2022

Patterns of Hatchery-Produced Returns of American Shad in the James River, Virginia

Patrick E. McGrath
Virginia Institute of Marine Science

Brian Watkins
Virginia Institute of Marine Science

Ashleigh Magee
Virginia Institute of Marine Science

Eric J. Hilton
Virginia Institute of Marine Science

Recommended Citation

McGrath, Patrick E.; Watkins, Brian; Magee, Ashleigh; and Hilton, Eric J., Patterns of Hatchery-Produced Returns of American Shad in the James River, Virginia (2022). *North American Journal of Fisheries Management*.
doi: 10.1002/nafm.10776

North American Journal of Fisheries Management
© 2022 The Authors. *North American Journal of Fisheries Management* published by Wiley Periodicals LLC on behalf of American Fisheries Society.
ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10776

ARTICLE

Patterns of Hatchery-Produced Returns of American Shad in the James River, Virginia

Patrick E. McGrath,* Brian E. Watkins, Ashleigh Magee, and Eric J. Hilton
Virginia Institute of Marine Science, William & Mary, 1370 Greate Road, Gloucester Point, Virginia 23062, USA

Abstract
American Shad *Alosa sapidissima* is an anadromous clupeid that once supported a robust fishery but has declined drastically throughout its native range due to overfishing, dam proliferation, and poor water quality. A hatchery program on the James River in Virginia was introduced in 1992 to support the recovery of stocks. Following a moratorium of the fishery enacted in 1994, a fisheries-independent survey was initiated in 1998 to monitor the population recovery efforts and status of American Shad stocks in Virginia. This paper examined 22 years of monitoring data for the James River and determined the effect of hatchery inputs on the James River stock of American Shad. The spawning stock index increased from 2.57 in 1998 to a peak of 9.33 in 2003 but has generally been declining since and has been at very low levels in most recent years. The hatchery prevalence for female American Shad (i.e., the percentage of fish derived from the hatchery) ranged between 3.6% and 60.5%. Years with higher spawning stock index values were significantly correlated to higher percentages of hatchery fish returning to spawn. The stock–recruitment relationship was best explained by the Ricker model, which had the lowest residual standard error and Akaike information criterion value. A threshold level of hatchery-released individuals (approximately 4 million larvae) was necessary to achieve the highest numbers of returning spawners, but stocking above 7 million larvae correlated with declining returns. Long-term monitoring of the James River American Shad spawning population allowed for the critical examination of the contribution of hatchery individuals to the yearly spawning run and the relative success rate of each hatchery year-class. From these data, we consider that the James River spawning stock of American Shad was dependent upon hatchery inputs, with ideal hatchery returns occurring during years of moderate levels of hatchery stocking.

Release of hatchery-reared fish is a popular tool in fisheries and can be used for stock enhancement, sea ranching, and restocking (Kitada 2018). Hatcheries can strengthen food security, aid in the recovery of endangered species, and provide greater opportunities for recreational fishing (Trushenski et al. 2018). Hatcheries also have negative effects, such as increased mortality, decreased growth rates, reduced reproductive fitness, and genetic drift (Hindar et al. 1991; Araki and Schmid 2010; Kitada 2018). Despite the many described negative attributes, supplementing natural populations with hatchery-produced fish persists for many species, including American Shad *Alosa sapidissima*.

American Shad is an anadromous species of the family Clupeidae (subfamily Alosinae) native to the coast of eastern North America and ranges from the St. Lawrence River, Canada, to St. John's River, Florida (Bigelow and Schroeder 1953; Munroe 2002), but has been widely established along the west coast of North America (Smith 1895). American Shad supported a robust fishery during the latter half of the 1800s (Walburg and Nichols 1967). Although declines in stocks coastwide began in the 1800s, landings throughout its native range decreased drastically in the 1900s, eventually leading to significant reductions or closures to most American Shad fisheries (ASMFC

*Corresponding author: patm@vims.edu
Received December 9, 2021; accepted April 12, 2022

2010; Latour et al. 2012). The precipitous drop in landings was attributed to overfishing, dam proliferation, and a decline in water quality (Rulifson 1994). To counter the decline in landings, American Shad have been stocked in the United States since the 1870s, with hatchery output reaching its highest level between 1872 and 1949 (Hendricks 2003). Despite the large production and release of larvae, American Shad populations continued to decrease, and since 1950, four distinct periods of decline have occurred in the commercial catches (Figure 1; ASMFC 2020).

American Shad are present in each of the four major tributaries of the Chesapeake Bay in Virginia: the James, York, Rappahannock, and Potomac rivers (all are managed by the Virginia Marine Resources Commission [VMRC] except for the Potomac, which is managed by the Potomac River Fishery Commission); each of these rivers supports a genetically distinct spawning stock (Hasselman et al. 2013; Aunins et al. 2014). The relative strength of the spawning stock of American Shad in Virginia over time closely reflects the rangewide trends for this species, and a moratorium on fishing was enacted for the Chesapeake Bay and its tidal tributaries in 1994 (VMRC Regulation 450-01-0069).

