Abstract. — Atlantic croaker. Micropogonias undulatus, collected from commercial catches in Chesapeake Bay and in Virginia and North Carolina coastal waters during 1988-1991 (n=1,967) were aged from transverse otolith sections. Ages 1-8 were recorded, but eight-year-old fish were rare. Marginal increment analysis showed that for ages 1-7, annuli are formed once a year during the period April-May. Otolith age readings were precise: >99% agreement within and between readers. Observed lengths-at-age were highly variable and growth rate decreased after the first year. Despite the high variability in sizesat-age, observed lengths for ages 1-7 fit the von Bertalanffy growth model ($r^2=0.99$; n=753) well. No differences in growth were found between sexes. Total annual instantaneous mortality (Z) estimated from maximum age and from a catch curve of Chesapeake Bay commercial catches ranged from 0.55 to 0.63. Our results do not indicate the existence of a group of larger, older Atlantic croaker in Chesapeake Bay compared with more southern waters and suggest that the hypothesis of a basically different population dynamics pattern for this species north and south of Cape Hatteras, North Carolina, should be reevaluated.

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Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus,* in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics*

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The Atlantic croaker, Micropogonias undulatus (Linnaeus), is one of the most abundant inshore demersal fishes along the Atlantic and Gulf of Mexico coasts of the United States (Joseph, 1972). Although recent commercial and recreational catches have come primarily from the South Atlantic Bight and the Gulf of Mexico, Atlantic croaker still support important fisheries along the Mid-Atlantic coast, especially from Maryland to North Carolina (Wilk, 1981). In Chesapeake Bay, they are caught by commercial and recreational fishermen during late spring and early fall migrations and, to a lesser extent, during the summer. In winter, Atlantic croaker leave the Bay to overwinter off the coast of Virginia and North Carolina, where they are caught by otter trawl and gillnet fisheries (Haven, 1959).

Little is known about age, growth, and mortality of Atlantic

croaker in the Middle Atlantic and Chesapeake Bay regions. Studies based on length frequencies (Haven, 1957; Chao and Musick, 1977) require considerable subjective interpretation given the extended spawning period of Atlantic croaker (Morse, 1980; Warlen, 1982; Barbieri et al., unpubl. ms.) and the difficulty in distinguishing modal groups at older ages (White and Chittenden, 1977; Jearld, 1983). Although scale-ageing has also been used (Welsh and Breder, 1923; Wallace, 1940; Ross 1988), problems in applying this method to Atlantic croaker have been widely reported (Roithmayr, 1965; Joseph, 1972; Barger and Johnson, 1980; Barbieri, 1993).

In this study we provide information on age, growth, and mortality of Atlantic croaker in the Chesa-

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peake Bay region using a validated otolith-ageing method. We also evaluate the relationship between otolith size and fish size and age, and discuss the implications of using otoliths for ageing Atlantic croaker. Finally, based on current information on growth, and size and age compositions in Chesapeake Bay, we discuss the hypothesis of White and Chittenden (1977) and Ross (1988) regarding the existence of a basically different population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina.

Methods

Atlantic croaker were collected between June 1988 and June 1991 from commercial pound-net, haulseine, and gillnet fisheries which operate from early spring to early fall in Chesapeake Bay. Local fish processing houses and seafood dealers were contacted weekly or fortnightly, and one 22.7-kg (50-lb) box of fish of each available market grade (small, medium, or large) was purchased. Although boxes of fish were not randomly selected, Chittenden (1989) found only minor among-box differences in Atlantic croaker length compositions in pound-net and haul-seine catches. Because nearly all variation in size compositions was captured by the within-box variation, box selection did not present a problem.

Since Atlantic croaker migrate from Chesapeake Bay in early fall to overwinter offshore (Haven, 1959), samples for the period November-March were obtained from commercial trawlers which operate in Virginia and North Carolina shelf waters. Young of the year (90-114 mm total length, TL) used to validate the first annulus on otoliths were obtained from the Virginia Institute of Marine Science juvenile bottom trawl survey.

