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[Article]

Relationships between Larval and Juvenile Abundance of Winter-Spawned Fishes in North Carolina, USA

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Abstract.—We analyzed the relationships between the larval and juvenile abundances of selected estuarine-dependent fishes that spawn during the winter in continental shelf waters of the U.S. Atlantic coast. Six species were included in the analysis based on their ecological and economic importance and relative abundance in available surveys: spot *Leiostomus xanthurus*, pinfish *Lagodon rhomboides*, southern flounder *Paralichthys lethostigma*, summer flounder *Paralichthys dentatus*, Atlantic croaker *Micropogonias undulatus*, and Atlantic menhaden *Brevoortia tyrannus*. Cross-correlation analysis was used to examine the relationships between the larval and juvenile abundances within species. Tests of synchrony across species were used to find similarities in recruitment dynamics for species with similar winter shelf-spawning life-history strategies. Positive correlations were found between the larval and juvenile abundances for three of the six selected species (spot, pinfish, and southern flounder). These three species have similar geographic ranges that primarily lie south of Cape Hatteras. There were no significant correlations between the larval and juvenile abundances for the other three species (summer flounder, Atlantic croaker, and Atlantic menhaden); we suggest several factors that could account for the lack of a relationship. Synchrony was found among the three southern species within both the larval and juvenile abundance time series. These results provide support for using larval ingress measures as indices of abundance for these and other species with similar geographic ranges and winter shelf-spawning life-history strategies.

More than 75% of the species important in fisheries off the southeast U.S. Atlantic coast have estuarine life stages (Fox 1992). The common life-history strategy for the majority of these species involves fall–winter spawning on the continental shelf followed by transport of larvae to nearshore habitats or through tidal inlets where they enter the estuary and settle in shallow nursery habitats (Miller 1988; Ortner et al. 1999). After a residency in estuarine habitats for one or more years, individuals emigrate from the estuary and enter the spawning stock.

A critical stage of this life-history pattern is the passage through narrow inlets or into mouths of estuaries that connect the ocean and estuarine habitats. These pathways to nursery habitats are few in number along much of the Atlantic coast of the United States and therefore serve as bottlenecks to recruitment for many species (Reyier and Shenker 2007). Coastal inlets and estuary mouths may also be suitable locations from which to observe and monitor the population status of these stocks, as every individual must pass through an inlet at least once during its life. For some species, however, the use of shallow nearshore ocean habitat may also be important (Able 2005).

The Beaufort Inlet Ichthyoplankton Sampling Program is the longest consecutive ichthyoplankton sampling program along the U.S. East Coast, providing a 22-year time series of larval fish ingress through Beaufort Inlet, one of five major inlets that connect the Atlantic Ocean to North Carolina estuaries. Research

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using these data has described the timing and variability of immigration (Hettler and Chester 1990) and the age and size characteristics of larvae (Warlen 1992), along with permitting inferences on the spawning sources and stock structure (Burke et al. 2000), mechanisms of larval transport (Hare et al. 1999), and relationships between environmental variables and recruitment (Hare and Able 2007).

Evidence suggests that year-class strength is strongly influenced by environmental conditions during larval transport and ingress, such as the processes associated with nearshore winds and river discharge, which drive water mass circulation along the coast (Checkley et al. 1988; Hare et al. 1999). For example, nearly 77% of the variation in the juvenile abundance of southern flounder *Paralichthys lethostigma* in North Carolina estuaries has been attributed to the wind direction and magnitude and precipitation coinciding with the peak ingress of southern flounder larvae (C. Taylor, unpublished data). It may be expected that species with common life history strategies (e.g., similar timing and location of spawning) would be influenced by similar environmental forces and show similar patterns of recruitment. However, it is also well known that subtle differences, such as species-specific larval behaviors, determine the effect of environmental factors on the transport to inlets (Hare and Govoni 2005).

There has not been an assessment of whether the larval ingress observed near inlets in the southeastern United States is similar among species, represents abundance in later life stages, or provides indicators of year-class strength for any of these species. For many species of commercially and recreationally important fishes, we lack fishery-independent estimates of population abundance at any life stage. Developing indices of abundance for managed species would help calibrate the stock assessment models used to inform management strategies.

