

## Estimating Proportion Mature at Age When Immature Fish are Unavailable for Study, with Application to American Shad in the York River, Virginia

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**Abstract.**—Estimating a maturation schedule for an anadromous fish based solely on in-river sampling is not feasible without some method of inferring the composition of fish still at sea. We developed a model to estimate the maturation schedule for American shad *Alosa sapidissima* in the York River, Virginia, based on the analysis of spawning marks on the scales of fish sampled from the mature population. The spawning histories of older fish are utilized to infer patterns at younger ages. The method of maximum likelihood was used to estimate the probabilities of American shad maturing at given ages. American shad collected in this study matured between ages 3 and 7. The proportions maturing at these ages were 1.8, 26.3, 52.4, 19.5, and 0%, respectively, for data collected during 1998; 5.4, 41.0, 31.6, 13.3, and 8.7% for data collected during 1999; and 0.3, 27.3, 49.6, 18.0, and 4.8% for data collected during 2000. They averaged 2.1, 32.5, 44.5, 16.8, and 4.1% for all 3 years. Maturity schedules were constructed by cumulating the maximum likelihood estimates and were found to generally overlap for the 3 years of data. Several assumptions underlie the model, but various analyses support these assumptions. However, the model was found to be sensitive to differential survival between immature and mature fish of the same age, particularly when mature survival is less than 75% of immature survival.

Estimating maturity at age may be a relatively straightforward process for species that do not exhibit differential habitat use by various ontogenetic components of the population. This is not the case for some anadromous fishes where the mature portion of the population is separated spatially from the immature during the spawning season. In these instances, in-river monitoring of the spawning run samples only the mature portion of the population, immature fish being unavailable. Without a method of inferring the numbers and ages of immature fish still at sea during the spawning season, unbiased estimation of a maturity schedule is impossible.

The American shad *Alosa sapidissima*, an anadromous clupeid that spends most of its life at sea, ascends coastal rivers to spawn. American shad on the Atlantic coast range from the St. Johns River, Florida, to Labrador, Canada (Walburg 1960; Dadswell et al. 1987). Age-0 American shad emigrate from natal rivers during fall and remain in oceanic waters until they reach sexual maturity. Most sexually mature fish return to their natal streams to spawn (Talbot and Sykes 1958; Walburg 1960; Carscadden and Leggett 1975a; Melvin et al. 1986). American shad native to rivers south of latitude 32°N are semelparous. Shad native to rivers north of this latitude exhibit increasing levels

of iteroparity with increasing latitude of the natal river (Leggett and Carscadden 1978).

The scales of American shad that have previously spawned are believed to exhibit spawning marks—characteristic scarlike rings on the scale caused by erosion or absorption of the scale when the shad enters freshwater to spawn (Moss 1946; Cating 1953; Judy 1961). It has generally been accepted that American shad eat very little while in freshwater and their growth ceases during the spawning migration. Annuli are recognized on scales of many fish species and are thought to mark a time when growth is impeded due to lower temperature or lack of food. Moss (1946) deemed it probable that a conspicuous mark would be found on shad scales due to cessation of growth and erosion or resorption of material from the scales during the spawning migration. Because this mark does not appear on all fish caught (thus it is not considered as a winter mark) but only on a portion of the catch, these marks are thought to represent fish that have previously spawned. Additionally, studies on other species, including singida tilapia *Tilapia esculenta* (Garrod and Newell 1958), rainbow trout *Oncorhynchus mykiss* (Carragher and Sumpter 1991), and Atlantic salmon *Salmo salar* (Persson et al. 1998), have suggested that synthesis and secretion of large amounts of the egg yolk precursor molecule, vitellogenin, may be related to mobilization of calcium from the scales. It is

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TABLE 1.—Spawning histories of American shad collected in the York River, Virginia, in 1998 ( $N = 286$ ), 1999 ( $N = 251$ ), and 2000 ( $N = 339$ ) and the 3 years combined. Ages are based on scale analysis. Table entries are numbers of fish.

Age at capture	Age at maturity							
	3	4	5	6	7	8	9	10
<b>1998</b>								
3	1							
4	1	73						
5	6	40	83					
6	2	10	27	14				
7	0	8	9	1	0			
8	0	2	7	0	0	0		
9	0	0	1	1	0	0	0	
<b>1999</b>								
3	2							
4	8	13						
5	7	72	51					
6	2	33	26	14				
7	0	7	5	0	2			
8	0	5	3	0	0	0		
9	0	0	1	0	0	0	0	
<b>2000</b>								
3	9	107						
4	1	30						
5	1	36	100					
6	0	3	18	16				
7	0	1	11	1	1			
8	0	1	1	0	0	0		
9	0	0	0	0	0	0	0	
10	0		1	0	0	0	0	0
<b>3 years combined</b>								
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

thus implied that scales can be partly demineralized to provide calcium for the formation of oocytes (Simkiss 1974). Judy (1961) validated the aging method of Cating (1953), which uses annuli and spawning marks to determine total age of shad.

Spawning marks have been used in previous studies (in conjunction with annuli) to investigate age at maturity by noting the first appearance of the mark on scales. For example, Leggett (1969, his Table 5) sampled 275 female American shad from the York River, Virginia, in 1967 and 1968 and used the scales to find age at first spawning; this information was then used to calculate the percentage of sampled fish spawning for the first time at each age. However, it would be incorrect to equate his results to a maturity schedule that estimates the proportion of the population maturing at each age because only the mature component

of an age-group was observed. Leggett (1969) collected data resembling the information contained in Table 1, summed each column, and divided by the total number of fish to obtain a schedule of age at maturity for sampled fish. However, in terms of the whole population, this is a biased estimate of the proportions mature at age because the data are incomplete wherever there is a blank in the table. Using the example in Table 1 for the 2000 study, we note that fish captured at age 3 represent the 1997 year-class. American shad older than age 3 originating from the 1997 year-class can only be captured in subsequent sampling years. Thus, observations on numbers mature at ages older than 3 for the 1997 year-class have yet to be made.

In theory, to determine a maturity schedule, one could examine fish of a single age that has completely recruited to the mature segment of the pop-

ulation. For example, if all age-9 fish are mature, then one could examine the spawning histories for this age-class and estimate a maturity schedule. However, in the York River, this is not feasible because of the difficulty in obtaining a large number of old fish.

