# AGE, GROWTH, AND MORTALITY OF KING MACKEREL, SCOMBEROMORUS CAVALLA, FROM THE SOUTHEASTERN UNITED STATES ${ }^{1}$ 

Allyn G. Johnson, William A. Fable, Jr., Mark L. Williams, and Lyman E. Barger ${ }^{2}$


#### Abstract

Age, growth, and mortality of king mackerel, Scomberomorus cavalla, from the southeastern United States were studied. Otoliths from 1,449 fish were used to estimate age composition, growth rates, and mortality rates of this species. Age composition varied between locations (Texas, Louisiana, Florida, South Carolina, and North Carolina). The majority of older fish were found in Louisiana waters. The oldest females were $14+$ years old and the oldest males were $9+$ years old. Compensatory growth was found in both sexes. The von Bertalanffy growth equations were as follows: Males (all areas) $1_{i}=965\left(1-e^{-0.28(t+1.17)}\right.$ ); females from Louisiana $1_{t}=1,529\left(1-e^{-0.14(1+208)}\right)$; and females (excluding Louisiana) $1_{t}=1,067\left(1-e^{-0.29(t+097)}\right.$ ) where $1=$ fork length ( mm ) and $t=$ years. The mean annual mortality rate determined by six methods of analysis ranged from 0.32 to 0.42 . The length-weight relations of king mackerel were for males: $W=0.8064 \times 10^{-5} L^{2.9928}$; for females: $W=0.8801 \times 10^{-5} L^{2.9827}$, where $W=$ weight in grams and $L=$ fork length in millimeters.


King mackerel, Scomberomorus cavalla, is a major recreational and commercial fisheries resource in the southeastern United States (Manooch 1979). Age, growth, and mortality information has been based on small specimens collected from a limited geographical area (Beaumariage 1973). A need has existed to reexamine age, growth, and mortality from broader geographically based samples.

King mackerel of Brazil have been studied intensively, but the great distance separating these Brazilian fish from those in the United States makes application of their results to king mackerel in United States waters a questionable practice (see Manooch et al. 1978 for annotated bibliography on this species).

A geographically comprehensive sampling of king mackerel in U.S. waters was initiated by us in 1977. Recreational landings were sampled because the sport fishery is less localized than the commercial fishery. We utilized samples from Texas to North Carolina to meet our objectives of determining the age composition, growth rates, length-weight relationships, and mortality rates of king mackerel from U.S. waters.

[^0]
## METHODS AND MATERIALS

King mackerel ( 7,723 fish) were collected from Texas, Louisiana, Florida, South Carolina, and North Carolina from June 1977 through August 1979 (Fig. 1). They were caught by recreational hook and line, except for some small individuals, which were caught in shrimp trawls at Cape Canaveral, Fla., in December 1978. The trawlcaught fish were used in determining the relation between otolith radius and fish length. In 1979, 121 fish samples were taken only in northwest Florida and were used to supplement existing samples for the marginal increment analysis.

Processing the fish samples involved several. steps. The fish were sexed when possible, measured to the nearest millimeter of fork length (FL), and weighed to the nearest gram. Otoliths were removed from the fish, cleaned, and stored either dry or in $100 \%$ glycerin.

The otoliths were examined under reflected light in a black-bottomed watch glass containing $100 \%$ glycerin with a binocular dissecting microscope at $28 \times$. The otolith radius ( OR ) was measured on the posterior surface from the focus to the distal margin along the axis approximating the extension of the sulcus acousticus. All measurements were made in ocular micrometer units ( $1 \mathrm{om} \mu=0.0363 \mathrm{~mm}$ ). Marks were counted and measured along the radius to their distal edge. The marks were opaque (light) under re-


Figure 1.-Location of king mackerel, Scomberomorus cavalla, sampling sites.
flected light, while the interspaces were hyaline (dark).

Otoliths were classified into age groups according to the number of opaque nonmarginal marks (following the method of Beaumariage 1973). Each otolith was examined by two readers. If the readers did not agree on the age of a fish, data for that fish were not used.

We determined the time of mark formation by comparing frequency per month of otoliths with opaque margins. A high percentage of opaque margins indicated recent mark formation.

Comparison of age estimations was made, based on surface (whole) and internal (sectional) examination of 133 otoliths. Three to 10 otoliths from each age ( $0+$ through $14+$ ) were used for the comparison. Three to six sections, each 0.15 mm thick, were made through the focus of each otolith, using a Norton ${ }^{3}$ diamond blade (SD519$\mathrm{N} 50 \mathrm{~m}-1 / 8$ ) rotating at about 285 rpm on an Isomet low-speed saw. The otolith was mounted in thermoplastic (quartz) cement (No. 70C Lakeside) and cooled with mineral spirits during sectioning. Later the cement was dissolved by soaking in $50 \%$ isopropanol. The free sections were then mounted on glass slides using Piccolyte ce-

[^1]ment and examined with a binocular dissecting microscope.
The relationship of the size of the aging structure (OR) to the size of the fish (FL) was determined by using least-square regressions with both linear and power curves. Once the relationship was established, fork lengths at earlier ages were back-calculated from surface otolith measurements, using methods adopted from Tesch (1971), Ricker (1975), and Everhart et al. (1975).

Otolith measurements were analyzed for implications of compensatory growth. A frequency distribution of otolith lengths from the focus to the proximal edge of the first opaque mark was developed. Both slow- and fast-growing fish were separated from those that grow at intermediate rates, and lengths at earlier ages were back-calculated for both the slow and fast growers.
A computer program by Abramson (1971) was used to fit von Bertalanffy theoretical growth curves. Each age was given equal weight, and mean back-calculated lengths were used in the computations.
Length-weight equations were developed for the entire king mackerel collection, and for males and females separately, by a computer program following Ricker's (1975) suggestions. Nonlogarithmic length intervals ( 50 mm ) and
weight intervals (computed by the program) were used. A maximum of 20 length-weight values was randomly selected for the analysis within each qualifying length and weight interval. If any length or weight interval contained fewer than 20 values, all were utilized.

