

A Mechanism to Explain Fluctuations in Population Size of the Far Eastern Sardine (*Sardinops sagax melanostictus*)

XIN-YANG LI, TSUYOSHI KAWASAKI and HITOSHI HONDA

*Fisheries Biology Laboratory
Faculty of Agriculture
Tohoku University
Japan*

Abstract

Environmental factors were examined and did not seem to be determinants of fluctuations in population size of the Far Eastern sardine. Summarizing traits of the sardine's life history and evaluating their consequences suggested that the surplus energy obtained by an individual could be largely regulated by population size-dependent migratory distance. Examining trajectories of body length against stock size suggested two distinctive processes of body condition degeneration and recovery in population growing and declining periods. All these, together with published experimental results on the relation between egg quality and larval survival for some close species, led to a hypothesis that the egg-recruit survival rate depends on adult body condition which is determined by degeneration and recovery processes corresponding to population growing and declining phases. The sardine's population fluctuations are broadly explained by this hypothesis.

Introduction

Catches of the Far Eastern sardine, *Sardinops sagax melanostictus*, have undergone long-term and drastic fluctuations. According to Ito (1961), prosperous periods in the sardine fishery history were 1560-1590, 1700-1720, 1800-1830 and around the mid-1930s. The sardine catch reached a new peak of 4.6 million tons around Japan in 1988, whereas it was only 9,000 tons in 1965. The mean interval between these peaks is about 100 years. The mechanisms responsible for the fluctuations have been a dominant focus of fisheries researchers (Tauti 1942; Nakai 1960a, 1960b, 1962a, 1962b,

1962c; Watanabe 1975, 1981, 1983, 1988; Kondo 1980, 1988; Kawasaki 1980, 1983; Kawasaki and Kumagai 1984; Kawasaki and Omori 1986; Wada 1988a, 1988b). While plenty of facts have been collected and some hypotheses on the mechanisms proposed, many researchers still feel that there is great need to seek more persuasive explanations for the fluctuations.

Although the fishing intensity was too limited to be an important regulator of the stock in the past years (say 1550-1850), the sardine population, after reaching a peak, always decreased, gradually fell into a trough and increased again (Ito 1961). These facts suggest that the population is strongly regulated by natural causes.

Environmental factors and peculiarities of the sardine's life history are examined to see which are likely to play a major role in regulating the populations.

Materials and Methods

All the names of stations and areas cited in the following text are indicated in Fig. 1.

Environmental Factors

The following time series are compiled and shown in Fig. 2: air pressure and temperature, precipitation, frequency of low pressure, the distance of Kuroshio Current from the coast, and macroplankton abundance in the spawning and nursery grounds of the sardine.

Stomach Contents

Sampling of sardines along the coast from Choshi to northern Aomori (Fig. 1) was carried out from April 1988 to December 1989, and 138 samples were collected. All fish were measured for standard length (SL) and weight (BW) and wet weight of stomach contents (SCW). For comparison, the same types of data for 1951-52 were compiled from "Data from survey of Iwashi resource (sardine, anchovy and round herring) in the Pacific Area off Honshu" (Tokai Reg. Fish. Res. Lab., Japan [ed.], 1953, 1954).

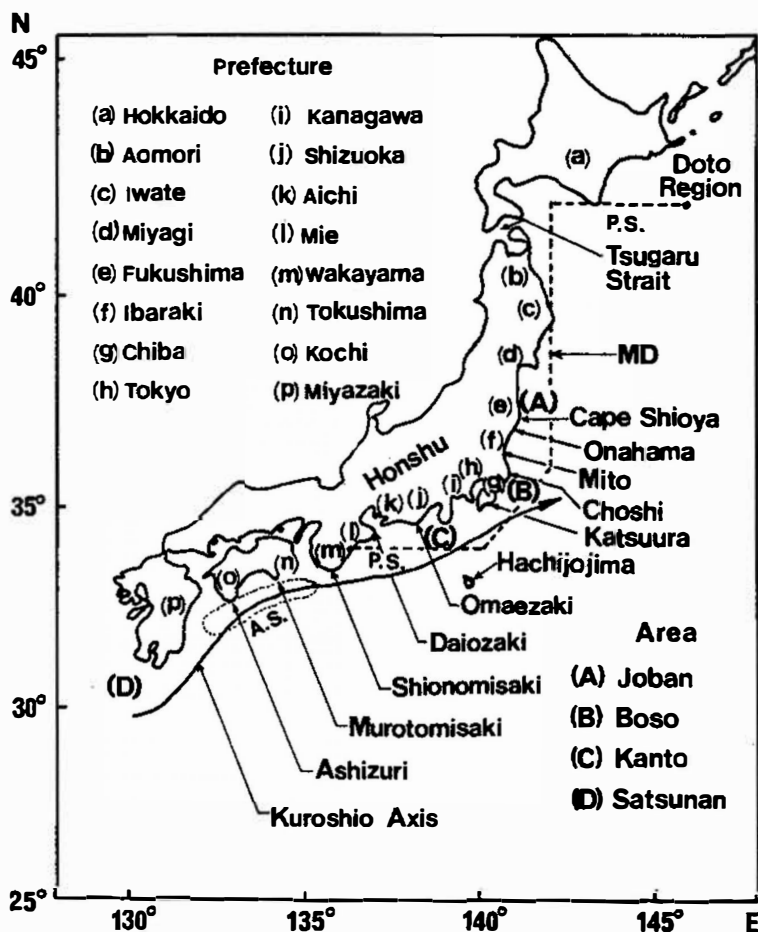


Fig. 1. Indicating: (1) localities; (2) distribution areas of Ashizuri (A.S.) and Pacific (P.S.) subpopulations; and (3) supposed migratory distance (MD) in estimating energetic cost for swimming.