In this paper, we develop a model to estimate a maturity schedule for American shad in the York River based on samples of all ages from the mature population. The spawning histories of older fish are used to infer maturity of younger age-classes. Ideally, the model would utilize information gained from the mature proportion of a year-class followed through time (i.e., a longitudinal study). However, this would require 5–10 years of sampling which, at present, has not been completed. As an alternative method, we developed a cross-sectional model of 1 year of sampling to estimate a maturity schedule for American shad. We then applied this model to 3 years of sampling (1998–2000) and expanded the model to use the 3-year combined dataset to increase sample size and to estimate an “average” maturity schedule. The method of maximum likelihood was used to estimate the probabilities of shad maturing at given ages.

### Methods

*Specimen collection.*—American shad were collected during the spawning run in the York River from late February to early May of 1998, 1999, and 2000 as part of an ongoing monitoring and stock assessment study (Olney and Hoenig 2001) that sampled shad with a 273-m staked gill net (12.4-cm stretched-mesh monofilament netting). The net was fished 2 d/week throughout the spawning period. All shad caught in the net were brought back to the laboratory for examination and collection of biological data. Only the data for female American shad were used for our study. Acetate impressions of shad scales were read on a microfilm projector following Cating’s (1953) method for determining age of shad and identifying spawning marks. For each fish, the age at capture and the age at first spawning were recorded. For example, an age-6 fish captured in 1999 with two spawning checks must have spawned for the first time in 1997 at age 4; it would be spawning for the third time but would not yet show evidence of a third spawning mark. We also noted any fish showing evidence of skipped spawning (i.e., formation of an annulus between spawning marks).

*Development of the model.*—We estimate the proportion of the American shad population becoming mature at each age from the ages and pre-

vious spawning histories of samples collected in 1 year (for each year of sampling), as well as from the 3-year combined dataset. We assume that all year-classes follow similar maturation schedules (e.g., scales from age-6 fish in 1999 presumably contain the same spawning history information, or number of spawning marks, as age-6 fish in all other years). In all 3 years of sampling, mature shad younger than age 3 were not observed, and the oldest virgin was age 7 (Table 1). Thus, we assume that the proportions maturing before age 3 and after age 7 are zero. Three other assumptions underlie the model: (1) that there is no difference in mortality between immature and mature fish of a given age, which implies no spawning-stress-induced mortality, no fishing mortality during the run, and no bycatch (fishing) mortality of immature shad; (2) that mature shad do not skip years of spawning; and (3) that early-maturing fish have the same catchability as late-maturing fish of the same age, which implies equal size (i.e., an age-5 fish that matured at age 3 is the same size as an age-5 virgin). These assumptions will be discussed following development of the maturity model.

To formally develop the model, let  $x_{ij}$  be the number of fish captured at age  $i$  ( $i = 3, \dots, 10$ ) that spawned for the first time at age  $j$  ( $j = 3, \dots, 7$ ); let  $p_j$  be the probability of a fish maturing at age  $j$ . If we consider the oldest age-class of fish first, then the likelihood of obtaining the observed set of spawning histories of the age-10 fish is the product of the probabilities for each individual spawning history within that set. An age-10 fish must fall into one of five categories of spawning history, as defined by the ages of maturity (i.e., ages 3–7). Thus, the observations on 10-year-olds constitute a sample from a multinomial distribution under simple random sampling of mature 10-year-olds, and the likelihood for age-10 fish ( $\Lambda$ ) is

$$\Lambda_{10} \propto \prod_{j=3}^7 p_j^{x_{10j}}. \quad (1)$$

The likelihoods for ages 7, 8, and 9 are constructed the same way. Hence, for  $i = 7, 8, 9$ , and 10, the likelihood is

$$\Lambda_i \propto \prod_{j=3}^7 p_j^{x_{ij}}. \quad (2)$$

Observations on age-6 fish are incomplete because we see the relative proportions maturing at ages 3, 4, 5, and 6 but do not observe that portion of

the year-class that will mature at age 7. Consequently, the likelihood for age-6 fish is

$$\Lambda_6 \propto \left(\frac{p_6}{1-p_7}\right)^{x_{66}} \left(\frac{p_5}{1-p_7}\right)^{x_{65}} \left(\frac{p_4}{1-p_7}\right)^{x_{64}} \left(\frac{p_3}{1-p_7}\right)^{x_{63}}$$

$$= \prod_{j=3}^6 \left(\frac{p_j}{1-p_7}\right)^{x_{6j}} \tag{3}$$

Similarly, for age-5 fish, we cannot observe the proportion maturing at age 6 or 7. Hence, the likelihood is

$$\Lambda_5 \propto \prod_{j=3}^5 \left(\frac{p_j}{1-p_7-p_6}\right)^{x_{5j}} \tag{4}$$

Likewise, for age-4 fish we have

$$\Lambda_4 \propto \prod_{j=3}^4 \left(\frac{p_j}{1-p_7-p_6-p_5}\right)^{x_{4j}} \tag{5}$$

Because the age-specific probabilities of shad maturing must sum to 1, we know

$$\sum_{i=3}^7 p_i = 1. \tag{6}$$

Therefore, in equations (1)–(5),  $p_7$  can be replaced by the expression

$$p_7 = 1 - \sum_{i=3}^6 p_i. \tag{7}$$

Because the probabilities associated with the various ages in the run are all independent, the overall likelihood, denoted by  $\Lambda$ , is simply the product of the individual likelihoods. Hence we have,

$$\Lambda = \prod_{i=4}^{10} \Lambda_i. \tag{8}$$

The maximum likelihood estimates are those values of the  $p_i$  ( $i = 3, \dots, 6$ ) that maximize the likelihood function. These can be found numerically with various software programs (e.g., using the Splus function `nlminb`). They can also be estimated quite easily via an analytical method (as outlined in Appendix 1). We estimated the variance–covariance matrix of the parameter estimates from the observed information matrix, which was approximated using finite differences. This was accomplished using the S-plus function `vcov.nlminb` (Venables and Ripley 1999). The variance–covariance matrix was then used to compute the correlation matrix for the maturity estimates.

