INTERACTION AMONG KRILL, WHALES AND OTHER ANIMALS IN THE ANTARCTIC ECOSYSTEM

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Abstract: A trial was made to establish a model dealing with the interaction among krill and other predators in order to estimate the valid exploitation level not to impair the stock of krill and whale, based upon the dynamics of prey and predotor. As the present knowledge of the basic biological parameters for the dynamics is still poor, the present report mainly aimes to set up the model and find out what parameters are important rather than to obtain the result itself.

At first the simple model with only one type of predator was used and the model was elaborated so as to include multiple predotors, and also to deal with the environmental influence.

Equilibrium state, in which the MSY level of exploitation rate can be expected, can be attained almost 100 years later if we start from the present level of stocks of both krill and whales.

According to the tentative calculation it was suggested that the influence of catch of krill upon the stocks of both krill and whales is very low even if 10% of the krill stocks is to be exploited for the period of 20 years or more. But the effect upon the stock of seal seems more significant than that upon whales when feeding competition is taken into consideration.

Sensitivity of each parameter upon the long term estimation of the krill stock was tested. The most sensitive parameters are the reproduction rate of krill, and the carrying capacity of krill in the Antarctic. The type of feeding competition should be studied.

1. Introduction

The conventional method of stock assessment of catch and effort statistics cannot be validly applied to the Antarctic krill in which case the predation by other animals, taking whales as an example, probablly exceeds much farther than that by human catch. Direct assessment employing acoustic devices will be most useful if the survey plan is established systematically and efficiently. It is, however, still required to solve the interaction of prey and predators which constitute the ecosystem in the Antarctic surrounding the krill adequately.

As a matter of fact, relevant information on biological parameters such as natural mortality, growth, reproduction, etc. on each component of the ecosystem is rather poor for solving the problem at present. The present report, therefore, aims to build up models on such interaction between krill and its predators by adopting available information and assumptions on the parameters even if they might be fragmental and speculative; and thus to try to find out; 1) the general pattern of such interaction and long

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trend of the change of the ecosystem; and 2) which parameters play the most important role in the dynamics of the ecosystem. Although several experimental calculations have been made along the line of the purpose, their numerical results are not themselves any final assesment. At the start the simplest model which deals with krill and whales as the only type of the predator was tried, then the model was elaborated to more complex types so as to deal with other types of predators.

2. Simple Model with Single Predator

2.1. Fundamental equations

HORWOOD (1981) presented the following equations which lead the dynamics of krill and whale under a simplified model based on the assumptions that 1) the predation by other animals than whale is considered to be at a constant rate; and 2) the whole baleen whale have the same biological parameters or they are considered as a single group.

Thus a set of simple simultaneous differential equations stands for the variation of stock size of both krill and whale, assuming a sigmoidal growth of the stocks (eqs. 1 and 2).

$$\frac{dZ}{dt}=Z\{P(1-Z/Q)-R-F1-SW\}, \qquad (1)$$

$$\frac{dW}{dt}=W\{T(1-W/UZ)-F2\}. \qquad (2)$$

Here Z is the stock size of the krill; W, that of whale; P and T stand for the annual reproduction rate of krill and whale respectivelly; Q, the carrying capacity for the krill in the Antarctic; R, the predation rate by other animals than whale; U, the nutritious turnover rate from krill to whale; $F1$ and $F2$ are the annual catch rate of krill and whale respectively.

If we consider the saturation of feeding may occur when abundance of food organism is very high, some modification may be made on eq. (1), namely,

$$\frac{dZ}{dt}=Z\{P(1-Z/Q)-R-F1\}-S'W\{1-\exp(-KZ/Q)\}, \qquad (1')$$

$$\frac{dZ}{dt}=Z\{P(1-Z/Q)-R-F1-S''K'W/(K'+Z)\}. \qquad (1'')$$

The former follows IVLEV (1965) and the latter does SHOEMAKER (1977). In the former S' means the amount of krill eaten by unit weight of whale, while in the latter case S'' has the same dimension as the original equation eq. (1).

2.2. Values of parameters tentatively adopted

2.2.1. P

HORWOOD adopted $P=1.0$. According to KAWAKAMI and DOI (1979), one adult female krill lays 7000 eggs of which 95% hatch successfully. Thus the number of female offspring from one adult is,

$$7000\times 0.95\times 0.5=3325.$$

The body length of a krill at copulation is 40 mm while that at one year of age is 25 mm. If the body weight is assumed proportional to the cubic of the body length, the ratio of the body weight of a krill of one year of age which enters the catchable stock is $(25/40)^3=0.244$. On the other hand, the natural mortality rate of the krill at one year after hatch was estimated as $M=5.5$. Therefore, the number of survived female at one year of age is,

$$3325\times \exp(-5.5)=13.6.$$

Thus the biomass ratio between the parent at spawning and one year of age is,

$$13.6\times 0.244=3.31,$$

therefore $P=\ln 3.31=1.19$.

The assumption P being 1.0 seems a little modest even though the difference is not very remarkable.

