Studies Relevant to Mechanisms Underlying the Fluctuation in the Catch of the Japanese Sardine, Sardinops melanosticta (Temminck & Schlegel)

Zinzirô NAKAI

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Introduction

Since about the inception of the present century the catch of the Japanese sardine, Sardinops melanosticta (TEMMINCK & SCHLEGEL), in the Far East has been subjected to extraordinary fluctuations. The yearly landings of the fish increased from slightly over 100,000 tons around 1910 to 2,700,000 tons in 1936 and 1937, and decreased since then, dropping to merely 160,000 tons in 1945. Since then the annual sardine catch ranged between 200,000 and 500,000 tons. In the prosperous period, the exploitation of this species played the most important role in Japanese fisheries, *i. e.* the annual sardine landings are averaged to have been 1,130,000 tons, or 42 percent of the total

output of the fisheries, for the period during 1929 through 1938. During the last half century the major fishing grounds of the sardine have shifted from certain areas to the others with change in the amount of catch.

It is axiomatic that the fishery biology is the study on fluctuations in size and distribution of any fish resource in question. In order to advance the study, it is needed to develop any overall research program that can provide the biological data indispensable to seek the mechanism of fluctuation in the population in the process of contribution of basic knowledges, and then to analyse and integrate all of the information obtained.

One of the peculiarities of fishery biology is to elucidate the manifestation of the fluctuation in the living resources, that receives strong influence of the ocean which has never been controlled by human energy. Therefore, any experimental approach is hardly applicable, and an everlasting accumulation of the data from the fields has been required in order to measure effects of numerous and mutually related factors on the fluctuation in the population. Another peculiarity of this kind of study is to make out that the fish population and the environments would largely fluctuate depending upon time and space. These peculiarities should be taken into consideration to promote the overall research program.

Before the World War II, no systematic investigation except one as below was conducted on the Japanese sardine, although many advanced reports on the biology of this fish appeared even in those years. The only systematic work was that continuously initiated by the Fisheries Experiment Station of the Government-General of Tyôsen during the period from 1936 to 1945. This consisted of two major projects: a survey on the amount and distribution of spawning activities in the waters surrounding Japan and Korea and a survey on migration, distribution and age composition of the grown fish exploited in the entire part of the western Japan Sea. The present author designed the program of and engaged in the investigation throughout the period. Unfortunately no unitary survey of the age composition of catch, one of the most important information for the study of fishery biology, covered the whole distribution range of the Japanese sardine until 1948, although the significant fishing area expanded over the surrounding waters of the Japanese Islands, Korea and Coast Range of USSR.

After the World War II, in accordance with the raised request for promotion of sardine resource investigations, a new cooperative system was established in 1949 by the Central Fisheries Experimental Station, Ministry of Agriculture and Forestry (renamed Tôkai Regional Fisheries Research Laboratory in 1949). The epoch-making systematic investigation, which was also designed by the present author, was thence commenced and is still actively managed under cooperation of regional fisheries research laboratories and Statistics and Survey Division, Ministry of Agriculture and Forestry, and the prefectural agencies. As the sardine fishery disappeared from Korea and Coast Range in 1943, the present investigation program has covered

whole the significant fishing area for this species.

The present paper provides various biological aspects of the Japanese sardine, and history of fluctuation in the catch and the population, on the basis of data obtained from the above two investigation programs as well as the other basic studies hitherto made. Among all the problems raised from these findings, those which are more specific and most important enough to be specially dealt with in this paper include: causes of the sharp increase in the catch that had lasted until about 1933, causes having brought forth the abrupt decrease in the 1940's and the more recent status of the sardine population. Basing on all this information, comments are given on the management and investigations of the sardine fishery in the waters surrounding Japan.

Methods and terminologies

The present study is mainly based upon the data from the two systematic investigations aforementioned, *i.e.* one carried out during 1936 through 1945 and the other conducted since 1949. Diverse methods and terminologies have been adopted in these two investigation programs. Following description covers the definitions that are important in explaining the fluctuation of the sardine population.

Positions of localities: In this paper, the Far Eastern sardine area is divided into



Fig. 1. Division of Far East sardine area.



Fig. 2. Geographical positions referred to in the text.

ten regions as shown in Fig. 1. Fig. 2 indicates geographical positions of the various localities appearing in the text.

Length of fish: Biologists engaging in the Cooperative Investigations have defined the body length as the distance from the anterior tip of lower jaw to the posterior end of silvery part exposed on the caudal peduncle when the scales are removed. The body length of the fish over 35 mm, which is evidently the "adult form", is measured on a measuring board by one mm unit.

Shirasu, postlarvae and juveniles less than 35 mm in body length, on which the caudal silvery area is not yet developed, are measured by total length instead of body length. In this case the total length is defined as the distance on the longi-

tudinal body axis between the anterior tip of the lower jaw and the posterior end of the ventral lobe of the caudal fin extended normally. The length is determined by one mm unit for *shirasu* taken by the commercial fishery, or by a unit less than one mm for specimens obtained by plankton net collection and by rearing experiment.

Commercial names for various sizes of sardine: Ôba, chûba, koba and koiwashi have been customarily and widely applied for diverse sized sardine in Japan. In this report, these commercial names are frequently appearing in Section 1-1 and in other descriptions when needed. The classification of these four groups, in this country, has been roughly used with some variations by locality and by age. The present author tried to make a presumed criterion for every size group of fish based on the responses from local fishermen's unions concerning this problem. The results obtained at the occasion are summarized as follows:

ôbafish over 17 cm in body length,

chaba....fish between 14 and 17 cm in body length,

kobafish between 6 and 14 cm in body length,

and koiwashi..fish between 3.5 and 6 cm in body length.

The terms, large-, medium- and small-sized sardine in this report are corresponding to ôba, châba, and koba together with koiwashi, respectively.

Age of fish: Since the 1930's, the age of sardine has been determined by scale reading methods, details of which are discussed in Section 1-5. The age of fish, except that caught during winter and early spring, is indicated by a capital Roman numeral corresponding to the number of annuli on the scale. In the winter season when the new annulus forms, some of a certain year-class already show a new annulus while others may have no new annulus formed. For the fish caught in the colder season of the year, the following modification has been applied. Since the major spawning season extends from January to May, a certain year class would possibly come into existence during the season of annulus formation. It has, therefore, been proposed that the age of the sardine older than juveniles, should be added one at every beginning of the calendar year. For a specimen that was born, for instance, in spring of 1949 and caught in December 1950, the age is expressed as I. If this fish was caught one month later, in January 1951, the age is expressed as II regardless whether or not a new annulus formed on the scale. In other words, the age of the fish caught in the season of the year is expressed by the number of annuli that formed in the preceding winters plus one corresponding to the annulus that newly formed or would form. In practice, when an annulus that has not become visible yet is added to the existing annuli for counting the age of a specimen, precaution is taken by making its age with a degree sign in order to distinguish that specimen from the others which have already formed the new annulus near the margin of the scale. In discussing the age of postlarvae or juveniles that should belong to a new year class, this modification is not applied. Instead, most of the young fish are

grouped into 0-age except a few landed in the later part of a year and stated as -I. The negative sign indicates that the fish belongs to the class of the next year. Thus, a postlarva taken in December 1949 is aged as -I and sorted into the 1950 year class.

Number of vertebrae: The number of vertebrae is defined as the total number of segments between and inclusive of the atlas, the segment just posterior to the basioccipital bone, and the urostyle. In quoting the vertebral data reported by some workers who did not count the urostyle, their counts are increased by one to conform to those of the present study.

Maturity: In general degree of the sexual maturity of fish is indicated by KG $\left(\frac{\text{gonad weight in gram}}{\text{cube of body length in cm}} \times 10^4\right)$ of FARRAN (1938). In addition, the maximum diameter and size frequency of ovarian eggs are occasionally used as indices of the maturity of female fish.

