AGE AND GROWTH OF LARVAE AND SPAWNING TIME OF ATLANTIC CROAKER IN NORTH CAROLINA[1]

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Abstract: The age and growth of larval Atlantic croaker, *Micropogonias undulatus*, was determined from daily growth increments on their otoliths. Smaller and younger larvae were found offshore near probable spawning areas while larger and older larvae were found near shore and in the lower estuary. A Laird-Gompertz growth model, $L_{(t)} = 0.926 \exp \{2.876 [1-\exp(-0.0428t)]\}$, described the growth of larvae to 62 days old. The age-specific growth rate, derived from this relationship, declined with fish age. Atlantic croaker spawned over a 5-month period from mid-September to late-February, with the majority probably spawning in October-November. Larvae were the same size, 9 to 11 mm SL, when they immigrated to the estuary in the period from late-October to mid-April, although mean age of fish entering in January and April (61 to 64 days) was almost twice that of fish entering earlier.

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The Atlantic croaker, an economically important fish in many areas of the coastal United States from New Jersey to Texas, spawns in the ocean and as late larvae move into estuarine nursery areas. While many studies have been published on this species, relatively little is known about its early life history. The only information that is available on growth of larval and early juvenile Atlantic croaker along the Atlantic coast has been obtained from examinations of shifts in modes of length-frequency distributions (Hildebrand and Cable 1930, Haven 1957). No definitive information is available on the age and growth of larval croaker in the ocean.

Recently, a technique has been developed that can yield valuable information on the age and daily growth patterns of fish. Pannella (1971, 1974) was the first to demonstrate that otoliths of some species of teleost fishes exhibit daily growth increments. Since then, increments on otoliths have been validated as daily growth rings for a number of other marine species (Liew 1974, Brothers et al. 1976, Struhsaker and Uchiyama 1976, Barkman 1978). Peters et al. (unpublished ms, Beaufort Laboratory) showed that growth increments were deposited daily on the otoliths of laboratory spawned and reared larval spot, *Leiostomus xanthurus*, a species in the same family as the Atlantic croaker. Enumeration of daily growth increments is a useful means of aging fish while either the age and size at capture or back calculation of lengths at ages prior to capture allows estimation of growth rates.

The objectives of this study were to use daily growth increments on larval Atlantic croaker otoliths to 1) measure their age and size in the ocean and as they enter the estuary, 2) estimate growth rates in North Carolina's coastal waters using age-size at capture data, and 3) estimate spawning times.

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METHODS

Fish Collections

Larval Atlantic croaker were collected off Beaufort during 5 cruises of the R/V *John DeWolf II*. These 2-day cruises were conducted monthly from November 1979 through March 1980 and each consisted of a transect of stations from Beaufort Inlet to about the 200 fathom contour (Fig. 1). All samples were obtained by either surface or standard double oblique (Powles and Stender 1978) plankton hauls with bongo nets (60 cm diameter frames) with mesh sizes of either 333 or 505 µm. Larvae were also collected with a surface tidal net (Hettler 1979) at Pivers Island (Fig. 1) from late-October to mid-April as they entered the lower Newport River estuary. Samples were preserved within about 5-minutes of collection with 95 percent ethanol so that the final alcohol concentration was 70 percent. The ethanol was changed in all samples at least once after initial preservation to prevent dissolution of otoliths in any samples that may have been inadequately preserved.

Otolith Preparation and Aging

The standard length (SL) of each fish was measured to the nearest 0.01 mm with an ocular micrometer on a dissecting microscope. The largest otolith pair (sagittae) was removed and the surrounding tissue was teased away. The otoliths were then cleaned in distilled water and mounted on a glass microscope slide under a thin layer of quick drying mounting medium.

Otoliths were examined with a compound microscope using transmitted light and fitted with a television camera. Growth increments were counted from otolith images on a video monitor at magnifications of 400X or 1,000X. The latter magnification was required to resolve adjacent growth increments on most otoliths. None of the otoliths required sectioning; however, otoliths from Atlantic croaker larger than 17 mm SL generally had to be ground before they could be aged using transmitted light.

