Abstract.—Larval Atlantic menhaden, *Brevoortia tyrannus*, were collected weekly during their expected recruitment (November–April) to the estuary near Beaufort, North Carolina, over seven consecutive years beginning 1985–86. The larval density in nighttime quantitative samples was calculated and ages determined from otolith microstructure. Back-calculated birthdates and larval abundance data were used to estimate the relative contribution of weekly age cohorts to seasonal recruitment of larvae. Summaries of these data were measures of the spawning distributions. Larvae were recruited to the estuary from mid-November through April, with about 86% collected during February–April. In all years, age and size of larvae increased linearly throughout recruitment until the end of March and then declined. The mean age of recruited larvae over all years was 61 days and the mean standard length was 24.6 mm. Atlantic menhaden spawning season was protracted, lasting 4–6 months. In every spawning season, a dominant birthweek mode in either December or January contributed from 25–43% of the total recruits. More than 76% of all spawning occurred in the December– January period. Individual birthweek cohorts recruited to the estuary over periods from one week to several months. Cohorts that usually contributed the greatest number of individuals to estuarine recruitment usually recruited over longer periods. Atlantic menhaden have apparently selected a spawning season and location that ensures transport of larvae across the southeast United States continental shelf and arrival of most larvae during a time when conditions are conducive to optimal survival in the estuary.

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Spawning time and recruitment dynamics of larval Atlantic menhaden, *Brevoortia tyrannus*, into a North Carolina estuary

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The Atlantic menhaden, *Brevoortia tyrannus*, is a commercially important clupeid that ranges on the east coast of the United States from the Gulf of Maine to the central coast of Florida. Tagging studies have shown that this species makes extensive seasonal migrations northward along the coast in spring and southward in fall and winter (Dryfoos et al., 1973; Nicholson, 1978). Most of the population is thought to overwinter in the area between Cape Hatteras, North Carolina, and northern Florida (Ahrenholz et al., 1987). Spatial and temporal trends in Atlantic menhaden spawning have been suggested by studies on the distribution of eggs and larvae (Reintjes, 1961; Kendall and Reintjes, 1975; Judy and Lewis, 1983) and studies on ovarian maturity and fecundity (Higham and Nicholson, 1964; Lewis et al., 1987). Those studies show that spawning occurs off New England from late spring to early summer and again in early fall, off the mid-Atlantic states in spring and fall and off the southeastern states from October to March. Maximum numbers of menhaden probably spawn in winter in offshore waters south of Cape Hatteras (Reintjes, 1969; Judy and Lewis, 1983) and waters off the North Carolina coast may be one of the major spawning grounds for Atlantic menhaden (Higham and Nicholson, 1964).

Plankton collections taken off North and South Carolina suggest that Atlantic menhaden may continuously spawn from late fall to early spring. Collections taken in the vicinity of Beaufort, North Carolina, from 1955 to 1961 (unpubl. data, National Marine Fisheries Service, Beaufort Laboratory, cited by Higham and Nicholson, 1964) showed larvae in samples beginning in November or early December and continuously thereafter until mid-April. Subsequent work supported these estimates of the timing of estuarine immigration of menhaden larvae. Lewis and Mann (1971) sampled larval menhaden semimonthly as the fish recruited to the estuary near Beaufort Inlet in the fall/winter 1966–67 and 1967–68 seasons, to estimate relative indexes of abundance. Densities of menhaden larvae recruited to estuaries were reported for North Carolina (Hettler and Chester, 1990; Warlen and Burke, 1990) and South Carolina (Allen and Barker, 1990).

Examination of otolith microstructure to count daily growth increments has made possible reasonably accurate estimates of the age and growth of the early life history stages of fishes. Age at estuarine recruitment can be tracked within and among seasons or years. Age at recruitment is also a measure of the total time from offshore spawning to recruitment to the estuary. Valuable new information on the early life history of larvae can be obtained when estimates of recruitment densities are combined with estimates of seasonal age composition of the catches. Back-calculated birthdate distributions of larvae in each sample can be multiplied by the catch density to determine the relative contribution of birthweek cohorts to the number of immigrants.

The purposes of this seven-year study were to document the duration and relative abundance of larval Atlantic menhaden recruitment to the estuary near Beaufort, North Carolina; to measure size and estimate ages of recruited larvae; to back-calculate birthdate distributions of larvae; and to determine the contribution of birthweek cohorts to the number of immigrants for an estimation of temporal spawning within and among sampling years.

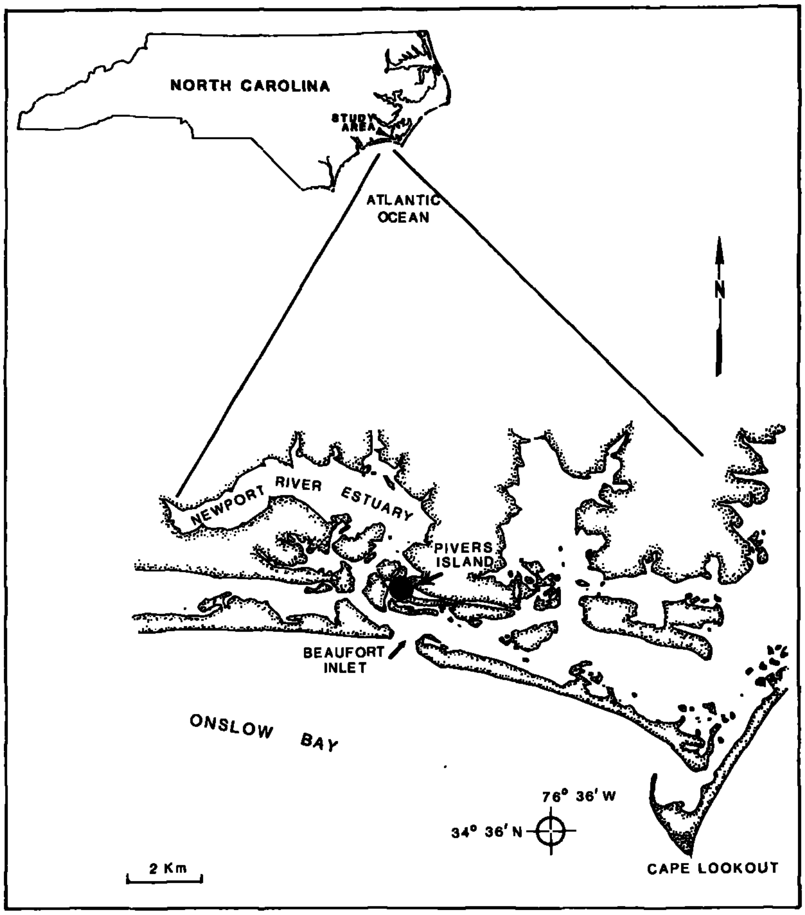

Figure 1
Location of the sampling site for larval Atlantic menhaden, *Brevoortia tyrannus*, in the lower Newport River estuary near Pivers Island, North Carolina.

