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[Article]

Effects of Winter Temperature and Flow on a Summer–Fall Nursery Fish Assemblage in the Chesapeake Bay, Maryland

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Abstract.—In temperate estuaries, nearshore nursery fish assemblages are influenced by environmental conditions that are present during and prior to the period of juvenile fish occurrence. An intensively sampled site (Patuxent River estuary) in mesohaline Chesapeake Bay provided 9 years of data for relating previous and current environmental variables with juvenile fish assemblages. Canonical correspondence analysis identified temperature and flow from the previous winter (January–March) and week and year of the assemblage sample as the most influential variables. In contrast, environmental variables at the time of sampling were not identified as important. High summer–fall abundances of Atlantic silversides *Menidia menidia*, striped bass *Morone saxatilis*, white perch *Morone americana*, and Atlantic needlefish *Strongylura marina* were positively associated with low winter temperatures and high winter flows. High abundances of bluefish *Pomatomus saltatrix*, spot *Leiostomus xanthurus*, bay anchovy *Anchoa mitchilli*, and northern puffer *Sphoeroides maculatus* were associated with low winter flows and high winter temperatures. The mechanisms by which winter conditions affect the summer–fall nursery fish assemblage were not directly addressed in this study, but winter conditions can affect subsequent spring and summer estuarine production, spawning and recruitment phenology, and distributions of juvenile fishes.

Fish assemblages in temperate estuaries are strongly influenced by environmental conditions (Attrill and Power 2002; Austin 2002; Jung and Houde 2003). Temporal and spatial variability in temperature, freshwater flow, salinity, dissolved oxygen, and turbidity are known to influence fish assemblage structure (Gunter 1956; Rogers et al. 1984; Szedlmayer and Able 1996; Marshall and Elliott 1998; Whitfield 1999; Akin et al. 2005). Numerous studies on temperate estuarine assemblage structure have focused on relations between current environmental conditions and assemblage structure (Rogers et al. 1984; Szedlmayer and Able 1996; Wagner and Austin 1999; Kimmerer 2002; Thiel et al. 2003), but the effects of prior environmental conditions have received little attention. However, recent evidence indicates that summer–fall fish assemblages in temperate estuaries are structured by environmental conditions present during the previous winter and spring.

Miller et al. (2006) showed that in U.S. mid-Atlantic estuaries, winter climate patterns were closely related to interannual changes in winter and spring freshwater flow. In turn, past studies have shown that spring flow influenced early life stages of estuary-spawning species, such as white perch *Morone americana* and bay anchovy *Anchoa mitchilli* (Secor 2000; Jung and Houde 2003; North and Houde 2003). Wood (2000) found that the timing of the winter–spring transition influenced subsequent summer–fall nursery fish assemblage structure in the Chesapeake Bay; coastal-spawning species (e.g., Atlantic menhaden *Brevoortia tyrannus* and spot *Leiostomus xanthurus*) were associated with warm, dry winter conditions, and anadromous species (e.g., striped bass *Morone saxatilis* and white perch) were associated with cold, wet winter conditions. Supporting these associations, Hare and Able (2007) showed that winter temperature was positively associated with subsequent abundance of Atlantic croaker *Micropogonias undulatus*.

Similarly, Attrill and Power (2002) showed that the North Atlantic Oscillation Index (NAOI), which primarily affects winter conditions, was the most important factor explaining the annual variation in various diversity indices (e.g., species number and Shannon–Weiner index) and individual species' abundance and growth in the Thames Estuary, UK. Hurst et al. (2004) showed that the Hudson River estuary fish assemblage structure from late August to November was strongly correlated with river flow during the preceding May–July but was not correlated with river flow during the summer–fall sampling period. Jung and Houde (2003) also showed that the assemblage structure in the main-stem Chesapeake Bay during 1997 was influenced by an anomalously high freshwater input during 1996.

Understanding estuarine fish assemblage structure requires the sampling of both temporal and spatial

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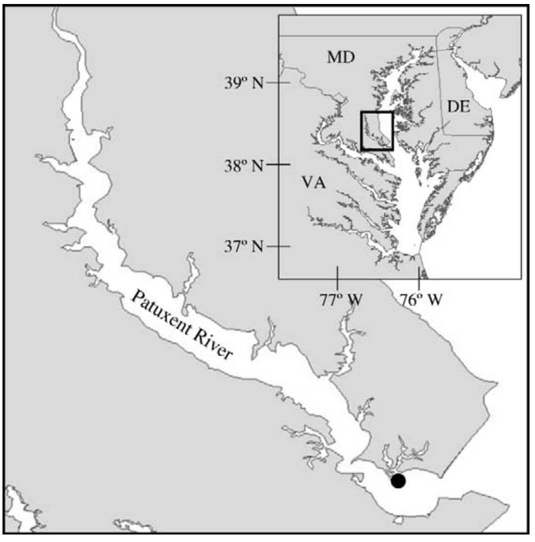

