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Age, Growth, and Mortality of Atlantic Croaker, Micropogonias undulatus, in the Chesapeake Bay Region

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Age, Growth, and Mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region

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

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

By

John R. Foster

2001

This thesis is submitted in partial fulfillment of the requirements for the degree of

Master of Science

John R. Foster

Approved, June 2001

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Peter A. van Veld, Ph.D.

TABLE OF CONTENTS

Page

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LIST OF TABLES

LIST OF FIGURES

Figure Page

ABSTRACT

Sectioned otolith age determination methodology was validated by individual age groups using mean monthly marginal increment analysis incorporating one-way ANOVA significance testing. One annulus was formed each year for ages 1-9 with the narrow opaque band forming from April to June. Precision in age determination from sectioned otoliths was very high, 100% within reader agreement and 97% between reader agreement.

Atlantic croaker were collected from commercial catches in the Chesapeake Bay region (N = 4862) from March, 1998 through March, 2000 to determine the impacts of relatively abundant unusually large fish on age, growth, and mortality information. Observed age compositions varied with biological year and by commercial grade. Ages 1-11 were recorded with ages 10 and 11 being rare. For unusually large fish (400+ mm TL), ages 4-11 were recorded, with ages 6-9 being abundant. Adjusted Age compositions varied with biological year but were similar to Observed Age compositions from Selected months in most years. Fluctuations occurred in year-class strength with year-classes prior to 1990 being much less important in Adjusted and Observed Age compositions from Selected months than the 1990 and subsequent year-classes.

There were differences in observed size compositions between sexes. While minimum sizes were similar, females were significantly larger on average than males, their pooled mean total lengths (TL) being 343 mm and 304 mm, respectively. Observed size-at-age varied by sex. Mean female size-at-age was significantly larger than males for ages 1-9. The von Bertalanffy growth model described growth of Atlantic croaker well though there were significant differences in growth between sexes. For females, L_∞ ranged from 399 mm to 535 mm, k ranged from 0.11 to 0.38, and t_o ranged from –4.44 to –0.95. For males, L_∞ ranged from 391 mm to 541 mm, k ranged from 0.08 to 0.18, and t_o ranged from –6.7 to –4.02. For sexes pooled, L_∞ ranged from 403 mm to 541 mm, k ranged from 0.10 to 0.34, and t_o ranged from –5.01 to –1.19.

Estimates of total annual instantaneous rates, Z, based on maximum age methods ranged from 0.4 to 0.51, the lowest reported from the Chesapeake Bay region. Catch-curve regression estimates of Z ranged from 0.45 to 0.85, though estimates agreed well at 0.45 – 0.46 when an influential observation was deleted from calculations. Estimates of natural instantaneous mortality rates, M, varied by method ranging from 0.15 to 0.39.

Age, growth, and mortality
of Atlantic croaker, *Micropogonias undulatus*,
in the Chesapeake Bay region

GENERAL INTRODUCTION

Range

Atlantic croaker, *Micropogonias undulatus*, inhabit coastal waters in the North Atlantic Ocean from the Bay of Campeche, Mexico to Cape Cod, Massachusetts (Welsh and Breder, 1923; Chao, 1978). This demersal species is highly abundant in coastal and estuarine waters over much of its range from Middle Atlantic to Gulf of Mexico coasts (Joseph, 1972).

Life history

Atlantic croaker undertake seasonal migrations. In the Chesapeake Bay region, they migrate into the Bay in the spring, from March to April, and leave in the fall, from about September to November, to overwinter along the continental shelf off the coasts of Virginia and North Carolina (Wallace, 1940; Haven, 1959).

Spawning begins as adults emigrate from the Chesapeake Bay and may continue over a large area from waters near to and possibly including the mouth of the Chesapeake Bay (Welsh and Breder, 1923) to shelf waters (Colton et al., 1979; Morse, 1980; Norcross and Austin, 1988). Recent work also suggests that some spawning may occur in the Bay itself (Barbieri et al., 1994b). Resulting post larvae and small juveniles are transported into the Chesapeake Bay system where they remain until migrating out of the Bay with the adults in the following fall (Haven, 1957; Chao and Musick, 1977; Norcross, 1983).

Commercial fishery

While the Atlantic croaker is an important commercial resource in the Chesapeake Bay region, annual landings have fluctuated greatly over the past

100 years (Joseph, 1972). Landings have ranged from a peak in 1945 of 26,000 metric tons to a low in 1968 of 2.8 mt (Rothschild et al., 1981; NMFS, personal communication[1]). In Virginia, there have been three distinct periods of relatively high landings separated by two periods of low landings, since 1950 (Figure 1). The first period of relatively high landings occurred from 1954 to 1959 when landings exceeded 2,000 metric tons annually with a peak of 6,440 occurring in 1957 (NMFS, personal communication[1]). Then from 1960 to 1974, landings fell below 2,000 metric tons (NMFS, personal communication[1]). A second brief episode of higher landings lasted from 1975 to 1978 with a peak of 3,901 metric tons occurring in 1977 (NMFS, personal communication[1]). Then from 1979 to 1992, landings fell below 2,000 metric tons for the second time, and in 1982 only 54 metric tons were harvested (NMFS, personal communication[1]). The third episode of increased landings began in 1993 and has continued through 1999 with an apparent peak in landings of 5,801 metric tons occurring in 1997 (NMFS, personal communication[1]).

Occurrence of large Atlantic croaker

Associated with the three most recent periods of high commercial landings in the Chesapeake Bay region has been the occurrence of unusually large Atlantic croaker, fish more than 400mm in total length. The presence of these large fish has been documented in previous reports (Hildebrand and Schroeder, 1928; Massmann and Pacheco, 1960; Ross, 1988; Barbieri, 1993), and in recreational catch records from the Virginia Saltwater Fishing Tournament from

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[1] NMFS, OFFICE OF SCIENCE AND TECHNOLOGY, F/ST1, Room 12362, 1315 East-West Highway, Silver Spring, MD 20910

1958 to 1972 and 1976 to 1999 (Figure 1; Claude M. Bain, III, personal communication[1]). Massman and Pacheco (1960) collected Atlantic croaker from the York River, Virginia in excess of 400 mm total length (TL) from 1950 to 1953 and from 1956 to 1958, and they collected fish greater than 500 mm TL in 1951, 1952, and 1958. Ross (1988) collected fish in North Carolina waters in excess of 400 mm TL and even 500 mm TL from 1979 to 1981. From 1958 to 1963, 931 citations for large Atlantic croaker, minimum weight of 0.91 Kg (2 lbs), were awarded by the Virginia Saltwater Fishing Tournament; from 1977 to 1983, 548 citations for large fish, minimum weight of 1.82 KG (4 lbs), were awarded, and from 1993 to 1998, 433 citations, minimum weight of 1.36 KG (3 lbs) were awarded (Claude M. Bain, III, personal communication[1]). The year-classes that produced these citation fish are not known, but they could reflect the episodic occurrence of strong or dominant year-classes as suggested by Barbieri et al. (1994a). Alternatively, Barbieri et al. (1994a) hypothesized that the proportional increase and occurrence of these large fish resulted from good survivorship in fish spawned early, July and August, coupled with lower survivorship in fish spawned later, November and December, due to very low water temperatures in nursery areas during the winter months (Massman and Pacheco, 1960; Joseph, 1972; Chao and Musick, 1977; Warlen and Burke, 1991). Early spawned fish have been shown to have higher growth rates than fish spawned later in the year (Warlen, 1982; Nixon and Jones, 1997) which could equate to very large adults.

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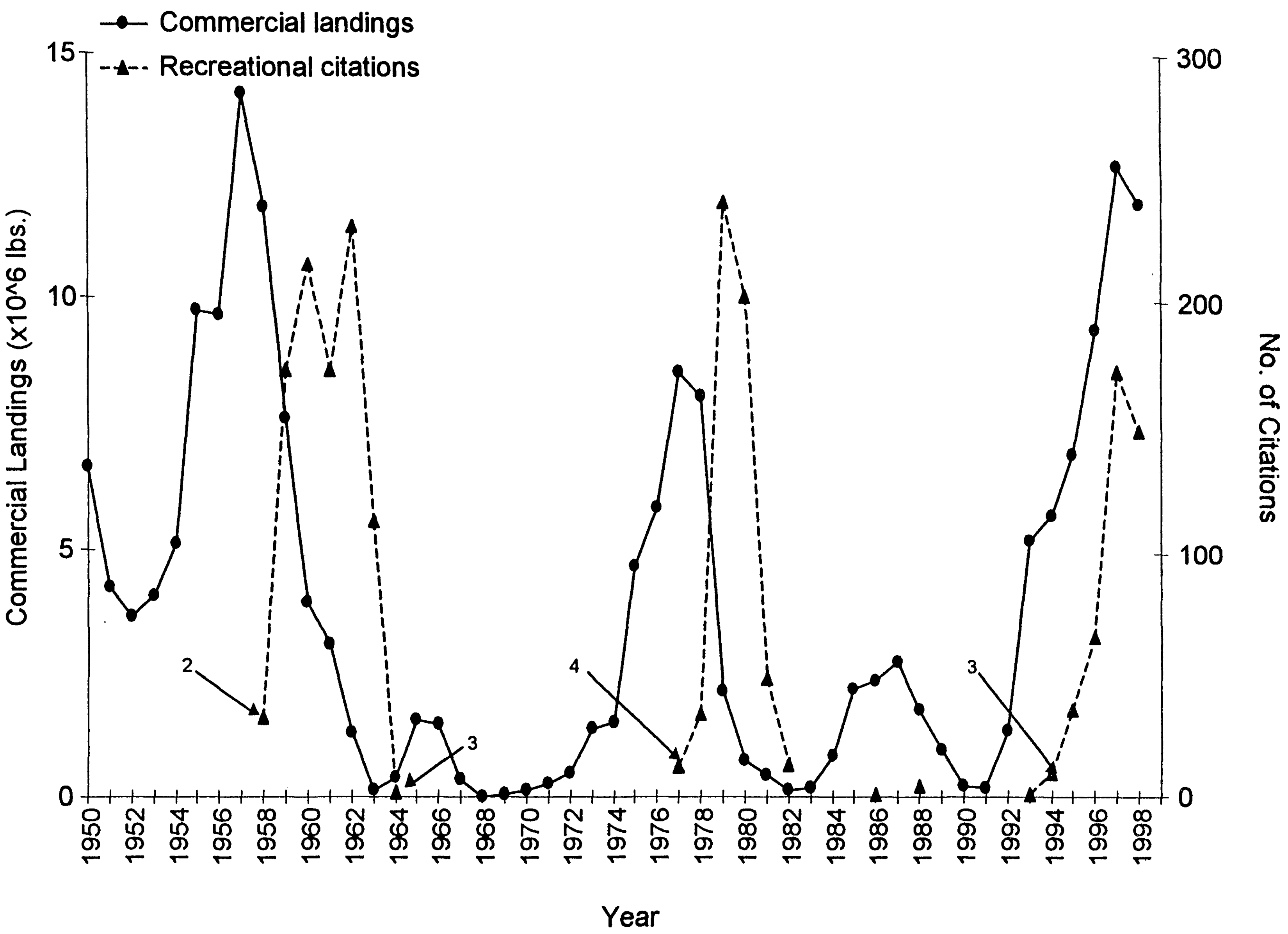
[1] Claude M. Bain, III, Virginia Saltwater Fishing Tournament, 986 South Oriole Drive, Suite 102, Virginia Beach, Virginia 23451

Figure 1. Annual commercial landings and recreational citations for Atlantic croaker in Virginia, 1950 to 1998. Commercial landings data from National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD. Recreational citation data from Claude M. Bain, III, Virginia Saltwater Fishing Tournament, Virginia Beach, VA. The four numbers adjacent to arrows indicate sizes (lbs.) required for recreational citations. Arrows point to the number of citations in the first year that citation size was implemented. No citation was offered for Atlantic croaker from 1972 to 1976.


Commercial landings
Recreational citations
Commercial Landings (x10^6 lbs.)
0
5
10
15
No. of Citations
0
100
200
300
Year
1950
1952
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2
3
4
3

Status of age, growth, and mortality information

While there is much recent information on age and size compositions, growth, and mortality of Atlantic croaker in the Chesapeake Bay and Middle Atlantic regions, it is incomplete and possibly inaccurate as it does not include exceptionally old, large fish. Barbieri et al. (1994a) described age, growth, and mortality of Atlantic croaker in the Chesapeake Bay region. That report, however, was based on a sample containing only one large fish, a fish just 400 mm TL. Presumably, large Atlantic croaker were rare in the Chesapeake Bay region then. Without the ability to collect them, Barbieri et al. could not describe the impact that the periodically occurring large fish might have on age, growth, and mortality estimates. Ross (1988) reported on age, growth and mortality of Atlantic croaker in North Carolina. His sample of 2,369 Atlantic croaker included 120 large fish with TL equal to or greater than 400 mm. Unfortunately, those 120 fish were aged using scales. Ross' (1988) results may have contained inaccuracies as problems with ageing Atlantic croaker based on scales have been reported (Roithmayr, 1965; Joseph, 1972; Mericas, 1977; Barger and Johnson, 1980; Barbieri, 1993; Barbieri et al., 1994a).

Description of thesis

There are three basic objectives to this study. The first is to determine the age composition of unusually large Atlantic croaker, currently present in the Chesapeake Bay region, using an accurate method for ageing based on sectioned otoliths. As the presence of these large fish may significantly change life history parameter estimates, the second objective is to revise information on age, growth, and mortality of Atlantic croaker. The final objective then, is to assess these changes through comparison with previous reports.

The thesis consists of three chapters. Topics related to age are covered in the first chapter. Specifically, I validate the sectioned otolith ageing method for ages 1-9 and provide information on the current age structure of Atlantic croaker in the Chesapeake Bay region with a focus on the age structure of unusually large fish. Based on the validated ageing method presented in Chapter 1, growth is addressed in Chapter 2, and information on mortality is provided in Chapter 3.

CHAPTER 1

Age Determination and Age Composition

INTRODUCTION

Studies on Atlantic croaker have used three main methods of age determination. Early work reported ages from length frequency distributions (Hildebrand and Cable, 1930; Gunter, 1945; Suttkus, 1955; Bearden, 1964; Hansen, 1969; Christmas and Waller, 1973; Hoese, 1973; Gallaway and Strawn, 1974), and scale ageing (Welsh and Breder, 1923; Wallace, 1940; White and Chittenden, 1977; Ross, 1988). Ageing Atlantic croaker with either of these two methods is problematic, however. Difficulties with the length frequency method arise from the protracted spawning period of Atlantic croaker (Morse, 1980; Warlen, 1982; Barbieri et al., 1994b) and difficulty distinguishing modal groups at older ages (White and Chittenden, 1977; Jearld 1983). Problems with scale-based ageing include poorly defined marks (Barger and Johnson, 1980), irregular frequency of marks (Haven, 1954), and difficulty in distinguishing marks (Roithmayr, 1965; Joseph, 1972; Mericas, 1977). As neither the length frequency nor scale method is wholly adequate (Barbieri et al., 1994a), sectioned otolith ageing has often been used since 1980 (Warlen, 1982; Music and Pafford, 1984; Barger, 1985; Barbieri et al., 1994a). Sectioned otoliths have been found superior to scales in definition and legibility of marks in two formal hard-part comparisons, both of which concluded that sectioned otoliths were the best structure for ageing Atlantic croaker (Barger and Johnson, 1980; Barbieri, 1993).

Validation of age determination methodology has been recommended for each age group and population examined (Beamish and McFarlane, 1983).

Both scale and otolith ageing has been validated using marginal increment analysis for Atlantic croaker populations in the South Atlantic and Middle Atlantic Bights (Music and Pafford, 1984; Ross, 1988; Barbieri et al., 1994a). For example, Ross (1988) reported validating scale-based ageing for ages 1 to 5, and Barbieri et al. (1994a) validated otolith-based ageing for ages 1 to 7. Older ages, however, have not been validated.

Many reports exist on Atlantic croaker age composition. While differing in geographic region, sampling regime, and age determination methodology, they often are similar in that they consist of predominantly young fish. For example, the maximum ages reported by Music and Pafford (1984) in Georgia waters was 5 years, but less than 1% of the fish were over age 2. Barger (1985) reported a maximum of age 8 in the Northern Gulf of Mexico with about 7% over age 3. Ross (1998) reported age 7 as the maximum, but only 9% were over age 3. Only Barbieri et al. (1994a) collected a relatively large number of older fish. The maximum age in that study was 8 with 35% of the fish over age 3 and 13% over age 5.

Given the occurrence of unusually large, potentially older, Atlantic croaker in the Chesapeake Bay region in recent years (see General Introduction), validating ageing techniques for older age groups and obtaining an age structure for a population with many older individuals may be possible. In this section, I validate an otolith-based ageing method and present age composition data with a focus on older individuals.

