Abstract–Age, size, abundance, and birthdate distributions were compared for larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly during their estuarine recruitment seasons in 1989–90, 1990–91, and 1992–93 in lower estuaries near Beaufort, North Carolina, and Tuckerton, New Jersey, to determine the source of these larvae. Larval recruitment in New Jersey extended for 9 months beginning in October but was discontinuous and was punctuated by periods of no catch that were associated with low water temperatures. In North Carolina, recruitment was continuous for 5–6 months beginning in November. Total yearly larval density in North Carolina was higher (15–39×) than in New Jersey for each of the 3 years. Larvae collected in North Carolina generally grew faster than larvae collected in New Jersey and were, on average, older and larger. Birthdate distributions (back-calculated from sagittal otolith ages) overlapped between sites and included many larvae that were spawned in winter. Early spawned (through October) larvae caught in the New Jersey estuary were probably spawned off New Jersey. Larvae spawned later (November–April) and collected in the same estuary were probably from south of Cape Hatteras because only there are winter water temperatures warm enough (≥16°C) to allow spawning and larval development. The percentage contribution of these late-spawned larvae from south of Cape Hatteras were an important, but variable fraction (10% in 1992–93 to 87% in 1989–90) of the total number of larvae recruited to this New Jersey estuary. Thus, this study provides evidence that some *B. tyrannus* spawned south of Cape Hatteras may reach New Jersey estuarine nurseries.

Recruitment of larval Atlantic menhaden (*Brevoortia tyrannus*) to North Carolina and New Jersey estuaries: evidence for larval transport northward along the east coast of the United States*

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The larvae of some species of fishes that spawn in the South Atlantic Bight (SAB; Cape Hatteras, North Carolina to Cape Canaveral, Florida) are transported northward to the Middle Atlantic Bight (MAB; Cape Cod, Massachusetts to Cape Hatteras, North Carolina) where they eventually use estuaries as juvenile nurseries. Kendall and Walford (1979) first suggested that spring-spawned bluefish, *Pomatomus saltatrix*, from the SAB are transported several hundreds of kilometers northward where they eventually enter estuaries in the MAB (Hare and Cowen, 1996). Nyman and Conover (1988) and McBride and Conover (1991) used otolith analyses to confirm the presence of a spring-spawned component from the SAB in the juvenile bluefish population in MAB estuaries. The larvae of several other species from more southerly areas are also expatriated to the MAB (Hare and Cowen, 1991; Cowen et al., 1993; McBride and Able, 1998). Tropical and subtropical planktonic invertebrates are also known to occur in the MAB

(Cox and Wiebe, 1979). Some seemingly unusual occurrences of Atlantic menhaden larvae in New Jersey during the winter suggested that the same pattern might occur for this species.

Atlantic menhaden, *Brevoortia tyrannus*, is a clupeid that migrates along the coast from the Gulf of Maine to Florida and adults spawn throughout this range. Studies (summarized in Warlen, 1994; Epifanio and Garvine, 2001) have shown that this species spawns off New England from late spring into summer and again in early fall, off the mid-Atlantic states in spring and fall, and in the SAB from October to March. Maximum numbers of Atlantic menhaden probably spawn during winter in offshore waters south of Cape Hatteras (Reintjes, 1969; Judy and Lewis, 1983) and North Carolina waters are likely one of the

major spawning grounds (Higham and Nicholson, 1964). The larvae are recruited to estuaries in North Carolina (Lewis and Mann, 1971; Warlen and Burke, 1990; Hettler and Barker, 1993; Warlen, 1994). For the purposes of this article, we define estuarine recruitment as the ingress or immigration of larvae to the estuary from the ocean.

A variety of field and laboratory observations suggest that spawning is not likely to occur at the temperatures found from late fall through spring in the MAB. Field observations in Naragansett Bay, Rhode Island (Govoni[1]), have indicated that peak densities of Atlantic menhaden eggs are found at 18–20°C and very few eggs are found at temperatures below 16°C. Kendall and Reintjes (1975) found Atlantic menhaden eggs at only one of 92 stations during one (9 November–14 December) of three late fall-winter cruises in the MAB. A summary of the Marine Monitoring Assessment and Prediction (MARMAP) collections, for November–April of the 1979–87 surveys in the MAB west of longitude 72°W from Montauk Point, New York, to Cape Hatteras, North Carolina, showed late-stage eggs in only 25 of 2247 plankton hauls (Berrien and Sibunka, 1999). Except in one haul in January near Cape Hatteras, all other Atlantic menhaden eggs found in this MAB survey were collected in November. Atlantic menhaden eggs were collected in Onslow Bay, North Carolina, in December 1992 only at temperatures of 17–23.5°C, and most were found at about 22°C (Peters[2]). During South Atlantic recruitment experiment studies (SABRE), eggs were found between the Gulf Stream and mid-shelf fronts (17–23°C) in Onslow Bay (Checkley et al., 1999). Reduced temperatures (14.8–15.7°C) appeared to diminish the ability to induce spawning of Atlantic menhaden in the laboratory (Fitzhugh and Hettler, 1995) as compared to temperatures >17°C. Even if spawning can occur at temperatures <15°C, there must be successful hatching and larval development to ensure larval survival. At 16°C, early larval growth in dry weight was about one-half that at 20°C (Powell, 1993). Therefore, we concluded that optimum temperature for hatching and larval survival and growth is probably ≥16°C.

From the above findings, we concluded that late-fall to early-spring water temperatures in the MAB are unsuitably low for Atlantic menhaden spawning. Water temperatures in the MAB to at least 300 km offshore are usually 7–14°C from mid-November through April (Benway et al., 1993a, 1993b). However, Atlantic menhaden larvae, probably spawned during that period, recruit to New Jersey estuaries from winter to spring (Witting et al., 1999). These two facts suggest a warmer water (i.e. southern) origin of the wintertime larval Atlantic menhaden recruits in New Jersey and prompted us to ask whether larval transport from the SAB could explain this occurrence. To test this hypothesis, we examined synoptic collections of larval At-

