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Age and Growth of Spanish Mackerel, Scomberomorus maculatus, in the Chesapeake Bay Region

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Age and growth of Spanish mackerel, *Scomberomorus maculatus*,

in the Chesapeake Bay region

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A Thesis

Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of

Master of Science

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by

Sarah K. Gaichas

1997

This Thesis is submitted in partial fulfillment of
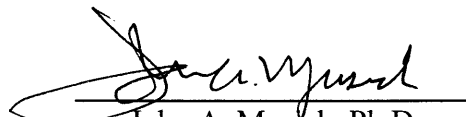the requirements of the degree of

Master of Science

Sarah K. Gaichas

Approved, July 1997

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ABSTRACT

Whole and sectioned otoliths, sectioned dorsal fin spines, sectioned pectoral fin rays, and stained vertebral centra from 60 fish were compared to determine the best method for ageing Spanish mackerel (*Scomberomorus maculatus*) in the Chesapeake Bay. Structure growth was proportional to fish growth for all five calcified structures, but the growth of the vascular core in dorsal fin spines may obliterate early growth history. For otoliths, fin spines, and vertebrae, the number of rings on each structure increased with body size, but the number of marks on pectoral fin ray sections was poorly related to body size. In a larger comparison, presumed ages from whole and sectioned otoliths were well correlated ($r=0.91$, $n=509$, $p=0.0001$), but whole otoliths underaged relative to sectioned otoliths for fish older than three. Whole otoliths were adequate for ageing young fish, but sectioned otoliths are better for ageing old fish and therefore for estimating growth and mortality.

Sectioned otolith ages were validated using ages-pooled plots of the monthly percent of otolith sections with zero marginal increment, and using one-way ANOVA and plots to evaluate differences between mean monthly marginal increments for all ages pooled, and for each presumed age group. Both ages pooled analyses indicated that annuli formed once per year with peak annulus formation in May, but examination of individual age groups revealed that age-one fish dominated pooled analyses. One annulus was formed per year in May-June for one, three, and four year old fish. Otoliths assigned age two appeared to form annuli in June or July during the period of Spanish mackerel residence in the Bay, although marginal increment analysis also indicated potential "annulus" formation in March and October.

A total of 4,194 Spanish mackerel was collected from Chesapeake Bay fisheries in 1988 and 1993-1995 to determine if a strong year class explained the recent period of high commercial landings, 1986-1995. Ages were based on 1,369 sectioned otoliths. Older, larger Spanish mackerel were more common in Chesapeake Bay in May through July of 1988 and 1993-1995, while small young-of-the-year fish did not appear in the fishery until August and September. Age compositions were very different between 1988 (ages 0 through 3 years) and 1993 (ages 0 through 6 years). Spanish mackerel landings in 1988 and 1993 were supported by different year classes. The 1987 year class was stronger than all other year classes in the 1988 and 1993 landings. Growth in Spanish mackerel was rapid and highly variable, with much overlap in size at age. Female Spanish mackerel were larger than males at all ages except 0, and von Bertalanffy growth models indicated that female Spanish mackerel grew to larger maximum lengths than males. Von Bertalanffy parameters were $L_\infty = 610.9$ mm, $K = 0.335$, and $t_0 = -1.1$ for sexes pooled; $L_\infty = 720.1$ mm, $K = 0.247$ and $t_0 = -1.36$ for females, and $L_\infty = 483.2$ mm, $K = 0.421$ and $t_0 = -1.32$ for males. Total mortality (Z) was between 0.53 and 0.58 for the entire period, based upon a maximum age of 8 years.

Plate 1. Spanish mackerel, *Scomberomorus maculatus*.
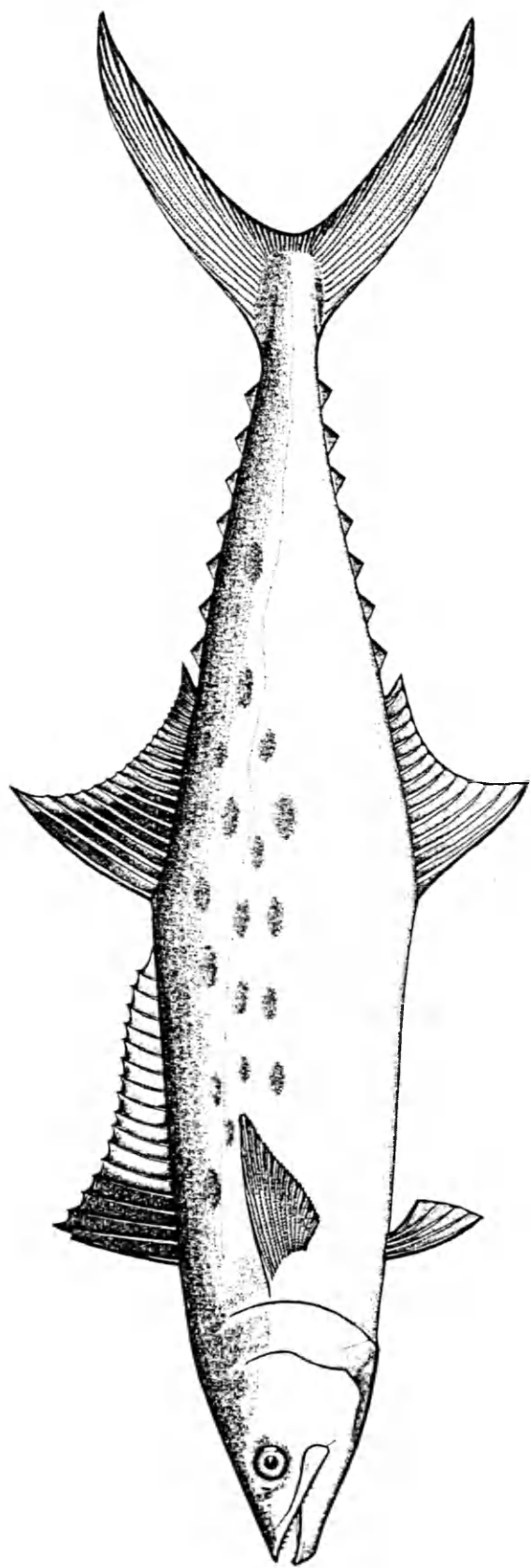
Spanish Mackerel, Scomberomorus maculatus

Drawn by Wm.Bunting, 1997

Age and growth of Spanish mackerel, *Scomberomorus maculatus*,

in the Chesapeake Bay region

General Introduction

The Spanish mackerel, *Scomberomorus maculatus*, is a member of the family

Scombridae, which also includes "true" mackerels (*Scomber*), bonitos (*Sarda*), and tunas

(*Thunnus*; Nelson, 1994). Scombrids are predatory, surface-schooling fishes with

pelagic eggs and larvae (Royce, 1972). Adaptations for high speed swimming in a

pelagic habitat characterize the family: all have streamlined bodies with finlets behind

the anal and second dorsal fins, a lunate caudal fin (Robins et al., 1986), and a narrow,

keeled caudal peduncle (Collette & Russo, 1978).

Worldwide, 18 species of *Scomberomorus* occupy tropical and warm temperate

continental shelf waters. In the western Atlantic, *S. maculatus* ranges from Massachusetts

to the Florida Keys, and throughout the Gulf of Mexico to the Yucatan peninsula

(Collette & Russo, 1984). Separate populations are thought to exist in the Gulf of

Mexico and along the U.S. east coast based upon morphometrics (Collette & Russo,

1984) and hemoglobin phenotypes (Skow & Chittenden, 1981). Spanish mackerel

migrate north seasonally along the U.S. east coast from wintering areas off southern

Florida. They appear off the Carolinas in March-April, in the Chesapeake Bay in May,

and in New York-Rhode Island waters by July (Earll, 1882; Beaumarriage, 1970). They

are resident in the Chesapeake Bay from May-September, and migrate out of the Bay by

mid-October (Earll, 1882; Chittenden et al., 1993a). Spanish mackerel are "multiple

spawners" (Hunter & Macewitz, 1985) which spawn repeatedly over a protracted season

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throughout their range in the Atlantic. Spawning occurs from April through September in

Florida (Powell, 1975), August through September in New York-New Jersey (Earll,

1882), and June through August in the Chesapeake Bay region (Cooksey, 1996).

Formal landings data for Spanish mackerel do not exist before 1879, although

anecdotal evidence indicates that the east coast commercial fishery developed in New

Jersey in 1873, and in Chesapeake Bay in 1875, coincident with the introduction of the

pound net in these areas (Earll, 1882). Chesapeake landings peaked in 1880 at 1.6

million pounds, with 1.8 million pounds total landed in the United States that year (Earll,

1882). Local landings have not approached that level since, indicating that the initial

fishery benefitted from a virgin stock (Chittenden et al., 1993b). Chesapeake landings

gradually declined to below eight hundred thousand pounds in 1890, to about five

hundred thousand pounds in 1900, and to below one hundred thousand pounds by 1910

(Chittenden et al., 1993b). By 1920, most east coast landings were in Florida (Trent &

Anthony, 1978), a trend which continues to this day (United States National Marine

Fisheries Service (NMFS), 1950-1994).

Although Florida landings have been on the order of a million pounds or more

annually, Chesapeake Bay Spanish mackerel landings have fluctuated markedly over the

past sixty years, ranging from lows below 5,000 lbs to peaks of 839,000 lbs in 1937 ,

(Lyles, 1969) and 514, 000 lbs in 1990 (NMFS, 1991; Chesapeake Executive Council,

1994). Furthermore, while nominal effort in terms of number of pound nets has steadily

decreased since 1930 from over two thousand to less than 250, catches increased in the

period 1986-1990, so that the recent CPUE greatly exceeds that of the 1937 landings peak

(Chittenden et al., 1993b). CPUE is a more reliable index of changes in abundance than raw landings data because it standardizes the effects of fishing effort on landings (Shepherd, 1988; Gulland, 1983; Royce, 1972). Therefore, the CPUE data indicate that Spanish mackerel may be more abundant in Chesapeake Bay now than they have been since 1929. The period of high landings since 1986 may reflect a combination of increased escapement from the Florida fishery due to recently implemented regulations. and the production of a strong year class in the mid-1980's (Chittenden et al., 1993b). One factor contributing to these fluctuations could be radical changes in year class strength, with one very strong year class supporting high landings throughout its lifespan. No data on the age composition of Spanish mackerel in Chesapeake Bay have ever been collected, and no general biological data on this species north of Cape Hatteras have been collected since the 1880's. Therefore, the objectives of this thesis are twofold: first, to describe age, growth, and mortality of Spanish mackerel in Chesapeake Bay, so that these life history parameters are available for management; and second, to test the hypothesis that the present abundance peak reflects a dominant year class.

Chapter 1

Comparison of calcified structures for ageing Spanish mackerel

Introduction

There has been disagreement over the most effective method for ageing Spanish mackerel, and the closely related king mackerel, *Scomberomorus cavalla*, which may result from geographic differences in interpretability of calcified structures. Although Klima (1959), Powell (1975), and Fable et al. (1987) used whole sagittal otoliths to determine ages in Florida Spanish mackerel, Schmidt et al. (1993) used transverse sections of otoliths to age Atlantic coast Spanish mackerel. Fable et al. (1987) found 97% agreement between whole and sectioned otolith ages and concluded that whole otoliths were adequate for ageing Spanish mackerel from Florida, where Gulf and Atlantic stocks mix. Similar comparisons of whole and sectioned otolith ages for king mackerel from both the Gulf and Atlantic, and from the Gulf of Mexico only, also found 97% and 87% agreement between structures, respectively (Johnson et al., 1983; Manooch et al., 1987). However, agreement was only 47% between whole and sectioned otoliths for Atlantic coast king mackerel (Collins et al., 1988). No comparison of whole and sectioned otolith ages exists for Atlantic coast Spanish mackerel, especially those caught north of Cape Hatteras, NC, a major zoogeographic boundary (Perry, 1985; Robins et al., 1986). Aside from scales, which were evaluated and dismissed by Klima (1959), no calcified structures other than otoliths have been rigorously examined in any Spanish mackerel population, even though fin spines, fin rays, and vertebrae have all been used to age other scombrids (Johnson, 1983; Beamish, 1981; Prince et al., 1985).

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Beamish and McFarlane (1983) have recommended that different ageing techniques be evaluated for precision and accuracy in each population to be examined, because readability of calcified structures may vary geographically, and because improved ageing methods may change perceptions of population dynamics. The importance of a preliminary comparison was demonstrated by Lowerre-Barbieri et al. (1993), who found weakfish (*Cynoscion regalis*) otolith sections to be far superior to the traditionally used scales in terms of precision and accuracy. Estimates of weakfish growth and mortality rates based upon scale ages, which were underestimates compared with sectioned otolith ages, may have led management to underestimate the vulnerability of weakfish populations to overfishing. Because no previous studies of Spanish mackerel age and growth exist for populations north of Cape Hatteras, NC, it was necessary to determine the most effective method for ageing fish in the Chesapeake Bay region.

The objectives of this study were twofold: first, to evaluate the potential of otoliths, fin spines, fin rays, and vertebrae for ageing Spanish mackerel; and second, to formally compare ages estimated from whole and sectioned otoliths, the previously used methods. The following criteria, slightly modified from Hill et al. (1989), were used to address the first objective, initial evaluation of calcified structures: presence of potential annual marks, proportionality of structure growth to body growth, increasing number of presumed annual marks with structure growth, precision of mark counts in repeated readings within and between readers, reader confidence in assigned ages, agreement between presumed ages assigned by different structures, and efficiency of processing. To address the second objective, a detailed comparison of presumed ages and age

compositions estimated from whole and sectioned otoliths was conducted using a large

random sample of fish from an entire year's collection.

Methods

Collection and Preparation of Calcified Structures

Spanish mackerel were collected every two weeks from May to September of 1993 and 1994 by purchasing a 50 lb box of each available market size grade from commercial pound net, gill net, and haul seine fishermen in Chesapeake Bay. Fork length (mm), total weight (g), and sex were recorded, and sagittal otoliths, spinous dorsal and soft-rayed pectoral fins were removed from each fish. Vertebral columns were also collected from a random sample of approximately 25% of the fish in each 50 lb. box. After removal, otoliths were stored dry while fins and backbones were stored frozen.

In preparation for further processing and reading, otoliths were soaked in bleach for 30 minutes, rinsed with hydrogen peroxide to neutralize bleach, rinsed three times with distilled water to remove all cleaning agents, and allowed to air dry. The right and left otoliths of each fish were assigned at random to be read whole or to be sectioned. Otoliths to be read whole were stored dry until reading. Otoliths to be sectioned were mounted sulcus side down on cardboard using thermoplastic cement. Transverse sections were made using a Buehler Isomet jeweler's saw with two blades separated by a spacer less than 0.5 mm wide. Sections were then mounted on microscope slides using thermoplastic cement and polished until the core and annuli were clearly visible.

Specific fin elements and vertebrae were chosen for the analysis on the basis of relative size and readability as determined by preliminary comparisons of all spines, rays,

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and vertebrae within two individual fish. The fourth dorsal fin spine and the fourth pectoral fin ray were selected because they were large enough to be handled and prepared easily, but the size of the interior vascular core was small relative to the cores of the first through third fin elements. Dorsal spines and pectoral rays numbered fifth and higher were too small and fragile to handle even with forceps. Caudal vertebrae were judged more readable than cervical or thoracic vertebrae. The 47th vertebra was selected because it was the largest of the more readable caudal vertebrae. Once chosen, the same numbered fin spine, ray, and vertebra was collected from each fish and prepared for reading.

Dorsal fin spines and pectoral fin rays were boiled in water for approximately 2 minutes and wiped clean with a cloth to remove excess tissue. They were then allowed to air dry, mounted on cardboard with thermoplastic cement, and cross-sectioned 3-5 mm from the base using the same equipment as described above for otoliths. Fin spine and ray sections were mounted on microscope slides with thermoplastic cement and polished to remove excess cement from their surfaces.

Vertebral columns were boiled in water for 3-5 minutes to remove excess tissue so that vertebrae could be accurately counted; then the 47th vertebra was separated from the column. Remaining tissue was peeled off the 47th vertebra and projecting spines and ribs were removed. Vertebrae were cleaned using bleach, hydrogen peroxide, and distilled water as described above for otoliths, and then stained by soaking for 45 minutes in a 0.05% solution of crystal violet (Johnson, 1979).

Initial Evaluation of Calcified Structures

Sixty Spanish mackerel between 239 mm and 608 mm fork length (FL) were selected from the 1,447 fish collected between May and September of 1994. To include as many age groups as possible in this analysis, equal numbers of fish were drawn from each of four fork length-based strata (200-299 mm, 300-399 mm, 400-499 mm, and 500+ mm FL). Whole and sectioned otoliths, the fourth dorsal fin spine, the fourth pectoral fin ray, and the 47th vertebra from each of these fish were used in the comparison. Before preparation and analysis, all calcified structures were assigned random numbers. Processing time was recorded for each calcified structure, and mean processing time by calcified structure was used to evaluate efficiency of preparation.

To determine the relationship between fish growth and calcified structure growth, several types of linear, areal, and volumetric measurements were made on each structure for comparison with fish fork length. Whole otoliths were weighed to the nearest 0.001 grams using an electronic balance. Whole otolith radius was measured from the focus to the posterior edge, and total length was measured from the rostrum to the posterior edge using an ocular micrometer (Figure 1a.). Linear and areal measurements for sectioned otoliths, dorsal spines, and pectoral rays were made using a compound video microscope with the Biosonics Optimas image analysis system. Sectioned otolith radius was measured from the center of the core to the distal edge of the ventral lobe, generally following the sulcal axis (Figure 1b.), and section area was calculated. Dorsal fin spine and pectoral fin ray section radius was measured from an estimated central point to the proximal edge of the section along the lateral axis (Figures 1c-d), and total area of

pectoral ray and dorsal spine sections, as well as area of dorsal spine cores was

calculated. Vertebral centrum radius and diameter were measured on the posterior face of

each stained centrum using an ocular micrometer (Figure 1e.). Linear regression was

used to determine if relationships between fish fork length and calcified structure size

were significant and increasing (Zar, 1984; SAS Institute Inc, 1988). Fits of the data to

more parameterized (ie. quadratic and cubic) models were not attempted for the

relationship of fish size to calcified structure size because predictive ability for back

calculating ages, etc. was not a priority in this initial evaluation.

To establish the presence of presumed annuli on each calcified structure and to

evaluate the relationship between calcified structure growth and number of presumed

annuli, calcified structures were examined and presumed annulus counts were compared

with the radial measurements described above. Whole otoliths were placed sulcus side

down in glycerine and examined on a black background with reflected light under a

dissecting microscope at 6X. Sectioned otoliths, dorsal fin spines, and pectoral fin rays

were examined under a compound microscope using transmitted light and a polarizing

filter at 2.5 to 20X, depending upon the size of the structure. Stained vertebral centra

were examined on a white background under reflected light with a dissecting microscope

(6X). Linear regression was used to determine if the relationship between calcified

structure size and number of presumed annuli was significant and increasing (Zar, 1984;

SAS Institute Inc, 1988).

Precision and confidence in repeated readings were used to evaluate the general

clarity of presumed annual marks on each calcified structure. To estimate within and

between reader precision, all calcified structures were examined twice by two different readers, with at least one week between repeated readings. Readings of calcified structures were done in a randomized order and without knowledge of fish size or date of capture. The confidence level for each reading was assigned by the reader using a scale of 1 (very low confidence) to 5 (very high confidence). Precision and differences between readings were evaluated by simple percent agreement, percent agreement $\pm$ one presumed annulus, average percent error (APE; Beamish & Fournier, 1981), and coefficient of variation (CV; Chang, 1982). Between reader percent agreement was calculated by averaging percent agreement between readers for the first reading and percent agreement between readers for the second reading.

To evaluate agreement between calcified structures from the same fish, presumed ages were compared using Spearman's rank correlation (Zar, 1984; SAS Institute Inc, 1988). Presumed age was defined as the number of presumed annuli on a given calcified structure for the purposes of this study. Agreement between structures was also calculated as simple percent agreement, percent agreement $\pm$ one presumed annulus, and using a test of symmetry as described in Hoenig et al. (1995). Individual calcified structures that showed no agreement in four readings were not included in between structure comparisons.

Detailed Comparison of Sectioned vs. Whole Otoliths

Presumed ages from sectioned and whole otoliths were compared in detail using an experiment designed to simulate "real world" production ageing. To represent only the most common age classes in proportion to their occurrence, a random sample of 545

otoliths was examined from the fish captured in 1993 which ranged in length from 192 to 658 mm FL. As in the preliminary evaluation of calcified structures, the right or left otolith was selected at random from each fish; however, the selected otolith was both aged whole and then sectioned and aged again, so that comparisons of whole and sectioned ages were from the same otolith. This design eliminated the potential for presumed age disagreements arising from differences between right and left otoliths. To re-evaluate precision in this larger experiment, a subsample of 133 sectioned otoliths was reread, with one month between repeated readings.

Whole and sectioned otolith presumed ages were compared using Spearman's rank correlation (Zar, 1984; SAS Institute Inc, 1988). Agreement between whole and sectioned otolith presumed ages was calculated as simple percent agreement, percent agreement $\pm$ 1 presumed annulus, and assessed using Hoenig et al.'s (1995) test of symmetry as described above. Differences between presumed age compositions from whole vs. sectioned otoliths were assessed with a Kolmogorov-Smirnoff two sample test (Worthington et al., 1995; Sokal & Rohlf, 1984). Differences between whole and sectioned otolith presumed ages were also examined for trends by fish fork length and sex.

Results

Initial Evaluation of Calcified Structures

All structures had marks which could be interpreted as annual. (Figures 1a-e.) Whole otolith annuli were identified as concentric wide relatively translucent "summer" bands bordered by narrow opaque "winter" bands in the posterior field of the otolith which were continuous around the otolith to the rostrum and anterostrum. The focus was usually clearly visible as a transparent point near the center of the distal face of whole otoliths. Sectioned otolith presumed annuli were identified as wide transparent areas bordered by narrow opaque bands originating at the sulcus and running parallel to the edge of the section. Marks visible on both the ventral and dorsal halves of the section were counted. The otolith core was usually identifiable as an opaque area medial to the sulcus acousticus on sections. Dorsal spines had concentric wide transparent areas bordered by very narrow opaque rings which were identified as annuli if they were continuous around the section. No growth center was identifiable in spines due to the vascularized core, so a growth center had to be estimated for radial measurements. Pectoral rays are composed of two asymmetrical elements which frequently became mis-oriented during sectioning; alternating transparent and opaque bands often appeared on each element in the section. Ages were assigned lower confidence if bands appeared on only one element. There was no growth center on fin ray sections, so it was estimated for radial measurements. Vertebral centra had visible presumed annuli only when stained

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Figure 1. Presumed annuli on calcified structures from a 575 mm FL female Spanish

mackerel, *Scomberomorus maculatus*, caught in Chesapeake Bay 5 July, 1994. Arrows

point to marks counted as presumed annuli.

1a. Whole otolith under reflected light.

1b. Sectioned otolith in transmitted light with a polarizing filter.

1c. Sectioned dorsal fin spine in transmitted light with a polarizing filter.

1d. Sectioned pectoral fin ray in transmitted light with a polarizing filter.

