CHANGES IN BIOLOGICAL PARAMETERS OF BALAENOPTERID WHALES IN THE ANTARCTIC, WITH SPECIAL REFERENCE TO SOUTHERN MINKE WHALE

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Abstract: Historical changes in biological parameters of the southern balaenopterid whales were comparatively examined by reviewing the reports and information as well as on the new analyses for the minke whale (*Balaenoptera acutorostrata*) in the Antarctic region during the 1920's and the 1982/83 season.

Two types of density-dependent changes were identified; changes by catch intensity itself for the blue (*B. musculus*) and the fin (*B. physalus*) whales and changes by interspecific competition for the sei (*B. borealis*) and the minke whales. However, further considerations would be needed in the changes of the sei whale.

Even though the recently proposed possible biases are considered, the following declining trend of age at sexual maturity for the minke whale is thought to be real; from 12-13 years in the mid-1940's to 7–8 years in the early 1970's and from 11-12 years in the late 1940's to 8 years in the mid-1970's, classified by the age of maturation which indicates cross sectional population (=year of catch). A change in pregnancy rate of the minke whale, from 0.55-0.59 in the 1940's to 0.78 in the 1970's was suggested by using a "balance equation".

1. Introduction

The density-dependent changes in biological parameters with changes in the level of populations are generally known. We can learn how changes are taking place in the population by observing the behavior of biological parameters, though a direct evaluation of population size changes seems to be rather difficult.

Several authors (Table 1) reported changes in biological parameters in the southern balaenopterid whales. Among those, observed changes in the blue and fin whales are clearly due to the direct whaling pressure on those species. On the other hand, for the sei (*Balaenoptera borealis*) and the minke (*B. acutorostrata*) whales indirect factors would be considered, because significant changes had taken place before the full scaled exploitations started. LAWS (1977a, b) reviewed the possible changes in the population of krill feeders suggested by the decreased population of the blue (*B. musculus*) and the fin (*B. physalus*) whales, which are caused by intensive whaling affecting the Antarctic marine ecosystem, and he speculated that changes in biological parameters of the sei whale may be due to the decreased population of the blue and the fin whales, as previously pointed out by the original authors themselves (GAMBELL, 1973; LOCKYER, 1974). For the changes in the minke whale also the same reasons have been considered by several authors (MASAKI, 1979; BEST, 1982; KATO, 1983a, b). It was considered that

Species	Parameter*	Locality	Observed** period	Author Mackintosh (1942), Laws (1961), Gambell (1973)		
Blue	Р	Antarctic, South Georgia	1932–59			
Fin	Р	Antarctic, South Georgia	1932-69	Mackintosh (1942), Laws (1961 Gambell (1973)		
	tm	Antarctic, Durban	1910-58YC	Lockyer (1972, 1979)		
Sei	Р	Antarctic, Durban	1946-69	Gambell (1973)		
		Antarctic	1956-75	Masaki (1978)		
	tm	Antarctic, Durban	1925-59YC	Lockyer (1974)		
Minke	Р	Antarctic	1971-80	Маѕакі (1979), Като (1982)		
	tm	Antarctic	1925-70YC	Masaki (1979)		
		Durban	1935-71YM	Best (1982)		
		Antarctic	1925-72YC	Като (1983b, 1985а)		
		Antarctic	1935-72YM	Като (1983b)		

Table 1. Summary of studies on changes in biological parameters of the southern balaenopterid whales.

* P, pregnancy rate; tm, age at sexual maturity.

** YC, year class; YM, year of maturation.

changes in biological parameters of the sei and the minke whales lead to an increase of recruitment to the population before the full scaled exploitation started.

However, COOKE and DE LA MARE (1983) and COOKE (1985) have recently proposed that declining trend of age at sexual maturity is produced by mathematical biases (truncation effect etc.). If their consideration is right, mast of changes in age at sexual maturity for balaenopterid whales which were reported in the past would be only an apparent trend.

The present study with newly gained information reconsiders the changes in biological parameters including pregnancy rate and sexual maturity age, taking into account the interspecific competition among the balaenopterid whales.

