PRELIMINARY ANALYSIS OF THE CATCH CURVE OF THE PACIFIC SARDINE, *Sardinops caerulea* Girard

BY SIGEITI HAYASI,[1] NANKAI REGIONAL FISHERIES RESEARCH LABORATORY, KOCHI, JAPAN

ABSTRACT

This is a report on a method of estimating age-dependent changes in rates of natural mortality and the age- and season-dependent changes in rates of availability of the Pacific sardine. It includes estimates of the virtual average catch curve and relative year class strengths and deviations of individual curves from these estimates. The calculations are carried out with each of three sets of data: total California catch, catch per unit of effort in central California, and catch per unit of effort in southern California.

The average catch curve allows an estimate to be made of the increase in the natural mortality rate during fully recruited ages. The deviations of individual curves are assumed to represent the annual changes in rate of availability of each year class under a certain condition. The deviations of different age groups in the same years are compared to give a general idea of age-dependent change in the rate of availability in a year. Availability is also examined in regard to ocean temperatures preceding the fishing season.

A detailed model is proposed to estimate parameters relevant to the sardine population on the basis of the above examination as well as on the basis of earlier estimates of rates of natural mortality and availability. Consideration of the detailed model indicates the necessity for several sources of information to establish methods for predicting the sardine catch.

A fisherman's income depends on the size and behavior of stocks of fish entering his fishing grounds as well as on the efficiency of his gear. A fishery biologist must predict the size of the fish stocks available to the commercial fisheries. Taylor's[2] multiple regression equation, based on temperature and salinity in the year of spawning and on body length at the end of the first year of life, predicts the virtual stock size of a Pacific sardine year class. Availability of this fish, however, varies from season to season (Widrig, 1954), thus complicating the problem of prediction. To be useful to the fishermen, therefore, forecasts are needed for particular seasons and they must be based on yearly changes in availability in addition to year-class strength.

Widrig (1954) used relative rate of availability of the Pacific sardine to estimate population sizes and Yamanaka[3] developed a method for estimating the absolute value of the rate. Both authors started from the formula:

$$Z = M - \log \{re^{-fQ} + (1-r)\} \quad (1)$$

where Z and M denote instantaneous coefficients of total and natural mortalities as defined by Holt, Gulland, Taylor, and Kurita (1959). Other symbols are defined as: f=amount of effort, Q=efficiency of unit effort, and r=rate of availability.

Widrig (1954) and Yamanaka[3] assumed that the rates of natural mortality and availability are constant for four age groups (III- to VI-year-old fish). Introducing age-dependent changes in these rates into the calculations complicates the problem. Because the above authors did not do so, it is necessary to check the assumptions of equation (1) from another point of view.

In this paper I am interested in three matters. First I determine, through a simple examination of the catch data, if there is evidence of age-dependent changes in natural mortality and in availability. I also compare the various estimates of availability and their relation to an environmental factor, ocean temperature. Then I present a method to estimate the parameters on more probable assumptions resulting from these examinations.

GENERAL STATEMENT

In the first examination of the age data, I made

no attempt to estimate the absolute value of rate of availability, but rather I estimated the fluctuations in it as related to season and age. Strictly speaking, availability should be divided into two categories: (a) accessibility, the fish stock (in terms of numbers) accessible within the range of the fishermen and (b) vulnerability, which depends on factors involving gear efficiency. Measuring vulnerability in the commercial catch requires more than the examination of age composition and the amount of effort. I comment on this problem later. In the absence of information to separate availability into its components, their separate effects are disregarded here and included in the changes in availability and mortality.

Two basic assumptions are requisite for the first study of the relation of fluctuations to season and age: first, that the total mortality coefficient fluctuates randomly around a mean; and second, that the rate of availability fluctuates around a logarithmic mean. Even though no fishery may satisfy these assumptions, they may be accepted for a first approximation when age and year class are significant sources of variation in catch compared to the interaction that is a measure of total effects of changes in rates of mortality and availability as well as survey errors. In other words, changes in mortality and availability are regarded as less important in determining the catch than age and year-class strength when the latter two are significant sources of variations.

FORMULATIONS

Without exception the number of the ith year class caught in the year when they were jth age, C_{ij}, is expressed as:

$$C_{ij}=N_{io}\cdot r_{ij}\cdot E_{ij}\cdot \prod_{a=0}^{j-1}\cdot S_{ij}=N'_{io}\cdot r_{ij}\cdot E_{ij}\cdot \prod_{a=tp}^{j-1}\cdot S_{ia} \quad (2)$$

where: S_{ij}=annual rate of survival of the ith year class at jth age, E_{ij}=rate of exploitation for the available part of the ith year class at jth age, tp=youngest age in maturing spawning products, N_{io}=initial stock size of the ith year class, N'_{io}=stock size of the ith year class at the beginning of the year when they were tp year (s) old.

Under conditions assumed above, it holds that

$$\log C_j=\log N'_o-\sum_{a=t_p}^{j-1} Z_a+\log r_j+\log E_j \quad (3)$$

where, $\log C_j$=logarithmic average of all catches of jth age fish over year classes, $\log N_o$=logarithmic average of recruitment stock sizes over

year classes, Z_a=average mortality coefficient at ath age over year classes, $\log r_j$=logarithmic average of availability rates at jth age over year classes, $\log E_j$=logarithmic average of exploitation rates at jth age over year classes and

$$\log C_{j+1}=\log N'_o-\sum_{a=t_p}^{j} Z_a+\log r_{j+1}+\log E_{j+1} \quad (3')$$

and then

$$\log C_{j+1}-\log C_j=-Z_j$$
$$+(\log r_{j+1}-\log r_j)+(\log E_{j+1}-\log E_j) \quad (4)$$

If jth age fish migrate with fish older by 1 year, formula (4) approaches $-Z_j$ for data available over a period of years, if there is no trend in the rates of exploitation and availability, or if the number of years is large. Thus, the logarithmic means of several ages of fish give a "standard virtual catch curve" for a given period under the above conditions. The standard curve becomes more reliable in estimates of $-Z_j$ as the period under consideration becomes longer and the catch curve of each year class becomes more stable.

