# Determining Age Frequency From Length Frequency

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## Scientific Summary

The major conclusions of this study are:

1. Application of age length keys yield maximum likelihood estimates of age composition if and only if the age length key is based on age samples drawn from the catch to be aged, otherwise biased estimates of catch at age are nearly certain.

   a. King mackerel age length keys samples were collected from USA catches during 1986, 1987, and 1988.

   b. Spanish mackerel age length key samples were collected from USA catches during 1987 and 1988.

   c. Age length key samples are unavailable for Mexican catches of king and Spanish mackerel.

2. Age determinations from hardparts can be inaccurate because of inaccuracies in interpreted age. Ageing errors can be due to random variability and due to systematic biases in making reliabe age determinations. Ageing errors can introduce biases in estimates of growth parameters, mortality rates, and abundance levels.

   2a. Spanish mackerel

   Estimates of back-calculated size at age reported by Fable et al. (1987) for Spanish mackerel appear to be biased. Von Bertalanffy growth parameters derived from back-calculated size at age may be biased.

   2b. King mackerel

   1. Collins et al. (unpublished) gave strong evidence that interpreted ages from whole otoliths were biased. Age determinations from Manooch et al. (1987) were from whole otoliths; growth parameter estimates may be biased.

   2. Sectioned otoliths indicated a destinct single annual peak

3. Stochastic ageing methods first described by Clark (1981) are recommended procedures for estimating the age composition of catches where age samples do not exist. The only information required in application are the size and the variance of size at age; these data can be derived from the mark-recapture statistics.

# Determining Age Frequency from Length Frequency

## I. Background

Many fisheries stock assessment techniques require the catch at age be known or estimatable (e.g., virtual population analyses (VPA), cohort analysis (see Gulland 1969, Ricker 1975, Pope 1972 for a review). Samples (of length) are usually readily available because measuring and recording lengths can be carried out with relatively little cost. The process of determing age is tedious and time-consuming. Currently used assessment techniques based upon length (see Pauly 1982; Jones 1979,1984; Pauly and Morgan 1987; Lai and Gallucci 1987,1988) assume equilibrium conditions of the stock under study unlike the traditional age-based methods. The length based methods usually assume all individuals grow according to a single schedule of growth (usually the von Bertalanffy curve (Bertalanffy 1934). As a result the methods of analysis used in the majority of stock assessment arenas today are age based procedures.

Determining age requires that boney structures (scales, otoliths, fin rays, opercula, etc.,) first be identified which reveal annual growth bands (rings or annuli). Validation of identified rings as reflecting true age must be carried out for all age classes present in the population (Beamish and McFarlane 1983, Chilton and Beamish 1982). Ideally, hardpart ages are validated with fish of known age using mark and release or holding experiments or from chemical marking (e.g., oxytetra- cycline OTC) injection) experiments. Older ages can sometimes be validated from determing the concentration of natural radio-nuclides present in a particular ageing structure (See Adelman 1987 for a review). Indirect validation of hardpart ages is used frequently when direct validation methods becomes unfeasible for a particular species or is too costly for the experimentor. These indirect validation techniques by necessity involve a degree of subjectivity and resulting ages can be biased. The majority of the indirect validation methods are based on comparing the mean lengths at hardpart age to the mean length (or modal length) identified from length frequency distributions or from tracking progressions of length frequency distributions over time (see Lai et al. 1987 for an example). Such techniques can be helpful in identifying ages in a length frequency but their overall performance depends upon the degree of overlap in size between ages. Generally, these procedures are helpful when few age groups are present and the sectioned otoliths, whole otoliths, fin rays) and/or different age readers. Such practices are often viewed as validation steps, however, these are not tests that confirm or reject the hypothesis that the rings identified as annuli are indeed annual and of a specific periodicity. Comparisons of age readings between and within age readers and between various boney structures as well as between ageing laboratories are useful; however, accuracy and precision (variability) of results have been shown to vary greatly between and within readers as well as between boney structures (See Kimura, Mandapat, and Oxford 1979, Boehlert and Yoklavich 1984 for a list of references on this topic).

## II. Establishing the Age Structure of Catches

### 1. Length Frequency Analyses

Determining the age structure of catches requires converting frequencies of size (usually length) into frequencies of age. Four length frequency methods have been used. The procedure, known as the Peterson Length Frequency Method (Peterson 1891 (cited in Ricker 1975)), considers a length frequency distribution as a group of length at age distributions; these are referred to as finite mixture distributions. Early users of the method separated the length distribution into age distributions visually. Later graphical techniques were used to isolate individual age components by assuming them normally distributed (Cassie 1954, Bhattacharya 1967 (cited in Macdonald 1987)). Recent length frequency analyses use multiple regression and likelihood estimation procedures to determine the age proportions for a length distribution (Hasselblad 1966; Kumar and Adams 1977 (cited in Clark 1981); Macdonald 1969, 1975, 1987; Macdonald and Pitcher 1979; Schnute and Fournier 1980 and Clark 1981). The major problems with all of these techniques that attempt to decompose a length frequency straight forwardly, include 1) the subjective nature of separating the age components, 2) the large amount of overlap in length between individual ages, and 3) sensitivity of the estimation methods used to input parameters (i.e., assumptions regarding the distribution and the number of components present in the length frequency). Estimates of negative age proportions are not uncommon in actual application (Rosenberg and Beddington 1987, Hampton and Majkowski 1987).

### 2. Age Length Keys

Converting length distributions into age distributions is avoid biases in resulting age densities (Knight 1970, Kimura 1977, Westrheim and Ricker 1978, Clark 1981, and Bartoo and Parker 1983 reviewed biases and problems in misuse of age length keys). There are few situations, excepting some of the North Sea groundfish fisheries, in which age length keys exist from all fisheries for which stock assessments are needed, either because of logistical problems in making reliable and accurate age determinations, because of the cost involved in obtaining age data, or because a long term sampling plan has not been established.

### 3a. Deterministic Growth Equations

Data often exist from mark-recapture experiments or from hardpart studies from which age can be described as a function of size. A growth equation such as the von Bertalanffy, the Richards equation (Richards 1959), or the Gompertz (Siliman 1934) curve can then be used to classify or slice lengths into ages. Ages derived from growth equations are used frequently as the basic input data in annual stock assessments from which regulatory advice is made. Ages determined by the growth equation method can be biased due to 1) inaccurate ages, 2) parameter estimations, 3) the deterministic form of the equation, and 4) growth differences between year classes (see Bartoo and Parker 1983 for more discussion). As lengths approach the asympotic size, the growth equation method may produce unreasonably old ages. Back-calculated lengths are often employed in modelling the size-age relation. Back-calculated sizes can be biased and have increased variability due to estimation, and frequently do not reflect the actual growth observed and should not be chosen over the actual length-age observations to model growth (McCaughran 1981).