lantic menhaden recruiting to estuaries in North Carolina and in New Jersey from fall to spring. We determined the duration of recruitment, age and size, relative abundance, spawning season, and relative contribution of cohorts of larvae spawned in a given calendar week to the estuarine recruitment of Atlantic menhaden larvae to an estuary in each area. These data were used to estimate the percentage of larval Atlantic menhaden collected in the New Jersey estuary that may have originated in the SAB.
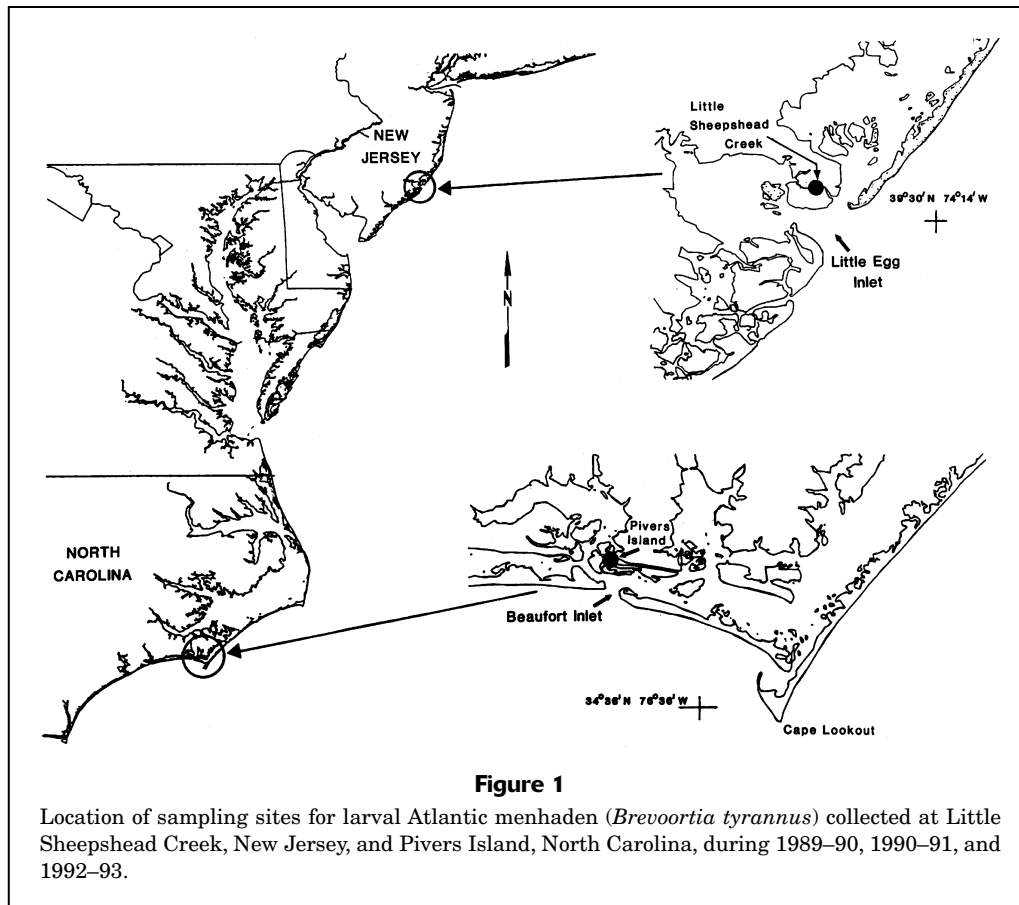
Methods

Larval occurrence and abundance

Sampling for larval Atlantic menhaden was conducted in North Carolina and New Jersey as these larvae recruited to the estuaries from the Atlantic Ocean. In North Carolina, larvae were collected at a station adjacent to Pivers Island in the lower Newport River estuary about 2 km inside Beaufort Inlet (Fig. 1). Nighttime sampling was conducted weekly at mid-flood tide during the expected recruitment period in three seasons (15 November 1989–2 May 1990, 14 November 1990–24 April 1991, and 19 November 1992–11 May 1993). Initial seasonal sampling was based on previous years' collections (Lewis and Mann, 1971; Warlen, 1994) that showed that Atlantic menhaden larval recruitment usually began no earlier than mid-November. End-of-year sampling terminated when larval density dropped to zero. Larvae were collected in four consecutive sets of a 1×2 m neuston net with 947-µm mesh fished (most sets 5–7 minutes long) just under the surface from a bridge platform. A flow meter was attached to the net to estimate the amount of water filtered. Details of the sampling protocol are given in Warlen (1994). Ichthyoplankton samples were preserved in 95% ethanol and diluted so that the final concentration was at least 70% ethanol. Catches were standardized as the number of larvae/100 m^3 of water filtered. The mean of the density data for the four net sets on a given night was used as the density estimate of Atlantic menhaden larvae recruiting during the flood tide.

In New Jersey, gear type and sampling effort were similar in concept but differed in some details (Witting et al., 1999). Ichthyoplankton were collected with a 1-m diameter (1-mm mesh) plankton net fitted with a flow meter. The net was fished during nighttime flood tides from a bridge spanning Little Sheepshead Creek about 3 km upstream from the mouth that is approximately 2.5 km inside Little Egg Inlet (Fig. 1). Water depth at this bridge and the Pivers Island bridge was approximately 4 m. Sampling was conducted over the same years as in North Carolina, and sampling was conducted year round in New Jersey. A mean larval density (number larvae/100 m^3 water fished) was calculated from all samples on each night (five surface and five bottom sets in 1989–90, three surface and three bottom sets in 1990–91, three mid-water sets in 1992–93) and was used to estimate Atlantic menhaden larval recruitment during the flood tide. Each net set lasted 0.5 hour. Current speeds were generally 25–50 cm/s,

[1] Govoni, J. J. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

[2] Peters, D. S. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

Figure 1

Location of sampling sites for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Little Sheepshead Creek, New Jersey, and Pivers Island, North Carolina, during 1989–90, 1990–91, and 1992–93.

and approximated those measured in North Carolina. As in North Carolina, samples were preserved in 95% ethanol.

We assumed that larval fish densities within and among years at a site were comparable (see Witting et al., 1999): therefore year-to-year relative abundances could be estimated at that site. However, differences between sites are not easily compared because the catch efficiency of the two types of passive nets is not known and there is no independent estimate of absolute abundance at either site.

Age, growth, and birthdate determination

Larvae were randomly subsampled from individual weekly net sets at both locations in proportion to their contribution to the total nightly catch. All larvae in catches up to 20 fish were used. In catches of >20 fish, subsample sizes were proportional to catch but generally no more than 50 fish were aged per week from any one site. Experienced otolith readers at the Beaufort Laboratory determined the ages of 1435 larvae from North Carolina and 444 from New Jersey for our study. Larvae were measured to the nearest 0.1 mm standard length (SL) with an ocular micrometer. Estimated age was the number of sagittal otolith growth increments (Maillet and Checkley, 1990) plus an empirically derived value for the number of days (five) from spawning to first increment formation (Warlen, 1992). Additionally, late-larval to early-juvenile Atlantic menhaden reared in the

laboratory through the winter at ambient water temperatures, formed daily otolith growth increments even when temperatures declined to 3°C (Ahrenholz et al., 2000). We assumed that the age at initial increment deposition in larval otoliths did not vary and that otolith increment deposition rate was constant within and between sampling seasons and the two sampling sites.

To reduce the chance of underestimating ages of larvae, we conducted a detailed examination of the otolith microstructure of larvae collected in the 1990–91 season. Otoliths from fish with our assigned January–February hatching dates were re-examined and their growth increments measured on an image analysis system. One reader made all counts and measurements in close consultation with two other experienced otolith readers. In contrast to the North Carolina larvae, New Jersey larval otoliths had areas in the middle portion of the counting path with narrower increments. However, New Jersey larvae did not have checks on their otoliths, which indicated that otolith growth did not stop. The otolith radius, standard length, and age relations suggested that New Jersey fish grew more slowly than North Carolina fish but did not indicate a systematic underestimation of the age of New Jersey fish due to narrow increments.