Estimation of Catches

The Far Eastern sardine population along the Pacific coast is divided into Ashizuri and Pacific Subpopulations (Ito 1961). But the separation is not so clear and communication between them can occur (Nakai and Hattori 1962). Watanabe (1983) attributes an increase in the number of eggs collected in the spawning grounds of Ashizuri Subpopulation in 1980-81 to substantial immigration of the

Pacific Subpopulation adults. In order to avoid the ambiguity in this separation, the two Subpopulations are treated here as a single fluctuating unit, called the Pacific Population.

The catches of sardine and anchovy were not consistently recorded separately before 1952. Kurita and Tanaka (1956) used regression techniques to estimate the catch of anchovy and then the sardine (by subtraction) totaled around Japan. Following their method and data, a prediction formula of the sardine catch, C_s , was obtained:

$$C_s = -41460 + 0.9472T - 1.375P \quad (n=14, r^2=0.993)$$

where T is the total catch and P the total boiled and dried production of the sardine and anchovy in tons. The 1920-52 catches of the Pacific Population were estimated using the above formula with T and P being the sums over the regions from Miyazaki to Hokkaido (Fig. 1), the coastal regions of the population range. Fig. 3 shows fluctuations in catch of the Pacific Population, where the 1953-88 catches were obtained from statistical yearbooks of the Japanese Ministry of Agriculture, Forestry and Fisheries.

Results

Are environmental factors the prime determinants of sardine fluctuations? If a factor plays a major role in regulating the population, it should be possible to distinguish between its fluctuation patterns during population growing and declining periods, and a turning point from one phase to the other.

ABIOTIC FACTORS

As shown in Fig. 2, the fluctuations in air pressure are irregular and show no difference between the sardine growing and declining periods. The last sardine growing period corresponded to a cold period, whereas the second corresponded to a warmer one. The collapse of the population began in the mid-1930s, but air temperature did not change much until the late 1940s. The population bounced back up quickly from the early 1970s, and while air temperature was at a high level during the 1970s, it was at a higher level during 1950-60 while the collapse still continued. Thus, the population

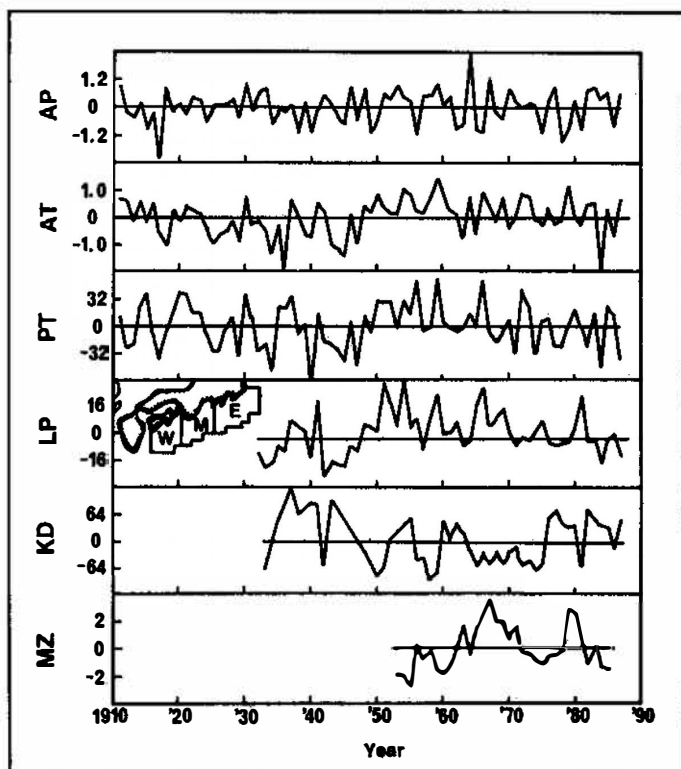


Fig. 2. Fluctuations in air temperature (AT, °C), air pressure (AP, mb), precipitation (PT, mm), frequency of low pressure (<990mb) passing through the three areas W, M and E (inset) during January-May (LP), the bigger distance of the Kuroshio path from Cape Daiozaki and Cape Omaezaki along longitudinal direction (KD, nautical miles) averaged over January-May (1933-59 data are obtained from Kawai 1972, and 1960-87 data from current maps published by Japan Water Way Department), and mean macroplankton biomass (MZ) in Tokai Area (after Suzuki 1987). AT, AP and PT are respectively calculated as the mean of anomalies at Ashizuri, Murotomisaki, Shionomisaki, Hachijojima, Katsuura, Choshi and Mito in each of the five months from January to May. Data are compiled from the Summary of Meteorological Information edited by Japan Meteorological Agency.

growing or declining phase was not likely determined by the air warming or cooling, and the switching of phases did not seem to be caused by changes in the air temperature. Similarly, fluctuations in precipitation, which showed close correlation with air temperature, did not seem to be determinants of the population fluctuations.