Estimates of annual mortality rate A (after Ricker 1975) were developed by catch-curve analysis of south Florida length-frequency data. These data were used because they best represented the king mackerel in U.S. waters according to Trent et al. (1981). Since these data were not separated by sex, two age-length keys were developed, one combining males and females assuming a $1: 1$ sex ratio and the other assuming a 1 male: 2 female ratio (the approximate ratio in our collection). The length-frequency data were converted to age-frequency distributions ( $N_{i}=$ number of fish caught in age-class $i$ ) by applying each of the combined age-length keys. Age classes I through X of the resultant catch curves were analyzed by

1. Heincke's (1913) method;
2. Jackson's (1939) method;
3. Rounsefell and Everhart's (1953) method;
4. Beverton and Holt's (1957) method, using the mean of values computed with their equation 13.4 between successive age groups;
5. Robson and Chapman's (1961) method, uncorrected for possible age-length key bias; and
6. finding the slope $(m)$ of a regression line fitted to $\ln \left(N_{i}\right)$ and $i$ and substituting in the equation $A=1-e^{m}$.

## RESULTS AND DISCUSSION

## Age

The validity of using otoliths for estimating the age and past growth history depends on these structures being directly correlated with the growth of the fish and on otolith mark formation being periodic. We found the otolith radii to be closely correlated to fork lengths, especially when the data were transformed to represent a "power" function. The "power curve" equation, $\mathrm{FL}=1.232 \mathrm{OR}^{1.331}$ with correlation coefficient $r$ $=0.987$, had a better fit than the linear equation, $\mathrm{FL}=5.559 \mathrm{OR}+84.818$ with $r=0.847$. This close correlation of OR and FL satisfied the first criterion for validation of otoliths as an age
determination structure. The second criterion, mark formation of known periodicity, needed further investigation. Beaumariage (1973) found king mackerel with opaque margins during 8 mo of the year (February-September); the highest percentage of otoliths with opaque margins occurred in May. He concluded, "Most otolith margins become opaque (form annuli) during April, May, and June...." Fish in our collections exhibited opaque margins in 11 mo of the year with the peak during May (54\%); however, few fish were collected during the winter months (NovemberFebruary). No month had a high percentage (over 75\%) of fish with opaque margins, and only one month (March) lacked fish whose otoliths had opaque margins (Table 1).

In recent years the use of whole otoliths for estimating the age of fish has been questioned. Beamish (1979) indicated that a fish's age may be underestimated using surface examination and that otolith sections are more reliable. However, we found $96.5 \%$ agreement between king mackerel age estimates (number of opaque marks) comparing surface and sectional readings. This indicates that our age estimations for whole otoliths are similar to those of sectioned ones.

The agreement between two readers about the number of marks on king mackerel otoliths was $98 \%$. The number of otoliths found to be usable was 1,449 .

## Age and Size Composition

Age composition of king mackerel varied greatly among the areas (Table 2). Younger fish were taken in northwest Florida, while older fish were caught off Louisiana, particularly in 1978. Fish of intermediate age were landed primarily in Texas, South Carolina, and North Carolina. The oldest females in our sample were $14+\mathrm{yr}$ (over $1,400 \mathrm{~mm} \mathrm{FL}$ ) and the oldest males were $9+$ yr ( 970 mm FL ).

Much age variation occurred within a single length group in our data (Tables 3,4 ) as it did in Beaumariage's (1973) data. For example, we found females $850-899 \mathrm{~mm}$ FL were $1-8 \mathrm{yr}$ old (Table 3).

## Back-Calculated Growth

The weighted means of the back-calculated fork lengths for male and female king mackerel from all areas and years sampled in this study are shown in Tables 5 and 6. Differences in mean

Table 1.-Percentages by month, area, and year of king mackerel otoliths having opaque margins. ( ) = total number of fish.

