

# IMMUNOGENETIC AND MARKING APPROACHES TO IDENTIFYING SUBPOPULATIONS OF THE NORTH PACIFIC WHALES<sup>1)</sup>

KAZUO FUJINO

To identify local subpopulations of whales, various methods have been applied. These include indirect methods basing upon oceanographic information, seasonal change of localization of whaling grounds and catch statistics, parasitological analysis, and direct methods of morphological and marking investigations. Recently another method using ecological characters was adopted to analyse mingling of southern humpback populations (Chittleborough, 1959).

Morphological and marking investigations are most frequently utilized among these. Most morphological characteristics are controlled with polygenic system and are apt to be affected by non-hereditary factors during growth of individuals, so that discrimination of different populations may sometimes run into difficulties. On the other hand, marking investigation gives the most definite informations about movements of marked whales. To deduce, however, distribution of general population to which marked whales are belonged, effects of various conditions when marked or recaptured and of ecological factors should be discussed.

From these reasons, another method of population genetics might bring more useful informations. In this method, some characters which are controlled with comparatively simple allele system, such as blood groups in human (Boyd, 1950) (Race & Sanger, 1954), in cattle (Owen, Stormont & Irwin, 1947), in fowl (Brile *et al.*, 1958) and pigmentations in insect (Komai, Chino & Hoshino, 1956) are used as genetic marker.

Recently serological characters have been utilized as 'genetic marker' to identify intraspecific subpopulations of marine animals commercially valuable in fisheries. These include studies on tuna (Cushing, 1956; Suzuki *et al.*, 1959), salmon (Takahashi & Suyehiro, 1957; Ridgway, Cushing & Durall, 1958), Pacific sardine (Sprague, 1959), Atlantic herring (Sinderman, 1959), fur-seal (Fujino & Cushing, 1960) and whales (Fujino, 1956; Cushing, Fujino & Takahashi, 1959).

In the present paper serological basic studies on whales, carried out since 1952, are summarized and analysis of raiation of the North Pacific finback whales by means of population genetics with blood group and

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marking investigations are discussed with attention to complementary relationships between these two methods.

#### BASIC PROBLEMS IN SEROLOGY

To identify whale populations by means of blood typing investigation, not only analysis of serological characteristics of themselves but also standardization of experimental methods and materials should be undertaken. Results of discussion on these technical problems are described in the following section. Other general methods used in successive sections are same as those in the literatures cited there.

*Technical problems, especially preserving methods of materials and blood typing with preserved materials*

a) Glycerol-freezing preservation technique of intact erythrocytes. Race and Sanger (1954) stated about studies on glycerol-freezing technique, 'There seems general agreement that antigens are well preserved at least up to a year and probably much longer. The method has been of great use in keeping available samples of blood representing rare genotypes'. Cushing *et al.* (1959) reported an application of this technique on marine animals of which sterile precautions are not available. After collecting blood samples are added equal volume of a mixture of four parts of glycerol and six parts of five percent sodium citrate solution (additional antimicrobial of guanofuracin was used at a concentration of 200 mg per liter against accidental warming), and then the mixture are kept frozen.

After transportation to laboratory, frozen samples are thawed under running water and are dialysed against 1.5 percent saline for two hours, and are washed several times with saline. Then the cells available for test will be obtained in good yield. All blood samples of finback and humpback whales, collected in 1958 and 1959, were analysed through this technique.

b) Blood typing of dried erythrocytes with  $^{131}\text{I}$ -labelled antibody. Fujino & Cushing (1959) developed another blood typing technique using dried erythrocytes and radioactive antibodies. Outlines of this technique are as follows. After being diluted one in ten with saline, one drop of fresh blood sample is dried on stripe of filter paper and is preserved in desiccator. Then  $^{131}\text{I}$ -labelled antibody is diffused on the filter paper with solvent of four per cent ammonium sulfate through the erythrocytes. Specific radioactivity on blood spot shows positive reaction between antibody and corresponding erythrocytes. According to their conclusive description, this technique will be useful in blood-typing of dried erythrocytes, but there are still general problems about preparation of

samples before applying to large scale of investigation.

c) Preservation of blood typing reagents. To undertake blood typing investigation of marine organisms in relation to fisheries problems, large number of sample should be tested for a long period. For this purpose it is desirable to use same standard reagents during a series of investigation. In past time many workers used formalin, merthiolate, carbolic acid and sodium azide as preservative of serum. While Race & Sanger (1954) stated that reagents for human blood typing can be preserved for long time by freezing at a temperature of  $-20^{\circ}\text{C}$  without preservative. As blood typing of marine animals, however, is sometimes carried out in field laboratory, it is required to add preservative to serums against warming during transportation. In practical, after inactivation serum reagents are added 1/10 volume of five per cent of carbolic acid or one per cent of sodium-azide, and are kept frozen at temperature  $-15$  or  $-20^{\circ}\text{C}$ . Another series of reagents divided from original serums have been kept frozen at same temperature without preservative for use in central laboratory. No significant differences in specificities and titers has been recognized between both series of reagents even after three years' preservation so far.

#### *Classification and genetics of blood group*

Agglutination or hemolysis reaction with immune antibody, isohemagglutinin and natural antibody are used for detecting blood group antigens. Summarized results of blood typing on four species of baleen whales and three species of toothed whales detected so far are shown in Table 1. Details by species will be described in following paragraphs.

a) Blue-white dolphin, *Stenella caeruleo-albus*<sup>1)</sup>. Two kinds of antigens are detected by agglutination and hemolysis reactions with rabbit immune serums, and isoagglutinins specific to these two antigens are found in low frequency (Yamaguchi & Fujino, 1953). Parenthesized figures in Table 2 show expected frequencies of occurrence of phenotypes calculated through hypothetical two allele system on population in Hardy-Weinberg's equilibrium.

It is not clear at present whether discrepancies between expected figures and observed those are caused by scantiness of samples tested or in compatibility of the allele system adopted.

Another kind of agglutinogen was detected in S. 23 dolphin cells, and occurred one out of ten individuals tested. No information on genetics on this antigen has not been obtained so far (Cushing, Fujino & Takahashi, 1959 ; Fujino & Cushing, 1959).

<sup>1)</sup> More recently these common name and scientific name are used for this species which blood typing were reported by Yamaguchi and Fujino (1953).

TABLE 1. BLOOD GROUPS IN VARIOUS SPECIES OF WHALES

Classification of whales	Whale species		Blood groups			Literature
	Common name	Scientific name	Phenotype	Detecting method of antigens		
Toothed whale	Blue-white dolphin	<i>Stenella caeruleo-albus</i>	Dc <sub>1</sub> Dc <sub>2</sub> , Dc <sub>1</sub> , Dc <sub>2</sub>	Agglutination and hemolysis reactions with immune antibodies	Yamaguchi & Fujino (1952)	
	Baird-beaked whale	<i>Berardius bairdii</i>	{ Br <sub>1</sub> Br <sub>2</sub> , Br <sub>1</sub> , Br <sub>2</sub> Pb <sup>+</sup> , Pb <sup>-</sup>			Fujino (1954)
	Sperm whale	<i>Physeter catodon</i>	{ P <sub>c1</sub> P <sub>c2</sub> , P <sub>c1</sub> , P <sub>c2</sub> Sp <sup>+</sup> , Sp <sup>-</sup>			Fujino (1953)
Baleen whale	Bryde whale	<i>Balaenoptera edeni</i>	Bb <sub>1</sub> <sup>+</sup> , Bb <sub>1</sub> <sup>-</sup> and Bb <sub>2</sub> <sup>+</sup> , Bb <sub>2</sub> <sup>-</sup>	Ditto and isoagglutination	Fujino (1953)	
	Fin whale	<i>B. physalus</i>	{ Bp <sub>1</sub> <sup>+</sup> , Bp <sub>1</sub> <sup>-</sup> and Bp <sub>2</sub> <sup>+</sup> , Bp <sub>2</sub> <sup>-</sup> Ju <sub>1</sub> Ju <sub>2</sub> , Ju <sub>1</sub> , Ju <sub>2</sub>			Agglutination reaction with immune and natural antibodies
	Blue whale	<i>B. musculus</i>	Bm <sub>1</sub> <sup>+</sup> , Bm <sub>1</sub> <sup>-</sup> and Bm <sub>2</sub> <sup>+</sup> , Bm <sub>2</sub> <sup>-</sup>	Agglutination and hemolysis with immune antibodies and isoagglutination	Fujino (1953)	
	Humpback whale	<i>Megaptera nodosa</i>	{ Mn <sub>1</sub> <sup>+</sup> , Mn <sub>1</sub> <sup>-</sup> and Mn <sub>2</sub> <sup>+</sup> , Mn <sub>2</sub> <sup>-</sup> 1, 2, 3, 4			Agglutination with anti-finback Ju immune and natural antibodies

TABLE 2. FREQUENCY OF OCCURRENCE OF BLOOD TYPES OF BLUE-WHITE DOLPHIN

Blood type	Male	Female	Sum
Dc <sub>1</sub>	.200	.187	.194 (.235)
Dc <sub>1</sub> Dc <sub>2</sub>	.500	.688	.583 (.500)
Dc <sub>2</sub>	.300	.125	.223 (.265)
No. of whales observed	20	16	36

b) Bairied-beaked whale, *Berardius bairdii*. Three kinds of antigens Br<sub>1</sub>, Br<sub>2</sub> and Pb are found by agglutination and hemolysis reactions with immune rabbit serums. According to phenotypic relationships Pb antigen seems to occur independently to Br<sub>1</sub> and Br<sub>2</sub> antigens. Frequencies of occurrence of phenotypes are shown in Table 3. Parentages of blood types are tested on two pairs of cow and fetus.

TABLE 3. FREQUENCY OF OCCURRENCE OF BLOOD TYPES OF BAIRD-BEAKED WHALE

Blood type	Male	Female	Sum	
Br system {	Br <sub>1</sub>	.820	.750	.804
	Br <sub>1</sub> Br <sub>2</sub>	.103	.083	.098
	Br <sub>2</sub>	.077	.167	.098
	No. of whales observed	39	12	51
Pb system {	Pb present	.125	.000	.100
	Pb absent	.875	1.000	.900
	No. of whales observed	32	8	40

After being tested with agglutination-inhibition reaction, blood types both of male fetus 8 feet 3 inch. long taken from 37 feet cow and of female fetus 8 feet 7 inch. long taken from 36 feet cow were identified as Br<sub>1</sub>Pb<sup>-</sup> which are same as those of their cow (Fujino, 1954).

Informations on isoagglutinin and allele system of three antigens have not been obtained yet.

c) Sperm whale, *Physeter catodon*. Three kinds of antigens of Pc<sub>1</sub>, Pc<sub>2</sub> and Sp are found by agglutination and hemolysis reactions with

TABLE 4. FREQUENCY OF OCCURRENCE OF BLOOD TYPES OF SPERM WHALES

Blood type	Male	Female	Sum	
Pc system {	Pc <sub>1</sub>	.400	.313	.346
	Pc <sub>1</sub> Pc <sub>2</sub>	.300	.313	.308
	Pc <sub>2</sub>	.300	.374	.346
Sp system {	Sp present	.400	.500	.462
	Sp absent	.600	.500	.538
No. of whales observed	10	16	26	

immune rabbit and fowl serums. According to phenotypic relationships, antigen Sp belongs into different allele system from those which antigens Pc<sub>1</sub> and Pc<sub>2</sub> are concerned. Frequency of occurrence of phenotypes is shown in Table 4.

Natural antibody specific to Sp antigen is detected in the serums of sei whales, *Balaenoptera borealis* and agglutinates Sp positive cells up to dilution of one in eight or one in sixteen (Fujino, 1954). No available data about isoagglutinin specific to known antigens and allele system has been obtained yet.

d) Bryde whale (Ogasawara whale), *Balaenoptera edeni*<sup>1)</sup>. Two kinds of blood group antigens Bb<sub>1</sub> and Bb<sub>2</sub> are detected by immune rabbit agglutinins and hemolysins in the Bryde whale taken from Bonin Islands' area, and occur as shown in Table 5 (Fujino, 1953). Sufficient data discussing on allele system of both antigens are not obtained yet. According to phenotypic relationships, however, antigens Bb<sub>1</sub> and Bb<sub>2</sub> seem to be controlled by different allele systems each other. No agglutinin, which has sufficient high titer and specificity to identify the known antigens, has been positively detected yet.

TABLE 5. FREQUENCY OF OCCURRENCE OF BLOOD TYPE ANTIGENS OF BRYDE WHALE<sup>1)</sup>

Present or absent of antigen	Male	Female	Sum	
Bb <sub>1</sub> antigen {	Bb <sub>1</sub> present	.364	.500	.407
	Bb <sub>1</sub> absent	.636	.500	.593
Bb <sub>2</sub> antigen {	Bb <sub>2</sub> present	.273	.300	.281
	Bb <sub>2</sub> absent	.727	.700	.719
No. of whales observed	22	10	32	

e) Finback whale, *Balaenoptera physalus*. At first two kinds of antigens Bp<sub>1</sub> and Bp<sub>2</sub> were found by immune rabbit agglutinins and hemolysins (Fujino, 1953). According to phenotypic relationships these

TABLE 6. TWELVE PHENOTYPES OF FINBACK BLOOD GROUPS CLASSIFIED WITH Bp AND Ju ANTIGENS\*

Bp antigen	Ju antigen					
	Ju <sub>1</sub>		Ju <sub>1</sub> Ju <sub>2</sub>		Ju <sub>2</sub>	
Bp <sub>1</sub> and Bp <sub>2</sub> present	Bp <sub>1</sub> Bp <sub>2</sub>	Ju <sub>1</sub>	Bp <sub>1</sub> Bp <sub>2</sub>	Ju <sub>1</sub> Ju <sub>2</sub>	Bp <sub>1</sub> Bp <sub>2</sub>	Ju <sub>2</sub>
Bp <sub>1</sub> present	Bp <sub>1</sub>	Ju <sub>1</sub>	Bp <sub>1</sub>	Ju <sub>1</sub> Ju <sub>2</sub>	Bp <sub>1</sub>	Ju <sub>2</sub>
Bp <sub>2</sub> present	Bp <sub>2</sub>	Ju <sub>1</sub>	Bp <sub>2</sub>	Ju <sub>1</sub> Ju <sub>2</sub>	Bp <sub>2</sub>	Ju <sub>2</sub>
Bp <sub>1</sub> and Bp <sub>2</sub> absent	O	Ju <sub>1</sub>	O	Ju <sub>1</sub> Ju <sub>2</sub>	O	Ju <sub>2</sub>

\* cited from Fujino (1956)

two antigens seem to be controlled by different allele system each other. Additional two antigens belong to Ju system were detected independently to the known two antigens by immune rabbit and fowl agglutinins. In consequence twelve phenotypes can be possible as shown in Table 6.

<sup>1)</sup> Sei whales taken from Bonin Islands' area (Fujino, 1953) are identified as different species from *Balaenoptera borealis* (Omura, Nishimoto & Fujino, 1952). More recently, these common name and scientific name are adopted to this species by Omura *et al.* (1957) and Omura (1959).

Another new antigen X were detected positively in Bp<sub>2</sub>Ju<sub>1</sub> and OJu<sub>1</sub> type cells, but relations to the known antigens have not been studied enough yet (Fujino, 1956).

Cushing *et al* (1959) stated that homozygous and heterozygous types, which belong to Ju system, reveal dosage effects against anti-Ju<sub>2</sub> antibody. This was confirmed with additional experiments using materials

TABLE 7. DOSAGE EFFECT IN HETEROZYGOUS TYPE OF FINBACK Ju BLOOD GROUP

Anti-Ju<sub>2</sub> no. 50 immune rabbit serum (absorbed)

Cells		Dilution									
		20	40	80	160	320	640	1280	2560	5120	10240
Ju <sub>1</sub>	503	—	—	—	—	—	—	—	—	—	—
Ju <sub>1</sub> Ju <sub>2</sub>	{ 181	##	##	##	##	##	†	†	+	—	—
	{ 455	##	†	†	+	—	—	—	—	—	—
Ju <sub>2</sub>	504	##	##	##	##	##	##	##	##	+	+

Anti-Ju<sub>2</sub> no. 34 immune rabbit serum (absorbed)

Cells		Dilution							
		10	20	40	80	160	320	640	1280
Ju <sub>1</sub>	503	—	—	—	—	—	—	—	—
Ju <sub>1</sub> Ju <sub>2</sub>	{ 181	##	##	##	##	##	†	+	—
	{ 455	##	##	##	†	+	+	—	—
Ju <sub>2</sub>	504	##	##	##	##	##	##	†	+

No. 2 horse serum (unabsorbed)

Cells		Dilution									
		1	2	4	8	16	32	64	128	256	512
Ju <sub>1</sub>	503	+	—	—	—	—	—	—	—	—	—
Ju <sub>1</sub> Ju <sub>2</sub>	{ 181	+	†	##	##	##	##	†	+	—	—
	{ 455	##	##	##	##	†	+	—	—	—	—
Ju <sub>2</sub>	504	+	†	##	##	##	##	##	†	†	+

Anti-Ju<sub>1</sub> no. 47 immune fowl serum (absorbed)

Cells		Dilution			
		10	20	40	80
Ju <sub>1</sub>	503	##	##	†	+
Ju <sub>1</sub> Ju <sub>2</sub>	{ 181	##	##	†	+
	{ 455	##	##	†	+
Ju <sub>2</sub>	504	—	—	—	—

which were collected by glycerol-freezing technique in 1959. Conversely, this phenomena may serve to distinguish heterozygous type from homozygous type.

Moreover another two types which revealed dosage effect against anti-Ju<sub>2</sub> serum were found among Ju heterozygous types (Ju<sub>1</sub>Ju<sub>2</sub>) as shown in Table 7. In this table results of reaction against anti-Ju<sub>1</sub>

serum show that there is no difference in antigenic activity between nos. 455 and 181 heterozygous erythrocytes after preservation. Large number of investigation about this point has not been carried out, but the results of Table 7 show that heterozygous type ( $Ju_1Ju_2$ ) may be subdivided into two groups, that is, stronger one and weaker one.