### 3b. Stochastic Growth Equations

Recent advances in estimating age densities from length densities revolve around the use of linear and non-linear least squares and maximum likelihood estimation techniques (see Clark 1981, Bartoo and Parker 1983, Shepherd 1985, Hoenig and Heisey 1987). These methods convert age densities from length densities by using the probability distribution of length within age categories (P[l:a]). The density of length is the y variable and the age density is treated as the unknown parameter vector and the P[l:a] matrix as the independent x variables. In other words, letting a be the number of ages and l the number of size categories where [P] is an l by a matrix whose columns sum to one, [L] is a column vector of length l rows, and [A] a column vector of a such that the equality holds. Linear and non-linear least squares estimation procedures can be used as well as likelihood methods.

Resulting estimates of the age distribution from the stochastic methods are unaffected by the distribution of age within length (i.e., the relative strengths of the year classes represented in the sample). Results are affected by differences in growth rates if growth has changed over time. Estimates are free of biases in year-class strength produced by incorrect application of age length keys. Estimates are also free of estimation biases produced from using a growth equation to slice lengths into ages. Knowledge of the mean size at age and the form of the variation in length about age must be known to obtain the P[l:a] matrix. If monthly samples are to be aged using age length keys, every gear-month-area strata must be sampled. If stochastic methods that incorporate the variation of length about age are used, the P[l:a]) need be available only for each month. In the frequent case where a length sample exists and no age length key is available, use of an age length key from another time can produce biased ages. Application of the stochastic methods will not produced biased results if P is known and growth differences have not occurred. If the P is to be estimated, accurate information regarding the mean size at age and the variation of size within an age must be available to avoid introducing additional biases. The main difficulty with use of the stochastic methods is with finding the solution for the parameter vector of ages. Common linear least squares was used used by Bartoo and Parker (1983) to obtain parameter estimates. In practice however, negative parameter estimates can arise as pointed out first by Clark (1981) who used constrained least squares to insure only positive values in the resulting age distributions. Shepherd (1985) suggested a logarithmic transformation of the parameter vector (the age vector) be used requiring that non-linear least squares estimation techniques be used (see Parrack (1986) for an application of the technique). Hoenig maximized a likelihood function to determine the parameter vector via the E-M (expectation-maximization) method (Dempster et al. 1977 (cited in Hoenig and Heisey 1987)). Hoenig incorporated the sample size of the age sample into the estimator and, in doing so considered that the P[l:a] is usually estimated and not known unlike the least squares techniques. In practical application both estimators, least squares and the likelihood function, require extensive adjustments when applied to an actual time series of fisheries statistics. The performance of these procedures to the knowledge then the age length key method can be biased greatly. In practice then, it is reasonable to use the age length key to age a catch sample if the key was drawn from that same strata; otherwise use of the P[l:a] procedure is appropriate. Of course, use of the age length key method requires first that age determinations are accurate and unbiased. Likewise, if the stochastic procedure is the method of choice the P[l:a] must be appropriate. Whether to use the least squares method of Shepherd, the likelihood estimator suggested by Hoenig, or another method for solving the equation can be best resolved by simulation studies of the estimators; estimator performance is most certain to be case specific.

## III. Objectives

This report describes procedures for determining the frequency of age from the frequency of length for king and Spanish mackerel stocks along the southeastern U.S. A summary of the available age and growth data available for use in converting length to age is first described for each species. Published growth data derived from hardparts and from mark-recapture experiments is reviewed and the differences between various studies in the literature summarized. Existing age length data for king and Spanish mackerel fisheries currently under assessment in the Gulf of Mexico and Atlantic are identified in the section on available data. Information on growth not yet reported in the published literature is also presented.

General fisheries methods currently used to establish age from size for many different resources throughout the world are reviewed in this document. Biases in resulting age estimates are reviewed for each ageing method and likely causes of such biases are given. Length frequency decomposition techniques are not treated in the sections that follow as potential ageing methods of king and Spanish mackerel. The length decomposition methods developed during the last decade may provide a way of converting king and Spanish mackerel lengths to ages. Presently, however these methods have not been thoroughly examined as methods for ageing king and Spanish mackerel from the southeastern United States. Reccomendations for determining ages from lengths for king and Spanish mackerel are given and the major points of this review paper are listed. The methods suggested here for use with king and Spanish mackerel employ traditional age-length keys and incorporate information on size at age and the variation of size at age to establish the most probable age for a given length. In doing so be discussed in this report, however, the primary focus of the manuscript is that of king mackerel from the southeastern U.S..

## IV. Data Available for Establishing Age of King Mackerel

### 1. Length Data and Age Length Data

Random samples of length from catches from the commercial and recreational Gulf of Mexico and Atlantic fisheries exist since the early 60's. Sufficient size and catch information exists since about 1979 to investigate historical population levels. Length samples from the Gulf of Mexico and Atlantic commercial and recreational fisheries exist in computer data files on the NMFS, NWAFC, B7800 computer. Aged samples do not exist for all catch samples that exist so the age composition of many catches must be estimated indirectly from size.

Johnson et al. (1983) presented sex specific age length keys for combined catches sampled from 1977 through 1979 throughout the entire Gulf of Mexico. The majority of fish in Johnson et al.'s study were from recreational hook and line catches however, trawl caught fish were included in the body size-otolith size relationship. An objective of the study of Manooch et al. (1987) was to generate current age length keys and estimate mortality rates for Gulf of Mexico king mackerel. Those authors developed age length keys from aged length samples collected during 1980-81, and 1984-85 from Northwest Florida, South Florida, Texas, and Louisana from recreational and commercial catches. Mortality rates were estimated for several fisheries (i.e., gillnet (1980, 1981, 1984), purse seine (1984), and recreational hook and line (1980) - Table 7, p. 107 in Manooch et al. 1987) however, age length keys were not presented. Sex-specific age length keys from that study were used to age length samples for the 1988 King mackerel annual stock assessment (Scott 1988). The NMFS, Southeast Fisheries Center, Panama City, Florida Laboratory has made routine collections of otolith samples for Gulf of Mexico and Atlantic king mackerel stocks and performed age determinations since 1986 (Grimes et al. 1987, Devries et al. 1988). Annual sex specific age length keys exist for the Gulf of Mexico, eastern Gulf of Mexico (Lousiana through the west coast of Florida, western Gulf of Mexico (Texas), and for the Atlantic geographical regions. Published age length keys do not exist for Atlantic king mackerel stocks before 1986. Age length keys have not been presented for king mackerel from Mexican catches.

(see Cummings 1985 for a list of references). Those studies used length at hardpart (whole otolith) age to model growth. Growth parameter estimates were obtained from graphical procedures (e.g, Walford plots) in some studies and in others from least squares fits to mean (or weighted means) back-calculated length at age estimates. Age determinations were indirectly validated using modal analyses. A review of the results and the major differences between studies carried out through 1985 was given by Cummings (1985, see Table 1 in Cummings). None of the hardpart studies that were conducted through 1985 validated ages used fish of known age; direct validation of hardpart ages does not exist for Gulf of Mexico king mackerel.

