AGE COMPOSITION, GROWTH, AND MATURATION OF THE PACIFIC SARDINE (*SARDINOPS SAGAX*) DURING 1994

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ABSTRACT

In conjunction with a study to estimate biomass based on daily egg production, Pacific sardine (*Sardinops sagax*) were independently aged by four or five readers using annuli in whole otoliths. Agreement among all five readers was only 31%, and an index of precision for estimated ages was 0.24. Ages ranged from one to seven years. The age composition of Pacific sardine in 1994 indicates a growing population or high adult mortality rates. Most of the biomass was in the youngest year classes. Very few fish were older than 4 years. Samples were taken from Baja California (26°40'N) to Monterey, California (36°40'N) during April and May 1994. Latitudinal clines in age of first maturity and size at age were found. Despite problems in age determination, it is clear that some sardines mature before their first birthday. Sardine in the south mature at a younger age than in the north. Most sardine in the current population mature at age one, rather than at age two as reported for the population prior to the collapse of the fishery.

INTRODUCTION

Pacific sardine (*Sardinops sagax*) dominated the Pacific coast fisheries of North America for much of the first half of the twentieth century, prior to successive years of low recruitment and unsustainable fishing mortality (Barnes et al. 1992). Following the collapse of the sardine fishery in the mid-1960s, a moratorium was placed on the commercial harvest of sardine in California (Radovich 1982).

Today the sardine fishery is rebuilding, as biomass during the past decade has increased (Deriso et al. 1996). The stock currently supports directed commercial fisheries in Ensenada (Baja California, Mexico), San Pedro (U.S.), and Monterey (U.S.). Determining the age composition of landings is important for investigating changes in abundance and suggesting management decisions. Unlike many commercial fisheries, age composition of sardine landings in California is relatively well documented for most of the twentieth century (Yaremko 1996). The methods of estimating age composition have varied over time from length-frequency analysis to annuli counts from either scales or otoliths. California Department of Fish and Game (CDFG) and others (Hester 1993) have conducted systematic port sampling and age determination of wetfish landings in the California commercial fishery since 1983.

In accordance with current practice, we chose otoliths over scales (or other hard parts) for determining sardine age. Otoliths are preferred for several reasons. (1) Samples were collected with trawl or purse seine gear, and at the time of collection, handling had abraded off the scales of many specimens. (2) Unlike scales, sardine otoliths do not require mounting or other preparation for ageing and can be stored with relative ease. (3) Otoliths are as reliable as scales (Mosher and Eckles 1954). (4) There is some evidence that annuli in otoliths form on an annual cycle (Barnes and Foreman 1994).

In this study we determined the age, growth, and maturation of Pacific sardine over a broad geographic range from Punta Eugenia, Baja California, to Monterey, California. This is the first attempt to address regional growth and maturation of Pacific sardine, which may show patterns similar to those found in northern anchovy (Parrish et al. 1985).

METHODS

Sampling

A daily egg production method (DEPM) biomass survey (Lasker 1985) was conducted from April 7 to May 14, 1994, to estimate current stock size (Lo et al. 1996). A total of 667 adult sardines were sampled to obtain adult reproductive data for DEPM calculations, and otoliths were removed for age determination. An additional 412 fish were sampled for age determination to encompass the size range of adults. Collection methods are described in Lo et al. 1996 and Macewicz et al. 1996. In most cases otoliths were removed at sea, cleaned, and stored dry in gelatin capsules. For a few samples taken from commercial purse seine catches landed in Ensenada, otoliths were removed in the laboratory from sardines taken at sea the night before.

Otolith Reading

An annulus was defined as one of a series of concentric zones on a structure that may be interpreted as annual markers. For sardine otoliths, an annulus is the interface between an inner translucent growth increment and the successive outer opaque growth increment (Fitch