Fish were measured for total length (TL, ± 1.0 mm), weighed for total weight (TW, ± 1.0 g), sexed, and both sagittal otoliths removed and stored dry. The left otolith was transversely sectioned through the core with the diamond blade of a Buehler low-speed Isomet saw. Sections 350–500 µm thick were mounted on glass slides with Flo-texx clear mounting medium and read under a dissecting microscope (6–12×) with transmitted light and bright field, with the exception of samples from the period April-May, when sections were also read with reflected light and dark field to help identify the last annulus.

Ages were assigned based on annulus counts; January 1 was taken as an arbitrary average birthdate when fish from one age class were assigned to the next oldest (Jearld, 1983). Although the average spawning date (average biological birthdate) of Atlantic croaker in the Chesapeake Bay region occurs in September (Barbieri et al., unpubl. ms.), we chose, for ageing purposes, to use January 1 as the average birthdate because annuli are formed during the period April-May (see Age determination below). To assess ageing precision, all otolith sections (n=1,967) were read twice by each of two readers, and agreement between readings and readers evaluated by percent agreement. All disagreements were resolved by a third reading with both readers.

Annuli were validated by the marginal increment method (Bagenal and Tesch, 1978). For each age, the translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 1). Measurements $(\pm 0.02 \text{ mm})$ were taken with an ocular micrometer at 25×.

To evaluate growth, observed lengths at ages 1-7 were fit to the von Bertalanffy model (Ricker, 1975) by using nonlinear regression (Marquardt method). Model parameters were the following: L_{∞} , the mean asymptotic length; K, the Brody growth coefficient; and t_0 , the hypothetical age at which a fish would have zero length (Ricker, 1975). To correct for growth after the time of annulus formation, only data for September, the peak spawning and thus average biological birthdate for Atlantic croaker in the Chesapeake Bay region (Barbieri et al., unpubl. ms.), were used for growth analysis.

To evaluate changes in otolith size relative to fish length and age, 30 randomly selected otoliths per age, for ages 1–7 (198–400 mm TL), were measured for maximum length (OL, ± 0.05 mm) and maximum thickness (OT, ± 0.05 mm), and weighed (OW, ± 0.001 g). After sectioning, otoliths were measured for otolith radius (OR, ± 0.02 mm), defined as the distance between the center of the core and the otolith outer edge along the ventral side of the sulcal groove (Fig. 1). Relationships between otolith measurements and fish TL were evaluated by regression analysis. The effect of fish age on these relationships was evaluated by analysis of covariance (ANCOVA).

Linear regression was used to determine a lengthweight relationship for fish ranging from 152 to 400 mm TL (36.3 to 967.0 g TW). Difference between sexes was tested by ANCOVA. The hypothesis of isometric growth (Ricker, 1975) was tested by *t*-test.

Instantaneous total annual mortality rates, Z, were estimated from maximum age by using Hoenig's pooled regression equation (Hoenig, 1983), by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972), and by the regression method with a catch curve of combined pound-net, haul-seine, and gillnet



data for all recruited ages having five or more fish (Chapman and Robson, 1960). To avoid sampling bias associated with individual gears, we considered the age-frequency distribution obtained from data from combined gears as the best estimate of Atlantic croaker age composition in Chesapeake Bay (Ricker, 1975). Commercial trawl collections were not used in this analysis because they had different length compositions than the other gears and could be biased towards small fish. Because in catch curve analysis the age group represented by the apex of the catch curve may or may not be fully recruited to the gears (Everhart and Youngs, 1981), mortality estimates were based on ages 3-7 only. Data from 1988 to 1991 were combined to minimize the effect of variation in year-class strength (Robson and Chapman, 1961). The right tail of the catch curve (Ricker, 1975) was tested for deviation from linearity by analysis of variance (ANOVA). Values of Zwere converted to total annual mortality rates, A, by using the relationship $A = 1 - e^{-Z}$ (Ricker, 1975).

All statistical analyses were performed by using the Statistical Analysis System (SAS, 1988). Rejection of the null hypothesis in statistical tests was based on α =0.05. *F*-tests in ANCOVA were based on Type III sums of squares (Freund and Littell, 1986). Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981). For the OL-TL, OW-TL, and TW-TL relationships, and for all ANCOVA and ANOVA analyses, data were \log_{10} -transformed to correct for non-linearity and heterogeneous variances. For the catch curve analysis, \log_{e} -transformed numbers at age were regressed on age. Unless otherwise indicated, back-transformed data and regression equations are presented in the results.