Year-class means of $\log C_{ij}$, $\log C_i$, are

$$\log C_i=\log N'_{io}-\sum_{a=t_p}^{t_i} k_aZ_{ia}+\log r_i+\log E_i \quad (5)$$

where $k_a=(t_1-a+1)/(t_1-t_p+1)$, and t_1=the oldest age in question. The last two terms are the year-class means of the logarithms of rates of availability and exploitation, respectively.

These means may not give a good estimate of year-class strength in the sardine because its life span is too short to allow changes in rates of availability and exploitation to cancel each other. It may be regarded, however, as a measure of the mean available stock size of each year class when the year class is found to be a significant source of variation.

Since the logarithmic mean of catches is

$$\log C=\log N'_o-\sum_{a=t_p}^{t_1} k_aZ_a+\log r+\log E \quad (6)$$

we can construct an "expected catch," E ($\log C_{ij}$), when $Z_{ia}=Z_a$ is common for the entire year class and $r_{ia}=r_i$ and $E_{ia}=E_i$ are common for all the age groups of any year class.

$$E (\log C_{ij})=\log C_i+\log C_j-\log C$$
$$=\log N'_{io}-\left\{\left(\sum_{a=t_p}^{j-1} Z_a\right.\right.$$
$$+\sum_{a=t_p}^{j-1} k_aZ_{ia}-\sum_{a=t_p}^{t_1} k_aZ_a\left.\right)\left.\right\}$$
$$+(\log r_i+\log r_j-\log r)$$
$$+(\log E_i+\log E_j-\log E) \quad (7)$$

Therefore,

$$\Delta_{ij} = \log C_{ij} - E\,(\log C_{ij})$$

$$= -\left\{ \sum_{a=t_p}^{j-1} Z_{ia} - \left(\sum_{a=t_p}^{j-1} Z_a + \sum_{a=t_p}^{t_i} k_a Z_{ia} - \sum_{a=t_p}^{t_i} k_a Z_a \right) \right\}$$

$$+ \{ \log r_{ij} - (\log r_i + \log r_j - \log r) \} + \{ \log E_{ij}$$

$$- (\log E_i + \log E_j - \log E) \} \qquad (8)$$

Among the variables in formula (8), we can determine combined effects of yearly changes in mortality coefficients and availability rate. Because $\Sigma_j \Delta_{ij} = 0$, the deviations of the same year class should be negatively correlated when the changes in rates of availability and exploitation are less important than change in mortality coefficients in determining the catch curves. On the other hand, significant positive correlation between deviations of any two age groups taken in the same seasons indicates that deviations in availability and exploitation are important.

A similar meaning attaches to any measure that is proportional to the available stock size, such as catch per unit of effort; here the change in rate of exploitation is disregarded. It should be noted that the deviations are affected by the year-class average of logarithms of availability and are not, then, a measure of relative availability on the same base.

TOTAL CALIFORNIA CATCH

Age composition of the California sardine has been reported for 26 seasons, 1932–33 through 1957–58 by Eckles (1954), Wolf (1961), Felin and Phillips (1948), Mosher, Felin, and Phillips (1949), Felin, Phillips, and Daugherty (1949), Felin, Daugherty, and Pinkas (1950, 1951), Felin, Anas, Daugherty, and Pinkas (1952), Felin, MacGregor, Daugherty, and Miller (1953, 1954, 1955), Felin, Wolf, Daugherty, and Miller (1958), Wolf, MacGregor, Daugherty, and Miller (1958), and Daugherty and Wolf (1960). When catch is plotted against age on a semilog scale for each year class, the catch curves are fairly smooth for fish older than age II of most year classes, but are very irregular for some year classes—especially those spawned in 1947 through 1949 (fig. 1). These irregular curves may be due to changes in availability and exploitation. The catch curves of some year classes indicate moderate irregularity. For instance, year classes 1930 through 1933 might have been highly available in the 1936–37 season.
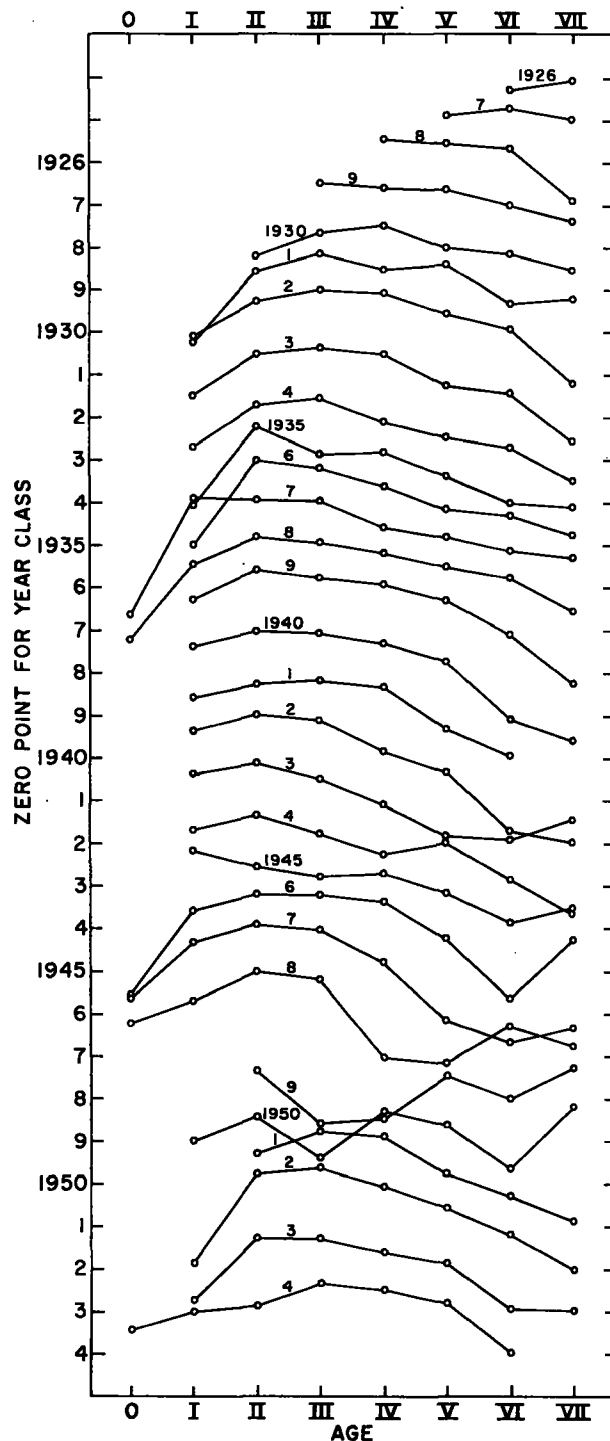

