

Interpreting Maturation Data for American Shad in the Presence of Fishing Mortality: A Look at Historical Data from the York River, Virginia

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Abstract.—To enable better monitoring, forecasting, and establishment of restoration targets, we undertook a study of maturation by American shad *Alosa sapidissima* in the York River, Virginia. Throughout the study, the need for historical information about the status of the stock and how it relates to the current depressed state was evident. We identified an early study (covering the years 1957–1959) that might allow reconstruction of maturation schedules for historical time periods and enable comparison with contemporary maturation schedules. When a commercial fishery is operating, mature survival can differ from immature survival for a given age because the immature fish remain offshore and do not experience the fishing mortality imposed on adults in the spawning river. Thus, a maturity model that can account for the relationship between mature and immature survival is required and was developed here. A process for reconstructing data matrices from published data summaries was developed that led to the discovery of errors in the historical source. For the year in which the errors could be corrected (1959), maturation parameters were estimated using the method developed here for various levels of the ratio of mature to immature survival (including that inferred from the exploitation rate reported in the historical study). Additionally, microfiche data were located that provided the information necessary to estimate maturation parameters for 1955 and 1956. The estimated maturation schedule for 1959 was earlier than the present estimated schedule, while those for 1955 and 1956 were later. Because a greater range of ages was sampled in 1955 and 1956 and the maturity estimates for those years were in agreement with each other and in line with ecological expectations, we accept those estimates over the ones obtained from the 1959 data and conclude that at present the maturation of American shad occurs earlier than it did during the historical period.

The scales of alosine fishes like the American shad *Alosa sapidissima* that have previously spawned exhibit spawning marks. These marks are characteristic scarlike rings and are presumed to be caused by the erosion or absorption of the scale when the fish enter freshwater to spawn. The number of spawning marks and annuli has been used to determine the age of a fish, the age at which it became mature, and how many times it has spawned (Cating 1953; Judy 1961).

This kind of age and spawning information is commonly tabulated in stock assessment reports. For American shad, Amendment I to the Interstate Fishery Management Plan for Shad and River Herring requires that Atlantic Coast states conduct spawning stock surveys (ASMFC 1999). As part of these surveys, states are required to take representative samples of adults to determine the sex and age composition as well as to obtain repeat-spawning information (for states north of South

Carolina; ASMFC 1999). However, the implications and uses of such data for understanding population dynamics are poorly understood.

At least three factors influence the distribution of spawning histories. First, the number of fish spawning for the first time increases relative to that of other years when a strong year-class matures and joins the spawning migration. Second, if the exploitation rate was high in the previous year the number of repeat spawners in the current year will be low. Third, for American shad, the southern stocks are largely semelparous. Those native to rivers at latitudes above 32°N exhibit increasing levels of iteroparity as the latitude of the natal river increases (Leggett and Carscadden 1978). Thus, it has not been clear what data on the occurrence of repeat spawning can tell us.

Previous studies have attempted to characterize the age of maturation for the American shad (see, for example, Nichols and Massmann 1963; Leggett 1969). Estimates of percentage mature at age were calculated by dividing the number of sampled fish maturing at a given age by the total number of fish sampled. Maki et al. (2001) showed that such cal-

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culations provide biased estimates of the percentages maturing at each age. Maki et al. (2001) developed a model utilizing the method of maximum likelihood to estimate the maturation schedule from data on age at capture and age at first spawning. However, using this method to obtain unbiased maturation estimates from samples taken from the spawning run requires that the mortality rates for mature and immature fish of the same age be equal. This assumption appeared reasonable for the case examined by Maki et al. (2001) because the stock they studied was under a moratorium in regard to the in-river harvesting of shad. Because of the moratorium, the in-river fishing mortality of mature fish was negligible and such fish were subject only to offshore intercept fisheries. Thus, the moratorium helped ensure that the assumption of equal mortality rates was at least approximately met by eliminating one source of differential mortality (Olney and Hoenig 2001). Differential mortality between immature and mature fish could also arise due to the unknown level of stress associated with spawning. However, American shad in the York River, Virginia, undergo a relatively short migration to the spawning grounds (Bilkovic 2002), spawn repeatedly (Maki et al. 2001), and may have energy reserves available for the postspawning migration (Glebe and Leggett 1981; Olney et al. 2001); therefore, they do not appear to have high spawning-induced mortality.

