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## Decadal Response of Marine Food-chain to Bottom-up and Top-down Controls

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### Abstract

Using a simple four-level food-chain model (nutrient, phytoplankton, zooplankton and fish), the phase relationships in a decadal time scale were investigated under a periodical nutrient supply, i.e. bottom-up control, and under a periodical flow-parameter from zooplankton to fish, i.e. top-down control. This model expressed seasonal changes imitating the spring bloom and assumed the possibility that the predation of fish could positively affect zooplankton productivity. In the model results, the bottom-up control revealed that decadal variation of annual mean zooplankton stock ( $\bar{Z}$ ) was stabilized and furthermore that the maximum of  $\bar{Z}$  led to 90° from that of the annual mean fish stock ( $\bar{F}$ ). On the other hand, the top-down control amplified the decadal variation of  $\bar{Z}$  and showed that the phase relation between  $\bar{Z}$  and  $\bar{F}$  was out of phase. The results were then applied to a diagnosis for the present marine ecosystem in the western Pacific.

**Key words:** Decadal response, Marine food-chain model, Bottom-up, Top-down

### Introduction

Climate regime shifts in the North Pacific have taken place in 1924/25, 1947/48, and 1976/77, as reviewed by Minobe and Mantua (1999). Previous studies of these shifts have focused on the dramatic changes that occurred coincidentally in both fisheries and climate during the winter of 1976/77. Since 1976, the Aleutian low has intensified during winter and has shifted further east. Although the important linkages are poorly understood, it has been inferred that such a regime shift may control long-term variations in the pelagic ecosystem, which would include marine fish (e.g. Kawasaki and Omori, 1995; Hare and Mantua, 2000).

In the western Pacific, the Pacific sardine catch peaked in abundance in the 1930s after the regime shift of 1924/25. The catch declined from the 1950s to the 1960s, and then began to rapidly increase after the shift of 1976/77. More recently, the sardine catch peaked in the late 1980s. Noto and Yasuda (1999) demonstrated that the climate changes in sea surface temperature in winter in the Kuroshio Extension regions are significantly related to the mortality of Pacific sardines. The annual mean biomass of zooplankton in the Oyashio Region peaked in the 1970s, then declined in the 1980s (Odate, 1994). Taniguchi (1999) pointed out that this lower zooplankton biomass in the 1980s might have been due to the existence of certain mechanisms that stabilized abundant biomass under increasing predation pressure from fish; increasing fish stocks likely maintained a high level of

nitrate transfer energy that extended the fish themselves. These findings suggest that the dominance and productivity of zooplankton and higher trophic level species are affected by changes in the ocean climate, but also that there is a significant phase difference between both decadal variations.

Although our goal is to understand how changes in ocean climate will alter the productivity of pelagic fish populations, it is not easy to examine ecological interactions within the marine food-chain. In general, there may be two candidates for energy flow controls through the marine food-chain from nutrients up to fishes, i.e. "bottom-up" and "top-down" controls. Bottom-up control would refer to the possibility that fish capacity responds to bottom-up energy flow through the plankton-based food-chain, starting from a variable nutrient supply depending on changing mixed layer depths or inflow of nutrient-rich waters from winter to spring. Top-down control indicates that variable physical forcing directly affects fish recruitment, e.g., large-scale effects of climate changes in wind fields on circulation and transport of heat and young fish, and then the predation on zooplankton by fish will change the dynamics at the lower trophic levels. In both controls, top-down indirect effects acting through trophic links may be also important (Abrams and Matsuda, 1993). For example, intense predation on zooplankton by fish temporally decreases zooplankton stocks and then increases phytoplankton stocks in a top-down manner, but such an increase in phytoplankton stocks may help

zooplankton recover their stocks through bottom-up processes (Taniguchi, 1999). Such process led us to expect that there is a reasonable phase difference between each biomass throughout the marine food-chain. Therefore, the observed phase difference between zooplankton and fish stocks provides useful information for diagnosing the present mass-balance ecosystem in any regional scale.

Models are needed that will integrate each food-chain component into a mass-balance ecosystem. In the present study, we assumed the possibility that the predation of fish could positively affect zooplankton productivity. The decadal phase relationships of zooplankton and fish are examined primarily by using a simple prey-predator model forced by both bottom-up and top-down controls.

### Model formulation

The main purpose of most marine ecological models has been to represent seasonal changes in relationship between nutrients, phytoplankton, and zooplankton in a particular regional area, as reviewed by Frost and Kishi (1999). These models are usually called *N-P-Z* models and reveal a complexity of species relationships and environmental influences. Such models lead to a better quantitative understanding of ecological relationships. Good agreement between models and observations was achieved by suitable adjustment of this model's parameters. However, an important aspect of their model's goal appears to be lost due to the numerous biochemical parameters as well as the excessive complexity of non-linear relationships.

It has been said that the explanation using the over-simplified model on marine food-chain may only arise out of a deep understanding of the true complexities of nature, e.g., excluding the presence of omnivory, physical refuges, and size structure of each trophic level etc. In the cases of small lake, bay, and coastal sea area, the development of more sophisticated conceptual models may be possible based on the observational or experimental information for aggregation of complex food webs. However, such realized model have been tested in few studies for the regional area (western, central, and eastern Pacific Oceans etc.) owing to poor knowledge gained from fundamental and applied research, basic predictions such as the effect of increased productivity on stocks of different trophic levels. Although simple set of rules for producer and consumer control cannot be universally applicable to understand the temporal variations of specific species, it is perhaps useful to illustrate basic view of control in food-chain which consists of total biomasses at three or four trophic levels. In the

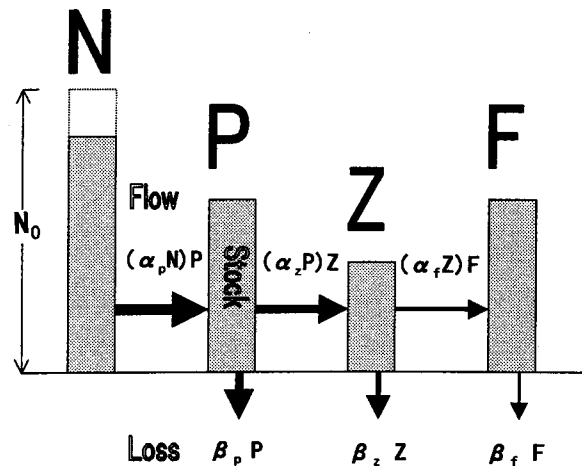


Fig. 1. Diagram of the dynamics of our food-chain model with four stock levels: *N* (nutrient), *P* (phytoplankton), *Z* (zooplankton), and *F* (fish).

present study, we took the following approach when designing a food-chain model: (1) We focused on the decadal response of each food-chain level rather than on seasonal changes. (2) We acknowledged that a deliberately simplified prey-predator model might continue to be an instructive tool, since the problem of overall food-chain efficiency is not yet well understood.

In our model, the simplest possible four-level food-chain was considered as illustrated in Fig. 1. The model has a single-nutrient and three-species food-chain (nutrient: *N*, phytoplanktons: *P*, zooplanktons: *Z*, and pelagic fishes: *F*). We used the letters *N*, *P*, *Z*, and *F* as both the names and variables. We let *N* be the stock of the nutrient at the lowest level of the food-chain, *P* takes in *N*, *Z* preys upon *P*, and *F* preys upon *Z*. Such prey-predator relations indicate a one-way energy flow from a lower to a higher level. That is, the reproduction of *P*, which occurs through a bacterial loop due to the decomposition from detritus of *P* and *Z*, was not considered because in order to consider the net-production of *P*, it would be important to discuss the long-term mass-balance of the marine food-chain. Also, *F* is a hypothetical entity consisting of all pelagic fishes in the regional area. Hence, variations not associated with the food supply of *F*, such as migration and year class fluctuations, were ignored, because decadal variations of fish abundance, the time scale of which is sufficiently longer than the life-span of any fish species, will occur due to long-term changes in fish capacity.

