Spawning time, growth, and recruitment of larval spot *Leiostomus xanthurus* into a North Carolina estuary

César Flores-Coto
Instituto de Ciencias del Mar y Limnología
Universidad Nacional Autónoma de México
México 04510 D.F.

Stanley M. Warlen
Beaufort Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Beaufort, North Carolina 28516-9722

Abstract.—Larval spot *Leiostomus xanthurus* were sampled weekly as they recruited to the Newport River estuary near Beaufort Inlet, North Carolina to determine their density, and age and size composition. Density data and otolith age distributions were used to calculate the relative contribution of birthweek cohorts to the seasonal recruitment of spot larvae. The protracted 1987–88 spawning season extended from mid-October to mid-March, with 90% in a 2-month period beginning mid-November. Larvae were recruited to the estuary over 5 months at a mean age of 82 d and mean standard length of 17.2 mm. Smaller, younger larvae generally immigrated to the estuary early (December–January) and late (late April), while larger, older larvae immigrated during the interim peak recruitment period (February to mid-April). In any recruitment week, larvae were from 2–10 birthweek cohorts, but recruitment was strongly influenced by the number of larvae of the dominant cohorts.

Larval spot were also sampled in the ocean between Cape Fear and Oregon Inlet off North Carolina to determine their distribution, abundance, and size and age composition. Age and size of larvae were inversely related to distance from shore. Highest densities of larvae were generally found outside the 30 m isobath. Distribution data supported the hypothesis that spot spawned south of Cape Hatteras on the outer continental shelf contribute to recruitment in Chesapeake Bay. A Kolmogorov-Smirnov test did not demonstrate a significant difference between birthdate distributions for ocean and estuarine larvae. This implied that mortality was not age-specific for larvae collected at different times. A Laird-Gompertz growth equation fit to age and size data for larvae collected in the ocean and estuary predicted that they grew from 1.2 mm at hatching to 16.1 mm in 80 d.

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Spot *Leiostomus xanthurus* is distributed from the Gulf of Maine to the Bay of Campeche, Mexico. The area of greatest abundance and the center of the commercial fishery on the Atlantic Coast extends from Chesapeake Bay to South Carolina (Johnson 1978, Mercer 1989). Spot spawn offshore during the fall and winter, and their larvae immigrate to nursery areas in estuaries (Hildebrand & Cable 1930, Fahay 1975, Chao & Musick 1977, Warlen & Chester 1985). Historically, spot have been among the most important commercial and recreational fishes in North Carolina (Miller et al. 1984, Mercer 1989). Hettler & Chester (1990), Warlen & Burke (1990), and Warlen (unpubl. data) have shown that larval spot are consistently the most abundant of the fall/winter spawning species whose larvae are found in Beaufort Inlet, North Carolina. The abundance of this species is probably a function of the relatively high densities of larvae that recruit into estuaries over an extended period of several months. Recruitment is defined as the movement (immigration) of spot larvae from the ocean into the lower estuary.

There have been studies on the early life history of spot regarding development (Fruge 1977, Fruge & Truesdale 1978, Powell & Gordy 1980), feeding (Govoni et al. 1983, 1985), distribution and abundance (Lewis & Judy 1983, Warlen & Chester 1985, Sogard et al. 1987), metabolic responses to cold (Hoss et al. 1988), and age and growth (Beckman & Dean 1984, Warlen & Chester 1985, Siegfried & Weinstein 1989). Although Beckman & Dean (1984) determined the relationship between spawning and part of the estuarine recruitment period, no studies have estimated the relative contribution of age (birthweek) cohorts to the number of estuarine recruits, or the seasonal changes in relative abundance of larvae that survive to reach the estuary. Such studies require systematic, quantitative sampling of larvae newly recruited to the estuary in order to estimate within-season relative abundances. Also, they require age determination of larvae throughout recruitment.

The density of larvae recruited from each birthweek gives an estimate of the spawning-date distribution of spot which can be compared with similar distributions determined from either offshore egg production (although these are difficult to obtain) or younger larvae caught off-

shore. If cohort survival is similar, the birthdate distributions would not be expected to differ. Age of larvae recruited to the estuary is a useful measure of the transport period from offshore spawning to recruitment into the estuary. Transport time may be expected to vary seasonally as a function of transport rate and spawning distance from shore (transport distance).

The objectives of this study were to (1) determine age and size of spot larvae immigrating into the Newport River estuary through Beaufort Inlet, (2) estimate the spawning season (back-calculated from ages of recruited larvae) and the relative contribution of birthweek cohorts to the total larval spot recruitment, (3) relate the density, age and size distributions, and back-calculated birthweeks of spot larvae collected off the North Carolina coast to the same cohorts collected later just inside the mouth of the estuary, and (4) estimate the growth rate of larvae.

Methods

Spot larvae used in this study were collected in both marine and estuarine areas. A 1×2 m neuston net frame with a 945 μm mesh net (Hettler 1979) was used to collect larvae (some specimens were early juveniles) at a station adjacent to Pivers Island in the lower Newport River estuary about 2 km inside Beaufort Inlet (Fig. 1). The fixed net was fished, with the top of the frame just under the water surface, from a bridge platform in the center of the channel. A flowmeter (General Oceanics model 2030) was attached to the mouth of the net to estimate the amount of water sampled. Four consecutive sets were made during nighttime hours at mid-flood tide, when current was the strongest. Because of the expected seasonal variation in larval fish densities, sets were 2–8 min long ($\bar{x}$=5 min) and sampled 58.4–443.0 m^3 of water. Samples were collected weekly from 10 November 1987 to 4 May 1988. The mean of data from all sets on a given night was used as the estimate of density of spot larvae.

Sampling for spot larvae was also conducted off the North Carolina coast from Cape Fear to Oregon Inlet (Fig.1) during two phases (12–13 January and 2–5 February) of cruise 172 of NOAA ship *Oregon II* in 1988. Sampling stations were arranged along a transect from Beaufort Inlet approximately south-southeast to the 400 m isobath, then along the Gulf Stream to about 36°N latitude, and finally inshore along a transect toward Oregon Inlet (Fig. 1). Additional stations along bands parallel to the coast were added in February in Onslow Bay. Samples at a station were obtained from either a day or night oblique plankton tow using a 60 cm Bongo frame fitted with 333 and 505 μm mesh nets and rigged with flowmeters. The amount of water filtered on a tow was depth-dependent and varied between 72.4 and 476.8 m^3. Ichthyoplankton samples from both estuarine and marine areas were preserved in 95% ethanol. Spot larvae from each sample were counted and density estimated as larvae/100 m^3.

