AGE DETERMINATION, REPRODUCTION, AND POPULATION DYNAMICS OF THE ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*[1,2]

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ABSTRACT

A validated scale method of age determination is described for the Atlantic croaker, *Micropogonias undulatus*. Two age-classes were usually observed, but only one was abundant. Mean total lengths were 155-165 mm at age I and 270-280 mm at age II based on three methods of growth estimation. Fish matured near the end of their first year of life when they were about 140-170 mm total length. Spawning occurred from at least September through March but there was a distinct peak about October. Somatic weight-length relationships varied monthly, and changes appeared to be associated with maturation and spawning. Somatic weight reached a maximum in June, and the minimum was observed in March. Maximum somatic weight loss (24%) occurred in March, but no data were obtained from December through February. In estuaries, age 0 croaker apparently occupied soft-substrate habitat and older fish occurred near oyster reefs. Life spans were only 1 or 2 yr, and the total annual mortality rate was 96%. The above life history pattern appears similar for croaker found throughout the Carolinian Province. Contrasts are presented to illustrate differences in the life histories and population dynamics of croaker found north and south of Cape Hatteras, N.C. A parallel is drawn with apparently similar changes in the American shad, *Alosa sapidissima*, and the suggestion is made that changes in the population dynamics of species that traverse the Cape Hatteras area may represent a general phenomenon.

The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), ranges in the western Atlantic from the Gulf of Maine to Argentina (Chao 1976). It is potentially a very important protein source because it is one of the most abundant inshore fishes of the northern Gulf of Mexico (Gunter 1938, 1945; Moore et al. 1970; Franks et al. 1972) and the Atlantic Ocean off the southeastern United States (Haven 1957; Bearden 1964; Anderson 1968).

Much work has been done on this species. However, many aspects of its life history and population dynamics are not clear; because no reliable method of age determination exists, and reproduction has not been studied intensively. A few early workers, including Welsh and Breder (1924) and Wallace (1940), attempted to age croaker using scales; but criteria for marks were not described and methods were not validated. More recent workers, in general, have not attempted to use hard parts to determine croaker age and growth. The scale method is difficult to apply to croaker (Joseph 1972), and this may be related to its migratory habits and extended spawning season (Suttkus 1955). Only Wallace (1940) studied reproduction using a large series of gonads. However, he worked north of Cape Hatteras, N.C. The life history of croaker found north of Cape Hatteras seems quite different from that of individuals in the Carolinian Province. Studies of reproduction in croaker found south of Cape Hatteras have been based on few fish (Gunter 1945; Bearden 1964) or fish less than 200 mm long (Hansen 1969).

This paper describes a validated method of age determination for croaker, their weight-length and girth-length relationships, habitat segregation between age-groups, spawning seasonality, somatic weight variation, growth, maximum size, life span, and total annual mortality rates. Finally, it contrasts the life histories of croaker found north and south of Cape Hatteras. Geographically, statements made herein apply to the Carolinian Province and/or more northerly waters. With modifications, particularly ones due to calendar differences in seasons, our findings may also apply in the southern hemisphere; but further work is needed there.

MATERIALS AND METHODS

Collections were made from commercial shrimp trawlers during 1974 in the Gulf of Mexico off

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Freeport-Galveston and Port Aransas, Tex., and Cameron, La. Fish were also collected by trawling in Palacios, Galveston, and Matagorda bays, Tex., and Calcasieu Lake, La. Additional fish, hereinafter termed reef fish, were captured by angling with dead shrimp bait (about 25 mm long) near an oyster bar in Galveston Bay. Collection months are indicated in Figure 1.

A sample was taken from each trawl catch by shoveling into a 25-liter container small portions of the catch from various areas of the deck. Unusually large fish were arbitrarily selected to obtain older fish to develop an ageing technique. Total length was measured on each croaker. Total and gonad weights and girth at the origin of the dorsal fin were determined for fish over a broad size range during each sampling period. Scales below the lateral line posterior to the pectoral fin were removed from 1,123 fish, were pressed on plastic slides, and were examined using a scale projector. Scales were examined from small numbers of croaker collected off Mississippi and Fort Pierce, Fla., and in Chesapeake Bay, Va., to judge whether or not the method of age determination proposed herein is valid throughout their range in the Carolinian Province and more northerly waters. The size and appearance of the gonads of more than 1,700 fish were examined, and ovaries were classified following Nikolsky (1963) as summarized by Bagenal and Braum (1971) except that the immature and resting stages were combined.

The regressions of somatic, gonad, and total weights, and girth on total length were computed to express the best linear or quadratic fit using the Statistical Analysis System (Service 1972). Sex data were pooled to compute total weight-length, somatic weight-length, and girth-length regressions, because F tests (Ostle 1963:204) indicated that pooled regression lines were appropriate.

SPAWNING

Spawning occurred over a protracted period extending at least from September to late March, but there was a distinct peak about October. The regressions of gonad weight on length were not significant during May, June, or July for either sex. The mean gonad weight in this period was 0.10 g, and its 95% confidence limits were 0.09-0.11 g. The regressions of gonad weight on length (Figure 2) indicate that gonad development in each sex began by late August, increased greatly during September, reached a peak in October, declined greatly by November, and was at the latter level in March. Similarly, the coefficients of determination (r^2) of the regression lines (Table 1) show that gonad weight variation in each sex was increasingly associated with length until October and then greatly declined. Therefore, it appears that peak spawning occurred in October. Fish captured in the Gulf and by the reef were in all stages of development during September, as were trawl-caught bay fish in October (Figure 3). Therefore, spawning apparently began at least by late September, and some individuals finished or had nearly finished spawning then. Most spawning occurred during October in agreement with the gonad weight-length analyses, because most fish captured in the Gulf were still immature in September. Most fish captured near the reef and in the Gulf were ripe or spent during October and November. Specimens captured in the Gulf during late March were in a resting stage or nearly spent, so that spawning is apparently completed by late March except by a few individuals.

Croaker started to mature at about 140-170 mm total length. Extrapolated x-intercepts or inflection points of the regressions of gonad weight on total length occur in that size range for each sex (Figure 2). Developing fish as small as 136 mm were observed.

Many aspects of croaker spawning appear similar throughout the Carolinian Province. The prolonged spawning period suggested by our data is consistent with frequently reported collections of fish about 25-40 mm long from October to June (many references including Suttkus 1955; Bearden 1964; Hansen 1969; Parker 1971; Swingle 1971; Christmas and Waller 1973; Hoese 1973). The apparent peak of spawning after September agrees with Pearson (1929), Hildebrand and Cable

TABLE 1.—Analyses for the regressions of gonad weight (Y) in grams on total length (X) in millimeters for each sex and month. All regressions were significant at $\alpha = 0.0001$.

