DENSITY DEPENDENT CHANGES IN GROWTH PARAMETERS OF THE SOUTHERN MINKE WHALE*

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ABSTRACT

Changes in growth parameters with time were examined for the southern hemisphere minke whales, using materials collected by Japanese Antarctic whaling expeditions in Areas III (0° ~ 70°E) and IV (70° ~ 130°E) during seasons from 1971/72 to 1982/83. Mean age at sexual maturity (50% maturation) for both sexes estimated from the transition phase in earplug declined from 12~13 years in the 1940s year-classes to 7~8 years in those of late 1960s to early 1970s, and the female trend agreed with the decline in mean age of females having a corpus luteum of first ovulation, but the mean body length of first ovulation remained constant around 27.5 ft (8.4 m) in all year-classes and in year of capture. Both analyses of growth curve and epiphyseal fusion of vertebrae suggested an increase in the growth rate and body length at attainment of physical maturity in recent year-classes, while it was not enough to examine changes in age at the attainment of physical maturity. These changes are thought to have resulted from the decline of possible competitative whale stocks such as blue and fin whales.

INTRODUCTION

Census data indicate that the populations of some penguins (Sladen, 1964) and pinnipeds (Laws, 1973; Payne, 1977) in the Antarctic had increased during 1940s to 1970s. Laws (1977a, b) considered these increases attributable to the decline of the populations of ecological competitors such as blue whale *Balaenoptera musculus* (Linnaeus, 1758), and fin whale, *B. physalus* (Linnaeus, 1758). The southern minke whales, *B. acutorostrata* (Lacèpéde, 1804), also share their habitat and food resources with the above whales, so they may have received same kind of similar or stronger influence from the changes.

Decline of minke whale age at sexual maturity from 14 years in the 1940s year-classes to 6 years in late 1960s year classes was suggested by the analysis of transition phase in earplugs (Masaki, 1979; Best, 1982; Kato, 1983a). And

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this was once considered indicating increase in minke whale population prior to the start of full exploitation in 1971/72 (International Whaling Commission (IWC), 1979).

Recently, however, Cooke and de la Mare (1983) expressed a doubt on the validity of transition phase analyses which had been adopted for several large whale stocks, and suggested that the apparent decline of age at sexual maturity could be the result of ageing errors and possible data handling biases such as truncated sampling problems. Since then, no general concensus has been obtained on this subject among the Scientific Committee of IWC in spite of many studies in this field (IWC, 1985).

Truncated samples will most seriously exaggerate the estimation of yearly trends of decline in age at sexual maturity (IWC, 1985). Kato (1983a) has solved this problem by excluding data possibly under the effect of the truncation bias. The present study compares annual changes in the age at sexual maturity suggested by his method with other changes in several parameters related to the growth of minke whales.

MATERIALS AND METHODS

Materials in this study were collected from minke whales taken by Japanese Antarctic whaling expeditions in 1971/72 to 1982/83 of austral summers in the waters south of 60°S to ice edge zone. To increase sample size, data from Areas III (0° to 70°E) and IV (70° to 130°E) were combined. Number of catches by the Japanese fleets by sex, whaling season and area is given in Table 1. Individual age was determined using growth layers in earplug, and assuming annual deposition of the layer (a pair of light and dark laminae to be formed annually--Best, 1982; Kato and Best, unpublished). Growth layers were counted with stereoscopic microscope ($6 \sim 10 \times$) by myself (for samples after 1978/79 season), or by Drs Yasuhiko Masaki and Seiji Ohsumi (before 1977/78 season). No systematic ageing error was detected among those three readers (IWC, 1984a).

Age and length at sexual maturity

Following parameters were calculated for each year-class group and year of capture using samples shown in Table 2.

L_{mov}: Mean body length of females soon after the attainment of sexual maturity (first ovulation), identified by the presence of a corpus luteum (CL) and no corpus albicans (CA) in the ovaries.

$L_{m50\%}$: Body length where 50% of females are sexually mature, using presence of corpus luteum or albicans in the ovaries as the indicator of sexual maturity. This length was calculated by fitting logtistic curve (weighted by sample size) to the proportion of sexually mature females at each length. If the Chi-square (goodness of fit) of the logistic curve to the observed values was low ($p > 0.95$), the $L_{m50\%}$ was not estimated. Although

TABLE 1. NUMBER OF CATCHES OF THE SOUTHERN MINKE WHALES BY THE JAPANESES FLEETS BY SEX, WHALING SEASON AREAS. DATA FROM INTERNATIONAL WHALING STATISTIS

Whaling season	Area III		Area IV		Whole Antactic*	
	Male	Female	Male	Female	Male	Female
1971/71	170	184	930	1,728	1,100	1,912
1972/73	–	–	1,116	975	1,116	975
1973/74	320	1,174	761	1,282	1,116	2,597
1974/75	554	805	430	410	1,247	2,252
1975/76	417	604	198	237	1,464	1,553
1976/77	446	939	521	429	1,678	2,272
1977/78	398	614	128	353	1,012	1,388
1978/79	642	958	386	573	1,097	1,635
1979/80	521	732	1,048	482	1,952	1,327
1980/81	327	292	529	664	1,472	1,647
1981/82	188	71	582	1,043	1,578	1,999
1982/83	–	–	530	490	1,083	2,140
Total	3,983	6,373	7,159	8,666	15,915	21,697

*) including Areas I (60°-120°W), II (60°W-0°), V (130°E-170°W) and IV (170°-120°W) as well as Areas III (0°-70°E) and IV (70°-130°E) where the present study has been done.

TABLE 2. NUMBER OF SAMPLES USED FOR ANALYSES OF AGE AND BODY LENGTH AT SEXUAL MATURITY

Parameter*	Data grouping	Number of samples examined		
		Male	Female	Total
L_{mov}	Year of capture	–	512	512
	Year-class	–	222	222
$L_{m50\%}$	Year of capture	–	12,332	12,332
t_{mov}	Year of capture	–	222	222
$t_{m50\%}$	Year of capture	–	6,872	6,872
	Year-class	–	6,872	6,872
t_{mp}	Year-class	1,121	1,721	2,842
	Year of maturation	1,538	2,272	3,810

*) L_{mov}, mean body length of females having CL of the first ovulation.
$L_{m50\%}$, body length at 50% sexual maturity.
t_{mov}, mean age of females having CL of the first ovulation.
$t_{m50\%}$, age at 50% sexual maturity.
t_{mp}, mean age at sexual maturity estimated from transition phase in earplug (both sexes).

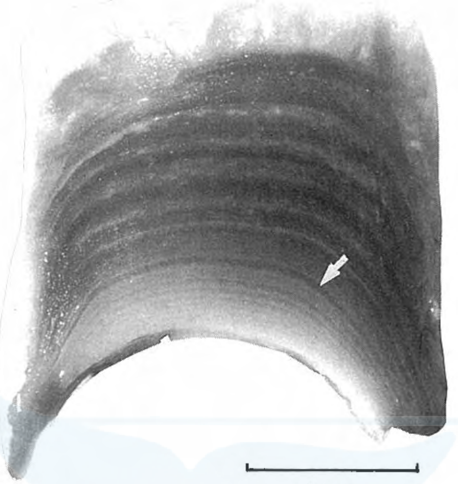

Fig. 1. Earplug core of southern minke whale, bisected to expose growth layers (a pair of light and dark laminae constitutes one growth layer). Arrow shows transition phase which is formed at the attainment of sexual maturity.

male minke whales in the Antarctic fishing ground are believed to mature at testis weight of 400g at heavier side (Ohsumi, Masaki and Kawamura, 1970; Ohsumi and Masaki, 1975; Masaki, 1979; Kato, 1982), this figure may underestimate mean testis weight at maturation for the population because mature males are more likely to come to the fishing ground than immature individuals of the same testis weight (Best, 1982; Kato, unpublished). Thus use of this maturity criterion will mislead the minke whale growth. Therefore this parameter was not estimated for males.

t_{mov}: Mean age of females having CL of the first ovulation, defined as item of L_{mov} above.

$t_{m50\%}$: Age where 50% of females are sexually mature defined as item of L_{mov} above.

t_{mp}: Mean age at sexual maturity estimated for both sexes using transition phase in the earplug (Fig. 1) as an indicator of sexual maturity (Lockyer, 1972; Kato, 1983b; Ohsumi, 1986a). In order to avoid trucated sampling problems, individuals of the following age ranges were selected for this analysis using criteria of Kato (1985), which principally selects ages (at capture) older than expected oldest immature individuals in each year-class.