The age of a larva in days was determined by counting the number of otolith growth increments and adding 5 days. Spot (Peters et al. unpublished ms, Beaufort Laboratory) and northern anchovy, *Engraulis mordax*, (Brothers et al. 1976) do not form otolith growth increments until completion of yolk-sac absorption—a time coinciding with first feeding. It was assumed that Atlantic croaker first fed at the same time as spot, 5 days (A.B. Powell unpublished ms, Beaufort Laboratory). Therefore, 5 days was added to the number of growth increments to estimate the age of fish from hatching.

Growth Estimations

Exponential, von Bertalanffy, and Gompertz mathematical models are commonly used to describe the growth of fishes. The Laird version (Laird et al. 1965) of the Gompertz growth equation has been successfully employed by Kramer and Zweifel (1970), Sakagawa and Kimura (1976), Zweifel and Lasker (1976) and Warlen and Chester (unpublished ms, Beaufort Laboratory) to model the growth of marine larval fishes. For this reason this model was selected to describe the growth in length of larval Atlantic croaker collected in the ocean and the lower estuary.

The Laird-Gompertz growth equation describes an asymmetric sigmoid curve of the form:

$$L_{(t)} = L_{(o)} \exp \{A_{(o)}/\alpha[1 - \exp(-\alpha t)]\}, \qquad (1)$$

where $L_{(t)}$ = length at time (t),

$L_{(o)}$ = length at t=o, assumed to be length at hatching,

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

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

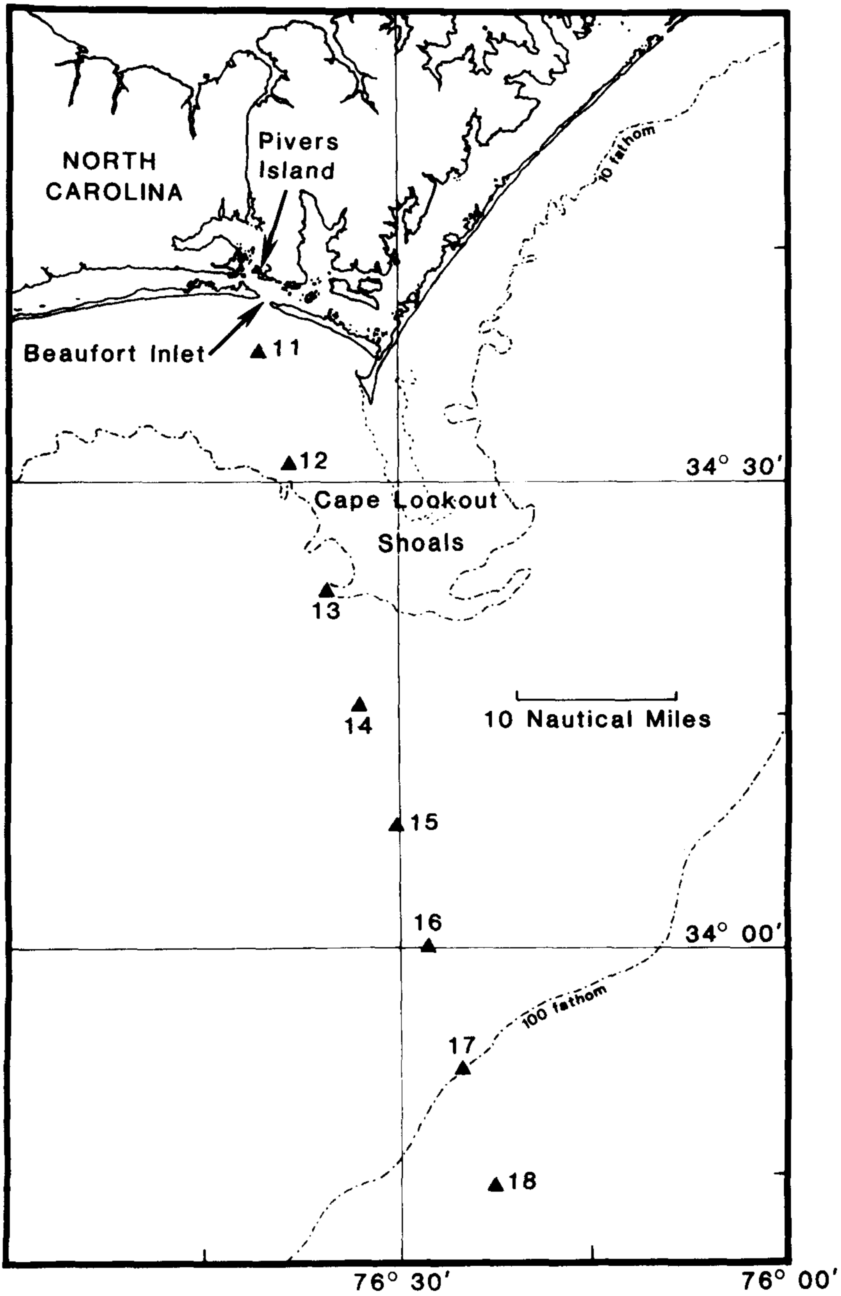

Fig. 1. Location of sampling sites for Atlantic croaker larvae in the mouth of the Newport River estuary at Pivers Island and in a transect offshore from Beaufort Inlet, North Carolina.

Marquardt's algorithm (Conway et al. 1970), an iterative, non-linear least squares method, was used to fit the model to the data and to estimate $L_{(o)}$, $A_{(o)}$ and α.

Once estimates of $A_{(o)}$ and α were obtained, it was possible to calculate the age specific growth rate, $A_{(t)}$, from the following relationship:

$$A_{(t)} = A_{(o)} \exp(-\alpha t). \tag{2}$$

Spawning Time Calculation

A spawning date was assigned to each ageable fish by subtracting the estimated age of the fish in days from the date of capture. For example, a 31-day-old fish caught on October 26, 1979, would have a September 25, 1979 spawning date.

RESULTS AND DISCUSSION

Age-Length at Capture