FIGURE 1.—Catch curves of Pacific sardine, year classes 1926 through 1954. Vertical scale equals log of millions of fish; distance between zero points for each year class equals 1.0 (i.e., 10,000,000 fish).

The age- and year-class mean of log C_{ij} for the 22 year classes from 1930 to 1951 are, nevertheless, regarded as sufficiently significant to give a reliable standard catch curve and estimates of year-class

strength of the available stocks. Analysis of variance of the means of logarithms of the total sardine catch in California for the year classes 1930 through 1951 gives the following:

Source of variation	Degrees of freedom	Mean square
Age	4	*6.1756
Year class	21	*1.3825
Residual	84	.2851

*Significant at a probability of less than 0.1 percent.

The average catches by age indicate that sardines are not fully recruited until age III (table 1). The increase in the mortality coefficient, even after age III, may be attributed partly to incomplete recruitment after this age and partly to an increase in natural mortality.

TABLE 1.—*Mean sardine catch (ln), total mortality coefficients, and change in mortality by age for the year classes 1930–51 and 1930–44 in California*

Age (j)	Mean catch (ln)		Mortality coefficient (Z_j)		$Z_{j+1} - Z_j$	
	1930–51	1930–44	1930–51	1930–44	1930–51	1930–44
	Millions of fish	Millions of fish				
II	310.0	646.7				
			−0.09	0.11		
III	340.9	579.9			0.72	0.60
			.63	.71		
IV	176.5	284.0			.32	.28
			.95	1.00		
V	65.1	104.9			.24	.23
			1.19	1.23		
VI	18.8	30.6				

Because of incomplete records, the expected catches of eight year classes, 1926–29 and 1951–57, are constructed through their mean catches and a standard catch curve, so that $\Sigma_j\Delta_{tj}$ reduced to zero. When these additional classes are included, the deviations of logarithmic catches of any two age groups in the same season are positively correlated with each other, where the effects of environment and fishing intensity might be expected to be common for all the age groups. The correlation coefficient is higher for combinations of adjacent age groups (fig. 2). On the other hand, correlation coefficients between deviations in two ages from the same year classes range from −0.690 to 0.307. This variability indicates that change in survival rate is less important than change in availability and exploitation.

From these observations in regard to assumptions given in the last two paragraphs of the
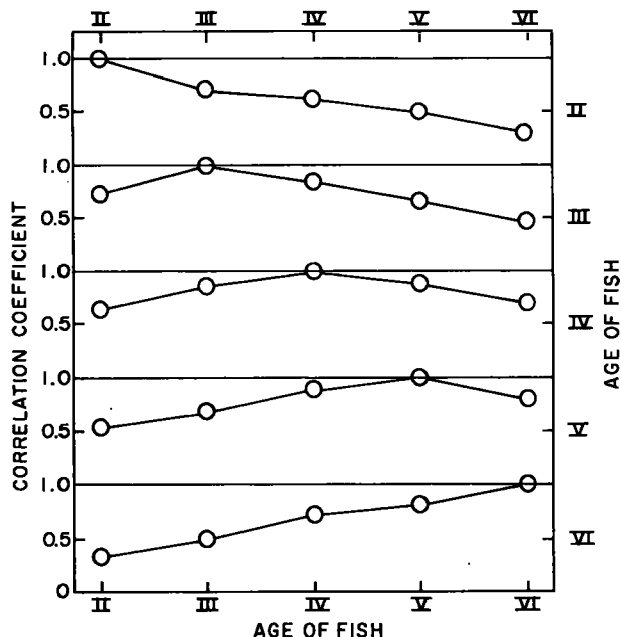

FIGURE 2.—Correlation coefficients between index of virtual availability of two age groups, based on the total catch in California, 1932–33 through 1957–58 seasons.

preceding section (on formulations), it may be assumed that the year-class-dependent change in total mortality coefficients is smaller than the seasonal changes in both availability and exploitation and that the migratory pattern differs from age to age but is similar for adjacent ages. The multiple correlation of deviations of age groups III to V in the same season was calculated to be as high as 0.815. These three age groups furnished the greater part of the period under discussion.

It is well known that the migratory pattern of the Japanese sardine and its fishing grounds are affected by changes in oceanographic conditions (Sako, 1939; Shimomura, 1954). Because sufficient information about the environment of the fishing grounds in California waters was lacking, I correlated the temperature anomaly at the pier of the Scripps Institution of Oceanography for July through September (just before the fishing season) with annual mean deviations in the catch of the three major age groups for 26 seasons (fig. 3). The correlation coefficient was 0.599, slightly over the 1-percent level of significance.