In addition to estimating three individual ma-

turity schedules based on the 1998, 1999, and 2000 samples, we combined the annual data to find an average maturity schedule based on all fish collected over the 3 years of sampling (Table 1). Now, the likelihood for age-4 fish becomes

$$\Lambda_4 \propto \prod_{j=3}^4 \left(\frac{p_j}{1-p_7-p_6-p_5}\right)^{\sum_{k=1}^3 x_{4jk}}, \tag{9}$$

where  $k$  is the year of sampling ( $k = 1998, 1999,$  and  $2000$ ). The other likelihood equations (for ages 5 through 10) are altered the same way to estimate the proportion maturing at each age for the combined years of data.

Model residuals were calculated and examined for any evident patterns. Note that the observed values are those shown in Table 1 and the expected values were calculated by multiplying the estimated probability of maturation at a given age by the total number of fish observed at a given age,  $N_i$  (i.e., row sums in Table 1). For example, the expected catch for 4-year-old fish maturing at age 4 is

$$E(x_{4,4}) = \frac{p_4}{1-p_5-p_6-p_7} N_4. \tag{10}$$

### Results

American shad ranged from ages 3 to 10 and had zero (virgin) to five spawning marks (Table 1). No instances of annuli between spawning marks were detected; thus, we conclude that none of the observed fish exhibited skipped years of spawning. The estimates of proportion mature ( $p_i$ ) derived numerically (Table 2) were equivalent to those calculated analytically. Model residuals (observed – expected) were examined; no clear patterns were detected (Figure 1). Correlation coefficients for pairs of estimated proportions ranged from –0.45 to 0.14. The largest negative values occurred between estimates of maturity at ages 5 and 6. Negative values are not unexpected because the maturity parameters must sum to 1, and thus, an overestimate of one proportion is likely to be associated with an underestimate of other proportions.

Maturity schedules were constructed by cumulating the maximum likelihood estimates with those from the combined data representing an average maturity schedule (Figure 2) for the 3 years of sampling. Maturity schedules for 1998, 1999, and 2000 had 95% confidence intervals that generally overlapped (Figure 3), and no temporal trends were observed over the 3 years. The largest

TABLE 2.—Maximum likelihood estimates (ML) of the proportion of American shad mature at age and the associated standard errors (SE) for 1998, 1999, 2000, and the 3 years combined.

Age	1998		1999		2000		3 Years combined	
	ML	SE	ML	SE	ML	SE	ML	SE
3	0.018	0.006	0.054	0.013	0.003	0.002	0.021	0.004
4	0.263	0.030	0.410	0.041	0.273	0.032	0.325	0.020
5	0.524	0.040	0.316	0.036	0.496	0.043	0.445	0.023
6	0.195	0.044	0.133	0.034	0.180	0.040	0.168	0.023
7	0.000	0.000	0.087	0.059	0.048	0.046	0.041	0.023

differences among years in estimates of  $p_i$  were observed for ages 3 and 4, which in 1999 were higher than in the other 2 years. Comparisons of maximum likelihood estimates of proportion mature with sample proportion estimates (as described by Leggett 1969) revealed consistent differences between the two methods (Figure 4). Results of a sensitivity analysis (Appendix 2) indicated that the model was sensitive to the ratio of mature to immature survival, particularly when the ratio was less than 0.75.

### Discussion

Maturity schedules derived by simply using the sample proportions (percentage of the sampled fish

maturing at given ages) yielded biased maturation parameters. Using sample proportions (Nichols and Massmann 1963; Leggett 1969; Carscadden and Leggett 1975b) shifted the maturity schedule to earlier ages because observations on numbers mature at some ages were not yet made. In our data, the sample proportion method yielded 94.4% maturity by age 5, whereas the maximum likelihood method estimated only 79.1% maturity by age 5 for the 3-year combined sample. Hence, use of an invalid method based on biased samples skews the estimate of maturity to earlier ages. The proposed maximum likelihood method yields asymptotically unbiased estimates, provided the assumptions are supported.

Some of the assumptions of the maximum likelihood method are testable. In our study, the assumption of no skipped spawning was supported by the absence of scales exhibiting one or more annuli between spawning marks. If annuli existed between spawning marks, they should be evident, despite the erosion producing the spawning marks, because the absorption process does not affect the posterior portion of the scale as much as the anterior portion. A spawning mark may erode away

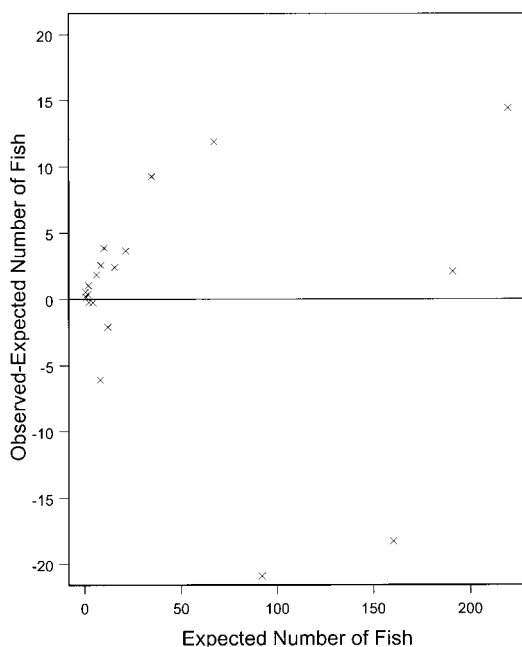


FIGURE 1.—Residuals from the maximum likelihood estimation of proportions of American shad maturing, based on 3-year combined data. Residuals from individual year estimates illustrated a similar lack of pattern (see Maki 2000).

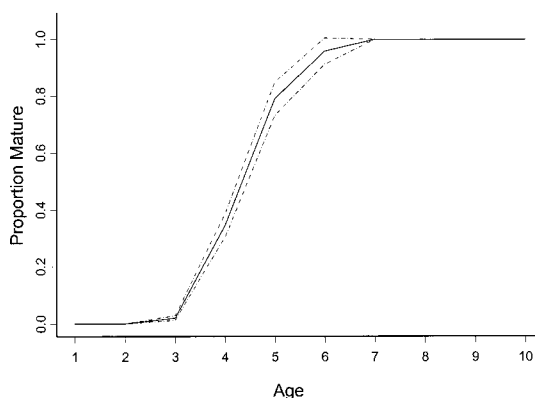


FIGURE 2.—Proportion of American shad maturing by a given age (solid line) and 95% confidence intervals (broken lines) for the 3-year combined dataset.