The primary goal of this research was to assess the utility of larval ingress measures as indices of abundance for commercially, recreationally, and ecologically important finfish species in North Carolina. There were two specific objectives: (1) to evaluate the relationships between larval abundance at ingress and juvenile abundance in estuarine nurseries and (2) to test for synchronous patterns in abundance between species during the larval and juvenile stages for representative species in North Carolina and the southeast U.S. Atlantic coast.

Methods

We selected six species for this analysis based on their importance in regional fisheries, ecological roles in coastal environments, and availability in existing fishery-independent monitoring programs (Table 1). These species are members of a guild of fishes that spawn on the continental shelf during the fall and winter and recruit to nursery habitats in estuaries in North Carolina. Our analyses drew from three long-term monitoring programs that have been operating in the state since 1987 or earlier.

TABLE 1.—Top 11 species captured in the Beaufort Ichthyoplankton Sampling Program. Rank is based on the cumulative number of larvae collected from 1987 to 2004. Representation in the juvenile surveys during the spring and summer is indicated with an x. Asterisks denote species selected for analysis in this article.

Taxon	Rank	Spring	Summer
Spot *Leiostomus xanthurus**	1	x	x
Pinfish *Lagodon rhomboids**	2	x	x
Atlantic croaker *Micropogonias undulatus**	3	x	x
Atlantic menhaden *Brevoortia tyrannus**	4	x	x
Speckled worm eel *Myrophis punctatus*	5		
Gulf flounder *Paralichthys albigutta*	6		
Pigfish *Orthopristis chrysoptera*	7		
Gobies Gobiidae	8		
Southern flounder *Paralichthys lethostigma**	9	x	x
Striped mullet *Mugil cephalus*	10		
Summer flounder *Paralichthys dentatus**	11	x	x

Larval sampling.—The Beaufort Inlet Ichthyoplankton Sampling Program has been in operation since late-1986 (Warlen 1994). Samples are collected from a bridge that spans a 40-m wide channel that is 1.5 km upstream from Beaufort Inlet (Figure 1). An estimated 10% of the water flowing through Beaufort Inlet passes through this channel (Churchill et al. 1999) and provides tidal exchange for the surrounding estuarine complex. The inlet is one of five major inlets providing pathways to estuarine nursery grounds in North Carolina. Several studies have demonstrated that the species assemblages and abundance patterns for larval fish sampled at this location are similar to those at other locations surrounding Beaufort Inlet (Hettler et al. 1997; Hettler and Hare 1998).

Larvae were collected with a 2-m^2 rectangular plankton net with 1-mm mesh and fitted with a flowmeter. The net was deployed at the surface during nighttime flood tides. The maximum channel depth (at high tide) is approximately 3 m. Four replicate sets were made weekly from November to April over the years 1986 to 2004. From 1986 to 1998, near-constant sample durations of 5 min were used, resulting in some variability in the total volume filtered. After 1998, a digital flowmeter was mounted in the net opening and filter volume was standardized to approximately 100 m^3. Samples were preserved in 95% solutions of ethanol and sorted and identified to species. Samples from the entire time span were standardized to the

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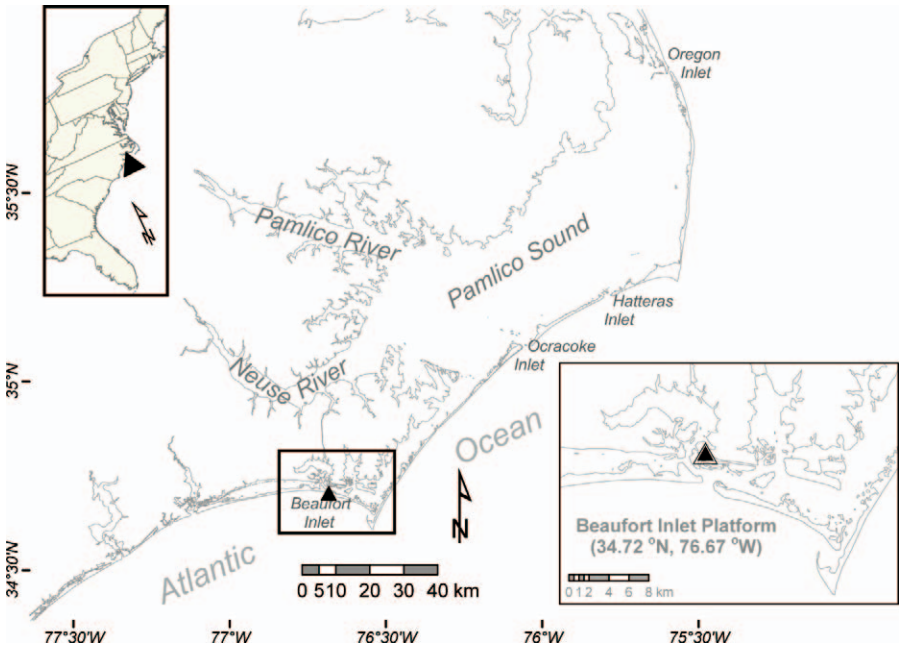