METHODS

Collection of Fish

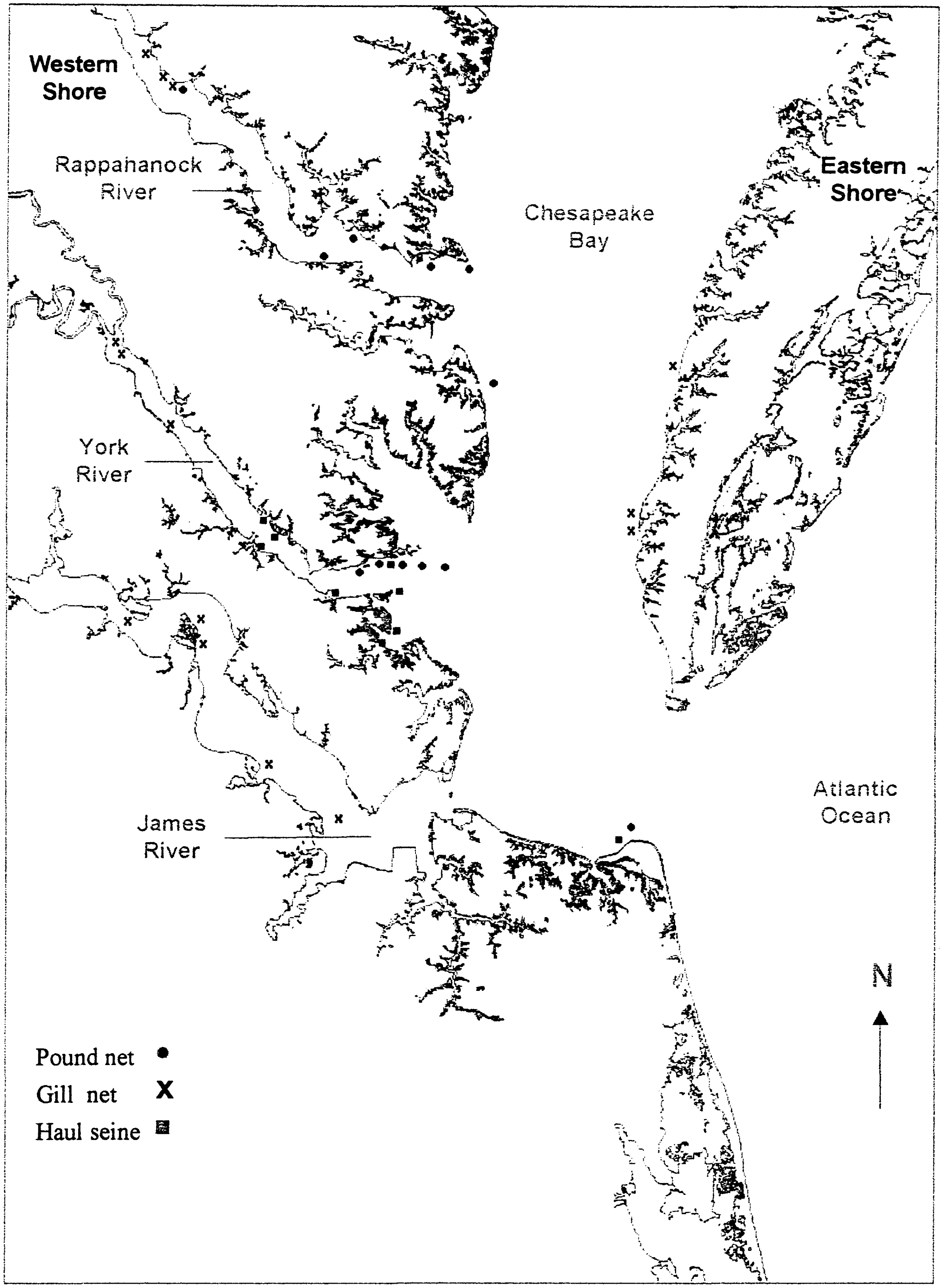
Atlantic croaker were collected twice monthly from 1998 to 2000 from catches of commercial pound-net, haul-seine, gill-net, and trawl-net fisheries along the Western Shore and Eastern Shore of the Chesapeake Bay region (Figure 2). Collections consisted of one 22.7 kg (50lb) box of fish from each available commercial grade: Small, Medium, Large, and Jumbo. While boxes were not selected randomly, most of the variation in length compositions has been shown to be captured by within-box variation for pound-net and haul-seine catches of Atlantic croaker (Chittenden, 1989).

Age Determination, Validation, and Precision

Ages were determined from transverse cross sections of saggital otoliths. For every fish, both saggital otoliths were removed and stored dry. The right or left otolith were randomly selected and a transverse cross section was cut through the core with a pair of diamond blades using a Buehler low-speed Isomet saw. Resulting sections, about 0.75 mm thick, were mounted on glass slides with Crystalbond™ 509 (polyethylene phthalate) and read under a dissecting scope with transmitted light.

Ages were based on counts of annuli. The annulus in Atlantic croaker is a bipartite mark consisting of a narrow opaque band and a broad translucent band when viewed under transmitted light (Barbieri et al., 1994a). The edge of the annular mark is considered to be the proximal edge of the distinct narrow opaque band, except for the first annulus which is a less distinct opaque band that may

Figure 2. Locations of Atlantic croaker collections from pound-net, gill-net, and haul-seine fisheries in the Chesapeake Bay region.


Western Shore
Rappahanock River
Chesapeake Bay
Eastern Shore
York River
James River
Atlantic Ocean
N
Pound net ●
Gill net X
Haul seine ▪

not be completely separate from the otolith core region (Barbieri et al., 1994a). As the average biological birthdate for Atlantic croaker in the Chesapeake Bay region occurs in September, following Barbieri et al., 1994a), I used September 1 was used as an arbitrary birthdate for promoting fish from one age-group to the next. All sectioned otoliths were read twice by two readers.

Presumptive annual marks were validated by age group using the marginal increment method (Bagenal and Tesch, 1978), where the marginal increment is the distance from the proximal edge of the last annulus (defined above) to the outer edge of the section along the ventral side of the sulcal groove. Marginal increments were measured using a calibrated digital imaging system and SPOT RT software version 3.0 (Diagnostic Instruments, Inc., 1997). Differences between monthly mean marginal increments were evaluated by one way ANOVA (Zar, 1984) for each individual age group.

Ageing precision was evaluated by percent agreement. Otolith sections from one hundred fish, ranging in size and age from 225-480mm TL and 1-9 years, were randomly selected from the total sample and read twice by two readers. Percent agreement was then calculated for both within reader and between reader agreement.

Age Composition

To describe age composition, the range of ages, mean age, age frequency distribution, and T_{99}, the 99th percentile of that distribution, were given for each biological year and for all fish pooled over all years. Biological years started on September 1 and ended on August 31. Collections were made during three biological years: Year 1 (03/98-08/98), Year 2 (09/98-08/99), and Year 3 (09/99-03/00). Observed age compositions were also reported for each commercial grade by biological year. As the Virginia Marine Resources Commission only reports commercial catches for Small, Medium, and Large grades, a frequency distribution was also constructed by pooling Large and Jumbo grades. An additional age frequency distribution was given for each biological year for Unusually Large fish, fish 400mm TL or greater. Differences in mean age among years were evaluated by one way ANOVA and Kolmogorov-Smirnoff two sample tests (Zar, 1984) were used to evaluate inter-annual differences between observed age compositions, observed age compositions by commercial grade, and observed age compositions of Unusually Large fish.

Ratio estimates (Cochran, 1977) were used to construct Adjusted Age Compositions to better reflect the actual composition of the commercial catch in Virginia. Estimates were based on Virginia Marine Resources Commission (VMRC) reports on total landings of each commercial grade each month. To construct an Adjusted Age Composition, for each year the number of fish in each age group was estimated for each market grade for each month and then summed across months and grades as:

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

where

N_i is the adjusted number of fish age i in Virginia's total annual commercial catch,

N_{ijk} is the adjusted number of fish age i in commercial grade j caught in month k,

n_{ijk} is the number of fish age i in the sample collected from grade j in month k,

w_{jk} is the total weight of the sample collected from grade j in month k, and

W_{jk} is the weight of the total commercial catch for grade j in month k.

Only observed ages and weights from Selected months in which Small, Medium, and Large grades were available were used to construct the Adjusted Age Compositions. Selected months were May - July, and September – November in 1998, April - June, October, and November in 1999, and January - March in 2000. Kolmogorov-Smirnoff (KS) two-sample tests (Zar, 1984) were used to evaluate differences between Observed and Adjusted Age compositions within and between years. Only Observed Age frequencies from Selected months were used in these comparisons.

To evaluate year-class strengths, individual age groups were converted to year-classes in each biological year. Observed and Adjusted Age Compositions were qualitatively evaluated for patterns in relative abundance of year-classes.

RESULTS

Age Validation and Precision

Atlantic croaker form one annulus a year, from April through June in the Chesapeake Bay region. Only one trough in monthly mean marginal increment values was present for ages 1-9 (Figure 3), indicating that only one annulus is formed each year. Mean values generally declined beginning in April signaling the onset of mark formation at each age. Mean values continued to decline through May to a minimum in June, indicating peak annulus formation in June. Mean values increased through July and August to a relatively stable plateau that lasted from September to March, indicating little or no otolith growth from September through March. ANOVA found significant differences between monthly means at each age (Table 1). Too few fish were collected to validate age beyond age 9.

Sectioned otolith age determination was very precise. Within reader agreement was 100% for reader 1 and for reader 2. Between reader agreement was 97% for both the first and second readings. The few disagreements reflect difficulties interpreting the otolith edge and were never greater than one year. Annuli were generally easily recognized even at the oldest ages (Figure 4).

Age Composition

Observed age compositions were generally similar overall, though they varied a bit by biological year. Ages ranged from 1 to 10 years in the first two years, from 1 to 11 in the third year (Table 2). Age 11 was the oldest observed age recorded. Second highest ages were 9 years in the first two years and 10 in

Figure 3. Mean marginal increments in Atlantic croaker by month for ages 1-11 years. Error bars represent 95% confidence intervals about the mean. Numbers above bars represent monthly sample sizes.

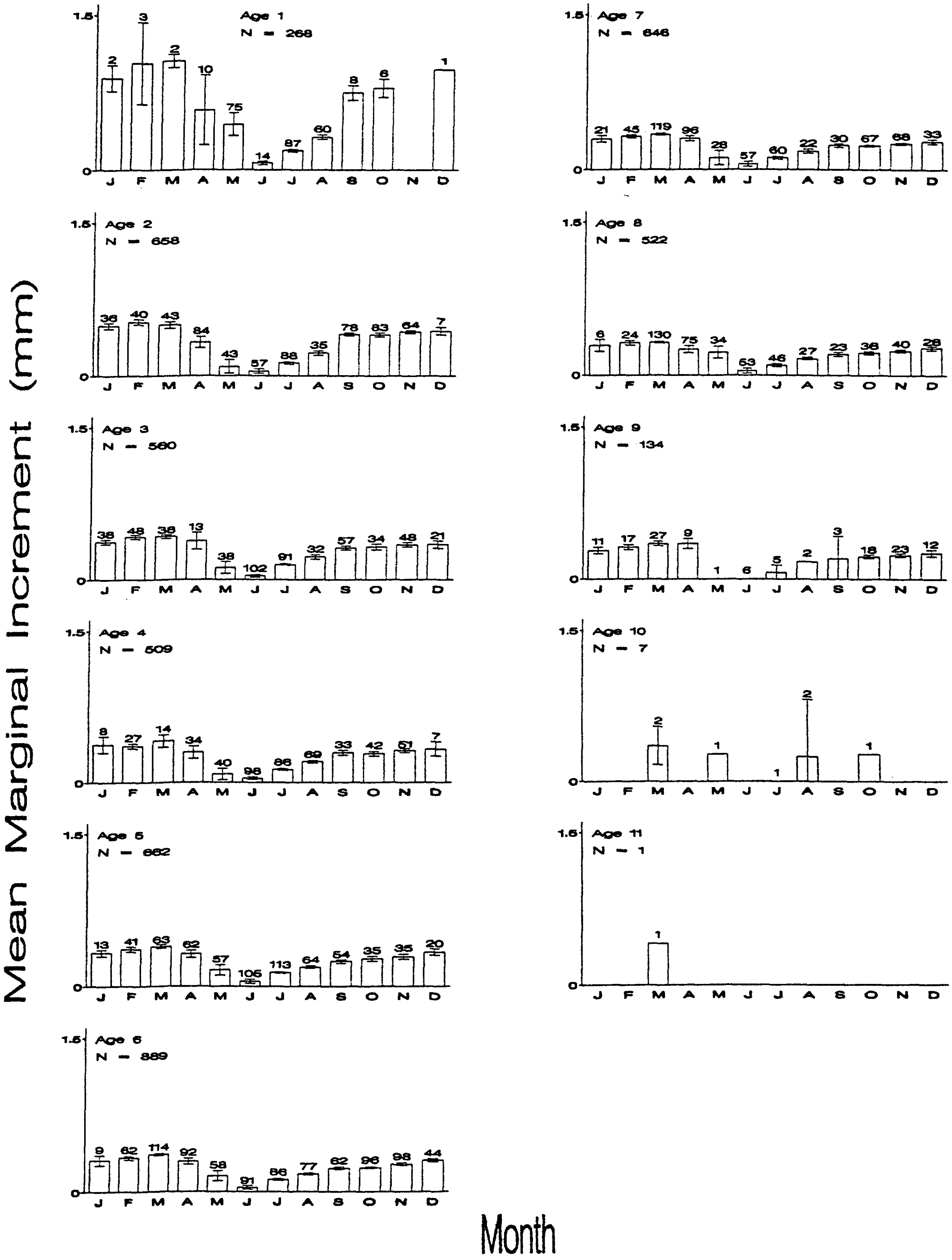

Mean Marginal Increment (mm)
Month
Age 1
N = 268
2
3
2
10
75
14
87
60
8
6
1
Age 2
N = 658
36
40
43
84
43
57
88
35
78
83
64
7
Age 3
N = 560
38
48
38
13
38
102
91
32
57
34
48
21
Age 4
N = 509
8
27
14
34
40
98
86
69
33
42
51
7
Age 5
N = 662
13
41
63
62
57
105
113
64
54
35
35
20
Age 6
N = 889
9
62
114
92
58
91
86
77
62
96
98
44
Age 7
N = 646
21
45
119
96
28
57
60
22
30
67
68
33
Age 8
N = 522
8
24
130
75
34
53
46
27
23
36
40
28
Age 9
N = 134
11
17
27
9
1
6
5
2
3
18
23
12
Age 10
N = 7
2
1
1
2
1
Age 11
N = 1
1
1.5
0
J F M A M J J A S O N D

Table 1. ANOVA tests for differences between monthly mean marginal increments for age groups 1-9 of Atlantic croaker from the Chesapeake Bay region. F values are significant at $\alpha = 0.05$, $p < 0.0001$.

Age	Source of Variation	df	SS	MS	F
1	Month	10	10.45	1.05	13.33
	Error	257	20.15	0.08	
	Total	267	30.60		
2	Month	11	16.49	1.50	94.60
	Error	646	10.24	0.02	
	Total	657	26.73		
3	Month	11	10.79	0.98	155.62
	Error	548	3.45	0.01	
	Total	559	14.24		
4	Month	11	6.79	0.62	76.25
	Error	497	4.02	0.01	
	Total	508	10.81		
5	Month	11	8.19	0.74	78.40
	Error	650	6.17	0.01	
	Total	661	14.36		
6	Month	11	8.31	0.76	103.56
	Error	877	6.40	0.01	
	Total	888	14.71		
7	Month	11	5.53	0.50	81.37
	Error	634	3.92	0.01	
	Total	645	9.44		
8	Month	11	4.21	0.38	50.52
	Error	510	3.87	0.01	
	Total	521	8.08		
9	Month	11	1.08	0.10	42.44
	Error	122	0.28	0.00	
	Total	133	1.37		

Figure 4. Transverse cross section of a sagittal otolith from an age 11 Atlantic croaker collected in March, 2000 from the Chesapeake Bay. Viewed with transmitted light, triangles indicate the narrow opaque bands of annuli which are easily identified beyond the first annulus.

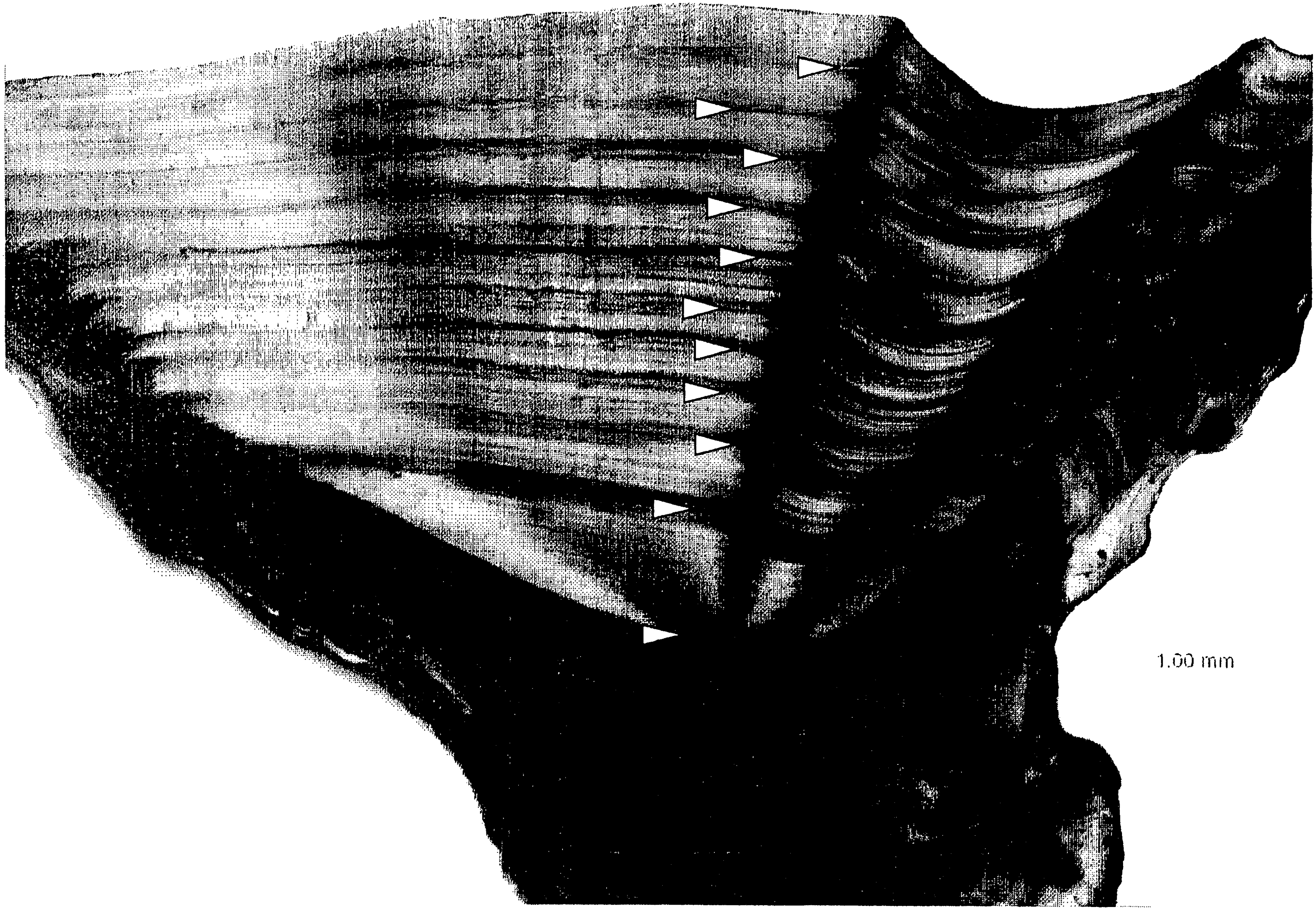

1.00 mm

Table 2. Observed minimum, maximum, T_{99}, and mean ages of Atlantic croaker from the Chesapeake Bay region for each biological year and pooled over the entire period, March, 1998 - March, 2000.