Larval spot were randomly sampled from each estuarine collection for aging. If the total number of larvae in a collection was ≤20, then all fish up to a maximum of 10 were used. If there were more than 20 specimens in a collection, then 10–40 larvae were taken for the sample depending upon the coefficient of variation (CV) of the standard length (SL) of 20 fish. If CV was 0.10–0.12, a subsample of 20 fish was taken. If CV was >0.12, the subsample was 30 fish, except when more than 1000 fish were caught, at which time 40 fish were used. Larvae were measured to the nearest 0.1 mm SL. Age was determined according to the method of Warlen & Chester (1985). The estimated age of a larva was the observed number of sagittal growth increments from one reading plus the estimated number of days from hatching to first increment formation (5 d). The precision in duplicate readings of otoliths from 25 larvae (range 32–86 d) was estimated from the differences in paired readings. The mean (±SD) difference was 1.52±1.26 growth increments, and the range was 0–4 increments. The birthdate (= spawning date) of each larva was back-calculated by subtracting its estimated age from the date of capture. Larvae spawned in a given calendar week were considered in the same calendar birthweek cohort. The spawning period of spot was estimated from the back-calculated birthdates of larvae recruited to the estuary over all seasons. For each weekly collection, the percentage of larvae from each birthweek cohort was determined. Each percentage was multiplied by the corresponding weekly density total (larvae/100 m^3) to give the density of larvae from each birthweek cohort. The densities for each birthweek cohort were summed over all collections and their percentage contribution to the total density (1540 larvae/100 m^3) for all birthweek cohorts was calculated. The Laird version (Laird et al. 1965) of the Gompertz growth equation was used to describe growth of spot larvae from the combined marine and estuarine collections. To stabilize the variance of length over the observed age interval, we used the log-transformed version of the Gompertz growth equation.

Results

Estuarine abundance and age/size distribution of larvae

Abundance of larvae A total of 9760 spot larvae was collected at Pivers Island between 2 December 1987

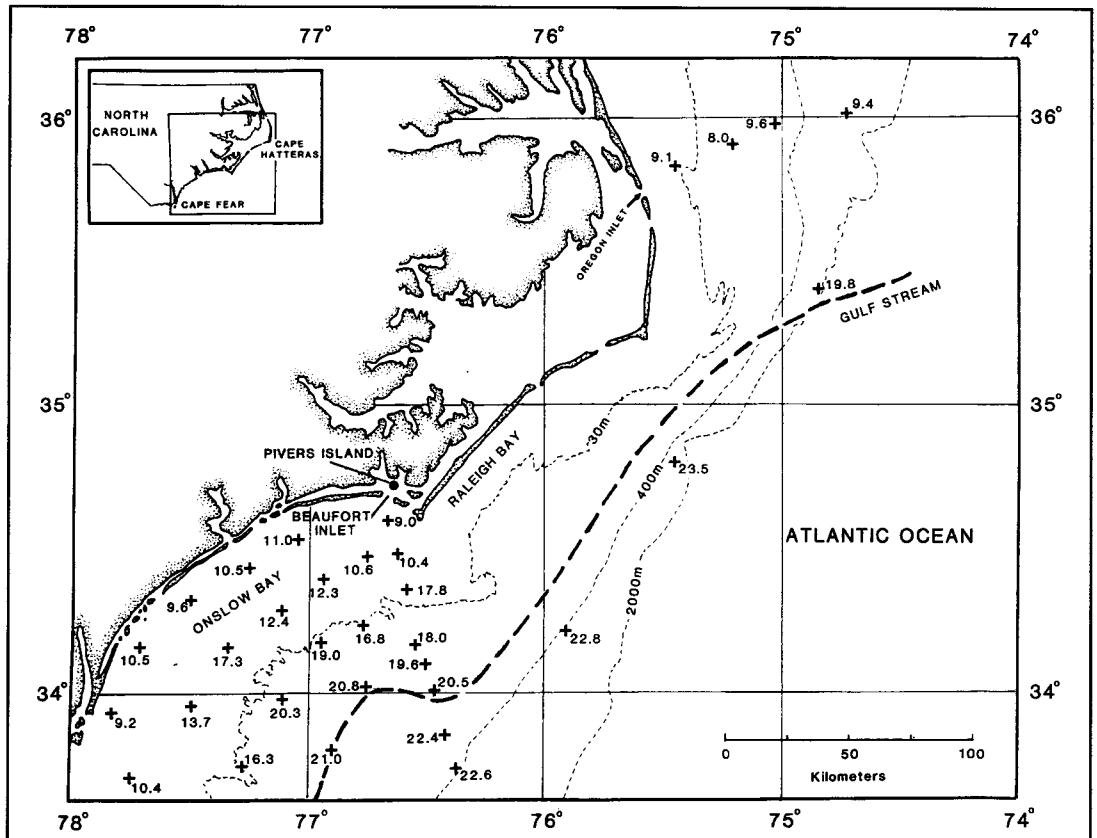

Figure 1

Location of sampling sites for spot *Leiostomus xanthurus* larvae at Pivers Island near Beaufort Inlet and ocean stations ("+") off the North Carolina coast. Surface-water temperatures are indicated for February 1988 stations.

and 4 May 1988 (Fig. 2). The 4th of May was considered the virtual end of the recruitment period, since spot densities had declined to <2 larvae/100 m^3 over the last 2 weeks of sampling. The sum of the weekly mean larval densities over all collections (1540 larvae/100 m^3) was used as the basis for determining the percentage of recruited larvae from each birthweek cohort. Larval density gradually increased during the first 10 weeks of sampling, varying from 0 to 40 larvae/100m^3 ($\bar{x}$=14.6). Approximately 9% of the larval spot recruitment occurred during this period. The period of highest density ($\bar{x}$=138.3 larvae/100 m^3) occurred during 10 February–13 April, when 88% of the larvae were recruited to the estuary. During this 10-week period, there was wide variation in relative abundance with four clear peaks, the largest occurring on 23 March when 34% of all larvae were collected. During the last 3 weeks of sampling, larval density declined to very low levels ($\bar{x}$=3.7/100 m^3) and represented less than 3% of the total spot larvae collected. There was variation in the catch densities among net sets on any given sampling night. Excluding the first 4 weeks when no spot larvae were collected in 41% of the sets, the average nightly coefficient of variation was 65.3% (range 20.3–119.5%).

We assumed that larvae caught each week were newly recruited to the estuary and that they were in transit to upper reaches of the estuary past Pivers Island. These assumptions are supported by the generally small standard error in the age of larvae within each collection (Fig. 3). The small observed within-sample variation in age is probably due in part to mixing of age cohorts in the ocean prior to estuarine recruitment. Since larvae were not accumulating in the lower estuary, there was no increase in standard error of mean age over time. Also, in the week following each of the four peaks (Fig. 2) densities were relatively low, a pattern that did not suggest substantial carryover of fish from week to week.