Year-classes before 1951; used all individuals (> 20 years)
1951–1955 year-class; over 19 years old at capture
(caught in 1971/72–82/83 seasons)

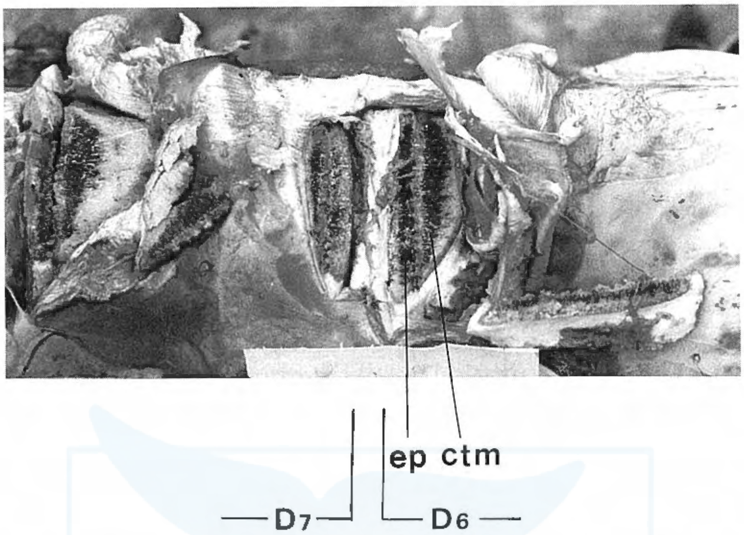

Fig. 2. The thoracic vertebrae of the southern minke whale, cut to expose boundary between the epiphysis (ep) and the centrum (ctm) at the 6th vertebra, ventral side.

1956–1960 year-class; over 15 years old at capture
(caught in 1972/73–82/83 seasons)
1961–1965 year-class; over 13 years old at capture
(caught in 1975/76–82/83 seasons)
1966–1970 year-class; over 12 years old at capture
(caught in 1979/80–82/83 seasons)

Growth curve

Apparent growth curves (mean body length on age at capture) were constructed for four year-class groups using each containing 10 year-classes. The total number of samples for this is 5,203 males and 6,998 females caught by Japanese fleets in 1971/72 to 1982/83 seasons.

Physical maturity

Materials were collected from 223 males and 356 females caught by Japanese whaling expeditions in 1978/79 and 1979/80 seasons. Only the 6th vertebral epiphyses and centrum of these individuals were cut with hand axe and observed with naked eyes for the presence of cartilage separating these bones (Fig. 2). The fusion of epiphyses to the centrum occurs lastly on the middle parts of thoratic (dorsal) vertebrae as in fin (Wheeler, 1930; Ohsumi, Nishiwaki and Hibiya, 1958) and minke whales (Kato, unpublished), and the southern minke whales have 11 to 12 thoracic vertebrae (Omura, 1975; Omura and Kasuya, 1976). The condition between epiphyses and centrum was initially classified into stages after Ohsumi, Nishiwaki and Hibiya (1958) and Laws (1961), then the absence of cartilage between the epiphyses and the centrum (stages *a* and *A* of Ohsumi *et al.* (1958) and *EJV* and *EJI* of Laws (1961)) was used as the indicator of physically mature individuals. Physically immature individuals of the present study therefore include stages *N* and *n* of Ohsumi *et al.* (1958) and *UTC* and *UFC* of Laws (1961). This study included data of limited number of whales examined by Dr P. B. Best (University of Pretoria, South Africa) on board *Nisshin Maru No. 3* in 1978/79 season.

Grouping of samples

Present analyses were done after grouping materials by year of capture, year-class, and year of maturation as defined below.

Year of capture: Used for L_{mov}, $L_{m50\%}$ and t_{mov}. Fishing season normally starts in November and closes in March of the next year.

Year-class (= year of birth): Year-classes were defined by;

Year-class = (starting year of the season) − (age at capture).

and used for L_{mov}, $t_{m50\%}$, t_{mp}, growth curve and physical maturity analyses. Both values of t_{mp} and $t_{m50\%}$ were calculated for each year-class, while L_{mov} and growth curve (as well as physical maturity) were analysed by combining year-classes of three and 10, respectively.

Year of maturation: Year of maturation of each individual was calculated as follows and used for t_{mp} analysis;

Year of maturation = (year of birth) + (age at transition phase)
= (starting year of the season) − (time after sexual maturity).

RESULTS

Age and body length at sexual maturity

1) Mean body length of females having CL of the first ovulation (L_{mov})

Since gestation of the minke whale lasts less than one year and the longevity of corpus luteum of ovulation must be shorter than this period (IWC, 1984b), females having a corpus luteum of pregnancy or ovulation (with no corpus albicans) were considered to have matured within one year.

Fig. 3 (left) shows body length distribution of recently matured females by year of capture. A mode existed at 27–28 ft (8.2–8.5 m), and L_{mov} ranged from 27.0 (8.2 m) to 28.0 ft (8.5 m) with no significant yearly trend ($0.1 < p < 0.2$, t-test of the regression coefficient of L_{mov} on year of capture).

Even when L_{mov} was analyzed by year-class group, the annual trend was also insignifiant ($0.2 < p < 0.3$; Fig. 3, right).

2) Body length at 50% sexual maturity ($L_{m50\%}$) for females

Fig. 4 shows $L_{m50\%}$ values as well as the relationships between sexual

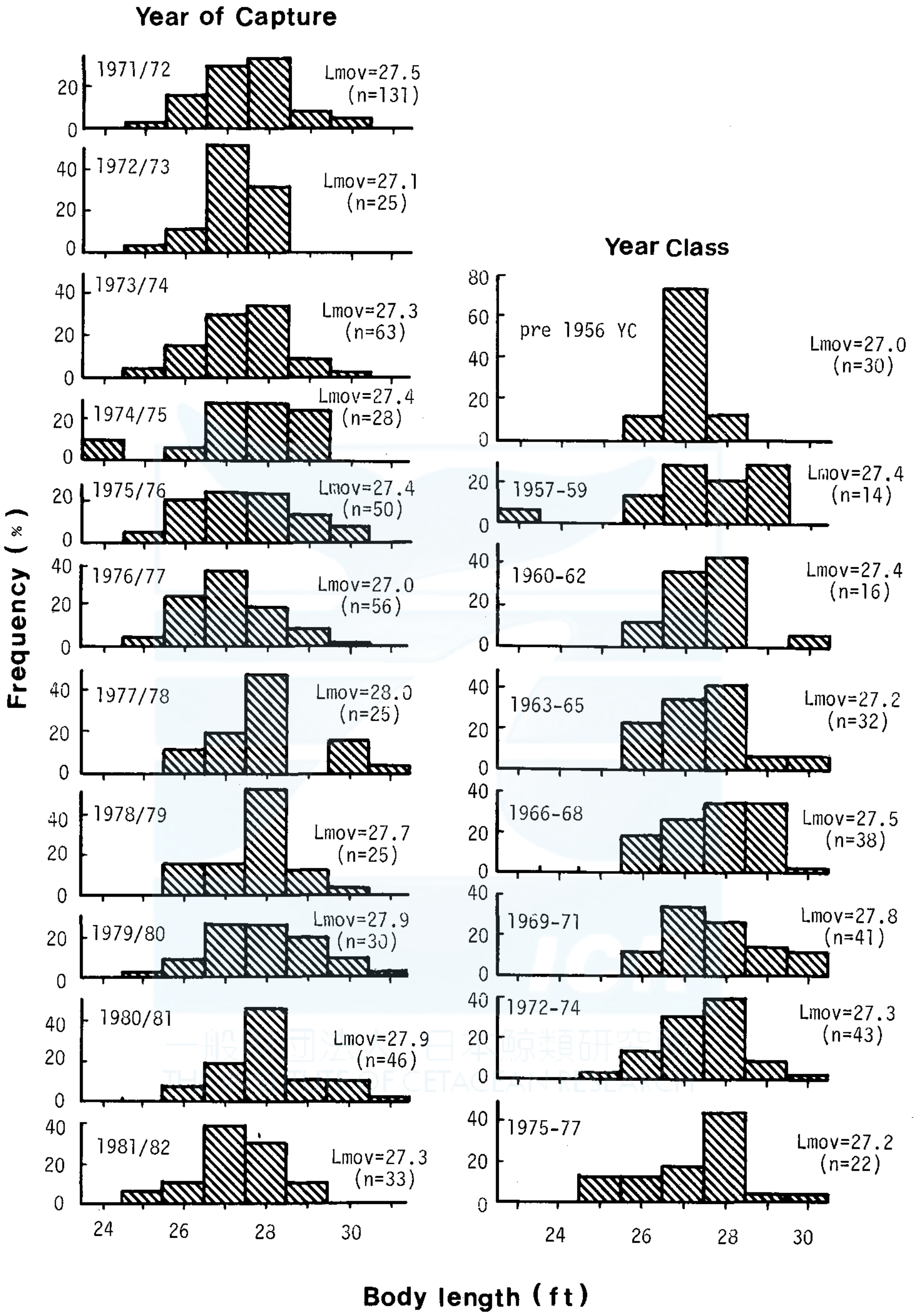

Fig. 3. Length distribution of females at the first ovulation having only one corpus letum and no corpora albicantia in the ovaries and *Lmov* for the southern minke whales in Areas III and IV. Grouped by year of capture (left) and year-class (right).