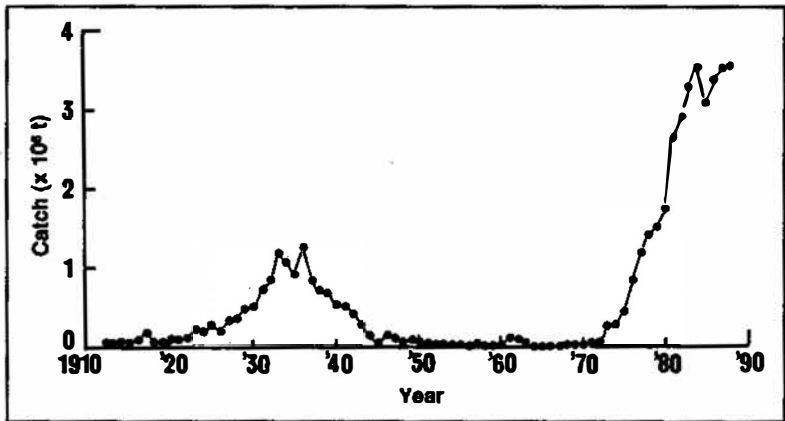


Fig. 3. Long-term fluctuations in catches of the Pacific Population of the Far Eastern sardine.

Low pressure passing over the spawning and nursery grounds might have some influence on the survival of larvae. Under strong low pressures, seawater can sometimes upwell and cause a sudden drop in sea surface temperature, which might be harmful to larvae. As Fig. 2 shows, the mean level of the low pressure frequency in 1936-50 was lower than in 1950-60, but the population collapsed drastically during the former period, and this collapse was apparently slowed down during the latter. The frequency of low pressures during the fast growing period was not at a level lower than that during the drastic declining period.

The Kuroshio Current flows through the spawning and nursery grounds of the sardine, and fluctuations in its path influence the transportation of fish eggs and larvae (Fujimoto and Hirano 1972). As Fig. 2 shows, in 1936-44 when the Current flowed far from the coast, the sardine population drastically declined, and in 1970-75 when the Current took a path very close to the coast, the population began increasing steeply. Apparently, the path fluctuated with higher frequency than the population did: during the declining period, the distance dropped three times to a trough, around 1950, the late 1950s and the mid-1960s, respectively. While the distance of the Kuroshio Current from the coast has been at high levels since 1976, the population has still been increasing. Thus, there was a possibility that the extreme positions of the Kuroshio path might trigger the collapse or recovery of the population, but the population might behave independently after that triggering.

BIOTIC FACTORS

According to Kondo et al. (1976), the principal food of postlarval sardines are the young stages of copepods. A time series of copepod biomass is not available; however, fluctuations in macroplankton biomass (Fig. 2) are presented for discussion. During 1963-71, the biomass was at a high level and the sardine was at a very low level. No sign of sardine recovery was observed until 1970. The macroplankton biomass dropped to a low level during 1972-78, but the sardine population surged at the same time. Thus, there was no evidence available that the recovery of sardine in the early 1970s was due to good food availability.

It seems unlikely that these abiotic and biotic factors are determinants of the long-term sardine fluctuations, although the unusual locations of the Kuroshio path might possibly trigger the collapse or recovery of the population.

Traits of Life History

The change of spawning grounds of the sardine population has shown to be closely related to its abundance levels. During the prosperous period around mid-1930s, the central spawning ground was located mainly in the Satsunan area (Nakai 1962c), which is probably the southwestern-most area of possible spawning grounds. As the population collapsed, the spawning ground gradually moved northeastward, and reached the Kanto area between the late 1950s and the early 1960s (Watanabe 1975), which is the northeastern-most area of spawning grounds to date. The population size has continued to grow since the late 1970s, and the major spawning ground has shifted southwestward. Fig. 4 shows the fractions of sardine eggs produced in the southwestern areas during 1978-86, where it can be noted that the shift proceeded obviously in two successive years, 1980-81, and did not change much thereafter. More than 90% of the eggs were produced in the southwestern areas during 1983-86.