Average growth of larvae was described by the Laird version (Laird et al., 1965) of the Gompertz growth equation (Zweifel and Lasker, 1976). The model was fitted to

data for SL and estimated age at time of capture. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation (Warlen, 1992). Because the conventional 3-parameter fit produced two cases where the estimates of the model intercept $(L_{(0)})$ were biologically unreasonable, all data sets were rerun by using a 2-parameter (i.e. $A_{(0)}$ and α) fitting procedure and by setting the intercept (third parameter) at 3.5 mm. This size at hatching was an intermediate value between the estimates of Powell and Phonlor (1986) for Atlantic menhaden hatching at 16° and 24°C. The overall average growth rate from hatching to a given age was the quotient of the predicted size at that age minus the size at hatching (3.5 mm) divided by that age. Differences in population growth curves between sampling locations in each year were tested by using a 2-parameter Hotelling's T^2 test of the model parameters (Bernard [1981] as modified by Hoenig and Hanumara[3]).

The birthdate (=spawning date) of each larva was back-calculated by subtracting its estimated age from the date of capture. Birthweek cohorts were defined as larvae spawned in a given calendar week. Density values and percentage age composition of each week's catch were used to estimate the estuarine recruitment of birthweek cohorts for each year and each location by using the methods of Warlen (1994). Birthdate distributions were used to estimate the percentage of larval recruits to the New Jersey estuary that could have originated in the SAB. The menhaden spawning season in North Carolina and New Jersey was estimated from the birthdate distributions of larvae that survived to enter the estuaries. The percentage distribution of spawning by week was based on the relative abundance of larvae collected throughout each recruitment year.

We assumed that larval Atlantic menhaden caught each week were newly recruited to the estuary and that they were in transit past the sampling sites to upper portions of the estuaries. This assumption is supported by the arguments in Warlen (1994), Churchill et al. (1999), and Forward et al. (1999) for the North Carolina sampling site and the patterns observed for other shelf-spawned estuarine dependent species such as summer flounder (*Paralichthys dentatus*) (Keefe and Able, 1993; Able and Kaiser, 1994) and other species for New Jersey (Witting et al., 1999).

Results

Timing and abundance of larval recruitment

The magnitude of larval Atlantic menhaden recruitment appeared to differ substantially between the two locations (Fig. 2). The sum of the weekly mean larval densities
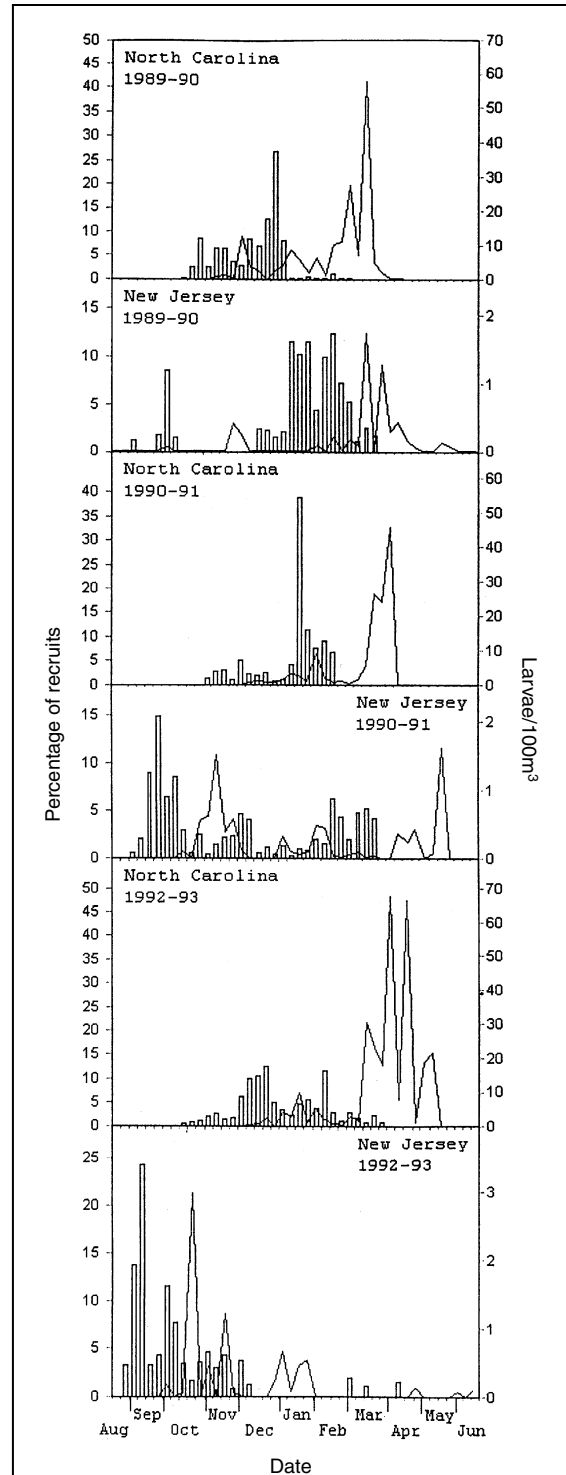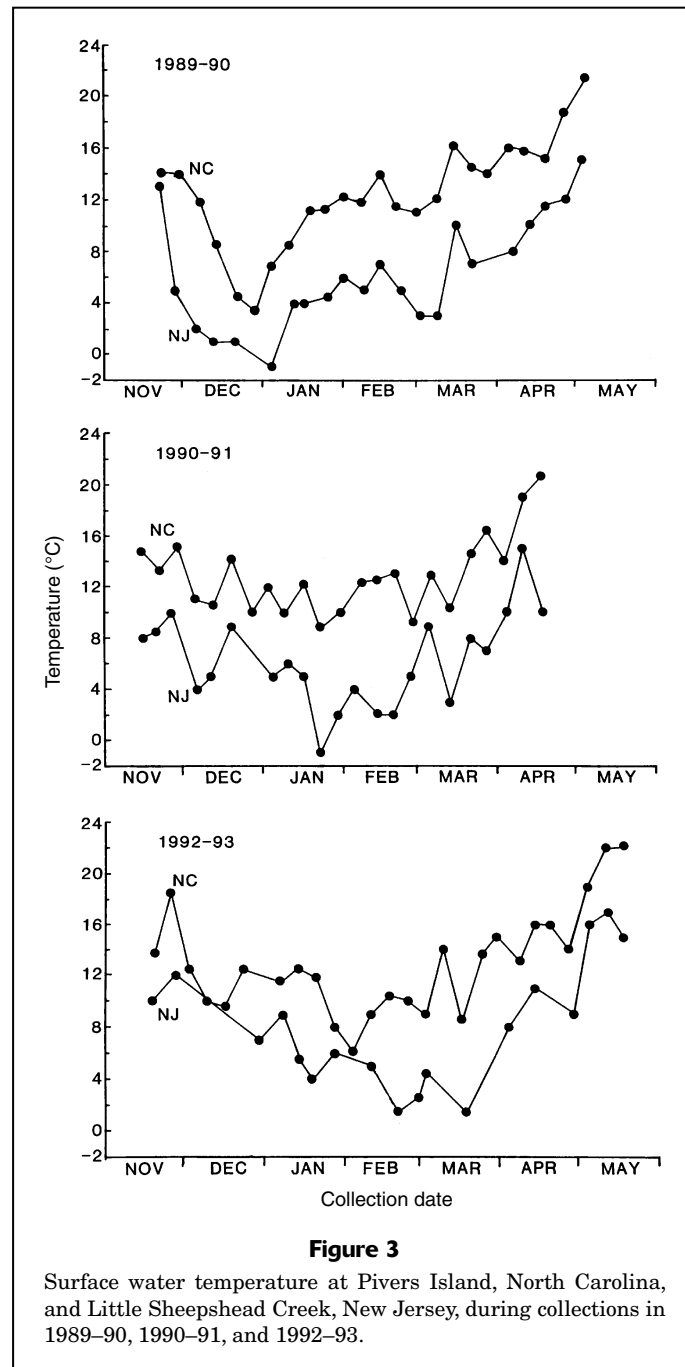
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[3] Hoenig, N. A., and R. G. Hanumara. 1983. Statistical considerations in fitting seasonal growth models for fishes, 25 p. ICES council meeting 1983/D.