There were two major reasons for the precipitous decline in abundance of American Shad in the James River: overfishing (primarily during the spring roe fishery) and dam proliferation (Weaver et al. 2003); these factors worked in concert with general poor water quality. Females are larger than males and typically mature at age 5, which coincides with the age at which they have fully recruited to the gill nets used in the roe fishery (Tuckey and Olney 2010). The removal of virgin females prior to spawning not just once but for multiple years greatly reduced spawning potential of the stock. In the James River, American Shad historically migrated as far west as Covington, Virginia, at river kilometer (rkm) 530 (measuring from the river mouth). In the mid-1800s, six dams, including Bosher's Dam at the fall line in Richmond, Virginia, were constructed, blocking access to spawning grounds above rkm 170 and confining American Shad to tidal waters. All of these dams, except for Bosher's Dam, were either naturally or artificially breached between 1989 and 1993. A fishway was installed in Bosher's Dam in 1999 that was specifically designed for passage of American Shad, coinciding with removing blockades to migration. Further, a hatchery program on the James River was initiated in 1992 to support recovery of American Shad stocks in Virginia.

In 1998, a fisheries-independent survey was initiated by scientists at the Virginia Institute of Marine Science (VIMS) to monitor the population recovery efforts and status of American Shad stocks in the James, York, and Rappahannock rivers in Virginia. This survey, which continues to the present, monitors both natural and hatchery returns in the James River through scanning otoliths of adults for oxytetracycline (OTC) marks (Latour et al. 2012), thus providing a unique opportunity to use the 22 years of monitoring data for the James River and evaluate the effect of hatchery inputs on the James River stock of American Shad. The natural recruitment of American Shad in the James River has been altered due to overfishing and dams. Therefore, we hypothesized that increased hatchery inputs of American

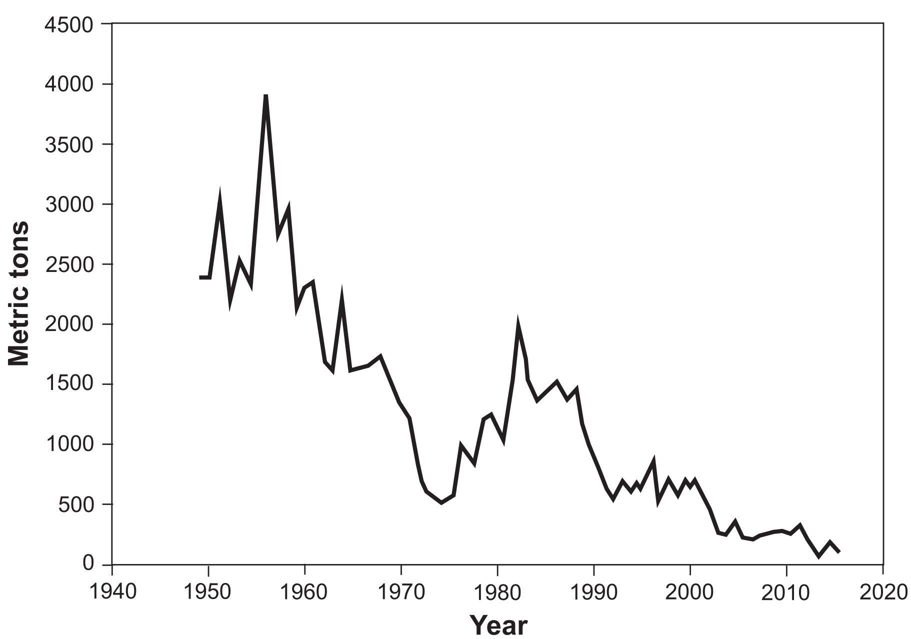

FIGURE 1. Commercial landings of American Shad in the USA, 1950–2018. Figure is redrawn from ASMFC (2020).

Shad larvae would lead to more returning adults as well as to a higher proportion of hatchery adults in the spawning stocks of that year-class.

METHODS

Larval inputs.— The hatchery program that produced the larvae of American Shad that were stocked into the James River was initiated by the Virginia Department of Game and Inland Fisheries (now the Virginia Department of Wildlife Resources) and began in 1992 with broodstock from the James River (Gunter 1997). All fry were marked by OTC, which labeled the otoliths with marks specific to the James River. Stocking commenced as early as the day following the final mark in a sequence, which was typically 3–7 d posthatch. In 1994, after 2 years of unsuccessful collection of sufficient numbers of broodstock, American Shad from the Pamunkey River, a tributary in the York River system, were used to collect gametes (Brown et al. 2000). The James River hatchery program increased larval production from a half million larvae in the first year to a peak of approximately 10 million larvae in 1998 (Table 1). Numbers of larvae released ranged between 6 and 9 million per year from 1999 to 2008. Production decreased after 2009, with a low of 1 million larvae in 2016. The decrease in larval release was mainly attributed to the lack of broodstock. In 2018, the hatchery program ceased stocking American Shad in the James River due to financial constraints and difficulty in obtaining broodstock.

Adult sampling.— Since 1998, scientists at VIMS have estimated the relative abundance of American Shad and assessed the status of stocks in Virginia through monitoring of the spawning runs in the James, York, and Rappahannock rivers (Hilton et al. 2022). This long-term, fishery-independent monitoring program is required for Virginia to be compliant with federal regulations, allowing for a limited bycatch fishery of American Shad (ASMFC 2009). The sampling techniques and locations were selected to be consistent with and directly comparable to those that generated historical commercial fishery logbook data collected by VIMS during the period of 1980–1993 in these rivers.

