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Cyclic Advantage Hypothesis for the Species Replacement of Pelagic Fishes.

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プランクトン食浮魚類の個体数変動：3すくみ説

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Abstract:

We consider a mathematical model which incorporates two factors affecting long-term fluctuation of planktotrophic pelagic fish: environmental fluctuation and interspecific competition. Long-term catch data of pelagic fishes in Japan suggest that the chub mackerel (labeled A) was replaced by the sardine (B), B was replaced by the anchovy, Pacific saury and horse mackerel, and these species (labeled group C) were replaced by A. If species A defeats B, B defeats C and C defeats A in interspecific competitive ability, the mathematical model predicts that the abundance of these three groups fluctuate forever and dominate in the cyclic order. We call this cyclic advantage hypothesis for species replacement. In this model, environmental fluctuation greatly affects when the next replacemtnt occurs, whereas cyclic relashionship in competitive ability determines what is the next dominant.

It is known that the catch abundance fluctuation of planktotrophic pelagic fishes is enormously large (fig. 1). This fluctuation qualitatively reflects the stock abundance fluctuation from year to year. The sardine (*Sardinops melanostictus*) was abundant in 1930s and in 1980s. The anchovy(*Engraulis japonica*), Pacific saury (*Calorabis saira*) and horse mackerels (*Trachurus japonica* and *Decapterus muroadsi*) were abundant in ca. 1960 and they are becoming dominant in 1990. The chub mackerel (*Scomber japonicus*) was dominant in 1970s and is at a very low stock level.

The purpose of this paper is to elucidate what is a major factor on such fluctuations. Some considered that the fluctuation of environmental condition is important. When the sardine increased rapidly in early 1930s and ca. 1980, the water temperature at the spawning area was significantly high (Sugimoto pers.comm.). Other people considered that interspecific relationships between these pelagic fishes are important. When the sardine stock declined in 1940s and now, the anchovy, Pacific saury and horse mackerel increased. When these 3 species decreased, in ca. 1970, the chub mackerel increased. When the chub mackerel decreased in 1980, the sardine became the dominant. It is called the species replacement of the pelagic fishes.

Some other people considered that both environmental fluctuation and species interaction are important for the stock fluctuation. I agree to this argument. I will show that the species interaction is a major factor on which species is the next dominant, and that the short-term fluctuation of environment determines when the next replacement occurs. Our hypothesis is called "the cyclic advantage hypothesis" for the species replacement of the planktotrophic pelagic fishes.

We have three questions: (1) Can we predict which fish will be the next dominant? Our answer from the cyclic advantage hypothesis is "Yes." After the sardine began to decline, the anchovy and other two species become to be the dominant. After the anchovy, the chub mackerel is the dominant. Finally, the sardine comes back to be the dominant after the chub mackerel.

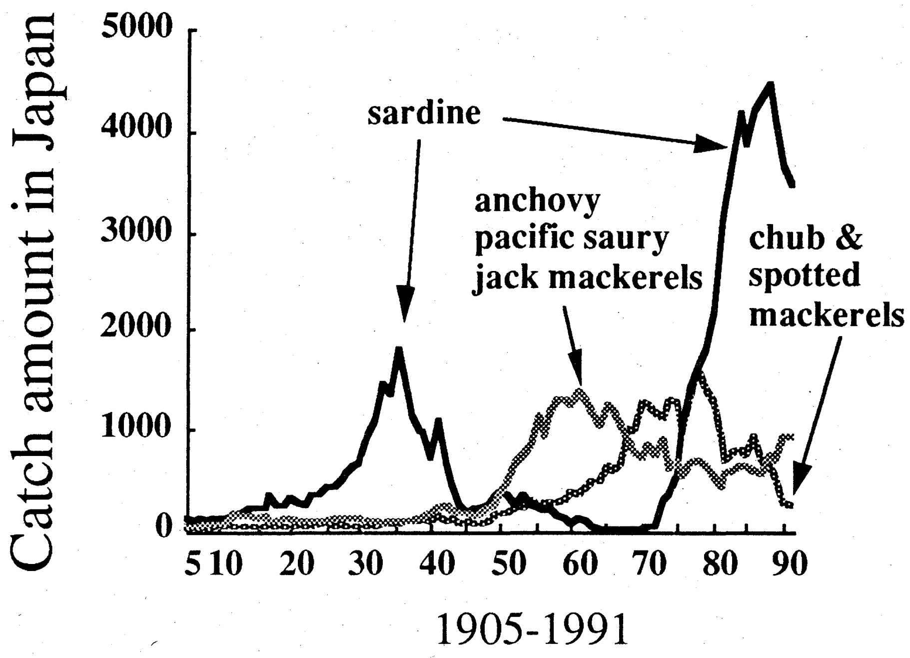


Figure 1. The long-term fluctuation of catch amount of pelagic fishes in Japan (Kawai & Takahashi 1983; Chikuni 1985, see also Matsuda et al. 1992b)