Migratory range has also exhibited a close relationship with the population levels. Kawasaki and Omori (1986) showed the supposed migratory range of the sardine around 1965 at a low stock level, and that in the early 1980s when stocks were at a high level, and found that the latter was much wider than the former. In regard to migration in the 1933-36 prosperous period, Nakai (1962c)

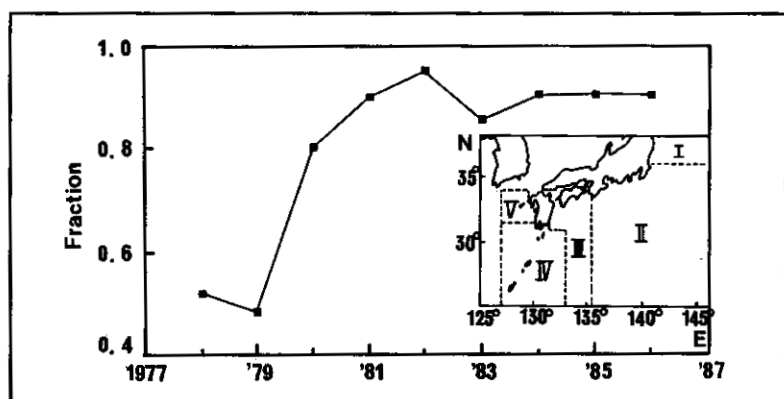


Fig. 4. Fluctuations in the fraction of sardine eggs collected in the areas III and IV indicated in inset. Data are obtained from Mori et al. (1988).

suggested that adult fish on the Pacific side passed through Tsugaru Strait, migrated southward to Satsunan area along the Japan sea coast of Honshu and completed their long "around Japan journey." On the basis of data obtained from a number of cruises, Wada (1988a) suggested that the migration range in the northwestern Pacific kept increasing during 1977-84 except for 1979.

In summary, the sardine has exhibited large expansions and contractions of range concomitant with changes in abundance. At high levels of abundance, sardines shifted their spawning ground southwestward and extended their migratory range. At low levels of abundance, sardines shifted their spawning ground northeastward and migratory range was greatly reduced. This dependence of range on stock level is very peculiar to the sardine population in comparison with other pelagic fishes in Japanese waters, such as anchovy and mackerel.

ENERGETIC COST FOR SWIMMING

The energy output required for swimming through a normal migratory distance is roughly calculated here to check its significance.

The distance along the migration route between Shionomisaki and Doto Region was estimated from a map to be about 1,646 km (Fig. 1). In hydrodynamics theory, the drag force, D , acting against a fish L cm long, swimming at a speed of V cm s⁻¹ is expressed as:

$$D = C_d \rho A V^2 / 2, \text{ and}$$

$$A = 0.4 L^2, C_d = 10.56 (V L / \nu)^{-0.58} \text{ (Ware 1978)}$$

where C_d is the drag force coefficient, ρ the density of seawater ($1.02 \text{ g}\cdot\text{cm}^{-3}$), A the wetted surface area, and ν the kinematic viscosity of seawater ($0.01 \text{ cm}^2\cdot\text{sec}^{-1}$). Due to lack of information about C_d for sardine, the experimental formula of C_d for salmon (Ware 1978) is used. Both species have similar streamlined bodies, and their C_d values may not be substantially different.

Taking the efficiency of converting chemical energy into propulsive power to be 0.20 (Brown and Muir 1970; Webb 1975), the energetic cost was calculated for a fish making a round trip between off Cape Shionomisaki and Doto Region at speeds of one and two body lengths a second. Body length is assumed to be 20 cm, which is the mean body length of 2- and 3-year-olds of the 1972 year class (Kondo et al. 1976). The energetic cost was calculated as the product of drag force D and swimming distance, $2 \times 1.646 \times 10^5 \text{ cm}$ here. It was then converted to equivalent sardine somatic mass using a conversion factor of 2.13 Kcal for one gram of flesh (Kagawa 1989). The results are:

speed (cm sec ⁻¹)	20	40
cost (Kcal)	29.05	77.74
sardine flesh (g)	13.64	36.50

It should be noted that the real migratory distance could be much larger than the one used here, considering that the fish might often make circles or go back and forth in search of prey. The increment of body weight from age 2 to 3 of the 1972 year class is 30 g (Kondo et al. 1976) and in comparison with the increment, the energetic cost for the round trip is high enough to be taken into consideration. The large difference in migratory range between periods of low and high population levels can certainly cause a large difference in the energetic cost for swimming.

MATURITY AND CONDITION FACTOR

The gonad index (GI) and condition factor (CF) show obvious differences at different population levels. Fig. 5 shows seasonal