| Area | Year | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Texas | 1977 | - | - | - | - | - | $\begin{aligned} & 26.7 \\ & (15) \end{aligned}$ | 28.6 | $\begin{aligned} & 0.0 \\ & (5) \end{aligned}$ | - | - | - | - |
|  | 1978 | - | - | - | - | - | $\begin{aligned} & 0.0 \\ & (5) \end{aligned}$ | $\begin{gathered} 0.0 \\ (17) \end{gathered}$ | $\begin{array}{r} 2.5 \\ (40) \end{array}$ | - | - | - | - |
| Louisiana | 1977 | - | - | - | - | - | $\begin{aligned} & 0.0 \\ & (4) \end{aligned}$ | - | - | $\begin{gathered} 0.0 \\ (15) \end{gathered}$ | $\begin{gathered} 0.0 \\ (22) \end{gathered}$ | $\begin{gathered} 0.0 \\ (18) \end{gathered}$ | - |
|  | 1978 | $\begin{aligned} & 0.0 \\ & (7) \end{aligned}$ | $\begin{gathered} 16.7 \\ \{6\rangle \end{gathered}$ | $\begin{gathered} 0.0 \\ (43) \end{gathered}$ | $\begin{aligned} & 40.6 \\ & (32) \end{aligned}$ | $\begin{aligned} & 0.0 \\ & (2) \end{aligned}$ | $\begin{aligned} & 15.4 \\ & (26) \end{aligned}$ | $\begin{aligned} & 6.5 \\ & (62) \end{aligned}$ | $\begin{aligned} & 13.5 \\ & (37) \end{aligned}$ | $\begin{aligned} & 0.0 \\ & (5) \end{aligned}$ | $\begin{gathered} 0.0 \\ (51) \end{gathered}$ | $\begin{gathered} 5.0 \\ (20) \end{gathered}$ | $\begin{gathered} 14.3 \\ (7) \end{gathered}$ |
| NW Florida | 1977 | $\sim$ | - | - | - | - | $\begin{aligned} & 18.2 \\ & (11) \end{aligned}$ | $\begin{aligned} & 9.4 \\ & (64) \end{aligned}$ | $\begin{gathered} 3.1 \\ (65) \end{gathered}$ | $\begin{gathered} 0.0 \\ (73) \end{gathered}$ | $\begin{gathered} 4.3 \\ (46) \end{gathered}$ | - | - |
|  | 1978 | - | - | - | - | - | $\begin{array}{r} 0.0 \\ (15) \end{array}$ | $\begin{gathered} 0.0 \\ (160) \end{gathered}$ | $\begin{gathered} 0.0 \\ (97) \end{gathered}$ | $\begin{gathered} 0.0 \\ (107) \end{gathered}$ | $\begin{aligned} & 11.1 \\ & \langle 135\rangle \end{aligned}$ | - | $\sim$ |
|  | 1979 | - | - | - | - | $\begin{aligned} & 61.2 \\ & (62) \end{aligned}$ | $\begin{aligned} & 20.0 \\ & (20) \end{aligned}$ | $\begin{aligned} & 19.2 \\ & (27) \end{aligned}$ | $\begin{gathered} 0.0 \\ (12) \end{gathered}$ | - | - | - | $\sim$ |
| SE Florida | 1978 | - | - | - | - | - | - | - | - | $\sim$ | $\sim$ | - | $\begin{gathered} 50.0 \\ (6) \end{gathered}$ |
|  | 1979 | $\begin{gathered} 83.3 \\ (6) \end{gathered}$ | - | - | - | - | - | - | - | - | - | - | - |
| South Carolina | 1978 | -- | - | - | - | - | - | - | - | - | $\begin{gathered} 2.9 \\ (104) \end{gathered}$ | $\rightarrow$ | - |
| North Carolina | 1978 | - | - | - | - | $\begin{aligned} & 0.0 \\ & \text { (5) } \end{aligned}$ | $\begin{aligned} & 63.6 \\ & (22) \end{aligned}$ | $\begin{aligned} & 38.5 \\ & (13) \end{aligned}$ | $\begin{aligned} & 26.7 \\ & (15) \end{aligned}$ | $\begin{gathered} 3.8 \\ (53) \end{gathered}$ | $\begin{gathered} 8.9 \\ (313) \end{gathered}$ | - | - |
| Total |  | $\begin{array}{r} 38.5 \\ (13) \end{array}$ | $\begin{gathered} 16.7 \\ (6) \\ \hline \end{gathered}$ | $\begin{gathered} 0.0 \\ (43) \\ \hline \end{gathered}$ | $\begin{array}{r} 40.6 \\ (32) \\ \hline \end{array}$ | $\begin{aligned} & 54.3 \\ & (70) \\ & \hline \end{aligned}$ | $\begin{array}{r} 23.7 \\ (118) \\ \hline \end{array}$ | $\begin{array}{r} 7.2 \\ (364) \\ \hline \end{array}$ | $\begin{array}{r} 44 \\ (271) \\ \hline \end{array}$ | $\begin{gathered} 0.8 \\ (253) \\ \hline \end{gathered}$ | $\begin{array}{r} 7.2 \\ (671) \\ \hline \end{array}$ | $\begin{array}{r} 2.6 \\ (38) \\ \hline \end{array}$ | $\begin{aligned} & 33.3 \\ & (13) \\ & \hline \end{aligned}$ |

Table 2.-Percentages of king mackerel by area and year within each age group, developed from age-length keys and lengthfrequency distributions.

| Area | Year | Age in years |  |  |  |  |  |  |  |  |  |  |  |  |  |  | No. fish |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |  |
| Males |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Texas | 1977 | - | - | 6.9 | 24.1 | 24.1 | 27.6 | 3.5 | 6.9 | 6.9 | - | - | -- | - | - | -- | 29 |
|  | 1978 | - | 2.6 | 1.9 | 13.5 | 16.5 | 20.6 | 32.5 | 3.6 | 3.3 | 5.8 | - | - | - | - | - | 533 |
| Lovisiana | 1977 | - | - | - | - | - | 100.0 | - | - | $-$ | - | - | - | - | - | - | 10 |
|  | 1978 | - | - | - | - | - | 20.0 | 24.0 | 36.0 | 8.0 | 12.0 | - | - | - | - | - | 25 |
| NW Florida | 1977 | - | 26.9 | 31.3 | 16.7 | 20.5 | 2.0 | 2.6 | - | - | - | - | - | - | - | - | 498 |
|  | 1978 | 1.8 | 93.1 | 2.7 | 1.2 | 0.4 | 0.8 | - | $\sim$ | - | - | - | - | - | - | - | 1,107 |
| South |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Carolina | 1978 | - | 21.1 | 8.8 | 21.8 | 13.6 | 13.6 | 19.7 | - | - | 1.4 | - | - | - | - | - | 147 |
| North |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Carolina | 1978 | - | 5.2 | 5.2 | 18.3 | 35.7 | 20.0 | 8.6 | 3.5 | 3.5 | - | - | - | - | - | - | 115 |
| Total males |  | 0.8 | 48.8 | 8.6 | 10.5 | 12.6 | 7.7 | 65 | 1.7 | 1.4 | 1.4 | - | - | - | - | - | 2,507 |
| Females |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Texas | 1977 | - | - | 27.9 | 48.8 | 7.0 | 9.3 | 4.7 | 2.3 | - | - | - | $\sim$ | - | - | - | 43 |
|  | 1978 | - | 4.1 | 8.5 | 5.8 | 37.3 | 23.6 | 9.9 | 10.8 | - | - | - | - | - | - | - | 780 |
| Louisiana | 1977 | - | 0.4 | 0.8 | 12.6 | 28.9 | 30.1 | 10.9 | 6.7 | 2.9 | 6.7 | - | - | - | - | - | 239 |
|  | 1978 | - | - | 0.4 | 1.3 | 6.0 | 14.4 | 24.4 | 11.9 | 7.7 | 7.7 | 10.9 | 8.8 | 4.4 | 1.3 | 0.8 | 479 |
| NW Florida | 1977 | - | 39.6 | 30.4 | 12.5 | 10.0 | 5.8 | 0.6 | 0.6 | 0.4 | - | 0.1 | - | $\sim$ | - | - | 1,393 |
|  | 1978 | 2.0 | 85.0 | 5.9 | 2.5 | 2.1 | 1.6 | 0.8 | - | - | - | 0.1 | - | - | - | - | 1,463 |
| South |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Carolina | 1978 | - | 17.3 | 3.6 | 26.5 | 21.7 | 5.6 | 11.2 | - | 4.4 | 5.6 | 2.4 | 0.8 | 0.9 | - | - | 249 |
| North |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Carolina | 1978 | - | 4.5 | 3.7 | 19.7 | 20.4 | 19.2 | 16.4 | 8.5 | 40 | 3.2 | -- | - | 0.4 | - | - | 402 |
| Total females |  | 0.6 | 37.9 | 10.9 | 9.9 | 11.1 | 8.6 | 0.3 | 4.0 | 2.2 | 1.7 | 1.7 | 1.1 | 0.7 | 0.2 | 0.1 | 5,216 |