The second question is: (2) can we predict when the next species replacement occurs? Our answer is said to be "No" if the environmental fluctuation is not predictable. This decidedly depends on the short-term fluctuation of environmental conditions. Our final question is: (3) can we make an optimal harvesting policy for each fish independent of other fishes? Our answer is "No." The optimal harvesting policy for each fish depends on which fish is currently dominant. When the sardine was dominant about several years ago, the future of chub mackerel was very pessimistic. However, when the anchovy was dominant as recently, the future of chub mackerel is a little bit optimistic.

There are at least four characteristic features of the long-term stock fluctuation of the sardine: (1) This has a long "period" of fluctuation. About 50 years passed from the last peak (ca. 1930) in the sardine stock to the last peak (ca. 1980), in spite of the fact that the generation time of the sardine is two or three years. (2) The fluctuation has a long history, at least for about

300 years. This suggests the stock fluctuation of the sardine is not induced by overexploitation. (3) There is a huge variation of the peak to the bottom in the stock abundance. According to the catch amount data, the ratio of the peak (1988: 4,490 kt) to the bottom (1967: 10 kt) is about 450 fold. This, however, seems to be underestimation. According to the estimated annual egg production, the peak (1986: 8985 billion eggs/year) is about 9,000 times larger than the bottom (1970: 1 billion eggs/year) as shown in fig. 2. The forth characteristic feature is that (4) both high-density phase and low-density phase are long. These continue for several generation time.

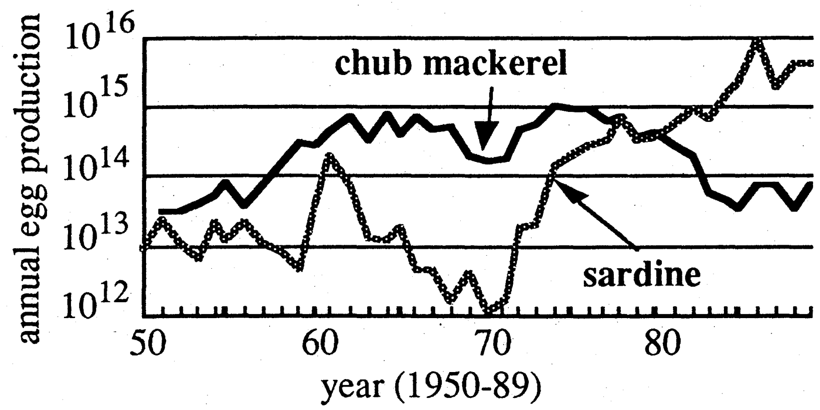


Figure 2. The long-term fluctuations of estimated annual egg production of the sardine and chub mackerel in the Pacific ocean off Japan (compiled by the Fisheries Agency of Japan, see also Matsuda et al. 1992a)

From the viewpoint of population ecology, there are several dynamic models which can exhibit a permanent oscillation of stock abundance. The simplest model is the single population dynamic model. It is known as Ricker's equation in fisheries science:

$$N_{t+1} = N_t \exp[r(1-N_t/K)], \qquad (1)$$

where N_t and N_{t+1} are respectively the stock abundances at the present and the next generations, r and K respectively denotes the intrinsic rate of increase and the carrying capacity. If r is sufficiently large, this system exhibit a chaotic behavior with a permanent oscillation. The low density phase continues for several generations, increases rapidly and collapsed drastically (fig. 3a). Figure 3b illustrates the reproduction curve of this system with the same parameter value as in fig. 3a. Note that, in this system, a high density phase can not continue for more than one generation. Although we know a typical example of this dynamics in nature: Lemming dynamics (Pitelka 1972), this does not explain the sardine's fluctuation.

