



Abstract—Ichthyoplankton data sets based on collections from estuaries in South Carolina, North Carolina, Virginia, Delaware, and New Jersey and from ocean cruises off the U.S. East Coast were examined to determine spawning locations in the ocean, cross-shelf distributions of larvae, and movements of spot (*Leiostomus xanthurus*) into estuaries. Spot spawn during fall and winter near the edge of the continental shelf, primarily south of Cape Hatteras in North Carolina. We documented additional spawning of spot north of Cape Hatteras, close to the coast, in summer and fall. Larval and early juvenile spot enter estuaries from November through May in South Carolina and North Carolina and from January through June in Virginia, Delaware, and New Jersey. Numbers of spot per volume of water sampled decreased from south to north among estuaries and in the ocean. Interannual variations in abundance were high, and no long-term trends were determined. Over the decades, median annual lengths of ingressing larval and juvenile spot decreased as annual mean water temperature increased in South Carolina and North Carolina. The timing of ingress was positively correlated with water temperature. Continued increases in water temperature on the East Coast will likely lead to additional changes in oceanic distribution and ingress patterns of spot. Our findings indicate the value of synthesizing information from long-term studies conducted across broad geographic scales.

Long-term dynamics of larval and early juvenile spot (*Leiostomus xanthurus*) off the U.S. East Coast: relating ocean origins, estuarine ingress, and changing environmental conditions

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The spot (*Leiostomus xanthurus*) is among the most abundant demersal fish species in the estuaries of the Atlantic and Gulf coasts of the United States and in the coastal ocean. As consumers of infauna and as prey for a range of piscivores, juvenile and adult spot play important ecological roles in shallow-water systems (Able and Fahay, 2010). Adults are harvested recreationally and commercially throughout their range (Hildebrand and Cable, 1930; Summers et al., 1985); however, harvests on the U.S. East Coast have been declining

(ASMFC¹). Although a considerable body of scientific literature is available on the biology and ecology of spot (Hales and Van Den Avyle²), there is a need for a bet-

¹ ASMFC (Atlantic States Marine Fisheries Commission). 2022. ASMFC stock status overview, 53 p. ASMFC, Washington, D.C. [Available from [website](#).]

² Hales, L. S., and M. J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic): spot. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.91). U.S. Army Corps Eng. TR EL-82-4, 24 p. [Available from [website](#).]

ter understanding of its life history, the factors determining temporal dynamics, and the status of populations. One shortcoming is the lack of broadscale, long-term knowledge of the recruitment dynamics of this species.

Along the East Coast, adult spot spend spring and summer in estuaries and the coastal ocean from New Jersey to Florida. In the fall, adults with ripening gonads occur near estuarine inlets (Hildebrand and Schroeder, 1928) before migrating across the continental shelf to spawn (Hildebrand and Cable, 1930). The presence of early-stage larvae indicates that spot spawn near the edge of the shelf between North Carolina and Cape Canaveral, Florida, from late fall to early spring (Powles and Stender³; Lewis and Judy, 1983; Warlen and Chester, 1985). Adult spot make offshore migrations when water temperatures are suitable for spawning. In the laboratory, spot spawn when water cools to between 17.5°C and 25.0°C (Hettler and Powell, 1981), with maximum egg production at 20°C (Powell and Gordy, 1980). Larvae hatch at ~1.6 mm standard length (SL) in about 2 d (Powell and Gordy, 1980).

Spot dominate larval fish collections in winter in ocean waters south of Cape Hatteras (SoCH) in North Carolina, and it is in these waters below this point where they reach maximum abundance on the offshore continental shelf in winter (Powell and Robbins, 1994). The presence of small spot larvae (<4.0 mm SL) offshore of North Carolina indicates that most spawning occurs SoCH (Quattrini et al., 2005). Most spawning takes place where waters of the outer continental shelf mix with waters of the Gulf Stream (Govoni and Pietrafesa, 1994; Govoni and Spach, 1999). Larval spot ranging from 2.8 to 5.9 mm SL have been collected in the region of the Charleston Gyre off South Carolina, where shelf and Gulf Stream waters are mixed and wrapped around eddies; larvae also have occurred in Gulf Stream waters within the core of eddies on the outer continental shelf (J. Govoni, personal commun.). Larval spot grow as they move across the shelf (Lewis and Judy, 1983; Warlen and Chester, 1985). Off North Carolina, larvae of different sizes were more abundant in different areas: small larvae in Gulf Stream and outer shelf waters, medium larvae (4.0–7.5 mm SL) inside the outer shelf mixing zone, and large larvae (>7.5 mm SL) in the mid-shelf water mass (Walsh, 2007).

Advection or transport of larval spot has both a cross-shelf (zonal) component and an along-shore (meridional) component (Hare et al., 1999). It is widely recognized that zonal movement of larvae occurs with prevailing currents that are directed southwestward and are inshore of spawning areas near Gulf Stream fronts (Haight⁴; Werner et al.,

1999; Blanton et al., 2003; Walsh, 2007). Newly hatched larvae are moved toward shore by Gulf Stream intrusions (Govoni and Pietrafesa, 1994) or eddies that strand on the shelf (Govoni et al., 2013).

Meridional transport moves larvae from ocean areas SoCH to waters north of Cape Hatteras (NoCH). Larvae entrained into the Gulf Stream by mixing and exchange with shelf waters at the Gulf Stream front (Govoni and Spach, 1999) can be transported northeastward. Larvae carried by the Gulf Stream could be moved into slope and shelf waters NoCH. Some young larvae remain in the Gulf Stream and have been collected off the coast of New England (Hare et al., 2001). Conversely, larvae in coastal waters off Virginia can be transported south into Onslow Bay, North Carolina (Stegmann and Yoder, 1996; Stegmann et al., 1999; Hare et al., 2001).

Some of the complexities of the transport of larval spot are a result of the nonuniform distribution of larvae in the water column (Hare and Govoni, 2005). Vertical position is important in their transport, zonally, across the shelf toward the East Coast by advection. Larvae and early juveniles in shelf waters <200 m deep are more abundant in the middle and deepest layers than in shallow layers (Hare and Govoni, 2005), and they are transported shoreward by residual lateral water movement at those depths (Pietrafesa and Janowitz, 1988; Hare et al., 1999). Investigating fish assemblages on the continental shelf off Georgia, Marancik et al. (2005) determined that transport of larvae could not be explained solely by 2-dimensional physical factors. Spatial and temporal variations occur in physical properties of shelf waters on multiple scales. Combined with largely unknown changes in behavior by developing larvae, the directions and rates of movement between spawning areas and estuaries remain difficult to resolve.

The age of larval and early juvenile spot (LEJ) collected in estuaries has provided some insights about transport duration. The youngest LEJ spot in Beaufort Inlet, in North Carolina, during 1978–1980 were 40 d old, and the average age was 59 d (Warlen and Chester, 1985). In North Inlet estuary, in South Carolina, during the winter–spring of 1981, the youngest larvae were about 60 d old and the average age was about 80 d (Beckman and Dean, 1984). Variations in both transport duration and environmental conditions across the shelf might account for much of the variation in ages and lengths observed among planktonic stages of spot found outside inlets and inside estuaries.

Larval and early juvenile spot arrive at inlets along the East Coast as far south as the Indian River Lagoon in southcentral Florida (Reyier and Shenker, 2007). Larval and early juvenile spot have been reported from inlets near St. Augustine, Florida (Korsman et al., 2017), the central coast of Georgia (Rogers et al., 1984), an estuary in northern South Carolina (Allen and Barker, 1990), various estuaries in North Carolina (Hettler and Chester, 1990; Hettler and Barker, 1993), Chesapeake Bay in Virginia (Olney and Boehlert, 1988; Ribeiro et al., 2015), the eastern shore of Maryland (Love et al., 2009), Delaware Bay

³ Powles, H., and B. W. Stender. 1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. Mar. Resour. Res. Inst., S.C. Wildl. Mar. Resour. Dep., Tech. Rep. 11, 47 p. [Available from [website](#).]

⁴ Haight, F. J. 1942. Coastal currents along the Atlantic coast of the United States. U.S. Dep. Commer., Coast Geod. Survey, Spec. Publ. 230, 73 p. Gov. Print. Off., Washington, DC. [Available from [website](#).]

(de Sylva et al.⁵; Ribeiro et al., 2015), and Little Egg Inlet in New Jersey (Able and Fahay, 2010). Although LEJ spot were not documented in early ichthyoplankton surveys in Rhode Island (Herman, 1963; Bourne and Govoni, 1988), recent reports indicate rare occurrences in Connecticut (Millstone Environmental Laboratory⁶) and Rhode Island (Schneider⁷).

The most complete understanding of the arrival of spot into estuaries has come from studies along the coast of North Carolina, where larvae and early juveniles reach inlets from late fall through spring (Warlen and Chester, 1985; Flores-Coto and Warlen, 1993; Ross, 2003). Studies in North Carolina have addressed distributions of LEJ spot from the outer shelf to the inner estuary (Lewis and Judy, 1983), ocean movements outside and through inlets (Pietrafesa and Janowitz, 1988; Hettler and Hare, 1998), differences in patterns between neighboring inlets (Hettler and Barker, 1993), demographics of early life stages within estuaries (Flores-Coto and Warlen, 1993), and temporal dynamics within estuaries (Warlen and Burke, 1990; Hettler et al., 1997; Joyeux, 1999). However, a large gap persists in our understanding of the broader spatiotemporal dynamics associated with the ingress of spot into estuaries on a coast-wide scale.

Given the ecological and economic importance of spot in estuarine systems, understanding connections between the ocean and estuaries and how they are influenced by the environment is extremely important. A review of the most recent stock assessment of spot (ASMFC⁸) listed several research priorities that justify this study. The following priorities were identified: 1) examining historical estuarine and oceanic ichthyoplankton data sets to investigate the magnitude of spawning and potential use of larval abundance time series in future assessments, 2) investigating environmental effects (e.g., temperature and large-scale oceanic cycles, such as the Atlantic Multidecadal Oscillation [AMO]) on recruitment of spot, and 3) developing a better understanding of patterns of larval migration into nursery grounds.

The goals of this study were 1) to synthesize and interpret ocean-based ichthyoplankton survey data regarding the origins and transport of larvae across the continental shelf; 2) to determine and compare long-term patterns of

ingress for larval and juvenile spot at multiple estuaries on the East Coast; 3) to explore relationships between spot abundance, size, and phenology and environmental conditions of estuaries and coastal waters during ingress; and 4) to consider effects of changing water temperatures on spawning, ocean transport processes, ingress, and landings of adult spot.

Materials and methods

Size classes

We designated 3 size classes for describing and comparing patterns of distribution of planktonic stages of spot in the ocean: small (nominal yolk sac and preflexion, ≤ 4.9 mm SL), medium (nominal flexion, 5.0–8.9 mm SL), and large (nominal postflexion, 9.0–20.0 mm SL). Specimens >16 mm SL, referred to herein as *early juveniles*, usually had a complete set of fins. Because 2 or 3 size classes often occurred in the same collection, we generally refer to the spot in this study as *larvae and early juveniles* of the species. Spot collected in estuarine ichthyoplankton collections included some specimens >28 mm SL; however, because their transition to the demersal phase had occurred (Hodson et al., 1981) and because they likely were not recent arrivals to estuaries, they were excluded from our analyses. In analyses of estuarine collections, we included all larvae and juveniles ≤ 27 mm SL.

Ocean

Data for larval spot from the ocean region NoCH (between 35°15'N and 42°0'N) came from 4 sampling programs conducted by the NOAA Northeast Fisheries Science Center. Details for the 4 programs, Marine Resources Monitoring, Assessment and Prediction (1977–1987), Herring and Sand Lance Program (1988–1994), Georges Bank Global Ecosystems Dynamics (1995–1999), and Ecosystem Monitoring (1999–present), can be found in Walsh et al. (2015). The basic station protocols were very similar among programs, providing consistency in sampling (Jossi and Marak, 1983; Ejsymont and Sherman, 2000). Samples were collected both day and night by using 61-cm-wide bongo nets (Table 1). Oblique tows were taken at 1.5 kt (0.77 m/s) with a minimum duration of 5 min, and nets were fished from the surface either to within 5 m of the seabed or to a maximum depth of 200 m. The volume of water filtered was measured with mechanical flowmeters mounted across the mouth of each net.

Shelf-wide station coverage extended from Cape Hatteras to the Gulf of Maine. A variety of sampling strategies were employed, including those that involved transects, fixed stations, and stations selected through a stratified random design. Most collections were processed at the Morski Instytut Rybacki in Szczecin, Poland, and the remaining collections were processed at

⁵ de Sylva, D. P., F. A. Kalber Jr., and C. N. Shuster Jr. 1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper water. Univ. Del. Mar. Lab., Info. Ser. Publ. 5, 164 p. [Available from [website](#).]