2.2.2. Q

There are various values for the estimation of the potential stock size of the Antarctic krill, as well as the value of the relationship between carbon fixation and phytoplankton productivity. According to HEMPELL (1970) the carbon fixation at south of 55° S is 1.6×10^9 t/year or 3.2×10^{10} t/year of phytoplankton adopting 20 as the conversion rate. While ARUGA (1970) obtained 30 gC/year/m^2 as carbon fixation. Adopting the same conversion rate for the area south of 45° S, total carbon fixation is 1.8×10^9 tC/year or 3.6×10^{10} t of phytoplankton per year. For the area south of 55° S the value is 2.4×10 t. If we consider that the standing crop of the zooplankton is about ten percent of the phytoplankton, half of which being the krill, the abundance of krill lies between 1.2 and 1.8×10^9 t. Thus we can suppose that the abundance of the Antarctic krill is in the lower level of the order of 10^9 t. The amount of primary productivity may have a year-to-year fluctuation considerably as the successive observation made in different years along nearly same cruising track shows.

By means of acoustic method DOI and KAWAKAMI (1979) estimated the abundance of the Antarctic krill being between one to two ($\times 10^9$) t for the minimum considerable value.

NEMOTO and MURANO (1979) gave the amount of the krill eaten by predators including only whales, seals, and birds as more than 0.337×10^9 t. In order that the krill stock may be sustained against the predation G, the following relationship

$$PZ(1-Z/Q)\geqq G, \quad (3)$$

must have the real solution for Z; namely

$$QP\geqq 4G, \quad (4)$$

for $P=1$ at the MSY level of Z.

Thus the value of Q should be at least four times as large as the amount of consumption by predators, namely $4\times 0.337=1.35$ ($\times 10^9$) t if the value by NEMOTO and

MURANO (1979) is adopted.

Accordingly, the value of Q may well be assumed to be in the lower level of the order of 10^9 t. Thus a modest value $Q=1\times10^9$ t is to be used tentatively in the computation hereafter. The current stock size of krill is naturally pretty lower than Q. The value $Q=1\times10^{10}$ t in HORWOOD's original report may seem rather an overestimation.

2.2.3. *R*

HORWOOD employed 0.05; while among the total amount of predation 0.337×10^9 t cited by NEMOTO and MURANO, 0.24×10^9 t are attributed to other predators than whale. The value 0.05–0.25 was used in the computation. The value should be improved by future study.

2.2.4. *S*

As has been explained in the previous section, S has different meaning in accordance with the type of model. For eq. (1) $S=5\times10^{-9}$, and for the eq. (1′) $S=5.0$ were adopted respectively.

The value of K in IVLEV's model (1965) and K' in SHOEMAKER's model (1977) are hard to obtain directly from available information. For the former $K=3$ was adopted arbitrarily meaning that the feeding approaches to the saturation state if the stock size of krill exceeds $Q/3$.

SHOEMAKER's coefficient K' and related S'' were obtained by the following assumptions: 1) The stock size of whale was 45 million t in 1920s and 8 million t in 1970 respectively (GAMBELL, 1974); 2) In both periods the krill is in a stable state, namely $dZ/dt=0$; 3) One ton of whale eat somewhat around 5 t of krill a year at present (ANONYMOUS, 1977) being 20 percent larger than that in 1920s (LOCKEYER, 1981), that is, 4.17 t/year. Thus

$$Z\{P(1-Z/Q)-R\}=G, \qquad (5)$$

stands for both initial and present states. The amount of krill eaten by whale G is therefore $45\times4.17\times10^6=188$ million t in the initial period and $8\times5=40$ million t for the present respectively. The value of Z can be obtained for the assumed value of R by putting $P=1$ and $Q=1.0\times10^9$. In such a case, however, R cannot exceed 0.13 so as Z may have real solutions. The value of K' and S'' can be obtained by solving the following set of equations;

$$\frac{S''}{K+Z}=5\,(\text{present});\quad =4.7\,(\text{initial}). \qquad (6)$$

For $R=0.05$, $S''=9.8(\times10^{-9})$ and $K'=1.2(10^9)$; while for $R=0.1$, $S''=14.5$ $(\times10^{-9})$ and $K'=0.6(\times10^9)$ were obtained respectively.

2.2.5. *T* and *U*

The value of HORWOOD's original report 0.05 and 0.1 were adopted.

2.3. *Stationary model*

The stock size of both krill and whale is a stationary state can be obtained by putting the left sides of the simultaneous differential equations as zero and solving them for various values for $F1$ and $F2$. IVELEV's model is rather hard to solve because of its shape. Therefore, the SHOEMAKER's model was tried.

