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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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AGE AND GROWTH OF LARVAL AND JUVENILE ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, FROM THE MIDDLE ATLANTIC BIGHT AND ESTUARINE WATERS OF VIRGINIA

by

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ABSTRACT

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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Sagittal otoliths were used to determine the age and growth of 605 larval and juvenile Atlantic croaker, *Micropogonias undulatus*, collected in the Middle Atlantic Bight (MAB) and estuarine waters of Virginia. A Laird-Gompertz model ($r^2 = 0.95$) was used to describe the growth of croaker up to 65 mm standard length (SL) and 142 days (t): $SL_{(t)} = 2.657 \text{ Exp } \{4.656 [1\text{-Exp } (-0.0081t)]\}$; $SL_{(t)}$ = standard length at day t. Generally, croaker collected inshore were larger and older than those collected offshore, indicating estuarine immigration from offshore spawning grounds. Back-calculated hatch-dates indicated spawning over an 8-month period from 05 July 1987 to 10 February 1988 with 82% of spawning occurring from August to October. Regression analysis indicated that early-spawned larvae (before October) grew more than 41% faster than late-spawned larvae (after September). Lapillar and sagittal otoliths were compared with light microscopy and found that lapillar otoliths underestimated age and were inadequate as a surrogate to sagittal otoliths in age determination. A fourth order polynomial best described ($r^2 = 0.99$) the relationship between SL and sagittal otolith maximum diameter (OMD). Contrary to the literature for other species, faster growing croaker had more than 12% larger otoliths than same size slower growing fish.

DEDICATION

This thesis is dedicated to my parents Phillip and Sachiko, and my brother Richard. Thank you so much for so many things, but mostly for your love and support. I couldn't have done it without you!

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INTRODUCTION

Atlantic croaker, *Micropogonias undulatus*, in all regions of its major range from the Chesapeake Bay to middle Florida and along the western and northern Gulf of Mexico (Ross 1988), are of great economic importance both commercially and recreationally. Historically, in the middle Atlantic region from New York to Virginia, croaker have ranked as one of the top five species that make up the annual total commercial catch of finfishes (HcHugh and Conover 1986). However, recruitment is highly variable in the species as seen in the commercial and recreational landings data. Virginia has generally accounted for the majority of the commercial catch of croaker in the western Atlantic, however, the commercial catch of croaker in Virginia, as in other regions of the Middle Atlantic Bight (MAB), has oscillated by as much as three orders of magnitude with an apparent overall decline since 1937 (Chesapeake Bay Program 1988; Virginia Marine Resource Commission, Commercial Fishery Statistics 1987, 1989). Virginia's recreational fishery has shown similar oscillations in abundance and have fluctuated by as much as two fold within two years (U.S. Department of Commerce, Marine Recreational Fisheries Statistics Surveys 1991).

One of the keys to effective fishery management is understanding the factors affecting year-to-year variability in recruitment. Knowledge of the age and growth characteristics of pre-recruits (larvae and juveniles) is vital to such work. Much of the information about the age and growth of pre-recruits has been based on daily growth increments in otoliths. Since Panella's (1971; 1974) pioneering work with daily growth increments in otoliths, immediate research focused on the validation of daily increments in the otoliths of an array of freshwater and marine species from various families (reviewed by: Campana and Neilson 1985; Jones

1986). In recent years researchers have recognized the ability to follow a fish's early life history by analyzing information recorded in the microstructure of otoliths. Researchers now analyze transitions throughout the development of a fish's early life history (Brothers and McFarland 1981; Victor 1982; Neilson et al. 1985), and the various factors affecting somatic growth (temperature, photoperiod, resource availability, pH, etc.) in relation to otoliths size, weight, or microstructure (Rice et al. 1985; Geen et al. 1985; Jones and Brothers 1987; Campana and Hurley 1989).

Although otolith daily increment analysis has become common practice, there are few age and growth studies published on the early life history of young (larvae and juvenile) croaker. Furthermore, age and growth information on young croaker collected in the MAB and estuarine waters of Virginia is totally lacking. The two studies that have been published have concentrated on larvae collected in coastal waters off North Carolina south of Cape Hatteras (Warlen 1982) and on larvae collected in coastal waters of the northern Gulf of Mexico off western Louisiana (Cowan 1988).

Previous Studies

Warlen (1982) found that larval croaker collected off North Carolina from 26 October 1979 to 17 April 1980 were spawned from 16 September 1979 to 24 February 1980, with peak spawning in October and November. Monthly mean standard lengths (SL) and ages ranged from 4 to 11 mm SL and 16 to 64 days (d) from October to April. Mean size and age progressively increased from the shelf to the estuary, indicating offshore spawning. Warlen suggested that transport rates and/or distances from spawning grounds are highly variable since mean larvae sizes of those entering the estuary remained relatively the same while mean ages increased by almost a factor of two as the season progressed. Due to seasonal variability in

the age of larvae entering the estuary, and the consistency of their size, Warlen suggested the presence of two sub-groups of croaker in North Carolina waters: a fast-growing group spawned early in the season and a slow-growing group spawned late in the season. Mean growth rates (mean SL/mean age) ranged from 0.272 mm/d in larvae collected on 26 October 1979 to 0.156 mm/d on 17 April 1980. Warlen stated that the slower growth rate found in late-spawned larvae is possibly due to colder ocean temperatures and less food availability in mid- to late-winter, or less likely, smaller egg size of late-spawned larvae and consequent reduced growth rate in early larval growth.

Cowan (1988) collected croaker larvae from the northern Gulf of Mexico late in the spawning season in mid-monthly cruises from December 1981 to April 1982. Based on 72 larvae, size ranged from 8 to 17 mm total length and were estimated to be 40 to 80 d old, with an estimated growth at 0.19 mm/d. Cowan noted the similarity of growth rates of late-spawned northern Gulf larvae (0.19 mm/d) and Warlen's (1982) North Carolina larvae captured late-season in April (0.16 mm/d). Cowan suggested the need to sample croaker larvae during peak spawning in the northern Gulf of Mexico to determine if two sub-groups with different growth rates occur in the Gulf as in North Carolina.

Stock Identification

Historically, croaker have been managed as a single stock in the western Atlantic along North America. However, White and Chittenden (1977) suggested that two stocks of croaker occur north and south of Cape Hatteras, North Carolina, based on differences of maximum size, life span, and total annual mortality of adult populations in the two regions. Ross and Sullivan (1987) could not identify separate stocks north and south of Cape Hatteras based on biochemical and tagging studies, although ten of 24 loci sampled indicated potential genetic

variation. It should be noted that minimal mixing between very large fish stocks is adequate to induce genetic homogeneity (Grant and Utter 1984; Mork et al. 1985) although the stocks, for management purposes, should be managed separately.

Temporal aspects of spawning also differ north and south of Cape Hatteras. Generally croaker spawn on the mid- to outer-continental shelf in deep, warm, saline waters (Warlen and Burke 1990). Norcross and Austin (1988) suggested that adult migration and spawning behavior is cued by water temperatures in response to seasonal wind patterns, and may be greatly variable from year to year. In the MAB north of Cape Hatteras, croaker spawn from August through December with peak spawning from late August through October (Wallace 1940; Haven 1957; Johnson 1978; Colton et al. 1979; Morse 1980; Chittenden et al. 1990). In contrast, croaker south of Cape Hatteras have been reported to spawn slightly later from September through March with peak spawning from late September through November (Hildebrand and Cable 1930; Warlen 1982).

Somatic and Otolith Growth Relationship

When a strong relationship exists between fish and otolith size through a life stanza, it is assumed that otolith increment widths reflect somatic growth. Although apparently straight forward, back-calculating growth from increment widths is subject to error when underlying assumptions are violated. The back-calculation of growth is based on the assumptions that increments are daily, and increment widths are a true indication of a fish's somatic growth for that day (Campana and Jones 1992). Furthermore, several recent studies (Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989) have indicated the confounding effects of feeding and temperature which can decouple the relationship between fish and otolith size, thus, invalidating generalized back-calculation formulas. Growth

variability effects on the somatic and otolith size relationship has not been investigated for wild or lab-reared croaker.

Purpose

The purpose of this study is to determine age and growth for larval and juvenile croaker collected in the MAB and estuarine waters of Virginia using the daily aging technique with otoliths. Specific objectives are to determine: spatial and temporal variability of size and age distributions, and size and age of entry into the bay, hatch-date distributions, and the length and peak of spawning. Estimated growth rates are used to determine seasonal and spatial differences in growth, and are compared with results for North Carolina and Gulf of Mexico provided by Warlen (1982) and Cowan (1988), respectively. Provided that the presence of separate stocks north and south of Cape Hatteras is debated, comparisons of early life histories between croaker from these two locations may provide valuable information in discerning separate stocks. Thus, comparisons of the early life histories of fish from this study are made extensively with North Carolina croaker larvae collected south of Cape Hatteras (Warlen 1982), and less extensively with croaker collected in the northern Gulf of Mexico (Cowan 1988). Finally, the relationship between otolith growth and somatic growth for field captured croaker are compared with results presented in the literature.

MATERIALS AND METHODS

Sampling Regime

Croaker larvae were collected in the ocean from the shore to the 91.5 m (50 fm) contour in the MAB from Cape Henlopen, Delaware to Cape Hatteras, North Carolina (see Cruise Report NOAA Ship FERREL S492, FE-87-09-SG, for sampling station locations). Sampling was conducted daily from 03 November 1987 to 15 November 1987 at random sites selected using the NMFS/MARMAP stratified grid system. A transect across the mouth of the Chesapeake Bay and secondary stations between the randomly selected sites were also sampled. Larvae were collected in oblique tows of 60 cm bongo nets with 505 μm mesh nets.

Additional croaker larvae and juveniles were collected monthly at three stations at Virginia's Eastern Shore (two seaside at Wachapreague Channel and Sand Shoal Channel, and one bayside at Occohannock Channel) and at two stations at the mouth of the York River (Guinea Marshes and Tue Marshes) from 29 September 1987 to 10 March 1988 in otter trawls (Figure 1). The trawl gears used were 4.88-m lined and unlined nets towed simultaneously. The lined net had a 6.35-mm mesh and 3.18-mm mesh liner, and the unlined net a 15.88-mm mesh. Croaker were also collected monthly from 21 September 1987 to 29 February 1988 at 8.05 km intervals along a 40.23-km transect running from the mouth of the York River to the mouth of the Chesapeake Bay. The trawl gear used was a 9.14-m lined net with a 15.88-mm mesh and 6.35-mm mesh liner. The same gear was used to sample the channels of the York and James rivers monthly from 25 January 1988 to 30 March 1988 at 8.05 km intervals from the mouth of the two rivers to 56.33 km upstream.

Weather permitting, all samples in estuarine waters were collected by otter trawls with a tow speed of 1.03 m/sec to 1.54 mm/sec over the bottom for five minutes. All specimens used in this study were preserved in 70% ethanol immediately upon collection, with ethanol changes within 24 hours and again after two days.

Otolith Extraction and Preparation

Prior to otolith extractions, SL measurements were recorded (n = 3,277; 126 from the MAB and 3,151 from Virginia's estuarine waters) to produce monthly length-frequency distributions. All specimens were measured to the nearest 0.01 mm using the Optimas image analysis system with an Olympus SZH stereoscopic microscope (specimens <20 mm SL), or with vernier calipers (specimens >20 mm SL).

For individuals used in the age and growth analysis, sagittal and lapillar otoliths were extracted under a stereoscopic microscope and stored dry for future analysis. At least 30 specimens were chosen at random from each station for each sampling date. All the individuals were used when samples had less than 30 specimens. A total of 605 individuals were used in the age and growth analysis; 40 from the MAB and 565 from Virginia's estuarine waters. Many of the larvae collected in the MAB were not used in the age and growth analysis because of problems with otolith preservation. However, length for the 40 larvae that could be used were representative of the entire collection (Chi Square goodness of fit test, α = .05), and thus, were deemed a valid sample of MAB larvae.

OMD measurements were taken to the nearest 0.01 mm using the Optimas image analysis system prior to embedding. Measurements were taken on otoliths from 39 of the 40 MAB larvae (for one individual, both sagittal otoliths were partially broken during dissection); for fish from estuarine waters otolith measurements were taken for 143 randomly selected

larvae and juveniles. Procedures described by Epperly et al. (1991) were used for the preparation of otoliths that required sectioning and polishing. Otoliths were sectioned longitudinally and ground and polished to the primordia one both sides. Generally, otoliths from fish <15 mm SL did not require grinding and polishing to distinguish daily increments and were placed directly on glass slides and embedded in Euparal with the proximal, sagittal plane up.

