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A REVIEW ON THE ANTARCTIC ECOSYSTEM MODELS

Abstract

Some published articles on the Antarctic krill biomass estimates and ecosystem models by Japanese scientists were reviewed. The concept and treatment of Lotka-Volterra type model by Yamanaka (1983) and Nagata (1983) were compared and some future modifications were discussed. While a network model such as developed by Doi (1879) is able to deal with many components in the Antarctic ecosystem simultaneously, it was felt a further review was needed to develop this model.

EXAMEN DES MODELES DE L'ECOSYSTEME ANTARCTIQUE

Résumé

Quelques articles sur les estimations de la biomasse de krill antarctique et sur des modèles de l'écosystème, publiés par des scientifiques japonais, ont été examinés. La conception et le traitement du modèle de type Lotka-Volterra par Yamanaka (1983) et Nagata (1983) ont été comparés et de prochaines modifications ont fait l'objet de discussions. Bien qu'un modèle de réseau comme celui développé par Doi (1879) soit en mesure de traiter simultanément un grand nombre de composants de l'écosystème antarctique, on a estimé qu'un nouvel examen était nécessaire à la mise au point de ce modèle.

ОБЗОР МОДЕЛЕЙ ЭКОСИСТЕМЫ АНТАРКТИКИ

Резюме

Были рассмотрены некоторые опубликованные работы японских ученых по оценке биомассы антарктического криля и моделям экосистемы. Было проедено сравнение концепции и трактовки модели типа Лотка-Волтерра Яманакой (1983 г.) и Нагатой (1983 г.) и обсуждены будущие модификации. Несмотря на то, что сетевая модель, которая была разработана Дои (1879 г.), учитывает многие компоненты экосистемы Антарктики одновременно было выражено мнение о том, что необходимы дальнейшие исследования для развития этой модели.

REVISION DE LOS MODELOS DEL ECOSISTEMA ANTARTICO

Sinopsis

Se revisaron algunos de los artículos publicados por los científicos japoneses sobre las estimaciones de biomasa del krill antártico y los modelos de ecosistemas. El concepto y tratamiento del modelo tipo Lotka-Volterra de Yamanaka (1983) y Nagata (1983) fueron comparados y se discutieron algunas modificaciones futuras. Mientras que un modelo de sistemas como el desarrollado por Doi (1879) es capaz de tratar simultáneamente muchos componentes del ecosistema antártico, se estimó que sería necesario efectuar una revisión adicional con el fin de desarrollar este modelo.

1. Krill biomass estimates by use of fish finder

The biomass of the antarctic krill was estimated by Doi and Kawakami(1878, 1979) and Hirayama et al.(1979) based on the record of fish finder. The fourth estimate was made by Doi (1982) based on the record of a scientific echo-integrator.

1-1. Estimates by fish finder

Doi and Kawakami(1978) estimated biomass of the Antarctic krill as 1,800 million tons for the whole Antarctic, from an analysis of data obtained from one boat operated in the area 65S-66S, 54E-58E in 1976/77 season. They (1979) made another estimate of 1,200 million tons based on the analysis of new data of the same kind obtained in 1977/78 in the area south of 61S, 110E-180. In their estimation biomass of patches detected between two adjacent stations was calculated utilizing average length and thickness, distance between patches and number of patches detected. They employed an assumption that the shape of a krill patch is shperoidal. Utilizing a value of 100 g/m^3 as an average of density of krills in a patch previously observed, an average density of krills in the Antarctic was estimated as 65.1 tons/km^2.

Hirayama et al.(1979) developed a model to simplify to utilize only averages of length of chord of patches and thickness and numbers of patches detected. They used data obtained by R/V Umitaka Maru in 1977/78 in the area of 120E -160E. Observed density of krills in a patch (146 g/m^3) was used together with two different assumptions on the shape of a patch (spherical and disk-shaped), which led to the estimates of biomass of the Antarctic krill of 13.7 and 3.6 hundreds million tons.

In the above three estimates there are some differences in parameters and data used as shown in Table 1.

Table 1. Comparison of data in the three reports

Authors	Doi and Kawakami		Hirayama et al.
Items	1978	1979	1979
Researched distance(km)	815.9	5,716	1,367
Mean diameter of patch(m)	*	*	102
Mean number of patch(/km^2)	*	*	4.78
Mean thickness of patch(m)	10	10	18.4
Krill density in a patch(g/m3)	**	100	146
Area of distribution(km2)	18.4*10^6		34*10^5
Biomass(million tons)	1,800	1,200	360-1,370

*observed values were used.
**four different values were used.

1-2. Estimate by echo-integrator

Doi (1982) reported on the results of target strength measurement and abundance estimate of the Antarctic krill based on the record of R/V Kaiyo Maru. The cruise was made in December 1980 in the area south of 61S, 60E-80E and in January 1981 in the area south of 63S, 30E-60E.

The estimate of biomass was made by stratifing research area into two strata; high SV (backscattering strength) area and low SV area. Those are given in average density in the above two areas as 0.313 and 0.259 g/m^3, which led to the estimates of 14.44 and 14.14x10^6 tons in these research area. If those estimates were simply expanded to the whole Antarctic an estimate of krill biomass is obtained as about

530 million tons. Since a revised estimate of target strength and some other correction factor were obtained recently, a revised estimate may be reported with them in near future.

2. Ecosystem modeling

There appears two different types of models in the published articles which deal with ecosystem modeling. They are Lotka-Volterra type model (Yamanaka, 1983; Nagata, 1983) and a network model (Doi, 1979).

2-1. Lotka-Volterra type model and the basic concept

In the Lotka-Volterra type model biomass of prey (x) and that of predator (y) are expressed in the simplest form as,

$$dx/dt = ax - cxy \qquad .....(1)$$

$$dy/dt = -by + dxy \qquad .....(2)$$

when no removal is made by fishery. With an assumption of logistic growth is introduced both for prey and predator, eqations become into the form,

$$dx/dt = p1x(1-x/X) - \mathrm{PREDATION} \qquad .....(3)$$

$$dy/dt = p2y(1-y/Y) \qquad .....(4)$$

p1 and p2 are intrinsic growth coefficient for prey and predator, respectively. X and Y are so called 'carrying capacity' for these species. Carrying capacity for prey (X) means an upper limit of biomass which can be attained only under a condition of average food availability and no removal by predation. Thus X is much larger than what it is attained in a real ecosystem. Since predator depends entirely on prey, their carrying capacity (Y) is relative to X and,

$$Y = rX \qquad .....(5)$$

r is so called 'ecological efficiency' or efficiency of energy transformation from one trophic level to the next, for which sometimes a value of 0.1 is assumed (Horwood, 1981).