⁶ Millstone Environmental Laboratory. 2021. Annual ecological report 2020: monitoring the marine environment of Long Island Sound at Millstone Power Station, Waterford, Connecticut, 205 p. Millstone Environ. Lab., Dom. Energy Nuclear Conn., Waterford, CT. [Available from the Millstone Power Station Environ. Lab., 314 Rope Ferry Rd. (Rte. 156), Waterford, CT 06358.]

⁷ Schneider, E. 2021. Personal commun. Rhode Island Div. Mar. Fish., 3 Fort Wetherill Rd., Jamestown, RI 02835.

⁸ ASMFC (Atlantic States Marine Fisheries Commission). 2017. 2017 spot stock assessment peer review, 9 p. Atlantic States Mar. Fish. Comm., Arlington, VA. [Available from [website](#).]

Table 1

Gear, tow type, mesh size, and years sampled for the ichthyoplankton collections used to assess the occurrence and length distributions of larval and early juvenile spot (*Leiostomus xanthurus*) during research cruises in the ocean north of Cape Hatteras in North Carolina (between 35°15'N and 42°0'N) and south of Cape Hatteras (below 35°15'N).

Region	Gear	Tow type	Mesh size (µm)	Years
North of Cape Hatteras	61-cm bongo	Oblique	505	1977–1994
	61-cm bongo	Oblique	333	1988, 1995–2018
South of Cape Hatteras	1-m Tucker trawl	Surface	333	1992
	Issacs-Kidd trawl	Midwater	Unknown	1979–1982
	1-by-2-m frame net	Neuston	950	1973, 1992–1995
	20-by-40-cm frame net	Neuston	947	1973–1975, 1977–1982, 1985, 1986, 1995
	61-cm bongo	Neuston	333	1988
		Neuston	505	1973, 1975–1982, 1985, 1986, 1988, 1992, 1993
		Neuston	838	1988
		Oblique	333	1988, 1990–1996, 1998–1999
		Oblique	505	1988, 1990, 1991
		Surface	333	1990–1995
		Surface	505	1990–1991
	Unknown	505	1973–1980, 1982, 1985, 1995	

the Narragansett Laboratory (Narragansett, RI) or the James J. Howard Marine Sciences Laboratory (Highlands, NJ) of the Northeast Fisheries Science Center or at the Atlantic Reference Centre (St. Andrews, Canada). A minimum of 50 randomly selected LEJ spot were measured to the nearest 0.1 mm SL. The total number of LEJ spot, concentration (number of spot per 100 m³), minimum SL, and maximum SL were available for 1 bongo-net collection at each station.

Data for larvae from the region SoCH (south of 35°15'N) came from 2 sources: the plankton archives at the Beaufort Laboratory of the NOAA Southeast Fisheries Science Center and the Marine Resources Research Institute of the South Carolina Department of Natural Resources. Collection gear and tow types used in sampling programs SoCH are provided in Table 1. The collections and data obtained from the Marine Resources Research Institute were from ichthyoplankton sampling programs conducted by the Southeast Fisheries Science Center, nominally between February 1973 and April 1995: Marine Resources Monitoring, Assessment, and Prediction and Southeast Area Monitoring, Assessment, and Prediction (Collins and Stender, 1989). The number of collections per date and the locations of tows varied among years. Collections were made with tows of 61-cm-wide bongo nets (with mesh sizes of either 333 µm or 505 µm) at stations over the inner (minimum depth of 9 m), middle, and outer continental shelf from just south of Cape Canaveral to off Cape Lookout in North Carolina. The total number of LEJ spot, minimum SL, and maximum SL were available for 1 bongo-net collection at each station on all dates.

Ichthyoplankton collections and data obtained from the Southeast Fisheries Science Center came from the South Atlantic Bight Recruitment Experiment and other

cruises conducted before and after the South Atlantic Bight Recruitment Experiment. Samples were collected primarily during the fall and winter in 1988 and 1990–1999 (Table 1). Collections were made with tows of a 61-cm-wide bongo net (with mesh sizes of either 333 µm or 505 µm) within 3 m of the surface and obliquely through the water column. Surface tows were also made with a 1-m-wide Tucker trawl net (with a mesh size of 333 µm). The volume of water filtered in bongo-net and Tucker-trawl collections was measured with a mechanical flowmeter mounted across the mouth of each net. Collections were also made by towing a neuston net with a 1-by-2-m frame (and a mesh size of 950 µm), with the top of the frame 0.25 m above the water's surface. Collections occurred primarily from off Charleston, South Carolina, to Cape Hatteras and targeted fish species that spawn on the shelf and, as juveniles, use estuarine habitats. Cross-shelf transects bisecting the cusped bays SoCH were the predominate sampling strategy for many of the cruises. In addition, concentration of spot (number of spot per 100 m³) was available for 1 bongo-net and 3 Tucker-trawl tows at each station.

Data from sampling in the ocean were grouped for analyses into 2 regions, NoCH and SoCH. Collections were made during all 12 months in each region (Table 2). Effort varied among months and years in both regions. The number of years during which collections were made within a given month varied from 13 to 41 NoCH and from 1 to 14 SoCH (Table 2). The total number of collections NoCH (number of samples [n]=28,280) was more than 9 times greater than that SoCH (n=3098) (Table 2). The full data set (with information from all collections) was used to describe seasonal patterns for the 2 regions based on presence or absence of and minimum and maximum lengths of

Table 2

Summary of monthly data used to assess the occurrence and length distributions of larval and early juvenile (LEJ) spot (*Leiostomus xanthurus*) collected during cruises north of Cape Hatteras in North Carolina (NoCH, between 35°15'N and 42°0'N) and south of Cape Hatteras (SoCH, below 35°15'N) between 1973 and 2018. The following information is presented for each month: the total number of years in which collections were made, the total number of collections with and without LEJ spot, the percentage of all collections with LEJ spot, the number of individuals caught in all collections taken that month, and the minimum and maximum lengths (standard lengths, in millimeters) of LEJ spot collected during the month.

Region	Month	No. of years collections made	No. of collections with LEJ spot	No. of collections without LEJ spot	Percentage of collections with LEJ spot	No. of specimens	Min. length	Max. length
NoCH	Jan.	25	23	1759	1.2	121	4	13
	Feb.	36	29	2417	1.2	138	3	17
	Mar.	39	36	2503	1.4	418	2	18
	Apr.	41	8	2874	0.3	33	7	19
	May	34	19	2961	0.6	57	2	20
	Jun.	31	11	2199	0.5	237	1	4
	Jul.	13	1	1021	<0.1	1	4	4
	Aug.	28	12	2658	0.4	118	1	3
	Sep.	35	39	1837	2.1	299	1	9
	Oct.	36	1	3008	0.4	2	6	11
	Nov.	37	8	3550	0.2	20	2	13
	Dec.	17	1	1305	<0.01	1	7	7
SoCH	Jan.	12	153	327	32	4276	2	17
	Feb.	14	184	485	28	5800	2	21
	Mar.	10	29	184	14	480	4	17
	Apr.	10	32	310	9	269	2	11
	May	7	0	244	0	0		
	Jun.	3	0	61	0	0		
	Jul.	3	0	73	0	0		
	Aug.	6	0	243	0	0		
	Sep.	9	1	277	<0.01	1	4	4
	Oct.	2	2	58	3	2	2	3
	Nov.	1	2	46	4	13	4	6
	Dec.	5	110	277	28	1137	2	12

LEJ spot. The decision to include all mesh sizes was based on studies comparing lengths of larval fish collected in nets with different meshes that were deployed at the same time. Johnson and Morse (1994) reported that the smallest larvae (2–3 mm SL) of 6 species were collected in nets with mesh sizes of both 333 μm and 505 μm . Only these 2 mesh sizes were used in the NoCH collections. Powell et al. (2000) noted that, although the smallest larvae caught in 333- μm -mesh nets (<3 mm SL) were not caught in 947- μm -mesh nets, 3–4 mm SL larvae were present in the collections made with nets with a mesh size of 947 μm . Most collections SoCH were made with nets with mesh sizes of 333 μm and 505 μm . The results of both studies indicate differences in the concentrations of larvae in most collections made by using nets with these mesh sizes.

Accordingly, concentrations of spot collected in the ocean were determined by using a subset of samples. Only collections made with 61-cm bongo nets with 333- μm -mesh nets towed obliquely through the entire water column were used to examine spatial and environmental patterns during the oceanic life stages. Concentrations

were binned into 2-month sampling periods: January–February, March–April, May–June, July–August, September–October, and November–December. Individual size classes were compared between the 2 regions with samples for the 2-month periods. Analysis of variance was done in Matlab⁹ (vers. 9.12; MathWorks Inc., Natick, MA) to determine if concentrations of spot among collections in the 2 regions were significantly different for each size class.

Cross-shelf (distance from shore) and environmental (sea-surface temperature and sea-surface salinity) patterns for the waters where spot were collected, by size class, were examined by using quotient analysis. Quotient analysis is relatively robust for data sets containing many values of 0, allowing regional analyses despite the rarity of spot larvae in collections NoCH (Bernal et al., 2007). With this analysis, the ratio of the proportion of

⁹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

larval occurrence to the proportion of observations was determined within environmental bins (distance from shore, temperature, and salinity) to discover where larvae were collected with higher (or lower) frequency than would be expected if larvae were evenly distributed. Quotient values >1 and above the upper confidence interval indicate a relatively higher occurrence of larvae, based on the number of observations, than expected. Quotient values just above or below 1 and below the upper confidence interval and above the lower confidence interval indicate occurrence at the expected level (van der Lingen et al., 2001). We examined the distance from shore (in kilometers), sea-surface temperature (in degrees centigrade), and sea-surface salinity for the locations where spot were collected for each of the 3 size classes of larvae (using Matlab).

Estuaries

Ichthyoplankton sampling in estuaries in South Carolina, North Carolina, Virginia, Delaware, and New Jersey resulted in data on abundance, lengths, and timing of ingress (phenology) of LEJ spot and on environmental parameters during ingress. Locations of the estuarine sampling sites are shown in Figure 1, and descriptions of the sampling gear, deployment strategies, and timing of collections for each site are provided in Table 3.

North Inlet estuary is a shallow, ocean-dominated salt marsh system with an extensive network of tidal creeks. Semidiurnal tides, with a mean tidal range of 1.4 m, maintain salinities at a range of 30–34 in the core of the estuary through most of the year. Water temperatures in the well-mixed salt marsh creeks of this system are usually 8–12°C

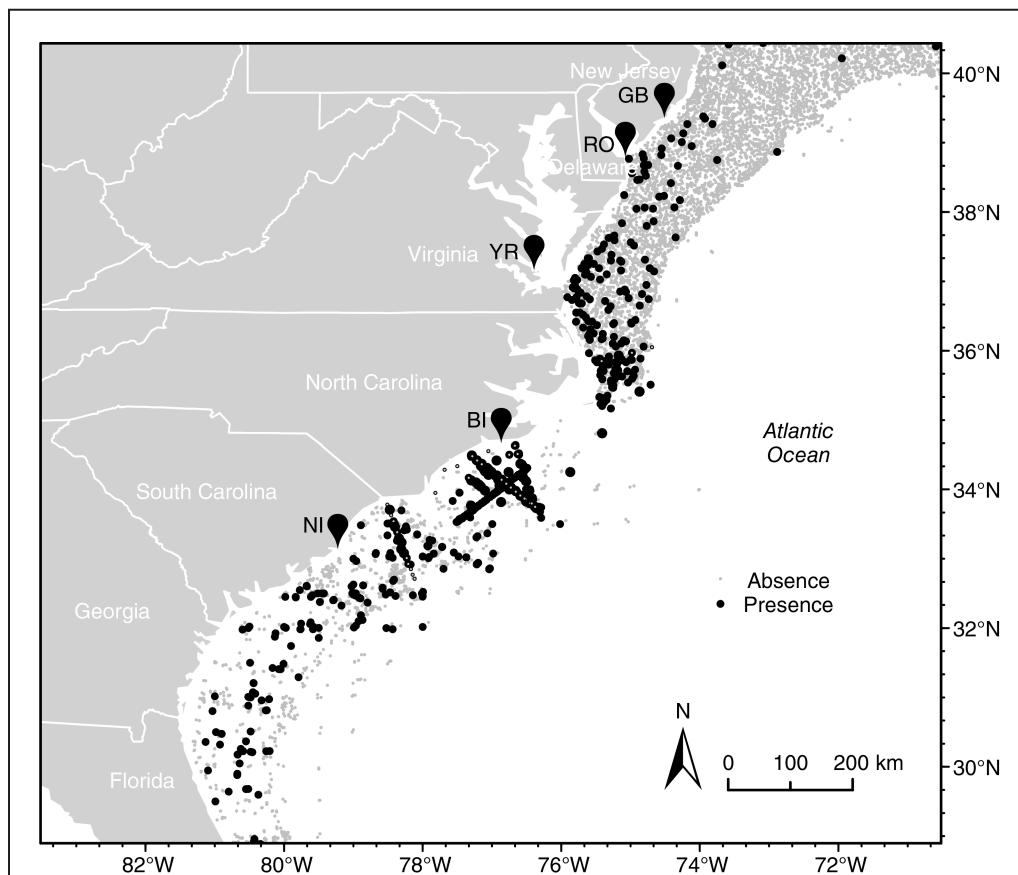


Figure 1

Map of presence (large black dots) and absence (small gray dots) of larval and early juvenile (LEJ) spot (*Leiostomus xanthurus*) in ocean-based collections made during 1973–2018 along the U.S. East Coast from central Florida to central New Jersey and included in this study. Although collections occurred north into the Gulf of Maine, so few LEJ spot were collected there (all far offshore) that these data were not plotted. The distribution of points represents all collections made during the cruises and sampling programs identified in Table 1. The dots in the lines that cross each other off the coast of North Carolina represent closely spaced sampling stations in roughly perpendicular transects. Balloons indicate the locations of the 5 estuaries where collections occurred: North Inlet (NI) in South Carolina, Beaufort Inlet (BI) in North Carolina, York River (YR) in Virginia, Roosevelt Inlet (RO) in Delaware, and Great Bay (GB) in New Jersey.