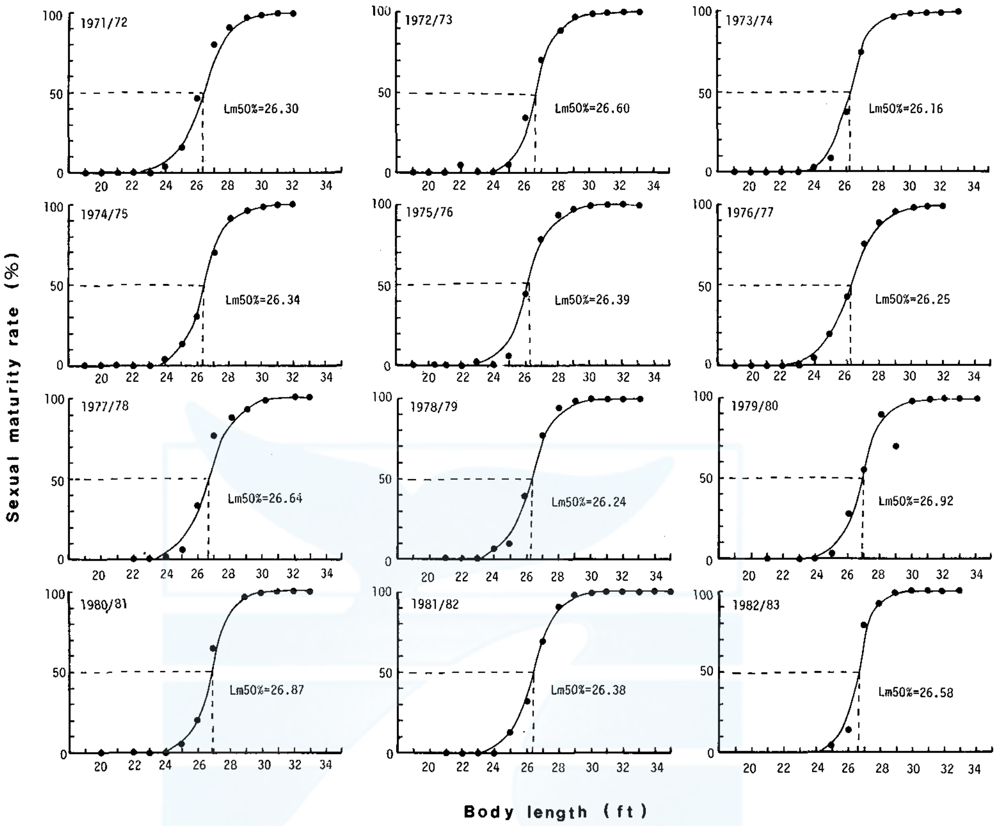

Fig. 4. Body length at 50% sexual maturity ($L_{m50\%}$) of the female southern minke whales collected in Areas III and IV, expressed for year of capture. Logistic curves are fitted by the least squares weighted by sample size.

maturity rate (proportion of sexually mature individuals in the sample) and body length analysed by the year of capture (1971/72 to 1982/83 seasons). The relationship was almost identical between seasons, and sexually mature individuals appeared at body length over 25 ft (7.6 m) and most of the individuals completed maturation below the length 28 ft (8.5m). $L_{m50\%}$ values were approximately at 26.5 ft (8.1 m), with no siginificant yearly trend ($0.1 < p < 0.2$, t-test of the regression coefficient of $L_{m50\%}$ on year of capture).

3) Mean age of females having CL of the first ovulation (t_{mov})

Fig. 5 shows distribution of age at the first ovulation (t_{mov}) by year of capture. The t_{mov} values have decreased from about 9 years in early 1970's

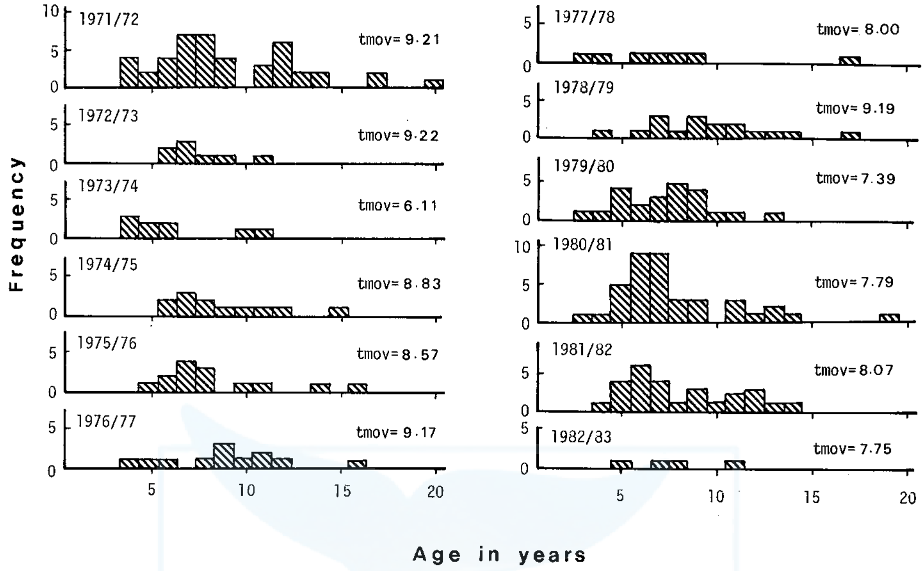

Fig. 5. Age distributions of females having only one corpus luteum and no CA in ovaries and t_{mov}, data from Areas III and IV.

to about 7 years in late 1970s and early 1980s. The trend was expressed by the following least square regression (t_{mov} on year of catch; weighted by sample size):

$$t_{mov} = 9.164 - 0.138t \quad \text{-------------------- Equation 1}$$
$$(r = -0.548,\ 1 < t < 12)$$

where, t is year of capture setting 0 for 1970/71.
Slope of the above regression was significantly different from zero (t-test, $p < 0.05$).

4) Age at 50% sexual maturity ($t_{m50\%}$) for female

Fig. 6 shows $t_{m50\%}$ values as well as the relationships between sexual maturity rate (proportion of sexually mature individuals) and age at capture for females. Except for the 1974/75 season when the value was apparently high (7.75 years), all the other figures of $t_{m50\%}$ ranged between 6 and 7 years with no specific annual trend. The regression coefficient of $t_{m50\%}$ on season was not significantly different from zero (t-test, $0.2 < p < 0.3$) as reported by Kato (1982).

Even if the relationship between sexual maturity rate and age is analysed by year-class using the same data set (Fig. 7), the $t_{m50\%}$ values were the same as above and showed no significant change among year-classes (t-test, $0.4 < p < 0.5$).

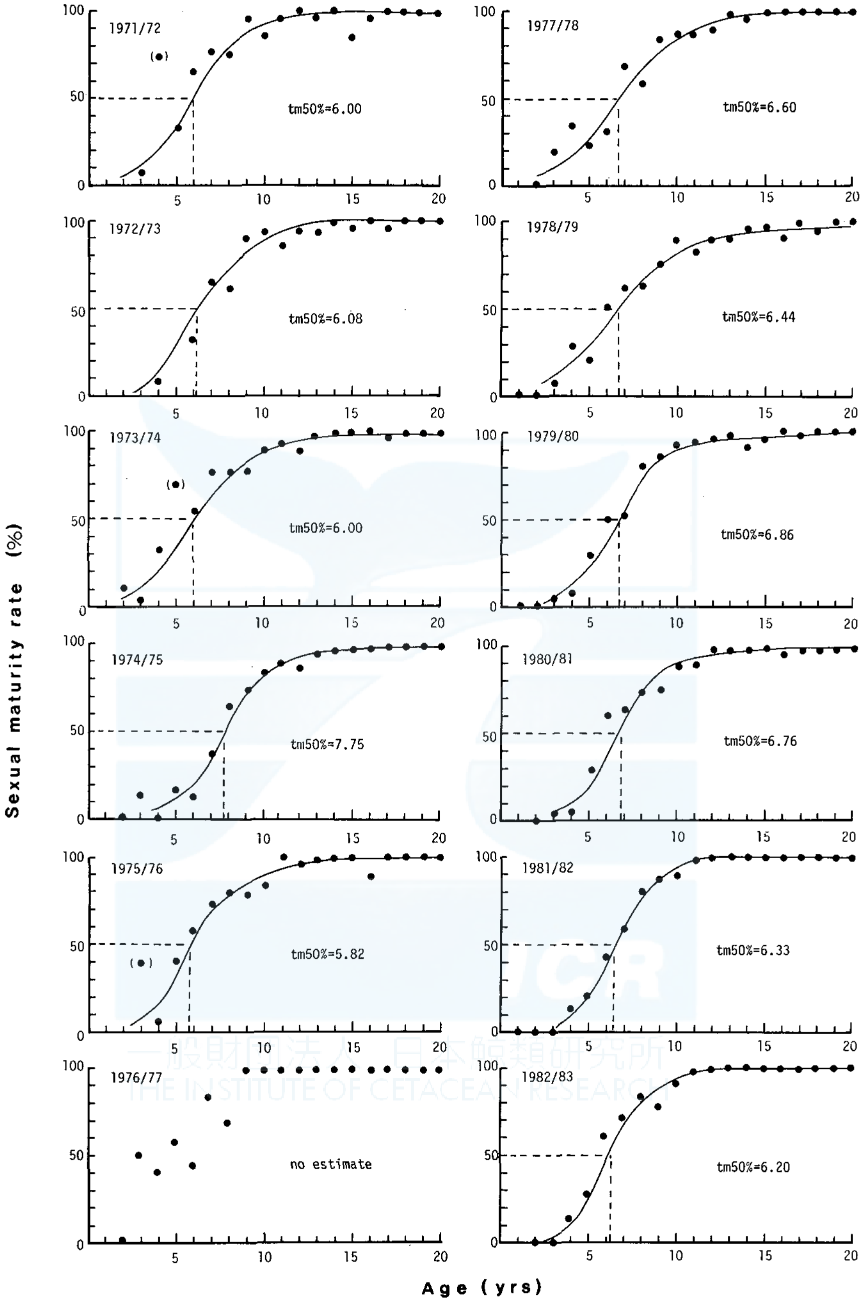

Fig. 6. Age at 50% sexual maturity ($t_{m50\%}$) of the female southern minke whales in Areas III and IV, expressed for each year of capture. Logistic curves are fitted by the least squares weighted by sample size (closed circles in parenthesis were not used for fitting logistic curve).