Developmental stages: Table 1 shows the standard and definition of the various developmental stages inclusive of the eggs, larvae and postlarvae. Some of these stages as well as sperm and unfertilized ova are illustrated in Fig. 3. Shirasu is appropriated to the postlarvae taken by the commercial fishery. The metamorphosing juvenile measuring 30-50 mm in total length is named *kaeri*. The fish over 35 mm is recently assigned to be the adult form.

Plankton net collection: Three types of nets have been widely employed to collect the eggs, larvae and postlarvae of the sardine as well as other plankton organisms for the cooparative investigations. They are maruchi type (130 cm in hoop diameter), marunaka type (60 cm in hoop diameter) and marutoku (45 cm in hoop diameter), all of which are conical in form (NAKAI 1962c). The straining parts of these nets are constructed of bolting silk cloth with about 0.3 mm aperature. Maruchi is towed horizontally on the surface for either 5 or 10 minutes at a speed of about one meter per second. Marunaka and marutoku are hauled from a depth of 150 m, or from the bottom when shallower, up to the surface at a speed between 0.8 and 1.3 meter per second. Since 1952 a flow meter is equiped at the mouth of marunaka and marutoku to measure the water volume actually strained while the net is hauled.

The collecting ability of *maruchi* horizontal towing and that of *marunaka* vertical hauling were compared at 81 stations in 1941. According to the experiments, *maruchi* was found to be as six times more efficient as *marunaka*.

Some closing nets have been also employed to survey the vertical distribution of the eggs and larvae. KITAHARA's quantitative net (HENSEN'S type) has been applied for the collection of microplankton that is thought to form one of the most important biological environments. It has 22.5 cm-diameter-hoop and 0.10 mm-aperature silk, being hauled vertically from a depth of 50 m up to the surface.

Estimation of age composition of catch: Scale reading has been conducted on a portion of samples used for measuring the length composition of the landings. The

Table 1. Definitions of early developmental stages of *Sardinops melanosticta* as used in the present study.

- A: Eggs inclusive of both unfertilized and fertilized. The fertilized eggs are specified by Aa, Aaa, Aab, Aac, Ab, and Ac, from the earliest stage of development until closure of the blastopore. However, "A" may be used in place of these subdivisions when they neither have been, nor could be, determined.
- A': Unfertilized egg.
- Aa : The stage in which the blastoderm grows until it occupies one-third of the yolk in the diameter that crosses at right angles with the basal periphery of the blastoderm.
- Aaa: The stage in which no cleavage occured.
- Aab: The stage in which the blastoderm grows until it occupies one-sixth of the yolk in diameter as defined above.
- Aac: The stage from the end of "Aab" till the blastoderm occupies one-third of the yolk.
- Ab: The stage that follows "Aa" until the blastoderm has grown to cover twothirds of diameter of the yolk.
- Ac: The stage that follows "Ab" until the blastoderm expands all over the yolk, closing the blastopore.
- B: Includes stages from the end of "A" till the tail-bud begins to separate off the yolk. When the subdivisions Ba, Bb, and Bc as defined below are not determinable, "B" may substitute them.
- Ba: The stage which takes place after closure of the blastopore, while the tailbud has not yet reached about the oil globule.
- Bb: The stage when the tail-bud has reached to the oil globule but not swelled notably.
- Bc: The stage when the tail-bud has raised conspicuously. A lateral view of the eggs at this stage shows a right angle bounded by the frontal line of the tail and by a tangent at the insertion of the tail-bud on the surface of the yolk.
- C : The stage from the end of "B" to hatching, which is divided into Ca and Cb as follows:
- Ca : The stage when the posterior part of the body extending free from the yolk remains shorter than the anterior.
- Cb: The stage after "Ca" till hatching.
- C'b: The stage immediately before hatching when a small projection is observed at the position of future opening (This stage is too critical to be applied to net-collections).
- Lar.: The larval stage that continues after hatching until the yolk sac has been absorbed and the mouth opens.
- P. L.: The post-larval stage that follows absorption of the yolk until the fish grows to "kaeri", which is an early juvenile of the sardines having passed the transparent stage with the pigments getting as clear as those of the adult.

Note:—In the text the egg fertilized and at the beginning of the incubation experiment will be tentatively called Aa', but it is left out of consideration here.

length composition has been converted to the age composition by multiplying the number or weight of fish in each length interval with the ratio of a-th age fish to all the fish used for age determination and fallen to the length class, then by

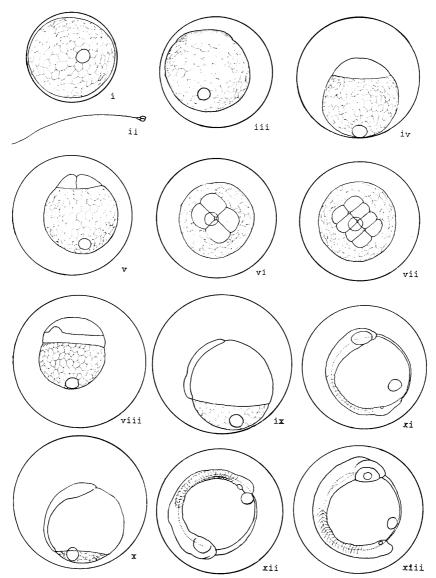
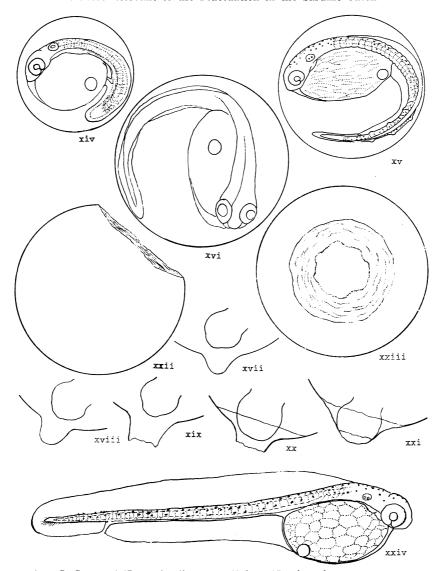


Fig. 3. Different developmental stages of Sardinops melanosticta in reference to Table 1* (after Nakal 1962b).

- i. A'-Stage: unfertilized egg, 1.020 mm in diameter, 0.974 mm in yolk diameter.
- A spermatozoon: 0.045 mm in total length, obtained off Hosojima, Miyazaki Prefecture, at 0120 on March 9, 1943.
- Aaa-Stage: egg membrane not yet heaved, 1.30 mm in diameter, one hour after fertilization.
- iv. Aaa-Stage: uncleavage, 1.42 mm in diameter, 1 hr. 8 min. after.
- v. Aaa-Stage: 1st cleavage 1.39 mm in diameter, 1 hr. 15 min. after.
- vi. Aaa-Stage: 2nd cleavage 1.39 mm in diameter, 1 hr. 35 min. after.
- vii. Aaa-Stage: 3rd cleavage 1.39 mm in diameter, 2 hrs. 5 min. after.
- viii. Aa-Stage: germ ring formed, 1.67 mm in diameter, 16 hrs. after.
- ix. Ab-Stage: 1.67 mm in diameter, 19 hrs. 5 min. after.
- x. Ac-Stage: 1.64 mm in diameter, 22 hrs. after.
- xi. Ba-Stage: myotome distinct, 1.59 mm in diameter, 25 hrs. after.
- xii. Ba-Stage: Kupfer's vesicle distinct, 1.59 mm in diameter, 33 hrs. after.
- xiii. Bc-Stage: optic vesicle distinct, 1.61 mm in diameter, 43 hrs. 15 min. after.



