Some Basic Problems in the Antarctic Krill Population

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南極オキアミ現存量に関する基本問題

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要旨: 南極オキアミの存在量，年生長率，carrying capacity，鯨，あざらし等による年捕食量，および人間による捕獲量をそれぞれ，Z, p, Z_∞, R および F_k で表わすと，オキアミ生存量の年変化は

$$dZ/dt = pZ(1-Z/Z_\infty)-(R+F_k)$$

をもって代表することができる．この式から $Z=0$ にならないための必要条件は，

$$(R+F_k) \leqq pZ_\infty/4 \quad \text{および} \quad Z \geqq (Z_\infty - Q)/2$$

であることが導かれる．ここに $Q \equiv Z_\infty[1-4(R+F_k)/pZ_\infty]^{1/2}$ である．

p, Z_∞ および R の現在最も確からしい値は $p=1.0$/年，$Z_\infty=10^9$ t, $R=1.1\times10^8$ t/年であるが，これ等の値から，オキアミ生存量の破滅的な減少を見ないような安全捕獲量の上限は，$F_k<1.1\times10^8$ t/年になる．ただし，この上限量まで南極オキアミを捕獲すると，鯨等のオキアミ捕食動物の量は増加しない．オキアミ捕獲量をこの上限値より十分少なくすれば，それだけ鯨等の生存量が増加することになる．

Abstract: Noting biomass, annual growth-rate, carrying capacity, annual consumption rate by Antarctic animals such as whales and seals and annual catching rate by mankind of Antarctic krill by Z, p, Z_∞, R and F_k respectively, a time-change rate of Z is simply expressed by

$$dZ/dt = pZ\,(1-Z/Z_\infty)-(R+F_k).$$

The critical condition for not resulting in a catastrophic vanishment of Z is given by $(R+F_k) \leqq pZ_\infty/4$ and $Z \geqq (Z_\infty - Q)/2$, where $Q \equiv Z_\infty[1-4(R+F_k)/pZ_\infty]^{1/2}$.

The most plausible numerical values of p, Z_∞, and R at present will be $p=1.0$ year^{-1}, $Z_\infty=10^9$ tons and $R=1.1\times10^8$ tons/year. If so, $F_k<1.1\times10^8$ tons/year will be the allowable upper limit for the krill catching at present. In such a case, however, an increase of whale biomass may not be expected. If F_k is considerably smaller than the critical value for $(R+F_k)$, an increase of whale biomass can be expected.

1. Introduction

The zooplankton, krill, is known as the major prey for whale, seal, squid and bird in the Southern Ocean. In particular, baleen whales and crabeater seals are known as the main predators of krill in the ocean south of the Antarctic Convergence. According to LAWS (1977a), it is estimated that krill biomass of about 190 million tons was annually consumed by baleen whales before 1904 when the commercial whaling started, but the consumption rate of krill by baleen whales at present has decreased down to

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about 43 million tons per year because of a decrease of baleen whale biomass caused by the whaling activities since 1904. LAWS (1977b) reported that the age of sexual maturity of sei whale has decreased from about 11 years to 7 years on average and that of fin whales from 8 years to 4 years during a period from 1930 to 1960. The age of sexual maturity of crabeater seals also has decreased from about 5 years in 1945 to 3 years in 1970 (LAWS, 1977b). According to LAWS, the observed shortening of the age of sexual maturity of whales and seals can be attributed to a considerable increase of their prey, that is krill, owing to a decrease of total biomass of baleen whale. LAWS (1977b) has reported also that the number of fur seal in Bird Island is increasing since 1950, and that the observed increase of fur seal biomass may be due to an increase of krill biomass.

The apparent amount of "surplus" krill at present will be about 150 million tons in comparison with the pre-whaling condition. The observed shortening of the sexual maturity age of whales and seals and the observed increase of biomass of fur seals in Bird Island can be naturally attributed to a considerable increase of the surplus krill biomass in the Southern Ocean. It would be suggested then that the potential biomass of krill, that is "the carrying capacity" of krill in technical term in the marine ecology, in the Southern Ocean is of a size, in which the estimated amount of surplus krill is not negligibly small.

It is presumed then that a catching of krill with rate of 10^2 million tons per year in the order of magnitude will give rise to a considerable effect on the marine ecosystem in the Southern Ocean. HORWOOD (1976) quantitatively discussed the populations of krill and whale in the Southern Ocean by taking into account the predator-prey relationship between whale and krill as well as their respective growth-rates. YAMANAKA (1983) has re-examined the Horwood model of krill-whale co-existence by taking into consideration reasonably modified interaction parameters between krill biomass and whale biomass and between phytoplankton and krill. YAMANAKA (1983) further discussed an effect on the Southern Ocean ecosystem of co-existence of seals which also feed on krill. The ecosystem models examined by HORWOOD and YAMANAKA consist of simultaneous differential equations representing changes with time of biomasses of krill and whale and/or seal respectively with appropriate mutual interaction parameters among them. It seems, however, that the interaction parameters among these species and their own growth rates have not yet been fully sufficiently determined at the present stage and all these parameters including the growth-rates are to be urgently studied on the basis of field survey data in the near future. Once these parameters are appropriately determined, the simultaneous differential equations ought to be numerically solved in response to appropriate initial and boundary conditions. At the present stage of knowledge of krill biomass, however, it seems likely that some key points of the problem of Antarctic krill population can be quantitatively pointed out for the purpose of finding the direction of future studies on this problem.