Age and length of larvae The weekly mean age of spot larvae caught at Pivers Island fluctuated between

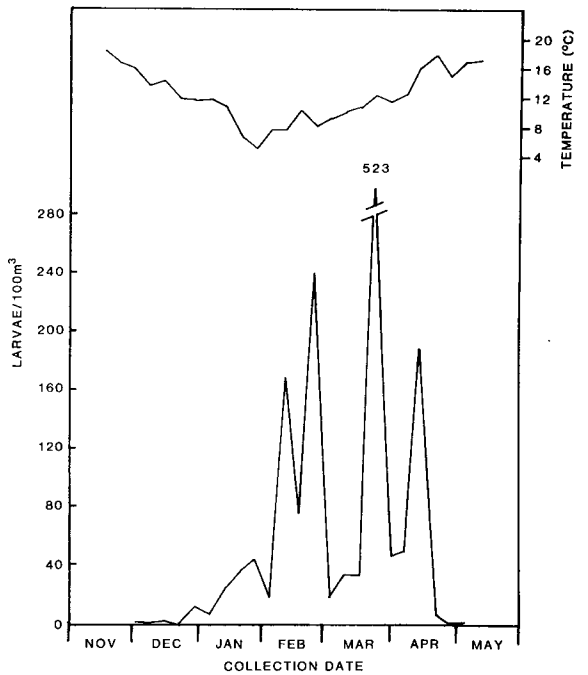

Figure 2
Weekly mean density (larvae/100 m³) of spot *Leiostomus xanthurus* larvae in collections at Pivers Island in the Newport River estuary, November 1987 to May 1988 (no larvae caught before 2 December). Mean weekly surface-water temperature calculated from hourly measurements at Pivers Island.

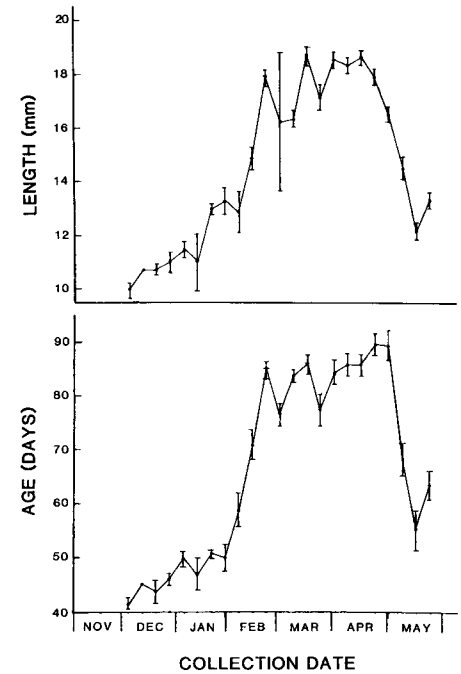

Figure 3
Mean standard length (mm±1SE) and age (d±1SE) of spot *Leiostomus xanthurus* larvae collected weekly, November 1987 to May 1988, at Pivers Island in the Newport River estuary (no larvae caught before 2 December).

37 and 108 d, ($\bar{x}$=82.4 d); weekly mean SL varied from 9.2 to 22.2 mm ($\bar{x}$=17.2 mm). The weekly mean age and SL of spot larvae (Fig. 3) increased from the beginning of the recruitment period, when the youngest and smallest larvae were caught, to the beginning of the period of peak recruitment density (10 February). Thereafter, average values remained high, only decreasing during the last 3 weeks. The age and size distributions of all spot larvae recruited to the estuary (Fig. 4) indicated that 68% were between 75 and 95 d, and 80% were between 15.1 and 20.0 mmSL. The mean age (±SE) and SL (±SE) of larvae corresponding to the three recruitment periods of different densities were 50.4 (±2.7), 84.6 (±1.4), and 62.6 d (±3.8), and 11.8 (±0.49), 17.7(±0.31), and 13.4 mm (±0.69).

Spawning time Spawning, which was continuous over a 5-month period, began near mid-October and ended about mid-March (Fig. 5). Over 99% of spawning occurred from 1 November to 24 January (22 weeks). Only about 1% was contributed by 9 weekly cohorts: 2 before and 7 after the main spawning period. Cohorts from 22 November to 10 January contributed >80% of total larvae (Fig. 5). The midpoint in spawning was the week of 20 December.

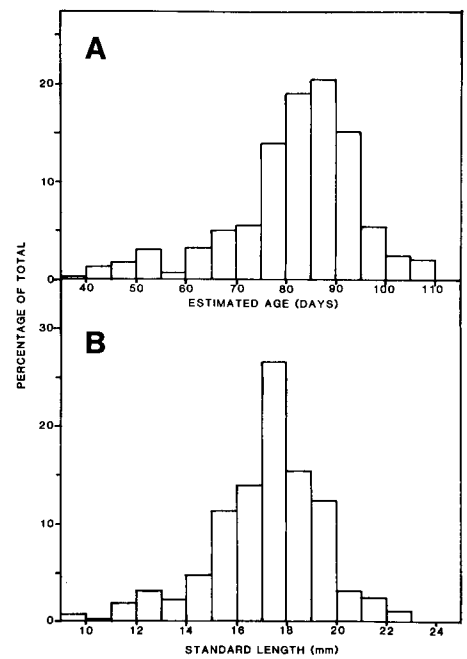

Figure 4
Percentage distribution of larval spot *Leiostomus xanthurus* recruited to the Newport River estuary, November 1987 to May 1988, by **(A)** estimated age (5d intervals) and **(B)** standard length (1 mm intervals).

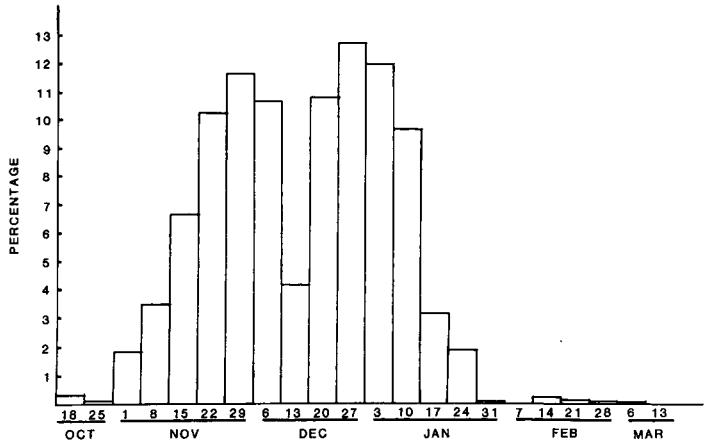

Figure 5

Percentage distribution of the number of larval spot *Leiostomus xanthurus* of back-calculated birthweeks recruited to the Newport River estuary, November 1987 to May 1988.

