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Macroscale Assessment of American Shad Spawning and Nursery Habitat in the Mattaponi and Pamunkey Rivers, Virginia

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Abstract.—Variation in habitat suitability can alter the growth and mortality of early life stages of fishes but is often difficult to measure, quantify, and apply to the entire system. We designed and tested habitat suitability index (HSI) models incorporating both proximate riverine parameters and surrounding landscape features as determinates of optimal spawning and nursery areas for American shad *Alosa sapidissima*. American shad eggs and larvae were collected in the Mattaponi and Pamunkey rivers, Virginia, during 1997–1999 as direct evidence of nursery habitat use and indirect evidence of spawning reaches. Hydrographic, physical habitat, shoreline, and land use features were examined for associations with the presence of eggs and larvae. Principal components analyses and logistic regressions indicated the importance of hydrographic parameters (current velocity, dissolved oxygen, and depth), physical habitat features (sediment type and woody debris), forested shoreline, and land use features to the presence of eggs. Larvae were more dispersed than eggs were, and distinct habitat associations for larvae could not be discerned. This corresponds to the hypothesis that sites are selected by spawners, and larvae (more so than eggs) are subjected to net downstream transport. Morphological features indicate the presence of three distinct regions along the Mattaponi and Pamunkey rivers. The presence of eggs is typically associated with upper and midriver regions, whereas larvae are dispersed among the three regions. The combination of remote sensing and on-site data collection and analyses used in this study may be an effective way to rapidly assess essential fish habitat when data are limited, allowing the linkage of fish population data with habitat evaluations. As more data become available and HSI models are refined, habitat ratings may be modified for a more precise delineation of specific reaches of critical fish habitat.

Essential fish habitat (EFH) is defined as ''those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity'' (Magnuson-Stevens Act, 16 U.S.C. 1801 et seq.). Embedded in the concept of EFH is the notion that habitat has a potential influence on fishery production. With new mandates to identify and protect EFH for all species managed under fisheries management plans, evaluation of fish habitat has become a priority.

An important step to understanding habitat influences on fishery production is to define the envelope of the habitat where the organism lives and the ecological factors influencing the habitat and its inhabitants (Odum 1971; Hoss and Thayer 1993). Until recently, habitat characteristics were referenced primarily on a microscale (centimeters–meters), in recognition of the small niche in which an estuarine organism physically is found. However, the process of managing a species often encompasses large areas, such that a macroscale (meters–kilometers) approach is more appropriate for quickly and accurately defining the habitat quality. With a macroscale watershed approach to habitat assessment, not only proximate (microscale) variables are examined but also the influence of landscape features on these proximate habitat variables.

Within coastal plain systems, the American shad *Alosa sapidissima*, an anadromous clupeid, is a prime example of a species affected by loss and degradation of habitat. Declines in Atlantic coastal stocks, attributed to habitat loss and flow alterations, have led to fishing moratoria in some areas (Mansueti and Kolb 1953; Walburg and Nichols 1967; Carlson 1968; ASMFC 1999). The American shad fishery peaked in the Chesapeake Bay in the late 1800s and declined after the turn of the century (Mansueti and Kolb 1953). Stocks continued to decline in the Chesapeake Bay region during the past few decades, probably as a result of overfishing, habitat degradation, and blockage of spawning runs. In-river fishing was finally closed for shad in Maryland (1980) and Virginia (1994). In Virginia, in addition to moratoria, passageways for fish are opening historic spawning grounds on the James and Rappahannock rivers, and hatchery efforts are taking place on the James and York river

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systems. Unfortunately, much of what is known about natural spawning and early life history is either anecdotal or incompletely described for all stocks (Massmann 1952; Bilkovic et al. 2002). It has been postulated that the larval stage (4–9 d) is the critical period at which American shad year-class strength is established (Crecco et al. 1983); therefore, varying habitat exposures during the early life stages may impact recruitment and the successful restoration of stocks.

To supplement restoration attempts underway in Virginia, our objective was to address the questions what is essential American shad spawning and nursery habitat and how can it be characterized over a large scale? Our chosen study area was the York River, a coastal plain system that currently has the largest spawning runs of American shad in Virginia (although now historically low; Olney and Hoenig 2001). Previous habitat suitability index (HSI) models developed and verified for the early life stages of American shad incorporated microscale measurements of hydrographic parameters, such as temperature, salinity, and water velocity (Stier and Crance 1985; Ross et al. 1993). In this study, we have proposed HSI models for the York River that include hydrographic parameters and expand on previous models by adding physical habitat and shoreline/landscape features. Although quantitative links between land use or macroscale variables and American shad populations have not been assessed previously, numerous studies have noted the potential influence on population and community dynamics of stream fish of landscape change resulting from land-use activities (Karr and Schlosser 1978; Limburg and Schmidt 1990; Schlosser 1991; Hall et al. 1996; Roth et al. 1996). We hypothesize that underlying relationships exist between macroscale habitat variables, which are measures of longitudinal heterogeneity of a river on a large scale, and the presence or absence of American shad eggs and larvae. We describe these relationships with multivariate statistical analyses and supplement the macroscale assessment with more detailed microscale habitat descriptors for two tributaries of the York River (Mattaponi and Pamunkey rivers).

Methods

Our approach followed a three-step process: (1) collect ichthyoplankton along the longitudinal axes of the Mattaponi and Pamunkey rivers (Bilkovic et al. 2002), (2) evaluate habitat for the area of collection, and (3) make quantitative comparisons between the presence or absence of eggs and larvae and the habitat evaluation.

Ichthyoplankton collections.—Presence/absence data on American shad eggs and larvae were obtained from ichthyoplankton surveys (March–May 1997–1999) conducted in the Mattaponi and Pamunkey rivers. Sampling encompassed the limits of the brackish water to the fall lines (the boundary between an upland region and a coastal plain, across which rivers from the upland region drop to the plain as falls or rapids)—on the Mattaponi River, river kilometers (Rkm) 68–124; on the Pamunkey River, Rkm 72–150—by using weekly oblique tows of a bongo frame and push-net deployments on each river.

Sampling protocol in 1997.—Exploratory sampling in the Mattaponi and Pamunkey rivers for eggs and larvae of American shad extended from March through April 1997. Sites were chosen based on a prior survey of American shad eggs in the rivers (Massmann 1952). The sampling protocol included weekly collections of ichthyoplankton during daylight hours using stepped oblique tows of a bongo frame fitted with two 333-μm mesh nets (60-cm diameter). Catches from both nets were combined. The same 10 stations were sampled weekly on each river within the tidal freshwater reaches. Stations are depicted as Rkm from the mouth of the York River, and were located at approximately 3.2-Rkm intervals.

Sampling protocol in 1998 and 1999.—In 1998 and 1999, station locations were extended upriver to include more shallow stations, given the low abundance of American shad eggs in 1997. Bongo nets could not be used, and sampling included surveys with push nets in the upper reaches of the rivers (31 March through 20 May 1998 and from 11 April through 7 May 1999). The weekly sampling on each river consisted of push nets towed approximately 1 m below the surface at each station. A push-net frame fitted to the bow of a 4-m boat (Olney and Boehlert 1988) accommodated two plankton nets (333 μm, 60 cm). Catches from both nets were combined. In 1998, eight stations per river were systematically sampled, bracketing 94–120 Rkm (Mattaponi River) and 109–131 Rkm (Pamunkey River). In 1999, two stations at 124 and 128 Rkm were added on the Mattaponi River; six upriver stations (135–154 Rkm) and one downriver station (104 Rkm) were added on the Pamunkey River (each spaced at 3.2-Rkm intervals). Bongo and push nets were fitted with a flowmeter for volumetric measurements, and tow times were adjusted (from 3 to 7 min) to meet a lower limit

TABLE 1.—Habitat suitability index (HSI) models for American shad egg and larval stages, with primary literature sources for the given ranges.