FIGURE 1.—Location of the Beaufort Ichthyoplankton Sampling Program observation platform near Beaufort Inlet, North Carolina.

number of individuals per 100 m^3. Samples from November to April were assumed to represent the year-class of the latter year (e.g., samples from November 1986 to April 1987 were considered part of the 1987 year-class).

Juvenile sampling.—Juvenile abundance data were derived from two North Carolina Division of Marine Fisheries surveys, the Estuarine Trawl Survey and the Pamlico Sound Survey. Abundance indices developed from these juvenile surveys are used in various stock assessment models for state and regionally managed fisheries. The Estuarine Trawl Survey samples approximately 100 fixed stations in shallow (<2-m) nursery habitats within Albemarle–Pamlico Sound estuarine systems (Figure 2) during April and May of each year. The samples are collected via a 1-min tow of a 3.2-m otter trawl with 6.4-mm mesh in the wings and body and 3.2-mm mesh in the cod end (West et al. 2006). The survey has been conducted since 1979; however, we used data for the period 1987–2004 to overlap with the ichthyoplankton program. All individuals were identified, counted, and measured to the nearest millimeter. The Pamlico Sound Survey samples approximately 54 stations chosen from a 0.5-degree grid subtended by the 2-m depth contour within Pamlico Sound and the Neuse and Pamlico rivers (Figure 2). Stations are selected through random sampling stratified by depth and region and sampled via double-rigged 9.1-m modified mongoose trawls with 22-mm mesh in the body and 19-mm mesh in the cod end (Fitzpatrick 2006). The survey has been conducted annually in June from 1987 to present; data from 1987 to 2004 were used for these analyses. Length frequency analysis was conducted to select the individuals from each survey that were members of the recruiting year-class; length modes were easily distinguished between age-0 and older age-classes for each species.

Statistical analysis.—We assessed the relationship between mean larval concentration and juvenile abundance using cross-correlation analysis for six species (Table 1). Data for all series were $\log_e$ transformed to approximate a normal distribution (i.e., $\log_e[L_t + 1]$ or $\log_e[U_t + 1]$, where L_t is the concentration of larvae per 100 m^3 in year t and U_t is the catch of juveniles per trawl in year t). We anticipated that some of the abundance and distribution patterns would be attributable to habitat type or region within the estuarine system (Burke et al. 1991; Walsh et al. 1999); therefore, we divided the juvenile survey stations into those located within river habitats (which would be characterized by soft sediments and low salinity) and those within sound habitats (which would be characterized by coarser sediments and higher salinity) (Figure 2). Spearman cross-correlations between larval concentration and juvenile abundance

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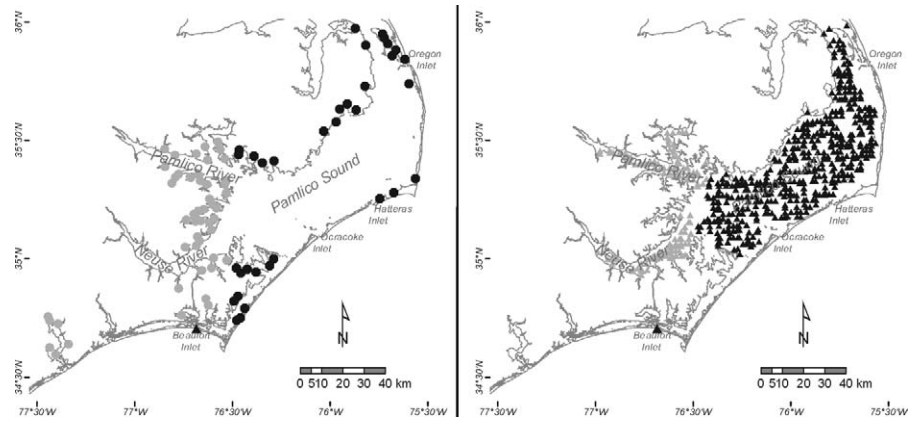