Sex	Month	Sample size	r^2	Equation
Males	August	67	0.46	$Y = -0.389 + 0.004X$
	September	108	0.68	$Y = -4.737 + 0.033X$
	October	64	0.73	$Y = -8.804 + 0.055X$
	November	46	0.32	$Y = -2.782 + 0.018X$
	March	35	0.43	$Y = -3.785 + 0.021X$
Females	August	92	0.47	$Y = -0.426 + 0.004X$
	September	286	0.63	$Y = -11.920 + 0.080X$
	October	154	0.67	$Y = -27.135 + 0.177X$
	November	69	0.28	$Y = -15.570 + 0.097X$
	March	41	0.32	$Y = -13.359 + 0.077X$

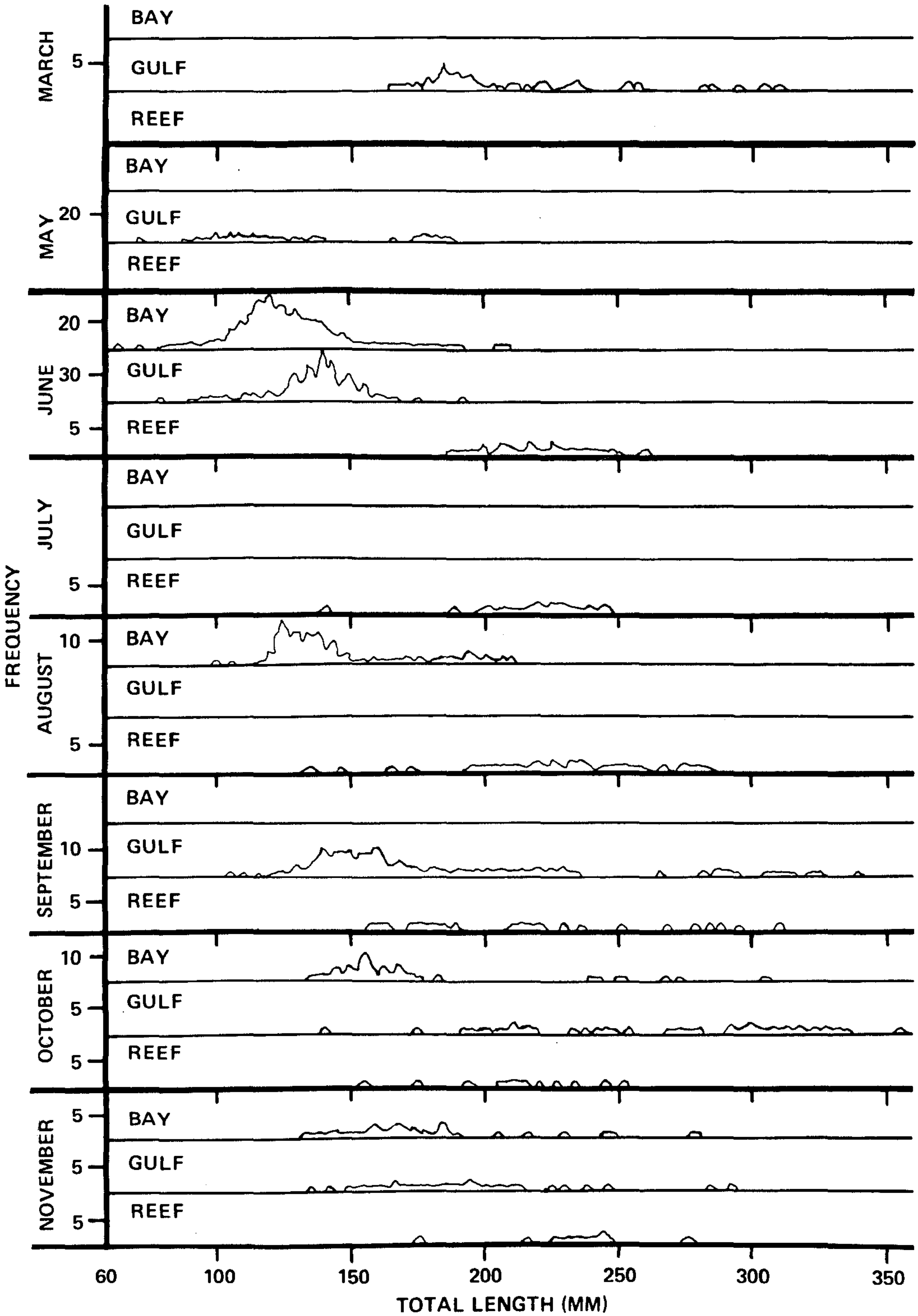


FIGURE 1.—Length frequencies of Atlantic croaker in each area each month. Frequencies are moving averages of three.

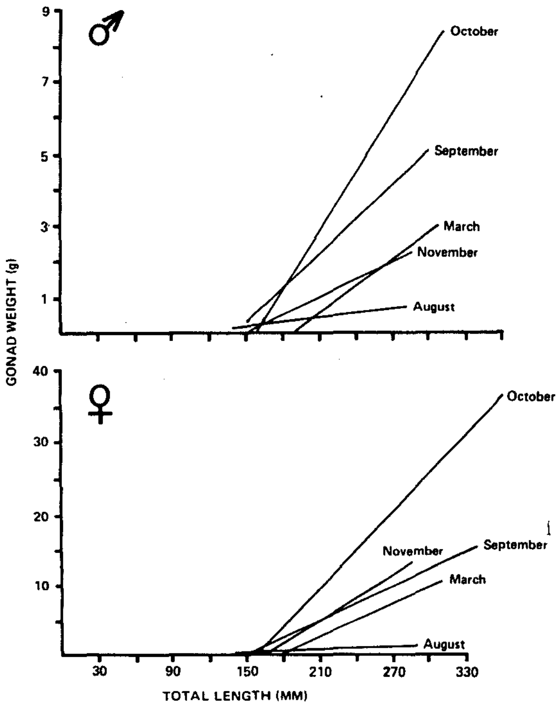


FIGURE 2.—Gonad weight-length regressions for Atlantic croaker by sex and month. The length of each line shows the observed size range.