Age and length of birthweek cohorts Larvae from the beginning and end of the spawning period reached the estuary at younger mean ages than those from the middle period (Fig. 3). Larvae from birthweek cohorts were recruited to the estuary over periods ranging from 2 to 10 weeks, with an average of 7 weeks for the main spawning period (Table 1). In all but four cohorts (25 October, 22 November, 6 December, and 3 January), at least 50% of the larvae from the cohort reached the estuary during a single week (Table 1).

The SL of larvae reaching the estuary (Table 2) follows a similar pattern to age. Except in one instance (3 February), the first two and the last five cohorts to reach the estuary had a mean SL <13.9 mm. In the middle period, the weekly mean SL of larvae was generally larger. The difference between the smallest and largest mean SL of larvae of any one birthweek cohort throughout the recruitment period varied from 0.3 to 11.7 mm. This was generally related to the total time during which a cohort recruited to the estuary.

Abundance of birthweek cohorts Several birthweek cohorts contributed substantially to more than one of the recruitment peaks. Three cohorts (13, 20, 27 December) contributed at least 50% of their respective total recruits to the large influx of larvae that occurred on 23 March (Table 1). The high densities of larvae (Fig. 2, Table 1) captured on 10 and 24 February, 23 March, and 13 April were collections to which some birthweek cohorts contributed ≥50% of their total recruitment (e.g., 1 and 8 November cohorts to catch of 13 April).

Oceanic abundance and age/size distribution of larvae

Abundance of larvae The highest densities of spot larvae collected offshore during January and February generally occurred in waters ≥30 m (Fig. 6). Densities there ranged from 24 to 68 larvae/100 m^3, but diminished toward the coast and further offshore toward the shelf break. In areas within 40 km of the coast at depths <30 m, densities were <5 larvae/100 m^3. Except for two larvae collected off Beaufort Inlet in January (Fig. 6A), no larvae were collected within 10 km of the coast. Larval densities in the estuary at Pivers Island were always higher than at any oceanic station <30 m deep within 40 km of the coast.

Spot larvae were collected at two of seven stations sampled east and north of Onslow Bay during January (Fig. 6A). In February, spot larvae were collected at all but one of these stations (Fig. 6B). Densities were relatively low except at the station nearest Onslow Bay.

Age and length distribution of larvae Ages of 351 spot larvae caught during oceanic sampling ranged from 9 to 69 d. Youngest larvae occurred farthest offshore, over the outer continental shelf and within the Gulf Stream (Fig. 7A,B). Age of larvae varied inversely with distance from shore along the Beaufort Inlet transect in January and February and the Oregon Inlet transect in February (Table 3, Fig. 7A,B). The mean age of larvae in Onslow Bay during February seems to increase toward shore from a dispersion center on the outer continental shelf south of Beaufort Inlet. Older larvae radiate to the north and west in Onslow Bay (Fig. 7B). Larvae in the transect across the continental shelf off Oregon Inlet (Fig. 7B) may have a general spawning area in common with larvae collected in Onslow Bay.

The length of larvae also varied inversely with distance from shore (Table 3, Fig. 7C,D). Smallest larvae were found on the outer continental shelf and over the continental shelf break. The mean size of larvae was 3.4 mmSL (range 2.1–10.1 mm) in January and 6.2 mmSL (range 2.5–12.7 mm) in February.

Spawning time Spot larvae collected off North Carolina were spawned over the period 8 November to 17 January (Fig. 8). As many as six cohorts were found in any one sample and the overall mean number of cohorts per sample was three. In 19 of 33 stations, ≥50% of the larvae were from one cohort, and in six stations ≥50% were from two consecutive cohorts. The remain-

Table 1

Relative abundance of back-calculated birthweek cohorts of larval spot *Leiostomus xanthurus* (larvae/100 m^3) recruited to the Newport River estuary, 2 December 1987 to 4 May 1988.

	Birthweek cohorts (week beginning)																						
	October		November					December				January					February				March		
Capture date	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	21	28	6	13	Total
Dec. 2	0.48	0.24																					0.72
9	0.07																						0.07
17		0.64	0.96																				1.60
22			0.33	0.08																			0.41
30				9.81	2.45																		12.26
Jan. 6					5.29	2.64																	7.93
12					14.64	8.79																	23.43
20					4.45	4.45	13.34	13.34															35.58
27						26.69	8.90	8.90															44.49
Feb. 3		0.78	1.56	2.34	2.34	5.46	3.90	2.34		0.78													19.50
10			25.72	41.16	51.45	46.30	5.14																169.77
17					9.99	16.65	26.64	16.65	3.33	3.33													76.59
24					12.97	45.37	116.67	51.85	12.97														239.83
Mar. 3						1.50	5.23	8.22	0.75	0.75	0.75												17.20
9								6.50	6.50	9.74	9.74		3.25										35.73
16								6.32	7.90	11.06	3.16	6.32											34.76
23								50.66	33.75	135.07	151.92	84.41	50.66	16.90									523.37
30										5.03	20.10	15.08		5.03									45.24
Apr. 6											10.95	25.59	14.63										51.17
13												54.05	81.08	27.03	27.03								189.19
20															2.12	0.71		3.53	1.41				7.77
27																		0.16	0.16	0.47	0.16	0.16	1.11
May 4															0.14				0.55	0.82	0.55	0.14	2.20
% of total	0.03	0.11	1.85	3.47	6.72	10.25	11.67	10.70	4.23	10.76	12.76	12.04	9.71	3.18	1.90	0.05	0.0	0.24	0.14	0.08	0.05	0.02	

Table 2

Weekly mean standard length (mm) of back-calculated birthweek cohorts of larval spot *Leiostomus xanthurus* recruited to the Newport River estuary, 2 December 1987 to 4 May 1988.

	Birthweek cohorts (week beginning)																					
	October		November					December				January					February				March	
Capture date	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	21	28	6	13
Dec. 2	10.3	9.2																				
9	10.7																					
17		10.8	10.7																			
22			11.3	10.0																		
30				11.6	11.3																	
Jan. 6					11.9	9.3																
12					13.4	12.5																
20					15.3	14.7	13.3	11.9														
27						13.8	13.0	10.0														
Feb. 3		17.3	16.7	17.1	16.6	15.0	14.1	11.5		9.6												
10			19.2	18.2	17.9	17.3	17.4															
17					16.6	16.8	17.3	15.8	13.2	13.6												
24					17.4	16.8	16.9	15.4	14.0													
Mar. 3						20.0	20.1	18.5	14.9	13.8	12.9											
9								19.6	17.3	17.6	16.3		13.7									
16								20.1	19.5	18.4	17.4	16.8										
23								21.2	20.6	19.2	18.2	17.0	17.0	15.3								
30										19.1	18.9	18.5		17.6								
Apr. 6											18.8	18.3	17.4									
13												16.2	16.4	17.8	17.7							
20															17.1	16.3		13.3	13.4			
27																		13.0	12.3	12.3	12.6	10.8
May 4															16.2				13.8	13.2	13.4	11.2