American Shad were caught in a staked gill net (274.3 m in length) set on the James River at rkm 16.1 from 1998 to 2019. The net consisted of 30 panels (9.14 m × 1.98 m) with 12.4-cm stretched-mesh monofilament. Because the fishery, and therefore the current monitoring program, targeted females for roe, there is a bias in the sample to female American Shad. Therefore, only mature females were included in our analyses. The fishing season was typically from February to May, but it ended in April during several years due to consecutive weeks with zero catches. Nets were set on two consecutive days of the week from 1998 to 2014 and then once a week from 2015 to 2019. Each set consisted of approximately 24 h of fishing.

TABLE 1. Hatchery input, American Shad spawning stock index, and hatchery prevalence from 1992 to 2019.

Year	Hatchery input (in millions)	American Shad spawning stock index	Hatchery percentage
1992	0.05		
1993	0.5		
1994	1.6		
1995	5.3		
1996	5.8		
1997	5.9		
1998	10.0	2.57	8.2
1999	7.3	2.99	3.6
2000	8.9	6.61	40.3
2001	9.3	5.01	40.2
2002	8.4	5.62	46.4
2003	8.7	9.34	51.4
2004	6.6	7.41	32.5
2005	6.0	7.16	23.8
2006	7.0	1.74	10.3
2007	6.5	4.45	32.2
2008	6.2	1.51	25.6
2009	3.8	2.69	8.9
2010	3.7	6.90	34.9
2011	2.4	9.00	39.0
2012	5.4	6.06	34.9
2013	4.8	4.48	60.5
2014	3.3	7.35	45.4
2015	3.5	1.25	44.4
2016	1.0	0.96	21.4
2017	1.9	3.83	25.7
2018	0.0	1.30	26.7
2019	0.0	0.35	28.6

Biological data.— All American Shad collected were measured to the nearest millimeter (both fork length and total length) and weighed to the nearest gram. Sex was determined by dissection, and maturity stage of females was determined via macroscopic examination of the ovaries following Olney et al. (2001). Sagittal otoliths were removed from every adult individual, and a subsample was screened for hatchery marks. For screening, otoliths were mounted on slides, then ground (600 grit) and polished (1,200 grit) on both sides by hand using wet, laboratory-grade sandpaper. An epi-fluorescent microscope was used to scan for hatchery marks. Otoliths have become the preferred structure to age American Shad since 2012 (Duffy et al. 2012; Elzey et al. 2015). However, to have a consistent aging method with our samples prior to 2012, scales were used for age determination. Scales of each fish were removed from a midlateral area on the left side posterior to the pectoral fin base, cleaned with a dilute bleach solution, mounted and pressed on acetate sheets, and read on a microfilm projector by one individual using the methods of Cating (1953).

Statistical analyses.— All statistical analyses were completed in R version 3.6.3 (R Core Team 2020). A daily catch per unit effort (CPUE) was calculated by totaling weight (kg) of maturing females per day per length of net. The graph of CPUE versus time was used to calculate a nonparametric index estimator defined as the area under the curve. The area under the curve was calculated via trapezoidal integration, and the estimator was used as a yearly spawning stock index (Olney and Hoenig 2001; Latour et al. 2012). The spawning stock index and the other variables used in this study were tested for normality by visual examination of quantile–quantile plots (Q–Q plots). Any variable violating normality was log transformed and rechecked with another Q–Q plot.

Hatchery prevalence was calculated as the percentage of otoliths with hatchery marks for each year. A correlation analysis was used to compare hatchery prevalence with the spawning stock index. We estimated the CPUE for each age-class in each year (aCPUE). The percentage of otoliths scanned for OTC marks and the level of effort (days fished) varied year to year. Therefore, aCPUE was calculated by dividing the number of fish at age with a hatchery mark for each year by the corresponding year's percent of otoliths scanned and effort (10^3 meter-day). Year-class CPUE (YCC) was calculated by summing aCPUE from multiple return years corresponding to each birth year. Three models were used to examine the relationship of the number of larvae stocked and the YCC (package "FSA" in R version 3.6.3; Ogle 2016). We fitted a linear model through the origin, which assumes the degree of successful year-classes remains constant across all levels of stocked larvae and has the form of

$$\text{YCC} = a(L),$$

where L = number of stocked larvae and a = a parameter controlling slope. Two other models are commonly used to analyze stock–recruit relationships: the Beverton–Holt (Beverton and Holt 1957) and Ricker (1975) models. The Beverton–Holt model assumes recruitment will approach an asymptote at some level of stocked larvae and has the form of

$$\text{YCC} = \frac{a(L)}{1 + b(L)}$$

and the Ricker model assumes a dome-shaped relationship, where maximum recruitment occurs at an intermediate level of stocked larvae and has the form of

$$\text{YCC} = a(L)e^{-b(L)},$$

where L and a have the same definitions as above and b is a parameter controlling the degree of density dependence. Model goodness of fit was compared through Akaike information criterion corrected for sample size (AIC_c), which prevents overfitting with small sample sizes (Bedrick and Tsai 1994; Burnham and Anderson 2004). The residual standard error, ΔAIC_c (the difference between the AIC_c value of a model and the lowest AIC_c value of all models), and the AIC_c weight (the odds that each model is the best representative of the data) were used to select the most parsimonious model; ΔAIC_c was evaluated at a threshold of 2 (Burnham and Anderson 2004).

An assumption of all three models is that mortality is approximately constant for each age of life. For our modeling purposes, we think it is reasonable to assume a constant rate of mortality for juveniles and adults over the study period since there were no changes in fishing pressure or catastrophic events during that period. However, mortality in the larval stage can be more variable, and years with extraordinarily good conditions could lead to unexplained higher recruitment levels, while extraordinarily bad conditions would lead to unexplained lower recruitment levels (Sinclair and Tremblay 1984; Houde 1989; Cushing 1990).