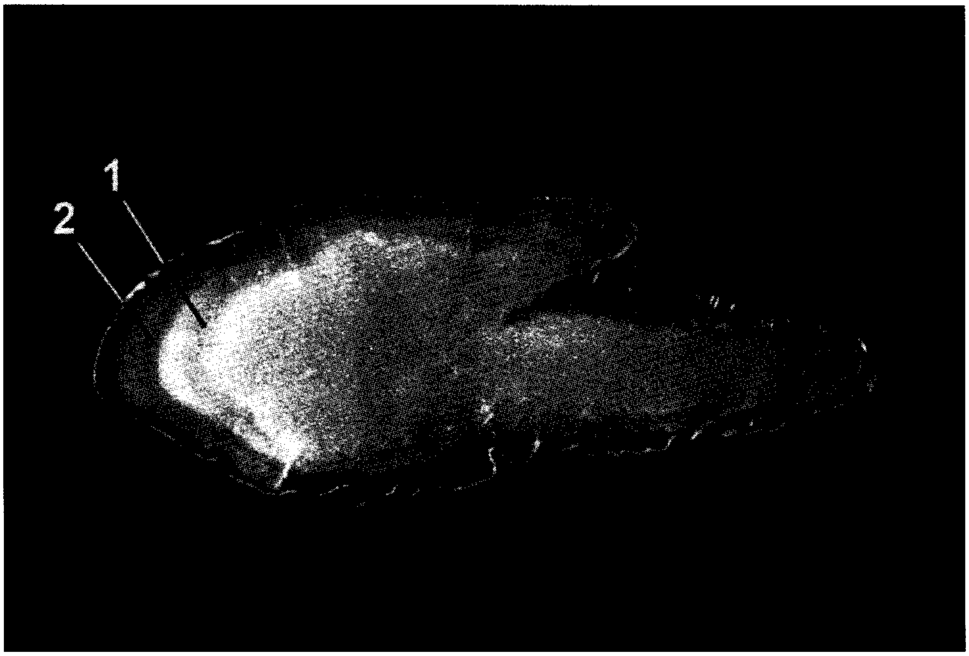

Figure 1. Sagitta of a 182-mm SL California sardine (*Sardinops sagax*), showing two annular increments.

1951; figure 1). Counting successive annuli in an otolith results in an estimate of age. The year class (year of birth) can be calculated by assuming a peak spawning season from the age and sample date. By convention, a year class consists of all fish hatched during a calendar year. Although some sardine spawning takes place year-round, most occurs in summer (Watson 1992). Because the actual hatch date for each individual is unknown, we assume that all individuals in each year class become one year old on January 1. This method differs from that used in California for Pacific sardine in the past. Murphy (1966), Walford and Mosher (1943), and Barnes and Foreman (1994) all assumed a July 1 birth date. The age of each fish reported here was the mean of four or five readers.

Annuli were identified by submerging each pair of sagittal otoliths under a depth of 4–5 millimeters of distilled water in a watch glass with black background to improve distinction between increments (Yaremko 1996). Under a stereoscopic microscope at 12–25× magnification and reflected light, opaque increments appeared white, and translucent increments appeared black or gray.

Age was not determined from otoliths that were deformed or partially crystallized (Blacker 1974). It is not uncommon for one or both members of a pair to be somewhat deformed; therefore both otoliths were examined. Readability of the pair was improved if they were placed in the watch glass side by side, sulcus side down, because annuli may be more distinct on one otolith than the other.

Otoliths were read within three minutes of immersion because water is quickly absorbed, reducing readability. Once saturated, the outermost opaque increments tend to fade or become indistinct from translucent increments. This can be a potential source of error, causing underestimation of true age. (Readability can be restored by drying.)

Each pair of otoliths was read by four independent readers. A portion of the sample was read by a fifth reader. Age reported here is the mean of all readers' results, rounded to the nearest whole number. Means with a decimal of 0.5 were rounded to the next highest whole number. Because of the assumed January birthdate and the date at which sampling was done (in the spring before the spawning peak), all fish that had no complete annulus were assigned to age 1, the 1993 year class. Since the fish were sampled in May, age-1 fish were roughly 10 months old.

The average percent error (*APE*) was calculated from

$$APE = \frac{100}{N} \sum_{j=1}^{N} \left[1/R \sum_{i=1}^{R} \frac{[X_{ij} - \bar{X}_j]}{\bar{X}_j} \right] \tag{1}$$

where N is the number of fish aged, R is the number of readers, X_{ij} is the ith reader's age determination for the jth fish, and $\bar{X}_j$ is the average age (Beamish and Fournier 1981).

The index of precision was calculated from

$$D = \frac{1}{N} \sum_{j=1}^{N} \frac{1}{\bar{X}_j \sqrt{R}} \sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - \bar{X}_j)^2}{(R-1)}} \tag{2}$$

where D is the coefficient of variation divided by $\sqrt{R}$ from equation 1 (Chang 1982). We report D times 100 to make it more comparable to APE.