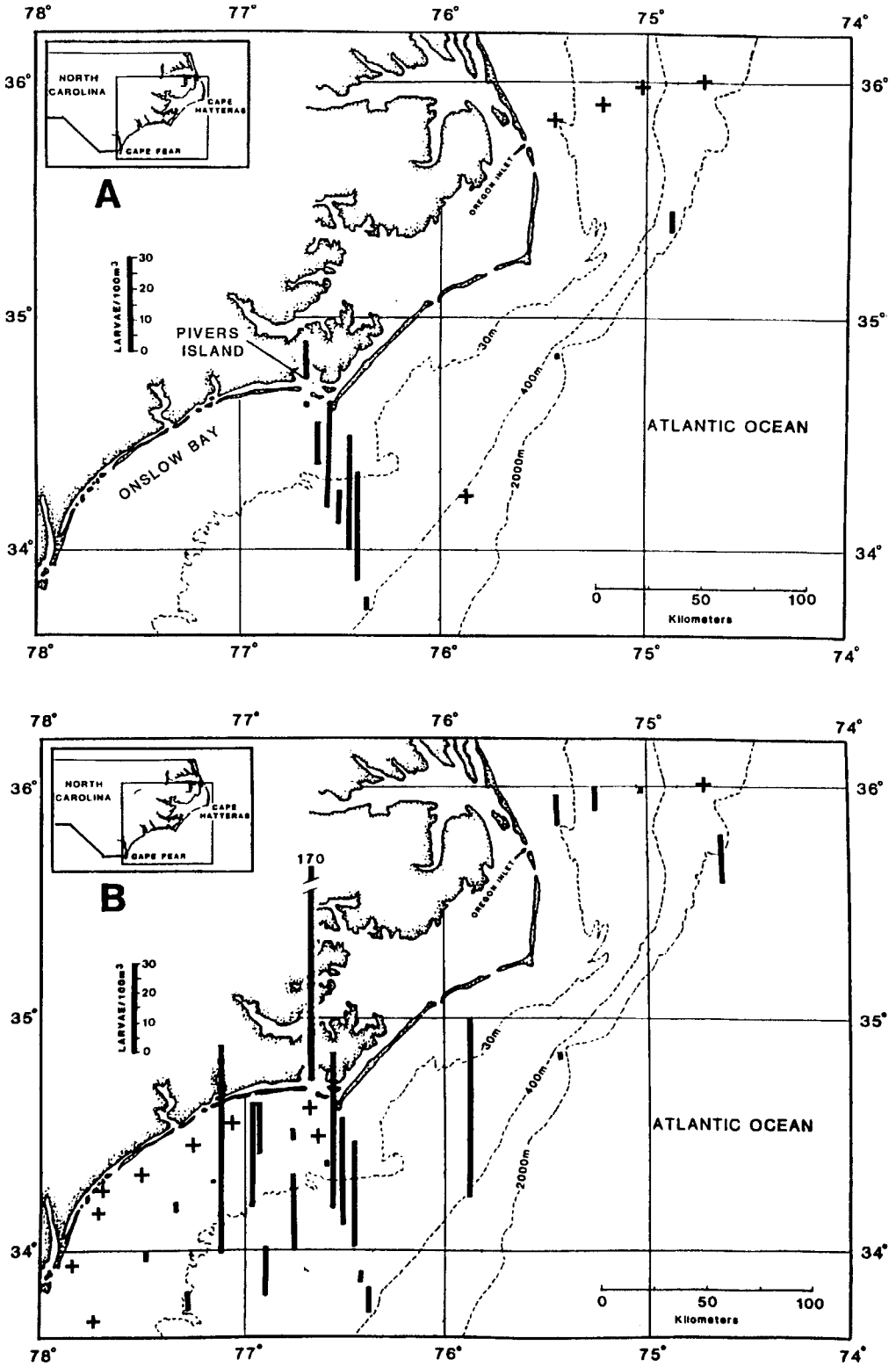

Figure 6

Density (larvae/100 m³) of spot *Leiostomus xanthurus* larvae collected in 1988 with bongo nets off the North Carolina coast during **(A)** 12–13 January, and **(B)** 2–5 February, and at Pivers Island with a neuston net. + indicates no larvae collected.

ing eight stations each had <5 larvae. There were eight different birthweek cohorts in January and nine in February. The principal cohorts in January were those of weeks beginning 20 and 27 December, which together contributed more than 88% of all larvae collected in the ocean (Fig. 8). These cohorts were the most important contributors to larvae recruited during the week of greatest abundance, 23 March (Table 1, Fig. 2). During February, larval cohorts were principally from birthweeks beginning 20 December–23 January. Larvae from these cohorts were caught later in the estuary and contributed heavily to the abundance peaks of 23 March and 13 April (Table 1).

A Kolmogorov-Smirnov two-sample test (Sokal & Rohlf 1981) was used to compare larval birthdate distributions for a 3-week spawning period, 13 December–2 January (Figs. 5&8), for larvae collected during January–February in the ocean and February–March in the estuary. There was no significant difference (max. diff. = 0.108, $P>0.05$) between birthdate distributions of 98 larvae collected in the ocean in January and 109 collected in February. There was also no significant difference between the pooled birthdate distribution data for larvae collected in the ocean in January and February (n=207) and for 134 larvae collected in the estuary at Pivers Island (max. diff. = 0.180, $P>0.05$).