Clark and Daugherty (1950) reported the catch per unit of effort and total effort of the purse seiners in California waters as well as at each of the three major ports, San Francisco, Monterey, and San Pedro, for the seasons 1932–33 through 1948–49. To eliminate the effects of improvement
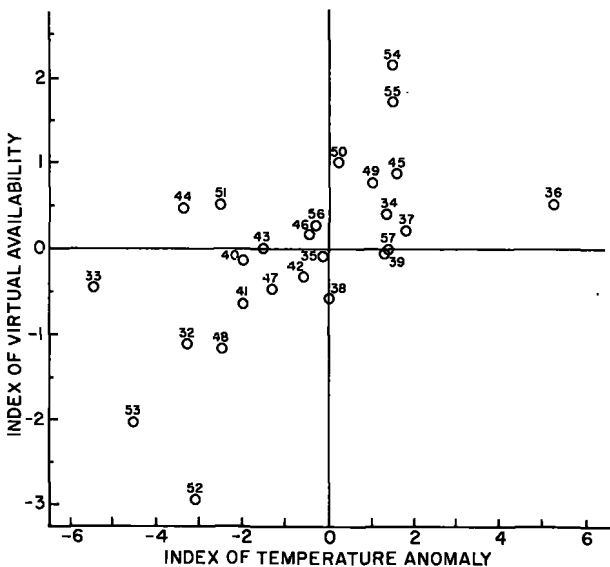
FIGURE 3.—Relation between temperature anomaly at pier of the Scripps Institution of Oceanography and virtual availability of sardines in California, 1932–33 through 1957–58 seasons. Numerals denote the fishing season, e.g., 32 indicates the season of 1932–33.

in the efficiency of individual boats, they adjusted the catch per unit of effort using as base year the 1932–33 season at each port. The same authors (1952) reported the data for the 1949–50 and 1950–51 seasons in all California waters, as well as at Monterey and San Pedro, and Clark (1956) published the data for the four seasons 1951–52 through 1954–55 in southern California. In the latter two works the authors chose the 1941–42 season as the new base year (Clark and Daugherty, 1950) to fit recent developments in the fishery.

Because fishing effort should be expressed on the same base year, I converted the catch per unit of effort in the whole fishing season to the value based on that of the 1941–42 season. Since the fishing grounds off California are divided into two regions of almost equal area, the north off San Francisco and Monterey and the south off San Pedro (Widrig, 1954), the total effective effort is calculated by dividing the total California catch by the sum of catches per unit effort in the two regions. The deviations of catch showed a significant multiple correlation coefficient of 0.594 with the temperature anomaly and the amount of fishing effort. Partial correlation coefficients were 0.293 for fishing effort and 0.585 for temperature anomalies.

CATCH PER UNIT OF EFFORT

Because fishing effort appeared to show a positive correlation with the deviation of catch from the expected value, I repeated the above calculations for total catch, using the catch per unit of effort. Present evidence indicates that the stock exploited in the waters off central California is mainly composed of fish spawned in the waters off southern California (northern subpopulation), whereas the stock in southern California includes fish spawned off central Baja California (southern subpopulation) as well as fish from the northern subpopulation (Felin, 1954; Marr, 1960). The effort data are not given after the 1951–52 season for central California where the fishery practically disappeared by 1954. Catch per unit of effort at San Francisco, Monterey, and San Pedro indicates that the available stocks off the two northern ports are correlated with a significant coefficient of 0.810 but that the stock off San Pedro is not correlated with either San Francisco (0.314) or Monterey (0.398) during the 19 seasons from 1932–33 to 1950–51. This lack of correlation may be attributed to differences in the subpopulation supporting the fisheries. It is also possible that the northern subpopulation, having migrated to central California, left only a minor portion of the stock in southern California or that major age groups differed between these regions.

Since it is desirable to forecast regional catches, the following discussion is based on data by region. In the northern waters the catch curves for ages II to VI, based on catch per unit of effort, were obtained for the 1930–44 year classes. The curves were fairly regular for most of the year classes, except the last. The following table shows that age and year class are significant sources of variation of logarithmic catch, as was true for total catch:

Source of variation	Degree of freedom	Mean square
Age	4	*4.4487
Year class	14	*1.2050
Residual	56	.1596

*Significant at a probability of less than 0.1 percent.

The following tabulation of the standard catch curve based on logarithmic means of the catch per unit of effort in central California for the year classes 1930–44 shows that there is less change in

mortality rate with age than was found for total catch (table 1):

Age (j)	Mean catch (thousands of fish)	Mortality coefficient (Z_i)
II	656.6	
III	592.5	0.10
IV	264.7	.81
V	102.5	.95
VI	33.7	1.11

The deviations from the expected catch for some year classes did not always indicate significant negative correlation; the coefficients range between −0.661 and 0.478. On the other hand, the deviations in the same season were always positively correlated; the coefficients vary between 0.280 and 0.850. It is again found that the closer the ages, the higher the correlation coefficients. The multiple correlation coefficient for the three major age groups is 0.877.

In the southern California catch, the curves were irregular for the year classes that occurred after 1947. The following analysis of variance of the means of logarithms of the catch per unit of effort in southern California for the year classes 1930-48 shows that age and year class are significant sources of variation:

Source of variation	Degrees of freedom	Mean square
Age	4	*1.6133
Year class	18	*2.0954
Residual	72	.1244

*Significant at a probability of less than 0.1 percent.

The standard catch curve is fairly smooth after age III; age-dependent changes in mortality are minor. The four year classes that were produced in 1945-48, however, may differ in survival rate as well as in stock size (table 2). The correlation coefficient between deviations of the same year class fluctuates broadly between −0.495 and 0.138. The correlations between deviations in the same season are always positive, 0.223 to 0.890, and are higher for two adjacent age groups; the multiple correlation coefficient for age groups III to V was as high as 0.910.