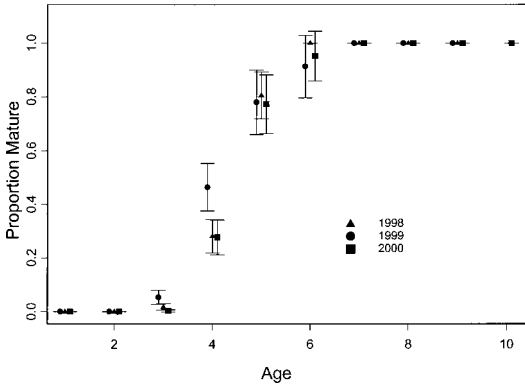


FIGURE 3.—Proportion of American shad maturing by a given age, as represented by 95% confidence intervals ( $\pm 2$  SEs) for 1998, 1999, and 2000.

a previous annulus in the anterior region of the scale but will usually leave evidence of the annulus in the posterior region (Cating 1953). Microchemical analysis of otoliths (Radtke et al. 1998; Campana 1999; Secor and Rooker 2000), specifically

strontium chronology, may be used to corroborate this morphological evidence. In a single American shad from the Chesapeake Bay region, the strontium chronology showed cycles that might be interpreted as spawning runs and indicated a possible year of skipped spawning (Secor and Rooker 2000). The skipped year result might have been obtained, however, because of inadequate sampling of that region of the otolith.

A test of the assumption of equal catchability between early- and late-maturing fish of the same age revealed no significant differences in size of American shad of a given age maturing in different years. The test was based on a comparison of mean total lengths for each shad age (Figure 5). Total lengths were used instead of weights because weights within an age category can be confounded by differential stages of gonad maturation. It is important to note that it is not necessary to assume that the sampling gear is not size selective. This method investigates each age-group independently. Thus, it does not matter if the gear selects unequally for ages 4 and 5, as long as it selects equal-

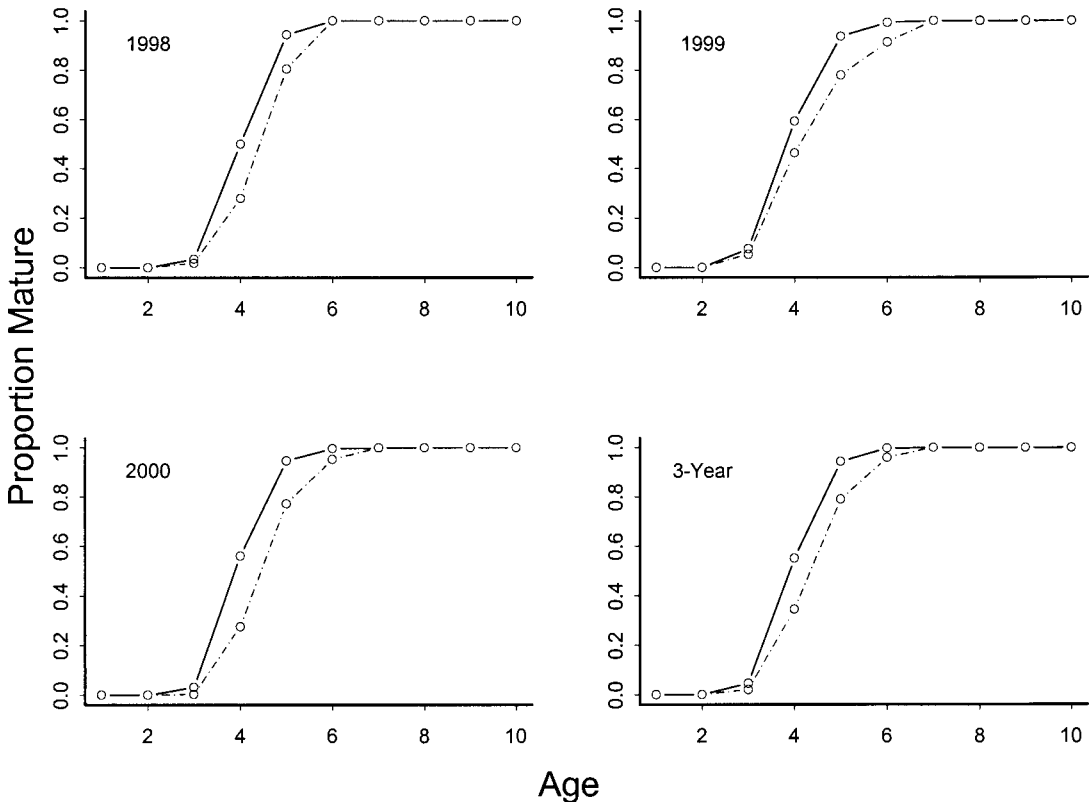


FIGURE 4.—Comparison of estimates of the proportion of American shad mature at age by the maximum likelihood method (broken lines) and by taking sample proportions (solid lines) for 1998, 1999, 2000, and the 3 years combined.

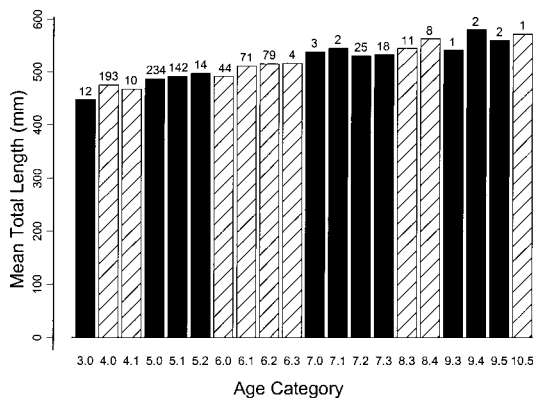


FIGURE 5.—Mean total length per age and spawning category (*a*, *b* represents fish of age *a* that have spawned *b* times before capture) of American shad collected in the York River, Virginia, during 1998, 1999, and 2000 combined. Numbers above bars are numbers of fish examined. Examination of age category and lengths in individual years yielded similar patterns (see Maki 2000).

ly for fish of a given age with different spawning histories.

