

**Abstract.**—Sagittal otoliths were used to determine age and growth of 605 larval and juvenile Atlantic croaker, *Micropogonias undulatus*, collected in the Middle Atlantic Bight and estuarine waters of Virginia. This study is the first to use age-based analysis for young Atlantic croaker collected in this region. A Laird-Gompertz model ( $r^2=0.95$ ) was used to describe the growth of Atlantic croaker up to 65 mm standard length (SL) and 142 days ( $t$ ):  $SL_{(t)} = 2.657 \exp \{4.656 [1 - \exp(-0.0081t)]\}$ ; where  $SL_{(t)}$  = standard length at day  $t$ . Spatial and temporal patterns in the size and age of Atlantic croaker showed a pattern of in-shore immigration from offshore spawning grounds, and faster early-season growth compared with late-season growth. Back-calculated hatching dates of Atlantic croaker collected in Virginia estuaries indicated a protracted spawning period over 8 months, from early July 1987 to early February 1988, with at least 82% of spawning occurring from August to October. Regression analysis indicated that early-spawned larvae (July through August) grew more than 39% faster than late-spawned larvae (September through February). Lapillar and sagittal otoliths were compared with light microscopy; ages were underestimated with lapillar otoliths, which were particularly inadequate in determining the age of older juveniles. The relation between SL and sagittal otolith maximum diameter was best described by a fourth order polynomial ( $r^2=0.99$ ) and faster-growing Atlantic croaker had larger otoliths (12%) than the same size slower-growing fish.

## Age and growth of larval and juvenile Atlantic croaker, *Micropogonias undulatus*, from the Middle Atlantic Bight and estuarine waters of Virginia

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Atlantic croaker, *Micropogonias undulatus*, range from New York to Florida and along the western and northern Gulf of Mexico (Ross, 1988; Atlantic States Marine Fisheries Commission, 1993). Historically, Atlantic croaker have ranked as one of the top five species in the commercial catch of finfishes in the middle Atlantic region (McHugh and Conover, 1986), although recruitment is highly variable in the species. In Virginia, annual commercial landings have varied by as much as threefold and have apparently declined overall since 1937 (Chesapeake Bay Program, 1988). Similarly, recreational landings have varied by as much as twofold over two years (U.S. Department of Commerce, 1991).

In species with substantial annual recruitment variability, change in the survival rate of prerecruits (larvae and juveniles) is a key factor in determining adult abundance (Houde, 1987). Determination of survival rates of prerecruits relies, in part, on daily age and growth information (Jones, 1992), and although otolith daily increment analysis has become common practice (Jones, 1992), there are few

published age and growth studies on the early life history of Atlantic croaker. Furthermore, there are no age-based estimates of growth for larval and juvenile Atlantic croaker for the Middle Atlantic Bight (MAB: shelf waters from Long Island, NY, to Cape Hatteras, NC) and estuarine waters of Virginia. Comparable age-based studies on the early life history of Atlantic croaker have concentrated on larvae collected in coastal waters south of Cape Hatteras, North Carolina (Warlen, 1982), or the northern Gulf of Mexico (Cowan, 1988).

North Carolina larvae (Warlen, 1982), collected south of Cape Hatteras at Beaufort Inlet, show a twofold decline in length-at-age between early- and late-season collections. Likewise, Cowan (1988) shows a similar slow growth rate for late-season larvae collected in the northern Gulf of Mexico. Warlen's (1982) back-calculated hatching dates indicate a broad spawning season from September to February, with peak spawning in October and November. On the basis of the pattern of progressive increase in mean size and age from the shelf to the estuary and on the basis of seasonal

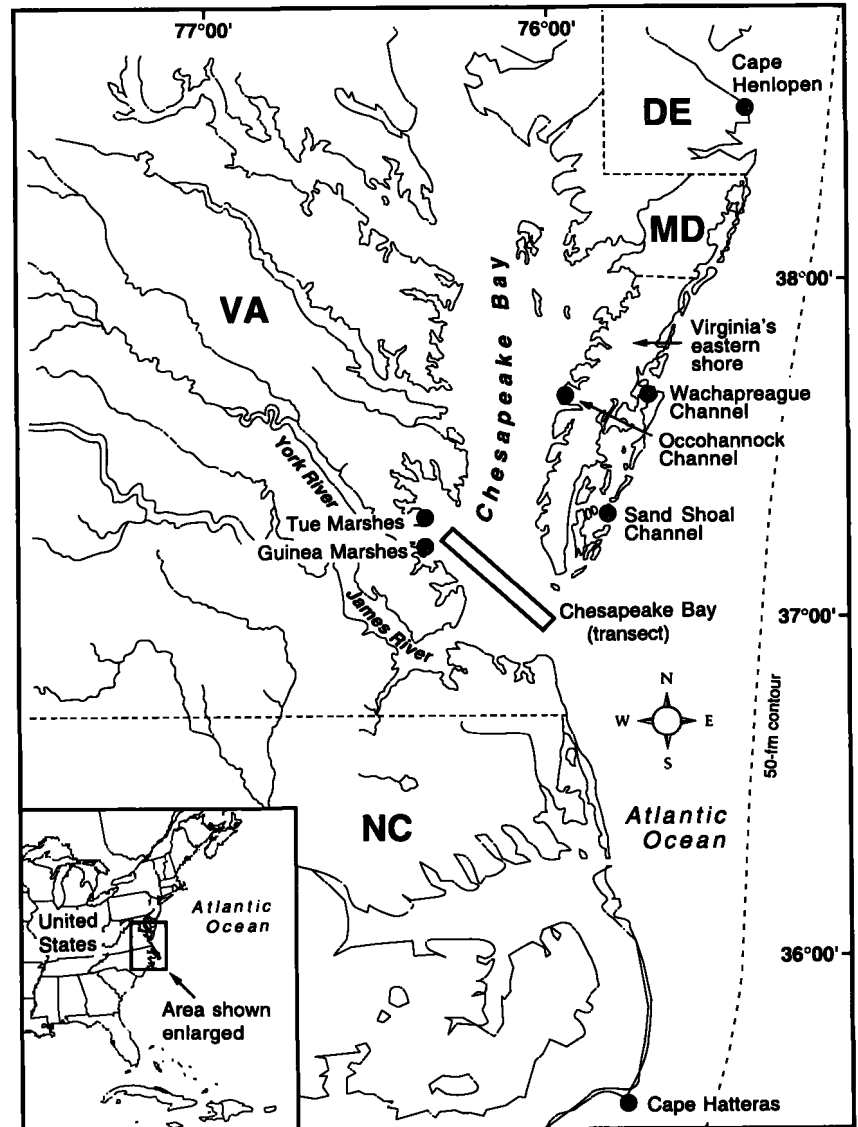
variability in age of larvae entering the estuary, Warlen (1982) postulates two offshore spawning locations for Atlantic croaker entering Beaufort. Warlen's conclusions imply potential differences in spawning source between larvae entering Chesapeake Bay and some of those entering Beaufort Inlet.