The mean age and length of Atlantic croaker larvae caught in the ocean was significantly smaller (t-test, $P < 0.01$) than those caught in the lower Newport River estuary (Table 1). These differences were expected since this species spawns offshore (Hildebrand and Cable 1930, Wallace 1940, Haven 1957, Powles and Stender 1978). Initial length after hatching is between 1.6 mm (A.B. Powell, personal comm., Beaufort Laboratory) and 2.0 mm (Middaugh and Yoakum 1974). Larvae caught in November and December on the mid to outer continental shelf (Stations 15-18) were 4 to 5 mm SL and were about 16 to 20 days old. In January, February and March, larvae were found in the same general area but were generally larger (5 to 8 mm SL) and older (25 to 34 days).

Generally, the age of larvae entering the estuary increases throughout the immigration period. While the larvae are similar in mean size throughout the estuarine immigration period the mean age of larvae differed by almost a factor of 2. Such a wide range of immigration ages may indicate spawning at variable distances from the inlet and variable rates of larval transport to the estuary.

Those larvae entering in January and April seemed to have had a growth rate much less than larvae entering in the early fall. For example, the average growth rate (mean SL/mean age) for the October 26 fish was 0.272 mm/day while the growth rate for fish caught April 17 was 0.156 mm/day. The relative success of immigration cohorts in utilizing the estuary as nursery grounds can be determined by measuring the growth rates of those fish as juveniles collected throughout their estuarine residency. Their past growth as larvae also can be estimated by back calculation.

The period of larval immigration into estuaries appears to be the same in North Carolina, late-October to mid-April, as it is in South Carolina, late-October through April (Bearden 1964). In addition, the size at immigration agrees very well with Bearden who found that Atlantic croaker larvae were 8 to 15 mm when they moved into South Carolina estuaries.

Growth of Larvae

A plot of the standard length and age at capture for larval Atlantic croaker (Fig. 2) suggested that there might have been 2 sub-groups of fish with different growth curves. The larvae represented by Curve A were those from collections through January 16 in the ocean and through January 3 at Pivers Island, while those in Curve B were caught after those dates in both areas.

Curve A probably represents the typical growth of larvae in coastal North Carolina waters since it is based on fish spawned during the peaks of the spawning season. These larvae were estimated to have grown from 3.1 mm SL at 13 days to 13.4 mm SL at 62 days (Fig. 2). The length at any time up to 62 days can be predicted from the Laird-Gompertz growth model:

Table 1. Mean standard length (mm) and age (days) of Atlantic croaker larvae from the ocean off Beaufort Inlet and the estuary at Pivers Island, North Carolina, October 1979 to April 1980.