Figure 2

Weekly mean density (larvae/100 m³) (line graph) and birthdate frequency distributions (bar graph) as calculated from relative abundances of larval Atlantic menhaden (*Brevoortia tyrannus*) in collections at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during 1989–90, 1990–91, and 1992–93.

Figure 3

Surface water temperature at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during collections in 1989–90, 1990–91, and 1992–93.

over all collections was a measure of the total abundance during a year. The total yearly densities (larvae/100 m^3) for North Carolina were 173 (1989–90), 128 (1990–91), and 286 (1992–93) and for New Jersey were 5.5 (1989–90), 8.4 (1990–91), and 7.3 (1992–93). Although there appeared to be generally large differences in overall abundance between the two areas, we could not determine how much of the 15–39× difference was due to the geographic location, the catch efficiency of the two types of gear, or to differences in sampling effort. Nightly mean densities were always low in New Jersey and, with one exception (20

October 1992), never exceeded 2.0 larvae/100 m^3, whereas in North Carolina nightly catches could exceed 40 larvae/ 100 m^3 every season (Fig. 2).

There were apparent differences in the timing of larval Atlantic menhaden entering estuaries in North Carolina and New Jersey (Fig. 2). Larval recruitment in New Jersey, which extended over a longer period (8–9 months) than that in North Carolina (5–6 months), began in October and ended in June (Fig. 2). Recruitment in New Jersey was discontinuous and was punctuated by periods of no catch, usually in late fall to early spring. The absences of

larval catches in some periods in New Jersey are associated with low water temperatures. There were no larvae caught in December–January of 1989–90 and 1990–91 and in February–March 1993 when water temperatures remained between 1.0 and 5.0°C (Fig. 3). In contrast, recruitment in North Carolina began in November and was continuous until ending in April or May (Fig. 2). Water temperature in North Carolina was warmer than in New Jersey and only twice dropped below 6°C (Fig. 3). In all three years in North Carolina, recruitment was characterized by a late season peak that occurred in March or April (Fig. 2). Predominant recruitment in New Jersey occurred either early (1992–93), late (1989–90) or with peaks early and late in the season (1990–91).

Larval age and size

Menhaden larvae entered both estuaries after development in the ocean. Most larvae were >1 month old and ≥ 17 mm long and there were no recently hatched specimens. However, the age and size of larvae entering the two estuaries differed within and between sites. The weekly mean age of Atlantic menhaden larvae collected in North Carolina increased linearly from early in the season to about the end of March in each year (Fig. 4). The weekly mean age over this period increased by a factor of 2–3×. In two years (1990, 1993) the mean age declined after March to levels approximating those early in the recruitment season. Larvae collected in the North Carolina estuary during peak recruitment were also the older (and larger) larvae. In New Jersey, although there was a general increase in larval age between October and December, there was no late season decline in mean age as we observed for North Carolina larvae. Larvae collected in New Jersey were generally younger than those collected in North Carolina for each of the three years (Fig. 5). The overall mean age of larvae collected in North Carolina for 1989–90, 1990–91, and 1992–93 were 60.7, 58.6, and 69.3 d as compared to 54.3, 52.7, and 50.9 d for New Jersey, respectively. The size of larvae showed seasonal trends similar to those for larval ages in each of the years, i.e. larval length increased and then decreased through time in North Carolina, whereas in New Jersey it increased but did not decline (Fig. 6). Larvae recruited in North Carolina were generally similar in size but were on average larger (24.9, 25.4, and 25.8 mm) than larvae recruited in New Jersey (22.2, 21.3, and 22.1 mm) in all three years (Figs. 6 and 7).

Growth of larvae

Larvae collected in North Carolina were generally older and larger and grew faster than larvae in New Jersey (Fig. 8). Population growth curves were significantly different between sampling locations in all years (Table 1). The predicted overall average growth rate from hatching to 65 d for larvae recruited in North Carolina was similar among years (0.35 mm/d for 1989–90, 0.36 mm/d for 1990–91, and 0.35 mm/d for 1992–93). Corresponding rates for larvae recruited to New Jersey were 0.30 mm/d for 1989–90, 0.31mm/d for 1990–91, and 0.32 mm/d for 1992–93.