The purpose of the present study was to examine age and growth of larval and juvenile Atlantic croaker from the MAB and estuarine waters of Chesapeake Bay by using daily growth rings on otoliths. Specifically, we investigated the variability of size, size and age of entry into Chesapeake Bay, calculated hatching-date distributions to estimate spawning periodicity, and estimated temporal and spatial differences in growth rates. In addition, we determined if there were significant differences in age counts between lapillar and sagittal otoliths and in size and age counts between left and right sagittal otoliths. Finally, we compared the relation between otolith growth and somatic growth for field-captured Atlantic croaker with results presented in the literature.

## Materials and methods

### Sampling regime

Larval Atlantic croaker were collected in the MAB (from Cape Henlopen, Delaware, to Cape Hatteras, North Carolina; Fig. 1) from 3 November to 14 November 1987 from the shore to the 91-m (50-fm) contour with a stratified grid system illustrated in the MARMAP Plankton Survey Manual (Jossi and Marak, 1983). Seven additional stations at 2-km intervals were sampled along a transect across the mouth of the Chesapeake Bay. Larvae were sampled in oblique tows with a 60-cm bongo sampler containing 505- $\mu$ m mesh. Larval and juvenile Atlantic croaker sampled by Norcross and Hata (1990) were collected monthly from 29 September 1987 to 10 March 1988 at three inshore stations at Virginia's Eastern Shore (Wachapreague, Sand Shoal, and Occohannock Channel) and at two stations at the mouth of the York River (Guinea and Tue Marshes;



**Figure 1**

Station locations in estuarine waters of Virginia for collection of larval and juvenile Atlantic croaker from 21 September 1987 to 30 March 1988.

Fig. 1) with two 4.9-m otter trawls (one lined, one unlined) towed simultaneously. The lined net had a 6.4-mm mesh and a 3.2-mm mesh liner, and the unlined net a 15.9-mm mesh. Additional larval and juvenile Atlantic croaker were collected monthly from 21 September 1987 to 1 February 1988 at 8.1-km intervals along a 40.2-km transect running from the mouth of the York River to the mouth of the Chesapeake Bay (Fig. 1) with an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Finally, juvenile Atlantic croaker sampled by Dameron et al.<sup>1</sup> were collected monthly from 25 January to 30 March 1988 in the channels of the York and James Rivers at 8.1-km intervals from the mouth of the two rivers to 56.3 km upstream (Fig. 1) with

an otter trawl with a 9.1-m lined net containing 15.9-mm mesh and a 6.4-mm mesh liner. Otter trawls were towed at 1.0 to 1.5 m/s over the bottom for five minutes. Specimens were preserved in 70% ethanol immediately upon collection. The ethanol was changed within 24 hours and again after two days.

### Otolith processing and data analysis

Standard length (SL) measurements were made on fish to the nearest 0.1 mm with an image analysis system for individuals <20 mm SL or with vernier calipers for individuals ≥20 mm SL. Sagittal and lapillar otoliths were extracted from at least 30 fish chosen at random from each station and sampling date ( $n=605$ , 40 from the MAB and 565 from estuarine waters). Otoliths were extracted from all individuals when samples contained less than 30 fish. Only 40 of the 126 larvae collected in the MAB were available for age analysis owing to inadequate preservation. Otolith maximum diameter (OMD) was measured on sagittae from rostrum to postrostrum to the nearest 0.1 mm with an image analysis system—39 otoliths from larvae collected in the MAB and 143 otoliths from randomly selected estuarine larvae and juveniles were measured.

The right sagittal otolith was used in age and growth analyses except when lost or damaged; then the left otolith was used. Procedures for the preparation of otoliths that required sectioning and polishing followed Epperly et al. (1991)—in short, otoliths were sectioned longitudinally, ground, and then polished to the primordia on both sides. Generally, otoliths from fish <15 mm SL did not require grinding or polishing to distinguish daily increments; they were placed directly on glass slides and embedded in Euparal. Otoliths were read at 1,000 $\times$ , under cross-polarized, transmitted light on a monitor with an image analysis system. All specimens were aged without knowledge of fish size or collection date. Three independent age counts were averaged to determine final ages. Age counts were estimated by adding 5 days to the number of daily increments in the otoliths by assuming that increment deposition begins at 5 days posthatching as in spot (*Leiostomus xanthurus*; Peters et al.<sup>2</sup>).

Paired  $t$ -tests were used to determine if there were significant differences in age estimates between lapillar and sagittal otoliths ( $n=32$ ) and in size and age counts between left and right otoliths ( $n=30$ ). Also, the precision of sagittal age counts by the primary reader and a secondary reader were compared ( $n=50$ ) with the indices of average percent error (Beamish and Fournier, 1981), coefficients of variation, and index of precision (Chang, 1982). A paired  $t$ -test also was used to determine if there was a significant difference in mean age counts between readers.

To generalize comparisons of mean growth rates and size-at-age of Atlantic croaker across capture sites, stations were grouped geographically into regions. These regions were designated as MAB, Chesapeake Bay, seaside Eastern Shore (includes the Wachapreague and Sand Shoal Channel stations), bayside Eastern Shore (includes the Occohannock Channel station), marshes (includes the Tue and Guinea marsh stations), and rivers (includes the James and York river transects). The length and age of fish were compared among regions sampled with similar gears with independent, two-sample  $t$ -tests.

Linear regression comparisons (Rawlings, 1988) were used to compare growth rates (slopes) and size at day 0 (y-intercepts) between early- (September through October) and late-captured (November through March) larvae ≤15 mm SL and ≤80 d. The analysis was restricted by size because larger, older juveniles were not available during early-season collections. Linear regression comparisons (Rawlings, 1988) were also used 1) to compare growth between early- (July through August) and late-season (September through February) spawned larvae (≤19 mm SL) and 2) to compare growth between early- and late-season spawned juveniles (19.1–65 mm SL). Early- and late-spawned larvae and juveniles were analyzed separately so that linear growth patterns could be described for the two life stages. We also used ANCOVA to compare mean size between early- and late-spawned juveniles.