FIGURE 1.—Map of the Patuxent River, Maryland (MD), indicating the study site (black circle) at the Chesapeake Biological Laboratory (CBL; University of Maryland Center for Environmental Science), where the effects of environmental variables on the nursery fish assemblage were examined. Inset shows the location of the study area within the Chesapeake Bay (VA = Virginia; DE = Delaware).

variation in species composition. Many studies have emphasized spatial sampling, including sites structured along an estuarine salinity gradient (e.g., Marshall and Elliott 1998; Jackson and Jones 1999; Martino and Able 2003; Thiel et al. 2003; Akin et al. 2005). In these studies, environmental conditions at each sampling site were relevant to and critical for characterizing the assemblage along the estuarine gradient, but preceding environmental variables were not examined. Hurst et al. (2004) emphasized that analyses of assemblage structure must account for the multiple time scales under which environmental factors and community composition may vary. Here, we emphasized temporal sampling by examining a single site, which allowed us to limit the influence of the spatial variation that occurs along estuarine gradients (Martino and Able 2003; Thiel et al. 2003; Akin et al. 2005).

We characterized the summer–fall nursery fish assemblage structure in the lower mesohaline Patuxent River estuary based on nine consecutive years (1999–2007) of approximately weekly sampling (May–October). We also collected approximately daily measurements of environmental variables year-round at the same site to describe the variability encountered by the fish community. The study site was situated in middle Chesapeake Bay, and its location at the mouth of a major Chesapeake Bay tributary made it a likely transition zone along the estuarine gradient where distributional shifts could occur. The species found at the study site are representative of the species that occur throughout mesohaline waters of the Chesapeake Bay (Murdy et al. 1997; Wagner and Austin 1999; Jung and Houde 2003). Based upon recent literature, we hypothesized that environmental conditions during winter and spring would influence spring–summer estuarine production and subsequent abundance and distribution patterns of juvenile fishes that use mesohaline habitats. Alternatively, environmental conditions at the time of sampling may be important in structuring the summer–fall nursery fish assemblage structure, influencing distribution of mesohaline species along the estuarine gradient. Although our single-site design is necessarily limited in scope and spatial variations were not accounted for, our intensive weekly sampling enabled us to test the importance of multiple environmental factors at different temporal scales.

Methods

Sampling methods.—The study site (Figure 1) was located at the mouth of the Patuxent River at the Chesapeake Biological Laboratory (CBL; University of Maryland Center for Environmental Science) and was characterized by mesohaline salinity levels (mean May–October salinity (practical salinity units) = 8–16 from 1938 to 2007; Beaven 1960). The nearshore nursery fish assemblage was sampled approximately weekly during summer–fall (mid-May to mid-October) from 1999 to 2007 ($N = 134$; mean $\pm$ SD = 15 $\pm$ 6 hauls/year). The study site has a mostly sandy bottom and little to no vegetation. Collections were made in water less than 1.5 m deep using a 30.0- $\times$ 1.2-m beach seine with a bag and 6.0-mm mesh. One seine haul was made within 1 h of the predicted low tide; the seine was extended 30 m out and returned to shore as a quarter circle sweep. All fish were identified to species (when possible), measured to the nearest millimeter, counted, and released.

Inland silversides *Menidia beryllina* and Atlantic silversides *Menidia menidia* were not differentiated from 1999 to 2001 and were therefore pooled (hereafter, "silversides") for analysis of the entire time series. However, Atlantic silversides were the dominant species (>99% of silversides in years when they were identified to species). Most species were represented by young of the year (age-0 fish), but white perch and striped bass were represented by both age-0 fish and age-1 and older (age-1+) fish and were classified separately for analysis. Hereafter, when species were represented by only one age-class, the age-0 or age-1+ designation is presented. Age-classes were not distinguished for the other species examined, even though

TABLE 1.—Mean, SE, and cumulative percent abundance (catch per unit effort [CPUE], fish/haul) and incidence (percentage of hauls in which a species was present) of nursery fishes collected by weekly beach seining in the Patuxent River estuary, Maryland, during May–October 1999–2007 (silversides = pooled inland silversides and Atlantic silversides; age-classes: 0 = age 0, 1+ = age 1 and older). Asterisks indicate use in canonical correspondence analysis.