Otolith Increment Analysis

I was unable to obtain known-age croaker in order to validate the assumption that increments formed daily in larval croaker. However, daily growth increments have been validated in the otoliths of larval spot, *Leiostomus xanthurus*, a sciaenid relative of croaker (Peters et al. 1978). Because of the similarities in the ecology and biology of spot and croaker, I assumed that the increments observed in the otoliths of croaker were formed daily.

General observation indicated that lapillar otoliths maintain a more spherical shape for a longer period of time than sagittal otoliths, potentially making them preferable to sagittae for determining growth. In croaker, the lapillus forms at the same time as the sagitta and therefore may give similar age counts. As part of a preliminary analysis it was determined if the two otoliths gave similar age counts. Results, as discussed later, indicated that sagittal otoliths were the better predictors of presumptive age, and thus, were used in all other analyses.

Right sagittal otoliths were used in the aging analyses except when lost or damaged (n = 13). No differences were found among age counts (t-test, $p < 0.05$) and size (t-test, $p < 0.05$) between left and right otoliths (n = 30). Age counts were estimated by adding 5 d to the number of daily increments counted in the otoliths by assuming that increments begin to form

at yolk-sac absorption. Peters et al. (1978) demonstrated that the first daily increment in spot, a related species of croaker, forms at first feeding about 5 d after hatching when yolk-sac absorption has been completed. Similar results have been found for northern anchovy (*Engraulis mordax*, Brothers et al. 1976), Pacific herring (*Clupea harengus pallasi*, McGurk 1984), and in Atlantic herring (*Clupea harengus harengus*, Lough et al. 1982; Geffen 1982). Thus, I assumed that initial increment deposition in croaker otoliths is at first feeding which occurs 5 d post-hatch when yolk-sac absorption is completed, as is shown in the closely related spot and many other species.

The Optimas image analysis system was also used to assist in aging. Otoliths were read on a monitor connected to a Olympus BHSM compound microscope using cross-polarized, transmitted light at 350-1000X. All specimens were aged without knowledge of fish size or collection date. Three independent age counts, with no knowledge of previous age counts, were averaged to estimate final ages. A random subsample of 50 specimens were read by a second investigator to calculate indices of precision and reproducibility of age counts. These indices included the average percent error (APE; Beamish and Fournier 1981) and the coefficient of variation (CV) and index of precision (D; Chang 1982).

Data Analysis

All statistical analyses were conducted using SAS (Statistical Analysis System: SAS/STAT User's Guide 1989; SAS System For Linear Models 1991).

A paired t-test was run on estimated age counts between lapilli and their corresponding sagittae from 32 randomly selected individuals to determine if the otoliths gave similar age counts. Regression analysis was also used to quantify relationships between lapillar and sagittal age counts.

To generalize spatial and temporal comparisons of size, age, and mean growth rates, stations were grouped together to form the following regions: MAB, Chesapeake Bay, seaside Eastern Shore (SES; includes the Wachapreague and Sand Shoal Channel stations), bayside Eastern Shore (BES; includes the Occohannock Channel station), marshes (includes the Tue and Guinea marshes stations), and rivers (includes the James and York river transects). Two-sample t-tests were used to compare SL and age estimates between offshore and inshore regions.

Regression analyses were used (Rawlings 1988) to compare growth rates (slopes) and size at day 0 (y-intercepts) between early- and late-captured larvae up to 15 mm SL and 80 d. The analysis was restricted to this size and age range for comparison with Warlen (1982). Simple linear regressions were also used to compare growth in SL of early- and late-season spawned larvae (< 19 mm SL), and then separately for juveniles (19.01 - 65.00 mm SL). Larvae and juveniles were analyzed separately so growth patterns could be described linearly at the two life stages, thus simplifying comparisons between early- and late-spawned fish. I also used an ANCOVA and calculated least square (LS) means to compare mean size between early- and late-spawned groups in juveniles after the assumption of equal slopes was tested.

Following earlier studies of larval fish growth (Sakagawa and Kimura 1976; Zweifel and Lasker 1976; Warlen 1982, 1992; Warlen and Chester 1985), I used a Laird-Gompertz growth model (Laird et al. 1965) to describe the growth of croaker larvae and juveniles up to 50 mm SL and 142 d. The equation is in the form: $SL_{(t)} = SL_{(0)} \text{ Exp } \{[A_{(0)}/\alpha][1 - \text{Exp } (-\alpha t)]\}$, where

$SL_{(t)}$ = standard length at day t,

$SL_{(0)}$ = assumed to be standard length at hatching (t=0),

$A_{(0)}$ = specific growth rate at hatching (t=0), and

α = rate of exponential decay of the specific growth rate.

The model was fitted to the data by iterative, non-linear least squares procedure using SAS (Statistical Analysis System: SAS System For Linear Models 1991). After estimates of $SL_{(0)}$, $A_{(0)}$, and α were determined, age-specific growth rates were calculated using the following equation:

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

A fourth order polynomial was used to describe the relationship between fish and otolith size. A fourth order polynomial has been used successfully in the past to describe the fish and otolith growth relationship in 14 to 62 d old Pacific herring (*Clupea pallasii*) (Moksness and Wespestad 1989). An ANCOVA and calculated least square (LS; adjusted treatment) means were used to compare mean otolith size between fast- and slow-growing groups. The analysis was restricted to fish from 11 to 37 mm SL in order to confine the analysis between similar sized fish from the two groups.

RESULTS AND DISCUSSION

Sagittal and Lapillar Otolith Comparison

A paired t-test run on sagittal and lapillar age counts ($n = 32$) indicated a significant difference between the two ($p < 0.01$). A linear regression between sagittal and lapillar age counts had a slope less than one, indicating that lapilli underestimated age, and with increasing age the underestimation worsened (Figure 2). It was assumed that sagitta increment counts were the more accurate predictors of age. Although the more accurate ageing structure has not been laboratorially validated, visual scrutiny of the microstructure in the two otoliths showed better defined rings in sagittal otoliths. Hence, age estimates for age and growth analyses were derived from sagittal otoliths.

Counts in lapilli replicated sagittal counts fairly well, and appear to be adequate in aging younger croaker up to about 95 d. Change in the shape of sagittal otoliths begins at about this time (sagittae begin to become oblong increasing growth along anterior and posterior axes), whereas lapilli remain concentric. It is possible that the croaker become conservative in putting on growth in lapilli at this stage, and thus, the ring widths may become to narrow to discern under normal light microscopy.

Precision and Reproducibility of Age Counts

Mean average percent error (APE) of age counts for the first reader was 4.8%, with a mean coefficients of variation (CV) of 6.4%, and mean index of precision (D) of 3.8%. For the second reader these indices were 8.4% (APE), 11.5% (CV), and 6.7% (D). Although age

counts varied more for the second reader, no significant differences were found between readers (t-test, $\alpha = 0.05$). The second reader's variability in age counts was attributed to overall unfamiliarity with reading daily increments in Sciaenid otoliths.

Spatial and Temporal Distribution

For larvae and juveniles collected from estuarine waters, size and age generally increased from September through January before declining in February (Figure 3). However, these later samples after January only represented fish collected in the York and James Rivers, except for a few from Guinea Marshes ($n = 7$); only one croaker was found in samples at other station locations (Table 1). The general decrease in size and age after January suggested movement of larger fish from the channels into shoal waters, probably in response to rising water temperatures in the shallower waters (Chao and Musick 1977), which may occur as early as January in Virginia.

Monthly length and age frequencies illustrated highly variable length distributions in comparison to respective age distributions in particular months (Figure 3). Fish collected in November appeared to have shown the presence of two distinct length modes. However, age frequencies clearly showed only one age cohort. This was also evident for fish collected in January, and indicated that size is not a good indicator of age in these fish.

Regional length and age frequencies illustrated general patterns of spatial size and age variability (Figure 4). I found significantly smaller and younger fish in the SES region than in the BES and marshes regions collectively (t-tests, $p < 0.0001$ for both comparison). Furthermore, significantly smaller and younger fish were collected in the Chesapeake Bay region than in the rivers region (size, $p < 0.05$; age, $p < 0.0001$). I cautiously draw note to the

size and age differences between the Chesapeake Bay and rivers regions since the rivers were only sampled during the later half of the sampling period.

I compared only those stations that were sampled with similar gear type to exclude the possible effects of gear selectivity. Within-gear comparisons suggested onshore immigration of croaker from offshore spawning sites. These results supported findings by Warlen (1982) for croaker in North Carolina. Although the phenomena of offshore spawning and consequent estuarine migration of croaker is documented by studies using the distribution of eggs and size of fish (Hildebrand and Cable 1930; Wallace 1940; Haven 1957; Colton et al., 1979; Morse 1980; Lewis and Judy 1983; Warlen and Burke 1990), this study and Warlen's are the only studies using age information from sagittal otoliths in croaker collected in the western Atlantic that support such findings. Because size has been shown to be highly variable at age, only age-based data provide reliable confirmation of cross-shelf transport of larvae.

Specimens collected at the most seaward site along the Chesapeake Bay transect (at the mouth of the bay) and at Wachapreague and Sand Shoal Channels were used to indicate the age of larval croaker entering Virginia nursery grounds. The youngest larvae collected at the mouth of the bay were sampled on 21 September 1987 and were aged at 24 d ranging from 6.05 to 7.57 mm SL (n = 3, Table 1 does not show this much detail). On average larvae from that sample were 38.1 d old at 10.7 mm SL (Table 1). Fish collected at Wachapreague and Sand Shoal Channels on the seaside of the Eastern Shore were probably better representatives of the typical age of newly recruiting larvae that enter Virginia nursery grounds. Smaller mesh nets (1/8 in. mesh liner) were used at these stations than in the Chesapeake Bay (1/4 in. mesh liner), and therefore, sampled the smaller newly recruiting larvae more effectively. Mean ages of larvae entering Wachapreague and Sand Shoal Channels were younger than were collected at the mouth of the bay (Table 1). The youngest larvae were sampled on 29 September 1987 at Wachapreague Channel and were aged at 20 d

ranging from 5.35 to 6.11 mm SL (n =2), and on 30 September 1987 at Sand Shoal Channel the youngest larvae were at 23 d ranging from 6.05 to 7.27 mm SL (n = 2, Table 1 does not show this much detail). On average fish from these samples were 25.7 d old at 7.25 mm SL, and 29.3 d at 8.27 mm SL for the two stations, respectively (Table 1).

Virginia larvae appear to enter nursery grounds at a slightly younger age than North Carolina larvae, perhaps due to shorter transport distances and/or rates from spawning grounds. In 1979-1980 the youngest croaker larvae (22 d at 7.4 mm SL) entered Beaufort Inlet on 26 October 1979 at 22 d and 7.4 mm SL (S. M. Warlen personal communication, NOAA, NMFS, Southeast Fisheries Center, Beaufort Laboratory, Beaufort, NC), and on average larvae were 33.2 d old at 9.04 mm SL. By 02 November 1979 recruiting larvae were as young as 29 d at 8.8 mm SL and on average were 36.0 d at 9.4 mm SL (Warlen 1982).

Warlen (1982) showed a general increase in the age of fish entering the Beaufort estuary as the season progressed which was suggested to be an effect of variable transport distances and/or rates to the estuary. Similar trends were seen in this study, and like Warlen variable transport distances and/or rates are used to explain the seasonal increase in size and age of croaker entering Virginia nursery grounds.

Hatch-Date Distribution

Back-calculated hatch-date distributions indicated spawning over an 8-month period from 05 July 1987 to 10 February 1988 with more than 82% of spawning occurring from August through October (Figure 5). Results are very similar when compared to earlier studies based on the presence of eggs in the ichthyoplankton that suggested a spawning period of 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. 1989).

Although the onset of spawning determined in this study is relatively early compared to previous reports for croaker recruiting into the Chesapeake Bay, females with post ovulatory follicles in their ovaries have occurred in trawls and pound nets in the Chesapeake Bay as early as July in recent years (Barbieri 1993).

Ripe females within the bay in July coupled with hatch-dates in July-August, and because sexually mature adults do not begin to migrate out of the bay until about this time, its apparent that croaker are being spawned within the bay or in proximal coastal waters. Although the paradigm that croaker spawn offshore still holds, it appears that they begin spawning in the bay and continue as they move offshore. The ultimate contribution of these inshore spawned larvae to the stock is unknown and is worthy of further study.

Compared to results for North Carolina larvae (Warlen 1982) the spawning period was longer and the onset and peak occurred earlier in Virginia. Mean monthly surface water temperatures were similar for the two locations and do not appear to have influenced the variability between spawning seasons (Figure 5). Typically the presence of eggs or unknown age larvae in the ichthyoplankton have been used to determine the periodicity of spawning. Only Warlen's (1982) and this study back-calculate hatch-date distributions in croaker using daily age information from otoliths.