Variable	Optimal range (HSI = 1)	Unsuitable range (HSI = 0)	Primary sources
Water temperature (°C)[a]	14.5–24.5	<8; >27	Stier and Crance (1985), Ross et al. (1993)
Dissolved oxygen (mg/L)[a]	>5.0	<4.0	Chittenden (1973), Stier and Crance (1985)
pH[a]	6.0–9.9	≤5.7; ≥10.0	Bradford et al. (1968), Stier and Crance (1985)
Current velocity (m/s)	0.3–0.7	0; >1.0	Stier and Crance (1985), Ross et al. (1993)
Salinity (g/L)	0–7.5	>7.5	Leim (1924), Limburg and Ross (1995)
Secchi depth (m)[a]	≥0.3	0	Leim (1924), Auld and Schubel (1978), Dadswell et al. (1983)
River depth (m)	1.5–6.1	≤0.15; ≥15.2	Massmann (1952), Wallburg and Nichols (1967), Stier and Crance (1985), Ross et al. (1993)
Woody debris surface area (m^2/1,000 m)	>3.8	0	Wallace and Benke (1984), Fajen and Layzer (1993)
Sediment size (3 categories)	≥2	1	Wallburg and Nichols (1967), Williams and Bruger (1972)
Overhang cover (5 categories)	≥0.5	0	Karr and Schlosser (1978)
Sinuosity	>1.3	1	Zimmer and Bachmann (1978), Platts et al. (1983), Decamps (1993)
Width : depth ratio	≥40	1	Rosgen (1996)
Forest/reach (%)	≥80	0	Correll et al. (1992), Wang et al. (1997)
Urban/reach (%)	≤10	100	Limburg and Schmidt (1990), Wang et al. (1997)
Agriculture/reach (%)	≤50	100	Lenat and Crawford (1994), Wang et al. (1997)
High erosion/reach (%)	>90	<7	Wang et al. (1998)

[a] Applicable to spawning adults as well as egg and larval stages.

of 50 m^3 of water filtered through both nets combined.

Development of HSI models.—Habitat suitability index models were based on an extensive literature review and were developed to describe potential influences on American shad production in the Mattaponi and Pamunkey rivers (Bilkovic 2000). We scaled hydrographic, physical habitat, and shoreline/landscape variables separately to denote suitability indices (SI) ranging from 0 (unsuitable) to 1 (optimal) for the life stages of the American shad that use riverine environments. American shad feeding and growth are presumed to be the greatest and mortality the least at optimal index scores. Decreased feeding and growth rates, increased mortality rates, and eventual death after prolonged exposures are expected for unsuitable index scores.

Unless otherwise noted, each variable and corresponding SI presented are applicable to the egg and larval life stages of American shad (Table 1). Throughout the literature, the effects of hydrographic variables on the early life stages of American shad were the ones most thoroughly studied by researchers. Thus, HSI models of water temperature, dissolved oxygen (DO), pH, salinity, and current speed are assumed to be the most accurate. Data for Secchi depth (turbidity) were deficient. Very little habitat suitability information was taken directly from York River studies, and we inferred that optimal ranges are similar across river systems. All of the physical HSI variables except depth were hypothesized as based on other systems and in some cases other species. Because no direct analysis on the effects of land use type or change on American shad was available in the literature, optimal and unsuitable ranges were often extracted from research that estimated indices of biological integrity (IBI). Researchers often apply IBI to measure the integrity of a system for biota, and the threshold amount of a particular land use that may affect a system can be obtained from this application (Karr 1991).

Tidal excursion.—The average tidal excursion (TE, m; the horizontal distance traveled by waterborne materials per stratum for an ebb cycle) is described by

$$\mathrm{TE} = [(2/\pi) \cdot u_t + Q/A] \times T/2, \qquad (1)$$

where u_t = maximum tidal current (m/s); $2/\Pi \cdot u_t$ = average tidal current (m/s); $T/2$ = ebb tidal cycle = 6.21 h; Q = median discharge (m^3/s); π = 3.14; and A = cross-sectional area (m^2). To estimate TE for the Mattaponi and Pamunkey rivers for the months of April and May, we used maximum tidal current amplitudes acquired from tide gauges maintained along the rivers by the Virginia Institute of Marine Science (VIMS) Physical Science Department (Sisson et al. 1997). Median monthly

TABLE 2.—Habitat variables examined for associations with the presence/absence of American shad eggs and larvae. See Tables 1 and 2 for variable units.

Variable	Nature of data	Measurement
Hydrographic		
Water temperature	Continuous	YSI[a] meter; every meter
Station depth	Continuous	Field measurements, topographic maps
Current velocity	Continuous	Marsh-McBirney current meter; surface
Dissolved oxygen	Continuous	YSI meter; every meter
pH	Continuous	pH meter; surface
Secchi depth	Continuous	Secchi disk
Physical habitat		
Woody debris surface area	Continuous	Surface area of woody debris per 1,000 m
Percentage of overhang	Categorical	Visual estimate (0, 1–25, 26–50, 51–75, 76–100%)
Sediment size	Categorical	Visual estimate (gravel, sand, mud/silt)
Sinuosity	Continuous	Channel length/straight line distance
Width : depth ratio	Continuous	Average width : average depth per 1,000 m
Number of creeks	Continuous	Counts of creeks per 1,000 m
Shoreline and land use		
Forest	Continuous	% per 1,000 m
Agriculture	Continuous	% per 1,000 m
Urban	Continuous	% per 1,000 m
High erosion	Continuous	% per 1,000 m

[a] Yellow Springs Instruments, Yellow Springs, Ohio.

discharge (1942–2000) was obtained from U.S. Geological Survey (USGS) stream gauge stations located approximately at the fall lines of the Pamunkey and Mattaponi rivers (Hanover station [number 01673000] and Beulahville station [number 01674500], respectively). Tidal excursion estimates were used to approximate the most appropriate distance between sampling locations, as well as the extent to which hydrographic values, which are dispersed by hydrologic forces, are applicable to a given portion of the river. Likewise, we assumed that the semibuoyant egg and the pelagic, weak-swimming early larval stages of American shad were subject to similar dispersal as hydrographic values.

Habitat measurements.—Hydrographic parameters measured during each ichthyoplankton sampling event from 1997 to 1999 included water temperature (°C), DO (mg/L), pH, and Secchi depth (m). Current velocity (m/s) was measured in 1998 and 1999 with a Marsh–McBirney current meter. Dissolved oxygen and water temperature were measured at 1-m depth intervals with a Yellow Springs Instruments meter, and median values were calculated. Current velocity and pH were measured once at approximately surface to 1-m depths (Table 2).

In the physical habitat analysis, we evaluated several morphological and instream habitat factors that were representative descriptors of a low-gradient coastal system: width, depth, sinuosity, overhang cover, woody debris, and sediment size. We modified overhang cover and sediment size metrics for coastal plain systems, which have limited riparian overhang and high percentages of fine sediment.