Larval birthdates

Back-calculated spawning dates varied between years in both locations but were most variable in New Jersey (Fig. 2). In New Jersey in the 1989–90 season there were two distinct groups of larvae. About 13% of the larvae were spawned early (September–October), then none to the middle of December, and the remaining larvae (87%) were spawned thereafter to the end of March. Larvae captured in North Carolina were spawned from the week ending 21 October 1989 continuously through the week ending 3 March 1990 and overlapped the later spawning dates for New Jersey larvae. Larvae spawned in March recruited to New Jersey but virtually none recruited to North Carolina.
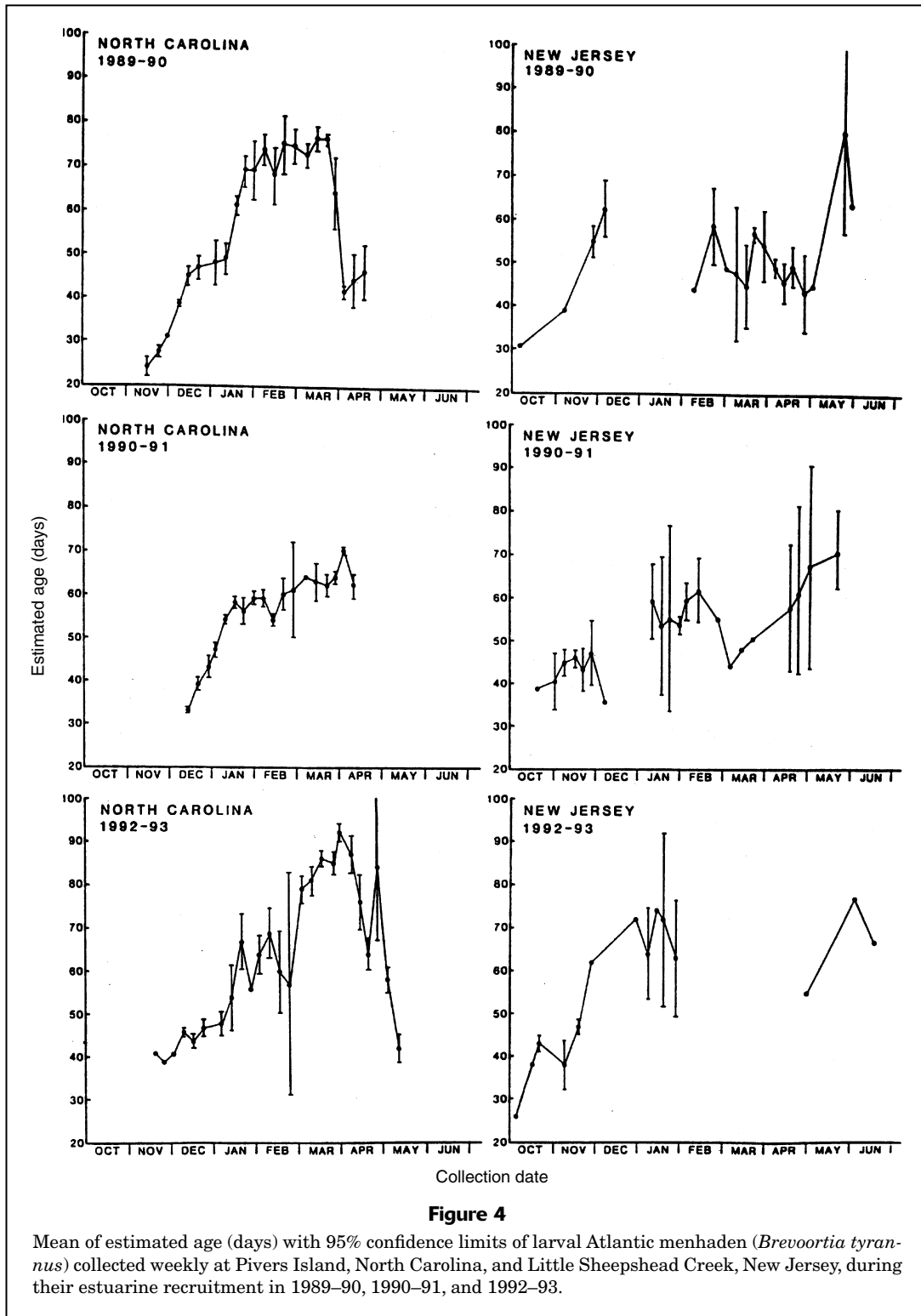
In the 1990–91 season, spawning dates of larvae collected in New Jersey (7 months) totally overlapped those collected in North Carolina (4 months) (Fig. 2). About 45% of the New Jersey larvae were spawned early (through week ending 27 October 1990) and the balance was distributed over the last five months with a mode in the week ending 23 February 1991. As in 1989–90, March-spawned larvae recruited to New Jersey but not to North Carolina. The highest frequency of spawning dates of larvae caught in North Carolina occurred from mid-January to the end of the season and peaked during the week ending 26 January 1991.

The spawning date distributions in 1992–93 were different from those in the previous two sampling seasons. About 77% of the New Jersey larvae were spawned by the end of October. An additional 18% of the total larvae entering the estuary were spawned in November to mid-December and only about 5% of the total were spawned in March–April. Larvae recruited to North Carolina had been spawned from October to April but there was no distinct mode as observed in the other two years. Late season spawning (March–April) contributed larvae to both New Jersey (≈5% of total) and North Carolina (≈13% of total). In both earlier years there were no April-spawned larvae and March-spawned larvae were only found in New Jersey.
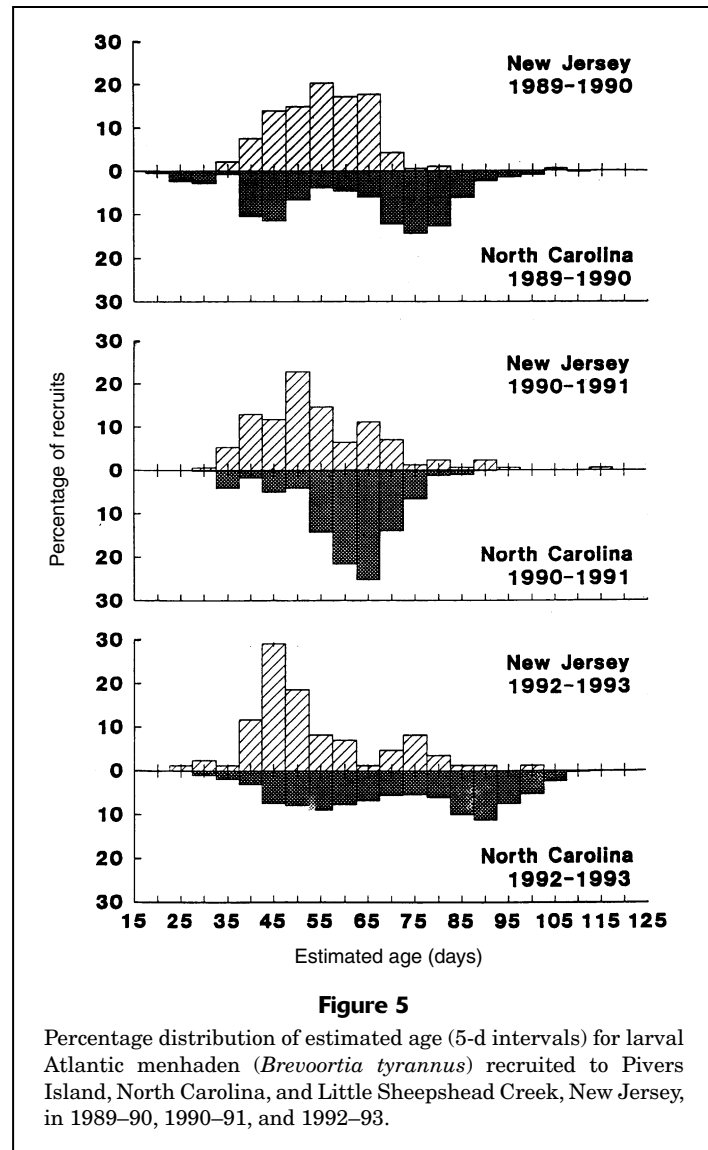
Discussion

Atlantic menhaden larvae recruited to the New Jersey estuary probably originate from two sources: locally (MAB) and from the SAB. Evidence of local spawning is seen in the larvae recruited to the New Jersey estuary from October through early December (Fig. 2). These larvae probably originated from local (i.e. New Jersey) spawning as adults begin their southward migration out of the MAB area in about November of each year (Higham and Nicholson, 1964). Schools of spawning-size adults (200 mm+) are captured in the commercial fishery in the fall and early winter as they move south along the coast from Maryland to North Carolina (Smith[4]). Spawning in the SAB produces larvae, some of which are transported northward and contribute recruits to New Jersey later in

Figure 4

Mean of estimated age (days) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

the recruitment season. Some larvae originating in the southernmost portion of the MAB in fall may even contribute some recruits to the SAB as three-dimensional circulation models have predicted (Quinlan et al., 1999; Rice et al., 1999; Stegmann et al., 1999). However, any adults that

might remain in the MAB after November would experience ocean temperatures on the continental shelf that are not only too cold to allow menhaden spawning but that also might prevent eggs from hatching or larvae from developing. Even if we accept the minimum temperature of 13°C