Information on American shad maturation is useful for forecasting in two ways. First, when an especially strong or weak year-class appears in juvenile monitoring, it helps us determine when the effects will be seen in the spawning runs. Second, knowing how the maturation of each cohort will proceed is necessary to forecast next year's run size from the current year's run data.

Therefore, it is useful to know whether maturation rates change appreciably over time. In addition to ongoing monitoring (Olney and Hoenig 2001), we are attempting to review all historical information about the status of the Virginia stocks in an effort to piece together a history of maturation schedules. This paper describes our endeavor to interpret historical information on the maturation of American shad in the York River, Virginia. These data were collected during a period of heavy commercial fishing and thus require a maturity model that accounts for the ratio of mature to immature survival being different from 1. The development of such a model will not only enhance the interpretation of historical maturation data but also allow interpretation of current mat-

TABLE 1.—Spawning histories of female American shad collected in the York River, Virginia, over three years of sampling (1998–2000). Table entries are numbers of fish; ages are based on scale analysis. The information in this table was summarized from Maki et al. (2001).

Age at capture	Age at maturity							
	3	4	5	6	7	8	9	10
3	12							
4	10	193						
5	14	142	234					
6	4	79	71	44				
7	0	18	25	2	3			
8	0	8	11	0	0	0		
9	0	2	2	1	0	0	0	
10	0	0	1	0	0	0	0	0

uration data for populations subject to commercial fishing (for which the survival of mature fish does not equal that of immature fish of a given age).

Reconstruction of Historical Data

Data collected by Nichols and Massmann (1963) were identified as potentially containing historical spawning and maturation data appropriate for estimating a historical maturity schedule. American shad maturity and spawning data can be tabulated in terms of age at capture and age at maturity (Table 1). Typically, however, historical papers present only summaries of the data on the age at capture, age at maturity, and number of previous spawns (as in Table 2). Nichols and Massmann (1963) provided such summaries for male and female American shad collected from the York River during 1957, 1958, and 1959. It is possible to construct tables similar to the one in Table 1 that have row sums (number captured at each age), column sums (number spawning for the first time at each age), and diagonal sums (number that spawned 0, 1, 2, . . . times previously) that are consistent with the data summaries. If the cells of the matrix are forced to be nonnegative integers, there is a finite number of solutions that yield the required column, row, and diagonal sums. A C++ program was utilized to attempt reconstruction of the historical data obtained from Nichols and Massmann (1963; see Appendix C of Maki 2000 for the program).

All attempts at reconstructing a data matrix for the three years of data presented in Nichols and Massmann (1963) failed. It was impossible to assign nonnegative integer values to all the cells of the data matrix in a way that yielded the appropriate row, column, and diagonal sums. However, a microfilm reel containing the raw data collected

TABLE 2.—Data for York River American shad samples collected by Nichols and Massmann (1963). Published data are summarized from Table 7 in Nichols and Massmann; revised data are adapted from a microfilm containing the raw data. Entries are numbers of fish.

Age (years) and prior spawns	Males		Females	
	Published	Revised	Published	Revised
Age at capture				
3	35	35	19	19
4	190	191	398	398
5	99	98	154	154
6	21	20	25	25
7	4	4	3	3
8	1	1	0	0
Total	350	349	599	599
Age of first spawn				
3	128	133	32	32
4	211	208	447	439
5	11	8	112	121
6	0	0	8	7
7	0	0	0	0
Total	350	349	599	599
Prior spawns				
0	193	192	526	525
1	83	82	58	57
2	65	67	15	17
3	5	4	0	0
4	4	4	0	0
Total	350	349	599	599

by Nichols and Massmann during 1959 was obtained from the National Marine Fisheries Service in Beaufort, North Carolina. Data summaries were recalculated from the raw data and used to determine where Nichols and Massmann had made errors (Table 2).