FIGURE 2.—Locations of fixed stations for sampling spring juvenile nursery abundance (left panel) and composite of trawling locations at which summer juvenile abundance observations were made (right panel), 1987–2004. Gray symbols indicate locations within river habitats, black symbols locations within sound habitats.

were calculated for each species and habitat type. The correlation coefficient was then compared with a distribution of the coefficients computed from 10,000 random permutations (bootstrap) of each time series sampled with replacement (Bjornstad et al. 1999). Statistical significance was evaluated nonparametrically as to whether the estimated correlation coefficients exceeded the 90th or 95th percentile (for positive values) or fell below the 10th or 5th percentile (for negative values). Initial examination of the relationships between larval and juvenile abundance suggested that the relationships were nonlinear and caused by density-dependent processes acting between life stages. We tested for this using a third-order polynomial regression model relating spring or summer juvenile abundance (the ordinate) to larval abundance (the abscissa). In no case were the polynomial terms significant; linear terms were only significant for species which also showed strong correlations between life stages.

We tested for synchrony among species within the larval and juvenile databases separately. Synchrony was tested both by pairwise cross-correlation and by analysis of the annual rate of change (first-order differences in each time series). We calculated the annual rate of change (z_t) for each species and life stage in log space, that is,

$$z_t = \log_e(L_t \text{ or } U_t) - \log_e(L_{t-1} \text{ or } U_{t-1}),$$

where L_{t-1} and U_{t-1} are the concentrations or abundances in the previous year. Spearman correlation coefficients were calculated for each pair of species within life stages. As with the cross-correlation of log abundance, correlation coefficient values were compared with a distribution of values generated from 10,000 permutations of the data series. In both methods, a positive value would indicate species that are in phase, a negative value species that are out of phase. A correlation with either sign could indicate population production being driven by similar environmental or biological forces.

Results

Comparison of Larval and Juvenile Abundance Patterns

We found significant positive correlations for three of the six species. The annual mean larval concentrations of pinfish, spot, and southern flounder at ingress were positively correlated to spring juvenile abundance, especially within the river habitats (Table 2; Figure 3). The correlations between larval concentration in the winter and juvenile abundance in the summer were significant for spot and southern flounder in river habitats and for pinfish in both river and sound habitats

TABLE 2.—Correlations between annual $\log_e$-transformed mean larval concentration and juvenile abundance within river and sound habitats during spring and summer sampling. Single asterisks indicate correlations exceeding the 90th percentile with 10,000 random permutations, double asterisks indicate correlations exceeding the 95th percentile.

	Spring		Summer	
Species	Rivers	Sounds	Rivers	Sounds
Pinfish	0.60**	0.33*	0.64**	0.63**
Spot	0.51*	0.45*	0.28*	0.03
Southern flounder	0.60**	0.33*	0.38*	0.20
Atlantic menhaden	−0.17	0.03	0.01	−0.33
Atlantic croaker	0.23	0.10	−0.02	−0.21
Summer flounder	−0.11	−0.30	0.30	0.40*