Methods

Larval collection

Larval Atlantic menhaden were collected at a station adjacent to Pivers Island (Fig. 1) as they recruited to the Newport River estuary from the Atlantic Ocean. Sampling, designed to cover the expected recruitment period of mid-November to April (Lewis and Mann, 1971), ran for seven consecutive years beginning with the 1985–86 sampling year. Larvae were sampled from 13 November 1985 to 23 April 1986 with a 60-cm bongo frame with paired 505-μm mesh nets and flow meters pulled by a 6.7-m boat. Tows were made weekly during nighttime hours just after mid-flood tide, when the current was strongest, to reduce potential net avoidance by larvae. Data from the catch of both nets from two consecutive tows, one surface-bottom-surface (double oblique) in 3–5 m of water and one just under the surface (subsurface), were averaged to estimate larval density (number larvae/100 m^3 water fished) and to provide fish for ageing. The lack of a significant difference (paired comparison *t*-test, $P>0.05$) in catch density from subsurface and double oblique tows allowed the paired data to be combined. In the other six sampling years (19 November 1986–30 April 1987, 10 November 1987–4 May 1988, 16 November 1988–3 May 1989, 15 November 1989–2 May 1990, 14 November 1990–24 April 1991, and 13 November 1991–6 May 1992) larvae were collected, with a 1×2 m neuston net frame fitted with a 945-μm mesh net and flow meter fished just under the water surface from a bridge platform over the center of the channel adjacent to Pivers Island. This location was only meters from the site sampled with the bongo nets in 1985–86. As in 1985–86, all samples were collected weekly during nighttime hours at mid-flood tide. Three consecutive sets were made each night in 1986–87 and four each night in subsequent years. Because of the expected seasonal variation in menhaden abundance, sets were between 2 and 16 minutes long; most were 5–7 minutes long. Volume of water fished by the net ranged from 41 to 805 m^3 but most sets filtered 150–350 m^3. Ichthyoplankton samples were preserved with 95% ethanol and diluted so that the final alcohol concentration was ≥70%. Samples not sorted within 24 hours were rinsed and represerved in 70% ethanol. As for bongo nets, these catches were standardized as the number of Atlantic menhaden/100 m^3 of water fished. The mean of the density data from all sets on a given night (bongo nets in 1985–86 and neuston nets in other years) was used as the estimate of density of Atlantic menhaden larvae recruited during the flood tide.

Simultaneous larval collections were made with bongo and neuston nets on 17 December 1986 (3 sets) and 18 March 1987 (4 sets) to test for differences in menhaden catch density between gear type. There were no significant differences in density of menhaden caught by gear type (ANOVA, $P>0.54$) or among sets (ANOVA, $P>0.24$). Hence, the catch data from bongo and neuston nets are comparable. The mean age or standard length (SL) also did not differ between the two types of nets.

Larval ageing

Larvae for ageing were subsampled from individual weekly night net sets in proportion to their contribution to the total nightly catch. In catches of up to 20 fish, all larvae were used. In catches of >20 fish, subsample sizes were proportional to catch but generally no more than 50 fish were aged per week. The ages of 3,864 larvae were determined.

The standard length of each larva to be aged was measured to the nearest 0.1 mm with an ocular micrometer. Sagittal otoliths were removed from their surrounding soft tissue, cleaned in distilled water, and placed on a glass microscope slide under a thin layer of Flo-Texx mounting medium. Otoliths were observed with transmitted light on a compound microscope fitted with a television camera. Growth increments were counted from images on a video monitor at microscope magnifications of 400× or 1,000×. One person made dual readings of otoliths from each fish. Readings were averaged if they differed by a count of four or less; if they differed by ≥5 increments, the fish was excluded from further analyses. Increment counts of about 2% of the aged fish differed by five or more. Estimated age was the number of increments counted plus an empirically derived value for the number of days (5) from spawning to first increment formation (Warlen, 1992). The otolith ageing technique for Atlantic menhaden larvae has been validated by Maillet and Checkley (1990), who established that larvae form one otolith growth increment per day. I assumed that the age at initial increment deposition did not vary and that the otolith increment deposition rate was constant within and between sampling seasons. A spawning date (birthdate) was assigned to each ageable larva by using the estimated age of the fish in days to back-calculate from the date of capture. Larvae spawned in a given calendar week were considered in the same calendar birthweek cohort.

Estuarine recruitment of birthweek cohorts

The percentage contribution of Atlantic menhaden larvae of all birthweek cohorts to the total recruitment was measured for each of the seven years from 1985–86 to 1991–92. For each weekly collection, the percentage of larvae spawned in each back- calculated birthweek was determined. Each percentage was then multiplied by the total larval density (number/100 m^3) for the week. Based on these results, density estimates were made for larvae from each birthweek cohort recruiting to the estuary on a given collection night.

Densities for each birthweek cohort were summed over all collections within a sampling year. The proportion that each birthweek cohort contributed was determined by dividing the individual birthweek sums by the total density of all birthweek cohorts for the recruitment year. These computations produced estimates of the relative contribution that each birthweek cohort made to the total recruitment of menhaden larvae into the estuary near Beaufort.

Results

Larval recruitment abundances

Larval Atlantic menhaden recruited to the estuary near Beaufort over a 5 to 5½ month period from mid-November to the end of April (Fig. 2). Larvae were generally recruited in highest densities during February–April and contained, on average, about 86% of the total estuarine recruitment during those months (Table 1). Recruitment was low in November and seldom extended into May. There was a distinct density mode in each of the seven years (Fig. 2). Except for 1988–89, modal density always occurred in March or April (Fig. 2, Table 2). Highest densities in a 3-week period (modal week plus adjoining weeks) in any year contributed 32–89% of the total density of Atlantic menhaden larvae for the year (Table 2).