		CPUE			
Species	Age-class	Mean	SE	Cumulative percent	Incidence (%)
Atlantic menhaden *Breroortia tyrannus**	0	63.81	42.90	42.9	11.2
Silversides *Menidia* spp.*		61.64	8.51	89.4	90.3
Spot *Leiostomus xanthorus**	0	4.90	1.41	92.9	47.8
Bay anchovy *Anchoa mitchilli**		4.13	1.83	95.8	9.7
Striped bass *Morone saxatilis**	0	1.39	0.38	96.8	19.4
Atlantic needlefish *Strongylura marina**	0	0.95	0.21	97.5	27.6
Striped anchovy *Anchoa hepsetus**		0.87	0.35	98.1	9.0
Atlantic croaker *Micropogonias ondulatus**	0	0.81	0.80	98.7	2.2
Blue crab *Callinectes sapidus**		0.63	0.11	99.1	30.6
Bluefish *Pomatomus saltatrix**	0	0.53	0.14	99.5	25.4
White perch *Morone americana**	1+	0.12	0.06	99.6	5.2
White perch *Morone americana**	0	0.07	0.04	99.6	3.7
Atlantic silverstripe halfbeak *Hyporhamphus unifasciatus**	0	0.05	0.05	99.7	1.5
Gizzard shad *Dorosoma cepedianum**	1+	0.04	0.03	99.7	2.2
Mummichog *Fundulus heteroclitus**		0.04	0.03	99.7	2.2
Striped killifish *F. majalis**		0.04	0.02	99.8	3.0
Summer flounder *Paralichthys dentatus**	0	0.04	0.02	99.8	3.0
Northern puffer *Sphoeroides maculatus**	0	0.04	0.02	99.8	3.0
Winter flounder *Pseudopleuronectes americanus**	0	0.04	0.02	99.8	2.2
Alewife *Alosa pseudoharengus**	0	0.03	0.02	99.9	1.5
Cownose ray *Rhinoptera bonasus**	0	0.03	0.02	99.9	1.5
Hickory shad *Alosa mediocris*	0	0.02	0.01	99.9	2.2
Striped bass	1+	0.02	0.01	99.9	2.2
Skilletfish *Gobiesox strumosus*		0.01	0.01	99.9	1.5
Summer flounder *Paralichthys dentatus*	1+	0.01	0.01	99.9	1.5
Northern pipefish *Syngnathus fuscus*		0.01	0.01	>99.9	1.5
Inshore lizardfish *Synodus foetens*		0.01	0.01	>99.9	1.5
Northern searobin *Prionotus carolinus*	0	0.01	0.01	>99.9	1.5
American eel *Anguilla rostrata*		0.01	0.01	>99.9	0.7
Blackcheek tonguefish *Symphurus plagiusa*		0.01	0.01	>99.9	0.7
Black drum *Pogonias cromis*	0	0.01	0.01	>99.9	0.7

multiple year-classes may have been present. Age designations were based on the work of Able and Fahay (1998) and on graphical analysis of length frequency distributions.

Salinity and temperature were measured approximately daily at the site over the entire sampling period. Patuxent River flow data were obtained from the U.S. Geological Survey station near Bowie, Maryland (132 km upstream from the river mouth). Principal components analysis was used to characterize associations between seasonal temperature, salinity, and flow.

Data analysis.—The association between summer–fall nursery fish assemblage structure and environmental conditions was examined using canonical correspondence analysis (CCA). As a direct gradient analysis, CCA has been widely used in community analyses and more recently has been applied to estuarine fish assemblage structure (Ter Braak 1986; Palmer 1993; Martino and Able 2003; Hurst et al. 2004; Veiga et al. 2006). In an extension of correspondence analysis (reciprocal averaging), the ordination axes in CCA are constrained to linear combinations of measured environmental variables (Ter Braak 1986). Therefore, CCA directly relates species' occurrences to environmental variables. The following environmental variables were used in CCA: mean winter (January–March) temperature, flow, and salinity; mean spring (April–June) temperature, flow, and salinity; mean monthly temperature, flow, and salinity; daily temperature and salinity; and year and week of the assemblage sample. Weekly abundance data from the seine haul was used to calculate catch per unit effort (CPUE) or catch per haul. Transformation ($\log_e$[CPUE + 1]) was used to reduce the influence of abundant species on CPUE and to approximate the normal distribution. Species occurring in more than 3% of all hauls or with a mean CPUE of more than 0.03 fish/haul were included in CCA (Wagner and Austin 1999; Martino and Able 2003). Twenty-one species × age-class combinations were included in the analysis (Table 1). The significance of CCA was tested with a Monte Carlo test (10^3 permutations) for the sum of all

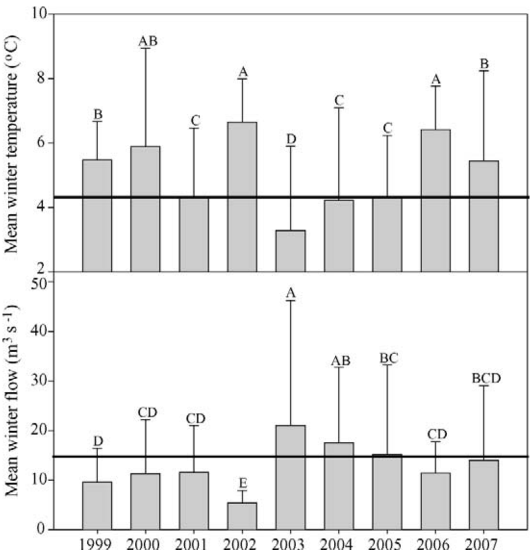

FIGURE 2.—Mean (±SD) winter (January–March) seawater temperature (°C) at the Patuxent River estuary study side and mean winter Patuxent River flow (m^3/s) at Bowie, Maryland (measured 132 km upstream from the mouth), during 1999–2007. Black lines indicate the historical mean winter temperature (1938–2007) and flow (1978–2007). Bars with the same letter are not significantly different ($P < 0.05$).