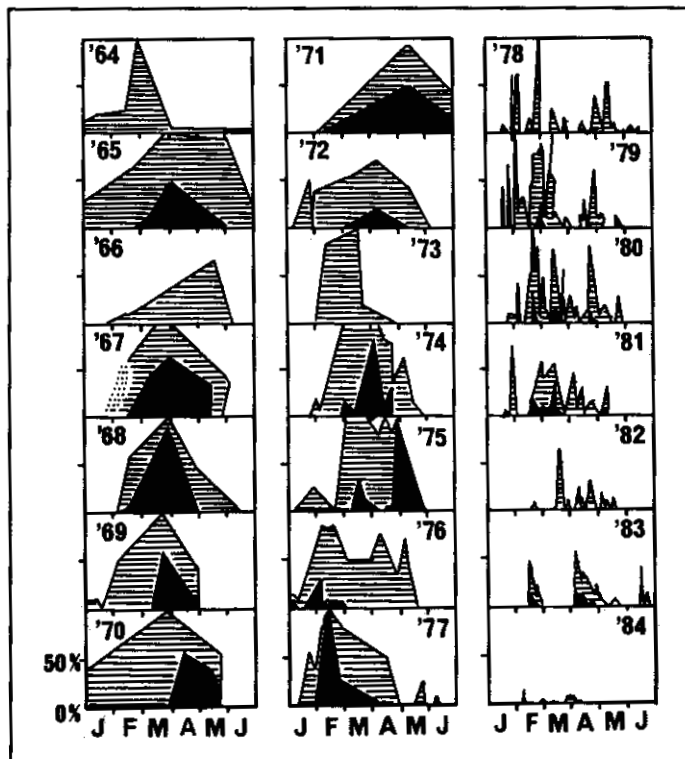


Fig. 5. Comparison between seasonal fluctuations in fractions of the fish greater than 10 (solid shaded area) in gonad index ($GI=10^4 \cdot \text{Gonad weight}/SL^3$) and between 4-10 (Hatched area) during 1964-70, 1971-77 (after Hiramoto 1981), and 1978-84 (after Survey Data of Fisheries Resources in the 200-mile Zone-The Pacific Subpopulation of Sardine, 1978-84. Tokai Reg. Fish. Res. Lab., Japan [ed.]).

variations in the fraction of fish 4-10 and larger than 10 in GI in Joban and Boso areas during 1964-84. The main spawning season is February-March. Most of the shoals passing through the two areas during January-June are either southward migration shoals or prespawning or spawning shoals (Hiramoto 1981). The three series of figures in the left, middle and right columns, respectively, illustrate the seasonal variations in GI during 1964-70 when the stock level was in a trough; 1971-77 when the stock was at an intermediate level; and 1978-84 when the stock reached a high level. The fractions of fish with GI greater than 4 during 1964-70 and 1971-77 are significantly higher than during 1978-84, and no discernible difference can be found between the first two periods, which suggests

that maturity progressed much more at low and intermediate stock levels than at high stock levels.

Fig. 6 compares seasonal variations in the fraction of the fish with CF greater than 14 in Joban and Boso areas during 1971-77 and 1978-84. Far fewer fish attained GI greater than 14 in the latter period, suggesting worse nutritional condition at high stock levels. Kondo (1980) investigated seasonal changes in CF and GI from October 1974 through March 1975, and showed that both the fat covering the visceral organs and CF decreased drastically from January to March, while there was a rapid increase in gonad weight. He suggested that fat is utilized for maturing the gonad as

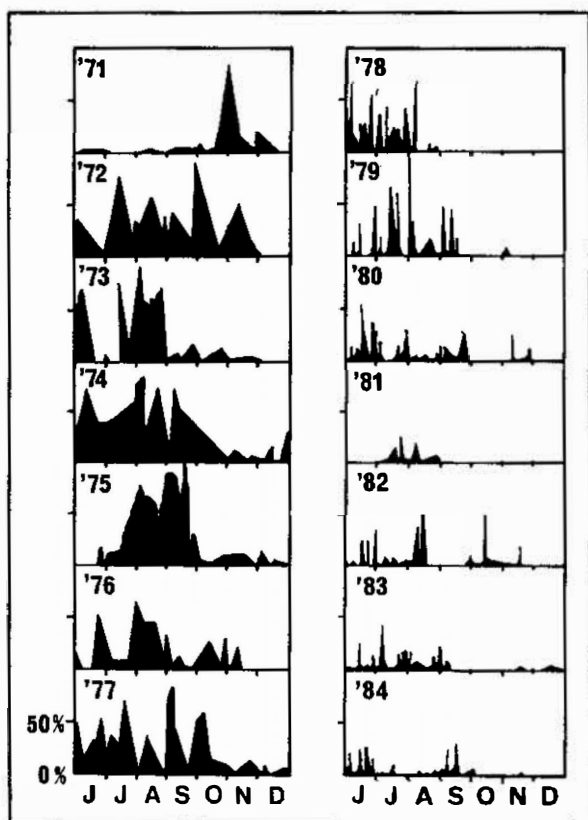


Fig. 6. Comparison between seasonal fluctuations in fraction of the fish greater than 14 in condition factor ($CF = 10^3 \cdot BW/SL^3$) during 1971-77 (after Hiramoto 1981) and during 1978-84 (after Survey Data of Fisheries Resources in the 200-mile Zone-The Pacific Subpopulation of Sardine, 1978-84. Tokai Reg. Fish. Res. Lab., Japan [ed.]).

well as the muscles, and maturity will be adversely affected if the fatness of the adults is poor and vice versa.

STOMACH CONTENTS

Fig. 7 shows curves of probability density function (estimated by dividing relative frequency by class length) for frequency distribution of the Stomach Contents Index ($SCI=10^3 \cdot SCW/BW$) for 1951-52 and 1988-89 periods. A much greater fraction of fish ate a small amount of food in 1988-89 when the stock level was very high (mean SCI, 3.67) than in 1951-52 when the stock level was much lower (mean SCI, 8.65).

In summary, as the stock level increased, the energetic cost for swimming would largely increase, the gonads would tend to develop poorly, and the food intake and condition factor would become very low.

Possible Mechanisms Underlying the Population Fluctuations

Blaxter and Hempel (1963) suggested that the relationship that smaller or poor quality eggs lead to higher larval mortality and vice versa, could have far reaching consequences on the population dynamics of some pelagic fishes.