The stationary value of krill Z_0 and corresponding whale W_0 can be expressed as,

$$\left.\begin{aligned} Z&=\frac{1}{2A}\cdot(-B+\sqrt{B^2-4AC}),\\ &A=-P/Q\\ &B=P(1-K'/Q)-(F1+R)-S''K'U(1-F2/K)\\ &C=K'(P-F1-R)\\ W&=UZ(1-F2/T). \end{aligned}\right\} \quad (7)$$

And corresponding catches for the krill and the whale are,

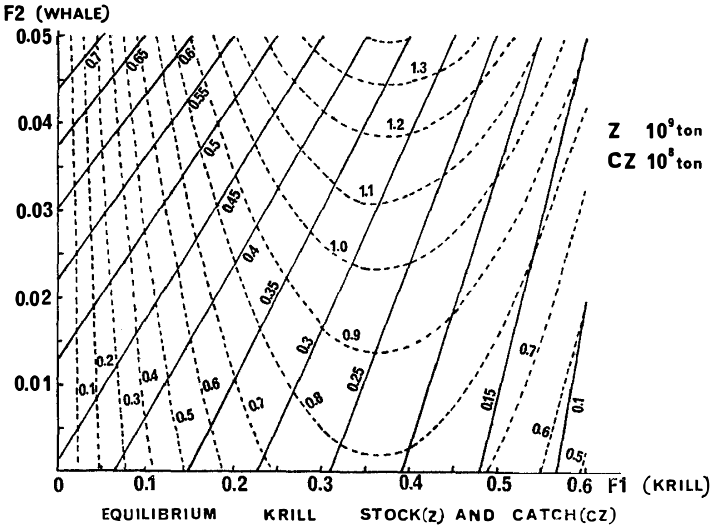

Fig. 1. Equilibrium krill stock (Z) and catch (CZ) for various values of fishing mortality of krill F1 and that of whale F2.

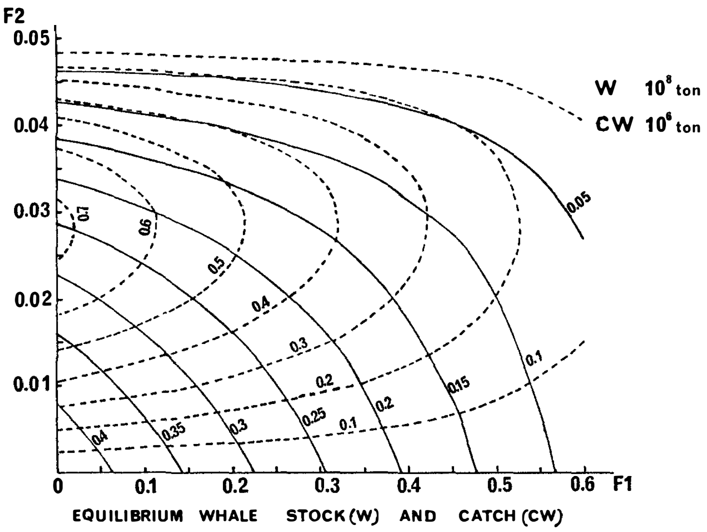

Fig. 2. Equilibrium whale stock (W) and catch (CW) for various values of fishing mortality of krill F1 and that of whale F2.

$$\left.\begin{aligned} CZ &= F1 \times Z_0, \\ CW &= F2 \times W_0, \end{aligned}\right\} \qquad (8)$$

respectively.

Figures 1 and 2 show a set of examples obtained in case of $R=0.1$; As to other parameters, $P=1.0$, $Q=1\times10^9$, $T=0.05$, and $U=0.1$ were used respectively.

It is shown that the MSY level of the krill, even though depending upon $F2$, is found in unrealistic high value of $F1$ compared with the present level of exploitation. Therefore, there seems to be no danger of overexploitation of krill at present circumstances.

2.4. Dynamic model

2.4.1. Decrease of whale and accompanying increase of krill in recent decades

The stationary state shown in the preceding chapter can be attained only after a long period of time. Trials were therefore undertaken to trace the change of both stocks by solving the simultaneous differential equations numerically by means of Runge-Kutta's method employing a computor.

To trace the past trend, however, the stock size of the whale has available time series data given by GAMBELL (1974). Assuming that krill was in the stationary state at the initial stage, the initial value of the krill stock can be obtained. And accordingly it is not necessary to solve the differential equation pertaining to the whale. Several values for R were adopted, but only to show that the general pattern of the trend does not change much. As to the value of Q two alternative methods were employed. At first it was set constant, and then it was dealt with a variable fluctuating in a normal