There are many different ways to handle the PREDATION term in equation (3). Horwood (1981) used a traditional expression as,

$$\mathrm{PREDATION} = exy \qquad .....(6)$$

A coefficient e is the instantaneous predation rate of the predators; unit biomass of predator takes e unit of prey biomass in unit of time. Thus the amount of krill eaten by one unit biomass of whale differs depending on the abundance of krill.

Yamanaka (1983) introduced a modification of predation taking a saturation effect of predation rate into account. When prey is much more abundant than a certain level, amount of predation by unit biomass of predator in unit of time (predation rate) should reach to a certain maximum level. He used Ivlev's (1965) model and Shoemaker's (1977) model for such saturation effect. Those are,

$$\text{PREDATION} = s\, y(1-\exp(-kx/Q)) \quad .....(7)$$

$$= s'k'y\, x/(k'+x) \quad .....(8)$$

In both of these expressions predation rate is a fuction of abundance of prey, and it reaches to a certain level (s in eqn.(7) and s'k' in eqn.(8)) ultimately.

Nagata (1983) also considered this effect and applied Shoemaker's model for predation of whales and seals on krills. To concentrate into a theoretical analysis on change of krill biomass with time, he simplified as,

$$\text{PREDATION} = R = \text{constant}$$

to deal with equation (3).

Another simplification might be possible to deal with PREDATION term. In the region over a certain level of prey abundance predation rate may be simplified as,

$$\text{PREDATION} = hy \quad ....(9)$$

without taking any density dependance on prey abundance into account (Shinozaki, 1967).

2-2. Yamanaka's analysis

Yamanaka (1983) set up Lotka-Volterra type model to deal with krill-whale system in the following form,

$$dZ/dt = Z\ (P(1 - Z/Q) - R - F1 - SW) \quad .....(10)$$

$$dW/dt = W\ (T(1 - W/UZ) - F2) \quad .....(11)$$

where Z, krill biomass; W, whale biomass; Q, carrying capacity for krill; R, predation rate by other predators than whale; U, efficiency of energy transformation; F1 and F2 are annual catch rates of krill and whale, respectively;

P,T are intrinsic growth coefficients; S, feedig rate of whale. He then applied Ivlev's and Shoemaker's models to incorporate saturation effect as previously explained in eqns. (7) and (8).

Yamanaka examinied values of parameters to adopt. P=1.0 was used following to Horwood (1981). Although a trial was made to estimate P value (intrinsitic growth rate of krill biomass) it was not valid, because no estimate of P can be derived when once an equilibrium status is assumed.

From eqn.(10) krill biomass (Z) has real solution for equilibrium status against pressure of predation (G=R+SW), when the condition,

$$PZ(1 - Z/Q) >= G \qquad .....(12)$$

or

$$QP >= 4G \qquad .....(13)$$

is satisfied. Hence predation on krill only by whales, seals, and birds is estimated as 0.337x10^9 tons by Nemoto and Murano (1979),

$$Q >= 1.35x10^9 \text{ tons}$$

was estimated taking P=1. After reviewing some previous knowledges to estimate a possible order of carrying capacity for krill (Q), it was concluded that Q may well be assumed to be in the lower level of the order of 10^9 tons.

With stationary model and parameters, Yamanaka calculated some diagrams for the solution of equilibrium catch on F1-F2 coordinates.

In the krill-whale system a hastorical trajectory of krill biomass can be obtained by adopting historical change of whale biomass (after Gambell, 1974) and assuming predation rate by other animals than whales (R). Fig. 1 is thus obtained to show historical trajectory of krill biomass. Hence R is rather small in this calculation krill biomass went up since 1920 when the system was at an stationary status.

The results of simulation to incorporate random fluctuation in carrying capacity for krill (Q) (Fig. 2) suggests that those fluctuation may mask the trend in a short period even though the general trend pattern is not affected. In a sensitivity test of the parameter values to the estimates, it was detected that P and Q have significant effects and hence important to have reliable estimates.

A multiple predator model was then developed to describe krill-whale-seal system;

$$dW/dt = W (T (1-(W+BSb/S)/UZ) - F2) \quad .....(14)$$

$$dB/dt = BTb (1 - (B+WS/Sb)/UbZ) \quad .....(15)$$

$$dZ/dt = Z(P(1-Z/Q)-R) - (SW+SbB)(1-\exp(-KZ/Q)) \quad .....(16)$$

where B, seal biomass; suffix b denotes parameters for seals; the rest are the same to the previous parameters.

When seal biomass was fitted to a logistic growth based on the previous knowledge, krill biomass showed an increase for about 30 years from the beginning and then stayed at a constant level despite the increasing predation of seals. This is due to a compensation by decreasing predation of whale whose biomass showed a decreasing trend in those years.

When F1 and F2 are set in a certain level and simulations were done to get future projection, as seen in Fig. 3 (without whale catch) and Fig. 4 (with whale catch), it was suggested that man's exploitation of krill have more significant effect on seals than on whales since they are much closer to their carrying capacity.

As a results of these analysis it was suggested that 1) the present level of exploitation of krill is very low and the exploitation of the order of hundred million ton per year may not adversely affect the whale stock and 2) key parameters such as P and Q are important to make a further research.

2-3. Nagata's analysis

Nagata (1983) considered theoretical aspects of krill-whale-seal-krill fishery system. When predation of whale and seal on krill set to a constant value (R) for simplification of the model, the following equations are obtained,

$$dZ/dt = pZ(1-Z/Z_\infty) - aZW(k/(k+Z)) - bZS(1/(1+Z)) - Fk$$

$$\simeq pZ(1-Z/Z_\infty) - (R+Fk) \quad .....(17)$$

where Z,W and S are biomass for krill, whale and seal, respectively; Z_∞,carrying capacity for krill; R, predation of whale and seal; Fk, catch rate of krill by fishery; the rest are parameters.

