AGE, GROWTH, AND DISTRIBUTION OF LARVAL SPOT, *LEIOSTOMUS XANTHURUS*, OFF NORTH CAROLINA

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ABSTRACT

Age and growth of the early life history stages of spot, *Leiostomus xanthurus*, were determined from daily growth increments on otoliths of larval and early juvenile spot collected from Beaufort Inlet, NC, to the continental shelf break during the fall and winter of 1978-79 and 1979-80. Spawning occurred on the mid to outer continental shelf between early November and early March, but appeared to be concentrated from mid-December through January. Generally, the youngest larvae were found further offshore; ages and lengths increased closer to shore. Larvae entered the estuary at an average age of 59 days (range 40-74 days) and an average size of 13.6 mm (range 11.3-15.6 mm). Significantly younger and smaller larvae immigrated at the beginning and end of the immigration period. Fish entered the estuary segregated by age as indicated by the small within-sample variation in age. A Gompertz growth equation was used to express the relationship between age and standard length for 69 larvae collected in 1978-79 and 557 collected in 1979-80. Spot grew from about 1.6 mm SL at hatching to 17-19 mm SL at 90 days. There were no significant differences in growth parameters between years; age-specific growth rates declined from ≅5%/day at age 10 days to <1%/day at age 90 days.

The larvae of a number of commercially important fishes that spawn on the outer continental shelf of the southeastern United States are transported shoreward to estuaries where development is completed (McHugh 1966; Chao and Musick 1977; Weinstein and Walters 1981; Warlen 1982). Although this general pattern of oceanic spawning and estuarine development has been known at least since publication of the work of Hildebrand and Cable (1930), most recent studies have considered only the estuarine phase (Chao and Musick 1977; Weinstein and Walters 1981), and virtually no quantitative data exist on age and size distribution or growth of larvae between the time of spawning and estuarine immigration.

Spot, *Leiostomus xanthurus*, spawn offshore and are widely distributed in coastal waters from the mid-Atlantic to Texas. Larvae have been reported from North Carolina to Massachusetts (Berrien et al. 1978), from the South Atlantic Bight (Fahay 1975; Powles and Stender 1976), and from the Gulf of Mexico (Fruge 1977; Govoni et al. 1983). Despite studies on egg and larval development (Fruge and Truesdale 1978; Powell and Gordy 1980), growth of juveniles (Weinstein and Walters 1981), and feeding ecology

of larvae (Govoni et al. 1983) and juveniles (Chao and Musick 1977), little is known of the early growth history of spot. Our objectives were to 1) determine the estimated age and size distribution of young spot from the time of hatching in the ocean to recruitment into the estuary, 2) estimate larval growth rates, 3) estimate spawning times, and 4) determine when young spot enter the estuary.

METHODS

Sources of Data

Larvae were collected off Beaufort, NC, during 11 2-d cruises of the RV *John de Wolf II*, from December 1978 to April 1979 (grid design, stations 1-10) and from November 1979 to March 1980 (transect design, stations 11-19) (Fig. 1). At all stations, except Beaufort Inlet, samples were obtained from oblique plankton hauls (Powles and Stender 1976) collected with 60 cm diameter bongo nets (mesh sizes 333 or 505 μm) rigged with flow meters. A surface tow was made at Beaufort Inlet. Larvae were also collected with a neuston net (Hettler 1979) about 1 mi inside the mouth of the Newport River at Pivers Island (Fig. 1) seven times from mid-December 1979 to mid-April 1980. Samples were preserved in 95% ethanol (final concentration ≅75%) within 5 min of collection.

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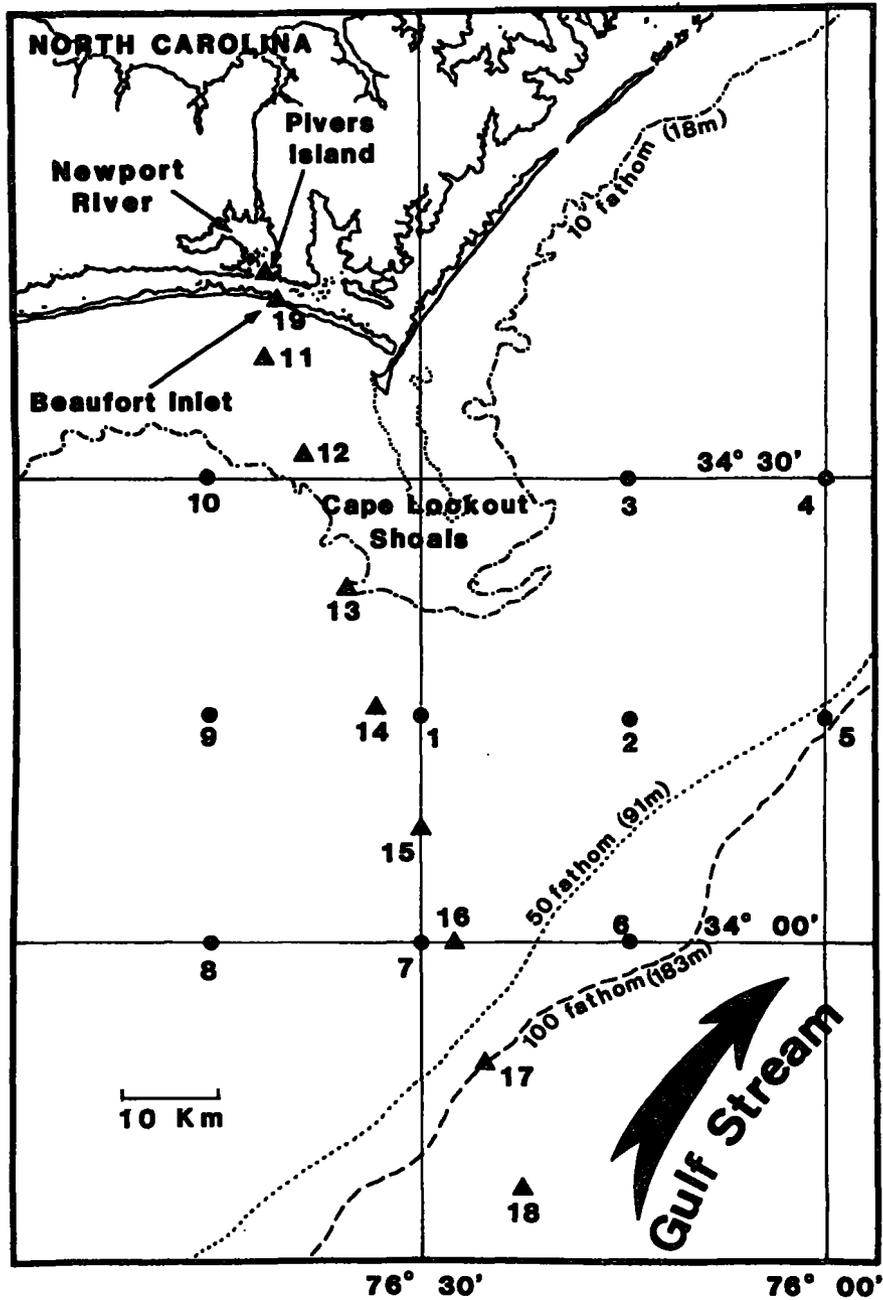
FIGURE 1.—Location of sampling sites for late-larval and early-juvenile spot in the mouth of the Newport River estuary at Pivers Island and for larval spot in the ocean off Beaufort Inlet, NC. Circles are stations sampled from December 1978 to April 1979 and triangles are those sampled October 1979 to April 1980.