Results

Age determination

Transverse otolith sections of Atlantic croaker show very clear, easily identified marks that can be used for ageing. Typical sections have an opaque core surrounded by a blurred opaque band composed of fine opaque and translucent zones (Fig. 1). This band represents the first annulus. The width of this annulus varies among fish, from a very narrow band that is almost continuous with the core, to a wide, well-defined band clearly separated from the core. Because of this variation in width and proximity to the core, the first annulus is sometimes difficult to identify. Subsequent annuli are represented by easily identified, narrow, opaque bands that alternate with wider translucent bands outside the proximal margin of the first annulus (Fig. 1).

Annuli are formed on otoliths once a year in the period April-May. For ages 1-7, mean monthly marginal increment plots show only one minima during the year, indicating that only one annulus is formed each year (Fig. 2). The trough starts abruptly in April, a period when there is, in general, maximum variation in the mean marginal increment, suggesting that some fish have begun to form the annulus while others have not. Lowest marginal increment values occurred in May, the most intensive period of annulus formation. Marginal incre-



ment values progressively rise to a somewhat stable maximum from October through March or April, indicating a period of little or no otolith growth. Because only two age-8 fish were collected, it was not possible to validate annuli beyond age 7.

To confirm our interpretation that the blurred opaque band around the otolith core represents the first annulus, (i.e., that fish hatched in the fall form a mark during their first spring), otolith sections of young of the year (94–114 mm) collected during the period March–June were examined. All those collected in March–April were developing fine opaque marks around the core, and all those in May–June had an opaque mark already formed (Fig. 3).

Otolith age readings were very precise, both within and between readers. Percent agreement was



Figure 3

Transverse otolith section of a young-of-the-year Atlantic croaker (114 mm TL) collected in June 1990 in Chesapeake Bay. The arrow indicates the outer edge of the first annulus formed during the period April-May. SG=sulcal groove; Ve=ventral; Pr=proximal; a=artifact of preparation. 99.5% for reader 1, 99.3% for reader 2, and 99.2% between readers. In all cases of disagreement, the difference never exceeded 1 year. Only one of the 1,967 left otoliths sectioned was crystallized and could not be read. In that case, the right otolith was read. Difficulty in ageing Atlantic croaker from otolith sections did not increase with increasing age. However, proper identification of the first annulus was very important. All disagreements, independent of age, were due to problems in identifying the first annulus.

Otolith size relative to fish size and age

Changes in otolith size relative to fish size were not constant along all axes (Fig. 4). Otolith maximum

length was the only axis that showed a linear, isometric increase with fish length. Otolith radius, the axis along which annuli were read in transverse sections, showed a non-linear relationship with fish length, and had the smallest r^2 of all variables (Fig. 4). The curvilinear relationship suggests that otolith growth relative to fish growth slows down along this axis as fish get bigger.

Despite its poor relationship with fish length, otolith radius showed a very strong linear relationship with fish age. An ANCOVA model showing length, age, and their interaction explained 97% of the variation in otolith radius (Table 1). All factors in the model were highly significant (P<0.01). Similar models for otolith maximum length, maximum thickness, and weight were also highly significant and had high coefficients of determination ($r^2 \ge 0.85$). However, significance for these models was due to fish length only, neither age nor the interaction factor was significant.

Growth

Observed lengths varied greatly within ages (Fig. 5). Atlantic croaker showed a rapid increase in size during the first year, but annual growth rate greatly decreased during the second year, remaining comparatively low thereafter (Fig. 5). On average, 64% of the cumulative total observed growth in length occurred in the first year and 84% was completed after two years.

No differences in mean lengths at age were found between sexes (*t*-test at each age; P>0.05 for all ages). Mean observed total lengths for pooled sexes were 201, 263, 274, 285, 290, 307, 309, and 313 mm, for ages 1–8, respectively.



Despite the high variability in sizes at age, observed lengths at ages 1–7 showed a very good fit to the von Bertalanffy growth model ($r^2=0.99$; n=753). Estimated model parameters, asymptotic standard errors, and 95% confidence intervals are given in Table 2.