From eqn. (17) change in krill biomass with time, Z(t), was solved analytically (his eqns (6)-(13)). Z(t) reaches to a stable equilibrium solution of,

$$\lim_{t\to\infty} Z(t) = (Z_\infty + Q)/2$$

$$Q = Z_\infty((1-4(R+Fk)/(pZ_\infty)))\hat{}0.5 \quad .....(18)$$

under the condition of,

$$R+Fk <= pZ_\infty/4 \quad \text{and} \quad Z_0 >= (Z_\infty - Q)/2.....(19)$$

On the other hand the final state biomass is zero if,

$$R+Fk > pZ_\infty/4 \text{ or } Z_0 < (Z_\infty - Q)/2 \quad .....(20)$$

The above relation between krill biomass at the final steady state and consumption rate by other animals is explained in Fig. 5.

Nagata considered the carrying capacity for krill (Z_∞), and suggested that an equilibrium of biomass of krill, whale, seal and other krill predators was near the critical point prepresented by,

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

in the pre-whaling period. Because very little observable effect only can take place on the age at sexual maturity and biomass of antarctic marine animals feeding on krill if Z_∞ has been much greater than $4R'/p$.

This idea is supported by a dicisive analysis as follows. In the krill-single predator system such as,

$$dZ/dt = pZ(1-Z/Z_\infty) - aW \quad .....(21)$$

$$dW/dt = qW(1-W/(lZ)) \quad .....(22)$$

Z and W, under the equilibrium condition in the pre-whaling period, can be solved as,

$$Z = Z_\infty(1-al/p) \quad .....(23)$$

$$W = lZ_\infty(1-al/p) \quad .....(24).$$

It is most likely that l, conversion factor, was naturally so adjusted that W could take its maximum value in that equilibrium state. Hence,

$$l = p/(2a) \text{ and thus } Z_0 = Z_\infty/2 \quad ....(25).$$

This condition on Z corresponds to

$$R = pZ_\infty/4 \text{ or } Q = 0 \quad ....(26).$$

If p=1.0 (after Horwood(1981) and Yamanaka(1983)) and R=2.5x10^8 tons/year is taken from Laws's (1979) estimate, the corresponding Z_∞ would be Z_∞=1.0x10^9 tons. This is a conservative estimate of Z_∞ since predation of seabirds, squid or other predators than whale and crabeater seal is not taken into account.

If present predation rate is adopted from Nemoto and Murano (1979), the estimate of Z_∞ goes up to $Z_\infty \simeq$14x10^8 tons and the natural consumption rate at present is estimatd as R - 2.1x10^8 tons/year. Assuming present krill biomass is at an equilibrium state, Z_0 is estimated by eqn.(18) as,

Z_0 = (14 + Q(R=2.1))/2 = 11.4x10^8 tons ....(27).

As shown in eqn.(20) if total removal from krill biomass, R+Fk, exceeds $pZ_\infty/4$= 3.5x10^8 tons/year, krill biomass will go down to zero. Therefore, allowable catch for krill fishery would be,

Fk <= 1.1x10^8 tons/year .....(28)

as far as R is kept constant at the above level.

Nagata concluded his remarks that while intrinsic growth rate of krill biomass (p) estimated by Horwood (1981) and Yamanaka (1983) would have a possibility of error, characteristics of krill biomass represented by Fig. 5 are invariable regardless of change of p as far as Z is given in unit of Z/Z_∞ .

2-4. Doi´s analysis

Doi (1979) set up a simulation model of a kind of network model for the analysis of the Antarctic ecosystem.

In his model thirteen species or components were chosen and connected in the way shown in Fig. 6. The flow of energy is in the direction from left to right in the figure i.e., from the producer to the consumer through predation process. The energy balance, for example, for the component 2, is shown in Fig. 7 and is expressed in a preservation equation as,

C1,2Q(2) - C2,3Q(3) - C1,2Q(2)RC(2)
food intake predation dissimilation

-C1,2Q(2)EC(2) - DC(2)Q(2) - FQ(2) = 0 .....(29)
egestion natural death catch

where Q(2), standing stock of species 2; Q(3), standing stock of species 3; RC(2), dissimilation rate; FQ(2), catch rate; C1,2, energy transformation coefficient from species 1 to 2 through the process of predation; C2,3, similar to C1,2 but for species 2 and 3.

The basic concepts and mathematical modifications to deal with model for non-equilibrium state are such that: (1) Every transfromation coefficient changes depending upon standing stock of prey as,

$$Cij = \widetilde{Cij}\ (1 - exp(-KijQi)) \qquad .....(30)$$

where Cij, coefficient for equilibrium state; $\widetilde{Cij}$, possible maximum value of coefficient $\widetilde{Cij}$ and estimated as $\widetilde{Cij} = n \times Cij$; Kij, constants; and (2) Every species has adaptability to adjust growth rate, fecundity, mortality rate etc. for existance. This function is dealt with the following expression to adjust mortality rate,

$$DC = DC_o(Q/Q_o)\hat{\ }a \qquad .....(31)$$

where DC, natural mortality coefficient; a, intrinsitic coefficient of adaptability for a species; subscript 0 denote initial state. a is estimated by simulation so as to explain historical change in biomass.

In Doi´s model standing stock of phytoplankton is kept constant and predation rate by krill (T1,3) and by other zooplankton (T1,2) are also set constant. The expression of change in biomass for krill is expressed in the equation,

$dQ(3)/dt = T1,3$
transportation from phytoplankton

$-C3,4(1-exp(-K3,4Q(3))Q(4)$
predation of squids

$-C3,5(1-exp(-K3,5Q(3))Q(5)$
predation of fishes

......

$-C3,13(1-exp(-K3,13Q(3))Q(13)$
predation of sei whale

$-DC(3)Q(3)$
natural death

$-FQ(3)$ .....(32)
catch by fishery

The equation for minke whale is,

$dQ(9)/dt = C3,9(1-exp(-K3,9Q(3))Q(9)(1-RC(9)$
predation on krill and net gain
$-EC(9))$

-DC(9)Q(9)
natural death

-FQ(9) .....(33)
catch by whaling

For the rest of the compoment differential equations are similar to the above in essence.