Figure 5

Percentage distribution of estimated age (5-d intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) recruited to Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.
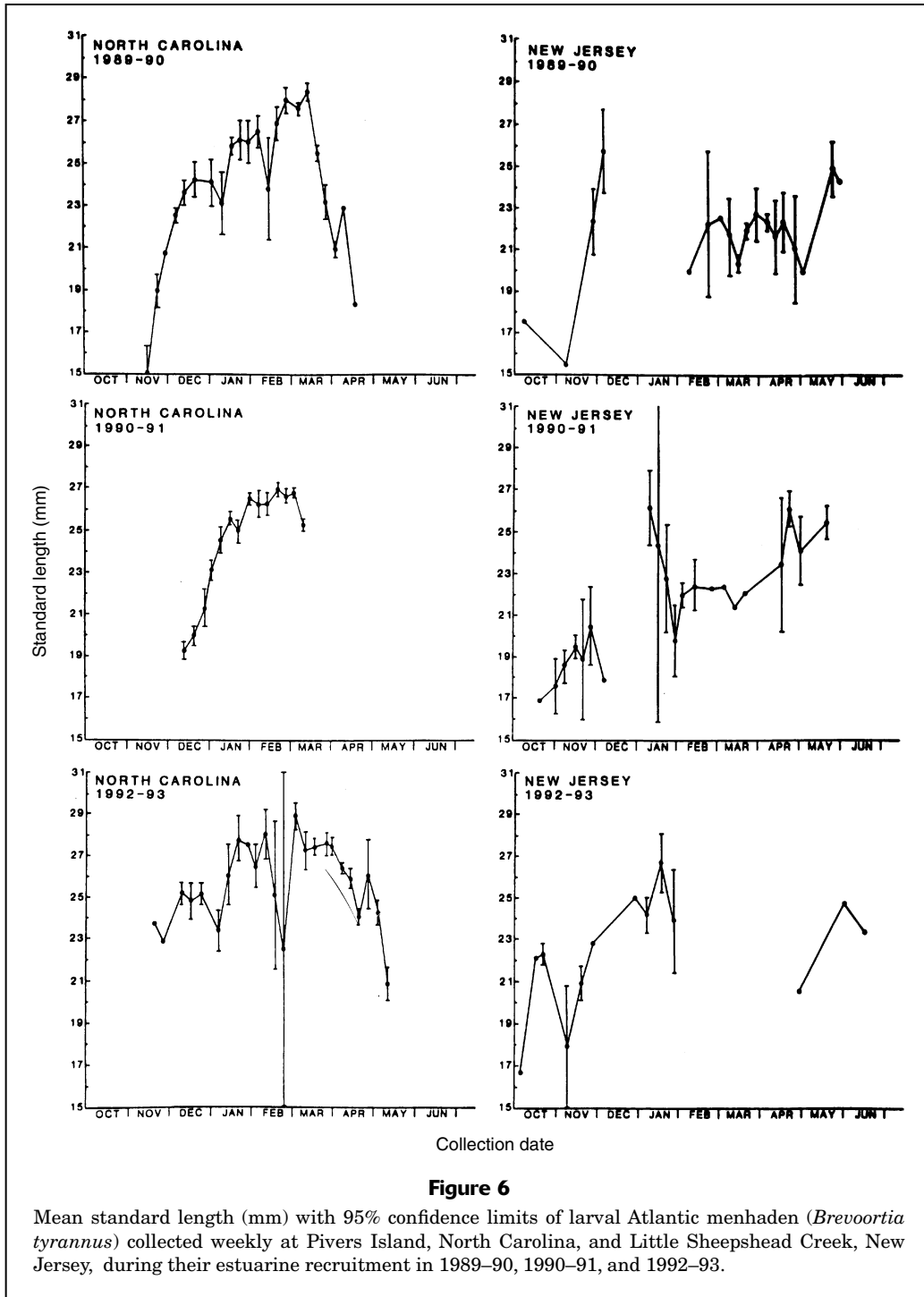
for Atlantic menhaden spawning suggested by Stegmann et al. (1999), there were no water temperatures above 12°C in the MAB in December through March (Fig. 9) during the three years of our study.

Two differing hypotheses could explain the occurrence of menhaden larvae recruiting to the New Jersey estuary in winter and spring. One is that larvae spawned in the MAB in October or November remain in the MAB until they move into estuaries in the spring. This hypothesis would require a retention mechanism to keep larvae on the continental shelf over the winter in water <10°C. No such mechanism is likely as field and modeling studies indicate persistent southwestward transport (Pietrafesa et al., 1994; Churchill and Berger, 1998; Werner et al., 1999). If larvae overwintered on the continental shelf, they would be about 150–210 d old when they recruited to the estuary 5–7 months after spawning. No Atlantic menhaden this old were found in any of the samples, or from any other studies
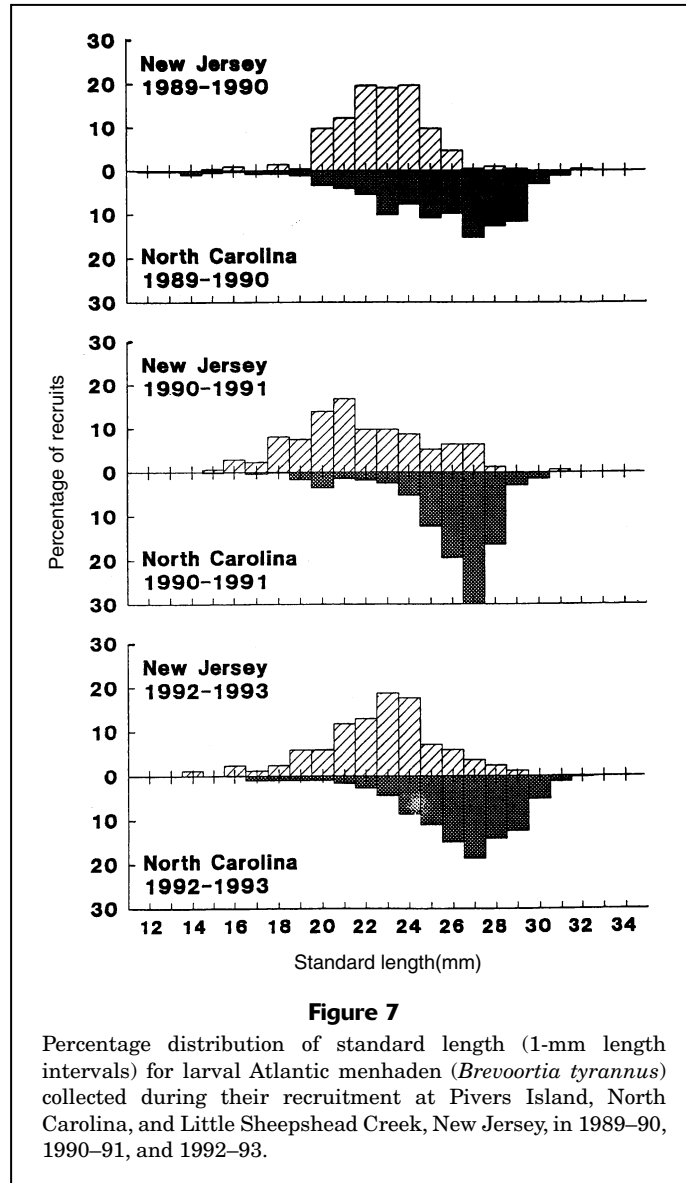
(Warlen, 1994; Rice et al., 1999), and underaging of larval otoliths in our study did not appear to be a problem.