We also report the mean and range of percent agreement, PA, for combinations of 2–5 readers, where percent agreement is the percentage of otoliths that all readers agree is a given age. There are 10 combinations of agreement between 2 readers with 5 total readers (e.g., R1 with R2, R1 with R3, etc.). Agreement may or may not exist for a particular fish among any combination of readers. For each combination we calculated the percent agreement. To combine data for all combinations of readers, we averaged percent agreement over combinations:

$$\overline{PA} = \sum_{r=1}^{R} \frac{PA_r}{R} \tag{3}$$

where

$$PA_r = \sum_{n=1}^{N} \frac{D_{r,n}}{N}$$

where R is the number of readers, N the number of fish aged, and $D_{r,n} = 1$ if agreement, 0 if disagreement.

Objective Criteria

Weight of the otoliths from sardines has been correlated with age (Pawson 1990; Fletcher 1991, 1995). In an attempt to obtain objective criteria (Boehlert 1985) to aid age determination, whole otoliths were weighed to the nearest 0.001 mg with an electrobalance after they had been cleansed with bleach and dried for two days in a desiccator. Weights of the otoliths and lengths of the fish were plotted by age class to determine whether our age determinations could be improved by cluster analysis or other statistical technique.

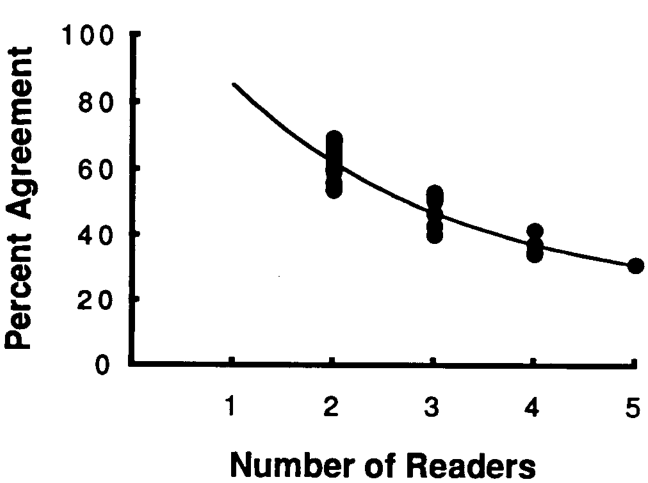

Figure 2. Percent agreement (PA) on age determination of Pacific sardine by two, three, four, and five readers. Equation fitted to the line is $PA = 19.6 + 102 * \mathrm{EXP}(-.44 * NR)$

Maturity

Maturation of females was determined from the histological state of the gonads. Presence of postovulatory follicles or yolked eggs was used as an indication of maturity (see Macewicz et al. 1996).

Geographic Areas

Samples were grouped into three regions: Monterey ($N = 152$), Southern California Bight ($N = 710$), and Baja California ($N = 212$). The Southern California Bight samples included all samples from 31°N to 34°N (see figure 3 in Lo et al. 1996). Monterey samples were all collected in Monterey Bay (north of 34°N), and Baja California samples were collected south of 31°N.

RESULTS

Reader Agreement

Age determinations for Pacific sardine were not very precise. The average percent error (APE) among readers was 16%, and the index of precision (times 100; Chang 1982) was 9. The mean agreement of five readers was 31%; of four readers, 37% (range 34%–42%); of three readers, 47% (range 40%–53%); and of two readers, 62% (range 54%–69%). Reader agreement was not correlated with experience. The two most experienced readers had the lowest agreement (54%). Agreement approaches an asymptote of about 20% as the number of readers who agree increases (figure 2). The percent agreement among five readers was negatively correlated with mean age ($N = 637$, $P < 0.01$).

Otolith Weight and Standard Length

It was not possible to use otolith weight with other data to estimate age of Pacific sardine. Otolith weight and fish length were plotted by mean age (figure 3). Fish assigned to age 1 and age 2 largely overlap in both length and otolith weight, whereas age-3 fish appear to be separate from younger and older fish. Some fish assigned to age 3 overlap with fish age 2 and also with fish age 5 and age 6. In addition, we were not able to use modal analysis of otolith weight to distinguish year classes (figure 4) as reported by Fletcher (1991, 1995). We decided that cluster analysis would not be a useful approach for estimating sardine ages.