The mean deviations for age groups III through V in central and southern California fluctuate similarly; the correlation coefficient between them was 0.810. Compared with the different regional fluctuations in catch per unit of effort of all the

TABLE 2.—*Mean sardine catch* (ln), *total mortality coefficients, and change in mortality by age for the year classes 1930-48 and 1930-44 in southern California*

Age (j)	Mean catch (ln)		Mortality coefficient (Z_i)		$Z_{i+1}-Z_i$	
	1930-48	1930-44	1930-48	1930-44	1930-48	1930-44
	Millions of fish	*Millions of fish*				
II	907.6	888.5				
			0.26	0.27		
III	701.9	680.2			0.77	0.61
			1.03	.87		
IV	251.1	283.6			.24	.33
			1.26	1.20		
V	71.1	85.2			.07	.29
			1.33	1.49		
VI	18.8	14.3				

age groups, this similarity may suggest that some younger and older age groups than those in question showed different changes in availability between these two regions.

The temperature anomaly at Scripps pier does not correlate well with the deviations in catch, but is slightly higher with those in central California (0.560) than with those in southern California (0.495).

DYNAMICS OF THE PACIFIC SARDINE FISHERY

This discussion deals with the age-dependent changes in rates of natural mortality and availability derived from information obtained thus far. A detailed model is presented for estimating the parameters inherent in the population dynamics of the Pacific sardine.

All three sets of data analyzed above indicate three characters of catch curves of the sardine: (a) the increase of the virtual total mortality coefficient with age; (b) the close relation between virtual indices of availability of two adjacent age groups; and (c) the dependence of the availability on temperature in the months just before the fishing season. To examine the reliability of these findings, similar analyses are repeated with estimates of these parameters as presented by Widrig (1954) and Yamanaka (footnote 3).

Previous authors assumed that the natural mortality coefficient was constant over the four age groups III through VI. In Widrig's study (1954) three appropriate values of the coefficients were assumed, and the rate of availability in a season was shown in relative rate to that of the 1936-37 season for each of these assumed coefficients. Yamanaka (footnote 3) assumed that the

natural mortality coefficient fluctuated around a mean and that the rate of availability fluctuated around a logarithmic mean for the 23 seasons from 1932–33 to 1954–55. Because the level of availability changed between the early and later years of the investigation, he divided the period into two parts; one from 1932–33 to 1945–46, and the other from 1945–46 to 1954–55. The present report examines only his final estimates based on the divided data. Because these authors first estimated the rate of availability in logarithms, my analysis of the rate is usually made with logarithmic rather than actual values.

As estimated by Yamanaka (footnote 3), the increase in virtual total mortality coefficients with age is comparable to decrease in availability of older fish. As expected from his assumption, availability should decrease with age if total mortality increases. Therefore, I conclude that the virtual coefficient of total mortality of the Pacific sardine increased with age for the period investigated.

The age-dependent change in the virtual coefficient of total mortality may be partly attributed to incomplete recruitment [4] in addition to a real change in natural mortality, insofar as it is estimated from the age composition of the commercial catch. Although no conclusive evidence is obtained, it seems to me that the increase in natural mortality with age is real rather than caused by incomplete recruitment for the fish at and older than the three ages discussed, since the fishery has exploited fish as young as age I and sometimes age zero. If this increase in natural mortality with age is real, the natural mortality coefficient of these fish is considered to increase linearly with age (table 1). A linear increase of the coefficient with age was postulated by Beverton and Holt (1957, pp. 69–71) for three species: two herrings, *Clupea harengus harengus* and *C. harengus pallasi*, investigated by Hodgson (1932) and Tester (unpublished, cited by Ricker, 1948) and the whitefish, *Coregonus clupeaformis*, of Lake Opeongo studied by Ricker (1949). A linear increase with age may not always hold, however, as was shown for the same species, or ecologically related ones, surveyed on other occasions: namely the whitefish of Shakespeare Island Lake, the

sauger, *Stizostedion canadense*, of Lake Opeongo (Ricker, 1949), and the herring, *C. harengus pallasi* (Tester, 1955).

It is noteworthy that total mortality coefficients are higher in southern California than in central California—also the increments, which average about 0.30 in southern California but 0.15 in central California, as previously shown. This difference is partly attributed to differential distribution of the fish by age; older fish migrate farther north. It should be noted, however, that Yamanaka (footnote 3) estimated the natural mortality coefficient of the sardines to be higher in the more recent years, when the southern subpopulation predominated, than in earlier years for the entire range of the fishery in California. Thus, both his and my results agree that the mortality rate is higher in the southern subpopulation than in the northern one.

It has been shown thus far that the rate of availability differed between age groups exploited in the same fishing season but that it was close for two adjacent age groups. A comparable result is obtained from the analysis of the availability rates as estimated by Yamanaka (footnote 3). As to the age-dependent change in availability, it has already been suggested that some species of fish school together by size or by age, including, among others, the herring, *C. harengus* (Hjort, 1926, p. 8); the sardine, *Sardinops melanosticta* (Yamanaka, 1955, p. 51); the anchovies, *Engraulis mordax* (Miller, 1955, p. 30), and *Cetengraulis mysticetus* (Howard and Landa, 1958, p. 394); the yellowfin tuna, *Thunnus albacares* (Schaefer, 1948, p. 199); and the skipjack tuna, *Katsuwonus pelamis* (Brock, 1954, p. 99).

As an approach to predicting catch, the temperature data at Scripps pier just before the fishing season were regarded as having been correlated with the preliminary estimates of availability. The correlation coefficients between temperatures and the logarithms of each series of estimates by Widrig (1954), based on assumed values of the natural mortality coefficients of 0, 0.2, and 0.4, are 0.256, 0.305, and 0.300, respectively. Since Yamanaka (footnote 3) estimated the natural mortality coefficient to be 0.35 for all the seasons, or 0.25 for 1932–33 through 1945–46 and 0.65 for 1945–46 through 1954–55, the most probable rate of Widrig's estimates of availability, based on the assumed natural mortality coefficient of 0.4, is best correlated with temperature. In Yamanaka's estimates, the correlation coefficient with

---

[4] Age of complete recruitment of a partially available population is defined as the age at which all the fish are potentially "catchable" by the fishery even if, actually, some of them do not always enter the fishing ground. When rates of availability are estimated for all the age groups appearing in the catch, the age of complete recruitment is determined by comparison of the average rate for each age.

temperature is 0.686—higher than that calculated by me or by Widrig (1954).