1e. Stained vertebral centrum under reflected light.

dorsal

focus

anterior
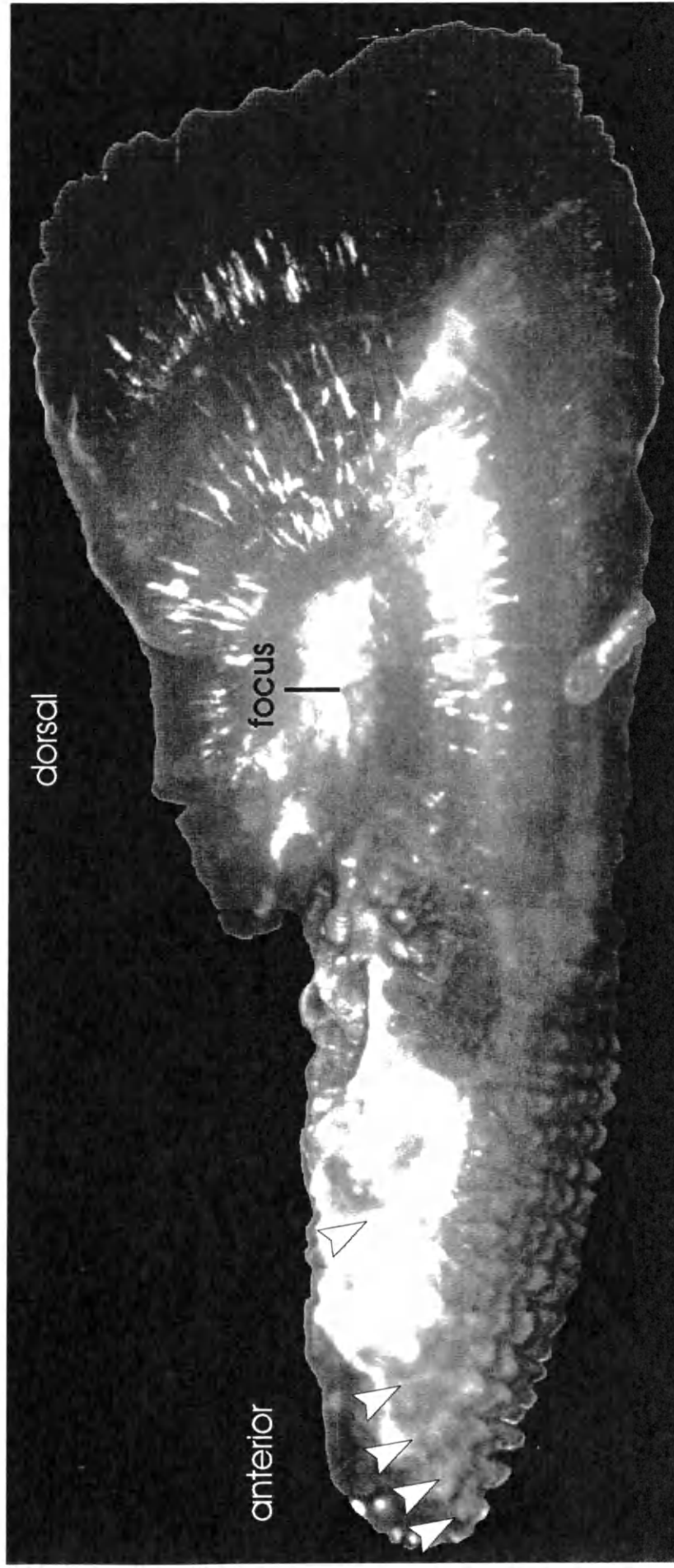
Total Length = 10.64 mm

Figure 1a

dorsal lobe

sulcus

core

ventral lobe

Total Length = 3.31 mm

Figure 1b
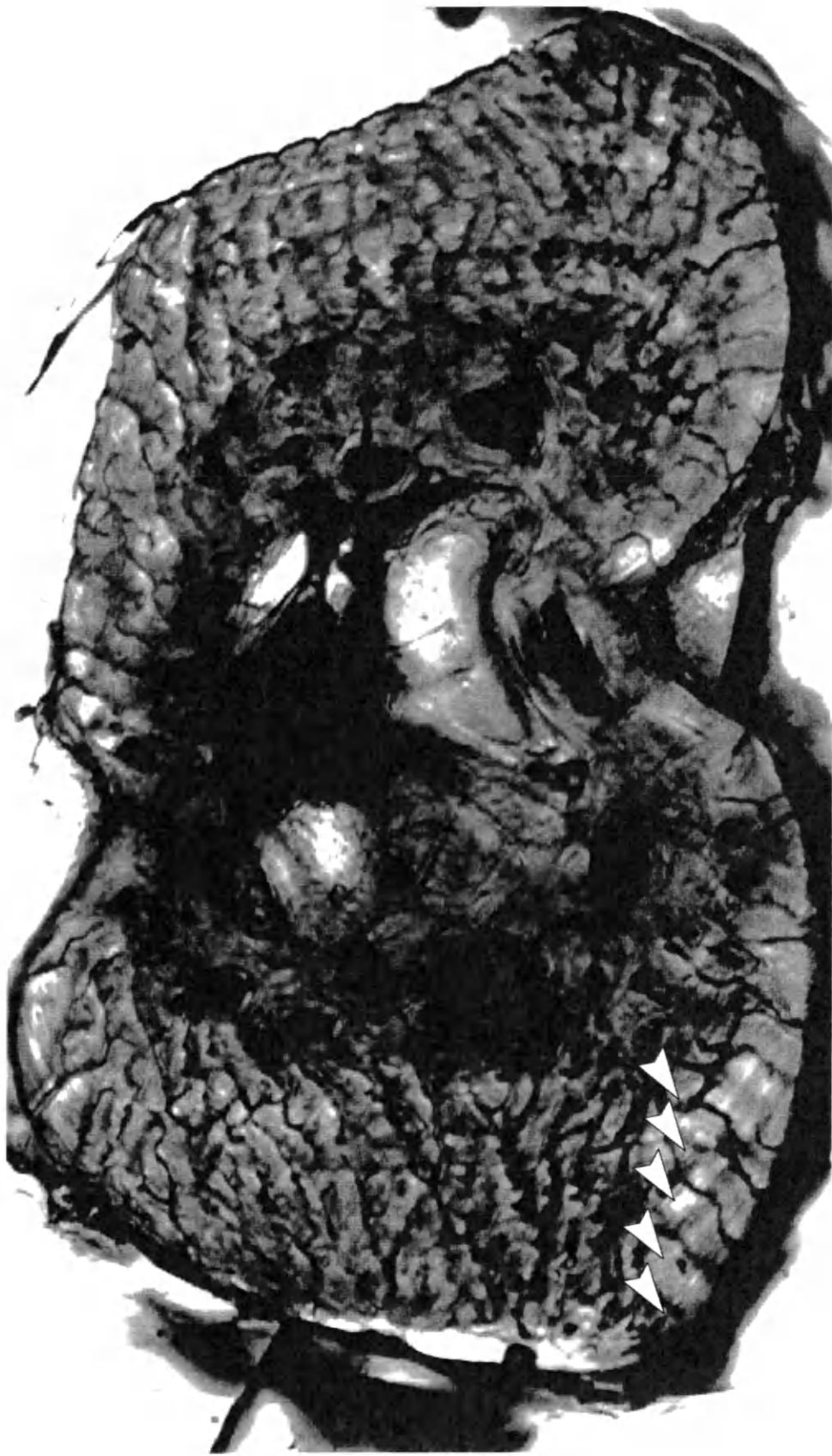
Diameter = 1.22 mm

Figure 1c

RAD = 1.33 mm

Figure 1d

focus
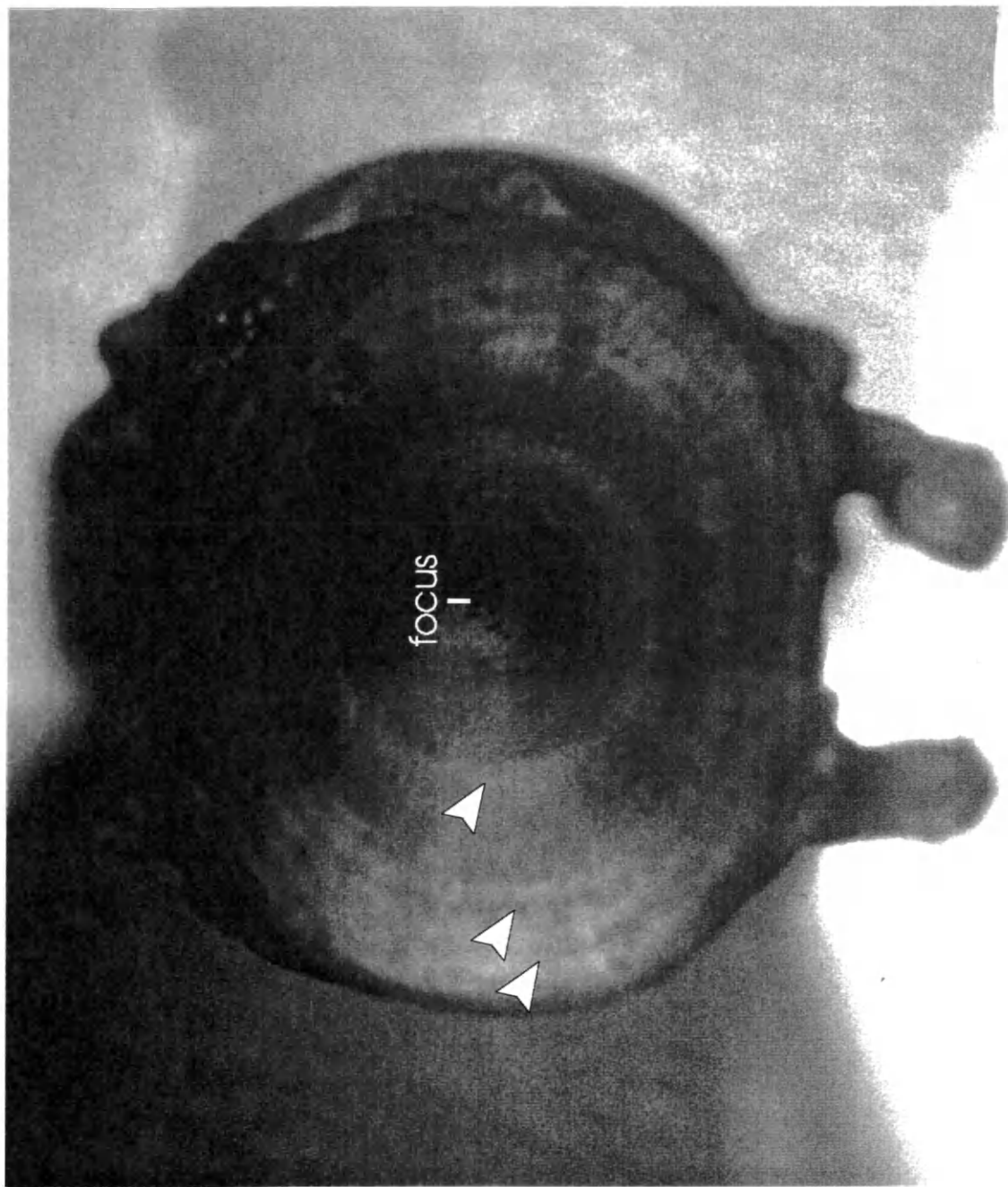
Diameter = 8.8 mm

Figure 1e

with crystal violet. Concentric narrow indentations in the overall uniform surface of the centrum were counted as annuli if they were continuous around the centrum. The growth center was clearly visible as a hole through the center of the bone on all vertebral centra.

Calcified structure size was directly related to fish size for all five structures, indicating that structure growth was proportional to body growth; however, the area of the vascular core in dorsal fin spines was also proportional to fish size, indicating that the growth of the vascular core in dorsal fin spines may obliterate early growth history. All regressions of structure size on fish fork length, including dorsal spine core area, were significant at $p<0.001$ and all slopes were positive (Table 1). A regression of spine core area on fish size indicates that fish over 500 mm FL have a spine core area which equals or exceeds the total spine area of 300 mm FL fish (Figure 2), suggesting that early growth history becomes lost as fish grow. Although all r^2 values were high, regressions of section area, core area, or whole structure diameter on fish length had much better r^2 fits than regressions of structure radius on fish length.

For all calcified structures except pectoral fin rays, the number of presumed annuli on each structure increased with structure size (Figure 3), and therefore body size. All regressions of otolith, spine, and vertebral radius on number of presumed annuli were significant at $p<0.001$ and increasing (Table 2). Sectioned otoliths had the best r^2 fit (0.71), followed closely by whole otoliths ($r^2=0.68$), vertebrae ($r^2=0.61$), and dorsal spine sections with a poorer fit ($r^2=0.31$). By contrast, the number of presumed annuli on pectoral fin ray sections was poorly related to ray size, and therefore body size.

Table 1. Regression equations and r^2 for relationships between calcified structure growth and fish growth for Spanish mackerel, *Scomberomorus maculatus*. All equations are significant with $p < 0.001$. WOWT = whole otolith weight, WOTL = whole otolith total length, WORAD = whole otolith radius, SOAR = sectioned otolith area, SORAD = sectioned otolith radius, SPAR = sectioned dorsal spine total area, SPRAD = sectioned dorsal spine radius, RAAR = sectioned pectoral ray area, RARAD = sectioned pectoral ray radius, VTDIAM = vertebral centrum diameter, VTRAD = vertebral centrum radius, FL = fish fork length.

Calcified Structure	Equations	r^2
Whole otolith	WOWT = -0.0133 + 7.69*10^{-5} (FL)	0.94
	WOTL = 1.56 + 0.0154 (FL)	0.93
	WORAD = 0.861 + 6.02*10^{-3} (FL)	0.88
Sectioned otolith	SOAR = -0.178 + 4.02*10^{-3}(FL)	0.87
	SORAD = 0.301 + 1.42*10^{-3} (FL)	0.69
Dorsal spine	SPAR = -0.371 + 2.08*10^{-3} (FL)	0.93
	SPRAD = -0.0581 + 1.12*10^{-3} (FL)	0.84
Pectoral ray	RAAR = -0.640 + 3.23*10^{-3} (FL)	0.87
	RARAD = -0.0918 + 2.31*10^{-3} (FL)	0.75
Vertebral centrum	VTDIAM = -1.21 + 0.0178 (FL)	0.97
	VTRAD = -0.422 + 7.74*10^{-3} (FL)	0.92

Figure 2. Regressions of dorsal spine total area and vascular core area on fork length in Spanish mackerel, *Scomberomorus maculatus*. Vascular core size in fish over 500 mm FL exceeds dorsal spine size of 300 mm FL fish, indicating the potential for growth increment resorption.
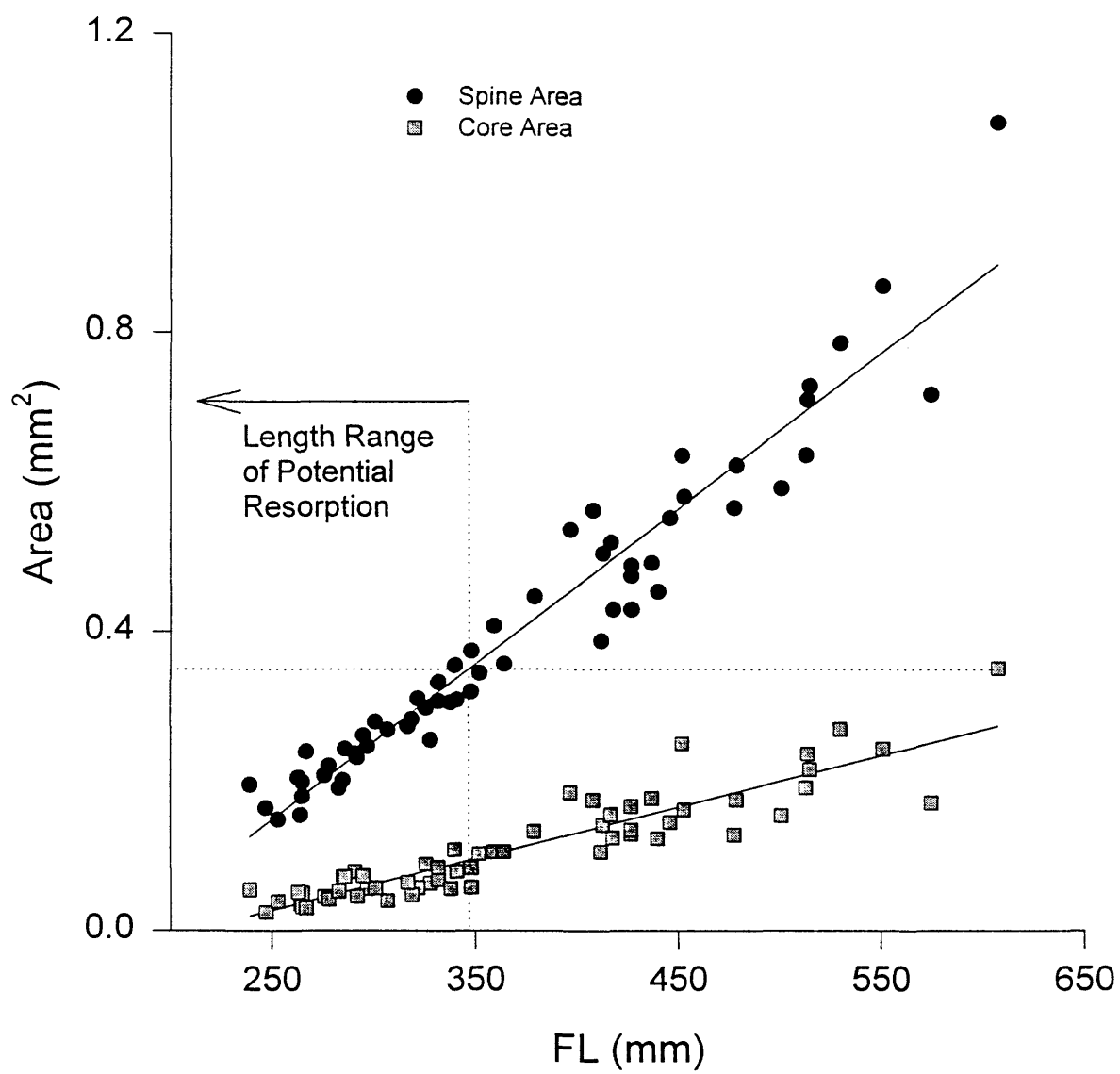
Figure 3. Relationship between the number of presumed annuli and fish length in whole

otoliths, sectioned otoliths, dorsal fin spines, pectoral fin rays, and vertebral centra of

Spanish mackerel, *Scomberomorus maculatus*.

Whole Otoliths

Sectioned Otoliths

Dorsal Spines

Pectoral Rays

Vertebral Centra

FL (mm)
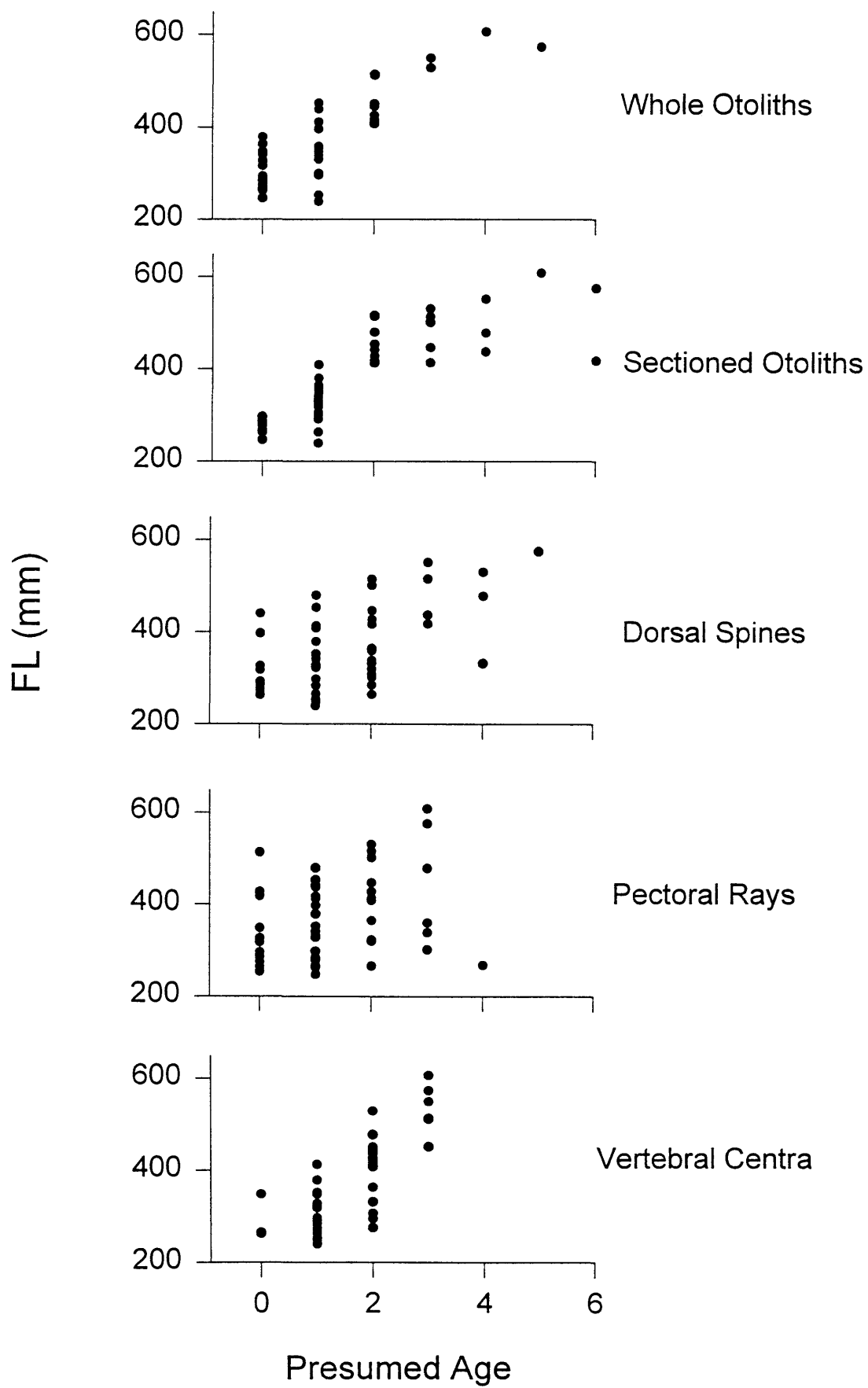
Presumed Age

Table 2. Regression equations, p values, and r^2 for relationships between calcified

structure size and number of presumed annuli for Spanish mackerel, *Scomberomorus*

maculatus. N = number of presumed annuli, WORAD = whole otolith radius, SORAD =

sectioned otolith radius, SPRAD = dorsal spine radius, RARAD = pectoral ray radius,

VTRAD = vertebral centrum radius.

Calcified Structure	Equation	p value	r^2
Whole otoliths	N = -3.80 + 1.59 (WORAD)	0.0001	0.68
Sectioned otoliths	N = -4.56 + 7.44 (SORAD)	0.0001	0.71
Dorsal spines	N = -0.657 + 6.12 (SPRAD)	0.0001	0.31
Pectoral rays	N = 0.410 + 1.24 (RARAD)	0.0309	0.09
Vertebral centra	N = -0.430 + 0.375 (VTRAD)	0.0001	0.61

Regression analysis showed a very poor relationship of number of presumed annuli to ray radius, with only marginal significance at p=0.031 and extremely poor fit to a linear model. The r^2 of 0.09 indicated that the number of rings had little to do with fin ray size (Table 2). For example, the highest count of 4 presumed annuli was read from one of the smallest fin rays in the sample (Figure 3).

Sectioned otoliths were most likely to identify older fish, and vertebrae were least likely to do so. Sectioned otoliths had the greatest maximum presumed age of six on the largest fish, while stained vertebrae had a maximum of only three presumed annuli even for the largest fish (Figure 3). Distributions of presumed ages from each structure also indicated that sectioned otoliths identified more fish over presumed age 3 than any other calcified structure, whereas vertebrae identified only presumed age three and under with presumed age two being most common (Figure 4). Presumed age one was most common in all other calcified structures except for whole otoliths, which found presumed age zero most common. Whole otoliths and dorsal fin spine sections gave maximum presumed ages of five for the larger fish in the sample, while pectoral fin ray sections had a maximum of four presumed annuli on one of the smallest fish.