The degree of maturity can affect the size of the eggs spawned. Nakai (1962b) showed a positive correlation between mean egg diameter of the third

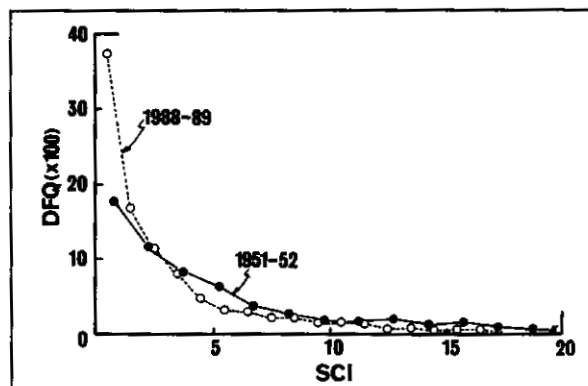


Fig. 7. Comparison between functions of probability density (DFQ) for relative frequency distribution of stomach contents index ($SCI=SCW/BW \cdot 10^3$) during 1951-52 ($n=1,207$) and 1988-89 ($n=2,688$). DFQ denotes the frequency occurring in each unit range.

egg group (the biggest one) and maturity coefficient of medium-sized female sardines. Blaxter and Hempel (1963, 1966) investigated many groups of Atlantic herring (*Clupea harengus*) for the effect of egg size on survival and size of larvae at different stages. They showed that overall growth rate to maximum

length is faster with larger eggs and a statistically significant relationship exists between egg weight and survival time (hatching to starvation) of larvae, the survival times increasing with bigger eggs. In the case of Japanese anchovy, Imai (1987) obtained similar results: maximum body length and mean survival time increased with egg diameter, and feeding success showed a positive correlation with egg volume. Although not yet experimentally investigated, the above results may hold true for the Far Eastern sardine.

POPULATION GROWING PERIOD

The above facts and arguments led to a hypothesis on the fluctuation mechanism in the growing period: the range of the population is determined by stock size. As a result, the amount of available food and the energetic cost for swimming through the range are stock size-dependent. The accumulated surplus energy determines the condition of spawning adults, which in turn determines the quality of eggs produced. The survival rate to recruitment is dependent on egg quality, and eventually the subsequent recruitment is stock size-dependent.

The total food intake of the sardine population, TF, and the migratory distance of a fish, MD, are likely to change with population size, B , in the ways indicated in Fig. 8. Initially, total food intake increases fast with population size at low levels when the amount of food available for an individual fish is great (two of the possible curves are given as L_1 and L_2), and slows down and approaches an asymptotic level (H_1) or even drops down (H_2) when population size reaches high levels, under which new feeding grounds for exploitation are gradually moved to offshore areas poor in food, and

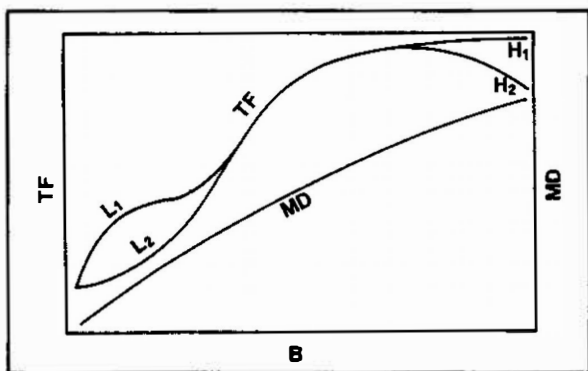


Fig. 8. Illustrating the possible ways of change of the whole population's food intake (TF) and the migratory distance of an individual (MD) with changing population size (B). L_1 and L_2 , and H_1 and H_2 , respectively, denote two possible TF curves under low and high population size levels.

meanwhile fish may have to decrease feeding frequency to make long migration possible. This is suggested by a much smaller SCI in 1988-89 than in 1951-52 as described in the forgoing part. As a result, migratory distance increases with population size at a higher rate than total food intake. According to our hypothesis, the stock-recruitment relationships for population growing periods can be described as follows:

$$R/B = k \cdot (TF_B/B \cdot d \cdot MD_B) \text{ or } R = k \cdot (TF_B \cdot d \cdot B \cdot MD_B)$$

where total egg production in number is supposed to be proportional to total biomass of adults and egg-recruit survival rate proportional to the surplus energy obtained by a unit weight of the sardine. R is recruitment in weight and B the population size in the same unit, k is a fractional exponent, and d is the hydrodynamic drag force acting on a unit weight of the sardine. If TF_B and MD_B take the shapes indicated in Fig. 8, a dome-shaped stock-recruitment relationship can certainly be obtained, causing a slowdown in population increase as observed in sardines.