We used Volterra's equation to describe the prey-predator relationship that incorporates a functional response in the consumers of *P*, *Z*, and *F*. The loss was assumed to be linearly proportional to the stock. Thus, difficult problems of growth and loss were by-

passed by deriving suitable constants. Time-varying stock at four levels took the form :

$$dN/dt = -(\alpha_p N)P + (N_0 - N)\theta[t-n]/t_a$$

$$(n=1, 2, 3 \dots \text{year}) \quad (1)$$

$$dP/dt = -(\alpha_z P)Z + (\alpha_p N)P - \beta_p P \quad (2)$$

$$dZ/dt = -(\alpha_f Z)F + (\alpha_z P)Z - \beta_z Z \quad (3)$$

$$dF/dt = (\alpha_f Z)F - \beta_f F \quad (4)$$

where  $t$  is time (unit is the year),  $t_a$  is the time-scale of the adjustment (a time step was used in our model),  $\alpha_p$ ,  $\alpha_z$ , and  $\alpha_f$  are coefficients of net food assimilation for  $P$ ,  $Z$ , and  $F$ , respectively;  $\beta_p$ ,  $\beta_z$ , and  $\beta_f$  are constant death rates for  $P$ ,  $Z$ , and  $F$ , respectively. In this paper, we refer to the coefficients of  $(\alpha_p, \alpha_z, \alpha_f)$  as the “flow-parameter”, and the rates of  $(\beta_p, \beta_z, \beta_f)$  as the “loss-parameter”. The  $\theta[t-n]$  is a delta-function, i.e.,  $\theta[0]=1$  at  $t=n$ , and  $\theta=0$  at the other time. The first term of right hand side of equation (1) represents only the continuous consumption of  $N$  by  $P$ . The second term indicates a one-time supply of  $N=N_0$  in a year and can express seasonal variations that imitated the spring bloom. Therefore, long-term ecosystem variations due to seasonal changes can be simulated in our model. The annual mean values can then be used to discuss the phase relations between the stocks of each component. As these equations and a yearly  $N$ -supply condition render analysis difficult, the model can be solved numerically by stepwise integration.

#### Choice for loss- and flow-parameters

The model we have just outlined has six parameters. In this system, assuming an average of lost time for  $P$  of several months ( $\sim 0.2$  year), then  $\beta_p=5 \text{ year}^{-1}$ . This lost time roughly corresponds to the duration of a typical spring bloom in the Oyashio Region (e.g. Sugimoto and Tadokoro, 1998). One would expect the average lifetime of many species of  $Z$  to be longer than that of  $P$ , hence the net loss of  $Z$  is roughly assumed to be half of that of  $P$ , i.e.  $\beta_z=2.5 \text{ year}^{-1}$ . Although the life-span of pelagic fish in the western Pacific (e.g. sardine, mackerel, anchovy, jack mackerel and saury) ranges from 1 to 6 years, we assumed a relative short lifetime of 2 years, in consideration of their natural death rate, i.e.  $\beta_f=0.5 \text{ year}^{-1}$ .

The reasonable flow-parameters of  $(\alpha_p, \alpha_z, \alpha_f)$  cannot be easily estimated. The parameter space of  $\alpha$  would be so large that we chose to concentrate our simulations on varying  $\alpha$ , holding the above loss-parameters fixed. For the sake of simplicity, we consistently used  $\alpha=\alpha_p=\alpha_z=\alpha_f$  flow-parameter, except for in the case of the top-down control. Then, taking a unit nutrient (e.g. carbon, nitrogen, etc.) supply of  $N_0=1$ , the values of  $\alpha$  from 0 to 50 changed.

## Model results

### Steady-state solutions of four-level and three-level chains

Assuming  $\alpha=\alpha_p=\alpha_z=\alpha_f$  and  $\theta=1$  of equation (1), the steady-state solution for four-level chain is

$$\text{Level 1 } N^* = (\beta_f + \beta_p) / \alpha$$

$$\text{Level 2 } P^* = (N_0 / (\beta_f + \beta_p) - 1 / \alpha) / t_a$$

$$\text{Level 3 } Z^* = \beta_f / \alpha$$

$$\text{Level 4 } F^* = P^* - \beta_z$$

Using the similar system studied by DeAngelis et al. (1996), they pointed out the following interesting properties of steady-state values: The stocks of all levels depend on the loss-parameter  $\beta_f$  of top predator level ( $F^*$ ). That is, the stocks of levels 1 ( $N^*$ ) and 3 ( $Z^*$ ) are linearly depend on the loss-parameter  $\beta_f$  and increase as the loss-parameter of top predator increases, whereas levels 2 ( $P^*$ ) and 4 ( $F^*$ ) decrease with increasing values of  $\beta_f$ . Only the stocks of trophic levels 2 ( $P^*$ ) and 4 ( $F^*$ ), on the other hand, depend on  $N$ -supply of  $N_0$ , both increasing as  $N_0$  increases. In the case of no fish ( $F=0$ ), the steady-state solution for three-level chain is as follows

$$\text{Level 1 } N^* = N_0 / (t_a \beta_z + 1)$$

$$\text{Level 2 } P^* = \beta_z / \alpha$$

$$\text{Level 3 } Z^* = N^* - \beta_p / \alpha$$

This case also shows that the stocks of all levels depend on the loss-parameter  $\beta_z$  of top predator level ( $Z^*$ ) and only the stocks of levels 1 ( $N^*$ ) and 3 ( $Z^*$ ) depend on  $N$ -supply of  $N_0$ .

From such steady-state solutions, we can approximately infer the decadal or long-term response of marine food-chain to bottom-up and top-down controls. In our chain system, there is obvious top-down control on the all species that are an odd number of levels below the top predator and that the top predator and species an even number of levels below it experience an influence from the primary production. That is, it is easily understand that the phase difference between  $[N, Z]$  and  $[P, F]$  variations will be out of phase. Given that flow-parameter  $\alpha$  is large and  $N_0$  large enough to support all trophic levels, further changes in  $N_0$  affect only the values of the top predator and species an even number of levels below it. In the bottom-up control,  $P$  and  $F$  will increase as  $N$ -supply of  $N_0$  increases, but the response of  $Z$  is unknown from the steady-state solution. The product of  $Z$  will be determined through the periodical transfer energy from  $P$  to  $F$ , and hence the phase relationship between  $Z$  and  $F$  (or  $P$ ) variations is an important key to diagnose the regional marine ecosystem.

( $\alpha=30$ )