Age Composition

Sardine in DEPM samples ranged from age 1 (1993 year class) to age 7 (1987 year class). Age composition comprised 21.4% 1993 year class; 41.4% 1992 year class; 28.3% 1991 year class; 6.3% 1990 year class; 2.6% 1989 year class; 0.3% 1988 year class; and 0.1% 1987 year class. The age composition of our samples was much younger than that reported for the California fishery during the

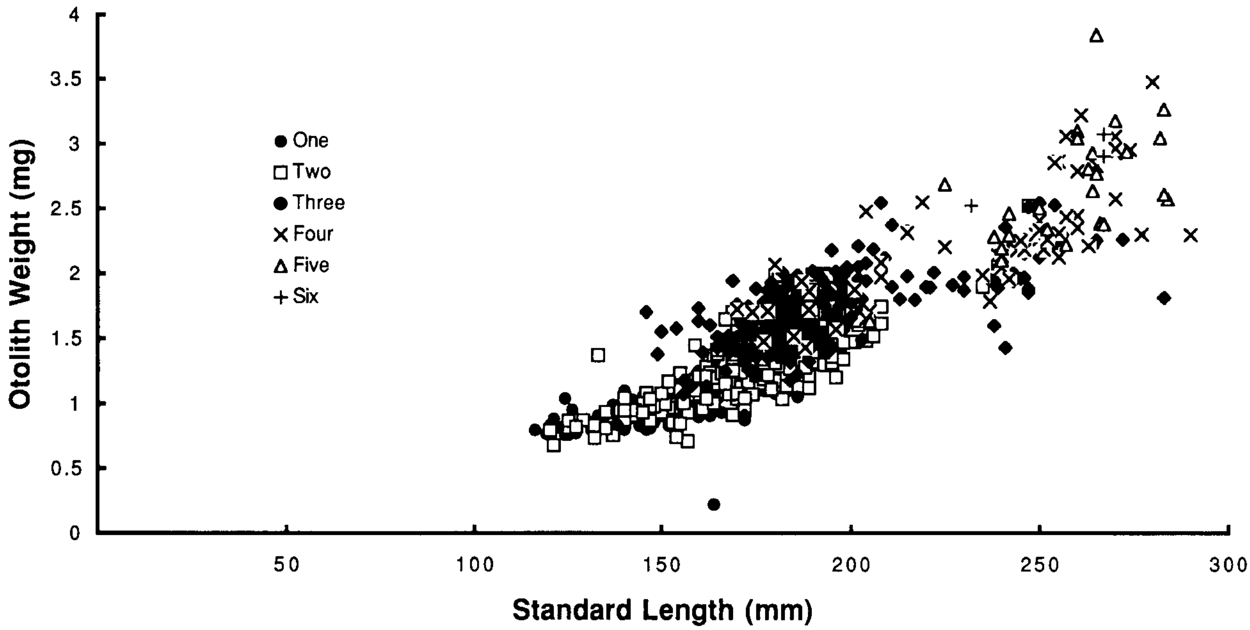

Figure 3. Otolith dry weight and standard length of Pacific sardine collected during the 1994 daily egg production method (DEPM) biomass survey.

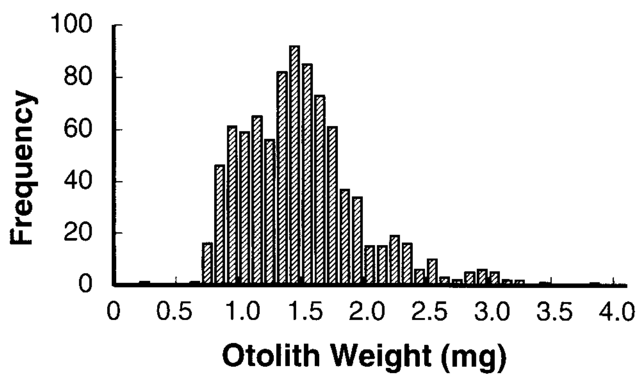

Figure 4. Distribution of otolith weights of Pacific sardine collected from 26°N to 36°N during 1994.