Clarity of presumed annuli on Spanish mackerel calcified structures was poor, as indicated by highly variable but generally low precision and confidence in readings for all structures. In general, reader one read otoliths and vertebrae most consistently, while reader two read vertebrae and fin elements most consistently. For reader one, sectioned otoliths had the highest within reader precision and confidence (79.3% agreement, Table 3; 3.2 confidence, Table 4). Reader one was nearly as precise with vertebrae (78.3%

Figure 4. Frequency distributions of presumed ages (years) from whole otoliths,

sectioned otoliths, dorsal fin spines, pectoral fin rays, and vertebral centra of Spanish

mackerel, *Scomberomorus maculatus*.
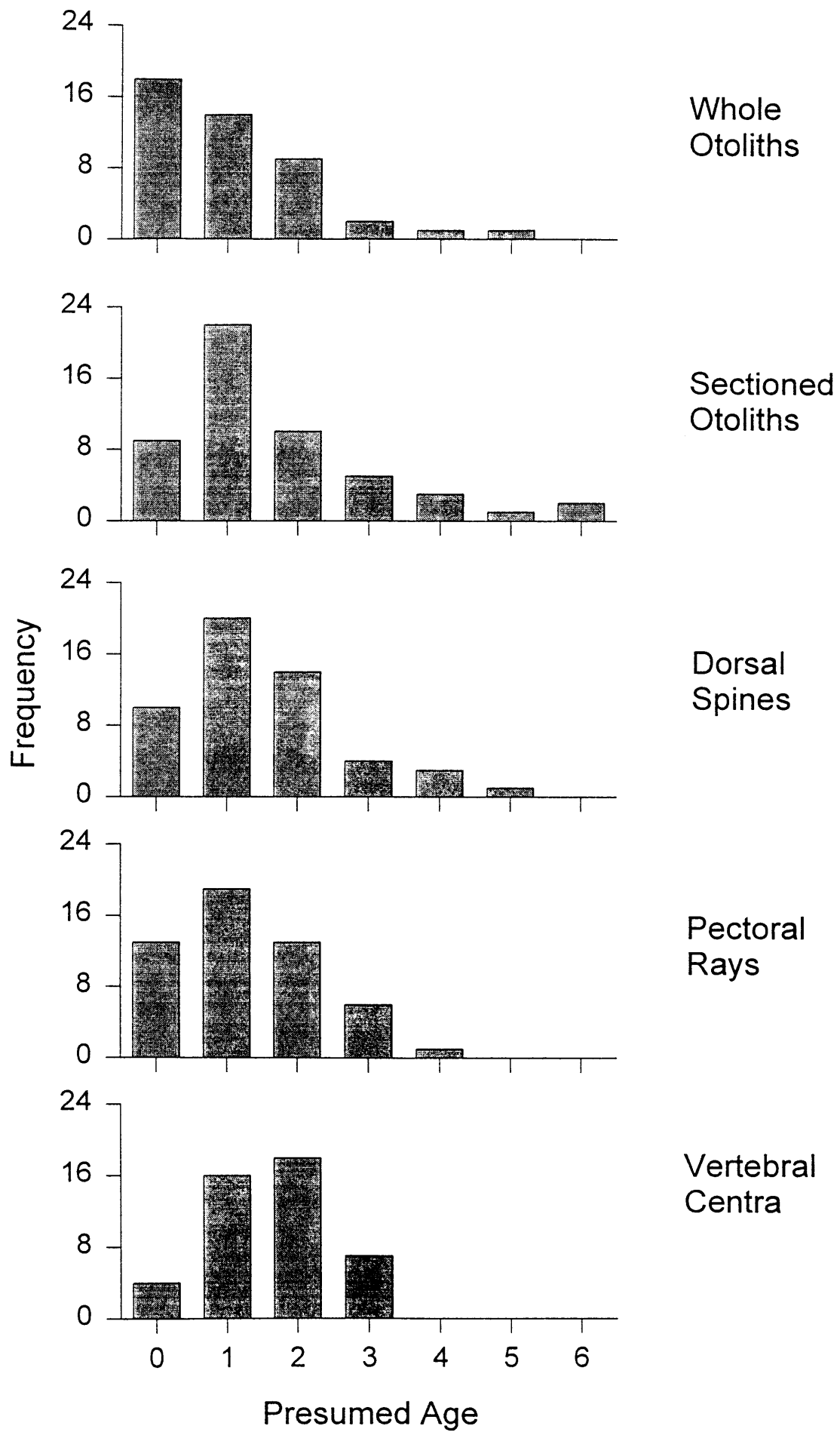
Table 3. Indices of precision overall, and for each reader in two readings of Spanish mackerel, *Scomberomorus maculatus* calcified structures. % Agree = simple percent agreement, % Agree ± 1 = percent agreement allowing for deviations of ± 1 presumed annulus, APE & CV = average percent error and coefficient of variation.

	Whole Otoliths	Sectioned Otoliths	Dorsal Spines	Pectoral Rays	Vertebral Centra
Reader 1					
% Agree	61.7	79.3	57.6	60.0	78.3
% Agree ± 1	100	100	93.2	93.3	100
APE & CV	0.26	0.14	0.22	0.21	0.12
Reader 2					
% Agree	51.7	56.9	64.4	66.7	78.3
% Agree ± 1	95.0	98.3	98.3	96.7	98.3
APE & CV	0.39	0.28	0.20	0.20	0.11

Table 4. Mean confidence levels assigned to Spanish mackerel, *Scomberomorus maculatus*, age readings by reader and structure.

Reader / Reading	Whole Otoliths	Sectioned Otoliths	Dorsal Spines	Pectoral Rays	Vertebral Centra
Reader 1					
First	3.10	3.15	2.47	1.86	2.34
Second	2.97	3.19	2.59	2.10	2.32
Reader 2					
First	2.17	1.68	1.97	1.68	2.69
Second	2.08	1.93	2.14	1.90	2.64
Mean	2.58	2.56	2.33	1.89	2.50

agreement), although mean confidence for vertebrae (2.3) was lower than for sectioned otoliths. Whole otoliths, spines, and rays had similar agreement for reader one (61.7% - 57.6%), although mean confidence varied greatly between pectoral rays (2.0) and whole otoliths (3.1). By contrast, reader two had the highest agreement and confidence for vertebrae (78.3%, 2.7), intermediate agreement for dorsal spines and pectoral rays (64.4% - 66.7%), and lowest agreement for whole and sectioned otoliths (51.6% - 56.9%). Reader two assigned lowest mean confidence to pectoral ray and sectioned otolith ages (1.8). Precision calculated as APE and CV was still generally low, and did not greatly change the rank order of structure precision for either reader (Table 3).

Between reader agreement for Spanish mackerel calcified structures was also generally low, ranging from 46% to 65% (Table 5). Spanish mackerel dorsal fin spines and sectioned otoliths had the highest between reader precision: 65% and 59% agreement respectively. Measured by APE and CV, Vertebrae had the least between reader error (0.29 APE, 0.31 CV), and sectioned otoliths and dorsal fin spines were nearly equivalent (0.35 APE for both, 0.38 and 0.39 CV respectively). Disagreement was highest for whole otoliths and pectoral fin rays.

Although overall precision and confidence in interpreting Spanish mackerel calcified structures were not high, within and between reader disagreements generally changed age by only one year. Percent agreement for reader one increased to 100% for whole and sectioned otoliths and vertebrae, and over 90% for fin spines and rays when allowing for differences of ± 1 year (Table 3). Similarly, percent agreement for reader two increased to over 95% for all structures when allowing for differences of ± 1 year (Table

Table 5. Indices of between reader precision for Spanish mackerel, *Scomberomorus*

maculatus calcified structures. % Agree = simple percent agreement, % Agree ± 1 =

percent agreement allowing for deviations of ± 1 presumed annulus, APE = average

percent error, CV = coefficient of variation.

Between Readers	Whole Otoliths	Sectioned Otoliths	Dorsal Spines	Pectoral Rays	Vertebral Centra
% Agree	45.8	58.6	65.3	47.5	53.3
% Agree ± 1	90.0	95.7	94.9	91.7	94.2
APE	0.58	0.35	0.35	0.40	0.29
CV	0.64	0.38	0.39	0.45	0.31
% disagreements exceeding 1 ring	10.0	4.3	5.1	8.3	5.8

Figure 5. Comparisons of presumed ages (years) from whole otoliths, sectioned dorsal

fin spines, sectioned pectoral fin rays and stained vertebral centra with sectioned otolith

presumed ages from Spanish mackerel, *Scomberomorus maculatus*. The diagonal line

represents 1:1 agreement. The number of fish each point represents is indicated.
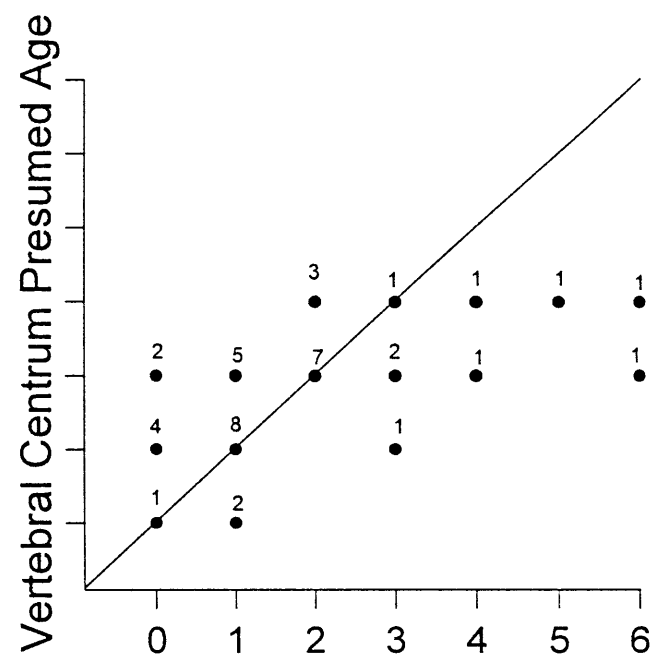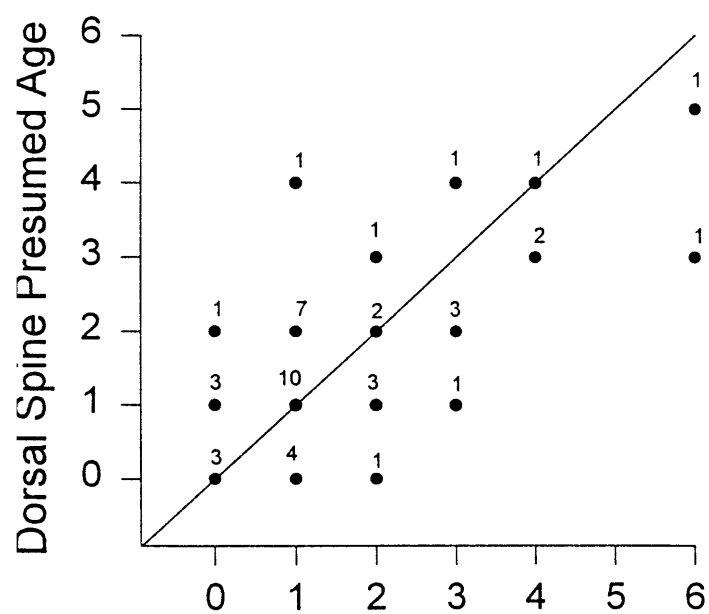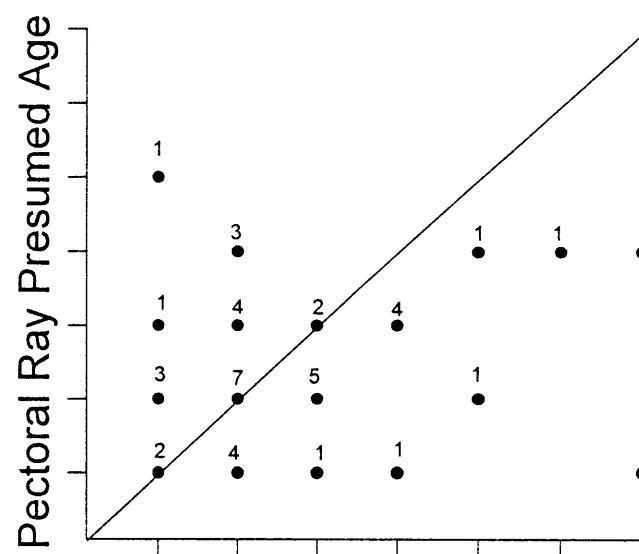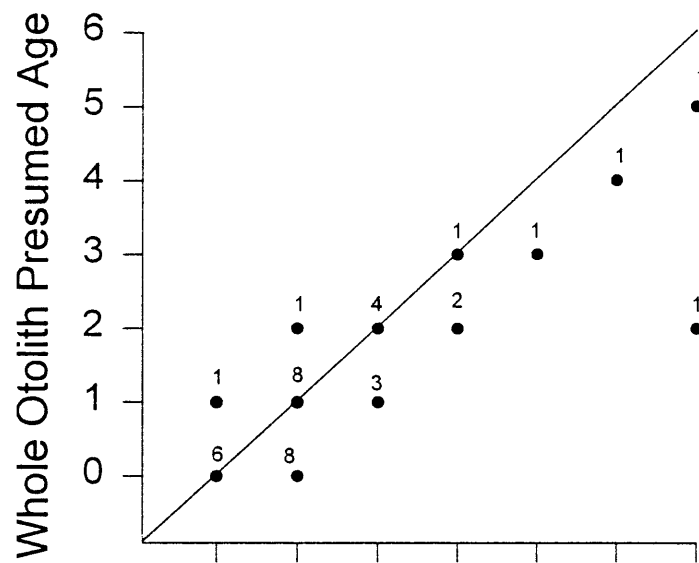
3). Between reader agreement for all structures also increased to at least 90% when allowing for differences of ±1 year (Table 5). Sectioned otolith precision increased to 95.7%; therefore 37.1% of all sectioned otolith readings differed by one year, while less than 5% differed by more than one year. Whole otoliths had the highest proportion of greater than one year differences between readers (10%, Table 5).

Both correlation analysis and percent agreement between structures indicated that different calcified structures from the same Spanish mackerel generally did not estimate the same presumed age, although whole and sectioned otoliths appeared to differ by only one year in estimated presumed age. Correlation between sectioned and whole otolith presumed ages was much higher (r=0.81, n=38, p=0.0001; Table 6, Figure 5) than correlations between any other pair of structures. Whole otolith presumed ages were slightly better correlated than sectioned otolith presumed ages with ring counts from fin spines and vertebrae. Conversely, ring counts from pectoral rays were completely uncorrelated with sectioned otoliths (r=0.18, n=34, p=0.2326) and vertebrae (r=0.28, n=39, p=0.0853), and had low correlations with whole otoliths and dorsal spines. Percent agreement between structures was generally low, but most disagreements were ±1 year. Whole and sectioned otoliths agreed only 50% of the time, but allowing for one year differences increased agreement to 97.4%; therefore less than 3% of differences exceeded one year (Table 6). For other between structure comparisons, differences exceeding one year ranged from a low of less than 8% for whole otoliths vs. dorsal spines to a maximum of 25% for sectioned otoliths vs. pectoral rays. Agreement between both otolith preparations and dorsal spines was generally higher than for other comparisons.

Table 6. Ring count agreement between Spanish mackerel, *Scomberomorus maculatus* calcified structures. r_s = Spearman's rank correlation coefficients, n = number compared, p = probability r_s = 0, % Agree = percent agreement between structures, % Agree $\pm$ 1 = percent agreement between structures allowing for deviations of plus or minus one ring.

	Sectioned Otoliths	Dorsal Spines	Pectoral Rays	Vertebral Centra
Whole otoliths vs.				
r_s	0.81	0.62	0.45	0.71
n	38	39	39	34
p	0.0001	0.0001	0.0037	0.0001
% Agree	50.0	48.7	56.4	41.2
% Agree $\pm$ 1	97.4	92.3	79.5	88.2
Sectioned otoliths vs.				
r_s	--	0.57	0.18	0.64
n	--	46	44	41
p	--	0.0001	0.2326	0.0001
% Agree	--	34.8	27.3	41.5
% Agree $\pm$ 1	--	89.1	75.0	82.9
Dorsal spines vs.				
r_s	--	--	0.37	0.56
n	--	--	46	39
p	--	--	0.0109	0.0002
% Agree	--	--	45.7	43.6
% Agree $\pm$ 1	--	--	80.4	84.6
Pectoral Rays vs.				
r_s	--	--	--	0.28
n	--	--	--	39
p	--	--	--	0.0853
% Agree	--	--	--	33.3
% Agree $\pm$ 1	--	--	--	82.1

Tests of symmetry showed that disagreements between whole vs. sectioned otoliths and whole otoliths vs. vertebrae presumed age comparisons were systematically biased (Table 7). Chi-square analysis showed that whole otoliths systematically underaged relative to sectioned otoliths for ages exceeding zero, and that vertebrae overestimated ages of zero and one year old fish relative to whole otoliths, and underestimated ages above three. For all other comparisons, no systematic ageing bias was detected by chi-square analysis, indicating that disagreements were randomly distributed throughout age classes.

Efficiency of processing, measured as mean preparation time, varied from 1 to 13 minutes per specimen among Spanish mackerel calcified structures. Because whole otoliths required only cleaning before they could be read, their processing was faster and easier than for any other structure, averaging one minute per otolith. Structures requiring cleaning and sectioning all had mean processing times between 10 and 13 minutes per specimen, and cleaning and staining vertebral centra required an average of nine minutes per vertebra (Table 8).

Detailed Comparison of Sectioned vs. Whole Otoliths

Presumed ages on whole and sectioned otoliths showed higher correlation and agreement in this detailed comparison than in the initial evaluation of calcified structures. Ages from whole and sectioned otoliths were well correlated (Figure 6; Spearman's rank r=0.91, n=509, p=0.0001). Whole and sectioned otolith presumed ages agreed for 83.3% of the fish examined. A Kolmogorov-Smirnoff two-sample test found no significant difference (p>0.10) between age compositions determined by whole

Table 7. Chi-square tests of symmetry for ring count comparisons between Spanish mackerel, *Scomberomorus maculatus* calcified structures.

	Sectioned Otoliths	Dorsal Spines	Pectoral Rays	Vertebral Centra
Whole otoliths vs.				
χ^2	12.44	8.98	9.57	14.13
df	7	6	7	7
p value	<0.10	<0.25	<0.25	<0.05
Sectioned otoliths vs.				
χ^2	--	8.08	14.25	13.87
df	--	9	12	10
p value	--	<0.75	<0.50	<0.25
Dorsal spines vs.				
χ^2	--	--	11.87	6.00
df	--	--	11	7
p value	--	--	<0.50	<0.75
Pectoral Rays vs.				
χ^2	--	--	--	10.75
df	--	--	--	7
p value	--	--	--	<0.25

Table 8. Mean processing times (minutes) for Spanish mackerel, *Scomberomorus maculatus* calcified structures.

Structure	Process	Mean Time per Specimen
Whole otoliths	Cleaning	1.0
Sectioned otoliths	Cleaning, sectioning, polishing	10.9
Dorsal spines	Cleaning, sectioning, polishing	10.0
Pectoral rays	Cleaning, sectioning	13.0
Vertebral centra	Cleaning, staining	8.9

Figure 6. Comparison of whole and sectioned otolith ages (years) from 509 Spanish

mackerel, *Scomberomorus maculatus*. The diagonal line represents 1:1 agreement. The

number of fish each point represents is indicated.
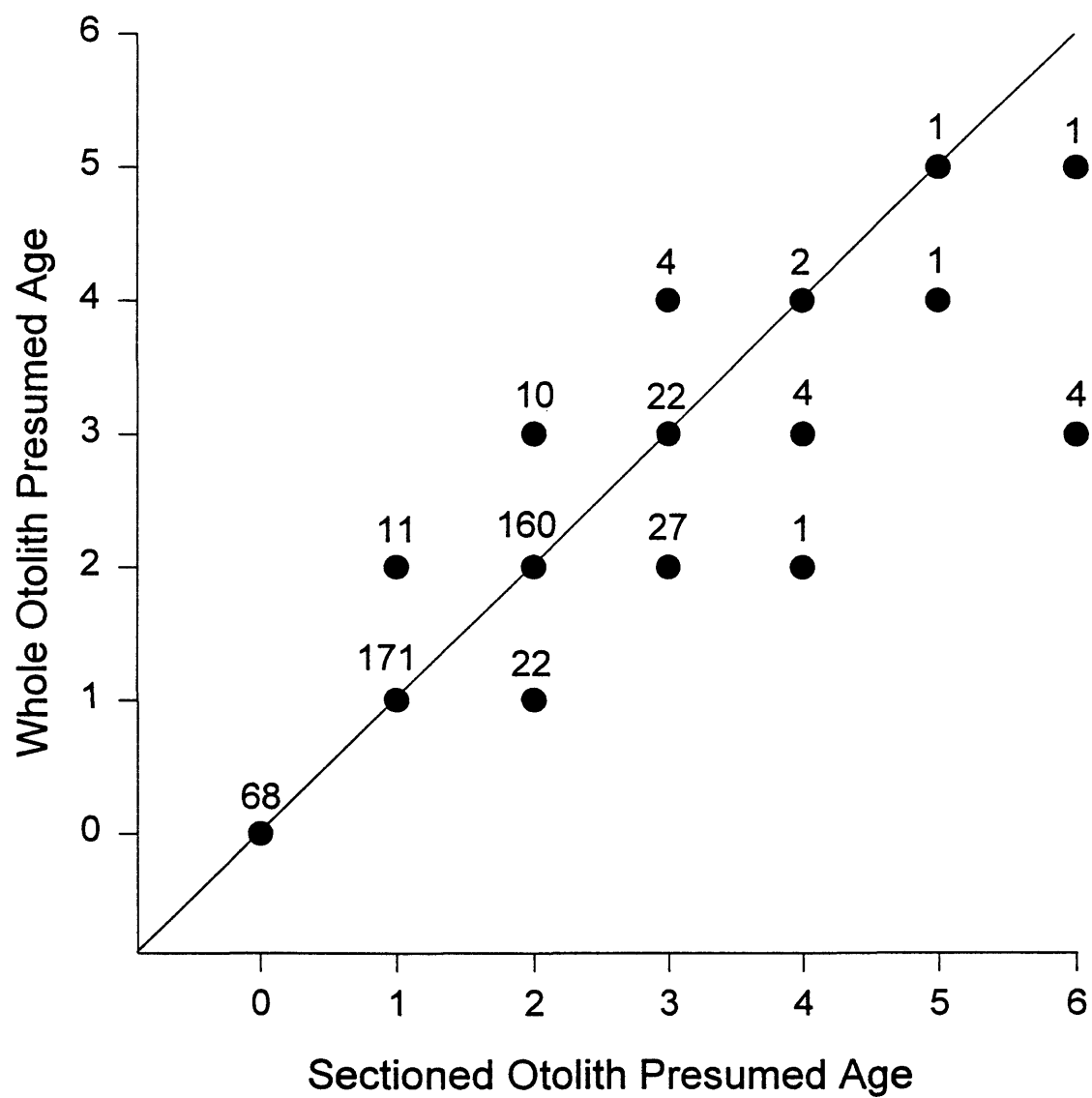
and sectioned otoliths; both methods estimate age structures dominated by presumed one and two year olds (Figure 7).

Although presumed ages were well correlated, the results of this detailed comparison agree with the initial evaluation of calcified structures in that whole otoliths underaged relative to sectioned otoliths. Whole otoliths more often underestimated than overestimated sectioned otolith presumed age for all ages over 1 (Figure 6). A test of symmetry revealed significant systematic differences in presumed ages assigned by the methods (χ^2=18.48, df = 7, p = 0.01). Disagreements were most dramatic for presumed age classes 4 through 6 as identified by sectioned otoliths. The majority (80%, four of five) of fish aged six by sectioned otoliths were aged three by whole otoliths. No six year olds were identified by whole otoliths.