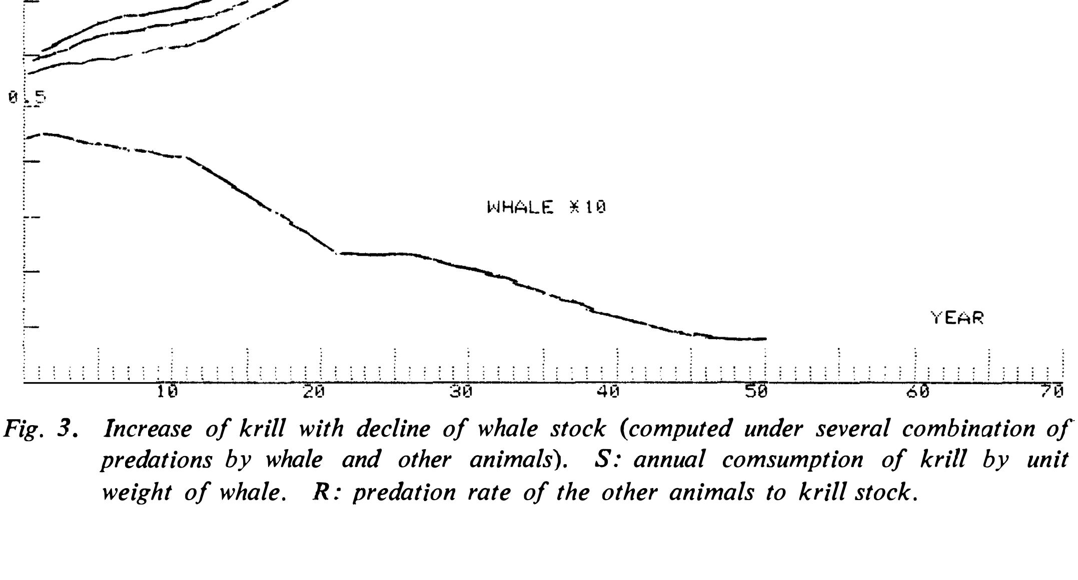

Fig. 3. Increase of krill with decline of whale stock (computed under several combination of predations by whale and other animals). S: annual comsumption of krill by unit weight of whale. R: predation rate of the other animals to krill stock.

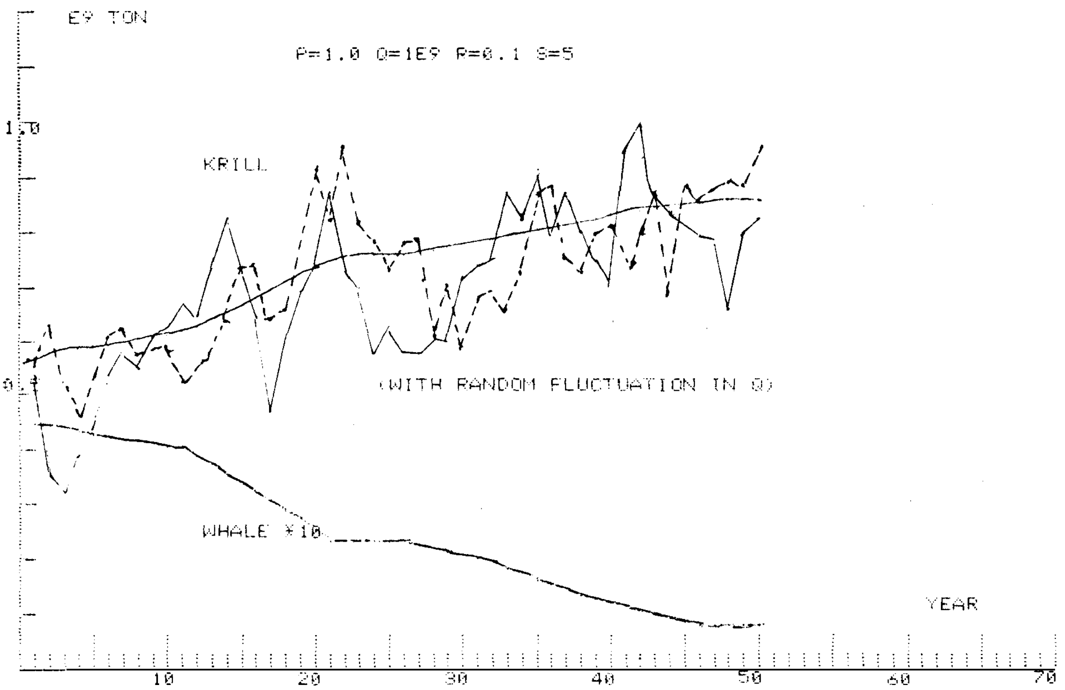

Fig. 4. Increase of krill with decline of whale, taking the random fluctuation in carrying capacity Q into consideration.

fashion around the mean value with 20% standard deviation, considering that the value of Q may be subject to environmental influence. Two sets of random series generated by computor were introduced. The results are shown in Figs. 3 and 4. They show the general increase of krill accompanying the decrease of whale in these decades. The fluctuation of Q by means of environmental variation may mask the trend in a short period even though the general trend pattern is not affected.

2.4.2. Effect of catch of krill upon both krill and whale stocks

The changes of both krill and whale were obtained by numerical solution of differential equations starting from the present level of stocks obtained by computation shown in the preceding chapter as the initial condition. The result naturally depends upon the parameter values adopted. But so far as those adopted in the previous chapters are concerned, the general trend does not change very severely. This point is to be discussed in the next chapter. Two alternative cases were tried again; the first being without whale catch of $F2=0$, and the second with $F2=0.025$ at which the whale stock can be sustained. In either case it takes several decades before the stable state can be attained. Moreover, even if ten percent of the krill stock may be taken annually for several decades, the influence upon the whale stock is rather slight. The catch of krill of ten percent ($F1=0.1$) means the annual catch of krill about 60 to 80 million t, almost comparable to the whole annual fisheries yield in the world (Figs. 5 and 6).