2. Problems of Ecosystem Consisting of Krill, Whales and Seals

The flow diagrams to show the predator-prey relationship in the Southern Ocean

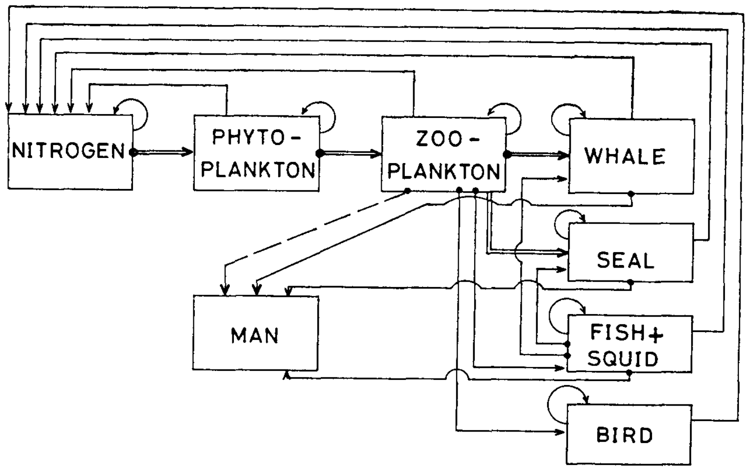

Fig. 1. Food-chain in the Southern Ocean ecosystem. Arrow lines show the energy flow directions including the feedback of energy as excrements and dead bodies. Thick lines indicate the main prey-predation chain. A broken line shows the present problem of man's fishery of krills.

ecosystem comprising phytoplankton, zooplankton and vertebrates can be approximately represented by Fig. 1, where the consumption of zooplankton, whale, seal and fish by mankind also is included. In Fig. 1, the arrows generally indicate the direction of flow and those arrows, which are closed with individual constituents, represent the growth of respective constituents (*e. g.* SHOEMAKER, 1977). The flow lines coming back to "Nitorogen" from "Zooplankton", "Whale", "Seal", "Fish+squid" and "Bird" show that these livings return nitrogen organism, through their death and excretion, to the water.

According to LAWS (1977b), the consumption rate of zooplankton (mostly krill) by birds and fish would be much smaller than that by whales and seals at present, though it is still difficult to estimate an exact value of the consumption of krill by birds and fish in the Southern Ocean. Therefore, whale and seal are the two main consumers of zooplankton in the flow diagram shown in Fig. 1.

Noting then the biomasses of krill, whale and seal by Z, W and S respectively, a mathematical model for representing an ecosystem consisting of the three species can be expressed by

$$\frac{\mathrm{d}Z}{\mathrm{d}t}=pZ\left(1-\frac{Z}{Z_\infty}\right)-\alpha ZW\left(\frac{k}{k+Z}\right)-\beta ZS\left(\frac{l}{l+Z}\right)-F_{\mathrm{k}}, \tag{1}$$

$$\frac{\mathrm{d}W}{\mathrm{d}t}=qW\left(1-\frac{W}{W_\infty}\right)-F_{\mathrm{w}}, \tag{2}$$

$$\frac{\mathrm{d}S}{\mathrm{d}t}=rS\left(1-\frac{S}{S_\infty}\right)-F_{\mathrm{s}}, \tag{3}$$

where

p, q and r: Growth-rate of krill, whale and seal respectively,
Z_∞, W_∞ and S_∞: Carrying capacity of krill, whale and seal respectively,
F_{k}, F_{w} and F_{s}: Catching rate of krill, whale and seal respectively,
α: Coefficient of feeding on krill by whale of unit mass,

β: Coefficient of feeding on krill by seal of unit mass,
k, l: Half-saturation coefficients for feeding on krill by whale and seal of unit mass, respectively.

Since both the carrying capacities of whale and seal, W_∞ and S_∞, should be primarily dependent on Z, both W_∞ and S_∞ approaching to zero if Z approaches to zero, $W_\infty = Zf(Z)$ and $S_\infty = Z\varphi(Z)$, where f and φ are functions of Z. Horwood (1976) assumed that $f(Z)=\text{constant}=\lambda$, and therefore $W_\infty=\lambda Z$. This simplest possible expression of W_∞ and S_∞ to satisfy the necessary condition for W_∞ and S_∞ may be adopted as the first approximation. Hence

$$\frac{dW}{dt}=qW\left(1-\frac{W}{\lambda Z}\right)-F_w\,, \tag{2*}$$

$$\frac{dS}{dt}=rS\left(1-\frac{S}{\mu Z}\right)-F_s\,. \tag{3*}$$

Simultaneous differential equations, (1), (2*) and (3*), can be numerically solved, if parameters p, q, r, λ, μ, α, β, k and l are approximately given, and F_k, F_w and F_s are assumed, and the initial conditions for Z, W and S at $t=0$ are adequately chosen.

Horwood (1976) discussed a special case that $S=0$, $k \gg Z$, and $d/dt=0$. Yamanaka (1983) discussed a little more generalized case that $S=0$ and $\beta S(l/(l+Z))=R=$ constant. As a set of the simultaneous differential equations, (1), (2*) and (3*), include so many parameters, which must be derived by processing a large number of ecological survey data, that only provisional quantitative discussions on $Z(t)$ and $W(t)$ have been made to date. In regard to the krill biomass, Z, for example, it is still difficult to estimate the magnitudes of α, β, k and l. At the present stage of knowledge about the Antarctic marine ecosystem, then, we may take a much more simplified model which contains as small number as possible of parameter in order to realistically estimate the krill biomass in the Southern Ocean.