We estimated river morphological and structural parameters (Table 2) in 1,000-m reaches from the fall lines to the mouths of both rivers. Each woody debris (instream woody debris that appeared to alter or impact the hydrology of the stream) counted was at least 0.15 m in diameter and 2 m long. Calculated as the surface area of a cylinder ($X = \Pi \cdot \text{diameter} \cdot \text{length}$), the minimum surface area of an individual woody debris was 0.94 m^2. Minimum surface area per 1,000-m reach segment was calculated by multiplying the number of woody debris counted by 0.94 m^2. Sinuosity was estimated by using shoreline coverages of the York River watershed (U.S. Department of Agriculture, Virginia Department of Conservation and Recreation). Channel length and the straight line distance between reaches of a length 20 times the average depth were determined by using Arc/Info Geographic Information Systems. The number of creeks draining into the main channel were counted per 1,000-m reach and verified with topographic maps. We visually evaluated categories of overhang cover (0, 1–25%, 26–50%, 51–75%, and more than 75%) and sediment size (3 = gravel, 2 = sand, 1 = mud/silt) at three locations in 300-m intervals per 1,000-m reach and then extrapolated average values over the entire reach. Overhang cover was defined as the percentage of river shaded by overhanging vegetation, either canopy or bank. Width:depth ratios were calculated from the av-

TABLE 3.—Median values and ranges of hydrographic, physical habitat, shoreline, and land use data collected in the Mattaponi and Pamunkey rivers, Virginia, 1997–1999.

Variable	Mattaponi River		Pamunkey River	
	Median	Range	Median	Range
Hydrographic features				
Temperature (°C)	15.5	12.0–22.0	15.2	11.8–19.4
Dissolved oxygen (mg/L)	9.1	6.8–12.6	9.2	7.3–11.5
pH	6.9	5.9–9.3	7.2	6.5–8.5
Secchi depth (m)	1.0	0.3–2.0	0.8	0.2–1.8
Depth (m)	3.3	0.9–10.0	3.7	0.9–12.0
Current speed (m/s)	0.5	0–1.1	0.4	0–1.2
Physical habitat				
Woody debris surface area (m^2/1,000 m)	7	0–83	16	0–57
Sinuosity	1.3	1.0–1.9	1.2	1.0–3.2
Width : depth ratio	33	12–224	31	8–284
Sediment size	1	1–3	1	1–3
Overhang cover	0	0–1	1	0–1
Width (m)	209	19–718	115	26–953
Number of creeks	3	0–16	2	0–13
Channel average depth (m)	5.5	0.6–16.2	3.7	0.8–17.7
Shoreline (percentage)				
Forest	86	0–100	97	15–100
Residential	7	0–77	3	0–85
Grass	0	0–100	0	0–18
Marsh	69	0–100	44	0–100
High erosion	0	0–50	0	0–35
Land use (percentage)				
Forest	62	0–100	69	0–100
Residential	0	0–19	0	0–94
Crop	6	0–75	12	0–90
Marsh	17	0–100	13	0–100

erage of five measurements, at 200-m intervals, per 1,000-m reach obtained from hydrographic coverages (width measures: U.S. Department of Agriculture, Virginia Department of Conservation and Recreation), topographic maps (depth measures for lower and midreaches), and field measurements (depth measures for upriver reaches).

Estimated riparian zone characteristics were based on the land immediately adjacent (0–10 m) to the river. Shoreline attributes of the rivers were continuously coded in the field by using a handheld GeoExplorer Global Positioning System (GPS) unit with a data dictionary that had been created to include the following shoreline classifications: (1) forest, (2) scrub–shrub, (3) grass/crop, (4) residential, (5) commercial, (6) bare, (7) timbered, and (8) developed. Because some classifications contained only small areas of land use; we simplified the shoreline attributes to three categories: (1) forest (forest and scrub–shrub); (2) grass/crop (grass, bare, and timbered); and (3) urban (residential, commercial, and developed). Erosion throughout the shoreline was estimated visually as high, low, or none, based on the percentage of stream bank with bare soil susceptible to wind or water erosion (Table 2). Line coverages were created from the GPS files by using shoreline information, and areas of shoreline features per 1,000-m reach were determined by using an Arc/Info frequency analysis.

Land use was evaluated within a 100-m buffer width on each riverbank. A 100-m width was used because several stream functions respond to riparian features within this distance from the stream (Large and Petts 1994; Phillips 1996). Land use percentages per 1,000-m reach were calculated from the MRLC (multiresolution land use characterization) database from the U.S. Environmental Protection Agency Region III Land Cover Data set, 1996 (thematic mapper [TM] data from 1992 to 1994, using the combined resources of the U.S. Environmental Protection Agency, USGS, and National Oceanographic and Atmospheric Administration), with Arc/Info frequency analysis. For this analysis, MRLC categories were combined into three broad classes: forest, agriculture, and urban (Table 2).

Statistical analysis.—Median values and ranges of hydrographic, physical habitat, and shoreline/land use parameters were similar for the Mattaponi and Pamunkey rivers; thus, we have combined data from both rivers for analysis (Table 3). The median

TABLE 4.—River features and land use for the upper, mid and lower regions of the Mattaponi and Pamunkey rivers.

Variable	Mattaponi River			Pamunkey River		
	Upper	Middle	Lower	Upper	Middle	Lower
River feature (average per 1,000-m reach)						
Woody debris (number of pieces)	37.4	7.1	2.8	30.4	13.4	6.3
Overhang (by category)	0.8	0.0	0.0	1.0	0.6	0.0
Number of creeks	1.7	2.6	6.3	1.7	2.3	5.4
Width (m)	38.0	321.5	310.5	36.9	213.2	402.5
Channel depth (m)	1.4	5.1	9.6	1.9	4.4	9.0
Sediment type (by category)	2.0	1.1	1.1	1.8	1.2	1.0
Sinuosity	1.4	1.2	1.5	1.3	1.6	1.8
Width : depth ratio	28.6	76.5	34.2	24.6	50.1	53.8
Dissolved oxygen	9.52	9.08	8.66	9.04	9.35	9.21
pH	6.88	7.09	6.88	7.26	7.23	7.31
Secchi depth (m)	1.20	0.99	0.65	1.23	0.92	0.50
Current speed (m/s)	0.51	0.31	0.46	0.37	0.35	0.26
Land use percentages						
Water	12.5	45.6	35.8	8.0	35.9	43.9
Developed	0.2	1.1	0.9	0.2	0.3	1.6
Grass	3.1	4.8	2.1	9.8	3.8	1.5
Crop	6.5	5.7	4.8	11.4	8.3	3.2
Forest	73.6	24.0	22.8	64.0	41.5	24.0
Marsh	4.1	18.7	33.6	6.7	10.2	25.9

of values was used for comparison to eliminate the effects of outliers or extreme values. Any ichthyoplankton density greater than zero was scored as present; densities of zero were scored as absent.

Relationships between the presence or absence of American shad eggs and larvae and habitat variables were explored with principal components analysis (PCA), using S-PLUS programming language. We used PCA because of its ability to describe the underlying data structure in multiple environmental variables. Given that the sampling encompassed an extensive spatial area and time period, we expected a skew distribution because of the many zero values (i.e., absence) in the data. To address our objectives, presence/absence data were sufficient for the analyses and eliminated expected data transformation difficulties. Hydrographic, physical habitat, and shoreline/land use datasets were analyzed separately. By the Kaiser criterion (Kaiser 1960) for retention of factors (eigenvalues >1), the first two principal components were retained in all cases. Scores for principal components 1 and 2 (PC1 and PC2) were displayed graphically with egg and larval presence/absence superimposed.

The PCA analysis correlations were then examined with binary logistic regression in the logit link (Minitab Version 12.0) with American shad egg and larvae presence/absence as the dependent variable and PC1 and PC2 scores as independent variables representing habitat. Logistic regression is an appropriate statistical test for presence/absence data; it attempts to express the probability that a species is present as a function of the explanatory variables (ter Braak and Looman 1995). General results displayed for the logistic regressions consist of estimates and standard errors of the coefficients, z-values, P-values, odds ratio, and a 95% confidence interval for the odds ratio. Additionally, the last log-likelihood from the maximum likelihood iterations is noted with the G statistic. This statistic tests the null hypothesis that all coefficients associated with predictors equal zero.