2. Materials and Methods

Historical changes in pregnancy rates and ages at sexual maturity of female for the blue, the fin and the sei whales were cited from the previous studies in the Antarctic region. The data of those studies, including that by the present author are summarized in Table 1.

Recently KATO (1985b) has developed further consideration on the sexual maturity age of the minke whale, in addition to my analysis presented at the Seventh Symposium on Polar Biology. This study was based mainly on the materials collected in higher latitudes (>60°S) in Areas III (0–70°E) and IV (70–130°E) during the 1971/72 and 1982/83 seasons. Approximate historical trend of pregnancy rate of the minke whale was estimated by using a "balance equation" for the biological parameters at the balanced level of population, as described in Section 5.

The pregnancy rate, except the minke whale, was estimated by (number of pregnant females)/(number of matured females). The sexual maturity age was estimated from the examination of the "transition phase" in earplugs (Fig. 1), the method originally



Fig. 2. Catches of Antarctic whaling by species from 1904–05 to 1982–83 season, based on MACKINTOSH and BROWN (1974) and the 'International Whaling Statistics. 1910 indicates 1909–10 season.

proposed by LOCKYER (1972). It was confirmed that this phase indicates age at attainment of sexual maturity, by LOCKYER (1972) and KATO (1983a, 1985b), for the fin whale and the minke whale, respectively.

Historical records of catch statistics in the Antarctic whalings during the 1904–05 to 1982–83 season are given in Fig. 2. These are based on MACKINTOSH and BROWN (1974) and the materials from the International Whaling Statistics.

3. Changes by Exploitation (Blue and Fin Whales)

MACKINTOSH (1942) and LAWS (1961) reported that the pregnancy rate of the blue and the fin whales had changed in accordance with the changes in the whaling intensity of both species during 1932 to the 1950's. With subsequent data series, GAMBELL (1973)



Fig. 3. Yearly changes in pregnancy rate (······), mean age at sexual maturity (by year class, female, ●—●) and catch () for the southern blue (upper) and fin (below) whales. Changes of biological parameters are from GAMBELL (1973) and LOCKYER (1974).

demonstrated that overall historical trends of pregnancy rate of the blue and the fin whales during the period from the 1930's to the end of the 1960's increased from 25% in the 1930's to 50–60% in 1950–60's and from 30% in the 1930's to 60% in the 1960's respectively (Fig. 3). Until the finding of earplugs by PURVES (1955), no reliable age character for baleen whales had existed, and no systematic sampling of earplug from the whales caught had been done during several periods after the finding of earplugs. This means there was no way to evaluate the value and behavior of sexual maturity age in earlier periods of exploitation.

LOCKYER (1972) has overcome this problem of the lack of age data in the past by using the "transition phase" in earplug which shows age at sexual maturity, and she indicated a declining trend of the year at birth of the fin whale by arranging to year class, from 10 years in 1910–30 year classes to 5–6 years at the end of the 1960's year classes (Fig. 3). As pointed out by several authors (FREE and BEDDINGTON, 1980; KATO, 1983a, b; COOKE and DE LA MARE, 1983; IWC, 1984), however, there are mathematical biases, so-called "truncation effect", among the estimates of relatively recent year classes, which would cause underestimation of mean ages at sexual maturity and over-representation of its declining trends. Recently, KATO (1985a) has tried to erase this bias from the examination on the minke whale by using the correlation between the ages at caught and at tmp and year of caught, and detected that this effect produced downward biases up to maximum two years.

From the above consideration, it is clear that the declining trend of sexual maturity age in the fin whale according to LOCKYER (1972) is over-representated, and the correction of biases as demonstrated in the minke whale by KATO (1985a) would be needed.

However, judging from the differences in mean ages at sexual maturity between the 1930's and the 1960's year classes, the declining trend of age at sexual maturity apart from its magnitude seems to be real, even though truncation effects exist in the observed values in recent year classes. Due to the lack of age data for the transition phase, the historical behavior of age at sexual maturity in the blue whale is not known, but similar phenomenon can be anticipated.