Put

$$\alpha Z W\left(\frac{k}{k+Z}\right)+\beta Z S\left(\frac{l}{l+Z}\right)\equiv R\,, \tag{4}$$

in eq. (1), then we get

$$\frac{dZ}{dt}=pZ\left(1-\frac{Z}{Z_\infty}\right)-(R+F_k)\,, \tag{5}$$

which contains 4 parameters, p, Z_∞, R and F_k. If we take one year as unit of t, then p is the annual growth rate of krill, Z_∞ the carrying capacity of krill, and $(R+F_k)$ is the annual rate of consumption of krill, which is the sum of natural consumption and man-made catching. Both parameters p and Z_∞ are the fundamental quantities to deal with the krill population, and therefore both parameters have been estimated to a certain extent. The annual consumption rate of krill by whale and seal at present are estimated anyhow ecologically (*e. g.* Laws, 1979a), because biomasses of whale and seal in the Southern Ocean are relatively well surveyed and the consumption rates of krill by whale and seal also are comparatively well studied.

3. Change of Krill Biomass with Time

The krill biomass, $Z(t)$, can be given by analytically solving eq. (5) with the initial condition that $Z=Z_0$ at $t=0$. $Z(t)$ is expressed by

$$Z(t)=\frac{(Z_\infty+Q)-\{((Z_\infty+Q)-2Z_0)/((Z_\infty-Q)-2Z_0)\}(Z_\infty-Q)\exp(-(pQ/Z_\infty)t)}{2[1-\{((Z_\infty+Q)-2Z_0)/((Z_\infty-Q)-2Z_0)\}\exp(-(pQ/Z_\infty)t)]}, \quad (6)$$

where

$$Q\equiv Z_\infty\sqrt{1-\frac{4(R+F_k)}{pZ_\infty}},$$

(for $(R+F_k)<pZ_\infty/4$ and $Z\geqq 0$),

$$Z(t)=\frac{Z_\infty}{2}+\frac{Z_0-(Z_\infty/2)}{1+((Z_0-Z_\infty/2)/Z_\infty)pt}, \quad (7)$$

(for $(R+F_k)=pZ_\infty/4$),

$$Z(t)=\frac{Z_\infty}{2}+\frac{Q^*}{2}\tan\left\{\arctan\left(\frac{2Z_0-Z_\infty}{Q^*}\right)-\frac{Q^*}{2Z_\infty}pt\right\}, \quad (8)$$

where

$$Q^*\equiv Z_\infty\sqrt{\frac{4(R+F_k)}{pZ_\infty}-1},$$

(for $(R+F_k)>pZ_\infty/4$ and $Z\geqq 0$).

In case of eq. (6) for $(R+F_k)<pZ_\infty/4$, eq. (5) can be rewritten as

$$\frac{dZ}{dt}=-\frac{p}{Z_\infty}\left(Z-\frac{Z_\infty+Q}{2}\right)\left(Z-\frac{Z_\infty-Q}{2}\right). \quad (5^*)$$

Hence,

$$\frac{dZ}{dt}>0 \quad \text{for} \quad \frac{Z_\infty-Q}{2}<Z<\frac{Z_\infty+Q}{2},$$

$$\frac{dZ}{dt}=0 \quad \text{for} \quad Z=\frac{Z_\infty+Q}{2} \quad \text{or} \quad Z=\frac{Z_\infty-Q}{2},$$

$$\frac{dZ}{dt}<0 \quad \text{for} \quad Z_\infty\geqq Z>\frac{Z_\infty+Q}{2}, \quad \text{or} \quad \frac{Z_\infty-Q}{2}>Z\geqq 0.$$

If $(Z_\infty-Q)/2<Z_0<(Z_\infty+Q)/2$, which is identical to

$$(R+F_k)<pZ_0\left(1-\frac{Z_0}{Z_\infty}\right), \quad \frac{dZ}{dt}>0,$$

Z increases from $Z=Z_0$ with an increase of t, approaching to $(Z_\infty+Q)/2$ at $t=\infty$. If $Z_\infty\geqq Z_0>(Z_\infty+Q)/2$, then $dZ/dt<0$, so that Z decreases from $Z=Z_0$ with t, approaching to $(Z_\infty+Q)/2$ at $t=\infty$.
If $(Z_\infty-Q)/2>Z_0\geqq 0$, then $dZ/dt<0$, so that Z decreases from $Z=Z_0$ with t, and becomes

$$Z=0 \quad \text{at} \quad t=t^*=-\frac{Z_\infty}{pQ}\, ln \left\{\frac{1-2Z_0/(Z_\infty-Q)}{1-2Z_0/(Z_\infty+Q)}\right\}. \tag{9}$$

If $Z_0=(Z_\infty+Q)/2$ or $Z_0=(Z_\infty-Q)/2$, then $dZ/dt=0$, and therefore $Z=Z_0=$constant regardless of t. $Z_0=(Z_\infty+Q)/2$ represents a stable equilibrium state, which is characterized by

$$\lim_{t\to\infty} Z=\frac{Z_\infty+Q}{2}$$

for both $Z_0>(Z_\infty+Q)/2$ and $Z_0<(Z_\infty+Q)/2$, as far as $(Z_\infty-Q)/2<Z_0<(Z_\infty+Q)/2$.

On the other hand, $Z_0=(Z_\infty-Q)/2$ represents an unstable equilibrium, which is characterized by

$$\lim_{t\to\infty} Z=\frac{Z_\infty-Q}{2} \quad \text{when} \quad Z_0>(Z_\infty-Q)/2\,,$$

and $Z=0$ at $t=t^*$, when $0<Z_0<(Z_\infty-Q)/2$.