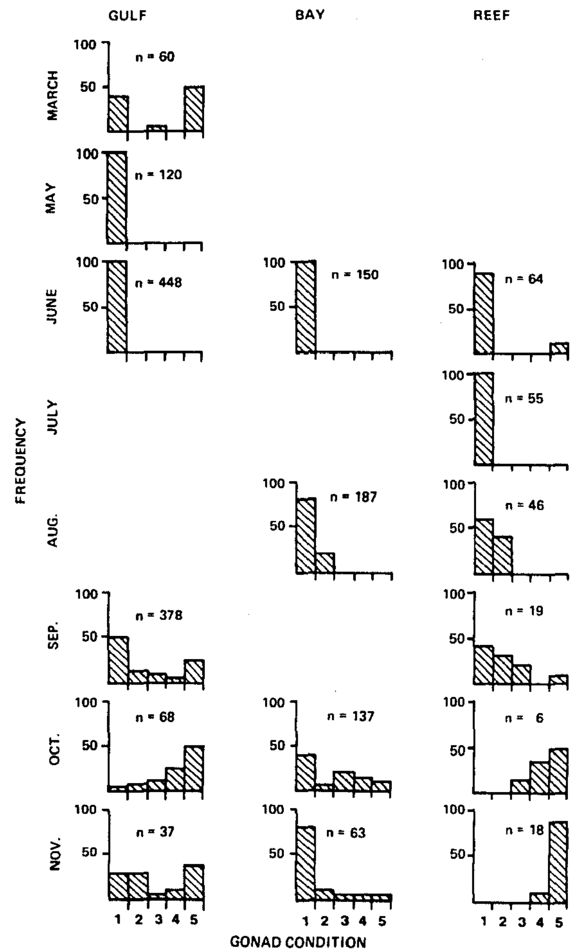


FIGURE 3.—Gonad condition of Atlantic croaker by months and areas. The ordinate represents percent of the sample. Gonad conditions on the abscissa are: (1) immature or resting, (2) maturation, (3) maturity, (4) reproduction, and (5) spent.

(1930), Suttkus (1955), and Bearden (1964); and size at maturity agrees with Pearson (1929), Bearden (1964), Hansen (1969), and Hoese (1973).

The general similarity of croaker reproduction suggests that 15 October, which approximates the time of peak spawning, would be appropriate as a defined hatching date in warm-temperate waters.

SOMATIC WEIGHT VARIATION

Somatic weight-length relationships varied monthly, and these changes appeared to be associated with maturation and spawning. Peak somatic weight occurred during June except in fish smaller than about 140 mm. Somatic weights predicted by the regression equations for other months (Table 2) were compared with predicted weights in June (Figure 4). The somatic weight of individuals smaller than about 140 mm increased from May to at least September. Fish about 140-160 mm showed progressive somatic weight loss from June to September-October. The smallest fish greater than 160 mm, in general, showed the greatest somatic weight loss (or smallest gain); and somatic weight loss, in general, seemed to progressively increase from June to September-October. Somatic weight loss during the fall in fish larger than 140 mm was greatest in September-

TABLE 2.—Analyses for the regressions of somatic weight (Y) in grams on total length (X) in millimeters for each month. All regressions were significant at $\alpha = 0.0001$.

Month	Sample size	r^2	Equation
May	120	0.99	$Y = 39.5303 - 0.8538X + 0.0057X^2$
June	686	0.99	$Y = 71.1692 - 1.3371X + 0.0076X^2$
August	299	0.99	$Y = 120.4035 - 1.9159X + 0.0092X^2$
September	501	0.97	$Y = 158.9511 - 2.3706X + 0.0103X^2$
October	265	0.98	$Y = 148.7089 - 2.2016X + 0.0097X^2$
November	162	0.91	$Y = 73.4739 - 1.2980X + 0.0072X^2$
March	93	0.99	$Y = 132.7087 - 1.8537X + 0.0080X^2$

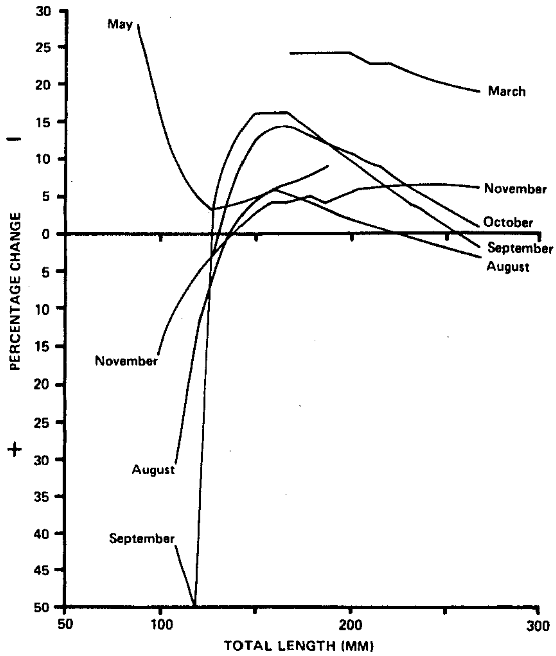


FIGURE 4.—Monthly somatic weight changes in Atlantic croaker. Percentage changes are in comparison to somatic weights in June. The lengths of the curves represent observed size ranges.

October just prior to the time of peak spawning. However, greatest somatic weight loss was observed in March when individuals of 170-250 mm had lost 20-24% of the June weight. The observed somatic weight-length relationships and apparent weight changes in November may be anomalous. Absolute somatic weight decreased in fish smaller than 140 mm, but the percentage weight loss in fish greater than 160 mm was about 5%. Croaker mature at about 140-160 mm, and most fish were small and immature in November. These smaller fish may have just begun to mature for spawning, and their inclusion in the data may have biased the observed pattern in November. This interpretation is supported by the regression coefficients of X and X^2 which were markedly smaller during November than during other months in the August-March period (Table 2).

Somatic weight changes have not been reported for croaker. Additional data, especially from the post-peak spawning period December to February, are needed to fully understand their annual cycle of somatic weight change. Possibly, the percentage of somatic weight loss may be greater in late fall and winter than we observed in March.

AGE DETERMINATION AND GROWTH

General Basis for the Method of Age Determination

Scale marks similar to annuli were distinguished by standard criteria, especially cutting over and differential spacing of circuli. Croaker appear to form two marks on their scales each year except that no mark is formed during their first winter. Some fish form no mark during their first year if 15 October is defined as the hatching date of croaker. Even-numbered marks (cold-period marks) form from about December to March, and odd-numbered marks (warm-period marks) form from about May to November. Fish that do not form a mark in their first year would not have mark numbering that corresponds to the typical odd and even system. Cold-period marks were most distinct and were used as "year" marks, although they represent 1-1½ yr of growth. Recognition of the first cold-period mark is the basis for this method. Subsequent marks, especially cold-period marks, seem to be easily identified.

Age determination was validated by: 1) establishing the time of year when each mark forms, 2) establishing age through analysis of length frequencies, and 3) showing that modes of back-calculated and observed lengths at each age agree with age determination by length frequencies.

Repeated reading suggests this method of age determination is consistent. We found 91% agreement between the first reading of scales from 200 fish (112 age 0 and 88 age I) and a second reading 3 mo later.