During the recruitment period, most Atlantic menhaden larvae recruited to the estuary in pulses. Mean density varied from zero to about 570 larvae/100 m^3 and most samples contained <20 larvae/100 m^3 (Figs. 2 and 3). Catch densities varied among sets on any given night and the standard deviation in catch densities generally increased with the mean catch den-

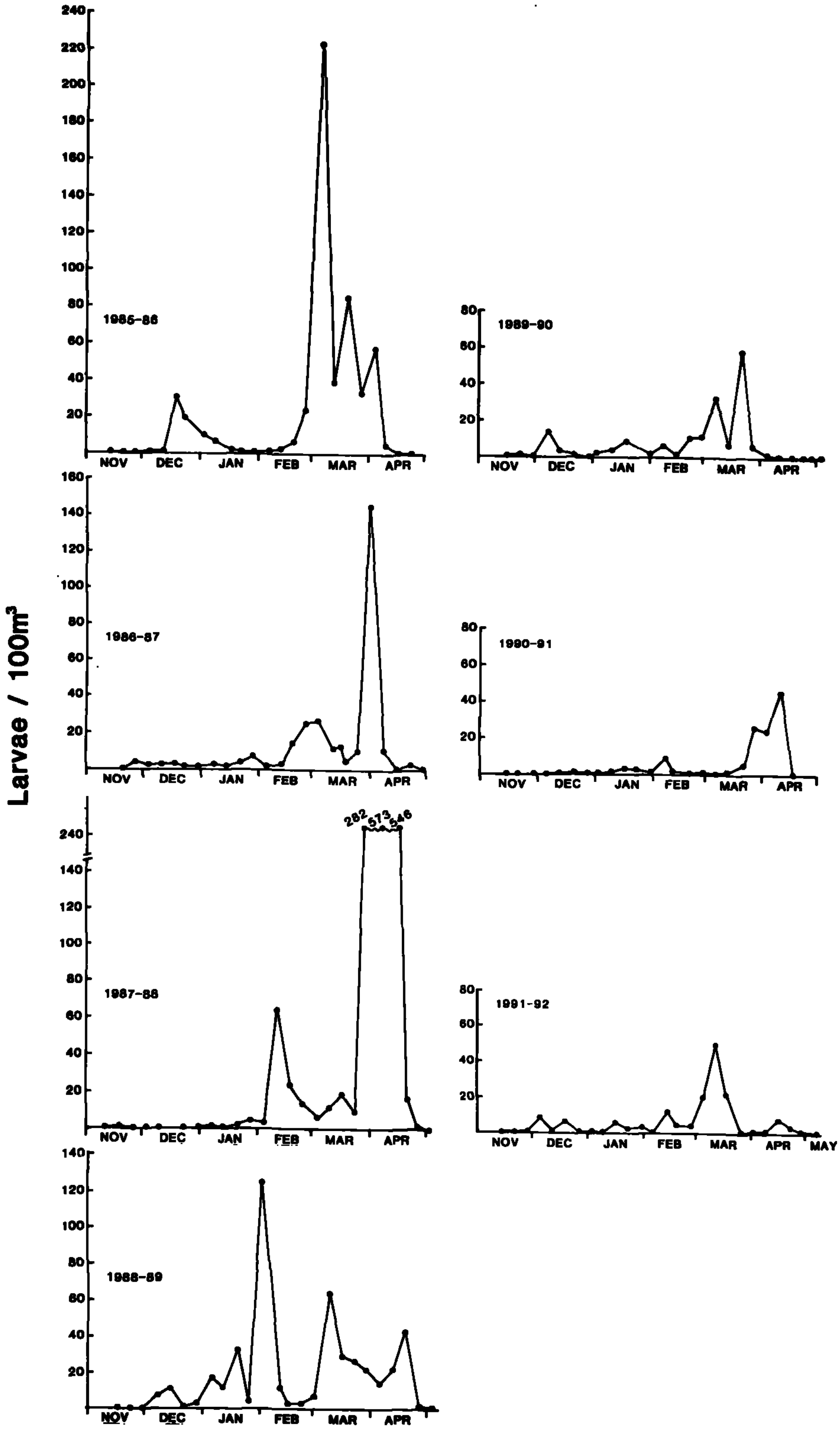

Figure 2

Weekly mean density (larvae/100 m^3) of Atlantic menhaden, *Brevoortia tyrannus*, larvae in collections at Pivers Island, North Carolina, in the lower Newport River estuary during seven consecutive estuarine recruitment years.

sity (Fig. 3). Relative abundance of larvae also varied among years (Fig. 2). The sum of weekly densities for individual sampling years differed by more than an order of magnitude (Table 2). Lowest relative abundances were observed for the last three sampling years.

I assumed that larval Atlantic menhaden caught each week were newly recruited to the estuary and that they were in transit past Pivers Island to upper portions of the estuary. These assumptions are supported by the presence of an abundance mode on 19 December 1985 (Fig. 2) and the presence of similar modes from bongo net sampling in the same estuary one-week later about 6 km up-estuary and two-weeks later about 11 km up-estuary (Warlen, unpubl. data). Also, the generally narrow 95% confidence limits in the age of larvae within each collection, along with no increase in the confidence limits through the recruitment year (Fig. 4), does not suggest an increase in the number of different birthweek cohorts in the lower estuary. In a number of cases, the week following a peak in density showed relatively low recruitment (Fig. 2), a pattern that did not suggest substantial carryover and accumulation of larvae from week to week. While a single sampling location may not reflect patterns of larval estuarine recruitment for all areas south of Cape Hatteras, it does provide a time-series description of relative larval recruitment abundances over several years inside a large inlet near the presumed major fall/winter spawning area.

Age and size of larvae

In every sampling year the age of larvae increased linearly throughout estuarine recruitment until about the end of March after which the mean age declined (Fig. 4). Linear regressions of the mean estimated age over time, excluding the end-of-season down trending values, were significant (ANOVA, $P<0.001$) for each recruitment year. Young larvae were always collected early in each recruitment year (Fig. 4). Virtually all larvae collected in November were less than 40 days old. Larvae collected about late March were 2–4 times older than larvae collected early in the recruitment year. Except in a few cases, the within-sample age variation was small and the 95% confidence limits were within ±5 days of the mean age.

Larvae recruited to the estuary during peak recruitment were also the older larvae. Peak recruitment densities were in February–April (Fig. 2) and those larvae were older, generally age 60–90 days or older, as in 1987–88 when some were up to age 115 days (Fig. 4). The recruitment-year mean age of larvae varied between 55 and 74 days for the seven years. The mean age of larvae over all years was 61 days.

The standard length of larvae also increased significantly (ANOVA, $P<0.001$) within each recruitment year. The mean size of larvae increased to the end of March then decreased slightly to

Table 1

Percentage of the sum of the weekly mean densities (number/100 m^3) of larval Atlantic menhaden, *Brevoortia tyrannus*, recruited to the estuary near Pivers Island, North Carolina, November–May of each recruitment year.