2.4.3. The sensitivity of the parameter values to the estimates

The parameter values hitherto adopted are all tentative. In order to investigate the sensitivity of them on the estimates of the krill stock size, a trial was made to shift each parameter by 10% and the effect on the estimate of the krill stock size was traced for the period of one hundred years. By this computation it was found that P the re-

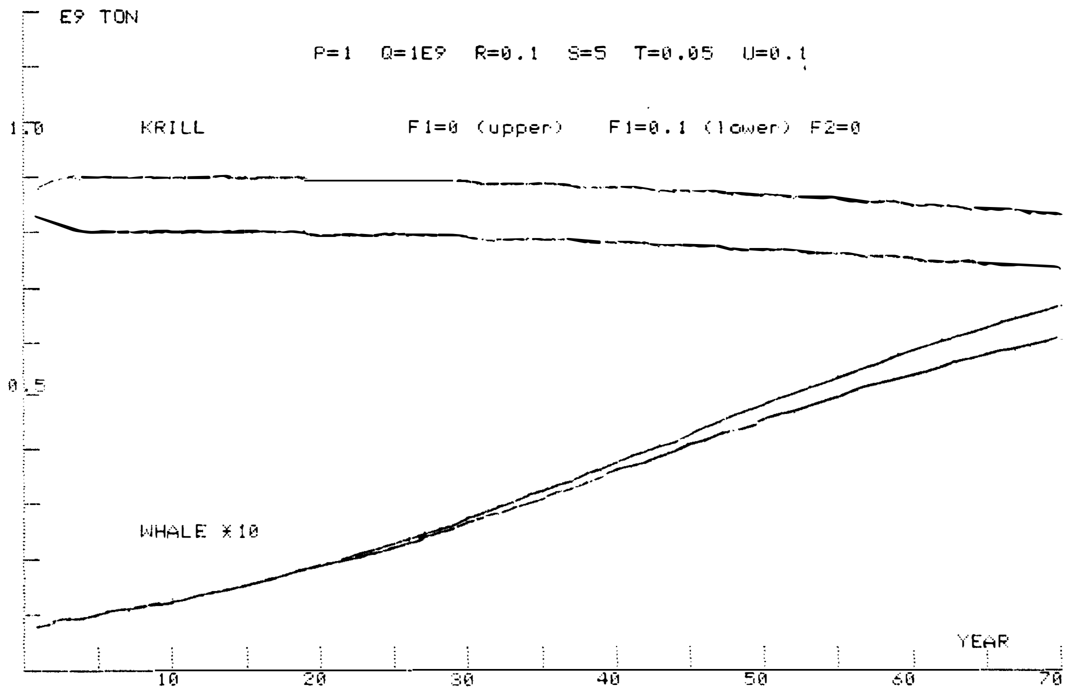

Fig. 5. Effect of krill catch upon whale stock (without whale catch) under two levels of krill exploitation.

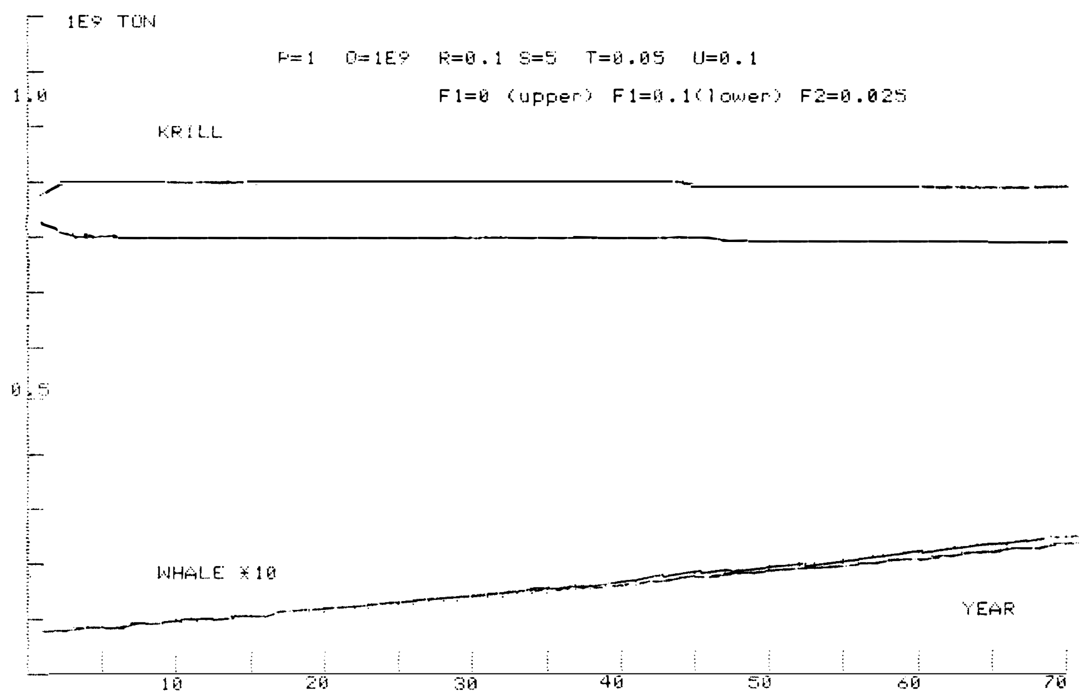

Fig. 6. Effect of krill catch upon whale stock (with sustainable level of whale catch) under two levels of krill exploitation.