Results

Distribution of American Shad Eggs and Larvae

Examination of morphological parameters indicated the existence of three distinct regions along the rivers (Table 4). The Mattaponi and Pamunkey rivers contain a downstream segment with wide, deep channels and extensive marshes (width: 200–600 m; depth: >5.7 m), a midriver segment with wide, shallow sandbars (width: 80–600 m; depth: 2–7 m, typically <5 m), and a predominantly forested upstream segment with shallow, narrow channels (width: <60 m; depth: <4 m).

Spawning of American shad on both of these rivers occurred predominantly within the upper and midriver segments in 1997–1999. On the Pamunkey River, larval American shad typically occupied nursery habitats in midriver to downstream segments, whereas in the Mattaponi River, larval

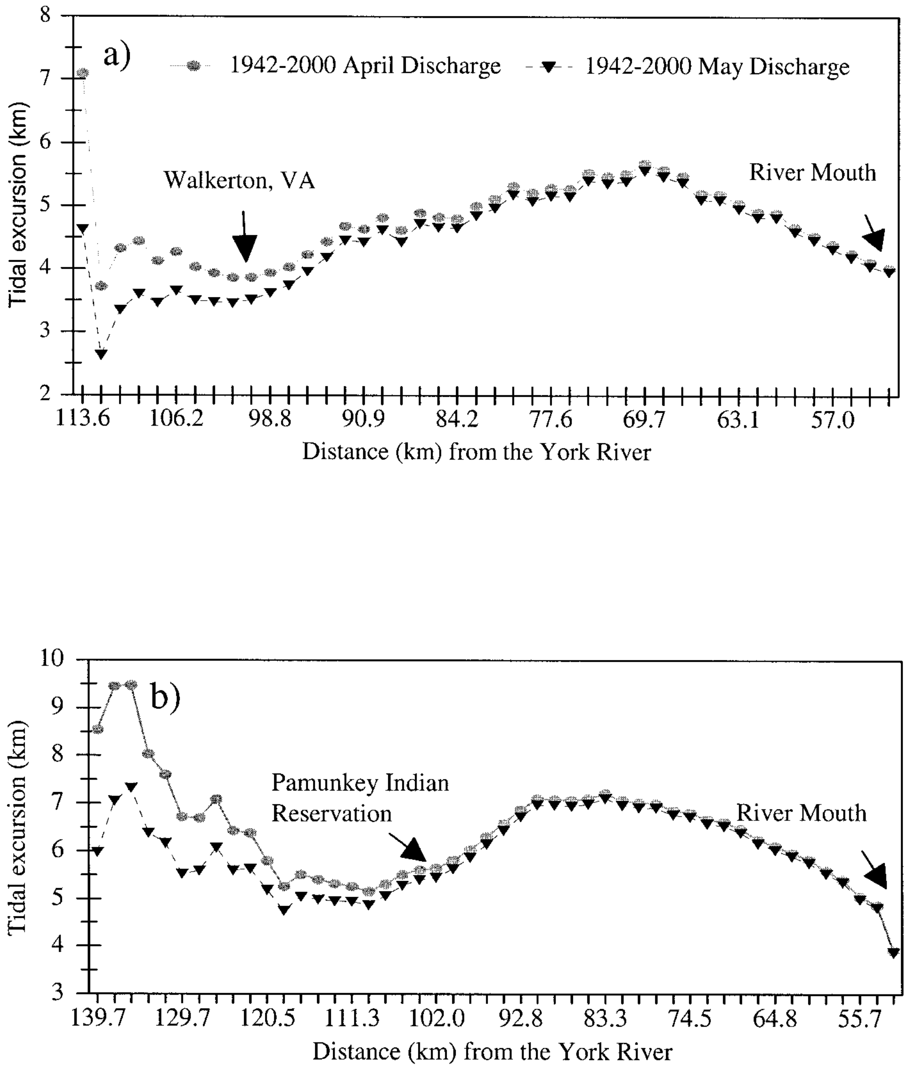

FIGURE 1.—Tidal excursion estimated from cross-sectional area, maximum tidal current, and median discharge for the **(a)** Mattaponi and **(b)** Pamunkey rivers from the fall line to the mouth. Discharge is a median monthly value (April and May) based on data from 1942 to 2000. Discharge measurements were obtained from the U.S. Geological Survey at Beulahville, Virginia, on the Mattaponi River and at Hanover, Virginia, on the Pamunkey River.

American shad were dispersed throughout all three regions. Eggs were collected from 80 to 124 Rkm and from 98 to 150 Rkm on the Mattaponi and Pamunkey rivers, respectively. Larvae were more dispersed than were eggs and were found throughout the range of 68–120 Rkm and 72–128 Rkm on the Mattaponi and Pamunkey rivers, respectively (Bilkovic et al. 2002).

Tidal Excursion

The average tidal excursion estimated per stratum for an ebb cycle for the Mattaponi and Pamunkey rivers did not descend below 3.2 Rkm with few exceptions (Figure 1). The highest tidal excursion distances for each month occurred near the fall lines in both rivers. Segments of relatively low tidal excursion were evident at midriver locations on the Mattaponi River (94–109 Rkm) and the Pamunkey River (94–124 Rkm). Increases in tidal excursion distance were apparent further downstream, declining near the mouths of both rivers (Figure 1). Because tidal excursion distance typically remained above 3.2 Rkm, the assumption was met that water-quality measurements and egg/

early larva dispersal may be extrapolated to locations between stations 3.2 Rkm apart.

Habitat Suitability Index Models

The ranges of the hydrographic parameters (DO, pH, Secchi depth, and temperature) observed with presence of eggs and larvae closely correspond to postulated HSI curves (Table 5). One exception was the absences in the upper optimal limit of temperature, which possibly reflects the limited number of samples. For both depth and current velocity, larvae displayed patterns differing in various way from that for eggs; accordingly, a distinct HSI model is required for larvae.

The least predictive HSI curves were those of the physical habitat. Reaches with low sinuosity values (1.2) contained similar densities of eggs and larvae as the reaches with high values. For both overhang cover and sediment size, eggs were distributed throughout the observed ranges, whereas larvae were collected in reaches with silt/mud only and overhang values of less than 1%. The HSI curve for woody debris surface area corresponded to the distribution of American shad eggs; larvae, in contrast, were often collected in reaches with suboptimal habitat (Table 5).

Postulated HSI curves for shoreline/land use were more predictive for eggs than for larvae. Eggs were collected primarily in reaches in which the shoreline was more than 60% forested or land use or both; larvae were dispersed throughout the range of sampled forest percentages. The relationships of the presence of eggs/larvae to shoreline and agricultural land use differ. Egg and larval densities were greatest in reaches with 0% agricultural shoreline, whereas there was a larger distribution of eggs and larvae throughout reaches of 0–35% agricultural land use. Also, declines in egg and larval densities occurred when more than 40% of the reach was agricultural land use. Shoreline was classified as grass throughout both agriculture and marsh areas, which may account for differences in the relationships of agricultural shoreline and land use to the presence of eggs and larvae. There was no distinct pattern between residential (which was less than 5% in any given reach) or marsh percentages of land use and egg/larval density, except that eggs were located primarily in reaches with less than 20% emergent marsh land use, whereas larvae were found largely in the areas with the greatest percentages of shoreline marsh. High erosion percentages were less than 15% throughout the Mattaponi and Pamunkey rivers, and the greatest egg and larval densities were found in reaches with 0% values. Of the reaches with 35–45% high erosion, no eggs were collected but larvae were observed (Table 5).