As shown in Table 8 natural antibodies specific to  $Ju$  antigen are detected positively in the serums of fowl, rabbit, pig, horse and cattle. As already reported in part by Cushing *et al.* (1959) no difference has been recognized on anti- $Ju_2$  specificity between immune and natural antibodies so far. Additional advantage, which these natural antibody occur in high frequency, will be potentially useful in large scale of blood typing investigations hereafter.

TABLE 8. ANTI-FINBACK  $Ju$  NATURAL ANTIBODIES FROM SERUMS OF VARIOUS SPECIES OF ANIMALS<sup>1)</sup>

Animal	Specificity of antibody	Agglutinin titer <sup>2)</sup>	Frequency of occurrence	Remark
Fowl	{ anti- $Ju_1$ anti- $Ju_2$	1:2 1:4	one out of three ditto	} detected from a same individual
Rabbit	anti- $Ju_2$	1:8~1:64	three out of five	
Pig	anti- $Ju_2$	1:256	only one tested	} Five out of eleven possess finback species specific antibody in common.
Horse	anti- $Ju_2$	1:64~1:2560	all of eleven	
Cattle	anti- $Ju_2$	1:32~1:40960	all of thirteen	

1) partly reported already by Fujino (1958) and Cushing, Fujino & Takahashi (1959).

2) agglutinin titer against homozygous type  $Ju_2$  in room temperature.

TABLE 9. BLOOD TYPE ANTIGENS OF FINBACK WHALES USED FOR LARGE SCALE OF INVESTIGATIONS IN VARIOUS AREAS

Year	East China Sea	Kamchatka off	South of east Aleutian	North of east Aleutian	Off Navarin and Olyutorskiy
1952		Bp			
54		Bp and $Ju$		Bp and $Ju$	
55		Bp and $Ju$	Bp and $Ju$	Bp and $Ju$	
56	$Ju$				
57	$Ju$				
58		$Ju$	$Ju$	$Ju$	$Ju$
59		$Ju$	$Ju$	$Ju$	

While Fujino (1958) stated that immune animal which has natural antibody specific to  $Ju$  antigen can produce more excellent antibody in specificity and titer against corresponding  $Ju$  antigen than other animals. Basing upon the above stated knowledges have been undertaken large number of blood typing of finback whales from various areas of the north Pacific.

Fujino (1956) stated that in large scale of investigation blood typing



TABLE 10. FREQUENCY OF OCCURRENCE OF Bp AND Ju BLOOD GROUP ANTIGENS OF FINBACK WHALES<sup>1)</sup>

Bp antigen	Off Kamchatka <sup>2)</sup>										South of E. Aleut.		North of E. Aleut.					
	1952		1954 & 55		South of E. Aleut.		North of E. Aleut.		Navarin		Olyutorskiy							
	male	female	sum	male	female	sum	male	female	sum	male	female	sum	male	female	sum			
Bp <sub>1</sub> { present absent	.310	.260	.285	.151	.148	.149	.000	.000	.000	.000	.000	.000	.000	.000	.000			
	.690	.740	.715	.849	.852	.851	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000			
Bp <sub>2</sub> { present absent	.190	.270	.230	.250	.264	.256	.526	.462	.500	.218	.221	.219	.782	.779	.781			
	.810	.730	.770	.750	.736	.744	.474	.538	.500	.782	.779	.781	726	701	1427			
No. of whales tested	100	100	200	232	197	429	19	13	32	726	701	1427						
Ju blood group	East China Sea		Off Kamchatka		South of E. Aleut.		North of E. Aleut.		Navarin		Olyutorskiy							
	male female sum		male female sum		male female sum		male female sum		male female sum		male female sum							
	.692	.781	.736	.833	.857	.844	.950	.919	.937	.981	.984	.982	.952	.914	.934	1.000	1.000	1.000
	.108	.094	.101	.048	.034	.042	.025	.030	.027	.007	.005	.006	.024	.029	.026	.000	.000	.000
Ju <sub>2</sub>	.200	.125	.163	.119	.109	.114	.025	.051	.036	.012	.011	.012	.024	.057	.040	.000	.000	.000
No. of whales tested	65	64	129	438	348	786	121	99	220	810	821	1631	41	35	76	8	5	13

1) Include data of Fujino (1953), Fujino (1956), Cushing, Fujino & Takahashi (1959) and additional those in 1959.

2) Figures in 1952 and 1954 & 1955 are noted separately here, because same reagents were not used in these years.

in Ju system can give higher precision than in  $Bp_1$  and  $Bp_2$  antigens because of some misclassification resulting from unknown antigen-antibody reactions involved. Therefore, Ju system alone is used for practical investigation ever since. Blood groups, which were adopted for investigations in various areas in each year, are shown in Table 9. Table 10 shows their frequency of occurrence obtained. In this table the results in 1952 are described separately from those in 1954 and 1955, because in 1952 no discussion was performed on the effect of X antigen which was found subsequently. It is clear from this table that  $Bp_1$  antigen which occurs in the area off Kamchatka does not occur in the area of east Aleutian and that frequencies of  $Ju_2$  antigen show geographical gradient descending from western to eastern sides of the north Pacific. Problems on identification and mingling of intraspecific subpopulations will be discussed later.

TABLE 11. SIZE DISTRIBUTION OF FIN WHALE FETUSES OF WHICH BLOOD GROUPS WERE IDENTIFIED

Body length in feet	Male			Female		
	$Ju_1$	$Ju_1Ju_2$	$Ju_2$	$Ju_1$	$Ju_1Ju_2$	$Ju_2$
4	1		1		1	
5				3		
6	4	1		6		
7	7	1		2		1
8	6	1		7		1
9	3			2		
10	3				1	
11	2	1		3		
12	3			2		
13	2	2		1		
14	1			1		
Sum	32	6	1	27	2	2

Parentages of blood types between cows and their fetuses taken and population genetics using relative frequencies of occurrence of each phenotype were used for finding allele system of blood types. Blood samples taken from umbilical cords of fetuses were used for analysis. Embryological problems of blood types in fetal stages were taken into consideration. After discussing developments of human blood types in fetuses by means of agglutination and agglutination-inhibition reactions, Mizu (1931) and Hirasawa (1935) stated that phenotypes in ABO and MN systems can be already identified approximately three months after fertilization. Therefore, data on whale fetuses, of which blood types were definitely identified with above stated two reactions alone are used for discussion of parentages of blood types in whales.

Table 11 shows body length distribution of fetuses of which blood

types were able to be identified. Judging from averaged growth curve estimated by Nozawa *et al* (Nozawa *et al.* 1956, pp. 44-55) and Ohsumi *et al.* (1958) it may be assumed that fetal blood types of the north Pacific finbacks can be identified already five or six months after fertilization. The parentages of blood types observed are shown in Table 12. According to this table Ju blood type seems to be hereditarily controlled by two allele system, but one exception of parentage has been observed. That is, Ju<sub>1</sub> type fetus was taken from Ju<sub>2</sub> type cow<sup>1)</sup>. This does not fit hypothesis in two allele system. Therefore, further discussions will be taken up by means of population genetics using relative frequency of occurrence of phenotypes as follows.

TABLE 12. PARENTAGES OF Ju BLOOD GROUPS OF FINBACKS<sup>1)</sup>

Mother whale		Blood groups of fetus		
blood group	no. of tested	Ju <sub>1</sub>	Ju <sub>1</sub> Ju <sub>2</sub>	Ju <sub>2</sub>
Ju <sub>1</sub>	56	53	3	0
Ju <sub>1</sub> Ju <sub>2</sub>	7	5	1	1
Ju <sub>2</sub>	7	1	4	2
Sum	70	59	8	3

<sup>1)</sup> Results in the years 1954, 55 & 59.

Phenotypic relationships of Ju blood types noted in Table 6 are discussed as follows from view points of presence or absence of antigens.

i) Erythrocytes lacking Ju<sub>1</sub> antigen are certain to have Ju<sub>2</sub> antigen, and erythrocytes lacking Ju<sub>2</sub> antigen are certain to have Ju<sub>1</sub> antigen. That is, no erythrocytes which has neither antigen Ju<sub>1</sub> nor Ju<sub>2</sub> has been observed.

ii) Erythrocytes possessing both antigens Ju<sub>1</sub> and Ju<sub>2</sub> exists.

Probable hypothetical two allele and three allele systems were discussed by means of population genetics. At first relations of dominancy among alleles were defined as follows. Parenthesized symbols mean frequency of occurrence of each gene. In two allele system, there is no relation of dominancy between  $j_1$  ( $p$ ) and  $j_2$  ( $q$ ) genes. In three allele A system,  $j_1^a$  ( $q$ ) gene is completely dominant against  $j_2$  ( $r$ ) gene and no relation of dominancy exist between  $j_2$  and  $j_1$  ( $p$ ) genes. In three allele B system,  $j_2^r$  ( $r$ ) gene is completely ressesive against  $j_1$  ( $p$ ) gene and  $j_2$  ( $q$ ) gene is equivalent to  $j_1$  gene. Then genotype-phenotype relations are given in Table 13. In two allele system one phenotype corresponds to each one genotype. In three allele A system Ju<sub>1</sub> phenotype includes four genotypes and other two phenotypes have one genotype each. In three allele B system phenotypes Ju<sub>1</sub>, Ju<sub>1</sub>Ju<sub>2</sub> and Ju<sub>2</sub> include two, one and three genotypes respectively.

<sup>1)</sup> According to the log supervised by Mr. K. Nasu, Whales Research Institute, these are no. 1542 cow 70 feet long and male fetus 8 feet and 6 inch. long taken in the area of the north of east Aleutian (54°27'N, 168°32'W) in Aug. 4, 1959.

TABLE 13. PHENOTYPE-GENOTYPE RELATIONSHIPS IN THREE KINDS OF ALLELE SYSTEMS

Phenotype	Genotype		
	two allele system	three allele A system	three allele B system
Ju <sub>1</sub>	j <sub>1</sub> j <sub>1</sub>	j <sub>1</sub> j <sub>1</sub> , j <sub>1</sub> j <sub>1</sub> <sup>a</sup> , j <sub>1</sub> <sup>a</sup> j <sub>1</sub> <sup>a</sup> , j <sub>1</sub> <sup>a</sup> j <sub>2</sub>	j <sub>1</sub> j <sub>1</sub> , j <sub>1</sub> j <sub>2</sub> <sup>r</sup>
Ju <sub>1</sub> Ju <sub>2</sub>	j <sub>1</sub> j <sub>2</sub>	j <sub>1</sub> j <sub>2</sub>	j <sub>1</sub> j <sub>2</sub>
Ju <sub>2</sub>	j <sub>2</sub> j <sub>2</sub>	j <sub>2</sub> j <sub>2</sub>	j <sub>2</sub> j <sub>2</sub> , j <sub>2</sub> j <sub>2</sub> <sup>r</sup> , j <sub>2</sub> <sup>r</sup> j <sub>2</sub> <sup>r</sup>

In a population at Hardy-Weinberg's equilibrium, following relations between frequencies of occurrence of phenotypes and those of genotypes can be formulated. That is, in two allele system,

$$\left. \begin{aligned} [Ju_1] &= p^2 \\ [Ju_1Ju_2] &= 2pq \\ [Ju_2] &= q^2 \\ p + q &= 1 \end{aligned} \right\} \quad (1)$$

, in three allele A system

$$\left. \begin{aligned} [Ju_1] &= (p+q)^2 + 2qr \\ [Ju_1Ju_2] &= 2pr \\ [Ju_2] &= r^2 \\ p + q + r &= 1 \end{aligned} \right\} \quad (2)$$

, and in three allele B system

$$\left. \begin{aligned} [Ju_1] &= p^2 + 2pr \\ [Ju_1Ju_2] &= 2pq \\ [Ju_2] &= (1-p)^2 \\ p + q + r &= 1 \end{aligned} \right\} \quad (3)$$

, where [Ju<sub>1</sub>], [Ju<sub>1</sub>Ju<sub>2</sub>] and [Ju<sub>2</sub>] mean frequency of occurrence of each phenotype and a relation of [Ju<sub>1</sub>] + [Ju<sub>1</sub>Ju<sub>2</sub>] + [Ju<sub>2</sub>] = 1 is provided.

TABLE 14. FREQUENCY OF OCCURRENCE OF PHENOTYPES AND GENES OF Ju BLOOD GROUPS OF FINBACK WHALES

Freq. of occurrence of phenotypes and genes	East China Sea		Kamchatka (A)		South of east Aleutian (B)		North of east Aleutian (C)		
	act. no.	freq.	act. no.	freq.	act. no.	freq.	act. no.	freq.	
Observed	[Ju <sub>1</sub> ]	95	.731	663	.844	206	.937	1602	.982
	[Ju <sub>1</sub> Ju <sub>2</sub> ]	13	.101	33	.042	6	.027	10	.006
	[Ju <sub>2</sub> ]	21	.163	90	.114	8	.036	19	.012
	sum	129		786		220		1631	
Two-allele system, exp. value	$\left\{ \begin{array}{l} p \\ q \end{array} \right.$	.787		.865		.951		.985	
	[Ju <sub>1</sub> ]	80	.620	588	.748	199.1	.905	1582.4	.9702
	[Ju <sub>1</sub> Ju <sub>2</sub> ]	43	.335	184	.234	20.5	.093	48.3	.0296
	[Ju <sub>2</sub> ]	6	.045	14	.018	0.4	.002	0.3	.0002
Three-allele system*	A $\left\{ \begin{array}{l} p \\ q \\ r \end{array} \right.$	.125		.062		.071		.027	
		.471		.600		.739		.863	
		.404		.338		.190		.110	
	B $\left\{ \begin{array}{l} p \\ q \\ r \end{array} \right.$	.596		.662		.810		.890	
		.085		.032		.017		.003	
		.319		.306		.173		.107	

\* Calculated for convenience of comparison under a hypothesis which population in each area is in Hardy-Weinberg's equilibrium.



Table 14 shows gene frequencies calculated from Table 10 through these formulas. Results of statistical tests shows that Ju blood type does not fit hypothetical two allele system. This confirm incompatibility of two allele system which was previously noted in parentages. Therefore, analysis of raiation and mingling of different populations will be discussed through three allele A and B systems.

Frequency of expected blood groups in fetuses from various matings can be noted in Table 15 through two ways of A and B systems.

Dosage effect in heterozygous types noted in Table 7 would propose existence of subtypes to which an additional gene will concern. However, informations sufficient to statistical treatment have not been obtained yet.

f) Blue whale, *Balaenoptera musculus*. Two kinds of antigens Bm<sub>1</sub> and Bm<sub>2</sub> are found in the erythrocytes of north Pacific blue whale with rabbit immune agglutinins and hemolysins. Frequencies of occurrence of antigens are shown in Table 16. Isoagglutinins specific to known

TABLE 16. FREQUENCY OF OCCURRENCE OF BLOOD TYPE ANTIGENS OF BLUE WHALES

Presence or absence of antigen	Male	Female	Sum
Bm <sub>1</sub> antigen { Bm <sub>1</sub> present	.033	.059	.043
	Bm <sub>1</sub> absent	.267	.411
Bm <sub>2</sub> antigen { Bm <sub>2</sub> present		.133	.059
	Bm <sub>2</sub> absent	.567	.471
No. of whales observed		30	17

antigens occur irregularly. Titers of anti-Bm<sub>1</sub> reach up to 1:4 or 1:64 and those of anti-Bm<sub>2</sub> up to 1:2 or 1:64 (Fujino, 1953). According to phenotypic relationships, antigens Bm<sub>1</sub> and Bm<sub>2</sub> seem to be controlled by genes belong to different allele systems each other, though informations enough to discuss has not been obtained.

g) Humpback whale, *Megaptera nodosa*. Two kinds of blood group antigens Mn<sub>1</sub> and Mn<sub>2</sub> are found in the north Pacific humpback whales

TABLE 17. FREQUENCY OF OCCURRENCE OF BLOOD TYPE ANTIGENS OF HUMPBACK WHALES

Presence or absence of antigen	Male	Female	Sum
Mn <sub>1</sub> antigen { Mn <sub>1</sub> present	.111	.118	.114
	Mn <sub>1</sub> absent	.278	.235
Mn <sub>2</sub> antigen { Mn <sub>2</sub> present		.056	.118
	Mn <sub>2</sub> absent	.555	.529
No. of whales observed		18	17

with immune rabbit agglutinins and hemolysins. Frequency of occurrence of each antigen is shown in Table 17. Isoagglutinins specific to known antigens were detected positively at high frequency. Out of ten

samples tested, three have anti-Mn<sub>1</sub>, three have anti-Mn<sub>2</sub>, two have both and two have none of agglutinins. Titers of anti-Mn<sub>1</sub> and anti-Mn<sub>2</sub> agglutinins reach up to 1:2 or 1:128 and 1:4 or 1:128 respectively. Table 18 shows results of isoagglutination (Fujino, 1953).