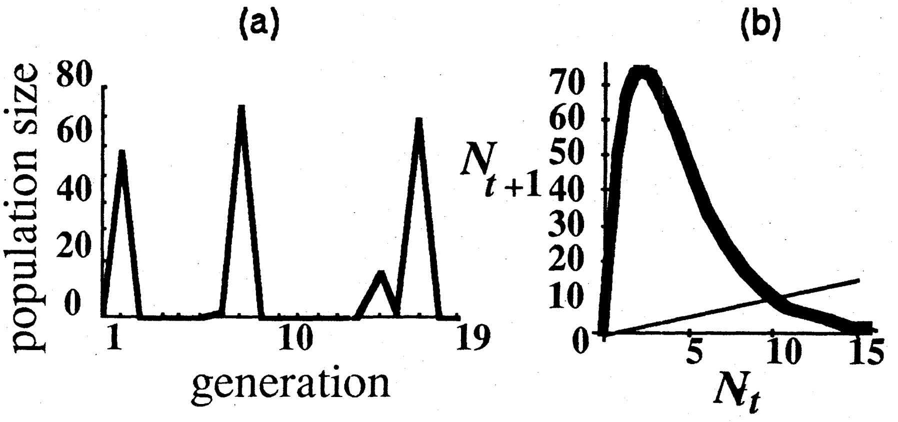


Figure 3. (a)A simulated fluctuation and (b) the re-production curve of the Ricker's eqn (1). $r = 4.5$, $K = 10$.

Although somebody consider the two species model for the sardine's dynamics. The Lotka-Volterra competition model is written as:

$$dN_1/dt = (r_1 - a_{11}N_1 - a_{12}N_2)N_1 \quad (2a)$$
$$dN_2/dt = (r_2 - a_{21}N_1 - a_{22}N_2)N_2 \quad (2b)$$

where N_i denotes the stock abundance of species i, r_i is the intrinsic rate of increase of species i, a_{ij} is the competition coefficient of species j from i. This system, however, does not produce a permanent oscillation: the two species coexist at an equilibrium state (fig. 4a) or either species wins (figs. 4b and 4c).

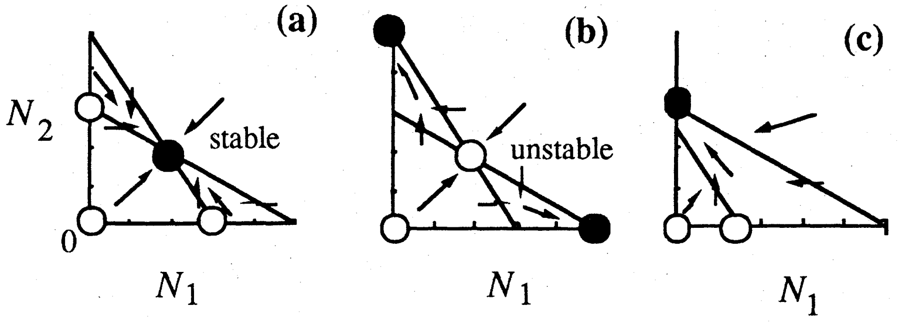


Figure 4. Phase diagrams of competition model (2): (a) two species coexist at an equilibrium, (b) either species goes to extinction, and (c) species 2 always wins. Closed and open circles are respectively stable and unstable equilibria.

Lotka-Volterra prey-predator dynamics is written by

$$dN/dt = (r - aN - bP)N \tag{3a}$$

$$dP/dt = (-\delta + bN)P, \tag{3b}$$

where N and P respectively denote the prey and predator abundances, r, a, b and δ are positive constants. It is well known that prey-predator dynamics produces permanent oscillations of both, not either, prey and predator populations. However, we have no data of long-term fluctuation of the prey or enemy of the sardine.Thus this does not explain the sardine's fluctuation either.

A system with two prey and one predator is written by

$$dN_1/dt = (r_1 - a_{11}N_1 - a_{12}N_2 - b_1P)N_1 \tag{4a}$$

$$dN_2/dt = (r_1 - a_{11}N_1 - a_{12}N_2 - b_2P)N_2 \tag{4b}$$

$$dP/dt = (-\delta + b_1N_1 + b_2N_2)P \tag{4c}$$

where N_1, N_2 and P respectively denote the prey abundance of species 1, 2 and the predator abundance. It is known that this system can produce permanent oscillations of two prey, but the predator density does not fluctuate very much (Fujii 1977). The parameter region which exhibits such a permanent fluctuation is very small.