Principal Components Analysis (PCA) and Logistic Regression

Hydrographic PCA.—The PCA of hydrographic data (1997 data were not included because current velocity was not measured that year) indicated American shad eggs typically were associated with areas of high DO, shallow depths, and high current. The presence of larvae was evident in high water temperature, high Secchi depth, and lower DO reaches and was more dispersed than the presence of eggs. PC1 loadings contrasted DO with water temperature and Secchi depth. PC2 loadings contrasted current velocity with depth and pH. Logistic regression indicated that PC1 and PC2 scores were associated significantly with the presence of eggs, whereas only PC1 scores were associated significantly with the presence of larvae (Figure 2; Tables 6, 7).

Physical habitat PCA.—The presence of eggs was associated with upstream or broad bar reaches, whereas larvae were more dispersed and associated with downstream reaches. Woody debris, increasing sediment size and overhang, are correlated parameters and characteristic of upstream reaches in the physical habitat PCA. Increasing width:depth ratios occurred at reaches with broad, shallow bars, typically in midriver. Increasing numbers of creeks and sinuosity were indicative of downstream, marsh reaches. PC1 loadings contrasted upstream reaches (woody debris, sediment size, and overhang) with mid- to downstream reaches (number of creeks, sinuosity, and width: depth ratios). PC2 loadings distinguished downstream reaches (marsh, sinuosity) from broad bars (increased width:depth ratios). Logistic regression indicated that PC1 and PC2 scores were associated significantly with the presence of eggs, whereas only PC1 scores were associated significantly with the presence of larvae (Figure 3; Tables 6,7).

Shoreline/land use PCA.—The presence of eggs was associated with forested reaches, whereas the presence of larvae indicated more dispersal within downstream, marshy reaches. Respective land use and shoreline features were correlated closely in the PCA. PC1 loadings contrasted forested with marsh shoreline/land use, which is indicative of upstream as opposed to downstream reaches. PC2 loadings distinguished urban shoreline/land use from marsh reaches. Logistic regression indicated that only PC1 scores were significantly associated

TABLE 5.—Median values and ranges of hydrographic, physical habitat, shoreline, and land use data collected in the Mattaponi and Pamunkey rivers, 1997–1999. The observed range is the range of values in which eggs and/or larvae were observed; the sampled range is the entire range of values measured during the data collection.

Variable	Life stage	Mattaponi River Median	Mattaponi River Range Observed	Mattaponi River Range Sampled	Pamunkey River Median	Pamunkey River Range Observed	Pamunkey River Range Sampled
Hydrographic features							
Temperature (°C)	Eggs	16.0	14.2–19.5	12.0–22.0	15.0	13.2–19.0	11.8–19.4
	Larvae	15.9	12.4–20.5	12.0–22.0	15.0	12.3–16.9	11.8–19.4
Dissolved oxygen (mg/L)	Eggs	10.8	7.5–12.4	6.8–12.6	10.2	8.0–11.5	7.3–11.5
	Larvae	8.2	7.5–11.3	6.8–12.6	9.3	8.0–10.6	7.3–11.5
pH	Eggs	6.9	6.5–7.9	5.9–9.3	7.2	6.5–8.5	6.5–8.5
	Larvae	6.9	6.5–9.3	5.9–9.3	7.2	6.5–8.5	6.5–8.5
Secchi depth (m)	Eggs	1.0	0.7–1.7	0.3–2.0	0.9	0.4–1.6	0.2–1.8
	Larvae	1.0	0.5–1.9	0.3–2.0	0.6	0.3–1.3	0.2–1.8
Depth (m)	Eggs	2.1	0.9–5.0	0.9–10.0	3.5	1.0–5.0	0.9–12.0
	Larvae	4.0	1.0–10.0	0.9–10.0	4.2	1.2–11.0	0.9–12.0
Current speed (m/s)	Eggs	0.49	0.3–0.9	0–1.1	0.44	0–1.0	0–1.2
	Larvae	0.47	0–0.6	0–1.1	0.40	0–0.5	0–1.2
River morphology							
Woody debris surface area (m^2/1,000 m)	Eggs	14.1	2.8–70.7	0–82.9	16.5	0–33.9	0–56.5
	Larvae	5.6	1.4–70.7	0–82.9	12.2	0–27.9	0–56.5
Sinuosity	Eggs	1.2	1–1.4	1.0–1.9	1.3	1.1–2.8	1.0–3.2
	Larvae	1.3	1.2–1.7	1.0–1.9	1.7	1.2–3.2	1.0–3.2
Width : depth ratio	Eggs	39.3	18.4–152.0	12.0–224.4	32.5	7.9–97.9	7.9–284.1
	Larvae	34.8	16.9–152.0	12.0–224.4	42.9	7.9–97.8	7.9–284.1
Sediment size	Eggs	2	1–2	1–2.5	1	1–2	1–3
	Larvae	1	1–2	1–2.5	0.5	1–2	1–3
Overhang cover	Eggs	0.1	0–1	0–1	0.1	0–1	0–1
	Larvae	0	0–1	0–1	0.05	0.05–1	0–1
Width (m)	Eggs	58.6	29.2–463.4	19.0–717.6	82.0	30.8–626.0	26.0–952.6
	Larvae	216.4	35.8–463.4	19.0–717.6	293.9	40.4–626.0	26.0–952.6
Number of creeks	Eggs	3	0–8	0–16	2	1–3	0–13
	Larvae	3	0–15	0–16	3	1–10	0–13
Average channel depth (m)	Eggs	2.1	0.9–8.8	0.6–16.2	3.3	1.2–7.0	0.75–17.7
	Larvae	5.8	0.9–12.8	0.6–16.2	5.9	2.1–12.2	0.75–17.7
Shoreline (percentage)							
Forest	Eggs	95.4	75.6–100.0	0–100.0	95.8	70.8–100.0	15.5–100.0
	Larvae	76.1	23.9–100.0	0–100.0	89.9	70.8–100.0	15.5–100.0
Residential	Eggs	4.6	0–24.4	0–77.0	3.2	0–29.2	0–84.5
	Larvae	9.8	0–38.5	0–77.0	10.1	0–29.1	0–84.5
Grass	Eggs	0	0	0–100.0	0	0–12.8	0–18.4
	Larvae	0	0–62.3	0–100.0	0	0–62.3	0–18.4
Marsh	Eggs	54.8	0–95.7	0–100.0	7.2	0–62.3	0–100.0
	Larvae	81.8	0–100.0	0–100.0	44.8	0–100.0	0–100.0
High erosion	Eggs	0	0–15.9	0–50.0	0	0	0–34.6
	Larvae	0	0–42.6	0–50.0	0	0–1.6	0–34.6
Land use (percentage)							
Forest	Eggs	77.4	22.6–98.5	0–100.0	71.0	20.9–99.7	0–100.0
	Larvae	68.4	0–91.1	0–100.0	65.7	0–99.7	0–100.0
Residential	Eggs	0.4	0–0.74	0–18.5	0	0–1.6	0–94.1
	Larvae	0.4	0–0.75	0–18.5	0	0–2.6	0–94.1
Crop	Eggs	5.8	0–32.3	0–75.0	10.5	0–79.1	0–90.0
	Larvae	6.3	0–64.1	0–75.0	8.4	0–57.2	0–90.0
Marsh	Eggs	11.1	0–54.0	0–100.0	6.9	0–37.8	0–100.0
	Larvae	20.5	1.4–100.0	0–100.0	12.2	0–100.0	0–100.0

with the presence of eggs and larvae (Figure 4; Tables 6, 7).