To examine the relationship between the above changes and the population levels for the blue and the fin whales, cumulative catches were adopted as indices indicating relative levels of populations for both species because of the lack of appropriate evaluation of them. As shown in Fig. 4, the pregnancy rate of both species increases and the mean age at sexual maturity for the fin whale decreases with increase of cumulative catches of each species. Correlations of regression each value of biological parameters on cumulative catches for both species were statistically significant as follows:



Fig. 4. Relationships between changes in biological parameters and cumulative catches in blue (upper) and fin (below) whales. Solid and dotted lines are regressions of pregnancy rate (○) and age at sexual maturity of females (●) on cumulative catch, respectively.

As pointed out previously, magnitude of decreasing mean age at sexual maturity for the fin whale is overestimated in recent year class by the truncation effect. However, even though this overestimation is taken into account, correlation between them is possibly significant. These may show that the above-mentioned biological changes which are increasing of pregnancy vote and decreasing of age at sexual maturity are the direct response to the density change (decrease) by catches, as pointed out by GAMBELL (1973), LOCKYER (1972) and LAWS (1977a, b).

Due to the lack of biological information, examination for the humpback, *Megaptera novaeangliae*, is difficult, but the status of this species seems to be the same as that of the blue and the fin whales.

4. Changes by Indirect Factor (Sei Whale)

Substantial exploitation of the sei whale stocks started in the mid-1960's, because the catches of this species in earlier periods had been very small (less than several hundreds), they can be thought as negligible in terms of density changes (Fig. 2) of the sei whale population itself.

GAMBELL (1973) reviewed the historical changes in pregnancy rate for not only the blue and the fin whales but also the sei whale. According to his illustration (Fig. 5), increasing pregnancy rate in advance of full exploitation from around 20% in the mid-1940's to 50% in the 1960's is remarkable.



Fig. 5. Same as Fig. 3 but for sei whale.

LOCKYER (1974) examined the trend of age at sexual maturity for the sei whale by using the transition phase of earplug, and detected a declining trend similar to that of the fin whale, from 11 years in the 1930's to 6–7 years at the end of 1950's (Fig. 5). Although the magnitude of declining trend seems to be overestimated by the truncation bias as mentioned previously, a real declining trend would also exist in the sei whale for the same reason as in the fin whale.

LAWS (1977a) considered that the above change in biological parameter detected in the sei whale was caused by decrease of the blue and the fin whale populations due to intensive whaling, which lead to greater availability of foods for sei whale. However, as pointed out by KAWAMURA (1978), there are segregation of preference on food species between the sei and other balaenopterid whales (Table 2). Moreover a latitudinal segregation in summer feeding ground also exists (Fig 6). These suggest little interspecific

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Whale species	Food species by order of preference				
Blue	Euphausia superba=Thysanoessa macrura				
Minke	E. $superba = Th$. macrura				
Fin	E. superba=Th. macrura>E. vallentini=Amphipoda>(Copepoda, fish)				
Humpback	E. superba>(gregarious fish)				
Sei	Copepoda (Calanus tonsus, C. simillimus, etc.)>E. vallentini=Amphipoda				
	>fish>Munida gregaria>E. superba				
Right	Copepoda				

Table 2. Species and the preference of food in the Southern Hemisphere baleen whales (after KAWAMURA, 1978).

(); local ocurrence.



competition between the sei and the blue/fin whales. (In terms of food and distribution, ecological aspects of the right whale are similar to the sei whale, but the right whale is not considered as a competitor because of its extremely reduced population before the beginning of modern whaling.)

On the other hand, GAMBELL (1968) found changes in migration pattern; the peak of the sei whale's migration to the Antarctic region was March in the 1930's but since the late 1950's it changed to January. Moreover, LAWS (1977a) in his review suggested latitudinal changes in the summer migration of the sei whale, migrating farther south. If the change in migration pattern as indicated above in the past was real, the significant competition between the sei and the fin/blue whales for habitat must exist.

Anyway, the significant changes in the biological aspect of the sei whales involve interesting features, and further considerations would be needed.