Table 3

Characterization of the estuarine sampling programs and data sets for collections of larval and early juvenile (LEJ) spot (*Leiostomus xanthurus*) in estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) during 1982–2017. Net size is the area of the mouth of the net. The sampling frequency at North Inlet was once every 2 weeks. Period of occurrence is based on the months of earliest and latest occurrences of spot at each estuary for all years of sampling combined. Number of dates includes both the number of samples in which LEJ spot occurred and the number of all samples collected over all of the years at each site. Percentage of dates is the frequency of occurrence in the time series.

Estuary	Gear	Net size	Mesh size (µm)	Period	No. of years	Time of day	Sampling frequency and period	Period of occurrence	No. of dates (% of dates)
North Inlet, SC	Rectangular net on epibenthic sled	0.13 m ²	365	1982–2017	36	Day	Biweekly, all year	1 Nov.–31 May	246/515 (48%)
Beaufort Inlet, NC	Rectangular net	2 m ²	1000	1985–2017	31	Night	Weekly, only 1 Nov.–31 May	1 Nov.–31 May	668/949 (70%)
York River, VA	Ring net	0.79 m ²	1000	2008–2014	7	Night	Weekly, all year	1 Jan.–30 June	91/187 (49%)
Roosevelt Inlet, DE	Ring net	0.79 m ²	1000	2006–2010	5	Night	Weekly, all year	1 Jan.–30 June	44/136 (32%)
Little Egg Inlet, NJ	Ring net	0.79 m ²	1000	1989–2017	29	Night	Weekly, all year	1 Jan.–30 June	63/707 (9%)

in winter and 26–30°C in summer (Allen et al.¹⁰). The sampling location was in Town Creek about 2 km from the inlet. Depth at the time of sampling during the daytime mid-ebb tides was 2.5–4.0 m, and surface current velocities were usually 1.0–1.2 m/s. Tows were made with a net, which had a diameter of 0.5 and a mesh size of 365 µm, fitted to the vertically oriented rectangular frame (mouth) of an epibenthic sled. Three consecutive (replicate) tows were made from a boat in the direction of the current along a 150-m path on every sampling date (Table 3).

Beaufort Inlet is the location of tidal exchange between the ocean and Back Sound, Bogue Sound, and several estuarine systems. Samples were collected from a fixed platform on Pivers Island Bridge in Beaufort, North Carolina (Table 3), about 1.5 km inside Beaufort Inlet. The bridge spans a channel that is 40 m wide and 7 m deep. An estimated 10% of the water entering Beaufort Inlet flows through this channel (Checkley et al., 1999). Tidal range was about 1 m. The seasonal temperature range was 8–30°C. Larvae were collected at night with a 2-m² rectangular plankton net that had a mesh size of 1000 µm and was fitted with a flowmeter. Four sequential (replicate) net deployments were made at maximum flood velocity. The net was deployed just below the surface during nighttime flood tides.

The site in the York River at Gloucester Point, Virginia, is located about 11 km from the river mouth and 47 km from the entrance to Chesapeake Bay. At this location, the

river is 700 m wide and 4 m deep. During this study, water temperature ranged from 2°C to 29°C, salinity ranged from 14 to 24, and current velocity ranged from 0.2 to 0.8 m/s (Chesapeake Bay National Estuarine Research Reserve in Virginia, Virginia Institute of Marine Science, Virginia Estuarine and Coastal Observing System [VECOS], available from [website](#), accessed July 2024). On each date of sampling, 3 consecutive (replicate) deployments were done with a 1-m-diameter ring net, which was fitted with a flowmeter and had a net mesh size of 1000 µm, from the pier (at the Virginia Institute of Marine Science) during a nighttime flood tide; the 3 deployments were timed with one at peak flood tide, one before peak flood, and another after peak flood.

Roosevelt Inlet, near Lewes, Delaware, is located at the mouth of the Broadkill River, about 5 km from the mouth of Delaware Bay. At this sampling location, the river is 60 m wide and 3 m deep. Water temperature varied from 1°C to 28°C, salinity ranged from 4 to 33, and tidal water velocity ranged from 0.3 to 0.5 m/s (Ribeiro et al., 2015). On each sampling date, 3 consecutive (replicate) deployments were done with a flowmeter-fitted, 1000-µm-mesh, 1-m-diameter ring net from a pier on flooding tides at night.

Little Egg Inlet, in New Jersey, connects the Great Bay–Little Egg Harbor estuarine system to the ocean. This polyhaline estuary has a broad, seasonal temperature range of –2–28°C, average water depth of 1.7 m, and a moderate tidal range of about 1 m (Kennish, 2003). Sheepshead Creek, located about 2.5 km from Little Egg Inlet, is among the several thoroughfares or “creeks” that run through a peninsula and serve to connect Great Bay and Little Egg Harbor. Portions of the flood tide waters from the ocean are diverted into the mouth of Little Sheepshead Creek, where the average depth is about 1.5 m

¹⁰ Allen, D. M., W. B. Allen, R. F. Feller, and J. S. Plunkett (eds.). 2014. Site profile of the North Inlet–Winyah Bay National Estuarine Research Reserve, 312 p. North Inlet–Winyah Bay Natl. Estuar. Res. Reserve, Georgetown, SC. [Available from [website](#).]

(Chant et al., 2000). Sampling was done from the bridge at Little Sheepshead Creek on flooding tides at night, with 3 consecutive (replicate) deployments of a 1000- μm -mesh, 1-m-diameter ring net fitted with a flowmeter.

Differences in the gear, timing, and frequency of the sampling among the 5 estuaries (Table 3) were considered in comparing the data sets. Sampling at North Inlet estuary differed most from that in the other estuaries, with tow collections low in the water column and close to the bottom, a net area and mesh size that were smaller than those of the gear used at other sites, and sampling done during the day. In a comparison of LEJ spot in collections at North Inlet estuary during simultaneous deployments (day and night, ebb and flood) of the epibenthic sled (mesh size: 365 μm) and fixed nets (mesh size: 1000 μm , similar to the mesh size of nets used for collections in Virginia, Delaware, and New Jersey), concentrations in the sled towed during the day were 2–4 times less than concentrations in a 0.79-m² fixed net used to sample during the flooding tide the same night (senior author, unpubl. data). Because the concentrations of LEJ spot in South Carolina appear to be biased low, comparisons of concentrations in South Carolina with those in other states should be made with this bias in mind. The potential effect on concentrations and fish lengths of using a much larger net (with a mouth area of 2 m²) in North Carolina, compared to the 0.79-m² nets used in Virginia, Delaware, and New Jersey, was not tested.

Length distributions in South Carolina were similar among all types of gear used at different tide stages and times of day (senior author, unpubl. data). Accordingly, the use of length distributions, the timing of occurrence (phenology), and temporal patterns of abundance of LEJ spot in South Carolina in comparisons of estuaries is considered valid and strong. The 1000- μm -mesh nets used at the other estuaries are appropriate for collecting larval fish with lengths >3 mm (Powell et al., 2000), well below the length of the smallest spot that have been documented in estuaries.

Because the ingress of LEJ spot was usually between November and May in South Carolina and North Carolina and between January and June in northern estuaries, periods of ingress rather than calendar years were used to define years for comparisons within and among estuaries. The first day of the month of earliest occurrence and the last day of the month of last occurrence in each time series were established as the end points of the period of occurrence (POC) at each estuary. The POCs used for comparing abundance and lengths during ingress among years were as follows: 1 November–31 May in South Carolina and North Carolina and 1 January–30 June in Virginia, Delaware, and New Jersey. Although LEJ spot usually first occurred in estuaries in South Carolina and North Carolina in November or December, the calendar year starting on 1 January of that POC was used to identify the year class. For example, if the first LEJ spot were collected in 1991 (before 1 January 1992), they were included in the analysis for the 1992 POC year class. If no larvae occurred before 1 January, zeros for all sampling dates back to the beginning of the POC (1 November in South Carolina and North Carolina) were used in the calculation of abundance for that

year. This approach enabled direct comparisons of ingress periods for each year class among estuaries.

Data were not grouped by calendar year for any analyses; therefore, the term *annual* always refers to the POC for that estuary. Mean annual concentrations for each estuary were based on the number of LEJ spot per cubic meter of water filtered in all collections between the designated start and end dates of the POC. In North Carolina, sampling ceased in late April or in mid-May during 16 of the 31 years (mostly during 1987–1997). However, in years when sampling occurred until the end of May, no or very few LEJ spot were collected during those final 2 weeks of the designated POC. All collections in North Carolina between 1 November and the last date sampled until May 31 were used in calculations for comparisons of abundance and length among years.

To determine interannual differences and long-term trends in the timing of ingress into estuaries for LEJ spot, we used the cumulative summation procedure to generate phenological metrics (Greve et al., 2005). Four metrics were selected to examine the timing of occurrence in the estuaries: early, middle, late, and peak dates within the POCs. Determination of the timing of these phenological events was based on abundance data. Calculations for the phenology analyses required a common time line for all estuaries. Calendar dates corresponding to the events were converted to day numbers 1–365 with 1 November as day 1 for all estuaries, even though ingress into the estuaries NoCH did not occur until January. To avoid bias associated with the tails (actual first and last dates of ingress) of the annual abundance curves, the earliest and latest dates of occurrence of larvae and juveniles each year were determined by summing concentrations for all dates within POCs and determining the dates on which 15% (early), 50% (middle), and 85% (late) of the total annual concentration (sum for all dates) were reached (Greve et al., 2005). The peak occurrence date for each year was the actual date on which the highest concentration was observed. Years in which larvae did not occur on at least 3 dates were not included in the analyses of these phenological metrics. Duration was defined as the number of days between the early (15%) and late (85%) dates of occurrence each year.

Water temperature and salinity measurements were made at the time of the ichthyoplankton collections on almost every date at all estuaries. Mean annual values were based on all sampling dates from the first to the last date of spot occurrences (i.e., during the POC for that estuary) each year. These mean annual values of water temperature and salinity were used in correlation analyses with abundance, phenology, and fish length at each estuary.

Relationships between climate events and the abundances and timing (phenological metrics) of LEJ spot were explored for each estuary. North Atlantic Oscillation (NAO) annual index data were obtained from the National Center for Atmospheric Research (indices produced by the Climate Analysis Section in Boulder, Colorado, based on Hurrell et al. (2003), available from [website](#), accessed July 2024). Atlantic Multidecadal Oscillation data were obtained from the Earth System Research Laboratory

(Enfield et al., 2001; data available from [website](#), accessed July 2024). Indices used for the El Niño–Southern Oscillation (ENSO) were obtained from the Oceanic Niño Index generated by the Climate Prediction Center of the National Weather Service (data available from [website](#), accessed July 2024). Average index values for the period from December through February were used to create climate event metrics for use in the correlation analyses. The designated period for the climate indices overlapped with the beginning of ingress of LEJ spot at all estuaries.

All statistical analyses and plots were configured by using SigmaPlot, vers. 10.0 (Grafiti, Pala Alto, CA). Abundance data for estuaries were converted to number of spot per cubic meter for analyses. Because abundance data were not normally distributed, a Kruskal–Wallis one-way analysis of variance on ranks was used to explore relationships between annual (POC) mean concentrations of spot at estuaries in South Carolina, North Carolina, and New Jersey, the estuaries with at least 29 years of data. Pairwise multiple comparisons were conducted with Tukey's honestly significant difference tests. Analyses with the Spearman's rank correlation coefficient were used to explore relationships between abundance, length, phenological metrics, climate index, water temperature, and salinity data within each of the 5 estuaries. Comparisons between annual median lengths of spot for pairs of estuaries with years in common were conducted by using Mann–Whitney rank sum tests. Linear regression was used to explore long-term trends in abundance, length, phenological metrics, water temperature, and salinity data at individual estuaries.