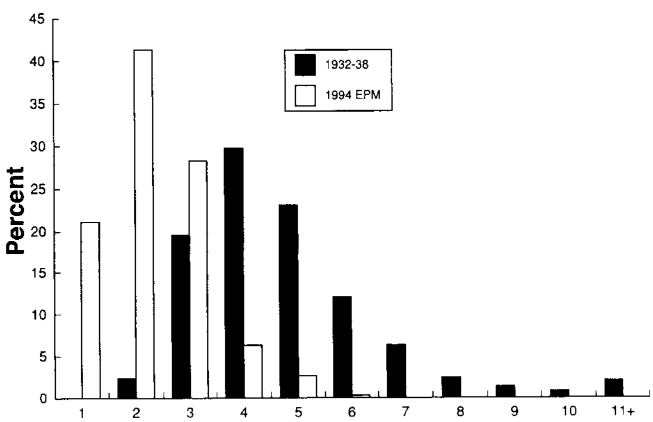

Figure 5. Comparison of age composition of Pacific sardine during 1932–38 (Moser and Eckles 1954) and 1994.

1930s (figure 5). Landings during the 1930s reached a maximum age of over 10, and at that time ages 6 and older accounted for 14.6% of all fish captured. In comparison, no fish older than 7 years were found in the samples collected during the DEPM survey.

Length at Age

Growth was estimated by fitting a von Bertalanffy equation to the size at age for all samples (figure 6). Length at infinity was 205.4 ± 1.6 mm SE; k was 1.19 ± 0.04 SE; and t_0 was fixed at zero because there were no data near the origin, and the parameter was not estimable (R^2 = .37). Length at infinity greatly underestimates the maximum size of sardine, but a large growth coefficient is consistent with fast growth.

Maturity

The age of 50% maturity could not be calculated, since more than 50% of age-1 fish were mature.

Regional Differences

Age composition varied with latitude in our samples. More young fish were found off Baja California than in the Southern California Bight or off Monterey (figure 7).

The length at age for Pacific sardine differed between regions (figure 8), although there was considerable overlap in size for the 1993, 1992, and 1991 year classes in each region. Mean sizes at ages of one-, two-, and three-year old fish indicate that fish were smaller at age off Baja

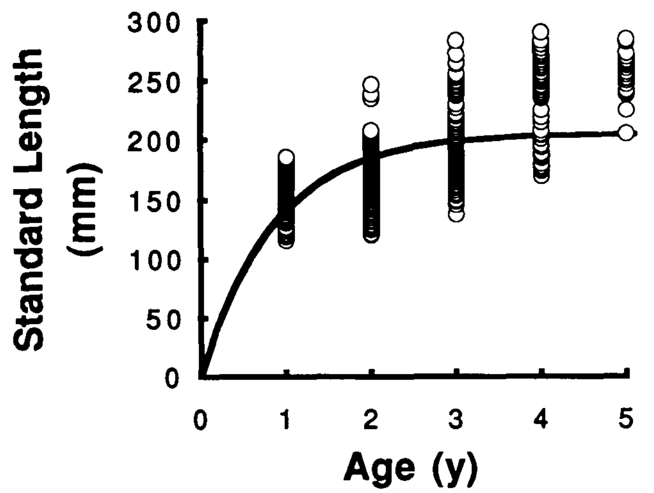

Figure 6. Length at age of Pacific sardine with Von Bertalanffy model. See text for details of the equation.