Capture date	Number of fish	Mean standard length (mm) ± S.E.	Mean age ± S.E.	Station no.
Ocean				
Nov. 15	37	4.25 ± 0.11	17.36 ± 0.32	15
Nov. 15	20	4.54 ± 0.10	17.65 ± 0.39	16
Nov. 16	38	4.26 ± 0.07	19.63 ± 0.28	15
Dec. 3	5	5.12 ± 0.79	19.20 ± 1.59	12, 13, 15-17
Dec. 4	19	3.99 ± 0.10	16.11 ± 0.43	18
Dec. 4	2	4.20 ± 0.0	18.00 ± 0.0	17
Dec. 4	1	7.30 ± 0.0	31.00 ± 0.0	13
Jan. 15	8	6.54 ± 0.37	27.38 ± 1.53	14-16
Jan. 16	5	7.36 ± 0.55	24.80 ± 0.86	15
Feb. 12	6	5.37 ± 0.37	26.50 ± 1.73	15, 17, 18
Feb. 13	9	5.86 ± 0.36	28.78 ± 1.29	14-16
March 20	4	7.15 ± 0.69	34.25 ± 3.73	14, 15
Estuary				
Oct. 26	10	9.04 ± 0.22	33.20 ± 1.37	P.I.[1]
Nov. 2	10	9.42 ± 0.26	36.00 ± 1.00	P.I.
Nov. 9	9	10.90 ± 0.30	44.67 ± 1.82	P.I.
Nov. 19	10	12.54 ± 0.59	51.20 ± 2.56	P.I.
Nov. 22	10	9.26 ± 0.13	39.10 ± 0.43	P.I.
Dec. 18	10	10.65 ± 0.18	41.50 ± 0.54	P.I.
Jan. 3	10	10.91 ± 0.25	53.30 ± 1.28	P.I.
Jan. 23	9	10.93 ± 0.25	61.11 ± 3.80	P.I.
Apr. 17	13	9.96 ± 0.21	63.69 ± 2.11	P.I.

[1]P.I. = Pivers Island

$$L_{(t)} = 0.926 \exp \{2.876 [1 - \exp(-0.0428t)]\}.$$

The value 2.876 is the constant, $A_{(o)}/\alpha$.

The larvae represented by solid triangles and by Curve B were smaller for their ages and thus fell well below the main group growth trend (Curve A). It may be that these fish represent cohorts having much slower growth rates. Such reduced growth rates could have been due to lower ocean temperatures in mid to late winter and to less than optimal food supplies, both of which could have limited growth of larvae. A less likely possibility is that small egg size in these later-spawned cohorts can scale down early larval fish growth. A seasonal decrease in egg size is characteristic of planktonic marine fish (Bagenal 1971). *Also, these relatively late spawned larvae might have come from parental stocks migrating* to North Carolina from northern areas and having different growth potential. Adults

