATES EXTRAPORATED TO UNSURVEYED AREA OF THE NORTHEASTERN PORTION OF THE RANGE (T3*)

Cruise no.	Month	Population in surveyed area	Unsurveyed area of distribution (n. mile^2)	Population in unsurveyed area	Total population
4	May	26,113	113,834	31,718	57,831
5	July – Aug.	11,662	112,852	17,710	29,372
6	July – Aug.	55,057	112,852	83,612**	138,669**
5+6	July – Aug.	27,844	112,852	42,235**	69,779**

*: see Fig. 9 for range.

**: low reliability due to poor model fit.

over months (May through September) and years (5 seasons). However, this does not necessarily imply that the densities of *truei*-types in the northern inshore and offshore areas are same in any particular month or year. Rather, we consider that the number of *truei*-types in the inshore area and that in the offshore area are negatively correlated, and that the densities are also dependent each other. Therefore, the estimates of *truei*-type population in the unsurveyed area thus extrapolated can be biased to the same direction as that in the surveyed area, and the bias can be amplified in the total population estimate. We feel that two extreme estimates of the total *truei*-type population in Table 8 (29,372 for cruise no. 5 and 138,669 for cruise no. 6) have higher probability of being far from the true figure than other figures. Additionally two figures in Table 8 using the cruise no. 6, i.e. 138,669 and 69,779, have lower reliability due to the poor goodness of fit of the model (Table 7). Only remaining estimate is 57,831 based on the cruise no. 4 in May 1986. As the conclusion, we consider that the population of the *truei*-type will be about 58,000 individuals. The confidence interval can not be estimated, but the c.v. has to be over 0.25 the figure calculated for surveyed area.

DISCUSSION

We made two assumptions in the present population estimate. They are (1) all the Dall's porpoises on the trackline are counted, and (2) Dall's porpoise schools do not respond to vessels. If Dall's porpoise schools respond to an approaching research vessel by moving toward or away from the vessel before the schools are detected by researchers the population estimate of the present study will be seriously under or over biased, respectively (Hammond, 1986). The response of the species to the vessel was investigated using helicopters (Bouchet, Braham and Tsunoda, 1983), and there was an attempt to calculate the correction factor (0.22–0.41) for the attraction of porpoises to the vessel (Turnock, 1987). However, the species could be either attracted to the vessel, neutral, or avoid the vessel depending on the area, season, growth stage, sex,

TABLE 9. GEOGRAPHICAL COMPARISON OF THE DALL'S PORPOISE DENSITY BASED ON DATA IN FIG. 8

Area	School density			Porpoise density		
	no. school sighted	transect length in n.m.	density /100 n.m.	no. individuals	transect length in n.m.	density /100 n.m.
Northern offshore*	30	815	3.7	116	755	15.4
Northern inshore**	84	1,111	7.6	364	976	36.9
Southern inshore***	135	1,777	7.6	389	1,435	27.1

*: 40°–45°N, 147°–155°E. **: Pacific area north of 40°N and west of 147°E. ***: Pacific area between 38° and 40°N, and west of 155°E.

and reproductive status (Kasuya and Jones, 1984). Therefore we felt it risky to use the above correction factor without further observation of the porpoise behavior. If we missed some individuals on the trackline, which we believe very possible especially for individuals that avoid vessels, it could have caused an underestimate. Additionally, present estimate of the Dall's porpoise population will also include possible underbias due to rounding of the sighting angle and radial distance (Buckland and Anganuzzi, 1987), which have not been considered in the present study.

Using sighting data obtained from the salmon research vessels cruising from Hokkaido to northern North Pacific in April to August (mainly June and July), Kato (1986) estimated the Dall's porpoise population of both color types in his *truei*-type area (40°–44°N, east of 155°E, which is slightly smaller than corresponding area of the present study), as about 64,000 individuals. Although Kato (1987) added 1986 data to the previous data set, expanded the southern range to 38°N (where some sighting efforts existed as well as the distribution of Dall's porpoises), and obtained the estimate of 125,000, this will be an overestimate due to the extrapolation of northern high density to southern low desnity area (Table 9). Our estimate of the Dall's porpoise in the similar area, 72,410 individuals (57,831 *truei*-types plus 14,579 *dalli*-types) is close to Kato (1986).