The total numbers captured at age were apparently tallied quite carefully. This is reflected by the fact that no differences were found for females for this total as calculated by Nichols and Massmann and our recalculations (Table 2). The tallies for number of spawning marks suggest that Nichols and Massmann counted the number of occurrences of 1, 2, 3, and 4 spawning marks. They then deducted the sum of these numbers from the total number of fish to derive the number of fish with no prior spawns. Errors in enumerating one or more of the categories (1, 2, 3, or 4 spawns) contributed to the error in the number of fish with no prior spawns. While no direct evidence was found on the microfilm, it is assumed that the errors in the number of fish maturing at each age resulted from a similar process of subtracting incorrect subtotals from the overall total.

As a result of the errors found in Nichols and Massmann's (1963) data, the recalculated summaries were utilized in the estimation of maturity

TABLE 3.—Spawning histories of female American shad collected in the York River in 1955 ($N = 603$), 1956 ($N = 699$) and 1959 ($N = 599$). Table entries are numbers of fish; ages are based on scale analysis. The information in this table was summarized from microfiche obtained from the Virginia Institute of Marine Science and the National Marine Fisheries Service.

Year	Age at capture	Age at maturity					
		3	4	5	6	7	8
1955	3	2					
	4	2	108				
	5	3	52	303			
	6	0	12	23	82		
	7	0	0	4	4	6	
	8	0	1	1	0	0	0
1956	3	24					
	4	13	238				
	5	10	65	205			
	6	4	17	14	93		
	7	0	1	0	3	9	
	8	0	0	0	0	0	3
1959	3	19					
	4	3	395				
	5	10	38	106			
	6	0	6	14	5		
	7	0	0	1	2	0	
	8	0	0	0	0	0	0

for 1959 (see below). Further information was not available for the data collected in 1957 and 1958. Thus, maturity was not estimated for these years. However, additional microfiche located at the Virginia Institute of Marine Science in Gloucester Point, Virginia, contained raw data for American shad collected in 1955 and 1956 as part of Nichols and Massmann's (1963) study (Table 3), thus allowing an estimation of maturity for these years as well.

Development of the Maturity Model

Maki et al. (2001) devised a maximum likelihood estimator for the proportion maturing at age j (p_j) when the value of the ratio of mature to immature survival (R) equals 1. However, during times of commercial fishing, it is extremely likely that this ratio will depart from 1. Estimating the proportion mature becomes more complex when this is the case since the proportion maturing at any age depends on both the biology of the species and the differential survival rates between mature and immature fish. For example, if 90% of age-4 American shad are mature but their survival after the spawning run is 0 ($R = 0$), the proportion maturing at age 5 can be as high as 100% and the p_j will no longer sum to 1.

Thus, to examine maturity during historical periods of commercial fishing (when $R \neq 1$), a dif-

ferent characterization of maturation is convenient. Therefore, we define the conditional maturation rate, π_j , to be the probability that a fish of age j matures during the year given that it is immature,

$$\pi_j = \frac{\text{(number age } j \text{ maturing)}}{\text{(number age } j \text{ maturing)} + \text{number age } j \text{ remaining immature)}.$$

These conditional rates do not vary with the survival ratio R except inasmuch as the basic biology changes. We estimated the conditional maturation rates for the data collected by Nichols and Massmann (1963) with a maximum likelihood model.