The assumption that there is no difference in mortality between immature and mature fish of a given age is somewhat problematic. Fishing for American shad in the Chesapeake Bay region has been under moratorium since 1980 in Maryland and since 1994 in Virginia. This leaves the modest offshore fishery that intercepts mixed stocks as the largest possible source of differential fishing mortality on the York River population (Olney and Hoening 2001). At present, there is no direct evidence of fishing mortality on immature fish, although some bycatch mortality might occur. Spawning stress could also cause differential mortality between mature and immature fish. Glebe and Leggett (1981) studied the bioenergetics of American shad homing to the St. Johns (Florida), York, and Connecticut rivers, and found that American shad consumed 30–80% of their energy reserves during the spawning migration. The highest values were for Florida fish, which are semelparous. York River migrants experienced smaller visceral and somatic weight losses relative to those of Connecticut and Florida, suggesting that shad of the York River may have energy reserves available for the postspawning migration. Because of the proximity of spawning grounds on the York River system (Bilkovic 2000), York River shad undergo a relatively short migration, which may reduce energetic expenditure and spawning stress. Based on our samples from staked gill nets (which

probably select for large fish), a high percentage of York River shad spawn repeatedly (44.5% or 390 of 876 fish sampled had spawned at least once before) suggesting that they experience reduced spawning-induced mortality relative to more southern populations, where most or all shad die after spawning. This estimate is based on a sample of females only and is almost twice that of the mean proportion of repeat spawners captured in pound nets in the York River (23%, males and females combined; Leggett and Carscadden 1978); however, those observations were made when an active fishery was in operation and fishing mortality reduces the proportion of repeat spawners.

The model was tested for sensitivity to differential survival of mature and immature fish of the same age. Data were simulated by assuming various magnitudes of the ratio of survival of mature to immature fish ( $R = 0.5$ – $1.0$ ; see Appendix 2) and then computing estimates of the maturation parameters. It is most likely that mature survival would be less than immature survival due to mortality associated with spawning. Thus,  $R$  values greater than 1 were not considered.

Differences between actual and estimated proportions maturing at age  $j$  were largest for fractions maturing at ages 4 and 5 (Figure A2.1). By age 7, no departures from the actual proportion maturing occurred. Additionally, departures from the actual parameter values were relatively small for values of  $R$  between 0.75 and 1.0. The same held true for the actual versus estimated proportions mature by age  $j$  (Figure A2.2). At more extreme values of  $R$  ( $< 0.75$ ), however, the estimated proportion maturing at age  $j$  differs increasingly from the true proportion maturing. In summary, when the difference in survival of mature and immature shad is small ( $1 > R > 0.75$ ), little discrepancy occurs between the maximum likelihood estimates and the true proportions maturing. However, if the magnitude of differential survival is high ( $R < 0.75$ ), parameter estimates computed with the model may be seriously biased when estimates are computed by assuming  $R = 1.0$ .

Maturity estimates for 1998, 1999, and 2000 were grossly similar, except that ages 3 and 4 in 1999 differed from the other 2 years. The estimates exhibited no temporal trends. The possibility of a temporal trend in the maximum likelihood estimates can be investigated in the future as more years of data are added to the maturity estimates. If maturation patterns are not changing over time or between cohorts, then combining the data leads to better precision because of increased sample

size. By analyzing each year of data separately, one cannot clearly tell to what differences in maturation are due (e.g., time, cohort size, etc.). Eventually, however, with enough years of data, the maximum likelihood method can be used in a longitudinal study, estimating maturity for one year-class throughout time. This will allow identification of differences in maturation between cohorts. If the longitudinal method is used, a likelihood ratio test could be utilized to examine differences in cohort-specific maturation parameters from combined data estimates.

The cross-sectional approach will still retain its value, however, when immediate predictive capabilities are required. For example, if one wished to forecast the size of a subsequent year's spawning run, a cross-sectional approach would be required because one must estimate the proportion that will become mature based on the performance of previously observed cohorts. Additionally, the approach developed here, whether used cross-sectionally or longitudinally, represents an advance over previous methods. The standard method (taking sample proportions) is also a cross-sectional view and any failing of the maximum likelihood method would also hold true for the sample proportion method. However, the maximum likelihood method represents an advance in estimating maturity because it eliminates the bias induced by the sample proportion method's failure to account for unsampled immature fish. Additionally, the maximum likelihood method is resilient to fluctuations in year-class strength because each age is investigated independently. Thus, any use of the maturity schedule (forecasting, etc.) will be improved. This is particularly important as Atlantic coastal states are required to conduct spawning stock surveys, as mandated by Amendment 1 to the Interstate Fishery Management Plan for Shad and River Herring (Atlantic States Marine Fisheries Commission 1999). As part of these surveys, states are required to take representative samples of adults to determine sex and age composition and (for states north of South Carolina) the level of repeat spawning. Additionally, several states are required to report annual juvenile abundance indices, which are used to assess juvenile production and predict future year-class strength.

The maximum likelihood method presented here is an important advance in determining maturation schedules in some anadromous fishes. However, further information is required to fully develop the model. Although the moratorium on in-river fishing reduces the differential survival between ma-

ture and immature American shad, the level of fishing mortality offshore is unknown. While Garmann (1992) suggested that carcasses of dead clupeids are an important source of marine-derived energy in Virginia rivers, there is no direct evidence of postspawning mortality of York River American shad. Estimates of relative survival rates for mature and immature shad are currently unavailable. If these estimates could be developed, the accuracy of the maturity model would increase.