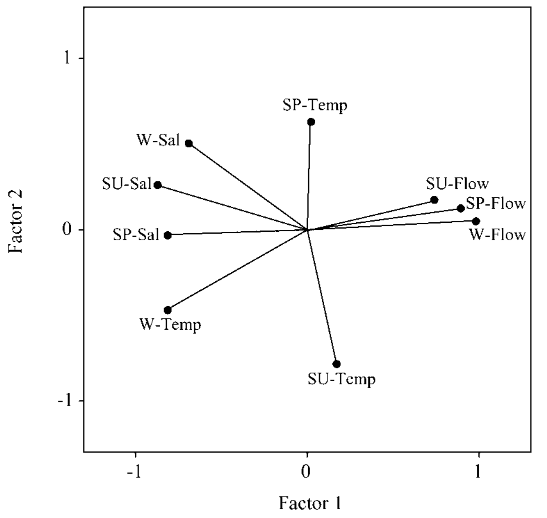

FIGURE 3.—Principal components analysis of seasonal temperature (temp; °C), salinity (sal), and flow (m^3/s) at the Patuxent River estuary study site, Maryland, during 1999–2007 (W = winter; SP = spring; SU = summer).

eigenvalues (Wagner and Austin 1999; Martino and Able 2003; Thiel et al. 2003). The significance of environmental variables in explaining assemblage structure was tested with a stepwise inclusion of variables into the analysis (Hurst et al. 2004). The CCA was performed in R software (version 2.4.0).

Univariate statistics were used to further analyze individual species' associations with the significant environmental variables from CCA. Individual species' abundances were compared with significant environmental variables using a Kruskal–Wallis test (nonparametric measures were necessary due to failed attempts to normalize the abundance data for univariate analyses). A chi-square contingency table analysis was also used to determine whether individual fish species were more likely to be present or absent in association with certain environmental conditions. If the analysis of variance was significant, then Duncan's multiple-range test was used to determine specific differences.

Results

Environmental Variation

The lower Patuxent River study site experienced significant interannual variability in seasonal (winter, spring, and summer) temperature, salinity, and flow ($P < 0.0001$). Although spring temperatures were not significantly different between years ($P = 0.10$), winter temperature varied significantly ($P < 0.0001$). Winter temperature ranged from 3.3°C to 6.6°C, salinity ranged from 9.0 to 18.0, and flow ranged from 5.4 to 21.0 m^3/s (Figure 2). Spring temperature ranged from 16.5°C to 19.0°C, salinity ranged from 8.8 to 14.0, and flow ranged from 5.2 to 24.3 m^3/s. Summer temperature ranged from 25.3°C to 28.0°C, salinity ranged from 10.5 to 16.1, and flow ranged from 2.8 to 17.8 m^3/s. Seasonal salinity and flow were inversely correlated in the principal components analysis, as was expected, and spring and summer temperature loaded orthogonally to salinity and flow (Figure 3). However, winter temperature was inversely correlated with winter flow.

Assemblage Structure

In a total of 134 seine hauls, we encountered 18,851 individual fish that represented 29 species (19 families) over the 9-year period (Table 1). The two most abundant species, age-0 Atlantic menhaden and silversides, made up almost 90% of the total catch. Age-0 spot and bay anchovy were the next most abundant species, together contributing 6% of the total catch. The most frequently encountered taxa (incidence > 25%) included silversides, age-0 spot, blue crabs, age-0 Atlantic needlefish, and age-0 bluefish.

Canonical correspondence analysis showed that winter temperature, flow, and salinity; week and year of the assemblage sample; and monthly temperature were important in structuring the nearshore fish