Estimated Age and Back-Calculated Length

We counted the number of growth increments on otoliths (e.g., Pannella 1971; Brothers et al. 1976) to estimate age (in days) of each larva. Laboratory-reared larval spot have been shown to deposit an average of 1 ring/d on their otoliths (Peters et al. 1978; Warlen 1984[2]), but do not begin to do so until 5 d after hatching, a time coincident with yolk-sac absorption and first feeding activity at 20°C (Peters et al. 1978). Therefore, we added 5 to the number of counted increments to estimate age. The spawning date of each larva was estimated by subtracting age in days from date of capture.

After we measured each larva in alcohol to the nearest 0.1 mm standard length (SL), we teased the largest pair of otoliths (sagittae) from the surrounding tissue, cleaned them in distilled water, and mounted them on a glass microslide under a thin layer of Flo-Texx[3] mounting medium. They were examined with a compound microscope fitted with a television camera. Growth increments were counted from images of otoliths on a video monitor at magnifications of at least 400×. For selected larvae, otolith radius and the growth increments along it were measured to the nearest 0.1 μm with a filar ocular micrometer. We then used Lee's (1920) modification of the direct proportion formula to back-calculate lengths and reconstruct the growth of each fish. In addition to the assumption that growth increments be daily, the reliability of back-calculated lengths requires that growth of the otolith must be linearly related to growth of the fish. We found, for larvae 2.2-12.4 mm SL, that the relation between body length and otolith radius was linear:

$$\text{body length (mm)} = 2.202 + 0.045 * \text{otolith radius (μm)}$$
$$n = 32, r^2 = 0.95. \tag{1}$$

Weight-Length Relationships

Because larval fish are not weighed in many ichthyoplankton field studies, a weight-length relationship is required to describe the growth of populations, assess production in terms of dry weight, and

estimate weight where only length is known. We determined a dry weight-length relationship from 125 laboratory-reared larvae and early juveniles (2.7-29.6 mm SL). Live fish were anesthetized in a solution of MS-222 (tricane methanesulfonate), removed from the solution, and measured to the nearest 0.1 mm SL. Fish were then rinsed in distilled water, placed on preweighed Nuclepore[R] membrane filters, freeze-dried, and weighed to the nearest 1 μg.

RESULTS

Spawning and Larval Movement

The temporal pattern of spawning found here, though perhaps influenced by the particular dates and stations sampled (Table 1), indicated that spot is a late October-early March spawner (Fig. 2). The majority (67%) of fish collected during the fall and winter of 1979-80 were spawned during December or January (Fig. 2).

The offshore larval distribution by estimated age and length suggests that spawning occurred over the outer continental shelf. Both mean age and length varied inversely with distance from shore (Figs. 3, 4). Youngest (<25 d) and smallest (<4 mm) larvae were found most often near or in the Gulf Stream, 80-100 km off Beaufort Inlet, paralleling the 183 m depth contour (stations 5, 16, 17, 18). However, comparable ages and sizes also were found in the mid-shelf area (stations 1, 14, 15) early in the spawning season (December 1978; November and December 1979). Older (40-50 d) and larger (>8 mm) larvae generally occurred closer to shore within about 40 km of Beaufort Inlet in <25 m of water (stations 10-13, 19), except during February and March 1980 when some larvae were caught 50 km offshore at station 14. Spawning apparently is continuous between late October and late February, since young larvae occurred every month at the three offshore stations (16-18). Most spawning off North Carolina probably occurs between 75 and 95 km offshore, except for some activity in the mid-shelf area early in the spawning season. Our age-length data provided no evidence that spot spawn near shore.

Estuarine Immigration

Larvae entered the Newport River estuary over a 4-mo period from about mid-December to mid-April (Figs. 2, 5). None were caught prior to December 1979 nor after 17 April 1980. Relative abundance of larvae collected at Pivers Island dur-

TABLE 1.—Number of larval spot per 100 m³ caught off North Carolina during the seasons of 1978-79 and 1979-80. N.S. = No sample taken.