Year	Min	Max	T_{99}	Mean	Std Error	N
1: 3/98-8/98	1	10	7	4.02	0.05	1367
2: 9/98-8/99	1	10	9	5.42	0.04	2360
3: 9/99-3/00	1	11	9	5.00	0.07	1132
All years pooled	1	11	9	4.93	0.03	4859

the third year. T_{99} was 7 years in year 1 and 9 in years 2, 3, and for all years pooled. Mean age was 4.02 in year 1, 5.42 in year 2, 5.0 in year 3, and 4.93 for all years pooled. Differences in mean ages between years were significant (ANOVA, F = 191.22, df = 4858, $p < 0.0001$).

Observed Age frequency distributions differed from year to year. Age 5 was most common in year 1, making up 22% of that distribution (Figure 5), but ages 1, 3 and 4 each made up 15 – 21%. Age 6 was most abundant in year 2, accounting for 27% of that frequency distribution. Age 3 was the most common in year 3, making up 22% of that distribution. Observed Age frequency distributions were significantly different between years 1 and 2, 1 and 3, and 1 and the pooled distribution (Table 3). Differences were not significant between years 2 and 3 nor between 2 or 3 and the pooled distribution.

Age composition of the Unusually Large fish varied by year. Ages ranged from 4 to 9 in year 1, though most fish were ages 5 - 7 (Figure 6). Age 7 alone made up almost 65% of the Unusually Large then. Ages ranged from 4 to 10 in year 2, though most fish were ages 6 - 8. Ages 8 and 6 were the most frequent ages, making up 42% and 27%, respectively. Ages ranged from 4 to 11 in year 3, with no fish being age 10. Most fish were ages 6 – 9. Ages 7 and 9 were the most frequent making up 28 - 32%. KS tests found significant differences in age frequencies between the three years (Table 4).

Adjusted Age Compositions varied greatly between biological years. Ages 1, 3, and 5 were most abundant in year 1, making up 31%, 22%, and 18%, respectively (Table 5, Figure 7). Ages 2 and 4 each made up 11 – 13%. Ages 2

Figure 5. Observed age compositions in each biological year and pooled over all years, March, 1998 - March, 2000. Numbers above bars represent sample sizes.

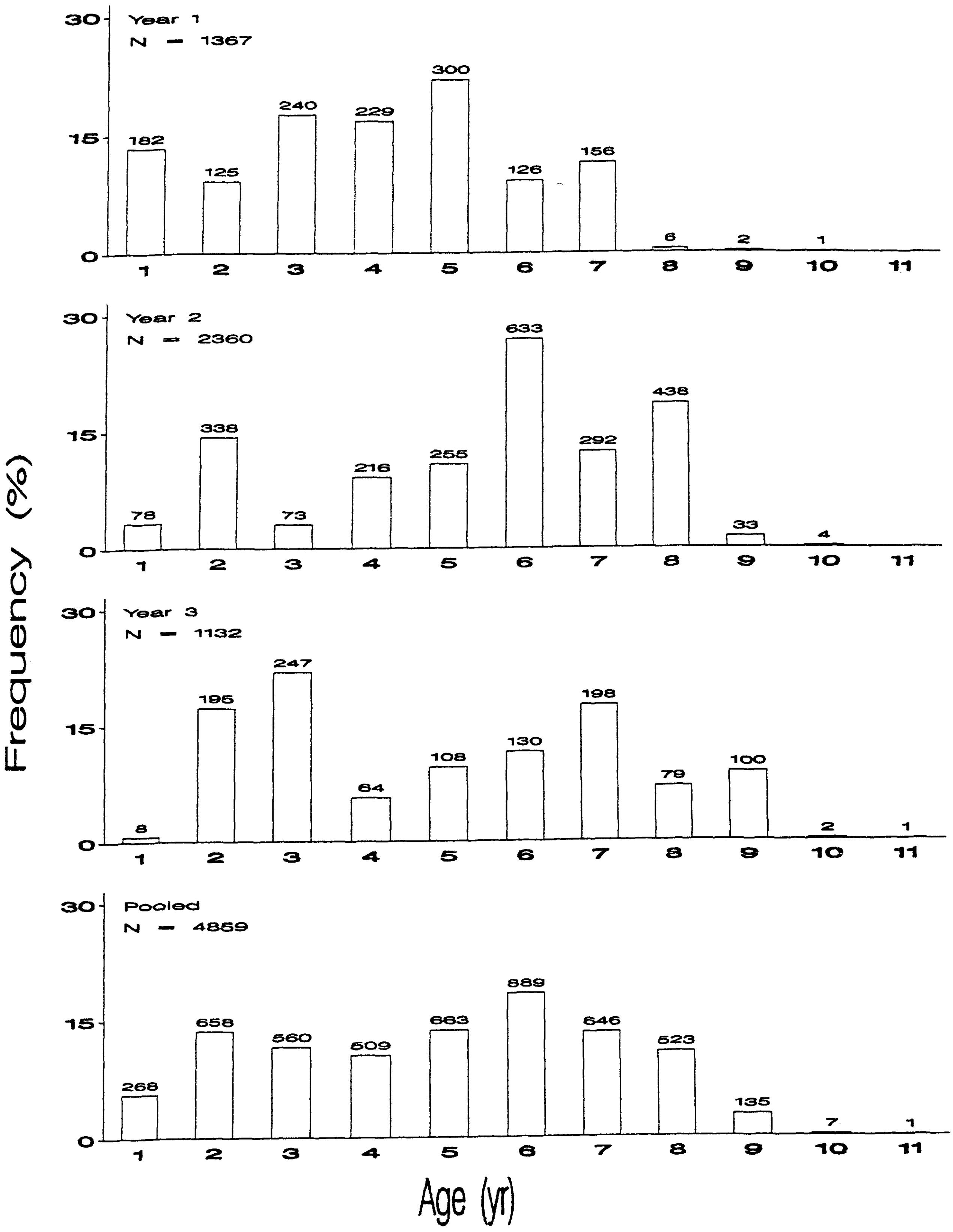

Frequency (%)
Year 1
N = 1367
30
15
0
182
125
240
229
300
126
156
6
2
1
1 2 3 4 5 6 7 8 9 10 11
Year 2
N = 2360
30
15
0
78
338
73
216
255
633
292
438
33
4
1 2 3 4 5 6 7 8 9 10 11
Year 3
N = 1132
30
15
0
8
195
247
64
108
130
198
79
100
2
1
1 2 3 4 5 6 7 8 9 10 11
Pooled
N = 4859
30
15
0
268
658
560
509
663
889
646
523
135
7
1
1 2 3 4 5 6 7 8 9 10 11
Age (yr)

Table 3. Kolmogorov-Smirnov two-sample tests for differences between: 1) observed age compositions of Atlantic croaker from the Chesapeake Bay region in each biological year, and 2) each annual composition and the composition pooled over the entire sampling period. "ns" indicates non-significance at $\alpha = 0.05$.

Years Compared	KS	D	KSa	P
1:2	0.19	0.39	2.67	<0.0001
1:3	0.12	0.24	1.64	0.009
2:3	0.10	0.20	1.35	ns
1:All	0.12	0.24	1.69	0.007
2:All	0.07	0.14	0.98	ns
3:All	0.05	0.10	0.68	ns

Figure 6. Observed age compositions in Unusually Large Atlantic croaker each year. Numbers above bars represent sample sizes.

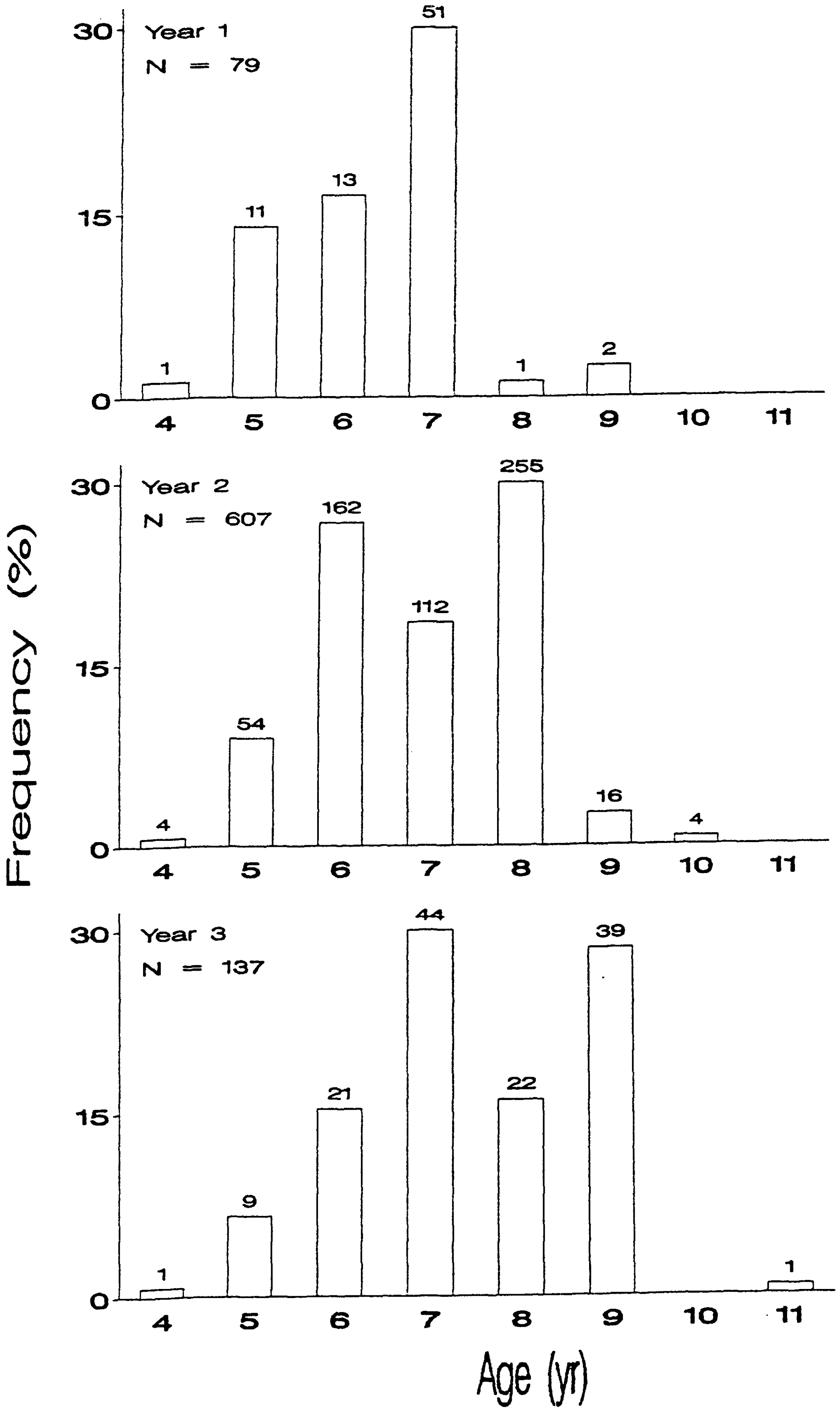

Year 1
N = 79
30
15
0
1
11
13
51
1
2
4
5
6
7
8
9
10
11
Year 2
N = 607
30
15
0
4
54
162
112
255
16
4
4
5
6
7
8
9
10
11
Year 3
N = 137
30
15
0
1
9
21
44
22
39
1
4
5
6
7
8
9
10
11
Frequency (%)
Age (yr)

Table 4. Kolmogorov-Smirnov two-sample tests for differences between observed age compositions of Unusually Large Atlantic croaker from the Chesapeake Bay region in each biological year, March, 1988 - March, 2000.

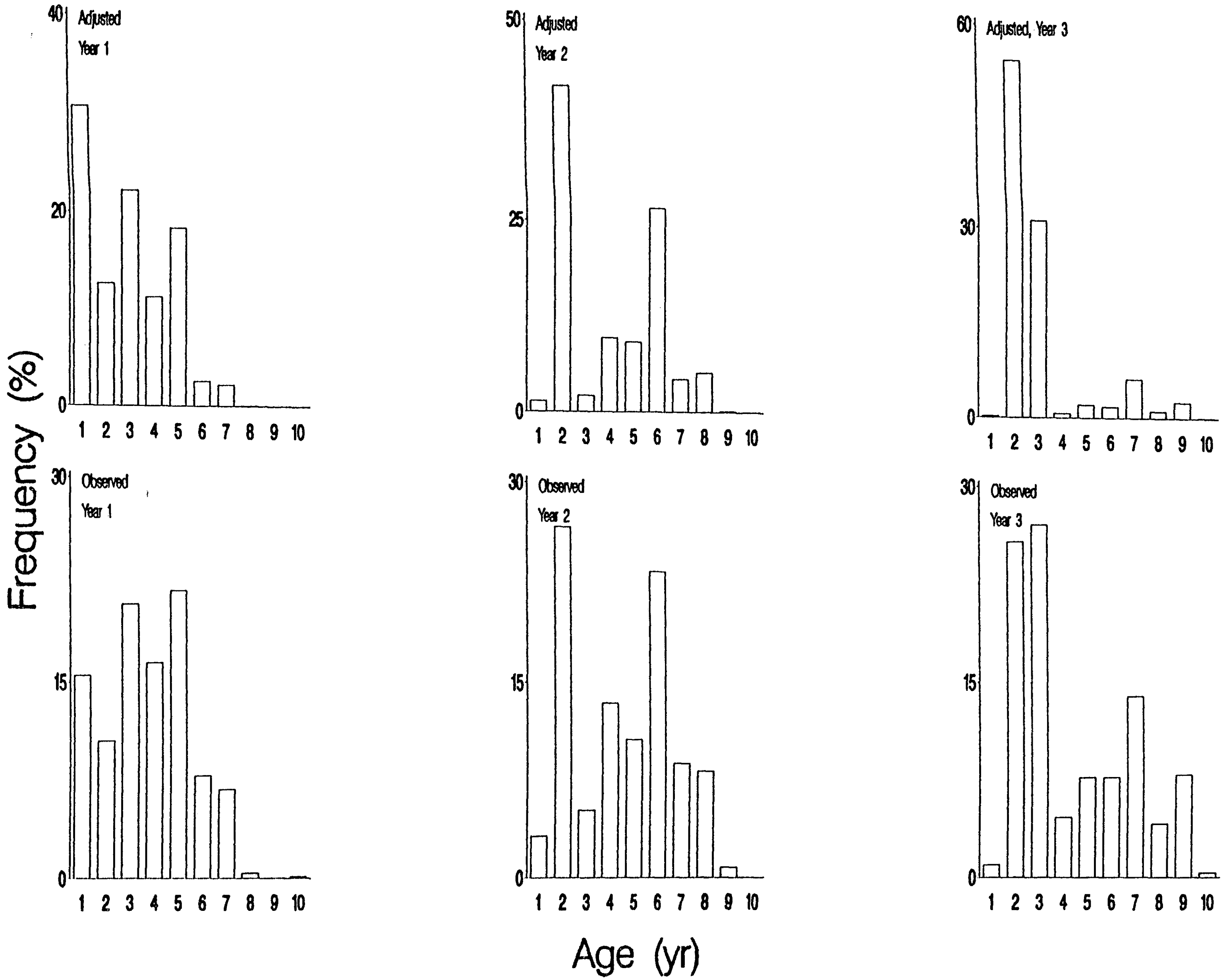
All results were significant at $\alpha = 0.05$.

Years Compared	KS	D	KSa	P
1:2	0.21	0.43	2.97	<0.0001
1:3	0.21	0.42	2.94	<0.0001
2:3	0.13	0.27	1.86	0.002

Table 5. Observed and Adjusted Age compositions of Atlantic croaker from Selected months during each biological year, March, 1998 through March, 2000.