TABLE 18. ISOHEMAGGLUTINATION IN Mn BLOOD TYPE ANTIGENS OF HUMPBACK WHALES

Serums	Erythrocytes									
	142	143	151	180	184	191	192	203	204	206
142	—	—	—	—	—	—	—	‡	—	—
143	—	—	‡	—	—	—	—	‡	—	—
151	—	—	—	—	—	—	—	‡	—	—
180	—	—	‡	—	—	—	—	‡	—	—
184	—	—	+	—	—	—	—	—	—	—
191	—	—	‡	—	—	—	—	‡‡	—	—
192	—	—	‡	—	—	—	—	‡‡	—	—
203	—	—	—	—	—	—	—	—	—	—
204	—	—	‡	—	—	—	—	‡‡	—	—
206	—	—	—	—	—	—	—	‡‡	—	—

Additional four kinds of blood types were temporarily classified on humpbacks taken from Okinawa waters with anti-finback Ju agglutinins (immune rabbit and fowl serums and natural antibodies from cattle and

TABLE 19. NEW BLOOD TYPES OF HUMPBACK WHALES TEMPORARILY CLASSIFIED BY ABSORBING TESTS OF ANTI-FINBACK Ju SERUMS

Blood types of absorbing erythrocytes	Blood types of erythrocytes used as agglutigen			
	1	2	3	4
1	—	—	—	—
2	+	—	—	—
3	+	+	—	—
4	+	+	+	—

TABLE 20. ISOHEMAGGLUTINATION IN HUMPBACK WHALE BLOOD TYPES CLASSIFIED BY ANTI-FINBACK Ju SPECIFICITIES

Serums	Blood types of erythrocytes					
	1 K 9	2 K24	3 R10	3 R29	4 K 4	4 R38
K 9	—	—	—	—	—	—
K24	‡‡	—	—	—	—	—
R10	‡‡	+	—	—	—	—
R29	‡‡	—	—	—	—	—
K 4	‡‡	‡	+	+	—	—
R38	‡‡	+	—	—	—	—

horse) as shown in Table 19. Isoagglutinins specific to these antigens were found. Especially agglutinin specific to type 1 erythrocytes were positively detected in all samples excepting type 1 individual out of

thirty-three those tested. Table 20 shows summarized results of the isoagglutination.

Any informations to discuss relationships between these four types and Mn antigens have not been obtained. Phenotypic relations noted in Table 19 would suggest existence of sub-blood types, but additional data should be collected to conclude on allele system definitely. Frequencies of occurrence of these four phenotypes of humpbacks taken from Okinawa area are shown in Table 21 (Cushing *et al.*, 1959).

TABLE 21. FREQUENCY OF OCCURRENCE OF HUMPBACK  
Ju BLOOD TYPES

Blood types				No. of whales observed	Locality taken
1	2	3	4		
.010	.040	.071	.879	99	Okinawa

*Serological constitution of whales from view points of human ABO blood types*

Natural antibodies specific to human ABO blood types were detected on whale serums by means of agglutination reactions. As shown in Table 22, anti-human A ( $\alpha'$ ) agglutinin was detected positively in all species tested, but anti-human B ( $\beta'$ ) agglutinin was found in finback and blue whales only. Agglutinin titers of anti-A reached up to 1:2 or 1:4 and those of anti-B up to 1:8 (Yamaguchi & Fujino, 1952; Fujino, 1953).

TABLE 22. FREQUENCY OF OCCURRENCE OF ANTI-HUMAN A( $\alpha'$ )  
AND ANTI-HUMAN B( $\beta'$ ) NATURAL ANTIBODIES IN  
SERUMS OF VARIOUS SPECIES OF ANIMALS

Whale species	Natural antibody				No. of whales tested	Locality taken	
	$\alpha'\beta'$	$\alpha'$	$\beta'$	$\alpha'$			
Toothed whale	blue-white dolphin	.000	.160	.000	.840	25	east side of Izu Penninsula
	sperm whale	.000	.154	.000	.846	13	
Baleen whale	bryde whale	.000	.188	.000	.812	16	} northern part of North Pacific
	fin whale	.096	.065	.065	.774	31	
	blue whale	.189	.297	.000	.514	37	
	humpback whale	.000	.400	.000	.600	15	

Friedenreich and With (1933) and Iseki and Murakami (1940) state that anti-human B and anti-human A natural antibodies in serums of animal does not have uniform construction in specificity and can be analysed into partial antibodies specific to corresponding partial antigens of human B and A blood groups. While Owen (1954) describes on heterogeneity of antibodies. However no analysis on these points of natural antibody of whales has been undertaken yet.

According to many studies it has been clarified that human blood type



antigens of A, B and O have mosaic constructions of partial antigens and that these partial antigens distribute in erythrocytes and body fluids of animals. Terashima (1942) reported that human A antigen can be analysed into four partial antigens  $A_I$ ,  $A_{II}$ ,  $A_{III}$  and  $A_{IV}$ . Friedenreich and With (1933) subdivide human B antigen into three partial antigens  $B_1$ ,  $B_2$  and  $B_3$ . Recently Furuhata (1957) proposed to substitute  $B_I$ ,  $B_{II}$  and  $B_{III}$  for three symbols noted above to avoid confusion with those of sub-blood types. Inoue (1943) reported that human O erythrocytes have a mosaic constitution which consists of three partial antigens  $O_I$ ,  $O_{II}$  and  $O_{III}$ .

After analysing B antigen by this method, Fujino (1958) reported that finback erythrocytes have  $B'_{IV}$  partial antigen of human B which has simpler structure serologically than  $B_{III}$  in guinea pig. Summarized results including additional species are shown in Table 23. Materials and methods in experiments are same as those noted by Fujino (1958). No analysis on blood group substances A and O has been undertaken.

TABLE 23. DISTRIBUTION OF PARTIAL ANTIGENS OF HUMAN B BLOOD TYPE SUBSTANCES

Whale species	Partial antigen	No. of whale, tested	
Toothed whale {	blue-white dolphin	$B_{III}$ and $B_{IV}'$	10
	sperm whale	ditto	25
	baird-beaked whale	ditto	8
Baleen whale {	fin whale	$B_{IV}'$	32
	sei whale	ditto	7

Schiff and Sasaki (1932) showed that secretion or non-secretion of blood type substance in human saliva is a hereditary character. Thereafter it has been clarified by many workers that this serological character can be identified with other body fluid than saliva. After analysing saliva of rabbit by the use of antibody specific to human A blood type, Koshino (1938 and 1939) stated that secreter-nonsecreter types can be distinguished in rabbit and that this serological property is closely related to producing ability of anti-human A antibody when used as immune animal. The author tried to analyse secreter-nonsecreter types in sperm whales using mucous membrane of second stomach as material. Human B blood type substance was used as indicator for analysis. After being washed, the mucous membrane of second stomach was ground down and was extracted with equal weight of 1.5 percent saline in refrigerator for 24 hours. Original sample for test were prepared by addition of 1/10 volume of five percent carboic acid to extracts after boiling for thirty minutes. After being inactivated, anti-human B type immune rabbit serum (agglutinin titer of anti- $B_1 = 1:2560$ , Fujino, 1958) was diluted 1:20 with saline and was added half volume

of human A type erythrocytes to absorb anti-human species-specific and anti-C agglutinin common to A and B cells.

Series of extracts prepared by successive dilution of original sample with saline was mixed with equal volume of absorbed anti-B<sub>1</sub> serum. After two hours' absorption in room temperature, results of agglutination inhibition tests were observed by mixing of human B type erythrocytes as shown in Table 24. It can be seen from this table that extracts of sample nos. 2, 3, 5, 6, 8 and 9 inhibit agglutination of anti-B<sub>1</sub> antibody significantly up to 1:4 dilution but others inhibit

TABLE 24. ANTI-HUMAN B AGGLUTININ-INHIBITING TESTS BY SALINE EXTRACTS OF STOMACH OF SPERM WHALES

No. of extracts	Dilution of extracts						
	1:1	1:2	1:4	1:8	1:16	1:32	1:64
1	+	‡	‡‡	‡‡	‡‡	‡‡	‡‡
2	—	—	—	+	‡	‡‡	‡‡
3	—	—	—	±	+	‡	‡‡
4	‡	‡‡	‡‡	‡‡	‡‡	‡‡	‡‡
5	—	—	—	±	+	‡	‡‡
6	—	—	—	±	+	‡	‡‡
7	+	‡	‡‡	‡‡	‡‡	‡‡	‡‡
8	—	—	—	—	+	‡	‡‡
9	—	—	—	+	‡	‡	‡‡
10	+	‡	‡‡	‡‡	‡‡	‡‡	‡‡
Control	‡‡	‡‡	‡‡	‡‡	‡‡	‡‡	‡‡

slightly. These facts seem to show existence of secrete-nonsecrete type in sperm whales. This serological property will serve for analysing of subspecific population in future. Relationship between these characters and known blood types of sperm whales has not been studied yet.

#### POPULATION ANALYSIS OF THE NORTH PACIFIC FINBACK WHALES

As regards raiation of the North Pacific fin whales several studies have been published as follows. After discussing seasonal change of localization of whaling grounds, catch statistics and oceanographic informations, Omura (1950) and Kasahara (1950) assumed that in the east (Pacific) and west (Japan sea) sides of Japan distribute different local populations which have different migratory courses each other. Basing upon geographical difference of frequency of occurrence of blood type, Omura (1955) and Fujino (1956) stated that fin whales distribute in areas around Aleutian Islands do not belong to one uniform population, but rather different local populations migrate to area off Kamchatka and area of north of east Aleutian. While Kawakami & Ichihara (1958) stated from results

of marking investigation that both populations in American and Asian sides migrate to same feeding area around Aleutian, but it is not clear whether these populations mingle in this area or are kept isolated each other. After comparing external dimensions of whale body, Ichihara (1957) found significant difference between fin whales from area around Aleutian and those from East China Sea, but does not discuss whether whales taken from these two areas belong to different populations or not. In the present report racial study of whales from these various areas will be discussed by means of population genetics with blood groups and marking investigations.

*Distribution of finback whales in the North Pacific*

Fin whales in the North Pacific have very widely geographical distribution, winter in lower latitude areas for breeding or calving and in summer season migrate northwards for feeding. Whaling grounds are formed in the waters adjacent to California, British Columbia, Alaska, Aleutian Chain, Kuril Islands and Japan during from June to October. Number of finback whales taken in the years 1949 to 1959 are shown in Table 25. In the areas of Okhotsk and Pacific sides of Japan number of catch has remarkably decreased in recent years. Whaling in the East China Sea has been resumed since 1955 after several years' suspension after World War II.

*Population genetics with blood types*

As already stated, several kinds of blood group antigens have been found in finback whales. Four antigens out of these are used for large scale of investigations as markers. Fujino (1956) stated that higher precision in blood typing can be expected in Ju system than in Bp system because of purification of typing reagents and phenotypic relationships. Therefore, Ju system alone has been used since 1956.

Cushing et al. (1959) stated that dosage effects were recognized between homozygous and heterozygous types in Ju system. Thereafter additional dosage effect was observed among heterozygous types as already shown in Table 7. On the other hand original anti-Ju<sub>2</sub> immune serums used in the years 1954 to 1959 have been always kept in high agglutinin titers and were used at dilutions 1:10 or 1:20 in actual typing. Therefore weaker heterozygous types seem to have been scarcely misclassified as Ju<sub>1</sub> homozygous type. From above-stated reasons Bp antigens were used for only qualitative comparison between populations and Ju antigens were used for qualitative and quantitative analysis of populations from different localities.

Geographical difference of distributions of Bp and Ju blood type antigens, which were shown in Table 11, will suggest existence of local populations of the North Pacific finback whales. After comparing by

year frequencies of occurrence in various areas, yearly fluctuation can be scarcely seen in the area of north of east Aleutian (area C) but can be recognized in the areas off Kamchatka (area A) and of south of east Aleutian (area B) (see Fig. 2). It can be assumed from these facts that whales which migrate to area C in these successive years, belong to the identical population, and that different populations migrate to areas A and B in different proportions by year. Concerning to this point,

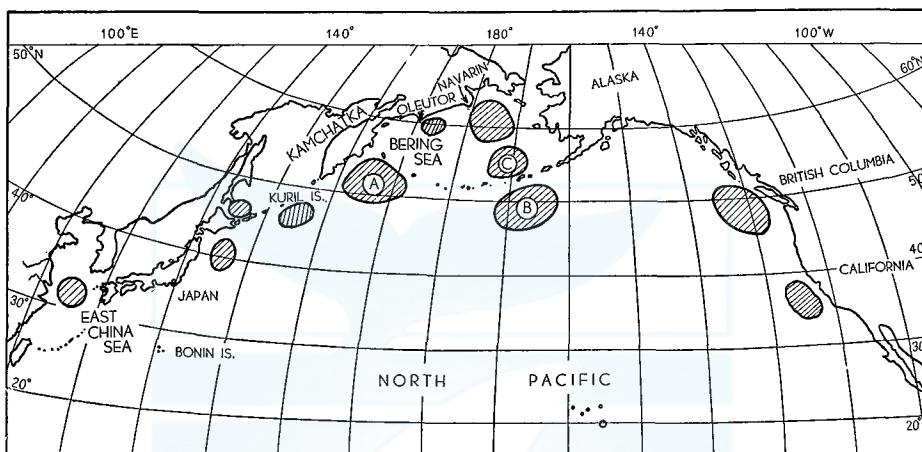


Fig. 1. Whaling grounds in the North Pacific Fin whale.

TABLE 25. NUMBER OF FINBACK WHALES CAUGHT IN VARIOUS AREAS OF THE NORTH PACIFIC, 1949~59

Area	Year											Sum
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	
Bonin	0	0	0	0	—	—	—	—	—	—	—	0 <sup>1)</sup>
Japan	1	0	0	22	12	0	225 <sup>2)</sup>	277	184	171	80	972 <sup>3)</sup>
{West												
{North-east	208	141	209	209	234	197	129	70	76	50	47	1570
Kuril	53	106	156	241	179	266	219	241	173	328	223	2185
Kamchatka & Bering (Pelagic)	64	92	90	447	615	1554	1439	1480	1486	1370	1582	10219
British Columbia	105	150	216	240	181	150	120	168	284	573	369	2556
California	10	—	9	—	—	—	—	3	22	109	105	258
Sum	441	489	680	1159	1221	2167	2132	2239	2225	2601	2406	17760

1) Whaling has ceased since 1953.

2) Whaling in the East China Sea has been operated since 1955.

3) Includes thirty-five Whales caught from Tsushima Strait, 1949~53.

Fujino (1953) stated that remarkable seasonal fluctuations of frequency of occurrence of Bp antigens were seen in the area off Kamchatka (area A) in 1952. This fact was confirmed with the results in Ju system obtained in successive years as shown in Table 26.

From these things it can be thought that migratory ranges of different local populations cover this area off Kamchatka and that relative size of these different stocks which actually migrate there fluctuates from year to year.

Number of whales tested in the East China Sea is small, but no remarkable yearly or seasonal fluctuations seem to be recognized judging from daily occurrence of blood types shown in Fig. 3.

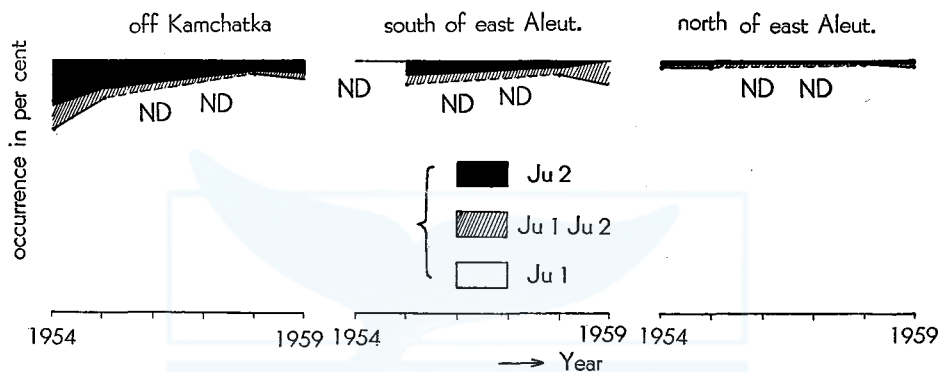


Fig. 2. Yearly fluctuation of frequency of occurrence of Ju blood groups. ND: No available data

TABLE 26. NON-RANDOM DISTRIBUTION OF BLOOD GROUPS BY YEAR OR BY SEASON IN THE WHALES TAKEN FROM AREAS OFF KAMCHATKA AND SOUTH OF EAST ALEUTIAN.

Area	Year and season	No. of whales observ.	Blood groups			Remark
			Ju <sub>1</sub>	Ju <sub>1</sub> Ju <sub>2</sub>	Ju <sub>2</sub>	
Off Kamchatka	1954 <sup>a</sup>	82	.646	.098	.256	June
	1954 <sup>b</sup>	234	.765	.068	.167	July~Aug.
	1955	113	.858	.027	.115	May~June
	1958 <sup>a</sup>	91	.989	.000	.011	May 23~June 9
	1958 <sup>b</sup>	28	.821	.036	.143	July 24~Aug 1
South of east Aleutian	1959	238	.929	.021	.050	May 27~June 27
	1955	32	.907	.031	.062	June (13), July (2) & Aug. (17)
	1958 <sup>a</sup>	140	.943	.021	.036	June 10~July 2
	1958 <sup>b</sup>	37	.946	.027	.027	July 14~July 23
	1959	11	.909	.091	.000	July 20~29

Even in case which yearly fluctuations are seen as stated above, it can be discussed by use of averaged figures of gene frequency whether two populations from areas of both side out of geographically neighbouring three areas mingle in the middle area or not. For this purpose it should be discussed whether continued ratios of corresponding gene frequencies from three areas are proportionate in three alleles or not. Gene frequencies are given in Table 13. Results of calculation in four

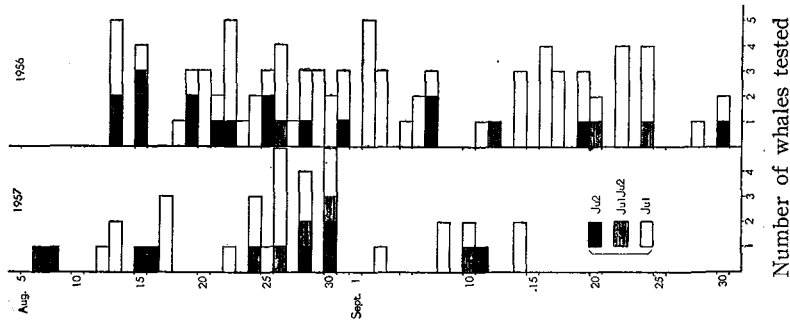


Fig. 3. Occurrence of Ju blood groups in daily catch in East China Sea.