In those simultaneous equations there are 137 variables,parameters and observed values parameters in all. Those are:

Variables; Q(2)-Q(14) for standing stock,
$Q_o(2)-Q_o(14)$ for initial state,

Parameters; T1,2, T1,3 for transportation from phytoplankton,
DC(2)-DC(14) for natural mortality,
RC(4)-RC(14) for dissimilation,
EC(4)-EC(14) for egestion,
21 Cij for transportation coefficient,
14 a for adaptability coefficient,
12 n for multiplier,
19 Kij for constants, and

Observed value; FQ(3), FQ(5), FQ(9)-FQ(14) for catch.

Among those variables and parameters QO, DC, RC, EC and FQ are adopted from previous publications. n are set rather arbitrary and K are solved by eqn.(30). Values of 'a' are tested in simulation for past trajectory. Cij are solved in the following procedure; twelve transportation coefficients were obtained from previous knowledges while the rest of them (9) were estimated by solving simultaneous equations for the initial state,

$$[Q]\ C - QQ = 0$$

where [Q] is a matrix to multiply for transportation coefficient vector (C) and QQ is negative production vector (as catch and natural death) estimated from some previous papers (Laws,1977; Project Team for Krill Biomass,1978; El Sayed,1977).

Historical catches of whales in the Antarctic was then utilized to estimate historical projections of 13 components in the network model. As shown in Fig. 8 reduction of whale biomass in those 70 years resulted in growth of krill biomass (3.7 times) while that of seals, penguines and sea birds are not so much remarkable. Krill biomass in 1976 was estimated as 3,700 million tons from the analysis. It is noteworthy that about 70% of predation on krill is made by squids.

A future projection was tried in nine cases of combinations of different catch regimes of krill and whale. Two of them were adopted from Doi (1979) as Fig. 9 and Fig. 10; the former is for 0 catch of krill and catch of whales at the level of 1975 and the latter is for 0 catch of whales with different catch level of krill. In the former case krill biomass is expected to decrease from 3,700 million tons to 2,900 million tons in about 30 years due to heavy predation by recovering fin and blue whales. When krill exploitation is to continue at the level of 10 million tons/year, krill biomass will reduce to about 2.6 billion tons after 30 years. While whale species will continue to increase under this scheme, sea birds and seals show a lesser increasing rate, squids stay at almost constant level and fish will continue to decline.

Doi noted in his remarks that only 17% of primary production of 30 billion tons is estimated to be consumed within the ecosystem and therefore suggested possibilities of much greater energy consumptions by components or outflow of energy from the Antarctic area. He stressed that further research should be focused on $\widehat{C}$, maximum transportation coefficient, and a, adaptability coefficient in the future study.

3. Some comments on ecosystem modeling

It is ovbious that ecosystem modeling is one possible approach in future study to get some practical and useful suggestions for a rational utilization and management of the Antarctic ecosystem. Although these three papers by Japanese scientists, dealing with absolute quantification, developed ways to approach to this difficult problem, they are not in a consistency not only in the modeling concept but also in the results. Informations used in these authors are also different and it is difficult to find immediately useful common suggestions from these works with regard to the Antarctic ecosystem management. Nevertheless they revealed some important points to be reviewed in future ecosystem medeling.
I want to make some comments to discuss this matter.

Lotka-Volterra type models are much simpler than other ecosystem models such as developed by Doi since they contain fewer variables and parameters to be used. At the same time they are definite limitation within themselves because of this simplification. When a simplified whale-krill system is adopted seal biomass is to be treated implicitly as only a part of 'predation other than whales' which is usually kept constant in the model. Even much complicated krill-whale-seal system is adopted, other important predators are hidden from the model, which may result in a projection totally different from different approach and modeling where those important predators are explicitly builted in. An example of this kind is observed in Yamanaka's analysis where predation by squid, fish and birds are adopted in the order of one tenth of that in Doi's model, and hence behavior of historical projection is different each other.

Another problems to consider on Lotka-Volterra type model are;

(1) Critical parameters such as Z_∞ and p,

(2) expression of PREDATION term in eqn. (3),

(3) expression of competition term in eqns (14)-(15),

(4) concept of transportation efficiency of predators.

These problems are to be discussed one by one.

(1) Yamanaka and Nagata considered a possible minimum value of carrying capacity for krill on the basis of balance at the equilibrium state. As discussed by Nagata necessary condition in equilibrium state is,

$$Z_\infty >= 4R/p.$$

There are some estimates of total predation, R, for pre-whaling period by several authors; Laws (1977) gave an estimate of 190 million tons of baleen whales and 80 million tons of seals; Nemoto and Murano (1979) gave similar figures of 180 and 64 million tons, respectively; They also gave an estimate of predation of birds as 39 million tons at present; Doi (1979) gave an estimate of 939 million tons including predation of squid, fish and birds as well.

If Doi's estimate is adopted carrying capacity for krill (Z_∞/p) should be over 37.56x10^8 tons, which is nearly four times of Yamanaka's estimate. Total predation in the pre-whaling period is a key information to estimate carrying capacity for krill.

As already suggested by Yamanaka and Nagata intrinsic growth coefficient of krill (p) is essential, influential and sensitive parameter. Nevertheless there is no valid basis to derive an estimate of p from them. It seems to be the best way to get some information on the possible range of this parameter by experimental culture.

(2) The PREDATION term has another important problem to consider. As explained in this report, different expression of this term will give us different results not only in the initial equilibrium solution with regard to Z_∞ but also in the projection.

(3) Competition between species in the same trophic level and feeding on the same sources are often expressed in the way adopted in eqns (14) and (15). In those equations feeding rate and biomass of competitors are dealt with in a manner so as to diminish the afford of capacity each other. In other words they are fully competitive in the ability and

range of feeding. Whales have superiority in feeding range over seals and hence negative effect from increase of seals may be less influential. On the contrary, the reverse effect of whales over seals may be much greater than a degree expressed by the ratio of feeding rate in eqns (14) and (15). A further modification is needed on this point based on their behaviour.