A Laird-Gompertz growth model (Laird et al., 1965) was used to describe the growth of Atlantic croaker larvae and juveniles ≤50 mm SL and ≤142 d:

$$SL_{(t)} = SL_{(0)} / \exp \{ [A_{(0)} / \alpha] [1 - \exp(-\alpha t)] \};$$

$SL_{(t)}$  = standard length at day  $t$ ;  
 $SL_{(0)}$  = assumed standard length at hatching ( $t=0$ );  
 $A_{(0)}$  = specific growth rate at hatching ( $t=0$ ); and  
 $\alpha$  = rate of exponential decay of the specific growth rate.

The model was fitted by an iterative, nonlinear least-squares procedure. Age-specific growth rates were subsequently calculated as

<sup>1</sup> Dameron, J. C., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program, bottom trawl survey. Annual data summary report series vol. 1987. Special Scientific Report 124, Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt., VA.

<sup>2</sup> Peters, D. S., J. C. Devane Jr., M. T. Boyd, L. C. Clements, and A. B. Powell. 1978. Preliminary observations of feeding, growth, and energy budget of larval spot (*Leiostomus xanthurus*). In Annu. Rep. NMFS, Beaufort, NC, p. 377–397.

$$A_{(t)} = A_{(0)} \exp(-\alpha t).$$

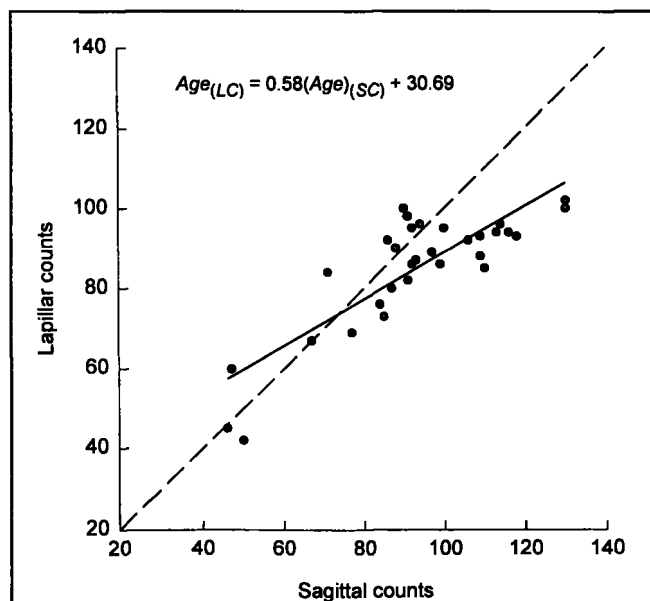
Finally, ANCOVA was used to compare mean otolith size between early-captured, fast-growing Atlantic croaker with late-captured, slower-growing Atlantic croaker between 11 and 37 mm SL.

## Results

### Otolith analysis

Age counts in sagittal and lapillar otoliths were significantly different ( $t$ -test,  $P=0.002$ ). For older age fish, lapillar counts underestimated sagittal counts, and the disparity increased with increasing age (Fig. 2). Also, no differences were found among size ( $t$ -test,  $P=0.49$ ) and age counts ( $t$ -test,  $P=0.85$ ) between left and right sagittal otoliths ( $n=30$ ).

Sagittal age counts by the primary reader showed good precision—the average percent error (APE) of counts was 4.8%, with a coefficients of variation (CV) and index of precision (D) of 6.4% and 3.8%, respectively. For the second reader's age counts these indices were 8.4% (APE), 11.5% (CV), and 6.7% (D). Although the second reader's age counts had relatively low precision, there was no significant difference in mean age counts between readers ( $t$ -test,  $P=0.27$ ).



**Figure 2**

Comparison of sagittal and lapillar otolith age counts ( $r^2=0.73$ ,  $n=32$ ) illustrating reproducibility of sagittal counts ( $Age_{SC}$ ) with lapillar counts ( $Age_{LC}$ ). Dashed line represents a one-to-one relation, and the solid line the regression describing the relation between sagittal and lapillar age counts.