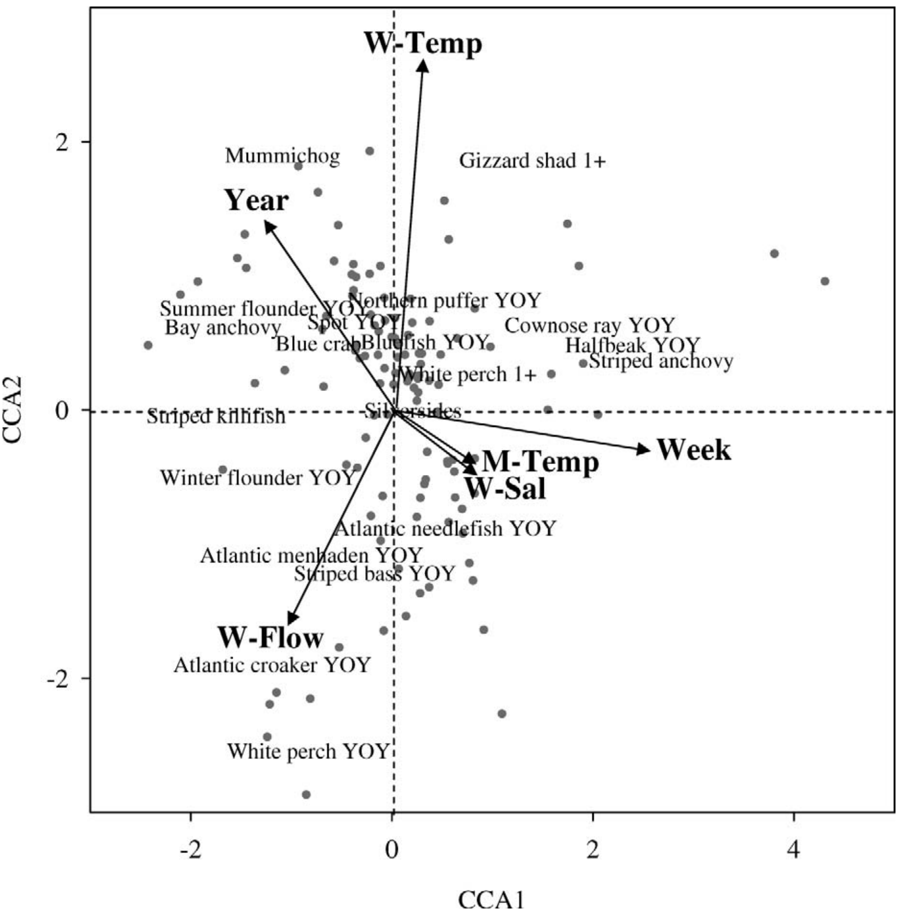

FIGURE 4.—Canonical correspondence analysis (CCA) ordination relating nursery fish assemblage composition to environmental variables (W-Flow = winter flow, m^3/s; M-Temp = monthly temperature, °C; W-Sal = winter salinity; W-Temp = winter temperature) for the Patuxent River estuary study site, Maryland, 1999–2007. Gray circles represent individual weekly seine hauls. A species' position on the axes is represented by the center of the species' name (YOY = age-0 fish; 1+ = age-1 and older fish); significant environmental variables are represented by arrows (relative lengths of arrows indicate relative importance). Species' positions relative to arrows reflect the species' distributions along each environmental variable.

assemblage (Figure 4; Tables 2, 3). The first and second canonical axes explained 10% of the variation in species composition and 55% of the species–environment correlation. The first canonical axis was strongly correlated with week of the assemblage sample. The second canonical axis was strongly correlated with winter temperature. The addition of the remaining variables did not significantly improve the model and were not included in the final CCA (spring temperature: $P = 0.57$; spring flow: $P = 0.75$; spring salinity: $P = 0.30$; monthly flow: $P = 0.13$; monthly salinity: $P = 0.90$; daily temperature: $P = 0.22$; daily salinity: $P = 0.91$). Monte Carlo-based permutation tests indicated that the resulting CCA ordination was highly significant ($P < 0.005$).

TABLE 2.—Summary of results from canonical correspondence analysis (CCA) used to examine the association between summer-fall nursery fish assemblage structure and environmental conditions in the Patuxent River estuary, Maryland, 1999–2007. Values for CCA axes 1–4 are presented.

	Axis			
Variable	1	2	3	4
Eigenvalue	0.23	0.15	0.12	0.09
Cumulative percentage of species variation	6.3	10.3	13.6	16.0
Cumulative percentage of species–environment variation	33.5	55.3	72.6	85.7
Sum of all unconstrained axes				0.68
Sum of all canonical axes				3.66

TABLE 3.—Canonical correlation coefficients describing the relation between nursery fish assemblage structure (from weekly beach seine sampling) and environmental variables (winter or monthly temperature, °C; winter flow, m^3/s; winter salinity) measured in the Patuxent River estuary, Maryland, 1999–2007 (**$P < 0.01$; ***$P < 0.001$).

Variable	Axis 1	Axis 2
Week***	0.85	−0.09
Winter temperature***	0.17	0.90
Year***	−0.44	0.49
Winter flow***	−0.30	−0.55
Monthly temperature**	0.40	−0.21
Winter salinity**	0.41	−0.26

Species that were associated with high winter flow and low winter temperature in the CCA ordination included age-0 white perch, age-0 striped bass, age-0 Atlantic menhaden, and age-0 Atlantic croaker. Species that were associated with low winter flow and high winter temperature included age-0 bluefish, age-0 spot, age-0 northern puffer, age-1+ gizzard shad, and mummichogs. The most frequently encountered taxon, silversides, was oriented towards the center of the axes, indicating frequent presence over all environmental conditions. Bay anchovy, age-0 spot, blue crabs, and age-0 bluefish occurred early in the season. Species that were associated with increasing summer and fall temperature and that appeared later in the season included age-0 cownose rays, age-0 Atlantic silverstripe halfbeaks, age-1+ gizzard shad, and striped anchovy.