Differences in presumed ages assigned by whole and sectioned otoliths were sex- and length-dependent. In general, males were more likely to be underaged by whole otoliths because they grew more slowly and more growth information was contained on smaller whole otoliths compared with female Spanish mackerel. Whole otolith presumed ages underestimated sectioned otolith presumed ages for male fish over 400 mm FL by one to three years (Figure 8). Presumed ages of some male fish over 350 mm FL were also underestimated by one year. For female Spanish mackerel, underestimation of presumed age by whole otoliths was less severe and did not occur exclusively over a particular size range. However, underestimation was more likely for females over 450 mm. In the range of 370 mm to 400 mm FL, whole otoliths appeared to overestimate the presumed age of females relative to sectioned otoliths (Figure 9). Tests of symmetry by

Figure 7. Frequency distributions of presumed ages (years) from whole and sectioned

otoliths of 509 Spanish mackerel, *Scomberomorus maculatus*.

Whole Otoliths

N = 509

Sectioned Otoliths

N = 509

Percent Frequency
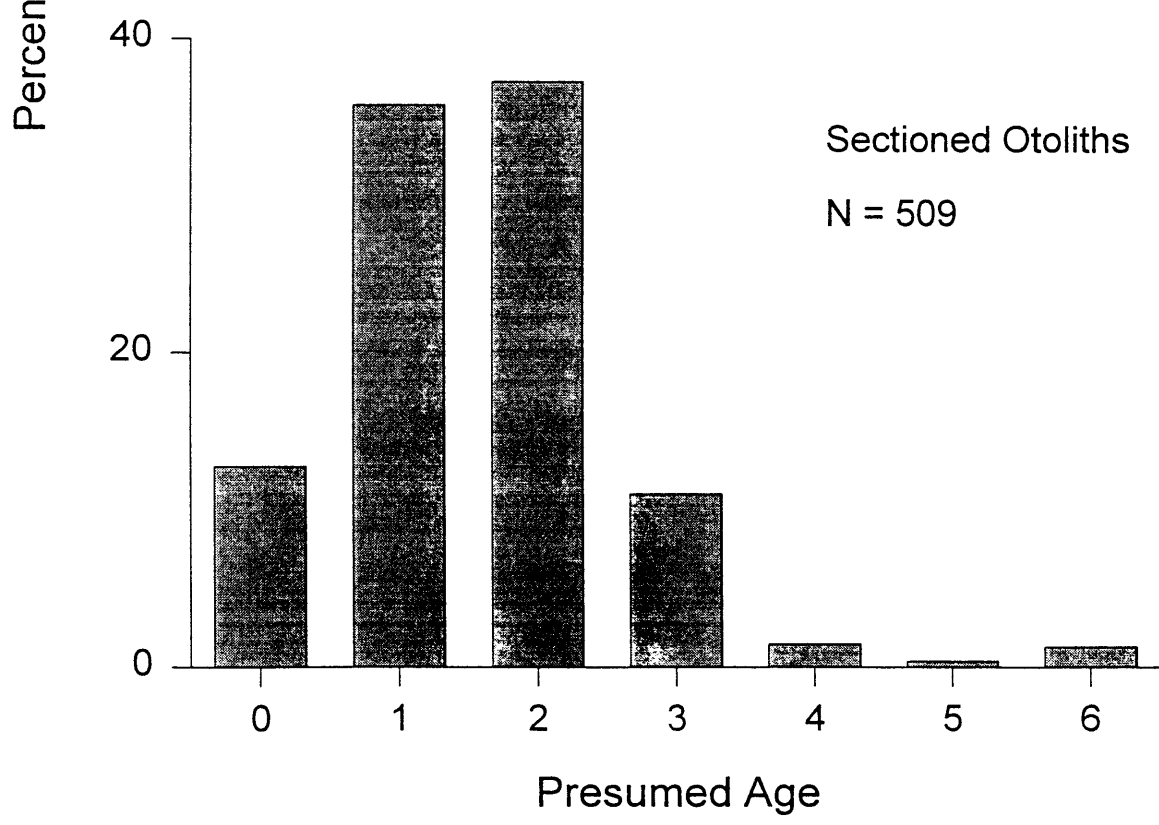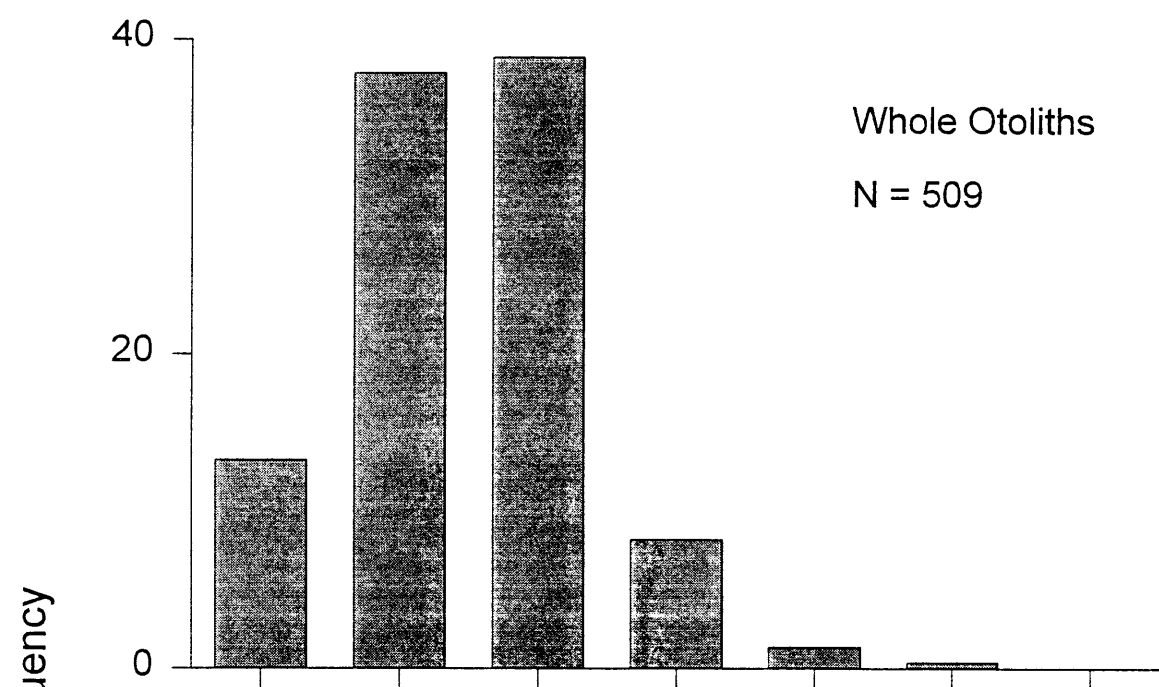
Presumed Age

Figure 8. Comparison of whole and sectioned otolith presumed ages (years) by FL for

210 male Spanish mackerel, *Scomberomorus maculatus*.
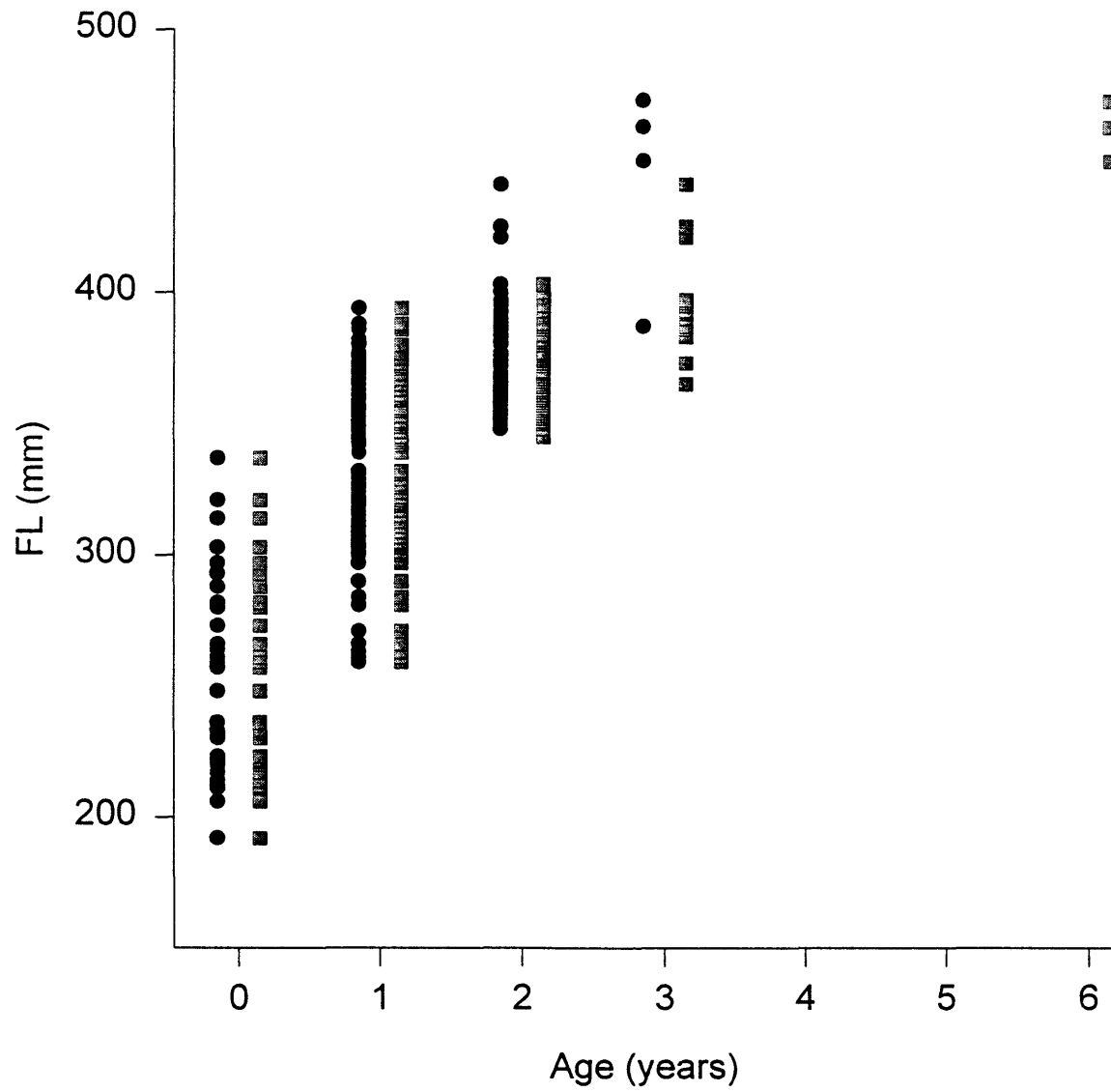
Figure 9. Comparison of whole and sectioned otolith presumed ages (years) by FL for

297 female Spanish mackerel, *Scomberomorus maculatus*.
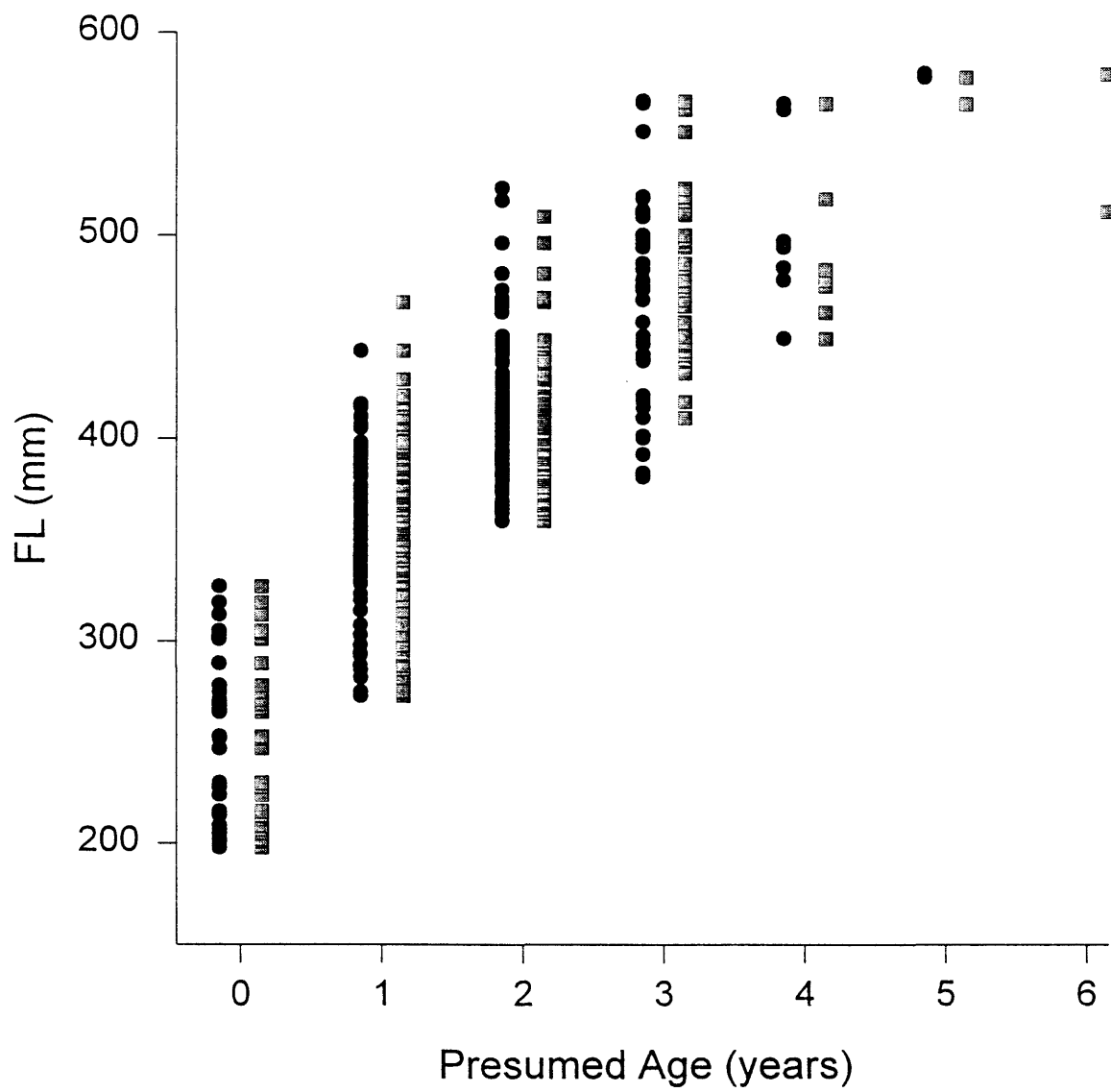
sex revealed significant bias between whole and sectioned presumed ages for males over one (χ^2=18.49, df=3, p<0.001), but no significant bias for females (χ^2=5.67, df=7, p<0.75).

Sectioned otoliths showed very high precision in repeated readings. Precision in a subsample of 133 sectioned otoliths was much higher than for the initial evaluation of calcified structures; agreement was 97%, and all disagreements were ±1 year. Error was distributed over all presumed age classes, with two disagreements between ages 1 and 2, one between ages 3 and 4, and one between ages 5 and 6.

Discussion

The initial evaluation of calcified structures indicates that pectoral fin ray sections and stained vertebrae should not be used for ageing Spanish mackerel. Counts of presumed annuli on these two structures were poorly related to fish size and presumed ages from other structures. Pectoral fin rays gave the highest presumed ages for some of the smallest fish, and presumed ages estimated from fin rays were completely uncorrelated with sectioned otolith ages. Vertebrae had a very narrow range of presumed ages compared to all other calcified structures: maximum presumed age was only three for vertebrae, compared with five for whole otoliths and spines, and six for sectioned otoliths. Although no previous studies examined the ageing potential of pectoral fin rays and vertebrae for Spanish mackerel or any other member of the genus *Scomberomorus*, both of these calcified structures have successfully aged other members of the family Scombridae. For example, albacore (*Thunnus alalunga*) fin ray ring counts increased with fish size as indicated by the von Bertalanffy growth function (Beamish, 1981). Vertebrae have been used to age other scombrids such as bluefin tuna, *Thunnus thynnus* (Prince et al., 1985; Lee et al., 1983) and little tunny, *Euthunnus alletteratus* (Johnson, 1983), primarily because they showed reasonably good agreement with ages estimated from other reliable calcified structures which were more difficult to obtain. Vertebrae are also used almost exclusively to estimate age in pelagic sharks (Cailliet et al., 1983; Schwartz, 1983; Pratt & Casey, 1983). However, vertebrae are not useful for ageing all

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pelagic fishes; Hill et al. (1989) found that counts of increments on vertebrae of Pacific

blue marlin (*Makaira nigricans*) were uncorrelated with counts from otoliths or fin

spines.

The initial evaluation of calcified structures demonstrated that dorsal spines have

potential for ageing Spanish mackerel, although growth of the vascular core may

obliterate early growth information for larger fish. This may explain why maximum ages

from dorsal spines were one year less than those from sectioned otoliths, even though

agreement between otolith and spine ages was better than for other structures examined,

and there was no systematic bias by age class in disagreement, indicating that errors were

random. There is resorption of early annuli in the spines of other scombrids, including

bluefin tuna, *Thunnus thynnus* (Compean-Jimenez & Bard, 1983); skipjack tuna,

Euthunnus pelamis (Antoine et al., 1983) and little tunny, *Euthunnus alletteretus* (Cayre

& Diouf, 1983; Johnson, 1983). In all of these cases, early growth of large fish was

estimated using the averaged early growth increments from the spines of smaller fishes of

the same species. Likewise, Hill et al. (1989) were able to statistically replace the

resorbed early annuli in dorsal and anal spines of Pacific blue marlin, *Makaira nigricans*,

with the cautionary statement that bias may have been introduced to the final age

estimates. Spanish mackerel dorsal spines may merit the extra effort necessary to

compensate for ring resorption, because sectioned dorsal fin spines had the highest

between reader agreement of any structure in the preliminary comparison, indicating that

they are relatively easy to interpret. The obvious advantage of dorsal fin spines over

otoliths is that fin spines may be removed without sacrificing the fish.

Sectioned otoliths gave the best information for ageing Spanish mackerel in the initial evaluation of calcified structures, although both whole and sectioned otoliths were initially difficult for readers to interpret consistently. Sectioned and whole otoliths had the best model fits of number of rings to structure radius, indicating the strongest relationship of number of marks to body size of all structures compared. This evidence, along with studies of marginal growth conducted by Powell et. al (1975) and Schmidt et al. (1993), indicates that marks on otoliths reflect fish age better than marks on the other structures. However, the precision of repeated readings on sectioned otoliths was not significantly greater than agreement for other structures, and was poorer for whole otoliths. Most disagreements were by $\pm$ 1 year, suggesting that either edge interpretation or first annulus identification was the problem, and not general illegibility. These problems were solved by training and increased experience reading Spanish mackerel sectioned otoliths, as evidenced by the great increase in precision between the initial evaluation of calcified structures (79% agreement for reader 1) and the detailed comparison of whole and sectioned otoliths (97% agreement). Previous studies reported high agreement between repeated readings on either whole or sectioned Spanish mackerel otoliths, but these studies were from different geographic areas. Fable et al. (1987) found 97.7% agreement between three readers of 520 whole otoliths collected in Florida. This suggests that Florida Spanish mackerel whole otoliths are considerably clearer than those of Chesapeake Bay Spanish mackerel, where agreement was only 45% between readers. Similarly, sectioned otolith clarity may vary geographically, because Schmidt et al. (1993) found 96.5% agreement between two readers for 1039 sectioned otoliths from fish

caught on the Atlantic coast south of Cape Hatteras, NC, whereas this study found 59% agreement between readers.

Agreement between sectioned and whole otolith presumed ages from Chesapeake Bay Spanish mackerel was much lower than reported in previous comparisons, perhaps due to geographic differences in growth and/or readability of otoliths. Fable et al. (1987) found 97.4% agreement between 70 whole and sectioned otolith age readings for Florida Spanish mackerel, but agreement between whole and sectioned otoliths was only 50% for 60 fish and 83.3% for 509 fish for Chesapeake Bay fish. Furthermore, there was a significant bias using the whole otolith method which underestimate age in larger, older Spanish mackerel. Clearly, whole otoliths cannot always be used to reliably age Spanish mackerel over their entire geographic range, or over the entire range of ages in a given population.

Since the primary objective of this study was to find the best method to age Spanish mackerel, whole otoliths must be still be considered because their processing time is minimal and they agree well with sectioned otoliths over part of the age range sampled. It has been shown that for some age and growth investigations such as determining age compositions, large samples evaluated with imprecise methods yielded better estimates than small samples evaluated with precise methods (Worthington, et al., 1995). In fact, there was no statistical difference between the 1993 age compositions of Spanish mackerel determined by whole or sectioned otoliths in this study. However, the results of both comparisons show that maximum age for Spanish mackerel was not correctly estimated by the less precise whole otolith method even with a relatively large

sample, so some amount of sectioning is necessary with this species even if whole otoliths are used to determine the majority of ages.

The most efficient method for ageing Spanish mackerel may be a combination of sectioning as many otoliths as time and resources allow and reading whole otoliths for the remainder of the sample comprised of small fish. The method currently in practice at the NMFS Southeast Fisheries Research Center in Panama City, Florida is to section otoliths for all Spanish mackerel over 500 mm FL (D. Devries, personal comm.). Although this practice may be effective for more southern populations of Spanish mackerel, the results of this study indicate that Chesapeake Bay Spanish mackerel are smaller than 500 mm FL when ages from whole and sectioned otoliths diverge, particularly for males. Differences in whole and sectioned age by length and sex are easily assessed by preliminary comparisons such as this study. If it were impossible to section all of the otoliths for an age and growth study in Chesapeake Bay, the results of this study indicate that it would be possible to section only the otoliths of male Spanish mackerel over 350 mm FL and of females over 475 mm FL, reading all other otoliths whole. To use a combination whole and sectioned otolith method for Spanish mackerel, I recommend calibration of the sex-length age deviation for different geographic areas, with recalibration over time using stratified sample as in initial evaluation of calcified structures.

Chapter 2

Validation of annual marks on sectioned otoliths of Spanish mackerel; a comparison of pooled and individual age-group analyses

Introduction

Beamish and McFarlane (1983) have recommended that ageing techniques be evaluated for precision and accuracy over the entire range of ages in each population examined. Their advice has generally been followed in that many age and growth studies now include some attempt at age validation, but a wide range of techniques are employed for validation. Although validation techniques from known age methods (Secor et al., 1995) and tetracycline marking (McFarlane & Beamish, 1992; Crabtree et al., 1996) to radiometric analysis (Fenton et al., 1991; Milton et al., 1994; Smith et al., 1995; Stewart et al., 1995), chemical analysis (Gauldie et al., 1995), and analysis of marginal growth (Barger, 1990; Morales-Nin & Ralston, 1990; Hyndes et al., 1992; Barbieri et al., 1993; Love et al., 1996) are all designed to prove that marks identified as annuli actually form on an annual basis, these techniques are not created equal. Known age methods and tetracycline marking provide convincing validation of ages, but only after large investments of time and holding space for live fish or effort in recapturing marked and released individuals; consequently they are most often employed in daily increment validation for larval and juvenile fish (Szedlmayer et al., 1991; Thomas et al., 1995). Radiometric and chemical methods often require pooling of otoliths and calibration with validated ages (Fenton & Short, 1992). Therefore, indirect validation by the analysis of marginal growth over time on otoliths (or any other structure employed for ageing) is often the only practical way to test the hypothesis that annuli actually form once per year.