Johnson et al. (1985) used the edge of whole otoliths to evaluate annuli timing and periodicity in king mackerel from the Gulf of Mexico and Atlantic. The majority of their fish were from the Gulf of Mexico (28% were from the Carolinas and southeast Florida). The major findings and points of interest of that study were as follows. In a sample of 133 otoliths examined they had 96.5% agreement between ages determined from both whole and sectioned otoliths. Marking occurred during eleven of twelve months (Table 1, p. 100 in Johnson et al. 1985). Marks were considered to be formed once yearly for the population and, usable for age determinations and subsequent computation of population age structure and mortality rates. Sexual dimorphism was assumed to exist however, back-calculated lengths at age were derived using a single body size-otolith size relation developed for sexes combined. Von Bertalanffy growth curves were developed separately for males and females using mean back-calculated length at age and weighting each age equally (Table 12, p. 104 - Johnson et al.).

Cummings (1985), while carrying out a review of king mackerel age and growth, used the Johnson et al. data set and presented reasonable evidence for inclusion of sex in the body size-otolith size relation (Pr[sexual dimorphism] > 0.99; $F_{2,173} = 59.32$). Marginal increment analysis results of Johnson et al.'s data (Figures 4-22, Tables 4-7 in Cummings 1985) in addition, to Johnson et al.'s periodicity findings did not support marking as a single yearly event for those data). Evidence was presented by Cummings suggesting that some fish marked more than once yearly and some fish did not mark at all. Growth model fitting of the Johnson et al. hardpart data was not pursued further by Cummings in that report.

Results from chemical marking experiments were given by recapture, time at liberty, and computed the size at the time of tetracycline injection (release). Estimated size at the time of marking (i.e., at the time of the tetracycline mark was deposited) was computed using the distance from the focus to the reader identified tetracycline mark and Johnson et al.'s (1985) empirical body size - otolith size power relation (Fl(mm) = 1.232 * Otolith Radius ** 1.331). Calculations were adjusted for the difference in measuring systems between the two studies (1 ocular unit = 0.0363 mm (Johnson et al. 1985) vs 0.0667 this unpublished study). Recall, sexual dimorphishm was not accounted for in Johnson et al.'s (1985) body size-otolith size relationship. For one of the three fish, the predicted size at release (i.e., at the tetracycline mark) as predicted by the age reader, was the same as actually observed. For one fish, the predicted size at the time of marking (i.e., at the time the tetracycline was injected) was 2% lower than the actual observed size at marking. The empirically predicted size at release of the other fish was 6.5% larger than actually observed.

Further investigations of the size-age relationship exist since Cummings (1985) review. Manooch et al. (1987) described the size-age relation for Gulf of Mexico fish using samples of whole otoliths collected during 1980-81, and 1984-85. The major findings from that study and analyses were the following. Age length keys were constructed using the combined samples and mortality rates estimated and presented for gillnet, purse seine, and recreational fisheries. These authors reported "whole otoliths were excellent for aging king mackerel and that rings were distinct, easily counted and measured". They reported for a sample of 24 fish 87% agreement between age determinations made from both sectioned and whole otoliths. The time of ring formation was evaluated by transforming the data and plotting the percent of otoliths with marginal rings (combined over sex, area, and age). Plots of the percent fish with marginal rings by month (Figure 1 in Manooch et al.) showed two destinct modes indicating marking occurred between January and October for the fish examined. The authors concluded rings (annuli) were formed annualy and on most fish during late winter and spring (February-May). They further noted that rings were apparently formed during late fall for some fish captured off northwest Florida. The fraction of fish thought to be marking in the fall was considered to a small fraction of the total number of otoliths examined; the proportion of all northwest Florida fish this fraction represented was not reported.

Manooch et al. employed sex specific body size-otolith size to estimate back-calculated sizes at earlier ages in Manooch et al's study differ from those used by Johnson et al.. Johnson et al. did not consider sex specific body size-otolith size relations in their study. Estimated weighted mean back-calculated sizes at age and the annual growth increments are nearly identical for the two studies (for ages 1-7 where about 95% of the observations existed). Although, almost identical back-calculated lengths at ages (females ages 1-7) and (males ages 1-6) were used in model fitting, estimated von Bertalanffy parameter values differ substantially between the two studies (see Tables 7 & 8 (Johnson et al.) and Tables 3 & 4 and Figures 4 & 5 in Manooch et al.). The two studies employed different magnifications in age determinations (28X (Johnson et al.), 50X (Manooch et al.) however, this alone does not explain the differences in resulting von Bertalanffy parameter estimates. Johnson et al.'s data set included males ages 1-9 and females ages 1-10 while, Manooch et al.'s collection contained fish of ages 1-14 (females, no age 13 females) and 1-11 (males). The differences in resulting parameter estimates are likely due to the older ages in the latter study. The one age 14 female (observed size = 1802 cm Fl) in Manooch et al.'s collection could be viewed as an outlier. The older ages in the Manooch et al. study were not well sampled ($n < 5$ (ages 10+ ), $6 > n < 8$ (ages 7-9 (males) and 8-9 (females)) however, these ages are very important in the parameter estimation. Caution should be taken when using the resulting parameter estimates that include those older age groups which are not well sampled. Further growth estimations incorporating larger samples of fish in the age 7+ (males) and age 8+ (females) age groups are needed. Parameter estimates presented by Johnson et al. are not within the estimated 95% confidence intervals presented by Manooch et al. for their estimates. The 0.95 confidence intervals presented by Manooch et al. may not be representative of the true confidence intervals since the mean distance from the otolith core to each annulus (across all fish) was used to compute mean back-calculated size at each age. The usual procedure is to compute for each fish the back-calculated size at each annulus and the corresponding average size over all fish at each annulus (the confidence interval's presented by Manooch et al. may be lower than if the mean back-calculated size at each annulus across all fish were used in growth estimations rather than the size computed for the mean otolith radius at each annulus). Manooch et al.'s estimated growth rate constants are lower for both sexes (0.2080-males, 0.1360-females) and, much lower for males than other published growth rate constant estimates for king mackerel from the southeastern U.S. presented through the time of this study (see Table 7, Manooch et al.).

of marking for fish captured from different areas (e.g., south Florida vs Louisana). General trends can be obtained from the data. The majority of fish in Manooch's study were ages 1-3 (77%) and were collected from south Florida (n=329, January-March, December), Norwthwest Florida (n=443, April-November), and Louisana and Texas (n=154, July-September). The otolith samples were from mainly from hook and line catches (62% males, 63% females) however, a large number of the samples did not have gear recorded (32% males, 35% females) thus, it is not known from what fishery those samples were drawn. The remaining samples were from gillnet or purse seine catches (6% males, 2% females). Marginal increment plots of the data separated by area (available upon request) indicate not only do fish captured off northwest Florida mark during the late summer and early fall, as Manooch et al. indicated, but also those captured further west. Of 151 fish sampled from Louisana and Texas between July and August 12% were recorded as marking by the age readers. Nine percent of the fish sampled from northwest Florida during August and September were marking. Fish captured off south Florida were sampled in Manooch's study, only during December and January through March, in sufficient numbers to examine mark formation (n=320). Only 9 fish were sampled between April and November from south Florida.