1978-79 cruise		Station number									
No.	Date	1	2	3	4	5	6	7	8	9	10
1	6-7 Dec.	1.9	0	0	0	0	0	0	0	0	0
2	4-5 Jan.	5.0	0	N.S.	N.S.	5.6	0	0	19.3	0	0
3	31 Jan.-1 Feb.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0	0
4	7-8 Mar.	1.8	6.4	N.S.	N.S.	N.S.	0	0	1.7	2.7	0
5	26-27 Mar.	0	0	N.S.	N.S.	N.S.	0	0	0	0	13.3
6	23-24 Apr.	0	N.S.	0	0	0	0	0	0	0	0

1979-80 cruise		Station number								
No.	Date	Inlet[1]	11	12	13	14	15	16	17	18
7	15-16 Nov.	N.S.	0	0	0	N.S.	43.1	3.3	N.S.	N.S.
8	3-4 Dec.	N.S.	0	0	3.1	1.1	0	4.0	1.1	45.0
9	15-16 Jan.	N.S.	2.4	0.4	0.7	108.6	8.8	4.1	N.S.	N.S.
10	11-13 Feb.	N.S.	0	0	4.1	31.5	17.9	0.6	0.3	2.3
11	19-20 Mar.	65.6	0	0	0.7	4.2	11.4	0.4	0.6	0

[1]Same as station 19.

ing the winter periods of 1967-70 showed major immigration peaks in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974). The duration of estuarine immigration generally reflected the duration of the spawning season (Fig. 2).

Statistically significant monthly variations (ANOVA, $P < 0.05$) in both age and length of larvae entering the Newport River estuary were observed from December to April (Fig. 5). Mean age at entry increased linearly from December to March and then decreased in April. Thus, larvae spawned at the beginning or end of the season spent relatively less time in the offshore environment than did larvae spawned in the middle of the season. Length followed a similar trend, except during January and early February when it remained about constant, indicating a declining rate of growth. As determined from seven samples collected at Pivers Island (Fig. 5) and one at Beaufort Inlet (19 March 1980), spot entering the estuary averaged 59 d-old (range 40-80).

In general, larvae entering the estuary together had similar spawning dates. As a rule, 50% of the fish in any Pivers Island sample had been spawned within a period of 5 d and all had been spawned within a period of 14 d (Fig. 2). The one exception was the last sample from Pivers Island in which several larvae were more than a month older than the majority of fish. We infer from the generally small variation in age of fish within a sample that a continuum of cohorts moved past Pivers Island enroute to the upstream parts of the estuary and that early juveniles entered the lower estuary segregated by age.

Growth Estimates

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture data for 1978-79 and 1979-80 (Fig. 6). Variance about the estimated growth curve was assumed to represent genetic differences in growth potential and the effects of differing environmental conditions over the year (Pennington 1979). To stabilize the variance of length over the observed age interval, we used the log-transformed version of the Gompertz growth equation:

$$\ln [L_{(t)}] = \ln [L_{(0)}] + \frac{A_{(0)}}{\alpha} [1 - e^{-\alpha t}] \qquad (2)$$

where $L_{(t)}$ = length at time t,
$L_{(0)}$ = length at $t = 0$,
$A_{(0)}$ = specific growth rate at $t = 0$,
α = rate of exponential decay of the specific growth rate.

The time origin ($t = 0$) was selected as hatching time (day 0) and values for $L_{(0)}$, $A_{(0)}$, and α were obtained by nonlinear regression. Age accounted for 96% of the variation in length for one year class (1978-79) and 91% of the variance in length for the other (1979-80) in the log-transformed models. We estimated that spot grew from about 1.6 mm SL at hatching to 17-19 mm at 90 d. The predicted size at hatching agrees well with laboratory observations of Powell and Gordy (1980). Population growth
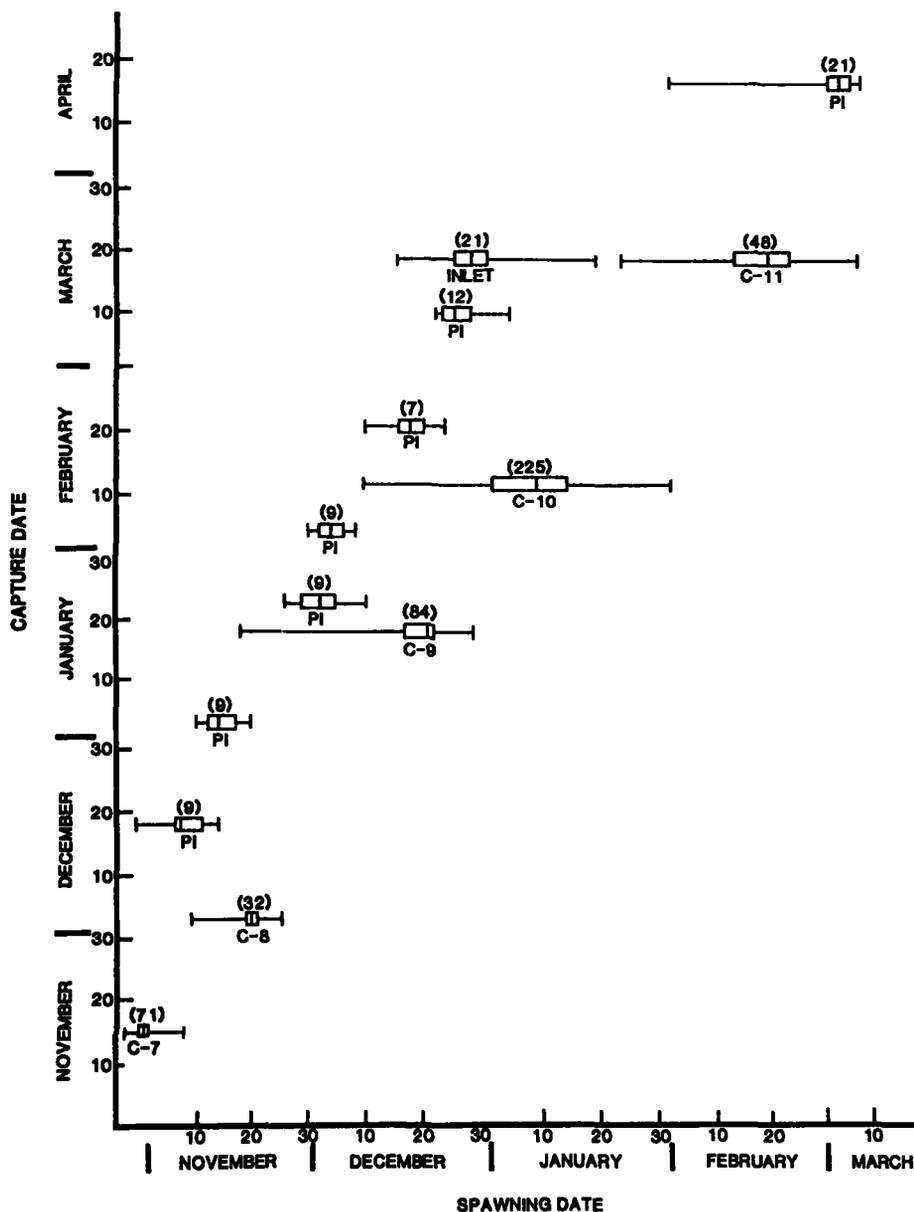
FIGURE 2.—Schematic plots of the spawning times of larval spot caught in the ocean (cruises 7-11 of RV *John de Wolf II*) and late-larvae/early-juvenile spot caught in the Newport River estuary at Pivers Island, NC. In each distribution, the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points.