TABLE 27. CORRELATION BETWEEN POPULATIONS TAKEN FROM NEIGHBOURING THREE AREAS REVEALED BY GENE FREQUENCIES

Combination of neighbouring three areas	Allele system	Gene freq.		Ratio of mingl. <sup>1)</sup>		Freq. of phenotype		$\chi^2$	
		obs.	exp. <sup>2)</sup>	b	1-b	obs.	exp. <sup>2)</sup>		
									, in middle area
a) { East China Sea Kamchatka East Aleutian (Sum of north & south)	A	p	.062	.087	.28	.72	Ju <sub>1</sub>	663	13.14
		q	.600	.630	.65	.35	Ju <sub>1</sub> Ju <sub>2</sub>	33	
		r	.338	.283	.77	.23	Ju <sub>2</sub>	90	
			*average	.57	.43		786		
	B	p	.662	.686	.77	.23	Ju <sub>1</sub>	644.5	
		q	.032	.059	.34	.66	Ju <sub>1</sub> Ju <sub>2</sub>	63.7	
r		.306	.254	.94	.06	Ju <sub>2</sub>	77.8		
		*average	.68	.32					
b) { East China Sea Kamchatka South of east Aleut.	A	p	.062	.090	.17	1.17	Ju <sub>1</sub>	663	24.18
		q	.600	.649	.52	.48	Ju <sub>1</sub> Ju <sub>2</sub>	33	
		r	.338	.265	.69	.31	Ju <sub>2</sub>	90	
			*average	.35	.65		786		
	B	p	.662	.679	.69	.31	Ju <sub>1</sub>	642.9	
		q	.032	.058	.22	.78	Ju <sub>1</sub> Ju <sub>2</sub>	62.1	
r		.306	.262	.91	.09	Ju <sub>2</sub>	81.0		
		*average	.61	.39					
c) { East China Sea Kamchatka North of east Aleut.	A	p	.062	.086	.36	.64	Ju <sub>1</sub>	663	11.45
		q	.600	.628	.67	.33	Ju <sub>1</sub> Ju <sub>2</sub>	33	
		r	.338	.286	.78	.22	Ju <sub>2</sub>	90	
			*average	.60	.40		786		
	B	p	.662	.687	.78	.22	Ju <sub>1</sub>	644.5	
		q	.032	.060	.35	.65	Ju <sub>1</sub> Ju <sub>2</sub>	64.5	
r		.306	.253	.94	.06	Ju <sub>2</sub>	77.0		
		*average	.69	.31					
d) { Kamchatka South of east Aleut. North of east Aleut.	A	p	.071	.051	1.26	-.26	Ju <sub>1</sub>	206	3.99
		q	.739	.682	.47	.53	Ju <sub>1</sub> Ju <sub>2</sub>	6	
		r	.190	.267	.35	.65	Ju <sub>2</sub>	8	
			*average	.69	.31		220		
	B	p	.801	.801	.35	.65	Ju <sub>1</sub>	206.4	
		q	.017	.014	.48	.52	Ju <sub>1</sub> Ju <sub>2</sub>	4.8	
r		.173	.185	.33	.67	Ju <sub>2</sub>	8.8		
		*average	.39	.61					

1) Ratio of mingling in the middle area of populations from western and eastern areas.  
 2) Calculated from figures of populations from areas of both side and averaged ratio of mingling.

combinations of neighbouring three areas among which gene frequencies reveal successive gradients are shown in Table 26. These include four cases of a) East China Sea : area A : sum of areas B and C, b) East China Sea : area A : area B, c) East China Sea : area A : area C, and d) area A : area B : area C.

From Table 26 it was denied that populations from both sides' areas mingle in middle area in any three cases a), b), and c) out of four through A or B allele systems. While in case of d) possibility of mingling seem to be assumed through B allele system only. This will be discussed later more in detail together with results of marking investigations. As results of emigration of marked whales show that some degree of minglings occur between west and east areas around Aleutian, it can be concluded that whales from East China Sea belong to a local populations which nearly isolated from populations that migrate to areas around Aleutian Chains. Results from areas off Navarin and Olyutorskiy Peninsulas are excluded from calculations because of scantiness of data available.

*Ratios of mingling of different populations calculated from blood type gene frequencies and rate of recapture of marked whales*

A. Rate of emigration of populations calculated from marking return. A part of marking investigations, which has been undertaken in the north Pacific since 1949, was already reported by Omura & Kawakami (1956) and Kawakami & Ichihara (1958). As shown in Table 28, number of finback whales recorded as 'Hit' reach up to 14 in the areas off

TABLE 28. NUMBER OF FINBACK WHALES MARKED IN VARIOUS AREAS OF THE NORTH PACIFIC, 1949~1959\*

Area	Year											Sum
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	
Bonin				1								1
Japan, Pacific	7		1		5							13
Kamchatka					22 <sup>1)</sup>	4	4 <sup>2)</sup>	1	2	28		61
East Aleutian						18 <sup>3)</sup>	15	16	10	8	10	77
South Aleutian						210 <sup>6)</sup>	32	57	34 <sup>4)</sup>	28	16 <sup>5)</sup>	377
North of Pribilof and Navarin						3	1		9			13
Sum	7	0	1	1	27	235	52	74	55	64	26	542

\* Includes whales recorded as 'Hit' only. 1), 2), 3), 4) and 5) include each one whale which was not recorded as 'Hit' but was recovered in successive years. 6) includes same type of three whales as above-noted.

Bonin Islands and Pacific side of Japan and to 528 in the area around Aleutian Islands. Seventy whales out of these have been recaptured in the areas around Aleutians, but no recovery has been reported from areas of East China Sea, north-east side of Japan, around Kuril Islands, off British Columbia and California in which whalings have been operated.

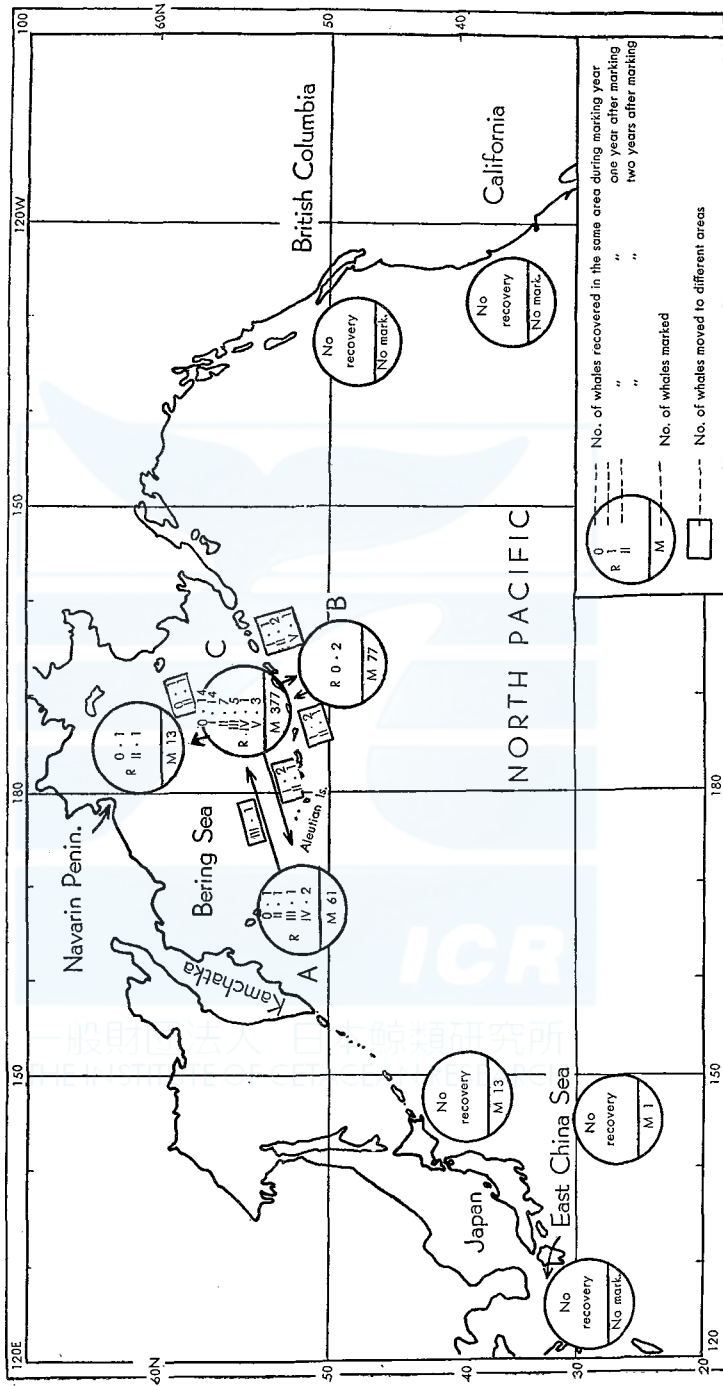


Fig. 4. Summarized results of movements of marked finback whales in the North Pacific (1953~1959).



Fig. 4 outlines interrelations among various whaling areas revealed by results of movement of marked whales. It can be thought to suggest existence of local populations that in spite of fairly large number of whales are taken from various areas noted above in every year no recovery of marker has been reported from these areas excepting those around Aleutians. Especially regarding to relations between populations in East China Sea and those around Aleutians, above-stated facts could be interpreted to confirm that the former is isolated from the latter as already concluded from blood typing investigations.

Relations among various areas around Aleutians will be analysed in following part. As shown in Fig. 4, 5 and 1 out of 61 whales marked in area A were recaptured in the same area and area C respectively. 44, 3, 2 and 4 out of 377 whales marked in area C has been recaptured in the same, A, north of Pribilof and off Navarin, and B areas respectively. Out of 77, 2 and 3 whales marked in area B have been recaptured in the same and C areas. Additional recaptures of one and three whales from those marked in areas C and B respectively were reported. As their markers, however, were recovered from freezing ship or oil-cooker of factory ship after treatment of whale body it is not clear whether these whales were recaptured from areas B or C. Judging from non-random geographical distribution in blood type gene frequency noted already, it can be thought that population which migrates to area C belong to different those migrate to area A, but above-stated results of marked whales show that mingling occurs in part between east and west populations. When two populations of west and east sides are temporarily called as I and II, above-stated situations may be interpreted as follows. These populations I and II are kept isolated each other in wintering breeding season and their feeding migratory ranges overlap in part in the areas around Aleutian Islands in summer season.

As Japanese pelagic whaling for baleen whales in the North Pacific has been operated by one company's whaling fleet, conditions at recovery of markers can be thought to be approximately identical by year and by area. Therefore problems of mingling between populations I and II in the areas A and C could be discussed quantitatively basing upon results of emigration of marked whales. Relative size of populations I and II which actually migrate to areas A and C can be calculated as average for periods of investigation from blood type gene frequencies and rate of emigration which is obtained as relative figures of rate of recapture against total catch in each area. As number of whales recaptured in the year of marking is remarkably effected by the season of marking and whaling operation, they are excluded from calculation.

Symbols listed in 'A Standard Terminology and Notation for Fishery Dynamics' (Holt et al., 1959) are applied to calculating results of marking investigation, and some other additional terms and symbols are adopted.

If average rate of recapture of whales marked in area A against catch in areas A and C in successive years after marking is given as  $r_1^1$  and  $r_2^1$ , and those of whales marked in area C against catch in area A and C is given as  $r_1^2$  and  $r_2^2$ , following representation will be possible.

$$\begin{aligned} \text{Rate of return of whales to area A: } & \frac{r_1^1}{r_1^1 + r_2^1} \\ \text{, rate of emigration of whales from areas A to C: } & \frac{r_2^1}{r_1^1 + r_2^1} \\ \text{, rate of return of whales to area C: } & \frac{r_2^2}{r_1^2 + r_2^2} \\ \text{, and rate of emigration of whales from areas C to A: } & \frac{r_1^2}{r_1^2 + r_2^2} . \end{aligned}$$

Whales against which marking investigations have been actually carried out in the various areas around Aleutian Islands should be thought to consist of not pure populations but rather parts of both populations I and II. If marking investigations in areas A and C, however, could be thought to have been undertaken against unmingled populations I and II respectively for convenience to calculation, ratios of mingling of both populations in areas A and C can be given by following formulas,

$$\left. \begin{aligned} \text{ratio of mingling in area A: } & m_{I:II}^A = N_1 \frac{r_1^1}{r_1^1 + r_2^1} : N_2 \frac{r_1^2}{r_1^2 + r_2^2} \\ \text{ratio of mingling in area C: } & m_{I:II}^C = N_1 \frac{r_2^1}{r_1^1 + r_2^1} : N_2 \frac{r_2^2}{r_1^2 + r_2^2} \end{aligned} \right\} \quad (4)$$

, where  $N_1$  and  $N_2$  are relative sizes of parts of populations I and II respectively which actually migrate to areas A and C.

Figures of  $r_1^1$ ,  $r_2^1$ ,  $r_1^2$ , and  $r_2^2$  can be calculated as follows. At first various symbols necessary for formulation are given. Term of  $u$  means average rate of recapture of whales, marked in area C in a year, against number of catch in area C in successive years. Number of catch, of whales recaptured, and of survivor in area C in successive years after marking are represented as follows.

Lapse of years after marking	0	1	2	...	$x$	
In area C, {	no. of whales recaptured	$R_0$	$R_1$	$R_2$	...	$R_x$
no. of survivor of initial stock in catch	$C_0'$	$C_1'$	$C_2'$	...	$C_x'$	

As it can be assumed that total number of whales recaptured up to  $x$  years after marking proportionates to total number of survivor of

initial stock, when marked, in catch,  $u$  will be given as rate of the former against the latter which is averaged for the figures of successive years as follows.

$$u = \frac{1}{x} \cdot \frac{1}{f} \left( \frac{R_1}{C'_1} + \frac{R_1+R_2}{C'_1+C'_2} + \dots + \frac{R_1+R_2+\dots+R_x}{C'_1+C'_2+\dots+C'_x} \right). \quad (5)$$

After averaging figures of  $u$  for different years with weight,  $r_2^2$  in formula 4 will be obtained through formula 5.

$$r_2^2 = \frac{2g}{x(x+1)} \left( \frac{u_0}{T_0-R'_0} \cdot x + \frac{u_1}{T_1-R'_1} \cdot (x-1) + \dots + \frac{u_{x-1}}{T_{x-1}-R'_{x-1}} \cdot 1 \right). \quad (6)$$

, where  $T$  means number of whales 'hit' in area  $C$ ,  $R'$  means total number of whales recaptured in the year of marking, that is, includes whales recaptured after emigrating to different areas,  $f$  means rate of recovery of marker from whales actually recaptured, and  $g$  means rate of confirming whales reported as 'Hit' against number of whales effectively marked. Figures of  $f$  and  $g$  are given as constant by year and by area. When various figures of area  $A$  are adopted to  $T$ ,  $C'$  and  $R'$  in formulas 5 and 6,  $r_1^2$  can be calculated by the same way as stated-above. To calculate  $r_2^2$ , figures of area  $C$  are adopted to  $T$  and those of area  $A$  are used for  $R'$  and  $C'$  in the same formulas.

Various figures used for these calculations such as number of whales hit, of those recaptured and of catch are shown in Tables 29 and 30. Calculation of number of survivor  $C'$  from number of catch  $C$  will be discussed later. Number of marked whales in Table 29 include whales reported as 'Hit' only and does not include finback whales recaptured from those reported as 'No verdict', 'Miss' or 'misconceived as different species' when marked. As remarked in the table, three and one whales marked in areas B and C respectively are excluded from 'number of whales recaptured' in this table, because their markers were recovered from cooker or refrigerated ship and their localities and dates of recapture are indefinite.

Figure of  $f$  was estimated from the experimental results on recovery of markers reported by Kawakami & Nasu (1956) as shown in Table 31. They stated that significant difference of rate of recovery was seen between standard type dart and dart with streamer in their experiments. In actual case, however, most streamer is fallen off from dart when recovered. Therefore  $f$  is calculated for all kinds of dart (1/ $f$  correction) from number of dart recovered on the treating deck of factory ship among standard type dart shot into finback whales, that is,  $f=17/35=0.485$ . In actual marking investigation, whales recaptured can be divided into two cases in which their markers were recovered from whales re-

TABLE 29. NUMBER OF FIN WHALES MARKED AND RECAPTURED

Marked in the areas:		Recaptured in the areas:																				
		Off Kamchatka						South of east Aleut.						North of east Aleut.								
		1953	54	55	56	57	58	59	1953	54	55	56	57	58	59	1953	54	55	56	57	58	59
Off Kamchatka	1953	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	54	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
South of east Aleutian	1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	54	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
North of east Aleutian	1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	54	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
North of Pribilof and off Navarin	1953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	54	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sum																						

- a) Includes whales recorded as 'Hit' only. There are one additional recapture from  
 b) A marker (no. 4452), which no information on marking was recorded, is excluded from  
 c), d) Marker no. 6860 was recovered in the year 1959. Markers of nos. 6859 and 7269

TABLE 30. NUMBER OF FINBACK WHALES TAKEN BY JAPANESE FLEET IN VARIOUS AREAS AROUND ALEUTIAN ISLANDS AND BERING SEA

Year	Area						Sum
	Off Kamchatka	East Aleutian		North of Pribilof	Off Navarin	Off Olyutorskiy	
		South	North				
1952	213						213
53	470						470
54	564	168	584				1316
1955	148	35	1177				1360
56	595	46	774				1415
57	280	500	286	158	174	6	1404
58	269	442	298		275	47	1331
59	694	53	703				1450
Sum	3233	1244	3822	158	449	53	8959

IN THE VARIOUS AREAS AROUND ALEUTIAN ISLANDS, 1953~1959

North of Pribilof and off Navarin							Sum of recapture	Number of whales marked		Remark
1953	54	55	56	57	58	59		recorded as 'Hit', $T_i^{a)}$	corrected $T_i \times 1/g$	
--	--	--	--	--	--	--	2	21 <sup>1)</sup>	26.2	
--	--	--	--	--	--	--		4	5.0	
--	--	--	--	--	--	--	2	3 <sup>2)</sup>	3.7	
--	--	--	--	--	--	--		1	1.2	
--	--	--	--	--	--	--	2	2	2.5	
--	--	--	--	--	--	--		28	34.9	
--	--	--	--	--	--	--		0	0.0	
--	--	--	--	--	--	--		0	0.0	
--	--	--	--	--	--	--	1	17 <sup>3)</sup>	21.2	One whale (mark no. J6149) recaptured from areas B or C in 1958, is not included in no. of recapture.
--	--	--	--	--	--	--	3	15	18.7	
--	--	--	--	--	--	--		16	20.0	
--	--	--	--	--	--	--	1	10	12.5	Two markers of no. 6860 & 6859, recovered from cooker, are not included in no. of recovery <sup>c)</sup> .
--	--	--	--	--	--	--		8	10.0	
--	--	--	--	--	--	--		10	12.5	
--	--	--	--	--	--	--		0	0.0	
--	--	--	--	--	--	--	22	206 <sup>b)</sup>	256.6	One marker of no. 7269, recovered from refrigerated ship, is not included in no. of recovery <sup>d)</sup> .
--	--	--	1	--	--	--	9	32	39.9	
--	--	--	--	--	--	--	4	57	71.0	
--	--	--	1	--	--	--	12	33 <sup>4)</sup>	41.0	
--	--	--	--	--	--	--	2	28	34.9	
--	--	--	--	--	--	--	4	15 <sup>5)</sup>	18.7	
--	--	--	--	--	--	--		0	0.0	
--	--	--	--	--	--	--		3	3.8	
--	--	1	--	--	--	--	1	1	1.2	
--	--	--	--	--	--	--		0	0.0	
--	--	1	--	--	--	--	1	9	11.2	
--	--	--	--	--	--	--		0	0.0	
--	--	--	--	--	--	--		0	0.0	
4							66	519 <sup>b)</sup>	646.7	

whales not recorded as 'Hit' in each of 1), 2), 3), 4), 5) and four those in 6) respectively. number of marking and recapture. were recovered in the same year of marking.