	Observed			Adjusted		
Year	Age	N	%	Age	N	%
1	1	156	15.48	1	3908950	30.89
	2	107	10.62	2	15958855	12.54
	3	208	20.63	3	28316289	22.25
	4	165	16.37	4	14259207	11.21
	5	218	21.63	5	23321242	18.33
	6	80	7.94	6	3258021	2.56
	7	69	6.85	7	2814684	2.21
	8	4	0.40	8	16647	0.01
	9	0	0	9	0	0
	10	1	0.10	10	4903	0.005
2	1	33	3.19	1	873027	1.35
	2	275	26.57	2	27043648	41.77
	3	54	5.22	3	1348303	2.08
	4	139	13.43	4	6249737	9.65
	5	110	10.63	5	5907385	9.12
	6	240	23.19	6	17214048	26.59
	7	91	8.79	7	2734363	4.22
	8	85	8.21	8	3303331	5.10
	9	8	0.77	9	77257	0.12
3	1	6	0.98	1	58167	0.21
	2	157	25.74	2	15408074	54.60
	3	165	27.05	3	8768174	31.07
	4	28	4.59	4	199572	0.71
	5	47	7.70	5	563428	2
	6	47	7.70	6	492556	1.75
	7	85	13.93	7	1727069	6.12
	8	25	4.10	8	292885	1.04
	9	48	7.87	9	704136	2.50
	10	2	0.33	10	4393	0.02

Figure 7. Adjusted and Observed Age compositions from Selected months in each biological year of sampling.


Adjusted
Year 1
Adjusted
Year 2
Adjusted, Year 3
Observed
Year 1
Observed
Year 2
Observed
Year 3
40
20
0
50
25
60
30
15
1 2 3 4 5 6 7 8 9 10
Frequency (%)
Age (yr)

and 6 were the most abundant by far in year 2, making up 42% and 27%, respectively. No other age made up more than 10%. Ages 2 and 3 made up most of the distribution in year 2, at 55% and 31%, respectively. KS tests found significant differences between years in the Adjusted Age frequencies (Table 6).

Observed Age compositions based on Selected months and Adjusted Age compositions were generally similar within years. Although Observed Age and Adjusted Age specific frequencies sometimes differed (Table 5) by as much as 15.4% in year 1 (for age 1), 28.84% in year 2 (for age 1) , and 28.86% in year 3 (for age 2), the general age frequency patterns did appear similar (Figure 7). KS tests found significant differences between Observed Age and Adjusted Age compositions based on Selected months in year 3 but not in years 1 or 2 (Table 7). Despite the significant difference in year 3, both Observed Age and Adjusted Age frequencies based on Selected months do show the same basic pattern in that year. Ages 2 and 3 were much more important than the other older ages, and both Observed Age and Adjusted Age showed similar patterns in those other older ages. The detected significance may, therefore, not have strong biological implications; rather it may reflect large sample sizes.

Atlantic croaker year-class strength seemed to vary greatly over the period 1987 – 1998. The 1987, 1988, and 1989 year-classes each made up only a small part of either the Observed Age or Adjusted Age based on Selected months, in any of the three years (Figure 8). These year-classes were about 8 – 11 years of age during the study period, so that either these year-classes were always weak, or they passed out of the fishery by age 8. The 1992 year-class

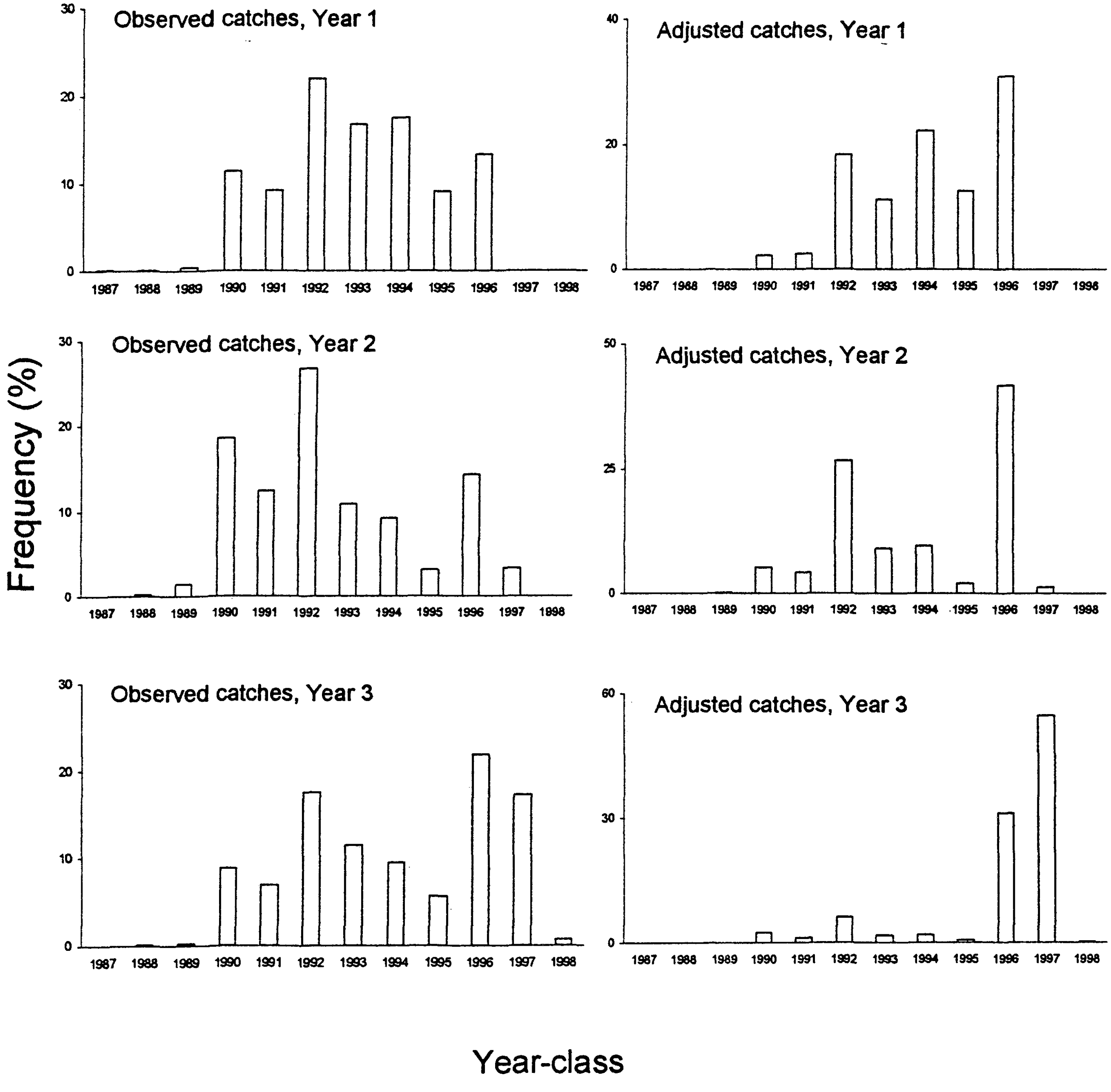
Table 6. Kolmogorov-Smirnov two-sample tests for differences between Adjusted Age compositions of Atlantic croaker from the Chesapeake Bay region from Selected months of each biological year of sampling. All results were significant at α = 0.05.

Years Compared	KS	D	KSa	P
1:2	0.16	0.32	2.23	<0.0001
1:3	0.16	0.31	2.15	0.0002
2:3	0.22	0.43	3.00	<0.0001

Table 7. Kolmogorov-Smirnov two-sample tests for differences between Observed and Adjusted Age compositions from Selected months in each biological year, March, 1998 - March, 2000. "ns" indicates non-significance at α = 0.05.

Year	KS	D	KSa	P
1	0.09	0.19	1.29	ns
2	0.07	0.13	0.91	ns
3	0.17	0.33	2.29	<0.0001

Figure 8. Observed and Adjusted catches based on Selected months, of Atlantic croaker in the Chesapeake Bay region by year-class, 1987 – 1998.


Observed catches, Year 1
Adjusted catches, Year 1
Observed catches, Year 2
Adjusted catches, Year 2
Observed catches, Year 3
Adjusted catches, Year 3
Frequency (%)
Year-class
0
10
20
30
25
40
50
60
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998

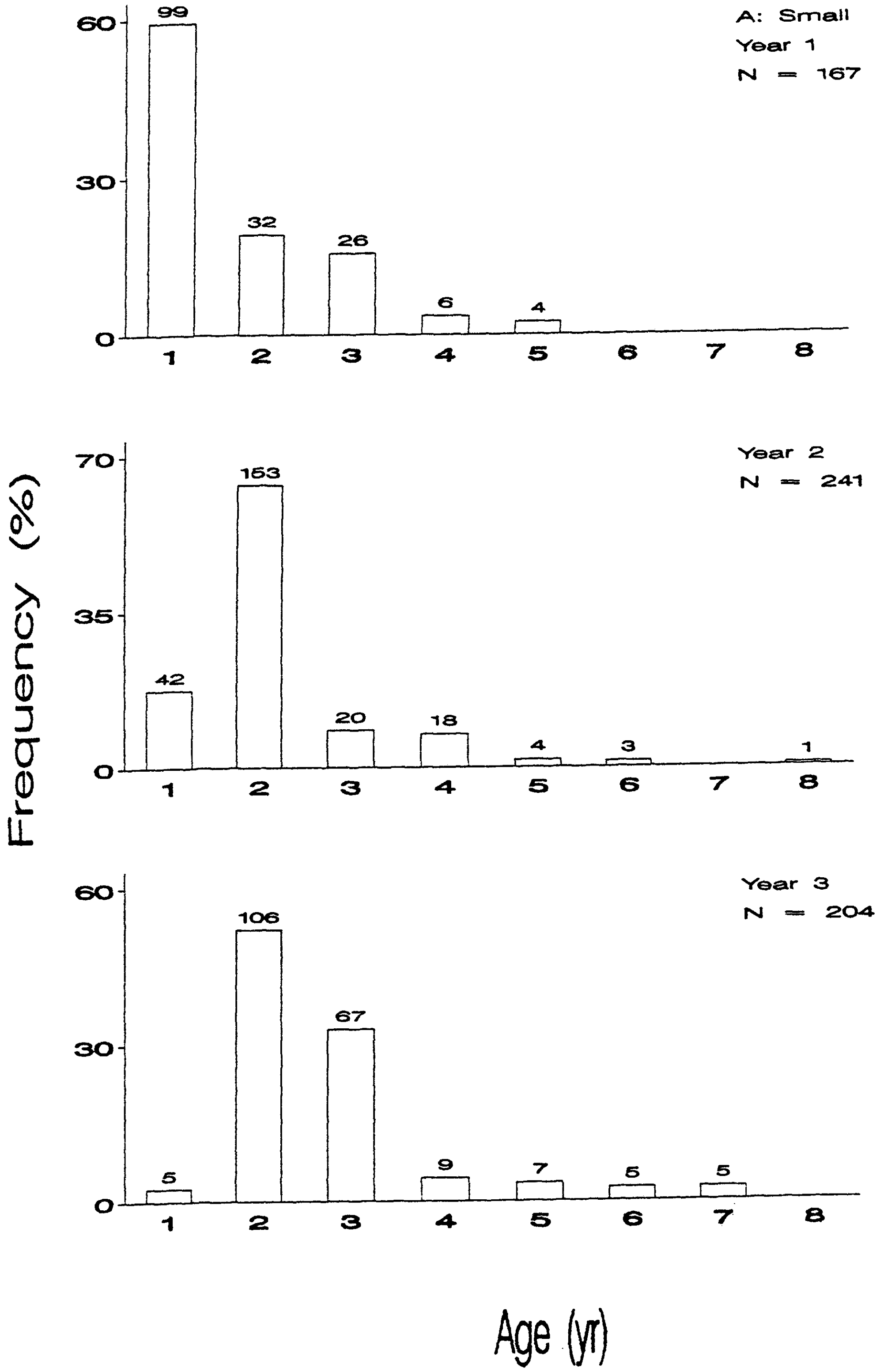
was apparently a very strong year-class. It made up roughly 18 – 28% of the Observed catch during the study period, and 18 – 25% of the Adjusted catch in years 1 and 2, though this year-class was 5 – 7 years old then. Except for the Adjusted catch in year 3, the 1992 year-class was generally at least as strong as, generally much stronger than, any of the year-classes following it from 1993 – 1996. The 1990 and 1991 year-classes were apparently also strong year-classes. They made up 8 – 20% of the Observed catch in the study period, a percentage that was generally about as large, or larger than, most of the year-classes following them from 1993 – 1996, this despite the age, 6 – 9 years, of the 1990 and 1991 year-classes in the period 1998-2000. The 1990 and 1991 year-classes were similarly strong in the Adjusted catch in years 2 and 3, though not in year 1. It was the 1990 and 1991 year-classes that produced most of the Atlantic croaker I collected at ages 7 – 9.