No difference in the length-weight relationship was found between sexes (ANCOVA; F=2.46; df=3,005; P=0.15). The equation for pooled sexes (Fig. 6) was

$$TW = 2.41 \times 10^{-6} TL^{3.30} (r^2 = 0.97; n = 3,006; P < 0.01).$$

The slope of the regression line (b=3.30; SE=0.0141) was significantly different from 3.00 (*t*-test; *t*=7.26; *P*<0.01), indicating allometric growth.

Size and age compositions

Length-frequency distributions of Atlantic croaker samples obtained from different fishing gears were similar (Fig. 7), with the exception of commercial trawl data which were dominated by fish smaller than 275 mm. The smallest Atlantic croaker cap-

Table 1

Summary of ANCOVA to evaluate the effect of Atlantic croaker (Micropogonias undulatus) total length (TL) and age on otolith maximum thickness (OT), maximum length (OL), weight (OW), and radius (OR). n = 210 for each analysis; $\alpha = 0.05$.

Otolith relation	Source of variation	r²	<i>P</i> -value
ОТ	model	0.85	0.0001
	TL		0.0001
	age		0.3263
	$TL \times age$		0.6214
OL	model	0.88	0.0001
	TL		0.0001
	age		0.9780
	$TL \times age$		0.7907
ow	model	0.90	0.0001
	\mathbf{TL}		0.0001
	age		0.0863
	$TL \times age$		0.1402
OR	model	0.97	0.0001
	TL		0.0001
	age		0.0001
	$TL \times age$		0.0008

tured by each gear was approximately 200 mm, although these data represent only market foodfish grades (small, medium, or large) and did not include smaller fish sold as scrap. The maximum length recorded was 400 mm, from a pound-net catch in 1988. However, for all gears 99% of the Atlantic croaker collected were ≤ 345 mm.

Age compositions from different gears were not as similar as length frequencies suggest (Fig. 7). Haulseines, gill nets, and commercial trawls caught a large proportion of fish at ages 1 and 2, and had age 2 as the first age fully recruited. Pound nets captured a comparatively larger proportion of fish at ages 4-7, and had age 3 as the first age fully recruited. Age-1 fish were not fully recruited to any of the gears sampled, but this may reflect, in part, the exclusion of scrap fish from our collections.

The maximum age sampled was 8 years. Despite the large sample size and the variety of gears used, only two eight-year-old fish were collected, one from a pound net in September 1988 (334 mm) and one from a gill net in September 1990 (293 mm).

Mortality

Instantaneous total annual mortality rates (Z)ranged from 0.55 to 0.63. Estimates obtained for a

Table 2
Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for Atlantic croaker (<i>Micropogonias unpulatus</i>) in the Chesapeake Bay region (1988–90).
95% confidence

Parameter	Estimate	Standard error	95% confidence intervals	
			Lower	Upper
L _{so}	312.43	7.44	297.82	327.04
K	0.36	0.08	0.20	0.52
t _o	-3.26	0.84	-4.91	-1.61

maximum age of 8 years were 0.55 (A=42%) by using Hoenig's (1983) method, and 0.58 (A=43%) by using Royce's (1972) method. A regression estimate obtained from the slope of the catch curve (Fig. 8) was 0.63 (A=47%); confidence intervals were 0.36(A=30%) and 0.90 (A=59%). The regression line did not deviate significantly from linearity (ANOVA; F=1.15; P=0.40).

Discussion

Age determination

Our criteria for ageing Atlantic croaker from otolith sections differ from those of Barger (1985), in that we considered the first annulus to be the blurred opaque band surrounding the otolith core. However, evidence from both studies seems to support our interpretation. Barger (1985) reported 58% of the otoliths in his samples had marks that were too thin or discontinuous and too close to the core to be considered annuli. By examining otoliths of young of the year during the period of annulus formation, we were able to validate this mark as the first annulus, formed during their first spring in the estuary. Because spawning of Atlantic croaker in the Chesapeake Bay area extends from late July to December (Barbieri et al., unpubl. ms.) and the first annulus is formed during their first spring after hatching, fish forming the first annulus could range from 5 to 10 months of age. As marginal increment plots indicated, all subsequent annuli formed at yearly intervals.