curves were not significantly different between years [Hotelling's T^2 test of $A_{(0)}$, α, and $L_{(0)}$; Bernard (1981) as modified by Hoenig and Hanumara (1983)]. Age-specific growth rates for both years declined from ≅5%/d at age 10 d to <1%/d at age 90 d.

To determine differences in growth rates for two

groups of larvae of different ages but from the same cohort, we back-calculated lengths at 5-d intervals up to 25 d for 10 larvae caught at stations 15 and 16 on 15-16 January 1980 and for 10 larvae caught at Beaufort Inlet on 19 March 1980 (Table 2). Although the estimated mean spawning date for
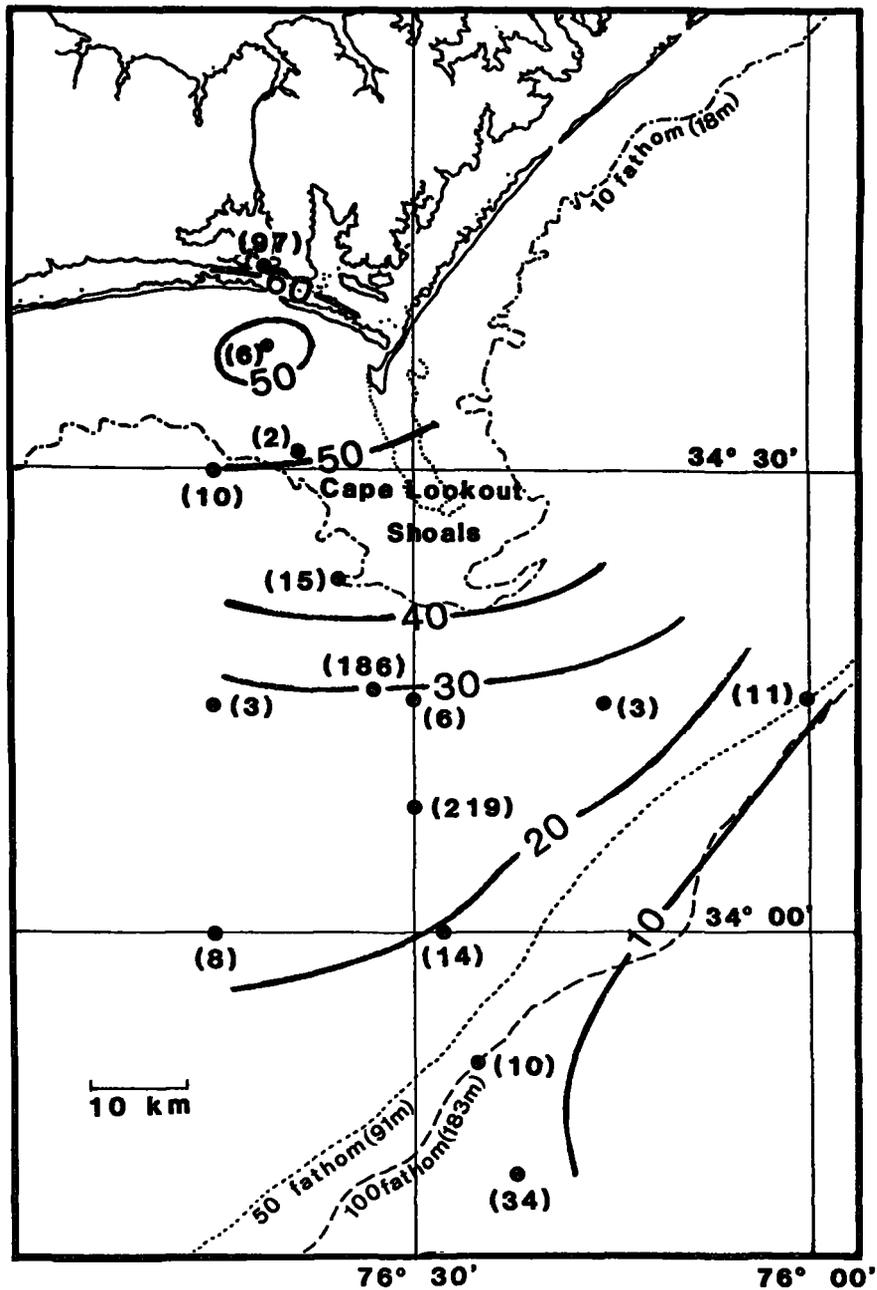