Recruitment year	Nov	Dec	Jan	Feb	Mar	Apr	May
1985–86	0.0	9.4	3.9	6.3	68.8	11.6	0.0
1986–87	1.6	4.1	5.5	15.1	18.5	55.2	0.0
1987–88	<0.1	<0.1	0.5	6.7	20.8	71.9	<0.1
1988–89	<0.1	5.0	14.4	30.9	32.2	17.4	<0.1
1989–90	1.2	10.7	12.8	16.9	57.0	1.4	0.0
1990–91	0.0	2.1	7.3	10.0	26.1	54.5	0.0
1991–92	0.5	10.4	8.5	13.5	57.5	9.5	0.1
Mean	0.5	6.0	7.6	14.2	40.1	31.6	<0.1

Table 2

Sum of weekly mean densities (number/100 m^3) by year, relative abundance (related to 1990–91), and peak recruitment density period (highest three consecutive sampling-date catches including the mode) of larval Atlantic menhaden, *Brevoortia tyrannus*, collected at Pivers Island, North Carolina, by recruitment year.

Recruitment year	Sum of weekly mean densities	Relative abundance	Peak recruitment density: Period of highest three consecutive catches			Peak recruitment density: % of year
1985–86	554	4.3	Mar	5–Mar	19	59.9
1986–87	288	2.3	Mar	25–Apr	8	57.7
1987–88	1581	12.4	Mar	30–Apr	13	88.6
1988–89	459	3.6	Jan	19–Feb	1	32.2
1989–90	173	1.4	Mar	7–Mar	21	53.4
1990–91	128	1.0	Mar	27–Apr	10	75.2
1991–92	163	1.3	Mar	4–Mar	17	56.7

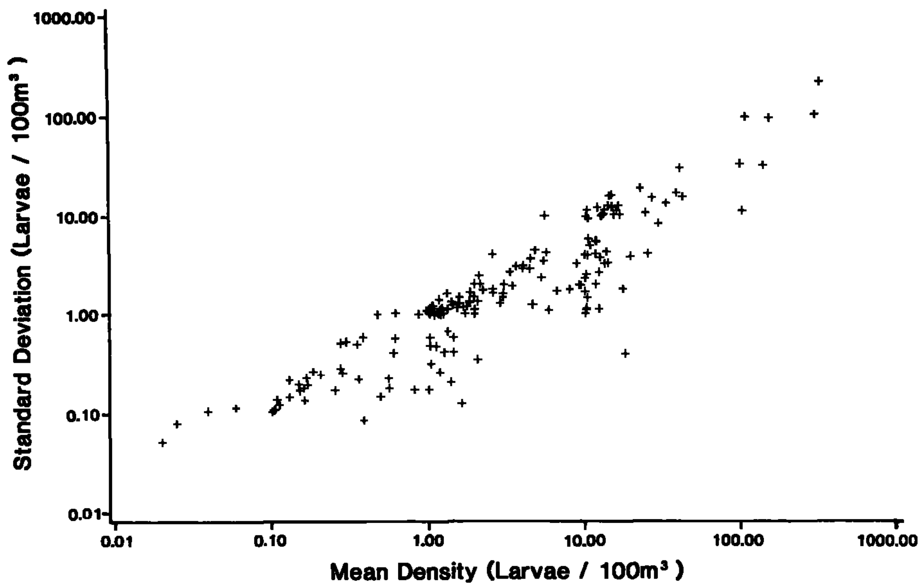

Figure 3

Plot of standard deviation versus mean density (larvae/100 m^3) for each collection night for larval Atlantic menhaden, *Brevoortia tyrannus*, sampled at Pivers Island, North Carolina, for seven consecutive recruitment years.

the end of the recruitment year (Fig. 5). Larvae recruited to the estuary were always >20 mm SL, except early in the recruitment year (November–December) when the mean size could be as low as 15 mm (Fig. 5). The overall recruitment year mean SL of larvae varied between 23.2 and 25.4 mm for the seven years and the mean SL over all years was 24.6 mm.

Spawning time

The menhaden spawning season in North Carolina was estimated from the birthdate distributions of larvae that survived to recruit to the estuary. The percentage distribution of spawning by week (Fig. 6) was based on the relative abundance of larvae collected at Pivers Island throughout the recruitment year. The spawning season was protracted, lasting four to six months (Fig. 6). Estimated spawning was variable among birthweeks. In every spawning season, there was a dominant birthweek mode that contributed from 25 to 43% of the total estuarine recruits. Except for 1987–88 (20 December 1987), these modes occurred very close to the new moon phase of the lunar cycle (10 January 1986, 31 December 1986, 9 December 1988, 28 December 1989, 15 January 1991, and 6 December 1991). Median spawning and modal spawning peaks were always in December or January as were the second and third quartile intervals of the distributions, except in 1989–90 when the second quartile interval extended into November (Fig. 6). Over all seven years, an average of more than 76% of all spawning occurred in December–January (Table 3). Earlier season spawning (October–November) contributed an average of 16% of the total, although November spawning alone could sometimes account for about 26% (Table 3). Little spawning occurred in February (. 7%) and in only two years did the March contribution exceed 1%.

The data suggest that within-season spawning frequency may be multimodal. There was an indication in 1985–86, 1986–87, 1989–90, 1990–91, and 1991–92 that a small, early mode may have occurred in October or November (Fig. 6). If there was an early mode in 1988–89, it may have blended with the mode for later spawned fish. A small, late season mode (February or March) may also have been present and was most evident in the 1986–87, 1988–89, 1989–90, and 1991–92 spawning seasons.

Recruitment of birthweek cohorts

Individual birthweek cohorts were recruited to the estuary over periods from one week to several months (Fig. 7). Those birthweek cohorts that recruited over the shortest time periods were generally spawned either early (October) or late (February–March) in the season. Birthweek cohorts spawned from mid-November through January usually recruited over

Table 3

Percentage monthly spawning of Atlantic menhaden, *Brevoortia tyrannus*, estimated from the density-weighted, back-calculated birthdate distributions of larvae recruited to the estuary near Pivers Island, North Carolina, during November–April each recruitment year.