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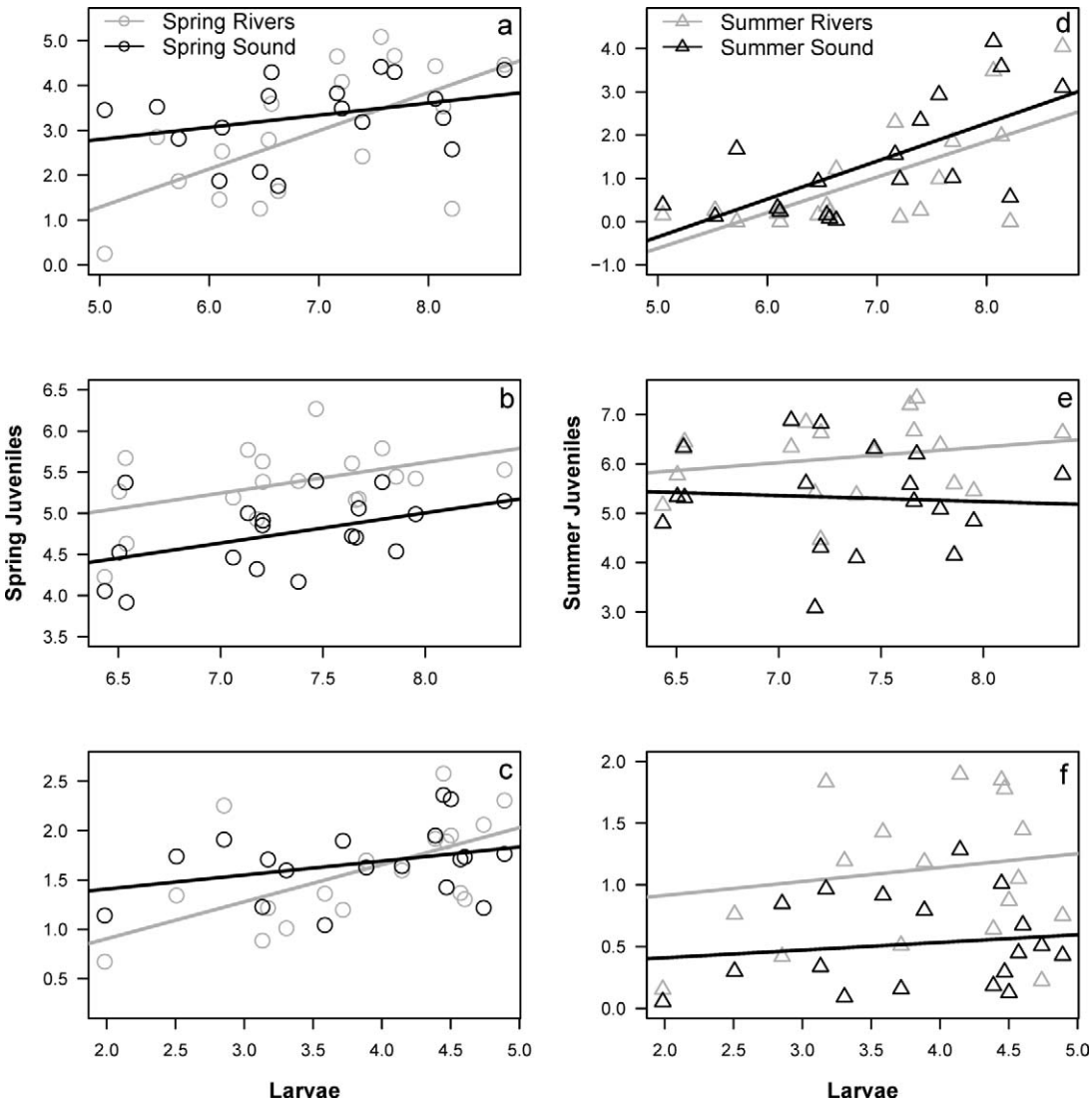


FIGURE 3.—Relationships between $\log_e$-transformed larval concentration and $\log_e$-transformed juvenile abundance for the spring nursery survey (left panels) and the summer sounds and rivers survey (right panels) for (**a**) and (**d**) pinfish, (**b**) and (**e**) spot, and (**c**) and (**f**) southern flounder. The lines are best linear fits for the subsets of juvenile abundance and are shown only for illustrative purposes.

(Table 2; Figure 3). In contrast, with one exception we failed to detect significant correlations between larval concentration and spring or summer juvenile abundance for Atlantic menhaden, Atlantic croaker, or summer flounder (Figure 4). Larval concentration and summer abundance in the sound habitats were weakly correlated for summer flounder (Table 2; Figure 4).

Synchrony among Species within Life Stages

We found evidence of synchronous patterns in the annual abundance of several species at both the larval and juvenile life stages. The larval abundances of pinfish and southern flounder were strongly correlated when we used log-transformed annual concentrations. In addition, there were significant relationships between the two flounder species (Table 3). These correlations may be affected by long-term trends and not reflect potential interannual patterns or step changes. Synchronous patterns assessed in terms of first-order differences showed a single significant pattern; ingressing larvae of Atlantic croaker were out of phase with pinfish (Table 3). Positive correlations were found between southern