(4) Carrying capacity of predators are usually expressed in a form in eqn. (5) based on the meaning of transportation coefficient in the ecosystem. Carryinf capacity is destined to vary from time to time due to change in biomass of prey. Change in the carrying capacity cause change in afford of growth capacity, which defines growth rate of prey biomass. Is it rational to define carrying capacity of predators in such way? Whales and seals are longlived animals and tolerant of starvation and hence the effect of shortage of prey should appear much indirect manner than the expression in eqn. (5) and perhaps with time lag. An alternative expression taking time lag effect into account or another modification is needed on this problem.

Network model has also many points to discuss. Doi´s network model has some advantages over Lotka-Volterra type models in dealing with numerous important components in the ecosystem simultaneously.

One of the shortcomings of this models is the great difficulty to decide or to assign adequate values for too many parameters. In Doi´s analysis some of them were adopted from previous publications, some were estimated in the tuning process for the initial equilibrium state and the rest were set rather arbitrary or estimated in a trial-and-error fitting process.

As pointed out by himself some of those parameters are influential to the results: possible maximum transportation coefficients ($\tilde{C}$ij) and adaptability coefficients (a) effect historical projection of components. Thus two points shold be noted with regards to those two sets of parameters. In the models expressed in the differential equation, there is no explicit definition of nature of biomass growth. Since maximum net growth coefficients are defined utilizing those two kinds of parameters in a linear form to its biomass, it could be understood from the equations that the nature of biomass growth is an exponential type instead of logistic growth. When looking into 'a' it ranges from 0 for plankton to 50 for sei and sperm whales although some of baleen whales are assigned a value of 1. Hence those two sets of parameters, Cij and 'a' should have some ecological basis, a further investigation is necessary to develope this model.

As already reffered to the difference between Yamanaka and Doi in dealing with squid, Doi´s estimate of 173 million tons of squid biomass in pre-whaling period has a great role in his analysis. They have been consuming 543 million tons of krill, 58% of total predation, in pre-whaling period, and in 1976 they still consume 75% of total predation. This is a point of further clarification before recalculation is to be done.

Although Doi's analysis showed many suggestive results, it envolves many problems in conceptual and procedual matters at the same time. It is thus difficult to judge immediately which type of approach -- Lotka-Volterra type model or network model -- would give us more useful suggestions at the present satus of knowledge. It is definitely clear, however, that common source of information especially on squid and fish biomass in pre-whaling period is needed whatever types of models is to be used in the analysis.

It is necessary to assume stability or equilibrium state in pre-whaling period to start with simulation for the Antarctic ecosystem regardless the type of the model. If this assumptiom is not fully supported the treatment and results have to ge changed. The higher the degree of yearly variation, the lesser is the possibility of existance of krill when carrying capacity for krill is taken such a conservative level to satisfy the equation,

$$Z_\infty = 4R/p.$$

Although it is not clearly known about the degree of annual variation of krill biomass it may be highly possible due to variation in climatorological factors such as solar radiation, ice coverage etc. as well as predation pressure. It seems to be difficult to measure yearly variation in primary production or in krill biomass directly but record of diet from whaling may be useful as an indirect information.

A further models to take into account seasonal variation or local ecosystem will be one of the possible direction of imporvement.

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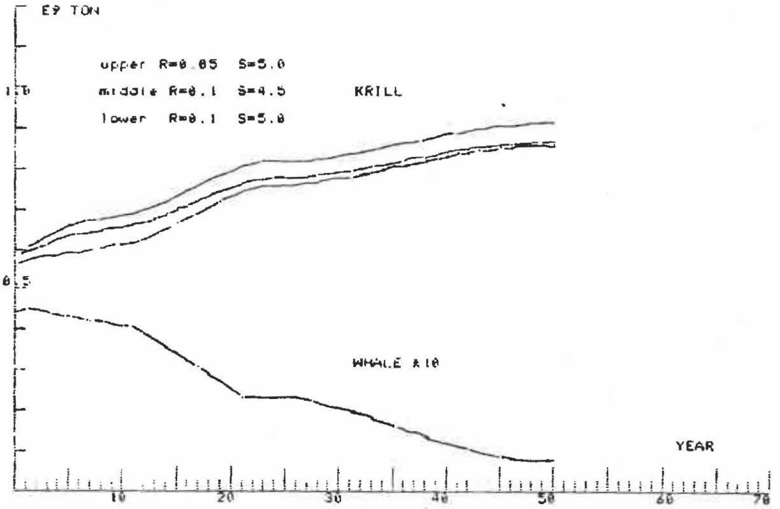

Fig. 1. Increase of krill with decline of whale stock (computed under several combination of predations by whale and other animals). S: annual comsumption of krill by unit weight of whale. R: predation rate of the other animals to krill stock. (by YAMANAKA, 1983)

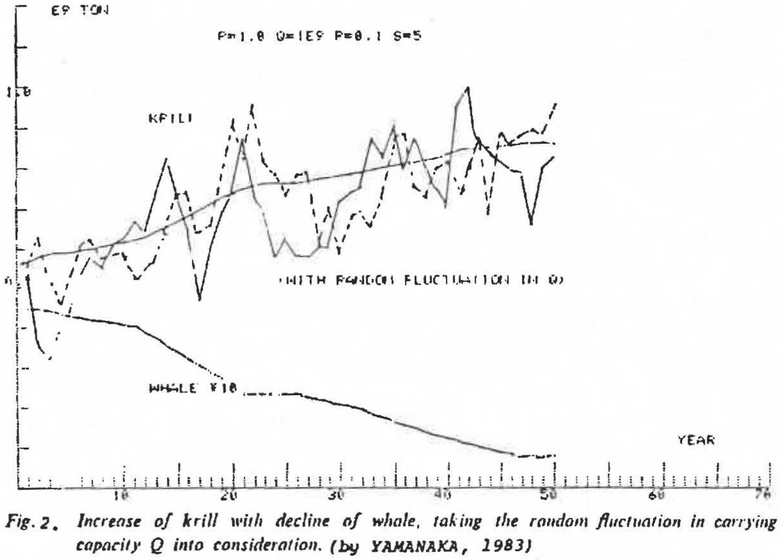

Fig. 2. Increase of krill with decline of whale, taking the random fluctuation in carrying capacity Q into consideration. (by YAMANAKA, 1983)