The abundance (CPUE) and incidence (presence in seine hauls) of several species varied significantly between sampling months (Table 4; Figure 5a). Striped anchovy and age-0 white perch were temporally restricted in their summer abundance and incidence (July–September and June–July, respectively; Figure 5a1, a5). Similarly, age-0 Atlantic menhaden were significantly more abundant in July and were only present during June–August (Figure 5a2). Silversides occurred frequently throughout the sampling period, exhibiting increased August–September abundance that was driven by recruitment of age-0 silversides to the study site (Figure 5a4). Age-0 spot and age-0 Atlantic needlefish occurred in all summer months but exhibited monthly pulses in abundance (May–June and August, respectively; Figure 5a3, a8). The incidence of age-0 bluefish was highest in June and then steadily decreased throughout the summer; abundance of this species showed monthly pulses, increasing in June and August (Figure 5a7).

Several species were also differentially influenced by flow and temperature measured during the preceding winter; dominant species exhibited positive relations with winter flow and negative relations with winter temperature (Table 3; Figure 5). Silversides

TABLE 4.—Significance (P-values) of tests examining the effects of environmental variables (winter flow, m^3/s; winter temperature [temp], °C) on abundance (catch per unit effort, fish/haul; Kruskal–Wallace tests) and incidence (percentage of hauls in which a species was present; chi-square analyses) of individual nursery fish species captured by beach seining in the Patuxent River estuary, Maryland, 1999–2007 (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Silversides are pooled inland silversides and Atlantic silversides.

Species	Effect	Abundance P	Incidence P
Striped anchovy	Month	<0.01**	<0.01**
	Winter flow	<0.01**	<0.01**
	Winter temp	0.12	0.14
Atlantic menhaden (age 0)	Month	<0.01**	<0.01**
	Winter flow	0.38	0.38
	Winter temp	0.01*	0.01*
Spot (age 0)	Month	0.06	0.11
	Winter flow	0.68	0.78
	Winter temp	0.02*	0.02*
Silversides	Month	0.57	0.40
	Winter flow	0.01*	<0.01**
	Winter temp	0.12	0.04*
White perch (age 0)	Month	0.26	0.26
	Winter flow	0.04*	0.04*
	Winter temp	<0.001***	<0.001***
Striped bass (age 0)	Month	0.34	0.38
	Winter flow	0.21	0.18
	Winter temp	<0.01**	<0.01**
Bluefish (age 0)	Month	<0.001***	<0.001***
	Winter flow	0.02*	0.03*
	Winter temp	0.01*	0.03*
Atlantic needlefish (age 0)	Month	0.05	0.08
	Winter flow	<0.01**	<0.001***
	Winter temp	<0.01**	<0.01**
Bay anchovy	Month	<0.01**	<0.01**
	Winter flow	0.49	0.50
	Winter temp	0.97	0.95
Blue crab	Month	0.89	0.92
	Winter flow	0.54	0.60
	Winter temp	0.63	0.50

(Figure 5b4, c4) and age-0 Atlantic needlefish (Figure 5b8, c8) had higher abundance and incidence with increased winter flow and decreased winter temperature. Age-0 white perch (Figure 5b5, c5) and age-0 striped bass (Figure 5b6, c6) were significantly more abundant in years with cold winter temperature. In contrast, age-0 spot (Figure 5b3, c3) showed increasing abundance and incidence as winter temperature increased. Similarly, age-0 bluefish (Figure 5b7, c7) occurred at higher abundance and incidence as winter temperature increased and as winter flow decreased. Striped anchovy exhibited higher abundance and incidence when winter flow was average to low (Figure 5b1).

Discussion

As shown by CCA, the summer–fall nursery fish assemblage structure at the lower Patuxent River site

