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In the Atlantic coastal region, American shad (*Alosa sapidissima*) is highly prized for its flesh and roe. Spawning runs have been heavily fished and since the late 1800s, landings have shown steady declines to the extent that Maryland declared a fishing moratorium in 1980, and Virginia followed in 1994 for Chesapeake Bay and its tributaries (ASMFC, 1999). Shad restoration projects are underway to restock depleted spawning runs, especially in regions where stream impediments have been or are being removed. Coastal ocean intercept gill-net fisheries have remained in place despite criticism and speculation about their impact on populations, particularly those river systems stocks that are depleted. The Atlantic States Marine Fisheries Commission Shad Board (ASMFC, 1999) adopted a fishery management plan for American shad and river herring that included a five-year phase-out of the ocean fishery and that required states to develop an approved fishing or recovery plan for each stock under restoration. In Virginia, this requirement applies to the James and York rivers.

Although the roe fishery for American shad has historically been important, there is little information about the specific spawning locations of these broadcast spawners. American shad are anadromous fish native to the Atlantic coast of North America, with a range extending from southeastern Labrador to the St. Johns River, Florida. In Chesapeake Bay tributaries, American shad deposit semidemersal eggs in the freshwater portions of the estuaries in the spring, usually beginning in March and ending by early June with peaks in April (Klauda et al., 1991). American shad have historically ascended farther upriver than at present, within tributaries where obstructions to movements upstream now exist. Prior to dam building in the 1800s on the James River, large numbers of American shad traveled over 335 miles from Chesapeake Bay into the Jackson and Cowpasture rivers (Mansueti and Kolb, 1953).

The York River, a coastal plain tributary located in the Chesapeake Bay watershed, is formed by the confluence of the Pamunkey and Mattaponi Rivers at West Point (Fig. 1). The Pamunkey River has a larger watershed (3768 km^2) and average spring discharge rate (47.5 m^3/s) than the Mattaponi River (2274 km^2; 27.2 m^3/s, respectively). Watershed sizes are based on U.S, Geological Survey digital line graph data (DLG) at 1:100,000. On these unobstructed rivers, annual releases of hatchery-reared American shad approximate two to four million fry through efforts of the Virginia Game and Inland Fisheries (VGIF) and an estimated 2.5 to 3 million fry are released by the Pamunkey tribal government. In addition there are unknown contributions from the Mattaponi tribal government (Gunther[1]). Current monitoring of adult catches indicates that the York River supports the strongest runs of shad in Virginia (Olney and Hoenig[2]). American shad in the York River are used as the source stock for hatchery efforts in the James and Potomac rivers. Thus, the restoration efforts in Virginia are dependent on the productivity of the York River.

Within the freshwater tidal portions of the Mattaponi and Pamunkey rivers, numerous other species spawn, including striped bass (*Morone saxatilis*) (McGovern and Olney, 1988; Grant and Olney, 1991). The Chesapeake Bay stock has rebounded after severe declines in the 1970s and early 1980s as a result of successful management and several years of successful reproduction (Olney et al., 1991; Field, 1997). The extent of the spawning area for both American shad and striped bass is in part a function of salinity and temperature. Striped bass spawn from the limit of brackish water to freshwater in the rivers of Chesapeake Bay from early April through the end of May (Setzler-Hamilton et al., 1981), and American shad spawn in freshwater (Leim, 1924). McGovern and Olney (1996) noted that the lower limit of striped bass spawning followed the 1 ppt salinity contour, and Secor and Houde (1995) postulated that the freshwater-saltwater interface may act as a down-river barrier to striped bass egg and larval advection. Based on suitable temperature ranges (12–24°C for striped bass [Setzler-Hamilton et al., 1980; Rutherford and Houde, 1995] and 12–25°C for Ameri-

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[1] Gunther, T. 2000. Personal commun. Virginia Game and Inland Fisheries, Richmond, Virginia 23230.

[2] Olney, J. E., and J. M. Hoenig. 2000. Monitoring relative abundance of American shad in Virginia's Rivers. March 1998–1999. Final report to the U.S. Fish and Wildlife Service and Virginia Marine Resources Commission, 53 p. Contract number F-116-R-1. Virginia Institute of Marine Science, Gloucester Point, Virginia.