It is important to note that mortality can bias estimates of hatch-date distributions (Campana and Jones 1992). Fish spawned earlier in the season will be underrepresented in samples because they have experienced higher cumulative mortality than later spawned fish. Measures of size- and age-specific mortality are needed to predict hatch-date distributions more accurately, but the likely implication is that early-season spawning percentages and estimated spawning peak were under-estimated for this study and Warlen's (1982).

Growth

Spatial and Temporal Growth Variability

A. By Capture Date

Mean growth rates (mean age/mean SL) were highly variable spatially, ranging from 0.172 mm/d in the MAB to 0.432 mm/d in the Chesapeake Bay (Table 1). However, appropriate spatial mean growth rate comparisons were difficult because mean ages were highly variable across stations at any particular time period. Comparisons between similar aged fish were important since mean growth rate differences may have been attributed to age and size partitioning; perceivably smaller, younger fish grow on a different scale than do larger, older fish.

Regressions were used to describe temporal growth variability and were restricted to similar aged fish. Striking variabilities in growth were observed between early- (before October) and late-captured groups (after November) for fish up to 15 mm SL and 80 d (Figure 6). Regression comparisons showed that the early-captured group (r^2 = 0.78) grew 35% faster than the late-capture group (r^2 = 0.77) based on LS means (ANCOVA; adjusted treatment means). Tests of homogeneity of regression coefficients indicated highly significant differences between slopes ($p < 0.0001$) with no significant difference between intercepts ($p = 0.1561$). These results suggested that the early-captured individuals were larger at age than the late-captured because of growth and not an initial larger size at hatch or age 0.

B. By Hatch-date

Spatial patterns in mean growth rate (mean SL/mean age) were apparent when fish were grouped by hatch-dates (Table 2). However, mean growth rate comparisons across

regions of capture were difficult because of similar problems seen in the capture-date data where mean ages were highly variable across regions at any particular time in the sampling period.

Although temporal mean growth rate comparisons were difficult, general patterns were seen within regions at all locations. Fish hatched early in the season in July and August experienced considerably faster growth than fish hatched in later months in September through January. The SES, BES, and marshes regions showed some decrease in growth for fish hatched in September and October. This seasonal variability in growth may have been attributed to exposure to higher water temperatures and increased food availability typical in July and August, or to improved survival of faster growing fish. Since similar trends were seen in the capture-date data it is suggested that growth differences, and not mortality, was the major contributor to growth variability.

Regression analyses indicated substantial differences in growth rate between early- and late-spawned larvae and further illustrated temporal growth variability (Figure 7). Regressions showed that the early-spawned larvae ($r^2 = 0.92$) grew more than 41% faster than the late-spawned larvae ($r^2 = 0.84$) based on LS means (ANCOVA; adjusted treatment means). Tests of regression coefficients indicated that the slopes were significantly different between early- and late-spawned groups of larvae ($p < 0.0001$). Comparisons of regression coefficients indicated significantly different y-intercepts, or size at age 0, between early- and late-spawned larvae ($p = 0.0095$). This contradicted with the previous intercept comparison between early- and late-captured larvae and suggested curvilinear growth in early larvae, as is typically seen in the early developmental growth of many fishes (Zweifel and Lasker 1976).

Further regression analyses between early- and late-spawned juveniles (Figure 8) indicated that once early-spawned larvae initiate faster growth (Figure 7), and size differences are established, they are maintained in the juvenile stage. Slope comparisons between early-

(r^2 = 0.92) and late-spawned (r^2 = 0.86) juveniles were not significantly different (p = 0.7537), however, an ANCOVA (Table 3A) indicated a significant difference between the two groups based on size adjusted by age (p < 0.0001) with the covariate (age) and main effects (fast vs slow grow fish growth) being highly significant (p < 0.0001 for both the covariate and main effects). Adjusted LS mean sizes indicated that early-spawned juveniles were 18% larger than similar aged late-spawned juveniles (Table 3A).

Hatch-dates of the faster growing early-spawned fish coincided very well with peak abundances of plankton in the Chesapeake Bay, which typically occur in July. (R. S. Birdsong, personal communication, Old Dominion University, Department of Biology, Norfolk, VA). Also, increased patchiness and falling abundance of plankton typically begin in September and October and coincide very well with the hatch-dates of slower growing fish. Increased patchiness of plankton communities may also explain the growth variability seen in the late-spawned fish that is not seen in the early-spawned larvae (Figure 7) and juveniles (Figure 8).

Growth Comparisons With Previous Studies

A. Comparisons to North Carolina Croaker Larvae (Warlen 1982)

Warlen (1982) fit separate Laird-Gompertz growth models to two variable growth groups, an early-captured slow-growing group collected from 26 October 1979 through 16 January 1980 and a late-captured fast-growing group collected after January 16 through April 17. For comparative reasons the linear regressions used to describe growth of early- and late-captured croaker larvae in Virginia were overlaid on the Laird-Gompertz growth curves used to describe the growth of North Carolina larvae (Figure 9). The pattern of faster early season growth is apparent in both data sets. For the most part, Virginia croaker appeared to have experienced increasingly faster growth at age in comparison to North Carolina larvae. It

should be noted that growth comparisons between studies are intended to point out possible trends only, due to limitations introduced by the differences in sampling gear and obvious time frame differences.

Warlen assumed that the early-captured fast-growing group observed in his data is the best representative of larval croaker growth in North Carolina, thus, growth model parameters from this study (for early- and late-captured fish collectively) were made with parameters estimated for the early-captured group from Warlen's study. A Laird-Gompertz growth model fit the Virginia data very well with no pattern to the residuals, although variance increased with age as result of variable growth (Figure 10). SL at hatch ($SL_{(0)}$) was 2.66 ± 0.33 mm SL for Virginia croaker, and was considerably higher than Warlen's estimate for North Carolina (0.926 mm SL). However, this estimate was much closer to previous observed sizes at hatch of laboratory spawned croaker from Chesapeake Bay (2.0 mm SL, Middaugh and Yoakum 1974) and North Carolina (2.43 mm SL, C. M. Jones, Applied Marine Research Laboratory, Old Dominion University, Norfolk, VA).

The rate of exponential decay of the specific growth rate (α) estimated for this study (0.0081 ± 0.0012) is considerably lower than Warlen's estimate of 0.0428 for North Carolina larvae (Figure 10). Illustration of the changes of age-specific growth (A_t: a function of the rate of exponential decay of specific growth in time) between the two populations indicated that North Carolina larvae experienced a decline of daily growth rate from 5.2% at day 20 to 0.9% by day 60, and Virginia larvae from 3.2% at day 20 to 2.3% by day 60 (Figure 11).

The estimates of larger size at hatch and a smaller rate of exponential decay of specific growth for Virginia croaker, relative to North Carolina croaker, are possible because mature croaker in Virginia are reported to be generally larger than mature croaker collected south of Cape Hatteras (White and Chittenden 1977). Conceivably, a smaller rate of exponential decay of specific growth indicates that Virginia fish experience smaller decreases in growth in time.

Therefore, Virginia croaker would potentially reach considerably larger sizes at later ages relative to North Carolina fish, at least through the juvenile stage.

Mean growth rate (mean SL/mean age) comparisons between Virginia and North Carolina croaker were made among similar aged fish from the two studies. For the most part, Virginia croaker grew faster than similar aged North Carolina croaker (Table 4). Seemingly, growth rates were similar between the two studies among larvae offshore. However, as fish grew older and were distributed in the more inshore locations, growth became increasingly faster in Virginia larvae. Striking growth difference were observed between Virginia larvae collected in the Chesapeake Bay on 16 October 1987 (n = 20; mean age = 53.05 ± 2.46) and North Carolina larvae collected in the estuary at Pivers Island on 19 November 1979 (n = 10; mean age = 51.20 ± 2.56) and on 03 January 1980 (n = 10; mean age = 53.30 ± 1.28). Virginia larvae captured on 16 October 1987 grew (0.432 mm/d) almost 44% faster than North Carolina larvae collected on 19 November 1979 (0.245 mm/d) and almost 53% faster than North Carolina larvae collected on 03 January 1980 (0.205 mm/d).

Although I have been using the regional designations of "Virginia" and "North Carolina" to simplify the discussion of growth rate differences, I cannot eliminate the real possibility that these differences could be temporal, year-to-year changes. However, whether spatial or temporal, or a combination of both, within season patterns among the two studies are similar while growth rates themselves differ.

B. Comparisons to Northern Gulf of Mexico Croaker Larvae

Cowan (1988) collected croaker larvae in oblique tows of 60-cm paired bongo nets (335 and 500 μm mesh) in coastal northern Gulf of Mexico waters off western Louisiana using oblique tows. Larvae were collected late in the spawning season from mid-December 1981 to

mid-April 1982. Larvae ranged from 8 to 17 mm total length and were estimated to be from 40 to 80 d old. Growth estimates based on a linear regression fit to 72 larvae was 0.189 mm/d. Cowan notes that this growth is fairly similar to, although slightly faster, than the mean growth rate (standard length/mean age: 0.156 mm/d) for late-season larvae captured in North Carolina in April 1980 (Warlen 1982). Late-season northern Gulf larvae grew slightly faster than Virginia larvae between 20 and 80 d collected late in the season after October (0.172 mm/d), however considerably slower than larvae collected early in the season before November (0.265 mm/d), based on growth estimated by regression analysis (Figure 6).

C. Implications Concerning Countergradient Variation in Growth

Results found in this study indicated that croaker north of Cape Hatteras may grow faster than fish south of Cape Hatteras. Presumably, fish inhabiting colder waters (north of Cape Hatteras) should have slower growth than fish inhabiting warmer waters (south of Cape Hatteras). However, evidence in other species suggests that this may not be the case. The capacity for growth in three anadromous (Conover 1990) and one coastal species (Conover and Present 1990), has been shown to be greater at higher latitudes where growing seasons are significantly shorter. Conover and Present (1990) demonstrated a genetic basis for the capacity for faster growth of Atlantic silversides (*Menidia menidia*) at higher latitudes (treatments were conducted on separate lab-reared progeny of ancestorial stocks collected in Nova Scotia, New York, and South Carolina). This phenomena of "patterns in genetic variation that show an inverse relationship to, and thereby compensate for, an environmental influence on phenotype are referred to as countergradient variation" (Conover 1990).

It is a paradigm that in young fish faster growing individuals have a greater chance of survival because of their larger size. The implications of subtle size differences in young fish,

and the benefits of larger size in regards to survival is extensively reviewed (Miller et al. 1988; Houde 1989; Buckley et al. 1991). Consequently, in higher latitude locations where growing seasons are shorter, and the duration and severity of winter is greater, selective pressure for faster growth and larger size is likely to be magnified.

Growth comparisons between young croaker from Virginia, North Carolina, and the northern Gulf of Mexico did not definitively support Conover's (1990) theory of countergradient variation in growth, although there was some indication of its possible presence in croaker north and south of Cape Hatteras.

Standard Length and Otolith Maximum Diameter Relationship (OMD)

A fourth order polynomial best described the relationship between sagittal OMD (x) and SL (y) for larvae and juveniles collectively (Figure 12). A linear regression (SL = 13.48(OMD) + 4.18) also fit the data well (r^2 = 0.98), however with strong patterns in the residuals which was greatly reduced in the polynomial model. A log-log transformation of fish and otolith length in larvae < 10 mm SL provided a good fit to the data (r^2 = 0.92, LOG(SL) = 1.16 LOG(OMD) - 3.89) and considerably reduced any patterns in the residuals. It was a similar case in juveniles > 10 mm SL (r^2 = 0.96, LOG(SL) = 1.28 LOG(OMD) - 3.76).

Test of homogeneity of regression coefficients indicated that the slopes of the fish and otolith size relationship between fast- (captured before November) and slow-growing groups (captured after October) were not significantly different (p = 0.5016). Upon meeting the assumption of equal slopes, an ANCOVA was run between fast (early-captured) and slow growing (late-captured) groups to compare adjusted mean otolith sizes calculated by least square (LS) means (Table 5). The covariate (standard length) and the main effects (fast vs

slow fish growth) were highly significant ($p < 0.0001$ for covariate and main effects, Table 5A). The calculated least square (LS) means indicated that otoliths from the fast-growing group were almost 13% larger than otoliths from similar sized fish from the slow-growing group (Table 5B). Plots of individual otoliths showed very little overlap between groups (Figure 13).