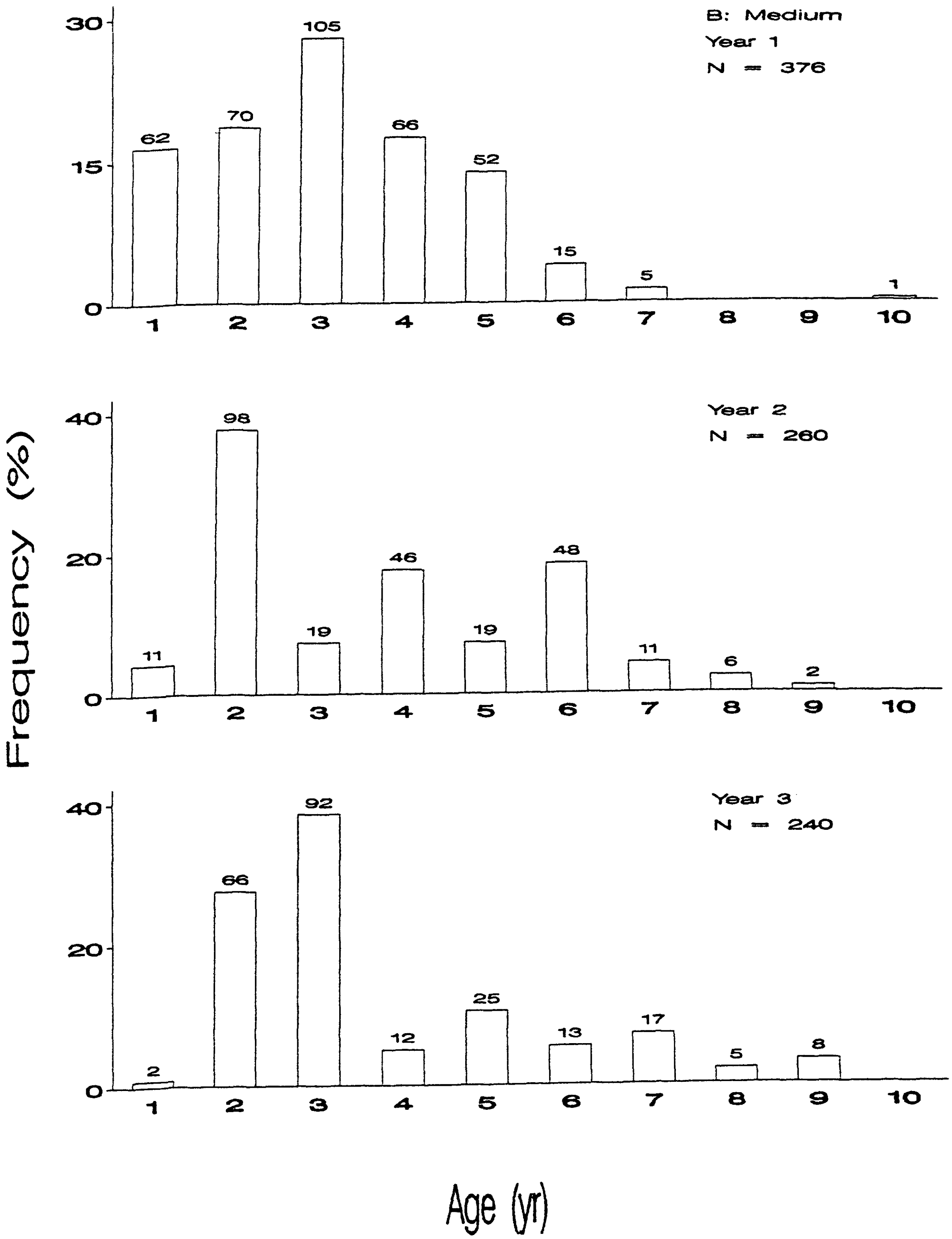
Age Composition by Commercial Grades

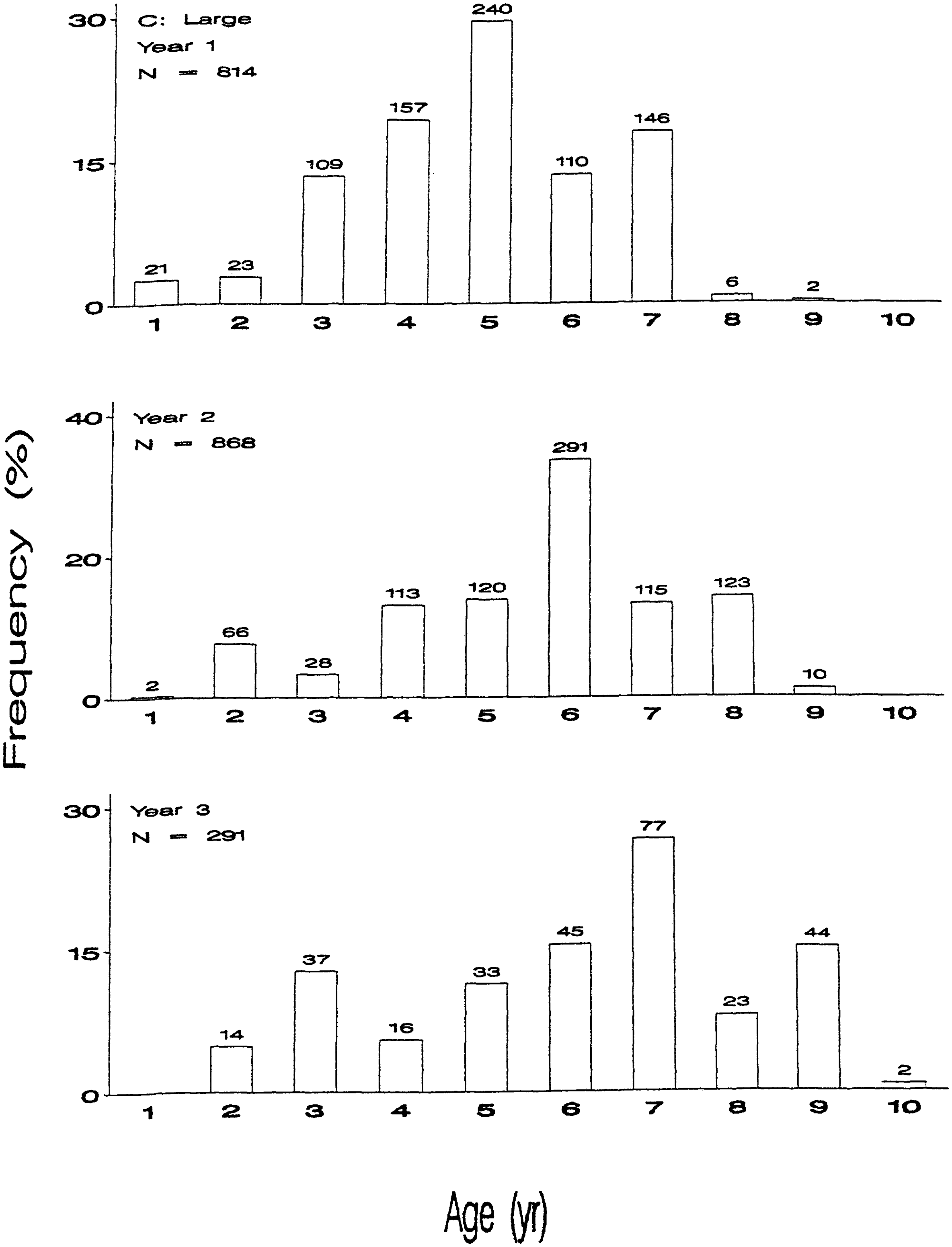
Atlantic croaker showed considerable inter-annual variation in age compositions within commercial grades. In Small grade fish, ages ranged from 1 to 5 in year one, with age 1 comprising almost 60% of the distribution (Figure 9a). Ages ranged from 1 to 6 in year 2, with age 2 comprising over 63% of that distribution. Ages ranged from 1 to 7 in year 3, with ages 2 and 3 making up 52% and 33% of that distribution respectively.

For Medium grade fish, ages ranged from 1 to 7 in year 1, with a single age 10 fish (Figure 9b). Most of that distribution was made up of ages 1 to 5 with age 3 being most common at 28%. Ages ranged from 1 to 9 in year 2, though

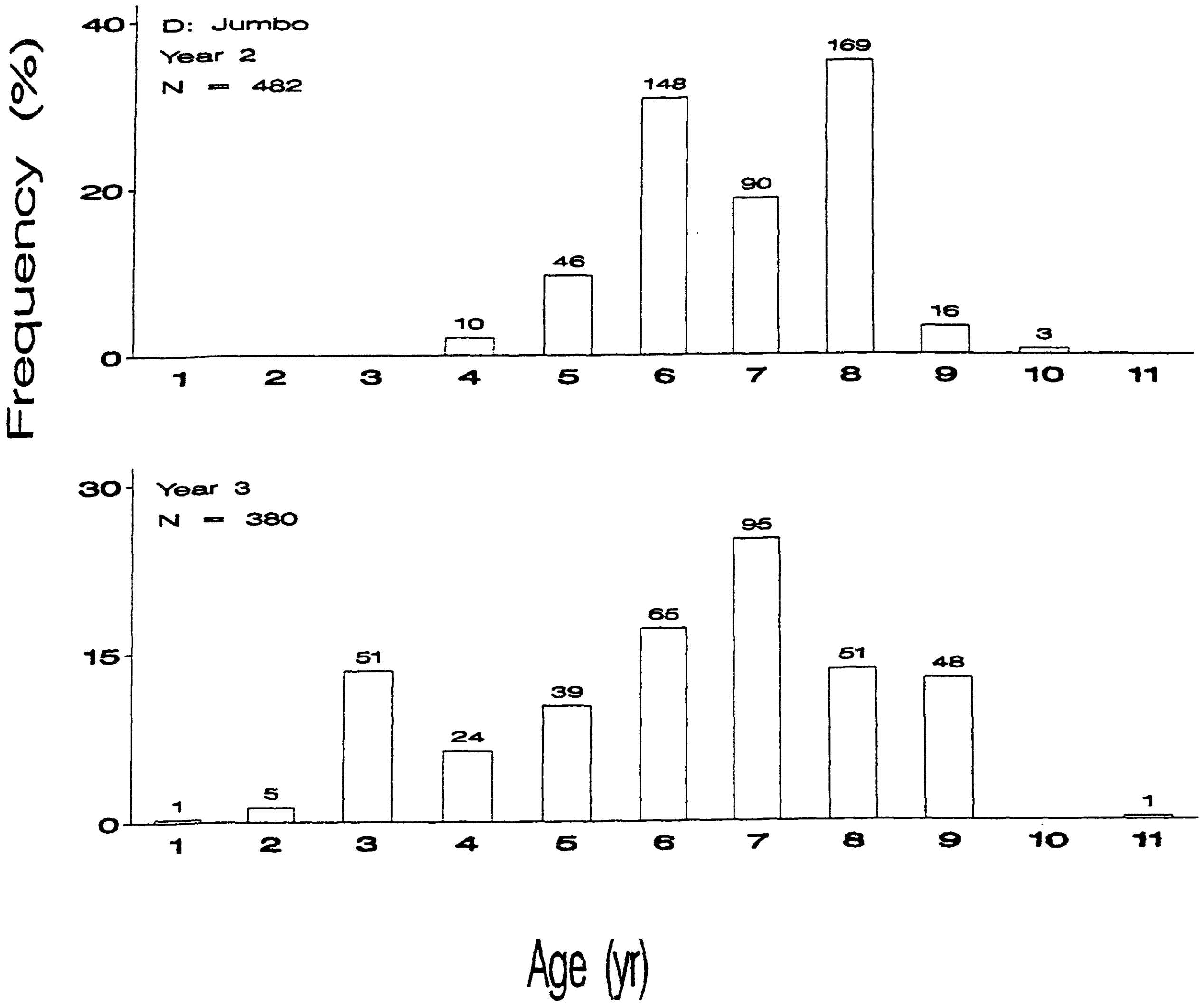
Figure 9. Observed age compositions in each biological year by Small (a), Medium (b), Large (c), Jumbo (d), Large and Jumbo (e), and ungraded (f) commercial grades. Numbers above bars represent sample sizes.


A: Small
Year 1
N = 167
60
30
0
99
32
26
6
4
1
2
3
4
5
6
7
8
Year 2
N = 241
70
35
0
42
153
20
18
4
3
1
1
2
3
4
5
6
7
8
Year 3
N = 204
60
30
0
5
106
67
9
7
5
5
1
2
3
4
5
6
7
8
Frequency (%)
Age (yr)

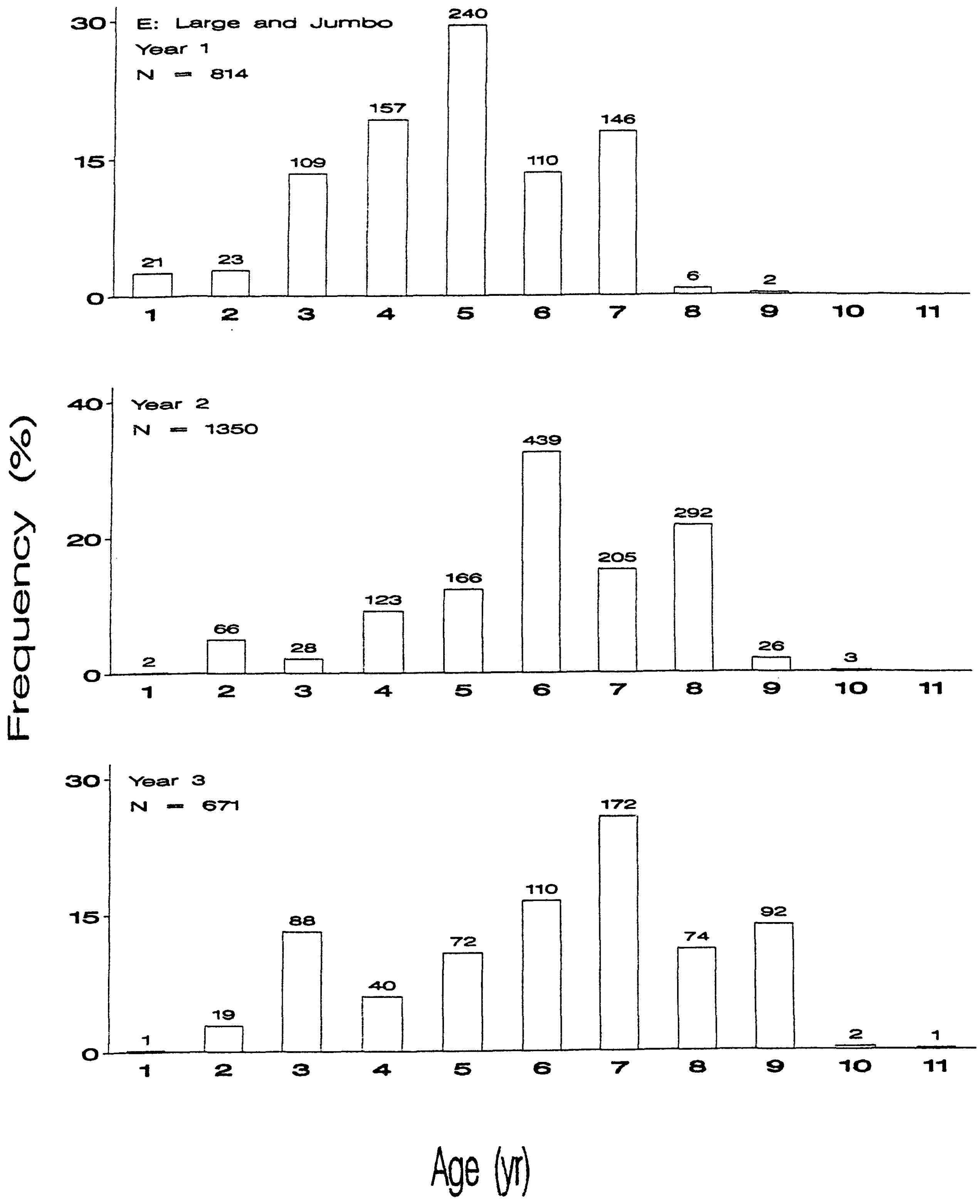

B: Medium
Year 1
N = 376
30
15
0
62
70
105
66
52
15
5
1
1
2
3
4
5
6
7
8
9
10
Year 2
N = 260
40
20
0
11
98
19
46
19
48
11
6
2
1
2
3
4
5
6
7
8
9
10
Year 3
N = 240
40
20
0
2
66
92
12
25
13
17
5
8
1
2
3
4
5
6
7
8
9
10
Frequency (%)
Age (yr)

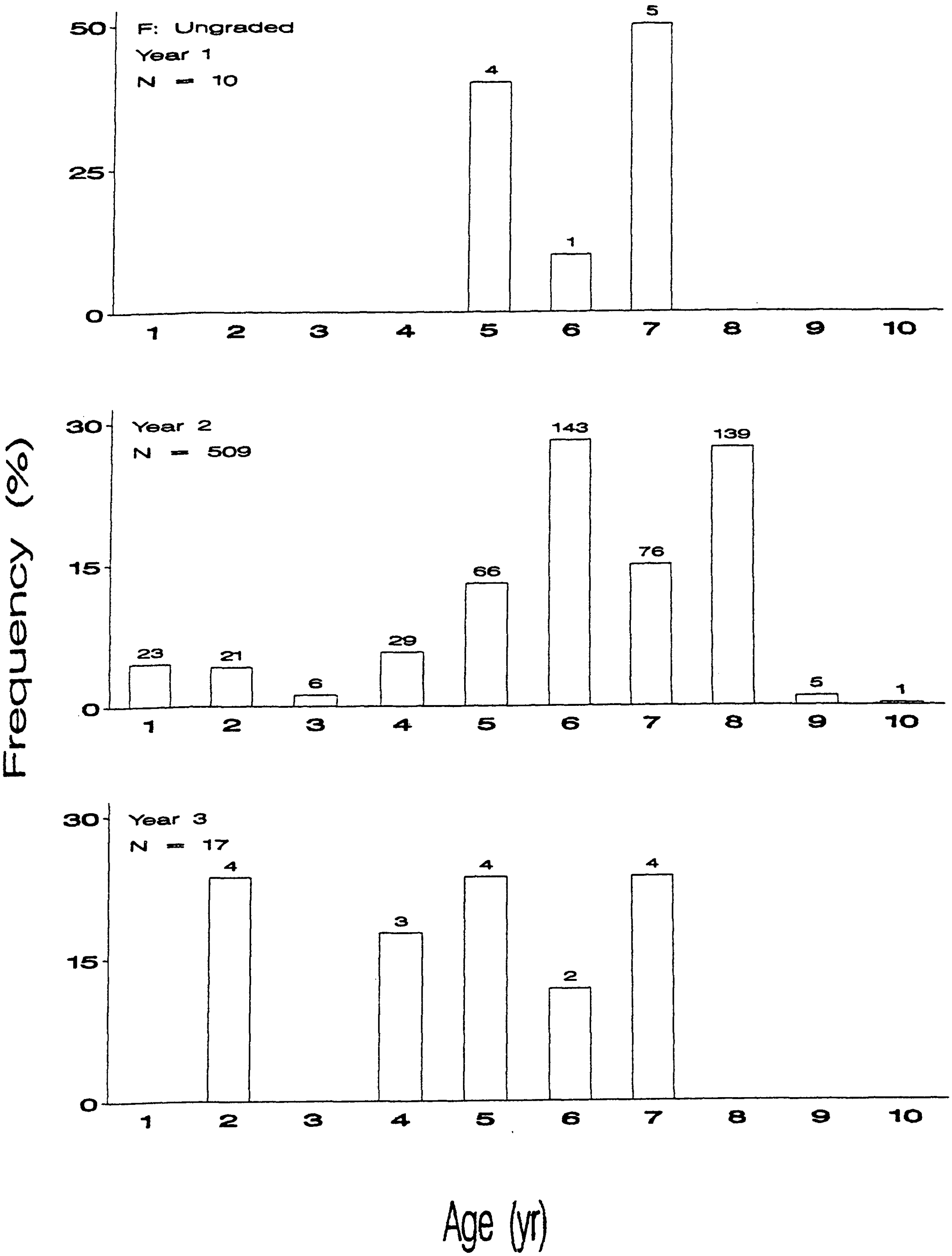


C: Large
Year 1
N = 814
30
15
0
21
23
109
157
240
110
146
6
2
1
2
3
4
5
6
7
8
9
10
Year 2
N = 868
40
20
0
2
66
28
113
120
291
115
123
10
1
2
3
4
5
6
7
8
9
10
Year 3
N = 291
30
15
0
14
37
16
33
45
77
23
44
2
1
2
3
4
5
6
7
8
9
10
Frequency (%)
Age (yr)



D: Jumbo
Year 2
N = 482
Frequency (%)
40
20
0
10
46
148
90
169
16
3
1
2
3
4
5
6
7
8
9
10
11
Year 3
N = 380
30
15
0
1
5
51
24
39
65
95
51
48
1
1
2
3
4
5
6
7
8
9
10
11
Age (yr)


E: Large and Jumbo
Year 1
N = 814
30
15
0
21
23
109
157
240
110
146
6
2
1
2
3
4
5
6
7
8
9
10
11
Year 2
N = 1350
40
20
0
2
66
28
123
166
439
205
292
26
3
1
2
3
4
5
6
7
8
9
10
11
Year 3
N = 671
30
15
0
1
19
88
40
72
110
172
74
92
2
1
1
2
3
4
5
6
7
8
9
10
11
Frequency (%)
Age (yr)


F: Ungraded
Year 1
N = 10
50
25
0
4
1
5
1
2
3
4
5
6
7
8
9
10
Year 2
N = 509
30
15
0
23
21
6
29
66
143
76
139
5
1
1
2
3
4
5
6
7
8
9
10
Year 3
N = 17
30
15
0
4
3
4
2
4
1
2
3
4
5
6
7
8
9
10
Frequency (%)
Age (yr)

ages 2, 4, and 6 were most common comprising 38%, 18%, and 18.5%. Ages ranged from 1 to 9 in year 3, though ages 2 and 3 made up most of the distribution, 28% and 38%, respectively.