- xiv. Ca-Stage: 1.47 mm in diameter, 49 hrs. 25 min. after.
- xv. Cb-Stage: 1.68 mm in diameter, 53 hrs. 35 min. after.
- xvi. C'b-Stage: the egg immediately before hatching, 1.71 mm in diameter obtained off Makurazaki, Kagoshima Prefecture, at 0842 on March 14, 1950 (The data is also for xvii-xxiii)
- xvii-xxi. Successive changes in a projection and an opening that occurred on the egg membrane at the time of hatchings: from the beginning of the projection at 8 hrs. 41 min. 50 sec. after (xvii) till the head completely came out about two minutes later (xxi); the whole body came out another two minutes later.
- xxii, xxiii. The empty egg from which the larva hatched out; 1.71 mm in diameter, opening, 0.57 mm in diameter. Note the loosen surrounding area of the opening.

xxiv. Larva; 12 hrs. after hatching out, total length 4.5 mm.

* Unless specified otherwise, the material in each figure was obtained before and during the fertilization experiment off Hosojima, Miyazaki Prefecture, which was commenced at 2145 on February 19, 1941. The sketches are not always in a natural position nor made on the same individual except v through vii.

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summing up the products for that age group, by the following formulae (NAKAI and HAYASHI 1962a).

$$N_a'' = \overline{N} \sum_i p'(n)i \cdot (n_{ai}/n_i),$$

$$W_a'' = W \cdot \sum_i p'(w)i \cdot (n_{ai}/n_i),$$

where,

 N_a'' : number of a-th age fish,

 W_a'' : weight of a-th age fish,

N: total catch in number,

W: total catch in weight,

p'(n)i: ratio of number of fish in i-th length class,

p'(w)i: ratio of weight of fish in i-th length class,

 n_{ai} : number of fish in *i*-th length class, which were determined to be a-th age,

 n_i : number of fish in i-th length class, which were determined by age.

Estimation of egg abundance in the sea: As the sardine spawn only in limited waters along the coast, the total egg abundance is estimated on the basis of the mean egg counts per haul, duration of time and survival rate for development in every month and subarea as well as coverage of the subarea. Subdivisions of the spawning area are arranged in reference to the horizontal distributions of eggs and collecting stations, topographical conditions of the spawning ground such as the distance from shore and the depth, and other knowledge pertaining to the spawning with the use of following formula (NAKAI and HATTORI 1962).

$$E = \sum_{i} (\bar{R} \cdot A_i / \bar{S} \cdot \Delta A) \sum_{j} (\bar{x}_{ij} \cdot D_j / d_{ij}),$$

where,

E: total egg abundance,

 x_{ij} : mean egg counts per haul in i-th subarea during j-th month,

 A_i : coverage of the sea in *i*-th subarea,

 ΔA : opening area of a plankton net,

R: mean straining coefficient of the net,

S: mean survival rate in egg stage,

 D_j : number of days in j-th month,

 d_{ij} : number of days required for hatching in i-th subarea during j-th month.

Variance of the estimate of egg abundance is computed by

Var.
$$(E) = \sum_{i} (R \cdot A_i / S \cdot A)^2 \sum_{j} (\sigma_{ij} \cdot D_j)^2 / d_{ij}^2 \cdot n_{ij}$$
,

where, Var. (E): variance of total egg abundance,

 σ_{ij} : standard deviation of mean egg counts per haul in *i*-th subarea during *j*-th month,

 n_{ij} : number of collections in *i*-th subarea during *j*-th month.

Chapter 1. Biological synopsis

Among several species of sardines distributed all over the Far Eastern waters the most commercially important is *Sardinops melanosticta* (TEMMINCK & SCHLEGEL). Related species occurring in subtropical regions as around the Ryûkyû Archipelago and Bonin Islands are *S. immaculata* (KISHINOUYE) and a few species belonging to the genus *Sardinella*: *S. sindensis* (DAY), *S. jussieu* (LACÉPÈDE), *S. melanura* (CUVIER), and *S. clupeoides* (BLEEKER). However, catches of the sardines other than *Sardinops melanosticta* have been insignificantly small. In a statistical reference at hand, some amounts of these sardines as well as anchovies landed on Okinawa and the neighbouring islands during 1913 through 1944 are combined together and made entry under a commercial name "*iwashi*". At no time during that period has landings of the *iwashi* on those islands ever reached beyond 300 tons a year. Therefore, one needs not to take those species but *S. melanosticta* into consideration in discussing sardine fisheries in the Far East.

In this paper, the English name "Japanese sardine" or simply "sardine" denotes only *Sardinops melanosticta*. "*Maiwashi*" is the Japanese standard common name of this species.

The general biology of the Japanese sardine is summarized in this chapter.

Section 1-1. Identity

Generic designation:

Genus Sardinops, Hubbs 1929

Type species: Maletta caerulea GIRARD 1854 (original designation)

"Clupeidae with the upper jaw not notably notched on the mid-line; the gill-rakers of the upper limb folded over those of the lower limb, which become markedly and progressively shortened toward the angle; carina of glossohyal not denticulate; no bilobed dermal flap on shoulder-girdle; opercle with strong and markedly oblique ridges; preopercular edge strongly sloping; interopercle widely exposed behind preopercle; scale-rows regularly spaced, the lateral scales all with subequal exposed area; radii on the scales nearly vertical, and paired on each side of median line; keels on ventral scutes weak, last two rays of dorsal and anal fins somewhat enlarged; a row of dark spots typically developed on upper sides behind head" (Hubbs 1929, p. 264).

Specific diagnosis:

Sardinops melanosticta (Temminck & Schlegel 1846)

1846 Clupea melanosticta, Temminck & Schlegel, p. 237, pl. 107, fig. 3.

1868 Clupea melanosticta, Günther, p. 443.

1900 Clupanodon melanostictus, JORDAN & SNYDER, p. 349.

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1906 Sardinella melanosticta, Jordan & Herre, p. 632.
1908 Clupea melanosticta, Kishinouye, pp. 101, 102, pl. 17 & pl. 21, fig. 1.
1912 Amblygaster melanostictum, Snyder, p. 402.
1930 Amblygaster melanostictus, Fowler, p. 590.
1931 Sardinia melanosticta, Schmidt, p. 19.
1935 Sardinia melanosticta, Okada, Uchida & Matsubara, p. 65, pl. 15, fig. 1.
1938 Sardinia melanosticta, Okada & Matsubara, p. 40.
1941 Arengus sagax, Fowler, p. 622 (non Jenyns 1842).
1955 Sardinops melanosticta, Matsubara, p. 191.
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"Cette troisième Clupe du Japon a le coaps plus comprimé et un peu plus élevé que la précédente, son ventre est tranchant et dentelé; l'anale est plus grande, enfin la distribution des teintes et les proportion des autres parties offrent des traits nombreux et faciles à saisir, au moyen desquels on puisse distinguer cette espèce deux précédentes.

La tête est quatre fois et un tiers, la hauteur du tronc cinq fois et un tiers dans la longueur totale du poisson. Le diamètre transversal du tronc fait la moitié du diamètre vertical. La longueur du museau, d'un tiers plus considérable que le diamètre de l'oeil, entre trois fois et un quart dans la longueur de la tête. La bouche est oblique et fendue jusque sous l'aplomb du diamètre vertical de l'oeil. La mâchoire supérieure est assez sensiblement échancrée de chaque côté. Il existe des dents en velours excessivement fines sur la langue, mais je n'en ai pu trouver ni dans les mâchoires ni dans les autres régions de la bouche. L'opercule forme, vers le bas, un angle arrondi et trèspeu saillant. Le ventre, quoique peu comprimé, est recouvert d'une rangée d'écailles assez dures et pourvues chacune au milieu d'une carène à pointe saillante en guise de scie. Les écailles des autres parties du corps sont de grandeur moyenne, très-minces et sujettes à tomber failement. L'anus s'ouvre sur le commencement du dernier tiers de la distance comprise entre l'extrémité du museau et l'énchancrure de la caudale. La linge latérale est droite, et un peu plus rapprochée de celle du dos que de celle du ventre.