The correlation coefficient based on the rate of availability is 0.757 and, thus, higher than that based on the logarithmic values.

Summarizing these examinations of the age composition of the sardine catch by Widrig (1954), Yamanaka (footnote 3) and the present study, I may be able to assume the following characteristics of the available sardine stocks:

a. The natural mortality differs by age and by subpopulation and probably by year class; therefore, I recommend that the rate be estimated for each age group with the data taken in the shortest period of years for which the analysis can be made and for each fishing ground in which the stock is more homogeneous.

b. The availability also differs by age of the fish. It is indicated, however, that the rates of two successive age groups are similar. This fact also indicates that the parameters should be estimated for each age group separately.

c. Availability seems to be correlated with temperature. This possibility should be studied in relation to temporal and areal patterns of the environment, as well as the general levels of availability. For instance, Craig (1960) demonstrated that the herring catch was related to increase in temperature and strength and direction of winds in early summer, even though the catch was not highly correlated with each of these factors. Factors such as these, regarded important in Japan, include temperature distribution, intensity of cold water masses (upwelling), and current strength and direction (Shimomura, 1954).

A more detailed model is presented on the basis of age specific mortality and availability characteristics. Because rates of availability of two adjacent age groups in any year may be assumed to be almost the same, the virtual survival rate, S'_{at}, obtained from age and catch data is expressed as:

$$S'_{at} = \exp{(Z'_{at})} = (N_{a+1 \cdot t+1})/(N_{at} r_{at})$$

$$= \{ r_{at} e^{-f_t Q_{at}} + (1 - r_{at}) \} e^{M_{at}} r_{a+1 \cdot t+1} / r_{at} \quad (9)$$

then

$$Z'_{at} = M_{at} - \log{\{ r_{at} e^{-f_t Q_{at}} + (1 - r_{at}) \}}$$

$$+ (\log{r_{at}} - \log{r_{a+1 \cdot t+1}}) \quad (9')$$

where a and t denote age of fish and season,

respectively. It is assumed that r_{at} and Q_{at} are equal to $r_{a \cdot t+1}$ and $Q_{a \cdot t+1}$ respectively.

The mean of virtual mortality coefficients for n seasons is the sum of means of the first and second terms, and $(\log{r_{a \cdot 1}} - \log{r_{a \cdot n+1}})/n$. Then, if Q remains constant for a long period of years so that the last term diminishes to zero, the means of the parameters including Q, M, and r are estimated as shown by Yamanaka (footnote 3). The value of Q, however, should be regarded as variable during rather short periods of years, partly depending on gear improvement, such as the several gear improvements in the sardine fishery in California. In addition, Q may vary because of biological and economic reasons even if the same type of fishing gear is used. The major factors relating to this quantity may be classified in the following three groups:

a. The first and most essential factor affecting Q depends on such variables as fish size, gear type, and speed of hauling. This factor and the mechanical selectivity discussed below, defined as q in the following discussion, determined the efficiency of a fishery for a particular size of fish distributed in a certain way.

b. The second factor, selectivity, is related to both the fish and the fishery. Two general categories of selectivity should be distinguished. The first is a mechanical selectivity, such as the size and number of fish retained by the gear, and is determined by the relation between sizes of mesh or hook and fish; the second is an economic selectivity, controlled by market performance by size or species. The former type of selectivity is included in the first category (a above) of factors controlling Q. The mean of the latter selectivity factor is included in the rates of natural mortality. The deviation from mean is included in availability.

c. The third factor, volume of the water in which the available part of the stock is distributed, also causes change in Q even though the rate of availability is constant. The same gear should be more effective or the same fishermen should locate the schools more readily when the fish are distributed in smaller volumes of water than in larger ones. Changes in patchiness and depth of distribution may not be as important as the size of the waters when the discussion concerns a whole season during which total effects may be nearly constant. Since sardines may remain in a particular stratum, the volume of water may be approximated by the area of fishing ground, A, that is

measured by location of the hauls or isothermal contours.

The first approach regards the value of Q as q/A.

Since catch per unit of effort is related to the mean density of the fish stock in the fishing ground, as well as to the efficiency of individual gear, this quantity should be adjusted by an appropriate measure (such as area of fishing ground) to yield the relative stock size and the virtual mortality coefficient (Gulland, 1955; Beverton and Holt, 1957). Watt (1956, p. 629) pointed out that the catch per unit of effort, obtained by dividing the total catch by total effort in a season, is not realistic when availability changes within the season. He, therefore, compared the stock sizes in 2 years by the catch per unit of effort in a particular month.

If a fishery is operated in several localities, there is no reason to believe that rate of availability (accessibility and vulnerability) is common for the total range of the fishery. Each locality should be studied, especially if the stocks in different areas are composed of different subpopulations.

Such studies require that the calculations be carried on for shorter periods and over smaller areas. Because the mean of the last term of equation (9) does not reduce to zero for such a situation, we have to assume the following:

a. M and q fluctuate around their means at random, and their variances are so small that these quantities may be regarded as constant.

b. There is a mean of r that gives a mean of the second term for any given set of q, f, and A.

c. The ratio of availabilities in 2 adjacent years fluctuates around a logarithmic mean at random.

d. The availability and gear efficiency are common for two adjacent age groups.