Results

Ocean

Larval and early juvenile spot were collected in the ocean from central Florida to Maine and from the coast to the edge of the continental shelf, but their occurrence north of New Jersey was very rare and is not shown in Figure 1. Overall, monthly estimates of frequency of occurrence in collections (number of samples with larvae per total number of samples) were low (average <0.1%) NoCH compared with estimates for collections SoCH (12.5%) (Table 2). Spot occurred NoCH during all 12 months. Frequencies of occurrence of 1.2–1.4% in January, February, and March represent the 3-month period of most frequent occurrence during the year. The highest frequency of occurrence (2.1%) was in September, and the lowest (0.01%) was in December (Table 2). Spot occurred SoCH only from September through April. Frequencies of occurrence of 28% in December, 32% in January, and 28% in February represent the 3-month period of most frequent occurrence SoCH. Spot were absent in SoCH samples from May through August, and occurrences in September and October were very low (Table 2).

During the months when LEJ spot were collected with oblique bongo-net tows in both regions, mean concentrations were significantly greater SoCH than NoCH for all 3 size classes whenever larvae occurred in both regions

(Fig. 2). Small spot larvae were present NoCH during all 2-month sampling periods (Fig. 2A) and had the highest mean concentrations from May through October (Fig. 2A). Medium and large larvae were present NoCH in all 2-month sampling periods except in July–August (Fig. 2, B and C). Medium larvae were most abundant in January–February (Fig. 2B), and the highest concentrations of large larvae occurred in January–February and March–April (Fig. 2C). South of Cape Hatteras, small and medium spot larvae

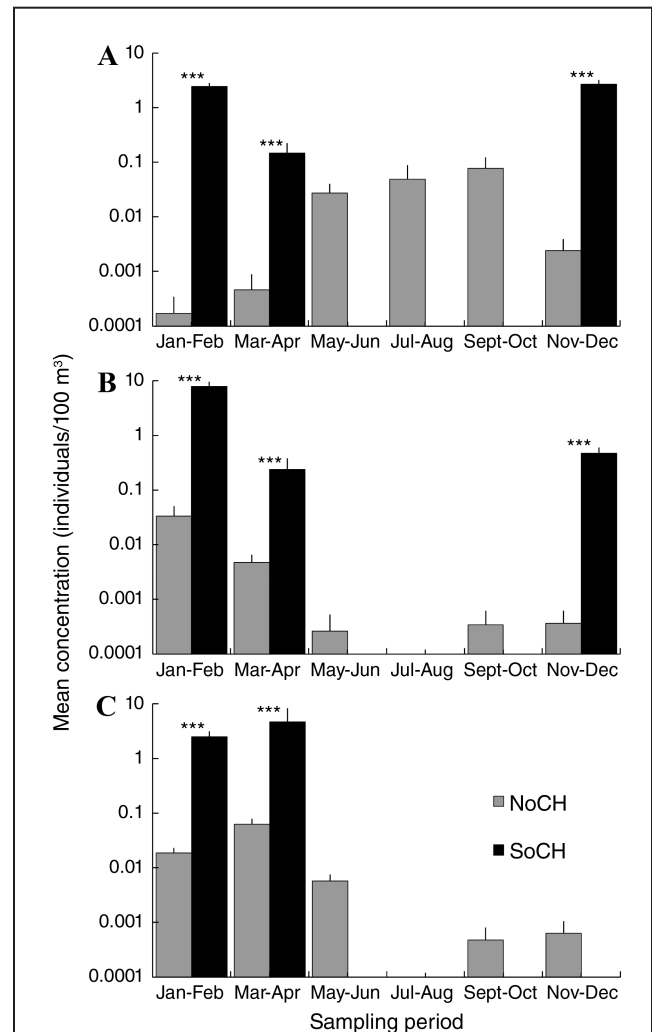


Figure 2

Mean concentration of (A) small (≤ 4.9 mm standard length [SL]), (B) medium (5.0–8.9 mm SL), and (C) large (9.0–20.0 mm SL) larval and early juvenile spot (*Leiostomus xanthurus*) collected from 1973 through 2018 during oblique tows of 61-cm-wide bongo nets (with a mesh size of 333 μ m). Collections occurred in 2 ocean regions: north of Cape Hatteras (NoCH, between 35°15'N and 42°0'N) in North Carolina and south of Cape Hatteras (SoCH, below 35°15'N). Asterisks (***) indicate significant differences ($P < 0.05$) in mean concentration between regions during 2-month periods. Error bars indicate the standard errors of the means. Data for the 3 size classes were analyzed independently.

were abundant during the 2-month sampling periods of November–December, January–February, and March–April (Fig. 2, A and B). Small larvae were most abundant in November–December and January–February, and medium larvae were most abundant in January–February. Large larvae occurred SoCH only from January through April,

and concentrations were higher there than NoCH throughout the year (Fig. 2C).

Results from quotient analyses indicate that spot larvae were produced at different locations across the continental shelf (east–west) in the 2 regions and in water masses with different environmental conditions (Fig. 3). North of

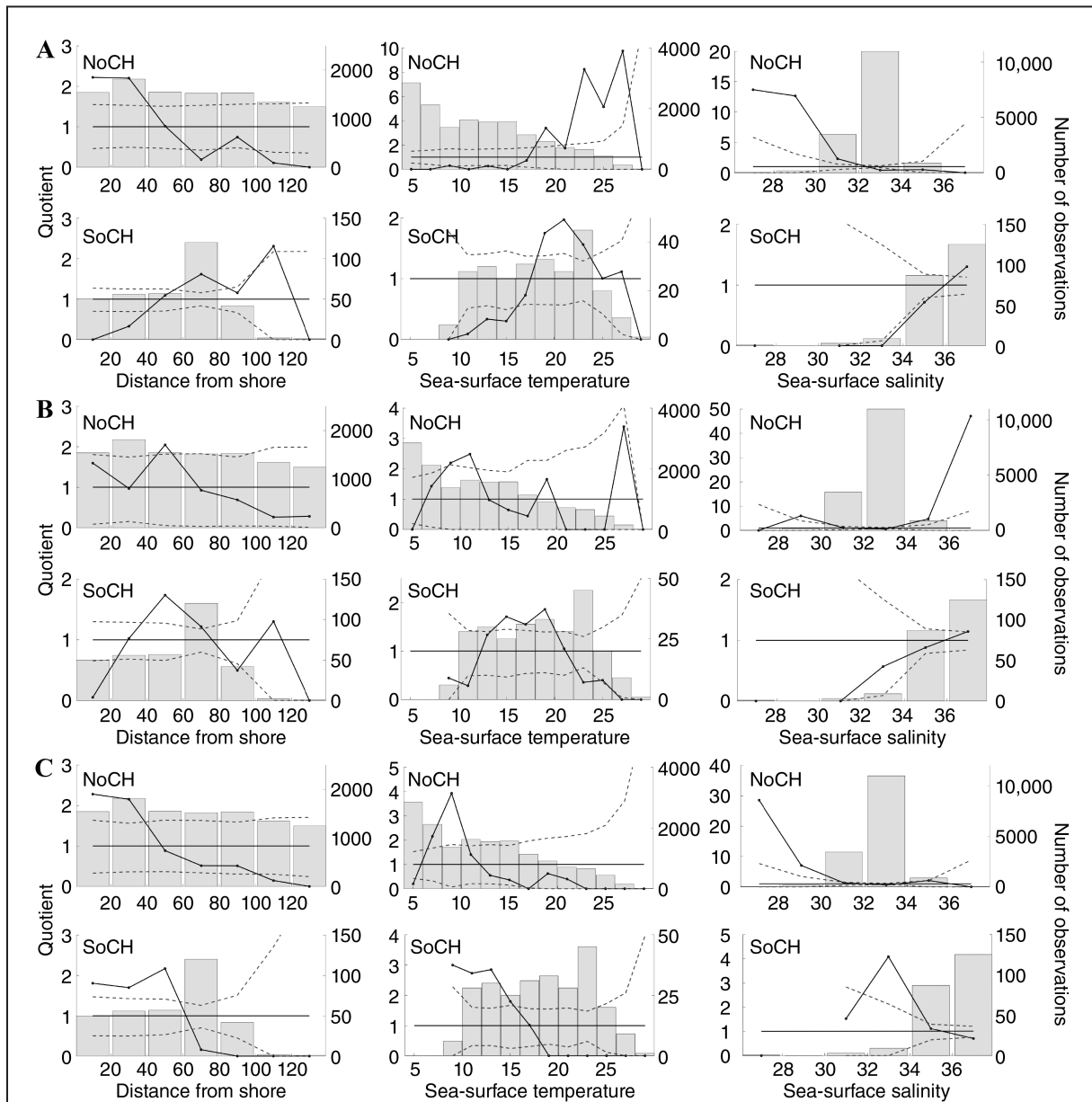


Figure 3

Ratio of the proportion of occurrence of larval spot (*Leiostomus xanthurus*) to the proportion of observations (quotient) for each bin of distances from shore, sea-surface temperatures, and sea-surface salinities from sampling on the U.S. East Coast during 1973–2018, by size class of spot: (A) small (≤ 4.9 mm standard length [SL]), (B) medium (5.0–8.9 mm SL), and (C) large (9.0–20.0 mm SL). The gray bars indicate total numbers of observations by bin. Collections were made by using oblique tows of 61-cm-wide bongo nets (with a mesh size of 333 μm) in 2 regions, north of Cape Hatteras (NoCH, between $35^{\circ}15'N$ and $42^{\circ}0'N$) in North Carolina and south of Cape Hatteras (SoCH, below $35^{\circ}15'N$). The solid lines connect the data points for ratios. The dashed lines are the upper and lower confidence intervals for the null hypothesis (i.e., even distribution across the sampling bins).

Cape Hatteras, small larvae occurred significantly more frequently on the inner shelf (<40 km from the coast) in warm coastal water, with sea-surface temperatures generally greater than 18°C and salinities less than 32 (Fig. 3A). South of Cape Hatteras, small larvae occurred significantly more frequently on the outer shelf (>60 km from the coast) in offshore water masses, with sea-surface temperatures between 19°C and 24°C and salinities greater than 34 (Fig. 3A). Medium larvae NoCH were generally on the middle to inner shelf in multiple water masses (Fig. 3B). In the region NoCH, medium larvae were in 1) warmer ($\geq 15^\circ\text{C}$) water masses in September–December, 2) colder ($< 15^\circ\text{C}$) and saltier (> 34) water masses in January–February, and 3) colder ($< 15^\circ\text{C}$) and fresher (< 34) water masses in March–April (Fig. 3B). In the region SoCH, medium larvae occurred significantly more frequently on the middle shelf (40–70 km from shore) (Fig. 3B), with sea-surface temperatures between 14°C and 20°C (Fig. 3B). Large larvae occurred NoCH more frequently on the inner shelf (Fig. 3C), and, SoCH, large larvae occurred on the inner shelf and middle shelf where water temperature and salinity were lowest (Fig. 3C).

Estuaries

Larval and early juvenile spot entered estuaries in South Carolina and North Carolina from November through May, and they entered estuaries in Virginia, Delaware, and New Jersey from January through June (Fig. 4). Within those POCs, frequency of occurrence varied among states: 48% in South Carolina, 70% in North Carolina, 49% in Virginia, 32% in Delaware, and 9% in New Jersey (Table 3). Early life stages of spot occurred during each of the 31 years in North Carolina, 35 of 36 years in South Carolina, all 7 years in Virginia, and all 5 years in Delaware, but they occurred during only 15 of 29 years in New Jersey.

Mean annual (POC) concentrations varied considerably among estuaries, and they differed by 3 orders of magnitude between the most (North Carolina) and least (New Jersey) abundant sites (Fig. 5). Long-term mean concentrations based on all years sampled at the sites were as follows: 0.4220 individuals/m³ in South Carolina, 0.6312 individuals/m³ in North Carolina, 0.0146 individuals/m³ in Virginia, 0.0042 individuals/m³ in Delaware, and 0.0004 individuals/m³ in New Jersey. An overall difference in median concentrations of LEJ spot was observed among sites (Kruskal–Wallis analysis of variance on ranks: $n=29$, $P<0.001$). Results from pairwise comparisons of mean annual concentrations when using the years in common indicate no difference in ranks between estuaries in North Carolina and South Carolina ($n=29$, $q=2.32$). Differences were observed between estuaries in North Carolina and New Jersey ($n=29$, $q=10.19$) as well as between those in South Carolina and New Jersey ($n=29$, $q=7.87$).

Interannual variation in mean concentrations were high at all estuaries. Minimum (non-zero) and maximum mean annual (POC) concentrations differed by a factor of 32 in South Carolina, 15 in North Carolina, 34 in Virginia, 42 in Delaware, and 65 in New Jersey (Fig. 5). Results from

linear regression analysis indicate no long-term trends for annual mean concentrations in any of the estuaries.