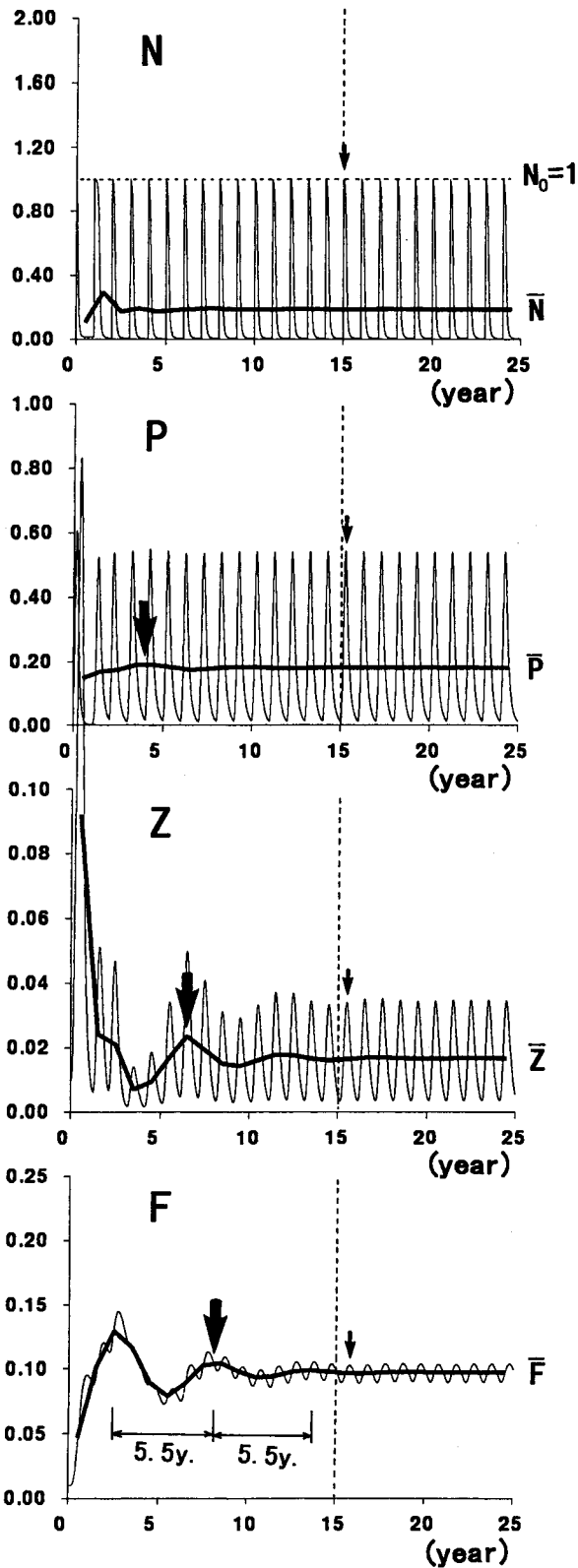


Fig. 2. Simulated time series of  $N$ ,  $P$ ,  $Z$ , and  $F$  for  $\alpha=30$  and  $N_0=1$ . The thick lines indicate annual mean values.

**Stock variations for a constant  $N_0$ -supply**

First, it is appropriate to consider the typical time variations of  $N$ ,  $P$ ,  $Z$ , and  $F$  stocks for  $\alpha=30$  under a constant  $N_0$ -supply ( $N_0=1$ ), shown in Fig. 2. Seasonal cycles of  $N$ ,  $P$ , and  $Z$  with large amplitudes are calculated, but the cycle of  $F$  is relatively small (thin lines). Here, we find that the calculated seasonal change of  $Z$  resembles that actually observed in the Oyashio Region, as shown later in Fig. 9(b). The obvious  $P$ -bloom accompanied by a decrease in  $N$ , followed by an increase in  $Z$  is depicted (small arrows). Note that this seasonal cycle is not the result of the prey-predator oscillation, but is caused by the limited nutrient supply in a single year. The ecological prey-predator oscillation can be seen only in the initial response of annual mean stocks (thick lines) as a damped oscillation with a 5.5-year period (thick arrows). All stocks show a monotonic approach to equilibrium, achieved over a long period of time.

In general, a prey-predator oscillation can occur when the prey increases due to a decline in the predator. In other words, energy must continuously be supplied to the prey. However, in our food-chain model, the lowest trophic level of  $N$  is always initialized each year and its stock decreases due to uptake by  $P$  during one year. Then, the oscillation loosens with time. This feature demonstrates that decadal prey-predator oscillation never occurs in marine ecosystems that have a dominant spring bloom.

To enhance the effect of intense predation pressure on  $Z$  by  $F$ , a calculation for the classical  $N$ - $P$ - $Z$  model (i.e.  $\alpha_f=0$ ) was also carried out. Figure 3 illustrates the equilibrium values for each stock as a function of  $\alpha$  for two cases: (a) the  $N$ - $P$ - $Z$  model and (b) the  $N$ - $P$ - $Z$ - $F$  model. In both models, it can be seen that the significant stocks appear in  $\bar{P}$  at  $\alpha\sim 5$ , in  $\bar{Z}$  at  $\alpha\sim 13$  and in  $\bar{F}$  at  $\alpha\sim 15$ . This implies that the energy flow from  $\bar{N}$  successively reaches the higher trophic level as the flow-parameter becomes larger. The response at  $\alpha>40$  in the  $N$ - $P$ - $Z$  model gives a low  $\bar{P}$ /large  $\bar{Z}$  (Fig. 3(a)), whereas the response at  $\alpha>20$  in the  $N$ - $P$ - $Z$ - $F$  model gives a low  $\bar{Z}$ /large  $\bar{P}$  and the  $\bar{F}$  value is large compared with  $\bar{Z}$  (Fig. 3(b)). Thus, the equilibrium stocks of  $\bar{N}$  and  $\bar{Z}$  tend to be smaller in the  $N$ - $P$ - $Z$ - $F$  model, indicating predation control by  $F$ .

The equilibrium mass-balance in the  $N$ - $P$ - $Z$ - $F$  model is as follows. For example, when  $\alpha\sim 30$ , the equilibrium values are  $\bar{N}\sim 0.5$ ,  $\bar{P}\sim 10^{-1}$ , and  $\bar{Z}\sim 10^{-2}$  (see Fig. 3(b)). The flow time from  $\bar{N}$  to  $\bar{P}$  can be roughly estimated by  $(\alpha_p \bar{N})^{-1}\sim 0.1$  year, and that from  $\bar{P}$  to  $\bar{Z}$  by  $(\alpha_z \bar{P})^{-1}\sim 0.3$  year, and that from  $\bar{Z}$  to  $\bar{F}$  by  $(\alpha_f \bar{Z})^{-1}\sim 3.3$  year, respectively. These estimated val-

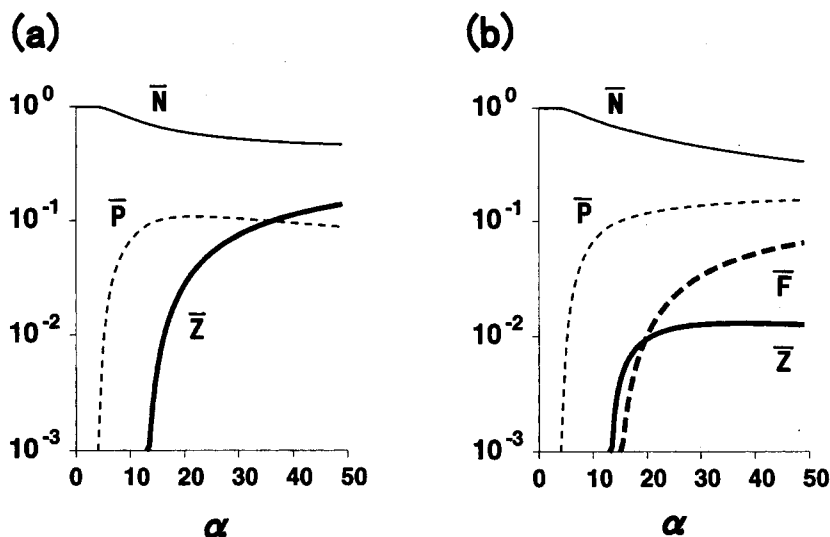


Fig. 3. The steady stock levels of  $\bar{N}$ ,  $\bar{P}$ ,  $\bar{Z}$ , and  $\bar{F}$  as the function of flow-parameter  $\alpha$  from 0 to 50 for  $N_0 = 1$  in (a) the  $N$ - $P$ - $Z$  model and (b) the  $N$ - $P$ - $Z$ - $F$  model.

ues have a similar order of lost time at the energy-supplied side, i.e.  $(\alpha_p \bar{N})^{-1} \sim \beta_p^{-1}$ ,  $(\alpha_z \bar{P})^{-1} \sim \beta_z^{-1}$ , and  $(\alpha_f \bar{P})^{-1} \sim \beta_f^{-1}$ . Therefore, an equilibrium mass-balance between energy loss and flow is achieved due to the dependence on magnitudes of each equilibrium stock level.