Contrary to our results Reznick et al. (1989) demonstrated that slower growing individuals of lab reared guppies (*Poecilia reticulata*) have larger otoliths than similar sized fast growing individuals when growth is controlled by feeding. Secor and Dean (1989) indicate similar results in otoliths from pond reared striped bass (*Morone saxatilis*), and extended these findings (Secor et al. 1989) to red seabream (*Pagrus major*) and spot (*Leiostomus xanthurus*). Mosegaard et al. (1988) found that in a long term experiment with Arctic char (*Salvelinus alpinus*), otoliths from slower growing fish reared at 8°C (small group) are significantly lighter than otoliths from similar sized faster growing fish reared at 13°C (large group). Also, otolith growth rate continued to increase above temperatures of maximum somatic growth rate. During exposure to temperatures above 13°C, otolith growth rate continued to increase while somatic growth remained constant. While previous studies regulated growth by varying food (Reznick et al. 1989; Secor and Dean 1989; Secor et al. 1989) or temperature regimes (Mosegaard et al. 1988), there is no quantitative data that can be tested to determine what factors are most influential in regulating the growth of wild-captured croaker used in this study. The underlying question, however, is to determine the extent of uncoupling of the fish and otolith growth relationship, and determine its significance when back-calculating growth.

SUMMARY

1. Age counts in lapillar otoliths replicate counts in sagittal otoliths fairly well up to about 95 d.

2. The phenomena of early-season fast growth seen by Warlen (1982) for croaker south of Cape Hatteras is also seen in croaker larvae from estuarine waters of Virginia. There may be a stock-wide pattern that is worthy of further study.

3. There is strong evidence that areas of the bay and coastal waters are used by different life history phases as indicated by spatial partitioning by age.

4. This study presents the first evidence from direct age analysis of larvae that they are spawned as early as July. This is confirmed by evidence from adult females sampled within the bay with post ovulatory follicles in their ovaries in July (Barbieri, 1993). July-August hatch-dates of croaker collected in October in Tue Marshes and the Chesapeake Bay also suggested that larvae are spawned within the bay or in proximal coastal waters because sexually mature adults do not begin to migrate out of the bay until about this time. The current paradigm holds that croaker go considerably offshore to spawn. Evidence from this study suggests that they begin to spawn in the bay and continue to spawn as they move offshore. The ultimate contribution of these

inshore spawned larvae to the stock is unknown and is also worthy of further study.

5. Growth comparisons with croaker larvae from North Carolina (Warlen 1982) and the northern Gulf of Mexico (Cowan 1988) did not definitively support Conover's (1990) theory of countergradient variation in growth, however, there was some evidence that Virginia larvae may grow faster than larvae from North Carolina south of Cape Hatteras.

6. A fourth order polynomial best fit the fish and otolith size relationship for larvae and juveniles, with faster growing fish having relatively larger otoliths than the same size slower growing fish.

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Table 1. Mean size, age, and growth rate (mean SL/mean age) of larval and juvenile croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia by capture date, station, and gear type.

Capture date	Sample size (n)	Mean standard length (SL) ± SE	Mean age ± SE	Mean growth
Middle Atlantic Bight (Oblique 60 cm bongo nets with 333 and 505 μm mesh)				
Nov. 3	9	7.83 ± 0.37	41.8 ± 1.2	0.188
Nov. 4	8	4.60 ± 0.40	22.9 ± 2.3	0.201
Nov. 6	2	8.94 ± 0.20	46.0 ± 2.0	0.194
Nov. 10	3	6.08 ± 1.31	34.7 ± 2.9	0.175
Nov. 13	13	6.99 ± 0.34	40.7 ± 1.8	0.172
Nov. 14	5	7.60 ± 0.29	31.6 ± 0.9	0.241
Seaside Eastern Shore (16 ft. lined and unlined nets)[1]				
Sep. 29	29	7.25 ± 0.34	25.7 ± 0.8	0.282
Sep. 30	32	8.27 ± 0.58	29.3 ± 1.2	0.283
Oct. 27	15	13.84 ± 0.94	44.5 ± 2.2	0.311
Oct. 28	28	10.97 ± 0.39	42.6 ± 0.9	0.257
Dec. 1	25	17.54 ± 1.11	70.1 ± 2.3	0.250
Dec. 2	8	15.30 ± 1.32	68.9 ± 2.2	0.222
Jan. 5	1	23.62 ± 0.00	100.0 ± 0.0	0.236
Bayside Eastern Shore (16 ft. lined and unlined nets)[1]				
Nov. 30	48	13.58 ± 0.59	64.7 ± 1.2	0.210
Chesapeake Bay (30 ft. net with 5/8 in. mesh and 1/4 in. mesh liner)				
Sep. 21	32	10.68 ± 0.58	38.1 ± 2.1	0.280
Oct. 16	20	21.18 ± 1.56	53.1 ± 2.5	0.399
Nov. 24	40	41.01 ± 1.46	97.0 ± 2.1	0.432
Jan. 15	37	36.12 ± 2.04	97.4 ± 3.5	0.371
Feb. 1	1	50.80 ± 0.00	125.0 ± 0.0	0.406
Marshes (16 ft. lined and unlined nets)[1]				
Oct. 2	60	11.79 ± 0.80	39.8 ± 2.0	0.296
Oct. 23	38	15.15 ± 1.46	49.3 ± 2.3	0.307
Dec. 3	30	12.47 ± 0.30	70.4 ± 1.0	0.177
Mar. 10	7	12.67 ± 0.39	54.7 ± 2.0	0.232
Rivers (30 ft. net with 5/8 in. mesh and 1/4 in. mesh liner)				
Jan. 25	37	31.55 ± 2.25	101.7 ± 3.0	0.310
Jan. 27	10	32.37 ± 4.71	104.8 ± 6.4	0.309
Feb. 22	30	31.02 ± 1.59	90.6 ± 3.4	0.343
Mar. 25	31	30.40 ± 1.95	88.3 ± 2.9	0.344
Mar. 30	6	38.88 ± 8.30	96.2 ± 11.1	0.404

[1]The lined net had a 1/4 in. mesh with an 1/8 mesh liner and the unlined net had a 5/8 in. mesh.

Table 2. Mean size, age, and growth rate (mean SL/mean age) for larval and juvenile croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia by hatch-month, region, and gear type.

Hatch month	Sample size (n)	Mean standard length (SL) ± SE	Mean age ± SE	Mean growth
	Middle Atlantic Bight[1]			
Sep.	19	7.94 ± 0.21	43.7 ± 0.9	0.182
Oct.	21	5.78 ± 0.35	29.7 ± 1.5	0.195
	Seaside Eastern Shore (Wachapreage Channel and Sand Shoal Channel)[2]			
Aug.	17	13.19 ± 1.51	41.0 ± 3.8	0.322
Sep.	115	11.03 ± 0.48	42.7 ± 1.8	0.258
Oct.	6	13.64 ± 0.78	56.5 ± 1.1	0.241
	Bayside Eastern Shore (Occohannock Channel)[2]			
Aug.	1	28.30 ± 0.00	94.0 ± 0.0	0.301
Sep.	32	14.35 ± 0.67	67.1 ± 1.2	0.214
Oct.	15	10.96 ± 0.23	57.5 ± 0.7	0.191
	Chesapeake Bay[3]			
Jul.	7	25.78 ± 6.51	77.3 ± 11.2	0.334
Aug.	74	28.94 ± 1.96	70.5 ± 3.8	0.410
Sep.	21	27.86 ± 3.42	78.4 ± 8.0	0.355
Oct.	21	35.36 ± 1.73	94.2 ± 2.7	0.375
Nov.	7	20.44 ± 1.33	71.6 ± 1.0	0.286
	Marshes (Guinea Marshes and Tue Marshes)[2]			
Jul.	10	23.96 ± 2.44	71.2 ± 3.0	0.377
Aug.	39	16.47 ± 1.18	48.6 ± 2.2	0.339
Sep.	75	9.78 ± 0.31	47.0 ± 2.2	0.208
Oct.	4	10.58 ± 0.64	60.0 ± 1.0	0.176
Jan.	7	12.67 ± 0.39	54.7 ± 2.0	0.232
	Rivers (York River and James River)[3]			
Sep.	13	48.46 ± 2.18	124.3 ± 1.7	0.389
Oct	25	32.06 ± 2.07	105.3 ± 2.2	0.304
Nov.	28	27.59 ± 1.98	91.5 ± 2.8	0.302
Dec.	32	31.77 ± 2.18	89.5 ± 2.9	0.355
Jan.	15	24.40 ± 1.67	74.4 ± 1.4	0.328
Feb.	1	10.56 ± 0.00	49.0 ± 0.0	0.216

[1]Gear type used was oblique 60 cm bongo nets with 505 μm mesh.

[2]Gear type used was a 16 ft. lined net with a 1/4 in. mesh and 1/8 in. mesh liner, and a 16 ft. unlined net with a 5/8 in. mesh.

[3]Gear type used was a 30 ft. lined net with a 5/8 in. mesh and 1/4 in. mesh liner.

Table 3. Growth comparison between early- (before September) and late-spawned (after August) croaker from 19.01-65.00 mm SL and 51-142 d using an analysis of covariance (ANCOVA) of the SL of fish (mm) with age (d) as the covariate. Calculated least squares (LS) means equals the mean SL of fish, adjusted for the effects of age.

ANCOVA			
A.	df	F-ratio	Prob. <p
Covariate			
Age	1	743.63	0.0001
Main Effect			
Fast Growth vs. Slow Growth	1	89.87	0.0001
Residual Sums of Squares (df)	5,489.19 (211)		
R^2	0.78		
B.	LS Means (mm) (SE)		
Fast Group: 39.52 (0.618)	Slow Group: 32.28 (0.431)		

Table 4. Mean growth rate (mean SL/mean age) comparisons between Virginia and North Carolina (Warlen 1982) croaker larvae of similar age by capture date and region.

Capture date	Sample size (n)	Mean standard length (SL) ± SE	Mean age ± SE	Mean growth	Region
Nov. 30-14	40	6.81 ± 0.42	36.2 ± 1.7	0.188	MAB
Mar. 20	4	7.15 ± 0.69	34.3 ± 3.7	0.209	Shelf (NC)
Oct. 28	43	11.97 ± 0.60	43.3 ± 1.4	0.277	SES (VA)
Nov. 9	9	10.90 ± 0.30	44.7 ± 1.8	0.244	Estuary (NC)
Dec. 18	10	10.65 ± 0.18	41.5 ± 0.5	0.257	Estuary (NC)
Oct. 2	60	11.79 ± 0.80	39.8 ± 2.0	0.296	Marshes (VA)
Nov. 22	10	9.26 ± 0.13	39.1 ± 0.4	0.238	Estuary (NC)
Dec. 18	10	10.65 ± 0.18	41.5 ± 0.5	0.257	Estuary (NC)
Oct. 16	20	21.18 ± 1.56	53.1 ± 2.5	0.432	Ches. Bay (VA)
Nov. 19	10	12.54 ± 0.59	51.2 ± 2.6	0.245	Estuary (NC)
Jan. 3	10	10.91 ± 0.25	53.3 ± 1.3	0.205	Estuary (NC)

Table 5. Otolith comparison between fast- (captured before November) and slow-growing (captured after October) croaker between 11-37 mm SL using an analysis of covariance (ANCOVA) of the otolith maximum diameter (OMD) of sagittae (mm) with SL of fish (mm) as the covariate. Calculated least squares (LS) means equals the mean OMD of sagittae, adjusted for the effects of SL of fish.

ANCOVA			
A.	df	F-ratio	Prob. <p
Covariate Standard Length	1	1,126.87	0.0001
Main Effect Fast Growth vs. Slow Growth	1	36.22	0.0001
Residual Sums of Squares (df)	1.16 (66)		
R^2	0.95		
B.	LS Means (mm) (SE)		
Fast Group: 1.538 (0.022)		Slow Group: 1.246 (0.023)	

Figure 1. Station locations in estuarine waters of Virginia for the collection of larval and juvenile croaker from 21 September 1987 to 30 March 1988.