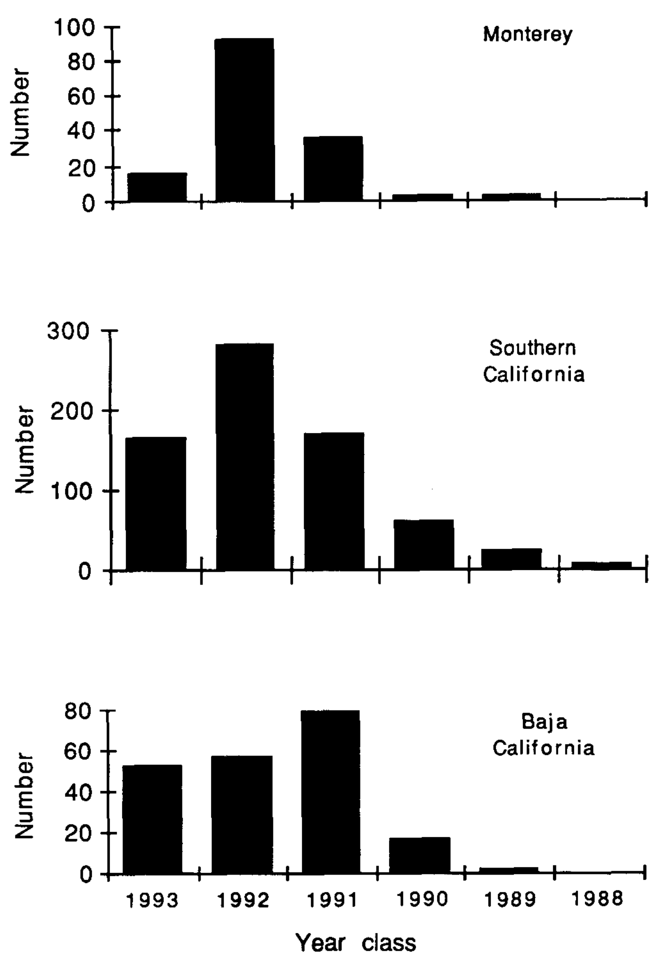

Figure 7. Age composition of Pacific sardine collected north of 34°N (Monterey); from 31° to 34°N (Southern California Bight); and south of 31°N (Baja California).

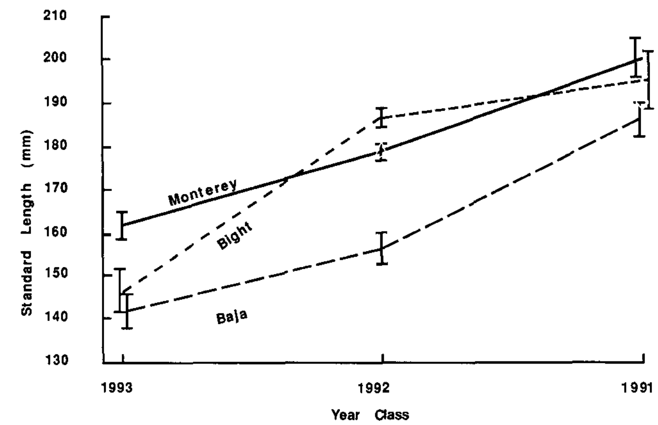

Figure 8. Length at age for Pacific sardine collected north of 34°N (Monterey); from 31° to 34°N (Southern California Bight); and south of 31°N (Baja California).

California and larger off Monterey. The one exception to this apparent cline in growth was age-2 fish collected in the Southern California Bight, which were larger than those collected off Monterey.

Maturation of Pacific sardine females appears to vary with latitude. Fish mature at a younger age in southern California and Baja California than off Monterey (figure 9). However, considering the small numbers of age-1 fish sampled both for age and maturity off southern Baja California (5) and off Monterey (14), these data must be considered as preliminary.

DISCUSSION

Validation

It is essential that the periodicity of annuli formation be validated before ages and year classes can be assigned with certainty. Barnes and Foreman (1994) documented the periodicity of annuli in otoliths of young sardines up to age 3. Their samples were collected from the Southern California Bight during the 1980s, in the early stages of the current resurgence in the population (Deriso et al. 1996). Earlier work by Walford and Mosher (1943) demonstrated an annual cycle in marginal increment width for otoliths taken from southern California landings during 1938 and 1939, implying the formation of annuli during that period.

The studies by Barnes and Foreman (1994) and Walford and Mosher (1943) provide some evidence for the formation of annuli in fish from California waters during different oceanographic regimes. This suggests that marks in Pacific sardine otoliths are not caused by transitory conditions. However, different oceanographic conditions or spawning behavior may cause the formation of two opaque growth increments per year for fish caught in Bahía Magdalena, Baja California Sur (Felix-Uraga and