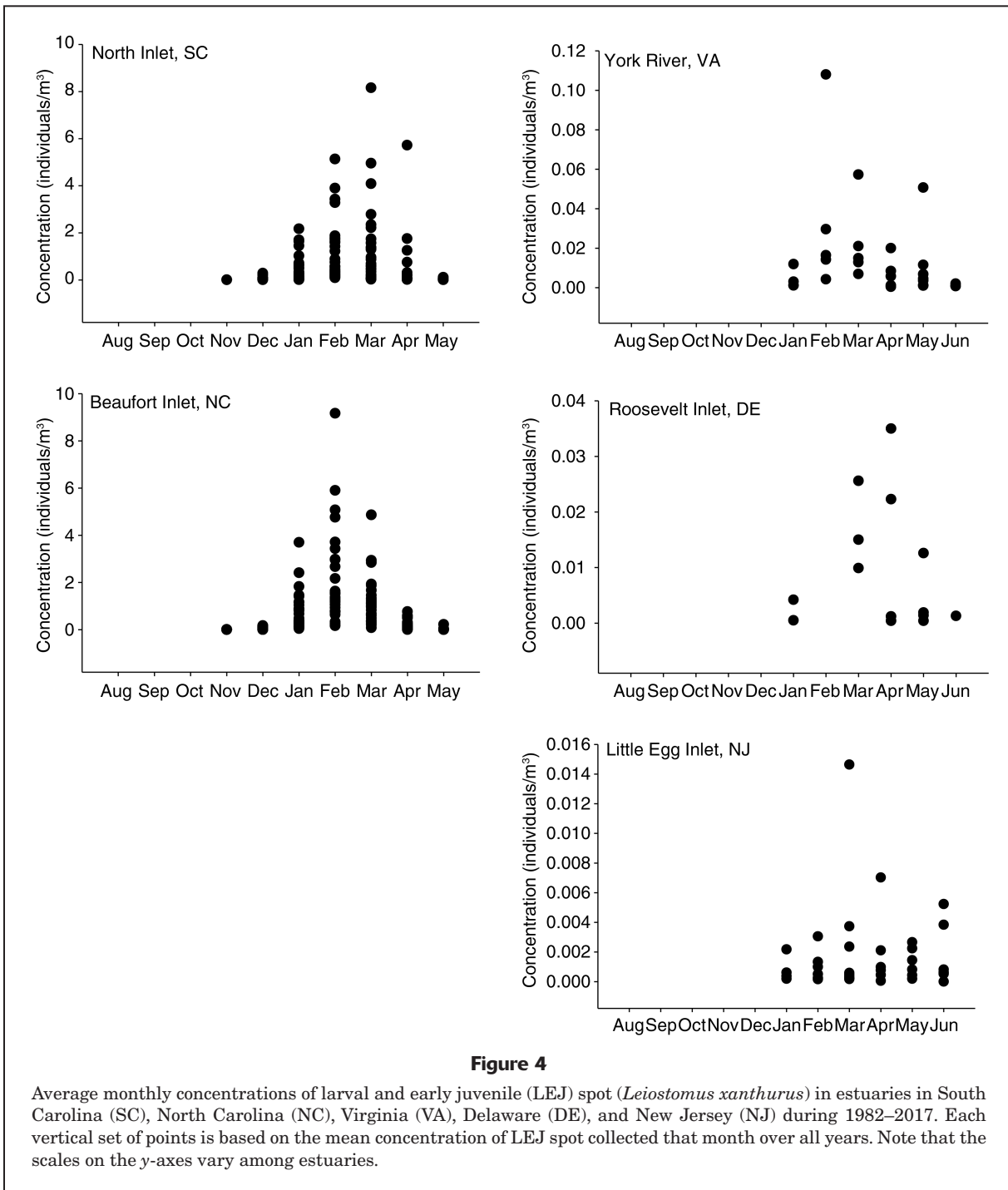
The highest concentration of LEJ spot for a single day during POCs at the 5 estuaries (total of 2494 collections) was 33.1546 individuals/m³ in North Carolina in 2005, and the next highest was 11.0775 individuals/m³ in South Carolina in 1984. Maximum concentrations for a single day were 0.0517 individuals/m³ in Virginia, 0.1388 individuals/m³ in Delaware, and 0.0282 individuals/m³ in New Jersey. In 2005, mean POC concentrations in both North Carolina (1.9990 individuals/m³) and South Carolina (1.2860 individuals/m³) were the highest among all years. In 1991, the only year during which no spot were collected in South Carolina, concentrations in North Carolina were the second lowest (0.2180 individuals/m³).

Mean annual (POC) water temperature increased between 1981 and 2017 in South Carolina (coefficient of determination [r^2]=0.17, $P=0.007$) and between 1987 and 2017 in North Carolina ($r^2=0.39$, $P<0.001$). No trend in temperature was observed in New Jersey (1989–2017) or during the shorter periods of sampling in Virginia and Delaware (Fig. 6). No correlations were found between mean annual concentrations of LEJ spot and mean temperature during the periods of occurrence within the estuaries. No long-term trends in salinity were found, and no correlations between salinity and mean annual concentrations of larvae were identified for any of the estuaries.

No correlations were found between mean annual water temperatures and the climate indices except for a positive relationship in North Carolina between mean annual water temperature and the AMO index ($n=31$, coefficient of correlation [r]=0.48, $P=0.006$). Mean annual concentrations of LEJ spot were not correlated with corresponding annual indices for ENSO, NAO, or AMO at any of the 5 estuaries.

The timing of the early (date when 15% of total annual abundance was reached) and late (date when 85% of total annual abundance was reached) occurrences of LEJ spot differed between estuaries south and north of Cape Hatteras. The date of early arrival (mean based on all years) was in late January in North Carolina and in early February in South Carolina (Table 4). The earliest mean dates in Virginia, Delaware, and New Jersey occurred in early to mid-March. The dates of late arrival were in mid-March in South Carolina and North Carolina and from late-April to mid-May in Virginia, Delaware, and New Jersey (Table 4). Similarly, middle dates and peak dates of ingress were earlier in North Carolina and South Carolina than at the northern sites. Average periods of duration were shortest in North Carolina and South Carolina (Table 4).

Positive relationships were found between many pairs of phenological metrics in North Carolina, South Carolina, and New Jersey, the 3 sites with the longest time series (Table 5). For example, the timing of the early and middle (date when 50% of the total annual abundance was reached) occurrences as well as the timing of middle and late dates across the years were positively correlated within each of these 3 estuaries. Dates of peak ingress were positively correlated with the dates of early, middle,

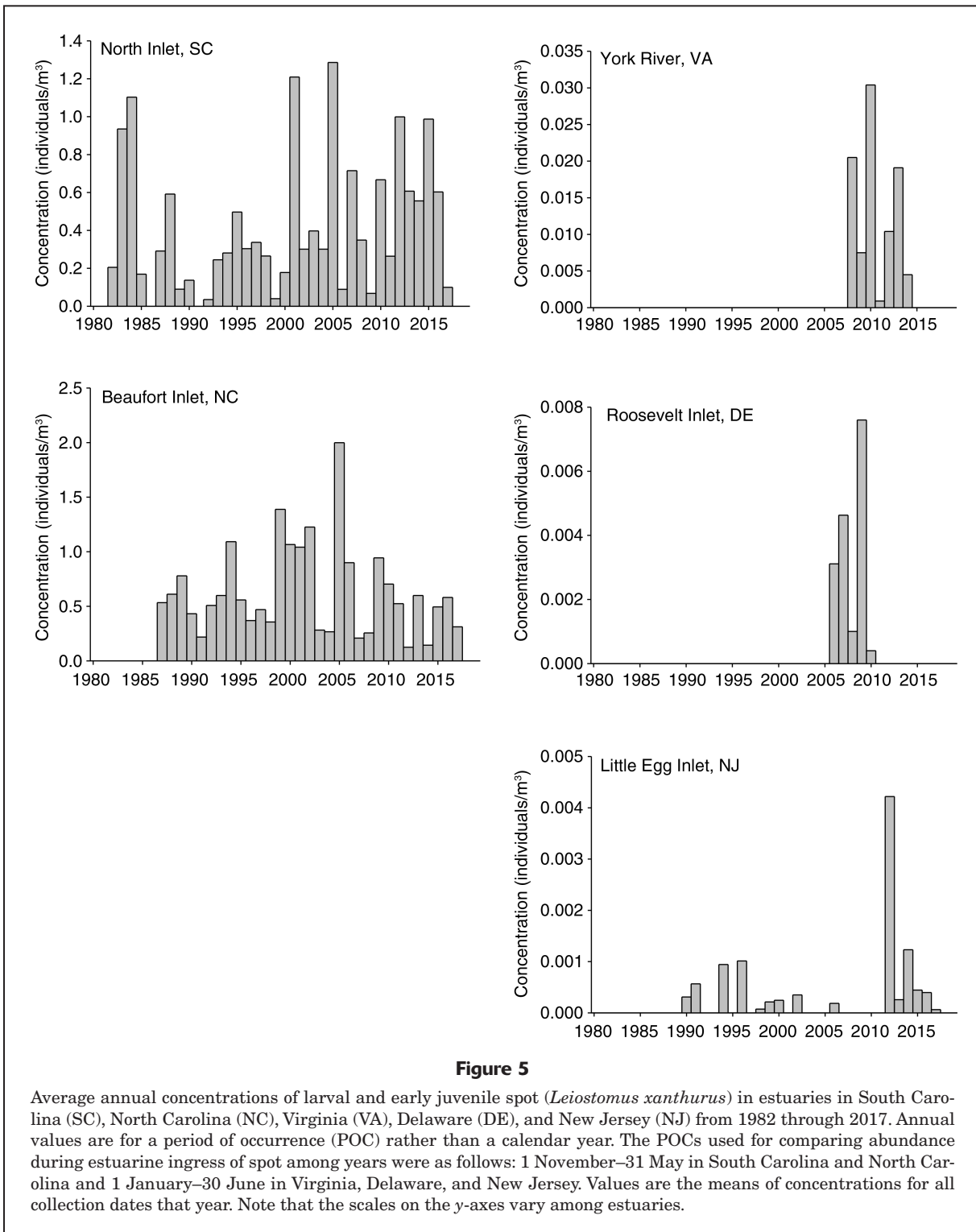


and late arrivals in South Carolina and New Jersey and with middle dates and late dates in North Carolina across the years (Table 5).

Long-term trends were not found for the timing of early or middle dates or for the durations of the ingress periods at any of the estuaries; however, long-term trends were found for late dates of arrival, which occurred later in South Carolina ($n=33$, $r^2=0.11$, $P=0.06$), North Carolina

($n=31$, $r^2=0.40$, $P<0.001$), and New Jersey ($n=12$, $r^2=0.55$, $P<0.01$) than in the other estuaries, and for peak dates, which occurred later in North Carolina ($n=31$, $r^2=0.21$, $P<0.01$) than at other sites.

Positive correlations were found between early, middle, and peak dates of ingress and water temperatures in South Carolina, Virginia, and New Jersey and between peak date and water temperature in North Carolina



(Table 5). Negative correlations were found between salinity and early and middle dates in North Carolina (Table 5).

Relationships between early, middle, and peak dates of ingress and the indices for ENSO, NAO, or winter AMO were not determined for most of the estuaries. The exceptions were the negative correlations between winter AMO

and duration of ingress in both South Carolina ($n=33$, $r=-0.38$, $P=0.03$) and Virginia ($n=7$, $r=-0.75$, $P=0.04$).