In a particular case given by eq. (7) for $(R+F_k)=pZ_\infty/4$, $dZ/dt\leqq 0$ and

$$Z=0 \quad \text{at} \quad t=t^{**}=\frac{2Z_0}{p(Z_\infty/2-Z_0)}\,, \quad \text{if} \quad Z_0<Z_\infty/2\,, \tag{10}$$

$$Z=Z_0\,, \quad \text{if} \quad Z_0=Z_\infty/2\,,$$

and

$$\lim_{t\to\infty} Z=Z_\infty/2\,, \quad \text{if} \quad Z_0>Z_\infty/2\,.$$

In case of eq. (8) for $(R+F_k)>pZ_\infty/4$ also, always $dZ/dt<0$, and

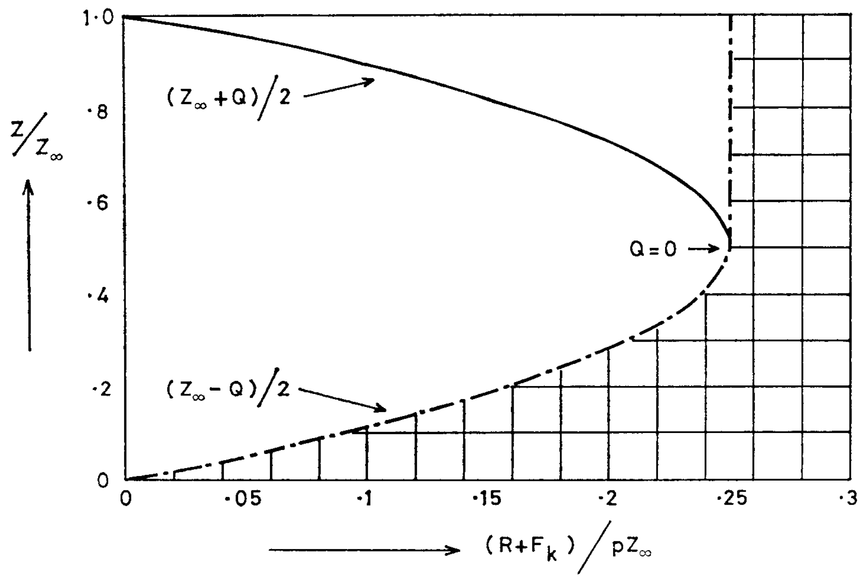

Fig. 2. Biomass of krill in unit of Z_∞, (Z/Z_∞), at the final steady state $(t=\infty)$ as a function of the consumption rate in unit of pZ_∞, $((R+F_k)/pZ_\infty)$. If $Z_0>(Z_\infty-Q)/2$ and $(R+F_k)<pZ_\infty/4$, the final state biomass is given by $(Z_\infty+Q)/2$. If $Z_0<(Z_\infty-Q)/2$ or $(R+F_k)>pZ_\infty/4$, the final state biomass is zero.

$$Z=0 \quad \text{at} \quad t=t^{***}=\frac{2Z_\infty}{pQ^*}\left\{\arctan\left(\frac{2Z_0-Z_\infty}{Q^*}\right)+\arctan\left(\frac{Z_\infty}{Q^*}\right)\right\}. \tag{11}$$

From the viewpoint of conserving the krill biomass, the condition of $\mathrm{d}Z/\mathrm{d}t \geqq 0$ must be maintained in order to keep the krill biomass (Z) above a certain preferable level, Z^0. Figure 2 shows the equilibrium curve of $\mathrm{d}Z/\mathrm{d}t=0$ in a Z *versus* $(R+F_k)$ diagram, where Z on the ordinates is given in unit of Z_∞, while $(R+F_k)$ on the abscissa in unit of pZ_∞. The upper half of the parabolic curve of $\mathrm{d}Z/\mathrm{d}t=0$ presents the stable equilibrium of $Z=(Z_\infty+Q)/2$ as a function of $(R+F_k)$, while the lower half presents the unstable equilibrium of $Z=(Z_\infty-Q)/2$. Figure 2 indicates that one of the necessary conditions for not resulting in the state of $Z=0$ is

$$(R+F_k)<\frac{1}{4}pZ_\infty, \tag{12}$$

and the additional necessary condition is given by

$$Z^0 \geqq \frac{Z_\infty-Q}{2}, \tag{13}$$

or

$$2Z^0 \geqq Z_\infty\left\{1-\sqrt{1-\frac{4(R+F_k)}{pZ_\infty}}\right\}. \tag{13*}$$

As far as the necessary conditions expressed by eqs. (12) and (13) are satisfied, the krill biomass (Z) can be maintained around the stable equilibrium value of $Z=(Z_\infty+Q)/2$.

Inequality relation eq. (12) for the allowed consumption rate, $(R+F_k)$, depends only on p and Z_∞. The other inequality relation eq. (13) for the allowable limit for $(R+F_k)$ also depends on p and Z_∞ in addition to the initial value of Z, namely Z_0. Therefore, the assessments of p and Z_∞ for the Antarctic krill biomass on the basis of marine survey data should be extremely significant. The present value of krill biomass, Z_0, also is important to set up the necessary management plan for krill catching in the future. In the present discussions, the natural consumption rate of krill by Antarctic animals, R, and the expected catching rate of krill by mankind, F_k, are taken into consideration as a single term of their sum $(R+F_k)$, which is the consumption rate of krill. In a practical management to evaluate an permissible value of F_k, therefore, we must always consider an appropriate value of R, which is the consumption rate of Antarctic krill mostly by baleen whales and crabeater seals and also by squid, fish and birds. The assessments of Antarctic biomasses of various species of whale and seal have been fairly extensively studied to date, and consequently their consumption rates of krill also have been estimated (*e.g.* LAWS, 1977a). As the permissible maximum value of $(R+F_k)$ for not resulting in the catastrophic decrease of Z is given by inequality relations eqs. (12) and (13) from the general krill ecosystem parameters, p and Z_∞, by taking into account the krill biomass at present (Z_0), the permissible upper limit of F_k can be evaluated by substracting an ~~appreciate~~ value of R from the permissible upper limit of $(R+F_k)$.