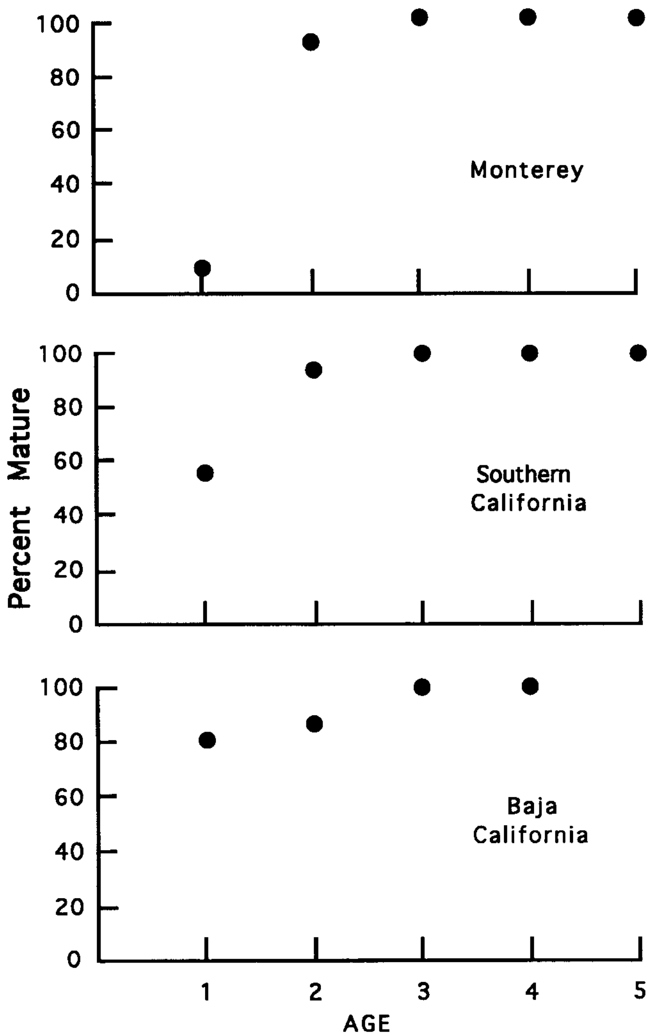

Figure 9. Percent maturity of Pacific sardine by age class for three geographic areas.

Ramirez-Rodriguez 1989). Kimura (1970) reported the formation of checks in scales of sardine reared in the laboratory. Unfortunately, otoliths were not taken from Kimura's samples. Thus errors due to variable periodicity are possible, but are probably associated with the more southern reaches of the population range.

In addition to validation, studies using age-composition data need to demonstrate reproducibility or verification of age assignments. There are two potential sources of ageing error in our study: (1) variable periodicity for major growth increments, and (2) indistinct or ambiguous appearance of major growth increments, complicated by false annuli or spawning checks in the otolith. We suspect that both sources of error are present to some extent in our results, although difficulties in interpreting otolith appearance are thought to be a greater problem than variable periodicity of annuli. Barnes and Foreman (1994) identified variable timing of the spawning peak as another potential source of ageing error, but that was not thought to be significant in this study.

The clarity of the annual pattern varies considerably from specimen to specimen, so interpretation of the annual growth patterns in otolith appearance was to some degree ambiguous in nearly 70% of our samples, as demonstrated by the low degree of agreement between all five readers. Ambiguous sardine otoliths create an element of subjectivity in age assignments, resulting in low precision. In this study two of our readers agreed on 64% of 1,035 otoliths. But in a recent ageing study involving specimens collected during 1988–92 (Hester 1993) the same readers achieved 70%–75% agreement in independent duplicate readings. This suggests that the otoliths in our study were more difficult to read. It is generally assumed that in any sample some fraction of otoliths is so unambiguous that all readers would assign the same age. In our study the fraction of unambiguous otoliths was about 20%.

Some ageing errors associated with simple annuli counts may be corrected by modeling age as a function of annuli count and other measurement data. Errors have been reduced by predicting age for individual Mediterranean sardines, *Sardina pilchardus*, by using otolith weight–fish length relationships for each year class (Pawson 1990). We anticipate that further work along similar lines will improve ageing results for Pacific sardine. But the apparently large variability in Pacific sardine growth rates among areas suggests that direct application of Pawson's (1990) method may not be appropriate for Pacific sardine. We suggest an expanded model for Pacific sardine that includes effects due to annuli counts, otolith weight, fish length, latitude of capture, and radial distance to each otolith annulus. One aspect of further ageing work should include counts of daily growth increments (Butler 1987) and injection with fluorescent dyes that mark the otolith to confirm growth rates and age assignments for different geographic regions.

Independent Criteria

Weight of the otolith and standard length of the fish did not clearly separate fish by assigned age. Fish aged one overlap fish aged as two-year-olds. This may be a result of ageing error for fish sampled over a broad geographic area, or a result of variation in spawning season and juvenile growth rates. Fish from southern California produce one translucent mark per year (Barnes and Foreman 1994), whereas Felix-Uraga and Ramirez-Rodriguez (1989) report that fish from southern Baja California produce two translucent marks per year. DEPM samples covered both regions, and readers used one criterion to assign an age for all samples. An alternate hypothesis is that fish from different regions have different allometric growth of the otolith.