We have suggested 15 October as a defined hatching date for croaker. Definition of a hatching date is essential in age and growth studies, so that year classes and age groups can be referenced. In the northern hemisphere 1 January is a standard defined hatching date. That date is convenient and has biological reality, especially for species that spawn in the spring and summer of one year. In more northerly waters, furthermore, growth seasons tend to be short; and spawning tends to be restricted in time and often occurs about when the annulus forms. Croaker of the Carolinian Province, in contrast, have a long, possibly year-round, growing season; and their spawning "season" is so long that it takes place over much of two calendar years. Therefore, it seems more convenient and biologically sound to select their peak spawning period as a defined hatching date upon which year class and age group terminology is based. Using an October hatching date, the year class would pertain to the fall calendar year and would include any fish of that spawning cycle hatched in the following winter and spring. A virtual annulus would be designated as of October.

Characteristics of Scale Markings Used to Determine Age

The first mark is typically a more or less indistinct mark formed in warm periods. It is characterized by cutting over in the lateral field, but it has little or no differential spacing of circuli before and after the mark (Figure 5a). This mark is often difficult to distinguish after the heavier second mark is formed. The typical second mark is formed in cold periods. It is the most diagnostic feature for age determination in croaker, and its recognition is the basis for our method. This mark is characterized by heavy cutting over of circuli and differential spacing of circuli in the lateral field (Figure 5b). Generally, circuli are closely spaced before the second mark and more widely spaced after it. When the first mark is absent or difficult to see, the typical second mark is readily distinguished. The third mark is typically formed in warm periods and is similar to the first mark (Figure 5c). We examined only six fish whose scales had the fourth mark, and its criteria may need modification. However, the fourth mark apparently forms in cold periods and apparently resembles the second mark in having heavy cutting over and differential spacing of circuli (Figure 5c).

Croaker from a broad geographical range seemingly can be aged by the method proposed, although further work is needed to establish this. Scales of fish from Mississippi, Fort Pierce (Figure 6a), and Chesapeake Bay (Figure 6b, c) showed markings similar to those on scales from Texas fish. Croaker scales from Florida generally had more or less indistinct cutting over and seemed

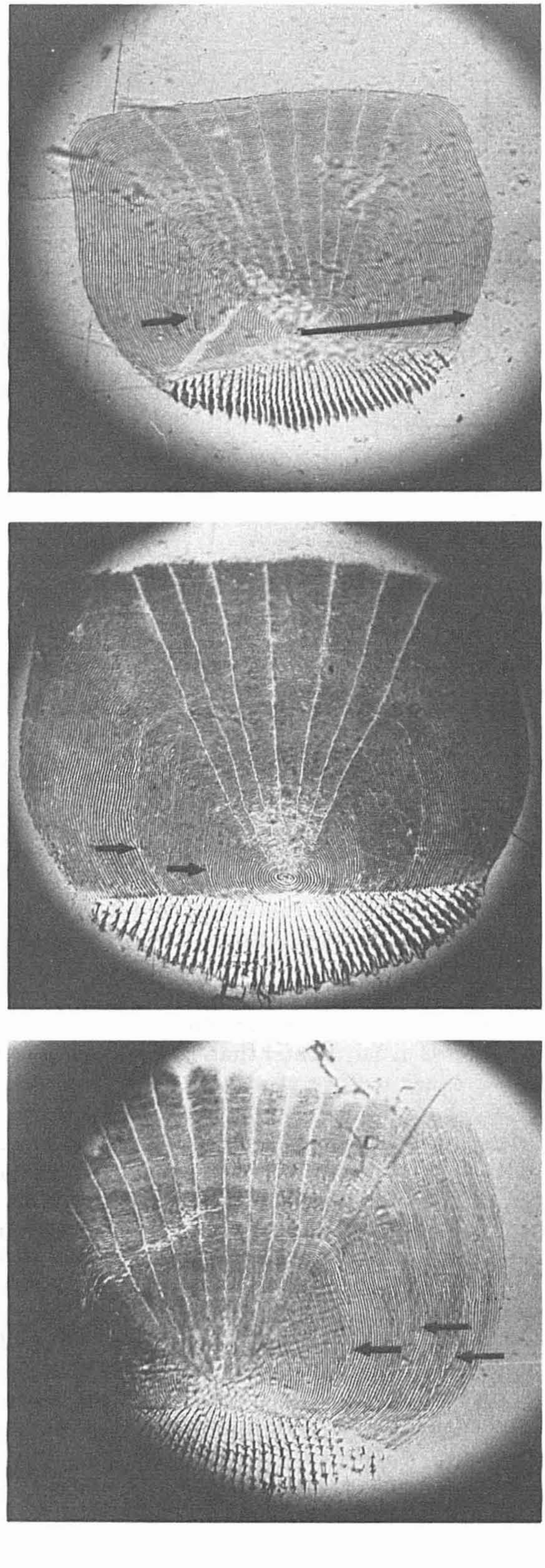
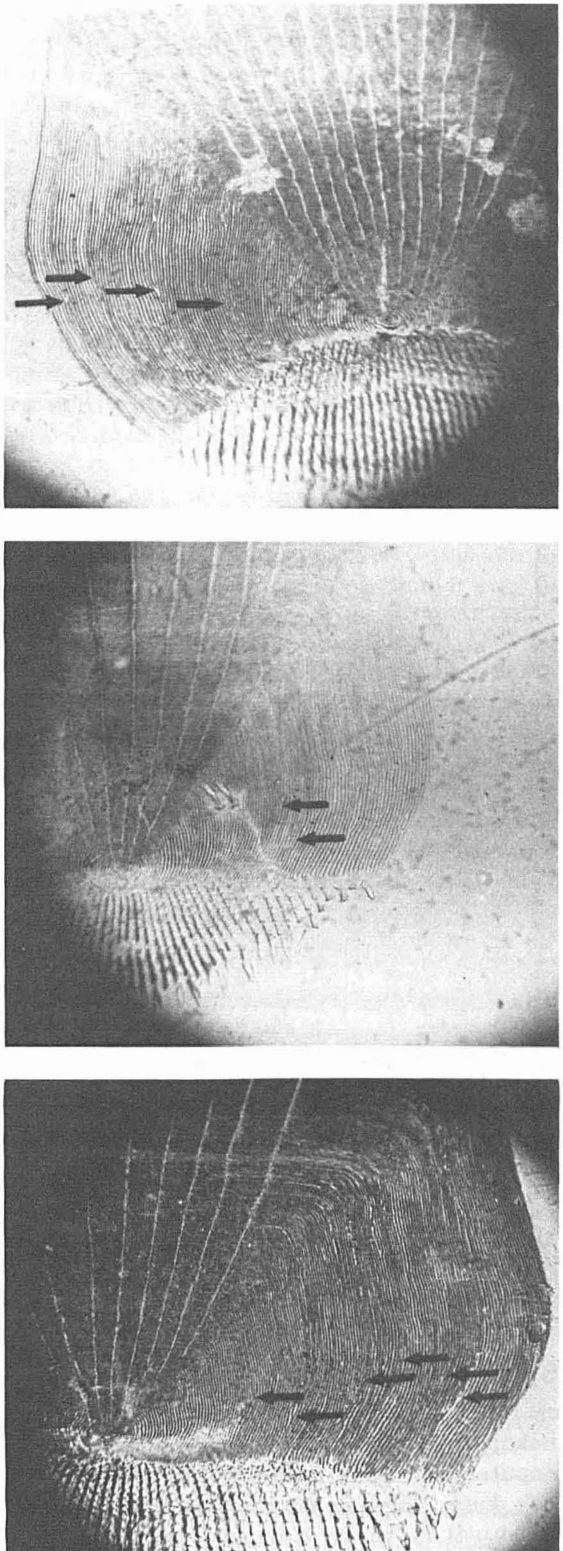