Laying aside the the question regarding time of marking for the Manooch et al. data and thus, assuming the hardpart ages as accurate, I examined the hypothesis that growth predicted from the back-calculated sizes as presented by Manooch et al. was the same predicted by the data that were not back-calculated. Least squares estimates of the von Bertalanffy growth parameters were derived separately for each sex using the Marquardt-Levenberg algorithm (Marquardt 1963). In my initial fittings all observations were used. Estimates produced for females (age 1-12 & 14) are within the 0.95% confidence intervals presented by Manooch et al. from back-calculated sizes for the growth rate constant but not for the asymptotic size ($L_\infty$ = 1652.56 mm Fork length (Fl), k=0.148). The estimates are not as different for males ($L_\infty$ = 1014.71 mm (Fl), k=0.2199), however, again only the growth rate constant estimate falls within Manooch et al's confidence intervals. The estimated $t_0$ values for females (+129.15) seemed unreasonable to this author thus, I re-examined the data for both sexes. Plots of the raw data (size on estimated age in years) indicated several possible outliers in the data and revealed a large amount of variation in size for the age 1 fish of both sexes. The one age 14 female (Fl=1802 cm) stands out. Also, the single age 12 female (Fl=1310 cm) and the age 11 male are possible abberant observations. I re-

All of these estimates, those from the observed sizes and from back-calculated sizes as reported by Manooch et al. are contingent on the assumption that the marks were indeed formed as once yearly annual events. If the equation parameters from the fits to the observed data for females are used and the initial $t_0$ stimates to compute theoretical size at age, non-sensical results are obtained ($t_0 = +129.14$ from the raw observations) thus, estimates of $t_0$ must be obtained elsewhere.

## 2b. Atlantic king mackerel

Waltz (1986) and Collins et al. (unpublished manuscript) carried out age and growth investigations from king mackerel sampled off the Atlantic coast between May 1983 and February 1987 (n = 183 males, 427 females). Recreational and commercial hook and line catches were the primary gears sampled for ageing structures although, young of the year fish were also sampled from research trawls, commercial shrimp trawls, gillnets, and seines. Sectioned and whole otoliths both were used by the authors in their analyses. Prior to Collins et al., growth information specific to Atlantic king mackerel stocks was unavailable. Beaumariage (1973) collected fish from both coasts of Florida but did not separate results by area when estimating growth parameters; nor did Johnson et al. (1985) who collected fish from both North Carolina and South Carolina and combined those observations with fish from the Gulf of Mexico (Tables 1,2 in Johnson et al.). Relative sex specific growth rates presented by Beaumariage separately for the East and for the West coasts of Florida suggests differences in growth between coasts might exist (Figures 12, 13 in Beaumariage). A growth study of Atlantic king mackerel such as the Collins et al. study is timely for several reasons including: 1) the lapse in time since the Florida study, 2) potential changes in growth over time in response to environmental and exploitation perturbations, 2) lack of specific growth information for the Atlantic stocks of king mackerel, 3) differences in results between previous age and growth hardpart studies carried out by Beaumariage, Johnson et al., and Manooch et al., and 3) the need for further validation work on age determination in such pelagic fishes as king mackerel. Separate Atlantic and Gulf migratory groups have been considered since 1985 in preparing annual stock assessments thus, the importance of stock specific biometrics is of interest.

The main points of interest in Collins et al.'s study and the findings are the following. Collins et al. performed marginal increment analyses and examined the edge of the otolith to included all of their samples in their comparisons, while the latter two studies compared readings using fewer otoliths. Some authors restrict comparisons to the larger sizes of fish on the basis that as fish grow larger and older the growth of the boney structure may change. Comparisons should not be limited to larger fish. Establishing ageing criteria for use in identifying the first major annulus may be difficult because of problems in destinguishing true annuli from false checks which can result from migrations, maturation, and other physiological changes. Collins et al. reported that differences in age determinations between the two techniques increased with age and that age readings differ at an earlier size for males than for females (Figure 3, Collins et al.). In Collins et al.'s study, agreement between readers in age determinations of whole otoliths was also much lower (77%) than in either of the two other studies (Johnson et al. 98% and Manooch et al. reported 86% agreement). Collins et al. reported difficulty in discerning marks from whole otoliths unlike, previous investigators. Comparisons in age determinations (using sectioned otoliths) made by different ageing laboratories were also made. A sample from the otoliths collected by Collins et al. were read by two age readers, one from the South Carolina Marine Resources Research Institute Laboratory and one from the NMFS, Southeast Fisheries Center, Beaufort, North Carolina Laboratory. Comparisons of the age determinations made from sections of 28 otoliths gave a 43% 1 to 1 agreement and a 75% + or - 1 agreement (Waltz, unpublished data, received by this author from C. Manooch). The majority of differences were with the larger fish.

The unpublished data from Collins study were made available in computerized form to this author for this review. As in earlier king mackerel age and growth studies, the temporal coverage of samples in this study was not sufficient to consider the time of mark formation separately by age for either sex. The observations from all ages and both sexes were thus considered in total. The results of Collins et al.'s marginal increment analyses and the results from examination of the otolith edge using sectioned otoliths presented in that study indicate rings form during late summer and early fall for Atlantic king mackerel. The results of their analyses for whole otoliths did not indicate a clear destinct time of mark formation. Plots of the percent of fish having zero marginal increments in a particular month as determined from whole otoliths revealed two destinct distributions (Figure 7, Collins et al.). This observation is also prominent when the raw marginal increment data are examined (i.e., untransformed). These results for whole otoliths in Atlantic king mackerel are very similiar to data. Collins et al. showed clear evidence that ages determined from whole otoliths were biased. Since growth parameters were derived using both sets of readings, comparisons however, can be made. Asymptotic sizes estimated from whole otoliths were lower for both sexes as compared with estimates obtained from sectioned otoliths (Table 8 Collins et al.). Whole ages gave estimates of growth rate constants much higher for males than estimates made from sectioned readings. Growth rate estimates from whole otoliths derived in this study are higher than any published king mackerel growth rate constants (see Cummings 1985, Table 1 and Manooch et al., Table 12). Collins et al. showed clearly, using indirect ageing validation procedures, that age readings from whole otoliths do not provide evidence of marking as a once yearly annual event in Atlantic king mackerel. Growth parameter estimates from whole otoliths should thus, not be used to model growth in Atlantic king mackerel.