TABLE 31. RATE OF RECOVERY OF MARKERS\*

	Fin whale		Humpback whale		Sperm whale	
	no. of hit	no. of recovery	no. of hit	no. of recovery	no. of hit	no. of recovery
With streamer	21	15	2	1	11	10
Without streamer	35	21 <sup>1)</sup>	3	3	20	18 <sup>2)</sup>

1) Includes four markers recovered from refrigerated ship.

2) Includes two markers recovered from refrigerated ship.

\* Cited from Kawakami & Nasu (1956).

corded as 'Hit' and from those not so recorded. Then  $g$  was calculated from Table 31 as a rate of number of whales recaptured from the former against total number of recapture, that is,  $g = \frac{66-9}{66+4+1} = \frac{57}{71} = 0.803$  ( $1/g$  correction). This denominator includes four whales of which localities

recaptured are indefinite and one whale recaptured from those on which no information is recorded at the time of marking.

$C'$  in formula 5 was calculated from number of catch  $C$  in each year which were given in Table 30. While initial stock at the year of marking gradually decreases with lapse of years through natural mortality and catch, it is recruited from younger generation in population. If stock number, number of recruitment and number of survivor of initial stock at the year of marking are represented as follows, stock in each year consists of survivor and recruit, and rate of recruit  $r$  and survival rate  $S$  have constant figures through full period of investigation, then formulas 7, 8 and 9 can be introduced.

Lapse of year after marking	0	1	2	...	$x$
Stock number	$N_0$	$N_1$	$N_2$	...	$N_x$
Number of annual recruitment		$R_1$	$R_2$	...	$R_x$
Number of survivor of initial stock when marked		$N_1'$	$N_2'$	...	$N_x'$

$$r = \frac{R_1}{N_1} = \frac{R_2}{N_2} = \dots = \frac{R_x}{N_x}, \quad (7)$$

$$S = \frac{N_1 - R_1}{N_0} = \frac{N_2 - R_2}{N_1} = \dots = \frac{N_x - R_x}{N_{x-1}}, \quad (8)$$

$$N_x' = N_0 \cdot S^x. \quad (9)$$

From formulas 7 and 8,  $N_x = N_0 \left( \frac{S}{1-r} \right)^x$ . Eliminating  $N_0$  from this relation and formula 9,

$$N_x' = N_x (1-r)^x. \quad (10)$$

If survival rates in sample of catch represent those of whole population,

$$\frac{C_x'}{C_x} = \frac{N_x'}{N_x} = (1-r)^x. \quad (11)$$

When stock is in a stabilized state,  $S+r=1$ . From this relation and formula 11,

$$C_x' = S^x \cdot C_x. \quad (12)$$

Survival rates  $S$  used for formula 12 are estimated from frequency distributions of number of corpus albicans in pregnant females taken and from those of number of lamination of ear-plug in each area. Data on ovaries used include major part of pregnant females taken during from 1952 to 1959, and data on ear-plug used base on the results collected in the three years 1957, 58 and 59 as shown in Table 32 and 34. At first it was discussed whether figures of survival rate

show significant differences or not during periods from 1952 to 1959 in which Japanese pelagic whalings have been operated. As regards averaged number of ovulation in a breeding cycle, Laws & Purves (1956) offered figure of approximate 2.8 for Atlantic finbacks, Purves & Mountford (1959) obtained approximately same figure for Antarctic finbacks. While, Nishiwaki et al. (1958) reported figures of 1.6 and 1.8 for the North Pacific and Antarctic finbacks respectively, so that significant discrepancy between results reported by both authors for Antarctic finbacks. In relation to this problem Laws (1960) states, 'There is still some uncertainty about the interpretation of the lamination of ear-plug at present.' Therefore age composition are obtained from frequency distribution of number of corpus albicans shown in Table 32 for two cases in which averaged number of ovulation is 1.6 or 2.8, and total survival rate  $S$  is calculated from these age compositions in two cases as rate of sum of five years' and older survivors against sum of four years' and older survivors as shown in Table 33. In Figure 5 survival curves for whole areas around Aleutian Islands against averaged number of ovulation 1.6 are drawn separately for three successive periods of years 1952-55, 1956-57, and 1958-59. Total survival rates for these three periods reveal gradual increase as shown by figures 0.8783, 0.9008 and 0.9095. Even if selective catching larger whales would effect upon the above-stated trend because of steadiness in whaling operation in recent years, it might be impossible to conclude that the north Pacific finback stock have depleted remarkably at present. After discussing separately by areas A, B and C, same trends can be clearly recognized. Of course these facts can be seen also in another case that averaged number of ovulation is 2.8 as shown in Table 35. In consequence, it may be possible for convenience of calculation to regard that the north Pacific finback stocks are nearly in a stabilized state. Then,  $C'_x$  in formula 5 will be calculated by formula 12, and total survival rates  $S$  can be given as averaged figures through whole periods for various areas. Total survival rates calculated from frequency distribution of number of lamination of ear-plug are shown in Table 35. It can be seen from this table that these figures are mostly consistent with those calculated from ovarian data in a case of averaged number of ovulation 1.6. According to Baranov (1918) mortality rates of a population may be calculated from the slope of the right limb of a frequency curve of ages. But frequencies of occurrence at peak and successive older several age groups in right limb of this curve drawn by ear-plug data may be assumed to be not representative of population because of size limitation in regulation of whaling. Therefore, number of survivors in these age groups were corrected by geometrical mean of survival rate calculated

from successive older three age groups. Total survival rate  $S$  was obtained as rate of survivors of age group  $t_{c+1}$  and older against those of minimum catchable age  $t_c$  and older. No significant difference in figure

TABLE 32. FREQUENCY DISTRIBUTION OF NUMBER OF CORPUS ALBICANS

No. of corpora albicans	Off Kamchatka (A)				South of east Aleutian (B)			
	1952~54	1955~56	1957~59	Sum	1954~55	1956~57	1958~59	Sum
0	23	13	25	61	6	12	10	28
1	26	9	20	55	11	9	16	36
2	30 25.6	9 10.2	21 22.6	60 58.4	4 5.2	16 12.4	7 8.6	27 26.2
3	28 25.0	7 10.4	27 22.8	62 58.2	3 5.0	16 12.4	4 8.2	23 25.6
4	21 24.0	13 10.2	20 21.2	54 55.4	2 3.4	9 12.4	6 7.4	17 23.2
5	20 21.4	14 11.8	16 20.4	60 53.6	5 3.4	12 11.6	8 7.2	25 22.2
6	21 19.4	8 10.8	12 18.6	41 48.8	3 3.8	9 10.0	12 7.0	24 20.8
7	17 18.0	17 9.8	17 20.0	51 47.8	4 3.6	12 9.6	6 6.8	22 20.0
8	18 16.2	2 8.8	18 18.0	38 43.0	5 3.0	8 8.8	3 5.8	16 17.6
9	14 13.6	8 8.4	27 18.2	49 40.2	1 3.0	7 8.6	5 4.0	13 15.6
10	11 10.8	9 5.6	16 17.6	36 34.0	2 2.2	8 7.6	3 3.8	13 13.6
11	8 7.6	6 5.8	13 15.8	27 28.6	3 1.2	8 6.4	3 3.8	14 11.4
12	3 5.6	3 4.6	14 11.6	20 21.8	1 1.2	7 5.2	5 3.0	12 9.4
13	2 3.8	3 3.6	9 9.8	14 17.2	0 0.4	2 5.0	3 2.6	5 7.0
14	4 2.4	2 3.2	6 8.0	12 13.6	1 0.4	1 2.6	1 2.0	3 5.0
15	2 2.2	4 2.4	7 5.8	13 10.4	0 0.6	2 1.6	1 1.0	3 3.2
16	1 1.8	2 2.0	4 4.8	7 8.6	1 0.6	1 1.2	0 0.4	2 2.2
17	2 1.0	1 1.6	3 3.6	6 6.2	1 0.4	2 1.2	0 0.2	3 1.8
18	0 0.6	1 1.0	4 2.4	5 4.0	0 0.4	1 1.0		1 1.4
19	0 0.4	0 0.8	1 1.6	2 2.8	0 0.4	1 1.0		1 1.4
20		1 0.6	1 1.2	2 1.8	0 0.2	1 0.6		1 0.8
21	0 0.2	1 0.4	0 0.4	1 1.0	1 0.2	1 0.6		2 0.8
22	0 0.2	0 0.4	1 0.4	1 1.0	0 0.2	0 0.6		0 0.8
23	1 0.2	1 0.4	0 0.2	1 0.8	0 0.2	1 0.4		1 0.6
24	0 0.2	0 0.2	0 0.2	0 0.6		0 0.2		0 0.2
25	0 0.2	0 0.2		1 0.4		0 0.2		0 0.2
26		0 0.2		0 0.2				
27		0 0.2		0 0.2				
28								
29								
30								
31						0 0.2		0 0.2
32						0 0.2		0 0.2
33						1 0.2		1 0.2
34		0 0.2		0 0.2		0 0.2		0 0.2
35		0 0.2		0 0.2		0 0.2		0 0.2
36	1 0.2	0 0.2	1 0.2	2 0.4				
37		0 0.2		0 0.2				
38		0 0.2		0 0.2				
39								
40	0 0.2			0 0.2				
41	0 0.2			0 0.2				
42	1 0.2			1 0.2				
43	0 0.2			0 0.2				
44	0 0.2			0 0.2				

$S$  was seen in two cases which three or four age were adopted as minimum catchable age  $t_c$ . As total survival rates calculated from ear-plug's data were consistent with one of two those calculated from ovarian data, figures calculated from only ovarian data were used for actual calculation of formula 12.





legal limit will recruit into catchable stock three years after marking. Therefore it may be mostly enough to make correction on number of catch and number of whales recaptured in one and two years after marking.  $e_1 e_2 C'_1$ ,  $e_1 e_2 R_1$  and  $e_2 C'_2$ ,  $e_2 R_2$  will be used in formula 5 instead

TABLE 33. NUMBER OF SURVIVOR AND DEATH OF FEMALE NUMBER OF CORPUS ALBICANS

Age	Off Kamchatka (A)				South of east Aleutian (B)			
	1952~54	1955~56	1957~59	Sum	1954~55	1956~57	1958~59	Sum
	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death	no. of survivor no. of death
4	284 12	146 7	246 9	626 18	51.8 2.6	141 6	91.5 4.2	283 12
5	272 13	139 5	237 8	608 23	49.2 2.4	135 5	87.3 4.1	271 12
6	259 14	134 8	229 8	585 15	46.8 2.4	130 5	83.2 4.1	259 12
7	245 22	126 7	221 7	570 16	44.4 2.0	125 5	79.1 3.1	247 12
8	223 5	119 6	214 6	554 19	42.4 2.1	120 6	76.0 3.5	235 11
9	218 14	113 4	208 6	535 23	40.3 1.9	114 6	72.5 3.0	224 11
10	204 15	109 10	202 5	512 24	38.4 2.1	108 6	69.5 4.0	213 10
11	189 16	99 7	197 5	488 26	36.3 1.9	102 6	65.5 4.3	203 13
12	173 17	92 8	192 6	462 28	34.4 2.6	96 5	61.2 6.0	190 14
13	156 19	84 7	186 7	434 30	31.8 2.7	91 6	55.2 5.5	176 15
14	137 20	77 8	179 8	404 42	29.1 3.4	85 6	49.7 4.7	161 17
15	117 24	69 9	171 9	362 48	25.7 5.5	79 8	45.0 5.0	144 17
16	93 21	60 8	162 15	314 49	20.2 6.6	71 8	40.0 4.0	127 18
17	72 18	52 8	147 28	265 57	13.6 4.2	63 9	36.0 4.0	109 17
18	54 14	44 5	119 20	208 39	9.4 1.9	54 10	32.0 3.9	92 18
19	40 9	39 6	99 15	169 27	7.5 1.3	43 12	28.1 6.4	74 17
20	31 10	33 5	84 16	142 22	6.2 0.7	31 10	21.7 6.4	57 16
21	21 4	28 6	68 12	120 19	5.5 1.0	21 4	15.3 6.1	41 11
22	17 4	22 3	56 11	101 17	4.5 0.5	17 4	9.2 4.4	30 8
23	13 2.5	19 4	45 9	84 17	4.0 0.4	13 2	4.8 2.5	22 4
24	10.5 2.0	15 3	36 9	67 14	3.6 0.3	11 1	2.3 1.5	18 3
25	8.5 2.0	12 2.5	27 6	53 20	3.3 0.5	10 1.5	0.8 0.8	15 2
26	6.5 2.0	9.5 1.5	21 6	33 11	2.8 0.3	8.5 1	0.0	13 2
27	4.5 0.5	8 1.5	15 4	22 7	2.5 0.3	7.5 0.5		11 1
28	4.0 0.5	6.5 1.5	11 4	15 4	2.2 0.3	7 1		10 1
29	3.5 0.5	5 0.5	7 3	11 3	1.9 0.4	6 1		9 1
30	3.0 0.5	4.5 1.0	4 2	8 2	1.5 0.3	5 0.5		8 1
31	2.5 0.3	3.5 0.5	2 1	6 2	1.2 0.4	4.5 1		7 2
32	2.2 0.2	3 0.2	1 0.5	4 1	0.8 0.2	3.5 1		5 1.5
33	2.0 0.4	2.8 0.3	0.5 0.3	3 1	0.6 0.3	2.5 1		3.5 1.3
34	1.6 0.2	2.5 0.5	0.2 0.2	2 1	0.3 0.1	1.5 0.5		2.2 0.2
35	1.4 0.4	2 0.2	0.0	1 0.5	0.2 0.2	1 0.5		2 1.0
36	1.0 1.0	1.8 1.8		0.5 0.5	0.0	0.5 0.5		1 1.0
37	0.0	0.0		0.0		0.0		0

of  $C'_1$ ,  $R_1$  and  $C'_2$ ,  $R_2$ , where  $e_1$  and  $e_2$  can be obtained approximately as follows.

$$e_1 = \frac{1}{\text{total survival rate for age groups older than two years of the stock}}$$

$$e_2 = \frac{1}{\text{total survival rate for age groups older than three years of the stock}}$$

However, survival curve has not been obtained for these younger part of the stock from data observed. Therefore, adopting the figure of death rate of 0.025, which was estimated arbitrarily for younger age groups by Ottestad (1956), against two and three age groups, calculation

FINBACKS, ESTIMATED BY FREQUENCY DISTRIBUTION OF OF PREGNANT FEMALES

North of east Aleutian (C)								Sum of three areas							
1954~55		1956~57		1958~59		Sum		1952~55		1956~57		1958~59		Sum	
no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death	no. of survivor	no. of death
536	43	278	27	212	14	1010	60	904	56	564	36	506	31	1960	120
493	45	251	28	198	16	950	90	848	64	528	40	475	27	1840	120
448	42	223	28	182	15	860	70	784	60	488	36	448	34	1720	120
406	46	195	33	167	8	790	90	724	64	452	38	414	26	1600	130
360	48	162	33	159	18	700	100	660	60	414	42	388	16	1470	110
312	46	129	26	141	13	600	90	600	56	372	37	372	11	1360	120
266	47	103	24	128	14	510	90	544	64	335	29	361	12	1240	100
219	42	79	12	114	12	420	70	480	56	306	24	349	19	1140	120
177	43	67	9	102	13	350	60	424	64	282	22	330	26	1020	110
134	36	58	7	89	14	290	60	360	68	260	22	304	34	910	110
98	25	51	5	75	14	230	50	292	52	238	20	270	37	800	100
73	18	46	5	61	16	180	40	240	56	218	20	233	28	700	100
55	16	41	4	45	10	140	30	184	48	198	21	205	33	600	100
39	11	37	5	35	9	110	20	136	37	177	21	172	30	500	90
28	8	32	4	26	7	90	20	99	31	156	24	142	22	410	80
20	7	28	5	19	3	70	20	68	20	132	22	120	20	330	70
13	4	23	3	16	3	50	8	48	12	110	22	100	20	260	60
9	2	20	4	13	1	42	4	36	8	88	18	80	17	200	40
7	1.5	16	3	12	1.5	38	8	28	6	70	13	63	13	160	20
5.5	0.5	13	2	10.5	0.5	30	2	22	2	57	10	50	12	140	30
5	0.5	11	3	10	0.8	28	4	20	4	47	7	38	8	110	20
4.5	0.5	8	1.5	9.2	0.2	24	2	16	4	40	7	30	7	90	20
4	0.3	6.5	1.5	9	0.0	22	2	12	1	33	6	23	5	70	10
3.7	0.6	5	1	9	0.0	20	1	11	3	27	4	18	2	60	10
3.1	0.1	4	1	9	0.0	19	2	8	1	23	5	16	2	50	10
3	0.2	3	1	9	0.4	17	2	7	1	18	4	14	1	40	10
2.8	0.3	2	0.2	8.6	0.6	15	3	6	2	14	3	13	1	30	5
2.5	0.3	1.8	0.4	8	0.4	12	2	4	1	11	3	12	2	25	5
2.2	0.2	1.4	0.4	7.6	0.6	10	1	3	1	8	2	10	1	20	5
2.0	0.2	1	0.5	7	1.0	9	2	2	1	6	1	9	1	15	5
1.8	1.8	0.5	0.5	6	1.0	7	2	1	1	5	1	8	2	10	5
0.0		0.0		5	1.0	5	2	0		4	1	6	1	5	5
				4	1.0	3	1			3	1	5	1	0	
				3	1.0	2	1			2	1	4	2		
				2	1.0	1	1			1	1	2	1		
				1	1.0	0				0		1			
				0								0			

will be given as follows.