POPULATION DECLINING PERIOD

As can be observed from the sardine fishery history, after reaching a peak the sardine population always decreased. At a same abundance level, on one side of a peak the population increases, but on the other side it decreases. If this is not caused by environmental factors, as suggested in the forgoing part, the reproduction rate defined as the ratio of recruitment to adult biomass was certainly lower in population declining periods than in growing periods. How could this occur? The change of body length with adult biomass is studied to seek a possible answer. The biomasses are estimated by dividing catches by exploitation rates, which are roughly estimated in the following way: Nakai (1960a) estimated adult annual survival rates in 1949-54 using catches at successive age-groups, the mean of which was 0.51. Wada (1988b) estimated those for 1974-80 year classes from available stock sizes at successive age-groups in Doto region, the average of which was 0.42. Supposing the natural mortality coefficient to be 0.37 (Yamanaka 1960), the exploitation rate during the above two periods, around 1952 and 1981, is 22% and 33%, respectively. According to Hiramoto (1981), in the late 1930s when powered fishing vessels became available, fishers began

offshore operations and reached as far as 30 km from the coast. Since then, the fishing ground has continued to expand with increases in both size and power of fishing vessels. In the early 1950s, the echo sounder was introduced into fishing, and the material for fishing nets was changed from cotton to synthetic fibers. Recently, new progress in equipment including computer technologies (Wada 1988b) suggest that the exploitation rate must have increased further.

It seems reasonable to assume that the stock level in the prosperous period around the mid-1930s and that of recent years may be similar. First, the ranges of population were similar in the two periods: the central spawning grounds were located in the southwestern-most Satsunan area and the northern limits of migration were remarkably extended (Nakai 1962c; Watanabe 1981, 1988). Second, the body length of 2-year-olds of 1936 and 1980 year classes were very small and close to each other. Fig. 9 shows that the body length of 2-year-olds is negatively correlated with stock level, which suggests that body size can be an index of stock level. The exploitation rate around 1936 can be estimated to be 12%, 8% or 24%, respectively, by assuming that the last population peak was as high as, one and a half times or half of, the recent one and that exploitation rates during 1982-88 were equal to that in 1981. Fig. 10 shows three cases of changes in exploitation rate during 1936-88 corresponding to the three levels of the last population peak assumed above, where a straight trend in the increase of exploitation

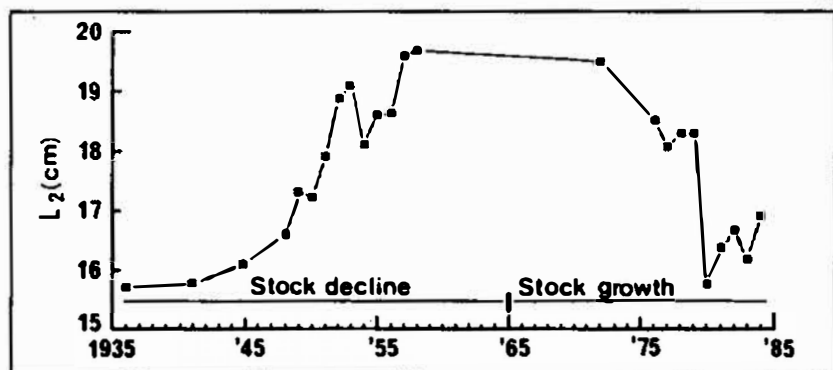


Fig. 9. Fluctuations in standard length of 2-year-olds (L_2). L_2 of 1936 year class is obtained from Aikawa and Konisi (1940), 1941 and 1945 year classes from Yasuda and Ogura (1950), 1948-58 year classes from Kondo et al. (1976), and 1976-84 year classes from Wada (1988a).

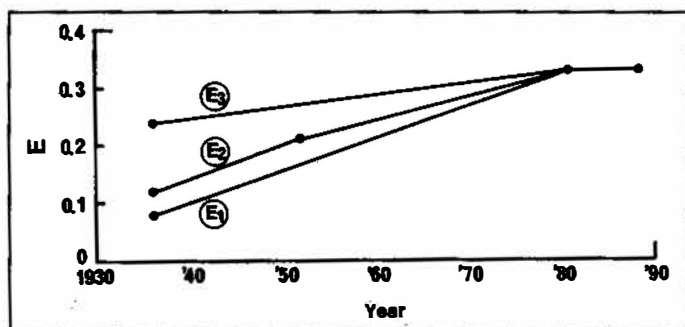


Fig. 10. Three cases of change in exploitation rate (E) of the Far Eastern sardine (E_1 - E_3). The 1952 and 1981 estimates in E_2 are obtained through adult survival rates. See text for explanation.

rate during 1936-52 and 1952-81 (E_2), and 1936-81 (E_1 and E_3) is supposed, respectively. The E_2 case was considered most possible.

The catchable biomass in a particular year during 1936-84 was estimated by dividing the catch by the estimated exploitation rate in that year. The number of fishing vessels operating in the fishing grounds dropped sharply during World War II (Kurita 1960), and the 1942-48 biomasses were interpolated by assuming a linear trend in the logarithmically transformed biomasses during this period.

Fig. 11 shows trajectories of body length of 2-year-olds against the estimated biomass corresponding to the three cases of the exploitation rates indicated in Fig. 10, where the trajectory in the population growing period is apparently different from that in the declining period in all the three cases, the body length being smaller in the declining period than in the growing period at a same biomass level. This suggests that while there might be some uncertainty about the estimates of biomass (particularly for the past), two distinctive processes of change of body length with population size certainly existed during different phases of population fluctuations.