It will have to be emphasized in the present discussion, however, that the equilibrium condition on $Z=(Z_\infty-Q)/2$ is unstable so that a small increase of $(R+F_k)$ near the state of $Z=(Z_\infty-Q)/2$ should cause a catastrophic decrease of Z. Since estimated values of p, Z_∞, Z_0 and R are inevitably associated with errors of a certain considerable amount, a sufficiently large value of a safety factor will have to be taken into consideration in determining the upper limit of $(R+F_k)$ by eq. (12) and that of Z_0 by eq. (13).

4. A Provisional Model of the Antarctic Krill Biomass

The general discussions of krill population in the foregoing section are primarily dependent on parameters p, Z_∞ and Z_0 in addition to the consumption rate, $R+F_k$.

(a) Growth rate (p)

HORWOOD (1976) assumed $p=1.0$ per year, while YAMANAKA (1979, 1983) estimated $p=1.2$ per year on the basis of birth rate, natural mortality rate and growth rate of body size of krill for the first one year of average krill life. Since an estimate of p for krill is entirely dependent on its spawning rate, hatching rate, growth rate of body size and natural mortality rate, no further discussion on p for krill will be made in this provisional note.

(b) Carrying capacity for krill (Z_∞)

HORWOOD (1976) assumed $Z_\infty=10^{10}$ tons, while YAMANAKA (1979, 1983) estimated $Z_\infty \gtrsim 10^9$ tons based on the following consideration. As generally discussed in Section 3, a necessary condition for not resulting in the vanishment of krill biomass is given by

$$pZ_\infty \geqq 4(R+F_k)\,. \tag{12}$$

In the period of 1920s, there was no man-made catching of krill ($F_k=0$), and the annual consumption rates of krill by whales, seals, birds and squid are estimated to be 188×10^6, 84×10^6, 39×10^6 and 64×10^6 tons/year respectively so that R in 1920 was about 3.0×10^8 tons/year. Putting $p=1.0$ per year, he has estimated that $Z_\infty \gtrsim 12\times10^8$ tons.

According to LAWS' assessment (1979a), the annual consumption rate of krill by baleen whales is 189.7×10^6 tons/year in the pre-whaling period and 42.8×10^6 tons/year at present, while the annual consumption rate of krill by crabeater seals is 63.2×10^6 tons/year. If we consider the consumption of krill only by baleen whales and crabeater seals according to these estimates, $R=2.53\times10^8$ tons/year before 1904. If we further consider the additional consumption by birds and squid according to YAMANAKA's reference data, $R=3.56\times10^8$ tons/year. Putting these values of R and $p=1.0$/year, eq. (12) suggests $Z_\infty \gtrsim 10.1\times10^8$ tons or $Z_\infty \gtrsim 14.2\times10^8$ tons. Thus, the lower limit of a possible value of Z_∞ can be roughly estimated as $Z_\infty \gtrsim 10^9$ tons.

It is difficult however to quantitatively evaluate the upper limit for Z_∞. A possible consideration in this regard may be concerned with the observed fact that the sexual maturity age of remaining whales and seals have been decreasing with time during a period of a considerable decrease of baleen whale biomass caused by the man-made catching activity. This observed fact suggests that an equilibrium of biomass of whales and seals and other animals feeding on krill with that of krill was near the critical point represented by $R=pZ_\infty/4$ in the pre-whaling period, because very little observable effect only can take place on the sexual maturity age and biomass of Antarctic marine animals feeding on krill if $Z_\infty \gg 4R/p$. It may thus be provisionally estimated that

$$Z_\infty \simeq 4R/p\,. \tag{14}$$

The above-mentioned idea to estimate Z_∞ may be more decisively descrived.

Replacing the consumption of krill by whales and seals in the pre-whaling period (when $F_k=F_w=F_s=0$) expressed by eqs. (1), (2*) and (3*) by a consumption of krill by a single predator, we can write as

$$\frac{dZ}{dt}=pZ\left(1-\frac{Z}{Z_\infty}\right)-\alpha^* W, \tag{15}$$

$$\frac{dW}{dt}=qW\left(1-\frac{W}{\lambda Z}\right), \tag{16}$$

where α^* denotes the consumption rate of krill by a unit biomass of the predator. It can be naturally assumed that the krill biomass (Z) and the biomass (W) of animals feeding on krill were in an equilibrium state during the pre-whaling period. Then,

$$pZ\left(1-\frac{Z}{Z_\infty}\right)=\alpha^* W \quad \text{and} \quad W=\lambda Z,$$

and consequently

$$Z=Z_\infty\left(1-\frac{\alpha^*\lambda}{p}\right) \quad \text{and} \quad W=\lambda Z_\infty\left(1-\frac{\alpha^*\lambda}{p}\right).$$