### Size and age distributions

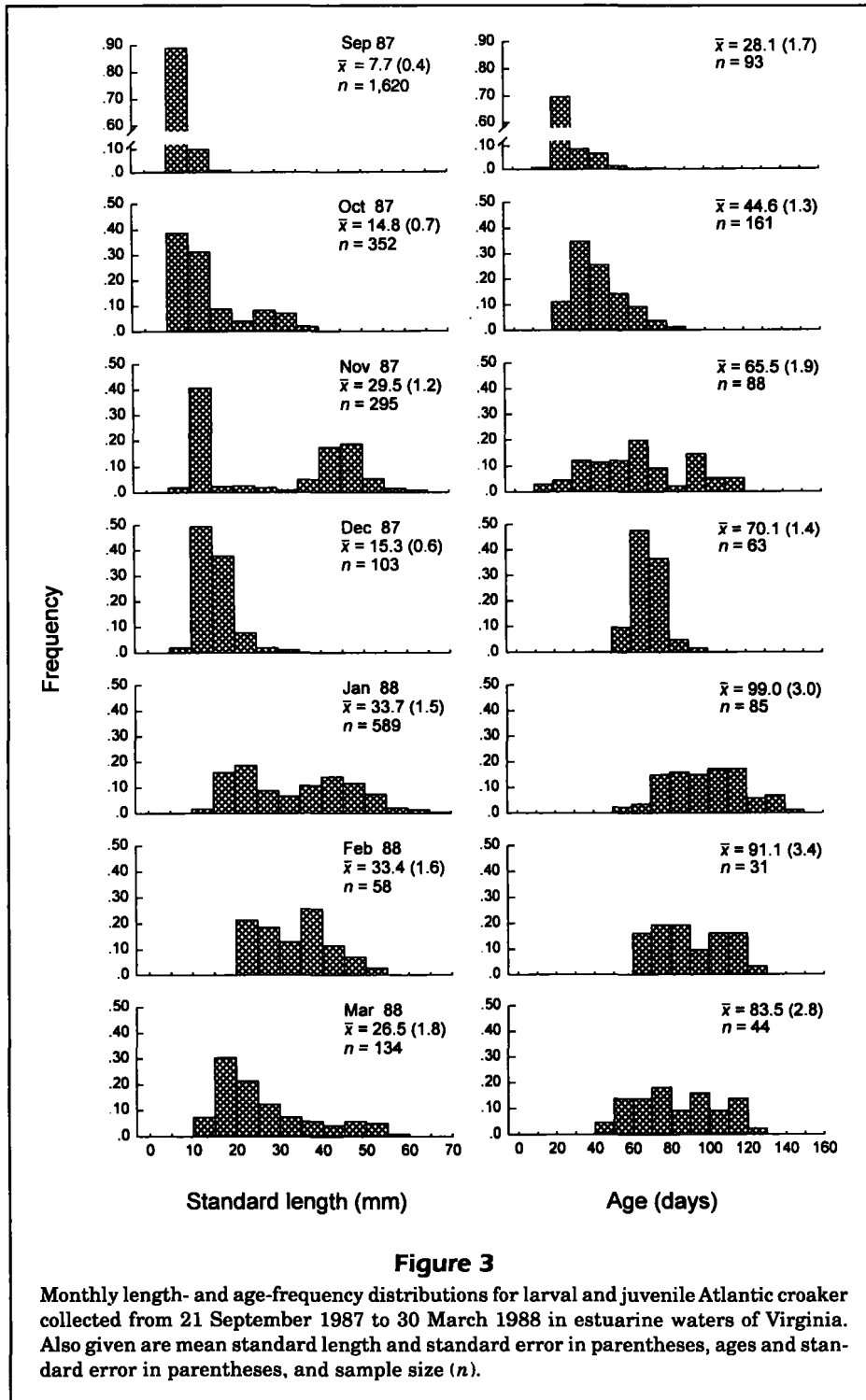
Monthly length- and age-frequency distributions showed that size and age of fish generally increased from September to January (Fig. 3). Size and age appeared to decline in February (although sample sizes were small) and mostly represented fish collected in the rivers after January. Also, length distributions were highly variable in comparison with respective age distributions (Fig. 3). For example, fish collected in November had two distinct length modes, whereas their age frequencies clearly had only one mode. This pattern was also evident for fish collected in October and January; thus size does not appear to be a good predictor of age in these fish.

Generally, smaller and younger fish were found in the seaside Eastern Shore region compared with the bay-side Eastern Shore or marsh regions ( $t$ -tests,  $P<0.001$ ) over the entire sampling season. This pattern was evident regardless of gear type. Significantly smaller ( $P=0.02$ ) and younger ( $P<0.001$ ) fish were found in the mainstem Chesapeake Bay compared with the rivers inland of the Bay. However, the rivers were sampled only during the later half of the sampling period.

The age of larval Atlantic croaker entering Virginia nursery grounds was examined from specimens collected at the mouth of the Chesapeake Bay (the most seaward station along the Chesapeake Bay transect) and at Wachapreague and Sand Shoal Channels. The youngest larvae (24 d) entered the mouth of the Chesapeake Bay on 21 September 1987 and measured 6.1 to 7.6 mm SL ( $n=3$ ). Fish collected at Wachapreague and Sand Shoal Channels were probably better representatives of the age of larvae that enter Virginia nursery grounds because smaller mesh nets (with 3.2-mm mesh liner which sampled smaller larvae more effectively) were used at these stations. The youngest larvae observed at Wachapreague Channel were collected on 29 September 1987 with a mean size and age of 7.3 mm SL and 26 d, respectively, with the youngest individuals (20 d) measuring 5.4 and 6.1 mm SL ( $n=2$ ). The youngest larvae observed at Sand Shoal Channel were collected on 30 September 1987 with a mean size and age of 8.3 mm SL and 29 d, respectively, with the youngest individuals (23 d) measuring 6.1 and 7.3 mm SL ( $n=2$ ). In conclusion, it appeared that the youngest larvae entered Virginian estuaries at an approximate age of 20 to 26 d, measuring 5.4 to 7.6 mm SL.

### Hatching-date distributions

Hatching-date distributions indicated a protracted spawning period of 8 months from 5 July 1987 to 10 February 1988 and with 82% of spawning limited to



August through October. Fish spawned earlier in the season are underrepresented in samples because they have experienced greater cumulative mortality than later spawned fish (Campana and Jones, 1992). Estimates of size- and age-specific mortality are needed to predict hatching-date distributions more accu-

rately, and these were not available. However, the result of greater accumulated mortality on early-spawned fish is to minimize the height of the estimated spawning peak. Hence, our results establish a lower bound of 82% of surviving juveniles spawned from August to October.

## Growth

Mean growth rates (mean SL divided by mean age) varied from 0.18 mm/d in the MAB to 0.41 mm/d in Chesapeake Bay (Table 1). Furthermore, early-spawned fish experienced considerably faster growth than late-spawned fish (Table 1).

Early-captured larvae grew 37% faster than late-captured larvae for individuals  $\leq 15$  mm SL and  $\leq 80$  d (Fig. 4A). Early-captured individuals were larger at age than late-captured individuals because of different growth rates and not because of larger size at

hatching, as indicated by tests of regression coefficients that showed highly significant differences between slopes ( $P < 0.001$ ) but not between intercepts ( $P = 0.16$ ).

Early-spawned larvae grew 39% faster than late-spawned larvae (Fig. 4B), and once these size differences were established, they persisted through the juvenile stage (Fig. 4C). There was a significant difference between slopes ( $P < 0.001$ ) for early- and late-spawned larvae, whereas, early- and late-spawned juveniles experienced similar growth according to tests of regression coefficients ( $P = 0.75$ ). Furthermore,

**Table 1**

Mean standard length (mm) and standard error (SE), age (d) (SE), and growth rate (mean SL/mean age) for larval and juvenile Atlantic croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia from 21 September 1987 to 10 March 1988 by hatching month, region, and gear type.