RESULTS

The spawning stock index for American Shad in the James River increased from 2.57 in 1998 to a peak of 9.33 in 2003 (Table 1; Figure 2). The peak spawning stock index value during the current monitoring program, however, was much lower than the peak (29.20) calculated from the historical logbook on the James River (Figure 2). The following years, the index fluctuated between relatively high index years in which values were above 6.00 (2004, 2005, 2009–2012, 2014) and low index years in which values were below 5.00 (2006–2009, 2013, 2015–2019). The geometric mean of the index from 1998 to 2019 was 3.42. The hatchery prevalence for female American Shad ranged between 3.6% and 60.5% (Figure 3). The Q–Q plots indicated that the spawning stock index, hatchery prevalence, and hatchery input all followed a normal distribution. The spawning stock index was significantly correlated to the prevalence of hatchery fish ($r = 0.51$, df = 20, $P = 0.02$).

The 1997 hatchery year-class had the highest CPUE (43.1 fish/meter-day; Figure 4). Year-class CPUE increased between 1992 and 1997 but then decreased to one of the lowest year-class CPUE values in 2001 (3.3 fish/meter-day). Year-class CPUE rose again from 2002 to 2009 but at its peak was still less than 50% of the 1997 year-class

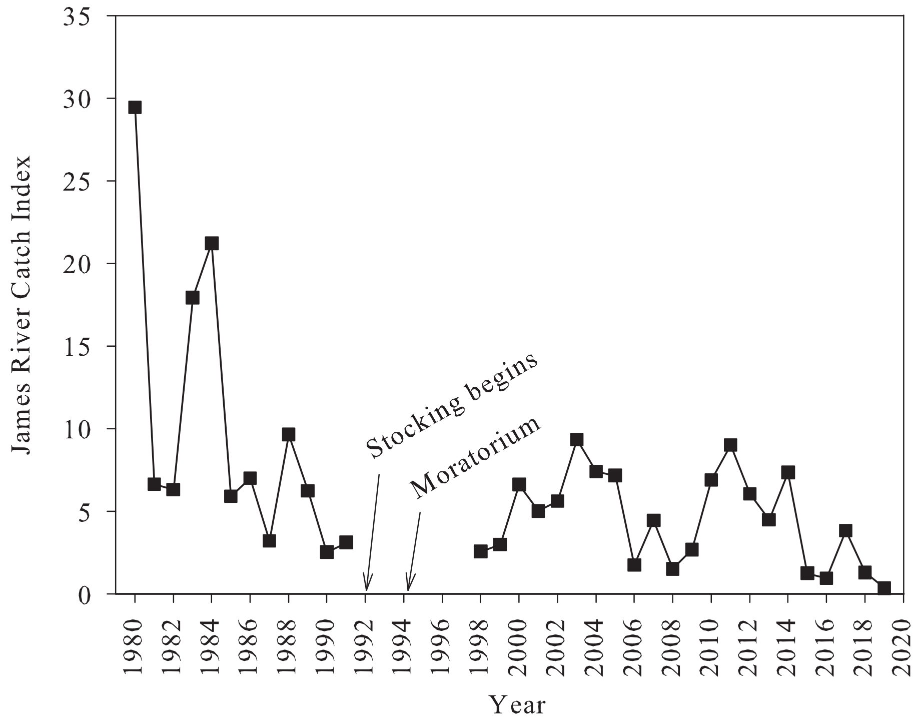

FIGURE 2. Historical and current spawning stock indices for American Shad in the James River.

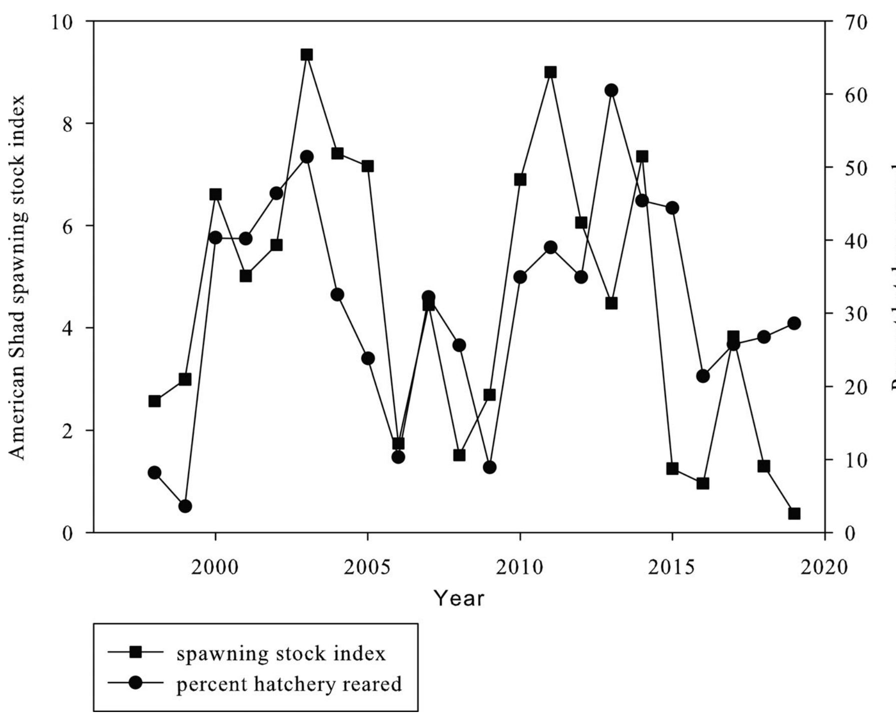

FIGURE 3. Comparison of the American Shad spawning stock index to the percent of spawning adults with OTC hatchery marks.