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FIGURE 3.—Contour plots of the mean ages of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the numbers of fish aged.
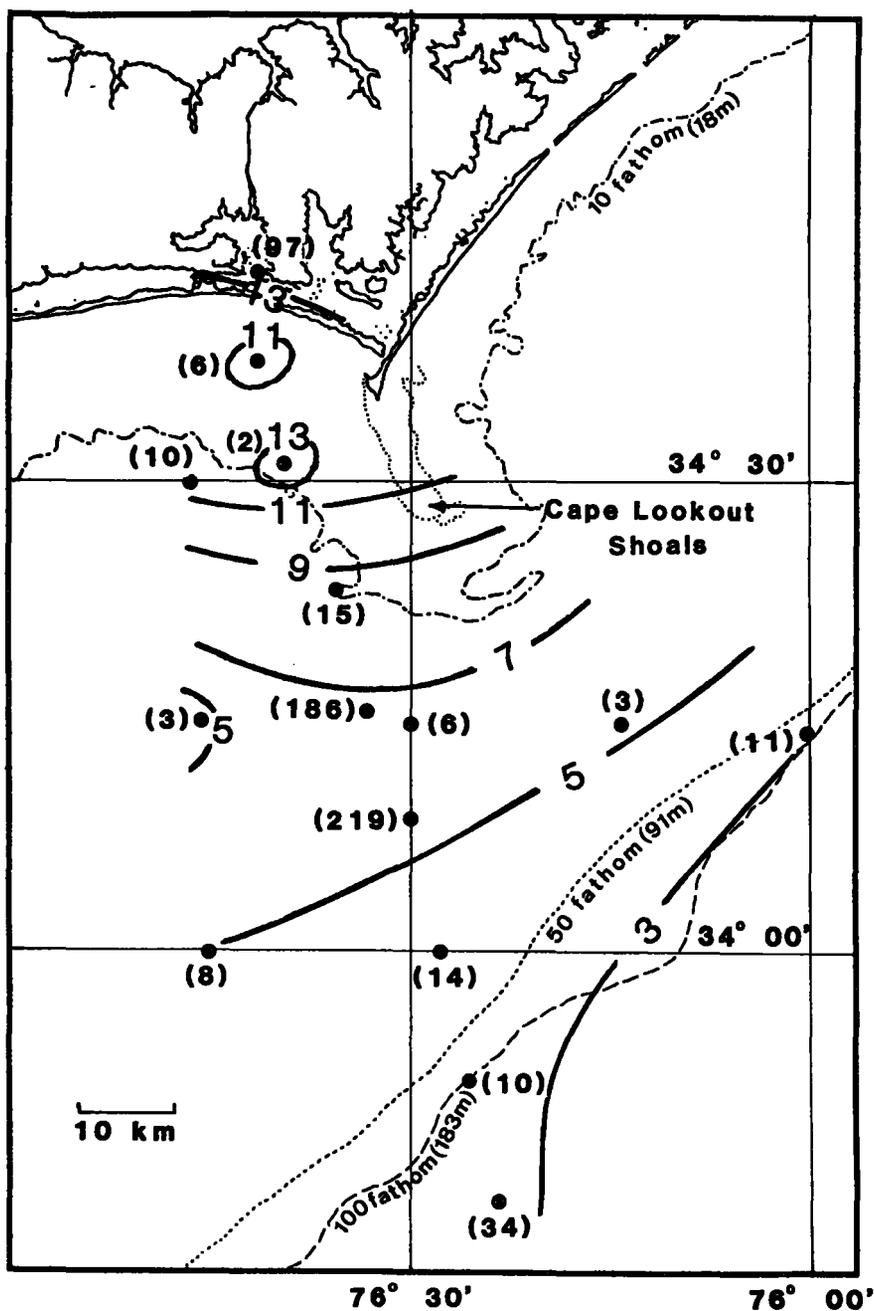
FIGURE 4.—Contour plots of the mean standard length of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the number of fish collected and measured.
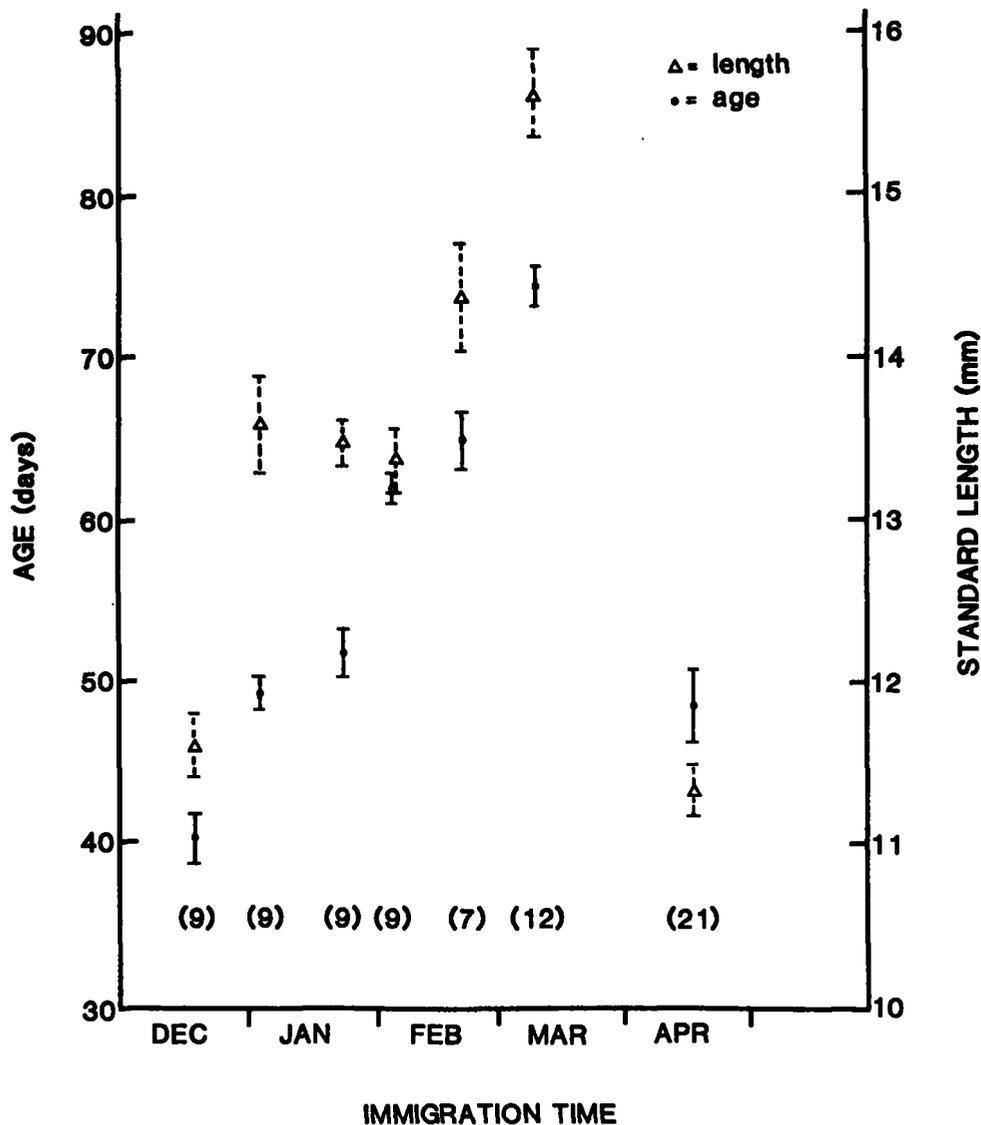
FIGURE 5.—Age (mean ±1 standard error) and standard length (mean ±1 standard error) of late-larval spot entering the Newport River estuary in North Carolina, December 1979-April 1980. The numbers of fish measured and aged at each sampling date are in parentheses.