Quant aux nageoires, la dorsale est un peu plus raprochée de l'extrémité du museau que de la base de la caudale, elle est beaucoup plus basse par derrière que par devant, où sa hauteur est un pue plus considérable que la moitié de la hauteur du tronc. Les pectorales naissent, un peu vers le bas, sous l'angle de l'opercule; leur longeueur fait un peu moins de deux tiers de la longueur de la tête. Les ventraux naissent sous la fin de la dorsale, et occupent le milieu de la distance comprise entre l'aiselle des pectorales et l'orifice de l'anus. L'anale est basse et de longueur moyenne. La caudale est profondément échancrée. B. 7; D. 17; A. 17; V. 8; P. 16; C. 16.

Les parties inférieures de ce poisson sont, à l'état frais, d'un blanc argenté; cette teinte passe au bleuâtre sur les flancs et au dessus de la ligne latérale, au bleu d'acier tirant au verdâtre sur le haut du dos qui est orné, de chaque côté, d'une triple rangée de points noirs excessivement fins. On observe sur la ligne latérale

une rangée de taches orbiculaires et noirâtres, au nombre de douze à quinze de chaque cote du corps. La caudale est d'un vert brunâtre foncé. Les autres nageoires et la tête sont d'un bleuâtre très-pale et unancé de brun jaunâtre où de brun rougeâtre; mais le dessus de la tête est d'un vert bleuâtre claire. L'iris de l'oeil est d'un blanc argenté.

Ce poisson dépasse rarement cinque à six pouces en longueur totale. Son nom japonais est Maiwashi. Il se pêche le long des côtés du Japon, particulièrement dans les mois d'automne, et le nombre qu'on en prend est souvent tellement considérable que l'on s'en sert comme engrais pour les terres" (TEMMINCK & SCHLEGEL 1846, as *Clupea*).

"B. 6. D. 17-18. A. 16-17. L. lat. 45. L. transv. 13.

The height of the body is less than the length of the head, which is contained thrice and three-fifths in the total (without caudal). Scales regularly arranged, thin, deciduous, with the margin entire. Lower jaw rather projecting beyond the upper; the maxillary extending beyond the front margin of the orbit. Bands of minute teeth on the palatine and pterygoid bones, and on the tongue; none on the vomer. Cheeks with venules; opercles smooth. Gill-rakers a little shorter than the eye, very fine, and closely set. Eye of moderate size, shorter than the snout, two-ninths of the length of the head. Ventral fin inserted below the posterior half of the dorsal fin, the base of which occupies the middle of the distance between the end of the snout and the route of the caudal fin. There are thirteen abdominal scutes behind the ventral fin. Sometimes a series of round bluish spots along the middle of the side. China and Japan" (GÜNTHER 1868, as Clupea).

Remarks: Fowler (1941, p. 620) synonimized Sardinops Hubbs 1929 and Sardina Antipa 1906 (which had been treated by Jordan 1918 as a synonym of Sardinia Poey 1860) with Arengus Cornide 1788. Thus, Fowler (loc. cit. p. 622) regarded

Country	Standard common names	Size of fish	Vernacular names
Japan	maiwashi	small size and juvenile	aoko, dobu, gakubari, goda, gotta, goza, hirago, hiyogo, koba, kobera, kobira, kobirago, masago, seirei, shirasu, tatsukuri.
		medium size	chûba, kochûba.
		large size	hirago, ôba, ôiwashi.
		general	ginmushi, himiiwashi, hira, hirago, hirago- iwashi, hirameiwashi, hirare, hirayuwashi, kabudaka, kakarimeiwashi, maio, morokuchi, murasaki, nanatsuboshi, nanman'yu, ohoso, omura, orasha, oiwashi, sashiamiiwashi, shoiwashi, yashi, yatsume, yuwashi, uwa.
Korea	chong-o-ri		
U. S. S. R.	Ivassi or ivashi (ИВАСИ)		

Table 2. Standard common names and vernacular names of the Japanese sardine.

Clupea melanosticta TEMMINCK & SCHLEGEL as a synonym of Arengus sagax (JENYNS). However, as there is a room for further discussion on Fowler's classification as pointed out by MATSUBARA (1955), the present author prefers to take the scientific name of Sardinops melanosticta for this species.

Common names: As sardine have been very popular among people almost in every part of Japan since early times, there may be more vernacular names than those enumerated in Table 2 at different localities and by size of fish. In some cases the vernacular names are loosely applied to different stages of anchovy and round herring; it is especially difficult, unless one is well acquainted with the vernacular usage at a particular locality, to distinguish by these names juvenile forms of these species from each other.

Subspecific fragmentation: TARANETZ (1937b) found no difference in the structure of the scutes of Sardinops melanosticta and S. caerulea; and slight differences in the number of gill rakers, numbers of scales on the lateral line and vertebrae, and on several other points. But on the basis of the fact that there are no distinct difference between the two forms, he considered that these are regarded as subspecific differences, i.e. as between Sardinops melanosticta melanosticta and S. melanosticta caerulea.

AMEMIYA and TAMURA (1943) also concluded that the differences between *Sardinops melanosticta* and *S. caerulea* should be that occurring within a single species, namely, between varieties or subspecies, as they could not find any specific differences in many of the characters examined, except head length and numbers of ventral scutes and vertebrae.

REGAN (1916) stated that the Japanese sardine could be statistically considered as a subspecies of *Sardina sagax*. Fowler (1941) considered *Clupea melanosticta* TEMMINCK & SCHLEGEL was conspecific with *Arengus sagax* (JENYNS 1842) which THOMPSON (1926) regarded identical with *Sardinops caerulea*.

Meristic variations: On the vertebral counts of the sardine, a tremendous amount of works has been published in Japan since the 1930's. Such examples as shown in Table 3 may give an aspect of the organized work on this problem. Adduction from several workers indicates the ranges of seven meristic characters listed in

Year	Number of individuals examined	Mean vertebral counts	Standard deviation
Up to 1940*	25, 855	50. 69	0. 55
1949**	1,099	50. 53	0.61
1950**	4, 348	50. 54	0.66
1951**	7, 347	50. 59	0.64

Table 3. Mean vertebral counts of sardine by year.

^{*} Calculated from AMEMIYA and TAMURA (1941).

^{**} After Nakai et al. (1955).

Charac- ters	TEMMINCK and SCHLEGEL 1846	Günther 1868	JORDAN and HERRE 1906	Kishi- Nouye 1908	SOLDATOV and LINDBERG 1930	Boese- MAN 1947	AMEMIYA and TAMURA 1943	TANAKA 1951
Dorsal fin	17	17, 18	16, 17	17-19	17-19(20)	18(I), 19(I)	18-20	16, 17
Pectoral fin	16	_	17	19		17	16-19	-
Ventral fin	8	_	8	8	(7)8(9)	_	7–9	_
Anal fin	17	16, 17	17	18, 19	(16)17-19(20)	18(I)	_	17
Caudal fin	16	_		_	_		· _	_
Scales: Transv. Lateral		13 45	 45	$\frac{12}{52-54}$	(48)49, 50(51)	=		— 45
Vertebrae	_	_	_	51	_	_	49-52	_

Table 4. Range of seven meristic counts of sardine by several authors.

Table 4.

Section 1-2. Distribution and migration

Delimitation of the total area of distribution: According to KISHINOUYE (1908), who gave the first significant scientific account of the distribution of the Japanese sardine, the species occurs in the coastal waters around Japan and Korea, but not in such areas as south of Izu Islands and Amami-Ôshima, western Hokkaidô, Kurile Archipelago and Sakhalin. However, the distribution range has changed during the the last half century (Sections 2-1, 2 and 3). Later investigations showed the fish to occur also in some other localities.

Japan—The fishing grounds are found in the coastal waters, excluding Bonin Islands and Ryûkyû. Though no precise record is available for Amami-Ôshima, it is said that the species has rarely been observed there. The centre of fisheries has been changing from year to year, the species at present being most abundant in the areas covering northwestern Kyûshû and the Japan Sea coast of Honshû (Section 2-1).