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Age validation by the analysis of marginal growth on otoliths falls into two general categories: the simpler method involves classification of the otolith margin as translucent vs. opaque to describe the monthly percent of opaque otolith margins over an annual cycle for pooled age groups (Barger, 1990; Morales-Nin & Ralston, 1990; Love et al., 1996). The second method involves measurement of the distance from the distal edge of the last opaque mark to the margin of the otolith and analysis of changes in the monthly mean of this measurement (Hyndes et al., 1992; Barbieri et al., 1993; Crabtree et al., 1996); this second method is properly termed "marginal increment analysis." In both cases, validation is considered successful if a single mode and minimum are present in an annual plot of the data. Many workers pool all age groups in these analyses for simplicity or to increase monthly sample size, although the results may not adequately represent the pattern for each individual age group (Hyndes et al., 1992).

Age and growth of Spanish mackerel, *Scomberomorus maculatus*, has been studied extensively only throughout its southern range (Klima, 1959; Powell 1975; Fable et al. 1987; Schmidt et al.,1993). Previous attempts at validation of Spanish mackerel ages all used the method of otolith marginal growth analysis with pooled age groups. Klima (1959), Powell (1975), and Fable et al. (1987), examined whole otoliths of Florida fish, and Schmidt et al. (1993) examined sectioned otoliths of southeast Atlantic Spanish mackerel. Klima (1959), Fable et al. (1987) and Schmidt et al. (1993) used the simpler method of comparing monthly percentages of opaque otolith margins to indicate annulus formation once per year, while Powell (1975) used pooled mean monthly measurements of marginal increments to reach the same conclusion. Although all of these studies

reported validation of ages, their results differ in terms of timing of annulus formation and interpretation of the first annulus, especially for whole otoliths.

Because there may be geographic differences in the appearance and readability of Spanish mackerel otoliths (Chapter 1) and the explanation for apparent fluctuations in abundance of Spanish mackerel north of Cape Hatteras may be based on changing age structure (Chapter 3), it was especially important to validate sectioned otolith ages for all age groups of Spanish mackerel in the Chesapeake Bay region. The objective of this study was to determine the timing and periodicity of annulus formation for each age group of Spanish mackerel by analyzing the marginal growth on sectioned otoliths, which were previously determined to be the best structure for ageing Spanish mackerel ranging north of Cape Hatteras (Chapter 1). Analysis was conducted by three methods (two for age groups pooled and one by individual age group) for comparison with previous studies and to evaluate the effects of pooling age groups. For the sectioned otolith method to be considered accurate for ageing Chesapeake Bay Spanish mackerel, marks identified as annuli would form once per year and at generally the same time of year for each age group.

Methods

Spanish mackerel were collected every two weeks during their seasonal residence in the Chesapeake Bay region between May and October of 1993-1995 by purchasing 50 lb boxes of each available market size grade from commercial pound net, gill net, and haul seine fisheries, following Chittenden (1991). Because marginal increment analysis requires collection of fish in all months of the year, additional Spanish mackerel were purchased in April 1993 (n = 53) and November 1994 (n = 3) from North Carolina, and between December 1994 and March 1995 (n = 398) from Florida. All fish were collected north of Cape Canaveral, FL to ensure that only Spanish mackerel from the Atlantic coast population were included in the analysis. Fork length (mm), total weight (g), and sex were recorded for each fish. Both sagittal otoliths were removed from each fish and stored dry.

Preliminary analysis indicated that marginal increment measurements from a minimum of 25 fish per month would be adequate to establish timing and frequency of annulus formation. An ANOVA of mean marginal increments from otoliths sectioned for a comparison of calcified structures (Chapter 1) found significant (p=0.003) differences between June and July, 1994 with only 19 otoliths in each month. Differences between June and July marginal increments were also found for individual age groups one (n=8 & 11; p=0.049), two (n=3 & 4; p=0.089), and three(n=4 & 3; p=0.005) in the preliminary analysis. For marginal increment analysis, all monthly collections of Spanish mackerel

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were stratified by fork length and equal numbers of fish were drawn from each stratum to include the entire range of age groups for each month. To ensure adequate representation of older age groups and to focus on fish captured north of Cape Hatteras, the number of fish included in the analysis per month was increased to 50 during the months of Spanish mackerel residence in the Chesapeake Bay region (April - October).

Otoliths randomly selected for marginal increment analysis were cleaned, sectioned, mounted, and polished by methods outlined in Chapter 1. Otolith sections were examined in transmitted light under a compound microscope with a polarizing filter at 10 and 20 x magnification. Presumed annuli were counted on the ventral lobe nearest the sulcus acousticus. Marginal increments (ie., the distance from the distal edge of the last opaque band to the edge of the section, Figure 10) were measured on each otolith section using a calibrated video microscope. All otolith sections were examined in a randomized order without knowledge of fish size or collection date. Three independent readings comprised of otolith examinations, presumed annulus counts, and marginal increment measurements were made on each otolith section. Qualitative comments on otolith appearance were recorded during each reading to assess trends in readability by age, sex, FL, time of year or collection location. Young of year fish with no visible annuli were recorded as age zero and omitted from further analysis.

Monthly patterns in the marginal growth of Spanish mackerel otoliths were assessed by three methods for each of the three readings: first, by ages pooled analysis of trends in percent of otoliths with opaque margins; second, by ages pooled analysis of trends in mean marginal increments; and third, by analysis of trends in mean marginal

Figure 10. Ventral portion of an otolith section from a 6 year old 575 mm FL female

Spanish mackerel, *Scomberomorus maculatus*, collected 5 July 1994. Arrows indicate

marks counted as annuli. Line indicates marginal increment measurement.

Marginal increment

increments separately for each age group. To compare results with previous studies, the quantitative measurement of zero marginal increment was assumed to be the equivalent of the qualitative assessment of an opaque otolith margin. Therefore, the percent of otolith sections with marginal increment measurements of zero were plotted by month for all otoliths. One-way ANOVA (Zar, 1984; Minitab Inc., 1996) was used to evaluate differences between mean monthly marginal increments for all age groups pooled, and for each presumed age group. The annual growth pattern of the otolith margin was evaluated by plotting mean monthly marginal increments for ages pooled and by individual age groups.

Results

Three general types of Spanish mackerel otoliths were identified during the independent readings of sections: "normal," "double-ringed," and "abnormal." "Normal" otolith sections were characterized by wide translucent areas bordered by narrow opaque bands originating at the sulcus and running parallel to the edge of the section (Figure 10). These alternating bands were visible on both the ventral and dorsal halves of the section, and the otolith core was usually identifiable as an opaque area medial to the sulcus acousticus. In all three readings, over 90% of otolith sections were considered "normal". "Double-ringed" otolith sections were characterized by wide a translucent areas bordered by twin narrow opaque bands separated by a narrow translucent area, but in all other aspects resembled "normal" otolith sections (Figure 11). These twin opaque bands were counted as a single presumed annulus when they were identified as "double rings" by the reader. The percentage "double-ringed" otolith sections was approximately 3% (13 out of 422 otoliths). No clear trends of right vs. left otoliths or male vs. female fish were present in "double-ringed" otolith sections. "Abnormal" otolith sections were characterized by inconsistent or unclear patterns of translucent and opaque areas so that it was difficult or impossible for the reader to draw any consistent conclusion about age (Figure 12). In at least two out of the three readings, 5.5% (23 out of 422) of otoliths were considered "abnormal." Only three otoliths were considered "abnormal" in all three readings, and only one of these had no age assigned to it in any reading. "Abnormal"

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Figure 11. Ventral portion of a "double-ringed" otolith section from an 8 year old 650 mm FL female Spanish mackerel, *Scomberomorus maculatus*, collected 19 June 1995. Double arrows indicate pairs of marks counted as annuli.
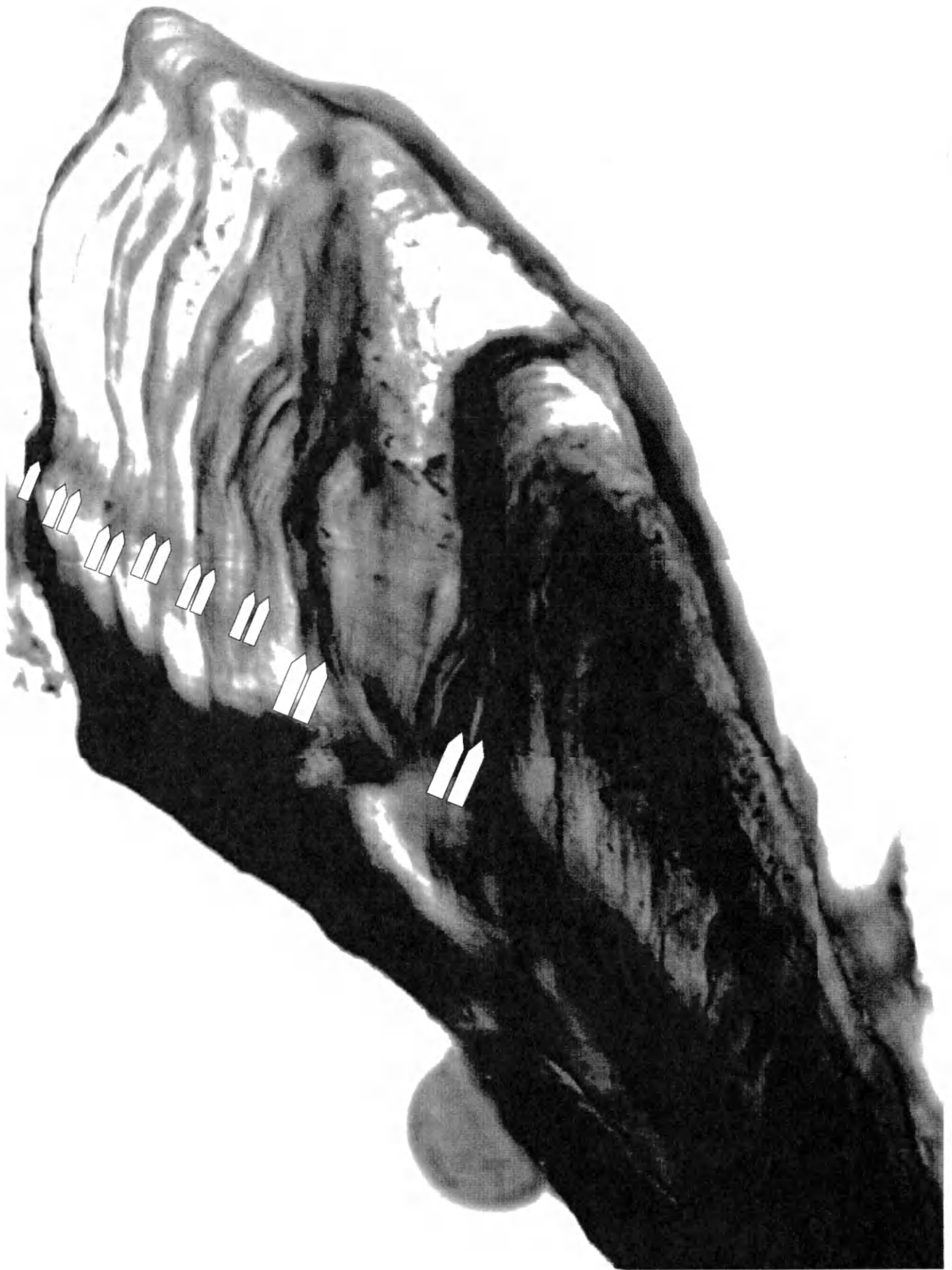
Figure 12. Ventral portion of an "abnormal" otolith section from a 508 mm FL female

Spanish mackerel, *Scomberomorus maculatus,* age undetermined, collected 2 February,

1995.

otolith sections showed no trends by sex, FL, right or left otolith, time of year, or

collection location.

Both types of ages pooled analysis indicated that annuli formed once per year,

with peak annulus formation in May, for all three readings. The monthly percent of

otoliths with zero marginal increment for each reading had a major peak in May, and

showed few otoliths with zero marginal increments appearing in September through

February (Figure 13). Pooled age ANOVA results for all three readings showed

significant differences between months (Table 9), and plots of mean marginal increments

for pooled ages also show minimal marginal increments in May, or May and June for

reading three, with marginal growth increasing after June to a maximum in September -

January (Figure 14). The apparent second minimum marginal increment in November in

all three readings was caused by a small (n = 3) number of older fish with reduced otolith

growth relative to the average young fish represented in all other months. Analysis

without the November data did not change the ANOVA results presented above.

Although the ages pooled analyses appeared to validate Spanish mackerel ages in

all three readings, individual age group analyses validated only age one fish in all three

readings. Patterns in the mean monthly marginal increments of one year old Spanish

mackerel matched those of the pooled analysis (Figures 15-16). In each reading, one year

olds had minimal marginal increments in May, with marginal growth increasing

throughout the summer and stabilizing at maximal growth in September through January

(ANOVA df = 141, 123, 133, $p < 0.001$; Tables 10-11).

Marginal increment analysis by individual age groups did not validate ages over

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Figure 13. Percent of Spanish mackerel, *Scomberomorus maculatus*, otoliths by month

with zero marginal increment (opaque margins) in readings one, two, and three.
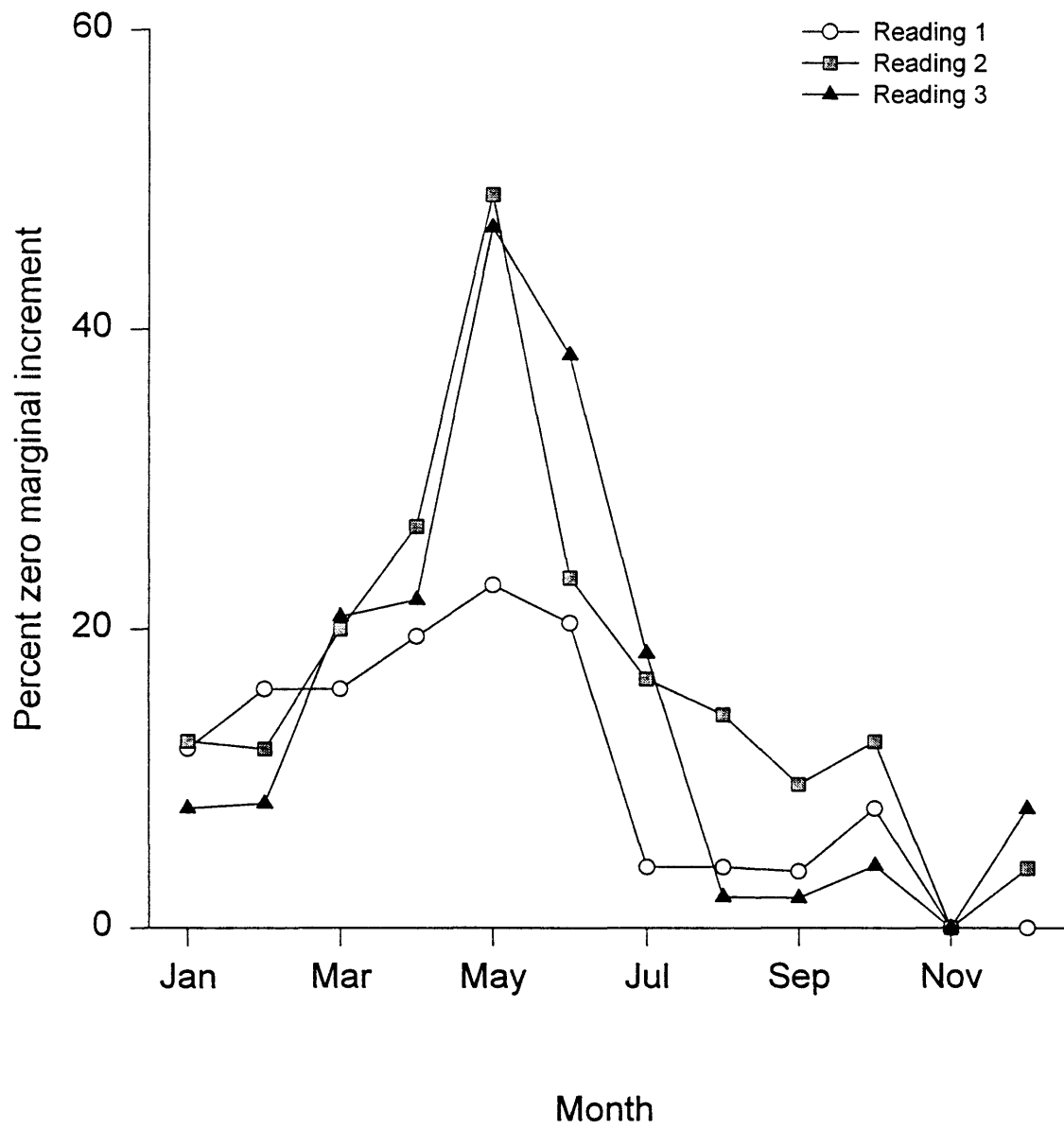
Table 9. Results of one way ANOVA testing for differences between mean monthly

marginal increments (mm) on sectioned otoliths for all ages pooled of Spanish mackerel,

Scomberomorus maculatus.

Reading One Ages Pooled

Source	df	SS	MS	F	p
Month	11	0.07765	0.00706	4.48	<0.001
Error	372	0.58607	0.00158		
Total	383	0.66372			

Reading Two Ages Pooled

Source	df	SS	MS	F	p
Month	11	0.11490	0.01045	7.23	<0.001
Error	365	0.52709	0.00144		
Total	376	0.64199			

Reading Three Ages Pooled

Source	df	SS	MS	F	p
Month	11	0.18733	0.01703	11.38	<0.001
Error	357	0.53444	0.00150		
Total	368	0.72177			

Figure 14. Mean marginal increments by month for all ages pooled of Spanish mackerel,

Scomberomorus maculatus, for readings one, two, and three. Error bars represent the

standard error of the mean, and numbers are sample size in each month.

Marginal Increment (mm)
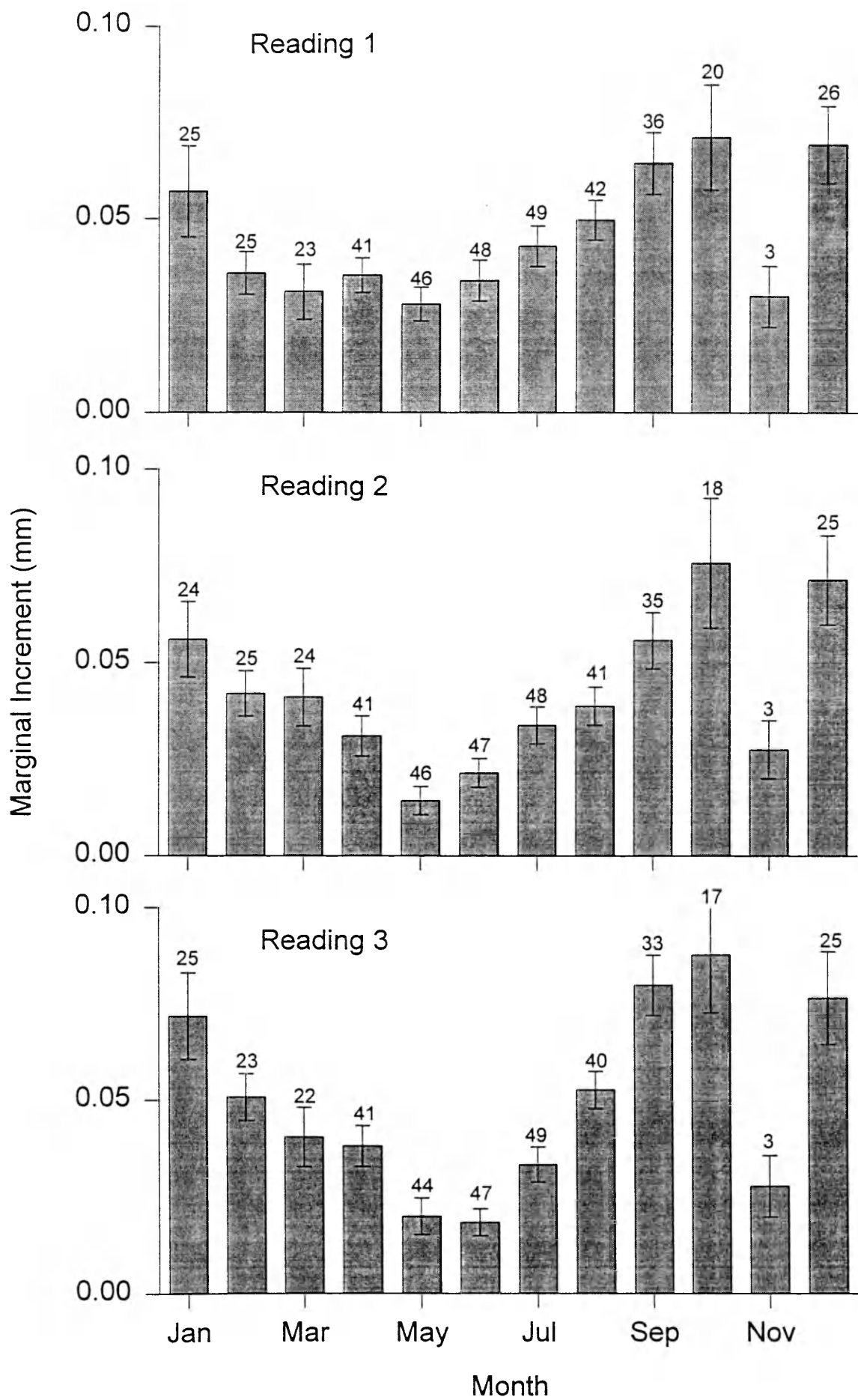
Figure 15. Mean marginal increments by month for ages one through six of Spanish