FIGURE 5.—Top. Scale from a 190-mm croaker showing mark 1. This fish was approaching age I when it was captured off Texas in September. The axis depicted shows how measurements were made to determine when each mark formed. Middle. Scale from a 255-mm croaker showing marks 1 and 2. This fish was approaching age II when it was captured off Texas in August. Bottom. Scale from a 310-mm croaker showing marks 2, 3, and 4. This was an age II+ fish captured off Texas in March.



difficult to read, possibly because the fish were collected in tropical waters of southern Florida where temperature changes are not as extreme as further north. Only six fish from Texas had scales with four marks. In contrast, scales from some Chesapeake Bay fish had six marks (Figure 6c). Croaker that live in the Carolinian Province south of Cape Hatteras live only 1 or 2 yr (see General Discussion) and, therefore, tend to have comparatively few marks on their scales. These fish might be easier to age than croaker that live north of Cape Hatteras. The latter fish apparently survive longer and, therefore, probably tend to have more marks on their scales.

Times of Mark Formation

The time when each annuluslike mark formed was determined by plotting for each month the distance from the scale margin to the last mark. Distance was measured across the lateral field of the scale (Figure 5a). Croaker generally form two marks per year except during their first year. Scales with no marks had the smallest distance between the scale margin and focus in May (Figure 7). The radius increased from May to October as scales grew during that period. Therefore, apparently no mark is formed during the first winter; and some croakers form no mark during the first year of life if 15 October is defined as their hatching date. Scales with one mark had the mark closest to the scale edge in warmer months. In March the mark was far removed from the scale margin, suggesting that the first mark normally forms in warm months. Apparently this mark formed on some fish throughout the period May to at least October. The increment between the scale margin and the first (or third) mark did not increase with time, but the reason for this is not clear. Scales with two marks showed the second mark closest to the scale margin in March. The increment between this mark and the scale edge increased until June and then remained nearly constant through November. Therefore, the second mark apparently forms during the colder

FIGURE 6.—Top. Scale from a 305-mm croaker showing marks 1, 2, 3, and 4. This was an age II+ fish when it was captured off Florida in March. Middle. Scale from a 293-mm croaker showing marks 1 and 2. This fish was approaching age II when it was captured in Chesapeake Bay in July. Bottom. Scale from a 508-mm croaker showing marks 1, 2, 3, 4, 5, and 6. This fish was approaching age IV when it was captured in Chesapeake Bay during July.

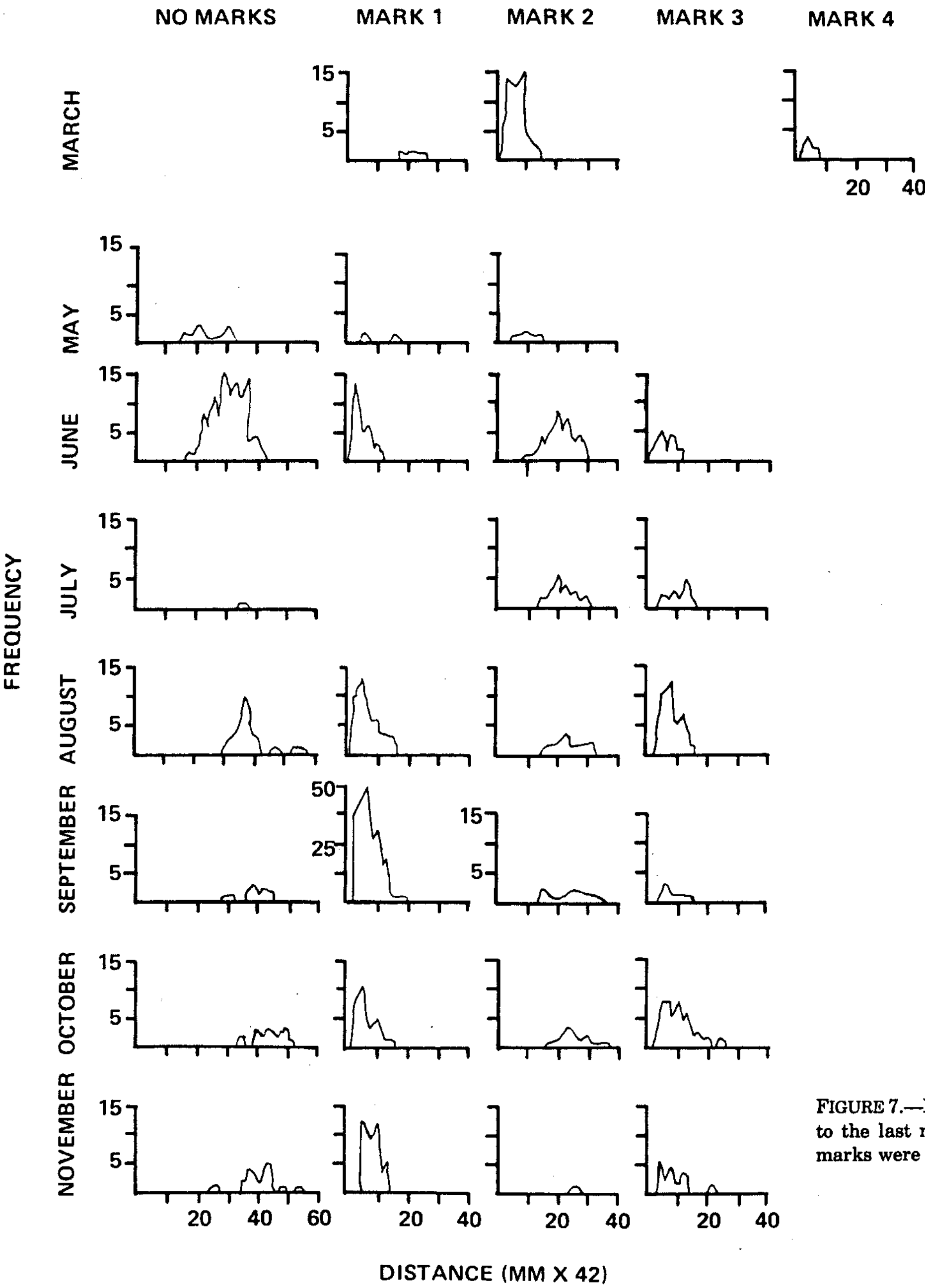


FIGURE 7.—Distance from scale margin to the last mark or to the focus if no marks were present.

months. Scales with three marks showed the third mark being formed throughout the warm months, the only period when scales with only three marks were available. Scales with four marks were observed only during March. The increment on these scales suggests that the fourth mark was formed during winter or spring. However, further data are needed to establish this.