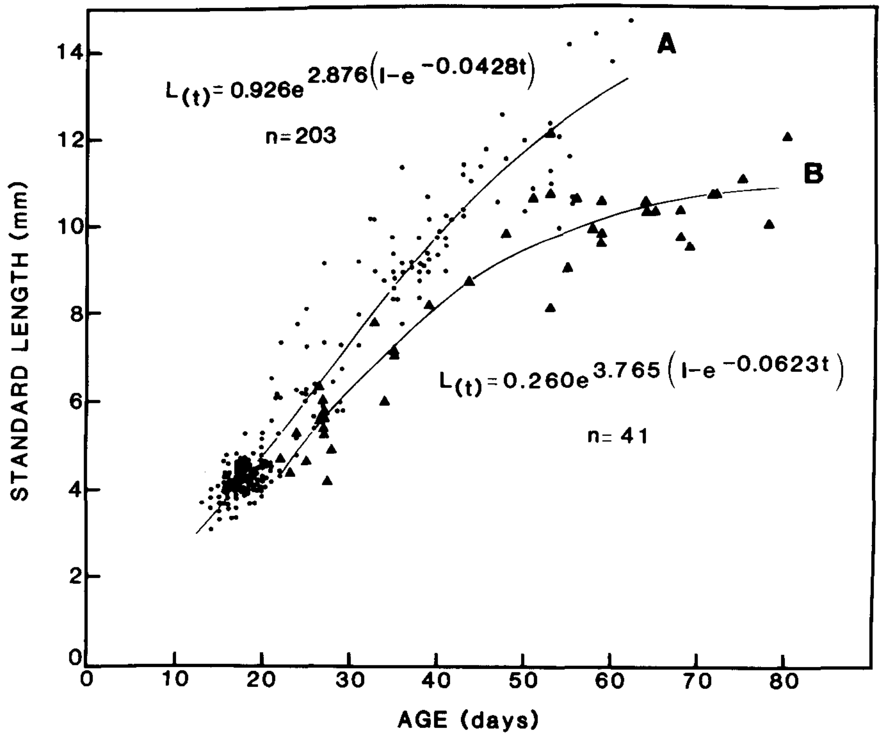

Fig. 2. Growth of 2 groups of larval Atlantic croaker collected from oceanic and estuarine waters of North Carolina. The Laird-Gompertz growth model of the form $L(t) = L(o) \exp \{A_{(o)} / \alpha \ [1\text{-}\exp(-\ \alpha\ t)]\}$ was used to describe the data. Curve A is for the larvae collected through January 16 in the ocean and through January 3 at Pivers Island, Curve B is for larvae caught after those respective dates in both areas.

tagged in the fall in Maryland-Virginia waters are known to migrate to waters off North Carolina (Haven 1959).

The early growth of many larval fishes is fundamentally exponential; however, as the fish grows, its growth rate undergoes some intrinsic exponential decay or retardation due to some unknown physiological mechanisms (Kramer and Zweifel 1970). Growth is due primarily to the multiplication of cells, but there appear to be genetically determined limitations on the growth parameters (Zweifel and Lasker 1976). The sign value for α in equation (3) indicates there is a reduction in the growth rate of Atlantic croaker larvae with time. The age specific growth rate (A_t) plotted against age of the fish (Fig. 3) shows a decline in daily growth rate from 12.3 percent at day-0 to 0.9 percent at day-60. We have found a similar pattern for larval-early juvenile spot (Warlen and Chester unpublished ms.) as have Sakagawa and Kimura (1976) and Zweifel and Lasker (1976) for the northern anchovy, *Engraulis mordax*.

Although Curve A (Fig. 2) appears to be a good approximation of the growth of larval Atlantic croaker, the estimate of the initial length (L_0= 0.926 mm) is below the actual size at hatching of 1.6 to 2.0 mm SL. Larvae probably grow about 1.0-1.5 mm to reach the 3.1 mm estimated size by day-13, a rate which is only about half that (2.8 mm) occurring in the succeeding 12 day period. Growth to day 13 probably consists of a sequence of