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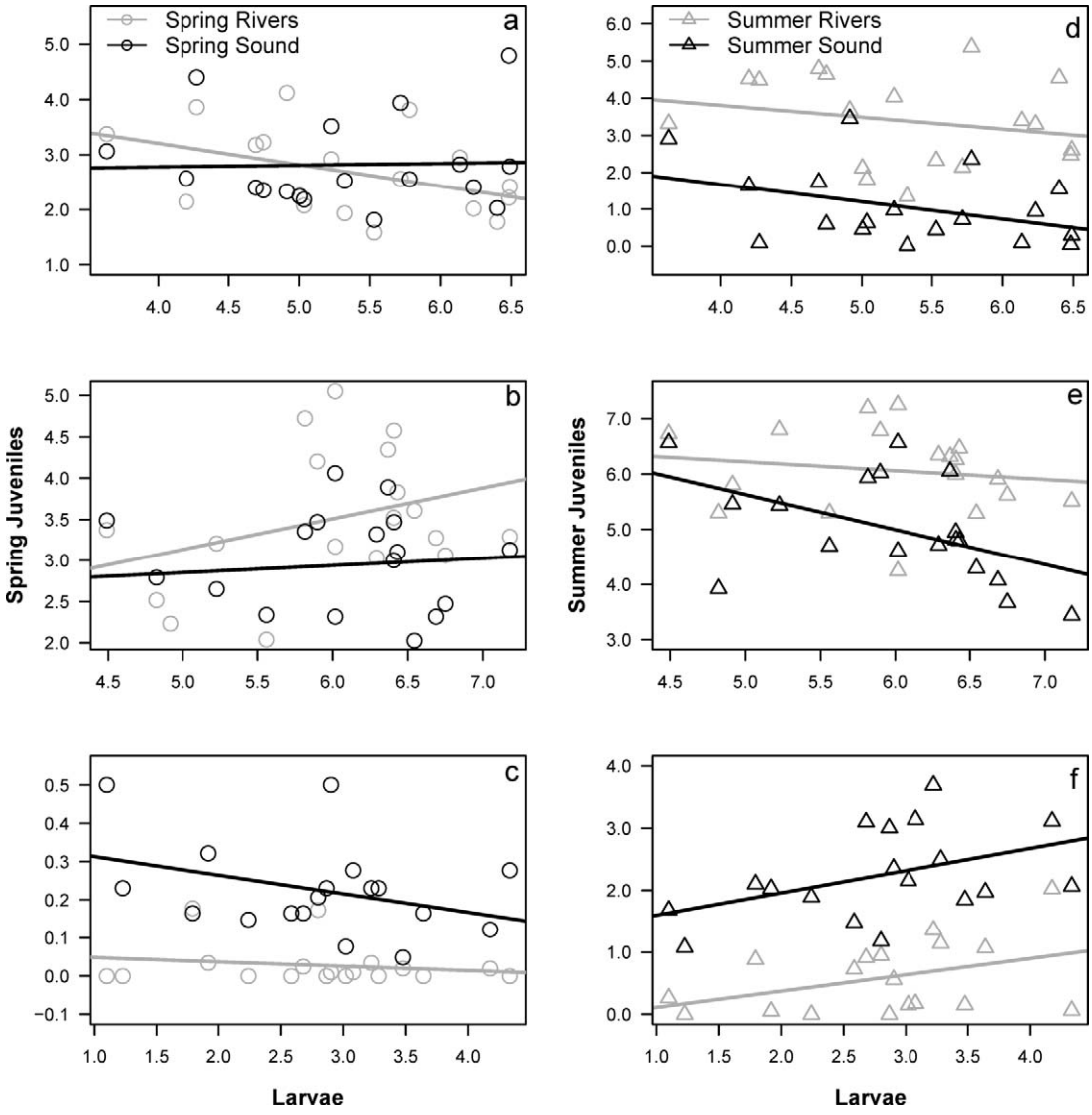


FIGURE 4.—Relationships between $\log_e$-transformed larval concentration and $\log_e$-transformed juvenile abundance for the spring nursery survey (left panels) and the summer sounds and rivers survey (right panels) for (**a**) and (**d**) Atlantic menhaden, (**b**) and (**e**) Atlantic croaker, and (**c**) and (**f**) summer flounder. The lines are best linear fits for the subsets of juvenile abundance and are shown only for illustrative purposes.

flounder and both pinfish and spot using abundance data from the spring juvenile survey (Table 4). When synchrony was assessed in terms of the annual rate of change, positive correlations were found among the two flounder species, spot, and pinfish (Table 4). Atlantic croakers were negatively related (out of phase) with pinfish and flounders. Atlantic menhaden were not related to any of the other species (Table 4). No relationships were found among any of the species within the summer juvenile time series.