length occurred from year to year and from area to area. Only data for Louisiana, however, where five or more individuals were used in computing a mean, showed the range of means within an age group to vary more than 100 mm .
In 2 yr of sampling in Louisiana, over 300 females were sampled, but too few males were col-
lected to back-calculate size at previous ages. Generally, the Louisiana fish were also much larger than those taken elsewhere, and we concluded that this must be an anomalous group of fish. We separated Louisiana females from other females for growth computations, except those dealing with compensatory growth.

JOHNSON ET AL.: AGE, GROWTH. AND MORTALITY OF KING MACKEREL
TABLE 3.-Length composition (\%) of female king mackerel by age group (locations combined).

| Length group (mm FL) | Age in years |  |  |  |  |  |  |  |  |  |  |  |  |  |  | Total no. fish |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |  |
| 350-399 | 100.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1 |
| 400-449 | 33.3 | 66.7 |  |  |  |  |  |  |  |  |  |  |  |  |  | 6 |
| 450-499 | 43.5 | 56.5 |  |  |  |  |  |  |  |  |  |  |  |  |  | 23 |
| 500-549 |  | 100.0 |  |  |  |  |  |  |  |  |  |  |  |  |  | 48 |
| 550-599 |  | 100.0 |  |  |  |  |  |  |  |  |  |  |  |  |  | 90 |
| 600-649 |  | 96.4 | 3.6 |  |  |  |  |  |  |  |  |  |  |  |  | 112 |
| 650-699 |  | 77.5 | 19.7 | 2.8 |  |  |  |  |  |  |  |  |  |  |  | 71 |
| 700-749 |  | 25.3 | 65.1 | 7.2 | 1.2 | 1.2 |  |  |  |  |  |  |  |  |  | 83 |
| 750-799 |  | 3.0 | 36.0 | 43.0 | 16.0 | 2.0 |  |  |  |  |  |  |  |  |  | 100 |
| 800-849 |  | 2.4 | 11.0 | 36.2 | 31.5 | 13.4 | 3.9 | 1.6 |  |  |  |  |  |  |  | 127 |
| 850-899 |  | 1.6 | 0.8 | 18.9 | 33.6 | 32.0 | 9.8 | 2.5 | 0.8 |  |  |  |  |  |  | 122 |
| 900-949 |  |  | 1.0 | 11.0 | 22.0 | 25.0 | 28.0 | 9.0 | 4.0 |  |  |  |  |  |  | 100 |
| 950-999 |  |  |  | 2.5 | 23.4 | 31.2 | 26.0 | 14.3 | 1.3 |  | 1.3 |  |  |  |  | 77 |
| 1,000-1.049 |  |  |  |  | 16.7 | 23.1 | 34.6 | 11.5 | 6.4 | 3.8 | 2.6 |  | 1.3 |  |  | 78 |
| 1,050-1,099 |  |  |  |  | 4.1 | 28.6 | 26.5 | 10.2 | 10.2 | 16.3 | 4.1 |  |  |  |  | 49 |
| 1,100-1.149 |  |  |  |  | 1.9 | 11.5 | 40.4 | 13.5 | 19.2 | 7.7 | 5.8 |  |  |  |  | 52 |
| 1,150-1,199 |  |  |  |  |  | 11.9 | 21.4 | 33.3 | 9.5 | 9.5 | 7.1 | 4.8 | 2.5 |  |  | 42 |
| 1,200-1,249 |  |  |  |  |  | 2.9 | 15.2 | 21.2 | 21.2 | 9.1 | 15.2 | 6.1 | 9.1 |  |  | 33 |
| 1,250-1,299 |  |  |  |  |  |  | 12.5 | 8.3 | 4.2 | 16.7 | 33.3 | 8.3 | 16.7 |  |  | 24 |
| 1,300-1,349 |  |  |  |  |  |  | 4.3 | 4.3 | 13.0 | 8.7 | 21.7 | 26.3 | 13.0 | 8.7 |  | 23 |
| 1,350-1,399 |  |  |  |  |  |  |  |  | 5.0 | 15.0 | 30.0 | 35.0 | 5.0 | 5.0 | 5.0 | 20 |
| 1,400-1,449 |  |  |  |  |  |  |  |  |  | 26.7 | 13.3 | 33.3 | 20.0 |  | 6.7 | 15 |
| 1,450-1,499 |  |  |  |  |  |  |  |  |  |  | 14.3 |  | 57.1 | 14.3 | 14.3 | 7 |
| 1,500-1,549 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 |
| 1,550-1,599 |  |  |  |  |  |  |  |  |  |  |  | 50.0 | 50.0 |  |  | 2 |