productivity of krill and Q the carrying capacity for krill have rather significant effect and thus the importance of improvement of those values is suggested. Moreover, those parameters pertaining to whale such as S, T and U are found that their variation may influence gradually with the lapse of time even though their relative contribution to

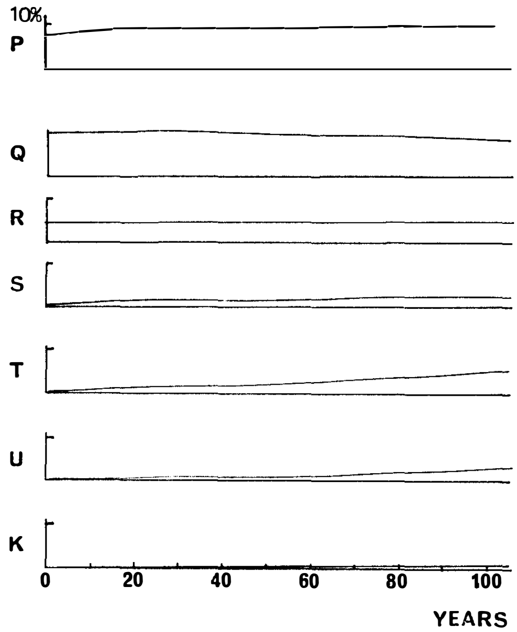

Fig. 7. Sensibility of each parameter. Effect of 10% shift of parameter on krill stock size estimation.

the krill stock estimation may not be severe in an early period. The shift of the value of R affects invariablly or rather homogeneously throughout the period (Fig. 7).

3. Model with Multiple Predators

The crabeater seal is nowadays considered as the more important predator of krill, (NEMOTO and MURANO, 1979). It has been shown that the seal has an increasing tendency. As informal information, NISHIWAKI (1965) showed that the number of the seal was two to five millions in 1950 but it has increased to as much as 15 millions nowadays.

The simultaneous differential equations for the dynamics with two kinds of predators on the common food, by ITO (1976) are;

$$\frac{\mathrm{d}W}{\mathrm{d}t}=W\left\{T\left(1-\frac{W+S_B/S}{UZ}\right)-F2\right\}, \tag{9}$$

and

$$\frac{\mathrm{d}B}{\mathrm{d}t}=B\cdot T_B\left\{1-\frac{B+WS/S_B}{U_BZ}\right\}, \tag{10}$$

where B means the stock size of the seal, S_B, T_B and U_B are the parameters corresponding to those of whale only with suffix respectively. In this case SHOEMAKER's model cannot be employed because of lacking information on the change of feeding during the period considered. Thus IVLEV's model was adopted as,

$$\frac{\mathrm{d}Z}{\mathrm{d}t}=Z\{P(1-Z/Q)-R\}-(SW+S_BB)\{1-\exp(-KZ/Q)\}. \tag{11}$$

Here $K=3$ was adopted again.

As we have very poor information on parameters with suffix B except S being estimated as 21.0, the following approach was therefore tried, namely; 1) The number of the seal was five million or $B=1.0\times10^6$ t in 1950 (the average body weight of a seal was taken as 200 kg), and it is 15 million t or $B=3.0\times10^6$ t in 1970. Employing the logistic curve the value of B in the year t (counted 1920 as start) can be expressed as,

$$B=A\exp(at)/\{1-b(1-\exp(at)\}, \qquad (12)$$
$$A=0.4, \quad b=0.05, \quad a=0.048.$$

By back calculation the value of B in 1920 was estimated as 0.4 million t; 2) As the growth of the seal can be considered faster than that of whale, T_B is taken larger than T; 3) The nutitional conversion rate from krill to seal is considered the same as that to whale, while the habitat is narrower.

The simultaneous differential eqs. (10) and (11) were solved numerically with the known value of time series of W used in Subsection 2.4.1. By trial and error, the combination of U_B and T_B was searched for so that the value of B at the terminal of estimation is conformed to the actual value. Thus $U_B=0.015$ and $T_B=0.13$ were selected. Another trial was also made in which the simultaneous eqs. (9) to (11) were solved from the initial stage by giving various values for U_B and T_B so as to obtain the values not only of B but also of W being conformed to the present value. In this case 0.13 was selected again as T_B, while U_B was 0.01 (Fig. 8).