Although the reliable annual mean stock levels in the actual marine ecosystem are not yet known, Taniguchi (1999) estimated average stocks of nitrate, phytoplankton, micro-zooplankton, and meso-zooplankton on the surface layer of different water masses in the subarctic Pacific in summer. In the Oyashio Region, the biomass ratio in weight of carbon such as nitrate, phytoplankton, micro-zooplankton and meso-zooplankton, which are given as a relative value to phytoplankton biomass, is as follows: ( $N : P : \text{micro-Z} : \text{meso-Z}$ ) = (6.4 : 1.0 : 0.1 : 0.7). Here, in consideration of the continuous uptake from a lower to a higher trophic level after the spring bloom, the annual mean ratio probably becomes larger in  $N$  and smaller in  $Z$  (= micro- $Z$  + meso- $Z$ ) than the corresponding estimated ratio in summer. That is, the inferred annual mean ratio will have the order of ( $\bar{N} : \bar{P} : \bar{Z}$ ) =  $10 \sim 10^2 : 1 : 1 \sim 10^{-1}$ . It should be noted that the range of  $\alpha > 20$  does not reflect a perfect correspondence with an actual marine ecosystem. However, the calculated equilibrium ratio in our model, i.e. ( $\bar{N} : \bar{P} : \bar{Z}$ ) = (5 : 1 :  $10^{-1}$ ), does not differ largely from this inferred annual mean ratio. We infer that a reliable marine ecosystem in the western Pacific can be represented to some degree by using a common flow-parameter of  $\alpha > 20$  in our model.

In the actual marine state, the magnitude of nutrient ( $N_0$ ) supply or predation pressure on  $Z$  by  $F$  is not the same each year, but varies with variations in the interan-

nual and decadal time scales. Next, we will consider two problems created by periodical changes in the  $N_0$ -supply and the flow-parameter  $\alpha_f$  from  $Z$  to  $F$ . These two parameter changes correspond to bottom-up and top-down forcings, respectively.

#### Long-term response of stocks forced by bottom-up control

Using our model forced by the periodical  $N_0$ -supply, the long-term response was examined. We assumed that

$$N_0(n) = 1.0 + N_a \sin(2\pi n/T_N) \quad (n=1, 2, 3 \text{ year}), \quad (6)$$

where  $N_a$  is the amplitude of the time-variance term and  $T_N$  is the forcing period from 2 to 50 years. When we chose a large amplitude of  $N_a > 0.2$ , the response exhibited somewhat irregular, but not chaotic behavior, e.g. a few secondary maxima between the forced primary maxima for  $Z$  and  $F$  stocks. In order to investigate the phase relationship between the stocks, we used  $N_a = 0.2$ , in which the stock response has the same periodicity as the forcing period. The calculations for such periodical forcing consisted of letting this system run for 100 years, and examining the final 50 years to take annual mean values at each stock.

Figure 4 shows the maximum/minimum ratio of each annual mean stock variation and the phase lag of the maxima of each stock from the maximum  $N_0$ -supply in both models of (a)  $N$ - $P$ - $Z$  and (b)  $N$ - $P$ - $Z$ - $F$ . The flow-parameter  $\alpha = 30$  was fixed. In the  $N$ - $P$ - $Z$  model (Fig. 4(a)), the maximum/minimum ratio of all stocks remained almost constant, regardless of any periodical variations. Over a long period of more than 10 years,

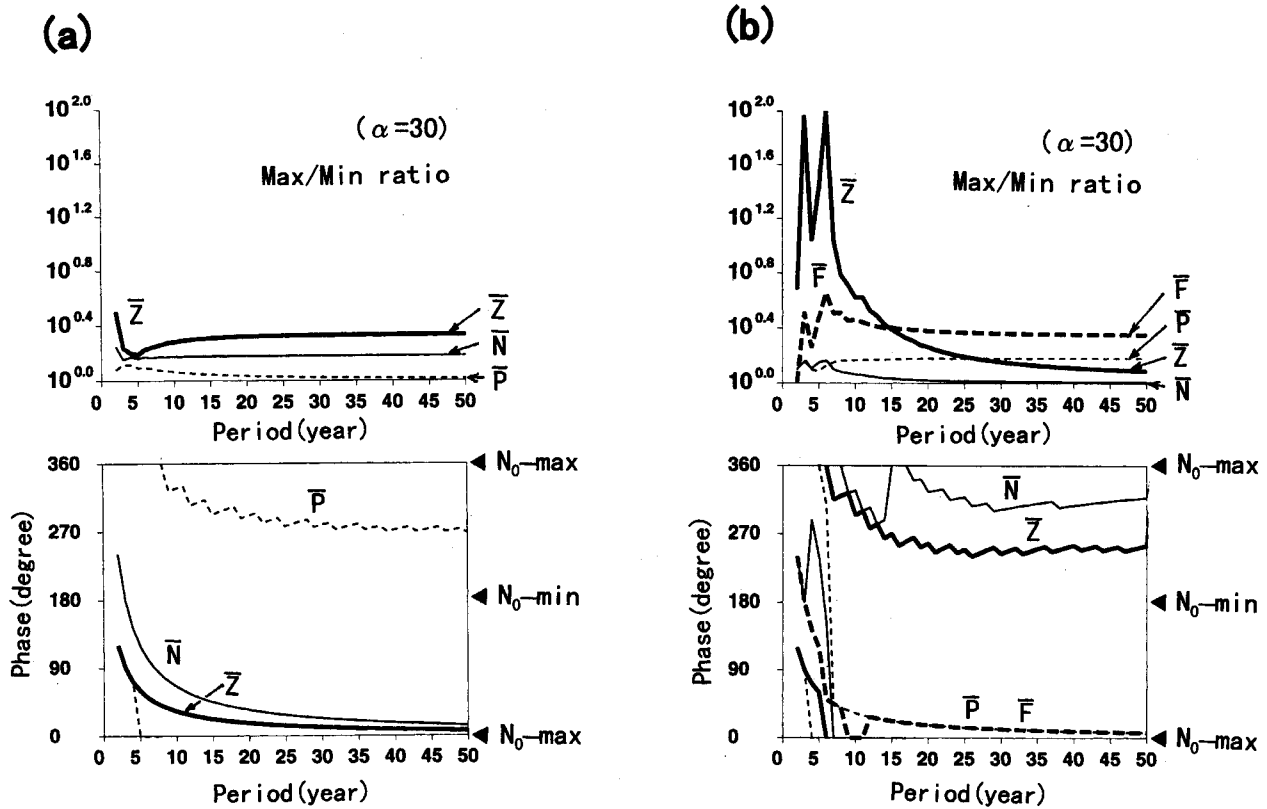


Fig. 4. Case for  $\alpha=30$  and temporal change of  $N_0$  in the periodical ranges from 2 to 50 years in (a) the  $N$ - $P$ - $Z$  model and (b) the  $N$ - $P$ - $Z$ - $F$  model. The upper panels show the maximum/minimum ratio of annual mean stocks and the lower panels show the phase lag of the maxima of each stock from the maximum of  $N_0$ -supply.

the  $\bar{N}$ - and  $\bar{Z}$ -variations were shown to have almost the same phase in the  $N_0$ -variation, whereas the maximum of  $\bar{P}$  led to about  $90^\circ$  ( $\sim 270^\circ$ ) from the maxima of  $\bar{N}$  and  $\bar{Z}$  with an increase in the forcing period. In the  $N$ - $P$ - $Z$ - $F$  model (Fig. 4(b)), the maximum/minimum ratio of  $\bar{P}$  and  $\bar{F}$  was almost constant throughout all periodical variations, and that of  $\bar{N}$  and  $\bar{Z}$  decreased to one with an increase in the forcing period, i.e., the stocks of  $\bar{N}$  and  $\bar{Z}$  become constant values as discussed in the steady-state solution. Over a long period of more than 10 years,  $\bar{P}$ - and  $\bar{F}$ -variations were shown to have almost the same phase in the  $N_0$ -variation, whereas the maximum of  $\bar{Z}$  always led to about  $90^\circ$  ( $\sim 270^\circ$ ) from the maximum of  $N_0$ . At a forcing period of less than 10-years, the  $\bar{Z}$ -variation was most dominant near the resonance periods ( $\sim 5$  years) of the prey-predator oscillation, as seen in Fig. 2. However, discussion of this short-term variation may not be meaningful, because our model cannot represent the lag-oscillation with a similar time scale, which is generated by both the occurrence of dominant year-class and fish age-structures.