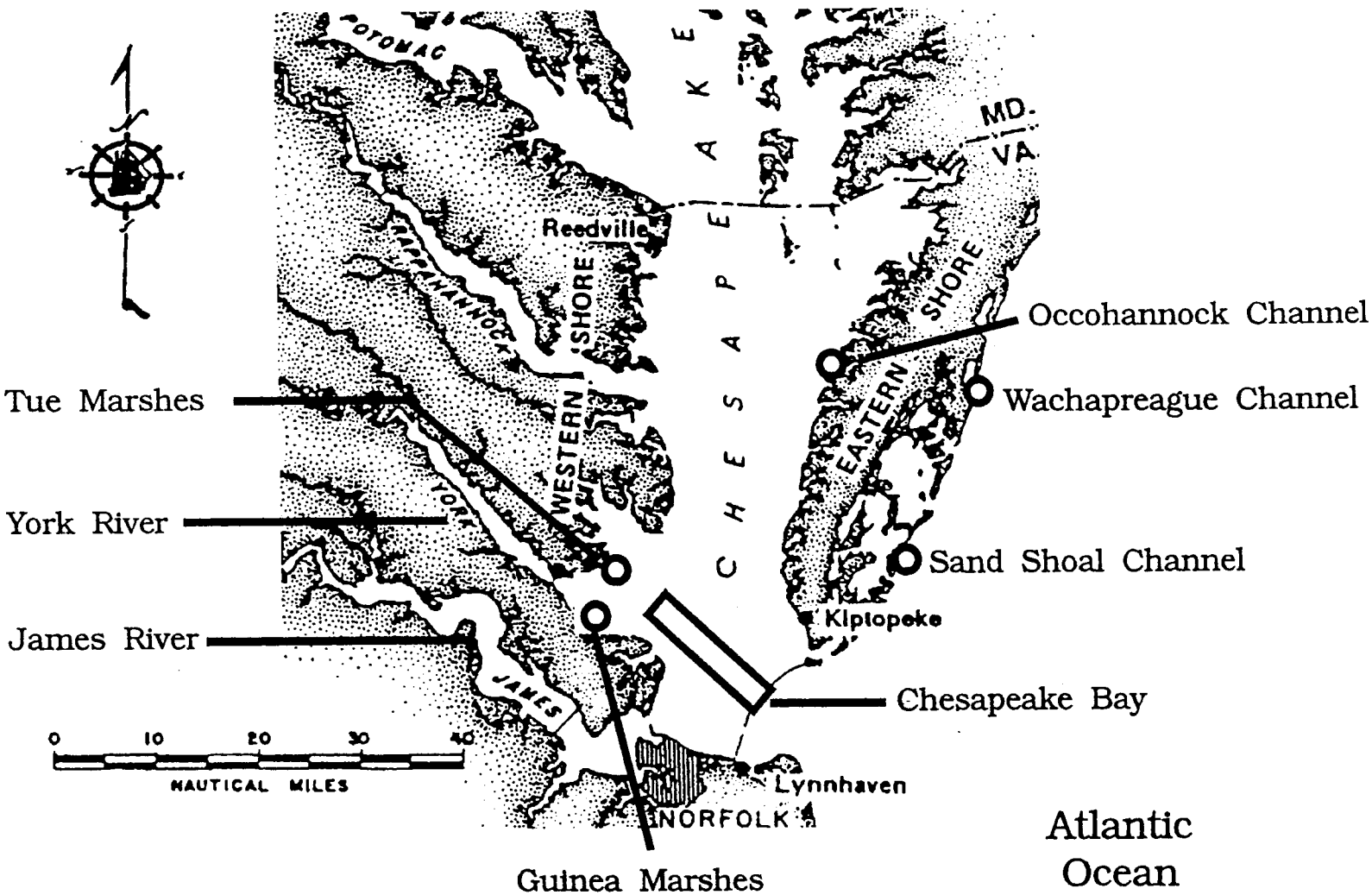

POTOMAC
RAPPAHANNOCK
YORK
JAMES
WESTERN SHORE
EASTERN SHORE
CHESAPEAKE
MD.
VA.
Reedville
Occohannock Channel
Wachapreague Channel
Sand Shoal Channel
Kiptopeke
Chesapeake Bay
Lynnhaven
NORFOLK
Tue Marshes
York River
James River
Guinea Marshes
Atlantic Ocean
0 10 20 30 40
NAUTICAL MILES

Figure 2. Comparison of sagittal and lapillar otolith age counts illustrating the reproducibilty of sagittal counts with lapillar counts. The solid line represents a one-to-one relationship, and the dashed line is the regression describing the relationship between sagittal and lapillar age counts.

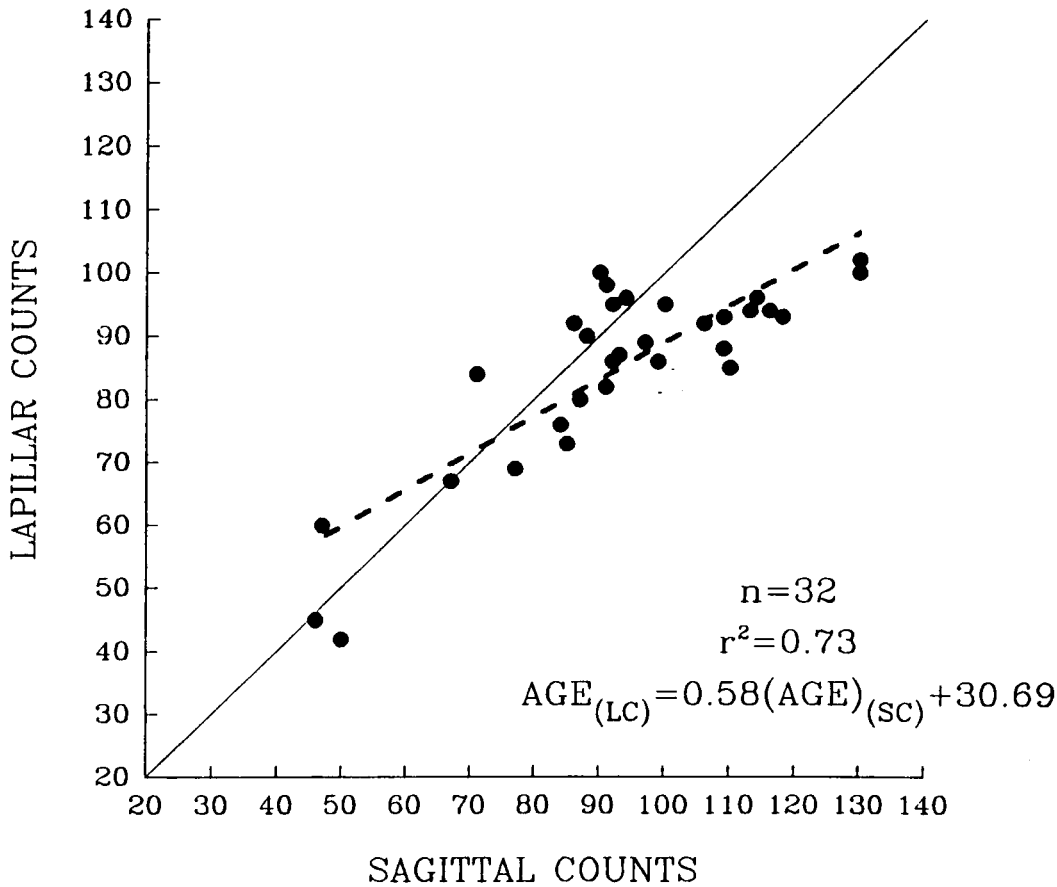

LAPILLAR COUNTS
SAGITTAL COUNTS
140
130
120
110
100
90
80
70
60
50
40
30
20
20 30 40 50 60 70 80 90 100 110 120 130 140
n=32
r²=0.73
AGE(LC)=0.58(AGE)(SC)+30.69

Figure 3. Monthly length and age frequency distributions for larval and juvenile croaker collected from 21 September 1987 to 30 March 1988 in estuarine waters of Virginia. Also given are mean SL (SE), ages (SE), and sample size (n).

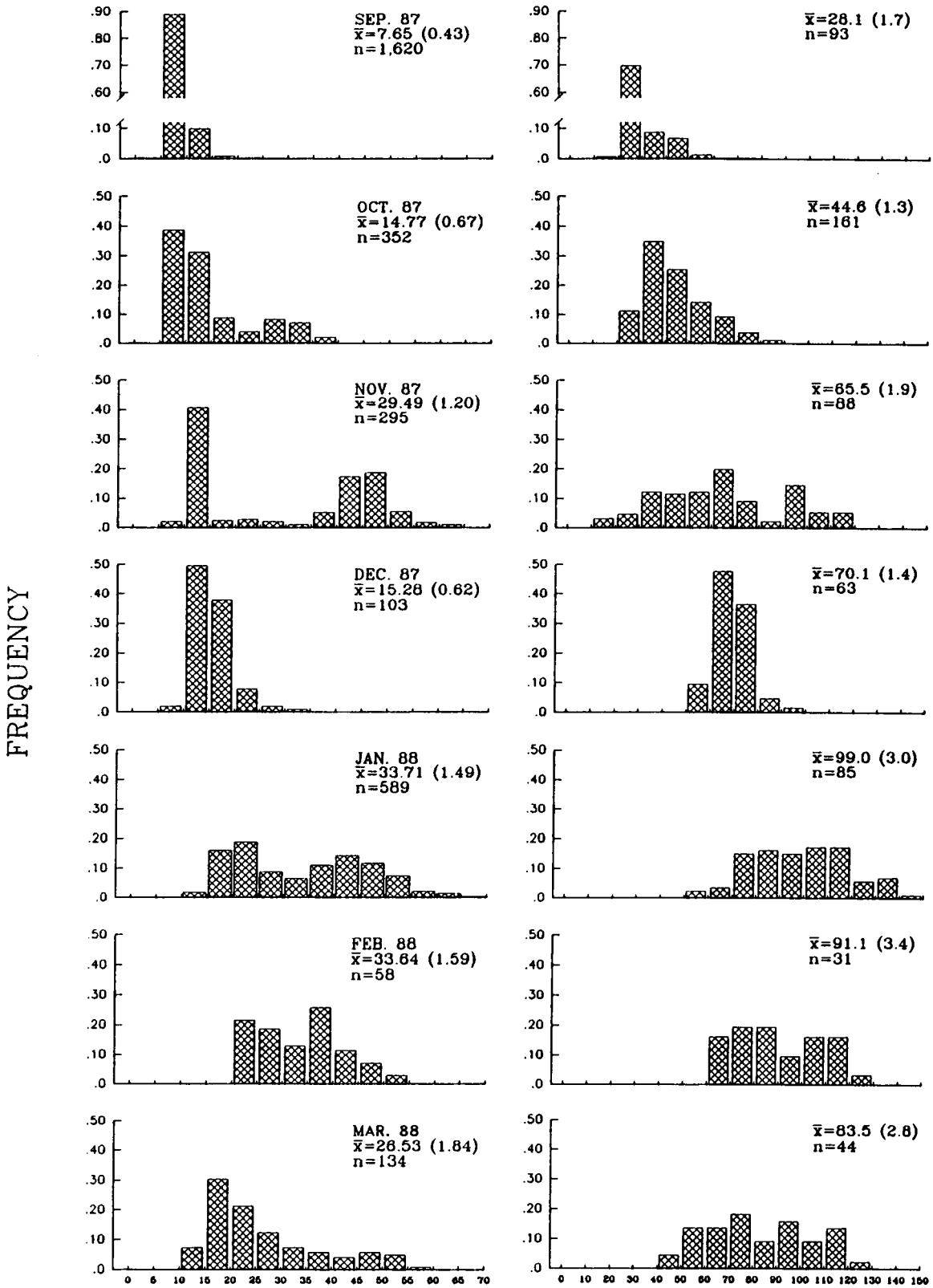

SEP. 87
x̄=7.65 (0.43)
n=1,620
x̄=28.1 (1.7)
n=93
OCT. 87
x̄=14.77 (0.67)
n=352
x̄=44.6 (1.3)
n=161
NOV. 87
x̄=29.49 (1.20)
n=295
x̄=65.5 (1.9)
n=88
DEC. 87
x̄=15.28 (0.62)
n=103
x̄=70.1 (1.4)
n=63
JAN. 88
x̄=33.71 (1.49)
n=589
x̄=99.0 (3.0)
n=85
FEB. 88
x̄=33.64 (1.59)
n=58
x̄=91.1 (3.4)
n=31
MAR. 88
x̄=26.53 (1.84)
n=134
x̄=83.5 (2.8)
n=44
FREQUENCY
STANDARD LENGTH (mm)
AGE (days)

Figure 4. Regional length and age frequency distributions for larval and juvenile croaker collected in the Middle Atlantic Bight and estuarine waters of Virginia. Each frequency distribution is cumulative over the entire sampling period (21 September 1987 to 30 March 1988) for each particular region. Also given are mean SL (SE), ages (SE), and sample size (n).