Growth Rates

It is difficult to compare size at age reported here with previous studies (Felin and Phillips 1948; Phillips 1948; Felin et al. 1958, etc.) because our samples are taken in April and May, and previous studies were taken from the commercial fishery, conducted between August and February. Marr (1960) reported calculated size at first annulus formation for year classes from 1934 to 1957. During 1934–43 and 1944–57, length at first annulus formation was 101 mm and 131 mm, respectively. Similar differences in sardine growth rates with population size have been found in Japan (Kawasaki and Omori 1995; Wada et al. 1995).

In this study, age-1 fish that are about 10 months old averaged 142, 162, and 146 mm in southern Baja California, southern California, and Monterey. It is uncertain whether these regional differences are due to differences in growth, small sample sizes, differences in spawning season, or inaccurate age determination. The average of all age-1 fish is 155 mm. This is larger than fish collected from 1934 to 1957 (Marr 1960) or fish reared in the laboratory (120 mm; Kimura and Sakagawa 1972). However, Felix-Uraga (1990) reports that sardine grow to 153 mm in one year in Bahía Magdalena. Thus sardine are apparently growing much faster now than previously reported. However, details of regional growth can best be documented with daily growth increments (Butler 1989), which were not examined in our study.

Age Composition

Age composition varied with latitude. This is consistent with findings from the historical fishery (Mosher and Eckles 1954). Hester (1993) reported similar latitude effects on age composition for samples collected from commercial fisheries in Ensenada, San Pedro, and Monterey during 1987–92.

Estimates of age composition from DEPM samples differ from those estimated from an age-structured stock assessment model of the population (Deriso et al. 1996). Age-2 (1992 year class) fish were most numerous in DEPM samples, whereas the population model indicates that age 1 (1993 year class) is most numerous (Deriso et al. 1996). This discrepancy may be due to assumptions about recruitment in the population model or due to size-specific gear selectivity in the DEPM sample. Lower selectivity for small, young fish results in underrepresentation of the two youngest year classes. Although 45% of DEPM specimens were obtained from commercial purse seine sets, these samples were taken inshore, whereas trawl samples were taken offshore. Perhaps for this reason, size composition did not differ between samples taken with the two gear types (Lo et al. 1996). Barnes et al. (1992) and Deriso et al. (1996) found sardine to be fully recruited to purse seine gear at age 3. Our results indicate that sardine were fully available to the DEPM sampling gear at age 2 or age 3, possibly because the high-speed midwater trawl obtains more representative samples of small, young fish than the commercial purse seines (Dotson and Griffith 1996).

Maturation

The age and size of maturation of sardine is a critical parameter, since the proportion of mature and immature fish is used to calibrate spawning biomass and total biomass (Lo et al. 1996; Deriso et al. 1996). Sardine appear to be maturing at an earlier age than previously reported. Murphy (1966) interpreted Clark's size at maturity for fish collected off Monterey during 1928–31 (Clark 1934) to indicate that 50% matured by age 2. MacGregor (1957) reported that 30% of age-1 fish and all age-2 fish were mature in samples taken off San Pedro during 1945 and 1946. Ahlstrom (1960) reported that Pacific sardine matured at 115 mm SL, with 50% mature at 125 mm in samples taken off Ensenada in 1958. It is important to note that 1958 was an El Niño year, with water temperatures 1°–2°C above normal. These fish were probably less than one year of age and are consistent with our age at first maturity for samples from southern Baja California. Thus maturation of sardine appears to be flexible. Interpretation of biological changes in response to population size or climatic regime is confounded by variation in seasonality and locality of sampling. The 1994 DEPM survey offered the first opportunity for studying maturation of Pacific sardine synoptically over a large geographic range.

CONCLUSION

The age composition of Pacific sardine in 1994 reflects a growing population and/or high adult mortality rates. Most of the biomass is in the most recent year classes. Very few fish are older than 4 years. During the 1930s the sardine population comprised many more year classes, and fish older than 8 years were not uncommon. The age composition of the population should be monitored carefully, because the present population, while growing, is very vulnerable to recruitment failure.

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