We propose the cyclic advantage model which consists of 3 competing species written as:

$$N_1' = c_1 + N_1\exp[r_1 - a_{11}N_1 - a_{12}N_2 - a_{13}N_3] \tag{5a}$$

$$N_2' = c_2 + N_1\exp[r_2 - a_{21}N_1 - a_{22}N_2 - a_{23}N_3] \tag{5b}$$

$$N_3' = c_3 + N_1\exp[r_3 - a_{31}N_1 - a_{32}N_2 - a_{33}N_3] \tag{5c}$$

where N_i and N_i' respectively denote the stock abundance of species i at the present and the next generations, c_i is a positive constant representing a constant immigration from outside, r_l is the intrinsic rate of increase of species i and a_{ij} is the competition coefficients of species j from i.. If species 1 defeats 2, 2 defeats 3 and 3 defeats 1, these 3 species can fluctuate permanently (Gilpin 1975). In mathematical terms, these cyclic advantage conditions in competitive ability when c_i is sufficiently small are written by:the following 6 inequalities:

$$a_{12}r_2 > a_{11}r_1 > a_{13}r_3 \; (N_2\Uparrow, N_3\Downarrow \text{ at } N_1 = r_1/a_{11}) \tag{6a}$$

$$a_{23}r_3 > a_{22}r_2 > a_{21}r_1 \; (N_3\Uparrow, N_1\Downarrow \text{ at } N_2 = r_2/a_{22}) \tag{6b}$$

$$a_{31}r_1 > a_{33}r_3 > a_{32}r_2 \; (N_1\Uparrow, N_2\Downarrow \text{ at } N_3 = r_3/a_{33}) \tag{6c}$$

The first two inequalities shown in the first line implies that species 2 increases and 3 does not increases when species 1 is dominant and nearly reaches its carrying capacity, r_1/a_{11}.The second line implies that species 1 does not increase but 3 increases when 2 is dominant. The last line implies that species 2 does not increase but 1 increases when 3 is dominant.

We consider such a cyclic advantage relationship actually exists in pelagic fishes. The three species are the sardine, anchovy and chub mackerel. In fig. 1, we summarized the anchovy, Pacific saury and horse mackerel into a single group, because the correlation coefficient in annual catch fluctuation of any pair of these three species are high (Table 1).

Table 1. Correlation matrix of annual catch fluctuation of pelagic fishes in Japan (1905-1990, see Matsuda et al. 1992b).

	(1)	(2)	(3)	(4)	(5)	(6)
1)sardine	**1**	**.32**	**.17**	**−.10**	**.05**	**−.33**
2)chub mackerels		**1**	**.49**	**.54**	**.50**	**−.56**
3)Pacific saury			**1**	**.82**	**.78**	**−.60**
4)anchovy				**1**	**.88**	**−.50**
5)horse mackerel					**1**	**−.59**
6)herring						**1**

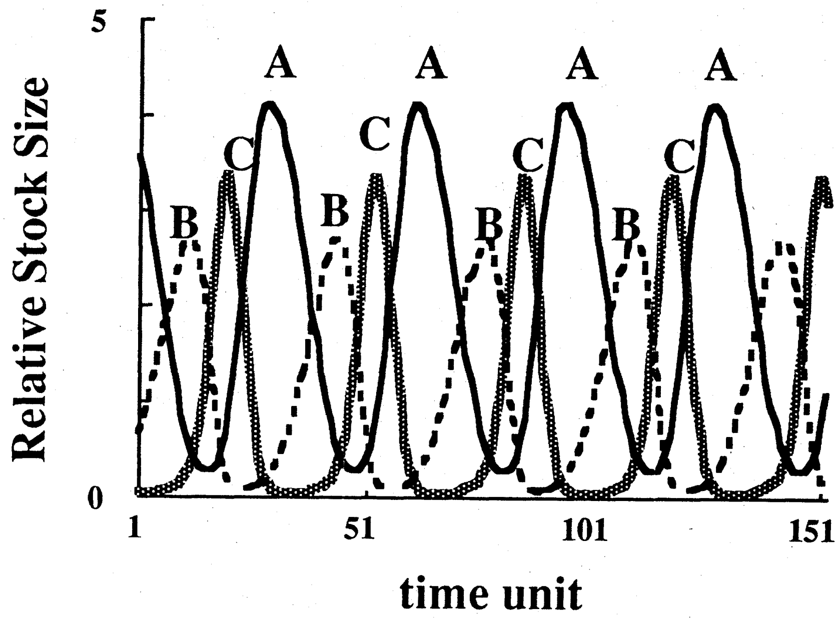
In the previous models, we implicitly ignored the environmental fluctuation. However, there is a large fluctuation of environmental conditions in nature. The environmental fluctuation affects on the survival rate of pelagic fishes at an early life stage. For simplicity, we consider that the rate of increase fluctuates due to environmental fluctuation from time to time, whereas the competitive coefficients are assumed to be constant. Random fluctuation of environment is expressed by

$$r_i = r_i^* + f_i Z_i(t), \tag{7}$$

where r_i^* is the average value of r_i, f_i is the amplitude of variation of r_i, and $Z_i(t)$ is the time-dependent random variable with no auto-correlation, which is called white noise. In computer simulations, we choose $Z_i(t)$ as the uniform random variable between −0.5 and 0.5.