CPUE. Year-class CPUE did not follow a normal distribution until the data was log transformed. Both the linear and Ricker model parameters were significant when modeling the stock–recruitment relationship (linear: $a = 0.35$, $P < 0.01$; Ricker: $a = 1.5$, $P < 0.01$, $b = 2.8$, $P < 0.01$), but the Beverton–Holt model parameters were not

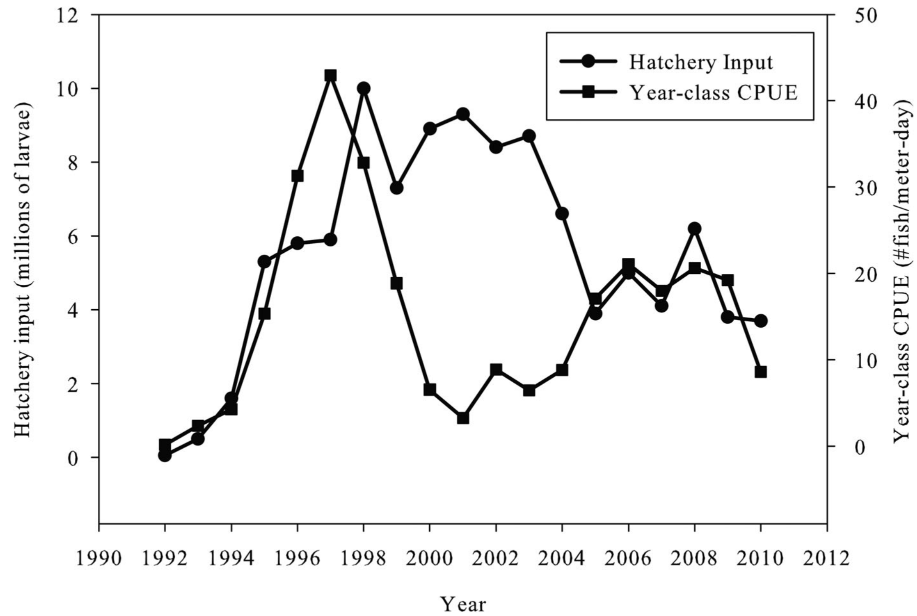

FIGURE 4. A comparison of year-class CPUE and hatchery input from 1993 to 2010.

significant ($a = 3.2$, P-value = 0.20, $b = 1.1$, P-value = 0.27). The Ricker model had the lowest residual standard error and AIC_c value and the greatest AIC weight. The ΔAIC values for the linear and Beverton–Holt models were both greater than the threshold of 2, and therefore the Ricker model was considered to be the best fit for the data (Table 2; Figure 5).

DISCUSSION

The peak of American Shad populations on the James River during the current monitoring period was one-third of the peak during the period of historical data collection from the fishery (1980–1993). The historical peak is certainly an underestimate of earlier (i.e., healthier) population values because data for direct comparison to our monitoring data do not exist until the 1980s, during a period when abundance was not sufficient to support a fishery. The first 4–6 years of monitoring the James River spawning stock population of American Shad were encouraging. However, beginning in 2006, the population has been in a 4- to 5-year cycle oscillating between very low index values and only slightly higher index values.

The lack of recovery of the James River stock of American Shad is despite a 26-year effort to supplement the population with hatchery-reared fish. Years with higher spawning stock index values were correlated to an increase in the percentage of hatchery fish returning to spawn. Aunins et al. (2014) conducted genetic analyses and concluded that the present population is mostly derived from hatchery fish and can no longer be distinguished genetically from the York River population. Therefore, it appears that the James River American Shad heavily relies upon hatchery inputs and is quite possibly dependent upon them.

Recently, otoliths have been identified as the most accurate and precise method for determining age for American Shad, with scales tending to underestimate age for older fish (~7 years and older; Duffy et al. 2012; Elzey et al. 2015). Incorrect aging would place fish into the wrong birth year and inflate the error in the stock–recruitment curve. While this might be the case, the population of American Shad in the James River is severely depleted and has a truncated age structure (Hilton et al. 2022). Most James River American Shad do not reach age 7, and any aging error therefore will have a minimal impact. The dome-shaped Ricker stock–recruitment model best described the relationship between hatchery input and year-class CPUE. A threshold level of hatchery-released individuals was necessary for success (approximately 4 million larvae), but stocking above 7 million larvae correlated with declining returns. Similarly, Ricker dome-shaped curves have been the best-fit models for describing the stock–recruitment relationship for river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*; Winters and Wheeler 1996; Devine et al. 2021) and Gizzard Shad *Dorosoma cepedianum* (Miranda et al. 2020). The highly variable and density-dependent mortality processes in the egg and larval stages often defines the transition of recruits to the more stable and density-independent mortality of older juveniles and adult fishes (Ricker 1954; Beverton and Holt 1957; Shepherd and Cushing 1980). These density-dependent processes (i.e., predation and starvation) play a major role in regulating fish population

TABLE 2. Model summaries for the spawner–recruit models fitted to ln (year-class CPUE) and hatchery input. AIC_c, Akaike information criterion corrected for sample size; n_{par}, the number of model parameters; RSE, the residual standard error; weight, Akaike weight; ΔAIC_c, the difference in AIC_c between the given model and the model with the lowest AIC_c value.