To formally develop the model, let x_{ij} be the number of fish captured in the river during the spawning run at age i ($i = 3, \dots, 7$) spawning for the first time at age j ($j = 3, \dots, i$), and let π_j be as defined above. The likelihood of obtaining the observed set of spawning histories for age of capture i is the product of the probabilities for each individual spawning history within that set. The observations from each age of capture category constitute a sample from a multinomial distribution under simple random sampling. Thus, the likelihood for age-4 fish is

$$\Lambda_4 \propto \left[\frac{R\pi_3}{R\pi_3 + \pi_4(1 - \pi_3)} \right]^{x_{4,3}} \times \left[\frac{\pi_4(1 - \pi_3)}{R\pi_3 + \pi_4(1 - \pi_3)} \right]^{x_{4,4}}.$$

The first factor gives the proportion of fish that matured at age 3. This is equal to the number of fish that matured at age 3 and survived divided by the sum of the number that matured at age 3 and survived plus the number that remained immature at age 3, survived to age 4, and are maturing at age 4. It is not necessary to specify survival rates for immature and mature fish separately; it suffices to specify the relative survival rates (R). The second factor can be interpreted as the number maturing at age 4 divided by the sum of the number maturing and the number already mature. The likelihood Λ_4 is a binomial function. Thus, the second factor can be expressed as 1 minus the first factor.

It follows from this that the likelihood for age-5 American shad is

$$\Lambda_5 \propto \left[\frac{A}{A + B + C} \right]^{x_{5,3}} \left[\frac{B}{A + B + C} \right]^{x_{5,4}} \times \left[1 - \frac{A - B}{A + B + C} \right]^{x_{5,5}}$$

where

$$A = R^2\pi_3, \quad B = \pi_4(1 - \pi_3)R, \quad \text{and} \\ C = \pi_5(1 - \pi_3)(1 - \pi_4).$$

The three factors represent the probabilities of maturing at ages 3, 4, and 5, respectively, given that a fish is age 5 and mature. Similar expressions hold for ages 6 and 7. The overall likelihood, denoted by Λ , is the product of the individual likelihoods. Hence,

$$\Lambda = \prod_{i=4}^7 \Lambda_i.$$

Comparison of Historical and Current Maturation

We applied the maximum likelihood model described in Maki et al. (2001) to female American shad samples collected in 1998, 1999, and 2000 in the York River, Virginia, during the spring spawning run (Table 1). Estimates of proportion mature (\hat{p}_j) were derived numerically utilizing the S-plus nlminb function (Insightful Corporation, 2001a). These values were computed under the presumably correct assumption that R equals 1 (since the population is currently under a moratorium in regard to in-river fishing) and were utilized to calculate values of π_j for the combined 1998–2000 data (see Appendix B in Maki et al. 2001; Table 4).

Reconstruction of data matrices for the 1957–1959 data collected by Nichols and Massmann (1963) was impossible due to errors in the published data. Therefore, estimation of π_j utilizing the maximum likelihood model described above was completed only for the data on females collected in 1959 (since they could be correctly tabulated based on raw microfiche data). Additionally, π_j were estimated for 1955 and 1956 based on additional microfiche data (Figures 1, 2).

Using the results of a tagging study, Nichols and Massmann estimated an exploitation rate of about 55% for 1959. The exploitation rate is related to the ratio of mature to immature survival and can be utilized to estimate R . Let μ be the exploitation rate, M the instantaneous natural mortality per

TABLE 4.—Estimates of conditional maturation-at-age parameters (π) derived from data for various years and ratios of survival rates (R). Data for 1955, 1956, and 1959 are from Nichols and Massmann (1963); data for 1998–2000 are from spawning stock surveys (Maki et al. 2001). As Nichols and Massmann did not collect any fish maturing at age 7 or above, π_6 was assumed to be 1.0 for 1955, 1956, and 1959; all age-7 fish in the current study were mature, so $R\pi_7$ was assumed to be 1.0 for 1998–2000.