An example of each stock variation with a forcing period of 50 years is shown in Fig. 5. In the  $N$ - $P$ - $Z$  model (Fig. 5(a)), the amplitude of the annual mean

value  $P$  was extremely small, but the peak value of the maximum envelope for a seasonal variation of  $P$  occurred at the same time as the maximum  $N_0$ -supply. On the other hand,  $\bar{Z}$  increased when the  $N_0$ -supply was largest. It is possible that the product of  $\bar{P}$  during the  $N_0$  increase was effectively transferred to  $\bar{Z}$ . In the  $N$ - $P$ - $Z$ - $F$  model (Fig. 5(b)),  $\bar{P}$  and  $\bar{F}$  increased and  $\bar{Z}$  decreased when the  $N_0$ -supply was the largest. Here,  $\bar{Z}$ -variation indicated the fluctuation as a saw-undulation and it was stabilized at a relatively constant level, even under the increasing predation pressure of  $\bar{F}$ . It is worth noting that the time when the annual mean  $Z$ -variation ( $\bar{Z}$ ) was at its maximum differed largely from the time with a maximum envelope of seasonal  $Z$ -variation. The peak value of the maximum envelope for seasonal variation of  $Z$  occurred at almost the same time as the maximum  $N_0$ -supply.

Figure 6 is identical to Fig. 4, except for changes in the flow-parameter  $\alpha$  from 0 to 50 at a fixed forcing period of 50 years. In both models, the maximum/minimum ratio of  $\bar{P}$ ,  $\bar{Z}$ , and  $\bar{F}$  became extremely large at  $\alpha \sim 5, 13$ , and 15, when the flow-parameter was close to the range of appearance for each stock, as seen in Fig. 3. At the range of  $\alpha > 20$ , the maximum/minimum

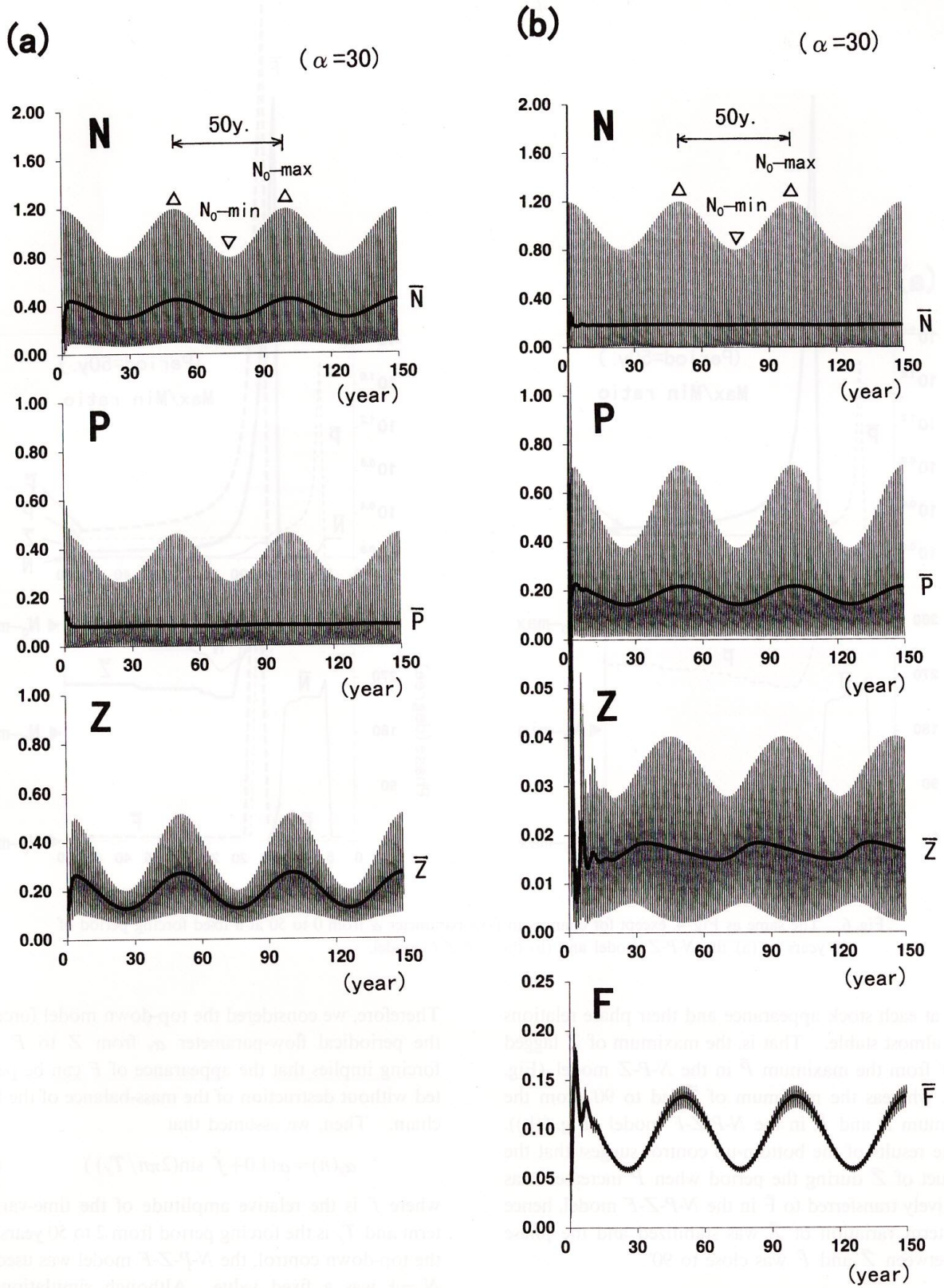


Fig. 5. Simulated time series of  $N$ ,  $P$ ,  $Z$ , and  $F$  for  $\alpha=30$  under the temporal change of  $N_0$  with a period of 50 years in (a) the  $N$ - $P$ - $Z$  model and (b) the  $N$ - $P$ - $Z$ - $F$  model. The thick lines indicate annual mean values.