Our sighting survey confirmed results of previous studies on the general pattern of distribution of two color types of Dall's porpoises in the Japanese coastal waters, i.e. Sea of Japan and southern Okhotsk Sea inhabited by *dalli*-types, and the Pacific coast of northern Japan and southern Kuril Islands by both *dalli*- and *truei*-types.

Although the previous studies (Kasuya, 1978, 1982) have assumed without firm data that the majority of Dall's porpoises that summer off the Pacific coast of northern Japan would be *truei*-types, the present study showed that the assumption was not always correct. Dall's porpoises which winter off the Pacific coast of northern Japan south of 40°N are composed mainly of *truei*-types (Kasuya, 1978, and also see below). They migrate in late summer and autumn to waters between 40° and 45°N and east of 145°E, and almost disappear from the Japanese coastal waters for some short period in September/October. We cosidered that their southbound migration probably start in October.

The Pacific coastal waters off Sanriku (38°–41°N) and southern Hokkaido (41°–43°N) are occupied mostly by *dalli*-types while *truei*-types are summering in an offshore northern area. This agrees with the fact that the Dall's porpoise catches of hand harpoon fishery which was landed in October and November at Otsuchi (39°20′N) and Yamada (39°30′N) Fish Markets on the Sanriku coast and reportedly caught off the Pacific coast of Hokkaido were mainly (87%) *dalli*-types (Anon., 1985b; N. Miyazaki, per. commn in 1986), but those taken off the Sanriku coast in January to March and landed at the same fish markets were mostly (96%) *truei*-types (Anon., 1985b; Kasuya, 1978). Such high *dalli*-type proportion was also confirmed in early November 1986 by one of the authors (T.M.) on the Kamaishi Fish Market (39°15′N) on the Sanriku coast.

Hand harpoon fishery for the Dall's porpoise had been operated only in winter season and off the Sanriku coast (Kasuya, 1978; 1982), and the annual catch during the 1960s and 1970s fluctuated between 5,000 and 9,000 individuals with the annual mean of 6,000 individuals (Kasuya, 1982). Kasuya (1978) considered on the *truei*-type stock that the population of 125 to 400 thousands will be required to sustain the mean annual take. The corresponding net annual recruitment rates were 0.048 to 0.015. The maximum net recruitment rate (R_{max}) of the offshore stock of *dalli*-type Dall's porpoise has been estimated to be 0.09 (Hester, 1986), 0.08 (Ohsumi, 1986), or 0.06 (Jones, Breiwick, Bouchet and Turnock, 1986). Although these estimates will need further improvement with improved biological parameters or refined model, it will be too optimistic to consider that the *truei*-type stock can sustain the annual take of over 10% of the population. If the present population of 60,000 individuals is not large enough to sustain the past level of the annual catch, then it means that the population has declined by the past catch. Although our data are unable to prove the past decline of the stock, we believe that such change could have occurred in the population.

Some fishermen from Iwate Prefecture (part of the Sanriku area) started in recent years the operation during other seasons and in other areas such as Sea of Japan off Akita Prefecture (41°N), off the Pacific coast of Southern Hokkaido, and in the southern Okhotsk Sea (Anon., 1985b; Kawamura *et al.*, 1983; Kasuya, unpublished), while operating the fishery off the Sanriku coast in winter as before. This expasion of fishery was due to the increased demand of porpoise meat. The total annual catch increased to around between 10,000 and 13,000 individuals, and there has been expressed a great concern on the effect of the catch on the Dall's porpoise populatin (IWC, 1984).

The results of the present study indicate that the recent hand harpoon fishery in northern Japan for the Dall's porpoise hunts *truei*-type population off the Pacific coast of Japan during winter and *dalli*-types in the Sea of Japan-Okhotsk Sea stock in summer operation. Available statistics of the fishery do not give the catch by color type or by month. With the absence of catch statistics by stock or any other alternative way to estimate it, we find it impossible to assess the effect of the current fishery on the Dall's porpoise stocks. However, it should be stressed that the current catch of Dall's porpoises by the Japanese harpoon fishery is still over 10% of the total number of Dall's porpoises known to migrate annually to the fishing grounds, i.e. 104,199 individuals (46,368 *dalli*-types plus 57,831 *truei*-types), and that there is a great risk of further depletion of one or more stocks of the species by the fishery.