It was of interest to investigate whether back-calculated sizes from section readings predicted the same growth as the observed data in the Collins et al. study. I derived least squares estimates of the von Bertalanffy growth parameters for the raw length at section age observations using the Marquardt-Levenberg algorithm; resulting parameter estimates for the asymptotic size are very similiar to those reported by Collins et al. ($L_\infty$= 923.19 mm (Fl) vs 942 males (Collins et al.), n=182; $L_\infty$ = 1156.49 mm (Fl) vs 1208 females (Collins et al.), n=423). Growth rates as predicted by the observed data were higher than predicted by the back-calculated sizes (0.294 vs 0.192 males, 0.154 vs 124 females). These growth rate constant estimates are within the 0.95% confidence intervals given by Mannoch et al. (1987). Asymptotic sizes are not within the estimated 0.95 confidence intervals reported by Manooch et al. for fish from the Gulf of Mexico.

## 3. Growth from Mark-Recapture Experiments

Mark-recapture experiments have been carried out by the Florida Department of Natural Resources (FDNR) and by the NMFS, SEFC, Panama City Laboratory. Methods of collection for these data have been described (Williams and Taylor (1978), Sutherland and Fable (1980)). Growth analysis results exist for the FDNR data alone (Williams and Godcharles 1984) and, also for the combined set of recaptures through August of 1985 (Cummings 1985). Williams and Godcharles (1984) derived least squares estimates of von Bertalanffy growth parameters for combined sexes for the FDNR

Godcharles study. Parameter estimates were essentially identical between the two analyses.

Returns available since, the previous marking results were presented by Williams and Godcharles and Cummings, were made available from these agencies for use in re-evaluating the size age relation. The total number of tags returned to date from FDNR releases is 1153 with an additional 334 returns available from the NMFS releases. Sufficient numbers of returns now exist having sex recorded and, the size range of these returns is adequate enough, for sexual dimorphism to be considered in further analyses of these data. Tagging continues to be carried out by the NMFS, SEFC Panama City, Florida laboratory. The last year of king mackerel tagging by the FDNR was 1985. Tagging of king and spanish mackerel is currently on-going at some state laboratories (i.e., North Carolina Department of Natural Resources).

The complete set of FDNR-NMFS king mackerel mark-recapture observations were analyzed to update the size-age relation and the results are reported here. The analyses were restricted to observations having positive growth. A total of 737 observations had usable information on growth. Release length ranged from 54 to 116 cm (Fl) and recapture size varied from 55 cm to 137 cm (Fl) for sexes combined. The average and maximum time at liberty were 1.46 and 8.37 years for sexes combined. Release length ranged from 67 to 108 cm (Fl) for males and recapture size ranged from 74 to 116 cm (Fl). The release size of females ranged from 54 to 115 cm (Fl) while recapture sizes of females ranged from 66 to 124 cm (Fl). Of the 737 observations 62 had sex recorded; of these 44 were females and 18 were males. The size-age relation was investigated for combined sexes and also for sexes separately. Data were not sufficient to investigate the size-age relation for separate geographical regions however, this information is summarized here for informational purposes. The majority of recaptures for which sex was recorded were from releases made off the Atlantic coast and of these, most were released off the east coast of Florida and recaptured from the east coast of Florida. There were 10 noteworthy exceptions. Three fish (females) released off Sebastian Inlet, Florida were recaptured off Key West, Florida; one female tagged off Sebastian Inlet, Florida was recovered off Texas. One fish (a female) was released and recaptured off Grande Isle, Louisana. Two fish (1 male and 1 female) released off Key West, Floridia were recaptured off Boyonton Beach, Florida. Two females tagged off Panama City, Florida were recovered off Key West, Florida. Another female released off Panama City was

Predicted size at recapture is estimated from observed size and lapsed time. Parameter estimates for sexes combined do not differ from those presented in previous analyses of the mark-recapture data ($L_{\infty}$ = 1237.78 mm (Fl), k= 0.1596) by Williams and Taylor (1978) or by Cummings (1985). The growth parameters presented here are the first sex specific estimates derived from mark-recapture observations for king mackerel from the southeastern United States. Estimated asympotic sizes were 1224.59 mm (Fl) for males and 1340.96 mm (FL) for females. Growth rate constants were estimated to be 0.1043 (males) and 0.1670 (females). Asymptotic sizes for both sexes are similiar to those suggested from hardpart studies. The estimate for females is within the 0.95% confidence interval specified by Manooch et al. but the male estimate is not. The 0.95% confidence intervals reported by Collins et al. do not contain either the female or male asymptotic size estimate. The growth rate parameter estimate for females is within Manooch et al.'s 0.95% confidence intervals but not Collins et al. The growth rate constant estimate for males is within Collins et al.'s 0.95% confidence intervals but not within Manooch et al's.

The size range of fish included in estimations seems adequate for modelling change in size (growth) over change in time for king mackerel. Keeping in mind that the mark-recapture statistics were from the Atlantic, specific differences in parameter estimates of $L_{\infty}$ and k from current estimates derived from hardpart ageing studies are the following. The growth rate constant (k) estimate for males is lower than the published estimates from hardpart studies (k = 0.10 vs 0.21 (Manooch et al.) and 0.28 (Johnson et al.). The estimate for females (k = 0.167) is larger than that reported by Manooch et al. (k = 0.14) and larger than that reported by Johnson et al. for all areas (k = 0.29). Estimates of asymptotic size reported in recent literature for males are lower than the estimate derived from mark-recapture statistics (1224 vs 965 (Johnson et al.), 1113 (Manooch et al.), and 942 (Collins)). The asymptotic size estimated here for females is much larger than that reported by Johnson et al. for all areas (1067) and by Collins et al. (1208) but lower than estimates reported by Manooch et al. (1417). The growth parameter estimates reported by Johnson et al. for Louisana females are very similiar to parameters derived in this study from mark-recapture data for fish released and recaptured mainly from the Atlantic ($L_{\infty}$ = 1529 Fl, k = 0.14 ). Growth parameter estimates reported by Nomura and Rodrigues (1967) for female king mackerel are nearly identical to the estimates reported here from marking experiments ($L_{\infty}$ = 1370, k= 0.15). Sample sizes from marked fish are recognized as small at this date

## V. Data Available for Establishing Age of Spanish Mackerel

### 1. Length Data and Age Length Data

Random samples of Spanish mackerel from the commercial and recreational fisheries exist since the mid 1980's in sufficient numbers to investigate changes stock dynamics using age structured analyses. Annual age length keys are unavailable before 1987 for fisheries off the southeastern U.S. Samples of length were sub-sampled for age data by the NMFS, SEFC, Panama City, Florida Laboratory during 1987 and 1988. Sex specific age length keys exist by geographical region (Atlantic, Gulf of Mexico) for 1987 and 1988. Annual age length keys were developed by the NMFS, SEFC, Panama City, Florida Laboratory age readers in 1987 and by the South Carolina Marine Resources Department in 1988. Annual age length keys do not exist for any Mexican catches to the knowledge of this author.