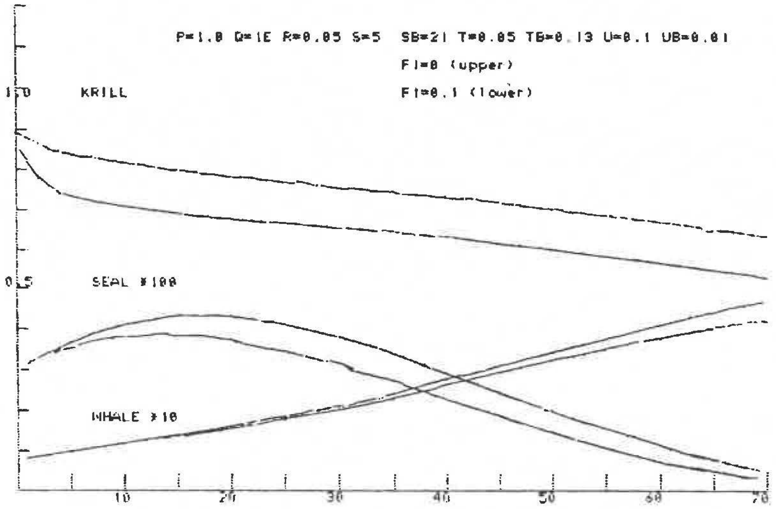

Fig. 3. *Effect of krill catch upon whale and seal (without whale catch).*
(by YAMANAKA, 1983)

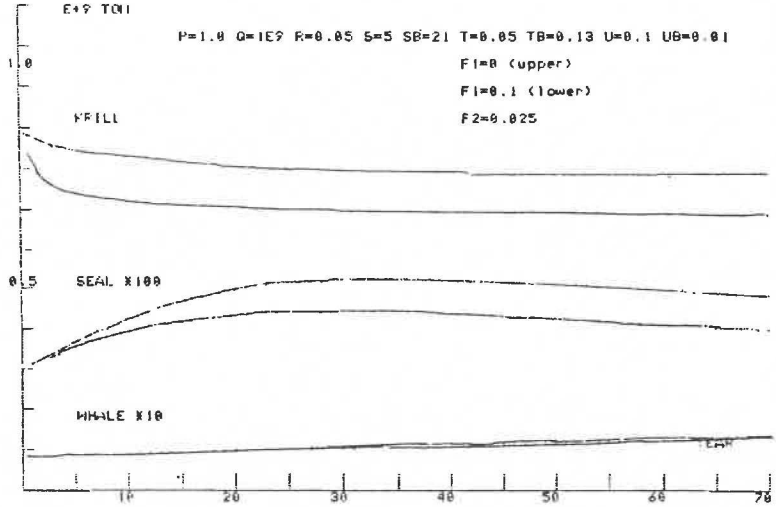

Fig. 4. *Effect of krill catch upon whale and seal (with sustainable level of whale catch).*
(by YAMANAKA, 1983)

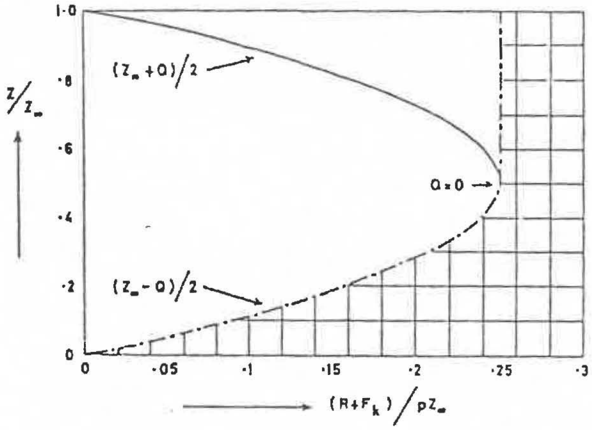

Fig. 5. *Biomass of krill in unit of* Z_∞, (Z/Z_∞), *at the final steady state* $(t=\infty)$ *as a function of the consumption rate in unit of* pZ_∞, $((R+F_k)/pZ_\infty)$. *If* $Z_0>(Z_\infty-Q)/2$ *and* $(R+F_k)<pZ_\infty/4$, *the final state biomass is given by* $(Z_\infty+Q)/2$. *If* $Z_0<(Z_\infty-Q)/2$ *or* $(R+F_k)>pZ_\infty/4$, *the final state biomass is zero.* *(by NAGATA, 1983)*

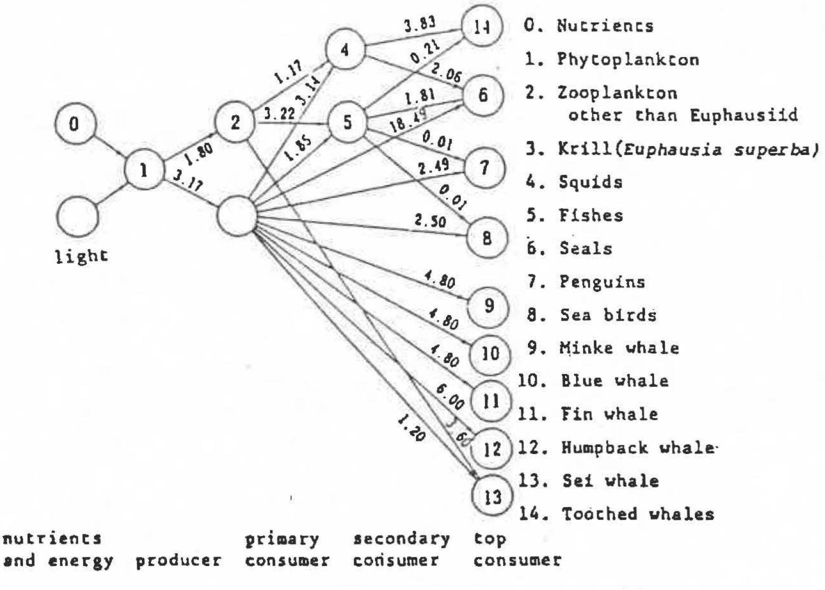

Fig. 6. Trophic network model in the Antarctic.
(by DOI, 1979)