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## Appendix 1

### Analytical Procedure to Estimate Probabilities of Maturation at Age

Consider the data in Table 1. The rows are the ages at capture, the columns are the ages at maturity. Let  $d_a$  be the column sum for age of maturity equal to  $a$  ( $a = 3$  to  $10$ ), and let  $R_a$  be the sum of all values in the rectangle for which  $(a, a)$  is the

upper right corner. It can be shown that  $R_a$  and  $d_a$  are minimal sufficient statistics. Consider the moment estimator,

$$e_a = \frac{d_a}{R_a},$$

which is a maximum likelihood estimator of

$$\frac{p_a}{\sum_{i=3}^a p_i}$$

Let  $\hat{p}_a$  be the maximum likelihood estimator of  $p_a$ . We solve for the  $\hat{p}_a$  by working backwards from the oldest age. Thus, for age-10 shad collected in this study (3-year combined dataset),

$$e_{10} = \frac{d_{10}}{R_{10}} = \frac{0}{1} = 0;$$

$e_{10}$  estimates  $\hat{p}_{10}$ , thus  $\hat{p}_{10} = 0$ . Similarly, for age-9 fish,

$$e_9 = \frac{d_9}{R_9} = \frac{0}{6}$$

estimates

$$\frac{p_9}{p_3 + p_4 + \dots + p_9} = \frac{p_9}{1 - p_{10}}$$

Solving for  $p_9$  we obtain

$$\hat{p}_9 = e_9(1 - p_{10}) = e_9(1 - 0), \quad \hat{p}_9 = 0.$$

Likewise, for eight-year-old fish,

$$e_8 = \frac{d_8}{R_8} = \frac{0}{25}$$

estimates

$$\frac{p_8}{p_3 + p_4 + \dots + p_8} = \frac{p_8}{1 - p_{10} - p_9}$$

Solving for  $p_8$  we obtain

$$\hat{p}_8 = e_8(1 - p_{10} - p_9) = e_8(1 - 0 - 0),$$

$$\hat{p}_8 = 0.$$

For seven-year-old fish,

$$e_7 = \frac{p_7}{1 - p_{10} - p_9 - p_8} = \frac{3}{73}$$

Solving for  $p_7$ ,

$$\hat{p}_7 = e_7(1 - p_{10} - p_9 - p_8) = (3/73)(1)$$

$$= 0.0410959.$$

For six-year-old fish,

$$e_6 = \frac{47}{268} = \frac{p_6}{1 - 0 - 0 - 0 - 0 - 0.0410959}, \quad \text{or}$$

$$\hat{p}_6 = 0.168166,$$

and so on for the other ages.

### Appendix 2

#### Sensitivity Analysis

In estimating the maturity parameters in the likelihood model, we assumed a ratio of mature to immature survival,  $R$ , equal to 1. When this is not the case, the situation is more complex because the proportion maturing at any age depends on both the biology of the species, and the differential survival rate between mature and immature animals. The parameter  $p_j$  used in the likelihood model is the number (no.) of maturing shad of age  $j$  divided by the total number surviving to age  $j$ ; that is,

$$p_j = \text{no. maturing}$$

$$\div (\text{no. maturing} + \text{no. already mature}$$

$$+ \text{no. remaining immature}).$$

Thus, when  $R = 1$ , if 90% of the shad at age 4 are mature, then no more than 10% of the shad at age 5 the next year can become mature (i.e.,  $p_5$  must be  $\leq 0.10$  and  $\sum_j p_j = 1.0$ ). In the presence

of a fishery, this is no longer the case, and the parameters may no longer sum to 1. For example, if 90% of shad at age 4 are mature but survival of mature age-4 fish after the spawning run is zero ( $R = 0$ ), the proportion maturing at age 5 ( $p_5$ ) can be as high as 100%. We can define conditional maturation rates ( $\pi_j$ ) to be the probability that an age- $j$  fish matures during the year, given that it is immature; that is,

$$\pi_j = \text{no. age } j \text{ maturing}$$

$$\div (\text{no. age } j \text{ maturing}$$

$$+ \text{no. age } j \text{ remaining immature}).$$

These conditional rates do not vary with  $R$ , except inasmuch as the basic biology might change.

Often, the relative survival rates may be unknown, and maturation could be erroneously estimated under the assumption that the ratio is 1. Therefore, a sensitivity analysis using varying levels of the ratio of mature to immature survival ( $R = 0.5, \dots, 1.0$ ) was used to test how the param-

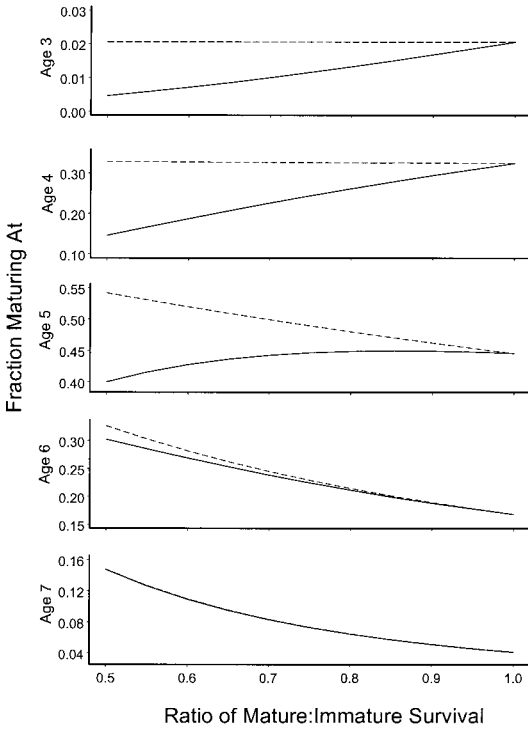


FIGURE A2.1.—Comparison of the true fraction maturing at age (broken line) with the estimated fraction maturing at age (solid line) for ratios of mature to immature survival ( $R$ ) between 0.5 and 1.0.

eters and parameter estimates would change with differential survival. For the analysis, total catches at age were held constant (i.e., the row sums of Table 1 remained constant as  $R$  was varied). The true parameter values when  $R = 1$  ( $p_j^{(1)}$ ) were set equal to 0.021, 0.325, 0.445, 0.168, and 0.041. New tables similar to Table 1 were constructed, each representing the expected catches for a different level of  $R$ . Each new data table was then used to estimate the maturity proportions (utilizing `nlnmb` in `Splus`).