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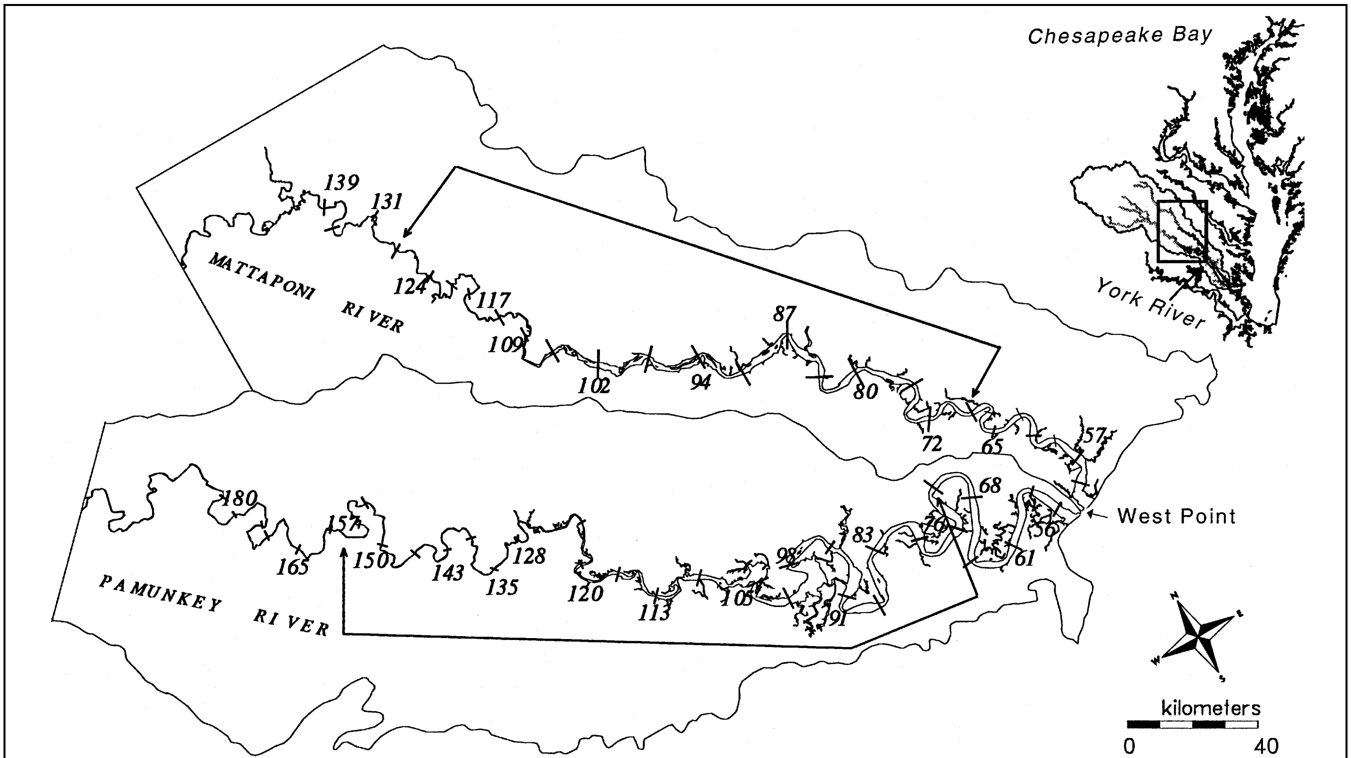

Figure 1

Extent of ichthyoplankton sampling by bongo net and pushnet in the Mattaponi and Pamunkey rivers (1997–99). Stations are denoted as the number of kilometers from the mouth of the York River.

can shad [Leach and Houde, 1999; Walburg and Nichols[3]] and salinity requirements for the early life stages of these species, the potential for spawning overlap spatially and temporally is high. Species interactions, including predation and competition by both adults and young, may play a role in the spawning and recruitment success of these species. Similar interactions have been postulated between American shad and other alosines in the Hudson River (Schmidt et al., 1988).

Our objectives were to describe the American shad spawning reaches in the Mattaponi and Pamunkey Rivers spatiotemporally, and to determine if striped bass also spawn within the identified spawning habitat of American shad. In year one, we completed an exploratory survey to map the distribution of the American shad spawning ground and the occurrence of striped bass within these reaches. In years two and three, sampling was modified to locate the upper limit of American shad and striped bass spawning within the two rivers.

[3] Walburg, C. H., and P R. Nichols. 1967. Biology and management of the American shad and the status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service, Special Scientific Report–Fish 550, 105 p. Fish and Wildlife Service, U.S. Dep. of Interior, Washington, DC 20005.

Materials and methods

Sampling protocol in 1997

Exploratory sampling in the Mattaponi and Pamunkey rivers for eggs and larvae of American shad and striped bass extended from March through April 1997. Sites were chosen on the basis of a prior survey of American shad eggs in the rivers (Massmann, 1952). Sampling protocol included weekly ichthyoplankton collections during daylight hours with 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 ten stations were sampled weekly on each river within the tidal freshwater reaches. Stations are depicted as river kilometers (rkm) from the mouth of the York River, for example, M68 is a station on the Mattaponi River that is approximately 68 river kilometers from the mouth of the York River. The stations were located at approximately 3.2-rkm intervals within the range of 72 to 106 rkm (P72 to P106) on the Pamunkey River and 68 to 102 rkm (M68 to M102) on the Mattaponi River (Fig. 1).