Discussion

Macroscale habitat evaluations can be used to distinguish spawning and nursery habitat for American shad within coastal plain systems. Because American shad are thought to spawn over large areas, often encompassing several habitat types (Ross et al. 1993), microscale habitat assessments fail to describe spawning reaches over large areas. Examining macroscale (m-km) habitat

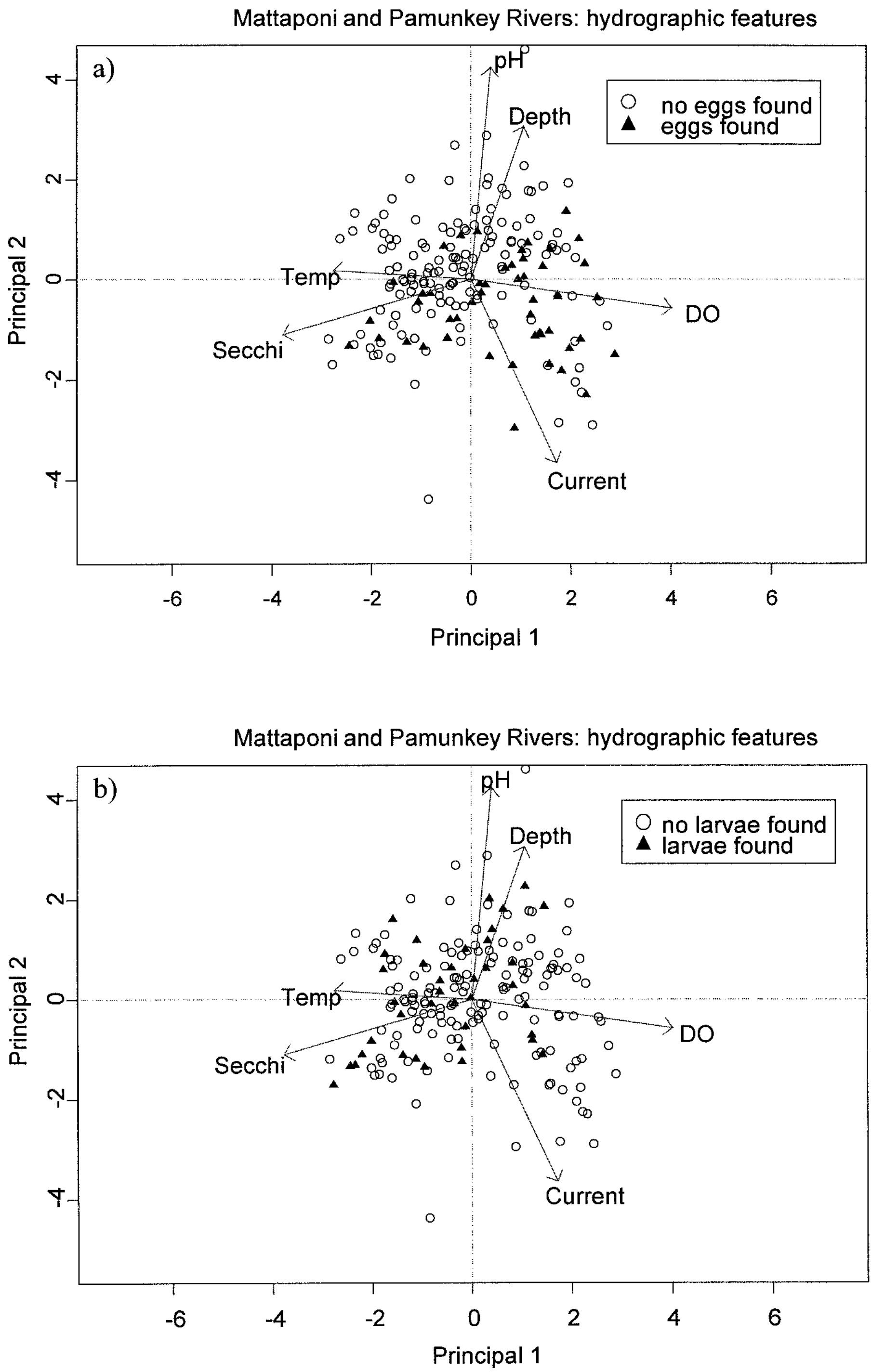

FIGURE 2.—Principal components analysis plots depicting the correlation of hydrographic variables (1998–1999) in the Mattaponi and Pamunkey rivers. On each of the plots, the first (PC1) and second (PC2) principal components are depicted on the *x*- and *y*-axes, respectively. The loadings of the variables are illustrated with the arrows. The loadings of PC1 contrasted dissolved oxygen (DO) with water temperature and Secchi depth, and those of PC2 contrasted current velocity with depth and pH. The presence of **(a)** eggs and **(b)** larvae (overlaid independently on the plots) is depicted as triangles, the absence as open circles. Abbreviations are as follows: Temp = water temperature, Depth = channel depth, Secchi = Secchi depth, and Current = current velocity.

TABLE 6.—Results of logistic regression of principal component (PC) scores 1 and 2 on the presence of American shad eggs in the Mattaponi and Pamunkey rivers. The following statistics are given: odds ratios (Ψ), the lower and upper 95% confidence limits, coefficients (β), standard deviations (SD), log-likelihood values (LL), the *G*-statistic for the log likelihood, and probability values (*P*-values) for the *G*-statistics; $P < 0.05$*, $P < 0.01$**.

Parameter grouping	β	SD	Ψ	Confidence limits Lower	Confidence limits Upper	LL	*G*	*P*-value
PC 1 scores								
Hydrographic	0.469	0.135	1.60	1.23	2.08	−95.6	26.6	0.001**
Physical habitat	0.460	0.405	2.51	1.13	5.55	−22.9	10.4	0.05*
Shoreline and land use	0.736	0.310	2.09	1.14	3.83	−23.6	7.3	0.02*
PC 2 scores								
Hydrographic	−0.536	0.161	0.59	0.43	0.80	−95.6	26.6	0.001**
Physical habitat	0.919	0.405	2.51	1.13	5.55	−22.9	10.4	0.02*
Shoreline and land use	0.088	0.478	1.09	0.43	2.79	−23.6	7.3	0.85

associations of American shad eggs and larvae provided insight into habitat suitability issues for an entire system. Using both micro- and macroscales, reaches over large distances (km) were delineated as spawning or nursery habitat and were then characterized further with microscale variables. Despite obvious limitations in macroscale assessment of variables that change laterally and longitudinally, the approach allowed for rapid assessment of systems for essential fish habitat when other data are limiting. In this study, microscale variables and egg and early larva dispersal governed by hydrologic forces are postulated to be relatable to larger areas (m-km) on the basis of tidal excursion estimates, which allows for application of local measurements over the entire river systems.

Macroscale examination of the distribution of American shad eggs indicated that spawning on the Mattaponi and Pamunkey rivers occurred predominately within the upstream and midriver segments. Spawning reaches were characterized by shallow depths (<5 m), high DO (>8 mg/L), and relatively high current velocity (0.3–1.0 m/s). Massmann (1952) also observed peak abundance of eggs along the middle segments of the Mattaponi and Pamunkey rivers, with extensive flats from Lester Manor (96.2–98.1 km) to Gregory's Bar (109.2–111.0 km) on the Pamunkey River and from Mattaponi (81.4–83.3 km) to Rickahock (92.5–94.4 km) on the Mattaponi River. Upstream and midriver reaches may be optimal spawning habitat because of the shallow water, the high DO, and the fast currents that may enhance mixing during spawning, prevent siltation or suffocation of eggs, and favor transport of hatchlings to salubrious feeding environments. Distributions of larvae extended into all three morphologic regions, the lowest densities being in upper reaches, presumably because of downstream drift. Peaks in larval density occurred in midriver reaches of both rivers, corresponding to the preponderance of upstream and midriver spawning with subsequent downstream transport of larval stages. Additionally, tidal excursion distances are typically lowest in midriver reaches, which may enhance larval retention (Figure 1). Spawning downstream may lead to larval transport out of favored nursery environments and increase mortality. However, a precise description of larval nursery habitats is difficult, given the lack of strong correlations between larval distribution and physical features evident in sta-

TABLE 7.—Results of logistic regression of principal component (PC) scores 1 and 2 on the presence of American shad larvae in the Mattaponi and Pamunkey rivers. See Table 6 for additional details.