mackerel, *Scomberomorus maculatus*, for reading one. Error bars represent the standard
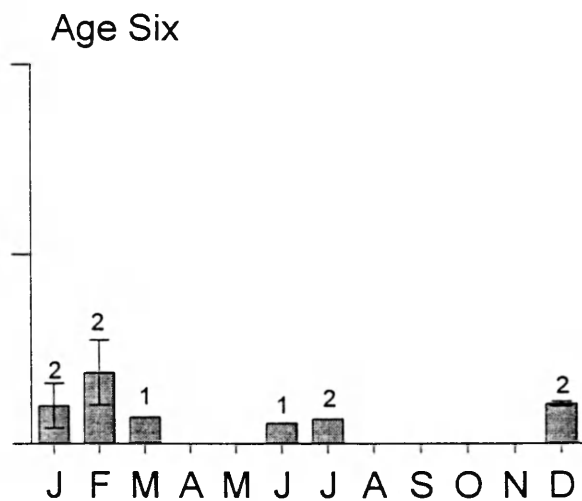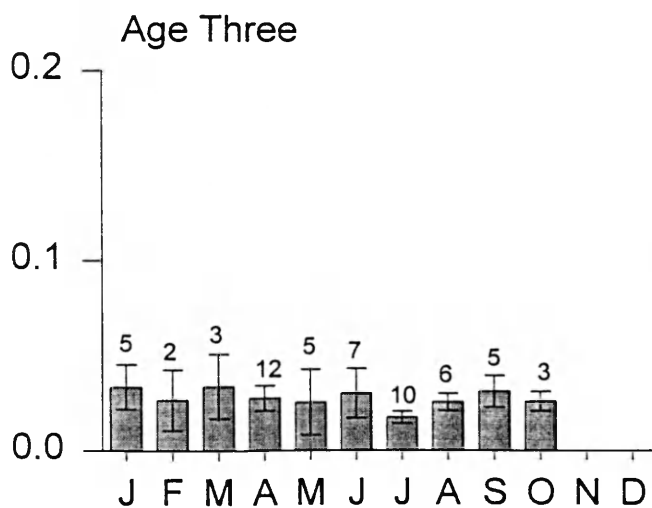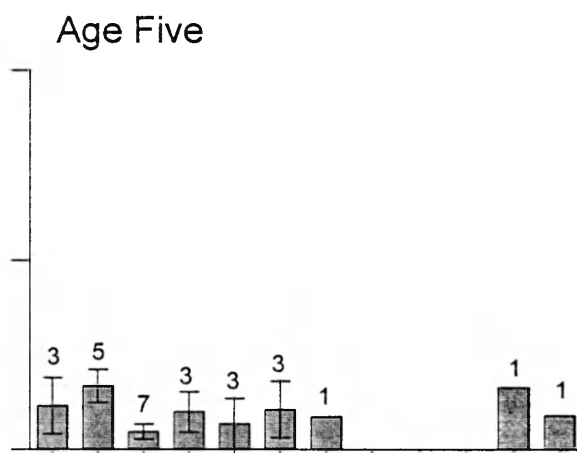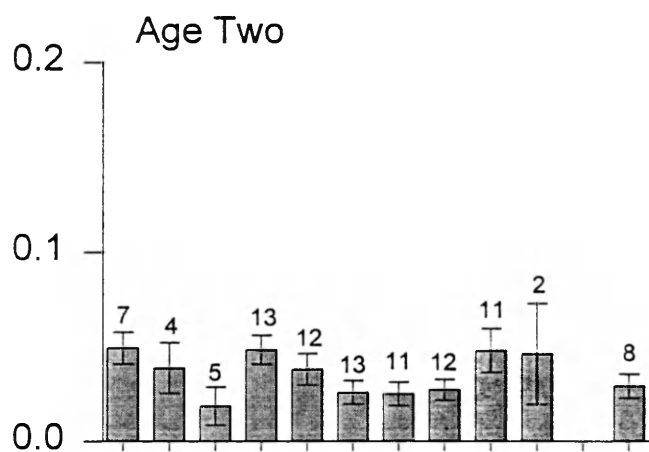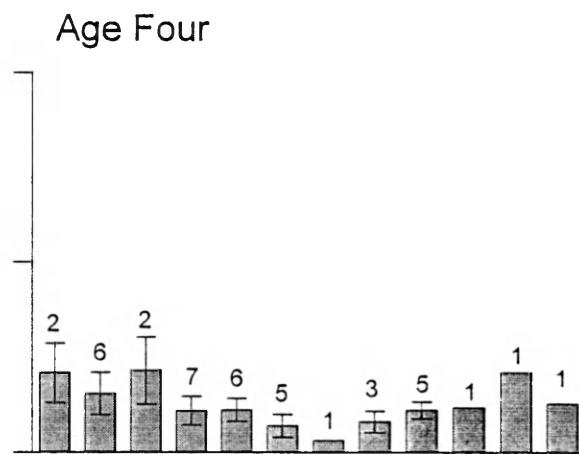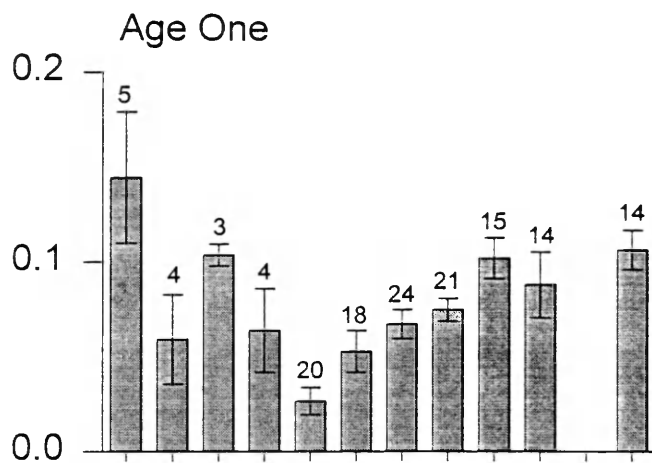
error of the mean , and numbers are sample size in each month.

Figure 16. Mean marginal increments by month for ages one through six of Spanish

mackerel, *Scomberomorus maculatus*, for reading three. Error bars represent the standard

error of the mean, and numbers are sample size in each month.

Table 10. Results of one way ANOVA testing for differences between mean monthly

marginal increments (mm) measured on sectioned otoliths during reading one for each

age class of Spanish mackerel, *Scomberomorus maculatus*.

Age One

Source	df	SS	MS	F	p
Month	10	0.11214	0.01121	6.14	<0.001
Error	131	0.23917	0.00183		
Total	141	0.35131			

Age Two

Source	df	SS	MS	F	p
Month	10	0.010564	0.001056	1.58	0.126
Error	87	0.058180	0.000669		
Total	97	0.068744			

Age Three

Source	df	SS	MS	F	p
Month	9	0.001445	0.000161	0.29	0.975
Error	48	0.026891	0.000560		
Total	57	0.028336			

Age Four

Source	df	SS	MS	F	p
Month	11	0.003015	0.000274	0.80	0.639
Error	28	0.009587	0.000342		
Total	39	0.012602			

Ages Five Through Eight Pooled

Source	df	SS	MS	F	p
Month	8	0.001858	0.000232	0.88	0.545
Error	37	0.009812	0.000265		
Total	45	0.011670			

Table 11. Results of one way ANOVA testing for differences between mean monthly

marginal increments (mm) measured on sectioned otoliths during reading three for each

age class of Spanish mackerel, *Scomberomorus maculatus*.

Age One

Source	df	SS	MS	F	p
Month	10	0.20985	0.02099	14.49	<0.001
Error	123	0.17811	0.00145		
Total	133	0.38796			

Age Two

Source	df	SS	MS	F	p
Month	10	0.031340	0.003134	4.41	<0.001
Error	88	0.062494	0.000710		
Total	98	0.093834			

Age Three

Source	df	SS	MS	F	p
Month	9	0.011733	0.001304	3.80	0.001
Error	45	0.015426	0.000343		
Total	54	0.027159			

Age Four

Source	df	SS	MS	F	p
Month	11	0.010648	0.000968	2.64	0.022
Error	25	0.009170	0.000367		
Total	36	0.019818			

Ages Five Through Eight Pooled

Source	df	SS	MS	F	p
Month	8	0.004800	0.000600	2.16	0.056
Error	35	0.009718	0.000278		
Total	43	0.014518			

one year old in the first reading, and only age groups one, three, and four years were validated in the second and third readings. No significant differences between mean monthly marginal increments were found for age groups two through four in the first reading (Table 10, Figure 15). Significant differences between mean monthly marginal increments were found for three and four year old fish in readings two and three (since the results from readings two and three agree, only the results of reading three are presented; Table 11). Minimum mean marginal increments occurred in May and June for three year olds, and in June for four year olds in reading three (Figure 16), suggesting that annuli formed once per year, but up to one month later for three and four year old Spanish mackerel relative to one year olds.

Two year old and five through eight year old Spanish mackerel age groups were not adequately validated by marginal increment analysis. Although a significant difference between months was detected for Spanish mackerel assigned age two in readings two and three (Table 11), minima occurred in the months of March and October, as well as June and July (Figure 16). For two year olds, March and October sample sizes are smaller (n < 5) than for other months. When data from these months were not included in the ANOVA, there were still significant differences between mean monthly marginal increments for two year olds, based upon differences between the June-July minimal growth and the early fall through winter maximal increments. Analysis by individual ages also revealed that five through eight year olds were not collected in enough months of the year for validation by marginal increment analysis.

Discussion

Marginal increment analysis of sectioned otoliths by individual age group adequately validated ages one, three and four for Spanish mackerel over their northern range in this study. Although the timing of annulus formation may be slightly later for older fish, readings two and three consistently indicated formation of a single annulus per year in May and June for these age groups. These results generally agree with previous studies, which established single annulus formation for pooled age classes anywhere between March and May (Fable et al., 1987), May and June (Klima, 1959), and May and July (Powell, 1975; Schmidt et al., 1993). However, unless the timing of annulus formation is identical for all age groups as has been shown for weakfish, *Cynoscion regalis* (Lowerre-Barbieri et al., 1993) and croaker, *Micropogonias undulatus* (Barbieri et al., 1993) the general agreement between studies in timing of annulus formation for ages pooled may not be applicable to all age groups, and may not constitute true validation.

The results clearly demonstrate that pooled age analyses of marginal growth were inadequate for validating Spanish mackerel ages in populations north of Cape Hatteras. Pooled analyses indicated validation for all three readings, although the results for individual age groups were inconsistent between readings, and clearly unvalidated in reading one. Both the percent of otoliths with zero marginal increments and the pooled ages mean monthly marginal increment plots were dominated by age group one, misrepresenting results for older age groups. Age one fish were numerically dominant and

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had the greatest annual change in mean marginal increments of any age group, due to higher growth rates. Hyndes et al. (1992) found a similar age group dominance using pooled age marginal increment analysis for whole otoliths of flathead, *Platycephalus speculator*.

The most serious drawback to the ages pooled marginal increment analyses was the misrepresentation of the age two pattern. There was no reading with in which the ages pooled mean marginal increment plots or monthly percentages of opaque margins correctly reflected the pattern of marginal increment growth for fish assigned age two, which were more numerous than all ages except one year olds. Small numbers of fish assigned age two in March and October may account for the minimal mean marginal increments in those months, but because some monthly sample sizes were even smaller for three and four year olds, this explanation is not satisfactory. The differences between timing of annulus formation for Atlantic (May-July; Powell, 1975 & Schmidt, 1993) and northern Gulf of Mexico (March-May; Fable et al., 1987) Spanish mackerel has been attributed to genetic distinction of stocks (Skow & Chittenden, 1981; Schmidt et al., 1993). If similar stock structure within the Atlantic existed, discrepancies between stocks might result in the apparent March and July peaks in annulus formation in two year olds.

Even when conducted for each age group, marginal increment analysis cannot distinguish true annuli from subannual checks unless it is used in conjunction with laboratory or tag-recapture studies of chemically marked fish. It is possible that fish were assigned age two when they were actually age one fish forming "double rings;" this may

have created the marginal increment minimum for two year olds in October. "Double rings" were easily identified in older fish where the pattern was well established. However, if a "double ring" forms in the first year of growth it is impossible to tell from a second true annulus unless the timing of annulus formation is already known.

Marginal increment analysis is inadequate for validating the ages of the oldest fish, which are by definition rare, but are disproportionally important in estimating growth and mortality. Validation was impossible for Spanish mackerel ages five and up due to insufficient samples in each month of the year. Although the ANOVA for combined ages five through eight showed significant differences between mean monthly marginal increments with a minimum in May and June, no fish over four were collected between August and October, so it was not possible to evaluate the pattern of marginal growth properly. Older age groups can only be truly validated by a different method, such as mark-recapture. Spanish mackerel fin spines may be considered for ageing live specimens (Chapter 1) in a study involving chemical marking.

Marginal increment analysis can be a useful tool for indicating potential sources of error in an ageing technique or analysis, but only if it is conducted for each age group separately. Ages pooled analyses of otoliths with opaque margins or marginal increments seem convenient and simple, allowing the more "important" analyses of age and growth to proceed with minimal interference. However, analysis by age group provides greater confidence in assigned ages and in subsequent age and growth studies (Barbieri et al., 1993; Lowerre-Barbieri et al., 1993; Crabtree et al., 1996). Even if satisfactory validation is not achieved for all age groups (as in the present study) the appropriate focus

of research can be determined to improve the situation; in this case, the investigation of "double ring" formation in young fish. The problematic mean monthly marginal increment pattern for fish assigned age two in this analysis refined techniques for subsequent analyses: the reader noted potential "double rings," which prevented inclusion in growth analyses (Chapter 3). Only fish collected in North of Cape Hatteras between May and September were included in further analysis, since only one "annulus" appeared to form during this period for each age group. An understanding of the limitations of marginal increment analysis and a given ageing technique may ultimately be more valuable than assuming validation using pooled age analyses of marginal growth.

Chapter 3

Age composition, growth, and mortality of Spanish mackerel

over the recent landings peak, 1988 - 1995

Introduction

Spanish mackerel abundance has fluctuated dramatically over the past century in the Mid Atlantic region, with Chesapeake Bay landings ranging from below ten thousand to over 1.5 million pounds (Earll, 1882; Lyles, 1969; Trent & Anthony, 1979; U.S. NMFS, 1950-1994). Peaks in Chesapeake landings occurred in the 1880-90's, the late 1930's, and again from 1987 to the present (Chittenden et al., 1993b). While the number of licenced pound nets in Chesapeake Bay steadily decreased since 1930 from over two thousand to less than 250, catches increased sharply in the period 1986-1990, so that the recent CPUE greatly exceeds that of the 1937 landings peak (Chittenden et. al., 1993b). This suggests that Spanish mackerel abundance in Chesapeake Bay may be much higher over the recent landings peak (1986-1995) than it has been since 1929. Due to this increased abundance, Spanish mackerel are now an economically important component of fisheries in the Chesapeake Bay (Chesapeake Executive Council, 1994).

The great fluctuations in abundance of Atlantic coast Spanish mackerel in the Mid Atlantic region are presently unexplained. Chittenden et al. (1993b) suggested that the recent period of high landings may reflect a combination of increased escapement from the Florida fishery due to recently implemented regulations, and the production of a strong year class in the mid-1980's. However, little information exists to evaluate any hypothesis explaining the fluctuations in abundance, because no data have ever been

collected on the age composition of Spanish mackerel in Chesapeake Bay, and there have

been no biological investigations of this species in its range north of Cape Hatteras, NC

since the work of Earll (1882) and Ryder (1882). Therefore, the objectives of this study

were twofold: first, to describe size, age and year class compositions, growth, and

mortality of Spanish mackerel in Chesapeake Bay, so that these life history parameters

were available for management; and second, to evaluate the hypothesis that the present

abundance peak could reflect a dominant year class. This was accomplished by

examining interannual variations in size and age compositions, growth, and mortality .

Methods

Collection of Fish and Otolith Preparation

A total of 4,194 Spanish mackerel were purchased from Chesapeake Bay

commercial fisheries between May and September of 1988 and 1993-1995. Over 98% of

these fish were captured in pound nets, with the remainder captured in gill nets and haul

seines. Total numbers of fish collected for individual years were 1163 in 1988, 1027 in

1993, 1430 in 1994, and 574 in 1995. Collection locations included Lynnhaven, the

lower York River, Mobjack Bay, Gwynn's Island, and the lower Eastern Shore (Figure

17). A 25 lb. or 50 lb. box of each available market size grade (i.e. small, medium, large,

or ungraded) was purchased every two weeks from each location where they were

available, although fish were generally sold by size grade only at the Lynnhaven location.

Although boxes could not be selected at random, size compositions in boxes from the

same market grade (including "ungraded") were assumed to be similar, because

Chittenden (1989) found that 98% of variation in fish length occurred within boxes, and

less than 2% of the variation occurred between boxes of weakfish (*Cynoscion regalis*)

and Atlantic croaker (*Micropogonias undulatus*) in the same market grade. All fish were

measured for fork length (FL, $\pm$ 1 mm), total weight, and gonad weight (TW and GW, $\pm$

0.1 g). A random subsample of fish were measured for girth (mm) anterior to the first

dorsal fin. Sex and gonad maturity stage were determined macroscopically. Both sagittal

otoliths were collected from each fish, and stored dry.

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Figure 17. Collection locations for Spanish mackerel, *Scomberomorus maculatus,* in

Chesapeake Bay.
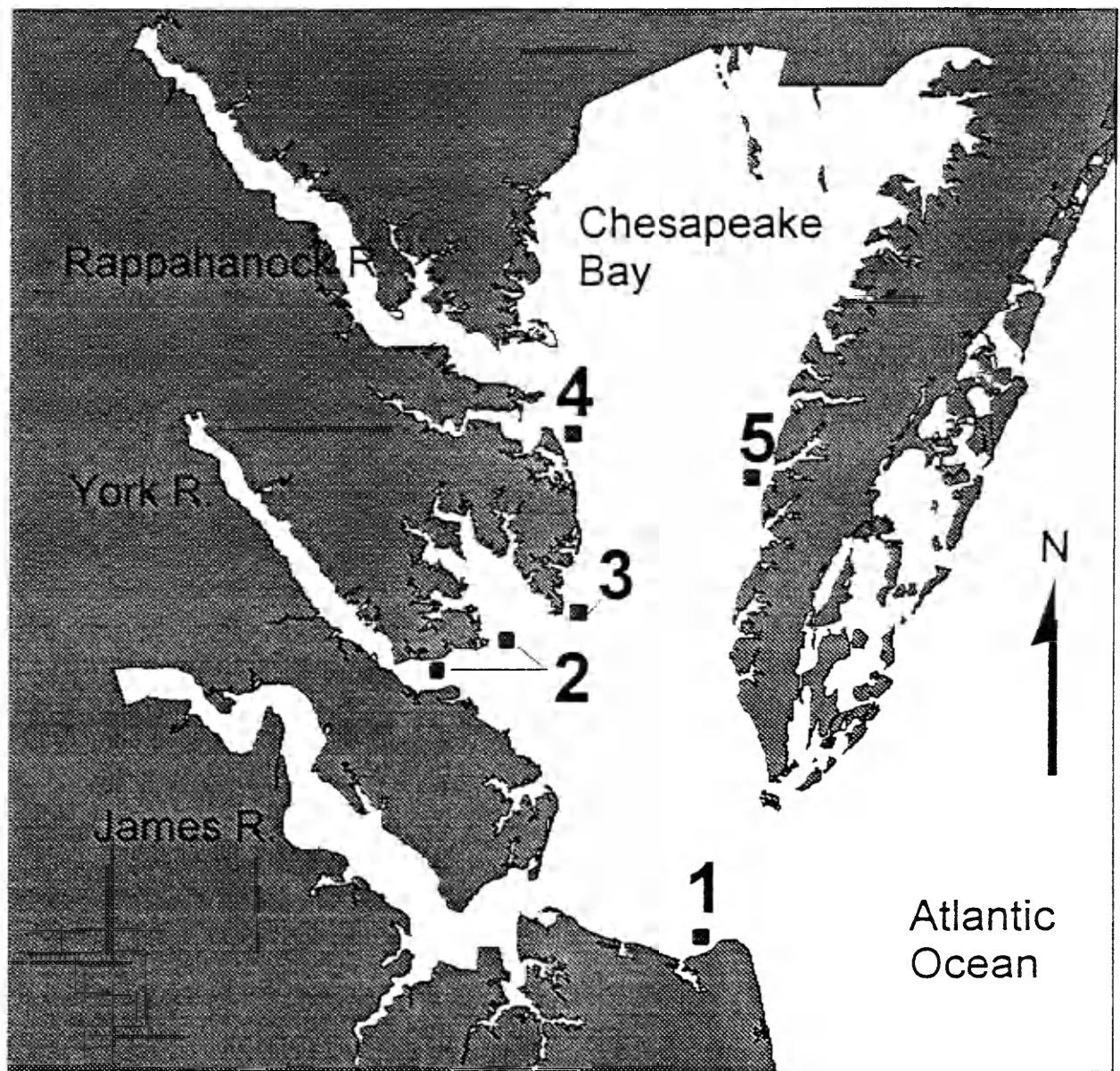
1: Lynnhaven
2: Lower York River
3: Mobjack Bay
4: Gwynn's Island
5: Lower Eastern Shore

The right or left otolith from each fish was selected at random, cleaned, and sectioned using methods outlined in Chapter 1. Otolith sections were examined in transmitted light under a compound microscope with a polarizing filter at 10 and 20X magnification. Annuli were counted on the ventral lobe nearest the sulcus acousticus. According to marginal increment analysis, May-June is generally the time of annulus formation for one through four year old Spanish mackerel in Chesapeake Bay (Chapter 2). Therefore, ages were assigned as follows so that all fish spawned in the same year had the same age: ages were annulus count + one for fish with wide translucent otolith margins in May or June, but were otherwise equal to annulus counts.

Size, Age, and Year Class Compositions

The size range of Spanish mackerel in Chesapeake Bay in 1988 and 1993-1995 was described using all 4,194 fish collected. Mean length was compared between collection years using one-way ANOVA (Zar, 1984). The overall range of ages in Chesapeake Bay was described using 1,369 aged fish collected in 1988 and 1993-1995. Mean size and age were compared by month over these years to evaluate seasonal patterns in size and age structure.

Length frequencies of Spanish mackerel collected in 1988 and 1993 were compared to evaluate changes over time. Differences in size compositions between years and sexes were assessed with a Kolmogorov-Smirnoff (KS) two-sample test (Sokal & Rohlf, 1981; Zar, 1984). Differences in mean FL for each year and between sexes were measured with a t-test (Zar, 1984).

To evaluate changes in age composition over the recent Chesapeake regional

landings peak, 550 fish were drawn from each of the 1988 and 1993 collections, which had roughly equal overall sample sizes and consistent collection protocols. Collections were stratified by market size grade (small, medium, large, or ungraded) and a random sample was selected from each grade. Numbers of fish selected were proportional to the total number collected in each grade, so that the subsample from each year reflected the composition of the collection from each year. Age compositions resulting from this raw data will be referred to as "collected age compositions" throughout this manuscript.

To adjust Spanish mackerel age compositions to reflect total fishery landings for each year, ratio estimates (Cochran, 1977) were used to extrapolate from the collected age compositions in each year. Because collections were made by market size grade and age compositions within grades differed by month, numbers at age within the landings were estimated for each market grade by month, then totaled across market grades and months to estimate numbers at age in total landings for each year:

$$N_i = \sum (\text{sum over } jk) \ N_{ijk} = (n_{ijk} / w_{jk}) * W_{jk} ,$$

where N_i = adjusted number of Spanish mackerel age i in total landings

N_{ijk} = adjusted number of fish age i landed in market grade j in month k,

n_{ij} = number of fish age i in subsample collected from market grade j in month k,

w_{jk} = weight of subsample (lbs) collected from market grade j in month k, and

W_{jk} = total weight landed (lbs) in market grade j in month k.

Spanish mackerel total monthly landings were provided by the Virginia Marine Resources Commission (VMRC). VMRC does not separate Spanish mackerel landings into market size grades. Landings by month (W_{jk}) for market grades "small," "medium,"

and "large" were provided by Lynnhaven Fish Company, the only wholesaler in the region who graded catches, and who landed over 50% by weight of Chesapeake Bay Spanish mackerel in 1988 and 1993 (VMRC, unpublished monthly landings). For the purposes of the ratio estimate, the monthly total weight landed (W_{jk}) for market grade "ungraded" was determined by subtracting the total weight of Lynnhaven's monthly landings from VMRC's total monthly landings. Ratio estimate adjustments were not attempted for grades and/or months where no collections were made; therefore, adjusted age compositions applied to over 80% of total landings for each year. Age compositions resulting from the ratio estimate adjustment will be referred to as "adjusted age compositions" throughout this manuscript. Differences in collected and adjusted age compositions between 1988 and 1993, and differences between collected and adjusted age compositions within years were evaluated with Kolmogorov-Smirnoff (KS) two-sample tests (Sokal & Rohlf, 1981; Zar, 1984).

To examine year class contributions to landings in 1988 and 1993, all age groups in the adjusted age compositions were converted to year classes (ie. the year in which a fish of a given age was spawned). Abundance of a particular year class which was an order of magnitude greater than all other year classes was the criterion for designation as a "strong" year class. Proportions of each year class in the landings for 1988 and 1993 were evaluated for the presence of a strong year class or classes.