Hatching month	Sample size	Mean standard length $\pm$ SE	Mean age $\pm$ SE	Mean growth
<b>Middle Atlantic Bight (MAB)<sup>1</sup></b>				
Sep	19	7.9 $\pm$ 0.2	43.7 $\pm$ 0.9	0.18
Oct	21	5.8 $\pm$ 0.4	29.7 $\pm$ 1.5	0.20
<b>Seaside Eastern Shore (SES: Wachapreague and Sand Shoal Channel)<sup>2</sup></b>				
Aug	17	13.2 $\pm$ 1.5	41.0 $\pm$ 3.8	0.32
Sep	115	11.0 $\pm$ 0.5	42.7 $\pm$ 1.8	0.26
Oct	6	13.6 $\pm$ 0.8	56.5 $\pm$ 1.1	0.24
<b>Bayside Eastern Shore (BES: Occohannock Channel)<sup>2</sup></b>				
Aug	1	28.3 $\pm$ 0.0	94.0 $\pm$ 0.0	0.30
Sep	32	14.4 $\pm$ 0.7	67.1 $\pm$ 1.2	0.21
Oct	15	11.0 $\pm$ 0.2	57.5 $\pm$ 0.7	0.19
<b>Chesapeake Bay<sup>3</sup></b>				
Jul	7	25.8 $\pm$ 6.5	77.3 $\pm$ 11.2	0.33
Aug	74	28.9 $\pm$ 2.0	70.5 $\pm$ 3.8	0.41
Sep	21	27.8 $\pm$ 3.4	78.4 $\pm$ 8.0	0.36
Oct	21	35.4 $\pm$ 1.7	94.2 $\pm$ 2.7	0.38
Nov	7	20.4 $\pm$ 1.3	71.6 $\pm$ 1.0	0.29
<b>Marshes (Guinea and Tue Marshes)<sup>2</sup></b>				
Jul	10	24.0 $\pm$ 2.4	71.2 $\pm$ 3.0	0.38
Aug	39	16.5 $\pm$ 1.2	48.6 $\pm$ 2.2	0.34
Sep	75	9.8 $\pm$ 0.3	47.0 $\pm$ 2.2	0.21
Oct	4	10.6 $\pm$ 0.6	60.0 $\pm$ 1.0	0.18
Jan	7	12.7 $\pm$ 0.4	54.7 $\pm$ 2.0	0.23
<b>Rivers (York and James River)<sup>3</sup></b>				
Sep	13	48.5 $\pm$ 2.2	124.3 $\pm$ 1.7	0.39
Oct	25	32.1 $\pm$ 2.1	105.3 $\pm$ 2.2	0.30
Nov	28	27.6 $\pm$ 2.0	91.5 $\pm$ 2.8	0.30
Dec	32	31.8 $\pm$ 2.2	89.5 $\pm$ 2.9	0.36
Jan	15	24.4 $\pm$ 1.7	74.4 $\pm$ 1.4	0.33
Feb	1	10.6 $\pm$ 0.0	49.0 $\pm$ 0.0	0.22

<sup>1</sup> Gear type used was oblique 60-cm bongo nets with 505- $\mu$ m mesh.

<sup>2</sup> Gear type used was a 4.9-m lined trawl net with a 6.4-mm mesh and 3.2-mm mesh liner and a 4.9-m unlined net with a 15.9-mm mesh. The lined and unlined nets were towed simultaneously.

<sup>3</sup> Gear type used was a 9.1-m lined trawl net with a 15.9-mm mesh and 6.4-mm mesh liner.

early-spawned juveniles were significantly larger (18%) than late-spawned juveniles when mean size was adjusted by age (ANCOVA,  $P < 0.001$ , Table 2B).

A Laird-Gompertz growth model fitted the entire range of Virginia data well ( $r^2 = 0.95$ ), although variance in size increased with age (Fig. 5). Standard length at hatching ( $SL_{(0)}$ ) estimated from the Laird-Gompertz growth model (Fig. 5) was  $2.7 \pm 0.3$  mm SL and was similar to size-at-hatching estimates for laboratory-spawned Atlantic croaker from the Chesapeake Bay (2.0 mm SL; Middaugh and Yoakum, 1974) and North Carolina (2.4 mm SL; Jones<sup>3</sup>), but considerably higher than Warlen's (1982) estimate of 0.9 mm SL for wild-captured Atlantic croaker larvae from North Carolina. The rate of exponential decay of the specific growth rate ( $\alpha$ ) was estimated at  $0.0081 \pm 0.0012$  (Fig. 6). Changes in age-specific growth ( $A_t$ , a function of the rate of exponential decay of specific growth in time) indicated that larvae experienced a decline of daily growth rate from 3.2% at day 20 to 2.3% by day 60 (Fig. 6).

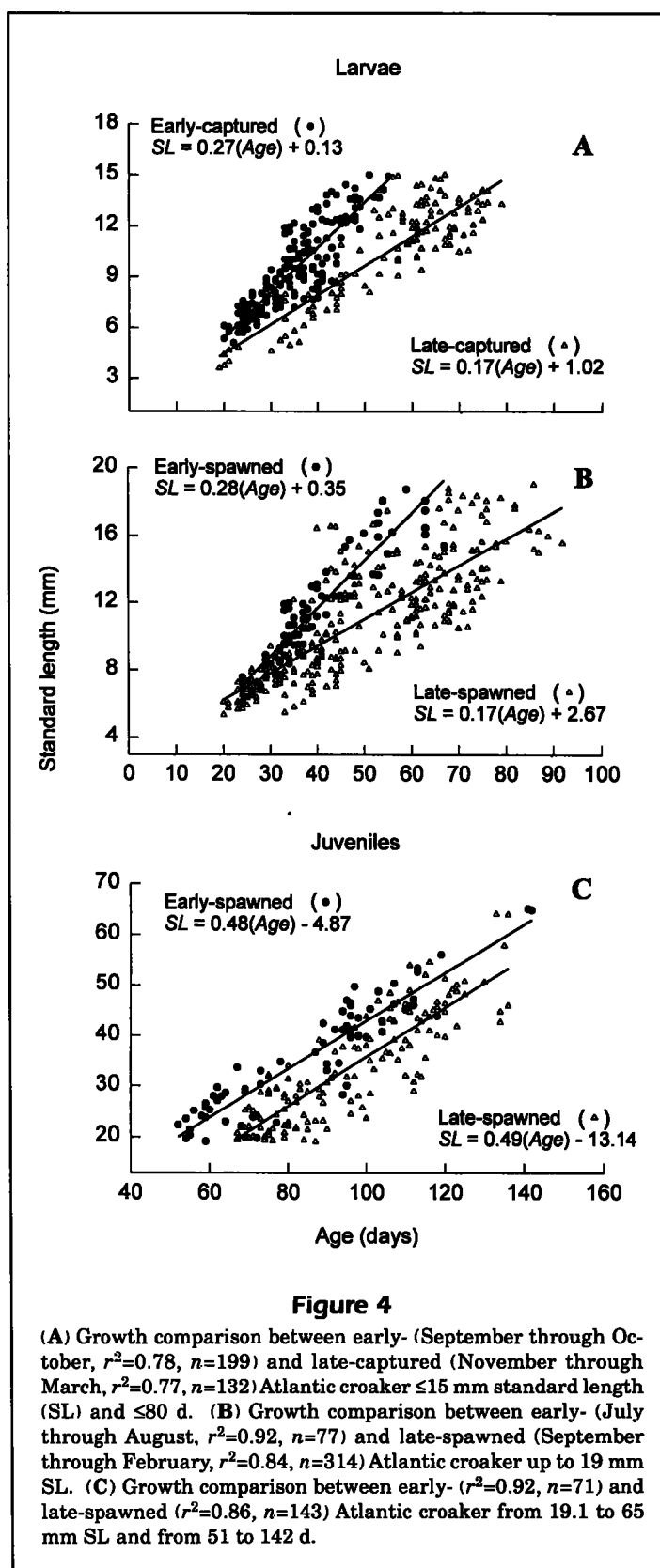
### Standard length and otolith maximum diameter (OMD) relation