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SEALS IN LOCH NESS

GORDON R. WILLIAMSON*

ABSTRACT

A Common or Harbour Seal *Phoca vitulina* L. lived in Loch Ness, Scotland, for seven months from November 1984–June 1985. Photographs of the seal are presented. This is the first time a seal has been proven in Loch Ness. Fishermen's reports indicate that Loch Ness is visited by a seal approximately once every two years.

INTRODUCTION

Loch Ness is one of Britain's largest and deepest freshwater lakes. It is long, narrow, deep and straight 38 km long, 1.7 km wide and 230 m deep, is 16 m above sea level and is connected to the sea by the 12-km-long River Ness. It lies in the valley of a former glacier. Many salmon *Salmo salar* L. migrate through Loch Ness. The temperature of Loch Ness surface water ranges 4–12°C (Wedderburn, 1907). The ecology of Loch Ness is described by Maitland (1981).

Common or Harbour Seals *Phoca vitulina* L. have a well-known habit of exploring up rivers and in northern Canada permanent populations of Common Seals live in freshwater lakes 300 km inland from the sea (Mansfield, 1967; Hewer, 1974; King, 1983). About 100 seals, both Common Seals and Grey Seals *Halichoerus grypus* Fabricius, live in the sea near Inverness. Individual seals of both species can regularly be seen 1 km up the River Ness in the middle of Inverness town, especially at high tides. There have been several reports of a seal in Loch Ness (Anon, 1933; 1934; 1934) and beyond Loch Ness in the River Oich (Harvie-Brown and Buckley, 1895, p183), but these reports were not supported by photographs and were not believed.

OBSERVATIONS AND DISCUSSION

Between November 16, 1984 and June 11, 1985, a seal was seen in Loch Ness by myself and other people. Photographs were taken (Figs 1 and 2). The seal was identified as a Common or Harbour Seal *Phoca vitulina* by its head profile, with turned-up nose by its grey colour with black spots and by its estimated length of 1.8m. The other species of seal found around Scotland, the Grey Seal, has a long straight nose, like an Alsatian dog.

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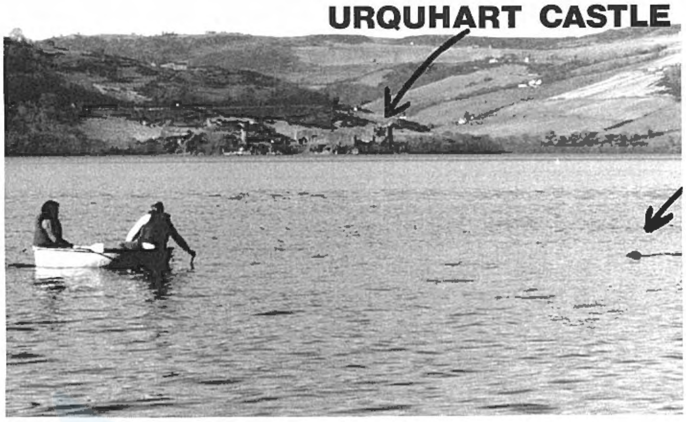

Fig. 1. Seal in Loch Ness with Urquhart Castle. February 27, 1985.

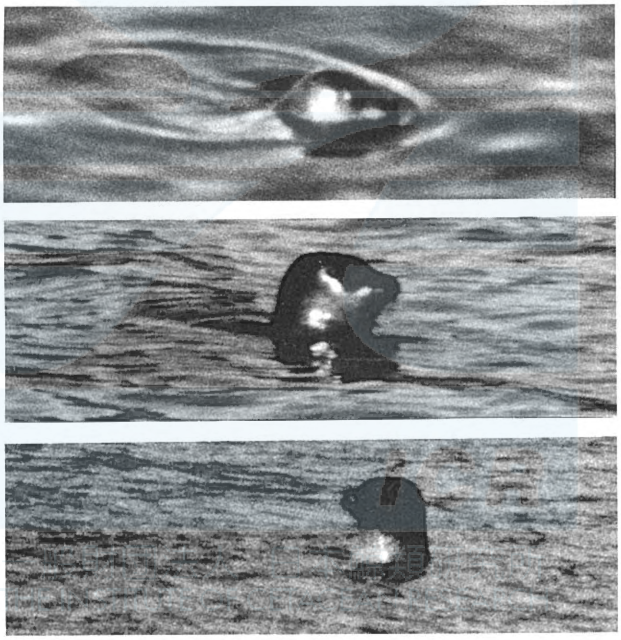

Fig. 2. Common Seal in Loch Ness. February 27, 1985.
Above: seal in natural swimming position.
Centre and below: seal with head raised in response to a low whistle sound made by me.