TABLE 4.-Length composition (\%) of male king mackerel by age group (locations combined).

| Length group ( mm FL ) | Age in years |  |  |  |  |  |  |  |  |  |  |  |  | Total no. fish |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |  |
| 400-449 |  | 100.0 |  |  |  |  |  |  |  |  |  |  |  | 4 |
| 450-499 | 15.2 | 84.8 |  |  |  |  |  |  |  |  |  |  |  | 33 |
| 500-549 |  | 100.0 |  |  |  |  |  |  |  |  |  |  |  | 51 |
| 550-599 |  | 98.3 |  | 1.7 |  |  |  |  |  |  |  |  |  | 60 |
| 600-649 |  | 93.0 | 5.3 |  | 1.7 |  |  |  |  |  |  |  |  | 57 |
| 650-699 |  | 37.5 | 37.5 | 14.6 | 10.4 |  |  |  |  |  |  |  |  | 48 |
| 700-749 |  | 11.9 | 35.7 | 31.0 | 16.6 | 2.4 | 2.4 |  |  |  |  |  |  | 42 |
| 750-799 |  |  | 11.1 | 27.8 | 46.3 | 13.0 | 1.8 |  |  |  |  |  |  | 54 |
| 800-849 |  |  | 2.0 | 15.4 | 34.6 | 21.2 | 19.2 | 3.8 | 3.8 |  |  |  |  | 52 |
| 850-899 |  |  |  | 15.0 | 5.0 | 35.0 | 30.0 | 10.0 | 5.0 |  |  |  |  | 20 |
| 900-949 |  |  |  |  | 14.2 | 42.9 | 42.9 |  |  |  |  |  |  | 7 |
| 950-999 |  |  |  |  |  |  | 25.0 | 25.0 | 25.0 | 25.0 |  |  |  | 4 |
| 1,000-1,049 |  |  |  |  |  |  |  | 25.0 |  | 75.0 |  |  |  | 4 |
| 1,050-1,199 |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 |
| 1.200-1.249 |  |  |  |  |  |  |  |  | 100.0 |  |  |  |  | 1 |

TABLE 5.-Weighted means of back-calculated fork lengths ( mm ) for female king mackerel from all areas, 1977-78.

| Age class | Texas |  | Louisiana |  | NW Florida |  | South Carolina | North Carolina |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1977 | 1978 | 1977 | 1978 | 1977 | 1978 | 1978 | 1978 |
| 1 | 487 | 457 | 504 | 502 | 463 | 443 | 415 | 393 |
| 11 | 688 | 673 | 718 | 714 | 670 | 687 | 638 | 627 |
| 111 | 777 | 748 | 824 | 824 | 755 | 764 | 750 | 738 |
| IV | 847 | 811 | 906 | 909 | 805 | 838 | 809 | 798 |
| V | '805 | 853 | 970 | 983 | 866 | 895 | 864 | 844 |
| VI | ${ }^{1} 849$ | 937 | 990 | 1,045 | '897 | '934 | 916 | 891 |
| VII | '932 | ${ }^{1} 885$ | ${ }^{1} 1,097$ | 1,096 | '963 |  | 941 | 939 |
| VIII |  |  | '1,203 | 1,148 |  |  | 996 | 992 |
| IX |  |  | ${ }^{1} 1,361$ | 1,202 |  |  | 1.033 | ${ }^{1} 1.000$ |
| $X$ |  |  |  | 1,252 |  |  | '1,034 |  |
| XI |  |  |  | 1,311 |  |  |  |  |
| XII |  |  |  | 1,332 |  |  |  |  |
| XIII |  |  |  | ${ }^{1} 1,350$ |  |  |  |  |
| XIV |  |  |  | ${ }^{1} 1,399$ |  |  |  |  |

'Lengths based on less than 5 samples.

Table 6.-Weighted means of back-calculated fork lengths (mm) for male king mackerel from all areas, 1977-78.

| Age class | Texas |  | Louisiana |  | NW Florida |  | South Carolina | North Carolina |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1977 | 1978 | 1977 | 1978 | 1977 | 1978 | 1978 | 1978 |
| 1 | 414 | 413 | - | - | 473 | 407 | 373 | 385 |
| 11 | 588 | 574 |  |  | 635 | 665 | 607 | 614 |
| III | 659 | 658 |  |  | 686 | ${ }^{1} 734$ | 715 | 702 |
| IV | 703 | 720 |  |  | 736 | ${ }^{1} 746$ | 746 | 747 |
| $V$ | 747 | 790 |  |  | ${ }^{1} 798$ |  | ${ }^{1} 769$ | 781 |
| VI | .1754 | 829 |  |  | '850 |  | ${ }^{1} 821$ | 795 |
| VII | ${ }^{1} 803$ | ${ }^{\text {'896 }}$ |  |  |  |  |  | ${ }^{1} 810$ |
| VIII | ${ }^{1} 789$ | ${ }^{1} 951$ |  |  |  |  |  |  |
| IX |  | '943 |  |  |  |  |  |  |

'Lengths based on less than 5 samples.

Back-calculations for male king mackerel from all areas combined are shown in Table 7. Growth is rapid until the third year of life, after which time the annular growth increment decreases and stabilizes at an average 42 mm FL.