Korea—In the pre-war period, sardine were chiefly fished along the Japan Sea coast of Korea (Section 2-1). Catches were also obtained from coastal waters along the Tsushima Straits but very little from the Yellow Sea coast of Korea. There is no information available as to the present status of the fish in these waters, but it is inferable that the fish would be present even if the stock was not large enough to be commercially exploited.

U.S.S.R.—TARANETZ (1937a) found the sardine in the years warmer than the usual, in the areas as far north as the Gulf of Tartary, Sakhalin and the eastern coast of the Kamtchatka Peninsula (Kronotzki Cape and other localities).

Chinese waters—GUNTHER (1868) collected a specimen of the Japanese sardine in China. On the other hand, KISHINOUYE (1908) stated that there was no reliable indication of the presence of the species in that locality. Also the author has not heard of the fish being caught there. It is probable that the species is scarce or not present at all in Chinese waters.

Differential distribution: The eggs and larvae used to appear around the Satsunan Area situated off the southern tip of Kyûshû until the years following the World War II, when the centre of the spawning ground was found to be moving to the northwestern waters off Kyûshû. More recently, the eggs and larvae have been found along the Japan Sea extending northward from Kyûshû to the western shore of Aomori Prefecture. These and other junior stages are frequently drifted away from the coastal areas mentioned above by the water current. Such occurrences in regard to geographic distributions of eggs, larvae and adult forms of sardine are described in Sections 1–3 and 2–3.

From February to March the eggs and larvae are distributed around Kyûshû. In May to June they move northward to the Japan Sea coast of northwestern Honshû, though they are sometimes found on a very small scale on the Pacific side, from Hyûga Nada to Kashima Nada.

The distribution of the fishing ground should be related to that of matured fish (Section 1-7).

Determinants of the geveral limits of distribution: On 23 October, 1923 an abrupt decrease in the surface temperature to 6.2° nearly 7°C lower than the average, was noticed around Cape Bolten on the eastern coast of North Korea (Fig 4). NAKAI (1939) postulated that the above phenomenon was directly responsible for the mass mortality immediately observed. On 12 to 14 November, 1933 a similar case but with lower mortality, was reported by KURAGAMI and KAWANA (1934), near Erimosaki, Hokkaidô where the water temperature dropped to 6°C.

As the sardine under experiment were able to live in water of 7-29°C (SUEHIRO 1936), the decrease of the temperature to 6-7°C should be regarded as responsible for physical disturbance of sardine resulting in death.

Sardine, being plankton feeders, are not distributed far offshore where planktonic organisms are scarce (NAKAI *et al.* 1955). From investigations carried out in the Japan Sea in 1940-41, NAKAI (1942) noticed that the migratory routes seemed to follow areas densely populated with food plankton.

Migration and local movements: In the prosperous period when any group of sardine greatly outnumbered the others, the migratory route of that particular group could usually be clearly traced. The group were spawned in the Satsunan Area, off-shore the southern tip of Kyûshû, in winter and early spring, and drifted along the Kuroshio Current up to the Bôsô Peninsula, Chiba Prefecture, in their planktonic life including egg and larval stages. After having passed the first year of life there,

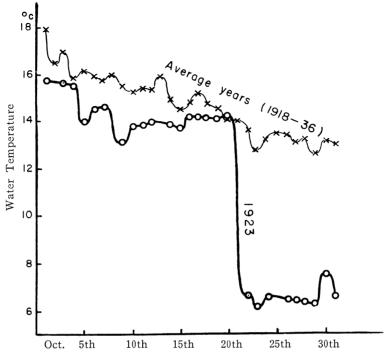


Fig. 4. Comparisons of water temperatures at the foot of Cape Bolten Lighthouse between October 1923 and the co-ordinate average 1918-36 (after NAKAI 1939).

I-age fish migrated northward up to Hokkaidô in the warmer months of the year (AIKAWA and KONISHI 1940, KAGANOVSKII 1931, NAKAI 1949 and 1960). In their second autumn, I-age fish took a southward trip to spend the winter in the waters around the Bôsô Peninsula. In the following spring the fish, II-age, migrated northward back to the waters around Hokkaidô. In the third autumn, the fish rapidly migrated, through the Tsugaru Straits and across the Japan Sea, down to the Satsunan Area for their first spawning. In the next spring the adult fish moved along the Japan Sea coast of Honshû and Korea, reaching the coastal waters of Hokkaidô, Sakhalin and the Coast Range in the early summer. In the autumn months, the adult fish were exploited in the coastal waters of Korea. In the subsequent years, the adults repeated the northward migration in spring and early summer and the southward one in autumn. Since the decline of catch after 1940, the dominant stock disappeared and any noticeable migratory route has not been found (Section 2-3).

Schooling: Sardine aggregate in the coastal area at the *kaeri* stage; but no sufficient evidence has been made available for discussing the schooling behaviour of adult fish.

Section 1-3. Spawning activity

The temporal and spacial variations of the spawning activities during 1949 through 1951 were determined on the basis of plankton net collection in the nation-wide scale.

Regional, seasonal and yearly variations: According to the aforementioned investigations, the sardine eggs were found to occur abundantly in the general area covering the Gotô Island, Iki Straits and Tsushima Straits from January to March. In April the distribution was plentiful in the waters reaching from the north of Yamaguchi Prefecture to the Noto Peninsula, and in May around the Noto Peninsula and Sado Island. The above fact indicates that locality of the spawning ground of sardine, which centered heavily at waters around the Gotô Islands in January to March appeared to transport northward as the season went on, having reached to the sea off the Noto Peninsula, the largest spawning centre next to the Gotô Islands area, about May. In the Pacific waters, the sardine eggs occurred but much less in amount than in the areas northwest of Kyûshû and in the Japan Sea. Barely appreciable amounts of the eggs were collected in the vicinity of the Ösumi Straits and Hyûga Nada in February and March: then in March through May the fish spawned in the sea extending from Sagami Nada to Kashima Nada, turning around the Bôsô Peninsula. In some years relatively thick spawnings were seen around the entrance to Tôkyô Bay and off Inubô Saki (cape), Chiba Prefecture (Fig. 5).

The sardine larvae were found distributed in the similar pattern as of the eggs, though the distribution range in Kyûshû area extended more southerly than that of the eggs (Fig. 6). This may be attributed to the dispersion of the larvae drifting in that direction along the surface current under the influence of the monsoon.

The above seasonal and spacial distribution pattern of the spawning activities did not indicate remarkable yearly fluctuation during 1949 through 1951. Although prevalent use of sonar fish finders introduced since 1951 gave rise to a fear of adverse effect on the sardine spawnings, the fact that no remarkable fluctuation was found between the spawnings in the three years seems to relieve the apprehension.

Through the investigations, the major spawning ground during the survey period was proved to have been located in the waters around Gotô Islands and Iki Straits: the number of eggs spawned there represented 34-52 percent of Japan's total. Among other areas, the vicinity of the Noto Peninsula produced 20-30 percent, and the western half of the Japan Sea, 15-16 percent of total egg abundance.

According to the investigations, the spawning amounts in March of 1949, 1950 and 1951 represented, in this order, 39, 35 and 29 percent of the yearly total. The second largest spawning occurred in May in 1949 and 1950, or April in 1951 (Fig. 7). Referring to region, the following are season-area combinations, in which the eggs were abundantly discovered, though scarcity of stations in the northeastern Pacific waters made the distribution picture thereof obscure:

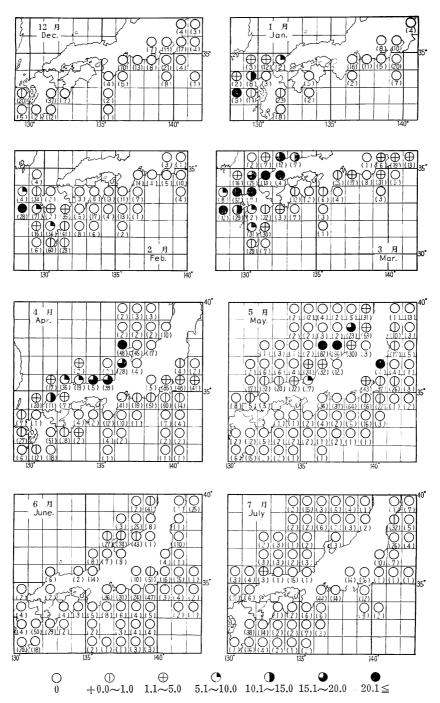


Fig. 5. Average distribution of sardine eggs in spawning month, 1949-51 (after Nakai and Hattori 1962).