The seal spent most of its seven months living on the south side of Loch Ness opposite Urquhart Castle (Fig. 3). However, the seal was seen in many parts of Loch Ness, including Fort Augustus 48 km from the sea. The seal was seen in the river exit of Loch Ness at Lochend on four separate occasions (Dec. 1, Dec. 21, Jan. 13, Feb. 8) yet it did not descend the river to the sea.

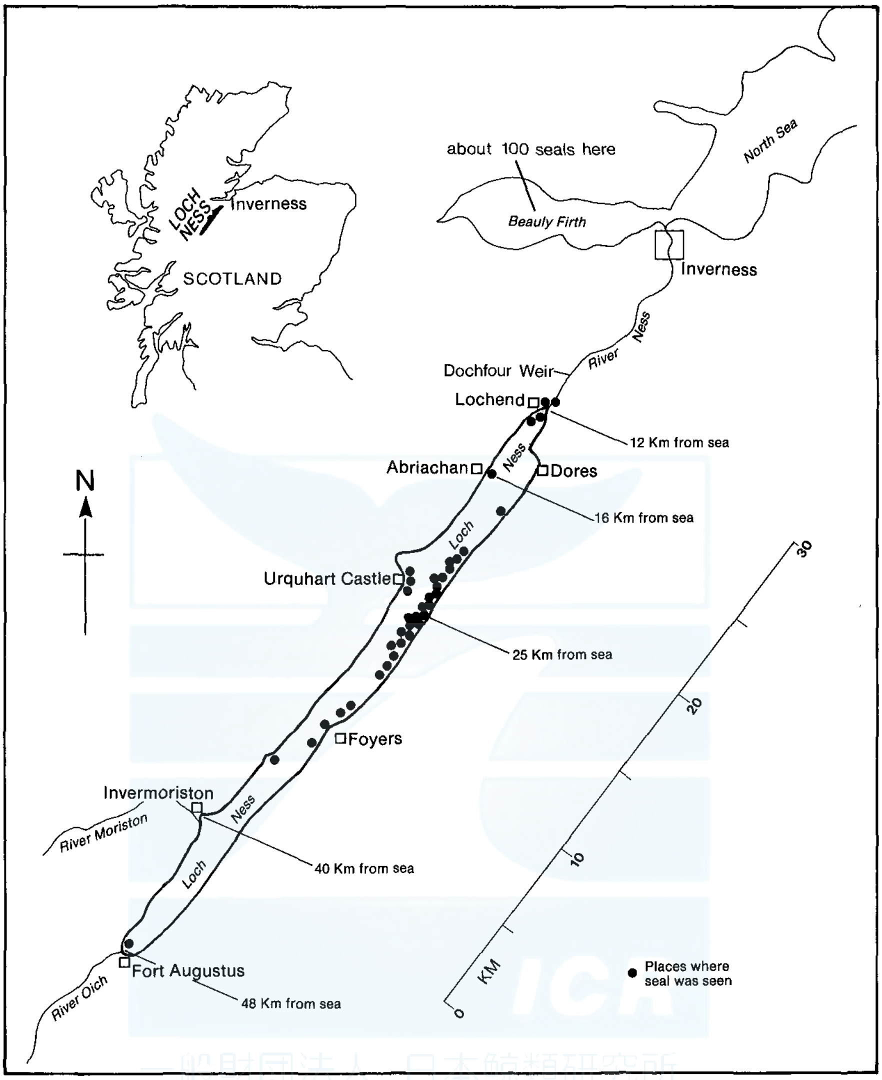

Fig. 3. Loch Ness showing places where the seal was seen.

This suggests that the seal "knew" where it was, was not "lost", and that it deliberately remained in Loch Ness. The seal appeared to be in vigorous good health throughout its stay in Loch Ness. The seal was shot on June 11, 1985.