Our findings on times of mark formation agree with Haven's (1954) suggestion that croaker form one fall and one winter mark each year in Chesapeake Bay and with Richards' (1973) computer-simulated findings that the related black drum, *Pogonias cromis,* forms one mark a year until maturity and two marks a year thereafter.

Age Determination and Growth by the Length-Frequency Method

Our length-frequency distributions suggest two croaker year classes occurred off Texas. One age group greatly predominated in the length frequencies of trawl-caught fish from the bay and Gulf during June (Figure 1). The size range of that age group was primarily about 100-150 mm in the bay and about 120-160 mm in the Gulf. Young-of-the-year first appear in Texas bays about November and increase in size from about 10-50 mm during January to 30-85 mm in March, 40-100 mm during May, and 70-130 mm in June (Gunter 1945; Parker 1971; Gallaway and Strawn 1974). Therefore, the fish we captured by trawling during June must be young-of-the-year. These young-of-the-year fish grew to about 110-170 mm in August, 120-175 mm in September, and 140-180 mm in October when they reached age I. Similar sizes in October have been recorded by Gunter (1945), Parker (1971), and Gallaway and Strawn (1974). The fish that became age I in October were about 130-190 mm in November, and fish captured in March were about 165-220 mm. The large fish caught in June by angling near the oyster reef were about 190-270 mm and apparently were survivors of the year class that became age I on the preceding 15 October. These age I+ fish were about 200-310 mm in September when they approached age II. This agrees with Gunter's (1945) size estimates for age II croakers off Texas.

With minor differences, length frequencies reported throughout the Carolinian Province by many workers, including Hildebrand and Cable (1930), Gunter (1945), Suttkus (1955), Bearden (1964), Hansen (1969), Christmas and Waller (1973), Hoese (1973), and Gallaway and Strawn (1974), show growth and age composition similar to our findings. Growth north of Cape Hatteras seems similar to that in the Carolinian Province. Haven (1957) presented monthly length frequencies of fish he considered young-of-the-year. His fish ranged from about 150 to 220 mm in September, but the mode was about 175-180 mm.

Agreement of Observed and Back-Calculated Lengths with Length-Frequencies

Observed sizes at ages 0, I, and II agree closely with ages determined by length frequencies (Figure 8). Only age 0 fish were captured in May and age I fish in July, so that graphs are not presented for these months. The frequencies show overlap in size between the various ages each month. This is to be expected, especially in a species having a prolonged spawning season, and makes it impossible to use the length-frequency method to assign age confidently where sizes at age overlap. The observed lengths of age 0 fish in September were primarily 130-170 mm (mean = 151 mm), but they ranged from about 110 to 220 mm. This age group was about 140-220 mm (mean = 158 mm) during October when they became age I and about 130-220 mm (mean = 172 mm) during November. The observed lengths of age I fish in September were about 200-340 mm with the mean being 253 mm. This age group was about 190-360 mm (mean = 274 mm) in October when they became age II.

Lengths back-calculated to cold-period marks reasonably agree with the sizes at age I estimated by length frequencies in October (Figure 9). However, cold-period marks apparently begin to form generally after October; so that the back-calculated lengths should be larger than the observed lengths in October. The similarity suggests Lee's phenomenon, possibly due to selective mortality favoring survival of smaller croaker. Back-calculated lengths were somewhat smaller than the sizes at age I+ in March, as would be expected. Back-calculated lengths from age I+ fish were primarily 110-210 mm at age I with a mean length of 165 mm. In agreement, back-calculated lengths from six age II+ fish had a mean of 181 mm at age I and 270 mm at age II. The body-scale regression equation used to back-calculate length was:

$$Y = 2.6000 + 4.6389X - 0.0122X^2$$

where Y represents total length in millimeters, and X represents the scale radius (millimeters × 42). The sample size was 1,123, and the total length range was 90-360 mm. About 88% of the variation in total length was associated with variation in scale radius.

Growth estimates based upon the length-frequency method and from observed and back-calculated estimates using the scale method show very close agreement. Mean lengths in October were about 155-165 mm at age I and 270-280 mm at age II depending upon how age was determined. The wide back-calculated and observed size ranges found at age may be due to the long