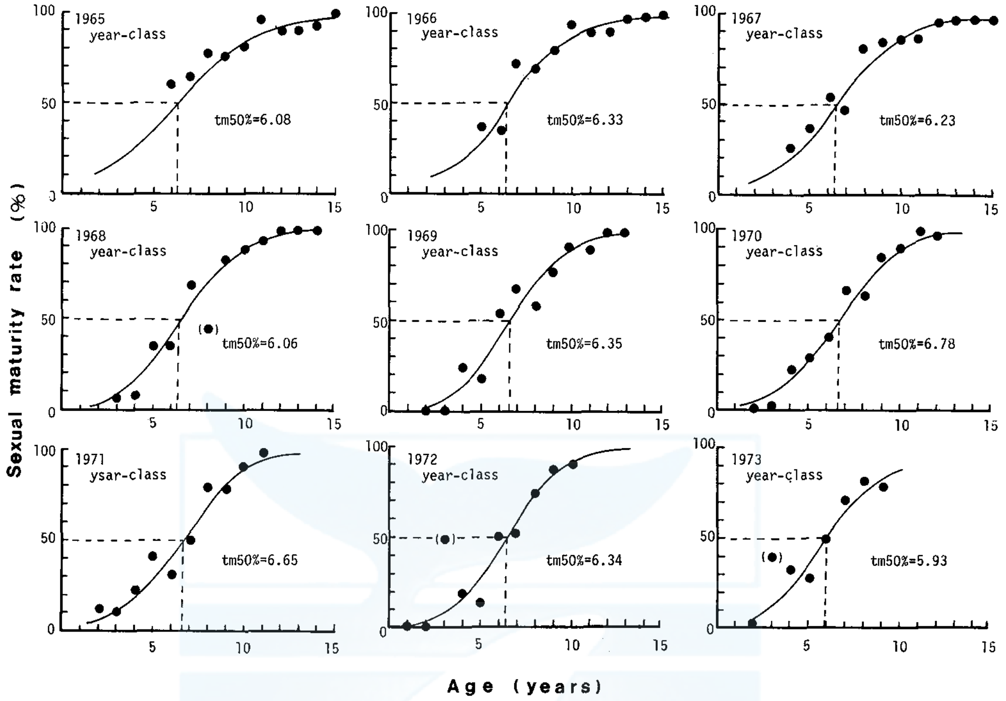

Fig. 7. Age at 50% sexual maturity ($t_{m50\%}$) of the female southern minke whales in Areas III and IV, expressed for each year-class. Logistic curves are fitted by the least squares weighted by sample size (closed circles in parenthesis were not used for fitting logistic curve).

5) Mean age at sexual maturity estimated from transition phase (t_{mp}) for both sexes

As indicated in Table 3 and Fig. 8 (left), the mean age at sexual maturity estimated from the transition phase in earplug (t_{mp}) seemed to be almost constant in both sexes in year-classes before 1940, but then it has declined from 12~13 years of year-classes in mid 1940s to 7~ 8 years of those in late 1960s. The regressions of t_{mp} for both sexes on year-class weighted by sample size are expressed by the following equations;

Male, $t_{mp} = 22.15 - 0.219k$ ($r = -0.971$, $45 \leq k \leq 70$) – Equation 2
Female, $t_{mp} = 21.64 - 0.206k$ ($r = -0.963$, $45 \leq k \leq 70$) – Equation 3

where, k is year-class setting 0 for 1900. Both of the slopes were significantly different from zero (t-test, $p < 0.001$).

The values of t_{mp} and its standard deviation for each year of maturation are given in Table 4, and are plotted in Fig. 8 (right). Due to the small sample size of the observed data, the values of t_{mp} and its standard deviation

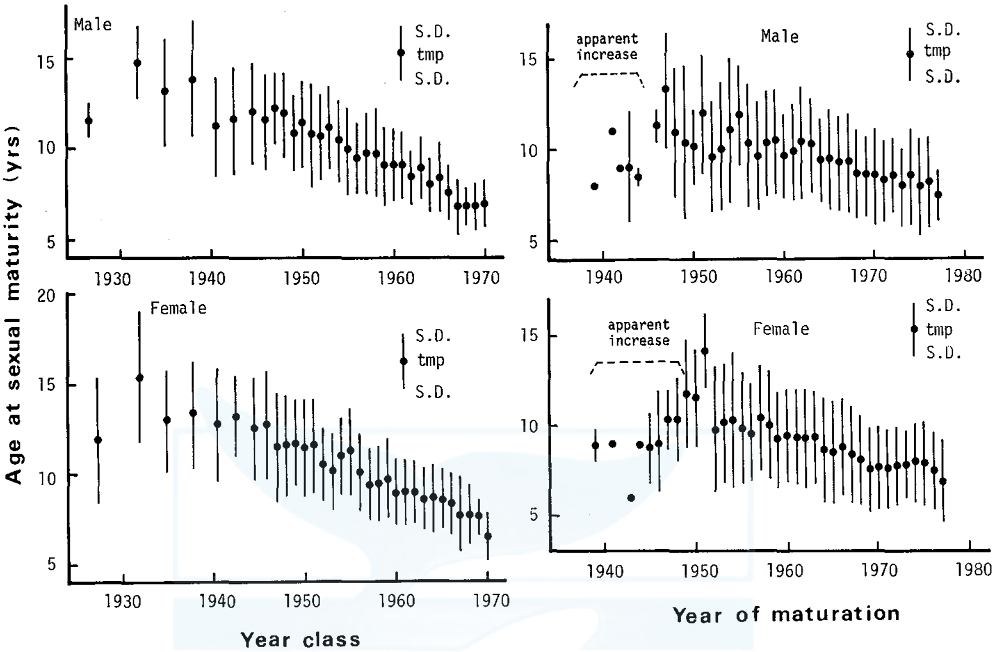

Fig. 8. Changes in age at sexual maturity deduced from transition phase in earplug for males (top) and females (bottom) of the southern minke whales. Range of one standard deviation (solid line) is expressed on each side of the mean age (*tmp*; closed circle). Samples are grouped by year-class (left) and year of maturation (right).

after 1978 were not examined for both sexes. Kato (1983a) pointed out the apparent increasing trends of *tmp* were to be produced by the procedure of converting data of year-class to year of maturation in the beginning several years of the time series of year of maturation, unless the time series of the data infinitely continued. Later this fact was identified again by the simulation study of Sakuramoto, Kato and Tanaka (1985). Therefore the apparent increasing trends of *tmp* values for both sexes before 1949 are artefact.

Then, only those trends from 1950 to 1977 have biological meaning. The *tmp* values declined from around 12 years in 1950s to 8 years in early 1970s. This is shown by the following least square regressions (*tmp* on year of maturation weighted by sample size):

Male, $tmp = 18.38 - 0.138t$ ($r = -0.921$, $50 \leq t \leq 77$ --- Equation 4

Female, $tmp = 19.59 - 0.152t$ ($r = -0.919$, $50 \leq t \leq 77$) --- Equation 5

where, t is year of maturation setting 0 for 1900. Both of the slopes were significantly different from zero (t-test $p < 0.001$).

TABLE 3. STANDARD DEVIATION (s.d.) AND THE MEAN (t_{mp}) OF AGE AT SEXUAL MATURITY ESTIMATED FROM TRANSITION PHASE IN EARPLUG FOR THE SOUTHERN MINKE WHALES COLLECTED IN AREAS III AND IV, 1971/72 TO 1982/83. YEAR-CLASS GROUPING