It is most likely that the conversion coefficient (λ) between the carrying capacity for the krill predator (W_∞) and the krill biomass (Z) was naturally so adjusted that W could take its maximum value in the equilibrium state. Hence,

$$\lambda=\frac{p}{2\alpha^*}, \tag{17}$$

which gives rise to

$$Z=Z_\infty/2. \tag{18}$$

In the diagram shown in Fig. 2, the condition expressed by eq. (18) just corresponds to

$$R=pZ_\infty/4.$$

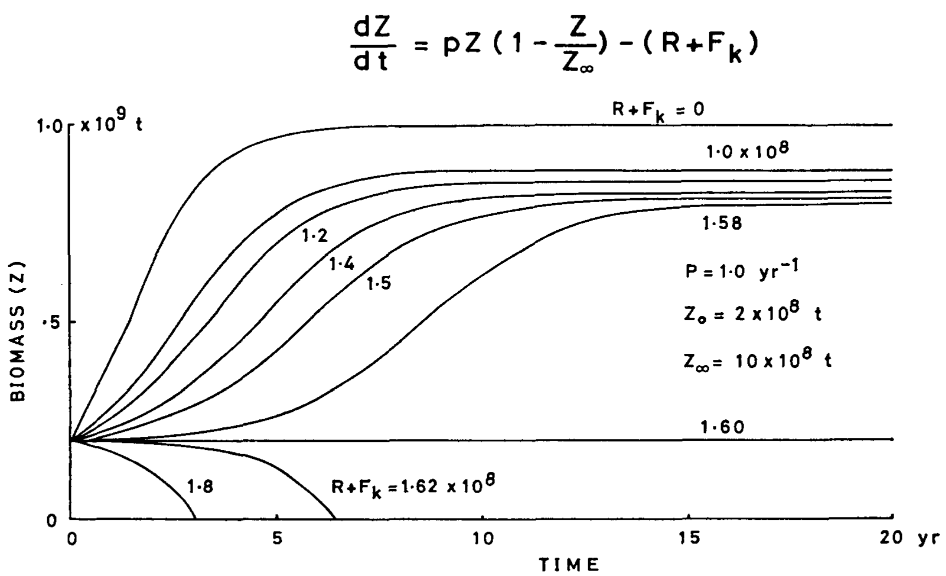

Fig. 3. Biomass of krill (Z) for $Z_0=2\times10^8$ tons.

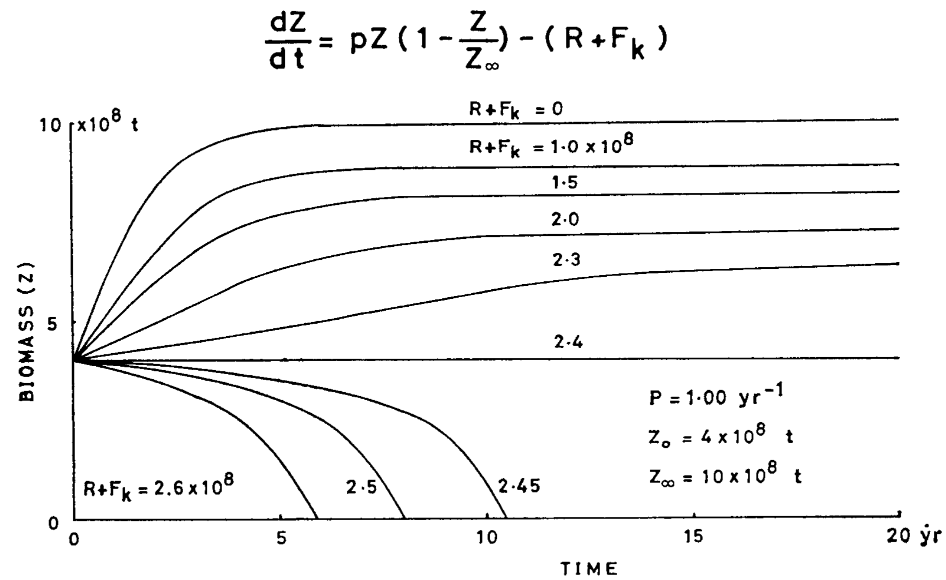

Fig. 4. Biomass of krill for $Z_0=4\times10^8$ tons.

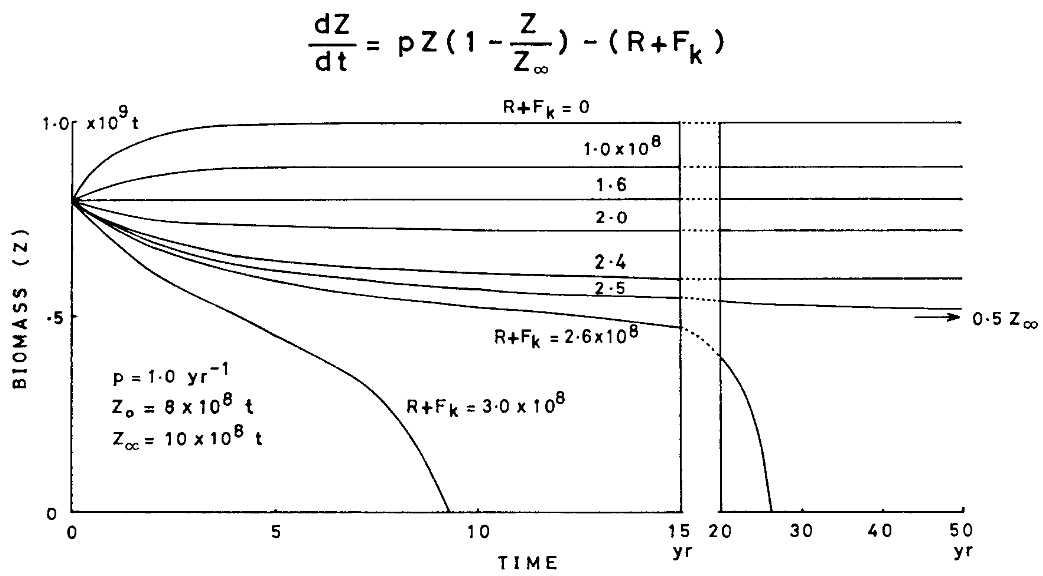

Fig. 5. Biomass of krill for $Z_0=8\times10^8$ tons.