Let  $X$  be the number of age-3 fish in the population,  $x_{ij}$  be the number of fish in a sample from the spawning run of age  $i$  that matured at age  $j$  ( $i = 3, \dots, 10; j = 3, \dots, i$ );  $N_i$  be the number of fish collected on the spawning run of age  $i$ ;  $S_I$  be the immature survival rate;  $S_M$  be the mature survival rate;  $p_j^{(r)}$  be the true fraction maturing at age  $j$  when  $R = r$ ;  $\hat{p}_j^{(r)}$  be the estimated proportion maturing at age  $j$  when  $R$  is assumed to be 1 but is really  $r$ ;  $m_j^{(r)}$  be the true proportion mature at age  $j$ ;  $\hat{m}_j^{(r)}$  be the estimated proportion mature at age  $j$  when  $R$  is assumed to be 1 but is really  $r$ ;

and  $\pi_j$  be the conditional probability of maturation given a fish is immature and age  $j$ .

The values of  $\pi_j$  can be computed from the true values of  $p_j^{(r)}$  when  $r = 1$ . Because all shad are immature at age 2, the unconditional, and conditional probabilities of their maturing at age 3 are the same, and

$$\pi_3 = p_3^{(1)}.$$

If a shad is immature when it turns 4,  $\pi_4$  is the probability that it matures at age 4. Thus,

$$\pi_4 = \frac{p_4^{(1)}}{1 - p_3^{(1)}}.$$

Similarly, for shad maturing at ages 5 and 6,

$$\pi_5 = \frac{p_5^{(1)}}{1 - p_3^{(1)} - p_4^{(1)}},$$

$$\pi_6 = \frac{p_6^{(1)}}{1 - p_3^{(1)} - p_4^{(1)} - p_5^{(1)}}.$$

For York River shad, all fish matured by age 7. Thus,  $\pi_7 = 1$ .

Because the conditional maturation rates are independent of the level of exploitation and, thus, remain constant as  $R$  is varied, they can be utilized to compute  $\hat{p}_j^{(r)}$  and  $\hat{m}_j^{(r)}$ . The procedure for constructing a table of expected catches for a given value of  $R$  is as follows.

The sample of age-4 fish from the spawning run contained shad maturing at ages 3 and 4. Those maturing at age 3 have undergone 1 year of mature survival since age 3, whereas those maturing at age 4 have undergone 1 year of immature survival. Thus, the expected catch of age-4 shad maturing at age 3 is

$$\begin{aligned} E(x_{4,3}) &= N_4 \frac{X\pi_3 S_M}{X\pi_3 S_M + X\pi_4(1 - \pi_3)S_I} \\ &= N_4 \left( \frac{\pi_3 R}{\pi_3 R + \pi_4(1 - \pi_3)} \right), \end{aligned}$$

and the expected catch of age-4 fish maturing at age 4 is

$$\begin{aligned} E(x_{4,4}) &= N_4 \frac{X\pi_4(1 - \pi_3)S_I}{X\pi_3 S_M + X\pi_4(1 - \pi_3)S_I} \\ &= N_4 \left( \frac{\pi_4(1 - \pi_3)}{\pi_3 R + \pi_4(1 - \pi_3)} \right). \end{aligned}$$