Age	Number of survivor	Number of death	Death rate
2	$a_2$	$a_2 - a_3$	0.025
3	$a_3$	$a_3 - a_4$	0.025
4	$a_4$	$a_4$	$1 - S$
older than 5	$a_5$		

TABLE 34. FREQUENCY DISTRIBUTION OF NUMBER OF LAMINATION OF EAR-PLUG OF THE NORTH PACIFIC FIN WHALES, SUM OF MALES AND FEMALES TAKEN DURING FROM 1957 TO 1959

No. of lamination of ear-plug	Off Kamchatka (A)		South of east Aleut. (B)		North of east Aleut. (C)	
	observ.	smooth.	observ.	smooth.	observ.	smooth.
2~ 3	0		0		4	
4~ 5	14		5		45	
6~ 7	34		13		87	
8~ 9	23	24.6	15	16.2	95	68.6
10~ 11	30	25.0	23	18.2	66	67.2
12~ 13	22	22.2	25	19.2	50	55.2
14~ 15	16	23.4	15	18.6	38	42.8
16~ 17	20	22.0	18	17.2	27	36.2
18~ 19	29	22.4	12	16.6	33	30.6
20~ 21	23	23.2	16	16.6	33	27.2
22~ 23	24	23.6	22	15.4	22	26.8
24~ 25	20	21.0	15	15.6	21	24.0
26~ 27	21	19.8	12	13.6	25	21.0
28~ 29	16	20.2	13	12.4	19	19.0
30~ 31	17	21.4	6	11.8	18	18.0
32~ 33	26	19.0	16	11.6	12	15.0
34~ 35	26	19.2	12	10.6	16	14.6
36~ 37	10	12.6	11	11.0	10	14.2
38~ 39	17	14.4	8	9.4	17	13.6
40~ 41	9	11.6	8	8.0	16	13.0
42~ 43	10	10.8	8	7.6	9	12.2
44~ 45	12	9.6	5	5.8	13	9.8
46~ 47	6	9.4	4	4.4	6	7.4
48~ 49	11	8.8	3	3.8	5	6.4
50~ 51	8	7.6	2	3.2	4	4.8
52~ 53	7	7.0	5	3.0	4	4.4
54~ 55	6	5.2	2	3.4	5	4.0
56~ 57	3	4.0	3	3.4	4	3.4
58~ 59	2	3.4	5	2.6	3	3.8
60~ 61	2	2.8	2	2.4	1	3.0
62~ 63	4	2.4	1	1.8	6	2.6
64~ 65	3	2.6	1	0.8	2	2.6
66~ 67	1	2.4	0	0.8	2	2.8
68~ 69	3	2.2	0	0.6	3	2.4
70~ 71	1	1.8	2	0.4	2	3.0
72~ 73	3	2.6	0	0.4	4	2.8
74~ 75	1	2.6	0	0.8	5	2.6
76~ 77	5	3.2	0	0.8	0	2.4
78~ 79	2	2.8	2	0.8	2	1.8
80~ 81	4	2.8	2	1.0	1	1.2
82~ 83	1	2.0	0	1.0	1	1.2
84~ 85	1	1.6	1	0.6	1	1.0
86~ 87	1	0.8	0	0.4	1	0.8
88~ 89	1	0.8	0	0.2	1	0.8
90~ 91	0	0.6	1	0.2	0	1.0
92~ 93	1	0.6		0.2	1	0.8
94~ 95	0	0.4		0.2	2	0.8
96~ 97	1	0.4		0.2	0	0.8
98~ 99	0	0.2			1	0.8
100~101	0	0.6			1	0.4
102~103	0	0.4				0.4
104~105	2	0.4				0.2
106~107		0.4				0.2
108~109		0.4				0.4
110~111		0.0				0.0

, then

$$a_2 = \frac{1-S}{S} \cdot \frac{a_5}{(0.975)^2}, \quad a_3 = \frac{1-S}{S} \cdot \frac{a_5}{0.975}, \quad a_4 = \frac{1-S}{S} \cdot a_5.$$

In consequence,

$$e_1 = \frac{a_2 + a_3 + a_4 + a_5}{a_3 + a_4 + a_5} = \frac{3.001 - 2.026 \cdot S}{1.975 - S}, \quad e_2 = \frac{a_3 + a_4 + a_5}{a_4 + a_5} = \frac{1.975 - S}{0.975}. \quad (13)$$

Figures  $e_1$  and  $e_2$  will be given after adopting those of  $S$  in Table 35 to formula 13. As in this case figures of  $S$  in any areas A, B and C give approximately same results to  $u$  in formula 5, averaged value by area around Aleutians was used. In consequence figures of  $e_1 e_2 = 1.4$ ,

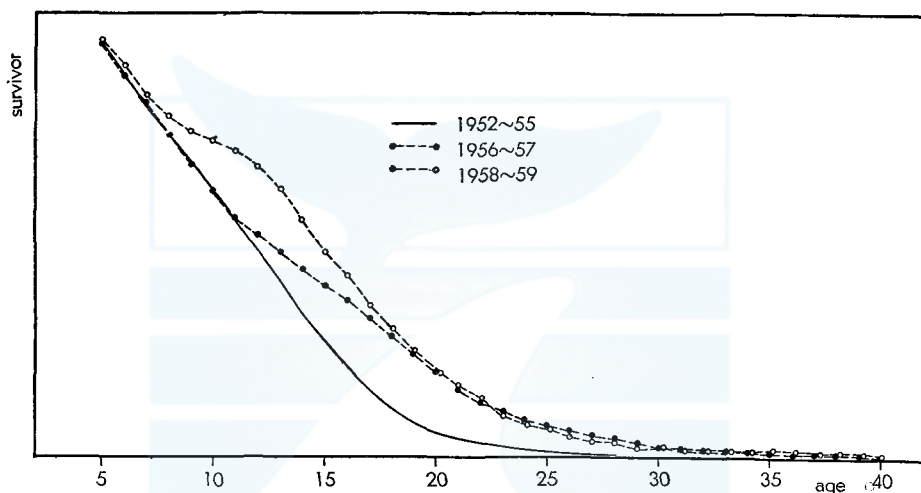


Fig.5. Age composition of the North Pacific Fin whales, estimated from distribution of frequency of corpus albicans of pregnant females.

TABLE 35. SURVIVAL RATES (S) OF THE NORTH PACIFIC FINBACKS

	Off Kamchatka (A)	East Aleutian		Whole area	
		south (B)	north (C)		
I	Season 1	.8261	.8386	.7505	.7914
	Season 2	.8490	.8562	.7496	.8248
	Season 3	.8729	.8609	.8075	.8440
	Average	.8573*	.8481	.7589*	.8192
II	Season 1	.9010	.9079	.8564	.8783
	Season 2	.9131	.9175	.8534	.9008
	Season 3	.9274	.9108	.8891	.9095
	Average	.9194*	.9133	.8714*	.8962
III	.9397	.9140	.8730	—	

Figures in columns I and II are calculated from freq. distribution of no. of corpus albicans of pregnant females as the average number of ovulation of 2.8 or 1.6 in one breeding season. Figures in column III are calculated from freq. distribution of no. of lamina of ear-plug.

Seasons 1, 2 and 3 correspond to three periods of 1952~54, 1955~56, and 1957~59 in area A, those of 1954~55, 1956~57, and 1958~59 in areas B and C and those of 1952~55, 1956~57, and 1958~59 in whole area.

\* These figures are used for calculation in formula 12 as survival rate (S).

$e_2=1.2$  and  $e_1e_2=1.2$ ,  $e_3=1.1$  were obtained against two cases of averaged number of ovulation 2.8 and 1.6 respectively. Thus various coefficients necessary for calculation of formulas 5 and 6 were obtained.

It should be discussed here that whether marked whales show random distribution in the stock, to which they belong, or not in various areas. For this purpose whether rate of recapture of marked whales fluctuate little or not from year to year were examined firstly on the data on 206 whales which were recorded as 'Hit' in area C in 1954. Table 36 shows

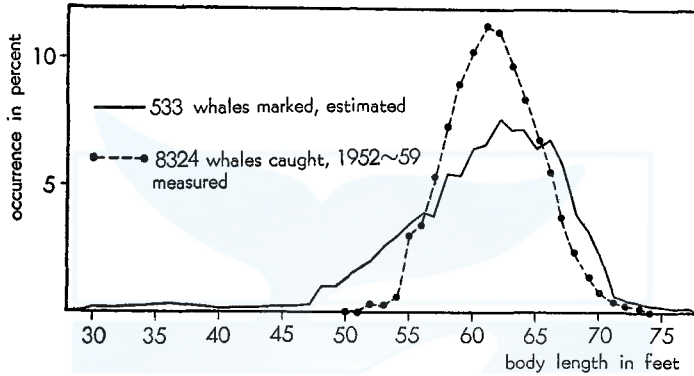


Fig. 6. Comparison of size distributions of whales caught (measured) and marked (estimated).

number of whales recaptured, number of catch and rate of recapture calculated from formula 5 for five years during from one year (1955) and five years (1959) after marking. But no  $1/f$  correction is made in those calculations. It can be seen from this table that yearly fluctuations of rate of recapture are very small as shown by figures of  $u=0.007300 \pm 0.000455$  and  $0.005950 \pm 0.000465$  against two cases of averaged number of ovulation 2.8 and 1.6. Number of whales recaptured from 1000 whales of annual catch are given by formula 14.  $y$  means number of whales recaptured in each year, and  $Y$  means total number of those, and I II correspond to two cases of averaged number of ovulation 2.8 and 1.6.

$$\left. \begin{aligned} y &= 7.30 \times 0.7589^x \\ Y &= 22.98(1 - 0.7589^x) \end{aligned} \right\} \text{I} \qquad \left. \begin{aligned} y &= 5.95 \times 0.8714^x \\ Y &= 40.32(1 - 0.8714^x) \end{aligned} \right\} \text{II} \qquad (14)^*$$

\* These formulas are given in general as follows.

$$y = 1000u \cdot S^x$$

, and

$$Y = 1000(u \cdot S + u \cdot S^2 + u \cdot S^3 + \dots + u \cdot S^x) = 1000 \frac{u \cdot S}{1 - S^x} (1 - S^x) \qquad (15)$$

, where  $S$  means survival rate and  $u$  means rate of recapture of marked whales against annual catch. If marked whales distribute at random in the stock to which they belong,

$$u = T/N \qquad (16)$$

, where  $T$  is number of whales marked effectively and  $N$  means stock number.

Calculated figures of  $y$  and  $Y$  are shown in Table 37 and Fig. 7. In this table observed values are obtained from Table 36 directly and expected those are obtained from formula 14. Figure 7 shows that number of whales recaptured in each year fluctuate along expected curve, but that observed values in total number of those are highly consistent with expected values in general. Curve  $Y$  in averaged number of ovulation 2.8, however, seem to have too low values in five (and may be also in successive) years after making, and this should be discussed

TABLE 36. ANNUAL RECAPTURE FROM 206 WHALES MARKED IN THE AREA OF NORTH OF EAST ALEUTIAN (C) IN 1954

Year	$x$	$R_x$		$C_x$		$S^{(c)}$	$C_x'$	$\Sigma R_x$	$\Sigma C_x'$	$\Sigma R_x / \Sigma C_x'$	
		obs.	cor. <sup>d)</sup>	obs.	cor. <sup>d)</sup>						
I <sup>a)</sup>	1955	1	7	9.8	1177	1648	.7589	1251	9.8	1251	.007834
	56	2	2	2.4	774	929	.5759	535	12.2	1786	.006831
	57	3	1	1	286	286	.4371	125	13.2	1911	.006907
	58	4	1	1	298	298	.3317	99	14.2	2010	.007065
	59	5	3	3	703	703	.2517	177	17.2	2187	.007865
II <sup>b)</sup>	1955	1	7	8.4	1177	1412	.8714	1230	8.4	1230	.006829
	56	2	2	2.2	774	851	.7593	646	10.6	1876	.005650
	57	3	1	1	286	286	.6617	189	11.6	2065	.005617
	58	4	1	1	298	298	.5766	172	12.6	2237	.005633
	59	5	3	3	703	703	.5024	353	15.6	2590	.006023

Means & stand. deviat., \* .007300 ± .000455, \*\* .005950 ± .000465.

a), b) In columns I and II, figures for correction of  $R_x$ ,  $C_x$  and survival rate  $S$  used correspond to those in two cases that average no. of ovulation in a breeding season is 2.8 and 1.6 respectively, that is, survival rate  $S=0.7589$ ,  $e_1e_2=1.4$  and  $e_2=1.2$  for the former and  $S=0.8714$ ,  $e_1e_2=1.2$  and  $e_2=1.1$  for the latter.

with additional data hereafter. Thus, following conclusion can be introduced. Whales in area C in the year 1954, distribute uniformly in the stock which migrate to the same area in successive years after marking. Gradual decrease in number of whales recaptured in successive years are caused by dilution of original stock in the year of marking with approximately constant rate of annual recruit from younger generation of the stock, and dilution of stock by mingling with different populations could be hardly supposed.

Table 38 shows rates of recapture against one thousand whales of annual catch on whales marked in the years besides 1954. It can be seen from this table that rate of recapture for years 1954, 55 and 56 are well consistent with each other. But figure for year 1958 is two times of the former and figure for year 1957 is very high. As  $r_2^2$  is obtained finally as averaged value of  $u$  with weight, it is little effected by figure for the year 1958, but is remarkably effected by figure for the year 1957. Detailed records on marking and recovery of whales marked in this year are shown in Table 39. According to this table, six whales (dart nos. J6815, J6801, J6802, J6837, J6829,

J6843) out of those marked in neighbouring area each other for several days in this year are taken in neighbouring area again in the year 1958, and this fact cause to make rate of recapture remarkably high. Therefore, it is more appropriate to remove data on whales marked in 1957 from calculation of  $r_2^2$  and  $r_1^2$  through formula 6. Results of actual calculation will be described later.

TABLE 37. NUMBER OF RECAPTURE FROM 1000 WHALES OF ANNUAL CATCH

Year	Years after marking, $x$	No. of annual receipt., $y$			Sum. of recapt., $Y$		
		observ.	expect.		observ.	expect.	
			I	II		I	II
1955	1	5.9	5.5	5.2	5.9	5.5	5.2
56	2	2.6	4.2	4.5	8.5	9.7	9.7
57	3	3.5	3.2	3.9	12.0	12.9	13.6
58	4	3.4	2.4	3.4	15.4	15.3	17.0
59	5	4.3	1.8	3.0	19.7	17.1	20.0

On the other hand rate of recapture of whales marked in area A show remarkable annual fluctuations. This seems to be caused by not only scantiness of number of whales marked but also non-random distribution of marked whales in the stocks which migrate to this area from year to year; in other words, migratory ranges of different populations cover this area. Practically, however, various causes and mechanisms

TABLE 38. RATE OF RECAPTURE OF WHALES MARKED AND RECAPTURED IN THE AREA OF NORTH OF EAST ALEUTIAN FROM 1000 WHALES OF ANNUAL CATCH<sup>a)</sup>

Year, marked	$x$	$u_x$	$T_x - R_x'$	$u_x / T_x - R_x'$	Weight	Average value with weight		
						not exclude 1957 & 58	exclude 1957	exclude 1957 & 58
1954	1	5.947	243.08	.02447	5	.08699	.02836	.02659
55	2	1.003	35.88	.02795	4			
56	3	2.018	71.25	.02832	3			
57	4	17.379	37.13	.46806	2			
58	5	1.633	32.94	.04957	1			

a) Figure corrected for  $f$  and  $g$  and calculated for average number of ovulation 1.6.

of yearly fluctuations can not be analysed in detail as undertaken on those in area C because of scantiness of data, so that  $r_1^1$  and  $r_2^1$  were calculated from figures of  $u$  in each year through formula 6.