Females from the combined areas (Table 8), excluding Louisiana, also showed rapid growth in the first 3 yr , after which the annual growth increment decreased to an average 40 mm FL. Females were larger than males for all ages.
Fish from Louisiana (all females) exhibited an impressive growth rate (Table 9). They averaged

69 mm longer than other females at age 1 , and by age 10 were 218 mm longer than their counterparts. The yearly growth increment was over 60 mm to age 6, an increment not maintained by other females, or males, past age 3 in other locations.

Our combined back-calculated data were compared with those from Beaumariage (1973) (Table 10). His data were converted to fork lengths from standard lengths (SL) using his equation: $\mathrm{FL}=1.096 \mathrm{SL}-17.143$. Disregarding Louisiana females, both male and female mean

Table 7.-Average back-calculated fork lengths (mm) at age for male king mackerel from all areas, 1977-78.

|  | Mean length at capture |  |  |  |  |  | in ye |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| class | ( mm FL ) | $N$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| 1 | 570.3 | 206 | 425.0 |  |  |  |  |  |  |  |  |
| II | 708.6 | 41 | 422.6 | 667.3 |  |  |  |  |  |  |  |
| 111 | 767.0 | 41 | 408.5 | 618.7 | 737.6 |  |  |  |  |  |  |
| IV | 772.5 | 44 | 403.3 | 594.6 | 677.5 | 747.9 |  |  |  |  |  |
| $v$ | 820.4 | 22 | 375.1 | 590.5 | 669.0 | 733.9 | 796.1 |  |  |  |  |
| Vi | 832.6 | 16 | 349.2 | 559.4 | 641.9 | 700.1 | 755.8 | 808.3 |  |  |  |
| VII | 852.3 | 3 | 389.6 | 579.3 | 648.6 | 717.7 | 752.7 | 802.1 | 838.3 |  |  |
| VIII | 920.0 | 2 | 415.2 | 578.8 | 649.2 | 714.5 | 773.1 | 817.3 | 862.5 | 896.0 |  |
| 1 X | 970.0 | 1 | 476.6 | 560.3 | 623.3 | 754.1 | 796.2 | 830.2 | 864.7 | 899.4 | 943.4 |
| Weighted mean |  | 376 | 414.1 | 613.4 | 689.2 | 734.0 | 777.4 | 809.3 | 850.8 | 897.1 | 943.4 |
| Annual increment |  |  |  | 199.3 | 75.8 | 44.8 | 43.4 | 37.9 | 41.5 | 46.3 | 46.3 |

TABLE 8.-Average back-calculated fork lengths (mm) at age for female king mackerel from all areas except Louisiana, 1977-78.

| Age class | Mean length at capture ( mm FL ) | $N$ | Age in years |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | 604.8 | 315 | 456.4 |  |  |  |  |  |  |  |  |  |
| 11 | 741.2 | 112 | 427.9 | 693.8 |  |  |  |  |  |  |  |  |
| III | 809.6 | 105 | 435.8 | 645.4 | 774.4 |  |  |  |  |  |  |  |
| IV | 858.7 | 100 | 426.2 | 648.9 | 753.5 | 830.2 |  |  |  |  |  |  |
| $\checkmark$ | 897.1 | 79 | 499.3 | 635.3 | 729.6 | 800.7 | 865.4 |  |  |  |  |  |
| VI | 933.7 | 44 | 405.1 | 630.3 | 727.2 | 791.6 | 848.2 | 908.3 |  |  |  |  |
| VII | 960.2 | 21 | 363.0 | 613.3 | 703.3 | 760.5 | 827.4 | 884.5 | 937.5 |  |  |  |
| VIII | 1,028.0 | 8 | 392.4 | 635,0 | 732.5 | 796.6 | 852.2 | 910.0 | 955.3 | 1,020.9 |  |  |
| ix | 1,056.0 | 6 | 337.4 | 609.2 | 732.0 | 790.9 | 847.3 | 893.9 | 938.1 | 987.7 | 1.034 .6 |  |
| X | 1,062.1 | 2 | 325.5 | 557.8 | 683.1 | 747.4 | 796.9 | 833.9 | 883.6 | 934.7 | 978.4 | 1,033.6 |
| Weigh | mean | 792 | 433.9 | 652.0 | 747.1 | 806.5 | 853.5 | 899.4 | 938.5 | 997.7 | 1,020.6 | 1,033.6 |
| Annua | ncrement |  |  | 218.1 | 95.1 | 59.4 | 47.0 | 45.9 | 39.1 | 59.2 | 22.9 | 13.0 |

Table 10.-Mean back-calculated fork length (mm) at ages, from Beaumariage (1973) and this study. Beaumariage's data were transformed from standard length by his formula $\mathrm{FL}=$ 1.096 SL - 17.143.


|  | Males |  |  | Females (except La.) |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Beau- <br> mariage | Johnson <br> et al. |  | Beau- <br> mariage | Johnson <br> et al. |  |
| 1 | 457 | 414 | 491 | 434 |  |
| 2 | 643 | 613 |  | 703 | 652 |
| 3 | 705 | 689 | 793 | 747 |  |
| 4 | 752 | 734 | 857 | 807 |  |
| 5 | 795 | 777 | 928 | 854 |  |
| 6 | 822 | 809 | 986 | 899 |  |
| 7 | 839 | 851 | 1,033 | 939 |  |

fork lengths at age were smaller in our study than in his in all cases but one ( 7 -yr-old males). Several explanations for the differences seem reasonable. First, our back-calculations employed a power curve, whereas his employed a linear equation. Secondly, our fish were sampled from a wide geographical range, which yielded fish with wide variation in age composition, whereas Beaumariage sampled from a more restricted area. Lastly, our sampling occurred almost 10 yr after his, and various changes may have occurred in the population owing to exploitation or other influences.