Parameter grouping	β	SD	Ψ	Confidence limits Lower	Confidence limits Upper	LL	*G*	*P*-value
PC 1 scores								
Hydrographic	−0.341	0.145	0.71	0.54	0.95	−92.8	6.3	0.02*
Physical habitat	−0.678	0.251	0.51	0.31	0.83	−21.6	9.5	0.007**
Shoreline and land use	−1.690	0.654	0.19	0.05	0.67	−18.4	13.7	0.01*
PC 2 scores								
Hydrographic	0.127	0.162	1.14	0.83	1.56	−92.8	6.3	0.43
Physical habitat	−0.137	0.394	0.87	0.40	1.89	−21.6	9.5	0.73
Shoreline and land use	1.128	0.936	3.09	0.49	19.36	−18.4	13.7	0.23

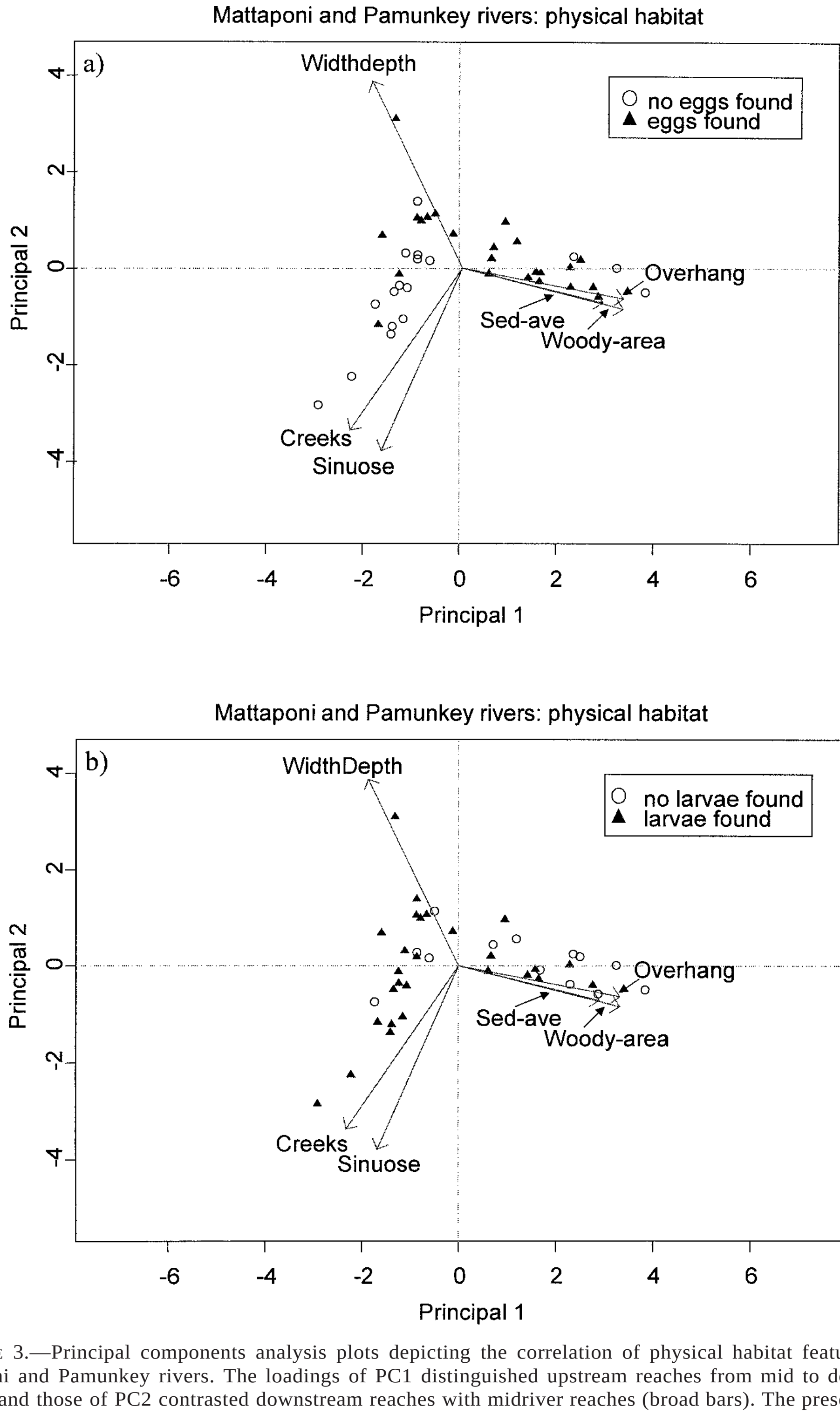

FIGURE 3.—Principal components analysis plots depicting the correlation of physical habitat features in the Mattaponi and Pamunkey rivers. The loadings of PC1 distinguished upstream reaches from mid to downstream reaches, and those of PC2 contrasted downstream reaches with midriver reaches (broad bars). The presence of **(a)** eggs and **(b)** larvae (overlaid independently on the plots) is depicted as triangles, the absence as open circles. Variables are as follows: Widthdepth = width to depth ratio, Creeks = number of creeks per reach, Sinuose = sinuosity (channel distance/straight line distance), Woody-area = woody debris per area, Sed-ave = average sediment size, and Overhang = overhang cover.