Calculated results of rate of recapture of whales marked in areas A, B and C are shown in Tables 40, 41 and 42. Table 40 shows comparison by two cases of averaged number of ovulation 1.6 and 2.8 in a breeding season which were adopted for calculation of survival rate from frequency distribution of number of corpus albicans of pregnant whales. It can be seen from this table that individual values of rate of recapture in case



of averaged number of ovulation 2.8 are somewhat higher than those in another case, but there is little difference in their relative values. Table 41 show comparison by two cases before and after  $1/g$  and  $1/f$  corrections. It may be seen in this comparison also that despite of

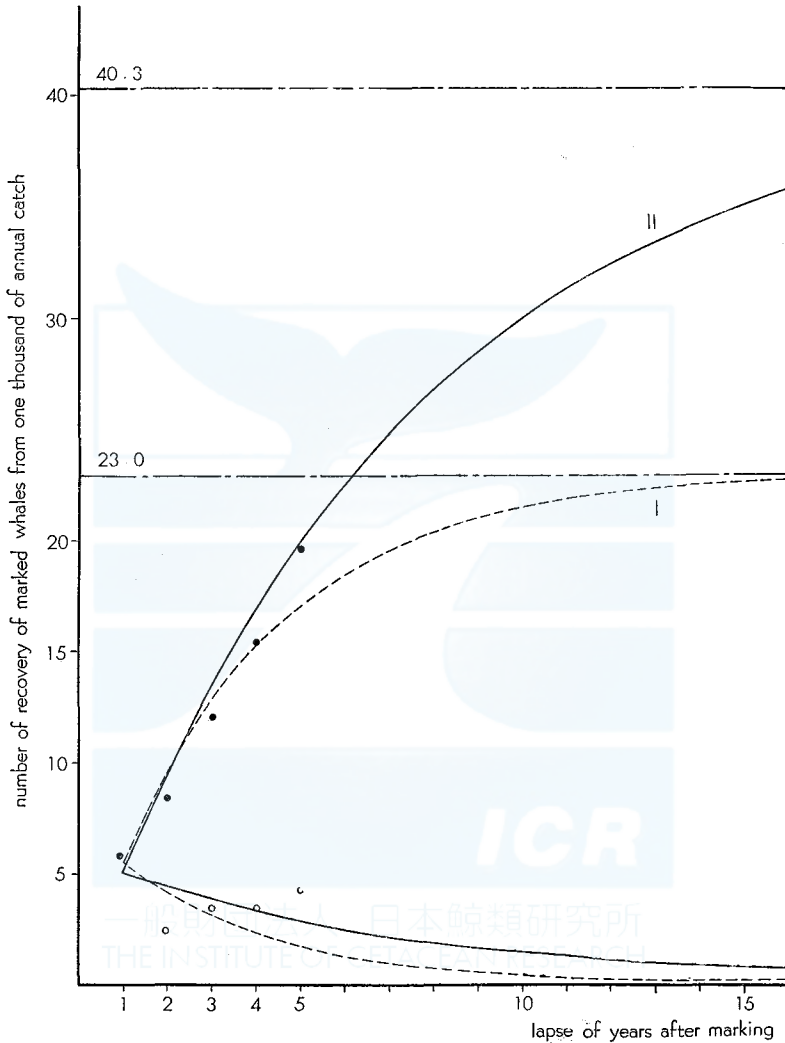


Fig 7. Annual recovery of whales marked in 1954 (206 whales marked) in the area C, north of east Aleutian, showing two cases I and II against survival rates of 0.7589 and 0.8714 respectively.

tolerable difference in individual values of rate of recapture, there is little difference in relative values. According to above-stated facts it can be concluded that errors in estimated values of averaged number of ovulation,  $g$  and  $f$  hardly effect on the results of rates of emigration.

In Tables 40 and 41 localities of recapture of two whales out of those marked in area B are indefinite, because their markers were recovered from oil-cooker or oil-separator of factory ship after treatment of whale

TABLE 39. REMARKS ON WHALES MARKED IN THE AREA OF NORTH OF EAST ALEUTIAN IN 1957 AND RECAPTURED IN SUCCESSIVE YEARS

, marked			, recaptured				
Date	Locality	No. of whales <sup>1)</sup>	No. of whales	Dart no.	Date	Locality	Area <sup>2)</sup>
June 10, 1957	( 55N 168~9W)	4	1	7269	June~July, 1957	NI <sup>3)</sup>	B or C <sup>6)</sup>
" 11, "	( 54N 168W)	1	1	7263	July 30, 1959	( 53N 168~169W)	C <sup>7)</sup>
" 25, "	( 54N 170W)	2					
" 29, "	( 55N 168W)	2					
July 6, "	( 56N 170W)	1	1	J 6506	Aug. 11, 1957	( 63N 178W)	off Navarin <sup>8)</sup>
Sept. 7, "	( 54N 167W)	2	1	J 6788 <sup>4)</sup>	June 30, 1959	( 53N 177~178W)	C
" 8, "	( 54N 168W)	3					
" 9, "	( 54N 169W)	2					
" 10, "	( 54N 168W)	6	4	* J 6815	July 4, 1958	( 54N 170W)	C
				* J 6801	" 11, "	( 54N 169W)	C
				* J 6802	" 11, "	( 54N 169W)	C
				J 6799	" 16, "	( 50N 170W)	B
" 11, "	( 54N 167W)	10	5	* J 6837 <sup>5)</sup> ( J 6831)	" 3, "	( 53N 169W)	C
				* J 6829	" 8, "	( 54N 166W)	C
				* J 6843	" 8, "	( 54N 166W)	C
				J 6807	" 9, 1959	( 53N 169W)	C
				J 6834	May 27, 1958	( 52N 171E)	A

1) number of whales recorded as 'Hit' only when marked, 2) areas temporarily classified as A (off Kamchatka), B (south of east Aleutian) and C (north of east Aleutian), 3) NI, no detailed information obtained, 4) recovered from whales recorded as 'Possible hit' when marked, 5) two markers in one whale, 6) recovered from cooker, 7) 8) recovered from refrigerated ship.

body. One was marked in area B (54°42' N, 159°25' W) in July 18, 1956 (marker number J6149) and was recaptured in area B or C during from June 29 to July 11, 1958. Another was marked in area B (50° 37' N, 168°33' W) in June 17, 1958 (marker number 6860) but locality

of recapture is indefinite because its marker was recovered from oil-separator Aug. 17, 1959. Therefore, as shown in Tables 40 and 41 rate of recapture are calculated against four cases of combination which each of these two whales is recaptured in area B or C. As rate of recapture show remarkable difference by case, rate of emigration from areas B to C is not able to be discussed quantitatively so far. Rate of emigration from areas B to C, however, show tolerably high value in all four cases, so that it is obvious that whales migrate to area B are closely related to those migrate to area C and it is difficult at present to suppose existence of the third different populations migrate to the middle area besides east (II) and west (I) populations.

TABLE 40. COMPARISON OF RATES OF RECAPTURE OF MARKED WHALES PER 1000 OF ANNUAL CATCH BY CASE OF AVERAGE NUMBER OF OVULATION 1.6 OR 2.8<sup>1)</sup>

		for no. of ovul. 1.6: recaptured from area of			for no. of ovul. 2.8: recaptured from area of				
		Kam- chatka	s. of e. Aleut.	n. of e. Aleut.	Kam- chatka	s. of e. Aleut.	n. of e. Aleut.		
		Marked in area of	Kamchatka	.13541	.00000	.00307	.16106	.00000	.00426
south of east Aleut.	1 <sup>2)</sup> 2 3 4			.18125	.05371		.19465	.07374	
				.00000	.00753	.06742	.00000	.00807	.08948
					.17372	.06402		.18658	.08648
				.00000	.07773		.00000	.10222	
	n. of e. Aleut.	.02404	.02208	.08699	.02663	.02797	.10392		
$\frac{r_1^1}{r_1^1+r_2^1} : \frac{r_2^1}{r_1^1+r_2^1}$		.978 : .022			.974 : .026				
$\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$		.217 : .783			.204 : .796				

1) f, g corrected.

2) Figures in columns 1, 2, 3 and 4 show those for four cases in which two whales recaptured from B, B and C, C and B and C areas respectively.

In Table 29 whaling grounds in the northern part of north Pacific are temporarily divided into four areas. Among these, however, area off Navarin and Pribilof is closely related to area of north of east Aleutian (c) as shown by results of emigration of whales in the year of marking, so that rates of recapture are calculated for two cases in which Navarin-Pribilof area is put together to area C or not. Little difference in rate of emigration was seen between two cases. Then figure of  $r_1^1, r_2^1, r_1^2$  and  $r_2^2$  and rates of emigration  $\frac{r_1^1}{r_1^1+r_2^1} : \frac{r_2^1}{r_1^1+r_2^1}$  and  $\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$  were calculated for two cases including data on whales marked in area C in 1957 or not. Though significant differences are seen between these two cases, but the latter figures were used for the successive calculations

because of the reasons noted already (p. 123, l. 21-24). Figures of rate of emigration from areas A to C, 0.978:0.022 in table 42 show that west sides' population hardly migrate to area C. This fact confirm the existence of west and east sides' populations which was clarified by blood typing investigations already. In following paragraph gene frequencies and relative sizes of populations I and II will be calculated from rates of emigration and gene frequencies in various areas through formula 4, and averaged ratios of mingling of populations I and II in areas A, B and C will be given.

TABLE 41. COMPARISON OF RATE OF RECAPTURE OF MARKED WHALES PER 1000 OF ANNUAL CATCH BEFORE AND AFTER f AND g CORRECTIONS<sup>1)</sup>

		not corrected for f and g recaptured from area of			corrected for f and g recaptured from area of		
		Kam- chatka	s. of e. Aleut.	n. of e. Aleut.	Kam- chatka	s. of e. Aleut.	n. of e. Aleut.
Marked in area of	Kamchatka	.07617	.00000	.00384	.13541	.00000	.00307
	south of	$\left. \begin{matrix} 2 \\ 3 \\ 4 \end{matrix} \right\}^{12)}$	.20646	.06468	.00000	.18125	.05371
	east		.00941	.08023		.00753	.06742
	Aleut.		.19704	.07757		.17372	.06402
			.00000	.09312		.00000	.07773
	n. of e. Aleut.	.02744	.03151	.10473	.02404	.02208	.08699
$\frac{r_1^1}{r_1^1+r_2^1} : \frac{r_2^1}{r_1^1+r_2^1}$		.952 : .048			.978 : .022		
$\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$		.208 : .792			.217 : .783		

- 1) Figures calculated for average number of ovulation 1.6 per breeding season.
- 2) Figures in columns 1, 2, 3 and 4 correspond to those in previous table.

B. Estimation of ratios of mingling of populations I and II by means of rates of recapture of marked whales and blood type gene frequencies. As stated already, various figures in Table 42 were calculated, for convenience, under hypothesis that marking in areas A and C were carried out against unmingled populations I and II respectively. But actually whales in areas A and C should be regarded as mingled those of populations I and II. Therefore figures of right and left terms in ratio of  $\frac{r_1^1}{r_1^1+r_2^1} : \frac{r_2^1}{r_1^1+r_2^1}$  show upper and lower limits in probable values respectively, and figures of left and right terms in ratio of  $\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$  show upper and lower limits respectively. Ratio of  $\frac{r_1^1}{r_1^1+r_2^1} : \frac{r_2^1}{r_1^1+r_2^1} = .978 : .022$  in Table 42 may be substituted by 1.000 : .000 without giving significant difference to final results of rates of emigration.

TABLE 42. COMPARISON OF RATES OF RECAPTURE BETWEEN TWO CASES IN WHICH RECAPTURES FROM WHALES, MARKED IN THE AREA OF NORTH OF EAST ALEUTIAN IN 1957, ARE EXCLUDED OR NOT<sup>1)</sup>

Marked in area of	Recapture from whales marked in 1957 are			
	included recapt. from area of		not included recapt. from area of	
	Kam- chatka	north of e. Aleut.	Kam- chatka	north of e. Aleut.
{ Kamchatka	.13541	.00307	.13541	.00307
{ n. of e. Aleut.	.02404	.08699	.01673	.02836
$\frac{r_1^1}{r_1^1+r_1^2} : \frac{r_2^1}{r_1^1+r_2^1}$	.978 : .022		.978 : .022	
$\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$	.217 : .783		.371 : .629	

1) Figures corrected for f and g, and calculated for average number of ovulation 1.6 per breeding season.

On the other hand intact figure of  $\frac{r_1^2}{r_1^1+r_2^2} : \frac{r_2^2}{r_1^1+r_2^2}$  can be used, because population I hardly migrates to area C. Schematic relationships of mingling of populations I and II in areas A and C may be shown as Fig. 8. Gene frequencies in both three allele A and B systems were adopted to calculations. Relationships stated above will be formulated as follows.

In area A

$$\left. \begin{aligned}
 p_A &= \frac{r_1^1}{r_1^1+r_2^1} N_1 p_1 + \frac{r_1^2}{r_1^2+r_2^2} N_2 p_2 \\
 q_A &= \frac{r_1^1}{r_1^1+r_2^1} N_1 q_1 + \frac{r_1^2}{r_1^2+r_2^2} N_2 q_2 \\
 r_A &= \frac{r_1^1}{r_1^1+r_2^1} N_1 r_1 + \frac{r_1^2}{r_1^2+r_2^2} N_2 r_2
 \end{aligned} \right\} (16)$$

, and in area C

$$\left. \begin{aligned}
 p_C &= \frac{r_2^1}{r_1^1+r_2^1} N_1 p_1 + \frac{r_2^2}{r_1^2+r_2^2} N_2 p_2 \\
 q_C &= \frac{r_2^1}{r_1^1+r_2^1} N_1 q_1 + \frac{r_2^2}{r_1^2+r_2^2} N_2 q_2 \\
 r_C &= \frac{r_2^1}{r_1^1+r_2^1} N_1 r_1 + \frac{r_2^2}{r_1^2+r_2^2} N_2 r_2
 \end{aligned} \right\}$$

, where  $N_1$  and  $N_2$  are averaged relative sizes of populations I and II which actually migrate to areas A and C,  $p_1 q_1 r_1, p_2 q_2 r_2, p_A q_A r_A$  and  $p_C q_C r_C$  are blood type gene frequencies of populations I and II and those of areas A and C respectively. Results of various figures on populations I

and II calculated from this formula and figures in Tables 13 and 42 are shown in Table 43. It is obvious from Table 43 that there is no difference in gene frequencies of population II between two cases including marking data in 1957 or not, but that there is some difference in those of population I. Moreover relative sizes of populations I and II show

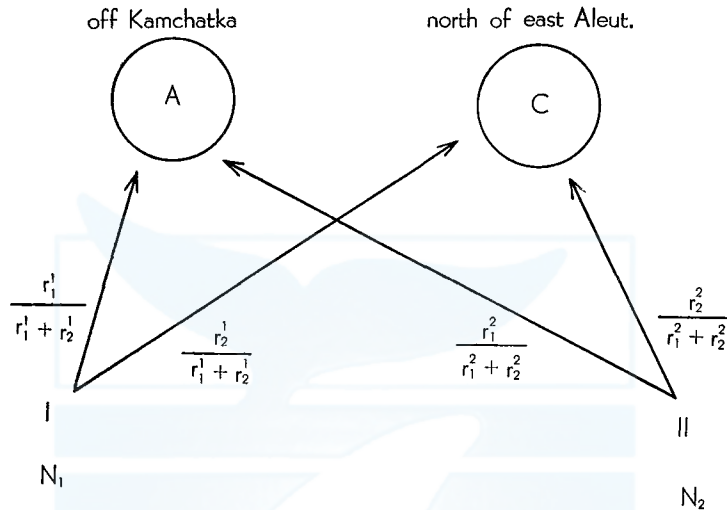


Fig. 8. Diagrammatic correlation between west (I) and east (II) populations estimated from the movements of marked whales.  $N_1$  and  $N_2$  mean relative size of each population actually migrate to areas A and C.

TABLE 43. GENE FREQUENCIES OF Ju BLOOD GROUPS AND RELATIVE STOCK NUMBER OF POPULATIONS I AND II

	Include recapture from whales marked in 1957		Exclude recapture from whales marked in 1957	
	popul. I	popul. II	popul. I	popul. II
A system	$p$	.075	.112	.026
	$q$	.500	.222	.869
	$r$	.425	.666	.105
B system	$p$	.575	.334	.896
	$q$	.043	.074	.002
	$r$	.382	.592	.102
Relative stock number	.74	1.26	.43	1.57

differences between both cases, and  $N_2$  is always larger than  $N_1$  as shown by  $N_2/N_1=1.7$  or  $3.7$ . Ratios of mingling of populations I and II in areas A and C are calculated from figures of  $N_1$  and  $N_2$  and those in Table 43 through formula 4 and mingling rate in area B is calculated from gene frequencies of populations I and II (Table 42). These results are shown in Tables 44 and 45. It can be seen from the latter table that the results show remarkable difference by allele systems A or B.

Ratios of mingling  $b$  and  $1-b$  in three alleles does not proportionate each other in A system, but approximately proportionate in B system. These facts were confirmed with chi-square tests of observed values against expected those in frequency of occurrence of phenotypes. Possibility of mingling shown in Table 44 is denied in A system but is affirmed in

TABLE 44. RATIO OF MINGLING OF POPULATIONS I AND II IN THE AREAS OFF KAMCHATKA, SOUTH AND NORTH OF EAST ALEUTIAN

		Kamchatka	S. of e. Aleut.		North of east Aleut.
			A system	B system	
Include recapture from whales marked in 1957	popul. I	.73	.51	.29	.02
	popul. II	.27	.49	.71	.98
Exclude recapture from whales marked in 1957	popul. I	.42	.29	.10	.01
	popul. II	.58	.71	.90	.99

TABLE 45. COMPARISON BETWEEN OBSERVED VALUE AND EXPECTED VALUE OF BLOOD GROUP GENE FREQUENCIES IN THE AREA OF SOUTH OF EAST ALEUTIAN

Allele system	Gene frequency		Ratio of mingl. <sup>1)</sup>		
	obs.	exp. <sup>2)</sup>	$b$	$1-b$	
Include recapture from whales marked in 1957	A $\begin{cases} p \\ q \\ r \end{cases}$	.071	.051	.92	.08
		.739	.681	.35	.65
		.190	.268	.27	.73
		average		.51	.49
	B $\begin{cases} p \\ q \\ r \end{cases}$	.810	.803	.27	.73
.017		.014	.36	.64	
.173		.183	.25	.75	
	average		.29	.71	
Exclude recapture from whales marked in 1957	A $\begin{cases} p \\ q \\ r \end{cases}$	.071	.051	.52	.48
		.739	.681	.20	.80
		.190	.268	.15	.85
		average		.29	.71
	B $\begin{cases} p \\ q \\ r \end{cases}$	.810	.818	.11	.89
.017		.024	.07	.93	
.173		.158	.13	.87	
	average		.10	.90	

1) ratio of mingling of populations I and II.

2) calculated from gene frequencies of populations I and II and averaged ratio of mingling.