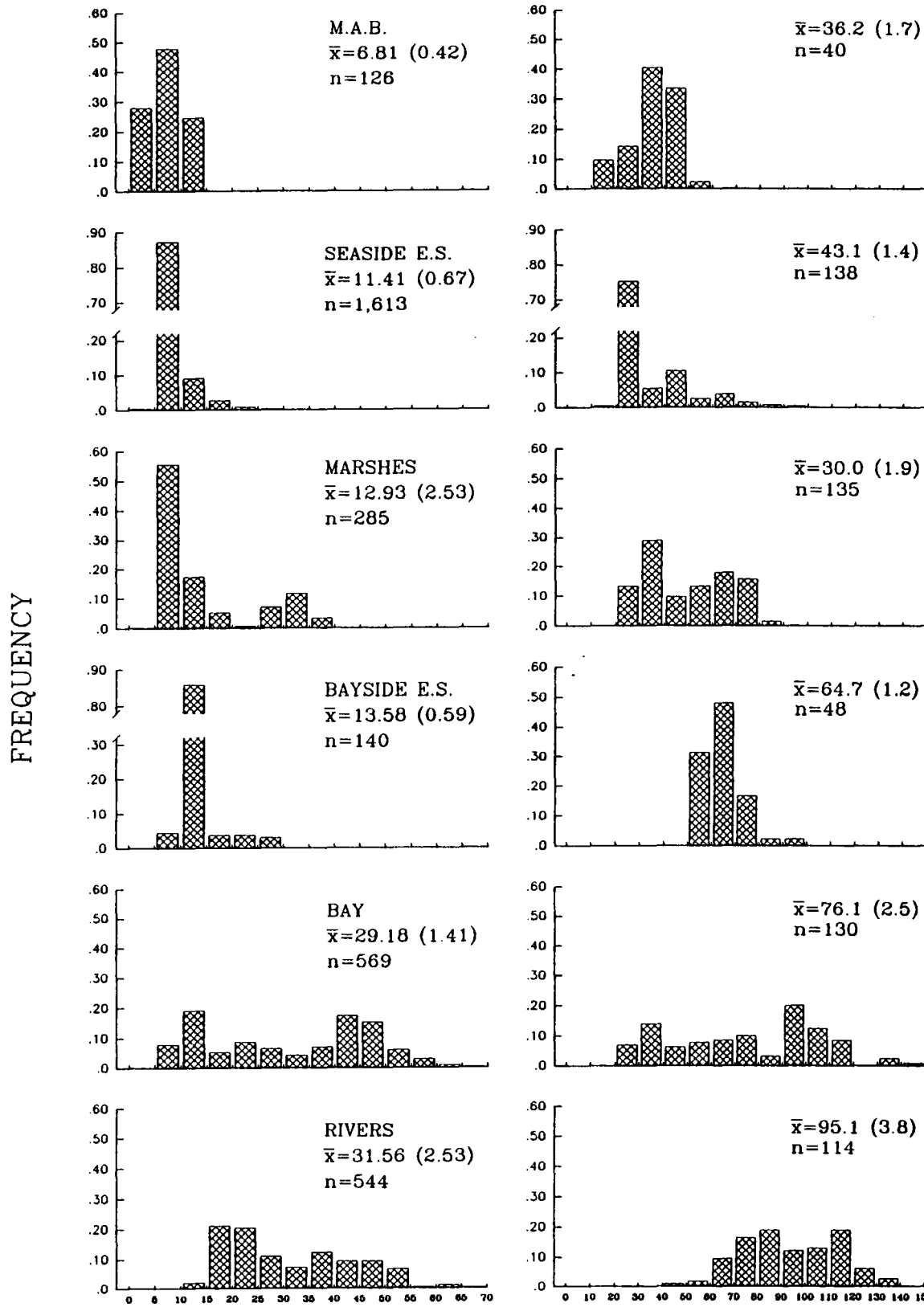

M.A.B.
x̄=6.81 (0.42)
n=126
x̄=36.2 (1.7)
n=40
SEASIDE E.S.
x̄=11.41 (0.67)
n=1,613
x̄=43.1 (1.4)
n=138
MARSHES
x̄=12.93 (2.53)
n=285
x̄=30.0 (1.9)
n=135
BAYSIDE E.S.
x̄=13.58 (0.59)
n=140
x̄=64.7 (1.2)
n=48
BAY
x̄=29.18 (1.41)
n=569
x̄=76.1 (2.5)
n=130
RIVERS
x̄=31.56 (2.53)
n=544
x̄=95.1 (3.8)
n=114
FREQUENCY
STANDARD LENGTH (mm)
AGE (days)

Figure 5. Comparison of hatch-date distributions between Virginia and North Carolina (Warlen 1982) croaker. Monthly mean surface water temperatures are shown for the Chesapeake Bay Bridge-Tunnel (July 1987 to April 1988) and for Myrtle Beach, South Carolina (closest location to Beaufort, NC with available data) (July 1979 to April 1980).

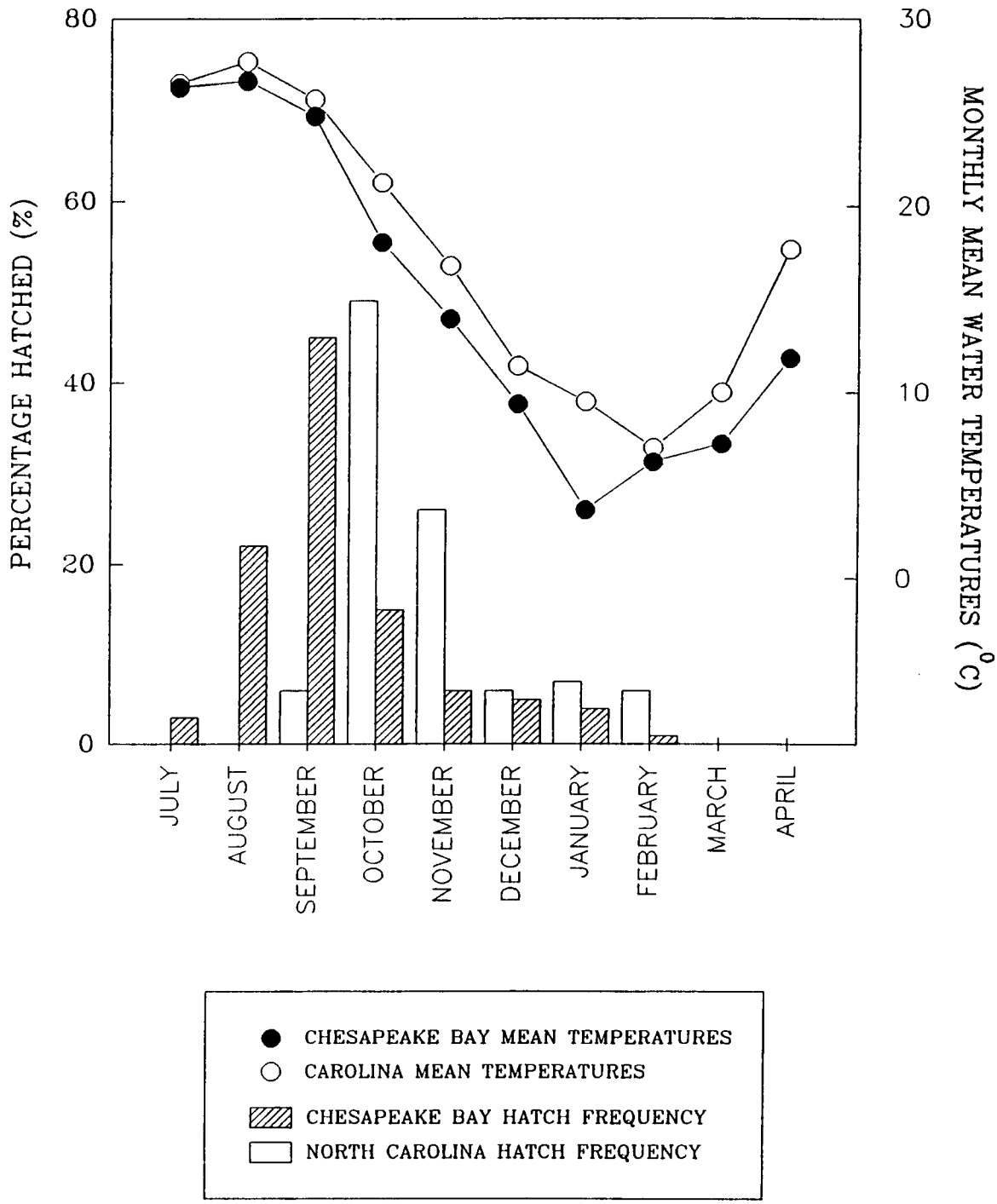

80
60
40
20
0
30
20
10
0
PERCENTAGE HATCHED (%)
MONTHLY MEAN WATER TEMPERATURES (°C)
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
APRIL
CHESAPEAKE BAY MEAN TEMPERATURES
CAROLINA MEAN TEMPERATURES
CHESAPEAKE BAY HATCH FREQUENCY
NORTH CAROLINA HATCH FREQUENCY

Figure 6. Growth comparison between early- (before November) and late-captured (after October) croaker up to 15 mm SL and 80 d.

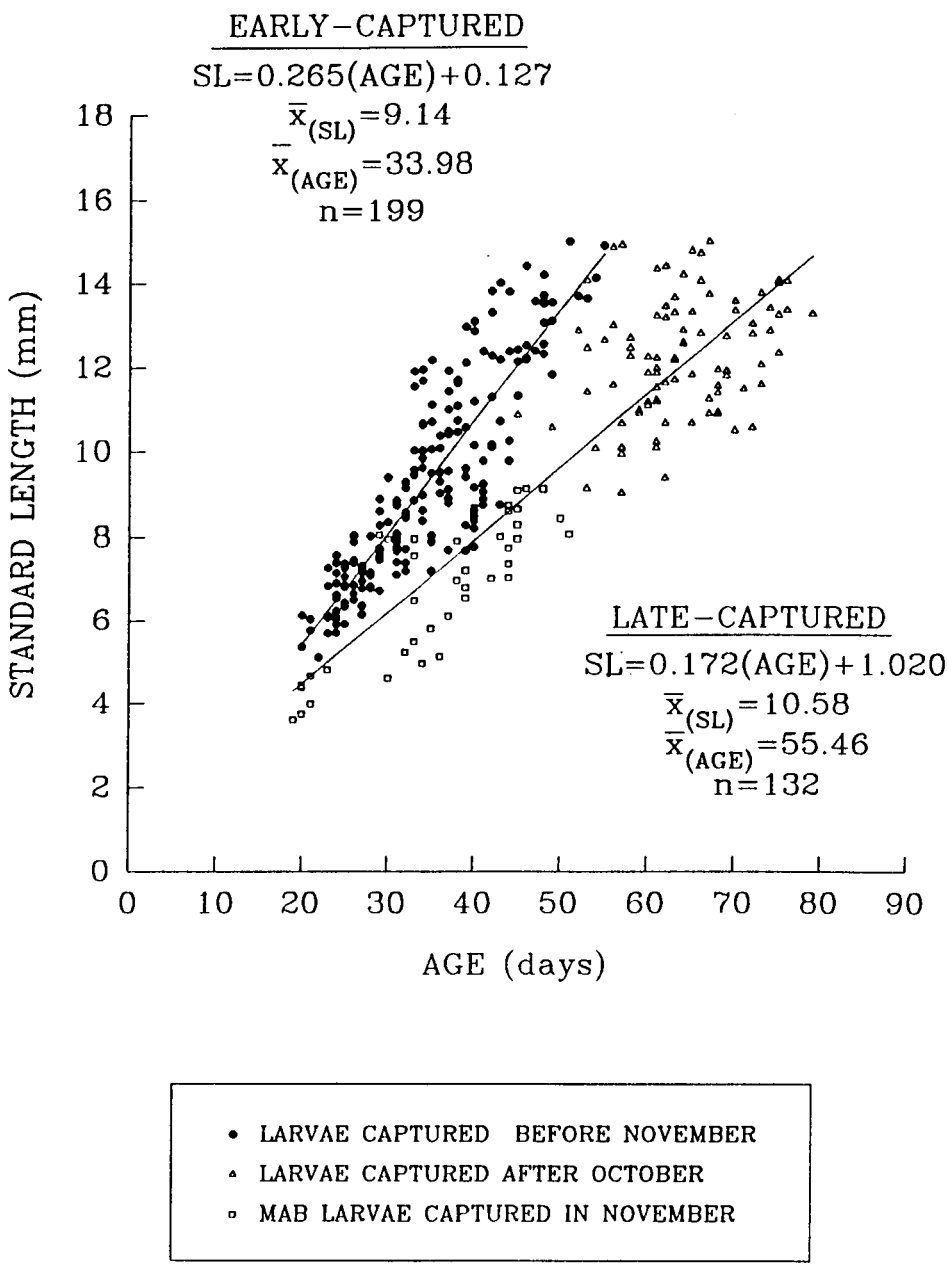

EARLY-CAPTURED
SL=0.265(AGE)+0.127
$\bar{x}_{(SL)}$=9.14
$\bar{x}_{(AGE)}$=33.98
n=199
LATE-CAPTURED
SL=0.172(AGE)+1.020
$\bar{x}_{(SL)}$=10.58
$\bar{x}_{(AGE)}$=55.46
n=132
STANDARD LENGTH (mm)
AGE (days)
0
2
4
6
8
10
12
14
16
18
0
10
20
30
40
50
60
70
80
90
• LARVAE CAPTURED BEFORE NOVEMBER
▲ LARVAE CAPTURED AFTER OCTOBER
▫ MAB LARVAE CAPTURED IN NOVEMBER

Figure 7. Growth comparison between early- (before September) and late-spawned (after August) croaker up to 19 mm SL.