5. Status of Minke Whale

5.1. Age at sexual maturity

Several authors (MASAKI, 1979; BEST, 1982; KATO, 1983b) observed declining trends of the mean age at sexual maturity estimated from examinations of the transition phase in earplugs, from 12–14 in the 1940's year class to 6–7 in the early 1970's year class. However, these observations are biassed to downward in recent year classes by trancation effect.



Fig. 7. Changes in mean age of sexual maturity estimated from the transition phase in earplug of female minke whale arranged by year class (left) and by year of maturation (right). Biases due to truncation effects were corrected by methods of KATO (1985a). Increase in the late 1930's to the 1940's in changes by year of maturation is apparent by the conversion effect suggested by KATO (1983b).

KATO (1985b) indicated modified trends of the mean age at sexual maturity (tmp) by year class free from truncation effects using the correlation procedure designed by KATO (1985a). Those are reproduced in Fig. 7 and if linear regressions are adopted to values of tmp between the 1945 and the 1969 year classes when the declining trend is observed, the following formulae are produced:

Male;
$$tmp = 12.31 - 0.222t$$
 $(r = -0.974, 0 \le t \le 27)$, (1)

Female; tmp = 12.47 - 0.209t (r = -0.972, $0 \le t \le 26$), (2)

where, t = year class (set 0 for 1945).

KATO (1985b) also arranged each estimate from by year class to by year of maturation. If this conversion is adopted, tmp by year of maturation can be considered to be a representative value of sexual maturity age in the population of certain year such as that in year of catch. From this treatment, a declining trend is also detected, 11-12 years at the end of the 1940's to 8 years in the 1970's by showing linear regressions for both sexes as below (Fig. 7);

Male;
$$tmp = 11.65 - 0.139t'$$
 $(r = -0.918, 0 \le t \le 22)$, (3)
Female; $tmp = 12.65 - 0.151t'$ $(r = -0.912, 0 \le t \le 26)$, (4)

where, t' = year of maturation (set 0 for 1949). Increases of tmp in the 1930's-1940's caused by "conversion effect" in KATO (1983b) are apparent and meaningless.

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Because the transition phase technique is thought to be an indirect estimation of age at sexual maturity, KATO (1985b) compared tmp values with other independent and direct estimates which are age at 50% of sexual maturity estimated from the relationship between the age and sexual maturity rate (tm 50%) and the mean age of animals having only one corpus luteum (tmov) during the periods when these estimates overlapped (Fig. 8). Substantial agreement was obtained between tmp and tmov (= year of catch), but those were about two years higher than tm 50% in both year class and year of maturation (= season caught). This discrepancy can be explained by the downward bias in tm 50% due to reproductive segregation in the sampling areas (higher latitudes), although tmp and tmov are thought to be free from such sampling effect (KATO, 1985b). From the above the age at sexual maturity demonstrated by the transition phase is thought to be valid.

As substantial exploitation of the minke whale had started in the 1971–72 Antarctic whaling season and the catches prior to this season were very small (Fig. 2, Table 3), direct catch did not affect the age at sexual maturity. From the viewpoint of interspecific competition on food and habitat, the minke whale is a more direct competitor of the blue and the fin whales than the sei whale. Plotted in Fig. 9 are the mean age at sexual maturity by year class against the cumulative catch of the blue and the fin



Fig. 8. Comparison of estimates of sexual maturity age of females by three different techniques in year class (upper) and year of maturation (below), after KATO (1985b). tm 50%, age at 50% of sexual maturity rate; tmov, mean age of females having only one corpus luteum in the ovaries; tmp, mean age at sexual maturity estimated from the transition phase in earplug.