Variation in the width of the first annulus also seems to reflect the protracted spawning period of Atlantic croaker. Early hatched fish (July–August) would probably be large enough by April or May to have this annulus close to, but not continuous with, the otolith core. In contrast, late-hatched fish (November-December) would be small in the spring and

would probably show the first mark and the core virtually fused together. Since Atlantic croaker also spawn over a long period in the Gulf of Mexico (White and Chittenden, 1977), this might explain why the first annulus was apparent in only a portion of Barger's (1985) fish.

Our interpretation of the first annulus is also consistent with evidence from another ageing method. Ross (1988) reported that some Atlantic croaker from North Carolina showed an early, age-0 scale mark, apparently formed during their first winter. However, they were not counted as annuli.

The high precision of repeated age readings and validation of annuli almost to the maximum observed age indicate that otolith sections represent a very reliable method for ageing Atlantic croaker. Identifying the first annulus may require some practice, but all other annuli are extremely clear and easy to identify. Otolith sections do not have the problems scales reportedly do, such as the occurrence of double marks (White and Chittenden, 1977; Music and Pafford, 1984; Ross, 1988; Barbieri, 1993), or marks that are poorly defined and difficult to distinguish (Joseph, 1972; Barger and Johnson, 1980; Barbieri, 1993).

The pattern of otolith growth relative to fish growth also indicated the high reliability of transverse otolith sections for ageing Atlantic croaker. Although otolith radius, the axis we used to read annuli, showed a poor correlation with fish length, the strong linear relationship between otolith radius and age indicates that otolith growth along this axis seems to be continuous with age, independent of fish growth. This supports previous suggestions (Mosegaard et al., 1988; Wright, 1991) that a process other than somatic growth governs the rate of otolith accretion. Because otoliths grow at a faster rate than the body during slow somatic growth, they are excellent structures for recording the seasonal cycle and age in slow-growing and old fish, especially those approaching asymptotic length (Casselman, 1990). The high correlation we found between otolith radius and age for Atlantic croaker seems to confirm this pattern.

Growth and mortality

High variability of observed lengths at age indicates that length is a very poor predictor of age for Atlantic croaker, especially beyond age 2. The wide range in lengths at age can be attributed to a combination of two factors: 1) most of Atlantic croaker's growth occurs during the first two years, becoming asymptotic after age 2; and 2) fish are born at different times during the extended spawning season and display different growth rates. Warlen (1982) reported that Atlantic croaker larvae caught later in the spawning season had slower growth rates than those taken during peak spawning. Since growth decreases sharply after their first year, such differences in growth rates among young of the year is likely to cause a large variation in lengths at age.

Growth parameter estimates reported here do not agree with previous reports for Atlantic croaker. However, comparisons with previous studies are difficult because other estimates were based on different ageing methods (White and Chittenden, 1977; Ross, 1988), different otolith-ageing criteria (Barger, 1985; Hales and Reitz, 1992), or a period before any significant fishery for Atlantic croaker occurred (Hales and Reitz, 1992). Methods used to estimate length-at-age data or to fit the von Bertalanffy model also varied. Previous studies on Atlantic croaker growth generally used back-calculated rather than observed lengths at age. Although backcalculation has been widely used and represents standard methodology in age and growth studies (Bagenal and Tesch, 1978; Jearld, 1983), recent evidence indicates that it may generate biased results (Campana, 1990; Ricker, 1992). By basing our growth parameter estimates on observed lengths at age of fish collected in September-the average spawning period of Atlantic croaker in the Chesapeake Bay area--we avoided problems related to back-calculation procedures or seasonal growth effects.

Our total mortality estimates are the lowest ever

reported for Atlantic croaker. However, the close agreement we found between estimates obtained from maximum age and from the catch curve indicates our values are probably realistic, at least for the Chesapeake Bay area. Comparisons with previous studies are difficult because other estimates were based on different ageing methods (scales and length frequencies), and on collections from a single sampling gear and different geographical areas (White and Chittenden, 1977; Ross, 1988).