Length distributions were similar in South Carolina, North Carolina, Virginia, and Delaware with the majority of ingressing LEJ spot measuring 12–17 mm SL (Fig. 7). Spot were smaller in New Jersey with LEJ spot

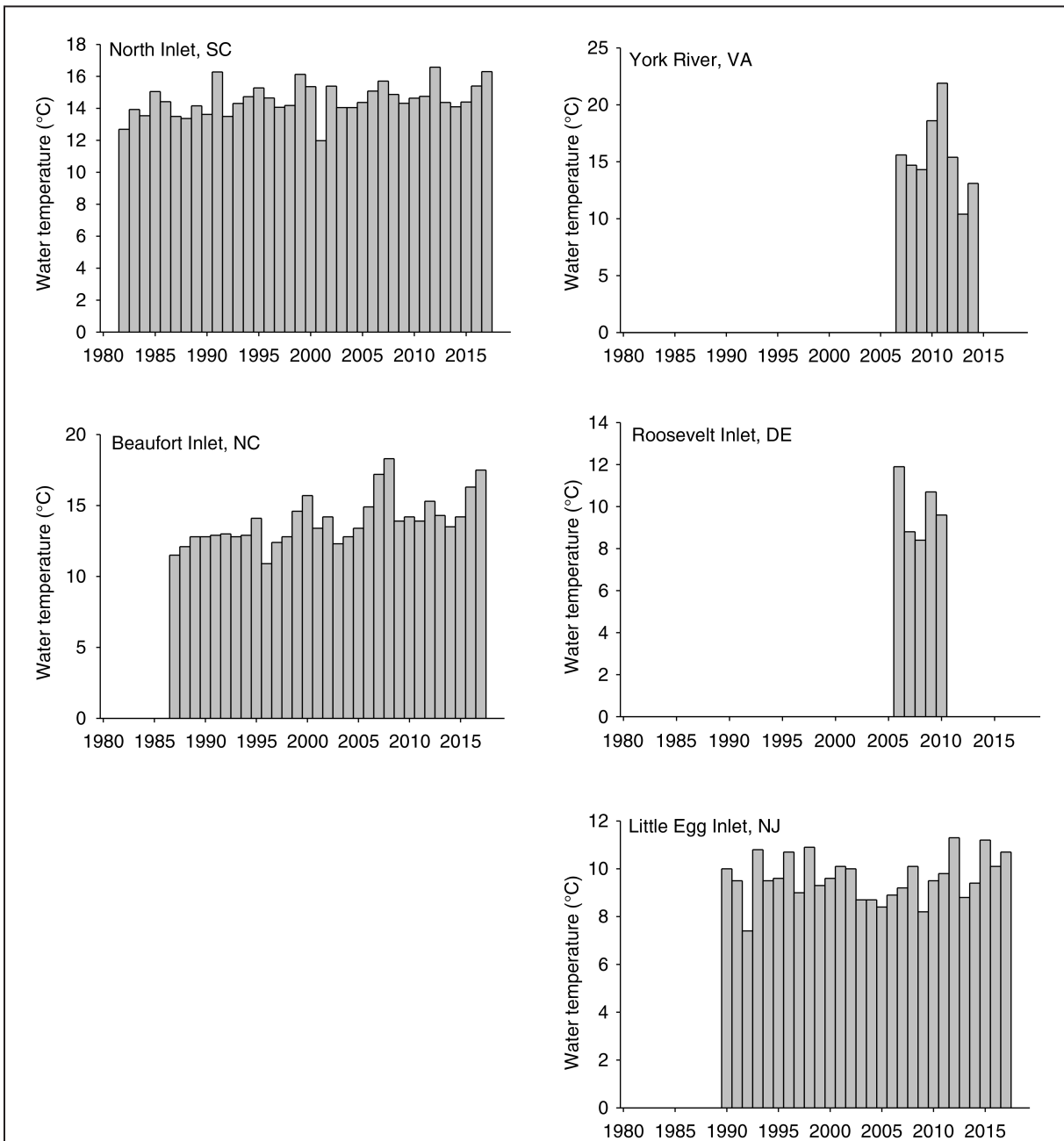


Figure 6

Average annual water temperatures for estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) where larval and early juvenile (LEJ) spot (*Leiostomus xanthurus*) were collected during 1982–2017. Annual values are for a period of occurrence (POC) rather than a calendar year. The POCs used for comparisons of temperatures among years were as follows: 1 November–31 May in South Carolina and North Carolina and 1 January–30 June in Virginia, Delaware, and New Jersey. Values are means of temperatures measured at the time of all collections of LEJ spot in each estuary that year. Note that the scales on the y-axes vary among sites.

at 9–12 mm SL accounting for the largest proportion of the annual catches. The largest individual in New Jersey was 19 mm SL, whereas juveniles at 23–26 mm SL were collected at the other 4 estuaries. The smallest spot collected in the estuaries were 5–7 mm SL in North Carolina and New Jersey, and the smallest spot collected in

South Carolina, Virginia, and Delaware were 8–9 mm SL (Fig. 7). Median lengths varied among years at all sites (Fig. 7). Long-term averages for median lengths were 14.4 mm SL in North Carolina, 15.3 mm SL in South Carolina, 11.4 mm SL in Virginia, 14.8 mm SL in Delaware, and 10.5 mm SL in New Jersey. Results of Mann–Whitney

Table 4

Phenology (timing of ingress) of larval and early juvenile (LEJ) spot (*Leiostomus xanthurus*) in estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) during 1982–2017. Dates of ingress of LEJ spot for each year were determined by using the cumulative summation method with dates corresponding to 15% (early), 50% (middle), and 85% (late) of the sum of concentrations (number of spot per cubic meter) for all dates that year. Dates identifying the early, middle, and late occurrences are the averages for all years combined in each time series. Peak date is the average of the dates with the highest concentration. Duration is the average number of days between the early and late dates of occurrence. Range of duration is based on the years with the smallest and the largest number of days between the actual first and last occurrences of LEJ spot in each time series.

Metric	SC	NC	VA	DE	NJ
Early date	5 Feb.	29 Jan.	6 Mar.	8 Mar.	14 Mar.
Middle date	18 Feb.	22 Feb.	29 Mar.	13 Mar.	2 Apr.
Late date	17 Mar.	14 Mar.	28 Apr.	24 Apr.	12 May
Peak date	25 Feb.	22 Feb.	30 Mar.	17 Mar.	21 Apr.
Duration (d)	37	43	53	77	60
Range of duration (d)	13–104	10–84	5–136	10–104	14–106

Table 5

Results from Spearman's rank correlation analyses of relationships between phenological metrics, water temperature, and salinity for spot (*Leiostomus xanthurus*) sampled in estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) over the time series from 1982 through 2017. Dates of ingress by LEJ spot each year were determined by using the cumulative summation method with dates corresponding to 15% (early), 50% (middle), and 85% (late) of the sum of concentrations (number of spot per cubic meter) for all dates that year. Peak date is the average of the dates with the highest concentration. Duration is the average number of days between the early and late dates of occurrence. Water temperature and salinity values were recorded on the phenological metric dates. Only Spearman's coefficients of multiple correlation with $P \leq 0.05$ are provided (cells with dashes had coefficients with $P > 0.05$). For North Carolina, correlation analyses with salinity were conducted with a number of samples (n) of 15.

Variables	Spearman's coefficient of multiple correlation				
	SC ($n=33$)	NC ($n=31$)	VA ($n=7$)	DE ($n=5$)	NJ ($n=12$)
Early vs. middle	+0.70, $P < 0.001$	+0.44, $P = 0.015$	–	–	+0.85, $P < 0.001$
Late vs. middle	+0.54, $P = 0.001$	+0.62, $P < 0.001$	+0.89, $P < 0.001$	–	+0.65, $P = 0.020$
Early vs. late	–	–	–	–	+0.66, $P = 0.019$
Early vs. peak	+0.44, $P = 0.010$	–	–	–	+0.65, $P = 0.022$
Middle vs. peak	+0.85, $P < 0.001$	+0.54, $P = 0.002$	+0.93, $P < 0.001$	+0.98, $P = 0.017$	+0.80, $P < 0.001$
Late vs. peak	+0.66, $P < 0.001$	+0.49, $P = 0.005$	+0.93, $P < 0.001$	–	+0.76, $P = 0.003$
Early vs. duration	–	–	–	–1.0, $P = 0.017$	–
Middle vs. duration	–	–	–	–	–0.60, $P = 0.036$
Late vs. duration	+0.51, $P = 0.018$	–	–	–	–
Early vs. temp.	+0.35, $P = 0.048$	–	+0.75, $P = 0.038$	–	+0.78, $P = 0.001$
Middle vs. temp.	+0.67, $P < 0.001$	–	+0.89, $P < 0.001$	–	+0.84, $P < 0.001$
Peak vs. temp.	+0.82, $P < 0.001$	+0.52, $P = 0.004$	+0.86, $P < 0.001$	–	+0.88, $P < 0.001$
Duration vs. temp.	–0.37, $P = 0.035$	–	–	–	–
Early vs. salinity	+0.39, $P = 0.026$	–0.63, $P = 0.011$	–	–	–
Middle vs. salinity	–	–0.69, $P = 0.004$	–	–	+0.84, $P < 0.001$
Peak vs. salinity	–	–	–	–	–
Duration vs. salinity	–	–	–	–	–

rank sum tests indicate no differences between pairings of median lengths in South Carolina, North Carolina, Virginia, and Delaware or between lengths in Virginia and New Jersey over the years; however, median lengths in North Carolina and South Carolina were larger than

those in New Jersey ($n=11$, $P < 0.001$) for both paired comparisons.

Median lengths decreased over the time series for both South Carolina ($n=34$, $r^2 = -0.16$, $P = 0.02$) and North Carolina ($n=16$, $r^2 = -0.28$, $P = 0.03$) but not for New Jersey (Fig. 7).

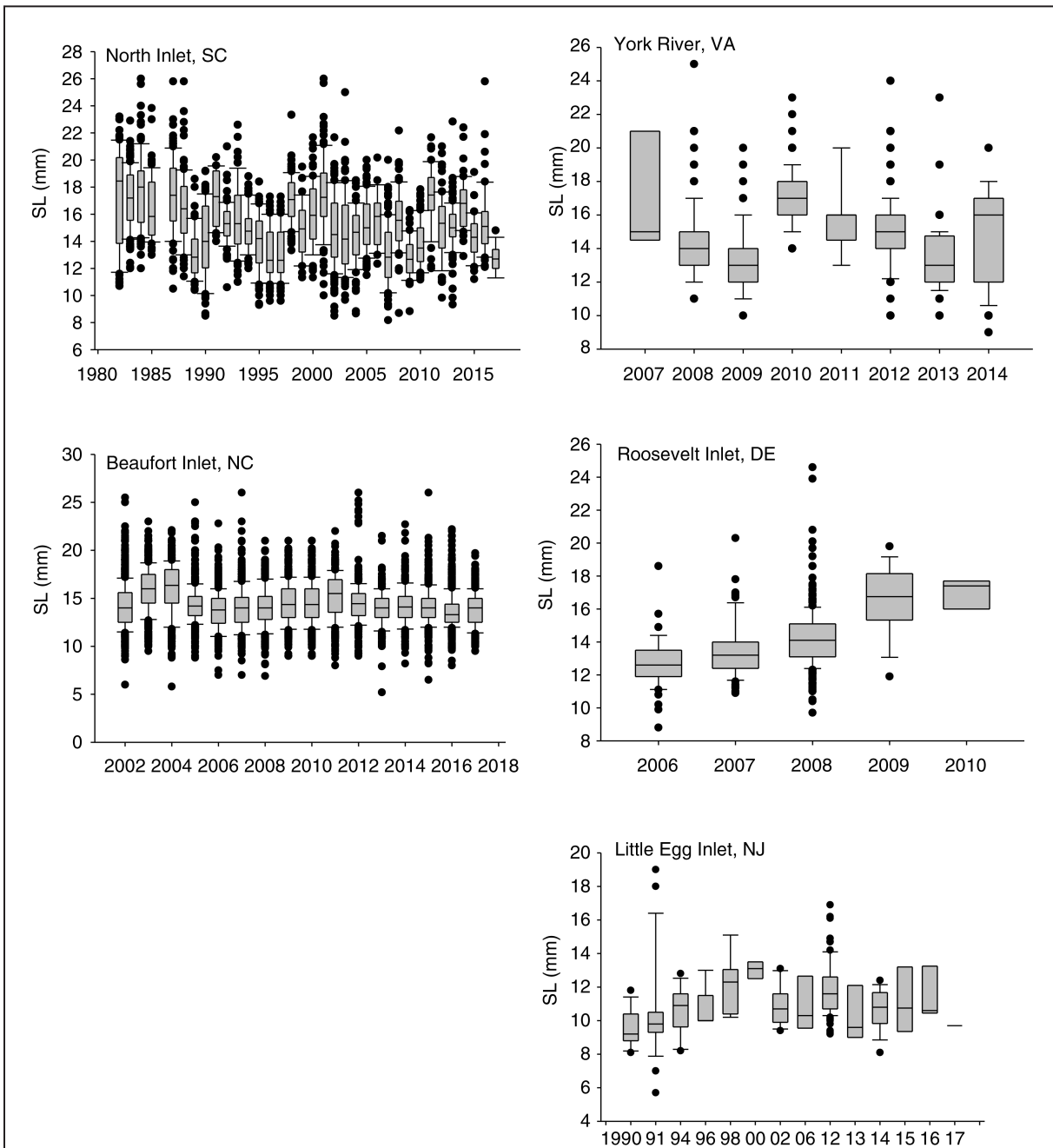


Figure 7

Standard lengths (SLs) by year for larval and early juvenile spot (*Leiostomus xanthurus*) collected in estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) from 1982 through 2017. Box plots show the distributions of all length data for years (all months combined) in which data were available for at least 10 individuals. Note that scales on both axes vary among sites and that years are not continuous for Little Egg Inlet estuary. In each box plot, the black line in the middle is the median. The upper and lower parts of each box represent the first and third quartiles (the 25th and 75th percentiles). The whiskers extend above and below each box no more than 1.5 times the interquartile range. Data points beyond the end of the whiskers are outliers.

Interannual variation in lengths was observed in the shorter-term data sets for Virginia and Delaware; the general increase in median lengths in Delaware and decrease in Virginia over periods of 4–6 years were similar to the cyclical patterns for equivalent spans of time in the longer time

series for South Carolina, North Carolina, and New Jersey. No long-term trends were found for minimum or maximum lengths in North Carolina, South Carolina, or New Jersey.