Recruitment year	Spawning month					
	Oct	Nov	Dec	Jan	Feb	Mar
1985–86	0.4	12.8	17.3	68.3	1.2	0.0
1986–87	4.2	7.3	64.4	21.1	2.9	0.1
1987–88	0.1	5.9	63.4	30.5	0.1	0.0
1988–89	0.6	26.5	49.2	9.1	12.9	1.7
1989–90	6.6	22.4	31.9	36.4	2.5	0.2
1990–91	0.0	8.4	11.6	54.2	25.8	0.0
1991–92	7.6	9.2	62.3	16.5	2.1	2.3
Mean	2.8	13.2	42.9	33.7	6.8	0.6

the longest time periods. However, 70% or more of any cohort were usually recruited in ≤3 consecutive weeks. In each recruitment year, those birthweek cohorts with the greatest numbers of individuals contributed most to the estuarine recruitment mode (Fig. 7). Also, within the larval catch of any given week, from one to 10 birthweek cohorts were represented (Fig. 7).

Discussion

Relatively large schools of larger-sized Atlantic menhaden, migrating from New England and mid-Atlantic states, along with local (North Carolina at least) Atlantic menhaden emigrating from estuaries, spawn off the southeast Atlantic states. The area from Cape Hatteras to about northern Florida is thought to be the major spawning location for this species (Higham and Nicholson, 1964; Reintjes, 1969; Nelson et al., 1977; Judy and Lewis, 1983; Lewis et al., 1987). Although the previous studies suggested that Atlantic menhaden spawn in the fall and winter off the southeast Atlantic states, none were able to estimate within season spawning intensity. The present study, which utilized samples collected throughout the recruitment year, estimated within season spawning intensity based on survivors entering an estuary. However, without any knowledge of egg production and the survival of cohorts between offshore spawning and estuarine recruitment, it was not possible to know how closely the estimates of the birthdate distributions represented the actual seasonal egg production.

In each year, the Atlantic menhaden spawning season was protracted. This long spawning season might indicate a "bet hedging" strategy (Lambert and Ware, 1984) where eggs are released continuously over the spawning season to ensure some reproduction during the most favorable periods for survival. Based on the birthdate distributions of larvae that recruit to the estuary, the most favorable period each year appears to be for those fish spawned in a relatively short period between early December and mid-to-late January. For all seven years, it was within this major spawning period that the week of peak spawning occurred. Larvae from this major spawning period are probably progeny of the large menhaden schools migrating southward from the New England and mid-Atlantic states. These schools, which contain many fish of spawning age (3+ years), are harvested from about late November to late January during the North Carolina fall purse seine fishery (Smith et al., 1987). Larvae spawned earlier (October–November), may originate from adults inhabiting North Carolina coastal waters and estuaries in the summer or from early fall adult immigrants to North Carolina waters (Wilkens and Lewis, 1971). Larvae spawned late (February–March) may have been spawned further south and immigrated to the estuary late in the season or were the offspring from northward migrating adults in early spring. This late spawned group contributed the younger, smaller larvae observed at the end of the recruitment year (Figs. 4 and 5).

Spawning locations, and routes and rates of transport probably account for the variation in age of larvae recruited to the estuary. While the precise locations of menhaden spawning are not known, the general area is thought to be on the mid- to outer-continental shelf off North Carolina (Checkley et al., 1988; Warlen, 1992). However, accounts of the occurrence of eggs are limited (Reintjes, 1969; Judy and Lewis, 1983) and no records of actual spawning events exist. Although some early season spawning may occur closer to shore, the largest contribution of recruited larvae to the estuary is later in the season, probably from the warm, plankton rich areas closer to the Gulf Stream. Water temperatures are generally ≥18°C (Govoni, 1993), even in winter. These warm temperatures are due, in part, to intrusions of warm surface water onto the middle continental shelf (Atkinson, 1985). Frequent upwelling events (Pietrafesa et al., 1985) stimulate primary productivity by providing nutrients (Atkinson, 1985; Yoder, 1985) for phytoplankton growth (Yoder et al., 1983)