Year	R	π_3	π_4	π_5	π_6	π_7
1955	1	0.00	0.05	0.27	1.00	
	0.7	0.00	0.09	0.35	1.00	
	0.5	0.01	0.15	0.43	1.00	
	0.475	0.01	0.16	0.44	1.00	
	0.4	0.01	0.19	0.49	1.0	
1956	1	0.01	0.08	0.21	1.00	
	0.7	0.02	0.14	0.27	1.00	
	0.5	0.04	0.22	0.34	1.00	
	0.487	0.04	0.23	0.35	1.00	
	0.4	0.06	0.29	0.39	1.0	
1959	1	0.01	0.23	0.67	1.00	
	0.7	0.01	0.32	0.75	1.00	
	0.5	0.02	0.41	0.80	1.00	
	0.45	0.03	0.44	0.82	1.00	
	0.4	0.03	0.48	0.84	1.0	
1998–2000	1	0.02	0.33	0.68	0.80	1.00

year, F the instantaneous fishing mortality per year, and S the annual survival, and let m index mature survival and i immature survival. The American shad fishery can be interpreted as a type-one fishery (Ricker 1975) in which all fishing occurs as a pulse at the beginning of the year and the population undergoes only natural mortality for the remainder of the year. As a result, the exploitation rate is equivalent to $1 - e^{-F}$.

There is no evidence of fishing mortality on immature American shad. Thus, immature shad are assumed to experience only natural mortality and

$$S_i = e^{-M}.$$

Mature shad experience both fishing and natural mortality. Hence,

$$S_m = e^{-M - F}.$$

R is the ratio of mature to immature survival. Thus,

$$R = e^{-F} = 1 - \mu.$$

As a result, Nichols and Massmann’s (1963) estimate of μ (0.55) yields a value of R equal to 0.45. Nichols and Massmann (1963) also listed fishing exploitation rates for 1955 (0.525) and 1956 (0.513), which yield values of R equal to 0.475 and 0.487, respectively.

Various values of R were utilized in the maxi-

mum likelihood estimation of π_j for the historical data, including the values 0.475, 0.487, and 0.45 predicted for the 1955, 1956, and 1959 data by Nichols and Massmann’s (1963) estimates of the exploitation rate. These were then compared with the values of π_j computed from the current maturation regime (1998–2000; Table 4). Because no fish captured in 1959 matured past the age of 6, π_6 was set equal to 1 for this year. Estimates for 1955 and 1956 were also made by setting π_6 equal to 1 (Figure 1), as were estimates of π_j for the combined historical data. Additionally, since fish also matured at the age of 7 in 1955 and 1956, estimates of π_j for 1955, 1956, and the combined historical data set were also made by setting π_7 equal to 1 and estimating π_6 (Figure 2). Since very few fish older than age 7 were collected, these fish were eliminated from the likelihood estimator. Standard errors for the conditional maturation parameters for all data sets were computed by bootstrapping (1,000 repetitions) the likelihood estimator using the S-plus function Bootstrap (Insightful Corporation 2001b; Table 5).

A mark-recapture experiment can be undertaken, as in Nichols and Massmann (1963), by tagging and releasing fish in the river near the mouth (below the commercial fishery). Then, an estimate of R can alternatively be obtained from the maximum likelihood method. The likelihood equation for obtaining R , denoted by Λ_r , can be expressed as

$$\Lambda_r \propto (1 - R)^y \cdot R^{n-y},$$

where y is the number of recaptures from the experiment and n is the number of animals marked. Now, the overall likelihood, denoted by Λ_R , becomes

$$\Lambda_R = \Lambda \cdot \Lambda_r.$$

This method was also utilized to estimate π_j for Nichols and Massmann’s (1963) 1959 data (as this was the year of their tagging study). An estimate of R equal to 0.552 was obtained and estimates of π_j were slightly lower than those estimated by the original likelihood equation (Λ) when R was input as a constant equal to 0.45 (Table 4). Standard errors for the parameter estimates (including R) were obtained by bootstrapping the maximum likelihood estimation (Table 6).