About 30 people reported about 60 separate sightings of the seal to me. Of these 30 observers, twenty-eight were local people who had close contact with the surface of Loch Ness – either fishermen in salmon-trolling boats or people who lived beside Loch Ness. Of the hundreds of thousands of people, locals and visitors, who drove along the roads beside Loch Ness during the 7-month period, only two (that I know of) – a pair of Australian tourists at

Fig. 4. Seal making successive jumps, as seen by fisherman Mr Gerry Breau.

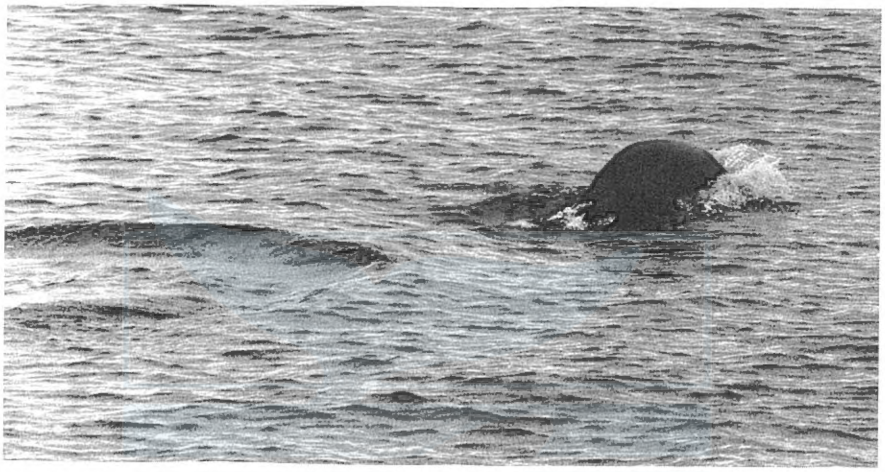

Fig. 5. A Common Seal jumping in sea near Orkney Islands. Photograph by Paul Thompson.

Urquhart Castle – noticed the seal. Common Seals spend only about 20% of the time at the surface, and make dives of 3–8 minutes duration (P. Thompson, pers. commn). Conclusion: in Loch Ness it is very hard to notice such a small animal as a seal unless you spend many hours close to the water. While at the surface, the seal breathed in and out about 24 times per minute (measured by observing the rise and fall of its back when the seal was floating horizontally).

The seal often followed the boats of salmon fishermen who troll along the sides of the Loch, often following a boat for half an hour, to the annoyance of the fishermen. One day fisherman Mr Gerry Breau accelerated his boat to try to get away from the seal, and the seal chased after the boat at top speed, leaping out of and into the water ten successive jumps like a porpoise (Fig. 4). However, this behaviour was only seen on one occasion.

Fishermen and river bailiffs informed me of the following sightings of seals in Loch Ness during recent years:

1972–80: About 4 seals seen in various parts of the Loch, including 2 together at mouth of River Moriston.
1981 April–August: 1 seal seen at mouth of River Moriston.
1984 November–June 1985: 1 seal seen in many parts of Loch (this report).

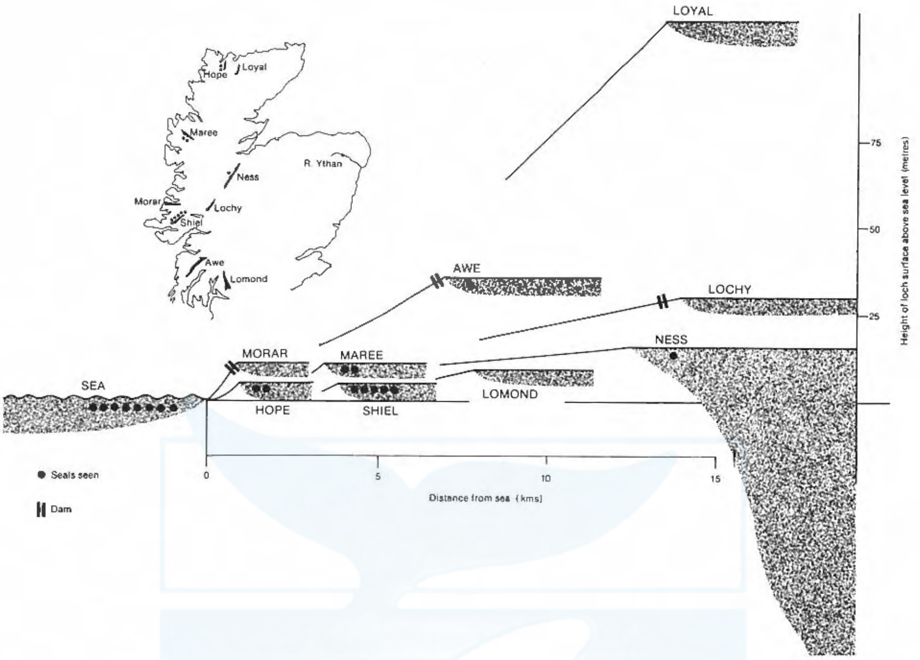

Fig. 6. Distribution of seals in Scottish lochs, probably *Phoca vitulina*.