On the basis of these assumptions, the virtual mortality coefficient of a certain age group of fish during the tth season, Z'_t, in an area is

$$Z'_{t'} = M_t - \log \{r_t \cdot \exp(-f_t q_t/A_t) + (1-r_t)\} + (\log r_t - \log r_{t-1}) \quad (10)$$

and the mean of the virtual mortality coefficients of the age group, Z', is

$$Z' = M - \log \{\bar{r} \exp(-f\bar{q}/A) + (1-\bar{r})\} + d \quad (11)$$

where $\bar{r}$ and $\bar{q}$ are estimated averages of r and q in the age group, which give the mean of the second term in the formula (10) for a given set of f and A, and $d = \log(r_1/r_0)/m - 1$.

The parameters, M, $\bar{q}$, $\bar{r}$, and d, may be estimated by the least-squares method if appropriate data which were taken in at least 6 successive years and a suitable computer are available to make the calculations.

Putting $a_t = \exp(-f_t \bar{q}/A_t)$, and $b_t = \log \bar{r} a_t + (1-\bar{r}) + d$, the expected virtual mortality coefficient, $E(Z'_t)$, equals $M - b_t$. The differences between observed and expected mortality coefficients, Δ's, are:

$$\Delta_1 = \log \{a_1 r_1 + (1-r_1)\} + (\log r_1 - \log r_2) - b_1,$$

$$\Delta_2 = \log \{a_2 r_2 + (1-r_2)\} - (\log r_2 - \log r_3) - b_2,$$

$$\cdot \qquad\qquad \cdot \qquad\qquad \cdot$$

$$\cdot \qquad\qquad \cdot \qquad\qquad \cdot$$

$$\Delta_5 = \log \{a_5 r_5 + (1-r_5)\} - (\log r_5 - \log r_1 + 5d) - b_5 \quad (12)$$

These equations give the rates of availability for these 5 years. Repeating this procedure for each successive 6-year period, we may obtain the running averages of the parameters on which a more advanced discussion can be made. When A is not accurately measured, the calculation of availability, based on the constant $Q = q/A$, may give some clues for estimating vulnerability. When fish show differential distribution by age, the mortality rate in the entire population may be estimated from the summation of the stock size of each age group in each locality. Before calculation, division of the area should be reexamined, such as by areal variation in fishing season and relative size of subpopulations (perhaps by scale characters as well as serological research).

Finally, it should be noted that this type of analysis does not provide absolute values of availability for a whole population. Estimates may differ from each other for availability of an age group in a season by six different series. If relative values of the estimated rates for successive seasons are comparable for all of the six series, however, the absolute rate may be surmised from information on the distribution of stocks and independent from fisheries, such as an egg census. As a matter of fact, estimates of availability rates in this type of analysis could be compared with geographic distributions of egg stocks. This comparison is based on the fact that the distribution of the parent stock of the Pacific sardine was represented by egg distribution for the 5 years

1952–56 (Ahlstrom, 1959, p. 204). Furthermore, a coincidence of distributions of parent stocks and their eggs was detected in the related species, *Sardinops melanosticta*, inhabiting the waters adjacent to Japan (Nakai, 1960, p. 821).

SUMMARY

The rate of natural mortality of the Pacific sardine seems to be higher in the older fish than in the younger ones and higher in the southern subpopulation than in the northern one. For this reason it is indicated that natural mortality should be estimated for the subpopulations by age from the catch data of two adjacent age groups.

Availability was found to differ by age as well as by season. High correlations were obtained between the rates of two adjacent age groups exploited in the same fishing season; therefore, this rate also should be estimated by examination of two adjacent age groups.

The data suggest that availability was positively correlated with water temperatures in July to September, immediately preceding the fishing season.

In addition to the above factors, others such as efficiency of gear and area of fishing grounds may affect the catch curves. The most promising procedures may be the comparisons of the total mortality coefficients, number of boats, and area of fishing grounds during the shortest time periods. Consideration of these facts indicates that running averages for six seasons should be computed for these factors.

ACKNOWLEDGMENTS

LITERATURE CITED

AHLSTROM, ELBERT H.
　　1959. Distribution and abundance of eggs of the Pacific sardine, 1952–56. U.S. Fish Wildl. Serv., Fish. Bull. 60: 185–213.

BEVERTON, RAYMOND J. H., and SIDNEY J. HOLT.
　　1957. On the dynamics of exploited fish populations. Great Brit. Min. Agr. Fish. Food, Fish. Invest. ser. 2, 19, 533 pp.

BROCK, VERNON E.
　　1954. Some aspects of the biology of the aku, *Katsuwonus pelamis*, in the Hawaiian Islands. Pac. Sci. 8: 94–104.

CLARK, FRANCES N.
　　1956. Average lunar month catch of sardine fishermen in southern California, 1932–33 through 1954–55. Calif. Fish Game 42: 309–322.

CLARK, FRANCES N., and ANITA E. DAUGHERTY.
　　1950. Average lunar month catch by California sardine fishermen, 1932–33 through 1948–49. Calif. Div. Fish Game, Fish Bull. 76, 28 pp.
　　1952. Average lunar month catch by California sardine fishermen, 1949–50 and 1950–51. Calif. Fish Game 38: 85–97.

CRAIG, R. E.
　　1960. A note on the dependence of catches on temperature and wind in the Buchan pre-spawning herring fishery. J. Cons. 25: 185–190.

DAUGHERTY, ANITA E., and ROBERT S. WOLF.
　　1960. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico in 1957–58. Calif. Fish Game 46: 189–194.

ECKLES, HOWARD H.
　　1954. Age determination of Pacific sardines from otoliths. [U.S.] Fish Wildl. Serv., Res. Rep. 37, 40 pp.

FELIN, FRANCES E.
　　1954. Population heterogeneity in the Pacific pilchard. [U.S.] Fish Wildl. Serv., Fish. Bull. 54: 201–225.