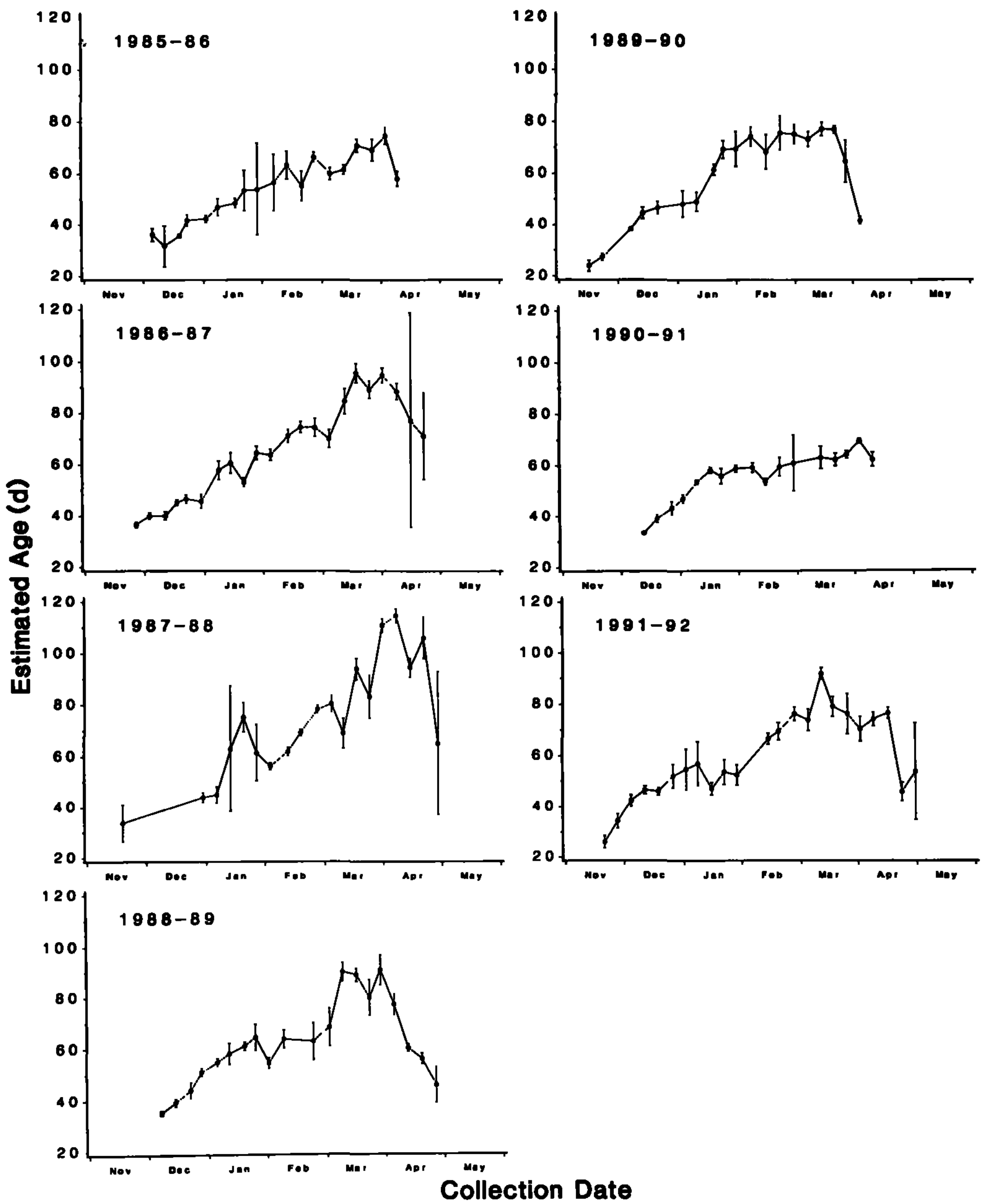

Figure 4
Mean of estimated ages (days) with 95% confidence limits of larval Atlantic menhaden, *Brevoortia tyrannus*, collected weekly over seven years during their estuarine recruitment at Pivers Island, North Carolina.

thus increasing secondary production (Paffenhöfer, 1985). This productive area is probably utilized by larval fishes spawned nearby.

Atlantic menhaden appear to spawn during periods (daily, seasonal) of lower light intensity. They probably spawn at night, and may have a diel pattern of ovulation and spawning that may be linked to the daily cycle of light and darkness as noted for many marine fishes (Bye, 1990). Reintjes (1969) examined Atlantic menhaden eggs at sea and concluded that estimated ages of groups of eggs of different stages suggested that "spawning occurred after mid-

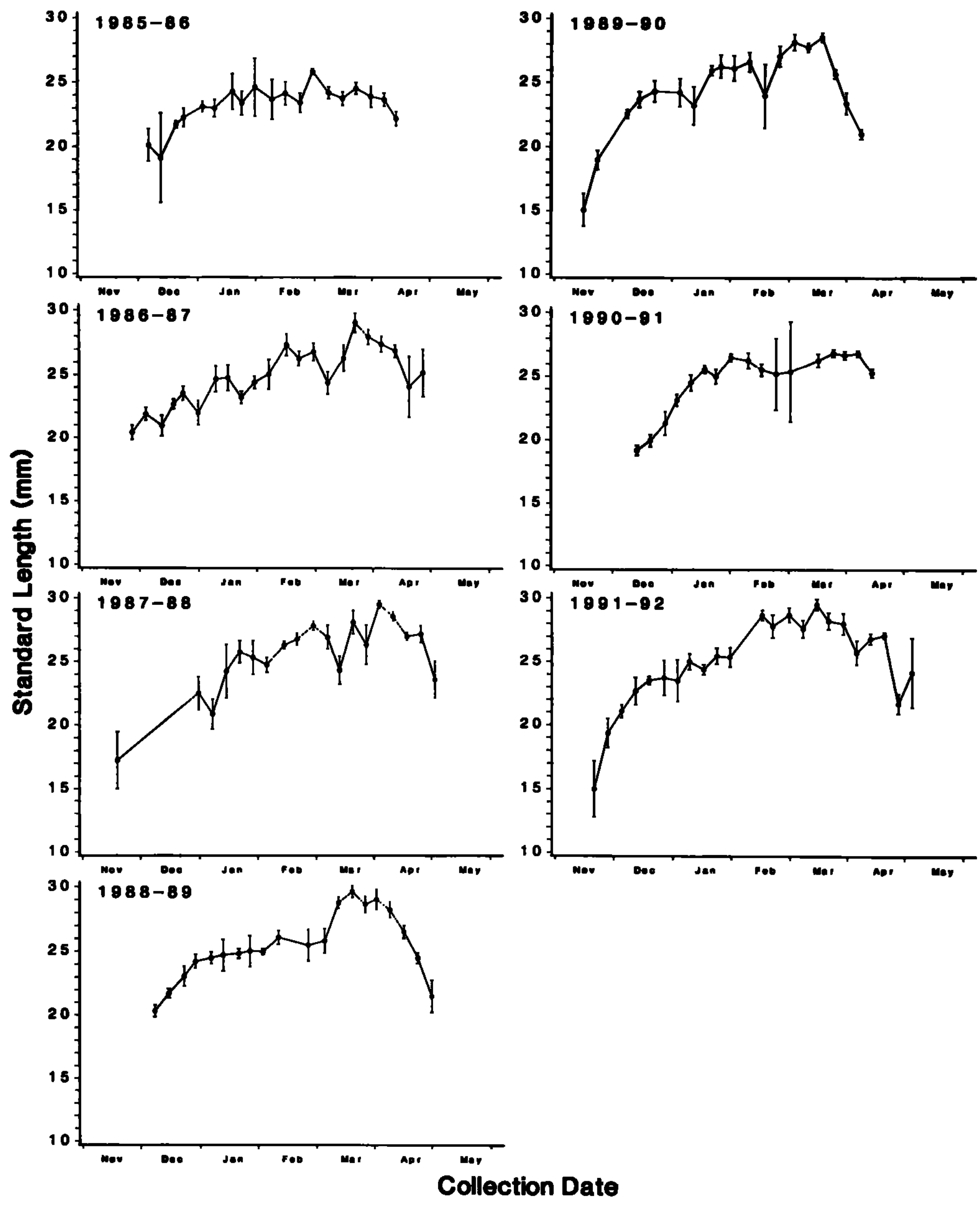

Figure 5
Mean standard length (mm) with 95% confidence limits of larval Atlantic menhaden, *Brevoortia tyrannus*, collected weekly over seven years during their estuarine recruitment at Pivers Island, North Carolina.

night but before dawn on three consecutive days." Ferraro (1981) also noted that Atlantic menhaden spawned at night and suggested that night spawning might be a means of reducing predation on spawners and eggs or of avoiding the deleterious effects of ultraviolet irradiation during early embryogenesis.