both groups was identical (22 December 1979), the variance about the mean was greater for Inlet-caught fish. Consequently, back-calculated lengths also were more variable for Inlet-caught fish (F-test, $P < 0.05$), but on the average they appeared to be larger at every age (t-test corrected for unequal variance, $P < 0.05$).

Significant differences were found for the weight-length relation (Fig. 7) of laboratory-reared larvae

$\leqslant 6$ mm and those >6 mm (ANCOVA, $P < 0.001$). We selected 6 mm as the dividing point because basic changes in body form had been observed to occur at around 6 mm (Powell and Gordy 1980). The length exponent for spot $\leqslant 6$ mm SL (4.201) was close to the mean value (4.152) reported by Laurence (1979) for larvae of seven marine fishes, while larvae > 6 mm (3.282) approached isometric growth (Ricker 1975).
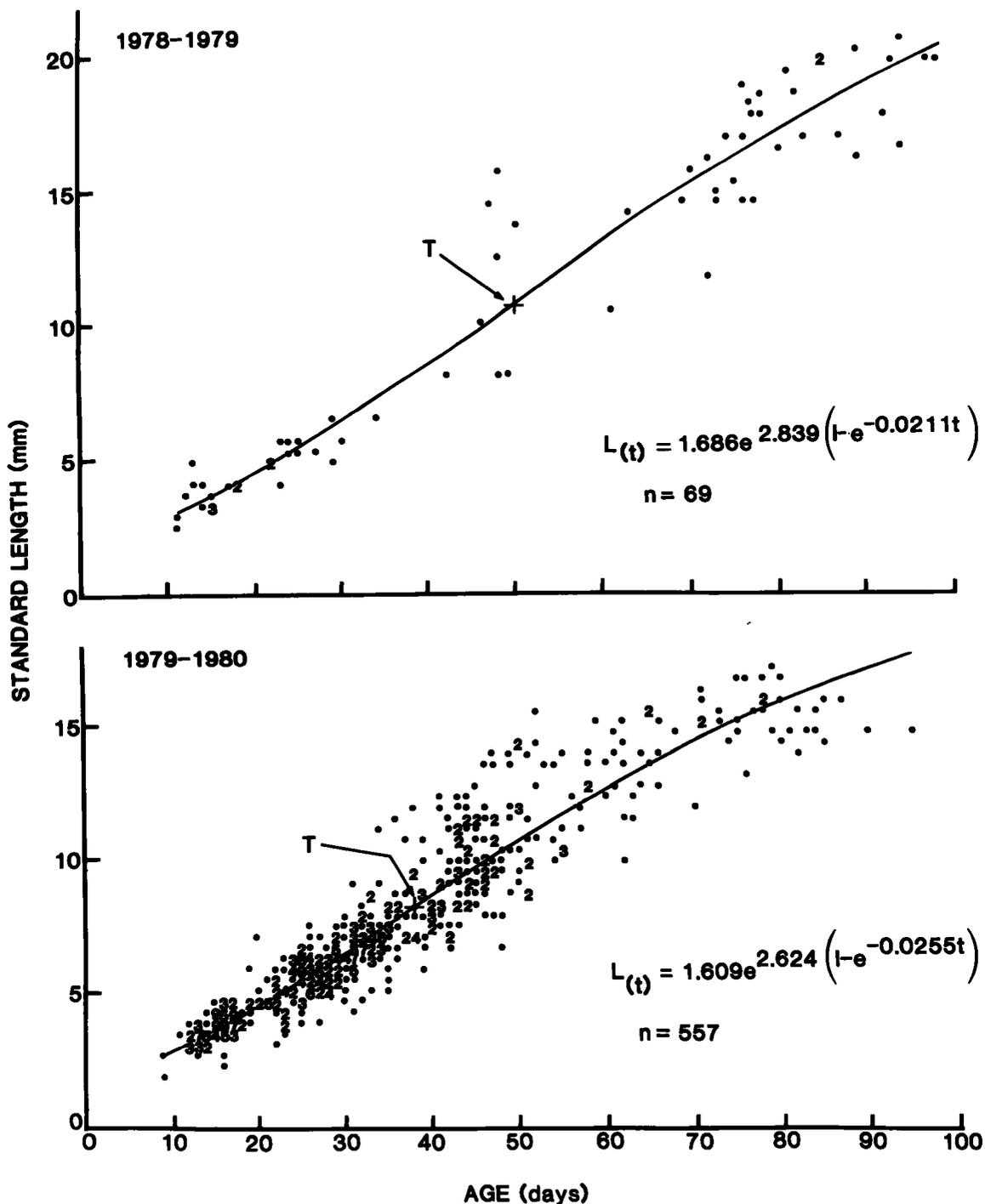
FIGURE 6.—Growth of larval and early-juvenile spot collected from oceanic and estuarine waters of North Carolina in the fall-winter, 1978-79 and 1979-80. The Laird-Gompertz growth model was used to describe the data. Estimates of the parameters were obtained by fitting the log-transformed version of the model to the data. "T" is the point of maximum absolute growth (inflection point) in the growth curve.