Discussion

We were unable to reconstruct a matrix for any of the data sets (male or female) reported by Nichols and Massmann due to errors in the data. Re-

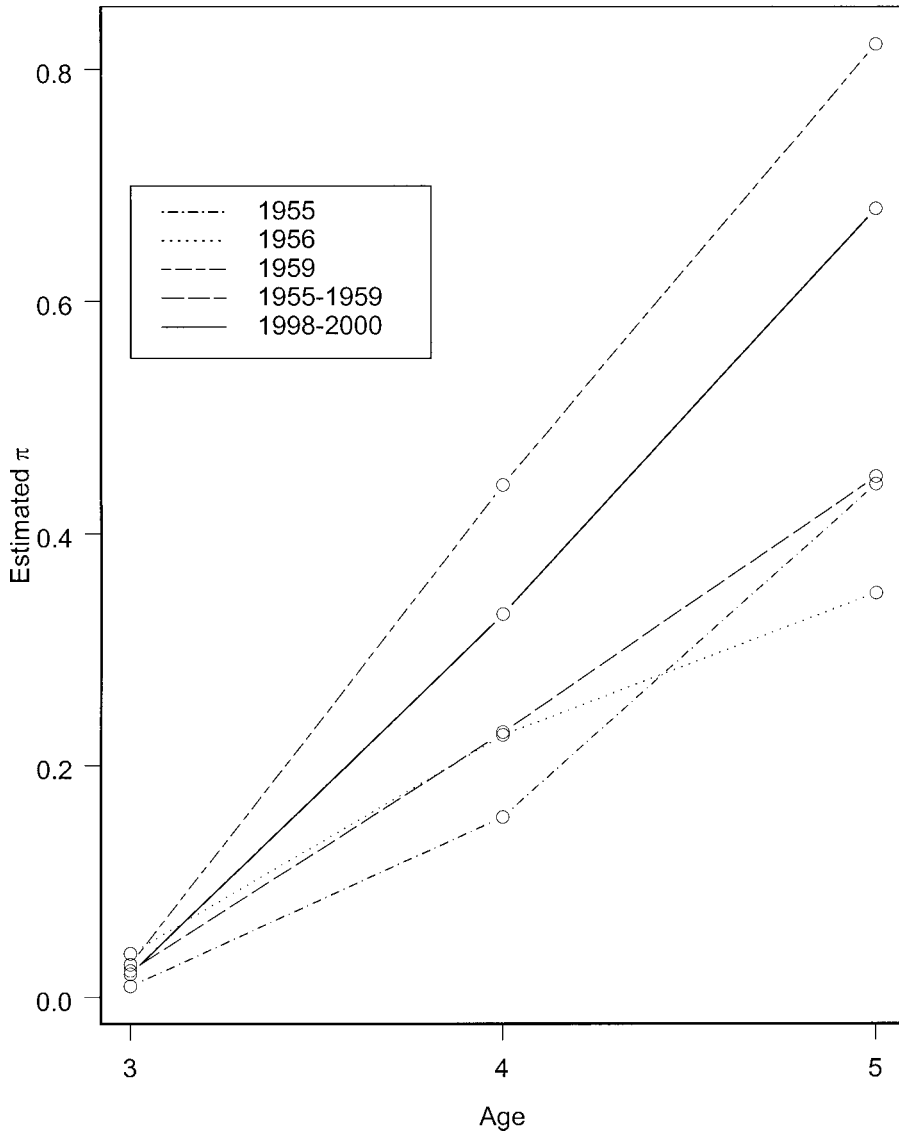


FIGURE 1.—Conditional maturation parameter (π_j) estimates for historical and current data when π_6 is assumed to equal 1; the subscripts indicate fish ages.

construction of the entire data table is not required in order to use the maximum likelihood procedure described in Maki et al. (2001; Appendix A) for estimating proportions mature. However, had we chosen to use only the minimally sufficient statistics (row and column sums) to estimate maturity, we would not have recognized the existence of errors in the data. This raises an important issue when utilizing historical data: all efforts must be taken to ensure the accuracy of the data before subjecting the information to further analysis.