### 2. Growth Curves from Hardpart Data

Several published growth curves exist for Spanish mackerel from the Gulf of Mexico. All have been derived using length at (unsectioned) otolith age. Klima (1959) sampled and presented age data for fish collected during 1959 from the commercial fishery off South Florida. Nomura (1967) using Klima's whole otolith data and the Walford graphical procedure (see Ricker 1975, p. 222-225) estimated von Bertalanffy growth curve parameters for Klima's South Florida fish and for fish from Brazil. Powell (1975) described growth using whole otolith samples collected from fish sampled between January 1968 and December 1969 from the commercial and sport fisheries off South Florida. Walford plots were presented for males and females and estimates of growth parameters made for the von Bertalanffy curve.

More recent studies since work by Klima (1959), Nomura (1967), and Powell (1975) exists. Fable et al. 1987 described age and growth using whole otoliths collected from 1978 through 1981 from Georgia through Texas. Sex specific von Bertalanffy growth curves were derived for fish from all areas and for fish from Florida only. Mean weighted back-calculated sizes, derived using a single body size-otolith size relation, were used in Fable et al's study although sexual dimorphism was assumed to exist and growth curves derived separately by sex.

The data from Fable et al.'s study were available in growth separately for males and females. There was little improvement in reducing the degree of Lee's phenomenon present in the data (the sex specific equation parameters and individual estimates of back-calculated sizes are available from the author). Other causes of the bias were not considered in this study. Bias due to the sampling gear is possible for these data since 58% of the samples were taken from gillnet catches. The growth rate parameter estimates from my fits were 0.125 (males) and 0.354 (females) and the asymptotic sizes were 924.0 mm Fl (males) and 710.5 mm Fl (females). Estimates of $t_0$ from my fits were -2.51 (males) and -0.92 (females). The estimates for males are very different from those presented by Fable et al..

Helser and Malvestuto (1988) presented information on age and growth using whole otoliths from 228 fish collected between May and August of 1986 from the recreational hook and line fishery off Alabama. Fish sampled in their study ranged in ages from 0 to 6 (males) and 0 to 4 (females) with about 90% being of age 3 or less. These authors used the Ford-Walford regression method to derive estimates of the asymptotic size and growth rate parameter respectively by sex (552 mm Fl, 0.29 (males), 604 mm Fl, 0.45 (females). Asymptotic sizes are lower than the largest sizes commonly encountered in the commercial and recreational fisheries for both sexes and are lower than published estimates.

Growth of Spanish mackerel from the Atlantic coast has not received the level of attention as fish from the Gulf of Mexico. Fable et al. (1987) reported information for 306 fish sampled from south Florida between 1978-1981. The results presented by Fable et al. (1987) suggested that Spanish mackerel from south Florida grew faster than fish from any other area in their study area (i.e., Northwest Florida, Texas, Mississippi/Alabama).

### 3. Growth from Marking Experiments

Mark-recapture experiments of Spanish mackerel have been carried out by the Florida Department of Natural Resources and by the NMFS, SEFC, Panama City, Florida Laboratory. Return rates have been low and growth information resulting from marking studies is virtually non-existant. Study results suggest non-reporting, tag loss, and negative growth (Sutherland and Fable 1980, Godcharles and Bullock 1984, Bill Fable personal communication).

## VI. Summary and Conclusions

for ageing king and Spanish mackerel. Information on growth required for application of the stochastic methods (size and variation of size at age) was reviewed for king and Spanish mackerel and growth results not reported to date in the literature summarized and presented. The methods reviewed here in addition to the existing database of age and growth data can be used to classify king and Spanish mackerel catch at length distributions available from the recreational and commercial fisheries into age densities.

The age length key is the preferred method for ageing catches because the age estimates are maximum likelihood estimates if the age data from which the key was drawn are representative of the catch strata to which they are being applied. Annual age length keys exist for the 1986-1988 U.S. king mackerel catches and for the U.S. 1987-1988 Spanish mackerel catches. Annual age length keys do not exist for U.S. catches prior to 1986 for king mackerel and prior to 1987 for Spanish mackerel and do not exist for any Mexican catches to the knowledge of this author. Age length keys must only be applied to length frequency samples that have been drawn from the same catch strata. The age length data and the length sample must both be from the same area, time, and gear partition that the catch is taken from. If age length keys are applied to a catch strata other than from which the length sample was drawn age estimates can be biased if changes in the population age structure (i.e, the age distribution) have occurred. Critical to application of the age length key method is that age determinations must be accurate and unbiased. It is imperative that an unbiased sampling plan be used to estimate the total length distribution of the catch and the age distribution of the sample.

Stochastic techniques (e.g., Shepherds and Hoenig's procedures) are preferred over the use of either a deterministic growth equation and presently over the length frequency analysis methods for ageing king and Spanish mackerel. These procedures are recommended in the cases where age length keys are unavailable for specific time-area-gear-sex catch strata. Specific attributes render these methods appropriate. Biases are eliminated in age estimates caused by 1) subjectively identifying age components in length frequency distributions, 2) sensitivity of the analyses to input data, and 3) use of a deterministic model. The stochastic methods are free of biases due to changes in year class strength but are affected by differences in growth if such exist. If the stochastic methods are used, changes in growth that may have occurred over time should be addressed in future work.

South American studies to describe the size-age relation of king mackerel caught off the U.S. coasts is unknown. The results from all of these studies provide the data needed to apply the stochastic ageing methods (i.e., the size and variation of size at age). Selection of the appropriate information to use in deriving the P[l:a] matrices (i.e., the growth parameters themselves or the size at age) must be made by weighing the relevance of the separate studies in this specific application. The dilemna is that several growth curves exist and most of them are based upon age determinations made of whole boney structures from two semi-tropical pelagic species for which direct evidence of age validation does not exist.

The Fable et al. (1987) study is the most current and complete Spanish mackerel growth study in terms of geographical coverage and life history stages sampled. Growth parameter estimates may be biased because Lee's phenomenon was evident in the back-calculated sizes at age. If the growth parameters are biased and are used to derive the distribution of length given age age estimates derived from the stochastic method will also be biased. If age estimates are biased VPA estimates of mortality rates and population size will be biased. Age determinations were made in the Fable et al. study from whole otoliths however, sectioned otoliths were used to construct the 1987 and 1988 annual age length keys. The presence or absence of differences in age determinations made from different ageing media has not been documented for Spanish mackerel. Studies addressing differences in growth between the Atlantic and Gulf of Mexico and changes in growth temporally are also needed for this species. Growth parameter estimates have not been reported for the age data used to develop the 1987 and 1988 annual age length keys. If temporal changes in growth have occurred, and if the Fable et. al. growth curves (representing samples from 1977-1981) are used to derive the P[l:a] and to age catches from other years, age estimates will be biased. Growth parameter information derived from mark-recapture statistics does not exist for Spanish mackerel.