By taking the minimum possible value of $R=2.5\times10^8$ tons/year, the corresponding reserved value of Z_∞ would be $Z_\infty=1.0\times10^9$ tons.

Then, assuming $p=1.0$/year and $Z_\infty=1.0\times10^9$ tons, numerical values of $Z(t)$ for different values of the consumption rate $(R+F_k)$ are illustrated in Figs. 3, 4 and 5 for three different cases of $Z_0=2\times10^8$ tons, 4×10^8 tons and 8×10^8 tons respectively. In Fig. 3 for $Z_0=2\times10^8$ tons, the $Z(t)\sim t$ curve for $(R+F_k)=1.6\times10^8$ tons/year presents the unstable equilibrium condition of $Z(t)=Z_0=$constant. If $(R+F_k)$ is a little smaller than the critical value (1.6×10^8 tons/year), say 1.58 tons/year for example, the $Z(t)$ value approaches with time to the stable equilibrium value of $(Z_\infty+Q)/2$ (8.03×10^8 tons in the present case), whereas the $Z(t)$ value becomes zero at $t=6.43$ years for $(R+F_k)=$ 1.62 tons/year which is only a little larger than the critical value. As far as $Z_0>(Z_\infty-$

$Q)/2$, that is, $\sqrt{1-4(R+F_k)/pZ_\infty}>1-2Z_0/Z_\infty$, $Z(t)$ can approach to a finite biomass, $(Z_\infty+Q)/2$ at the final stage of $t\to\infty$. As numerically demonstrated in Fig. 3, the transition from the state of $Z(t)\to(Z_\infty+Q)/2$ to the state of $Z(t)\to 0$ is extremely sensitive to the consumption rate, $R+F_k$, around its critical value corresponding to the unstable equilibrium of Z.

In Fig. 4 for $Z_0=4\times10^8$ tons, the $Z(t)\sim t$ curves for $(R+F_k)=0$ through $(R+F_k)=2.45\times10^8$ tons/year are characteristically same as those shown in Fig. 3; namely, these curves are mathematically represented by eq. (6) and the unstable equilibrium condition takes place at $(R+F_k)=2.4$ tons/year, which corresponds to the special condition of $Z_0=(Z_\infty-Q)/2$ in this case. The curve for $(R+F_k)=2.5\times10^8$ tons/year presents the case of $Q=0$, which is mathematically given by eq. (7), while the curve for $(R+F_k)=2.6\times10^8$ tons/year is a case of $(R+F_k)>pZ_\infty/4$ which is mathematically given by eq. (8). Numerical examples of $Z(t)$ characteristics illustrated in Figs. 3 and 4 represent those of the cases of $Z_0<Z_\infty/2$.

In Fig. 5 for $Z_0=8\times10^8$ tons, which is an example of the cases of $Z_0>Z_\infty/2$, characteristics of the $Z(t)\sim t$ curves are somewhat different from those in Figs. 3 and 4. The $Z(t)$ values for $(R+F_k)=0$ through $(R+F_k)=2.4\times10^8$ tons/year approach to their final values given by $(Z_\infty+Q)/2$ at $t\to\infty$, and their mathematical expression is given by eq. (6), while the $Z(t)$ value for $(R+F_k)=2.5\times10^8$ tons/year corresponds to the case which is mathematically expressed by eq. (7) where $Z_0>Z_\infty/2$. When $(R+F_k)$ exceeds the critical value, $(R+F_k)=2.5\times10^8$ tons/year, $Z(t)$ should be expressed by eq. (8) and consequently $Z(t)$ becomes zero at $t=t^{***}$ given by eq. (11). In the case of Fig. 5, therefore, the $Z(t)$ curve for $(R+F_k)=1.6\times10^8$ tons/year presents the stable equilibrium condition corresponding to $Z(t)=Z_0=$constant.

The three numerical examples shown in Figs. 3, 4 and 5 cover characteristics of all possible cases which can take place depending on mutual relations among p, Z_∞ and Z_0 with a changing parameter, $(R+F_k)$.

A significant point concluded from the present simple mathematical discussion will be that the stable equilibrium state for $Z(t)$ can take place only if $Z_0>Z_\infty/2$. In the present simple model of $Z_\infty=10^9$ tons and $p=1.0$ year^{-1}, it is assumed that the equilibrium state in the pre-whaling period with a krill consumption rate of $R=2.5\times10^8$ tons/year corresponds to $Z=Z_\infty/2$ at $R\simeq pZ_\infty/4$. In accordance with a decrease of baleen whale biomass caused by the whaling activity, R has decreased from 2.5×10^8 tons/year to about 1.1×10^8 tons/year at present (LAWS, 1977a). Hence, Z has already recovered to $Z_0=\{Z_\infty+Q(R=1.1\times10^8)\}/2=8.7\times10^8$ tons. This is approximately identical to the model case shown in Fig. 5. Since $(R+F_k)_c=2.5\times10^8$ tons/year is the critical consumption rate, $(R+F_k)\lesssim2.2\times10^8$ tons/year may be allowable in order to safely keep the krill biomass (Z) around the stable equilibrium condition which corresponds to $Z>Z_\infty/2=5\times10^8$ tons. If R is continuously kept at 1.1×10^8 tons/year, $F_k\lesssim1.1\times10^8$ tons/year becomes the permissible limit for the expected krill catching rate.