Growth

To describe Spanish mackerel growth in the Chesapeake Bay region for management purposes, age and growth data from fish captured in 1988 and 1993-95

were used to calculate mean fork length at age, von Bertalanffy growth parameters, length-weight, and length-girth relationships. Analyses were conducted with sexes pooled as well as by sex, because Spanish mackerel are not externally sexually dimorphic and differential management by sex would be impossible. Mean fork lengths at age were compared using t-tests for each age group. Seasonal growth rates for individual age groups were estimated using linear regression of fish length on month within years. The growth parameters K, t_0 and L_∞ were calculated by fitting observed lengths at age to the von Bertalanffy growth function using the Marquardt algorithm in Fishparm (Saila et al., 1988) and the SAS PROC NLIN (SAS Institute, 1988). Only fish collected in the month of June each year were included in the von Bertalanffy analysis to eliminate seasonal variations in growth. June was chosen for this analysis because it is close to the time of annulus formation for all age groups (Chapter 2), and because the oldest fish were present then. Length-girth relationships were determined by linear regression, and length-weight relationships were calculated using linear regression with log-transformation and non-linear regression (SAS Institute, 1988). Linear regression equations for were compared using ANCOVA with type III sums of squares (Steel & Torrie, 1980; Freund et al., 1986).

Mortality

Total mortality rates (Z) of Spanish mackerel in the Chesapeake Bay were estimated for each year and overall from maximum age using both of Hoenig's (1983) equations:

$$\ln Z = 1.44 - (0.982) * \ln t_{max} \text{ (for all taxa)},$$

$$\ln Z = 1.46 - (1.01) * \ln t_{max} \text{ (for fish)},$$

and Royce's (1972) equation:

$$Z = 4.6 / t_{max},$$

where t_{max} = maximum observed age. These equations were used to provide a range of estimates. Maximum age was determined from sectioned otoliths of all fish over 500 mm FL, and a random sample of half the male fish over 400 mm FL collected in 1988 and 1993-95.

Results

Size, Age, and Year Class Compositions

Spanish mackerel size varied moderately by year. Overall, fish averaged 353 mm FL between 1988 and 1993-1995, and ranged from 192 mm FL to 658 mm FL (Table 12). Mean length was greatest in 1993 (378 mm), smallest in 1994 (337 mm), and intermediate in 1988 and 1995 (350-351 mm). The greatest range of fish lengths, including the largest and smallest Spanish mackerel, were collected in 1993. Lengths ranged from 221 mm to 585 mm in 1988, and from 204 mm to 608 mm and 650 mm in 1994 and 1995, respectively. Differences in mean length were significant between years (ANOVA, F = 104.94, df = 4193, p < 0.0001).

Older, larger Spanish mackerel were most common in Chesapeake Bay in May through July of 1988 and 1993-1995, while small young-of-the-year fish did not appear in the fishery until August and September. The oldest (ages 6 +) fish were only collected in May - July , and the largest and oldest fish (over 600 mm FL, age 8) were only collected in June (Table 13). Mean length was relatively stable in May - August, ranging from 365 mm FL - 380 mm FL, but was lowest in September (324 mm FL). Mean age was greatest in May and June (2.18 and 1.99 years, respectively), and lowest in September (0.61 years). Age 0 (young-of-year) fish do not appear in landings until August.

Spanish mackerel length frequencies were roughly similar in appearance in 1988 and 1993; both were basically unimodal, symmetrical, and normal (Figure 18). Length

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Table 12. Mean, standard error, and range of fork length (mm) of Spanish mackerel,

Scomberomorus maculatus, captured in Chesapeake Bay 1988 and 1993-1995.

Year	N	Mean	StdErr	Min	Max
1988	1163	349.58 1.590		221	585
1993	1027	378.27 2.023		192	658
1994	1430	337.15 1.522		204	608
1995	574	351.48 1.941		204	650
All Years	4194	352.63 0.915		192	658

Table 13. Mean, standard error, and range of length (mm) and age (years) by month of

Spanish mackerel, *Scomberomorus maculatus*, collected between 1988 and 1993 in

Chesapeake Bay.

Length

Month	N	Mean	StdErr	Min	Max
May	71	378.17	8.60	247	541
June	355	379.93	4.22	239	658
July	402	366.05	2.35	286	575
August	277	377.92	2.28	251	488
September	264	325.45	5.18	192	576
All months	1369	364.85	1.84	192	658

Age

Month	N	Mean	StdErr	Min	Max
May	71	2.18	0.15	1	6
June	355	1.98	0.06	1	8
July	402	1.36	0.04	1	6
August	277	1.34	0.04	0	4
September	264	0.61	0.06	0	4
All months	1369	1.42	0.03	0	8

Figure 18. Length frequencies (FL mm) of Spanish mackerel, *Scomberomorus*

maculatus, collected in Chesapeake Bay in 1988 and 1993.

1988
n = 1163

1993
n = 1074

Number of Fish

FL (mm)
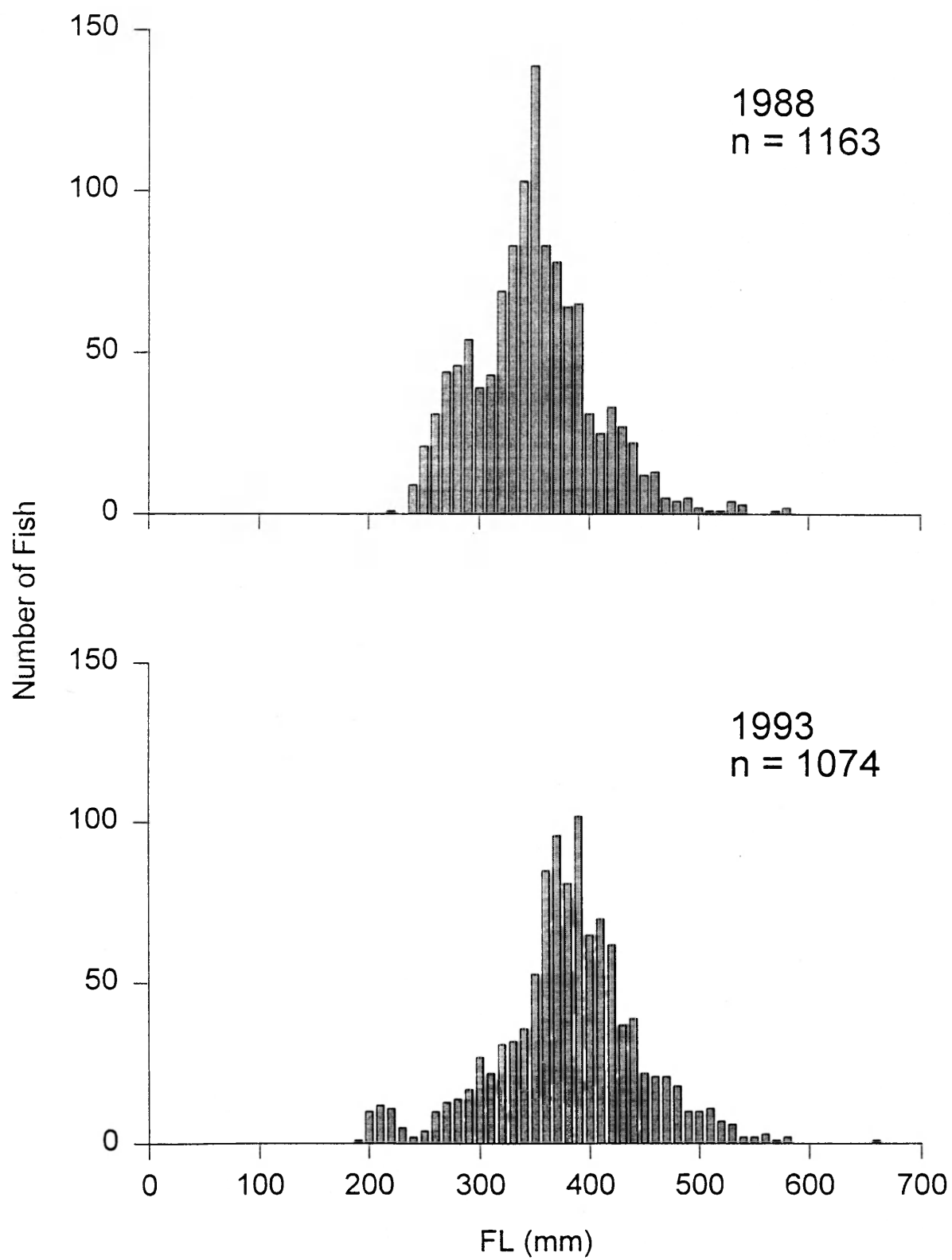
frequencies did not show the distinct multiple modes necessary to determine age by the Peterson method, except that a small mode of age 0 fish is visible in the 1993 length frequency. Mean and median lengths were nearly equal within each year, being respectively 350 mm and 348 mm in 1988, and 385 mm and 386 mm in 1993.

Despite their similar appearance, Spanish mackerel length frequency distributions were significantly different between 1988 and 1993 (KS, D = 0.307, p < 0.01). Fish collected in 1993 were larger than those in 1988. Mean length in 1993 (385 mm) was significantly larger (unpaired t = -13.92, df = 2161, p < 0.0001) than the 1988 mean, (350 mm). Furthermore, the largest fish were collected in 1993. Maximum size was 658 mm FL in 1993 as opposed to 585 mm FL in 1988, and more fish were larger than 500 mm FL in 1993 (22) than in 1988 (6).

Collected and adjusted age compositions of Spanish mackerel were generally similar within each year. Percentages estimated for each age group were within ± 6% between collected and adjusted estimates in 1988 (Table 14). For 1988, the collected age composition was not significantly different from adjusted age composition (KS, D = 0.0439, p > 0.10). Similarly, percentages of each age group were within ± 8% between collected and adjusted age compositions in 1993. Despite this general agreement, significant differences were found between collected and adjusted age compositions in 1993 (KS D = 0.0871, p < 0.01), with the largest difference for age group 0 (16.5% collected vs. 4% adjusted).

Both collected and adjusted age compositions of Spanish mackerel were very different between 1988 and 1993. Only ages 0 through 3 years were identified in 1988,

Table 14. Collected and Adjusted (see methods) age compositions of Spanish mackerel, *Scomberomorus maculatus* in 1988 and 1993.

| | Collected | | | | Adjusted | | | |
| | 1988 | | 1993 | | 1988 | | 1993 | |
Age	N	%	N	%	N	%	N	%
0	77	14.7	69	12.7	46331	16.5	8854	4.0
1	381	70.7	194	35.8	179711	64.2	91844	41.8
2	69	12.7	202	37.3	46718	16.7	96926	44.0
3	11	1.9	60	11.0	7187	2.6	19911	9.1
4	0	0.0	8	1.5	0	0.0	1405	0.6
5	0	0.0	2	0.4	0	0.0	203	0.1
6	0	0.0	7	1.3	0	0.0	800	0.4

whereas ages 0 through 6 were found in 1993 (Figure 19). Age one fish dominated

collected and adjusted 1988 age compositions (71% and 64%; Table 14), but age one and

two fish were codominant in 1993 (36% and 37%, respectively in collected, and 42% and

44% in adjusted age compositions). In 1988, 98% and 97% of the fish were age two or

younger in collected and adjusted age compositions, respectively. In 1993, however,

86% of fish in collected age compositions were age two or younger, and 89.8% were two

and under in adjusted age compositions. A Kolmogorov-Smirnoff two sample test found

significant (p<0.01) differences between the 1988 and 1993 age compositions, using both

collected and adjusted data.

Spanish mackerel landings in 1988 and 1993 were supported by different year

classes, and different numbers of year classes. 1988 landings were primarily supported

by the 1987 year class as one year old fish, which composed 64% of the catch based on

adjusted age compositions (Table 14, Figure 20). Most of the remaining 1988 catch was

supported by the 1988 and 1986 year classes, together totalling 33% of landings, with the

1985 year class comprising under 3% of landings. In 1993, landings were supported

jointly by the 1992 and 1991 year classes as one and two year old fish, which together

composed 86% of the 1993 catch. The 1990 and 1993 year classes together composed

13% of 1993 landings, with combined 1989, 1988, and 1987 year classes composing just

over 1% of 1993 landings.

The 1987 year class was stronger than all other year classes in the 1988 and 1993

landings. Numbers of fish estimated by adjusted age compositions and totaled across

years are greatest for the 1987 year class (180,511 fish, 36% of total, Table 15) followed

Figure 19. Collected and Adjusted (see methods) age compositions of Chesapeake Bay

Spanish mackerel, *Scomberomorus maculatus* in 1988 and 1993.
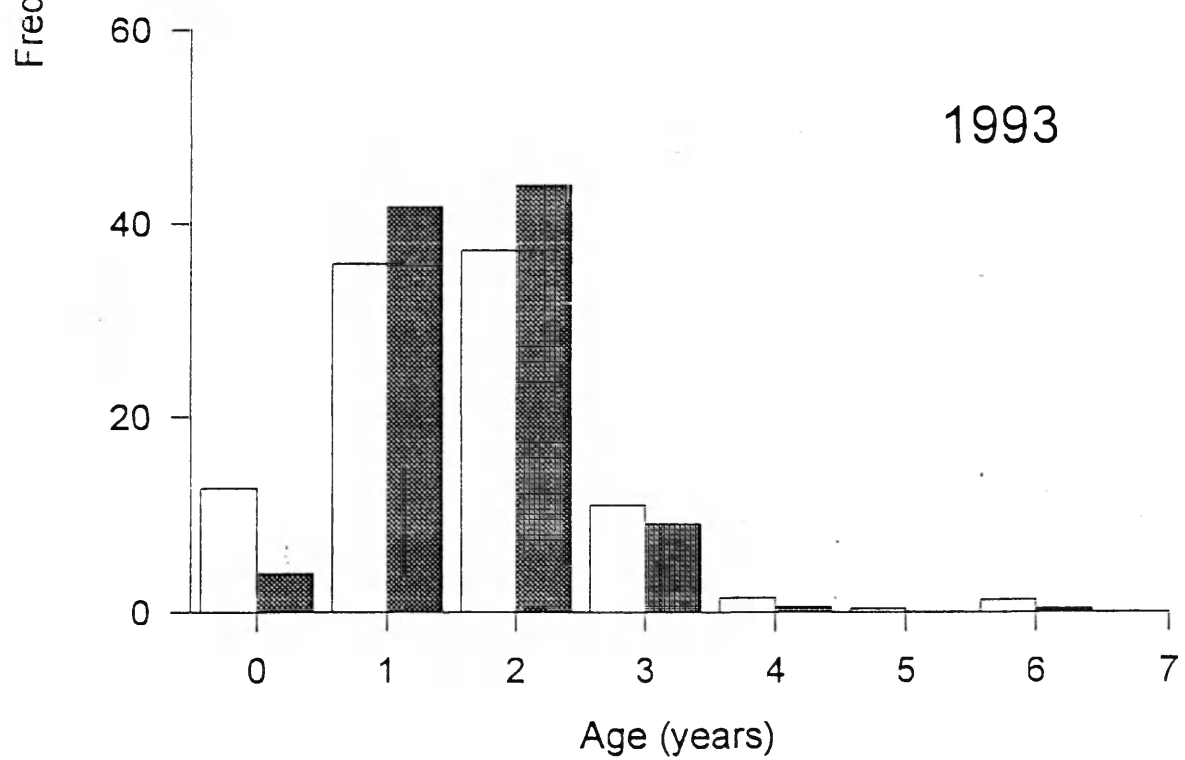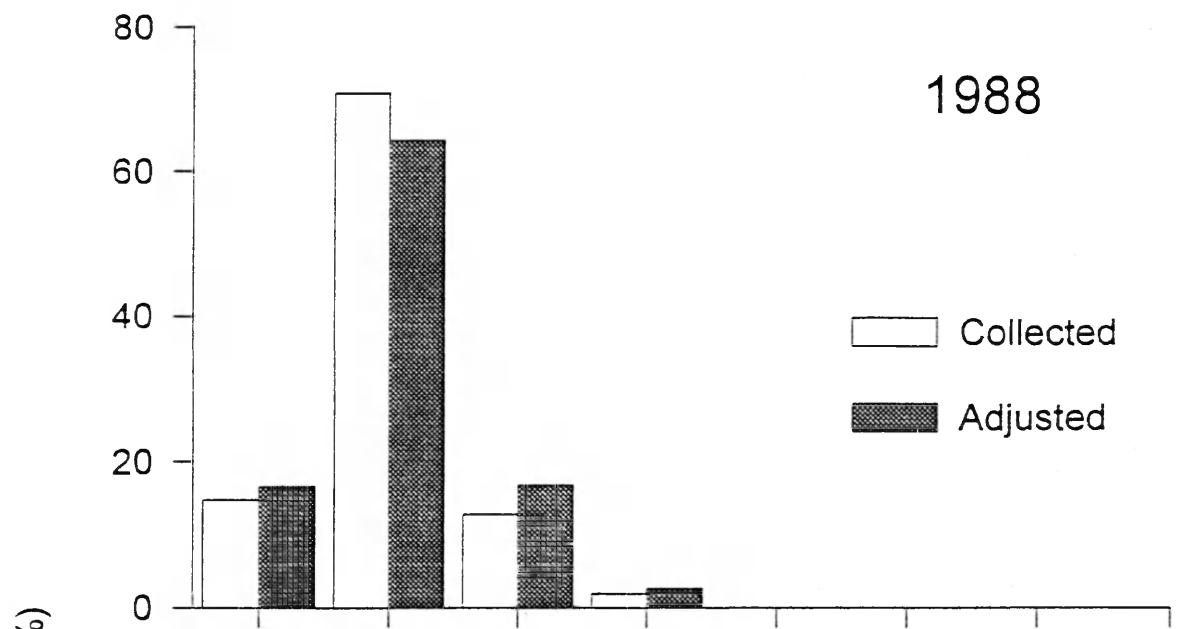
Figure 20. Year class composition of 1988 and 1993 landings of Spanish mackerel,

Scomberomorus maculatus, in Chesapeake Bay.
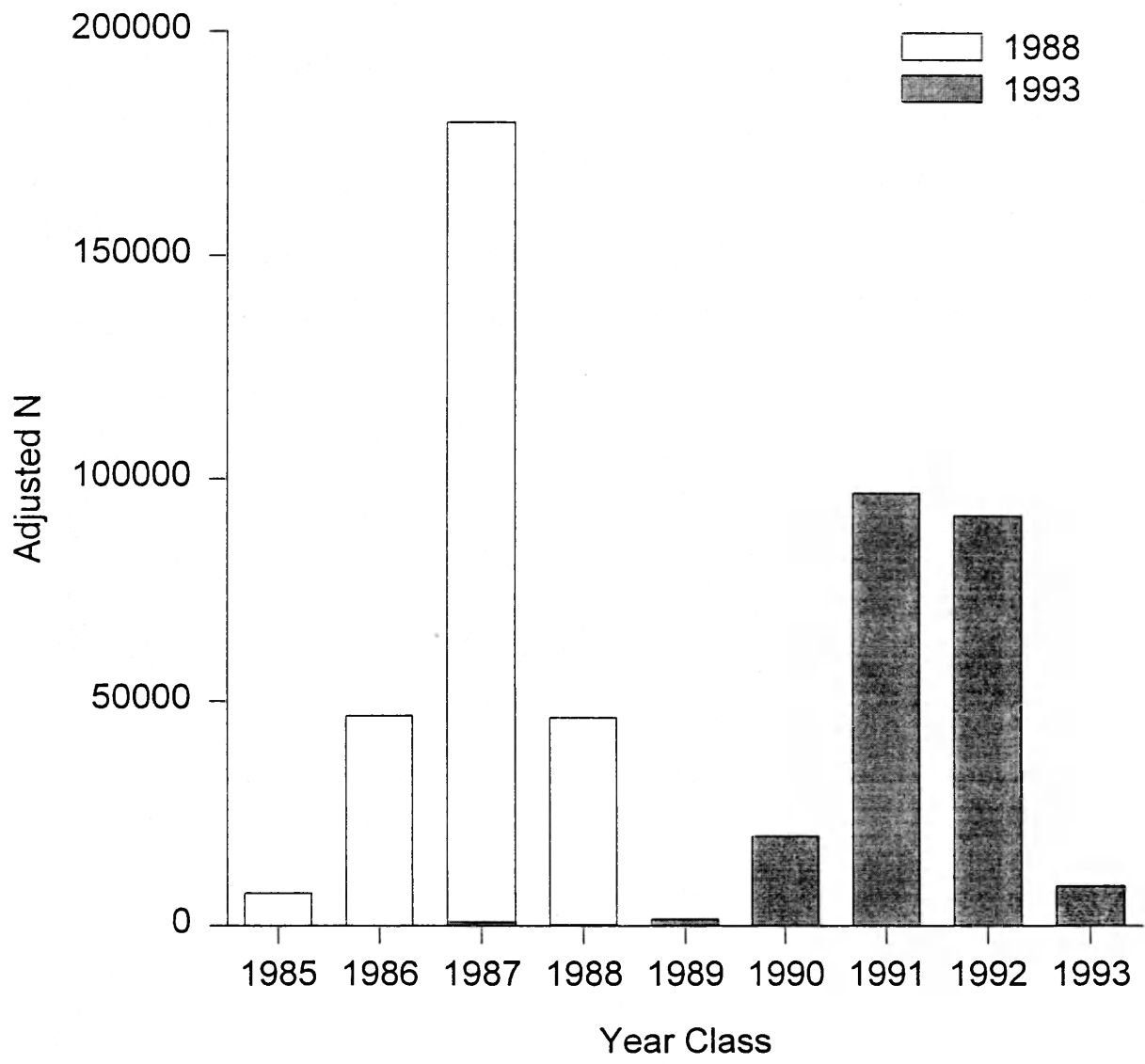
Table 15. Year class composition of combined 1988 and 1993 landings of Spanish

mackerel, *Scomberomorus maculatus* in Chesapeake Bay.

Year Class	Age(Year)	Adj. N	Age(Year)	Adj. N	Total	%
1985	3 (1988)	7187			7187	1.44
1986	2 (1988)	46718			46718	9.35
1987	1 (1988)	179711	6 (1993)	800	180511	36.11
1988	0 (1988)	46331	5 (1993)	203	46534	9.31
1989			4 (1993)	1405	1405	0.28
1990			3 (1993)	19911	19911	3.98
1991			2 (1993)	96926	96296	19.39
1992			1 (1993)	91844	91844	18.37
1993			0 (1993)	8854	8854	1.77

Total   499890

by the 1991 (96,926 fish, 19%) and 1992 (91,844 fish, 18%) year classes. All other

individual year classes contributed to less than 10% of Spanish mackerel combined

landings in 1988 and 1993.

Growth

Growth in Spanish mackerel was rapid and highly variable, with much overlap in

size at age. With data pooled over 1988 and 1993-1995, mean lengths at age were 347

mm for age 1, 404 mm for age 2, 456 mm for age 3, 476 mm for age 4, 515 mm for age 5

and 508 mm for age 6 (Table 16). Lengths ranged from 239-531 mm at age 1, 307-528

mm at age 2, 365-576 mm at age 3, 400-565 mm at age 4, 384-658 mm at age 5, and

418-658 mm at age 6 (Figure 21). Even young-of-the-year fish, though incompletely

recruited to the fishery, ranged in size from 192-365 mm FL. Length is a very poor

predictor of age in Spanish mackerel; given these ranges of size at age, a 420 mm

Spanish mackerel could be anywhere from 1 to 6 years old.

Part of the variation in length at age was due to growth within the year. Age one

Spanish mackerel grew rapidly within each year, with linear regressions indicating a

mean growth rate of over 30 mm per month for one year old Spanish mackerel within

their period of residence in Chesapeake Bay (FL = 120.6 + 31.26 Month, r^2 = 0.47 for

1988; and FL = 121.9 + 32.46 Month, r^2 = 0.59 for 1993). This growth rate did not

change between 1988 and 1993 (ANCOVA, p>0.10). Aside from a very weak

relationship for 1993 two year olds (FL = 342.8 + 7.27 Month, r^2 = 0.07), no significant

monthly growth rate was detectable by linear regression for any other age groups.

Another major component of the variation in length at age was sex. Within years,

Table 16. Mean and range of length at age for sexes pooled of Spanish mackerel,

Scomberomorus maculatus, collected in Chesapeake Bay 1988 and 1993-1995.