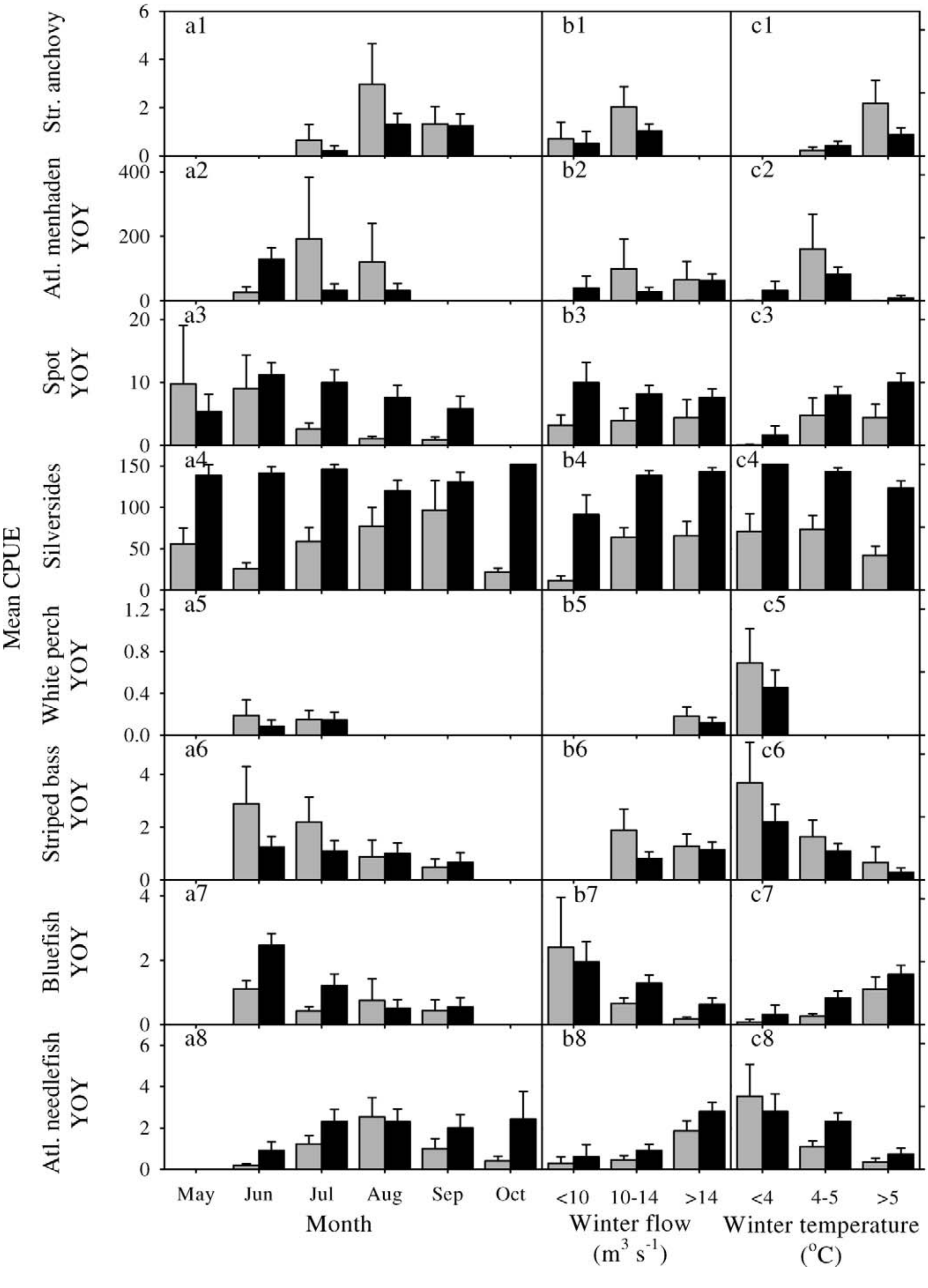

FIGURE 5.—Mean (±SE) abundance (catch per unit effort [CPUE], fish/haul; gray bars) and incidence (percentage of hauls in which a species was present; black bars) of nursery fishes (Atl. = Atlantic; str. = striped; silversides = pooled inland silversides and Atlantic silversides; YOY = age-0 fish) collected by beach seining in the Patuxent River estuary, Maryland, in relation to **(a)** month of the assemblage sample, **(b)** winter flow (m^3/s), and **(c)** winter temperature (°C). Table 4 summarizes the results of Kruskal–Wallis tests (CPUE) and chi-square analyses (incidence).

was strongly influenced by environmental variables from the previous winter. Winter temperature and flow were most influential, whereas environmental variables measured at the time of sampling were not identified as important. Similarly, spring variables did not explain significant variation in the summer–fall assemblage. These results were similar to those of Hurst et al. (2004), who showed that previous environmental variables were important in explaining the Hudson River fish assemblage over a 21-year period. Also, Attrill and Power (2002) showed that winter conditions (i.e., NAOI) were important in explaining assemblage composition, abundance, and growth on an annual basis in the Thames Estuary.

The mechanisms by which winter conditions influence the summer–fall nursery fish assemblage were not directly addressed by this study. Hurst et al. (2004) identified two sources of variation in estuarine assemblage structure: (1) physical factors that create habitats that are suitable for the success of individual species and (2) the recruitment dynamics of individual species. Winter conditions may influence both of these sources of variation. First, winter temperature and flow may affect nursery stability and production differentially among species (i.e., anadromous versus coastal-spawning species). For example, it is well known that nursery zones expand for anadromous species during years with cold, wet winter conditions (Secor 2000; Jung and Houde 2003; North and Houde 2003). During those years, high flow also intensifies the formation of the maximum turbidity zone and provides favorable early foraging conditions for estuary-spawning fishes (North and Houde 2003). Similarly, Weinstein et al. (1980) suggested that the nursery zone boundaries for Atlantic croaker, spot, and flounder in North Carolina estuaries are dictated by freshwater flows and tend to shift as flows change. Gibson (1994) and Ross (2003) found that fish population abundances were correlated with the availability of nursery habitat that promotes growth and survival. The lower Patuxent River study site was situated in a transitional zone along the riverine–estuarine gradient and the upper–lower Chesapeake Bay gradient; distributional shifts related to availability of nursery habitats may occur in this zone. Second, winter conditions may influence the timing of migration and spawning of adult fish, as well as the survival of eggs and larvae to juvenile stages (recruitment dynamics). For example, the timing of spring spawning is a critical determinant of recruitment success in anadromous species, such as striped bass and American shad *Alosa sapidissima* (Limburg 1995; Secor and Houde 1995).