Sampling protocol in 1998 and 1999

In 1998 and 1999, station locations were extended upriver to include more shallow stations owing to the low abundance of American shad eggs in 1997. Bongo nets could not be used, and sampling included pushnet surveys in the upper reaches of the rivers (from 31 March through 20 May 1998 and from 11 April through 7 May 1999). The weekly sampling on each river consisted of pushnet tows at approximately one meter below the surface at each station. A pushnet frame fitted to the bow of a 14-foot 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 M94 to M120 and P109 to P131. In 1999, two stations at M124 and M128 were added on the Mattaponi River; we added six upriver stations (P135–P154) and one downriver station (P104) on the Pamunkey River (each spaced at 3.2-rkm intervals, Fig. 1). Bongo and push nets were fitted with a flow meter for volumetric measurements and tow times were adjusted (three to seven minutes) to meet a lower limit of 50 m^3 of water filtered through both nets combined.

Laboratory procedures and data analysis

Ichthyoplankton samples were preserved in 10% phosphate-buffered formalin. Ichthyoplankton were sorted and larval fish and eggs were identified (Lippson and Moran, 1974; Jones et al.[4]), enumerated, and removed from the original, whole sample. Densities were reported as number per 100 m^3. Relative abundance in both rivers was calculated by average density of each life stage (egg, yolksac larva, and postyolksac) multiplied by total volume of spawning or nursery area sampled. Total volume of spawning or nursery area sampled was determined separately for each species by including locations within the sampling region where eggs (spawning reaches) or larvae (nursery reaches) were collected. River volumes were calculated by using bathymetric surveys and corresponding areal estimates from a digitized record of the mean high-water shoreline position as shown on the 7.5 minute topographic map series of the U.S. Geological Survey completed by Comprehensive Coastal Inventory, Virginia Institute of Marine Science (Bilkovic, 2000). For purposes of comparison, we used data on the abundance of American shad and striped bass juveniles in the Pamunkey and Mattaponi rivers. The data were taken from annual surveys of juvenile abundance conducted by the Virginia Institute of Marine Science (Austin et al., 2000; Olney and Hoenig[2]).

Results

Trends in density (numbers/100 m^3) of eggs for each river and species by date and station are depicted for 1997–99 in Figures 2 and 3. Average density (total eggs or larvae per total volume filtered) of each species per river is depicted in Figure 4. On the Mattaponi River (1997–99), American shad eggs were collected over a 44-km reach (M81–M124) and the highest densities occurred between M96 and M124. Striped bass spawning occurred over a 27-km reach and the highest densities in the sampled area occurred between M68 and M87, downstream of the primary spawning reaches of American shad (Figs. 2–4). On the Pamunkey River, American shad eggs were collected over a 53-km reach (P98–P150), and the highest densities were found between P104 and P131. Striped bass spawning occurred over a 60-km reach (P72–P131), and the highest densities were found between P72 and P87. There was some spatial overlap in spawning of these species, but the primary spawning reaches were separate. Temporal overlap in spawning of American shad and striped bass occurred throughout the sampled period in both rivers (Figs. 2–3).

On the Mattaponi River, American shad larvae (total length, 6.1–19.2 mm) were collected from M68 to M124, and the highest densities were observed between M94 and M102—a reach that is downstream of the spawning habitat. On the Pamunkey River, American shad larvae (total length, 6.6–12.2 mm) were collected between P76 and P128. Densities were highest at P102, 105, and 124. Larval striped bass were collected from M68 to M94 and from P72 to P109, and peak catches (>1/m^3) were collected from M68 to M80 and from P72 to P91. In both rivers, we observed overlap in American shad nursery grounds and striped bass spawning reaches. However, the highest densities of larval striped bass were downstream of the primary shad spawning and nursery areas (Fig. 4).

Average density of individual life stages of American shad was higher in the Mattaponi River than in the Pamunkey River; the opposite pattern was apparent for striped bass (Table 1). Estimates of the relative numbers of American shad and striped bass (average density × river volume) suggested that abundance of American shad eggs and larvae was higher on the Mattaponi River than on the Pamunkey River by a factor of 5.5 and 4.4, respectively. Relative abundance of striped bass eggs and larvae was higher on the Pamunkey River than on the Mattaponi River by a factor of 29 and 9.9, respectively (Table 2).

Discussion

Over the three years of surveys, eggs and larvae of American shad were rare compared to those of striped bass (Table 1). Despite our successive efforts to relocate sampling stations upstream of known striped bass spawning habitat (Grant and Olney, 1991; Olney et al., 1991), striped bass eggs and larvae were more abundant (~114 times and ~38 times, respectively) than those of American shad (Table 2). These differences could be attributed to the relative sizes and egg production of the spawning stocks because the number of mature American shad presently in the York River system is believed to be low in relation to historic run sizes (Nichols and Massmann, 1963; Olney

[4] Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval, and juvenile stages. Vol. 1, Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service report FSW/OBS-78/12. Fish and Wildlife Service, U.S. Dep. Commer., Washington DC 20005.