Energy in excess of maintenance requirements may be channeled into somatic or reproductive tissue. Roff (1983, 1984) found that gonad weight is generally proportional to body weight in many species of fish, which led him to assume that a fixed fraction of surplus energy is channeled into either somatic or gonad tissue. Following Roff's argument, the total surplus energy obtained by an individual during the prerecruit period (the recruitment age of sardine is 2 or 3 years) can be considered to change in a way

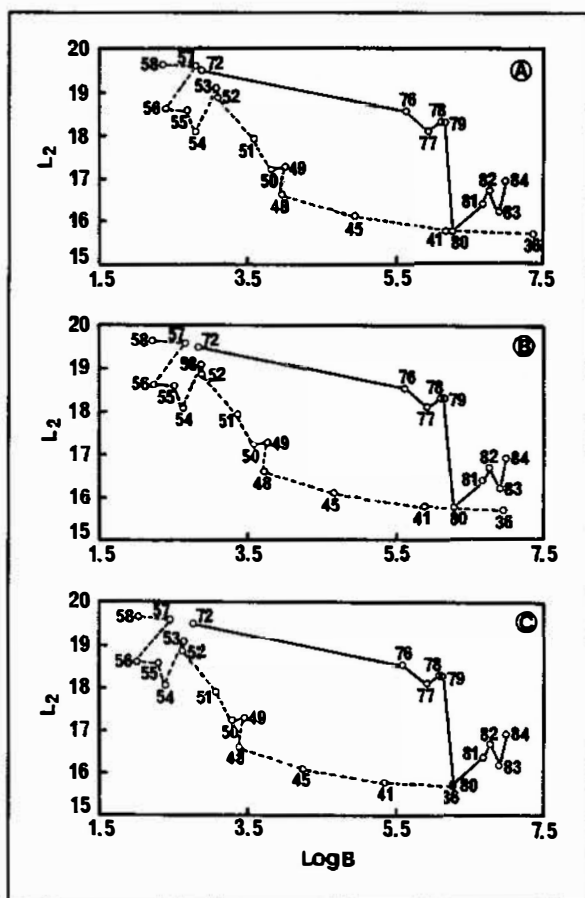


Fig. 11. Trajectories of standard length of 2-year-olds (L_2) against logarithm transformed biomass ($\log B$). 1936-58 year classes correspond to a population declining period, and 1972-84 ones correspond to a population growing period. (A), (B) and (C) correspond to the three cases of exploitation rates E_1 , E_2 and E_3 (Fig. 10), respectively. B is in 10^4 t, and L_2 in cm (Fig. 9).

similar to that of the body length, or the prerecruit sardines accumulated less surplus energy during the population declining periods than during growing periods, which can be considered the direct reason for the lower reproduction rate in population declining periods. A possible explanation for this phenomenon is as follows:

Consider possible processes of degeneration and recovery of body condition of adults with changing population size. When the population reaches high levels, increase in energetic cost for

swimming, decrease in food intake and other crowding effects can become significant, and the body condition degenerates gradually. As the population size continues to increase, all the negative factors can turn to be crucially harmful, and the condition of the fish drops steeply. The population collapses and the condition recovers. Situations where the condition recovers exactly along the trajectory of degeneration seem unlikely to occur when taking into account the tendency frequently observed in body condition of many animals, i.e., once collapsed, even if the living condition gets better, the body condition cannot recover soon to the same level as it was before the collapse. The lower surplus energy obtained in a declining population can be explained by such a recovery process of body condition.

Discussion

Lluch-Belda et al. (1989) synthesized information on sardine stocks in five regions of the world: the western (Japan system) and eastern (California Current) boundary areas of the North Pacific, the eastern boundary (Humboldt Current) of the South Pacific, and both the northern (canary Current) and southern (Benguela system) boundaries of the eastern Atlantic. They showed that all the five sardine stocks exhibit large expansions and contractions of range with changes in abundance. In their study of variations in parent stock and recruitment of pilchard (*Sardinops ocellata*) in the southern Benguela system, Shelton and Armstrong (1983) showed that the gonad condition factors during 1958-61 when population level was high were obviously lower than during 1970-71 and 1980-81 when population level was low. They suggested that gonad weight as well as age at maturity may have important regulatory consequences in the dynamics of the South African pilchard. These common traits of all the sardine stocks may explain to some extent their peculiar fluctuation pattern with continuously growing and declining periods occurring alternatively over a relatively long period.

Catches of sardines in the Japan system, California Current and Humboldt Current show approximately parallel trends with mean air temperature for the northern hemisphere from 1910s to 1980s (Kawasaki and Omori 1986), whereas catches in the Canary Current and Benguela system are not in phase with the mean air temperature (Lluch-Belda et al. 1989). As discussed earlier,

agreement was not found between the fluctuation in the sardine population size in the Japan system and in the air temperature over the coastal areas, suggesting that the air temperature might not be a direct factor for the sardine population dynamics.

Begon and Mortimer (1981) argued that unrestrained population growth is unknown, and unrestrained decline leading to extinction is extremely rare; they concluded that all natural populations are regulated to some extent by density-dependent processes. We propose that the sardine population fluctuations are largely due to a self-regulating process in which adult body condition is regulated by population size.

Acknowledgement

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