The CCA ordination explained a small but significant amount of species variation (10%) and a substantially larger amount of the species–environment variation (55%). As was emphasized by Gauch (1982) and Ter Braak (1986), ordinations that explain low percentages of variation still can be informative, since inherent noise in the data makes it impossible to explain 100% of the variation. The unexplained variation in the fish assemblage may indicate the importance of biotic interactions in structuring assemblages (Marshall and Elliott 1998; Martino and Able 2003; Akin et al. 2005), and these were not explicitly considered in our analysis. Many authors have shown the importance of biotic factors (e.g., competition, predation [i.e., piscivores, humans, and otherwise], and feeding behavior) and the interaction of biotic and abiotic factors (Livingston et al. 1976; Ogburn-Matthews and Allen 1993; Lankford and Targett 1994; Thiel et al. 1995; Nemerson and Able 2004; Akin et al. 2005) in structuring assemblages. While biotic interactions were not measured in this study, CCA showed that abiotic variables exerted a strong influence on fish assemblage structure. Further, the univariate effects of month, winter temperature, and winter flow on individual species' abundance and incidence were in agreement with the multivariate CCA and provided further evidence for the importance of abiotic variables in structuring the fish assemblage.

Although our study was limited to a single site, we found that winter conditions had a significant influence on the summer–fall nursery fish assemblage. The lower Patuxent River summer–fall nursery fish assemblage was similar in composition to other described Chesapeake Bay fish assemblages and was also similar in structure (e.g., low diversity and high dominance) to other temperate estuarine fish assemblages (Allen 1982; Jackson and Jones 1999; Wagner and Austin 1999; Whitfield 1999; Jung and Houde 2003; Akin et al. 2005). Our study site was dominated by silversides and age-0 Atlantic menhaden, which made up almost 90% of the total catch. Although these taxa showed similar mean abundances, silversides had a high incidence (encountered in 90% of all hauls), whereas Atlantic menhaden had a relatively low incidence (encountered in 11% of all hauls). Atlantic menhaden also showed a large amount of variation in abundance; CPUE ranged from 0 to almost 5,000 fish.

Species groupings identified by CCA were similar to those reported in other Chesapeake Bay studies (Wood 2000; Jung and Houde 2003); anadromous species were associated with cold, wet winter conditions, and some coastal-spawning species (e.g., age-0 bluefish, age-0 spot, bay anchovy, and striped anchovy) were associated with warm, dry winter conditions. Other coastal-spawning species, including age-0 Atlantic menhaden and age-0 Atlantic croaker, were associated with cold, wet winter conditions. Jung and Houde (2003) grouped age-0 Atlantic menhaden with the anadromous species and designated age-0 Atlantic croaker as intermediate between coastal spawners and anadromous species (similar to our study), but these classifications were in disagreement with those of Wood (2000) and Hare and Able (2007). Age-0 Atlantic menhaden abundance is positively correlated with spring and summer plankton blooms (Friedland et al. 1989; Luo et al. 2001; Love et al. 2006), which in turn are positively correlated with high winter flows (Fisher et al. 2006; Paerl et al. 2006), suggesting a possible link between high winter flow and age-0 Atlantic menhaden production. However, large Atlantic menhaden schools were rarely captured in this study, and the variability in abundance and low catchability may have confounded the association of age-0 Atlantic menhaden with environmental variables. Both Atlantic menhaden and Atlantic croaker spawn in late fall and early winter (Able and Fahay 1998), and summer seine surveys may not effectively sample all periods of age-0 occurrence for these species. Atlantic croakers were also rare in Maryland Department of Natural Resources (MDNR) seine survey data, which provided a more spatially extensive evaluation of nursery assemblage structure (Durell and Weedon 2005). Although Atlantic croakers were absent from samples in most years, MDNR seine survey data showed that age-0 fish were present during 2002 and 2006, which were relatively warm and dry years; this result is contrary to our findings but agrees with reports by Wood (2000) and Hare and Able (2007). In summary, our results support those of studies indicating that cold, wet winter conditions are favorable for anadromous species, whereas the association between warm, dry winter conditions and summer–fall assemblages varies among coastal-spawning species. In our study, age-0 bluefish, age-0 spot, and age-0 northern puffers showed the strongest associations with warm, dry winter conditions.

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