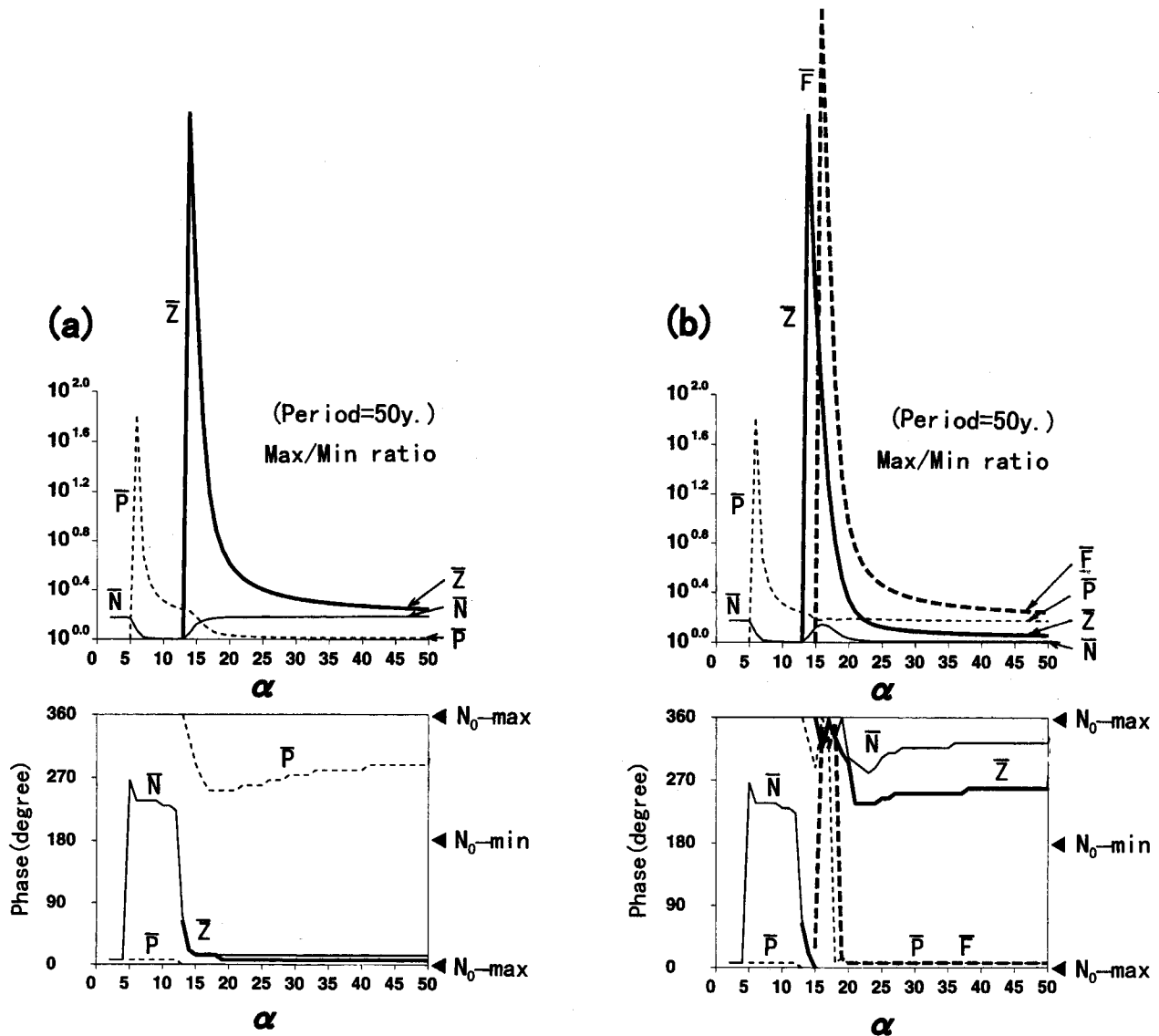


Fig. 6. The same as Fig. 4, except for changes in flow-parameter  $\alpha$  from 0 to 50 at a fixed forcing period of 50 years in (a) the *N-P-Z* model and (b) the *N-P-Z-F* model.

ratio at each stock appearance and their phase relations were almost stable. That is, the maximum of  $\bar{Z}$  lagged to  $90^\circ$  from the maximum  $\bar{P}$  in the *N-P-Z* model (Fig. 6(a)), whereas the maximum of  $\bar{Z}$  led to  $90^\circ$  from the maximum  $\bar{P}$  and  $\bar{F}$  in the *N-P-Z-F* model (Fig. 6(b)).

The results of the bottom-up control suggest that the product of  $\bar{Z}$  during the period when  $\bar{P}$  increased was effectively transferred to  $\bar{F}$  in the *N-P-Z-F* model, hence long-term variation of  $\bar{Z}$  was stabilized and the phase lag between  $\bar{Z}$  and  $\bar{F}$  was close to  $90^\circ$ .

**Long-term response of stocks forced by top-down control**

A top-down system will work due to the extreme occurrence of *F*, but excessive setting of  $\bar{F}$  values easily breaks the mass-balance of the lower trophic levels.

Therefore, we considered the top-down model forced by the periodical flow-parameter  $\alpha_f$  from *Z* to *F*. This forcing implies that the appearance of *F* can be permitted without destruction of the mass-balance of the food-chain. Then, we assumed that

$$\alpha_f(n) = \alpha(1.0 + f \sin(2\pi n/T_f)) \quad (7)$$

where  $f$  is the relative amplitude of the time-variance term and  $T_f$  is the forcing period from 2 to 50 years. In the top-down control, the *N-P-Z-F* model was used and  $N_0=1$  was a fixed value. Although simulations for various relative amplitudes of  $f (< 1)$  were carried out (not shown), the system qualitatively exhibited similar phase relations between the stocks, hence  $f=0.5$  in the following calculations.

Figure 7(a) shows the maximum/minimum ratio of

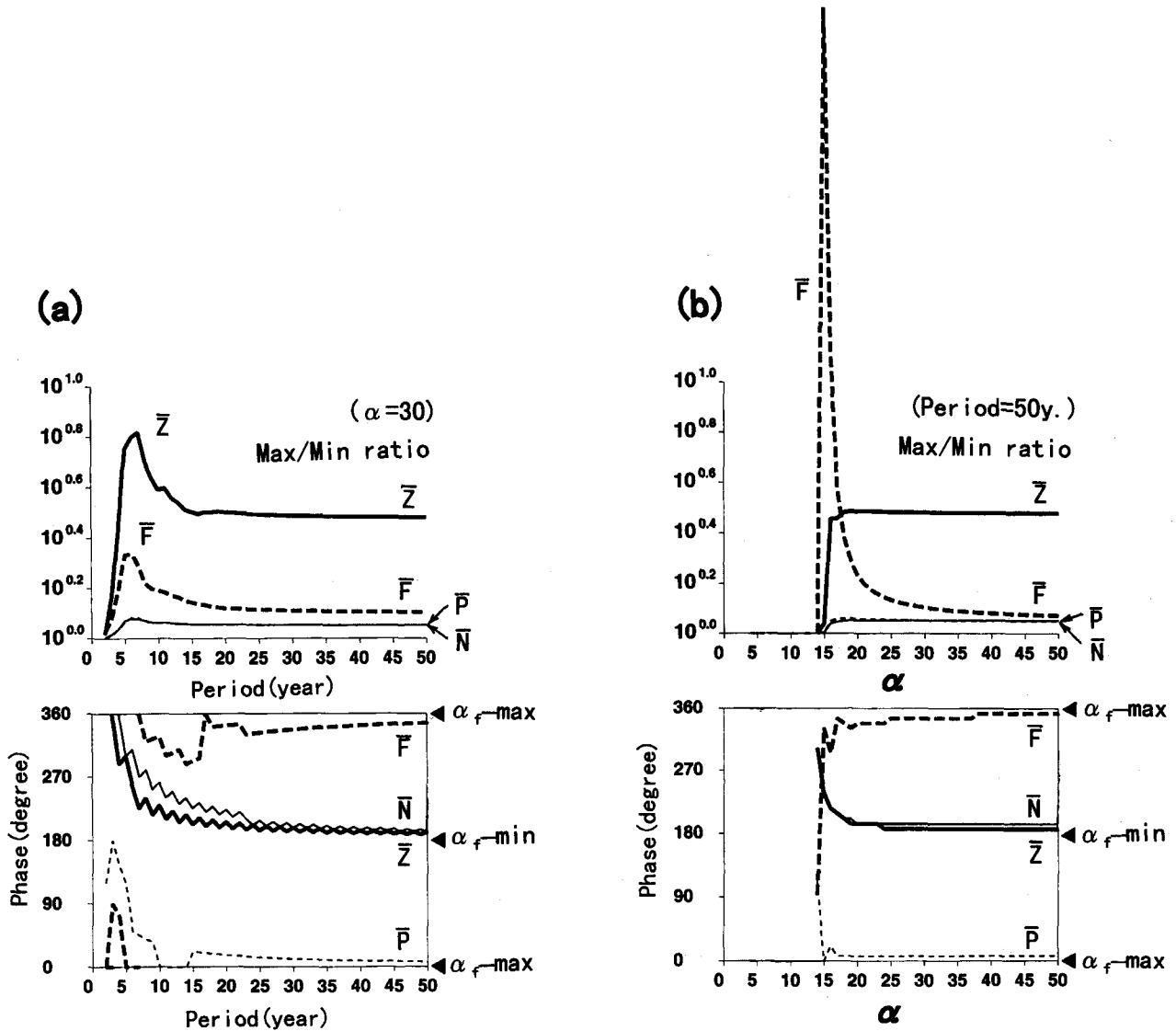


Fig. 7. (a) Case for  $\alpha=30$  and temporal change of flow-parameter  $\alpha_f$  from Z to F in the periodical range from 2 to 50 years in the N-P-Z-F model. The upper panel shows the maximum/minimum ratio of annual mean stocks and the lower panel shows the phase lag of the maxima of each stock from the maximum flow of  $\alpha_f$ ; (b) is identical to (a), except for changes in flow-parameter  $\alpha_f$  from 0 to 50 at a fixed forcing period of 50 years.