Model	n_{par}	RSE	AIC_c	ΔAIC_c	Weight
Ricker	3	0.613	42.57	0.00	0.94
Beverton–Holt	3	0.704	48.12	5.55	0.06
Linear	2	1.090	63.87	21.30	0.00

stability (Ricker 1954; Beverton and Holt 1957; Cushing 1975). Density-dependent mortality previously has been described for many clupeids, including Atlantic Herring *Clupea harengus* (Cardinale and Arrhenius 2000), Gizzard Shad (Miranda et al. 2020), river herring (Winters and Wheeler 1996; Devine et al. 2021), Sprat *Sprattus sprattus* (Casini et al. 2014), and American Shad (Crecco et al. 1986; Savoy and Crecco 1988).

Hatchery-stocked larvae are not exempt from density-dependent processes. Survival of Atlantic Salmon *Salmo salar* from fry to yearling was significantly greater at lower stocking densities versus higher densities (McMenemy 1995). Logsdon and Anderson (2018) also found the Ricker model to fit best when describing the relationship between stocked Walleye *Sander vitreus* fry and year-class strength. Many stocking programs exist without the benefit of knowing the stock–recruitment relationship. Although more data are needed to determine how analysis of American Shad stocking in the James River relates to other stocking programs, we have shown that in at least some instances there appears to be a threshold of the number of larvae stocked above which produces negative results (i.e., lower larval survival). We did find, however, that the highest hatchery output year (1998) produced a moderately strong year-class. Environmental conditions that year might have led to an unusually low mortality rate. Crecco et al. (1986) found that adding climatic data to Ricker stock–recruitment curves for American Shad in the Connecticut River improved the models dramatically. Interestingly, they found May water flow and May–June rainfall to be negatively correlated to mortality rates; the spring of 1998 was one of the highest flow rates for the James River during the span of this study (U.S. Geological Survey 2021).

American Shad hatcheries have had mixed success in supplementing year-classes throughout the native range (Bailey and Zydlewski 2013). Reasons for successes and failures are complex and multifaceted, and it is difficult to compare between river systems. For example, the Rappahannock River was stocked for several years but the program ended due to consistently low percentages of hatchery fish found in the spawning runs. Hatchery supplementation of American Shad in the Rappahannock River coincided with the removal of Embry Dam. The natural population benefitted from the opening of 170.6 km of spawning habitat (A. L. Weaver, presentation given at the International Conference on Engineering and

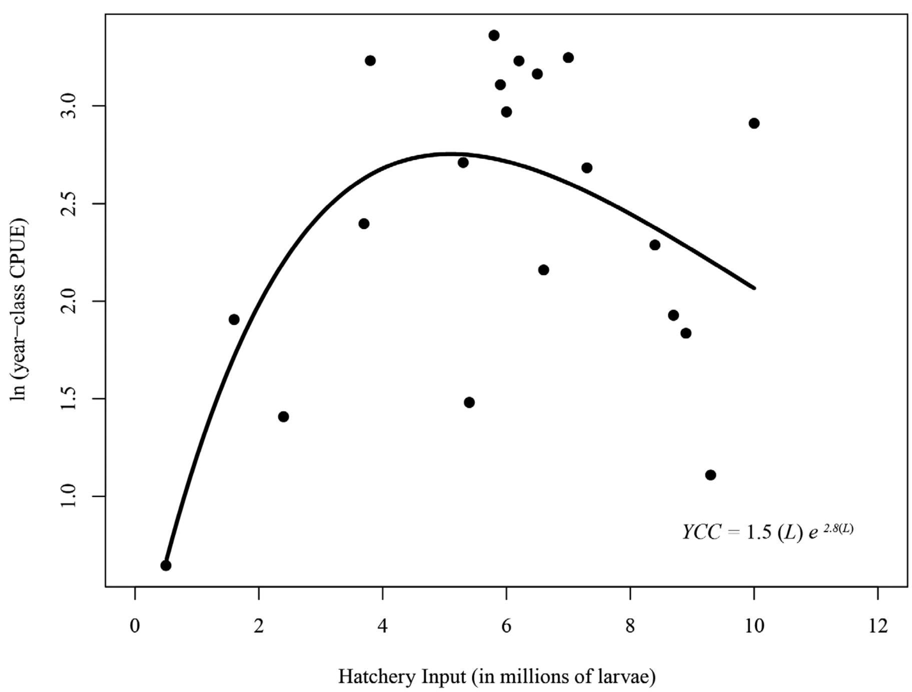

FIGURE 5. Comparison of hatchery input and ln (year-class CPUE) from 1993 to 2012. The black line indicates the Ricker curve model.

Ecohydrology for Fish, 2013). In this case, the production resulting from this newly accessible spawning habitat may have greatly outweighed the input of hatchery individuals.