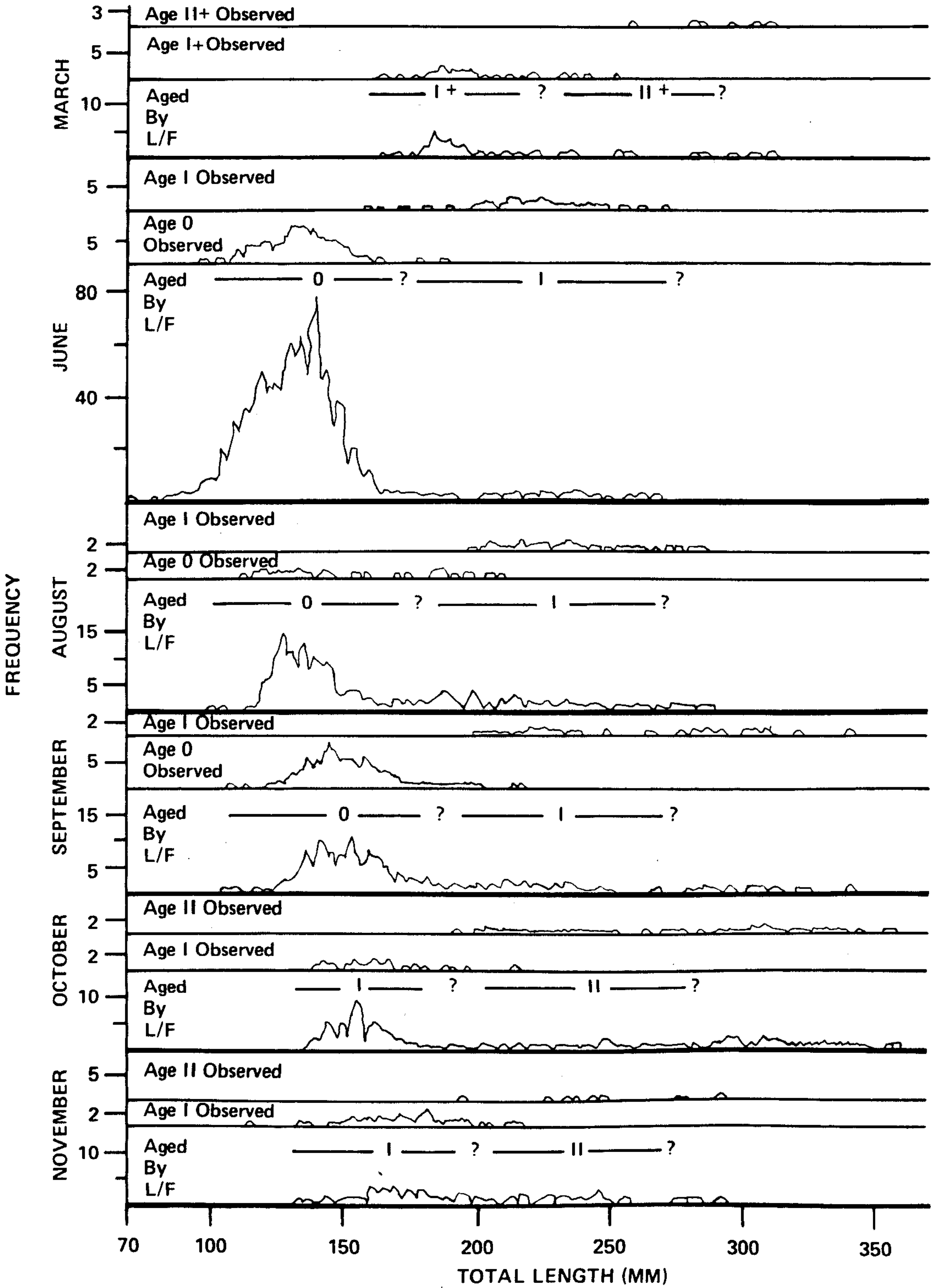


FIGURE 8.—Length compositions comparing observed ages with ages determined by the length-frequency method. Frequencies are moving averages of three.

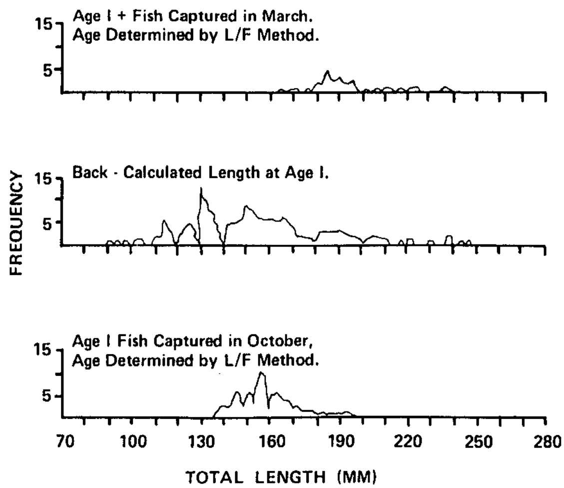


FIGURE 9.—Back-calculated length frequencies at age I and length frequencies (L/F) of age I fish in October and age I+ fish in March. Frequencies are moving averages of three.

spawning season and/or prolonged time span when the cold-period mark may form.

HABITAT SEGREGATION BETWEEN AGE GROUPS

A portion of all croaker age groups apparently utilized bays as feeding grounds during the warmer months, but age I and older fish seemed to occupy different habitat than young-of-the-year. Croaker captured by angling near the oyster reef from June to August were about 200-270 mm in length (Figure 1) and seemed common there. In contrast, trawl-caught bay fish were generally much smaller than 200 mm. Reef and trawl-caught bay individuals were then about age I+ and age 0, respectively. Many other workers, including Reid (1955), Perret (1966), Nelson (1969), Hansen (1969), Parker (1971), Hoese (1973), and Gallaway and Strawn (1974), have also captured few individuals greater than 200 mm by trawling in bays, but they captured many small specimens like we did. Therefore, although capture by angling may have selected larger fish near the reef, the two age-groups seem to segregate by habitat: young-of-the-year occupy soft substrates, and age I and older fish occur near oyster reefs (and similar hard substrates?). This agrees with Harden Jones' (1968) generalization that the feeding grounds of adult fishes are separate from their spawning grounds and nurseries.

Age I and older fish seemed to remain near oyster reefs until they migrated to sea to spawn. Fish caught near oyster reefs were much larger than those caught by trawling in the Gulf or bays until September-October (Figure 1). Specimens larger than 191 mm were not collected in the Gulf until September, which is about when spawning begins in the northern Gulf (Gunter 1945; Suttkus 1955; present study). Simmons and Hoese (1959) captured fish less than 175 mm long throughout the summer as they migrated to the Gulf, but these workers captured fish similar in size to our reef fish only during September.

The larger young-of-the-year began moving to sea by late spring or early summer. Trawl-caught fish in the bay were smaller than those in the Gulf during June (Figure 1) when modal length for young-of-the-year was about 120 mm in the bay and about 140 mm in the Gulf. The difference in size between young-of-the-year in the bay and Gulf agrees with Gunter (1945), Haven (1957), and Reid and Hoese (1958) who found a size gradient in estuaries, the smallest young-of-the-year being farthest up the estuary. Haven (1957) and Hoese et al. (1968) suggested that the gradient was due to gradual seaward dispersal of the largest young, and Parker (1971) and Franks et al. (1972) suggested that young-of-the-year began moving to sea at about 85-100 mm long. Evidently the Gulf becomes a very important nursery by midspring or early summer, because young croaker compose about 24-29% by number of the fishes found on the white shrimp grounds of the Gulf then (Miller 1965, table 3; Chittenden and McEachran 1976).

MAXIMUM SIZE AND AGE, LIFE SPAN, AND MORTALITY RATE

Croaker in the Carolinian Province are typically small and have a short life span and high mortality rate. Most fish we collected were less than 200 mm long and the largest was 357 mm. The largest croaker observed in warm-temperate waters generally have been less than 300 mm (many workers including Hildebrand and Cable 1930; Reid 1955; Bearden 1964; Miller 1965; Nelson 1969; Hansen 1969; Parker 1971; Hoese 1973), although some workers captured fish as large as 330-380 mm (Pearson 1929; Gunter 1945; Suttkus 1955; Franks et al. 1972; Christmas and Waller 1973). Rivas and Roithmayr (1970) found a 668 mm specimen, but this is exceptional.