The relation between sagittal OMD and SL was best described by a fourth order polynomial (Fig. 7). A simple linear model also described the OMD and SL relation fairly well ( $SL = 13.5$  (OMD) + 4.2,  $r^2 = 0.98$ ); however, there were strong patterns in the residuals. Otolith growth was similar between early-captured (fast growers captured from September to October) and late-captured (slow growers captured from November to March) groups when compared by slope ( $P = 0.50$ ). However, a significant difference was observed between the two groups when otolith size was adjusted for fish size (ANCOVA,  $P < 0.001$ , Table 3A). Size-adjusted means indicated that otoliths from the early-captured group were almost 13% larger than otoliths from the late-captured group (Table 3B). Plots of individual otoliths showed very little overlap between groups (Fig. 8).

## Discussion

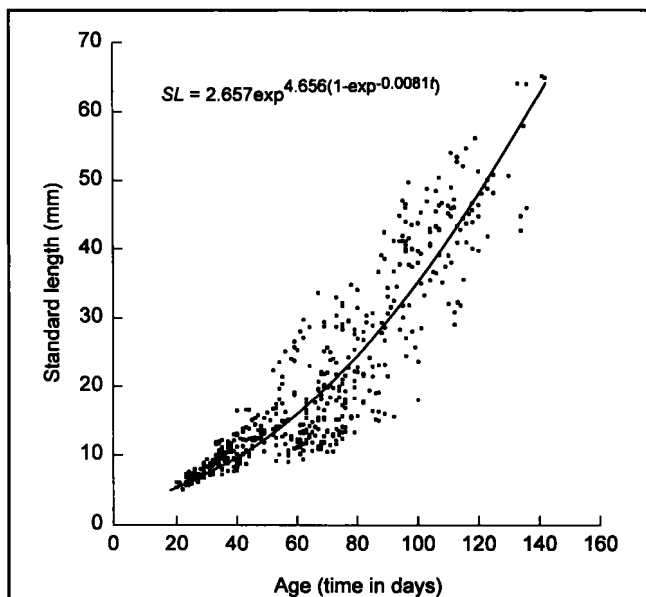
### Otolith analysis

We were unable to obtain known-age Atlantic croaker to validate the assumption that incre-



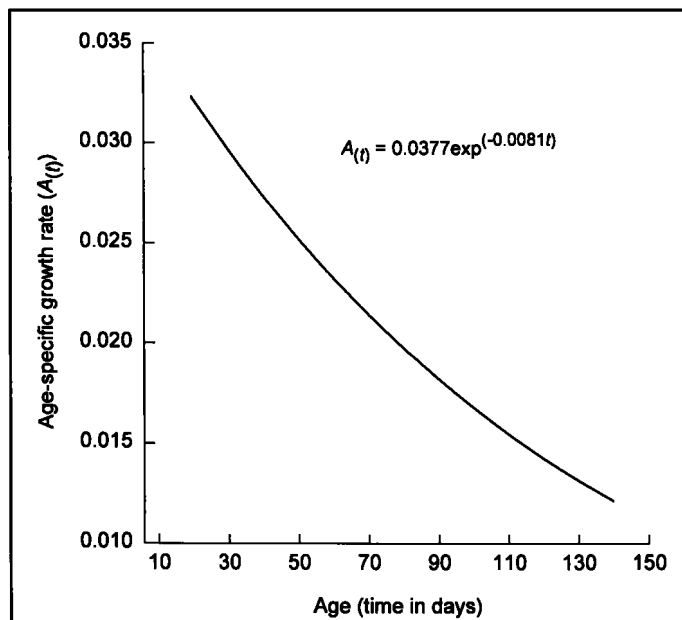
<sup>3</sup> Jones, C. J. 1995. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529. Unpubl. data.

ments form daily in larvae. However, daily growth increments have been validated in the otoliths of larval spot, *Leiostomus xanthurus*, a sciaenid relative of Atlantic croaker (Peters et al.<sup>2</sup>), and we assumed,



**Figure 5**

Laird-Gompertz growth model describing growth of Virginia larval and juvenile Atlantic croaker  $\leq 65$  mm standard length (SL) and  $\leq 142$  d ( $r^2=0.95$ ,  $n=605$ ).



**Figure 6**

Age-specific growth rate relation determined from the equation  $A_{(t)} = A_{(0)} \exp(-\alpha t)$  with  $A_{(0)}$  and  $\alpha$  from the Laird-Gompertz growth equation (Fig. 2).

therefore, that increment deposition is daily in Atlantic croaker. Peters et al.<sup>2</sup> also demonstrated that the first daily increment forms in the sagittae of spot at the time of first feeding, which occurs in spot about 5 d after hatching at 18 and 20°C (Powell and Chester, 1985); thus, we added 5 days to our increment counts.