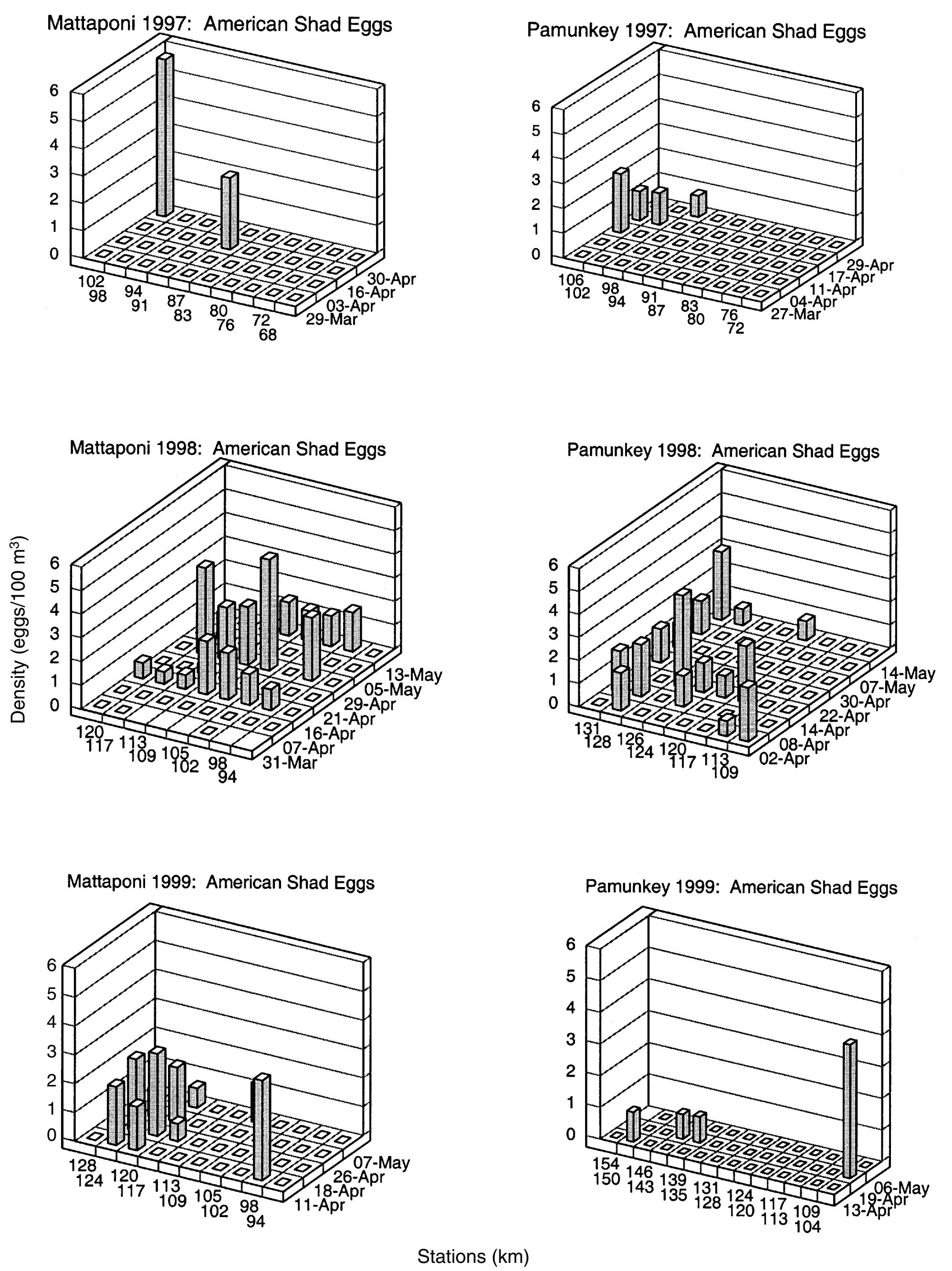

Figure 2

American shad egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River.

and Hoenig[2]). In contrast, striped bass stocks are at record levels of abundance (Field, 1997) and support a large recreational and commercial fishery in the York River.