each annual mean stock variation and the phase lag of the maxima of each stock from the maximum flow of  $\alpha_f$  for  $\alpha=30$ . Over a long period of more than 10 years, the maximum/minimum ratio of all stocks remained almost constant, and  $\bar{P}$ - and  $\bar{F}$ -variations had almost the same phase in the  $\alpha_f$ -variation, whereas the maxima of  $\bar{Z}$  and  $\bar{N}$  led to about  $180^\circ$  from the maximum of  $\alpha_f$ . An example of each stock variation with a forcing period of 50 years for  $\alpha=30$  is shown in Fig. 8. It is found that the amplitude of  $\bar{Z}$  was extremely large and that the maximum for  $\bar{Z}$  occurred at the minimum of  $\alpha_f$ . Unlike in the case of the bottom-up control, the time when the annual mean Z-variation ( $\bar{Z}$ ) had a maximum value coincided to the time with a maximum

envelope of seasonal Z-variation. Figure 7(b) is identical to Fig. 7(a), except for changes in flow-parameter  $\alpha_f$  from 0 to 50 at a fixed forcing period of 50 years. The maximum/minimum ratio of  $\bar{Z}$  was the largest among all of the stocks in the range of  $\alpha > 20$ , the phase difference between  $\bar{Z}$  and  $\bar{F}$  was close to  $180^\circ$ .

The results of the top-down control suggested that long-term variations in  $\bar{Z}$  were amplified by both effects of continuous energy flow from  $\bar{P}$  and the variable predation pressure of  $\bar{F}$ , hence the phase relation between  $\bar{Z}$  and  $\bar{F}$  was out of phase.

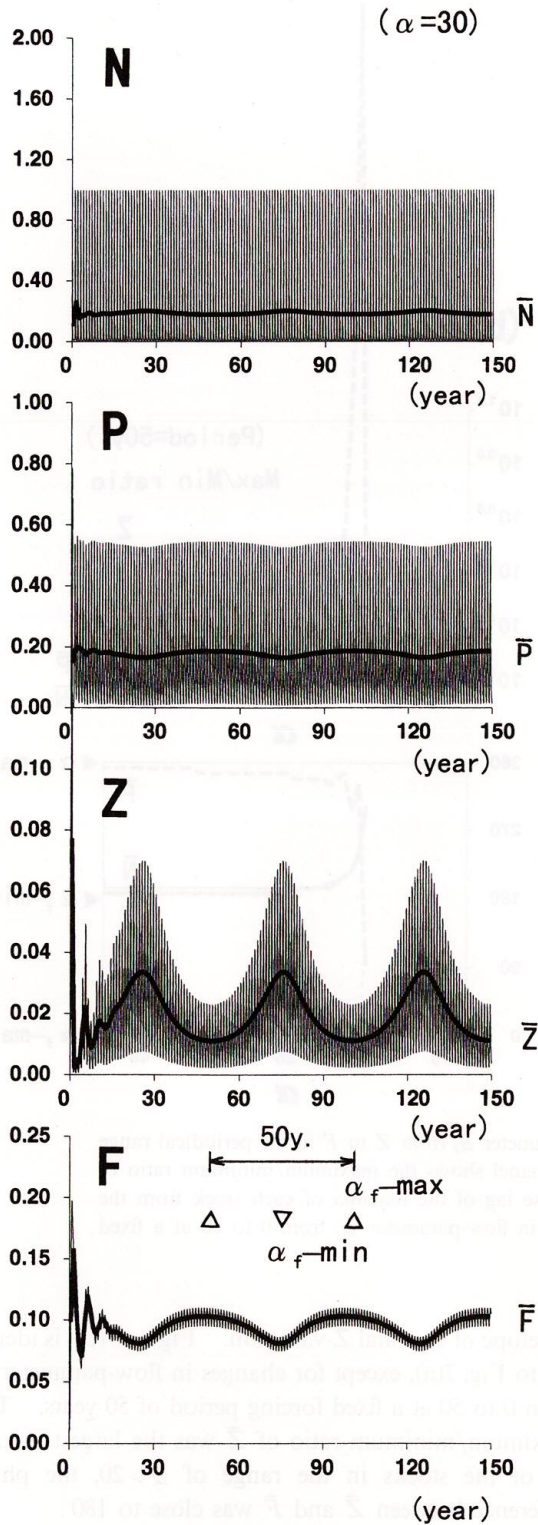


Fig. 8. Simulated time series of  $N$ ,  $P$ ,  $Z$ , and  $F$  for  $\alpha = 30$  under the temporal change of flow-parameter  $\alpha_f$  with a period of 50 years in the  $N$ - $P$ - $Z$ - $F$  model. The thick lines indicate annual mean values.

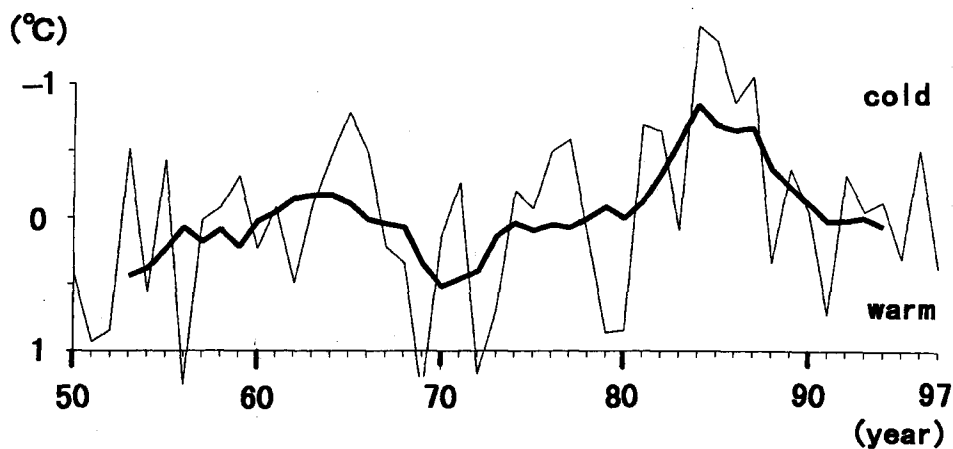
### Discussion and conclusion

In the present study, we assumed the possibility that the predation of  $F$  could positively affect  $Z$  productivity. The decadal relationships between the variations of  $Z$  and  $F$  were examined primarily by using a simple  $N$ - $P$ - $Z$ - $F$  model forced by bottom-up and top-down controls. In model results, their phase relations and the long-term amplitude of  $Z$ -variations had entirely different responses to both controls. In the case of the bottom-up control, the decadal variation of the annual mean  $\bar{Z}$  was stabilized and the maximum of  $\bar{Z}$  led to a  $90^\circ$  difference from that of  $\bar{F}$ , whereas in the case of the top-down control, the decadal variation of  $\bar{Z}$  was amplified and the phase relation between  $\bar{Z}$  and  $\bar{F}$  was out of phase.