In South Carolina and North Carolina, median lengths of LEJ spot ingressing between November and January

were smaller than those for LEJ spot arriving in February and March when annual maximum median lengths occurred in both estuaries; however, median lengths in South Carolina and North Carolina decreased in April and May (Fig. 8). Some larvae <10 mm SL occurred during

all months at the estuaries in South Carolina and North Carolina. Monthly length distributions were different in Virginia and Delaware, where median lengths increased from March to the end of the ingress period in June (Fig. 8). The distribution of lengths was more even across months

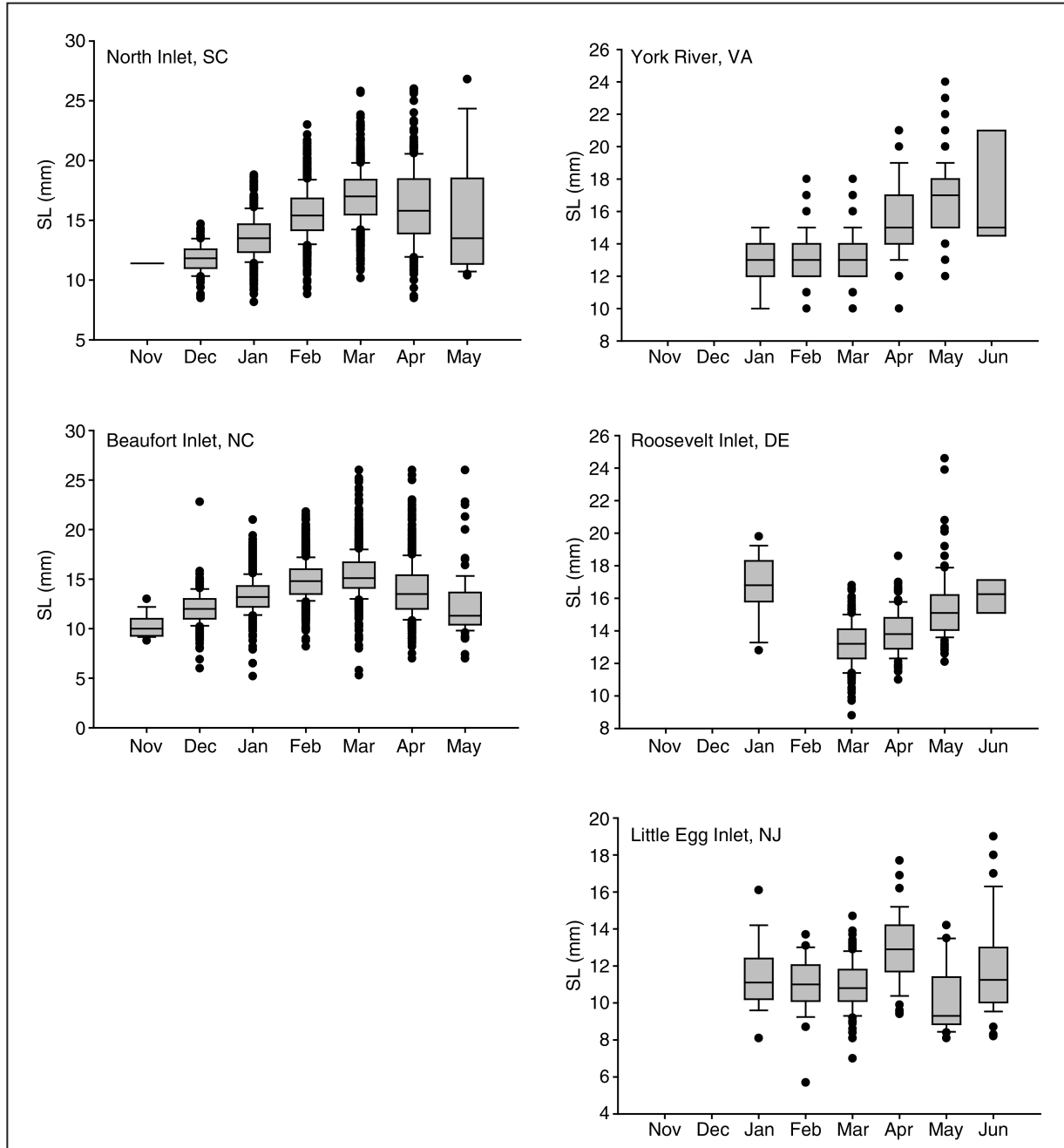


Figure 8

Standard lengths (SLs) by month for larval and early juvenile spot (*Leiostomus xanthurus*) collected in estuaries in South Carolina (SC), North Carolina (NC), Virginia (VA), Delaware (DE), and New Jersey (NJ) from 1982 through 2017. Box plots show distributions of all length data for months (all years combined) in which data were available for at least 10 individuals. Note that the scales on the y-axes vary among sites. In each box plot, the black line in the middle is the median. The upper and lower parts of each box represent the first and third quartiles (25th and 75th percentiles). The whiskers extend above and below each box no more than 1.5 times the interquartile range. Data points beyond the end of the whiskers are outliers.

in New Jersey, where LEJ spot were comparatively small throughout the ingress period (Fig. 8).

Median annual lengths of LEJ spot decreased with increasing annual mean water temperature in South Carolina ($n=34$, $r=-0.37$, $P=0.03$) and North Carolina ($n=16$, $r=-0.67$, $P=0.005$), but relationships between length and water temperature were not evident in Virginia, Delaware, or New Jersey. Median annual length and mean annual salinity did not appear to be related in any of the estuaries.

Discussion

Spawning locations along the East Coast

This first broadscale analysis of the early life history of spot on the East Coast by using novel data sets resulted in new information about the origins of larval spot on the continental shelf. Previous investigators focused on the outer shelf SoCH as a likely primary location of spot spawning, with most spawning found to occur in winter (Lewis and Judy, 1983; Warlen and Chester, 1985; Flores-Coto and Warlen, 1993; Govoni et al., 2013). These previous studies were limited to that area. Our analysis of >31,000 ocean ichthyoplankton collections from Florida to Maine over several decades added spatial resolution to earlier findings that early-stage larvae were consistently found in greatest abundance near the edge of the continental shelf south of the latitude $35^{\circ}15'$ (Cape Hatteras) during winter. In the region SoCH, mean concentrations of LEJ spot were more than 100 times higher and frequencies of occurrence of LEJ spot in collections were more than 10 times higher than in the region NoCH.

Our observations of LEJ spot in multiple water masses with relatively high salinity NoCH indicate that some larvae spawned SoCH were entrained into the Gulf Stream and transported northward (Hare et al., 2002; Govoni et al., 2013). Results from previous studies on ocean currents and the distribution of larvae of other ocean-spawned species indicate that larvae produced SoCH can be transported onto the shelf NoCH (Grothues and Cowen, 1999; Hare et al., 2001; Grothues et al., 2002; Hare et al., 2002; Warlen et al., 2002). The species other than the spot that spawn in the ocean and enter estuaries NoCH as larvae and early juveniles include the Atlantic menhaden (*Brevoortia tyrannus*) (Warlen et al., 2002), Atlantic croaker (*Micropogonias undulatus*) (Norcross, 1991), summer flounder (*Paralichthys dentatus*) (Hoey et al., 2020), bluefish (*Pomatomus saltatrix*) (Hare and Cowen, 1996), and speckled worm eel (*Myrophis punctatus*) (Able et al., 2011).

We found evidence for a second source of larval spot NoCH. The occurrence of small larvae (≤ 4.9 mm SL) <40 km from shore NoCH from May through November indicates an origin other than outer continental shelf spawning SoCH. The highest concentrations of small larvae on the inner shelf NoCH occurred from July through October, when water temperatures were at annual highs. The greatest frequency of occurrence of small larvae NoCH was in September–October. The occurrence of small larval

spot NoCH is best explained by adults spawning on the inner shelf or mid-shelf before spawning begins on the outer continental shelf SoCH in winter. Adult spot with developing ovaries have been found in lower Chesapeake Bay in September and October (Hildebrand and Schroeder, 1928). Whether adults that spawn on the inner shelf NoCH before November continue to migrate and spawn near the edge of the shelf in winter is unknown. Regardless, there are 2 sources of larvae for NoCH estuaries: 1) winter–spring spawning on the outer shelf from near or south of Cape Hatteras and 2) summer–fall spawning on the shelf NoCH. The absence of larvae SoCH from May through August and their near absence from September through November indicate that spawning in summer and early fall is not an important source of larvae for estuaries SoCH.

Ingress into estuaries

The timing of ingress of LEJ spot (January–June) in northern estuaries (Virginia, Delaware, and New Jersey) was similar in most years. Arrival of larvae and early juveniles of a wide range of sizes (8–18 mm SL) in all 3 estuaries NoCH from January through June indicates that they could have originated from both sources of larval production as described in the previous section. A comparison of the ingress of Atlantic menhaden between the estuaries in New Jersey and North Carolina revealed that larvae arriving in New Jersey early in the annual ingress period probably were spawned off New Jersey by adults migrating toward primary winter spawning areas in deep waters and that larvae arriving later in winter were likely from spawning activity SoCH (Warlen et al., 2002). Norcross and Bodolus (1991) suggested that LEJ spot recruiting to Chesapeake Bay in winter and spring arrived 1–3 months after being produced at the edge of the continental shelf near Cape Hatteras, about 250 km to the south. How much winter spawning on the outer shelf SoCH contributed to LEJ spot in northern estuaries is unknown. However, because concentrations of all sizes of spot larvae in the ocean NoCH in winter were orders of magnitude less than those SoCH, it is likely that spawning NoCH from May through October was an important annual source of larvae for estuaries NoCH.

In New Jersey, LEJ spot arrived later and were smaller than those in Virginia and Delaware, indicating that delivery processes differed NoCH. Episodes of southerly winds in winter, and more frequently in spring, could facilitate the northward transport of larvae produced on the outer shelf around Cape Hatteras during winter (Norcross and Bodolus, 1991). Southerly winds could also affect the movement of larvae produced on the inner shelf NoCH in the fall. Wind events have been thought to be at least partly responsible for the high interannual variability in ingress observed in northern estuaries (Ribeiro et al., 2015). The ingress of smaller larvae in New Jersey could also be due to slow growth rates between fall spawning NoCH and ingress into this northernmost estuary. Larvae arriving in New Jersey during the winter and spring could

also be delivered more directly from the outer shelf by Gulf Stream eddies (Gangopadhyay et al., 2019, 2020) and other ocean processes that transport larvae to the coast more rapidly (Hare and Cowen, 1996).

The occurrence of LEJ spot in New Jersey during only 15 of the 28 years and at concentrations that were the lowest among the 5 estuaries indicates that Little Egg Inlet estuary in New Jersey is probably near the current northern limit of distribution of LEJ spot in estuaries on the East Coast. We were able to find records of spot in early life stages from only 2 estuaries north of New Jersey. Spot were rare in ichthyoplankton collections from Niantic Bay in Connecticut (eastern Long Island Sound) between 1976 and 2020, where a total of 12 larvae were collected on 11 dates from 1988 to 2019 (Millstone Environmental Laboratory⁶). They were also sparse in a survey conducted between 2002 and 2008 in Narragansett Bay in Rhode Island, with only 5 larvae collected on one date at a single station in 2007 (Schneider⁷). Studies of age and growth and chemical composition in otoliths of spot from the ocean and estuaries could further refine our understanding of the ocean origins and transport of LEJ spot to northern estuaries (Bath Martin et al., 2004; Bath Martin and Thorrold, 2005).

Spawning by spot on the outer shelf SoCH was almost certainly the source of LEJ spot entering estuaries in North Carolina and South Carolina. Larval and early juvenile spot in North Carolina were generally more abundant and smaller than those in South Carolina, and the timing of early, late, and peak occurrences was somewhat earlier. These findings indicate that Beaufort Inlet in North Carolina is more proximal to the main source of larvae in the ocean SoCH than North Inlet estuary in South Carolina. Consistently larger median lengths of spot arriving in South Carolina compared to those of spot arriving in North Carolina at the same time could result from longer transport across the shelf. Larval and early juvenile spot approaching the coast SoCH could be affected by the southward-directed coastal current (Blanton et al., 2003), possibly explaining the later timing and larger size of ingressing larvae and early juveniles in North Inlet estuary.