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Season	Japan	USSR	Brazil	S. Africa	Norway	UK	Netherland
1951-52		9					
195 2 –53							
1953-54						3	
1954–55				-			
1955-56		41				1	
1956-57		46					
1957-58		493					
1958-59		102				1	
1959-60		203				1	1
196061		162		Box sales of	-		
1961–6 2	-	2	-				
1962-63		21					
1963-64	96	5					
1964–65	2	4			1		
1965-66		8			2		
1966-67	1	14			3		-
1967–68	597	8	-				
1968-69	42	17					
1969-70	_	30			1		
1970–71	4	40	900		32		
1971–72	3013	41	702	135			
1972–73	2092	3653	650	173			
1973–74	3713	4000	765	117			
1974–75	3500	3500	1039	110			
1975–76	3017	3017	776			_	_
1976–77	3950	3950	1000				
1977–78	2400	2600	690				
1978–79	2733	2733	739				—
1979–80	3279	3879	902				
1980-81	3120	3120	749				_
1981–8 2	3577	3577	854				
198 2 –83	3223	3223	625			_	

Table 3. Catch statistics of the minke whale by country and season in the SouthernHemisphere.Data from International Whaling Statistics.



Fig. 9. Relationship between the minke whale's age at sexual maturity of female (by year class) and cumulative catches of the blue and fin whales combined.

whales combined by the corresponding year class. The correlation coefficients of linear regression mean age on catch were highly significant (r = -0.927; t-test, p < 0.001). This may indicate that a decrease of age at sexual maturity depends on the decrease of population of the blue and the fin whale which are most positive competitors in the Antarctic region.

5.2. Possible changes in pregnancy rate

KATO (1982) reported a constant trend of observed pregnancy rate at around 0.9 in the 1971–72 to 1980–81 season in the Antarctic whaling ground. However, as suggested by the previous author (OHSUMI and MASAKI, 1975), there is reproductive segregation in the Antarctic whaling ground where not only matured but also pregnant females dominated. This phenomenon has caused overestimation of pregnancy rate in the whaling ground.

BEST (1982) examined the pregnancy rate of this species off Durban (30° S, 31° E) from the female's sexual status in the population based on materials collected from 1971 to 1973 and estimated the pregnancy rate to be 0.78. Although small samples were used, his examination is theoretically appropriate, and seems to be only acceptable value of true pregnancy rate at present. This value can be adopted as a true rate of pregnancy in the 1970's.

There is no way to evaluate directly the pregnancy rate in the past (prior to the 1970's). However, adopting the "balance equations" among biological parameters when the population is balanced (Recruitment rate = Mortality rate), the pregnancy rate in the past can be estimated, under the same assumptions as on the natural mortality coefficient. The balance equation is expressed as follows:

$$P = 2(1 - e^{-M})e^{((tm'-1)M + Mj)},$$
(5)

where P = pregnancy rate, tm' = age at the first parturition, M = natural mortality coefficient and Mj = juvenile mortality coefficient (j=0-1). In terms of the nature of cetacean natural mortality, natural mortality in the first year (juvenile mortality) generally seems to be higher than other age classes. Although the exact value of juvenile mortality coefficient has not been obtained, Scientific Committee of IWC (1981) considered its value to be roughly two or three times larger than M.

Age-specific changes in natural mortality rate have been reported in the toothed whale (KASUYA and MARSH, 1984). In this connection, DE LA MARE (1985) suggested that age-dependent mortality rate also existed in baleen whales including the minke whale by the examination of catch curve (age distribution). However, he did not take acount of the factor of population increasing effect in the construction of catch curve. For the mortality estimation of the minke whale, the use of catch curves is not suitable because catch curves were skewed by increasing recruitments. Then, the value of 0.085 (KATO, 1984) estimated by the technique using interspecific relationships between M and maximum body length among the balaenopterids, which was originally proposed by OHSUMI (1979a), was tentatively adopted as a representative M throughout life.

Judging from the behavior of age at sexual maturity arranged by year of maturation, a decline seems to start at the end of the 1940's from 11–12 y. Then I assumed that the population was in the balanced level in the 1940's and earlier.

Accepting the above, biological parameters at the balanced population level were set as follows:

tm';
$$12.15(tm) + 0.92$$
 (gestation period in years)
M; 0.085
Mj; Option 1 (*Mj*=2*M*)-0.170, Option 2 (*Mj*=3*M*)-0.255.

Putting the above values in eq. (5), the pregnancy rate in the 1940's was calculated to be 0.54 and 0.59 in options 1 and 2, respectively. Accepting those values as the pregnancy rate in the 1940's the magnitude of increasing rate of pregnancy rate between the 1940's and the 1970's is calculated to be 0.19-0.24 y.