Estimates of π_j for the historical data were made

by introducing various levels of R into the likelihood equation (Λ ; Table 4). The values of π_j decreased with increasing levels of R . However, it appears that for modest errors in the estimation of R (for instance, if R is assumed to be 0.45 when it is actually 0.40), the resulting estimates of π_j are not greatly altered. All parameter estimates, with the exception of the last parameter estimated (π_5 or π_6) in each case, were characterized by low standard errors (Table 5). This is most likely due to the low numbers of older fish collected during times of heavy commercial fishing. The best op-

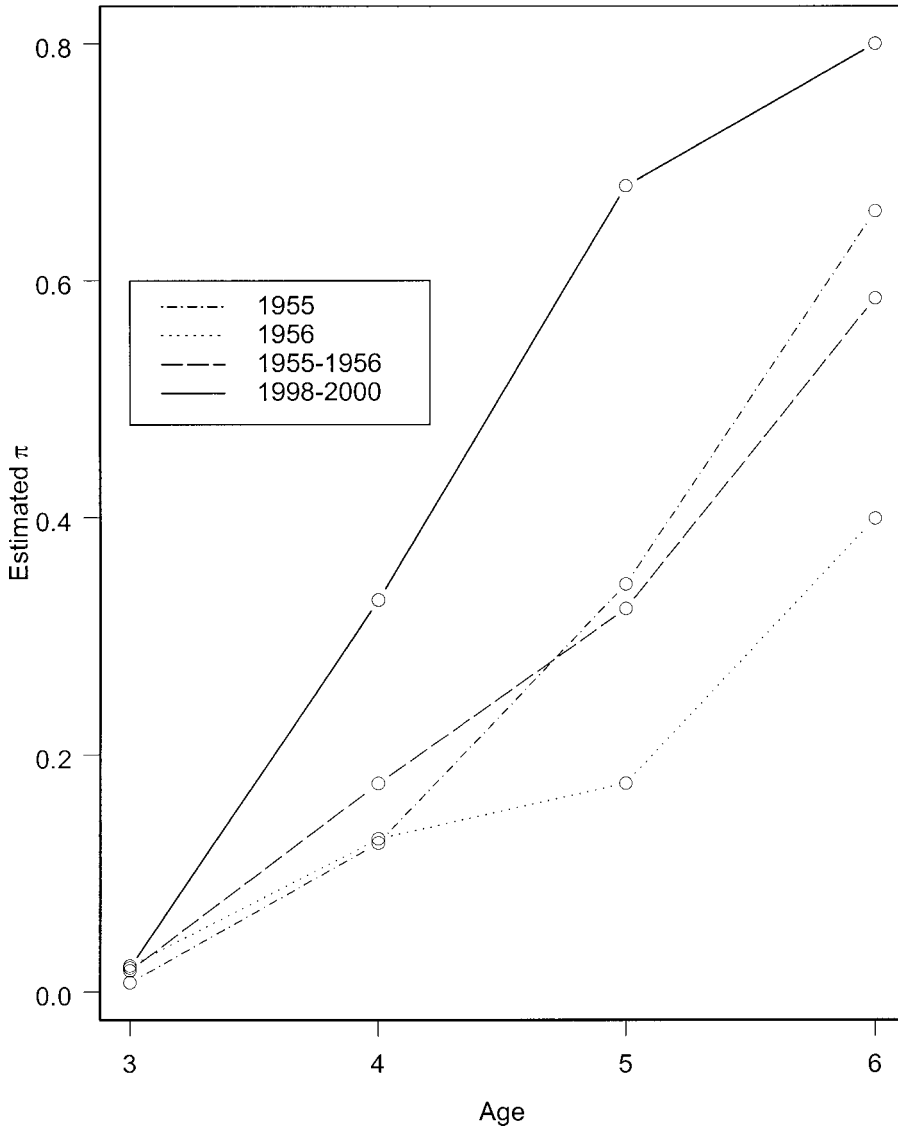


FIGURE 2.—Conditional maturation parameter (π_j) estimates for historical and current data when π_7 is assumed to equal 1. Since none of the fish collected in 1959 matured after age 6, the π_j for 1959 were not estimated under this assumption.

TABLE 5.—Standard errors derived from bootstrapping for all estimated conditional maturation parameters. Estimates were derived under two separate circumstances, (1) constraining π_6 to equal 1.0 and (2) estimating it.