Our length frequencies suggest that two year classes occurred, but only one was abundant. This agrees with other reported length frequencies from warm-temperate waters (see references cited in section on Age Determination and Growth by the Length-Frequency Method). Therefore, the typical croaker life span in warm-temperate water appears to be only 1 or 2 yr. Age II+ fish captured in March were the oldest fish we examined in agreement with other estimated maximum ages from the Carolinian Province (Gunter 1945; Suttkus 1955; Bearden 1964; Hoese 1973). Fish associated with oyster reefs are larger and a year older than trawl-caught bay or Gulf fish during the summer. However, the abundance of these age I croaker must be small compared with the abundance of age 0 croaker, because the geographical area occupied by oyster reefs is comparatively small.

Croaker have a high total annual mortality rate as their short life span requires. We found only six age II+ fish in 1,123 aged. Greatest mixing of age-groups probably coincides with fall spawning in the Gulf. We observed 11 age I+ and 250 age 0+ fish in random samples from trawl catches made 25-27 September 1974, so that the observed total annual mortality rate was about 96% assuming negative exponential survivorship. This must approximate the total annual mortality rate throughout the Carolinian Province because maximum sizes and ages, length frequencies, and life spans appear similar throughout this area. The observed total annual mortality rate agrees closely with the theoretical total annual mortality rate. Following the reasoning of Royce (1972:238) the negative exponential survivorship relation $S = N_t/N_o = e^{-Zt}$ can be solved for an approximate instantaneous total mortality rate over the entire life span which can be used to estimate average annual total mortality rates. A species with a life span of 1 or 2 yr would have a theoretical approximate total annual mortality rate of 90-100%.

TOTAL WEIGHT-LENGTH AND GIRTH-LENGTH RELATIONSHIPS

The regression of total weight in grams (Y) on total length in millimeters (X) was expressed by the equation:

$$\log_{10} Y = -5.26 + 3.15 \log_{10} X.$$

This relationship was based on a sample size of 2,081 fish in the length range 90-360 mm. About 98% of the variation in $\log_{10}$ total weight was associated with variation in $\log_{10}$ total length. The arithmetic mean $\log_{10} X$ was 2.21056, and arithmetic mean $\log_{10} Y$ was 1.71546.

The regression of girth in millimeters (Y) on total length (X) in millimeters was expressed by the linear equation:

$$Y = -11.84 + 0.71X.$$

This relationship was based on a sample size of 2,081 fish in the length range 90-360 mm. The arithmetic mean girth was 108.07 mm. About 94% of the variation in girth was associated with variation in total length.

GENERAL DISCUSSION

Many aspects of the life history of Atlantic croaker in the Carolinian Province appear different than those of fish found in cold-temperate waters north of Cape Hatteras except that the growth rates appear similar. In general, our data and the literature agree that in warm-temperate waters: 1) peak spawning occurs about October but the spawning season is long and lasts from about September to at least March, 2) maturity is reached at about 140-180 mm long as the fish approach age I, 3) maximum size is about 300-350 mm and most fish are so small (about 200 mm or less in length) that they do not support commercial food fisheries, 4) the life span is about 1-2 yr and maximum age is typically about 2 yr, 5) most fish live only to about age I, and 6) total annual mortality rate is about 95%. In contrast, fish living north of Cape Hatteras generally:

1) Have a spawning season (July or August-December?) that starts earlier and may end earlier (Welsh and Breder 1924; Hildebrand and Schroeder 1928; Wallace 1940; Pearson 1941; Massmann and Pacheco 1960). However, the time when spawning ends is not certain. Haven (1957) captured many young 20-30 mm TL from February to April, but their significance is not clear; they could represent late-winter spawning or, perhaps, fall spawning with little or no overwinter growth. Peak spawning seemingly occurs no later than midfall, because all the adult fish that Wallace (1940) examined had spent or

recovering gonads in late November and thereafter.

2) Reach maturity when greater than 200 mm long as they approach at least age II (Welsh and Breder 1924; Wallace 1940; Haven 1954).
3) Have a maximum size of about 500 mm (Hildebrand and Schroeder 1928; Gunter 1950) and large average size so that they have supported important commercial food fisheries (Gunter 1950; Haven 1957; Joseph 1972).

Maturity is reached about 1 yr later in cold-temperate waters and typical sizes are much larger, although growth rates appear similar. Therefore, the typical maximum age is probably about 2-4 yr north of Cape Hatteras. If so, the total annual mortality rate must be lower north of Cape Hatteras. Assuming negative exponential survivorship, the theoretical approximate total annual mortality rates would be 90, 78, and 68% for life spans of 2, 3, and 4 yr, respectively.

The existence of an abrupt change at Cape Hatteras in the life histories and population dynamics of species whose ranges traverse this area has apparently not been recognized, particularly as a possible general phenomenon; although Cape Hatteras has long been recognized as a significant zoogeographic boundary [see Briggs' (1974) review]. Gunter (1950) noted differences in the sizes and some aspects of the life histories of certain fishes of the Gulf of Mexico and mid-Atlantic coast of the United States. However, he gave no consideration to the possibility that an abrupt change might occur near Cape Hatteras. Although the Cape Hatteras connection has not been recognized, the pelagic, anadromous American shad, *Alosa sapidissima,* also shows changes in life history there that are similar to those herein documented for croaker. Runs of shad native to streams north of Cape Hatteras consist primarily of somewhat older fish (ages IV-VII and older) and include many repeater spawners in contrast to the younger fish (ages IV-VI) and the complete or virtual absence of repeat spawners south of Cape Hatteras (for pertinent literature see Walburg and Nichols 1967; Chittenden 1975). La Pointe (1958) reported similar growth rates in shad native to streams throughout their range. Therefore, the geographic differences in age compositions should result in differences in life spans, ages at maturity, maximum ages, maximum and average sizes, and mortality rates as in croaker.

The life histories and population dynamics of two species with different life styles but primarily coastal habit have been shown to change abruptly at Cape Hatteras. This may represent a general phenomenon as Gunter (1950) apparently observed. However, similar comparisons are necessary in other species, especially noncoastal forms, to see how far the inference extends.

The reason for the geographical differences in population dynamics is not clear. However, shad exhibit great somatic weight loss (about 25-55% depending upon sex and size) associated with migration and spawning (Leggett 1972; Chittenden 1976). Leggett (1972) suggested that the low frequency of repeat spawning shad in southern streams might be due to increased use of body reserves during spawning migrations that occur at higher average temperatures. Croaker also show somatic weight loss associated with maturation and spawning, although we did not observe weight loss comparable to that in shad. However, we had no data for the post-peak spawning period December-February when weight loss may have been greater. It is pertinent here that Chittenden has observed many emaciated spot, *Leiostomus xanthurus,* in the Gulf of Mexico during January, which is about when this species spawns. The observed differences in population dynamics north and south of Cape Hatteras may be largely the result of different temperature regimes that affect age at maturation, spawning-associated somatic weight loss, and the magnitude of a subsequent post-spawning mortality.

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