Despite the proximity and resemblance of the Pamunkey and Mattaponi Rivers, patterns of spawning and recruitment of American shad and striped bass are opposite for each tributary. We observed annual differences in abundance of eggs and larvae of these species that are concordant with indices of juvenile production. In our surveys, eggs and larvae of American shad were more abundant on the Mattaponi River and striped bass eggs and larvae were more abundant on the Pamunkey River (Tables 1 and 2). Similarly, mean recruitment (the mean index of juvenile abundance or JAI) of American shad

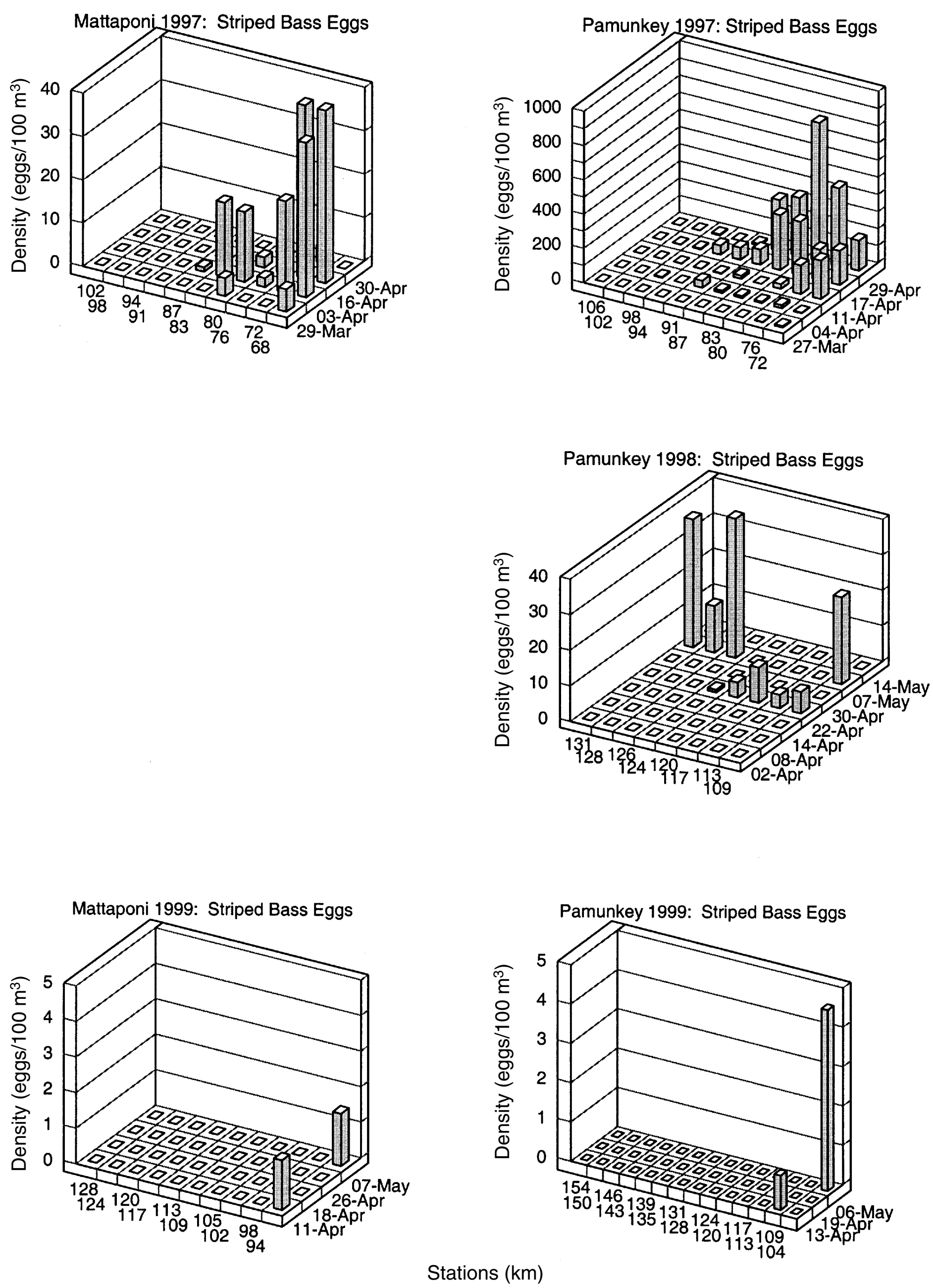

Figure 3

Striped bass egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River. In 1998, no striped bass eggs were collected on the Mattaponi River.

was higher on the Mattaponi River (1997–99; Mattaponi JAI, 1648.5; Pamunkey JAI, 112.7), and mean recruitment of striped bass was higher on the Pamunkey River (1997–99; Mattaponi JAI, 1.6; Pamunkey JAI, 4.9). The approximate volume of the Pamunkey River, from the fall line to river mouth (1.9×10^8 m^3) is 1.2 times that of the Mattaponi River (1.6×10^8 m^3). Thus, equal populations of eggs or larvae that are homogeneously distributed on each tributary would be expected to be at the most 1.2 times as concentrated on the Mattaponi River. Because we observed differences in egg density that were much greater than double (~17 times in the case of striped bass) and in the unexpected direction (Pamunkey River egg densities > Mattaponi River egg densities), it is unlikely that