Number of sardine eggs per one square meter of the area in 1° square of Latitude and Longitude. Not adjusted for the amount of water strained by the net. Numerals within parentheses show number of hauls.

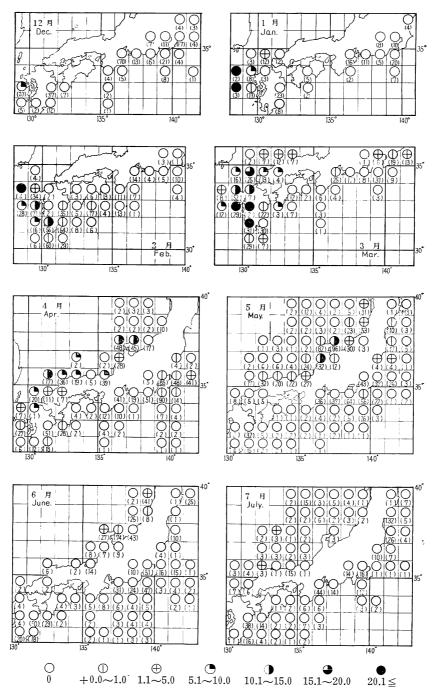


Fig. 6. Average distribution of sardine larvae by spawning month, 1949-51 (after Nakai and Hattori 1962).

Number of sardine larvae per one square meter of the area in 1° square of Latitude and Longitude. See footnote of Fig. 5 for other information.

- 1. Pacific waters north of Lat. 36°N up to the coast of Hokkaidô: May to July in general.
- 2. Pacific waters south of Lat. 36°N, east of Long. 135°E: March to May in 1949 and 1950, March to June in 1951.
- 3. Pacific waters between Long. 135° and 131°E: April 1949, January to March in 1950 and 1951.
- 4. South of Lat. 32°N, west of Long. 131°E: February to March in the three years.
- 5. North of Lat. 32°N, west of Long. 131°E: January to April 1949 and 1950, December 1951.
- 6. Japan Sea between Long. 131° and 135°E: July 1949, March to May in 1950 and 1951.
- 7. Japan Sea south of Lat. 42°N, and east of Long. 135°E: April to June in the three years.

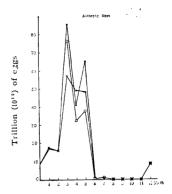


Fig. 7. Monthly fluctuation in abundance of sardine eggs, 1949-51 (after NAKAI and HATTORI 1962).

O: 1949, ●: 1950, ×: 1951.

During the period the number of eggs spawned in the waters around Japan was estimated to be 200-230 trillions with coefficients of variation of about 10 percent (Table 5). In the light of the variation coefficients, annual differences in the estimates of egg abundance are deemed negligibly small. The fact that no remarkable

Table 5. Abundance of sardine eggs in Japanese waters, 1949-51 (after NAKAI *et al.* 1955).

(Unit: Trillions of Eggs)

Year	Egg abundance	Variation coefficient
1949	198. 00	% 12
1950	234. 86	9
1951	197. 59	10

change was found among the annual total egg abundances suggests that the population of the parents have been in stability till 1951 since they were born. Therefore, it is hardly conceivable that the fishing intensity exerted at least in these years was so heavy as to have had an adverse effect on the stock of sardine. In the present study, however, time factor affecting the distribution could not be taken enough into account because of insufficient

amounts of data. For this reason further consideration has to be paid in that respect along with methods for sampling and estimation.

Spawning hours of the day: In ascertaining as to what time of the day the sardine are likely to spawn for the most, the egg of stage Aa, the very earliest period of life, is defined as that which blastoderm keeps growing until to expand, in lateral view, to one-third of the yolk in diameter. During the survey period, 3,128 eggs of stage Aa were collected from 353 vertical hauls out of 3,666 stations integrally occupied in the spawning area-months exclusive of many other stations, which failed in securing an exact time of the occurrence, or when the covering area-months of them produced no egg of this stage.

The occurrence of stage Aa was the most abundant during 0700 (7 o'clock a.m.)

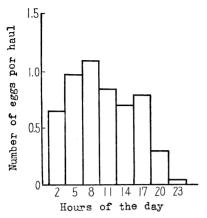


Fig. 8. Number of sardine eggs at Aa-stage by hours of the day, 1949-51 (after NAKAI and HATTORI 1962).

to 0900 hours, followed by other times of the day from 0100 to 1800 (6 o'clock p.m.) hours, but an abrupt decrease in number was noticeable during the night from 1900 to 2400 hours (Fig. 8). Such a wide range of the occurring time might have been resulted from entire region of Japanese waters during the three years, in which temperature and other factors controlling the growth of Aa stage must have been different depending upon locality and season.

However, at the average spawning temperature of 14.2°C obtained for the survey period, 18 hours would be required to complete stage Aa, and therefore nine hours for the

early half of the duration (Section 1-4). By retroceding nine hours back from 0700-0900 hours, when the majority of the youngest eggs occurred, it may be resonable to assume that the most active spawning of a day would have taken place during 2200 to 2400 hours of the previous night. The estimation is nearly in agreement with the result of study on the sardine in the Japan Sea by ITÔ and YAMAGUCHI (1952) and on the related species in California by Ahlstrom (1943), as those authors determined the spawning time of respective species to be 2000 to 2400 hours.

Distance of spawning ground offshore: Sardine eggs occurred and were success-

fully collected at 659 stations out of 4,704 occupied in the whole area during the survey period. Frequency of successful stations on the continental shelf bounded by 200 m-depth contour line (C-0) was 19 percent to the total stations occupied. The frequency in the zones 10, 20 and more miles seaward from the continental edge (C-1 to C-3) was 8, 4 and only 0.4 percent, respectively. The high frequency for inshore stations (C-0) where the eggs were collected would become still higher when stations taken in enclosed waters, such as Tôkyô Bay, Mikawa Bay and Ise Bay hardly producing sardine eggs, are excluded from the total stations occupied. Consequently, it may be concluded that sardine spawn in profusion over the continental shelf but rarely in the high sea beyond 20 miles seaward of 200-m depth contour

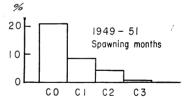


Fig. 9. Ratio of stations at which the sardine eggs were collected to the total stations occupied in each distribution zones*, 1949-51 (after NAKAI et al. 1955).

- * Distribution zones
- C-0: Inshore of 200-m depth contour line.
- C-1: 10 miles seaward of the line.
- C-2: Between 10 and 20 miles seaward of the line.
- C-3: More than 20 miles seaward of the line.

(Fig. 9).

As to frequency of successful inshore stations within 10 miles off the contour lines (C-0 to C-1) in the course of the survey period, the peaks appeared in April in 1949 and 1950, or in March in 1951, with a few favorable months on each side of the modes (Fig. 10).

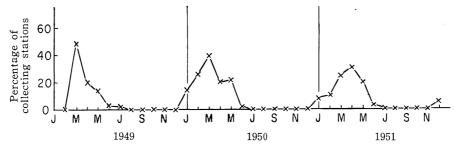


Fig. 10. Ratio of inshore stations* collecting sarding eggs by month, 1949-51. (after Nakai et al. 1955).