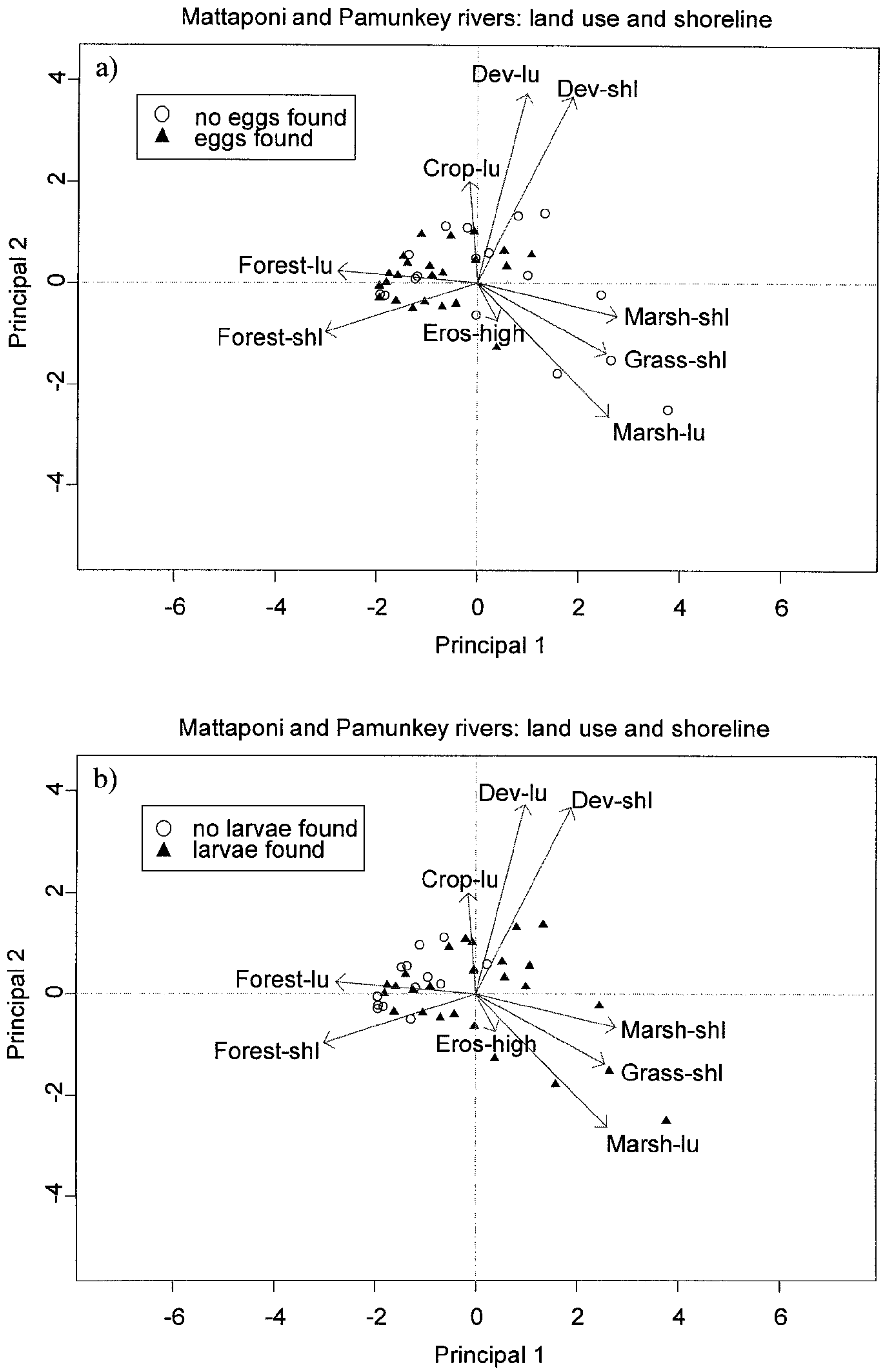

FIGURE 4.—Principal components analysis plots depicting the correlation of shoreline and land use features in the Mattaponi and Pamunkey rivers. The loadings of PC1 contrasted forested with marsh shoreline and land use, and those of PC2 distinguished urban shoreline and land use from marsh reaches. The presence of **(a)** eggs and **(b)** larvae (overlaid independently on the plots) is depicted as triangles, the absence as open circles. Variables are as follows: Dev-shl = percent developed and residential shoreline, Dev-lu = percent developed and residential land use, Crop-lu = percent agricultural land use, Forest-shl = percent forested shoreline, Forest-lu = percent forested land use, Eros-high = percent high erosion, Marsh-shl = percent marsh shoreline, Marsh-lu = percent marsh land use, and Grass-shl = percent grass shoreline.

tistical comparisons. Logistic regression results consistently indicated that scores for both principal components were significant for presence of eggs, but only one was typically significant for the presence of larvae (Tables 6, 7). This implies that the patterns for eggs are stronger than for larvae and that spawning habitat may be more accurately described than nursery habitat—most probably because of site selection by spawners. The less distinct pattern in distribution of larvae may be expected when the effects of downstream transport of larvae are considered.

Distinct associations of habitat with egg distribution may indicate active selection by spawners or be a function of the area itself. Research in other systems elucidated depth and current ranges associated with American shad similar to those observed in the Mattaponi and Pamunkey rivers. American shad spawning takes place in areas dominated by extensive shallow flats (Bigelow and Welsh 1925; Massmann 1952; Jenkins and Burkhead 1994). Ross et al. (1993) noted that the greatest spawning activity occurred at less than 1 m deep, in low-turbidity (<2 nephelometric turbidity units [NTU]) reaches of the Delaware River. Although some spawning was observed in all of the habitats examined, the greatest activity was in the runs and the lowest in the pools and riffle pools, indicating some habitat selection by spawners. Upstream habitats are considered important to larval and juvenile stages for feeding (Massmann 1963; Crecco and Blake 1983). Selection by spawners of reaches with extensive deadfall (where important larval and juvenile shad prey items originate) may occur to ensure retention within favorable upstream and midriver nursery habitats. Peaks in density of eggs and larvae in high-width:depth ratio reaches, which represent broad midriver bar reaches, substantiate the importance of these areas as spawning and nursery zones. American shad eggs were primarily collected in reaches that were more than 60% forested and less than 20% emergent marsh, indicative of upstream and midriver reaches, whereas larvae were more dispersed. These patterns are most probably descriptive of the morphology of the rivers, because marshes dominate in the downstream reaches of both of the rivers below the observed spawning reaches but within the nursery zones. Although shoreline residential percentages exceeded residential land use values, the impact of developed areas may be minimized in these rivers, which lack intense urbanization. Limburg and Schmidt (1990) observed increased variability in oxygen saturation levels near urban areas in the Hudson River and declines in the abundance of eggs and larvae of anadromous fishes in reaches where urbanization was greater than 10%. The Hudson River contains much more intense urbanization than do the Mattaponi and Pamunkey rivers, which may account for the differing results.

Annual indices of abundance of juvenile American shad present a consistent pattern of greater abundance in the Mattaponi than in the Pamunkey River (mean recruitment [1991–1999]: Mattaponi juvenile *Alosa* Index [JAI], 1522.6; Pamunkey JAI, 247.0) (Bilkovic et al. 2002). Although habitat features are a possible explanation to variations in abundance, the variables examined in this model exhibited no clear difference between the rivers that would account for these variations in production. Additional characteristics to be considered include biotic controls, discharge, and fishery impacts. Variation in these components between rivers could lead to differing abundances of juveniles. Crecco and Savoy (1985) observed high larval survival rates in the Connecticut River associated with low flows, high water temperature, and high zooplankton densities. To date, within the Mattaponi and Pamunkey rivers, consistent correlations have not been shown between abiotic factors (river flow, temperature, and precipitation) and annual JAIs for blueback herring *A. aestivalis* (Dixon 1996) or American shad (Bilkovic 2000). The tidally dominated Mattaponi and Pamunkey rivers have mean daily flow rates during spawning and larval development period nearly an order of magnitude lower than the rates in the Connecticut River, which may account for inconsistent relationships between systems.

In the present study, we examined water temperature and current velocity (related to discharge); however, zooplankton densities were not analyzed. Efforts should be made to assess the survival of early life stages of American shad in these systems in relation to prey abundance.

A future effort could incorporate variables influencing fish populations that are independent of habitat features into the HSI models. For example, Platts and Nelson (1988) noted the need for incorporating natural fluctuations of fish populations into the habitat-based models used to evaluate land use effects. As populations of American shad fluctuate, spawning reaches will presumably expand or shrink. If restoration efforts are successful, the availability of suitable or preferred spawning areas may become limiting. If populations of American shad increase, habitat protection and restoration efforts should be expanded to match potential spawning and nursery habitat to ensure continued increases.

This study addresses one aspect of a very complex management issue. Each major river along the Atlantic coast appears to have a discrete spawning stock of American shad, and the reproductive biology of American shad varies latitudinally, thus necessitating that stocks be managed separately. To further complicate the issue, a mixed stock fishery still exists,the impact of which on individual stocks is unknown. Additional information on the river-specific reproductive biology (batch sizes and numbers, percent of repeat spawning, and fecundity) and on the survivability of each life stage (spawning adult through subadult) is necessary to promote management efforts.

Overall, this study provides a watershed tool for assessing essential fish habitat. It proceeds beyond typical HSI models, which do not include physical habitat, riparian integrity, or landscape features. Relationships between habitat variables and the distribution of spawned eggs were determined for two river systems. Future research may provide additional information on the functional relationship of egg and larval density with habitat features and be incorporated into this analysis for reevaluation and refinement of habitat suitability assessment. Deficiencies in available data for this analysis include certain variables for land use and physical habitat. Therefore, future studies on the effects of physical habitat and land use on the riverine life stages of American shad are necessary for refinement of HSI models. This may clarify the potential influences driving variations in productivity in these two rivers.

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