## Compensatory Growth

Compensatory growth (Ricker 1975) appeared to occur in both male and female king mackerel. Length-frequency distributions of otolith measurements from the focus to the proximal edge of the first opaque mark in both sexes showed a normal distribution of values. After examination of the distributions, we defined slow-growing fish (both sexes) as those with an increment of $50 \mathrm{om} \mu$ or less, fast-growing males as those with an increment of $81 \mathrm{om} \mu$ or more, and fast-growing females as those with an increment of 86 om $\mu$ or more.

Back-calculated lengths for these fish are shown in Table 11. While fast-growing males grew 525 mm in year 1 , they grew only 135 mm in year 2. The slow-growing males grew 303 mm in their first year, but made up some of their size difference by growing 285 mm in their second year. Females showed a similar trend, with fastgrowing fish having a first-year increment of 559 mm and a second-year increment of 184 mm . The slow-growing females grew 282 mm in year 1 and 334 mm in year 2 . Beyond age 2, yearly growth increments were similar within each sex. Growth compensation in king mackerel is

Table 11.-Annual fork length increments (mm) computed from backcalculations on fast- and slow-growing male and female king mackerel (from all areas combined).

| Age | Males |  | Females |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Fast | Slow | Fast | Slow |
| 1 | 525 | 303 | 559 | 282 |
| 2 | 135 | 285 | 184 | 334 |
| 3 | 87 | 85 | 101 | 99 |
| 4 | 53 | 72 | 89 | 67 |
| 5 | 104 | 63 | 75 | 63 |
| 6 |  | 49 | 64 | 66 |
| 7 |  |  | 46 | 75 |
| 8 |  |  | 52 | 65 |
| 9 |  |  | 53 | 47 |
| 10 |  |  | 44 | 47 |
| 11 |  |  | 51 | 67 |
| 12 |  |  | 34 | 10 |
| 13 |  |  | 67 | 35 |
| 14 |  |  | 11 | 100 |

probably the result of an extended spawning season. Long spawning seasons and multiple spawns are discussed by Beaumariage (1973) and would result in great size variation in young-of-theyear king mackerel. Some of that size variation would be decreased as the smaller fish continue to grow at a higher rate in their second year than do larger fish in their second year. Although the slow-growing fish make up some difference in size during year 2 , they remain smaller than the fast growers throughout their lives.

## Theoretical Growth

The von Bertalanffy theoretical growth parameters computed from back-calculated fork lengths are shown in Table 12, along with those reported by other authors. The von Bertalanffy $(1938,1957)$ growth equation is the following:

$$
1_{t}=L_{\infty}\left(1-\mathrm{e}^{-k\left(t t_{0}\right)}\right)
$$

where $1_{t}=$ length at age $t$,
$L_{\infty}=$ asymptotic length,

$$
k=\text { growth coefficient, and }
$$

Table 12.-von Bertalanffy growth parameters for king mackerel.

| Author | $\stackrel{k}{\text { value }}$ | $\left.{ }_{(m m}^{L}{ }^{\circ} \mathrm{F}\right)$ | $\begin{gathered} t_{0} \\ (\mathrm{yr}) \end{gathered}$ |
| :---: | :---: | :---: | :---: |
| Males |  |  |  |
| Johnson et al., all areas | 0.28 | 965 | -1.17 |
| Beaumariage (1973) | 0.35 | 903 | -2.50 |
| Nomura and Rodrigues (1967) | 0.18 | 1,160 | -0.22 |
| Females |  |  |  |
| Johnson et al., excl. La. | 0.29 | 1,067 | -0.97 |
| Johnson et al., La. | 0.14 | 1,529 | -2.08 |
| Beaumariage (1973) | 0.21 | 1,243 | $-2.40$ |
| Nomura and Rodrigues (1967) | 0.15 | 1,370 | -0.13 |

$t_{0}=$ time when length would theoretically be zero.

Our theoretical growth parameters are between those calculated by Beaumariage (1973) and Nomura and Rodrigues (1967). Beaumariage's theoretical growth parameters were calculated by employing observed sizes of fish at each age, while Nomura and Rodrigues apparently combined both back-calculated lengths and empirical lengths in their calculations. We employed mean back-calculated lengths at age in our computations, which may account for some of the differences between our values and those of the other investigators.

## Length-Weight Relationship

The length-weight values for king mackerel computed for the equation $W=a L^{b}$, where $W$ is weight in grams and $L$ is fork length in millimeters, are presented in Table 13. Male lengthweight values from our study were within the confidence intervals set by Beaumariage (1973), but for both our female and combined sexes, length-weight values were below his lower confidence intervals.

## Mortality

Mortality estimates are presented in Table 14. The mean annual mortality rate ( $\mathrm{A}=0.37$ ) is lower than Beaumariage's (1973) estimate ( $\mathrm{A}=$ 0.54 ). We feel that our results are more concordant with generally accepted techniques of catchcurve analysis, in that our catch-curves were developed from age-frequency data, as opposed to the length-frequency catch-curve used by Beaumariage. We also feel that our results are less influenced by the effects of gear selectivity than Beaumariage's results, since Trent et al. (1981) stated that commercial hook-and-line gear excludes small and large king mackerel to a greater extent than does recreational hook-and-line gear. Nevertheless, there are many difficulties in using catch-curve analysis in our study. Specific problems are related to the Beverton and Holt (1957) and Robson and Chapman (1961) techniques. The first technique involves using several consecutive years of data, which were unavailable in our study. With the second technique, we used age-length keys as the basis for our catch-curves but were unable to make corrections for the bias when such keys were used (Rob-

Table 13.-Summary of length-weight relations of U.S. king mackerel. $W=$ weight in grams; $L=$ fork length in millimeters.