Year class	Male			Female		
	t_{mp}	s.d.	n	t_{mp}	s.d.	n
1924	13.00	–	1	18.00	–	1
1925	11.00	–	1	–	–	–
1926	–	–	–	–	–	–
1927	–	–	–	–	–	–
1928	–	–	–	11.00	–	1
1929	–	–	–	10.00	–	1
1930	13.00	–	1	9.00	–	1
1931	15.40	5.122	5	14.00	3.266	3
1932	15.33	0.471	3	22.00	–	1
1933	13.67	3.682	3	15.00	2.608	5
1934	13.67	3.682	3	14.20	1.720	5
1935	12.75	2.681	4	12.90	2.548	10
1936	12.75	2.681	4	12.67	3.300	9
1937	10.67	3.399	3	14.83	3.023	6
1938	16.25	2.385	4	12.25	3.269	8
1939	14.00	2.204	7	13.57	2.195	7
1940	11.50	2.617	10	11.40	3.231	10
1941	10.89	2.885	9	13.80	2.822	15
1942	9.16	2.115	6	13.47	2.329	17
1943	12.56	2.715	16	13.00	2.134	18
1944	11.09	2.503	11	13.04	2.091	24
1945	12.53	2.849	15	12.08	3.370	25
1946	11.54	2.664	26	12.78	3.071	27
1947	12.25	4.122	20	11.53	3.154	40
1948	11.94	2.488	31	11.68	2.823	56
1949	10.79	2.041	24	11.77	3.370	57
1950	11.38	2.518	39	11.45	2.745	76
1951	10.81	2.891	48	11.60	2.673	62
1952	10.49	2.493	59	10.55	2.033	69
1953	11.17	2.325	43	10.25	2.193	77
1954	10.43	2.330	44	11.04	2.172	53
1955	9.96	2.410	26	11.27	2.497	55
1956	9.45	1.958	58	10.11	2.168	129
1957	9.75	2.306	53	9.41	2.054	96
1958	9.72	2.420	46	9.48	2.103	80
1959	9.02	2.184	61	9.71	2.220	69
1960	9.09	2.032	44	8.97	1.865	69
1961	9.05	1.965	73	9.01	1.941	99
1962	8.46	1.562	63	8.99	1.742	90
1963	8.94	1.605	50	8.65	1.717	100
1964	8.00	1.469	38	8.67	2.030	60
1965	8.34	1.882	41	8.62	1.747	66
1966	7.49	1.517	39	7.86	1.398	37
1967	6.72	1.484	25	7.80	2.111	35
1968	6.85	1.079	27	7.81	1.704	16
1969	6.85	1.292	13	7.72	0.989	18
1970	6.95	1.356	19	6.50	1.402	14

Growth curve

The growth curves (mean body length plotted on age at capture) are shown in Fig. 9 and the corresponding body length values in Table 5. The mean body lengths of the recent year-classes came always above those for the same age in earlier year-classes, the difference was significant in 9 (female)

TABLE 4. STANDARD DEVIATION (s.d.) AND THE MEAN (*tmp*) OF AGE AT SEXUAL MATURITY ESTIMATED FROM TRANSITION PHASE IN EARPLUG FOR THE SOUTHERN MINKE WHALES COLLECTED IN AREAS III AND IV COMBINED, 1971/72 TO 1982/83. YEAR OF MATURATION GROUPING

Year of maturation	Male			Female		
	tmp	s.d.	n	*tmp*	s.d.	n
1936	11.00	–	1	–	–	–
1937	13.00	–	1	–	–	–
1938	–	–	–	–	–	–
1939	8.00	–	1	10.00	0.816	3
1940	–	–	–	–	–	–
1941	11.00	–	1	10.00	–	1
1942	9.00	–	1	18.00	–	1
1943	9.00	3.000	2	7.00	–	1
1944	8.50	0.500	2	10.00	–	1
1945	–	–	–	9.33	2.115	6
1046	11.00	0.943	3	10.00	2.739	4
1947	13.40	3.250	5	11.33	1.700	3
1948	11.00	3.674	4	11.40	2.417	5
1949	10.40	4.224	5	12.73	0.119	9
1950	10.14	2.167	7	12.75	2.634	8
1951	12.08	3.430	13	15.17	2.115	6
1952	9.87	3.145	6	10.32	3.588	11
1953	10.80	3.682	10	11.16	3.498	19
1954	11.17	4.079	12	11.35	3.838	20
1955	12.00	2.852	15	10.90	3.161	20
1956	10.39	3.630	18	10.63	2.836	32
1957	9.70	3.035	20	11.33	3.107	42
1958	10.41	2.949	22	11.09	3.029	33
1959	10.51	2.943	39	10.27	2.585	49
1960	9.75	2.332	40	10.15	2.776	59
1961	9.69	2.681	47	10.43	2.775	125
1962	10.40	3.178	57	10.37	2.808	120
1963	10.01	2.651	59	10.43	2.775	125
1964	9.48	2.469	66	9.75	3.077	120
1965	9.50	2.898	80	9.64	2.906	119
1966	9.34	2.610	99	9.78	2.803	140
1967	9.37	2.849	105	9.43	2.650	175
1968	8.77	2.528	113	9.13	2.571	173
1969	8.62	2.326	104	8.56	2.476	187
1970	8.58	2.688	120	8.71	2.052	172
1971	8.41	2.350	103	8.81	2.189	137
1972	8.72	2.170	95	8.83	2.128	135
1973	8.01	2.239	67	8.87	2.041	110
1974	8.64	2.708	69	8.08	2.193	60
1975	7.96	2.724	62	8.90	2.414	31
1976	8.22	2.620	23	8.57	2.129	29
1977	7.57	1.450	14	7.89	2.315	27

and 10 (male) of the 15 pairwise comparison for each sex (t-test, $p < 0.05$; Table 5). The magnitude of the difference of mean body length between pairs tended to be larger in younger age classes, but it should be noted that there are still statistically significant difference of mean body lengths between pairs which are age 25 years in males and ages 25 and 28 years in females (t-test, $p < 0.05$; Table 5), which were close to or over the age at physical maturity (see below).

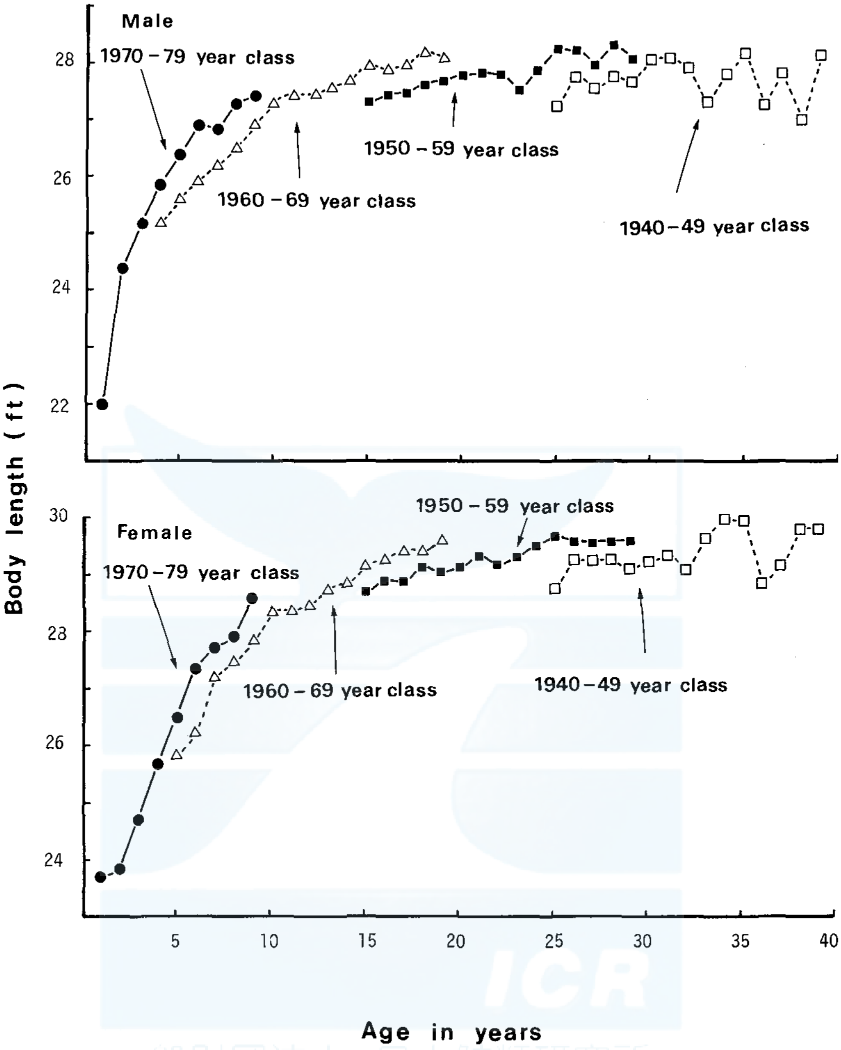

Fig. 9. Mean body length plotted on age at capture of the southern minke whales in each 10 year-class group. Data from Areas III and IV combined, 1971/72 to 1982/83.