6. Discussion

From the present analysis, it is thought that biological parameters of balaenopterid whales have changed in accordance with decrease in their density possibly caused by reduction of population size itself or reduction of ecological competitors, even taking into account that some biases affected yearly trend of biological parameters.

The historical changes in biological parameters in the minke whale can be explained by an ecological response to the reduction of the blue and the fin whale populations, which suggest a relative decrease of the minke whale, subsequently leading to increased availability of food. Increasing availability of food may lead to a faster growth rate of the minke whale. This possible phenomena may be supported by the findings by KATO (1985b), namely, animals of recent year classes grew faster than those of old year classes. And mechanism of this whale seems to be simpler than the case of the sei whale. From the points of the interspecific competition on habitats, both blue and minke whales distribute in ice edge zone. By my sighting experience during the IWC/IDCR (International Decade of Cetacean Research) sighting and marking cruises in the Antarctic region, the blue and the minke whales were observed in close association and occasionally the two species formed a mixed school (in Area III during the 1979–80 cruise).

I assumed in the previous chapters that the significant changes in the minke whale population had begun at the end of the 1940's when exploitation of the blue and the fin whales was reopened after World War II. However, before this period, as the blue whale had been heavily exploited in the late 1920's to the earlier 1940's (Fig. 2), the existence of a gradual change in the minke whale population is undeniable. In this connectoin, OHSUMI (1979b) considered that the increase of the minke whale had started in the 1920's. Earlier exploitations of the blue whale in the 1920–30's may have provided favorable conditions for other whales such as the fin whale and the humpback whale. Therefore, it is thought both factors caused by catch intensity and interspecific competition affect changes in populations of exploited species. In other words, both factors are comingled in the changes of biological parameters. Future study may need examination of this point, by appropriate analysis of the changes in population level for each species of baleen whales.

LAWS (1977a, b) and KAWAMURA (1978) pointed out the necessity of taking into

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account the existence of other krill-feeders such as pinnipeds and penguins, considering the ecosystem changes in the Antarctic region. SLADEN (1964) suggested increases in the chinstrap and the Adélie penguin, and PAYNE (1976) reviewed the number of pups of southern fur seal, *Arctocephalus gazella*, and recorded the increased number from 12 in 1933–36 to 1000 in 1957–1970's at South Georgia. LAWS (1973) estimated that population size of fur seal expanded from 100 to 60000. These are direct information of increasing population of krill-feeder.

LAWS (1977b) reported that the biological change in crabeater seal, Lobodon carcinophagus, was a decline in age at sexual maturity, based on the transition phase in the cementum of teeth similar to that in earplug, from 4 years in the 1940's to 2.5 years at the end of the 1960's. However, this trend involves "truncation effect", and the magnitude of this bias has not been evaluated. Recently, BENGSTON and LAWS (1983) gave an alternative interpretation of the trend of sexual maturity age by year class; age-specific-mortality rate porduces an apparent declining trend. However, sample size of age data in crabeater seal seems to be small and those had been collected only in two seasons, which may not be sufficient to judge whether the declining trend is real or artificial because the magnitude of the decline would not be so large as that in baleen whales, considering their longevity and the general nature of flexibility of changes in age at sexual maturity. Anyway, the crabeater seal is distributed mainly in the ice edge zone where the minke whale concentrated in the summer feeding season and the blue whale was once abundant. From my experiences during the IDCR sighting and marking cruise (1978–79 to 1980–81 cruise), the habitats of the crabeater seal and the minke whale are very close to each other. Moreover, taking account of their abundance (1.5 million), this seal is one of the important components in the Antarctic ecosystem.

Impacts of whaling seems to affect also the population of the krill indirectly; mortality rate by predators may be one of the factors to regulate the population size, when the abundance of most dominant predators (baleen whales) was reduced by whaling, and substantial changes in the krill population may have taken place.

In the future, quantitative evaluation of historical change of krill-feeding animals including baleen whales should be focused on the simulation study which will provide reasonable interpretation on the interspecific competiton.

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