Sagittal otoliths of Atlantic croaker begin to increase growth along their anterior and posterior axes during the late-larval stage, whereas lapilli maintain concentric growth through the juvenile stage, potentially making lapilli preferable when using otoliths to backcalculate growth. In examining the potential for using lapillar counts as a surrogate to sagittal counts, we found under light microscopy that lapillar counts increasingly underestimated sagittal counts as fish increased in age. The microstructure in sagittal otoliths also had better defined increments, leading us to assume that sagittal counts were more accurate predictors of age than lapillar counts. No differences in the size and age counts between left and right sagittal otoliths warranted the replacement of lost or damaged right otoliths with left otoliths.

### Size and distribution

Offshore spawning and subsequent estuarine migration of Atlantic croaker have been thoroughly documented by studies with egg and larval size distributions (Hildebrand and Cable, 1930; Wallace, 1940; Haven, 1957; Colton et al., 1979; Morse, 1980; Lewis

**Table 2**

Growth comparison between early- (July through August) and late-spawned (September through February) Atlantic croaker from 19.1 to 65 mm SL and from 51 to 142 d with an analysis of covariance (ANCOVA) of standard length (SL) of fish (mm), with age (d) as the covariate. Size adjusted means equals the mean SL of fish, adjusted for the effects of age.

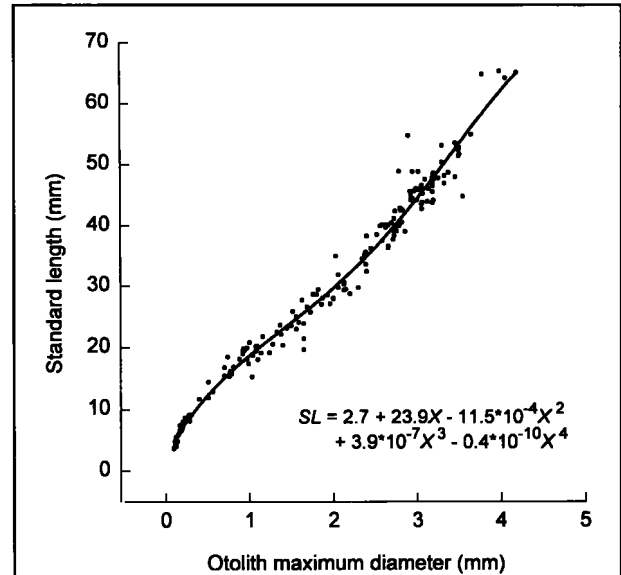
A	ANCOVA		
	df	F-value	P-value
Covariate age	1	743.6	$P < 0.001$
Main effect			
Early-spawned vs. late-spawned	1	89.9	$P < 0.001$
Residual sums of squares (d)	5,489.2 (211)		
$r^2$	0.78		
B	Size adjusted means (mm) (SE)		
	Early-spawned: 39.5 (0.6)	Late-spawned: 32.3 (0.4)	



**Table 3**

Otolith comparison between faster-growing early-captured (September through October) Atlantic croaker and slower-growing late-captured (November through March) Atlantic croaker between 11 and 37 mm standard length (SL) with an analysis of covariance (ANCOVA) of the otolith maximum diameter (OMD) of sagittae (mm), with SL of fish (mm) as the covariate. Size-adjusted means equals the mean OMD of sagittae, adjusted for the effects of SL of fish.

ANCOVA			
A	df	F-value	P-value
Covariate standard length	1	1,126.9	$P < 0.001$
Main effect			
Early-captured vs. late-captured	1	36.2	$P < 0.001$
Residual sums of squares (d)			
	1.16 (66)		
$r^2$	0.95		
B Size adjusted means (mm) (SE)			
Early-captured:	1.54 (0.02)	Late-captured:	1.25 (0.02)

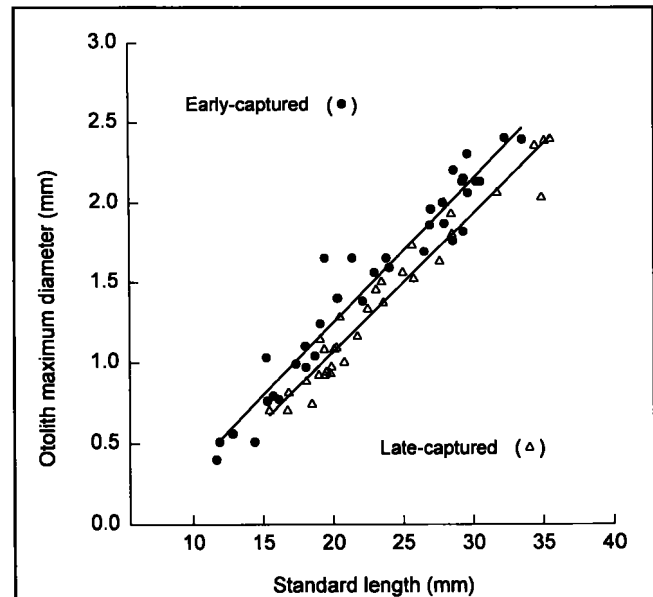


**Figure 7**

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) ( $r^2=0.99$ ,  $n=182$ ).

and July, 1983; Warlen and Burke, 1990). However, only two studies (Warlen, 1982; this study) used daily age information from otoliths to support such findings. Daily age information is critical because size-at-age is highly variable in this species, and age-based data provide reliable confirmation of cross-shelf transport of larvae. Warlen (1982) found a general increase in the age of fish entering the Beaufort estuary as the season progressed, and suggested this increase in age was an effect of variable transport distance or rates to the estuary (or both). Seasonal trends observed in this study may be attributed to similar processes.

Mean ages generally increased over time, lagging about 10 d between monthly sampling dates, suggesting constant recruitment over the entire sampling season. However, mean ages in the rivers declined after December. Our samples collected in January along river transects show a gradient of smaller, younger individuals upstream and of larger, older individuals downstream. Bottom waters in the York River experience a winter temperature gradient, with the lowest temperatures occurring in upper reaches of the river (Chao and Musick, 1977; Dameron et al.<sup>1</sup>; Land et al.<sup>4</sup>) and the higher temperatures in the Bay mainstem. This bottom water temperature gradient coupled with the increase in size of Atlantic croaker



**Figure 8**

The relation between otolith maximum diameter (OMD) (mm) and standard length (SL) of fish (mm) illustrating otolith and somatic growth relation between faster-growing, early-captured (September through October) Atlantic croaker ( $n=36$ ) and slower-growing, late-captured (November through March) Atlantic croaker ( $n=32$ ) between 11 and 37 mm SL.