Similar computations were made for both cases by the similar method to that in Subsection 2.4.2. The results are too suggestive because of many asumptions. The

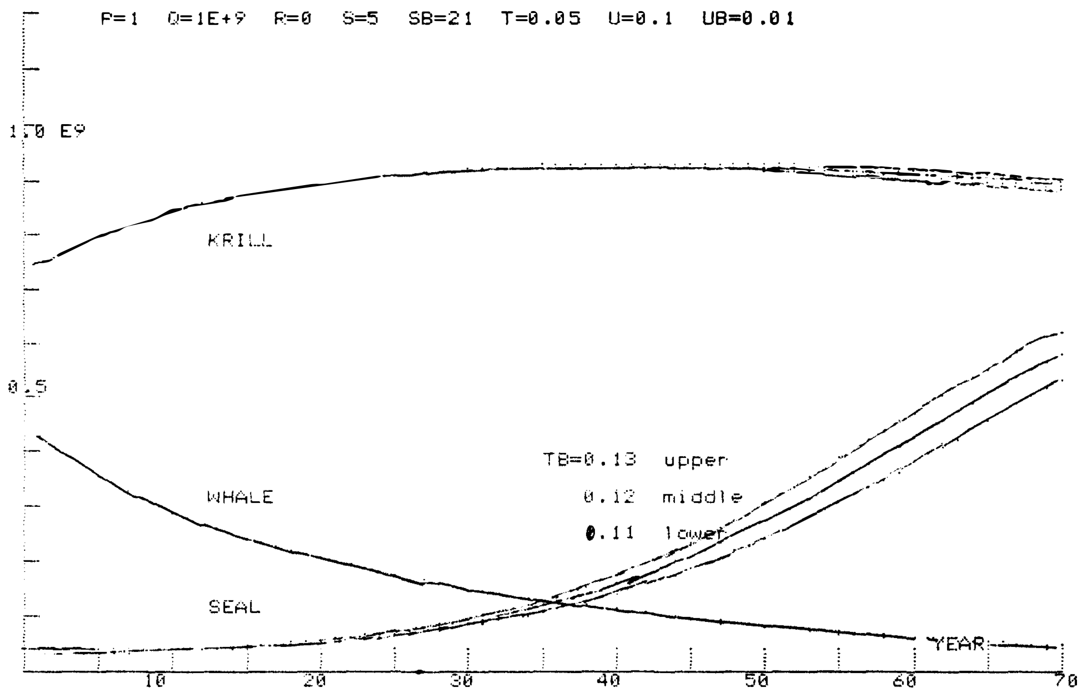

Fig. 8. Back estimation of effect of catch of whale on krill and seal, in order to determine suitable value of T_B the reproductivity of seal so as to make the change of whale and seal stock conform to actual one.

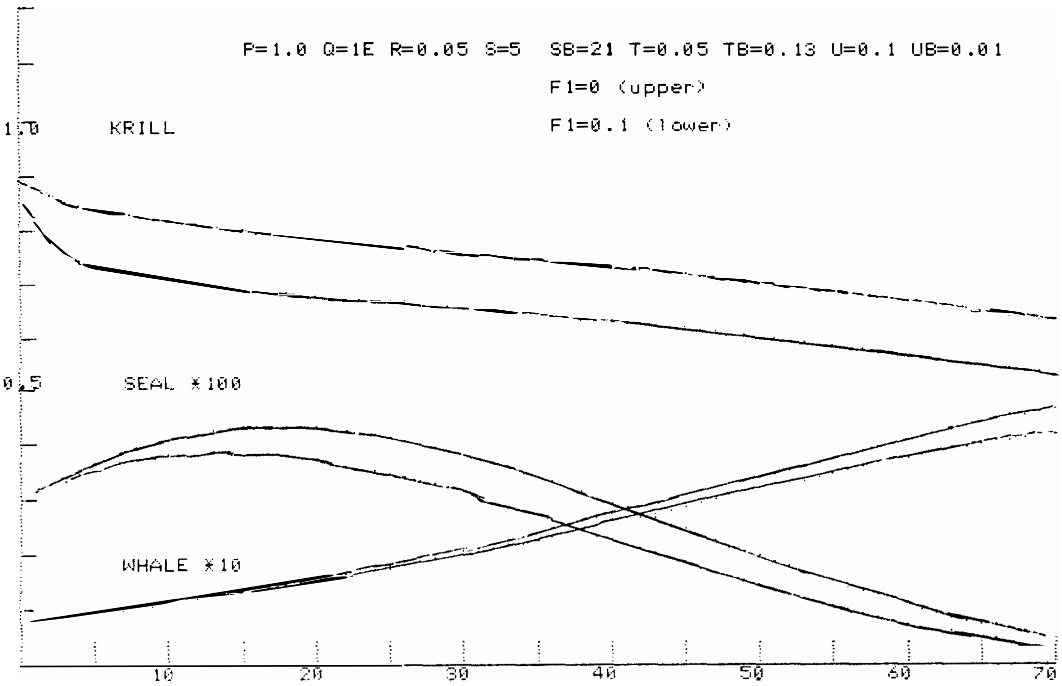

Fig. 9. Effect of krill catch upon whale and seal (without whale catch).