1985 October: An adult and a 4-month-old young Common Seal seen together at Dochfour Weir and near Foyers (identified from photographs taken by Mr John Bailey).

This totals about 8 seals in 15 years (1972–86): an average of one seal entering Loch Ness every two years. Two seals together were seen on two occasions. The number of seals reported by individual fishermen varied greatly: one man had seen six seals during the period, some men have never seen a seal yet.

Seals in Loch Ness lived in good health and the place at which seals were most commonly seen was the mouth of the River Moriston (Fig. 3), although the present seal was not seen there. Seals lived in Loch Ness for up to seven months. What finally happens to seals that enter Loch Ness? Local men told me that several seals have been shot by salmon fishermen. One rainy January day some years ago when the River Ness was in spate, a big seal was seen swimming down the River Ness at Dochgarroch near Dochfour. It seems that most seals that enter Loch Ness get shot, but a few return to the sea.

A seal making successive jumps, especially if seen silhouetted against the setting sun, etc. could well look like a many-humped serpent or monster (Figs 4–5). Perhaps a proportion of sightings of the "Loch Ness Monster" and other "sea-serpents" may be sightings of jumping seals. A successive-jumping seal looks more like a "sea-serpent" than a dolphin: a seal jumps equal-length jumps in fast close-spaced rhythm; whereas a dolphin jumps regularly and the jumps are spaced further apart.

The distribution of seals in the larger Scottish lochs is shown in Fig. 6 and was discovered by interviewing fishermen and river bailiffs etc. In near-to-the-coast Loch Shiel, Hope and Maree, seals are seen as follows:

L. Shiel : one or two seals seen most years, may stay several months, once five seals seen together.
L. Hope : one seal six weeks in loch June–July 1983, one definite Grey Seal one month in loch August 1984.
L. Maree: one seal seen 1981, five seals seen Sept–Oct 1983.

In lochs which have hydroelectric dams blocking their outlet river, such as Lochs Morar, Lochy and Awe, seals are not seen. In former times in Loch Awe, however, when the outlet river flowed freely to the sea, seals were seen: "The seal comes up from the ocean, through a very rapid river, into Loch Awe in quest for salmon, and retires to the sea at the approach of winter". (Anon, 1793, p260). "For ten years, up to 1883, we saw one or more seals in Loch Awe almost every year, most frequently in the Autumn, but also in April in some years". (Harvie-Brown, 1891). In Loch Lomond, which is near the sea and whose river is unobstructed, seals have not been reported (P.S. Maitland pers. commn): perhaps the industrial pollution in the Firth of Clyde during the past century is the cause.

The former occurrance of seals in Loch Awe is interesting for it proves that seals can ascend rivers at least four times steeper than the R. Ness (slope of R. Awe 5.1m/km, R. Ness 1.3m/km). (Fig. 6).

In rivers on the east coast, the furthest upstream places and distances above tidewater at which individual seals have been seen are:

R. Spey : Aberlour 27 km
R. Deveron : Bridge of Marnoch 30 km
R. Ythan : Fyvie 37 km (A young Common Seal was photographed Nov. 30, 1984).
R. Don : Grandholme Works 2 km (Industrial pollution and weirs in river).
R. Dee : Park Inn Pool, Drumoak 19 km
R. Tay : Caputh 24 km.

CONCLUSION

The data presented prove that a Common or Harbour Seal lived in Loch Ness during seven months of 1984–85, indicate that Loch Ness is entered by a seal about once every two years, and prove that a seal can live for many months in Loch Ness. The route of entry of a seal must be from the sea up the River Ness. These data suggest that past reports of seals in Loch Ness were true and that seals have probably been visiting Loch Ness for thousands of years.

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