π	$\pi_6 = 1$				π_6 estimated		
	1955	1956	1959	1955-1959	1955	1956	1955-1959
π_3	0.004	0.009	0.008	0.004	0.004	0.008	0.003
π_4	0.025	0.030	0.041	0.017	0.026	0.041	0.022
π_5	0.053	0.044	0.060	0.031	0.061	0.059	0.042
π_6					0.118	0.146	0.090

TABLE 6.—Conditional maturation-at-age (π) and survival ratio (R) parameter estimates for the 1959 data collected by Nichols and Massmann (1963) obtained from the overall likelihood equation (Λ_R ; see text) and their associated standard errors. Note that π_6 is assumed to be 1.

Parameter	Estimate	Standard error
π_3	0.020	0.006
π_4	0.383	0.042
π_5	0.790	0.068
R	0.552	4.64×10^{-7}

portunity to collect older maturing fish is during a moratorium, as is the case with the current (1998–2000) data.

Analysis of Nichols and Massmann's (1963) estimate of the exploitation rate for 1959 yielded an R value of 0.45. The π_j estimated utilizing this value of R were higher than those derived from data from recent years. However, the estimates of π_j for 1955 and 1956 yielded the opposite result (Figures 1, 2). The estimates for those two years were in close agreement and suggest that maturation now occurs at earlier ages than it did during 1955 and 1956. The model, being cross-sectional in nature, is not designed to measure year-to-year changes in maturation rates. However, it seems unlikely (though not impossible) that maturation rates changed so drastically from 1956 to 1959.

In cases such as this, other researchers have attempted either to contact those responsible for collecting the historical data or to obtain the original fish hard parts utilized in the historical analysis (J. Carscadden, Department of Fisheries and Oceans, personal communication). In our study, however, we were unable to contact the original investigators or track down the scales collected during the 1950s. Therefore, it is necessary to make a judgment call as to which data set, if any, is credible.

As sample sizes were relatively similar for all three years (Table 3), this does not seem a likely explanation for the disparity between the estimated parameters. However, a greater number of older fish (age 5 and older) were collected in 1955 and 1956 than in 1959. It is unknown whether the sampling protocols were different between the early and late years of historical collection, whether older fish were simply relatively few in number in 1959, or whether there were discrepancies in aging methodologies between the years.

In addition to spanning a greater range of ages, the 1955 and 1956 data and resulting π_j estimates are more closely in line with ecological expectations for maturation. It is not unlikely that the

current average age of maturation of American shad is earlier than during the historical period, which was a time of heavy commercial fishing. By reducing stock biomass, exploitation could release a fish stock from some of the pressures of intra-specific competition. This could enable faster growth and earlier maturation if maturation is size dependent (Law 2000).

Based on the facts that a greater range of ages were collected in 1955 and 1956, that these two years of data produced estimates of π_j in close agreement with each other, and that the estimates for these two years are in line with ecological expectations, we believe that the maturation of American shad now occurs at an earlier age than it did during the 1950s. This acceleration of maturation may be due to the current low population levels following decades of heavy commercial fishing. We acknowledge, however, that readers may reach other conclusions.

The model developed here is not only useful for interpreting historical maturation data but can also be used with current data when R can be estimated. For example, commercial fisheries for American shad occur on several Atlantic Coast systems, including the Hudson, Delaware, and Connecticut rivers. If the ratio of mature to immature survival of fish of a similar age can be estimated, the maturity model introduced here can be used to estimate π_j . While estimating survival is not an easy task, an estimate of the ratio of mature to immature survival can be made from estimates of exploitation rates (as discussed above). For example, an in-river tagging study that is well designed and implemented could provide an estimate of the exploitation rate and thus an estimate of R . This value of R , together with observations on mature samples collected during the spawning run, can then be utilized in the maximum likelihood estimation of π_j (alternatively, R can be estimated concurrently with π_j as part of the likelihood estimation by utilizing information on the number of marked and recovered animals). Thus, the model allows comparisons of maturation parameters at any point in history and for any rate of exploitation, provided that R is estimable.

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