Discussion

The life stage at which year-class strength is established is variable among estuarine-dependent fish species, but for many species the greatest control occurs during the larval and early-juvenile stages (Houde 1987). The positive correlations between larval abundance at Beaufort Inlet and juvenile abundance in nursery habitats within the Albemarle–Pamlico estuarine system suggests that year-class strength is established in the early life stages for species such as

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TABLE 3.—Results of tests for synchrony in annual larval concentrations between species using $\log_e$-transformed concentrations and $\log_e$-transformed first differences. Species abbreviations are as follows: Bt = Atlantic menhaden, Lr = pinfish, Lx = spot, Mu = Atlantic croaker, Pd = summer flounder, and Pl = southern flounder. Single asterisks indicate positive values above the 90th percentile or negative values below the 10th percentile of 10,000 random permutations; double asterisks indicate positive values above the 95th percentile or negative values below the 5th percentile.

	Bt	Lr	Lx	Mu	Pd	Pl
Concentrations						
Bt						
Lr	0.15					
Lx	0.37	0.38				
Mu	0.20	0.07	0.27			
Pd	0.08	0.21	−0.27	0.40		
Pl	0.36	0.50**	0.52**	0.27	0.42*	
First differences						
Bt						
Lr	0.21					
Lx	0.31	0.38				
Mu	−0.01	−0.48*	0.05			
Pd	−0.15	0.02	−0.38	0.16		
Pl	0.26	0.27	0.31	0.38	0.18	

TABLE 4.—Results of tests for synchrony between species in annual spring juvenile abundance at the fixed stations using $\log_e$-transformed values of abundance and $\log_e$-transformed first-differences. See Table 3 for additional details.

	Bt	Lr	Lx	Mu	Pd	Pl
Abundances						
Bt						
Lr	−0.46					
Lx	−0.11	0.28				
Mu	−0.05	−0.17	0.14			
Pd	0.23	−0.10	0.31	−0.32		
Pl	−0.22	0.57**	0.65**	−0.18	0.22	
First differences						
Bt						
Lr	−0.21					
Lx	−0.08	0.48				
Mu	−0.06	−0.64**	−0.02			
Pd	0.15	0.68**	0.53**	−0.44**		
Pl	−0.11	0.62**	0.77**	−0.26	0.59**	

spot, pinfish, and southern flounder. The factors that determine the abundance of larvae or the strength of a recruiting year-class have been associated with the environmental conditions in the nearshore coastal ocean during the late larval stages (Nelson et al. 1977; Checkley et al. 1988; C. Taylor, unpublished data). In a modeling study, Quinlan and Crowder (1999) found that population growth in Atlantic menhaden is most sensitive to the number of larvae arriving at an inlet and survival just after ingress. Our results suggest that the supply of larvae to the estuary determines the abundance of juveniles in nursery habitats for pinfish, spot, southern flounder, and perhaps other species with similar life-history strategies and geographic distribution. Whether juvenile abundance is linked to year-class strength remains to be determined, but juvenile indices are often used as tuning indices in stock assessments. Based on metrics derived for this study, larval supply at Beaufort Inlet does not determine juvenile abundance for Atlantic croaker, Atlantic menhaden, and summer flounder.

The lack of significant correlations for these three species does not necessarily mean that there is no relationship between larval ingress and juvenile abundance. There are three possible reasons for this lack of significance. First, larval sampling occurred at a single inlet and this inlet may not be representative of the larval supply into all four major inlets of the Albemarle–Pamlico estuarine system. Summer flounder, Atlantic croakers, and Atlantic menhaden spawn both north and south of Cape Hatteras (Checkley et al. 1999; Burke et al. 2000). During years of relatively high reproductive output in spawning habitats to the north of Cape Hatters, larvae would be more likely to enter the estuary through Oregon Inlet, which is near the border of North Carolina and Virginia. Alternatively, the movement of water masses may have favored the transport of larvae to inlets other than Beaufort Inlet. Years with high ingress through Oregon Inlet may result in high juvenile abundance, but this would not be documented at Beaufort Inlet. This scenario would not be surprising, as the southern orientation of Beaufort Inlet means that it would be subjected to different oceanographic conditions than the southeast- and east-facing Ocracoke and Oregon inlets (Hare et al. 1999). The weaker relationship between larval abundance and summer juvenile abundance for summer flounder suggests that strong year-classes are still evidence of successful spawning and recruitment through inlets both north and south of Cape Hatteras; therefore, juvenile abundance estimates for summer flounder may only be relevant if they are derived from summer surveys in the sound habitats of the Albemarle–Pamlico estuarine system.