Early life stages of spot also arrive in estuaries in Georgia during winter and early spring (Rogers et al., 1984). Cross-shelf transport of larvae has been observed at least as far south as central Georgia (Marancik et al., 2005). The arrival of LEJ spot in estuaries in northern and central Florida could result from spawning on the outer shelf as far south as Cape Canaveral (Fahay, 1975). Larval and early juvenile spot occurred in the Guana-Tolomato-Matanzas estuary near St. Augustine, Florida, from December through April (Korsman et al., 2017); lengths of 8.5–12.5 mm SL and average concentrations around 0.3 individuals/m³ were similar to those of LEJ spot collected in North Inlet estuary. Lower concentrations were reported for collections in the Indian River Lagoon near Melbourne, Florida, near the southernmost extent of estuarine ingress for LEJ spot (Reyier and Shenker, 2007). Spot in demersal (juvenile and adult) stages occur in Florida south of the Indian River Lagoon (Snyder and Burgess, 2016), but they

do not appear to be as common as they are from central Florida to New Jersey. Spot are common in coastal waters and estuaries of the Gulf of Mexico, and spawning of spot there could contribute larvae and early juveniles to the east coast of Florida. Govoni et al. (2015) suggested that larvae of the chain pearlfish (*Echiodon dawsoni*) could be transported from the Gulf of Mexico to waters off the east coast of Florida and off states northward through the Loop Current and Gulf Stream; a similar pathway could be possible for spot as well.

The availability of records for many continuous years from South Carolina (36 years), North Carolina (31 years), and New Jersey (29 years) enabled comparisons of timing of ingress among and within the estuaries in these states. The timing of phenological events varied geographically; however, within each estuary, correlations between dates of early, middle, peak, and late occurrences were positive, indicating consistent relationships among these measures of timing among years. Strong relationships among phenological metrics within estuaries indicate largely symmetric patterns of ingress for each estuary over the years. However, these patterns varied among estuaries. Long-term trends with later dates of late arrival were identified for LEJ spot in South Carolina, North Carolina, and New Jersey. Peak ingress dates at all 3 of these sites were positively correlated with water temperature, indicating that peak ingress occurred later as water temperature increased. Positive correlations between water temperature and early and middle ingress dates in South Carolina, Virginia, and New Jersey also indicate responses by LEJ spot, with ingress delayed with increasing water temperatures. Thaxton et al. (2020) did not detect any long-term trends for phenological metrics for LEJ spot in Beaufort Inlet but found that ingress of many larval and early juvenile fish, including spot, occurred earlier during warm years. Differences in results between our study and the study by Thaxton et al. (2020), both of which used ichthyoplankton data from the same source in North Carolina, could be due to the use by Thaxton et al. (2020) of a shorter time series (1987–2013) and a different source of water temperature data (ocean-based sea-surface temperature). Results from analyses of sea-surface temperature off the Carolinas through 2015 do not indicate a warming of ocean waters (Shearman and Lentz, 2010; Morley et al., 2017); however, in a more recent analysis of temperatures in the region from North Carolina through the Florida Keys, an upward trend in sea-surface temperature beginning in 2014, particularly in winter and spring, was identified (Craig et al., 2021). High spatial and temporal variability within data sets for LEJ spot and water temperature present major challenges to understanding the relationships of water temperature and various aspects of LEJ spot in the ocean, but efforts to explore the influence of temperature on abundance, movements, and growth of LEJ spot in the ocean will be important for interpreting patterns of ingress into estuaries as environmental conditions change.

Warming temperatures could affect the size of larvae reaching the coast in several ways. For instance, if ocean water temperatures increase in the coming years, adults

migrating offshore could find suitable temperatures for spawning closer to the coast. If more spawning took place west of the long-recognized main spawning areas near the edge of the continental shelf, transport distances to estuaries would be shorter and smaller larvae might be expected to arrive at estuarine inlets. The occurrence of larval spot <4.9 mm SL within 40 km of the coast SoCH between December and April could indicate that some spawning occurs on the shelf, and that could be the source of small larvae collected in North Carolina and South Carolina in April and May. Warlen and Chester (1985) suggested that small LEJ spot collected toward the end of the ingress period might have originated from spawning at different locations than those arriving earlier in the year. The pattern that we observed for median lengths of LEJ spot in estuaries in South Carolina and North Carolina increasing between December and February and then decreasing in March and April had been previously reported for estuaries in North Carolina (Warlen and Burke, 1990; Flores-Coto and Warlen, 1993). Variations in the rates of transport across the shelf could also account for differences in the length of spot arriving in estuaries among years (Lewis and Judy, 1983) as well as within years.

The wide ranges of lengths of spot observed on most dates at all 5 sites of our study could be attributed to the presence of 2–10 birth-week cohorts throughout an ingress period of 4–5 months (Flores-Coto and Warlen, 1993). Beckman and Dean (1984) identified 3 primary cohorts of LEJ spot in North Inlet estuary, with length ranges of up to 10 mm SL within cohorts. It is not clear whether larvae collected in an estuary on a particular date were all or mostly new arrivals or if there was a mixture of new arrivals and LEJ spot that had already occupied the area for days or weeks. Wide ranges in lengths could also be related to differences in growth rates. Variation in growth can be expected within and between years as environmental factors, such as temperature, food supply, winds, and current velocities, vary during the months of cross-shelf transport (Govoni et al., 2010). Beckman and Dean (1984) determined that most 16-mm-SL spot entering North Inlet estuary were between 60 and 100 d old; therefore, it is possible that LEJ spot of the same length collected early in the ingress period (from January through March) had grown faster than those collected late in the period (in April and May).

Whether growth rates, rates of larval transport to the coast, or locations or timing of spawning for spot have changed is unknown. Clearly, more efforts are needed to understand many aspects of the early life history of spot in the ocean. The reestablishment of regular ichthyoplankton cruises SoCH (which currently take place NoCH) coupled with ongoing long-term collections of LEJ spot in estuaries would help answer many questions. Presently, long-term sampling programs are continuing in the estuaries in South Carolina, North Carolina, and New Jersey.

Variation of lengths, timing, and abundance of LEJ spot in estuarine collections could also be related by conditions close to shore. Upon arrival at inlets, passage of larvae into estuaries can be influenced by short- and long-term fluctuations in tide, sea-level pressure gradients, wind, or

a combination as well as by other physical and biological factors (Pietrafesa and Janowitz, 1988; Hare et al., 2005; Hale and Targett, 2018; Whitfield et al., 2023a). Teodósio et al. (2016) suggested that ingress of larvae could not occur without behavioral responses to sensory cues, such as visual, sound, odor, and geomagnetic signals, that aid in navigation toward suitable estuarine nursery areas. Hettler and Hare (1998) determined that patterns in concentrations of larval spot outside of Beaufort Inlet were complex and probably were influenced by both the physical processes that supply larvae to inshore areas and the physical dynamics near the inlet. Certain conditions outside the inlet likely favor concentrating LEJ spot and influence ingress more than other conditions (Flores-Coto and Warlen, 1993). Several investigators have noted the importance of wind in the timing of estuarine ingress of LEJ spot and other species (Love et al., 2009; Schieler et al., 2014; Thaxton et al., 2020). Variations in the abundances, timing of occurrences, and lengths of LEJ spot between neighboring inlets in North Carolina (Hettler and Barker, 1993) and Florida (Korsman et al., 2017) were thought to be due to differences in local physical conditions controlling ingress.

The lack of significant relationships between salinity and the abundance and median lengths of LEJ spot in the 5 estuaries indicates that they were not very responsive to variable salinity conditions during winter. In addition, the almost total absence of correlations between early, middle, and late dates of occurrences in the estuaries with salinity indicates that ingressing spot did not have high sensitivity to variation in salinity. In laboratory studies of behavioral responses of larval spot (from 4 d to 4 weeks old) to rates of salinity change, De Vries et al. (1995) found that salinity gradients in the ocean were not likely to affect depth regulation, which could influence delivery to estuaries. As planktonic spot transform to juveniles and develop a demersal lifestyle, they occur across a wide range of salinities and, in river-driven estuaries, move toward tidal fresh water following ingress (Rogers et al., 1984).

Relationships between indices for NAO, AMO, or ENSO and the abundance and distribution of fishes in the North Atlantic Ocean have been reported by investigators interested in understanding how a changing climate affects fish and fisheries (Hare and Able, 2007; Thaxton et al., 2020; Gillanders et al., 2022; Whitfield et al., 2023b). In our study, very few correlations were found between LEJ spot and winter values for these broadscale indices. No relationships between the 3 indices and either abundance or the timing of ingress were found at any site; however, we found that the AMO index was positively correlated with water temperature in North Carolina between the mid-1980s and 2017, when water temperature increased in the estuary.

Although many environmental factors affect fish ecology, water temperature is most frequently identified as the most important in driving long-term changes in fish populations and their distribution. Several studies have produced evidence of latitudinal shifts in the distributions and timing of occurrence of some fish species in the North Atlantic

Ocean in recent decades with changes in temperature regimes (Perry et al., 2005; Nye et al., 2009; Walsh et al., 2015). Responses to changing temperature vary considerably among species and life stages of fish and zooplankton, even within the same assemblage (Allen et al., 2008; Morley et al., 2017; Morson et al., 2019; Thaxton et al., 2020). In an analysis of long-term data sets for larval and trawl-caught fish in the shelf ecosystem of the northeastern United States, Walsh et al. (2015) found seasonal and spatial (latitudinal) shifts for many species but not for either larval or adult spot in the ocean. However, their analysis ended with collections made in 2008, prior to the increases in ocean water temperatures and marine heat wave events that started around 2010 (NEFSC¹¹). For Little Egg Inlet estuary, Morson et al. (2019) reported an increasing presence of southern species and decreasing occurrence of northern species in association with warming temperatures.

A northerly shift in areas with temperatures around 20°C could result in a shift in the spawning of spot northward and westward away from the outer edge of the shelf SoCH. Such a shift could have major effects on the supply of spot larvae to estuaries both SoCH and NoCH. In addition, increasing winter water temperatures could provide expanded suitable habitats for juveniles and adults in northern estuaries. Our knowledge of the life history and ecology of spot is far from complete, but established relationships between water temperature and spawning and the observed long-term changes in lengths of early life stages and the timing of ingress in relation to changing temperature indicate that the occurrence and abundance of spot in estuaries of the East Coast will continue to be affected by the changing climate.

Conclusions

Our synthesis of data on LEJ spot from ichthyoplankton collections across the continental shelf north and south of Cape Hatteras and collections from 5 estuaries along the U.S. East Coast revealed new patterns of larval production, cross-shelf movement, and ingress into estuaries that could only be determined with data collected over multiple decades at multiple sites. Results of analyses of the oceanic data collected NoCH indicate for the first time that adult spot produce larvae on the inner shelf in summer and fall. Patterns of abundance, length, and timing of ingress in estuaries NoCH indicate that larvae spawned on the inner shelf supplemented those originating from the outer shelf. Ingressing spot in North Carolina and South Carolina originated from spawning near the edge of the shelf SoCH.

Over the decades, the lengths of LEJ spot arriving in the estuaries in North Carolina and South Carolina decreased. This change coincided with increasing water temperature over the same period. The timing of ingress became later

over the decades, with the early, middle, and peak dates of ingress correlated with increasing water temperatures in South Carolina, North Carolina, and New Jersey. These relationships, which could be determined only from long-term data sets, indicate that the current trend for increasing ocean and estuarine water temperatures along the East Coast will lead to changes in the timing and locations of spawning, larval transport, and ingress of spot into estuaries. Given the important ecological and economic roles of spot, especially in estuaries, changes in their distribution and abundance could affect the structure of coastal food webs and both the recreational and commercial harvests of this species.

Resumen

Se examinaron de datos de ictioplancton colectados en estuarios de Carolina del Sur, Carolina del Norte, Virginia, Delaware y Nueva Jersey así como de cruceros oceánicos frente a la costa este de EE.UU., para determinar los lugares de desove en el océano, la distribución de larvas entre plataformas y los movimientos de la croca (*Leiostomus xanthurus*) en los estuarios. La croca desova durante el otoño y el invierno cerca del borde de la plataforma continental, principalmente al sur del cabo Hatteras en Carolina del Norte. Documentamos desoves adicionales de la croca al norte del cabo Hatteras, cerca de la costa, en verano y otoño. Las larvas de esta especie entran en los estuarios de noviembre a mayo en Carolina del Sur y Carolina del Norte y de enero a junio en Virginia, Delaware y Nueva Jersey. El número de crocas por volumen de agua muestreada disminuyó de sur a norte entre los estuarios y en el océano. Las variaciones interanuales en la abundancia fueron elevadas y no se determinaron tendencias a largo plazo. Durante décadas, la mediana de la longitud anual de las larvas y juveniles de croca que ingresaban disminuyó al incrementarse la temperatura media anual del agua en Carolina del Sur y Carolina del Norte. El momento de la entrada se correlacionó positivamente con la temperatura del agua. Es probable que el aumento continuo de la temperatura del agua en la costa este provoque cambios adicionales en la distribución oceánica y en los patrones de entrada de la croca. Nuestros hallazgos indican el valor de sintetizar la información procedente de estudios a largo plazo realizados en escalas geográficas amplias.

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¹¹ NEFSC (Northeast Fisheries Science Center). 2021. 2021 state of the ecosystem: Mid-Atlantic, revised, 42 p. Report to the Mid-Atlantic Fishery Management Council. [Available from [website](#).]

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