FELIN, FRANCES E., RAY ANAS, ANITA E. DAUGHERTY, and LEO PINKAS.
　　1952. Age and length composition of the sardine catch off the Pacific Coast of the United States in 1951–52. Calif. Fish Game 38: 427–435.

FELIN, FRANCES E., ANITA E. DAUGHERTY, and LEO PINKAS.
　　1950. Age and length composition of the sardine catch off the Pacific Coast of the United States and Canada in 1949–50. Calif. Fish Game 36: 241–249.
　　1951. Age and length composition of the sardine catch off the Pacific Coast of the United States and Canada in 1950–51. Calif. Fish Game 37: 339–349.

FELIN, FRANCES E., JOHN S. MACGREGOR, ANITA E. DAUGHERTY, and DANIEL J. MILLER.
　　1953. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico in 1952–53. Calif. Fish Game 39: 409–417.
　　1954. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico in 1953–54. Calif. Fish Game 40: 423–431.

　　1955. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico in 1954–55. Calif. Fish Game 41: 285–293.

FELIN, FRANCES E., and JULIUS B. PHILLIPS.
　　1948. Age and length composition of the sardine catch off the Pacific Coast of the United States and Canada, 1941–42 through 1946–47. Calif. Div. Fish Game, Fish Bull. 69, 121 pp.

FELIN, FRANCES E., JULIUS B. PHILLIPS, and ANITA E. DAUGHERTY.
　　1949. Age and length composition of the sardine catch off the Pacific Coast of the United States and Canada in 1948–49. Calif. Fish Game 35: 165–183.

FELIN, FRANCES E., ROBERT S. WOLF, ANITA E. DAUGHERTY, and DANIEL J. MILLER.
　　1958. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico in 1955–56. Calif. Dep. Fish Game, Fish Bull. 106: 7–12.

GULLAND, J. A.
　　1955. Estimation of growth and mortality in commercial fish populations. Great Brit. Min. Agr. Fish. Food, Fish. Invest., ser. 2, 18(9), 46 pp.

HJORT, JOHAN.
　　1926. Fluctuations in the year classes of important food fishes. J. Cons. 1: 5–38.

HODGSON, WILLIAM C.
　　1932. The forecasting of the East Anglian herring fishery. J. Anim. Ecol. 1: 108–118.

HOLT, SIDNEY J., J. A. GULLAND, CLYDE C. TAYLOR, and SUSUMU KURITA.
　　1959. A standard terminology and notation for fishery dynamics. J. Cons. 24: 239–242.

HOWARD, GERALD V., and ANTONIO LANDA.
　　1958. A study of the age, growth, sexual maturity, and spawning of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama. Inter-Amer. Trop. Tuna Comm., Bull. 2: 391–467.

MARR, JOHN C.
　　1960. The causes of major variations in the catch of the Pacific sardine (*Sardinops caerulea* Girard). Proc. World Sci. Meet. Biol. Sardines Related Species, FAO U.N., Stock Area Pap. 3: 667–791.

MILLER, DANIEL J.
　　1955. Studies relating to the validity of the scale method for age determination of the northern anchovy (*Engraulis mordax*). Calif. Dep. Fish Game, Fish Bull. 101: 7–34.

MOSHER, KENNETH H., FRANCES E. FELIN, and JULIUS B. PHILLIPS.
　　1949. Age and length composition of the sardine catch off the Pacific Coast of the United States and Canada in 1947–48. Calif. Fish Game 35: 15–40.

NAKAI, ZINZIRO.
　　1960. Changes in the population and catch of the Far East sardine area. Proc. World Sci. Meet. Biol. Sardines Related Species, FAO U.N., Stock Area Pap. 3: 807–853.

RICKER, WILLIAM E.
    1948. Methods of estimating vital statistics of fish populations. Ind. Univ. Publ., sci. ser. 15, 101 pp.
    1949. Mortality rates in some little-exploited populations of freshwater fishes. Trans. Amer. Fish Soc. 77: 114–128.
SAKO, NOBURU.
    1939. On the iwashi fishing grounds around Inubo Saki (Cape). Suisan Kenkyushi 34: 305–310, 327–332, 366–371. [In Japanese.]
SCHAEFER, MILNER B.
    1948. Size composition of catches of yellowfin tuna (*Neothunnus macropterus*) from central America and their significance in the determination of growth, age and schooling habits. *In* Milner B. Schaefer and John C. Marr, Contributions to the biology of the Pacific tunas, pp. 197–200. [U.S.] Fish Wildl. Serv., Fish. Bull. 51.
SHIMOMURA, TOSHIMASA.
    1954. Predictions of fish catch based on the oceanographic condition. Kagaku 24: 438–500. [In Japanese.]
TESTER, ALBERT L.
    1955. Estimation of recruitment and natural mortality rates from age composition and catch data in British Columbia herring populations. J. Fish. Res. Bd. Can. 12: 649–681.
WATT, KENNETH E. F.
    1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. J. Fish. Res. Bd. Can. 13: 613–645.
WIDRIG, THEODORE M.
    1954. Method of estimating fish populations, with application to Pacific sardine. [U.S.] Fish Wildl. Serv., Fish. Bull. 56: 141–166.
WOLF, ROBERT S.
    1961. Age composition of the Pacific sardine 1932–1960. U.S. Fish Wildl. Serv., Res. Rep. 53, 36 pp.
WOLF, ROBERT S., JOHN S. MACGREGOR, ANITA E. DAUGHERTY, and DANIEL J. MILLER.
    1958. Age and length composition of the sardine catch off the Pacific Coast of the United States and Mexico, 1956–57. Calif. Dep. Fish Game, Fish Bull. 106: 13–17.
YAMANAKA, ICHIRO.
    1955. An ecological inference of statistics concerning the size composition (I). Annu. Rep. Jap. Sea Reg. Fish. Res. Lab. (2): 48–54.