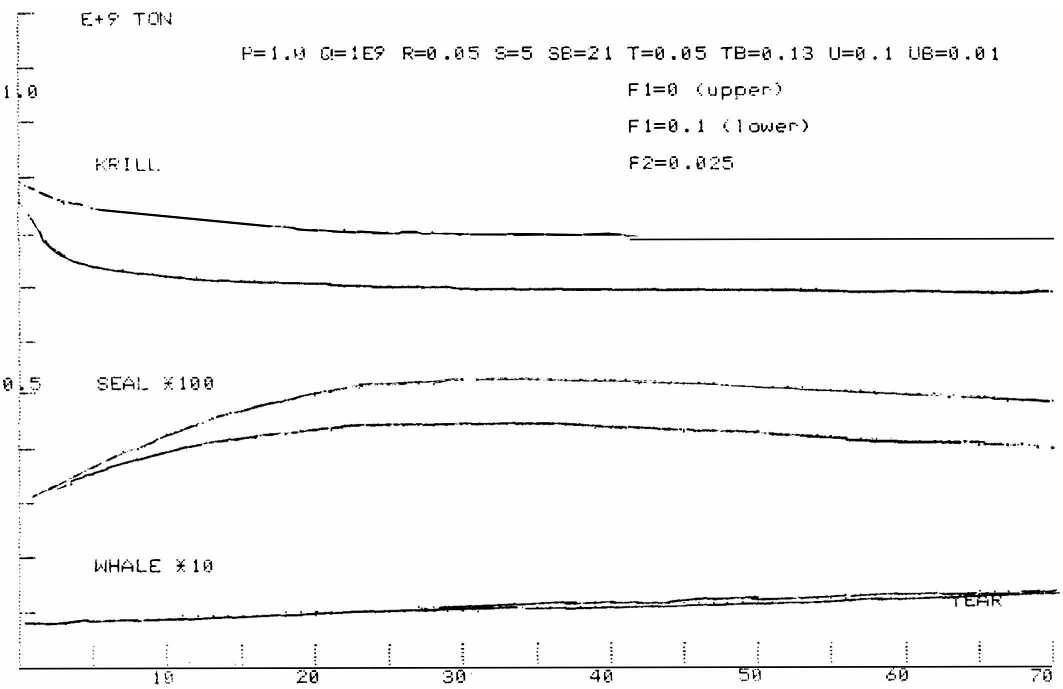

Fig. 10. Effect of krill catch upon whale and seal (with sustainable level of whale catch).

trend of seal increment may be unrealistic. The mechanism of food competition needs further improvement. It may be said, however, that the 10% catch of krill does not cause any severe influence on the recovery of whale, whereas its influence upon the seal may be more significant (Figs. 9 and 10).

4. Discussion

The trials of computation hitherto made were mostly with the value of Q as 1.0 ($\times 10^9$). As has been already discussed this value may be rather modest. Accordingly, the values pertaining to the krill stock estimation which is in the higher level of the order of 10^8 t may be also rather modest. It seems more reasonable, from the view of predation of other animals than whale, to consider the value of Q to be at least 1.3–1.4 times larger, and accordingly the present krill stock size is in the lower level of 10 t order. Such difference, however, does not make any substantial change in the general pattern of the interrelation between krill and its predators.

Among various tentative assumptions on biological parameters, those pertaining to other animals than whale are rather far from credible. Those on predation by birds, squids and fishes which certainly influence krill were dealt synthetically as R in the present report.

DOI (1979) employed an alternative method to solve the ecosystem dynamics by means of the energy flow among trophic levels. In this case the values of excretion, respiration, etc., of phyto- and zooplankton, krill and several types of predators were adopted from available sources, and then the energy flow coefficients were solved by means of the simultaneous differential equations on the energy flow. Because of the uncertainty of the relevant parameters employed, iteration by trial and error was made. The result showed that the catch of krill of the order of 10^8 t, or of the order of ten percent of the estimated stock size, will not give any adverse effect on the whale stock even if such exploitation lasts for three decades; thus being conformed to the tentative result of the present report.

GULLAND (1970) suggested 50 million t for the lower limit of the potential yield of the krill. His value, although rather modest, seems to be fairly conformed to the results obtained by the present author.

5. Conclusion

As mentioned in the beginning, it is not the main purpose of this paper to give any final and quantitative result on the analysis of the ecosystem surrounding the krill. Tentatively, however, it has been suggested that the present level of exploitation of the krill is very low compared with the MSY level; and that the exploitation of the order of hundred million t per year may not adversely affect the whale stock even if such exploitation would last for couple of decades.

Through computations dealt hitherto, it was shown that the main cause of the variation of the krill stock size is the feeding competition of the predators. The parameters pertaining to it are the key to solve the problem. As to parameters pertaining to the krill itself, the reproduction rate and the value of the carrying capacity are of importance.

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(*Received November 16, 1982; Revised manuscript received December 21, 1982*)