King mackerel growth information presented by Manooch et al. (1987) and Collins et al. (unpublished) in addition, to that derived from mark-recapture data (presented in section III) is recommended over results from earlier studies reported by Beaumariage (1973) and Johnson et al. (1985). Manooch et al. described growth for the Gulf of Mexico while the latter two studies document growth in the Atlantic. The current studies are more comprehensive in terms of geographical, temporal, and life history stage coverage. The recent studies are also more thorough

~~by Manooch et al. from whole otoliths for Gulf of Mexico king~~ mackerel do not support marking as an annual discrete event thus, ages interpreted from whole otoliths are likely in error. If age determinations are biased then mortality rates and abundance size estimates will be in error. Parameter estimates of the asymptotic size and growth rate constant are not radically different between the Atlantic studies but the differences are enough to cause concern. Estimates of asymptotic size reported by Collins et al. for the Atlantic (940 mm (Fl) - males, 1208 mm (Fl) - females) are lower than those derived from mark-release data (1225 mm (Fl) - males, 1340 mm (Fl) - females) and, are also lower than the largest sizes observed in the recreational and commercial fisheries. The differences are greater for males. The lower asymptotic size values are probably due to the larger sizes not being sampled in the study. Future studies will no doubt improve these estimates. The major concerns however, are the large negative estimates of the $t_0$ (theoretical size at age 0) values reported by Collins et al. (-2.50 males, -3.74 females) which yield negative ages at small sizes when used in the usual manner to compute age. These values are 2-3 times smaller than the values reported in the literature for other scombrids. Athough, the $t_0$ parameter is not needed for computing relative age, use of these specific values and the respective $L_\infty$ and k values to determine age is questioned. The possibility of introducing a positive bias in the number of fish at young ages exists if these parameter values are used to convert lengths to ages. If numbers caught at younger ages are overestimated then mortality rates and abundance levels will be be in error. Growth parameters estimates derived from mark-recapture data are free from the problems associated with age determination and are appealing and recommended for ageing for that reason. Systematic ageing errors associated with establishing absolute age for hardparts are eliminated. Growth is modelled from the change in growth and the change in time. Relative age can be computed using only the asymptotic size and growth constant estimates. Errors in recorded sizes and time at liberty can introduce errors in growth estimates.

# LITERATURE CITED

Adelman, I.R. 1987. Uptake of radioactive amino acids as indices of current growth rate of fish: A review, p 65-80 In: R. C. Summerfelt and G. E. Hall (eds.) Age and growth of fish. "Papers presented at the International Symposiumon Age and Growth of Fish, Des Moines, Iowa, June 9-12, 1985". Iowa State University Press, Des Moines, Iowa, 544p.

Bartoo, N.W. and K.R. Parker. 1982. Stochastic age-frequency estimation using the von Bertalanffy growth equation. Fish. Bull. 81(1):91-96.

Beamish, R.J. and G.A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735-743.

von Bertalanffy, L. 1934. A quantitative theory of organic growth. Human Biology. 10(2):181-213. [cited in Richer 1975].

Bhattacharya, C.G. 1967. A simple method of resolution of a distribution of Gaussian components. Biometrics 23:115-135.

Boehlert, G. and M.M. Yoklavich. 1983. Variability in age estimates in Sebastes as a function of methodology, different readers, and different laboratories. Calif. Fish and Game 70(4): 210-224.

Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Australian Journal of Mar. and Freshw. Res. 5:513-522.

Chilton, D.E. and R.J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60. 102p. Published by Government of Canada Fisheries and Oceans.

Clark, W.G. 1981. Restricted least-squares estimates of age composition from length composition. Can J. Fish. Aquat. Sci. 38:297-307.

Collins, M.R., D.J. Schmidt, C. Wayne Waltz, and J.L. Pinckney. [Forthcoming]. Age and growth of king mackerel

Dempster, A.P., N.M. Laird, and D.B. Rubin. 1977. Maximum likelihood from incomplete data via the EM algorithm (with discussion). J. of the Royal Stat. Soc. Ser. B 39:1-38.

Devries, D.A., K.L. Lang, and C.B. Grimes. 1988. Ageing of king mackerel, *Scomberomorus cavalla*, from the U.S. south Atlantic and Gulf of Mexico, 1987. NOAA, NMFS, SEFC, Panama City Laboratory unpublished manuscript, 22 p.

Fabens, A.J. 1965. Properties and fitting the von Bertalanffy growth curve. Growth 29:265-289.

Fable, W.A., A.G. Johnson, and L.E. BArger. 1987. Age and growth of Spanish mackerel, *Scomberomorus maculatus*, from Florida and the Gulf of Mexico. Fish. Bull. 85(4):777-782.

Fridrikson, A. 1934. On the calculation of age distribution within a stock of cod by means of relatively few age determinations as a key to measurements on a large scale. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 86:1-14.

Godcharles, M.F., and L.H. Bullock. 1988. Spanish mackerel pilot tagging project. Brief synopsis: December 1984-December 1987 Unpublished manuscript, Fl. Dept. Natural Res., 3 p.

Grimes, C.B., V.M. Pettigrew, S.P. Naughton, and J.H. Finucane. 1987. Ageing of the king mackerel, *Scomberomorus cavalla*, from the U. S. south Atlantic and Gulf of Mexico, 1986. NOAA, NMFS, SEFC, Panama City Laboratory, Jan. 1987. unpublished manuscript, 32 p.

Gulland J.A. 1969. Manual of methods for fish stock assessment. Part 1: Fish population analysis. FAO Man. Fish. Sci. 4:154p. [ed.] 1977. John Wiley & Sons. New York and Toronto. 372p.

Hampton, J. and J. Majkowski. 1987. An examination of the accuracy of the Elefan computer programs for length-based stock assessment. p 203-216 In D. Pauly and G.P. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p., Manila.

Hasselblad, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.

Hoening, J.M. and D.M. Heisey. 1987. Use of a log-linear model with the EM algorithm to correct estimates of stock composition and to convert length to age. Trans. Am. Fish. Soc. 116:232-243.

Jones, R. 1979. An analysis of a Nephrops stock using length composition data. Rapp. P.- V. Reun. Cons. int. Explor. Mer, 175: 259-269.

Jones, R. 1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fisheries Circular No.734, 60 p.

Johnson, A.G., W.A. Fable Jr., M.L. Williams, and L.E. Barger. 1983. Age, growth, and mortality of king mackerel, Scomberomorus cavalla, from the southeastern United States. Fish. Bull. 81(1):97-106.

Ketchen, K.S. 1949. Stratified subsampling for determining age distributions. Trans. Am. Fish. Soc. 79:205-212.

Kimura, D.K. 1977. Statistical assessment of the age-length key. J. Fish. Res. Board Can. 34:317-324.

Kimura, D.K. , R.R. Manadapat, and S.L. Oxford. 1978. Method validity, and variability in the age determination of yellowtail rockfish (Sebastes flavidus), using otoliths. J. Fish. Res. Board Can. 36:377-383.