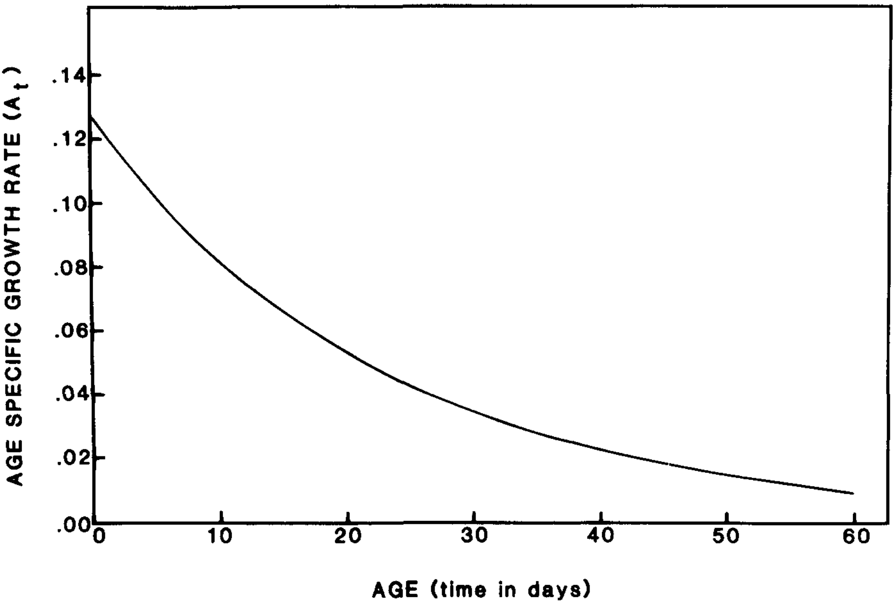

Fig. 3. Relationship of age specific growth of Atlantic croaker larvae with their age from the equation $A_{(t)} = A_{(o)}\exp(-\alpha t)$. Estimates of $A_{(o)}$ and α are from the Laird-Gompertz growth equation fit to larval length data from R/V *John DeWolf II* and Pivers Island collections (Fig. 2).

moderate growth for a short period after hatching, a period of minimal growth to approximately first feeding (ca. 5 days), and finally a more rapid growth phase—reaching 3.1 mm at age 13-days. Zweifel and Lasker (1976) suggest that this pattern is a general phenomenon "found to be almost universal in larval growth". They applied a 2-stage Laird-Gompertz growth curve to the 2 growth cycles, 1 cycle from hatching to depletion of the yolk sac and the other beginning at first feeding. Such a 2-stage model may well be appropriate for Atlantic croaker larvae when growth data for days 0-12 becomes available.

Spawning Times

Atlantic croaker were estimated to have spawned over approximately a 5-month period, from mid-September to late-February (Table 2). Based on the limited number of samples, the major spawning season occurred from late September through November. Relative abundance data of larval Atlantic croaker collected at Pivers Island from November 1967 through April 1968 (Fig. 4, from unpublished data from R. M. Lewis, Beaufort Laboratory) shows major peaks of larval immigration in early-December and mid-January. The age of those fish, if similar to those caught in December 1979 and January 1980, would have estimated spawning peaks in October and November. These data agree with Johnson (1978) who stated that Atlantic croaker generally spawn south of Cape Hatteras from September to March with a peak around October or November.

The Atlantic croaker spawning season in North Carolina waters is probably very similar to that in South Carolina. As discussed earlier, recruitment of larvae into estuaries of both states took place during the same period and if it is assumed that ages at recruitment are similar in both areas, then spawning times also would be similar.

Table 2. Range and average spawning dates of Atlantic croaker larvae from the ocean off Beaufort Inlet and the estuary at Pivers Island, North Carolina, October 1979 to April 1980.

Capture date	Number of fish	Range of spawning dates	Average spawning date
Ocean			
Nov. 15	37	Oct. 25 - Oct. 31	Oct. 29
Nov. 15	20	Oct. 24 - Oct. 31	Oct. 28
Nov. 16	38	Oct. 21 - Oct. 29	Oct. 27
Dec. 3	5	Nov.8 - Nov. 17	Nov. 14
Dec. 4	19	Nov. 15 - Nov. 21	Nov. 18
Dec. 4	2	Nov. 16	Nov. 16
Dec. 4	1	Nov. 11	Nov. 11
Jan. 15	8	Dec. 10 - Dec. 24	Dec. 19
Jan. 16	5	Dec. 20 - Dec. 25	Dec. 22
Feb. 12	6	Jan.8 - Jan. 21	Jan. 16
Feb. 13	9	Jan. 9 - Jan. 20	Jan. 15
Mar. 20	4	Feb. 5 - Feb. 22	Feb. 15
Estuary			
Oct. 19	0	-	-
Oct. 26	10	Sept. 19 - Oct. 4	Sept. 23
Nov. 2	10	Sept. 24 - Oct. 4	Sept. 27
Nov.9	9	Sept. 16 - Oct. 5	Sept. 25
Nov. 19	10	Sept. 18- Oct. 15	Sept. 29
Nov. 22	10	Oct. 12 - Oct. 16	Oct. 14
Dec. 18	10	Nov. 4 - Nov. 9	Nov. 7
Jan. 3	10	Nov. 4 - Nov. 19	Nov. 11
Jan. 23	9	Nov. 4 - Dec. 6	Nov. 23
Apr. 17	13	Jan. 30 - Feb. 24	Feb. 13