The relatively constant year-to-year spawning mode during December–January, observed in this study, occurs when the daily hours of darkness are maximal, $13^{1}/_{2}$–14 hours between sunset and sunrise, and when overcast days are more frequent. Peak spawning in each year (except 1987–88) also occurs very

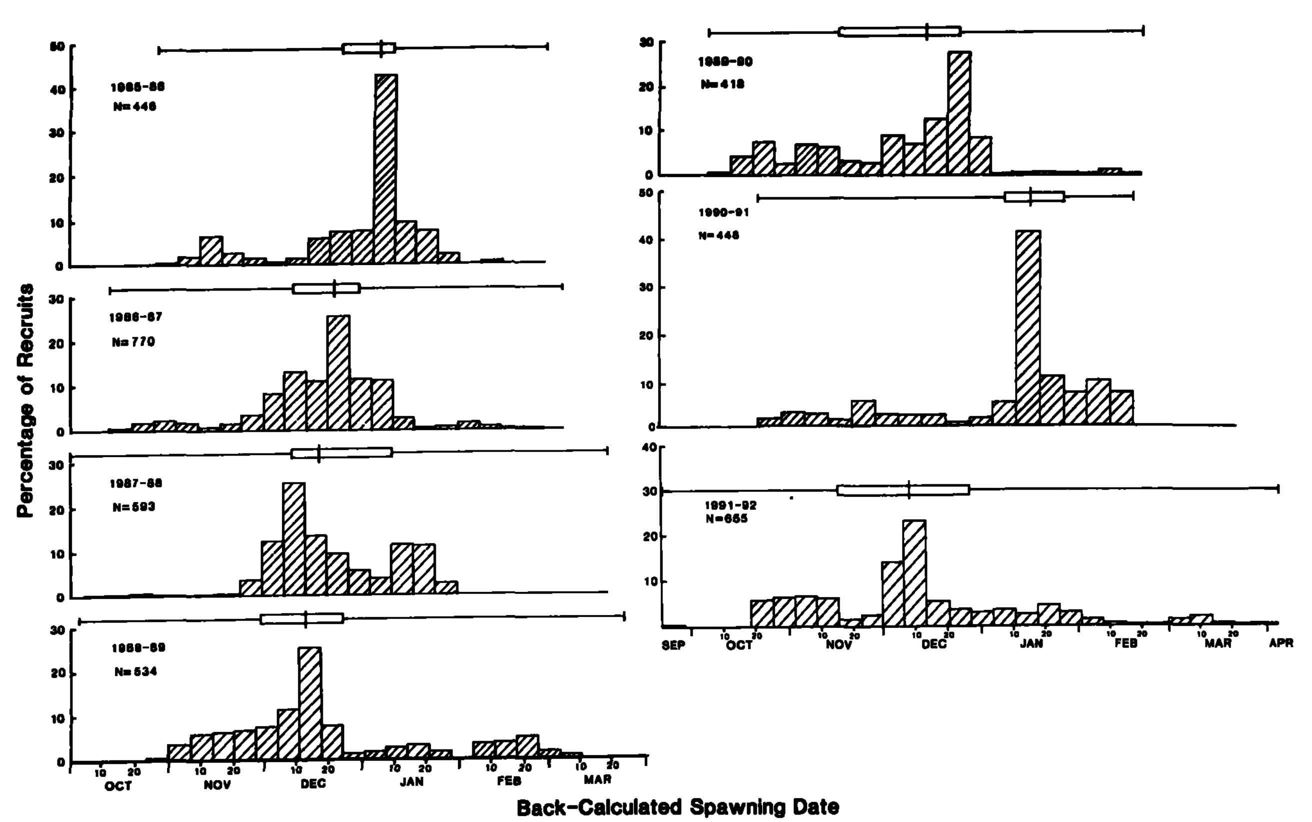

Figure 6

Birthdate frequency distributions calculated from the relative abundances of larval Atlantic menhaden, *Brevoortia tyrannus,* collected in the lower estuary at Pivers Island, North Carolina, in each of seven recruitment years. In each distribution, the vertical line is the median value and the box represents the 2nd and 3rd quartile intervals (central 50%). Lines beyond the boxes represent the range of data.

close to the new moon phase of the lunar cycle, which would also reduce available light during spawning.

Spawning of Atlantic menhaden off the southeastern Atlantic states is apparently timed to ensure transport of larvae across the continental shelf and arrival of most of the larvae (about 85% on average) during a time of optimal survival conditions in the estuary. Atlantic menhaden larvae that recruit to the estuary during the peak period (February–April) arrive when the water temperature is rising, prey abundance is high, and predator abundance and estuarine resident larval fishes and invertebrate (ctenophore) competitor abundances are low (Warlen and Burke, 1990). Some Atlantic menhaden larvae (about 15%) recruited to the estuary early in the season, November–December, before the period of coldest water temperatures in January (Warlen and Burke, 1990). These early recruited larvae may experience cold-related mortality if estuarine water temperatures drop to <4°C (Lewis, 1966; Wilkens and Lewis, 1971). However, larval Atlantic menhaden may tolerate lower temperatures than larvae of other species (e.g. spot, *Leiostomus xanthurus*) that recruit over the same period in the Beaufort area (Hoss et al., 1988). In milder winters, earlier recruited larvae may survive overwinter and, in the following spring and summer, may be larger than the more abundant Atlantic menhaden larval groups recruited several months later. Ahrenholz et al. (1989) observed a multi-modal distribution in lengths of juvenile menhaden collected in the summer in North Carolina which may reflect several seasonal abundance groups of immigrating larvae (early, middle, late) from a single spawning season.

Variation in egg production, mortality of eggs and larvae, and losses of larvae by advection to other areas of the coast probably account for the observed differences in relative recruitment abundances at the Pivers Island collection site. There was more than an order of magnitude difference between the relative abundances of the most abundant and the least abundant years. Lewis and Mann (1971) also ob-