An alternative but more feasible hypothesis for the observed winter-spawned larvae collected in New Jersey from December to the end of the recruitment season (May–June) is that they were spawned in the SAB and were transported northward to the MAB. We used the density-weighted, back-calculated spawning date distributions of larvae collected in New Jersey that were spawned from November to April as the best estimator of the percentage of the total recruits that were spawned in the SAB. If we use the portion of larvae spawned December or later as the most conservative estimator, then the contribution of larvae from the SAB, of all New Jersey recruits, was 87% in 1989–90, 47% in 1990–91, and 10% in 1992–93. If larvae spawned November or later are considered to be from the SAB where there was spawning, then the estimate (87%) is the same for 1989–90 but increases to 55% in 1990–91 and to 23% in 1992–93.

Figure 6

Mean standard length (mm) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

Although the estimated percentage of larvae contributed to the New Jersey estuary from the SAB varied between 10% and 87%, the actual numbers of contributed larvae were relatively low, over an order of magnitude less than that observed for North Carolina, because of the overall low number of larvae recruited there. However, the total contribution of SAB larvae to New Jersey recruitment over the entire season may actually be greater than esti-

mated from the birthdate distributions. The contribution of larvae spawned in the MAB to recruitment in New Jersey is based on the presence of early season larvae, but for these fish to contribute to the population the next spring, they must survive the winter in the estuary. If the winter water temperature in New Jersey estuaries drops below the lethal limit for Atlantic menhaden larvae (<5.0°C; Lewis, 1965), there will be decreased survival for the fall

Figure 7

Percentage distribution of standard length (1-mm length intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected during their recruitment at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.
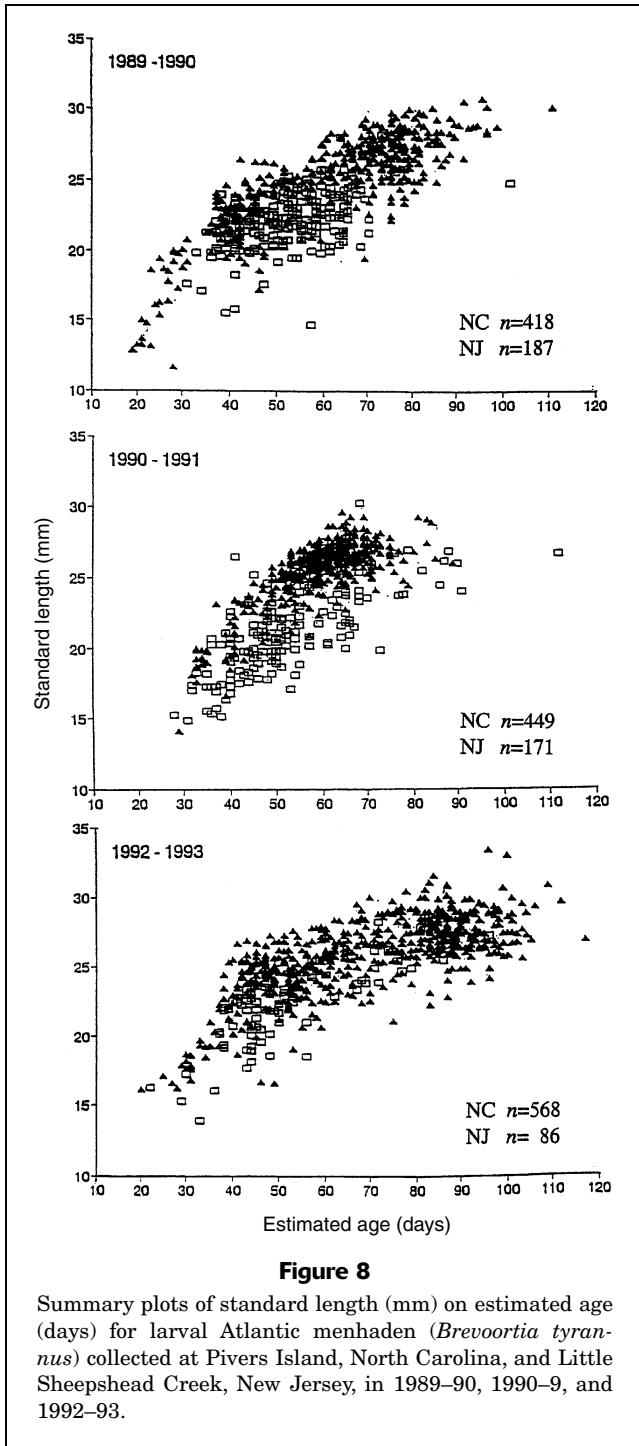
recruited larvae. Temperatures this low are often found during winter in New Jersey estuaries (Able et al., 1992) and result in mortality of several other estuarine species (Szedlmayer et al., 1992; Keefe and Able, 1993; Hales and Able, 2001). We did not catch Atlantic menhaden larvae in the New Jersey estuary at any time when the surface water temperature was <5°C. Temperatures <3°C deterred larval Atlantic menhaden entry into estuaries, inhibited movements into tributaries, and caused mass mortalities in Indian River, Delaware (Reintjes and Pacheco, 1966). Alternatively, larvae recruiting in March or later have less chance of encountering lethal temperatures and experiencing cold-related mortality and hence their proportion of the total year's recruitment may increase.
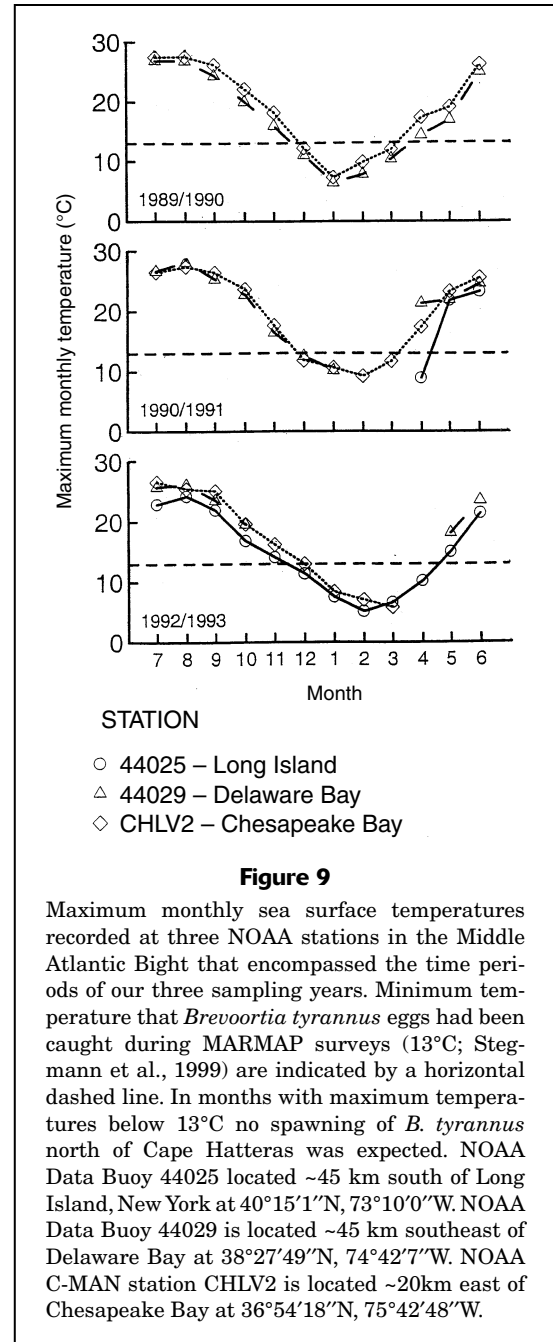
The precise mechanisms responsible for larval Atlantic menhaden transport from the SAB to the MAB are unknown. However, it seems likely that larvae may be trans-ported northward by the Gulf Stream. Atlantic menhaden larvae that are spawned on the outer continental shelf of North Carolina (Checkley et al., 1988; Warlen, 1992; Govoni and Pietrafesa, 1994) may be entrained in meanders that impinge onto the shelf (Pietrafesa et al., 1985) and carried northward out of the SAB. Govoni and Spach (1999) estimated offshore fluxes of Atlantic menhaden larvae from the North Carolina shelf to the Gulf Stream during the winter. Modeling results supported these empirical findings and indicated that export from the North Carolina shelf is influenced by both wind and bathymetry (Hare et al., 1999). Once in the Gulf Stream, larvae can be transported rapidly (≈100 cm/s) to the northeast (Hare[5]).