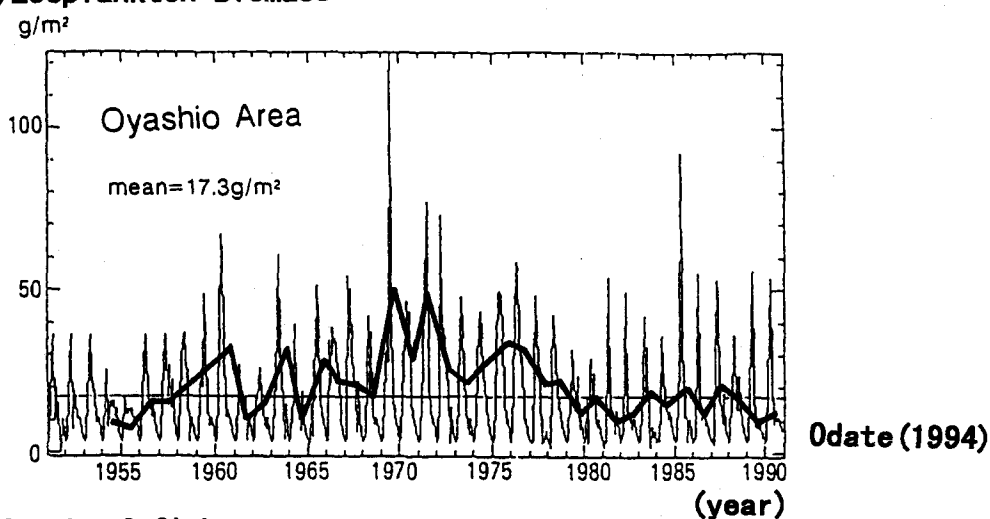
The model employed here is based on unknown parameters, but the present results can be roughly applied to a diagnosis of the present state of the marine ecosystem in the western Pacific. An increase in the total catch of all species in this area is produced primarily by an increase in the population of Pacific sardine (Kawasaki, 1993). Yasuda et al.(1999) studied the relation between decadal variations as regards numbers of Pacific sardine and ocean/climate from 1600 to 1990. They found that high sardine catches occurred eight times during this period. Therefore, we concluded that the decadal periodicity of the western Pacific marine ecosystem will be about 50 years. Thus, the results in Fig. 5(a) show a case that is not influenced by fish; in Fig. 5(b) and Fig. 8 the bottom-up and top-down control cases are shown, respectively.

Figure 9(a) shows year-to-year variations in sea surface temperature (SST) anomalies in the Oyashio Region ( $36^\circ$ - $42^\circ$ N,  $142^\circ$ - $150^\circ$ E) during the winters from January to March 1950-1997 (data sets were provided by the Japan Meteorological Agency). A thick line indicates the winter SST of a 5-year running mean. In this region, a clear decrease in winter SST occurred after the climatic regime shift in the 1970s. This change occurred when the southward intrusion of the primary branch of nutrient-rich Oyashio water was intensified (Sekine, 1999; Hanawa, 1995). Unfortunately, there is no reliable data concerning interannual variations of chlorophyll, which represent the phytoplankton biomass. Figures 9(b) and (c) show seasonal and interannual variations of zooplankton biomass in the Oyashio Region during 1951-1991 (adapted from Odate, 1994; Sugimoto and Tadokoro, 1997) and year-to-year variations in the annual catch of five dominant pelagic fish species in the neighboring waters of Japan during 1960-1997 (FAO statistical yearbooks), respectively. From the 1970s to the 1980s, the winter SST

(a) Winter-SST anomaly (36°-42°N, 142°-150°E)



(b) Zooplankton Biomass



(c) Catch of fishes

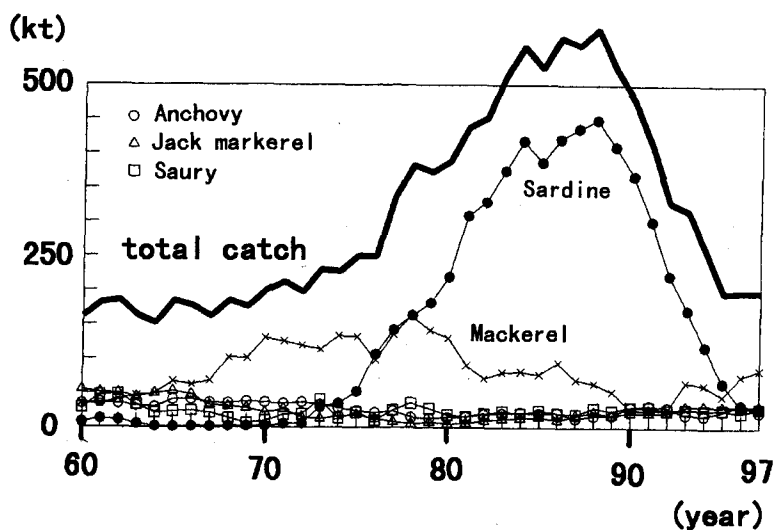


Fig. 9. (a) Year-to-year variations of SST anomalies during winters from 1950 to 1997 (thin line) and the 5-year running mean (thick line) in the following regions of sea : 36°-42°N, 142°-150°E (Data were taken from JMA). (b) Long-term variations of monthly (thin line) and yearly (thick line) mean values of zooplankton biomass from 1951 to 1990 in the Oyashio Region (adapted from Odate,1994 ; Sugimoto and Tadokoro 1997). (c) Year-to-year variations in the annual catch of five species and their total catch (thick line) in the neighboring waters of Japan from 1960 to 1997 (FAO statistical yearbooks).

decreased (Fig. 9(a)), i.e. rich nutrients might have been supplied to the Oyashio Region, and the total catch increased (Fig. 9(b)). Annual mean zooplankton biomass peaked in the 1970s, and then decreased in the 1980s. However, the maximum values of seasonal zooplankton biomass in the 1980s were never small (Fig. 9(c)). We infer that the spring bloom might have dominated during the cold period in the 1980s. If cold oceanic conditions in spring/winter imply higher biological productivity in spring, due to the large nutrient supply, then the direct correlation between the lowest (nutrient) and highest (fish) stock levels can be qualitatively understood from the bottom-up model results, as shown in Fig. 5(b). That is, increases in phytoplankton ( $\bar{P}$ ) production due to increases in nutrient ( $N_0$ ) supply in the 1980s were efficiently transferred from grazing zooplankton ( $\bar{Z}$ ) to fish ( $\bar{F}$ ), following which a higher capacity of fish ( $\bar{F}$ ) occurs in almost the same low SST phase (i.e. high  $N_0$ ). Of course, there is the possibility that the zooplankton stocks was large enough to support the fish stock, such that the observed phase relationship between zooplankton and fish catches would be apparent. In this case, high zooplankton must correspond to high nutrient supply (i.e. low SST) from the *N-P-Z* model results (Fig. 5(a)). However, such a relationship cannot be seen in Fig. 9. Although the specific mechanisms involved in the western Pacific marine ecosystem remain unclear, we suggest that the observed relationship between zooplankton and fish stocks is similar to that effected by the bottom-up response.

The present results are only a first approximation because the model employed here is very simple and also because the magnitude of the parameters is not yet known. Hence, our results allow for only a qualitative view of the problem. It is nonetheless possible that such a view may be all that is required at the present stage of study, because an accurate estimation of each stock level remains very difficult or even impossible. The most difficult component to average annually is the amount of phytoplankton, because the seasonal maximum value at spring bloom occurs during a short period of a few months. Therefore, it is difficult that the spring bloom period can be captured by snapshot ship-observations. In the past, it has been incorrect to consider the chlorophyll data that was not collected at the time of the spring bloom as representative of the year. For this reason, approaches to the decadal marine ecosystem would inspire little confidence if based on either the estimations of observed stock levels, or on excessively complex ecosystem models. We believe that it may be helpful to search for more reasonable parameters, such as net conversion efficiency between the stocks and their loss rate, and to examine the regional response

with the aid of a simple model based on these parameters.

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