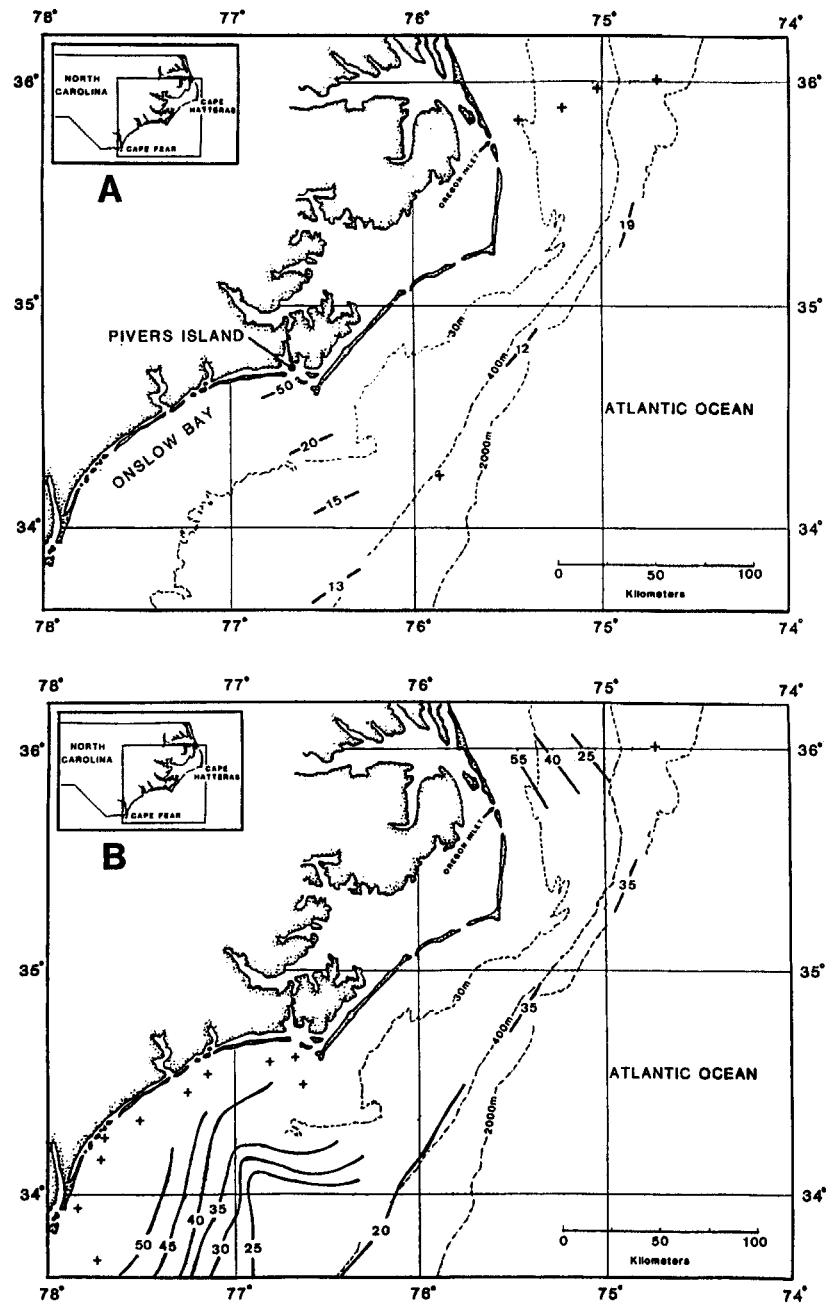

Figure 7

Contour plots of the mean age (d) on **(A)** 12–13 January, and **(B)** 2–5 February, and mean standard length (mm) on **(C)** 12–13 January and **(D)** 2–5 February, of spot *Leiostomus xanthurus* larvae collected off the North Carolina coast in 1988. + indicates no larvae collected.

Growth rate

The overall growth rate of larval spot was estimated from 312 estuarine and 351 oceanic specimens combined. Larvae ranged from 9 to 108 d and 2.1 to 22.2 mmSL (Fig. 9). From the Laird-Gompertz model (Fig. 9), we predicted that spot grew from 1.2 mm at hatching to 19.1 mm in 95 d, an overall average growth rate of 0.188 mm/d. The size at hatching, estimated from the Laird-Gompertz model (1.2 mmSL), was less

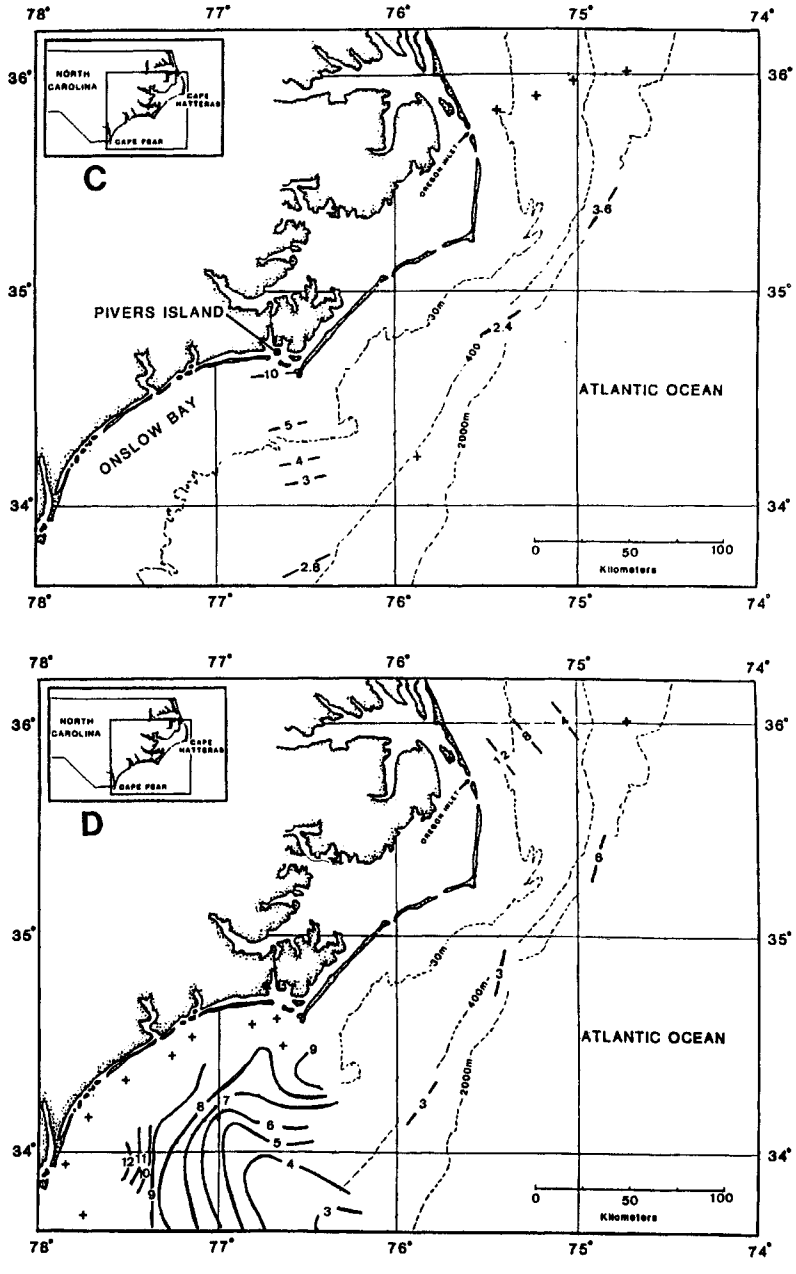

Figure 7 (continued)

than the 1.6–1.7 mmSL measured on laboratory-reared larvae by Powell & Gordy (1980) and estimated from wild specimens by Warlen & Chester (1985). In the log-transformed model (Fig. 9), age accounted for 98% of the variation in length. Age-specific growth rate declined from 5.8%/d at age 10 d to <0.7%/d at age 100 d. Maximum absolute growth rate occurred when larvae were 9.3 mmSL and 46 d old.