* Occupied in the zones extending from the shore to 10 miles beyond the 200 m-depth counter line. The number of such stations was 5,112 throughout the period.

On the one hand, eggs in A-stage, both fertilized and unfertilized but whose blastopore has not yet disappeared, are abundant in waters on the continental shelf. On the other hand, they were decreasing in number with the distance increasing seawardly, and almost ceased to exist in the high sea more than 20 miles off the 200-m depth contour. In the zone C-1 the eggs in stage C with the tail bud separating off the yolk were found dominant over the earlier stages. These evidences indicate that the greater majority of eggs are spawned closely to the coast, and when developed, some portion of them are carried offshore by currents.

Water temperature and chlorinity in spawning grounds: In connection with the development of sardine eggs, the environmental conditions such as temperature and chlorinity of spawning grounds were investigated. The ranges of surface temperature in waters where the eggs of stage-Aa occurred were in Centigrade: 11.1-17.6° in 1949, 12.0-18.6° in 1950 and 12.6-19.1° in 1951; the annual average weighted by number of eggs of Aa-stage in each successive year, 13.2°, 14.8° and 14.4°; the three year average weighted alike was 14.2°. When weighted by number of stations where the eggs occurred, the annual average temperatures are successively 14.8°, 15.4° and 14.9°, and the three-year average 15.1°. It is conceivable from these findings that the spawning of sardine during the three years was at its height within the temperature range of 13 to 16° (Fig. 11). Chlorinities of surface water at stations hauling the eggs of stage Aa ranged from 18.3 to 19.4 permil throughout the survey period with a single exception of 17.6 permil. Chlorinity of 18.82 permil was the three-year average weighted by number of Aa-eggs and 18.95 permil was that by

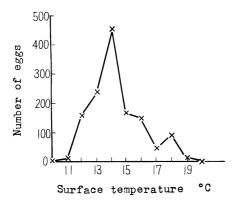


Fig. 11a. Relationship between number of sardine eggs at Aa-stage and surface temperature, 1949-51 (after NAKAI and HATTORI 1962).

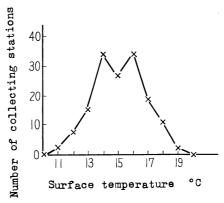


Fig. 11b. Relationship between number of stations collecting sardine eggs and surface temperature, 1949-51 (after NAKAI and HATTORI 1962).

frequency of collecting stations. Sardine seem to spawn plentifully in waters where the chlorinity ranges from 18.5 to 19.2 permil, as the eggs of Aa stage were more oftentimes collected within that range.

Section 1-4. Early development

When essential data are available, total number of eggs spawned by the fish population, which produces pelagic eggs, can be estimated on the basis of net collection. Primary data that have to be provided for the estimation include the rate of fertilization, and the duration of time required for and the survival rate during the embryonic development. These factors are affected by the environmental conditions as well as genetical, physiological and ecological features of the parents and eggs.

Rate of fertilization: In the previous works, no satisfactory accounts have been given on fertilization rate of sardine under rearing condition (Fisheries Institute of Kyôto Prefecture 1930, 1931, KOBAYASHI 1944, MILLER 1952). No report based on the net collection appeared with regard to the fertilization rate of the Japanese sardine. The following paragraphs present the author's estimates of the rates on the bases of a rearing experiment and an examination of the egg samples collected by the plankton nets.

(i) Rearing experiment: For determining fertilization rate and time for completing fertilization, a rearing experiment was conducted in February 1941. The materials* thus far examined were obtained from the sardines caught by drift net

^{*} The unfertilized egg obtained from the parent fish was measured 1.020 mm in diameter and 0.974 mm in yolk diameter. The spermatozoon was measured 0.045 mm in total length. The head of it was apparently consisted of two parts of equal size, and was measured 0.0016 mm in length. The middle piece (neck) was measured 0.0014 mm in length (Fig 3).

off Hosojima, Miyazaki Prefecture. They were fertilized artificially by the dry method with sea water being added five to ten minutes after the beginning of the work. During the first 25 hours of the experiment, samples were eight or nine times taken out of the eggs under breeding to count the number of the fertilized

ones and the unfertilized ones which were determined as such by width of the perivitel-line space and the egg diameter (Figs. 3 and 12). With a view to keeping a bias of the sampling at minimum, the water was stirred around slowly before each sampling. Soon after taking them out of the water with help of a pipette the eggs were fixed in ten percent formalin. In the aquarium the water temperature was 16.0°C at the start, lowered to 15.6°C and rised again to 16.2°C during the earliest six hours of the work (Fig. 13).

The earliest activity occurred with fertilization rate at 22-25 percent in the first one hour when the temperature was at 16.0°C. In the period of lower temperature, the eggs stopped, for a while, being fertilized. Two hours after the work set in, the temperature started to rise and was restored to 16.2°C shortly before another hour past. It was

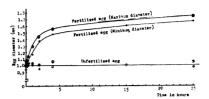


Fig. 12. Comparisons of development between diameters of fertilized eggs and unfertilized eggs in the experiment (after NAKAI 1962b).

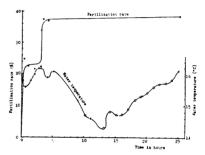


Fig. 13. Changes of fertilization rate and water temperature (after NAKAI 1962b).

about that time when the second activity commenced to take place with the rate rising to 38 percent. Then the fertilization apparently ceased to continue any longer. The fact that the first and the second activities were both nearly coincidental in the temperature standing at around 16°C with an apparent intermission in lower temperature may indicate 16°C as a lower limit of temperature good for fertilization. If the temperature could be kept above that level, the eggs might have been fertilized at a higher rate with the effective period for activity possibly extending longer.

A general picture that has been made clear so far is that fertilization rate under the experimental condition was slightly less than 40 percent, that the effective period for making the ova and sperms fertilized lasted at least for about five hours after catch of their parents, that the eggs were fertilized immediately after encounter with the sperms, and that occasionally they would be fertilized at intervals of time.

(ii) Study relevant to net collection: It has been known from the above experiment that about 40 percent of eggs were capable of being fertilized under rearing conditions in five to six hours after catch of their parents. However, these results obtained from only a couple of parents do not seem to warrant a few ques-

tions as to whether they were really satisfactory and conclusive.

For this reason it is not feasible to assume this value for fertilization rate in nature. According to the net samplings in spawning surveys since 1936, the surface collections for eight years ending in 1943 indicate that the number of sardine eggs collected at 676 stations was 395,910 of which no more than seven collected at merely four stations were determined as unfertilized eggs. Scarcity of unfertilized eggs in the netted samples may be interpreted that, in case of natural spawning, almost all the sardine eggs can be fertilized in such a short spell with very little space and time to cover in their prefertilization period. However, if the fish discharged the ova and sperms on a layer near the bottom to let them stay there and fertilized little by little through the pre-fertilization period effective for about five hours, and if only fertilized eggs floated up to the surface with no regard to the rate, few or no unfertilized eggs would possibly be collected by surface haulings.

Although neither these questions nor fertilization rate in nature have been made certain so far, samples taken from the bottom of stations where eggs in the early stages occurred heavily presented very few amounts of unfertilized eggs as well. From these findings it may be appropriated to support the above assumption—fertilization in nature would be carried out for practically all the eggs almost a moment after being discharged.

Effect of temperature on embryonic development: Except a few cases referred to by Nishikawa (1903), no satisfatory result has likely been described in regard of the relationship between temperature and development of the eggs of Japanese sardine. For a related species, Pacific sardine, two workers have made their effort on this subject (Ahlstrom 1943, Miller 1952).

The materials and data for the present works include those obtained from the artificial fertilization at the sea off Hosojima in 1941 and the pelagic eggs and the surface temperature made available from surveys carried out in the waters around Kyûshû and off the Pacific coast during 1949 through 1951.