TABLE 5. CHANGE IN MEAN BODY LENGTH (FT) AT AGE OF SOUTHERN MINKE WHALES INDICATEDS FOR FOUR YEAR-CLASS GROUPS (YCG). AREAS III AND IV

‹Male›

Age	1940 – 1950 YCG				1950 – 1959 YCG				1960 – 1969 YCG				1970 – 1979 YCG		
	Mean	s.d.	n	t(df)1)	Mean	s.d.	n	t(df)1)	Mean	s.d.	n	t(df)1)	Mean	s.d.	n
1	–	–	–	–	–	–	–	–	–	–	–	–	22.0	2.61	6
2	–	–	–	–	–	–	–	–	–	–	–	–	24.4	2.02	75
3	–	–	–	–	–	–	–	–	–	–	–	–	25.2	1.65	143
4	–	–	–	–	–	–	–	–	–	–	–	–	25.8	1.34	138
5	–	–	–	–	–	–	–	–	25.6	1.92	68	3.49(212)4)	26.4	1.39	146
6	–	–	–	–	–	–	–	–	25.9	1.93	66	4.28(207)4)	26.9	1.33	143
7	–	–	–	–	–	–	–	–	26.2	1.88	95	3.32(250)4)	26.8	1.26	157
8	–	–	–	–	–	–	–	–	26.5	1.40	114	4.87(282)4)	27.3	1.26	170
9	–	–	–	–	–	–	–	–	26.9	1.38	145	2.96(254)3)	27.4	1.21	111
10	–	–	–	–	–	–	–	–	27.3	1.42	172	–	–	–	–
11	–	–	–	–	–	–	–	–	27.4	1.40	225	–	–	–	–
12	–	–	–	–	–	–	–	–	27.4	1.25	288	–	–	–	–
13	–	–	–	–	–	–	–	–	27.5	1.27	247	–	–	–	–
14	–	–	–	–	–	–	–	–	27.6	1.31	249	–	–	–	–
15	–	–	–	–	27.3	1.21	81	3.38(289)4)	27.9	1.28	210	–	–	–	–
16	–	–	–	–	27.4	1.14	81	2.40(263)2)	27.8	1.29	184	–	–	–	–
17	–	–	–	–	27.5	1.07	82	2.94(253)3)	28.0	1.24	173	–	–	–	–
18	–	–	–	–	27.6	1.27	91	3.22(241)3)	28.2	1.22	152	–	–	–	–
19	–	–	–	–	27.9	1.29	102	0.84(252)	38.0	1.28	108	–	–	–	–
20	–	–	–	–	27.8	1.33	119	–	–	–	–	–	–	–	–
21	–	–	–	–	27.9	1.26	147	–	–	–	–	–	–	–	–
22	–	–	–	–	27.8	1.26	138	–	–	–	–	–	–	–	–
23	–	–	–	–	27.5	0.79	83	–	–	–	–	–	–	–	–
24	–	–	–	–	27.9	1.31	90	–	–	–	–	–	–	–	–
25	27.3	1.31	21	3.77(100)4)	28.3	0.98	81	–	–	–	–	–	–	–	–
26	27.9	1.11	28	1.54(82)	28.3	1.23	56	–	–	–	–	–	–	–	–
27	27.8	1.45	47	0.45(97)	27.7	1.15	52	–	–	–	–	–	–	–	–
28	27.9	1.27	27	1.27(61)	28.3	1.06	36	–	–	–	–	–	–	–	–
29	27.8	1.33	26	0.84(58)	28.1	0.95	34	–	–	–	–	–	–	–	–
30	28.2	1.23	36	–	–	–	–	–	–	–	–	–	–	–	–
31	28.1	1.13	28	–	–	–	–	–	–	–	–	–	–	–	–
32	28.0	0.88	33	–	–	–	–	–	–	–	–	–	–	–	–
33	27.4	1.19	23	–	–	–	–	–	–	–	–	–	–	–	–
34	27.9	1.32	27	–	–	–	–	–	–	–	–	–	–	–	–
35	28.2	0.98	11	–	–	–	–	–	–	–	–	–	–	–	–
36	27.3	0.91	14	–	–	–	–	–	–	–	–	–	–	–	–
37	27.8	1.03	12	–	–	–	–	–	–	–	–	–	–	–	–
38	27.0	1.41	2	–	–	–	–	–	–	–	–	–	–	–	–
39	28.2	1.48	10	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 5. (Cont.)
‹Female›

Age	1940 – 1950 YCG				1950 – 1959 YCG				1960 – 1969 YCG				1970 – 1979 YCG		
	Mean	s.d.	n	t(df)[1]	Mean	s.d.	n	t(df)[1]	Mean	s.d.	n	t(df)[1]	Mean	s.d.	n
1	–	–	–	–	–	–	–	–	–	–	–	–	23.7	1.97	6
2	–	–	–	–	–	–	–	–	–	–	–	–	23.8	2.20	77
3	–	–	–	–	–	–	–	–	–	–	–	–	24.7	1.78	141
4	–	–	–	–	–	–	–	–	–	–	–	–	25.7	1.94	130
5	–	–	–	–	–	–	–	–	25.0	2.11	74	1.81(233)	26.5	1.64	161
6	–	–	–	–	–	–	–	–	26.3	1.95	89	4.47(244)[4]	27.3	1.70	157
7	–	–	–	–	–	–	–	–	27.2	1.71	131	2.17(273)[2]	27.7	1.71	144
8	–	–	–	–	–	–	–	–	27.5	1.62	158	2.29(308)[2]	27.9	1.52	152
9	–	–	–	–	–	–	–	–	27.9	1.56	222	4.17(336)[4]	28.6	1.26	116
10	–	–	–	–	–	–	–	–	28.4	1.50	245	–	–	–	–
11	–	–	–	–	–	–	–	–	28.3	1.48	329	–	–	–	–
12	–	–	–	–	–	–	–	–	28.5	1.95	351	–	–	–	–
13	–	–	–	–	–	–	–	–	28.8	1.36	326	–	–	–	–
14	–	–	–	–	–	–	–	–	28.9	1.40	279	–	–	–	–
15	–	–	–	–	28.9	1.43	90	1.53(350)	29.2	1.32	262	–	–	–	–
16	–	–	–	–	29.1	1.32	132	0.96(375)	29.3	1.37	245	–	–	–	–
17	–	–	–	–	29.0	1.27	133	3.20(346)[3]	29.4	1.27	215	–	–	–	–
18	–	–	–	–	29.3	1.56	145	2.06(338)[2]	29.3	1.35	195	–	–	–	–
19	–	–	–	–	29.1	1.30	186	3.63(304)[4]	29.6	1.12	118	–	–	–	–
20	–	–	–	–	29.2	1.34	225	–	–	–	–	–	–	–	–
21	–	–	–	–	29.4	1.17	210	–	–	–	–	–	–	–	–
22	–	–	–	–	29.2	1.29	208	–	–	–	–	–	–	–	–
23	–	–	–	–	29.3	1.28	201	–	–	–	–	–	–	–	–
24	–	–	–	–	29.5	1.23	156	–	–	–	–	–	–	–	–
25	28.8	1.28	41	4.07(169)[4]	29.7	1.21	130	–	–	–	–	–	–	–	–
26	29.7	2.17	51	0.61(147)	29.5	1.22	98	–	–	–	–	–	–	–	–
27	29.3	1.44	56	0.87(145)	29.5	1.18	91	–	–	–	–	–	–	–	–
28	29.5	1.35	47	0.44(104)	29.6	1.18	59	–	–	–	–	–	–	–	–
29	29.1	1.27	63	2.05(111)[2]	29.6	1.29	50	–	–	–	–	–	–	–	–
30	29.3	1.38	41	–	–	–	–	–	–	–	–	–	–	–	–
31	29.4	1.50	40	–	–	–	–	–	–	–	–	–	–	–	–
32	29.1	1.47	54	–	–	–	–	–	–	–	–	–	–	–	–
33	29.7	1.25	40	–	–	–	–	–	–	–	–	–	–	–	–
34	30.1	1.10	39	–	–	–	–	–	–	–	–	–	–	–	–
35	30.0	1.39	19	–	–	–	–	–	–	–	–	–	–	–	–
36	28.8	2.00	28	–	–	–	–	–	–	–	–	–	–	–	–
37	29.2	1.47	17	–	–	–	–	–	–	–	–	–	–	–	–
38	29.8	0.94	12	–	–	–	–	–	–	–	–	–	–	–	–
39	29.9	1.21	13	–	–	–	–	–	–	–	–	–	–	–	–

1) t-value and degree of freedom between nearest YCGs.
2) difference between adjacent YCG is statistically significant at $0.01 < p < 0.05$.
3) difference between adjacent YCG is significant at $0.001 < p < 0.01$.
4) difference between adjacent YCG is significant at $p < 0.001$.

TABLE 6. RELATIONSHIP BETWEEN BODY LENGTH AND PHYSICAL MATURITY IN THE SOUTHERN MINKE WHALES TAKEN IN 1978/79 AND 1979/80 IN AREAS III AND IV

Body length	Male				Female			
(ft)	Immat.	Mat.	To.	Mat.rate(%)	Immat.	Mat.	To.	Mat.rate(%)
18	–	–	–	–	1	0	1	0.00
19	–	–	–	–	–	–	–	–
20	–	–	–	–	–	–	–	–
21	–	–	–	–	–	–	–	–
22	5	0	5	0.00	4	0	4	0.00
23	–	–	–	–	12	0	12	0.00
24	5	0	5	0.00	10	0	10	0.00
25	16	2	18	11.11	10	0	10	0.00
26	33	6	39	15.38	19	0	19	0.00
27	37	14	51	27.45	42	7	49	16.67
28	43	21	64	32.81	53	11	64	17.19
29	15	13	28	46.42	56	22	78	28.21
30	5	6	11	54.54	47	27	74	36.48
31	1	1	2	50.00	18	14	32	43.75
32	–	–	–	–	0	1	1	100.00
33	–	–	–	–	0	2	2	100.00

TABLE 7. RELATIONSHIP BETWEEN AGE AND PHYSICAL MATURITY IN THE SOUTHERN MINKE WHALES TAKEN IN 1978/79 AND 1979/80 IN AREAS III AND IV