Age	Mean FL	n	Std Deviation	Minimum	Maximum
0	268.4	182	33.7	192.0	365.0
1	347.1	690	38.0	239.0	531.0
2	404.1	337	34.4	307.0	528.0
3	456.0	111	50.4	365.0	576.0
4	476.0	25	41.8	400.0	565.0
5	515.2	11	96.3	384.0	658.0
6	508.7	12	72.1	418.0	658.0
7	-----	---	----	-----	-----
8	650.0	1	----	650.0	650.0

Figure 21. Range and mean of lengths for each age of Spanish mackerel,

Scomberomorus maculatus, collected in Chesapeake Bay between 1988 and 1993-1995.

Bars represent ranges, and points means of fork lengths (mm). The age 0 bar is not

closed to represent incomplete recruitment to the fishery.
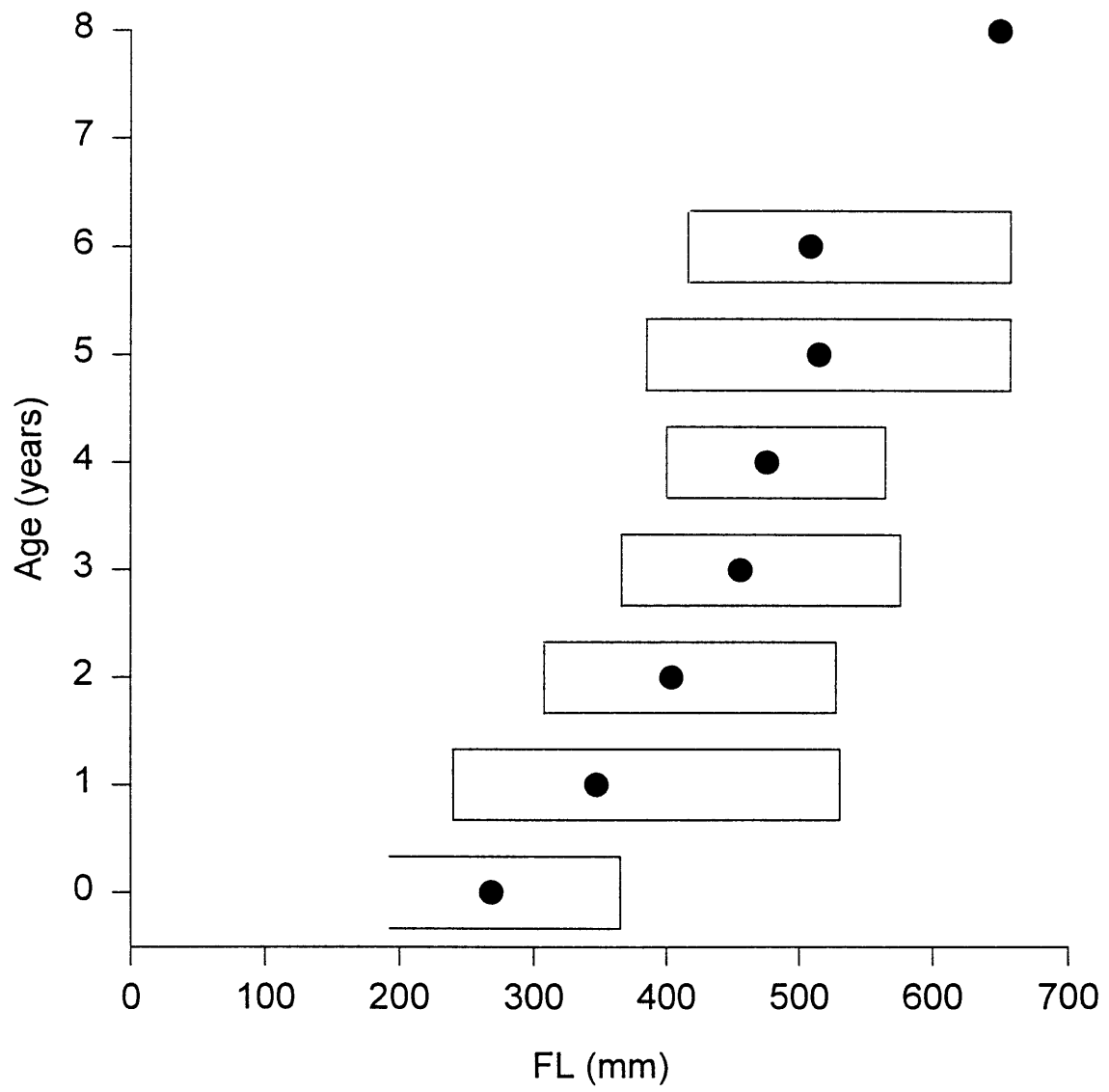
female Spanish mackerel were larger than males at all ages except for incompletely

recruited age 0 fish (Table 17). In 1988, mean fork length at age was significantly greater

for females than males for 1 through 3 year olds. Similarly, 1993 females were

significantly larger than males for ages 1 through 3 years. Mean lengths of females were

also greater than those for males at ages 4 and 6, although sample sizes were too small for

t-tests or differences were not significant.

Observed Spanish mackerel lengths at age from June showed an adequate fit to

the von Bertalanffy growth model, which improved somewhat when sexes were modeled

separately. The sexes pooled model predicted a mean asymptotic length (L_∞) of 610.9

mm with a growth rate (K) of 0.335 and t_0 of -1.1 (Figure 22, n = 335, r^2 = 0.76).

Separate von Bertalanffy growth models indicated that female Spanish mackerel grew to

much larger maximum lengths than males. Model parameters for females were L_∞ =

720.1 mm, K = 0.247 and t_0 = -1.36 (n = 209, r^2 = 0.83). Model parameters for male

Spanish mackerel were L_∞ = 483.2 mm, K = 0.421 and t_0 = -1.32 (n = 126, r^2 = 0.79).

Although length at age and growth rates were different for male and female

Spanish mackerel, there was no sexual dimorphism in length-weight or length-girth

relationships. Fork length-total weight and fork length-girth relationships for each year's

collections were not significantly different between sexes (ANCOVA, p>0.10; Table 18,

Figure 23).

Mortality

Maximum age, and therefore total mortality estimates, varied by year between

1988 and 1993-1995. Overall maximum observed age for all Chesapeake collections was

Table 17. Mean fork length (FL mm) at age of female and male Spanish mackerel,

Scomberomorus maculatus collected in 1988 and 1993.

1988

Age	Mean FL Females	n	Mean FL Males	n	t	p
0	276.6	36	279.6	27	0.70	0.4850
1	360.1	229	330.5	152	8.80	0.0001
2	436.7	34	403.6	35	7.27	0.0001
3	509.1	8	413.7	3	6.28	0.0003

1993

Age	Mean FL Females	n	Mean FL Males	n	t	p
0	252.7	32	250.1	36	0.26	0.7925
1	361.8	99	335.9	94	4.86	0.0001
2	404.6	132	368.5	70	12.80	0.0001
3	477.2	43	395.7	17	10.71	0.0001
4	490.0	2	459.0	1	-----	------
5	571.5	2	-----	--	-----	------
6	583.3	3	465.8	4	2.76	0.1063

Figure 22. Observed lengths at age and fitted von Bertalanffy regression lines for

Spanish mackerel, *Scomberomorus maculatus*, collected in Chesapeake Bay in June of

1988 and 1993-1995.
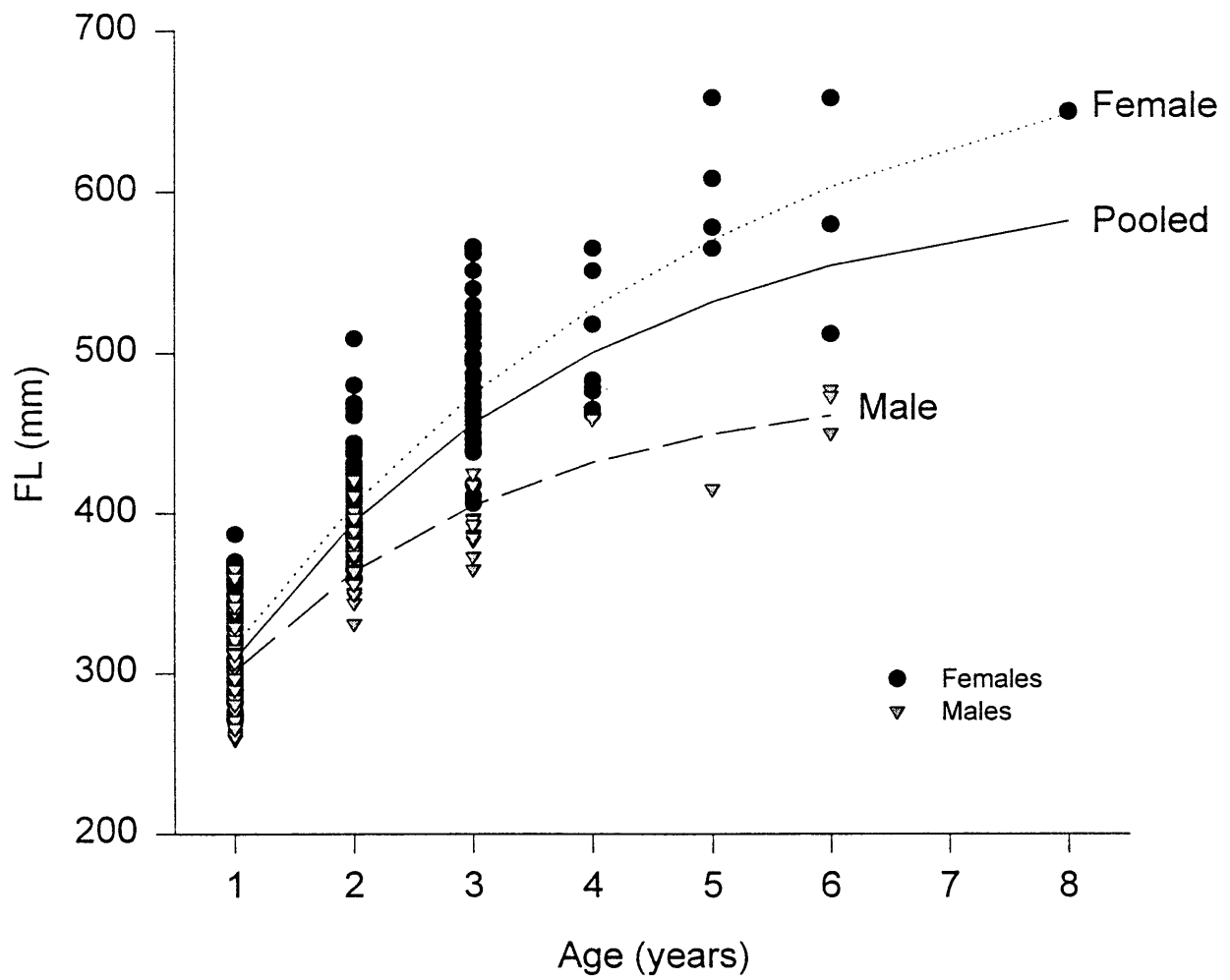
Table 18. Length weight and length girth relationships for Spanish mackerel, *Scomberomorus maculatus* collected in Chesapeake Bay, 1988 & 1993-1995. FL = fork length (mm), TW = total weight (g), GTH = girth (mm). Pooled relationships include unsexed, young-of-the-year fish.

Length-weight	Equation	n	r^2
Pooled	$TW = 7.06*10^{-6} \, FL^{3.04}$	1369	0.99
Females	$TW = 7.00*10^{-6} \, FL^{3.04}$	804	0.99
Males	$TW = 9.09*10^{-6} \, FL^{2.99}$	551	0.99

Length-girth	Equation	n	r^2
Pooled	$GTH = 33.0 + 0.366 \, FL$	648	0.77
Females	$GTH = 37.8 + 0.355 \, FL$	416	0.74
Males	$GTH = 29.3 + 0.372 \, FL$	237	0.74

Figure 23. Sexes pooled fork length-total weight relationships for 1988 and 1993-1995

collections of Spanish mackerel *Scomberomorus maculatus* in Chesapeake Bay.
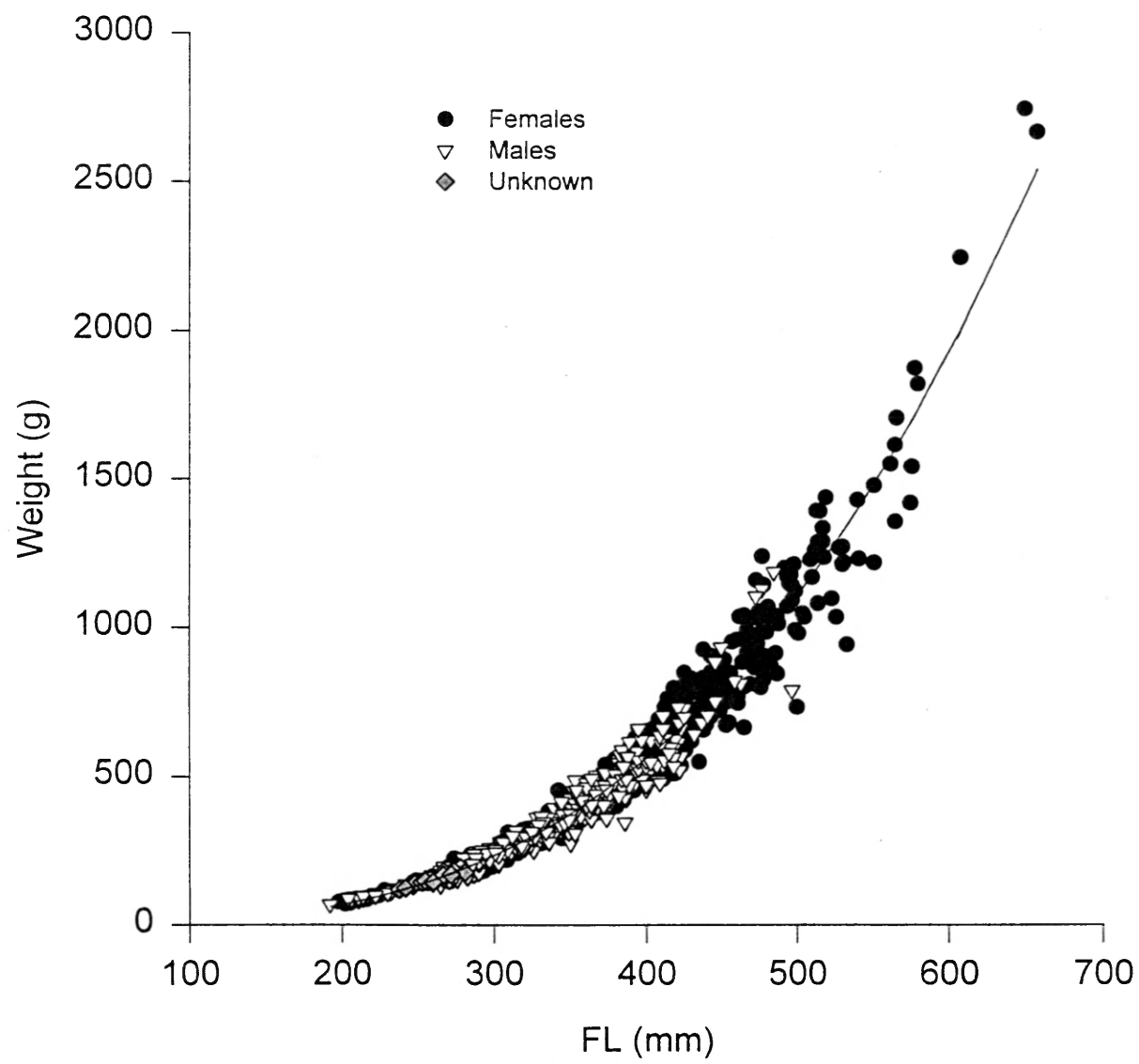
8 years (Figure 24), giving total mortality estimates between 0.53 and 0.58 (Table 19). In 1988, maximum age for both sexes was 3 years, giving total mortality estimates between 1.41 and 1.53. In 1993 and 1994, maximum age was 6 years for both sexes, giving total mortality estimates of 0.70 - 0.76. In 1995, maximum age was 5 years for male Spanish mackerel and 8 years for females, resulting in total mortality estimates of 0.84 - 0.92 for males and 0.53 - 0.58 for females.

Figure 24. Otolith section from an 8 year old 650 mm FL female Spanish mackerel,

Scomberomorus maculatus, collected 19 June 1995.

Table 19. Annual maximum age and total mortality (Z) estimates for Spanish mackerel,

Scomberomorus maculatus collected in Chesapeake Bay in 1988 & 1993-1995.

Estimates of Z follow: Hoenig's (1983) equations for (1) fish only, and (2) all taxa; and

(3) Royce's (1972). F=females, M=males.

Year	Max age (years)	n at Max Age		Z (1)	(2)	(3)
1988	3 (F&M)	5 (F)	2 (M)	1.41	1.43	1.53
1993	6 (F&M)	3 (F)	5 (M)	0.70	0.73	0.76
1994	6 (F&M)	1 (F)	1 (M)	0.70	0.73	0.76
1995	8 (F) 5 (M)	1 (F)	3 (M)	0.53 0.84	0.55 0.87	0.58 (F) 0.92 (M)
Overall	8 (F) 6 (M)	1 (F)	6 (M)	0.53 0.70	0.55 0.73	0.58 (F) 0.76 (M)

Discussion

Spanish mackerel age compositions have changed greatly over the recent period of high landings in Chesapeake Bay, 1986-1996. Age compositions expanded from fully recruited age groups 1 to 3 in 1988 to age groups 1 through 6 in 1993. Although previous studies did not examine interannual variations in age compositions, the compressed age structure found in Chesapeake Bay in 1988 is unusual. Klima (1959) found age groups 0 through 5 between 1956-1958 in southeast FL; Powell (1975) found fish up to 8 years old between 1968 and 1969 in Florida; and Fable et al. (1987) found ages 0 through 9 between 1977 and 1981 collecting from both coasts of Florida. These studies used whole otoliths, which underestimated ages of older Spanish mackerel compared with sectioned otoliths (Gaichas et al., in review), so it is possible that the age ranges for these studies are even greater than reported. Indeed, Schmidt et al (1993) used sectioned otoliths to age Spanish mackerel from the southern Atlantic coast and found ages ranging from 0 through 11. When age compositions were combined over years in the present study, results were similar to previous studies; ages for Spanish mackerel collected in Chesapeake Bay between 1988 and 1995 ranged from 0 to 8 years.

Spanish mackerel exhibited rapid and highly variable growth in Chesapeake Bay between 1988 and 1995. The expansion of age structure between 1988 and 1993 was not obvious in length frequency distributions, due to the wide ranges of size at age. Powell (1975), Fable et al. (1987), and Schmidt et al. (1993) also reported wide ranges of

100

Spanish mackerel size at age, and estimated L_∞ ranging from 645 to 741 for females and

from 515 to 776 for males, and K ranging from 0.24 to 0.45 for females and from 0.27 to

0.48 for males. Von Bertalanffy parameter estimates for female fish collected in

Chesapeake Bay are similar to estimates from previous studies: L_∞ =720.1 and k=0.25.

Mean asymptotic length predicted by the model for male Spanish mackerel, L_∞ =483.2,

was somewhat smaller than previously reported. Mean observed fork lengths at age in

Chesapeake Bay by sex and for sexes combined were also smaller than mean observed

lengths at age reported in Powell (1975), Fable et al. (1987), and Schmidt et al. (1993) for

all ages. Mean length at age was not compared with the results of Klima 1959, due to

general disagreement in the literature over Klima's identification of the first annulus

(Powell, 1975; Fable et al. 1987). Differences were greatest between this study's length

at age results and those of Powell (1975) and Fable et al. (1987), probably due to a

combination of stock differences between the Atlantic and Gulf of Mexico populations of

Spanish mackerel (Skow & Chittenden, 1981; Collette & Russo, 1984) and the use of

whole vs. sectioned otoliths to estimate age. Although ageing techniques and stock

sampled were more comparable between this study and Schmidt et al. (1993), mean fork

length at age was still smaller for Chesapeake Bay Spanish mackerel at all ages.

Differences in collection methods could account for a difference in mean length at age:

over 98% of fish collected from Chesapeake Bay were captured in pound nets, a gear that

is generally not size selective. However, fish collected for Schmidt et al.'s 1993 study

were captured by "hook and line, trawls, gill nets, and block (stop) nets," all of which are

size selective.

Spanish mackerel in Chesapeake Bay appeared to have decreasing annual total mortality over the period 1988-1995 based upon estimates of Z from maximum age. Although no other estimates of mortality for Spanish mackerel are reported in the literature, Z can be calculated from maximum ages in other studies to compare with Chesapeake Bay estimates. Using Hoenig's (1983) equation for all taxa, the estimate of overall Z based upon Klima's (1959) maximum age of 5 is 0.87, based upon Powell's (1975) maximum age of 8 is 0.55, based upon Fable et al.,'s (1987) maximum age of 9 is 0.48, and based upon Schmidt et al.'s (1993) maximum age of 11 is 0.40. As with all other age and growth parameters, the mortality estimate for 1988 (1.43) is unusually high in comparison with previous studies, but the estimates for 1993 (Z=0.73) and for the overall period 1988-1995 (Z=0.55) fall within the range of results from previous studies.

There was evidence of a strong (1987) year class moving through the annual Chesapeake Bay landings. However, the 1987 year class alone did not support landings throughout the period of 1988-1993. As expected, younger age groups dominated the landings in each year: fish aged 2 and under composed 97.4% and 89.8% of 1988 and 1993 landings, respectively. Because Spanish mackerel are sexually mature by age one (Powell, 1975; Schmidt et al., 1993) or by a fork length which corresponds to mean length at age one estimated in this study (Finucane and Collins, 1986; Cooksey, 1996), it is possible that the large 1987 year class reproduced very successfully as age one fish in 1988. There is evidence that Spanish mackerel reproduce in the Chesapeake Bay region: both female and male Spanish mackerel were collected from Chesapeake Bay with ovaries and testes in the running ripe stage of development (Cooksey, 1996), and very

small (28-184 mm FL, n=31) juvenile Spanish mackerel were collected in Virginia waters by the VIMS seine and trawl surveys between 1993 and 1995.

Fisheries theory states that the expansion of age compositions over time is characteristic of "colonization" and population growth, usually in the absence of heavy fishing pressure. By contrast, as a "new" fishery on a stock progresses, theory states that age compositions should compress over time (Weatherly, 1972). The situation for Spanish mackerel in Chesapeake Bay is consistent with neither theory: age compositions appear to have expanded over time although fishing has continued throughout the period of high landings, 1986-1995. One explanation for this pattern is that a strong year class or classes, including the 1987 year class, may have experienced high reproductive success, contributing to a self sustaining Chesapeake Bay fishery in which F is apparently low enough to allow moderate population expansion.

The question remains as to why Spanish mackerel reappeared in Chesapeake Bay in 1986. There are several explanations for these apparent population dynamics. First, the entire Atlantic stock may have experienced strong year classes in the mid-late 1980's, resulting in a density-dependent range expansion. Second, environmental parameters in Chesapeake Bay may have changed between the early part of the 20th century and the mid-late 1980's, resulting in a shift from very unfavorable to very favorable environmental parameters for Spanish mackerel. Environmental factors affecting Spanish mackerel populations may include temperature, turbidity, or other water quality parameters as well as the population dynamics of other fish species including prey and competitors. Third, gear restrictions and other fishery regulations which were instituted

in the Florida Spanish mackerel fishery in 1985 (Chittenden et al., 1993b) may have

increased escapement from that region to the Chesapeake Bay region. Most probably a

combination of these factors contributed to the 1986-1995 period of high landings in the

Chesapeake region. Further study is required to compare fluctuations in landings and age

compositions coastwide to determine if this phenomenon is unique to Chesapeake Bay, or

if it represents a coastwide fluctuation in age and growth parameters.

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