Geographic comparisons

The possible existence of two groups of Atlantic croaker, exhibiting different life history and population dynamics attributes north and south of Cape Hatteras, North Carolina, has been extensively discussed in the scientific literature (Chittenden, 1977; White and Chittenden, 1977; Ross, 1988). Ross (1988) hypothesized that these groups may overlap and mix in North Carolina and stated that, if the Atlantic croaker designated in his study as "northern" were fish migrating south from the Chesapeake and Delaware Bay areas, their larger sizes (350–520 mm TL) and older ages (5-7 years, as aged by scales) would be consistent with the proposed northern group life history pattern. However, our results do not support the hypothesis of a group of larger, older Atlantic croaker in Chesapeake Bay, at least in recent years.

Maximum length and size ranges reported here are consistent with recent data from North Carolina, both for inshore waters as well as for the offshore trawl fishery. Since 1982, Atlantic croaker trawl catches in North Carolina have been dominated by small fish. Fish larger than 300 mm TL and older than 3 years have represented less than 1% of the recent catches (Ross, 1991). Although records of large fish do exist, Atlantic croaker as large as those reported by Ross (1988) have never been common in commercial catches from the Chesapeake Bay region. Even in the early 1930's, when the winter trawl fishery had just been established off the coasts I

of Virginia and North Carolina and catches of Atlantic croaker were dominated by large fish, most fish measured 260–360 mm TL (Pearson, 1932). Length frequencies of Atlantic croaker sampled from commercial pound nets in the lower Chesapeake Bay in 1922 (Hildebrand and Schroeder, 1928) and during 1950–1958 (Massmann and Pacheco, 1960), as well as from pound nets and haul-seines in Pamlico and Core sounds, North Carolina (Higgins and Pearson, 1928), show the same pattern.

Recreational catch records also indicate that the large Atlantic croaker reported by Ross (1988) have not been common in the Chesapeake and Delaware Bay areas. Between 1960 and 1970 the minimum citation weight for Atlantic croaker in the Virginia Saltwater Fishing Tournament ranged from 0.91 to 1.36 kg. Although 741 citations were issued during this period, only 1.9% were for Atlantic croaker \geq 1.82 kg. Between 1977 and 1982, however, although the minimum citation weight was raised to 1.82 kg, 599 citations were issued, including 47 entries for Atlantic croaker ≥2.27 kg (483–610 mm TL). The largest number of citations occurred in 1979 and 1980, coinciding with Ross's (1988) sampling period in North Carolina. Records from the Delaware State Fishing Tournament show the same pattern as that from Virginia. The number of citations was very small during the early 1970's, reached a peak in 1980, and decreased rapidly thereafter. Although complete information covering their entire range is not available, state records of Atlantic croaker along the east coast of the United States show the same pattern. Records from Georgia to New Jersey were broken during the period 1977–82. indicating that 1) unusually large fish occurred during this period and have not occurred since; and 2) their occurrence was not limited to areas north of North Carolina.

In conclusion, recent size and age composition data do not indicate the existence of a group of larger, older Atlantic croaker in the Chesapeake Bay region compared with more southern waters. Historic information agrees well with our results and indicates that fish >400 mm TL have not represented a large proportion of Atlantic croaker in this area. The abundance of unusually large fish during the period 1977-82 apparently constituted an unusual event and may reflect passage through the fishery of a few strong year classes that seemingly disappeared after 1982. Similar episodes-the occurrence of larger fish for a few years-have been previously reported for Atlantic croaker in Chesapeake Bay (Hildebrand and Schroeder, 1928; Massmann and Pacheco, 1960), suggesting the phenomenon happens periodically. An increase in survivorship of early spawned fish, combined with higher mortality of late-spawned fish as a result of low winter temperatures in estuarine nursery areas (Massmann and Pacheco, 1960; Joseph, 1972; Warlen and Burke, 1991) could account for an increase in the proportion of larger fish in certain years and explain the episodic occurrence of large Atlantic croaker in this area.

Our results for Chesapeake Bay, together with records of large fish south of North Carolina during 1977–82, suggest that the hypothesis of a basically different life history and population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina, should be reevaluated. However, sampling programs over time describing size and age compositions of Atlantic croaker throughout their range are still necessary to fully evaluate this question.

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