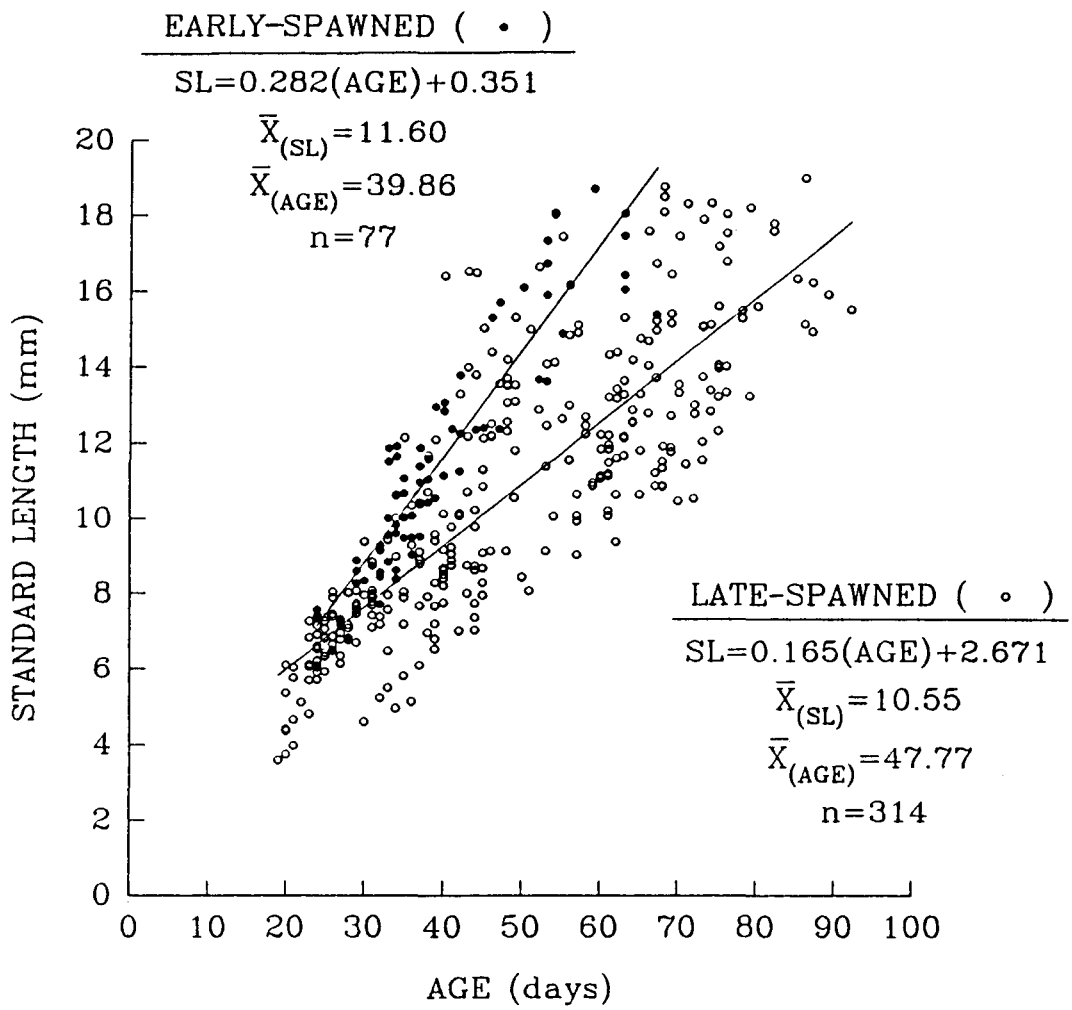

EARLY-SPAWNED (•)
SL=0.282(AGE)+0.351
$\bar{X}_{(SL)}$=11.60
$\bar{X}_{(AGE)}$=39.86
n=77
LATE-SPAWNED (∘)
SL=0.165(AGE)+2.671
$\bar{X}_{(SL)}$=10.55
$\bar{X}_{(AGE)}$=47.77
n=314
STANDARD LENGTH (mm)
AGE (days)
0
2
4
6
8
10
12
14
16
18
20
0
10
20
30
40
50
60
70
80
90
100

Figure 8. Growth comparison between early- (before September) and late-spawned (after August) croaker from 19.01-65.00 mm SL and 51-142 d.

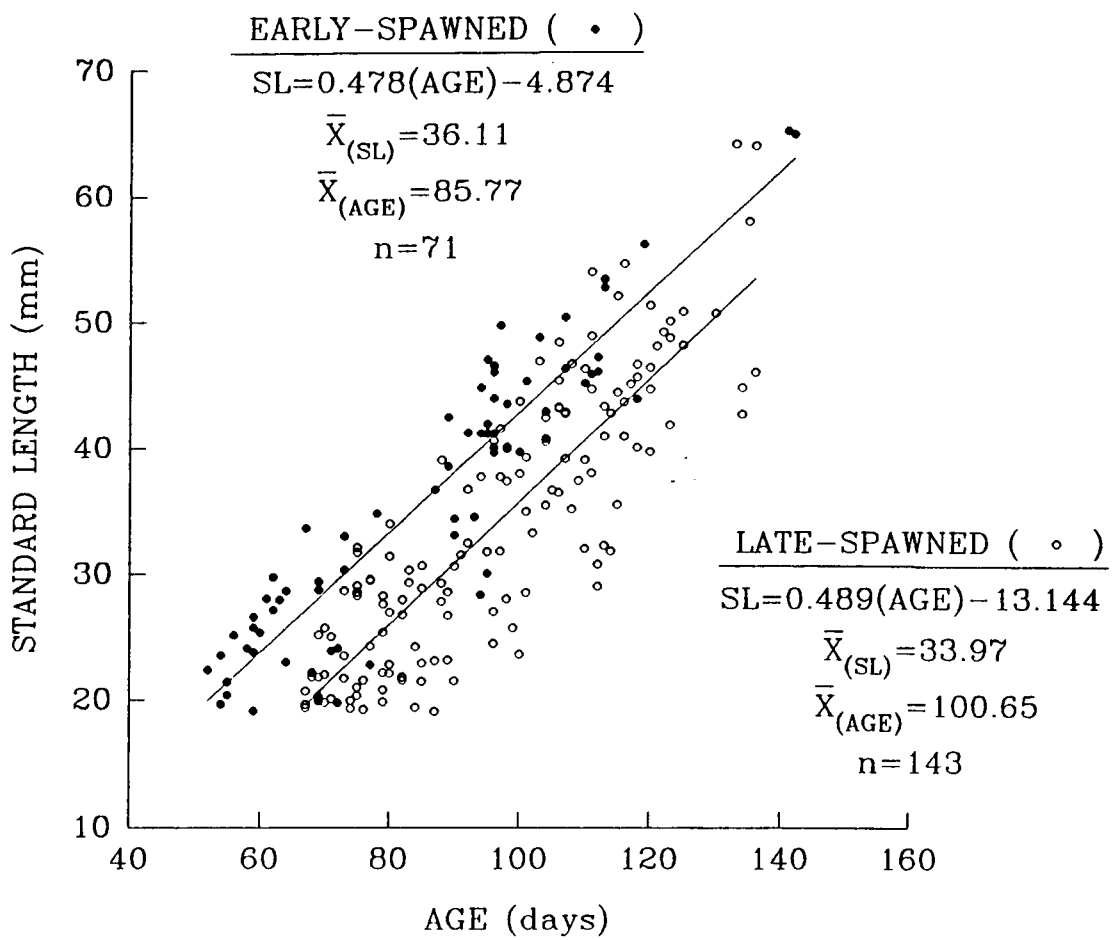

EARLY-SPAWNED (•)
SL=0.478(AGE)-4.874
$\bar{X}_{(SL)}$=36.11
$\bar{X}_{(AGE)}$=85.77
n=71
LATE-SPAWNED (◦)
SL=0.489(AGE)-13.144
$\bar{X}_{(SL)}$=33.97
$\bar{X}_{(AGE)}$=100.65
n=143
STANDARD LENGTH (mm)
AGE (days)
70
60
50
40
30
20
10
40
60
80
100
120
140
160

Figure 9. Growth comparison between Virginia (——) and North Carolina (- - - -) (Warlen 1982) croaker larvae up to 15 mm SL and 80 d. A) represents larvae caught early in the season for the two studies (Virginia: 29 September-28 October 1987; North Carolina: 26 October 1979-16 November 1980), and B) for larvae caught late in the season (Virginia: 03 November 1987-30 March 1988; North Carolina: 23 January-20 March 1980).

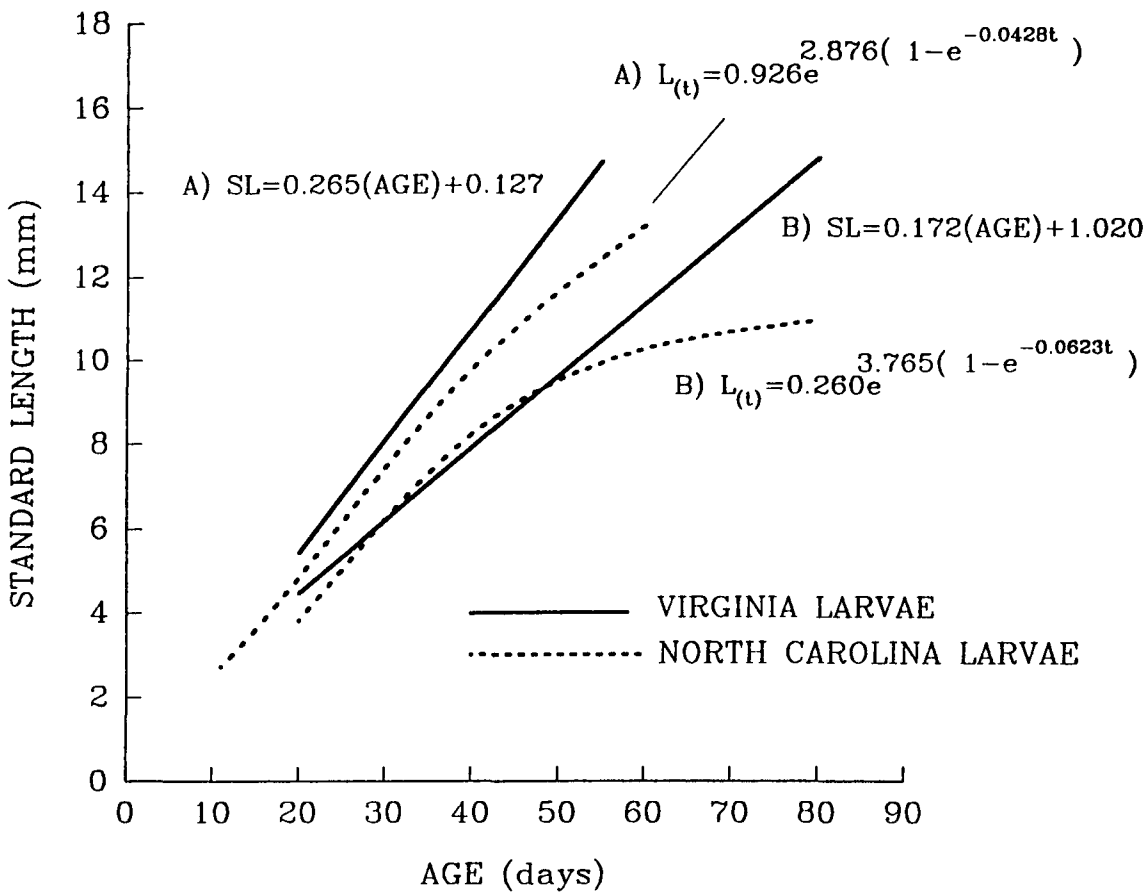

STANDARD LENGTH (mm)
AGE (days)
A) SL=0.265(AGE)+0.127
A) $L_{(t)}=0.926e^{2.876(1-e^{-0.0428t})}$
B) SL=0.172(AGE)+1.020
B) $L_{(t)}=0.260e^{3.765(1-e^{-0.0623t})}$
VIRGINIA LARVAE
NORTH CAROLINA LARVAE

Figure 10. Laird-Gompertz growth model describing growth of Virginia larval and juvenile croaker up to 65 mm SL and 142 d.