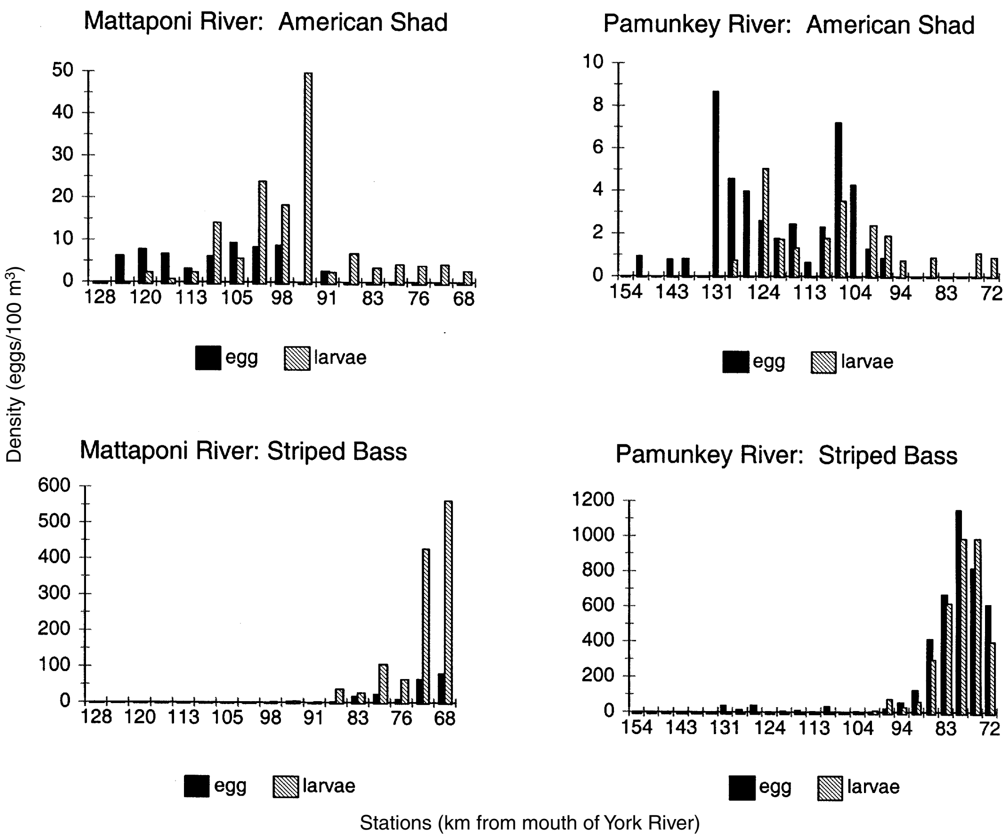

Figure 4

Total American shad and striped bass density (eggs and larvae) distinguished by river, species, and life stage for 1997–99 bongo and pushnet collections. Note differences in scaling on the y-axis.

Table 1

Average density (total numbers/total volume filtered) of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). Values are reported as numbers per 100 m^3.

			Larvae		
Species	River	Eggs	Yolksac	Postyolksac	Total larvae
American shad	Mattaponi	59.1	32.8	67.3	100.1
	Pamunkey	33.7	11.5	6.2	17.6
Striped bass	Mattaponi	205.3	392.1	792.4	1184.5
	Pamunkey	4016.5	2625.9	909.8	3535.7

tributary volume alone is responsible for the contrasting patterns. Instead, differences in discharge, river sinuosity, habitat, stock size, or combinations of these factors may be responsible.

Temporal and spatial overlap in spawning distributions of American shad and striped bass occurs in the York River system but the primary spawning grounds of these species are disjunct. Evidence of spawning and peak egg abundance for both species was apparent throughout the water temperature range of 13–19°C in both rivers. Trends of general abundance for both years and rivers indicated that American shad spawn in regions upstream of striped bass primary spawning grounds (Fig. 4). Trophic interactions, especially predation and competition, may explain the disjunct spawning habitats of these species in the York River. Striped bass may be important predators on American shad in freshwater (Mansueti and Kolb, 1953; Walburg and Nichols[3]). Although recent studies have failed to detect

Table 2

Relative abundance (average density × river volume, numbers × 10^8) and ratios of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). River volume (10^7 m^3) consists of reaches where eggs (spawning reaches) or larvae (nursery reaches) were found.

	River volume			Larvae		
Species	Spawning reaches	Nursery reaches	Eggs	Yolksac	Postyolksac	Total larvae
American shad						
Mattaponi	6.1	9.4	0.36	0.27	0.63	0.94
Pamunkey	1.9	12.0	0.07	0.13	0.07	0.21
Mattaponi: Pamunkey	3.2	0.8	5.5	2.0	8.8	4.6
Striped bass						
Mattaponi	7.9	3.3	1.6	1.3	2.6	4.0
Pamunkey	12.0	11.0	47.0	29.0	10.0	39.0
Pamunkey: Mattaponi	1.5	3.3	29.0	22.3	3.8	9.9