(i) Rearing experiment: It is impossible to compare the time-temperature relationships in detail with the obtained data, for everyone of the experiments was not provided with satisfatory conditions in respect of sampling and proceeding temperatures. Nevertheless, every stage prior to gastrula was found to have been nearly in agreement with the result of the Pacific sardine (MILLER 1952) despite the mean temperature of the former being somewhat higher than that of the latter. On the other hand, another experiment of the Japanese species (KOBAYASHI 1945) is about one hour late from the development by the other authors (Table 6). According to KOBAYASHI (*loc. cit.*), the temperature, which was 13.5° at about one hour after pouring the sperms over the ova, was made to keep 20.0°C for the following period. There is no information about the mean temperature for 200 minutes that followed the fertilization in his study. But it may be reasonable to analogize from

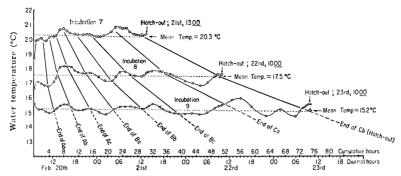


Fig. 14. Development of eggs under three different temperature levels. (after Nakai 1962b).

Table 6. Comparison between the present and the previous works on the time required for early development of sardine eggs (after NAKAI 1926b).

		Japanes	Pacific sardine			
Cleavage division	One of the present experiments		Ковачаѕні (1944)		Miller (1952)	
	Time passed (hrs. mins.)	Time intervals (mins.)	Time passed (hrs. mins.)	Time intervals (mins.)	Time passed (hrs. mins.)	Time intervals (mins.)
First cleavage Second cleavage Third cleavage Fourth cleavage Fifth cleavage Sixth cleavage Seventh cleavage	1 08 1 35 2 05 2 25 2 35 2 45	27 30 20 10 10	2 20 2 40 2 50 3 20 —	20 10 30 —	1 30 2 00 2 15 2 30 3 00 3 30	30 15 15 30 30
Temperature range	18. 2-18. 6°C		13. 5–20. 0°C		16. 8°C	

Table 7. Time required for completing different developmental periods from beginning of experiment and mean temperature in incubations Nos. 7 to 9 (after NAKAI 1962b).

Series number of experiment	No. 7		No. 8		No. 9	
To* the end of	Time required (hrs.)	Mean temp. (°C)	Time required (hrs.)	Mean temp. (°C)	Time required (hrs.)	Mean temp. (°C)
Aa	2	20.00	3. 5	17. 02	5	15. 21
Ab	4	20.01	7	17. 16	10	15. 34
Ac	6	20.10	10	17.40	15	15. 30
Ba	9	20.14	15	17. 51	22	15. 24
Bb	12	20.20	20	17.50	29	15. 27
Вс	15	20. 23	25	17. 51	37	15. 28
Ca	22	20. 27	36	17. 56	55	15.26
Cb	30	20.34	50	17. 46	75	15. 23

^{*} From stage at the time the incubation experiment began.

these results that the mean temperature for that period did not exceed 16.8°C and would remain somewhere around 16°C at best.

A close check of the results obtained reveals that in a certain series of the present experiment the duration between two stages succeeding one after another is generally getting shorter with the progress of cleavage (Table 6). But no such tendency is always apparent in the work by Kobayashi (1944) and Miller (1952). In regard to a factor responsible for this difference which has not been made clear so far, further effort has to be made.

In order to see the influence of temperatures on the length of time required for development from the Aa' stage to hatching, three glass jars, each containing ten eggs, were prepared at 20.3°, 17.5° and 15.2° (Fig. 14). Time needed for hatching* five to seven eggs out of ten was 30, 50 and 75 hours after the beginning of

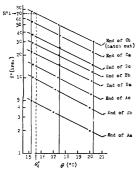


Fig. 15. Relationship between temperature (θ) and time required for the period from stage Aa' to a given later stage (H') (after Nakai 1962b).

each breeding (Table 7). According to the result, logarithm of time is nearly in linear relation with temperature within the above thermal range. These lines are almost parallel with one another (Fig. 15).

These facts indicate that among the different breedings the relationship between temperature and time leading to any developmental stage is definite. For instance, at the mean temperatures, 20.3°, 17.5° and 15.2°C, the times needed for hatching are 30, 50 and 75 hours, respectively, the times reaching stage Ca, 15, 25 and 37 hours, those up to stage Ba, 6, 10 and 15 hours, those up to stage Ab, 4, 7 and 10 hours. When the time duration at 20.3°C is taken as the standard, the ratios between the fertilization and these stages are roughly averaged to be 1, 1.7 and 2.5. On

the analogy of these findings it may be assumed that the time-temperature relationship for the period from immediately after fertilization until the beginning of the development of the materials incubated in separate vessels is the same as those calculated above. In that case and when one knows the mean temperature and length of the period before the separation, the length of time needed for them growing at anyone of changing temperatures during that period can be readily estimated as follows.

$$H_i = H'_i + H''_i \cdot \frac{H'_i}{H'_{i'}}$$

^{*} At the time of hatching, a portion of the egg membrane nearest to the head of the embryo produces a small swelling. The larva is ready to come out through an opening that is formed at the tip of the swelling. It normally takes four minutes and ten seconds for the larva to complete hatching in the rapid case. See Fig. 3 for the details of the process of hatching and the empty egg from which larva came out.

where, H_i : estimated length of time elapsing from fertilization to a given stage, S_a , at a temperature, θ_i ,

 H_i' : length of time from a mid-stage, S_m , to S_a at a temperature, θ_i' ,

 H_i'' : length of time from fertilization to S_m , at the mean temperature, θ_i' , for the period,

 $H'_{i'}$: length of time from stage S_m to S_a at a temperature, $\theta'_{i'}$.

In the work under report the eggs had been bred in the first aquarium for nine hours after the outset of fertilization till Aa stage when they were separated into three different jars at the mean temperature of 15.6°C. Let S_m represent the stage when they were separated under different temperatures; θ'_i , 15.6°C, H''_i , 9 hours (NAKAI 1962b); S_a the stage at hatching; then H'_i , is read 70 hours (Fig. 15).

When θ_i is 15.2°C, H'_i is 75 hours as computed above; accordingly from the above formula, H_i at 15.2°C is 75+9×(75/70)=85 hours. In case θ_i is 17.5° or 20.3°C, H'_i is 50 or 30 hours, respectively; therefore, H_i is 56 or 34 hours accordingly; the length of time elapsing from fertilization to hatching at the different temperatures, 15.2°, 17.5° and 20.3°C are 85, 56 and 34 hours, respectively.

Now, the same procedure can be applied to obtaining H_i needed for attaining successive stages of S_a , each corresponding to the three different temperatures.

Linear relationship was seen between the logarithms of reciprocals of H_i , or V_i , and of absolute temperatures, T_i (Fig. 16), verifying the Arrhenius's equation.

$$\frac{V_2}{V_1} = e^{\frac{\mu}{2} \left(\frac{1}{T_1} - \frac{1}{T_1}\right)}$$

where μ is the temperature characteristics.

Numerical values of μ for eight developmental stages were coincidently estimated to have been around 31,000 (Table 8). The present estimates, however, are fairly higher than the value calculated as 22,500 by AHL-STROM (1943) for the Pacific sardine. Expressing the ratio of elapsing time to the temperature difference of 10°C as Q_{10} , one may derive from the numerals $Q_{10} = 6.0$ when

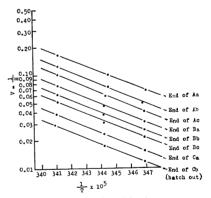


Fig. 16. Relationship between reciprocal of absolute temperature (1/T) and that of time computed as required for the period from fertilization to each later stage (1/H=V) (after NAKAI 1962b).

the hatching takes place within the temperature range of about 15-20°C. Applying the equation proposed by HIGURASHI and TAUTI (1925),

$$He^{a\theta} = C$$

where, H: the number of days required for hatching,

 θ : temperature in degree of Centigrade,