Kimura, K.K. and S. Chikuni. 1987. Mixtures of empirical distributions: an iterative application of the age-length key. Biometrics 43:23-35.

Klima, E.F. 1959. Aspects of the biology and the fishery for Spanish mackerel, Scomberomorus maculatus (Mitchill), of southeren Florida. Fla. Bd. Conserv. Tech. Ser. No. 27: 39 p.

Knight, W. 1970. Some remarks on the behaviour of growth and mortality estimates based on age-length keys. ICNAF Res. Bull. 7:52-55.

Kumar, K.D., and S.M. Adams. 1977. Estimation of age structure of fish populations from length frequency data, p. 256-281. In W. Van Winkle [ed.] Proceedings of the conference on assessing the effects of power-plant induced mortality on fish for Quanitative Science, School of Fisheries, Univ. of Washington, Seattle.

Lai, H.L. and V.F. Gallucci. 1988. Effects of parameter variability on length-cohort analysis. J. Cons. int. Explor. Mer. 45:82-92.

Libby, D.A. 1985. A comparison of scale and otolith aging methods for the alewife, Alosa pseudoharengus. Fish. Bull. 83(4):696-701.

Macdonald, P.D.M. 1969. FORTRAN programs for statistical estimation of distribution mixtures: some techniques for statistical analysis of length-frequency data. Fish. Res. Board Can. Tech. Rep. 129:45p.

Macdonald, P.D.M. 1975. Estimation of finite distribution mixtures, p. 231-245. In R. P. Gupta [ed.] Applied statistics. North-Holland, Amsterdam. 416 p.

Macdonald, P.D.M. 1987. Analysis of length-frequency distributions, p. 371-384 In. R. Summerfelt and G. E. Hall (eds.) The age and growth of fish. 1987. "Papers presented at the International Symposium on Age and Growth of fish, Des Moines, Iowa, June 9-12, 1985". The Iowa State University Press, Ames, Iowa 50010, 544p.

MacDonald, P.D.M. and T.J. Pitcher.1979. Age groups from size frequency data: a versatile and efficient method of analyzing distributing mixtures. J. Fish. Res. Bd. Can. 36:987-1001.

Manooch, C.S., S.P. Naughton, C.B. Grimes, and L. Trent. 1987. Age and growth of king mackerel, Scomberomorus cavalla, from the U.S. Gulf of Mexico. 1987. Marine Fisheries Review 49:102-108.

Majkowski, J. and J. Hampton. 1982. The effect of parameter uncertainties in an age-length relationship upon estimating the age composition of catches. Can. J. Fish. Aquat. Sci. 40:272-280.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of non-linear parameters. J. Soc. Industrial and Applied Math 11(2):431-441.

McCaughran, D.A. 1981. Estimating growth parameters for

Nomura, H., and M.S. de Sousa Rodrigues. 1967. Biological notes on king mackerel, Scombermorus cavalla (Cuvier), from northeastern Brazil. Arq. Estac. Biol. Mar. Univ. Fed. Ceara 7:79-85.

Parrack N.C. and D.B. McClellan 1986. Trends in Gulf of Mexico red snapper population dynamics, 1979-1985. NOAA, NMFS, SEFC, Miami Laboratory, Coastal Resources Division Contrib. No. CRD-86/87-4.

Pauly, D. 1982. Studying single species dynamics in a tropical multispecies context, p 33-70 In D. Pauly and G. I. Murphy (editors) Theory and management of tropical fisheries. ICLARM Conf. Proc. 9, Manila, 360 p.

Pauly D. and G.R. Morgan. 1987 [eds.]. Length-based methods in fisheries research. ICLARM Conference Proceedings 13, 468 p. Int. Ctr. for Living Aquat. Res. Mange., Manila, Philippines, and Kuwait Inst. for Sci. Res., Safat, Kuwait.

Pauly, D., M.L. Palomares, and F.C. Gayanilo. 1987. VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981, p. 142-166. In D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, Manila, 351p.

Peterson, C.G. 1891. Eine Methode zur Bestimmung des Alters und Wuchses der Fische. Mitteilungen. Deutscher Seefischerei Verein 11:226-235. [cited in Richer 1975].

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. ICNAF Res. Bull. 9:65-74.

Powell, D. 1975. Age, growth, and reproduction of Spanish mackerel, Scomberomorus maculatus. Fl. Dept. Nat. Res. Mar. Res. Publ. No. 5, 21p.

Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling. 1986. Numerical Recipes, the art of scientific computing. Cambridge University Press, Cambridge. 818 p.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of the Fish. Resh. Board of Canada. 382 p.

Rosenberg, A.A. and J.R. Beddington. 1987. Monte Carlo testing of two methods for estimating growth from length frequency data, with general conditions for their applicbility, p.283-289 In D. Pauly and G.P. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p., Manila.

Schnute, J. and D. Fournier. 1980. A new approach to length frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37:1337-1351.

Scott, G.P. and D.M. Burns. 1988. Updated assessment information on the status of the king mackerel resource in the southeastern U.S. Mackerel Stock Assessment Panel Rep. No. MSAP/88/2, 77 p.

Shepherd, J.G. 1985. Deconvolution of length compositions. ICES Methods WG 1985:Working Paper, 7p.

Shepherd, J.G. 1987. A weakly parametric method for the analysis of length composition data, p. 113-120 In D. Pauly and G.P. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p., Manila.

Siliman, R.O. 1967. Analog computer models of fish populations. fish. Bull. 66:31-46.

Southwards, G. M. 1976. Sampling landings of halibut for age composition. Int. Pac. Halibut Comm. Sci. Rep. 58:31 p.

Sullivan, P.J., H.L. Lai, and V.F. Gallucci. 1988. A catch-at-length analysis that incorporates a stochastic model of growth. Can. J. Fish. Aquat. Sci. XX:XXX

Sutherland, D.F., and W.A. fable, Jr. 1980. Results of a king mackerel (*Scomberomorous cavalla*) and Atlantic Spanish mackerel (Scomberomorous maculatus) migration study. NOAA. Tech. Memo/NMFS-SEFC 12:32 p.

Tanaka, S. 1953. Precision of age-composition of fish estimated by double sampling method using the length for

Westrheim, S.J. and W.E. Ricker. 1978. Bias in using an age-length key to estimate age-frequency distributions. J. Fish. Res Board Can. 35:184-189.

Williams, R.O., and M.F. Godcharles. 1984. King mackerel taggging and stock assessment. Fla. Dept. Nat. Res, Completion Rpt. of P. L. 88-309 Project No. 2-341-R, paper presented at Second Annual Stock Assessment Workshop, NMFS, SEFC, Miami, Florida, SAW/84/GCP/14:121 p.

Williams, R.O., and R.G. TAylor. 1978. King mackerel tagging and stock assessment study. Fla. Dept. Nat. Res. Completion Rpt. of P. L. 88-309 Project No. 2-254-R.