The Susquehanna River is the largest tributary of Chesapeake Bay to be stocked with hatchery-produced American Shad and offers a good comparison to the trends found in the James River because it also still has a dam. Both rivers have structures to pass fish upstream, but their effectiveness is uncertain. The Pennsylvania Fish Commission began operating the Van Dyke Hatchery in 1976, and by 2001, fish counts at the lowermost dam on the Susquehanna River grew from only a few hundred to over 200,000 fish (Brown and St. Pierre 2001). Although the Susquehanna and James rivers are comparable in some respects, stocking intensity on the Susquehanna River does not mirror that of the James River stocking and sampling techniques for returning adults are different. However, both rivers experienced increases in American Shad spawning stock abundance in the late 1990s and early 2000s, followed by a steep decline beginning in 2005 (Hendricks and Trynineski 2013). Stocking efforts of both programs were unable to increase the spawning population to historical levels.

Conclusion

Long-term monitoring of the James River American Shad spawning population allowed for the critical examination of the contribution of hatchery individuals to the yearly spawning run and the relative success rate of each hatchery year-class. Although American Shad populations did not rebound as planned, from these data we consider that the James River spawning stock of American Shad was dependent upon hatchery inputs, with ideal hatchery returns occurring during years of moderate levels of hatchery stocking. Hatchery operations for American Shad on the James River ceased in 2018 due to financial constraints, difficulty in obtaining broodstock, and the apparent ineffectiveness of restoring the natural population. Because the age-5 year-class is the first year of full recruitment to the gear used for monitoring the spawning stock, the full consequences of the termination of hatchery inputs on the James River should be evident in 2023. We will continue to monitor the American Shad population and see if the natural population may rebound due to lack of density-dependent pressure from stocked larvae or if it may further decline because spawning American Shad are dependent upon the returning hatchery adults.

ACKNOWLEDGMENTS

We thank the numerous people who have contributed to the collection of data over the course of this study. We also thank Eric Brittle and Alan Weaver with the Virginia Department of Wildlife Resources and Mike Odum with the U.S. Fish and Wildlife Service for hatchery release data. The VIMS Alosine Monitoring Program has been supported since 1998 by VIMS and by the Virginia Marine Resources Commission and U.S. Fish and Wildlife Service through the Wallop-Breaux Sport Fish Restoration Act (F-116-R1 to R23). This is contribution number 4093 of the Virginia Institute of Marine Science, William & Mary. Open access funding enabled and organized by ProjektDEAL. There is no conflict of interest declared in this article.

ORCID

Patrick E. McGrath https://orcid.org/0000-0002-0089-6308
Eric J. Hilton https://orcid.org/0000-0003-1742-3467

REFERENCES

Araki, H., and C. Schmid. 2010. Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. Aquaculture 308:S2–S11.

ASMFC (Atlantic States Marine Fisheries Commission). 2009. Amendment 2 to the interstate fishery management plan for shad and river herring. ASMFC, Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2010. Amendment 3 to the Interstate Fishery Management Plan for shad and river herring (American Shad management). ASMFC, Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2020. 2020 American Shad stock assessment and benchmark peer review report. ASMFC, Arlington, Virginia.

Aunins, A. W., J. M. Epifanio, and B. L. Brown. 2014. Genetic evaluation of supplementation-assisted American Shad restoration in the James River, Virginia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 6:127–141.

Bailey, M. M., and J. D. Zydlewski. 2013. To stock or not to stock? Assessing the restoration potential of a remnant American Shad spawning run with hatchery supplementation. North American Journal of Fisheries Management 33:459–467.

Bedrick, E. J., and C. Tsai. 1994. Model selection for multivariate regression in small samples. Biometrics 50:226–231.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Her Majesty's Stationery Office, London.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service Fishery Bulletin 74:1–577.

Brown, J. J., and R. A. St. Pierre. 2001. Restoration of American Shad *Alosa sapidissima* populations in the Susquehanna and Delaware rivers, USA. MTS (Marine Technology Society)/IEEE (Institute of Electrical and Electronics Engineers) Conference and Exhibition 1:321–326.

Brown, B. L., T. P. Gunter, J. M. Waters, and J. M. Epifanio. 2000. Evaluating propagation-assisted restoration of American Shad. Conservation Biology 14:294–303.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Cardinale, M., and F. Arrhenius. 2000. Decreasing weight-at-age of Atlantic Herring (*Clupea harengus*) from the Baltic Sea between 1986 and 1996: a statistical analysis. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 57:882–893.

Casini, M., T. Rouyer, V. Bartolino, N. Larson, and W. Grygiel. 2014. Density-dependence in space and time: opposite synchronous variations in population distribution and body condition in the Baltic Sea

Sprat (*Sprattus sprattus*) over three decades. PLoS (Public Library of Science) ONE 9(4):e92278.

Cating, J. P. 1953. Determining age of Atlantic Shad from their scales. U.S. Fish and Wildlife Service Fisheries Bulletin 54:187–199.

Crecco, V. A., T. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American Shad recruitment: a predictive approach. Canadian Journal of Fisheries and Aquatic Sciences 43:457–463.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Oxford, UK.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26:250–293.

Devine, M. T., J. Rosset, A. H. Roy, B. I. Gahagan, M. P. Armstrong, A. R. Whiteley, and A. Jordaan. 2021. Feeling the squeeze: adult run size and habitat availability limit juvenile river herring densities in lakes. Transactions of the American Fisheries Society 150:207–221.

Duffy, W. J., R. S. McBride, M. L. Hendricks, and K. Oliveira. 2012. Otolith age validation and growth estimation from oxytetracycline-marked and recaptured American Shad. Transactions of the American Fisheries Society 141:1664–1671.