Age class	Male				Female			
(years)	Immat.	Mat.	To.	Mat.rate(%)	Immat.	Mat.	To.	Mat.rate(%)
1– 3	6	0	6	0.00	13	0	13	0.00
4– 6	13	0	13	0.00	23	0	23	0.00
7– 9	24	1	25	4.00	41	0	41	0.00
10–12	21	5	26	19.23	42	7	49	14.17
13–15	18	5	23	21.73	39	8	47	17.02
16–18	19	6	25	24.00	29	9	38	23.68
19–21	12	6	18	33.33	21	6	27	22.22
22–24	4	12	16	75.00	11	10	21	47.61
25–27	6	8	14	57.14	17	11	28	39.28
28–30	2	5	7	71.42	9	8	17	47.05
31–33	2	4	6	66.67	3	5	8	62.50
≧34	1	3	4	75.00	4	12	16	75.00

Physical maturity

Table 6 shows the relationships between physical maturity and body length. Physically mature animals appeared at the body lengths over 25 (7.6 m) and 27 ft (8.2 m) in males and females, respectively, and the proprtion of

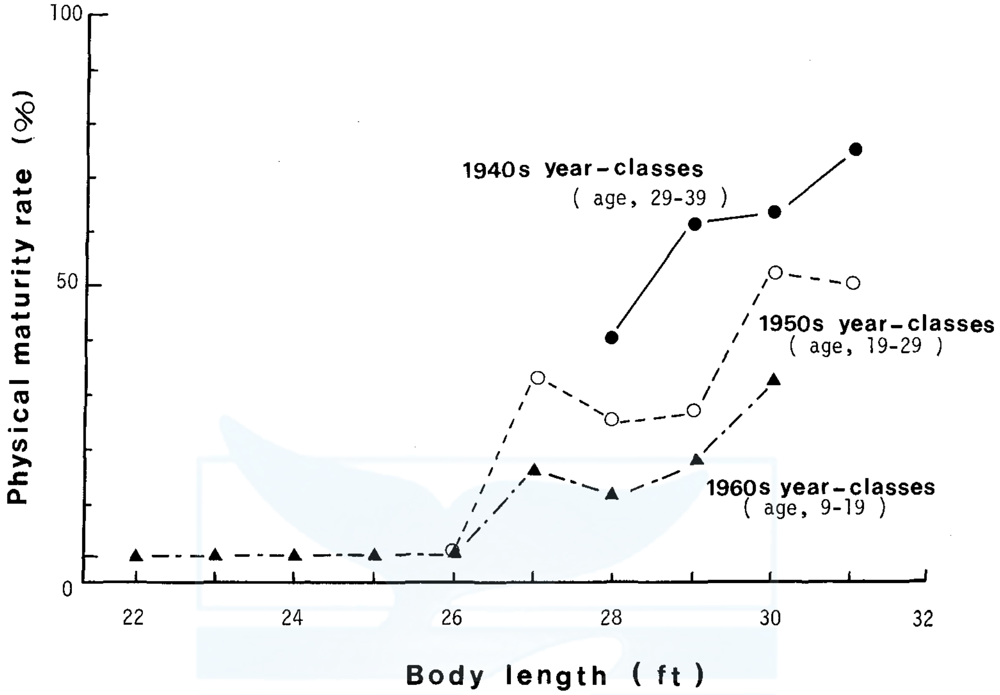

Fig. 10. Relationship between physical maturity rate and body length of female southern minke whales in Areas III and IV. The physical maturity is determined by the fusion of epiphysis with the centrum of the 6th theoracic vertebra.

physically mature individuals increased with increasing of body length.

When physical maturity is compared with age, the physically mature animals first appear at the age of 7~9 years and 10~12 years in males and females, respectively (Table 7). And the proportion of physically mature individuals increases slowly with increasing age in both sexes.

The physical maturity rate (proportion of physically mature individuals) and body length are compared in Fig. 10 between year-classes (10 year-classes combined) among females for which sample size was relatively large. Although the proportion of physically mature individuals increased with the increase of body length in all three year-class groups examined, it is always higher in the earlier year-classes of the same body length, which are older at capture. The proportion of physically mature individuals is statistically different between three year-class groups (1940~'49, 1950~'59, 1960~'69) and for the two length groups (28~29 ft, 30~31 ft) compared ($p<0.001\sim0.05$, χ^2 – test; Table 8).

TABLE 8. COMPARISON OF PHYSICAL STATUS OF FEMALES BETWEEN YEAR-CLASS GROUPS (YCG) IN EACH BODY LENGTH CLASS

Body length Class (ft)	Physical status	Number of animals			Test
		1940s YCG	1950s YCG	1960s YCG	
28–29	Immature	8	23	58	$\chi^2 = 14.248$
	Mature	10	8	9	df=2, $p < 0.001$
30–31	Immature	5	19	27	$\chi^2 = 7.412$
	Mature	10	20	11	df=2, $p < 0.05$

The body lengths of females at 50% physical maturity are estimated to be approximately 28.4 ft (8.7 m) and 29.8 ft (9.1 m) for the 1940s and 1950s year-class groups, respectively. Less than 50% of individuals are physically mature in the 1960s year-class group in all length classes.

Any examination on the age at physical maturity for year-classes has not been made out due to the small sample size and too short time series of the data to be analyzed.

DISCUSSION

Age and body length at sexual maturity

Present study indicated for the southern minke whales that the mean body length of females at the first ovulation (L_{mov}) and the mean length where 50% of the females were sexually mature ($L_{m50\%}$) remained constant at about 27.5ft (8.4 m) and 26.5ft (8.1 m), respectively, during the seasons studied (1971/72 to 1982/83). The mean of 12 $L_{m50\%}$ values is 26.5 ft (8.1 m), and is close to the corresponding figures of 26 ft (7.9 m) estimated for samples in late 1960s to early 1970s (Ohsumi, Masaki and Kawamura, 1970; Ohsumi and Masaki, 1975) or 26.3 ft (8.0 m) estimated for 1971/72 to '76/77 samples (Masaki, 1979). But these values are lower than L_{mov} estimated in the present study by about 0.5~1.5ft (0.15~0.45m).

The present study estimated $L_{m50\%}$ by fitting logistic curve to sexual maturity rate. This procedure should give value which is substantially close to the mean body length at the first ovulation if there is no sample bias, because the curve is symmetric at the point of 50% maturity and the fitness of the present data is good. DeMaster (1984) indicated using artificial data set that different methods may produce different estimates of mean age (or length) at sexual maturity, and that the estimate obtained by least square method ($L_{m50\%}$ or $t_{m50\%}$) is always higher than the mean of the individual ages at maturation (L_{mov} or t_{mov}). This is totally reversed to the result of this study ($L_{m50\%} < L_{mov}$), and I suspect that there must be some biological bias in the present minke whale data.

Ohsumi and Masaki (1975), Masaki (1979) and Best (1982) pointed out, for the southern minke whale stocks, that sexually mature animals tend to segregate in the Antarctic whaling ground. This causes samples to overrepresent the proportion of sexually mature animals, and consequently underestimates the population mean of body length where 50% of individuals are sexually mature, even when $L_{m50\%}$ correctly represents the mean value for the population migrating into the whaling ground. On the other hand, L_{mov} is free from such segregation by maturity. This will be the reason of the discrepancy of 0.5 to 1.5ft (0.15–0.45m) observed between $L_{m50\%}$ and L_{mov}, and the latter will represent the mean body length of females at the attainment of sexual maturity in the southern minke whale population.

Fig. 11 compares t_{mov}, $t_{m50\%}$ and t_{mp} values obtained by two different data groupings, i.e. year-class and year of capture (equivalent to year of maturation). Estimate of t_{mp} covers longer period (28~40 years), while $t_{m50\%}$ and t_{mov} only nine and 11 years, respectively. In years when comparison is possible (1971~78) in the grouping year of capture the t_{mp} values agree with the t_{mov} values in both absolute figures and trend. However, $t_{m50\%}$ values are always about 0.5~2 years lower than t_{mov} or t_{mp} in both groupings (χ^2–test, $p < 0.05$), as pointed out by Cooke (1985). This discrepancy can be explained by the segregation of sexually mature animals in the Antarctic whaling ground, as considered above for body length at sexual maturity. This is supported by Best (1982). He estimated $t_{m50\%}$ of female minke whales to be about 8 years using samples collected off Durban during breeding season in the early 1970s, which is higher than $t_{m50\%}$ obtained from the Antarctic ground in the present study, but is very close to t_{mov} and t_{mp} of the present study. Thus the t_{mp} and t_{mov} are considered to be free from the segregation and give correct value for the population.

It is known that truncated sampling seriously biased t_{mp} value downward in recent year-classes (Free and Beddington, 1980; IWC, 1984a). However, the present study used only samples which are free from this bias. Another possible factor that may cause bias in the transition phase analysis is the ageing error. Cooke and de la Mare (1983) argued that an apparent decline of t_{mp} is produced by assuming a mean ageing error of 25~50% of the true age, even when true t_{mp} remained constant over the period. However, comparison of age readings between readers showed that ageing error of experienced readers is not proportional to the age of whales, but that it is always 2~4 layers (IWC, 1984a). Following this result Sakuramoto, Kato and Tanaka (1984) and Sakuramoto, Tanaka and Kato (1985) showed that the observed declining trend of t_{mp} is real based on a simulation under the assumption of ageing error of 2~4 layers (absolute values which is independent of the age of whales) for each of the transition phase age and age at capture.