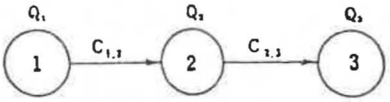

Fig. 7. Energy flow between three species.
(by DOI, 1979)

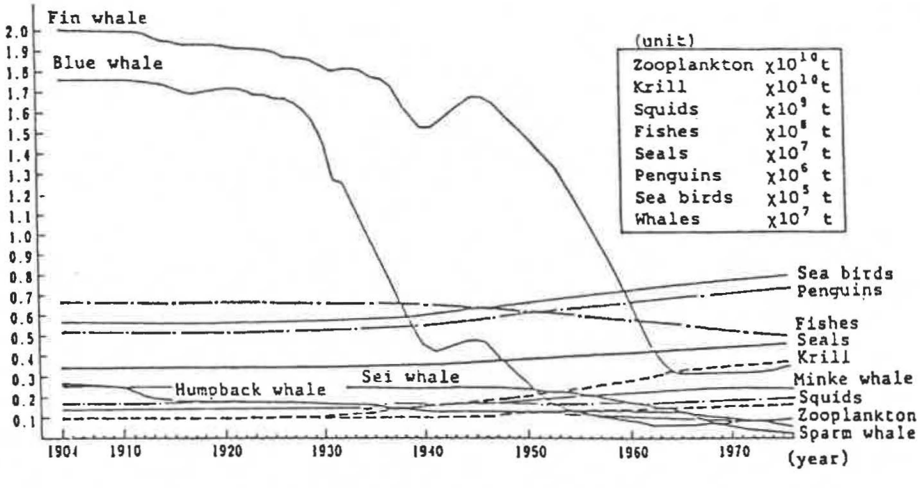

Fig. 8. Estimated historical trajectories for each species.
(by DOI, 1979)

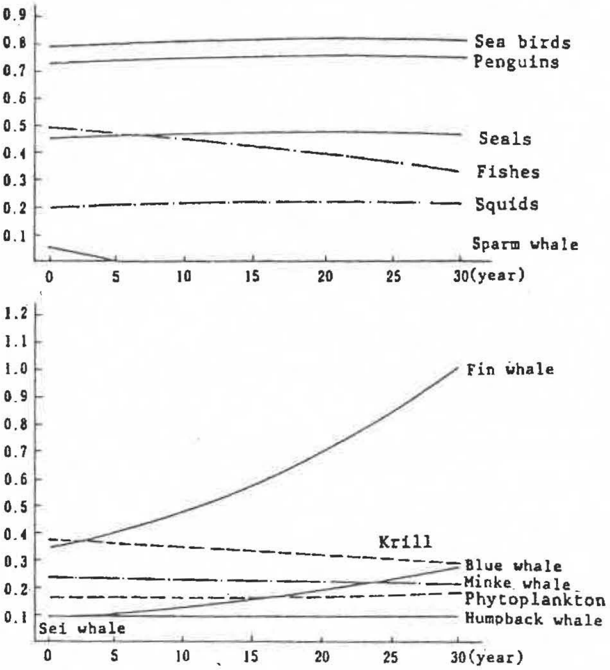

Fig. 9. Future projections for each species under exploitation of whale. *(by DOI, 1979)*

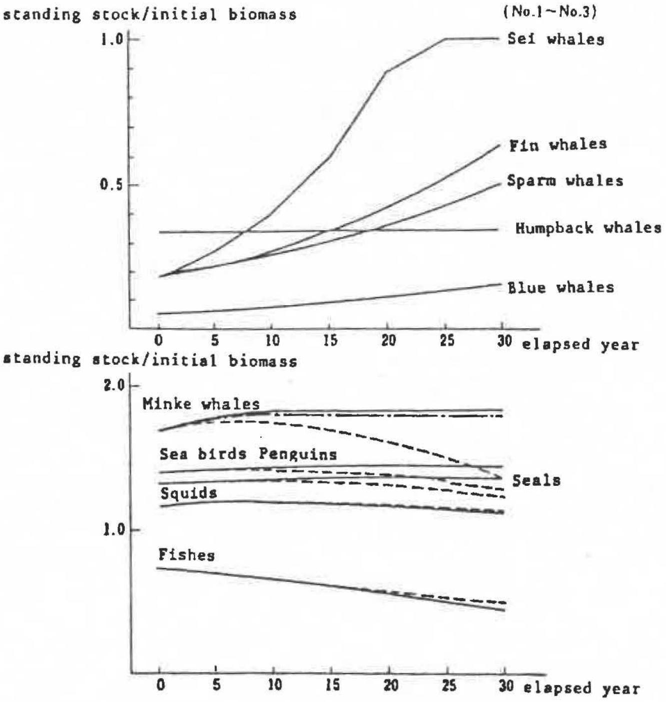

Fig. 10 Future projections for each species under exploitation of krill. *(by DOI, 1979)*

Table 1.	Comparison of data in the three reports
Fig. 1.	Increase of krill with decline of whale stock (computed under several combination of predations by whale and other animals). S: annual consumption of krill by unit weight of whale. R: predation rate of the other animals to krill stock. (by YAMANAKA, 1983)
Fig. 2.	Increase of krill with decline of whale, taking the random fluctuation in carrying capacity Q into consideration. (by YAMANAKA, 1983)
Fig. 3.	Effect of krill catch upon whale and seal (without whale catch). (by YAMANAKA, 1983)
Fig. 4.	Effect of krill catch upon whale and seal (with sustainable level of whale catch). (by YAMANAKA, 1983)
Fig. 5.	Biomass of krill in unit of Z_∞, (Z/Z_∞), at the final steady state $(1=\alpha\delta)$ 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. (by NAGATA, 1983)
Fig. 6.	Trophic network model in the Antarctic. (by DOI, 1979)
Fig. 7.	Energy flow between three species. (by DOI, 1979)
Fig. 8.	Estimated historical trajectories for each species. (by DOI, 1979)
Fig. 9.	Future projections for each species under exploitation of whale. (by DOI, 1979)
Fig. 10.	Future projections for each species under exploitation of krill. (by DOI, 1979)