Within-season growth was compared for similar-age larvae collected at Pivers Island between early (early February) and late (early April) portions of the peak recruitment period and between early (early February) and post-peak recruitment periods (late April). The mean growth rate (0.195 mm/d) of 15 larvae (17.7±1.30 mmSL, 82.5±2.56 growth increments) collected 3 and 10 February (early peak) was not significantly different (t-test, P=0.09) from that (0.204 mm/d) of 15 larvae (18.2±0.98 mmSL, 81.9±3.19 growth increments) collected 6 and 13 April (late peak). However, the mean growth (0.214 mm/d) of 12 larvae (14.9±1.45 mmSL, 62.3±3.77 growth increments) collected on 3 February (early peak) was significantly different (t-test, P<0.01) from that (0.194 mm/d) for 10 larvae (13.4±0.64 mmSL, 60.7±3.43 growth increments) collected in late April (post-peak).

Discussion

The spawning period of spot in the 1987–88 season was apparently a continuous process occurring over 5 months from mid-October to mid-March. Although spawning was protracted, the greatest concentration occurred in the 2-month interval from mid-November to mid-January when 90% of the estuarine-recruited larvae were spawned. This information, while generally agreeing with earlier work on fish collected in North Carolina (Hildebrand & Cable 1930, Warlen & Chester 1985) and South Carolina (Beckman & Dean 1984), is the first to be estimated from back-calculated birthweek distributions on larvae collected weekly over the entire estuarine recruitment period. The contribution of birthweeks to the larval catch each week was based on

Table 3

Linear regressions of mean estimated age (d) and mean standard length (mmSL) of spot *Leiostomus xanthurus* larvae on collection distance (km) from shore.

Transect/ month	Stations along transect	Variable	Intercept	Slope	Correlation Coefficient
Beaufort Inlet	8	Age	44.875	–0.364	0.905
January		SL	10.227	–0.088	0.886
Beaufort Inlet	7	Age	68.345	–0.515	0.936
February		SL	13.465	–0.104	0.953
Oregon Inlet	3	Age	71.279	–1.526	0.999
February		SL	15.756	–0.363	0.997

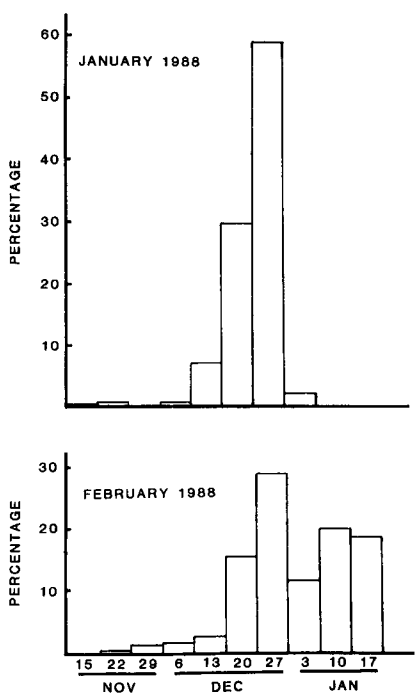

Figure 8

Percentage distribution of back-calculated birthweeks for spot *Leiostomus xanthurus* larvae caught in 1988 off the North Carolina coast: **(top)** 12–13 January and **(bottom)** 2–5 February.

the percentage age composition and density of larvae.

The seasonal differences in age and size of larvae at estuarine recruitment (Fig. 3) suggest that spawning may have been nearer the coast at the beginning and end of the spawning season. As adult spot emigrate from the estuary to offshore waters in fall, at a time of decreasing photoperiod and water temperature (Mercer 1989), they probably seek suitable water temperatures for spawning (17.5–25°C) (Hettler & Powell 1981). This temperature range is present over much of the North Carolina continental shelf water (Stefánsson et al. 1971) in the early months of spawning. During later spawning (mid-December to February), nearshore waters are cooler and well mixed and water above 17.5°C is generally restricted to areas on the outer continental shelf (Stefánsson et al. 1971, Atkinson 1985). Also, in winter the extent of this potential spawning area may be influenced by the Gulf Stream and its occasional wave-like perturbations (cyclonic meanders and filaments) along its western edge which can intrude onto the continental shelf. It is known that average surface-water temperatures on the outer continental shelf are moderated by the Gulf Stream (Atkinson 1985). The winter (January and February) distribution patterns of age and size of spot larvae in Onslow Bay, with the youngest, smallest larvae occurring only furthest offshore, support the idea that spawning may occur some 90 km offshore. Spawning that occurs further offshore as the spawning season progresses has been suggested for spot (Lewis & Judy 1983, Warlen & Chester 1985) and Atlantic croaker *Micropogonias undulatus* (Warlen 1982). Norcross & Austin (1988) also suggested that the area of warm water encountered upon migration of Atlantic croaker from Chesapeake Bay onto the continental shelf determines spawning location.

Differences in age at estuarine recruitment may also be due to differences in transport rate that result from the degree to which favorable currents facilitate more rapid transport of larvae toward shore. Different transport rates and spawning distances from shore could also act in concert to produce the observed differences in age and size at recruitment. Although some of the physical processes that could affect larval transport have been discussed (Checkley et al. 1988, Miller 1988, Pietrafesa & Janowitz 1988), precise larval-fish transport mechanisms still remain unknown.

The higher abundance of spot larvae in water deeper than 30 m may be a function of spawning location and subsequent larval transport toward shore. The reduced abundance observed inshore of the 30 m isobath may reflect fewer numbers of larvae present or their reduced vulnerability to capture by bongo nets. Mortality will also reduce larval abundance over time. Kjelson et al. (1976) and Miller et al. (1984) suggest that spot larvae offshore are more pelagic but that inshore they are more benthic-oriented. Spot larvae caught from shore to the 30 m isobath were 40–61 d old and 8.2–12.1 mm SL, and correspond to the early stages of the transformation period (Govoni 1980 and 1987, Powell & Gordy 1980) when spot begin to be more benthic.

Larval spot are recruited from offshore spawning areas to estuaries bordering Onslow Bay. Fish of the same ages also are found along the offshore to onshore Oregon Inlet transect (Figs. 6,7). This data and the fact that larval spot were found in and near the Gulf

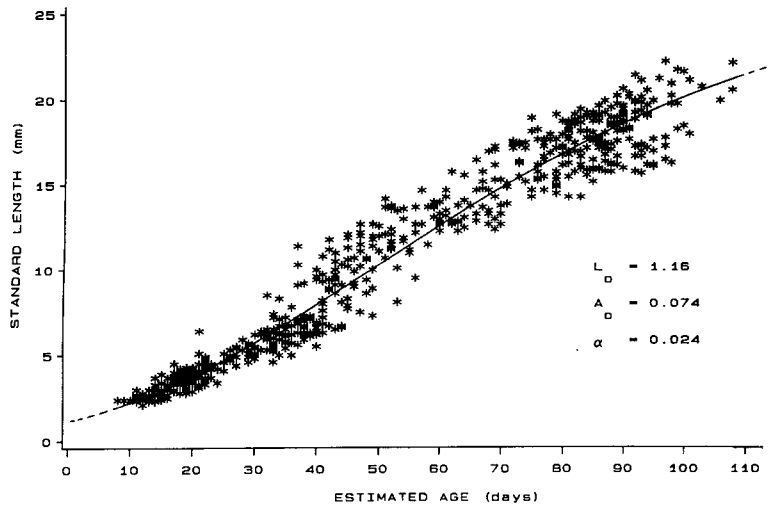

Figure 9

Growth of larval spot *Leiostomus xanthurus* collected from the estuary and oceanic waters off North Carolina, November 1987 to May 1988. A Laird-Gompertz model was fit to the age/size data for 663 fish. Estimates of the parameters were obtained by fitting the log-transformed version of the model to the data. L_0=length at hatching, A_0=specific growth rate at hatching, and α=exponential decay of the specific growth rate.