A second possible reason for the uncoupling of larval and juvenile abundance is the design of the juvenile sampling programs. Both the spring and summer surveys are conducted using stratified fixed or random sampling designs based on geography and not the habitat or physicochemical features in the estuary. Atlantic croakers, for example, are known to select nursery habitats that are near the tidal–fresh margin of the estuary (Ross 2003; Searcy et al. 2007b). Very few stations in either juvenile sampling program are located in these regions of the estuary; therefore,

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Atlantic croakers may be poorly represented and juvenile abundances underestimated. Similarly, the summer survey is based on geographic and depth strata and ignores sediment and other benthic characteristics that are important in the distribution of summer flounder (Burke et al. 1991; Walsh et al. 1999). In years when surveys undersampled the preferred sandy substrates, summer flounder abundance would be underestimated. The behavior of pelagic schooling species like Atlantic menhaden probably results in poor capture success when using a bottom trawl. Further studies of species–habitat relationships will help refine the inferences drawn from juvenile sampling programs and may improve estimates of juvenile abundance for species that are closely associated with specific habitat types.

A third reason for the uncoupling between larval and juvenile abundances is mortality and cohort restructuring between the larval and juvenile measurements. At least 2 months separate the final larval sample and the juvenile survey. Previous work on settlement dynamics in estuarine-dependent fishes has found evidence that predation and density-dependent processes have a significant effect on the survival of early-settled fishes such as some flounders (Van der Veer 1986), Atlantic croakers (Searcy et al. 2007a), and Atlantic menhaden (Light and Able 2003). Mortality may vary annually and prevent a strong relationship between early larval and juvenile abundance patterns. The strong relationships that we found for pinfish, spot, and southern flounder, and to a lesser extent for summer flounder, suggest that major cohort restructuring is not occurring in these species, but it may be present in Atlantic croakers and Atlantic menhaden.

The patterns of synchrony among many of our species and within the larval and juvenile life stages suggest that similar biophysical or environmental processes are acting on the early life stages of many species that share the winter shelf-spawning strategy. Offshore larvae of spot and southern flounder are found at similar time periods (Hettler and Chester 1990) and at similar depths (Hare and Govoni 2005) and are probably subject to similar flow regimes in a vertically structured water column. Synchrony among the southern species (spot, pinfish, and southern flounder), coupled with the strong correlations between larval and juvenile abundance for these species, provides support for exploring the use of larval ingress measurements as indices of abundance and year-class strength for these and other species that have this life-history strategy. In contrast, the negative correlation between Atlantic croaker and pinfish larvae and juveniles and Atlantic croaker and summer flounder juveniles may be related to the timing of spawning and the transport pathways used by larvae as they move toward the coast and into the estuarine system. There are several species that are not represented in the juvenile surveys in nursery habitats in North Carolina and elsewhere but that serve as important fisheries or ecological resources. For species for which we lack other fishery-independent measures of abundance, the magnitude of larval ingress could be used as a tuning index for stock assessments (Gledhill and Lyczkowski-Shultz 2000). When there are good juvenile abundance data, larval data may serve as supplemental information that is more directly related to spawning biomass. The strong indication of synchrony among the various species further suggests that an index for one species may be useful in the management of other species. Species that are not economically valuable (e.g., pinfish) but that share life history traits with valuable species (e.g., summer flounder) may provide an independent source of data to guide decisions by fishery managers when environmental forcing is suspected.

Since inlets and estuary mouths are few along much of the eastern U.S. Atlantic coast, observation platforms similar to the ichthyoplankton platform at Beaufort Inlet could be designed for other inlets (e.g., Sullivan et al. 2006) and may be a cost-effective complement to spatially extensive estuarine trawl survey programs. Indeed, the U.S. Commission on Ocean Policy has recommended coordination among observation platforms and the development of additional ones to monitor chemical, physical, and biological variables (U.S. Commission on Ocean Policy 2004). As we have shown in this article, corroboration and validation of larval ingress dynamics via independent data sets would strengthen the inferences drawn from such observations.

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article honors the memory of J. Patrick Monaghan, who passed away during the preparation of the initial data for this work and whose insight and guidance helped establish this interinstitutional effort.

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