<sup>4</sup> Land, M. F., P. J. Geer, C. F. Bonzek, and H. M. Austin. 1994. Juvenile finfish and blue crab stock assessment program. Bot-

tom trawl survey. Annual data summary report series. Volume 1988. Spec. Sci. Rep. Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 171 p.

downstream may indicate movement of larger, older individuals into deeper, warmer waters of the mainstem Chesapeake Bay. Atlantic croaker's sensitivity to low temperatures (Massmann and Pacheco, 1960; Joseph, 1972) may further explain the movement of older and larger fish from the rivers into warmer Bay waters.

### Hatching-date distributions

Our estimate of a protracted spawning season from early July 1987 to February 1998, with peak spawning in September, is similar to earlier reports in studies that used the presence of eggs or early larvae to estimate spawning. These studies suggest a protracted spawning period from August through December with peak spawning from August to October (Wallace, 1940; White and Chittenden, 1977; Johnson, 1978; Colton et al., 1979; Morse, 1980; Chittenden et al.<sup>5</sup>). Although our observation that spawning may begin as early as July has not been reported elsewhere, ovaries containing postovulatory follicles recently have been observed in Atlantic croaker from the Chesapeake Bay as early as July (Barbieri et al., 1994). Furthermore, because sexually mature adults do not begin to migrate out of the Chesapeake Bay until early July, and mainly in August and September (Wallace, 1940), limited spawning of Atlantic croaker may occur in proximal coastal waters as suggested by Haven (1957).

### Growth

When comparing temporal patterns in growth, it is best to analyze differences between groups by spawning date, rather than by capture date; otherwise older fish are under represented because of their greater accumulated mortality (Campana and Jones, 1992). Temporal growth variability was observed when the data were analyzed both by capture date and spawning date, although a 6% greater difference was observed when the data were analyzed by spawning date.

Seasonal variability in the growth of larval and juvenile Atlantic croaker may result from higher water temperatures or increased food in July and August (or both) (Alden et al.<sup>6</sup>) or from improved

survival of larger, faster-growing fish (Miller et al., 1988; Isley and Grimes, 1996). Hatching dates of faster-growing, early-spawned fish coincided with peak mean surface water temperatures in July and August (26.3° and 26.7°C, respectively; U.S. Department of Commerce<sup>7</sup>) and with peak plankton abundances in the Chesapeake Bay which typically occur in July (Alden et al.<sup>6</sup>). Furthermore, hatching dates of slower-growing fish coincided with increased patchiness and falling plankton abundances which typically begin in September and October (Alden et al.<sup>6</sup>). Warlen (1982) reported similar seasonal growth patterns for North Carolina Atlantic croaker larvae and speculated that slow growth observed in late-captured fish (mid-January to mid-April) might be attributed to colder ocean temperatures and low food availability in mid- to late-winter, or less likely, to smaller egg size of late-spawned larvae.

Recently immigrated larvae collected in Virginia estuaries in this study were larger at age than North Carolina larvae. Monthly mean growth rates (mean SL/mean age) of estuarine collected larvae (26–65 d) in this study ranged from 0.26 to 0.40 mm/d and were considerably higher than weekly mean growth rates (0.16–0.27) for similar age (32–64 d) North Carolina larvae collected in estuarine waters (see Warlen 1982, Table 1). Because this study and Warlen's (1982) were conducted in different years, we cannot eliminate the real possibility that these differences may be temporal, year-to-year changes. Further inter-year studies within Virginia and North Carolina, showing consistent patterns of growth variability, are needed to conclude that there are regional growth differences. However, whether spatial or temporal, or a combination of both, within-season patterns among the two studies are similar, whereas growth rates themselves differ.

Apparently, Atlantic croaker larvae immigrating into estuaries of Virginia and North Carolina can be categorized as early-spawned, fast growers or as late-spawned, slow growers. These seasonal growth differences, coupled with a spatially and temporally extended spawning season suggest that Atlantic croaker encounter variable environmental factors that may affect their survival. Identifying factors that may enhance survival or affect mortality rates of these spatially and temporal explicit groups are of major interest and are worthy of further study.

<sup>5</sup> Chittenden, M. E., C. M. Jones, L. R. Barbieri, S. J. Bobko, and D. E. Kline. 1990. Initial information on the Atlantic croaker, a final report on development of age determination methods, life history-population dynamics information, and evaluation of growth overfishing potential for important recreational fishes. Final Rep. to Virginia Mar. Res. Comm. VMRC I, Va. Inst. Mar. Sci., College of William and Mary, Gloucester Point, VA, 88 p.

<sup>6</sup> Alden, R. W., III, R. S. Birdsong, D. M. Dauer, H. G. Marshall, and R. M. Ewing. 1992. Virginia Chesapeake Bay water quality and living resources monitoring programs: executive report, 1985–89. Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA 23529, Report 849, 33 p.

<sup>7</sup> U.S. Department of Commerce, National Ocean Service, NOAA, Ocean and Lake Level Division Database, Rockville, MD 20874, June 1992.

## Standard length and otolith maximum diameter (OMD) relation

We found that in wild-caught larval Atlantic croaker, faster-growing individuals have larger otoliths than similar-size slower-growing individuals. Our results differ from results found for laboratory-reared guppies (*Poecilia reticulata*) (Reznick et al., 1989), pond-reared striped bass (*Morone saxatilis*) (Secor and Dean, 1989), red seabream (*Pagrus major*), and spot (*Leiostomus xanthurus*) (Secor et al., 1989). In these studies, where food ration was controlled, slower-growing individuals had larger otoliths than similar-size faster-growing individuals. However, in Arctic char (*Salvelinus alpinus*), otolith growth rate has been found to continue increasing while somatic growth remains constant when exposed to temperatures above 13°C (Mosegaard et al., 1988). In our study, the early-captured, faster-growing Atlantic croaker, may have experienced otolith growth that exceeded their maximum somatic growth rate.

Unfortunately, there are no quantitative data that can be tested to determine what factors influenced the growth of Atlantic croaker in our samples and what were the subsequent effects on the otolith growth-somatic growth relation. The underlying issue, however, is to examine how the fish and otolith-size relation is affected by temperature responses of somatic growth rate at particular food levels (Mosegaard et al., 1988) and to determine its significance when backcalculating growth from increment widths (Campana and Jones, 1992).

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