Larvae collected in the ocean (Table 2) appeared as distinct cohorts in each month. In any sample, fish were similar in age and size (Table 1). The cohort spawned in one month was not found again in oceanic samples in any succeeding month because the larvae are constantly being transported from offshore areas of spawning to inshore nursery areas. Nelson et al. (1977) suggested that zonal Ekman transport was the most significant mechanism responsible for movement of larval Atlantic menhaden, *Brevoortia tyrannus*, from offshore spawning grounds to inshore nursery grounds in the same study area. This mechanism is probably also largely responsible for transporting Atlantic croaker larvae into the Newport River estuary. As larvae reach the estuary there seems to be some mixing of cohorts as indicated by the relatively higher standard error of the mean age in the Pivers Island samples (Table 1).

The best indicator of the spawning time of marine fishes is the presence of their eggs in the plankton. However, eggs are often difficult to collect and when collected cannot be identified to species because the eggs have not been described. Consequently, many

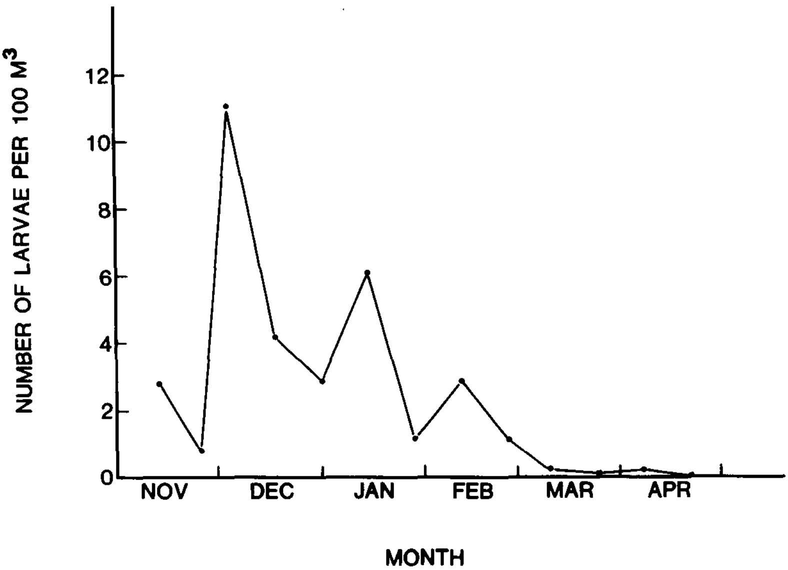

Fig. 4. Mean semimonthly number of Atlantic croaker larvae per 100 m^3 water sampled at Pivers Island from November 1967 to April 1968 (unpublished data from R. M. Lewis, NMFS, Beaufort Laboratory, Beaufort, N.C.).

estimates of spawning times have been based only on the presence of larvae of unknown age in ichthyoplankton samples over time. These estimates are necessarily less precise than estimates based on aged larvae. For example, Hildebrand and Cable (1930) estimated Atlantic croaker spawning time, from September to May off Beaufort using larvae of unknown ages. Their larvae collected in September were 4.2 mm long and were probably spawned in September. Few or no larvae were that small in their March to May collections, suggesting that those larvae were probably spawned earlier. Many of those fish (9 to 12 mm) could have been 37 to 55 days old (Fig. 2). Depending on the exact date(s) of capture, their May caught fish were probably spawned in March or April and their April fish in February or March. Therefore, the extent of the spawning season was probably less than they suggested.

Adult Atlantic croaker move from estuaries at a time of decreasing photoperiod and dropping water temperatures to spawn in Continental Shelf waters that are still warm, 18 to 25°C, (Fahay 1975) and where phytoplankton and zooplankton (food for larvae) levels are still relatively high (Turner et al. 1979). In addition, the warm water temperatures undoubtedly facilitate rapid growth of larvae. Larvae of the same species spawned in the winter in the same area do not have these advantages. Atlantic croaker larvae spawned in winter and recruited into the estuary later have lower growth rates as indicated by the greater age at size (Table 1). The relative success of the seasonal spawning cohorts, in terms of their survival and production of adult biomass, remains to be tested.

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