While there is no independent parameter, such as t_{mov} of females, to confirm the male t_{mp} estimate, I consider the decline of male t_{mp} is also valid because the male trend is almost the same as that of females and the recent increase of

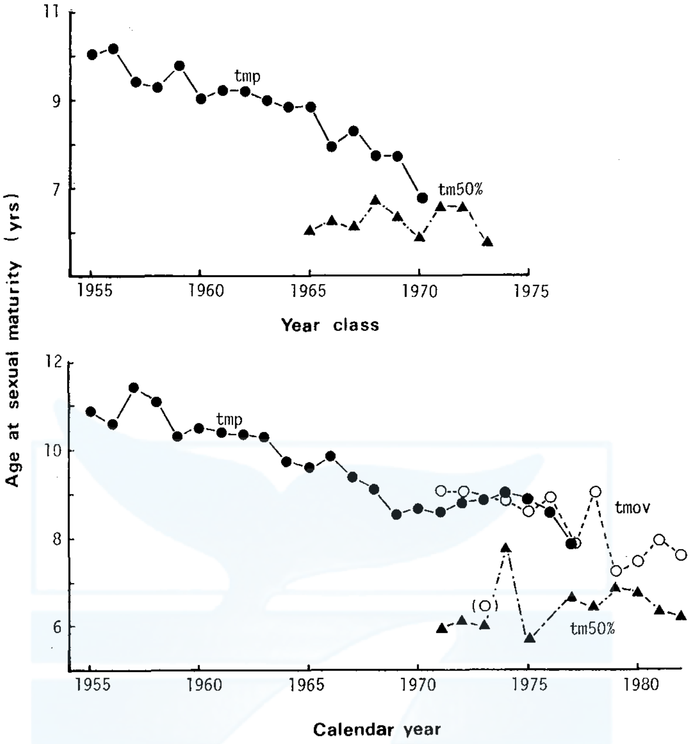

Fig. 11. Comparison of three kinds of estimates of age at sexual maturity for female southern minke whale (Areas III and IV). $t_{m50\%}$; age at 50% maturity rate, t_{mov}; mean age of females having corpus luteum of the first ovulation, t_{mp}; mean age of transition phase in earplug.

the growth rate has been identified in both sexes.

Thus I conclude that the age at sexual maturity of the southern minke whale declined from 12~13 to 7~8 years in the past 30 years, while female body length at sexual maturity remained unchanged at around 27.5 ft(8.4m) at least in the past 20 years. Similar finding has been made by Ohsumi (1986b) in the North Pacific fin whale stock. He found that the female age at sexual maturity ($t_{m50\%}$ and t_{mov}) delined from 12 years in the middle 1950s to 6 years in the middle 1970s, while body lengths at sexual maturity ($L_{m50\%}$) remained unchanged at around 57ft and 61ft in males and females, respectively.

Growth curve and physical maturity

The present study showed that recent year-classes attains larger body size than the previous ones of the same age and attaine larger size at ages close to the attainment of physical maturity. If the growth increase had appeared only in the young fast growing ages, it would be possible to attribute it to an artefact due to possibly intensified fishery selection for larger whales. However, the increase of the growth rate in older age classes strongly suggests that the recent increase in growth rate is real.

The analysis on epiphyseal fusion at the 6th thoracic vertebra showed physical maturity rate in recent year-classes is lower than that in earlier year-classes of the same body length. One possible explanation for this would attribute it to the fact that samples of earlier year-classes tend to include older individuals than those of recent year-classes, and reject the possibility that the body length at physical maturity have increased over the period. Other explanation will consider that the attainment of physical maturity is not dependent on age but on physiological factors which can be decided by some environmental factors such as nutrition, and that the recent increase in body length at physical maturity is real. However, due to short data series available, it is inconclusive which interpretation is more appropriate.

Possible factors causing changes in growth parameters

It is generally known on various mammal and fish populations that growth parameters, such as age at sexual maturity, change with the depletion of the stock or increase of food availability. As shown in Fig. 12, for the southern minke whale stocks, since changes in growth parameters were observed in the period prior to the start of full-exploitation of this stock, the reasons causing such changes will be required for another factors rather than stock depletion. Laws, Parker and Johnstone (1975) reported for the African elephant, *Loxodonta africana*, that the mean ages at sexual maturity differ between populations in different habitats, and attributed it to difference on food availability. Yamagishi (1977) made a detailed cohort analysis of human growth in comparison with the historical changes in food availability, and concluded that recent Japanese year-classes grew faster and to larger body size mainly by improved nutrition in the adolescent growth spurt stages.

From analogizing above studies, the decline in the age at sexual maturity and increases in growth rate (and presumably in body length at physical maturity) will be attributable to the increase of food availability of minke whales (*per capita*) in the Antarctic feeding ground, which is considered to have been produced by the depletion of whale stocks such as blue, fin and humpback whales which share an ecological niche with minke whales (Gambell, 1973, 1975; Laws, 1977a, 1977b).

Laws (1977a) estimated that extra food availability for krill-feeders brought from the depletion of large whale stocks due to the past Antarctic whaling will be about 147,000,000 tons/year during 1920s to 1970s. Additionally, Lockyer (1981) estimated through the analyses of energy cost and growth of the southern minke whale that females will require 3.5% of the additional food to attain sexual maturity one year earlier. In order to make rough examination if the above increase in food availability allows for minke whales

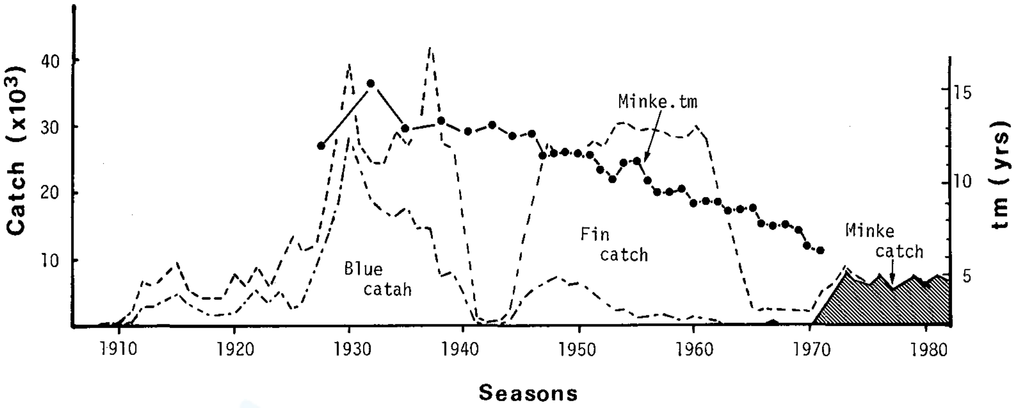

Fig. 12. Historical changes in mean age at sexual maturity of females (t_m, •—•) deduced from transition phase in earplug in the present study female by year-class and in the catch by the whole Antarctic (▨) for the southern minke whales, as well as blue (—·—) and blue + fin (—–—) whale catches. Catch data from International Whaling Statistics.

to decrease juvenile period from 12 years in middle 1940s to 7 years in early 1970s, I have made a calculation assuming;

(a) Mean food intake for both sexes in 1940s was 280kg/day whale (Ohsumi, 1979), which was constant within feeding season.
(b) Minke whales feed in the Antarctic for 135 days and feed nothing outside the Antarctic.
(c) Total minke whale population in 1940s was 382,074 as calculated from sighting surveys in late 1970s to early 1980s (IWC, 1985). (possible increase of the total population size from 1940s to 1970s suggested by the decline of age at sexual maturity was not incorporated)

These assumptions give total krill consumption by the southern minke whale population at the Antarctic as about 14,442,400 tons/year in 1940s. This has to be increased to 14,442,400 × $(1+0.035)^5$ in 1970s, or net increase of food intake of about 108,400 tons/year to allow the five year decrease of the prepubertal stage. This is only 1/1,356 of the food surplus estimated by Laws (1977a). And even under the extreme assumptions of two folds population size in 1940s and daily food consumption during the period, it is still only 1/352 of the food surplus produced by the depletion of the large whale stocks. Thus, there is still room to support the possible increase of other krill-feeder populations such as seabird and seals indicated by seveval authors (Sladen, 1964; Laws, 1973, 1977b; Payne, 1977). The total biomass of above competitors is estimated to be 3,561,000 tons, which is brought from 580,000 tons of seabirds (Group of specialist on living resources of the southern ocean, SCAR and SCOR, 1977) and 2,981,000 tons of seals, including all seal species which have the possibility to feed krill regardless of its amount, based on Øritsland (1977), Laws (1977a) and Gilbert and Erickson (1977), and is about 1.11 folds of the total minke whale biomass (382,074 × 7.0 tons (average body weight)). Furthermore, the biomass of several species of fishes and squids, which are yet other krill-feeders at the Antarctic, will not exceed 10 folds of the minke whale biomass (Mr Ichii, pers. comm.), though the practical estimation on the biomass of these fishes has not been done. Then, the total biomass of krill-feeders other than minke whales in the Antarctic is about 29,420,000 tons (about 11 folds of minke whale biomass). However, even when food requirement of those krill-feeders has historically increased, I consider that there has been an ample supply of krill to allow the changes in minke whale growth parameters in the present study judging from considerably small proportion of aditional food requirements for these changes to the food surplus brought from the stock depletion of the large whales.

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