In Large grade fish, ages ranged from 1 to 9 in year one (Figure 9c). Age 5 was most abundant making up 29% of that distribution, although ages 3, 4, 6, and 7 were also common. Ages ranged from 1 to 9 in year 2, with age 6 fish making up 34% of the distribution. Ages 4, 5, 7, and 8 were also common. Ages ranged from 2 to 10 in year 3. Age 7 was most common accounting for 26%. Ages 3, 5, 6, and 9 were also abundant although each made up less than 15%.

Jumbo grade fish were not collected in the first year. Ages ranged from 4 to 10 in year 2, with ages 6 and 8 making up 31% and 35%, respectively (Figure 9d). Ages ranged from 1 to 11 in year 3, with age 10 being absent. Age 7 was most abundant, making up 25%. Ages 3, 6, 8, and 9 were also common making up 13 - 17% each.

The pooled Large and Jumbo grades age composition was identical to the Large grade in the first year, as jumbo fish were not collected that year (Figure 9e). Ages ranged from 1 to 10 in year 2, with ages 6 and 8 making up 33% and 22%, respectively. Ages 5 and 7 were also common making up 12% and 15%. Ages ranged from 1 to 11 in year 3. Age 7 was most common making up 26%. Ages 3, 5, 6, 8, and 9 were also abundant accounting for 10 - 16% each.

In ungraded fish, ages ranged from 5 to 7 in year one (Figure 9f). Ages 5 and 7 were most abundant making up 40% and 50%, respectively. Ages ranged from 1 to 10 in the second year, with ages 6 and 8 making up over half the distribution at

28% and 27%, respectively. Age 2 and ages 4 - 7 were present in year 3. Ages 2, 5, and 7 were most common each making up 24%.

DISCUSSION

Age Determination

I have validated sectioned otoliths for ageing Atlantic croaker in the Chesapeake Bay region at ages 1 – 9 years. My validation extends previous marginal increment validation of sectioned otoliths, validated to age 7 (Barbieri et al., 1994a), and Barger's (1985) validation of pooled ages, a method considered inadequate in other species (Gaichas, 1997). My validation includes formal significance testing using ANOVA, something absent in previous studies (Barger, 1985; Barbieri et al., 1994a). As a result, sectioned otolith validation is now on a statistically sound basis, not just a qualitatively based assessment. Finally, with the oldest recorded Atlantic croaker being age 15 (Hales and Reitz, 1992), sectioned otolith age determination is now validated by individual age group for 60% of the life span of the species.

Age Composition

My findings indicate the presence of unusually large numbers of older fish in the Chesapeake Bay region in recent years. Fish ages 7-11 made up over 27% of my Observed Age composition, a finding very different from previous studies where fish ages 7 and older made up only 0 – 2% of the observed age compositions (Music and Pafford, 1984; Barger, 1985; Ross, 1988; Barbieri et al., 1994a). Over a four year period, 1988 – 1991, Barbieri et al. (1994a, see Figure 7) collected only 34 Atlantic croaker ages 7 – 8 from the Chesapeake Bay region, roughly 2% of their observed age composition. In contrast, I collected 1169 fish ages 7 – 8 over a three year period, 1998 – 2000, using the same collection procedure, about 24% of my Observed Age composition. In addition, I collected 143 fish ages 9 – 11, ages absent in Barbieri et al. (1994a). This large difference indicates that Atlantic croaker population age structure has changed greatly in the Chesapeake Bay region since 1991.

Fluctuations in Year-Class Strength

My results indicate that Atlantic croaker year-class strengths have changed greatly since 1987. The 1987, 1988, and 1989 year-classes were consistently weak generally making up less that 1%, of the Observed Age composition, when they were ages 8 – 10 in year 1, 9 and 10 in year 2, and 10 and 11 in year 3. Stronger year-classes then followed starting with the 1990 year-class which made up 9 – 19% of the Observed Age composition each year, when those fish were ages 7 – 9. The 1992 year-class was very strong making up 17 – 27% of the Observed Age composition each year, when it was ages 5 – 7. These large changes in year-class strength probably explain the large differences in observed age compositions that Barbieri et al. (1994a) and I found. The 1987 – 1989 year-classes that I found were weak, were 1 – 4 years of age from 1988 – 1991, when Barbieri et al. (1994a) collected, yet these ages made up about 84% of their observed age compositions. The 1986 and older year-classes, ages 5 – 8 from 1988 - 1991 when Barbieri et al. (1994a) collected, made up only 16% of their observed age composition. The first strong year-class I found, the 1990 year-class, was only age 1 in 1991, may not have been fully recruited to the fishery when Barbieri et al. (1994a) collected them, and would have made up, at most, 12% of their observed age composition. The strong

1992 year-class was wholly absent. It appears, therefore, that Barbieri et al. (1994a) collected during a period of weak year-classes. As a result, their age composition contained very few older fish. In contrast, I collected during a period of both strong and weak year-classes. As a result, I found large numbers of old fish.

CHAPTER 2

Size Composition and Growth

INTRODUCTION

Studies of size and growth of Atlantic croaker have a long history. Early workers presented size-at-age data based on length frequencies or ages determined from scale readings (Welsh and Breder, 1923; Hildebrand and Cable, 1930; Gunter, 1945; Suttkus, 1955; Bearden, 1964; Hansen, 1969; Hoese, 1973; White and Chittenden, 1977). More recently, researchers have reported sizes-at-age based on scale or sectioned otolith readings, and they have modeled growth using the von Bertalanffy (1938, 1957) curve in adults (Music and Pafford, 1984; Barger 1985; Ross, 1988; Hales and Reitz, 1992; Barbieri et al., 1994a) and a Laird-Gompertz model in larvae and juveniles (Laird et al., 1965; Nixon and Jones, 1997).

While size-at-age and von Bertalanffy growth parameters are difficult to compare between reports on adult Atlantic croaker, past collections have generally been made up of predominantly small fish. For example, maximum sizes were 389 TL for Music and Pafford (1984), 417 for Barger (1985), and 400 for Barbieri et al. (1994a), with most fish being under 300 mm. Although Ross (1988) collected over 100 large fish, fish ranging from 400 to 533 mm TL, he aged them using scales, an ageing method with many problems (Roithmayr, 1965; Joseph, 1972; Mericas, 1977; White and Chittenden, 1977; Barger and Johnson, 1980; Jearld, 1983; Barbieri, 1993). Thus, the effects that large fish have on estimates of growth are unclear, because most work has been based on predominantly small fish or age determination using scales.

In this chapter, I investigate the effects of large fish on size composition and growth estimates by presenting length frequencies, observed size-at-age data, estimates of maximum length, and a length-weight relationship. I also model adult growth using the von Bertalanffy (1938, 1957) model. Lastly, I compare my results with work done by Barbieri (1993) and Barbieri et al. (1994a) during a period of time when large fish were not common in the Chesapeake Bay region.

METHODS

Size Compositions and Size-at-Age

Size compositions and sizes-at-age were described from Atlantic croaker (n=4862) collected in the Chesapeake Bay region and aged using sectioned otoliths (Chapter 1, Methods). To describe size compositions, size range in total length (TL), mean TL, length (TL) frequency distribution, 99.5, 99, and 90 percentiles ($L_{99.5}$, L_{99}, L_{90}), and the percentage of Unusually Large fish, fish 400 mm TL or larger were reported for each year and for all data pooled. To describe sizes-at-ages, mean size-at-age was estimated for each age group and for each sex within age groups.

Mean total lengths were compared between years and between sexes within years using one-way ANOVA and unpaired t-tests, respectively (Zar, 1984). Length frequencies were compared among years using a Kolmogorov-Smirnoff two-sample test, and finally, mean sizes-at-age were compared between age groups and between sexes within age groups using one way ANOVA and unpaired t-tests, respectively (Zar, 1984).

Growth Models

Growth of adults was modeled using the von Bertalanffy (1938, 1957) model. In doing so, growth curves were fit to observed age and length (TL) of each fish collected (Chapter 1, Methods), by least squares non-linear regression (PROC NLIN; SAS Institute, 1999) using the equation (Ricker, 1975),

$$L_t=L_\infty(1-e^{(-k(t-t_o))}),$$

where L_t = TL at age t,

L_∞ = average theoretical maximum size,

k = Brody growth coefficient,

t = age,

t_o = theoretical age when length would be zero, the x-intercept.

Parameters were estimated for each separate sex and for sexes pooled, in three ways: 1) using un-weighted least squares non-linear regression of TL on age. 2) using weighted least squares non-linear regression of TL on age. In doing so TL's within an age group were weighted by 1/n, the inverse sample size for their age group. 3) by fitting only TL and age data from September collections in 1998 and 1999. This latter approach was taken to reduce variation due to within year growth. September was chosen as it best represents the average biological birthdate of Atlantic croaker spawned in the Chesapeake Bay region (Barbieri, 1993). As a result, September sizes should most accurately estimate sizes-at-annual age. Finally, differences in parameter estimates between sexes were evaluated using likelihood ratio tests (Kimura, 1980; Cerrato, 1990).

Length-Weight Relationships

Length-weight relationships were determined from all fish collected (n=4862) using un-weighted non-linear regression (PROC NLIN; SAS Institute, 1999) and the equation,

$$W = a(L)^b,$$

where W = total weight (TW),

L = TL,

a, *b* = empirical parameters.

Relationships were determined for all females, all males, and for all fish, sexes pooled. Differences in parameter estimates between sexes were evaluated using likelihood ratio tests (Kimura, 1980).

RESULTS

Size Composition

Observed size compositions varied moderately by biological year. Sizes ranged from 208 to 537 mm TL, $L_{99.5} = 464$, $L_{99} = 455$, and $L_{90} = 415$, with a mean size of 332 mm TL for pooled data (Table 8). Sizes ranged from 208 to 495 mm, $L_{99.5} = 448$, $L_{99} = 439$, and $L_{90} = 374$, with a mean of 306 mm in year 1. Sizes ranged from 210 to 537 mm, $L_{99.5} = 468$, $L_{99} = 460$, and $L_{90} = 423$, with a mean size of 348 mm in year 2. Sizes ranged from 208 to 474 mm, $L_{99.5} = 460$, $L_{99} = 447$, and $L_{90} = 403$, with a mean of 332 mm in year 3. Mean lengths were significantly different between years (ANOVA, $F = 245.70$, df =2, 4858, $p < 0.0001$). Unusually Large fish made up 16.9% ($n = 823$) of the observed size composition for pooled data, 5.8% ($n = 79$) in year 1, 25.72% ($n = 607$) in year 2, and 12.1% ($n = 137$) in year 3. Most of the Unusually Large Atlantic croaker were female. Of the 823 fish in the pooled data, 94% were female and only 6% were male. All fish over 457 mm TL were female.

Female and male size compositions were distinctly different within each year. Females were larger overall, with a mean size of 343 mm TL and a size range of 210 mm TL to 537 mm TL (pooled Data, Table 9). Males had a mean size of only 304 mm and a size range of 208 to 457 mm. Both sexes were smallest in year 1. The mean size of females was 313 mm with a range of 215 to 495 mm then, and the mean size of males was 290 mm with a range of 208 to 457 mm. Both sexes were largest in the year 2. The mean female was 360 mm with a size range of 210 to 537 mm then, and the mean male was 312 mm with a

Table 8. Mean, minimum, maximum, $L_{99.5}$, L_{99}, L_{90}, and standard error of mean total length (TL mm) for Atlantic croaker each year in the Chesapeake Bay region.

Year	N	Mean	Std Error	Min	Max	$L_{99.5}$	L_{99}	L_{90}
1	1367	305.72	1.34	208	495	448	439	374
2	2360	348.04	1.25	210	537	468	460	423
3	1132	332.12	1.60	208	474	460	447	403
pooled	4859	332.42	0.85	208	537	464	455	415

Table 9. Mean, minimum, maximum, and standard error of mean total length (TL mm) of female and male Atlantic croaker each year in the Chesapeake Bay region.

Females

Year	N	Mean	Std Error	Min	Max
1	928	312.99	1.71	215	495
2	1765	360.26	1.42	210	537
3	824	341.10	1.87	220	474
pooled	3517	343.30	1.00	210	537

Males

Year	N	Mean	Std Error	Min	Max
1	439	290.35	1.88	208	457
2	595	311.80	2.01	211	446
3	308	308.05	2.65	208	420
pooled	1342	303.92	1.27	208	457

size range of 211 to 446 mm. Females had a mean size of 343 mm in year 3, with a size range of 220 to 474 mm. Males had a mean size of 308 mm then, with a size range of 208 mm to 420 mm. There were significant differences in mean lengths between the sexes in all years (Table 10). Mean sizes were significantly different between each year for females (ANOVA, $F = 215.79$, $df = 2, 3516$, $p < 0.0001$) and for males (ANOVA, $F = 29.71$, $df = 2, 1341$, $p < 0.0001$).

Length frequency distributions varied between years. The distribution appeared unimodal in year 1, distributed about the 300 mm interval (Figure 10). It appeared unimodal but skewed towards larger sizes in year 2, with a peak at 400 mm. The distribution was largely unimodal in year 3, with a peak at 350mm. KS tests found length frequency distributions were significantly different between each year (Table 11), but individual length frequencies were not significantly different from the pooled length frequency distribution.

Size-at-Age

Mean lengths increased with age. Observed mean length increased from 247 mm at age 1 to 387 mm by age 10 (Table 12). The one age 11 fish collected was 403 mm. Differences between means at age were significant (ANOVA, $F = 726.83$, $df = 9, 4858$, $p < 0.0001$).

Mean lengths-at-age differed by sex. Females were significantly larger at each age than males except at age 10 (Table 13). Differences between females and males generally increased from 15.86 mm at age 1 to 47.62 mm at age 9. Though not significant, the difference between female and male mean size was 56 mm at age 10.

Table 10. Unpaired t-tests for differences in mean total lengths (TL mm) of female and male Atlantic croaker in the Chesapeake Bay region. All results significant at $\alpha = 0.05$ with $p < 0.0001$.

Year	t	df
1	8.92	1104
2	19.69	1226
3	10.21	630
pooled	24.34	3087

Figure 10. Length (TL mm) frequency distributions of Atlantic croaker in the Chesapeake Bay region each year. Lengths are grouped by 25 mm size intervals. X-axis values are size interval midpoints, and numbers above bars represent sample sizes in each interval.

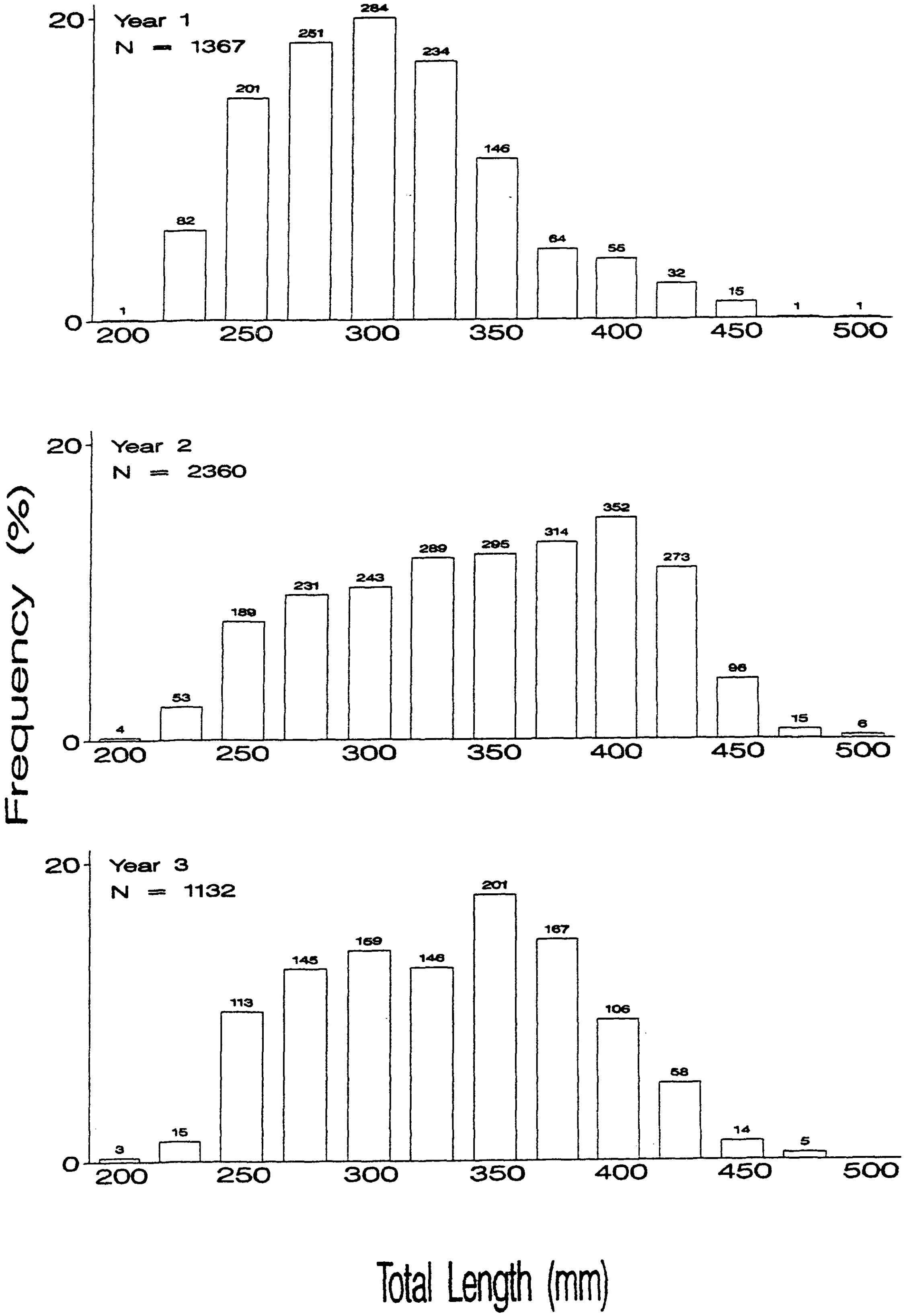

Frequency (%)
Total Length (mm)
Year 1
N = 1367
1
82
201
251
284
234
146
64
55
32
15
1
1
Year 2
N = 2360
4
53
189
231
243
289
295
314
352
273
96
15
6
Year 3
N = 1132
3
15
113
145
169
146
201
167
106
58
14
5
0
20
200
250
300
350
400
450
500

Table 11. Kolmogorov-Smirnov two-sample tests for differences between length frequencies of Atlantic croaker from the Chesapeake Bay region each year, and between each year and all years pooled. "ns" indicates non-significance at α = 0.05.