TABLE 2.—Mean back-calculated standard length of 10 spot from each of two collections of the same cohort (average spawning date 22 December 1979) taken about 2 mo apart in 1980.

| Age (d) | 15-16 January | | | 19 March | | |
| | Stations 15-16[1] | | | Station 19 (Beaufort Inlet)[2] | | |
	SL (mm)	SD	N	SL (mm)	SD	N
5	3.1	0.13	10	3.5	0.39	10
10	3.7	0.15	10	4.4	0.49	10
15	4.6	0.32	10	5.1	0.62	10
20	5.1	0.34	7	6.0	0.67	10
25	6.0	0.35	2	7.0	0.80	10

[1]Larval mean age, 23 d; mean size, 5.7 mm
[2]Larval mean age, 83 d; mean size, 15.0 mm

DISCUSSION

Although spot is a winter spawner, it spawns in relatively warm water. Very young larval spot (≤15 d) occurred only in water above 19.3°C, an observation corroborated by experimental evidence indicating that spot spawn only between 17.5° and 25°C (Hettler and Powell 1981). In late fall and early winter off North Carolina, such warm temperatures are found only on the outer continental shelf near the Gulf Stream. Newly ripe adults probably emigrate in the fall of the year from the cooling waters of bays and sounds in Virginia (Hildebrand and Schroeder 1928), North Carolina (Roelofs 1951), and South Carolina (Dawson 1958) to spawn in such warm waters. Hildebrand and Schroeder (1928) and Dawson (1958) also suggested that spot spawn along the outer continental shelf.

Warm coastal waters in the fall and the influence of warm Gulf Stream waters later in the season may provide a suitable spawning temperature regime over a long period. The extended (4.5 mo) spawning season of spot is typical of the general pattern for Atlantic coast sciaenids (Powles 1981). The spawning season of spot in North Carolina in 1979-80 was similar to that found by Hildebrand and Cable (1930) in North Carolina and by Dawson (1958) in South Carolina. Because most of the larvae caught off North Carolina were spawned in December and January, we conclude that these are the months of peak spawning. This conclusion is supported by the observation that peak estuarine immigration occurs in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974) for fish we estimate to have been about 2 mo-old. Hildebrand and Cable (1930) and Lewis and Judy (1983) also inferred, from length-frequency information, that peak spawning occurs in December and January.

The trend of decreasing larval age and size (Figs.

2, 3) with distance from shore supports the idea that spot spend virtually their entire larval period in the ocean. Berrien et al. (1978) and Lewis and Judy (1983) also noted an inverse trend of size with distance from shore in the same area to 79 km offshore. A similar trend may exist in the Gulf of Mexico where Fruge (1977) found small larval spot to be most abundant 60-80 km off the Louisiana coast. By the time larvae have been transported to shore and enter estuarine nursery areas, they have reached the late larval or early juvenile stage.

Although the mechanism is unclear by which larval spot from 74 to 93 km offshore arrive at the estuary in about 60 d, their initial onshore movement is probably a passive transport by water currents in Onslow Bay. A consistent counterclockwise eddy (Stefansson et al. 1971) and a strong indication of bottom drift in a northerly direction on the outer and mid-continental shelf and directly to the coast inshore during January-April (Bumpus 1973) could aid in the transport of larvae. Nelson et al. (1977) considered that zonal Ekman transport was a significant mechanism for movement of larval Atlantic menhaden, *Brevoortia tyrannus*, from offshore spawning grounds to inshore nursery grounds in the same study area at about the same season of year. Data from recent years, however, does not lend support for this hypothesis (Schaaf[4]). A recent analysis by Yoder (1983) suggested that mean Ekman transport does not favor onshore flow in surface waters during winter off the southeastern United States. Rather, cross-shelf transport of larval fishes may depend on highly variable, short-term meteorological events which reverse the mean surface flow. Variations in transport rates of larvae in the ocean as well as spawning at variable distances from shore may be responsible for the seasonal differences in age and length at immigration (Fig. 5). In addition, factors affecting growth, such as temperature and the distribution of food organisms, interact with the physical factors of transport to produce the temporal pattern of age and length observed in a given year.