Elzey, S. P., K. A. Rogers, and K. J. Trull. 2015. Comparison of four aging structures in the American Shad (*Alosa sapidissima*). U.S. National Marine Fisheries Service Fishery Bulletin 113:47–54.

Gunter, T. P. 1997. American Shad restoration project report. Virginia Department of Game and Inland Fisheries, Ashland.

Hasselman, D. J., D. Ricard, and P. Bentzen. 2013. Genetic diversity and differentiation in a wide-ranging anadromous fish, American Shad (*Alosa sapidissima*), is correlated with latitude. Molecular Ecology 22:1558–1573.

Hendricks, M. L. 2003. Culture and transplant of alosines in North America. Pages 303–312 *in* K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Hendricks, M. L., and J. D. Tryninewski. 2013. Hatchery contribution and cohort analysis of adult American Shad collected in the Susquehanna River based on tetracycline tagging. Pages 215–254 *in* Susquehanna River Anadromous Fish Restoration Committee. Restoration of American Shad to the Susquehanna River annual progress report. U.S. Fish and Wildlife Service, Washington, D.C.

Hilton, E. J., P. E. McGrath, B. E. Watkins, and A. R. Magee. 2022. Monitoring relative abundance of American Shad and river herring in Virginia's Rivers. 2021 Annual Report to the Virginia Marine Resources Commission, Contract F-116-R24, Ft. Monroe.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48:945–957.

Houde, E. D. 1989. Subtleties and episodes in the early life of fishes. Journal of Fish Biology 35:29–38.

Kitada, S. 2018. Economic, ecological and genetic impacts of marine stock enhancement and sea ranching: a systematic review. Fish and Fisheries 19:511–532.

Latour, R. J., E. J. Hilton, P. D. Lynch, T. D. Tuckey, B. E. Watkins, and J. E. Olney. 2012. Evaluating the current status of American Shad stocks in three Virginia rivers. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:302–311.

Logsdon, D. E., and C. S. Anderson. 2018. Impacts of Walleye fry stocking on year-class strength in lakes with Walleye spawn-take operations. Minnesota Department of Natural Resources, Investigational Report 569, St. Paul.

McMenemy, J. R. 1995. Survival of Atlantic Salmon fry stocked at low density in the West River, Vermont. North American Journal of Fisheries Management 15:366–374.

Miranda, L. E., D. M. Norris, V. R. Starnes, N. M. Faucheux, and T. Holman. 2020. Stock–recruitment dynamics of a freshwater clupeid. Fisheries Research 221:105378.

Munroe, T. A. 2002. Herrings: family Clupeidae. Pages 111–160 *in* B. B. Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington, D.C.

Ogle, D. H. 2016. Introductory Fisheries Analyses with R. The R Series. CRC Press, Taylor & Francis Group, Boca Raton, Florida.

Olney, J. E., and J. M. Hoenig. 2001. Managing a fishery under moratorium: assessment opportunities for Virginia's stocks of American Shad (*Alosa sapidissima*). Fisheries 26(2):6–12.

Olney, J. E., S. C. Denny, and J. M. Hoenig. 2001. Criteria for determining maturity stage in female American Shad, *Alosa sapidissima*, and a proposed reproductive cycle. Bulletin Francais de la Peche et de la Pisciculture 362:881–901.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Department of Environment, Fisheries and Marine Service, Ottawa.

Rulifson, R. A. 1994. Status of anadromous *Alosa* along the east coast of North America. Pages 134–158 *in* J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous Alosa symposium. American Fisheries Society, Tidewater Chapter, Bethesda, Maryland.

Savoy, T. F., and V. A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American Shad, *Alosa sapidissima*. U.S. National Marine Fisheries Service Fishery Bulletin 86:467–482.

Shepherd, J. G., and D. H. Cushing. 1980. A mechanism for density dependent survival of larval fish as the basis of a stock–recruitment relationship. Journal du Conseil international l'Exploration de la Mer 39:160–167.

Sinclair, M., and M. J. Tremblay. 1984. Timing of spawning of Atlantic Herring (*Clupea harengus harengus*) and the match–mismatch theory. Canadian Journal of Fisheries and Aquatic Sciences 41:1055–1065.

Smith, H. M. 1895. A review of the history and results of the attempts to acclimatize fish and other water animals in the Pacific states. Bulletin of the United States Fish Commission 15:379–475.

Trushenski, J. T., G. E. Whelan, and J. D. Bowker. 2018. Why keep hatcheries? Weighing the economic cost and value of fish production for public use and public trust purposes. Fisheries 43:284–293.

Tuckey, T. D., and J. E. Olney. 2010. Maturity schedules of female American Shad vary at small spatial scales in Chesapeake Bay. North American Journal of Fisheries Management 30:1020–1031.

U.S. Geological Survey. 2021. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation). Available: https://doi.org/10.5066/F7P55KJN. (November 2021).

Walburg, C. H., and P. R. Nichols. 1967. Biology and management of the American Shad and status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Special Scientific Report Fisheries 550.

Weaver, L. A., M. T. Fisher, B. T. Bosher, M. L. Claud, and L. J. Koth. 2003. Boshers dam vertical slot fishway: a useful tool to evaluate American Shad recovery efforts in the upper James River. Pages 339–347 *in* K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Winters, G. H., and J. P. Wheeler. 1996. Environmental and phenotypic factors affecting the reproductive cycle of Atlantic Herring. ICES (International Council for the Exploration of the Sea) Journal of Marine Science 53:73–88.