| Sex | No. fish | Range ( mm FL ) | $W=a L^{\circ}$ |  | $\begin{gathered} 95 \% \\ \text { confidence interval } \end{gathered}$ |  | Correlation coefficient (r) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | $a$ | $b$ | Lower | Upper |  |
| Male | 701 | 428-1,355 | $0.8064 \times 10^{-5}$ | 2.9928 | 2.9572 | 3.0284 | 0.9909 |
| Female | 2,023 | 351-1.554 | $0.8801 \times 10^{-5}$ | 2.9827 | 2.9562 | 3.0092 | 0.9910 |
| Sexes combined | 2,821 | 351-1.554 | $0.8464 \times 10^{-5}$ | 2.9881 | 3.0153 | 3.0153 | 0.9899 |

Table 14.-Estimated annual mortality rate (A) by estimation technique, assuming 1:1 and 1:2 male:female ratios.

| Male:Female ratio | Estimation technique |  |  |  |  |  | Mean A |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Heincke (1913) | Jackson (1939) | Rounsefell \& Everhart (1953) | Beverton \& Holt (1957) | Robson \& Chapman (1961) | Regression analysis |  |
| 1:1 | 0.35 | 0.34 | 0.42 | 0.42 | 0.32 | 0.35 | 0.37 |
| 1:2 | 0.34 | 0.35 | 0.42 | 0.42 | 0.33 | 0.36 | 0.37 |

son and Chapman 1961). This was a result of the age-length keys being developed for a different fish sample than the one being analyzed for mortality rates. The difficulties in applying Robson and Chapman's technique resulted in an implication that king mackerel are not fully recruited into the south Florida recreational fishery until age 7 , after which the annual mortality rate is 0.53 . This mortality estimate is similar to Beaumariage's $(\mathrm{A}=0.54)$, but the age at recruitment was found by Beaumariage to be $2-3$. His estimate was based on a smaller age range (0-7) than was ours. This difference probably influenced the resulting mortality estimates.

Many difficulties are also involved in the basic concept of using catch-curve analysis to estimate mortality in king mackerel. Rounsefell and Everhart (1953) emphasized that catch-curve analysis is based on false assumptions when applied to most pelagic species, including mackerel. Robson and Chapman (1961) reiterated this warning, stating, "if year classes...vary in strength and survival rates vary from year class to year class and age to age, then the age-frequency distribution in the catch of a single season provides no identifiable information whatsoever regarding [mortality rates]...." These comments force us to state our mortality findings with some wariness.

## ACKNOWLEDGMENTS

We thank Michael Crow, Mark Farber, and Dennis Lee of the National Marine Fisheries Service, Miami Laboratory, Miami, Fla., for their constructive reviews of this manuscript.

## ADDENDUM

Fischer (1980) reported on the length-weight relationship of king mackerel off Louisiana. His length-weight values are similar to ours.

## LITERATURE CITED

abramson, N. J.
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101, 149 p.
Beamish, R. J.
1979. Differences in the age of Pacific hake (Merluccius productus) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36:141-151.

Beaumariage, D. S.
1973. Age, growth, and reproduction of king mackerel, Scomberomorus cavalla, in Florida. Fla. Mar. Res. Publ. $1,45 \mathrm{p}$.
Beverton, F. J. h., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric., Fish. Food (G.B.), Ser. II, 19. 533 p.

Everhart, W. H., A. W. Eipper, and W. D. Youngs.
1975. Principles of fishery science. Cornell Univ. Press. Ithaca, N.Y., 288 p.
Fischer, M.
1980. Size distribution, length-weight relationships, sex ratios, and seasonal occurrence of king mackerel (Scomberomorus cetealla) off the southeast Louisiana coast. La. Dep. Wildl. Fish. Tech. Bull. 31:1-21.
Heincke, $F$.
1913. Investigations on the plaice. General report. I. Plaice fishery and protective measures. Preliminary brief summary of the most important points of the report. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 16, 67 p.
Jackson, C. H. N.
1939. The analysis of an animal population. J. Anim. Ecol. 8:238-246.

Manooch, C. S., III.
1979. Recreational and commercial fisheries for king mackerel, Scomberomorus cavalla, in the South Atlantic Bight and Gulf of Mexico, U.S.A. In E. L. Nakamura and H. R. Bullis, Jr. (editors), Proceedings of the mackerel colloquium, p. 33-41. Gulf States Mar. Fish. Comm., Brownsville, Tex.
Manooch, C. S., III, E. L. Nakamura, and A. B. Hall.
1978. Annotated bibligraphy of four Atlantic scombrids: Scomberomorus brasiliensis, S. covalla, S. mar\%latus, and S. regalis. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 418,166 p.
Nomura, H., and M. S. S. Rodrigues.
1967. Biological notes on king mackerel, Scomberomorus cavalla (Cuvier), from northeastern Brazil. Arquivos do Estocão de Biologia marinha do Universidade Federal do Ceará. 7(1):79-85.
Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Robson, D. S., and D. G. Chapman.
1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.
Rounsefell, G. A., and W. H. Everhart.
1953. Fishery science: its methods and applications. John Wiley and Sons, Inc., N.Y.. 444 p.
Tesch, F. W.
1971. Age and growth. Im W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2 d ed., p. 98-130. Blackwell Sci. Publ., Oxford.
Trent, L., R. O. Williams, R. G. Taylor, C. H. Saloman, and C. S. Manooch III.
1981. Size and sex ratio of king mackerel, Scomberomorus conalla, in the southeastern United States. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-62, 59 p. National Marine Fisheries Service, Panama City, Fla.
von Bertalanffy, L.
1938. A quantitative theory of organic growth (inquiries on growth laws. I). Hum. Biol. 10:181-213.
1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217-231.


[^0]:    ${ }^{1}$ Contribution No. 82-29-PC, Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, Panama City, Fla.
    ${ }^{2}$ Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, 3500 Delwood Beach Road, Panama City, FL 32407-7499.

[^1]:    ${ }^{3}$ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