The consumption rate of krill by birds and squid has not yet been well known (*e.g.* LAWS, 1977b). If we adopt the consumption rate by bird and squid accepted by YAMANAKA (1979, 1983), Z_∞ becomes $Z_\infty\simeq14\times10^8$ tons and the natural consumption rate at present is estimated as $R\simeq2.1\times10^8$ tons/year. Then, the present krill biomass is estimated as $Z_0=\{Z_\infty+Q(R=2.1\times10^8)\}/2=11.4\times10^8$ tons and $(R+F_k)=2.6\times10^8$ tons/

year gives the stable equilibrium state of $Z(t)=Z_0=$constant. As the critical consumption rate in this case is evaluated as $(R+F_k)_c=3.5\times10^8$ tons/year, again $F_k\lesssim1.1\times10^8$ tons/year will be the practical upper limit for the allowable krill catching rate, as far as R is kept constant. In the above discussion, the upper limit of permissible value of $(R+F_k)$ is arbitrarily defined as $(R+F_k)_c-(3\times10^7$ tons/year). This kind of safety factor will have to be considered more practically.

In the present note, the consumption rate of krill by Antarctic animals feeding on krill is simply taken into account as a varying numerical parameter, R. It may be obvious, however, that we must deal with simultaneous differential equations, (1), (2*) and (3*) in general, in order to consider necessary conditions for conserving whale, seal and other animals at their adequate biomass levels.

5. Concluding Remarks

In the foregoing section, few discussions only are made on a numerical estimate of the annual growth rate (p) of krill biomass, and p is taken as $p=1.0$ year^{-1} according to approximate estimates made by HORWOOD (1976) and YAMANAKA (1979, 1983). There would be a possibility that this estimated value of p is somewhat erroneous.

In equations (6) through (8), however, the krill consumption rate, $(R+F_k)$, is always presented in form of $(R+F_k)/pZ_\infty$ in either Q or Q^*, and $Z(t)$, Z_0, Q and Q^* are expressible in terms of $Z(t)/Z_\infty$, Z_0/Z_∞, Q/Z_∞ and Q^*/Z_∞, respectively. As far as Z is given in unit of Z_∞ on the ordinates and $(R+F_k)$ in unit of pZ_∞ on the abscissa in Fig. 2, therefore, all characteristics of the krill biomass represented by Fig. 2 are invariable regardless of a change of p. If we keep the assumption for estimating Z_∞ by eq. (14), we get $Z_\infty=2\times10^9$ tons corresponding to $p=0.5$ year^{-1} in case of $R=2.5\times10^8$ tons/year, for example. In this case, Figs. 3, 4 and 5 correspond to the initial conditions of $Z_0=4\times10^8$, 8×10^8 and 16×10^8 tons respectively and units for both ordinates and abscissa in these figures must be doubled, because the Z_∞ value is doubled on the ordinates and the time scale $(1/p)$ also is doubled on the abscissa, as given by eq. (6) through eq. (8).

Thus, the conclusion of numerical examples of the stable equilibrium state and the unstable equilibrium state of Z given for the case of $p=1.0$ year^{-1} and $Z_\infty=10^9$ tons in the foregoing section holds, almost as it is, in the present case of $p=0.5$ year^{-1} and $Z_\infty=2\times10^9$ tons, so far as we are concerned with $Z(t)/Z_\infty$ and Z_0/Z_∞. For example, the stable equilibrium state $(Z_0=(Z_\infty+Q)/2)$ takes place for $(R+F_k)=1.6\times10^8$ tons/year in the present case too, as it is so in Fig. 5.

In this note on the Antarctic krill population, the numerical value of pZ_∞ is derived by eq. (14) from the R value estimated for the pre-whaling period. As numerically discussed in this section and the foregoing section, the general conclusion in regard to the allowable upper limit of F_k is not too much sensitive to individual parameters, p and Z_∞, as far as eq. (14) can approximately hold. It must be emphasized, however, that the $(R+F_k)$ value must be maintained within the allowable state defined by $(R+F_k)<pZ_\infty/4$ and $Z>(Z_\infty-Q)/2$, or in other expressions, by $Q>0$ and $Z>(Z_\infty-Q)/2$, which is represented by a domain without lattice coordinates in Fig. 2.

In this note, the critical value for the total consumption rate of krill, $(R+F_k)$, only is discussed. If F_k increases up to the allowable upper limit of $(R+F_k)$, R cannot increase at all; it means that the biomasses of whale and seal cannot increase anymore. The annual feeding rate on krill by a baleen whale is estimated as about 5 times as much as its weight (*e.g.* LAWS, 1977a). An increase of R, ΔR, caused by an increase of whale biomass by ΔW will therefore be $\Delta R=5\Delta W$. Then, R_p denoting the present consumption rate of krill by whales and other marine vertebrates, we may approximately put $(R+F_k)=(R_p+5\Delta W+F_k)$. The next problem to be studied will be an appropriate assessment of the R-value as a function of time with the aid of eqs. (1), (2*) and (3*), even though the problem will be much more complicated.

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