B system. This fact confirm that B allele system can better interpret the results observed than A system as assumed already by quantitative comparisons of blood type gene frequencies only. But additional basic discussions on phenotype-genotype relationships should be undertaken hereafter before reaching definite conclusions on allele system. In present paper, for convenience, three allele B system and rates of emigration excluding marking data in 1957 are adopted finally. Then ratio of mingling in area B is obtained as  $m_{I,II}^B = .10 : .90$ . According to the results discussed above, it can be concluded that population I migrate to areas A and B but does hardly to area C, and population II migrate not only to area C but also to areas B and A, that is, migratory ranges of

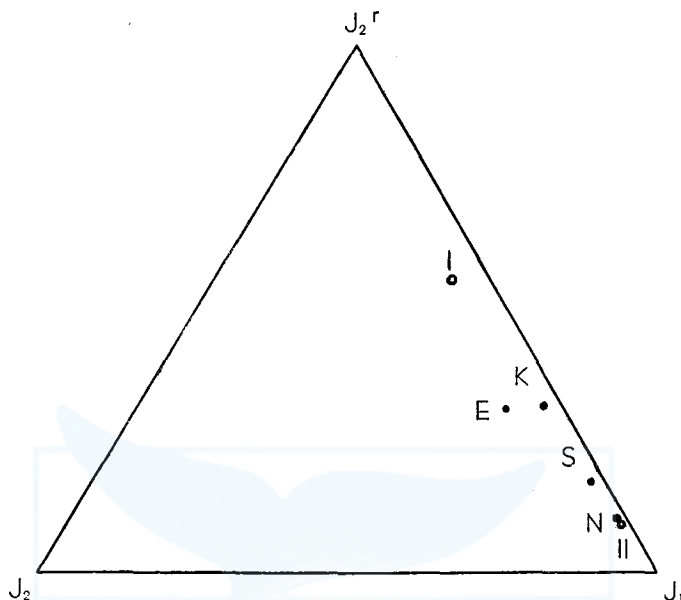


Fig. 9. Relative positions of the local populations of the North Pacific Finback whales in the triangular coordinates, expressed through the three allele B system of  $J_u$  blood group.

E: East China Sea                      S: South of east Aleut. (observed)  
 K: Kamchatka                            N: North of east Aleut.  
 I: Population I                          II: Population II

TABLE 46. SUMMARY OF VARIOUS FIGURES DISCUSSED IN THIS SECTION

a) Blood group gene frequencies<sup>1)</sup>

Gene freq.	$\begin{cases} p \\ q \\ r \end{cases}$	Popula- tion I	Kam- chatka	South of east Aleut.		North of east Aleut.	Popula- tion II
				obs.	exp. <sup>2)</sup>		
	$p$	.334	.662	.810	.818	.890	.896
	$q$	.074	.032	.017	.024	.003	.002
	$r$	.592	.306	.173	.158	.107	.102
Freq. of pheno- types	$\{ [J_{u_1}] \}$	.503	.844	.937	.928	.982	.985
	$\{ [J_{u_1}J_{u_2}] \}$	.053	.042	.027	.039	.006	.004
	$\{ [J_{u_2}] \}$	.444	.114	.036	.033	.012	.011

<sup>1)</sup> in three allele B system only, <sup>2)</sup> calculated from ratio of mingling.

b) Averaged ratio of mingling between populations I and II:

Population	$\begin{cases} I \\ II \end{cases}$	Area		
		Kamchatka	South of east Aleut.	North of east Aleut.
I		.42	.10	.01
II		.58	.90	.99

c) Relative stock number of populations I and II actually migrate to the areas off Kam-  
 chatka and north of east Aleutian:

$$N_1=0.43$$

$$N_2=1.57$$



populations I and II overlap in areas A and B. Relative size of both populations which actually migrate to area A fluctuate from year to year, and gene frequencies observed in area A fluctuate correspondingly. As blood typing data, however, have not been obtained during full period for marking investigation, there are assumed to be some bias in observed values of gene frequency of population I, because they were obtained as averaged figure by year. On the other hand, gene frequency of population II is not affected by this and seems to include little bias. Even if there is some bias in gene frequencies of population I, these figures will be available for discussing yearly fluctuation of ratio of mingling between both populations in various areas. For this purpose additional number of whales should be observed hereafter. Summarized results of various figures in this paragraph are shown in Table 46.

#### DISCUSSION AND SUMMARY

In the present paper after analysing sub-populations of the north Pacific finback whales, the author clarified that two different populations, which their migratory ranges overlap each other in feeding season, distribute in areas around Aleutian Chains, and that whales taken from East China Sea belong to a different local population which is isolated from above those. Various assumptions were rendered during these analysis, so that it should be discussed here that how do they effect upon final conclusions in the present report.

*Problems in immunogenetics.* Despite of somewhat lower precision in blood typing Bp antigen, the facts that Bp<sub>1</sub> antigen occurs in area off Kamchatka (A) and while does not in area of north of east Aleutian (C) are sufficient evidence to show existence of local populations in these two areas. On the other hand, it can be supposed that misclassification of Ju blood types hardly has happened, because of obverse and reverse correlations between Ju<sub>1</sub> and Ju<sub>2</sub> antigens, dosage effect between homozygous and heterozygous types and purification of standard reagents. Moreover, as specific agglutinin has sufficient high titer even after dilution with saline for actual use, it can be hardy assumed that weaker heterozygous type was misclassified as homozygous type Ju<sub>1</sub>. As regards allele system of Ju blood type, after discussing discrepancies from Hardy-Weinberg's Equilibrium in frequency of occurrence of phenotypes and parentages between cows and fetuses, two allele system is denied and then at least three alleles should be supposed. Then problems of identification and mingling of populations were investigated through two kinds of hypothetical three allele systems A and B. It was discussed whether continued ratios of gene frequencies between neighbouring three areas

reveal approximately same figures in three alleles each other or not. Consequently it was clarified from discussions through both allele systems A and B that whales taken from East China Sea belong to a local population isolated from those around Aleutians. As regards correlations between three areas off Kamchatka (A), south of east Aleutian (B), and north of east Aleutian (C), after above-stated discussion it was denied through A system that populations from both side's areas mingle in middle area but it was affirmed through B system. On the other hand, as emigration of marked whales between both side's areas, have been reported it is not probable that mingling in middle area is completely denied, so that A allele system seems to give results contradictory to the facts observed. In other words, though direct evidences have not been obtained yet, B allele system could better interpret the facts of observation than A system at present. As revealed by the rate of emigration of marked whales, populations in the areas A and B are mingled those of populations I and II. But results of discussions on figures in Table 27 and successive those, which were calculated through formulas 2 and 3, can lead to final conclusions in the present paper.

According to the phenomena of dosage effect in Ju heterozygous types, additional alleles related to possible sub-types can be supposed, but available data are too scanty to discuss this problem definitely. Existence of this new fourth allele, however, might not effect upon analysing results of racial study basing on three allele systems.

*Effects of estimation of various figures in calculation of ratio of mingling and some biological factors to the results discussed in the present paper.* To calculate rate of emigration, it was presumed for convenience that marking in areas A and C were performed against unmingled populations I and II. As population II, however, actually migrate to area A, rate of emigration of population II to this area is obtained as a upper limit averaged for period of investigations. According to same thinking it can be thought that major part of population I distribute to area A and a part to area B, but it scarcely migrate to area C. This fact is confirmed by the blood typing evidences that  $Bp_1$  antigen occurs in area A but does not in area C at all.

Effects of errors in estimates of  $f$ ,  $g$ ,  $e_1$ ,  $e_2$  and  $S$  in formulas 5 and 6 to ratios of mingling and other final results in present report will be discussed here. At first  $g$  means rate of confirming number of whales hit, against those effectively marked and was given as rate of number of whales recaptured from those recorded as 'hit' when marked against total number of recapture. Coefficient  $f$  means rate of recovery of marker from whales recaptured, and was estimated experimentally.

Actually one whale is shot by two or more darts in low frequency, so that it could be approved that rate of recovery of marker  $f$  is equal to rate of confirming recaptured whales. As stated in discussions on Table 41, figures  $f$  and  $g$  thus obtained fairly effect upon values of  $r_1^1$ ,  $r_2^1$ ,  $r_1^2$  and  $r_2^2$ , but hardly do to rates of emigration calculated as relative value of these. Figures of  $e_1$ ,  $e_2$  and  $S$  were calculated for two cases assuming average number of ovulation per breeding season 2.8 or 1.6. Errors of estimate of  $e_1$  and  $e_2$  effect upon only first and second terms of numerator and denominator in formulas 5 and 6. As regards estimate of survival rates  $S$  matters are as follows. For example populations I and II migrate to area A and some geographical segregation by age in a population may be supposed. As being obvious from formula 12, however, errors of survival rate  $S$  estimated from ovarian data of catch in each area effects a little upon only first term and hardly upon second term and after as negligible minute more than two orders of each denominator of formula 5 and will bring scarce difference on final figures of rates of emigration. Estimates of  $e_1$ ,  $e_2$  and  $S$  show different figures by two cases in which averaged number of ovulation is 2.8 or 1.6, and give some differences to individual figures of  $r_1^1$ ,  $r_2^1$ ,  $r_1^2$  and  $r_2^2$ , but hardly bring difference to rates of emigration of their relative values.

Significant difference is seen in figure of  $r_2^2$  calculated from formula 6 for area C between two cases including marking data in 1957 or not (see Table 42). According to detailed records in marking logs, in spite of scantiness of number of whales marked, those marked in closely neighbouring areas at approximately same time are recaptured in closely neighbouring areas again in a successive year. This makes figure of  $u$  for this year higher, so that some bias is brought to figure of  $r_2^2$ . Therefore it is more appropriate that the data in this year is excluded. Thus after being corrected with  $f$  and  $g$  coefficients and adopting figures of  $e_1$ ,  $e_2$  and  $S$  in the case which average number of ovulation is 1.6, rates of emigration was finally calculated from data of marking investigation excluding these in 1957. On the other hand, regarding area A it is assumed from yearly fluctuations of frequency of occurrence of blood type that relative size of populations I and II which migrate to this area vary from year to year. But analysis stated above for area C could not be performed for area A because of scantiness of number of whales marked and recaptured in each year, so that intact figures of  $r_1^1$  and  $r_2^1$  obtained from formulas 5 and 6 are used for calculation of rates of emigration.

Next problems to be discussed are how do ecological factors during migration of whales effect upon the results in previous discussions. Regarding ecology of whales in general, some degrees of seasonal or

geographical segregations by sex, pregnancy and some other physiological factors have been observed. In the north Pacific finback whales, however, slight segregations by pregnancy only have been observed. Sufficient data to estimate quantitatively biases in rates of recapture which seem to be caused by individual factors have not been obtained yet. But the fact, that rates of recapture  $r_2^2$  for area C against number of survivor in catch keep approximately constant value from year to year, would suggest that the above-stated various factors against biological segregations hardly effect upon rates of recapture finally. On the other hand, such analysis has not been performed for data on area A, so that it must be kept in mind that some degree of biases in rates of recapture are involved. This means that ratio of  $\frac{r_1^2}{r_1^2+r_2^2} : \frac{r_2^2}{r_1^2+r_2^2}$  includes some degree of error. Errors in this ratio and in rates of emigration which is caused by bias between periods for blood typing and those for marking investigations, might bring somewhat effects upon gene frequency of population I and figures of  $N_1$  and  $N_2$ . But these figures must have sufficient precision to discuss problems involved in present paper. Higher precision could be expected through discussions with additional data hereafter.

*Other biological evidences suggesting existence of local populations.* After comparing morphological characteristics, following differences, which may confirm the existence of local populations, have been observed between whales from East China Sea and those from areas around Aleutian Islands. That is, whales from East China Sea 1) have lower growth rate in body length, attain sexual maturity at averaged body length of 57 or 58 feet in male and of 60 or 61 feet in female approximately three feet smaller (Fujino, unpublished data), 2) are different significantly in external body proportions (Ichihara, 1958) and in shape of skull (Fujino and Ichihara, unpublished data), and 3) have shorter baleen plates in same ages and in same body lengths than those from areas around Aleutians. Full discussions on these points will be published later (Fujino, to be published in next issue). Such significant difference have not been recognized between whales from area off Kamchatka and those from area of east Aleutians. Therefore it can be assumed that differentiation between populations I and II is situated in earlier stage than that between those and populations in East China Sea. In the areas of Okhotsk sea and off Pacific coast of Japan sufficient investigations have not been carried out in recent years because of poor catch, but shape of baleen plates from these whales reveal same characteristics as those from Aleutian waters (Fujino, unpublished data).

Results of discussions in the present paper can be summarized as

follows.

1) After studying technical problems in large scale of blood typing investigations on whales, standardization in basic methods has been established as follows. Glycerol freezing technique has potential value in preserving intact erythrocytes used for analysing blood type antigens, and standard reagents can be preserved by adding preservatives at concentration of 0.5% carbolic acid or 0.1% sodium azide and by being kept frozen for several years in good condition available for testing. Preservatives will serve against accidental warming during transportation between central and field laboratories.

2) Blood type antigens and other serological constitutions were analysed in four species of baleen whales and three species of toothed whales and allele systems in some species among these were discussed. Especially in Ju blood types of finback whales, two allele system was denied and two kinds of three allele systems were discussed.

3) Racial study on the north Pacific finback whales were performed by means of population genetics with blood types. As Ju antigens have higher precision than Bp antigens in large scale of investigation, the former was used for quantitative analysis.

4) Basing upon non-random geographical distribution in frequency of occurrence of blood types and rates of emigration of marked whales, it became to be obvious that different local populations of finback whales distribute in various areas of the North Pacific including East China Sea, west and east sides' areas around Aleutian Islands.

5) According to comparison of continued ratios of blood type gene frequencies of populations from neighbouring three areas, finback whales in East China Sea belong to a local population which is isolated from those in areas around Aleutians. Furthermore, this fact was confirmed significantly by comparison of morphological characteristics such as growth rate in body length, body length at which sexual maturity is attained, external body proportions and shape of skull, shape and growth rate of baleen plate.

6) Rate of emigration which was calculated from results of marking investigations strongly confirm the existence of the two different populations in the west (population I) and east (population II) sides' areas around Aleutian Islands which was previously clarified by blood typing investigations, and that population I hardly migrate to the area north of east Aleutian (area C), but population II distribute not only to area C but also to area off Kamchatka (area A). In other words, migratory ranges of populations I and II are overlap in the areas A and south of east Aleutian (B), but relative sizes of both populations which actually migrate to these areas fluctuates from year to year.

7) Gene frequencies of populations I and II are estimated by blood type gene frequencies observed in various areas and rates of emigration of marked whales through three allele B system. These includes  $p_1 : .334$ ,  $q_1 : .074$ ,  $r_1 : .592$  in population I and  $p_2 : .896$ ,  $q_2 : .002$ ,  $r_2 : .102$  in population II. These figures will be useful for estimating annual ratio of mingling between populations I and II in various areas around Aleutian Islands, although some bias may be involved in figures of population I. Additional data could be serve to bring these values higher precision.

8) After estimating relative sizes of populations I and II which actually migrate to areas A and C, it became to be clarified that population II has larger stock number than the other. Higher precision in estimating these actual figures should be expected by additional data hereafter.

9) Shape of baleen plates of finback whales from area of Okhotsk and Pacific sides of the north eastern Japan is different from that from East China Sea and reveals same type as that from areas around Aleutians, though the data obtained are very scanty so far. Whether whales from these areas belong to population I or other will be discussed after obtaining informations available in future.

10) In spite of fairly abundant annual catch, no recapture of whales, which was marked in the areas around Aleutians has been reported from areas off British Columbia and off California. This fact might suggest existence of another different population in these areas, so that it can be concluded that at least four different local populations of finback whales distribute in the north Pacific Ocean.

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一般財団法人 日本鯨類研究所  
THE INSTITUTE OF CETACEAN RESEARCH

APPENDIX. FREQUENCY DISTRIBUTION OF NUMBER OF CORPORA  
ALBICANS IN PREGNANT FEMALES TAKEN FROM THE NORTH  
PACIFIC FINBACK WHALES

	Off Kamchatka (A)								South of east Aleut. (B)						North of east Aleut. (C)					
	1952	1953	1954	1955	1956	1957	1958	1959	1954	1955	1956	1957	1958	1959	1954	1955	1956	1957	1958	1959
0	1	13	9	4	9	7	2	16	6			12	8	2	31	25	10	10	8	26
1	6	12	8	2	7	4	4	12	8	3	2	7	15	1	23	40	19	9	6	14
2	5	16	9	4	5	6	5	10	4			16	6	1	16	21	20	14	6	15
3	2	12	14	2	5	10	5	12	2	1		16	4		18	33	14	7	5	10
4	1	11	9	2	11	4	6	10	1	1	2	7	4	2	9	21	9	2	4	14
5	2	10	8	6	8	4	4	18	5			12	7	1	12	24	10	4	3	7
6	1	7	13	2	6	3		9	3			9	10	2	7	16	8	1		13
7	2	10	5	5	12	2	3	12	2	2		12	6		6	14	4	2	3	10
8	2	11	5		2	8	3	7	4	1		8	3		3	6	5		2	7
9	1	5	8	2	6	7	3	17	1			7	5		4	5	1	2	2	6
10	4	3	4	4	5	3	7	6	2		1	7	2	1	2	4	3	2		1
11	1	5	2		6	5	3	5	3		3	5	2	1	1	5	4	2	2	5
12	1		2		3	4	1	9				7	4	1		2	1	2		
13	1		1		3	1	1	7				2	2	1		2	1	2		1
14		3	1		2	1	1	4	1			1	1		1					2
15			2		4	1	1	5				2	1				2	1		
16		1			2	2	1	1	1			1				1				1
17		1	1		1			3	1			2					1			2
18					1	2		2									2		1	
19												1			2					1
20					1			1				1								
21					1				1		1						1			1
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41																				
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Sum	30	122	101	33	102	76	53	167	45	8	10	136	80	13	136	219	117	60	44	140