Years Compared	KS	D	KSa	P
1:2	0.34	1	1.86	0.002
1:3	0.28	0.63	1.61	0.0111
2:3	0.46	1	1.66	0.0079
1:All	0.09	0.48	0.47	ns
2:All	0.40	1	0.89	ns
3:All	0.20	0.66	0.63	ns

Table 12. Observed mean total length (TL mm), 95% confidence limits, standard error, and sample size for age 1-10 Atlantic croaker in the Chesapeake Bay region.

Age	N	Mean TL	CL	Standard Error
1	268	247.07	244.29 - 249.86	1.41
2	658	267.76	265.94 - 269.59	0.93
3	560	292.52	289.80 - 295.24	1.39
4	509	313.74	310.72 - 316.77	1.54
5	663	339.43	336.21 - 342.66	1.64
6	889	360.58	357.81 - 363.36	1.41
7	646	374.11	370.85 - 377.37	1.66
8	523	395.44	391.93 - 398.95	1.79
9	135	386.13	379.16 - 393.09	3.52
10	7	386.71	345.33 - 428.09	16.91
11	1	403		

Table 13. Minimum, maximum, and mean total length (TL mm), standard error, and sample size by sex for age groups 1-10 of Atlantic croaker in the Chesapeake Bay region with t-tests for between sex differences in mean size-at-age. "ns" indicates non-significance at α = 0.05.

	FEMALES				MALES				t-test		
Age	N	Min-Max	Mean	Std. Error	N	Min-Max	Mean	Std. Error	t	df	p
1	193	210-339	251.51	1.70	75	208-300	235.65	2.02	6.01	181	<0.0001
2	448	212-357	271.53	1.18	210	217-330	259.73	1.31	6.69	524	<0.0001
3	384	234-395	299.22	1.69	176	226-375	277.90	2.03	8.07	411	<0.0001
4	359	239-417	323.50	1.78	150	218-354	290.38	2.01	12.34	377	<0.0001
5	475	263-487	351.12	1.89	188	259-403	309.92	2.03	14.84	504	<0.0001
6	658	254-465	372.24	1.50	231	259-446	327.39	2.24	16.63	450	<0.0001
7	487	282-495	383.71	1.74	159	263-457	344.71	3.12	10.91	264	<0.0001
8	417	283-537	405.22	1.73	106	279-440	356.94	3.72	11.76	154	<0.0001
9	90	315-475	402.00	3.73	45	304-417	354.38	4.78	7.86	96	<0.0001
10	5	356-429	402.80	12.57	2	300-393	346.50	46.50	1.17	1	ns

Growth

The von Bertalanffy growth curve well described growth of adult Atlantic croaker in the Chesapeake Bay region. Coefficients of determination, r^2, were above 0.98 for all curves (Table 14), implying good statistical fits and suggesting that the von Bertalanffy model is reasonable for adult Atlantic croaker in the Chesapeake Bay region (Figure 11).

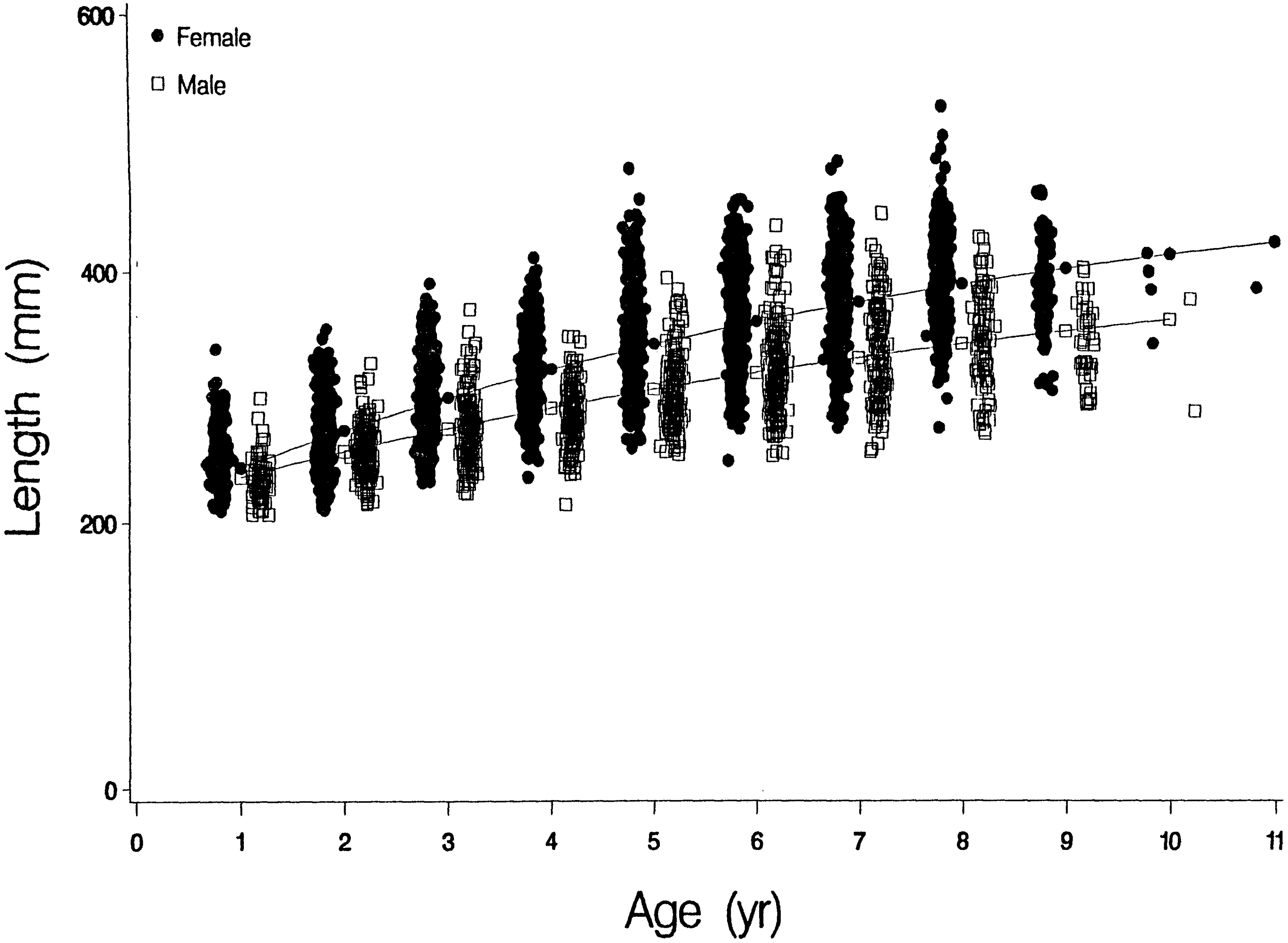
Both male and female Atlantic croaker grow rapidly in the first year or two, then growth slows greatly. Males reach about 235 mm TL at age 1, about 40 – 60% of L_∞(Figure 11, Tables 13, 14). Males then grow much less rapidly after age 1, reaching about 260 mm at age 2 (48 – 66% of L_∞) 278 mm at age 3 (51 – 71% of L_∞), and 290 mm at age 4 (54 – 74% of L_∞). Similarly, females reach about 251 mm at age 1, roughly 47 – 63% of L_∞. Females then grow much less rapidly after age 1, reaching 271 mm at age 2 (51 – 68% of L_∞), 299 at age 3 (56 – 75% of L_∞), and 323 at age 4 (60 – 81% of L_∞).

Von Bertalanffy parameter estimates differed greatly by fitting method and sex. Values of L_∞ ranged from 390.8 mm TL (Table 14: males, all collections, weighted) to 541.2 (pooled, all collections, unweighted; males, September collections, unweighted). Values of k ranged from 0.08 (males, all collections, unweighted) to 0.38 (females, September, unweighted). Values of t_o ranged from –6.7 (males, all collections, unweighted) to –0.95 (females, September collections, unweighted). Estimates of L_∞ were largest, except for males, in unweighted regressions using all collections, values being 535.1mm TL, 501.6, and 541.2 for females, males, and sexes pooled, respectively. L_∞ estimates were

Table 14. von Bertalanffy growth parameter estimates with sample sizes, 95% confidence intervals (CI) and coefficients of determination (r^2) for each of three types of regression fitting. See text for explanation of fitting methods.

			L_∞		k		t_o	
	N	r^2	Estimate	CI	Estimate	CI	Estimate	CI
1. All collections - unweighted								
Pooled	4859	0.99	541.2	492.9 - 589.4	0.10	0.08 - 0.12	-5.01	-5.75 - -4.26
Females	3517	0.99	535.1	493.6 - 576.8	0.11	0.09 - 0.14	-4.44	-5.11 - -3.76
Males	1342	0.99	501.6	400.1 - 603.1	0.08	0.04 - 0.13	-6.70	-8.68 - -4.71
2. All collections - weighted								
Pooled	4859	0.99	439.0	430.7 - 447.4	0.17	0.16 - 0.19	-3.57	-3.91 - -3.23
Females	3517	0.99	441.6	434.4 - 448.9	0.19	0.18 - 0.21	-3.09	-3.39 - -2.79
Males	1342	0.99	390.8	374.4 - 407.1	0.18	0.14 - 0.22	-4.10	-4.94 - -3.25
3. September collections - unweighted								
Pooled	348	0.99	403.4	385.3 - 421.5	0.34	0.25 - 0.43	-1.19	-1.83 - -0.55
Females	301	0.99	399.0	381.9 - 416.1	0.38	0.27 - 0.49	-0.95	-1.64 - -0.26
Males	47	0.99	541.2	140.1 - 942.4	0.11	-0.08 - 0.29	-4.02	-8.39 - 0.35

Figure 11. Observed total lengths-at-age and fitted von Bertalanffy growth curves by sex for Atlantic croaker in the Chesapeake Bay region. Data points have been jittered by sex for illustrative purposes.


Female
Male
Length (mm)
600
400
200
0
Age (yr)
0
1
2
3
4
5
6
7
8
9
10
11

smallest, except for males, in unweighted regressions using September collections, values being 399 mm TL, 541.2, and 403.4 for females, males, and sexes pooled, respectively. L_∞ estimates were intermediate for females (441.6 mm TL) and sexes pooled (439 mm) and smallest for males (390.8 mm) in weighted regressions using all collections. Estimates of k were largest, except for males, in unweighted regressions using September collections, values being 0.380, 0.107, and 0.342 for females, males, and sexes pooled, respectively. k estimates were smallest in unweighted regressions using all collections, values being 0.112, 0.083, and 0.098 for females, males, and sexes pooled, respectively. Estimates of k were intermediate for females (0.194) and sexes pooled (0.342) and largest for males (0.178) in weighted regressions using all collections. Estimates of t_o were largest in un-weighted regressions using September collections, values being -0.95, -4.02, and -1.19 for females, males, and sexes pooled, respectively. t_o estimates were smallest in un-weighted regressions using all collections, values being -4.44, -6.70, and -5.01 for females, males, and sexes pooled. Estimates of t_o were intermediate in weighted regressions using all collections, values being -3.09, -4.10, and -3.57 for females, males, and sexes pooled, respectively.

The significance of between sex differences in von Bertalanffy parameter estimates varied with regression type. Values of L_∞ for females (441.6) were significantly higher than for males (390.8) in weighted regressions using all collections (Table 15). Female/male differences in L_∞ were not significant in either un-weighted regressions, all collections or September collections.

Table 15. Kimura (1980) likelihood ratio tests for between sex differences in estimates of von Bertalanffy growth parameters for Atlantic croaker in the Chesapeake Bay region by three different regression fits. See text for explanation of regression fits. "ns" indicates non-significance at $\alpha = 0.05$.

Parameter	Female	Male	N	df	X^2	p
1. All collections - unweighted						
L_∞	535.1	501.6	4859	1	0.24	ns
k	0.11	0.08	"	1	1.17	ns
t_o	-4.44	-6.70	"	1	5.85	<0.025
L_∞, k, t_o				3	974.71	<0.001
2. All collections - weighted						
L_∞	441.6	390.8	4859	1	27.19	<0.001
k	0.19	0.18	"	1	1.09	ns
t_o	-3.09	-4.10	"	1	9.40	<0.005
L_∞, k, t_o				3	1373.59	<0.001
3. September collections - unweighted						
L_∞	399.0	541.2	348	1	2.38	ns
k	0.38	0.11	"	1	4.89	<0.05
t_o	-0.95	-4.02	"	1	4.87	<0.05
L_∞, k, t_o				3	13.01	<0.005

Female/male differences in *k* were significant only in the un-weighted regression using September collections, for which *k* was 0.38 in females versus 0.11 in males. Between sex differences in t_o and the overall curve (all parameters combined) were significant in all regressions.

Length-Weight

Estimated length-weight relationships were:

$$TW = 4.2\text{x}10^{-5}(TL)^{2.79} \quad (r^2 = 0.99),$$

$$TW = 2.3\text{x}10^{-5}(TL)^{2.89} \quad (r^2 = 0.99),$$

$$TW = 3.1\text{x}10^{-5}(TL)^{2.84} \quad (r^2 = 0.99),$$

for females, males, and sexes pooled, respectively. Kimura's (1980) likelihood ratio tests found significant differences between the sexes in parameters *a*, *b*, and the overall curve (both parameters combined) (Table 16).

Table 16. Kimura (1980) likelihood ratio tests for between sex differences in total length-total weight relationship parameters. All differences were significant at $\alpha = 0.05$, $p < 0.001$.

Parameter	Female	Male	N	df	X^2
a	4.2×10^{-5}	2.3×10^{-5}	4862	1	13.46
b	2.79	2.89	4862	1	11.85
a, *b*			4862	2	89.72

DISCUSSION

Size Composition

The size structure of Atlantic croaker in the Chesapeake Bay region has changed greatly over the past decade in that much larger fish have been present, and in large numbers, in recent years. I found a maximum size of 537 mm TL in contrast to the maximum of 400 mm found by Barbieri (1993). I found 838 fish, 16.9% of my overall collection, as large or larger than the 400 mm maximum that Barbieri (1993) found. Of my fish, 3 were greater than 500 mm TL. 90% of the fish I collected were smaller than 415 mm in contrast to the 90% smaller than 295 mm that Barbieri (1993) found. Indeed, 90% of Barbieri's (1993) fish from 1988 – 1991 were about 40 mm smaller than the overall mean length, 332 mm, I found from 1998 – 2000. The maximum size that I found, 537 mm, is generally much larger than those in most other reports outside the Chesapeake Bay region (417 mm TL – Barger, 1985; 389 mm – Music and Pafford, 1984; 357 mm – White and Chittenden, 1977). Ross (1988) reported about 100 fish from 400 – 533 mm, the only other study to report many large fish like I found in the 400 – 540 mm size range.

The size structure of Atlantic croaker in the Chesapeake Bay region has expanded in recent years rather than just shifting towards larger sizes. The size range that I found, 208 to 537 mm TL, is about 129 mm longer than the size range of 200 to 400 mm TL that Barbieri et al. (1994a) reported. Because minimum sizes are similar (208 mm TL in my study, 200 mm in Barbieri et al.

1994a), the change in size structure appears to reflect a recent expansion into larger sizes.

Size-at-Age and Growth

I found large between sex differences in size-at-age of Atlantic croaker. Between sex differences have not been reported in previous studies, most of which have simply pooled sexes for size and growth analyses (Music and Pafford, 1984; Barger, 1985; Ross, 1988; Barbieri et al., 1994a). Barger (1985) and Barbieri et al. (1994a), however, found no between sex differences though they formally tested for them. Music and Pafford (1984) observed a larger maximum total length and weight for females, but they did not formally test for between sex differences.

I found that most Unusually Large Atlantic croaker in the Chesapeake Bay region are female. This finding is new. Though a few studies have reported very large Atlantic croaker (Hildebrand and Schroeder, 1928; Massmann and Pacheco, 1960; Ross, 1988), these studies did not describe the sex composition of the very large fish.

The von Bertalanffy growth parameter estimates I found generally agree with previous reports except for that of Ross (1988). Estimates of k (0.36) and t_o (-3.26) found by Barbieri et al. (1994a) fall within the range of values I found for k (0.08 – 0.38) and t_o (-6.70 – -0.95), though their L_∞(312.43) falls below the range I found (390.8 – 541.2). Barger (1985) reported values of 419.2, 0.273, and -1.405 for L_∞, k, and t_o, respectively, all of which fall within the range of values I found. Ross (1988) reported values of 645, 0.2, and -0.6 for L_∞, k, and t_o, respectively, of which only k (0.2) falls within the range of values I found.