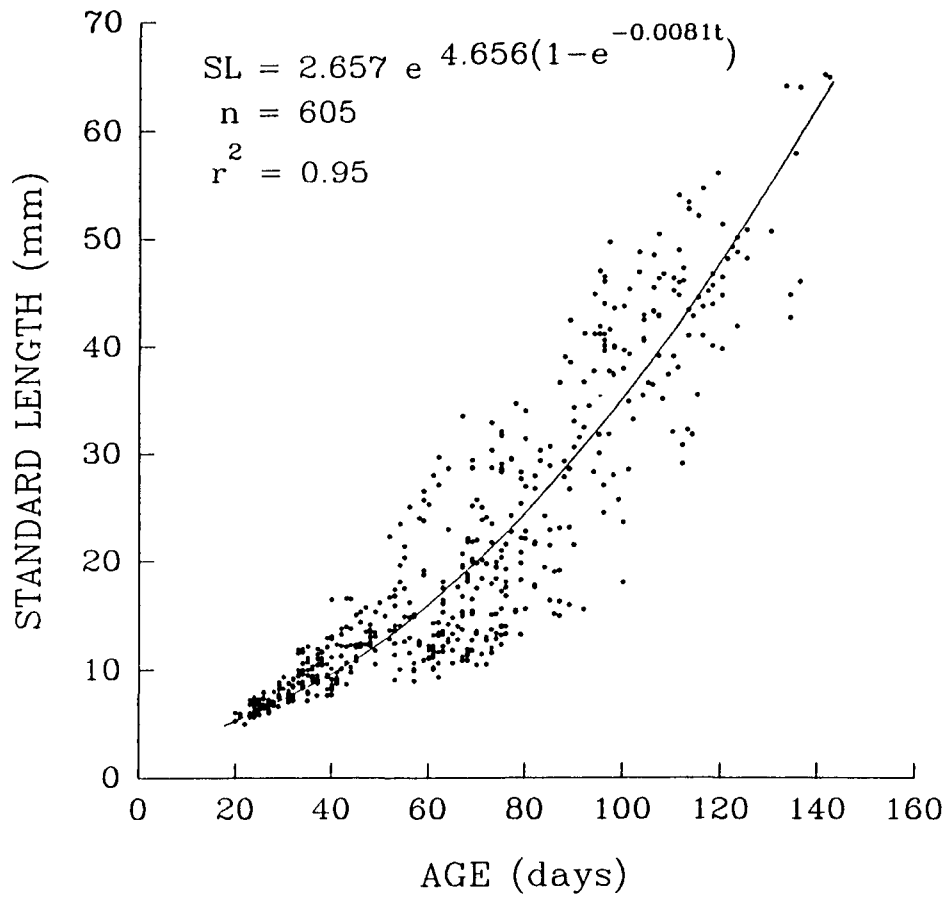

SL = 2.657 e 4.656(1−e−0.0081t)
n = 605
r2 = 0.95
STANDARD LENGTH (mm)
AGE (days)
0
10
20
30
40
50
60
70
0
20
40
60
80
100
120
140
160

Figure 11. Comparison of age-specific growth rate between Virginia and North Carolina (Warlen 1982) croaker larvae up to 90 d. Dotted portion of the lines represent extrapolated data; the youngest larvae was 13 d in North Carolina samples and 19 d in Virginia.

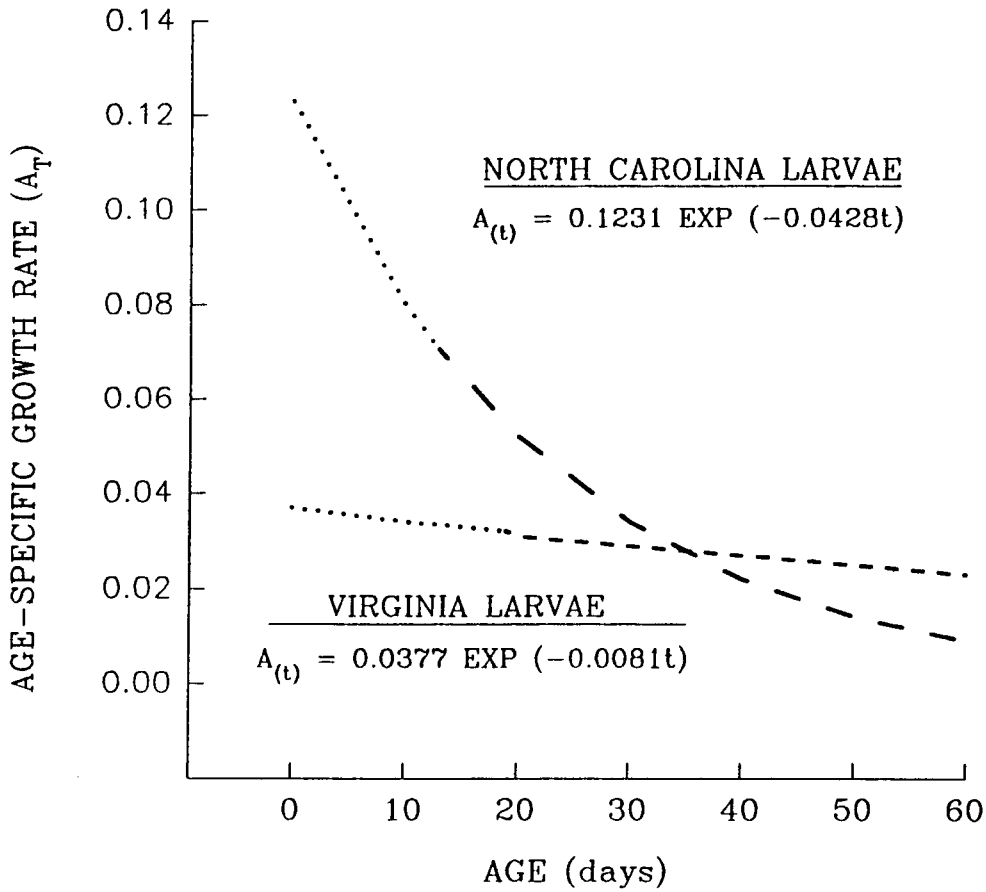

AGE-SPECIFIC GROWTH RATE (A_T)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
NORTH CAROLINA LARVAE
$A_{(t)}$ = 0.1231 EXP (−0.0428t)
VIRGINIA LARVAE
$A_{(t)}$ = 0.0377 EXP (−0.0081t)
0
10
20
30
40
50
60
AGE (days)

Figure 12. The relationship between otolith maximum diameter (OMD) (x) and SL of fish (y) as described by a fourth order polynomial: $y = 2.71 + 23.92\ x - 11.48 * 10^{-4}\ x^2 + 3.94 * 10^{-7}\ x^3 - 0.41 * 10^{-10}\ x^4$; $r^2 = 0.99$; $n = 182$.

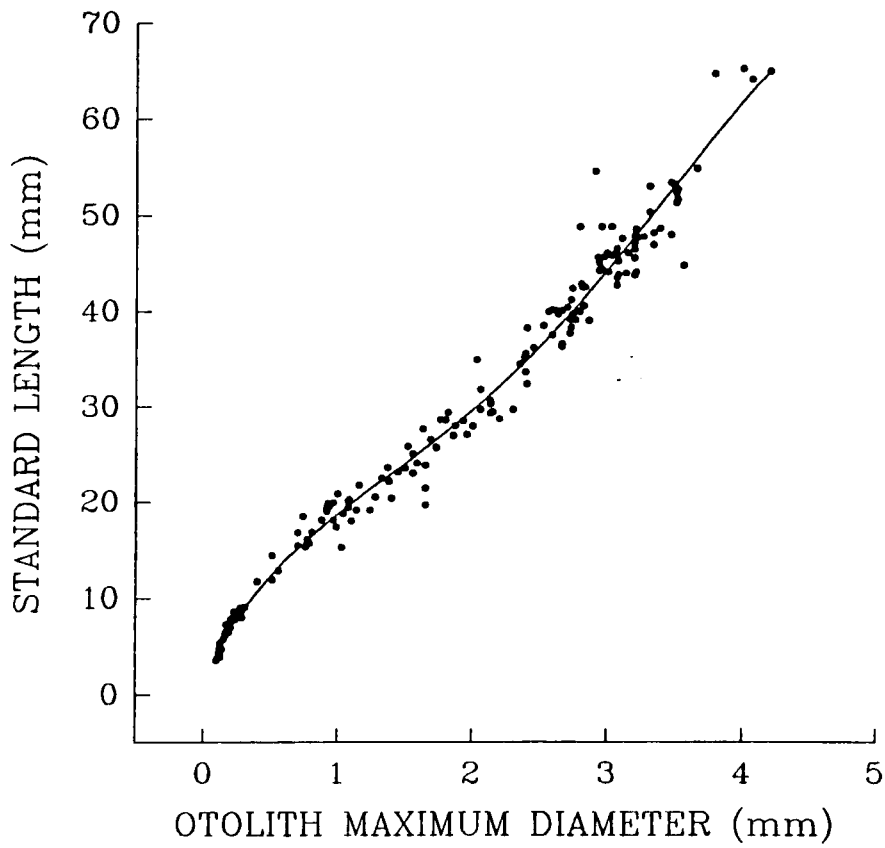
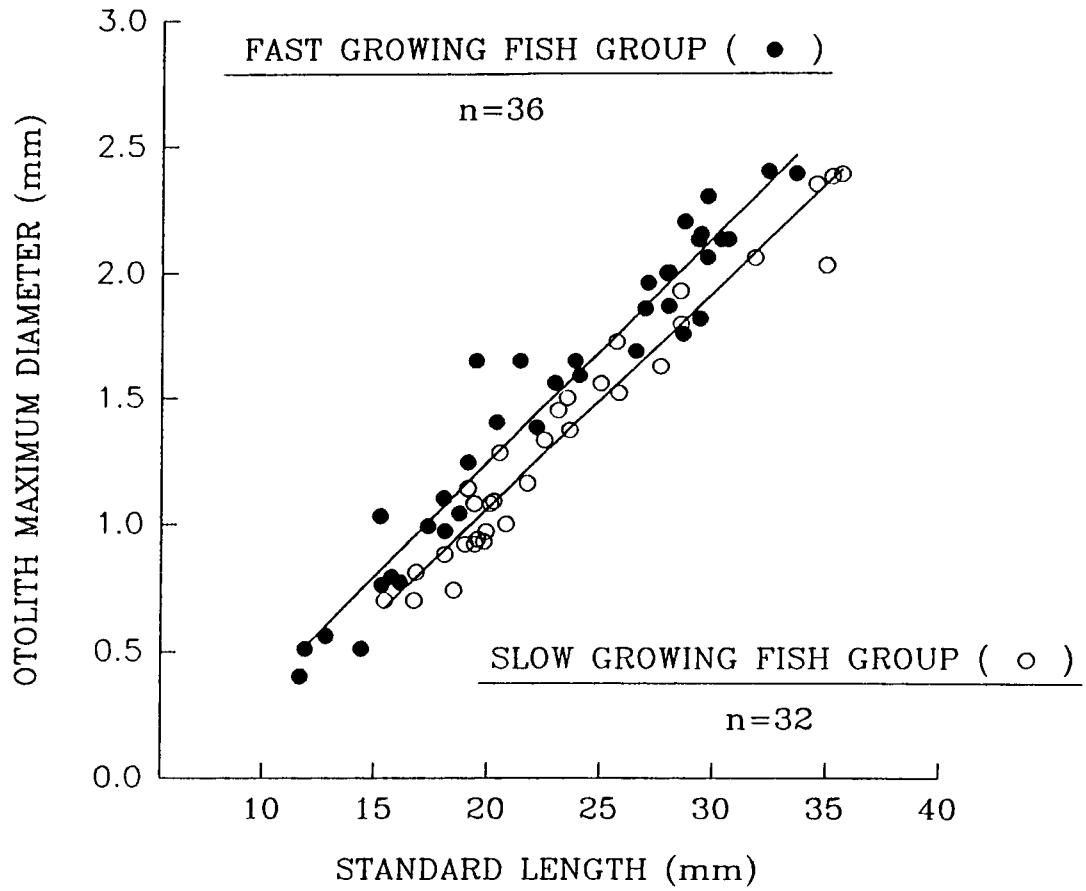

STANDARD LENGTH (mm)
70
60
50
40
30
20
10
0
0
1
2
3
4
5
OTOLITH MAXIMUM DIAMETER (mm)

Figure 13. The relationship between otolith maximum diameter (OMD) (mm) and SL of fish (mm) illustrating otolith and somatic growth relationship between fast- (captured before November) and slow-growing (captured after October) croaker between 11-37 mm SL.


FAST GROWING FISH GROUP (●)
n=36
SLOW GROWING FISH GROUP (○)
n=32
OTOLITH MAXIMUM DIAMETER (mm)
STANDARD LENGTH (mm)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
10
15
20
25
30
35
40