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[5] Hare, J. A. 1999. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC.

Figure 8

Summary plots of standard length (mm) on estimated age (days) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–9, and 1992–93.

STATION

○ 44025 – Long Island
△ 44029 – Delaware Bay
◇ CHLV2 – Chesapeake Bay

Figure 9

Maximum monthly sea surface temperatures recorded at three NOAA stations in the Middle Atlantic Bight that encompassed the time periods of our three sampling years. Minimum temperature that *Brevoortia tyrannus* eggs had been caught during MARMAP surveys (13°C; Stegmann et al., 1999) are indicated by a horizontal dashed line. In months with maximum temperatures below 13°C no spawning of *B. tyrannus* north of Cape Hatteras was expected. NOAA Data Buoy 44025 located ~45 km south of Long Island, New York at 40°15′1″N, 73°10′0″W. NOAA Data Buoy 44029 is located ~45 km southeast of Delaware Bay at 38°27′49″N, 74°42′7″W. NOAA C-MAN station CHLV2 is located ~20km east of Chesapeake Bay at 36°54′18″N, 75°42′48″W.

Warm core ring streamers and surface intrusions of warmer water could assist in transporting larvae from the Gulf Stream to the MAB continental slope (Hare and Cowen, 1991, 1996). Larvae must then cross the shelf-slope front and once larvae are in shelf waters they may be transported south and westward along the coast and toward shore by the predominant winds from the northeast which induce an Eckman drift westward toward shore.

Biological mechanisms such as vertical migrations and directional swimming behavior, can modulate transport by placing larvae in water masses favorable to cross slope or cross shelf transport (Hare and Cowan, 1996). Cowen et al. (1993) and Hare and Cowen (1993) have described this general scenario for several species that may be transported to the MAB from the SAB.

Regardless of the type of transport mechanisms, it is clear that larvae of a number of other species are transported from the SAB to the MAB. The larvae of *Anguilla rostrata*, which originate in the Sargasso Sea (Schmidt,

Table 1

Estimates of Gompertz growth model parameters ($A_{(0)}$, α) with standard errors in parentheses for larval Atlantic menhaden collected in 1989–90, 1990–91, and 1992–93 in North Carolina and New Jersey and results of Hotelling's T^2 tests comparing growth models between sites for each year. In each model fit, $L_{(0)}$ was set at 3.5 mm standard length. * Significant at 0.01.

	Year		
Statistics	1989–90	1990–91	1992–93
Growth model[1]			
North Carolina			
$A_{(0)}$	0.113 (0.002)	0.101 (0.001)	0.113 (0.002)
α	0.054 (0.001)	0.048 (0.001)	0.055 (0.001)
New Jersey			
$A_{(0)}$	0.129 (0.008)	0.092 (0.003)	0.104 (0.005)
α	0.068 (0.005)	0.046 (0.002)	0.051 (0.003)
Hotelling's T^2			
Sample size			
n_1—NC	418	449	568
n_2—NJ	187	171	85
$F(0.01, f_1, f_2)$[2]	5.30	5.30	5.30
$F_{(calculated)}$	153.87*	127.81*	7.12*

[1] $L_{(0)}$ = length at hatching, $A_{(0)}$ = specific growth rate at hatching, α = exponential decline in $A_{(O)}$.

[2] 0.01 = level of testing, f_1 = np (=no. of parameters), $f_2 = n_1 + n_2 - np - 1$.

1922; McCleave and Miller, 1994), occur in and near the Gulf Stream in the SAB and appear as glass eels in the New Jersey collections at approximately the same time as menhaden larvae (Witting et al., 1999). The same general track is presumed for *Conger oceanicus* which also spawn in the Sargasso Sea (Miller, 1995) and are also collected at the New Jersey study site, although they occur later (May–June) (Able and Fahay, 1998; Witting et al., 1999). Similarly, other species which presumably spawn in the SAB such as *Chaetodon* spp. (McBride and Able, 1998), *Mugil curema* (Collins and Stender, 1989), and *Lutjanus griseus* (Able and Fahay, 1998) also enter the New Jersey study site (Able et al., 1997; Witting et al., 1999). Larval spot, *Leiostomus xanthurus,* spawned south of Cape Hatteras may also be transported to estuaries in the MAB (Norcross and Bodolus, 1991).

In summary, although the SAB may be a very important spawning area for Atlantic menhaden, all larvae produced in the SAB are not retained there; some are transported to the MAB. We believe the birthdate distribution data suggest that Atlantic menhaden larvae spawned in the SAB are an important but variable source of recruits (10–87%) for the MAB based on the collections from New Jersey. The number of winter-spawned larvae ultimately recruited to New Jersey probably depends on the initial number of larvae transported northward from the SAB, the efficacy of the transport mechanisms, and the mortality of larvae during the process. Obviously, the estimates for this single New Jersey estuary may differ from other areas in the MAB. As a result of the above variables and recent insights from the SABRE program, it appears that larval

Atlantic menhaden supply is very complex with frequent exchanges between the MAB and the SAB, as well as the contribution from local spawning. Ultimately, we need to know which spawning seasons and sites contribute most individuals to nursery habitats (Beck et al., 2001) and to the adult population.

The relative contribution of SAB menhaden larvae, and those of other species, to other estuaries in the MAB might clarify the importance of MAB estuaries and contribute to an improved understanding of recruitment mechanisms for shelf-spawned estuarine-dependent fishes in the MAB. Additional evidence for the contribution of SAB larvae to the MAB could come from analyses of the elemental composition of the primordium (nucleus) of larval otoliths from both New Jersey and North Carolina. The laser ablation inductively coupled plasma mass spectroscopy (ICPMS) technique (Campana et al., 1994; Thorrold et al., 2001) might be used to discriminate among larvae to determine if they have similar or different geographic origins. Similarities in elemental composition of New Jersey and North Carolina larvae with the same winter-spawned birthdate would be an important step toward validating the common geographic origin of the larvae recruited to New Jersey and perhaps elsewhere in the MAB.

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