Figure 5 illustrates resultant stock fluctuations from simulations with the same parameter values of r_i^* and a_{ij}. Under a constant environment which corresponds a case where f_i=0 and $r_i = r_i^*$, the dynamical behavior would be recognized as a limit cycle. The period of this cycle is about 51 time units. The species replacement occurs in cyclic order, ABCABC... Under a randomly fluctuating environment, the stock abundance unpredictably varied with time. Even a

(a) constant environment



(b) random environment

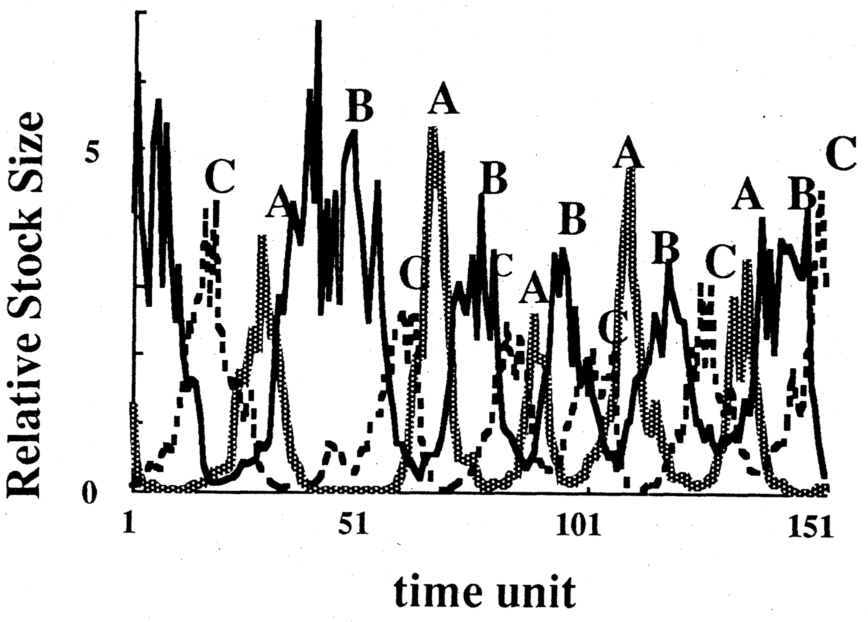


Figure 5. Simulations of the cyclic advantage model under (a) constant environment and (b) randomly fluctuating environment. Parameter values are: $(r_1, r_2, r_3) = (0.9, 0.8, 0.7)$, $(a_{11}, a_{12}, a_{13}, a_{21}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}) = (0.2, 0.4, 0.1, 0.1, 0.2, 0.4, 0.4, 0.1, 0.2)$, c_i=0.02, f_i=0 for (a) and f_i=1 for (b).

case when the survival rate at an early life stage (corresponding the value of r_i) fluctuates 10 times from year to year, the species replacement is infrequently and occurs in still cyclic order. The "period" of stock fluctuation is not constant; often falls in 60 to 90 time units. That is why we can not predict when the next replacement occurs but we can predict which is the next dominant as mentioned above.

We have three major conclusions: (1) The cyclic advantage hypothesis predicts which is the next dominant. The sardine increases after the chub mackerel is dominant. The anchovy increases after the sardine. The chub mackerel increases after the anchovy. This is testable. If the sardine increases just after the anchovy is dominant, this hypothesis falls into error. This is testable in the future in spite of the fact that long years must be required. (2) Cyclic advantage hypothesis does not predicts when the next replacement occurs, which depends on the short-term fluctuation of the environment. The environmental factor affects on the species replacement as a trigger.

Furthermore, (3) species replacement of pelagic fishes is inevitable. We should not expect a constant catch amount of each species every year. We should make a fish market which demands the currently dominant fish species. Canadian and American people can consume the Pacific saury when this is abundant. The mortality from exploitation is not significant when the fish is dominant, but is critical when it is rare. Fishermen should focus their catch effort on the currently dominant fishes.

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