Stream (Fig. 6) suggest that larvae are being transported to areas north of Onslow Bay. The origin of these larvae is probably south of Cape Hatteras and most likely Onslow Bay or southward. These data support the hypothesis of Norcross and Bodolus (1991) that spot spawned south of Cape Hatteras on the outer continental shelf contribute to recruitment in Chesapeake Bay. Spring (March–May) spawned bluefish *Pomatomus saltatrix* are also thought to be transported to the Middle Atlantic Bight from spawning areas near the edge of a northerly flowing warm-water mass (Gulf Stream) in the South Atlantic Bight (McBride & Conover 1991).

The extended recruitment period of 5 months (Fig. 2) is a reflection of the length of spawning period (Fig. 5), although the time from spawning to recruitment varies throughout the season. The beginning of the maximum recruitment period coincides with increasing estuarine water temperature. Warlen & Burke (1990) found that peak immigration into North Carolina estuaries of fall–winter spawned ichthyoplankton matched the period of rising water temperature. This idea agrees with the fact that spot abundances are low during cold periods. Low water temperatures (<10°C) can cause cold stress by increasing larval respiration rate and can kill spot larvae (Hoss et al. 1988). The maximum estuarine recruitment period in North Carolina probably varys slightly from year to year, but is basically midwinter to early spring. Our estimate of the maximum recruitment period (mid-February to mid-April) is similar to that (February–March) recorded by Hettler & Chester (1990) and that (mid-January to mid-March) found by Warlen & Burke (1990). Apparently once spot larvae are in the estuary they move toward fresher water and utilize upper reaches of estuaries as nursery areas (Weinstein et al. 1980, Allen & Barker 1990). Peak recruitment of spot to the marshes of the Cape Fear River estuary in North Carolina occurred during March and April (Weinstein 1979). Interannual variations may be expected as a consequence of the seasonal changes that trigger emigration of the adults from estuaries to oceanic spawning areas and the subsequent transport rates of larvae back to the estuary.

The sum of the weekly mean larval densities over all collections (1540 larvae/100 m^3) was almost double that of 1985–86 (estimated from Fig. 2 of Warlen & Burke 1990), but less than that of 1989–90 and about equal to 1986–87 and 1988–89 (S.M. Warlen, unpubl. data). Allen & Barker (1990) also recorded variable patterns of larval spot abundance in South Carolina estuaries during 1981–84. The four highest peaks of recruitment density (10 and 24 February, 23 March, 13 April), that contributed about 74% of all spot larvae, could be consequences of concentration mechanisms of larvae outside the inlet and the subsequent facilitation of the influx of pooled larvae to the estuary. Lyczkowski-Shultz et al. (1990) suggested that larvae of spot, as well as other offshore spawners, accumulate in nearshore areas to develop and grow prior to recruitment. Tide may be an important mechanism which forces the larval gathering process outside and inside inlets (Pietrafesa & Janowitz 1988). The higher abundance of larvae just inside the inlet compared with the abundance at inshore stations seems to be a common feature for many estuarine-dependent species (Warlen 1982, Lewis & Judy 1983, Warlen & Chester 1985).

Because any birthweek cohort can be widely dispersed in the ocean, their larvae may reach the estuary over a period of 2–10 weeks. However, in general, >50% of the larvae of any birthweek cohort are recruited to the estuary in one week (Table 1). Birthweek cohorts of 25 October to 15 November had bimodal

recruitment, with small groups of younger larvae of each cohort reaching the estuary earlier, and larger groups of older (and larger) larvae recruited later (Tables 1, 2). The groups are clearly separated by a period of no recruitment, and the separation becomes less evident with later birthweek cohorts. The existence of two groups of recruits from early cohorts could result from dispersion of larvae spawned over the mid-continental shelf at different spawning locations and with different rates of transport to the estuary. Birthweek cohorts after November do not appear to be recruited to the estuary as distinct early and late groups.

The results show that the abundant larval cohorts of birthweeks 20 and 27 December, caught in January and February in Onslow Bay, contributed substantially to recruitment over the last four weeks in March. Birthweek cohorts of 3, 10, and 17 January were well represented in two later estuarine recruitment peaks. The comparison of birthdate distributions of larvae collected in the ocean in January and February and later in the estuary in February and March provided an opportunity to assess the relative survival of cohorts. The Kolmogorov-Smirnov tests showed no significant difference between ocean and estuarine birthdate distributions for larvae spawned over a period (13 December–2 January) of intense spawning. Therefore, we conclude that earlier (oceanic) and later (estuarine) larvae were from the same birthdate distribution, and that survival for the daily cohorts between 13 December and 2 January was not age-specific. The lack of seasonal sampling of larvae in the ocean precluded similar comparisons of birthdates throughout the spawning season.

During their oceanic existence, spot larvae grew rapidly from a hatching size of about 1.6 mmSL to a mean size of 17.2 mmSL at estuarine immigration. The growth curve was sigmoidal and similar to those found by Warlen & Chester (1985) for spot larvae in North Carolina during 1978–79 and 1979–80. Parameter estimates of the growth model for larval spot in 1987–88 in North Carolina, i.e., length at hatching ($L_{(0)}$=1.156), specific growth rate at hatching ($A_{(0)}$=0.074), and the exponential decline of the specific growth rate ($\propto$=0.024), were comparable to the growth parameter estimates for 1978–79 and 1979–80 ($L_{(0)}$=1.686, 1.609; $A_{(0)}$=0.060, 0.067; $\propto$=0.021, 0.026) found by Warlen & Chester (1985). Maximum growth rate (9.3 mm, 46 d-old larvae) was between the values that they report (8.0 mm, 46 d old; and 10.7 mm, 45 d old). There did not appear to be large differences in within-season growth of spot, although significant differences could be demonstrated. Mean growth was about 0.19–0.21 mm/d for larvae collected during and after the peak immigration period.

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