CHAPTER 3

Mortality

INTRODUCTION

Few workers have reported total annual mortality in Atlantic croaker (White and Chittenden, 1977; Ross, 1988; Barbieri et al., 1994a). White and Chittenden (1977) targeted Atlantic croaker in the warm temperate waters of the Gulf of Mexico, but the pertinence of that study to Atlantic croaker farther North is not clear. Only, Barbieri et al. (1994a) and Ross (1988) have studied Atlantic croaker total annual mortality in the middle Atlantic region of North Carolina and the Chesapeake Bay.

Two principal methods have been used to estimate total annual instantaneous mortality (*Z*) in Atlantic croaker in the middle Atlantic and Chesapeake Bay regions. Ross (1988) and Barbieri et al. (1994a) used regression analysis of catch-curves as described by Chapman and Robson (1960). White and Chittenden (1977) and Barbieri et al. (1994a) estimated *Z* from maximum ages based on negative exponential survivorship as described by Royce (1972). Barbieri et al. (1994a) also estimated *Z* based on maximum age using Hoenig's (1983) pooled regression equation.

Previous estimates of *Z* have varied greatly. White and Chittenden (1977) reported a total annual mortality rate of 96% ($Z = 3.2$) for Atlantic croaker in the Northwestern Gulf of Mexico. In contrast, Ross (1988) reported a *Z* of 1.3 for the Pamlico Sound area and Barbieri et al. (1994a) obtained estimates for the Chesapeake Bay region of *Z*, 0.55, 0.58, and 0.63 using Hoenig's (1983) method, Royce's (1972) method, and regression analysis of a catch-curve, respectively. It is not clear why these estimates range so widely, but it may be due in part to different geographic regions, fishing and natural mortality rates, and methods of age determination and fish collection. The impacts of large fish on estimates of total annual mortality are also unclear. Of the previous studies of mortality in Atlantic croaker, only Ross (1988) collected many fish greater than 400mm total length. However, he used scales and length frequencies to determine ages, methodologies that have often been questioned in this species (Roithmayr, 1965; Joseph, 1972; Mericas, 1977; White and Chittenden, 1977; Barger and Johnson 1980; Jearld, 1983; Barbieri, 1993).

In this chapter, I estimate total annual instantaneous mortality, *Z*, and instantaneous natural mortality, *M*, for adult Atlantic croaker in the Chesapeake Bay region, and compare these estimates with those of Barbieri (1993), Barbieri et al. (1994a), and Barbieri et al (1997).

METHODS

Total annual instantaneous mortality

Instantaneous total annual mortality, *Z*, was estimated from Atlantic croaker (n=4862) collected in the Chesapeake Bay region and aged using sectioned otoliths (Chapter 1, Methods). *Z*, was estimated in three ways: 1) using Royce's (1972) method as described by Chittenden and McEachran (1976), 2) Hoenig's (1983) method, and 3) by regression analysis of a catch-curve (Ricker, 1975).

Assuming negative exponential survivorship (Gulland 1969) and following Royce's (1972) method for estimating natural mortality in unexploited fish stocks, Chittenden and McEachran (1976) described a simple equation to estimate *Z*:

$$Z = 4.6 \,/\, \text{life span},$$

where life span is the maximum age recorded, and the constant, 4.6, comes from the expression (ln100 – ln1), which represents a 99% reduction in the size of an average year-class from mortality over the fishable life span.

Hoenig (1983) described several equations to estimate *Z* from maximum age, based on regression analysis of observed total annual instantaneous mortality rates on maximum observed ages. I used the predictive equation for all taxa:

$$\ln(Z) = a + b\ \ln(t_{\max}),$$

where Hoenig gave values of $a = 1.44$ and $b = -0.982$, and $t_{\max}$ is the maximum observed age.

I estimated maximum age for the Royce (1972) and Hoenig (1983) methods in three ways: 1) as the mean of the three observed maximum ages in 1998, 1999, and 2000, 2) as T_{99} for all years pooled, and 3) as the single maximum observed age over the period 1998 – 2000 (Chapter 1, Table 2).

I used the Adjusted Age Composition (see Chapter 1) to estimate *Z* via regression analysis of a catch-curve. The Adjusted Age Composition was based on pooling all age data from 1998 – 2000 to reduce the effects of variation in year-class strength (Robson and Chapman, 1961). Following Chapman and Robson (1960) and Ricker (1975), only recruited age groups containing five or more fish were used in calculations, and age data were based on collections from all gear types to minimize sampling bias associated with individual gears. Finally, following the above guidelines, ages 3 through 10 were used to construct an initial catch-curve. Catch-curves were also constructed using ages 3 through 9, 2 through 10, and 3 through 9 to evaluate the effects of specific age groups on estimates of *Z*.

Z values were converted to *S* and 1 – *S* following Ricker (1975).

Instantaneous natural mortality

Instantaneous natural mortality rates, *M*, were estimated in 4 ways: 1) using the predictive equation of Alverson and Carney (1975), 2) using Pauly's (1980) equation, and 3) using Royce's (1972) and 4) Hoenig's (1983) methods based on maximum age as described by Barbieri (1993).

The Alverson and Carney (1975) equation estimates M from maximum age and the Brody growth coefficient of the von Bertalanffy growth equation (see Ricker, 1975):

$$t_{\max} \times 0.38 = (1/k) \times \ln [\, (M+3k) / M \,],$$

where: $t_{\max}$ = maximum fish age (as described above) and k = Brody growth coefficient. Values of k, and values of L_∞ for the Pauly (1980) method below, were based on estimates of these parameters for both sexes pooled (see Chapter 2).

The Pauly (1980) equation estimates natural mortality from the von Bertalanffy growth parameter estimates L_∞ and k, and mean annual water temperature:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log k + 0.4634 \log T,$$

where: L_∞= theoretical asymptotic maximum length, k = Brody growth coefficient, and T = mean annual temperature of water inhabited by Atlantic croaker in the Chesapeake Bay region. Mean temperature estimates were 20.11 C and 19.46 C. Estimates were based on temperature data from March through November, 1998 and 1999, at the ambient condition monitoring station at the Virginia Institute of Marine Science (2001) and the Virginia Institute of Marine Science, Juvenile Fish and Blue Crab Trawl Survey (2001), respectively.

Reasoning that Z approximates M when fishing is light or absent, Barbieri (1993) used Royce's (1972) and Hoenig's (1983) methods, as described earlier, to calculate M based on the maximum age before significant modern fisheries developed. That maximum age (15 years) was obtained from Hales and Reitz (1992) who aged otolith sections from Indian middens deposited from 1600-1700 A.D. near St. Augustine, FL.

RESULTS

Maximum Age

Estimates of maximum age were generally similar. Maximum age values were 9 years based on T_{99} for all years pooled, 10 years based on mean of the three observed maximum ages in 1998, 1999, and 2000, and 11 years based on the maximum individual age observed. These values generally agree with observed maximum age values of 10 and 11 for 1998 – 1999 and 2000, respectively (see Table 2 in Chapter 1).

Total Annual Mortality and Survivorship

Estimates of total annual mortality and survivorship were generally similar among maximum age methods. Values of *Z* ranged from a low of 0.40 to a high of 0.51 for maximum ages 11 and 9, respectively (Table 17). Values of 1 – *S* ranged from 0.33 to 0.40 for maximum ages 11 and 9, respectively, and values of *S* ranged from 0.67 to 0.60 for these respective maximum ages.

Estimates of total annual mortality and survivorship based on catch-curve analysis varied. Estimates of *Z* ranged from 0.45 to 0.85 (Table 18). Estimates of 1 - *S* ranged from 0.36 to 0.57, and S ranged from 0.43 to 0.64. The smallest *Z* values, 0.45 and 0.46, best statistical fit (r^2 = 0.84 and 0.89), and smallest confidence intervals (0.22 – 0.67, 0.30 – 0.62) were obtained when age 10 was dropped from the catch-curve. The largest *Z* values, 0.85 and 0.78, poorest statistical fit (r^2 = 0.67 and 0.70), and widest confidence intervals (0.26 – 1.44, 0.33 – 1.23) were obtained when all fully-recruited ages 3 through 10 plus

Table 17. Estimates of total annual instantaneous mortality, *Z*, 1 - *S*, and *S*, based on maximum age methods for listed maximum ages.

Method	Max Age	*Z*	1 - *S*	*S*
Royce (1972)	9	0.51	0.40	0.60
	10	0.46	0.37	0.63
	11	0.42	0.34	0.66
Hoenig (1983)	9	0.49	0.39	0.61
	10	0.44	0.36	0.64
	11	0.40	0.33	0.67

Table 18. Catch-curve regression estimates of *Z*, 1 - *S*, and *S*, with coefficients of determination (r^2) and 95% confidence intervals (CI), based on listed ages.

		Z		1 - *S*		*S*	
Ages	r^2	Estimate	CI	Estimate	CI	Estimate	CI
3 - 10	0.67	0.85	0.26 - 1.44	0.57	0.23 - 0.76	0.43	0.24 - 0.77
3 - 9	0.84	0.45	0.22 - 0.67	0.36	0.20 - 0.49	0.64	0.51 - 0.80
2 - 10	0.70	0.78	0.33 - 1.23	0.54	0.28 - 0.71	0.46	0.29 - 0.72
2 - 9	0.89	0.46	0.30 - 0.62	0.37	0.26 - 0.46	0.63	0.54 - 0.74

age 2, the peak of the curve, were used (Figure 12). The latter two catch-curves, however, included an influential observation, age 10, in the calculations. Abundance at that age was far below the regression line and, as a result, would greatly affect all regression calculations. Deleting age 10 greatly reduces values of Z from 0.85 and 0.78 to 0.45 and 0.46, increases r^2 from 0.67 and 0.70 to 0.84 and 0.89, and greatly narrows confidence intervals from 0.26 – 1.44 and 0.33 – 1.23 to 0.22 – 0.67 and 0.30 – 0.62.

Instantaneous Natural Mortality, M

Estimates of M ranged from 0.15 to 0.39 with an average of 0.28. The Alverson and Carney (1975) equation gave estimates ranging from 0.17 to 0.39, the largest value overall, with an average of 0.29 (Table 19). The Pauly (1980) equation gave estimates ranging from 0.15, the lowest overall value, to 0.37 with a mean of 0.26. The Royce (1972) and Hoenig (1983) equations gave similar values of 0.31 and 0.30, respectively.

Figure 12. Catch-curves, with regression estimates of Z, $1 - S$, S, and r^2 values, based on pooled Adjusted Age Composition over age ranges: A) 3-10, B) 3-9, C) 2-10, and D) 2-9. The "□" symbol indicates an influential observation.

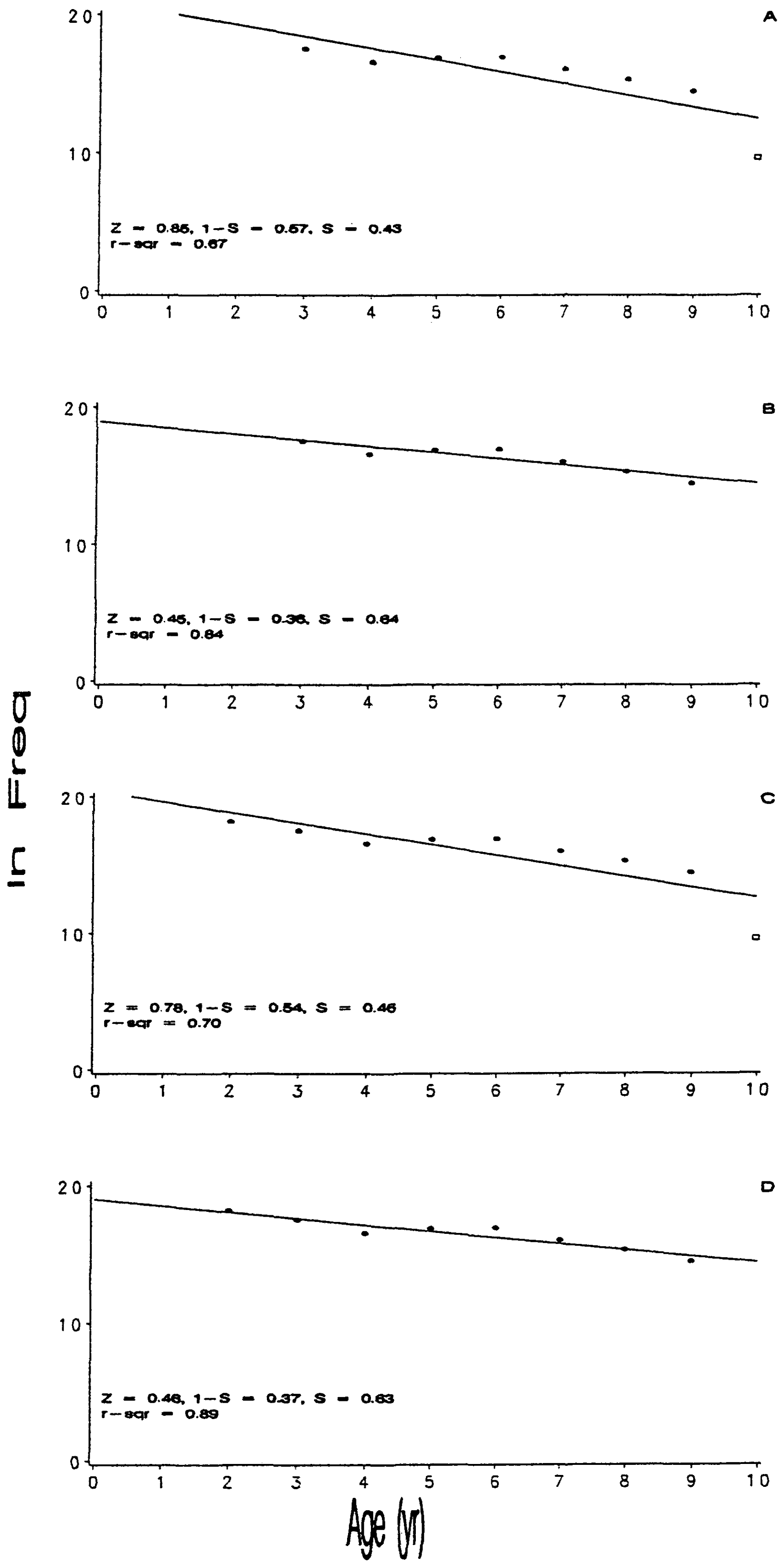

A
Z = 0.85, 1-S = 0.57, S = 0.43
r-sqr = 0.67
B
Z = 0.45, 1-S = 0.36, S = 0.64
r-sqr = 0.84
C
Z = 0.78, 1-S = 0.54, S = 0.46
r-sqr = 0.70
D
Z = 0.46, 1-S = 0.37, S = 0.63
r-sqr = 0.89
0
10
20
0 1 2 3 4 5 6 7 8 9 10
ln Freq
Age (yr)

Table 19. Estimates of instantaneous natural mortality rates, *M*, for Atlantic croaker in the Chesapeake Bay region. See text for description of how parameters were estimated.

Method	Estimates for equation parameters			*M*
Alverson and Carney (1975)	Max Age = 15	$k = 0.10$		0.39
	"	$k = 0.17$		0.31
	"	$k = 0.34$		0.17
Pauly (1980)	$L_\infty = 541.2$	$k = 0.10$	T = 20.11	0.22
	$L_\infty = 439.0$	$k = 0.17$	"	0.23
	$L_\infty = 403.4$	$k = 0.34$	"	0.37
	$L_\infty = 541.2$	$k = 0.10$	T = 19.46	0.15
	$L_\infty = 439.0$	$k = 0.17$	"	0.23
	$L_\infty = 403.4$	$k = 0.34$	"	0.36
Royce (1972)	Max Age = 15			0.31
Hoenig (1983)	Max Age = 15			0.30

DISCUSSION

I found that estimates of *Z* for Atlantic croaker in the Chesapeake Bay region were 0.40 – 0.51 for maximum age methods and 0.45 to 0.84 for the catch-curve method. When age 10, an influential observation, is dropped, my catch-curve estimates, 0.45 and 0.46, agree well with a mid-range value of 0.46 from my maximum age methods, and they indicate 95% confidence limits of 0.22 – 0.67 and 0.30 – 0.62 about *Z*, respectively. My values of *Z* from maximum ages fall just below those of Barbieri et al. (1994a), 0.55 and 0.58. However, Barbieri et al.'s (1994a) catch-curve estimate of 0.63 falls in the center of my range of values (0.45 – 0.85) for catch-curves. Both my maximum age and catch-curve based estimates, as well as those of Barbieri et al. (1994a), fall well below the catch-curve based estimate, $Z = 1.3$, reported by Ross (1988) for North Carolina and the maximum age based estimate of total annual mortality of 96% ($Z = 3.22$) reported by White and Chittenden (1977) for the Northwestern Gulf of Mexico.

I found values for *M* of 0.15 – 0.39 for Atlantic croaker in the Chesapeake Bay region. My values calculated using Alverson and Carney (1975) and Pauly (1980) empirical equations agreed well ranging from 0.17 – 0.39 and 0.15 – 0.36, respectively. My values based on Royce (1972) and Hoenig (1983) maximum age methods, as described by Barbieri (1993), were very close (0.31 and 0.30, respectively) and fell within the range of values I calculated using the empirical equations. My estimates generally agree well with those of Barbieri (1993), 0.29

– 0.36, suggesting that these values are reasonable for adult Atlantic croaker in the Chesapeake Bay region.

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