American shad in the diets of striped bass (Manooch, 1973; Austin and Walter[5]), this absence may be due to current low numbers of American shad in relation to other clupeids. Correspondingly, American shad juveniles have the potential to prey upon striped bass larvae (McGovern and Olney, 1988). Competition for food may occur between the early life stages of these two species as well. According to several studies, larval and juvenile stages of striped bass and American shad feed on similar prey items (Massmann, 1963; Markle and Grant, 1970; Setzler-Hamilton et al., 1981; Gardinier and Hoff, 1982; Crecco and Blake, 1983; Johnson and Dropkin, 1997; Ross et al., 1997). Distinct spawning locations of these species may act to minimize competition between larval- and early juvenile-stage fish, which use nursery locations downriver of spawning reaches. There is also potential overlap in habitat use between the juveniles of these species because both species occupy shallow nearshore waters. Some habitat overlap may be avoided by differing inshore-offshore diel migration patterns. American shad occupy nearshore areas during daylight and move offshore during night hours (Schmidt et al., 1988), whereas striped bass have been observed to predominately occupy nearshore habitats during both day and night hours (Boynton et al., 1981; Rudershausen and Loesch, 2000).

Locations of striped bass spawning grounds on the Pamunkey River in this study corresponded to those of previous studies. Primary spawning reaches on the Pamunkey River were previously reported from 8–48 km above West Point (Rinaldo, 1971); at approximately 27 km (Pamunkey) and 14 km (Mattaponi) above the mouth of each river (Tresselt, 1952); and within the first 40 km of tidal freshwater of both rivers (Grant and Olney, 1991). In the our study, some striped bass eggs were collected on the Pamunkey River upstream of previously reported locations, but in lower abundance than occurred downstream. In the Mattaponi River, striped bass eggs were absent in upstream locations, an observation in agreement with previous surveys (Tresselt, 1952; Rinaldo, 1971; Grant and Olney, 1991; McGovern and Olney, 1996).

On both rivers, American shad were collected in higher abundance upriver of previously reported primary ranges by Massmann (1952). He observed peak egg abundance from 96.2 to 111.0 rkm on the Pamunkey River and from 81.4 to 94.4 rkm on the Mattaponi River. This is in part because we sampled farther upriver than Massmann. However, in those upriver reaches that both studies sampled, eggs were found in higher abundance in 1997–99. Shifting spawning habitats (possibly due to changes in population structure and size, climate, or river discharge), sampling deficiencies, unknown catchability differences between the studies, or some combination of these factors may explain these historical differences. As populations of American shad fluctuate, the spawning area used will likely expand or shrink. If restoration efforts are successful, the availability of suitable spawning areas may become a limiting factor to population growth. Further studies of habitat suitability for spawning within this system are underway to elucidate potential spawning reaches and optimal areas.

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[5] Austin, H. M., and J. F. Walter. 1998. Food habits of large striped bass in the lower Chesapeake Bay and its tributaries March 1997–May 1998. Final report to the Marine Recreational Fisheries Advisory Board and Commercial Fisheries Advisory Board, VMRC, 56 p. Contract number RF-97-08 and CF09709-08. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

ing Advisory Board of the Virginia Marine Resources Commission (grant numbers F-116-R-1 and F-116-R-2), and by the Anadromous Fish Conservation Act, Public Law 89-304 (grant-in-aid projects AFC-29 and AFC-27-1, grant numbers NA96FA0192 and NA76FA0361) from the National Marine Fisheries Service. This manuscript is a portion of a dissertation prepared by the senior author in partial fulfillment of the requirements for the doctoral degree, School of Marine Science, Virginia Institute of Marine Science (VIMS), College of William and Mary.