Tableau 1.	Comparaison des données contenues dans les trois rapports
Fig. 1.	Accroissement du krill en conjonction avec la diminution du stock de baleines (calculés d'après plusieurs combinaisons des activités prédatrices des baleines et autres animaux). S: consommation annuelle de krill par unité de poids de baleine. R: taux d'activité prédatrice des autres animaux sur le stock de krill. (d'après YAMANAKA, 1983)
Fig. 2.	Accroissement du krill en conjonction avec la diminution du nombre de baleines, en prenant en considération la fluctuation, prise au hasard, de la capacité de reproduction Q. (d'après YAMANAKA, 1983)
Fig. 3.	Effet de la prise du krill sur les baleines et les phoques (sans tenir compte de la capture des baleines). (d'après YAMANAKA, 1983)
Fig. 4.	Effet de la prise du krill sur les baleines et les phoques (en tenant compte d'un niveau de capture acceptable de baleines). (d'après YAMANAKA, 1983)
Fig. 5.	Biomasse du krill en unité de Z_{∞}, (Z/Z_{∞}), à l'état final stable $(1=\infty)$ comme fonction du taux de consommation en unité de pZ_{∞}, $((R+F_k)/pZ_{\infty})$. Si $Z_0>(Z_{\infty}-Q)/2$ et $(R+F_k)<pZ_{\infty}/4$, la biomasse à l'état final est donnée par $(Z_{\infty}+Q)/2$. Si $Z_0<(Z_{\infty}-Q)/2$ ou $(R+F_k)>pZ_{\infty}/4$, la biomasse à l'état final est zéro. (d'après NAGATA, 1983)
Fig. 6.	Modèle du réseau trophique en Antarctique. (d'après DOI, 1979)
Fig. 7.	Courant d'énergie entre trois especès. (d'après DOI, 1979)
Fig. 8.	Trajectoires diachroniques estimées pour chaque espèce. (d'après DOI, 1979)
Fig. 9.	Trajectoires prospectives pour chaque espèce sous un régime d'exploitation des baleines. (d'après DOI, 1979)
Fig. 10.	Trajectoires prospectives pour chaque espèce sous un régime d'exploitation du krill. (d'après DOI, 1979)

Таблица 1. Сравнение данных, содержащихся в трех докладах

Рис. 1. Увеличение количества криля в результате сокращения запаса китов (вычислено по нескольким комбинациям охотник-жертва в отношении китов и других животных). S: годовое потребление криля на единицу массы кита. R: уровень хищничества других животных по отношению к запасу криля.
(По Яманака, 1983 г.)

Рис. 2. Увеличение количества криля в результате сокращения запаса китов с учетом произвольного колебания переносимого объема Q (по Яманака, 1983 г.)

Рис. 3. Влияние вылова криля на китов и тюленей (без вылова китов)
(По Яманака, 1983 г.)

Рис. 4. Влияние вылова криля на китов и тюленей (с поддерживаемым уровнем вылова китов).
(По Яманака, 1983 г.)

Рис. 5. Биомасса криля в единицах Z_∞, (Z/Z_∞); гомеостаз $(1 = \infty)$; как функция уровня потребления в единицах pZ_∞, $((R + F_k)/pZ_\infty)$. Если $Z_0 > (Z_\infty - Q)/2$ и $(R + F_k) < pZ_\infty/4$, результат описывается формулой $(Z_\infty + Q)/2$. Если $Z_0 < (Z_\infty - Q)/2$ или $(R + F_k) > pZ_\infty/4$, то окончательное состояния биомассы равняется нулю. (По Нагата, 1983 г.)

Рис. 6. Модель трофической сети в Антарктике
(По Дои, 1979 г.)

Рис. 7. Поток энергии между тремя видами
(По Дои, 1979 г.)

Рис. 8. Предполагаемые исторические траектории для каждого вида.
(По Дои, 1979 г.)

Рис. 9. Предполагаемые тенденции каждого вида при эксплуатации китов.
(По Дои, 1979 г.)

Рис. 10. Предполагаемые тенденции каждого вида при эксплуатации криля
(По Дои, 1979 г.)

Cuadro 1	Comparación de los datos en los tres informes
Ilustración 1.	Aumento del krill con la disminución de las existencias de ballenas (calculado de acuerdo con varias combinaciones de depredación efectuada por ballenas y otros animales). S : consumo anual de krill por peso unidad de ballena. R : tasa de depredación de los otros animales con respecto a la existencia de krill. (por YAMANAKA, 1983)
Ilustración 2.	Aumento de krill con la disminución de ballenas, tomando en consideración la fluctuación fortuita en la capacidad de acarreo Q (por YAMANAKA, 1983)
Ilustración 3.	Efecto de la captura de krill en las ballenas y focas (sin que haya captura de ballenas). (por YAMANAKA, 1983)
Ilustración 4.	Efecto de la captura de krill en las ballenas y focas (con un nivel sustentable de captura de ballenas) (por YAMANAKA, 1983)
Ilustración 5.	Biomasa del krill en unidad de Z_∞ $(Z/Z_\infty$, en la condición estable final $(1 = \infty)$ como función de la tasa de consumo en unidad de pZ_∞ $((R + F_k)/pZ_\infty)$. Si $Z_o > (Z_\infty - Q)/2$ y $(R + F_k) < pZ_\infty/4$, la condición final de la biomasa la da $(Z_\infty + Q)/2$. Si $Z_o < (Z_\infty - Q)/2$ o $(R + F_k) > pZ_\infty/4$, la condición final de la biomasa es cero. (por NAGATA, 1983)
Ilustración 6.	Modelo de sistema trófico en el Océano Antártico. (por DOI, 1979)
Ilustración 7.	Corriente de energía entre tres especies. (por DOI, 1979)
Ilustración 8.	Trayectorias históricas calculadas para cada especie. (por DOI, 1979)
Ilustración 9.	Proyecciones futuras para cada especie bajo la explotación de la ballena. (por DOI, 1979)
Ilustración 10.	Proyecciones futuras para cada especie bajo la explotación del krill. (por DOI, 1979)