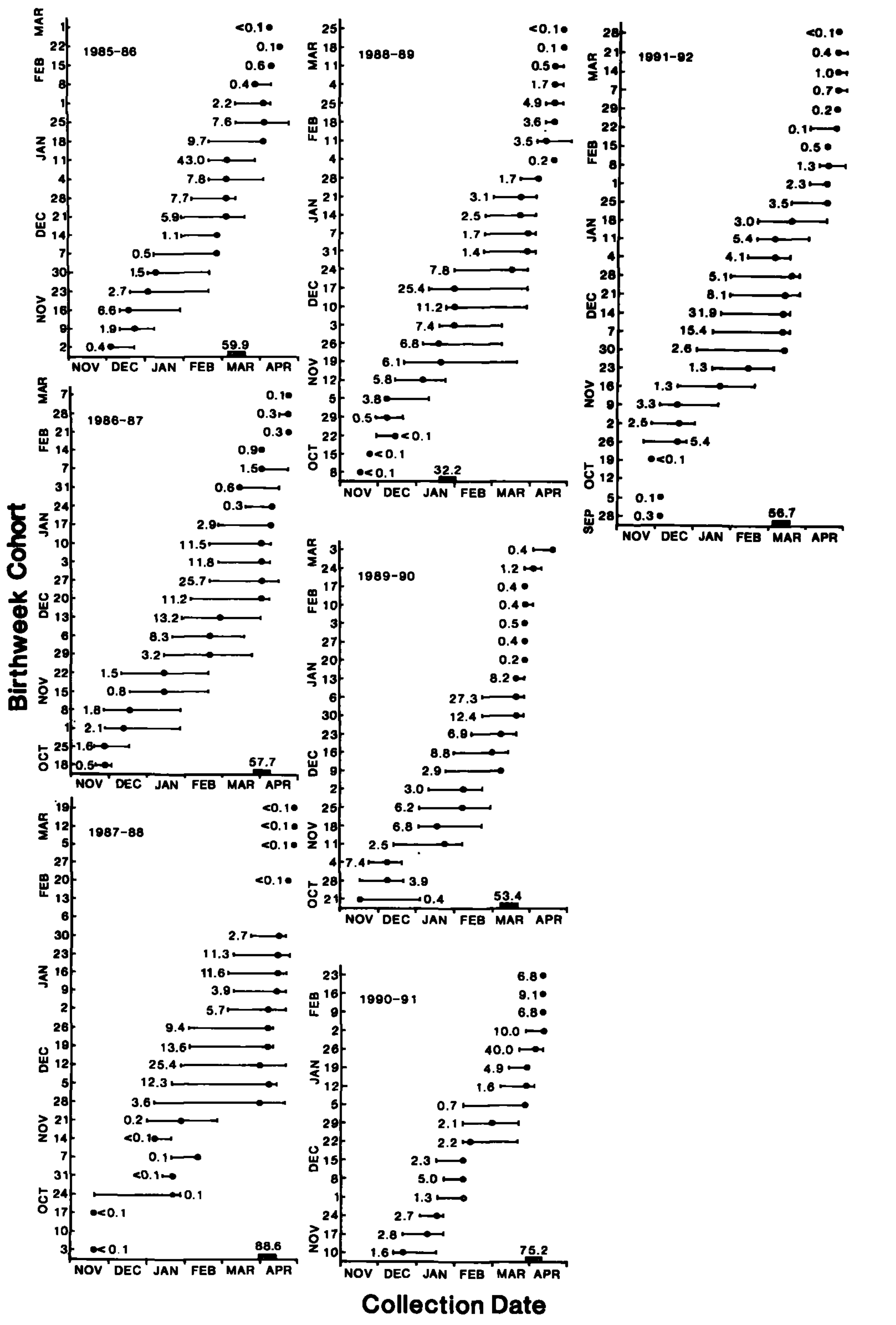

Figure 7

Percentage of total recruitment by birthweek cohort by year. The temporal range of collections of each birthweek cohort is denoted by a horizontal line and the mode by a closed circle. The peak recruitment density period (highest three consecutive sampling-date catches including the mode) and its percentage in each sampling season is indicated by the bar on the abscissa.

served a similar difference (13-fold) in relative abundances of Atlantic menhaden larvae at Pivers Island between 1966–67 and 1967–68. Their low year (1967–68) estimate was about one half that of the low year (1990–91) estimate in this study. Although relative abundances give estimates of larval recruitment among years, it is not known how representative the estimates are of coastwide year-class strength of the species. Virtual population analyses (VPA) indicate that recruitment to the commercial fishery to age-1 from the 1987–88 year class was about double that of the previous two years, 1985–86 and 1986–87 (Vaughan, 1993). In comparison, the estimate of larval recruitment for 1987–88 was about 3–5 times larger than the 1985–86 and 1986–87 estimates.

An increase in SL of Atlantic menhaden larvae recruited through each of seven seasons has also been observed in earlier studies. Higham and Nicholson (1964) noted that in plankton collections taken in the vicinity of Beaufort, North Carolina, Atlantic menhaden larvae were smallest in December and largest in April. Lewis and Mann (1971) found that the condition factor (weight/length^3) of larval Atlantic menhaden also increased throughout the season. Checkley et al. (1988) showed that the mean SL of Atlantic menhaden larvae about 10 km offshore increased over the period from January 15 to early March. The mean SL of Atlantic menhaden collected by Hettler and Chester (1990) increased from 16.0 mm in November to 27.6 mm in March then decreased to 24.0 mm in April. Similar trends in increasing size of larvae collected throughout the recruitment season have been observed for spot (Allen and Barker, 1990; Flores-Coto and Warlen, 1993), Atlantic croaker, *Micropogonias undulatus* (Allen and Barker, 1990; Warlen and Burke, 1990) and pinfish, *Lagodon rhomboides* (Warlen and Burke, 1990), all species that recruit to the estuary with Atlantic menhaden.

The total time required for transport of larvae from the area of hatching offshore to the estuary can be estimated from the ages of larvae caught at Pivers Island. The observed similarities in patterns of ages over each of the seven recruitment years suggest that similar transport mechanisms operate from year to year. Youngest larvae, which are only recruited at the beginning or end of each season, must be recruited most efficiently to the estuary, while at other times in the season transport becomes less efficient as larvae require longer to get to the estuary. Also, as the season progresses it is likely that spawning may occur further offshore (Warlen, 1992) as suitable spawning temperature water is found farther offshore and, consequently, larvae must be transported a greater distance to estuaries. The extended period of transport allows for mixing of birthweek cohorts offshore as evidenced by the greater mix of birthweek cohorts during the late season recruitment peaks. Mixing could also occur if there is "pooling" of larvae outside the inlet. Warlen (1992) suggested that larval Atlantic menhaden transported from offshore in North Carolina to the estuary was rapid in November–December. However, in the January–March period transport was only rapid to about the mid-shelf frontal zone, after which the overall transport rate was much slower. It is this latter spawned group that apparently makes up the largest fraction of estuarine immigrating larvae each recruitment season.

In summary, during an extended period (fall/winter/early spring) Atlantic menhaden spawn and their larvae are recruited to estuaries in the northern portion of the South Atlantic Bight. Although there is variation, consistent temporal patterns of spawning, recruitment density, and age and size trends are observed from year to year. Back-calculated modes in spawning suggest the importance of short periods within the total spawning season and peaks in estuarine recruitment suggest the importance of larval across-continental-shelf transport and near-shore concentrating mechanisms.

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