Literature cited

ASMFC (Atlantic States Marine Fisheries Commission).
1999. Amendment 1 to the interstate fishery management plan for shad and river herring, 76 p. ASMFC, 1444 Eye St. NW, 6th Floor, Washington, D.C. 20005.
Austin, H. M., A. D. Estes, and D. M. Seaver.
2000. Estimation of juvenile striped bass relative abundance in the Virginia Portion of Chesapeake Bay. Annual progress report, 32 p. Virginia Institute of Marine Science, Gloucester Point.,VA.
Bilkovic, D. M.
2000. Assessment of spawning and nursery habitat suitability for American shad (*Alosa sapidissima)*. Ph.D. diss., 216 p. Virginia Institute of Marine Science. Gloucester Point, VA.
Boynton, W. R., T. T. Polgar, and H. H. Zion.
1981. Importance of juvenile striped bass food habits in the Potomac estuary. Trans. Am. Fish. Soc. 110:56–63.
Crecco, V. A., and M. M. Blake.
1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Trans. Am. Fish. Soc. 112:498–507.
Field, J. D.
1997. Atlantic striped bass management: Where did we go right? Fisheries 22(7):6–8.
Gardinier, M. N., and T. B. Hoff.
1982. Diet of striped bass in the Hudson River estuary. N.Y. Fish and Game Journal 29:152–165.
Grant, G. C., and J. E. Olney.
1991. Distribution of striped bass *Morone saxatilis* (Walbaum) eggs and larvae in major Virginia Rivers. Fish. Bull. 89:187–193.
Johnson, J. H., and D. S. Dropkin.
1997. Food and prey selection of recently released American shad (*Alosa sapidissima*) larvae. J. Freshwater Ecol. 12: 355–358.
Klauda, R. J., S. A. Fischer, L. W. Hall Jr., and J. A Sullivan.
1991. American shad and hickory shad. *In* Habitat requirements for Chesapeake Bay living resources (S. L. Funderburk, S. J. Jordan, J. A. Mihursky, and D. Riley, eds.), p. 9-1–9-27. Chesapeake Research Consortium, Inc., Annapolis, MD.
Leach, S. D., and E. D. Houde.
1999. Effects of environmental factors on survival, growth, and production of American shad larvae. J. Fish Biol. 54: 767–786.
Leim, A. H.
1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to factors limiting its abundance. Biol. Board of Canada, Contr. to Can. Biol. 2(11):161–284.
Lippson, A. J., and R. L. Moran., ed.
1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary, 282 p. Maryland Department of Natural Resources, Baltimore, MD.
Manooch, C. S.
1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. Ches. Sci. 14:73–86.
Mansueti, R. J., and H. Kolb.
1953. A historical review of the shad fisheries of North America. Ches. Biol. Lab. Publ. 97:1–293.
Markle, D. F , and G. C. Grant.
1970. The summer food habits of young-of-the-year striped bass in three Virginia rivers. Ches. Sci. 11:50–54.
Massmann, W. H.
1952. Characteristics of spawning areas of shad, *Alosa sapidissima* (Wilson) in some Virginia streams. Trans. Am. Fish. Soc. 81:78–93.
1963. Summer food of juvenile American shad in Virginia waters. Ches. Sci. 4:167–171.
McGovern, J. C., and J. E. Olney.
1988. Potential predation by fish and invertebrates on early life history stages of striped bass in the Pamunkey River, Virginia. Trans. Am. Fish. Soc. 117:152–161.
1996. Factors affecting survival of early life stages and subsequent recruitment of striped bass on the Pamunkey River, Virginia. Can. J. Fish. Aquat. Sci. 53: 1713–1726.
Nichols, P. R., and W. H. Massmann.
1963. Abundance, age and fecundity of shad, York River., 1953–1959. Fish. Bull. 63:179–187.
Olney, J. E., and G. Boehlert.
1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chespaeake Bay. Mar. Ecol. Prog. Ser. 45:33–43.
Olney, J. E., J. D. Field, and J. C. McGovern.
1991. Striped bass egg mortality, production, and female biomass in Virginia Rivers, 1980–1989. Trans. Am. Fish. Soc. 120:354–367.
Rinaldo, R. G.
1971. Analysis of *Morone saxatilis* and *Morone americana* spawning and nursery areas in the York and Pamunkey Rivers, Virginia. M.S. thesis, 56 p. College of William and Mary, Gloucester Point, VA.
Ross, R. M., R. M. Bennett, and J. H. Johnson.
1997. Habitat use and feeding ecology of riverine juvenile American shad. N. Am. J. Fish. Manage. 17:964–974.
Rudershausen, P. J., and J. G. Loesch.
2000. Feeding habits of young-of year striped bass, *Morone saxatilis*, and white perch, *Morone americana*, in lower James River, VA. Va. J. Sci. 51:23–37.
Rutherford, E. S., and E. D. Houde.
1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in the Chesapeake Bay. Fish. Bull. 93:315–332.
Schmidt, R. E., R. J. Klauda, and J. M. Bartels.
1988. Distributions and movements of the early life stages of three species of *Alosa* in the Hudson River, with comments on mechanisms to reduce interspecific competition. *In* Fisheries research in the Hudson River (C. L. Smith, ed.), p. 141–168. The Hudson River Environmental Society, State University of New York, Albany, NY.
Secor, D. H., and E. D. Houde.
1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries 18: 527–544.
Setzler-Hamilton, E. M., W. R. Boynton, J. A. Mihursky, T. T. Polgar, and K. V. Wood.
1981. Spatial and temporal distribution of striped bass

eggs, larvae and juveniles in the Potomac estuary. Trans. Am. Fish. Soc. 110:121–136.

Setzler-Hamilton, E. M., W. R. Boynton, K. V. Wood, H. H. Zion, L. Lubber, N. K. Mountford, P. Frere, L. Tucker, and J. A. Milhursky.
1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). U.S. Dep. Commer., NOAA Tech. Rep. NMFS 433.

Tresselt, E.F.
1952. Spawning grounds of the striped bass, *Roccus saxatilis* (Walbaum), in Virginia. Bull. Bingham Oceanogr. Coll. 14 98–110.