The expected catches for age-5 shad for a fixed value of  $R$  become

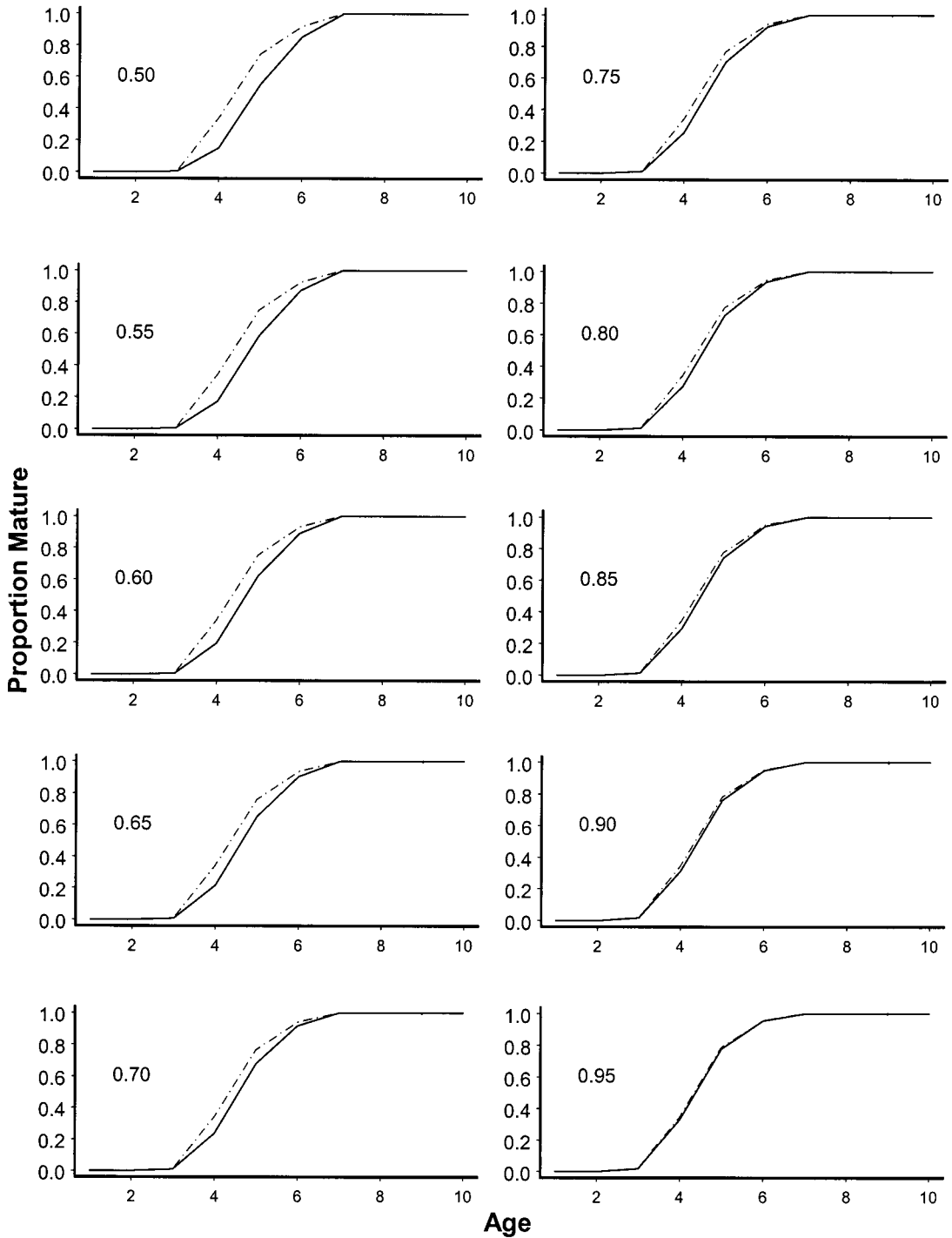


FIGURE A2.2.—Comparison of the actual proportion mature by age (broken line) with the estimated proportion mature by age (solid line) for values of  $R$  between 0.50 and 0.95. At  $R = 1$ , the two curves are equal.

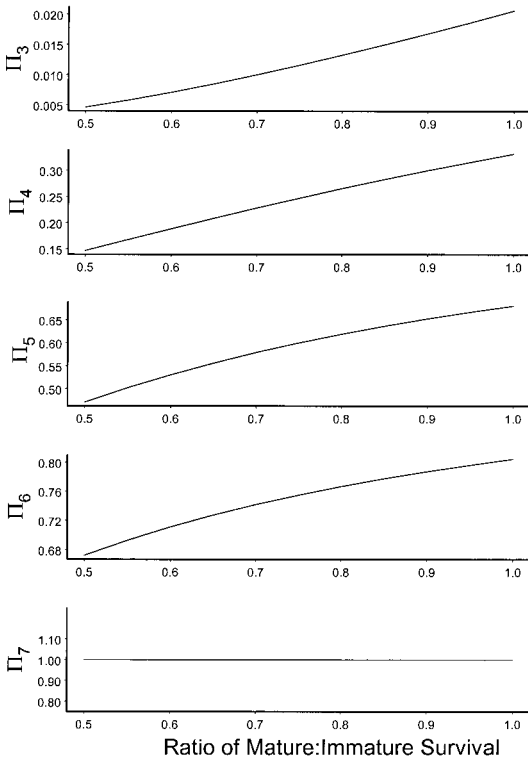


FIGURE A2.3.—Estimates of the conditional maturation rate,  $\pi_j$  (the conditional probability of maturation, given that a fish is immature and age  $j$ ), calculated from the biased estimates of fraction mature at age (achieved by wrongfully assuming that  $R = 1.0$ ). The true  $\pi_j$  is the value when  $R = 1.0$ .

$$E(x_{5,3}) = N_5 \{ (\pi_3 R^2) / [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4)] \},$$

$$E(x_{5,4}) = N_5 \{ [\pi_4(1 - \pi_3)R] \div [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4)] \},$$

$$E(x_{5,5}) = N_5 \{ [\pi_5(1 - \pi_3)(1 - \pi_4)] \div [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4)] \}.$$

This process was similarly executed to fill in the rows of the new tables for ages of capture equal to 6, 7, 8, 9, and 10. Maximum likelihood estimates  $\hat{p}_j^{(r)}$  were computed using the Splus function `nlminb` under the assumption that  $R = 1$ , when the true values of  $R$  ranged from 0.5 to 1.0 (Figure A2.1). These biased estimates can be compared

with the true fractions maturing at age  $p_j^{(r)}$ , which are based on the  $\pi_j$  values and the level of  $R$ . The true fractions maturing at age are computed as follows:

$$p_j^{(r)} = \text{no. maturing at age } j \div (\text{no. matured previously and survived} + \text{no. maturing at age } j + \text{no. remaining immature}).$$

Thus,

$$p_3^{(r)} = \pi_3,$$

$$p_4^{(r)} = \frac{\pi_4(1 - \pi_3)}{\pi_3 R + \pi_4(1 - \pi_3) + (1 - \pi_3)(1 - \pi_4)},$$

$$p_5^{(r)} = [\pi_5(1 - \pi_3)(1 - \pi_4)] \div [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4) + (1 - \pi_3)(1 - \pi_4)(1 - \pi_5)],$$

and so on for the true proportions maturing at ages 6 and 7. When  $R$  is wrongfully assumed to be equal to 1, the estimates of proportion maturing depart from the true fraction maturing at age  $j$  (Figure A2.1). This difference is smallest for the oldest age of maturation, and there is no difference between the estimated and true values of the fraction maturing at age 7.

The values of  $\hat{p}_j^{(r)}$  were cumulated to produce the estimated proportion mature at age  $\hat{m}_j^{(r)}$  for cases where it is wrongfully assumed that  $R = 1$ . These values were then compared with the true proportion mature at age,  $m_j^{(r)}$ , which were calculated using the true  $\pi_j$  and the values of  $R$ . The true proportion mature at age were determined as follows:

$$m_4^{(r)} = \frac{\pi_3 R + \pi_4(1 - \pi_3)}{\pi_3 R + \pi_4(1 - \pi_3) + (1 - \pi_3)(1 - \pi_4)},$$

$$m_5^{(r)} = [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4)] \div [\pi_3 R^2 + \pi_4(1 - \pi_3)R + \pi_5(1 - \pi_3)(1 - \pi_4) + (1 - \pi_3)(1 - \pi_4)(1 - \pi_5)],$$

and so on for age six. Because all shad are mature by age seven,

$$m_7^{(r)} = 1.$$

Again, the greatest differences between actual and estimated values of the proportion mature occurred for ages 4 and 5, whereas the differences were minimal for age 6, and zero for age 7 (Figure A2.2). Additionally, large values of  $R$  ( $>0.75$ ) showed little distinction between the true and estimated values.

Values of  $\hat{p}_j^{(r)}$  were utilized to estimate the conditional probabilities of maturation at age (given that a fish is immature), for values of  $R$  ranging from 0.5 to 1.0. The  $\pi_j$  are independent of the magnitude of  $R$ , but estimates of the  $\pi_j$  are too low when estimated under the assumption that  $R = 1$  and  $R$  is in fact less than 1 (Figure A2.3).