Young spot undergo several environmentally related changes in growth during their larval and juvenile stages. Growth in length of larval spot is rapid (initially approaching 7%/d) and coincides with the winter peak of plankton productivity in the relatively warm water of the outer continental shelf (Turner et al. 1979; Turner 1981; Yoder et al. 1981;
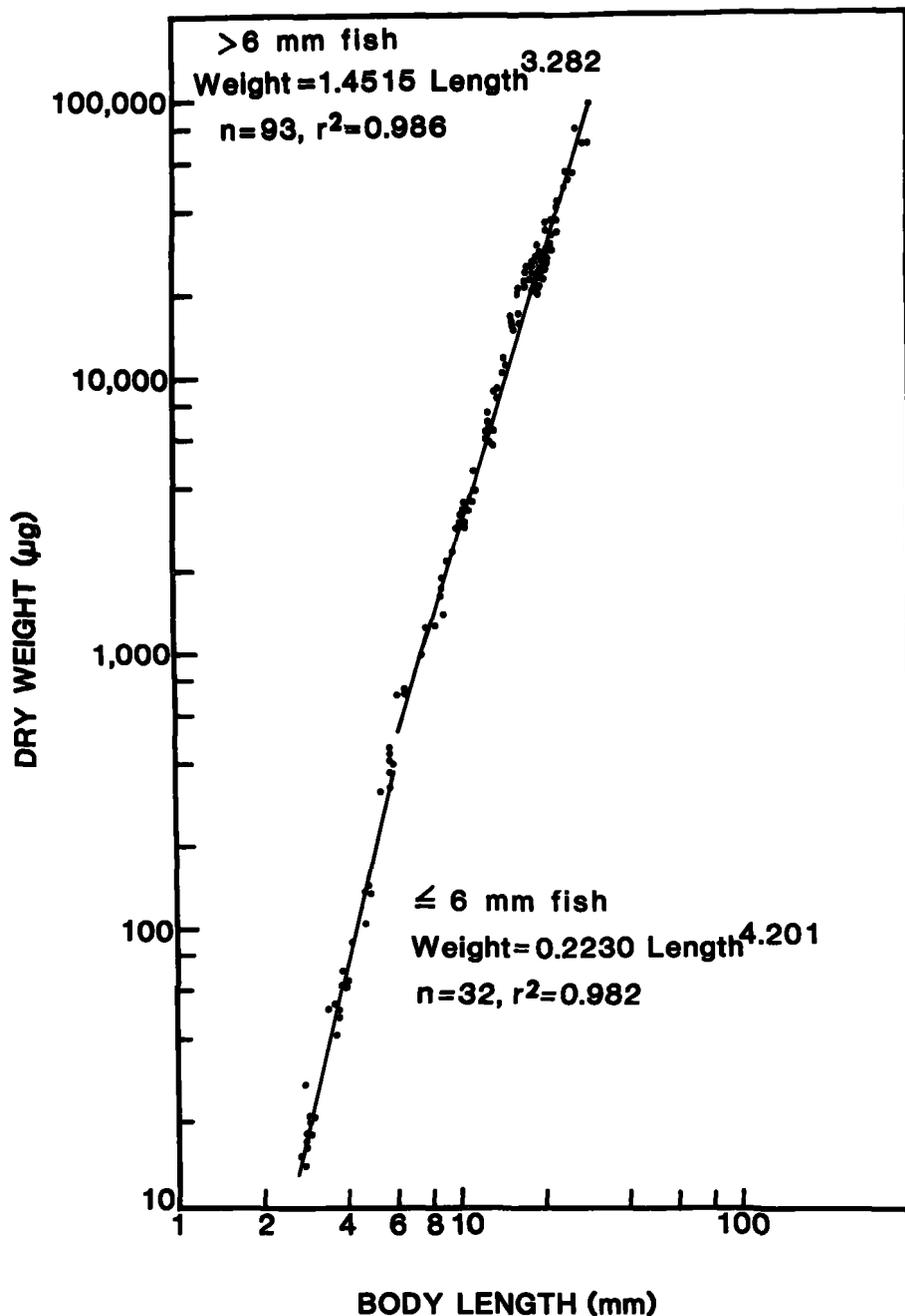
FIGURE 7.—Relationships between dry weight and standard length of spot for length classes ≤6 mm and >6 mm. Fish were from laboratory spawned and reared stocks.

Yoder et al. 1983). By the time larvae enter the cooler (often <10°C) coastal and estuarine waters, growth rate has slowed considerably (<1.5%/d). The asymptote of 22.2 mm SL (Fig. 6, 1979-80 data) estimated by our growth model corresponds closely to the size of juvenile spot collected early in their estuarine residency (Weinstein and Walters 1981). Increase in length of newly immigrated spot is relatively slow (≅0.5%/d from December to March, estimated from figure 3 of Weinstein and Walters 1981), and it is

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not until after the usual peak in plankton abundance (Thayer et al. 1974) and increases in water temperature that growth rates accelerate and persist at a high level through the summer ($\cong$1.0%/d from April to August, estimated from figure 3 of Weinstein and Walters 1981).

Within the same cohort, older fish had statistically larger back-calculated sizes at each age than did younger fish (Table 2). One explanation is that size-selective mortality (e.g., predation, Bailey 1984) favors survival of faster growing larvae and that the apparent growth rate depends on the size (and age) of larvae on which it is calculated. Alternatively, the two groups may have been spawned in different locations and experienced different environmental conditions that could affect growth.

ACKNOWLEDGMENTS

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